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OPERANT METHODOLOGY OUT OF THE LAB AND APPLIED TO
ENRICHMENT WITH CAPTIVE CHIMPANZEES (*PAN TROGLODYTES*)

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submitted in partial fulfilment
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ABSTRACT

A group of socially-housed chimpanzees, maintained in a zoo facility, were given the opportunity to access each of several purpose-designed and built enrichment items. Each item was made freely available in the chimpanzees' regular setting, with their normal activities available. The time members of the group spent engaging with each item gave an assessment of their relative preference for the items. The group were shown to have the greatest preference for a foraging enrichment item (Screwfeeder) and the least preference for an audiovisual enrichment item (TV/Video). Individual preferences for the items were evident. The chimpanzees were then taught to operate a weighted lever to get access to an item. Once all chimpanzees had operated the lever for access to the items, the number of lever operations required for access to each item was systematically doubled over a series of 3 hr sessions until the chimpanzees did not gain any access to that item for two consecutive sessions. One item was presented for two series of increases. The group response rates for an item increased with increased response requirement and then decreased with further increases, reflecting data from individuals in other research. The highest response requirement that maintained the group behaviour differed over the items. The number of times an item was accessed (consumption) was plotted against the response requirement (price) on logarithmic coordinates. Lines fitted to the data (demand functions) were shallowest for a foraging enrichment (Screwfeeder) and steepest for the audio enrichment (Musicbox). There were not enough data points to fit a function for the audiovisual enrichment. Differences in individual's demand within the group were evident. In general, the rank order of preference for the items and the rank order based on the parameters of the demand functions (slope or elasticity and initial intensity) was broadly the same. Three individual chimpanzees were exposed to two series of increasing response requirement for access to the Screwfeeder whilst housed alone, in one hour sessions. Response rates were again bitonic and the linear demand functions for these individuals were steeper (more elastic) than the functions fitted to data for group responding and differed idiosyncratically from the data for these individual when responding as part of the group. Thus the change of social setting had a different impact on the behaviour of each of the individuals. These results show that an animals' demand for a commodity is altered by the environment in which it is tested.

Overall the research provides the first example of operant methodology in a zoo setting with a group of chimpanzees. It is also the first research to show differential responding for access to different enrichment items by a group and how this relates to their preference (based on time allocation) for those items.

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DEDICATION

This thesis is dedicated to my family and their encouragement over this very long haul. Some of my greatest supporters, who would have been the proudest of all, are not with us to see its conclusion. I hope somehow that they can see that I have made it.

My immense gratitude, love and a thousand other things (including wedgies) go to my angel and other half, Serge. This journey has required much of me and has had implications for our life. Yet, his support and confidence in me has been unwavering (although sometimes rebuffed in frustration). Without him I am sure I would never have reached my goal. I look forward to our exciting future ahead without this shackle and, I promise, less fleece.

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OPERANT METHODOLOGY OUT OF THE LAB AND APPLIED TO
ENRICHMENT WITH CAPTIVE CHIMPANZEES (*PAN TROGLODYTES*)

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ABSTRACT

A group of socially-housed chimpanzees, maintained in a zoo facility, were given the opportunity to access each of several purpose-designed and built enrichment items. Each item was made freely available in the chimpanzees' regular setting, with their normal activities available. The time members of the group spent engaging with each item gave an assessment of their relative preference for the items. The group were shown to have the greatest preference for a foraging enrichment item (Screwfeeder) and the least preference for an audiovisual enrichment item (TV/Video). Individual preferences for the items were evident. The chimpanzees were then taught to operate a weighted lever to get access to an item. Once all chimpanzees had operated the lever for access to the items, the number of lever operations required for access to each item was systematically doubled over a series of 3 hr sessions until the chimpanzees did not gain any access to that item for two consecutive sessions. One item was presented for two series of increases. The group response rates for an item increased with increased response requirement and then decreased with further increases, reflecting data from individuals in other research. The highest response requirement that maintained the group behaviour differed over the items. The number of times an item was accessed (consumption) was plotted against the response requirement (price) on logarithmic coordinates. Lines fitted to the data (demand functions) were shallowest for a foraging enrichment (Screwfeeder) and steepest for the audio enrichment (Musicbox). There were not enough data points to fit a function for the audiovisual enrichment. Differences in individual's demand within the group were evident. In general, the rank order of preference for the items and the rank order based on the parameters of the demand functions (slope or elasticity and initial intensity) was broadly the same. Three individual chimpanzees were exposed to two series of increasing response requirement for access to the Screwfeeder whilst housed alone, in one hour sessions. Response rates were again bitonic and the linear demand functions for these individuals were steeper (more elastic) than the functions fitted to data for group responding and differed idiosyncratically from the data for these individual when responding as part of the group. Thus the change of social setting had a different impact on the behaviour of each of the individuals. These results show that an animals' demand for a commodity is altered by the environment in which it is tested.

Overall the research provides the first example of operant methodology in a zoo setting with a group of chimpanzees. It is also the first research to show differential responding for access to different enrichment items by a group and how this relates to their preference (based on time allocation) for those items.

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DEDICATION

This thesis is dedicated to my family and their encouragement over this very long haul. Some of my greatest supporters, who would have been the proudest of all, are not with us to see its conclusion. I hope somehow that they can see that I have made it.

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Captive Animal Well-Being

An animal in the wild spends much of its time in the search of food, water, shelter or a mate. Competing with other animals, escaping from predators, rearing and protecting young, social activities, or protecting territory take up the active hours of the animal's life. For captive animals, food and water is supplied, territory is already delineated, social groupings are usually fairly stable and structured, there are usually no predators to avoid, and mates are selected for them (National Research Council/Institute for Laboratory Animal Research (NRC/ILAR), 1998; Savage-Rumbaugh, Wamba, Wamba & Wamba, 2007). Being placed or reared in captivity has eliminated most of the time normally spent in 'survival mode' (Seidensticker & Forthman, 1998; Shepherdson, 1998). With all this 'free time', captive animals often show stereotypic or abnormal behaviour patterns (Markowitz, 1982; Appleby, 1997), or as Sommer (1974) observed, the 'hard' zoo, with its architecture and routines and management, often distorts the behaviour of animals. Since legislation governing the care of captive animals has mandated that their psychological requirements be catered to, research has been undertaken to find ways of improving animals' environments and developing practical, objective measures of the effects environmental resources have on their well-being (Mench 1998; NRC/ILAR, 1998; Shepherdson, 1998; United States Department of Agriculture, Animal and Plant Health Inspection Service (USDA/APHIS), 1999; Young, 2003).

Psychological Well-Being

While an animal's physical health can be based on objective measures, its psychological well-being requires more complex assessment and methods of promotion. One reason for this may be that there is lack of clarity as to the meaning of the term. Despite numerous attempts, the concept of psychological well-being has not been precisely defined or directly measured (partially as a result of the lack of clarity in the definition of the term) (Brinkman, 1996; Crockett, 1998; Novak & Drewsen, 1989; Novak & Petto, 1991; Novak & Suomi, 1988; Petto, Novak, Fingold & Walsh, 1990; Suomi & Novak, 1991; Young 2003). It has been suggested that the best indicators of psychological well-being include a synthesis of physical and behavioural measures (Appleby, 1997; Boinski, Swing, Gross & Davis, 1999; Broom & Johnson, 1993; Dawkins, 2004; Novak, 1989; Novak & Drewsen, 1989; Snowden & Savage, 1989; Woolverton, Ator, Beardsley & Carroll, 1989). This present

research will focus on aspects of psychological well-being related to behavioural measures and expression.

Psychological Well-Being Represented Behaviourally

Researchers have shown that changes made to the environmental conditions of captive animals can lead to changes in their behaviour. Views as to how these changes in behaviour reflect psychological well-being differ. Many agree that psychological well-being in captive animals is evidenced by the reduction or elimination of stereotypic or self-destructive behaviours, or a drop in levels of aggressive behaviour (e.g., Akers & Schildkraut, 1985; Brent, Lee & Eichberg, 1991). Stereotypies are defined as repetitive, unvarying and apparently functionless behaviour patterns (Mason, 1991). Captive animals might exhibit a high degree of species-typical behaviours, or have behavioural time budgets more closely resembling their wild counterparts, to represent psychological well-being (e.g., Brent & Eichberg, 1991; Maki, Alford, Bloomsmith & Franklin, 1989). In some cases, improvements in psychological well-being might be evidenced by enhanced captive breeding (Chamove, 1989; Shepherdson, 1998). However, a difficulty with these views of behaviour being representative of psychological well-being is whether it is the animal's behaviour being considered to be representative of its species, or 'normal', or based on what are deemed to be the 'needs' of the animal. Each aspect of behaviour as a representation of psychological well-being of captive animal has been a source of much discussion as to how it should be interpreted and/or utilised (Besch, 1990).

Abnormal behaviours, such as stereotypic pacing, self-injury, and regurgitation/reingestion, have been cited as principal indicators of distress and compromise to the well-being of animals (Bayne, Hurst & Dexter, 1992; Broom, 1983; Broom & Johnson, 1993; Carlstead, 1998; Mason, 1991a, b; Olfert et al., 1993; Toates, 1997; Wemelsfelder, 1993). There is much debate about whether abnormal behaviour patterns indicate some compromise of well-being, or whether they are an adaptation to the environment or coping mechanisms (reviewed by Mason, 1991a, b; Carlstead, 1998; Veasey et al., 1996). There is also the possibility that an animal's behaviour may not indicate current suffering or environmental conditions but rather reflects past events (Mason, 1991b; NRC/ILAR, 1998).

There is a general consensus that the promotion of 'species-appropriate'

behaviour, appropriate both in form and quantity, should be a central focus of captive animal management (Brent & Stone, 1996; Chamove & Anderson, 1989; Forthman & Ogden, 1992; Markowitz, 1997a, b; Olfert, Cross & McWilliam, 1993; Poole, 1991, 1992; Rose, 1994; Toates, 1997). The underlying assumption in this view is that a captive animal's well-being is enhanced if it exhibits 'natural behaviour' and the optimal situation in which to encourage this is a 'natural environment' (Maki & Bloomsith, 1989; Newberry, 1995; Schapiro & Lambeth, 2007; Seidensticker & Forthman, 1998; Shepherdson, 1998, Veasey, Warran & Young, 1996). However, a problem with providing a natural environment is that there is no single standard for it or for natural behaviour (Clarke, Juno & Maple, 1982; Rosenblum & Andrews, 1995; Woolverton et al., 1989). As Shepherdson (1998) suggests, it is also a mistake to assume just because something is natural that it is positive. For example, conspecific competition for mates, hunger, predators, or disease, all take place for animals in the wild but it could be argued that they may not improve the psychological well-being of animals (Poole, 1998; Veasey et al., 1996).

Questions have also been raised as to what extent it is desirable that the behaviour of captive animals resembles that performed in more extensive or natural environments (Newberry, 1995; Poole, 1998; Shepherdson, 1998; Veasey et al., 1996). Animals descended from former zoo animals may have become adapted to life in captivity and as such may not benefit from exhibiting some behaviour seen in the wild. To aid in a judgement of psychological well-being Newberry (1995) suggested that it is necessary to describe the behaviour being encouraged and to justify how the animal will benefit from exhibiting that behaviour. Newberry (1995) also recommended that for assessing captive animal well-being, it is more useful to emphasise the function of behaviour in specific environments rather its degree of 'naturalness'. Some behaviour currently considered atypical might instead be seen as a selective advantage for individuals performing it in a captive environment.

Given the difficulties of judging what behaviours are representative of psychological well-being, designing methods of promoting enhanced well-being can be hampered.

Needs

Whilst still a source of debate, many accept that animals have complex 'needs' and that these should influence the way in which they are maintained in captivity

(Dawkins, 1988; Poole, 1992; Shepherdson, 1998). Jensen and Toates (1993) defined a 'need' as "a state, which if not attained causes suffering to an animal as indexed by disturbed behaviour, an increased risk of pathology and/or a hormonal profile consistent with stress".

Some animal needs are deemed fundamental to their survival in captivity, such as for food and water. While the non-satisfaction of other types of needs, rather than being fundamental, can change the form and function of the behaviour of captive animals. An example of the latter type of need would be that the lack of 'appropriate' social conditions during the rearing of primates has been shown to be associated with abnormal patterns of behaviour (Schapiro, Bloomsmith, Suarez & Porter, 1995). For non-human primates regulations based on needs, assessed to be fundamental, have been set down as to the appropriate husbandry and conditions that should be maintained when animals are held in captivity. These include guidelines for such things as enclosure construction, sanitation, veterinary care, feeding and watering and protection from the elements (New Zealand Government, 1999; NRC/ILAR, 1998; USDA/APHIS, 1985). Regulations also take into consideration recommendations, such as those made by the Jane Goodall Institute (1998), as to the social and caging needs of primates, including a concern for social hierarchy and the provision of such things as manipulanda, food variety and toys.

In the absence of fundamental research, studies of needs can be based on pragmatic experimentation, involving changes in enclosure conditions. These can be carefully thought out, or inspired trial and error. As Newberry (1995) suggests, one can then measure an animals' responses to the modifications. Increases in desirable activity and/or decreases in undesirable activity can lead to judgements about the enhancement, or otherwise, of well-being. We can also measure physiological indicators of stress; these can include neurological symptoms and non-invasive assays of stress hormones (Broom & Johnson, 1993). Both the behavioural and physiological indicators may suggest evidence of a need having been satisfied for an animal.

Data on the perceptual worlds of animals can aid our assessment of relevant factors that may be considered to be a need for a captive animal. Colour is clearly irrelevant to animals with monochromatic vision; odour is not of high relevance to animals with a poor sense of smell, and so on. As Robinson (1998) points out, we often neglect the olfactory environment because of our own sensory biases. In many

captive environments, because of considerations of hygiene, all the odour marks the macrosmatic animals make are regularly removed, and in the process the individuals personal security and home range markers. By alternating the presence of individual animals in the same enclosures we may provide threatening situations through the persistent odour markers of rivals. However, as Broom and Johnson (1993) put forward, there is the possibility that threat and fear may be may not be negative factors for an animal.

Robinson (1998) suggests that, despite some recent emphasis on variability of intraspecific behaviour, there are many areas of behaviour where we should expect that selection may have operated to reduce variability. These should be the areas where needs are easiest to assess. For instance, hunting animals should have little variability in their response to the movement of prey-sized objects. Hughes and Duncan (1988) have argued that animals are strongly driven to perform some behaviours even in the absence of any necessity, physiological or otherwise, to do so. If this is the case, then deprivation of functional behavioural opportunities may at times be a potentially negative factor and where a need may be identified.

Great Apes in Captivity

Great Apes are frequently kept in captivity although they can pose a considerable challenge to maintain, as the likes of Byrne (1999), the Institute of Laboratory Animal Resources (NRC/ILAR, 1998) and the Jane Goodall Institute (1998) suggest, not least due to their high intelligence. Byrne (1999) reviewed all primate species' propensity to suffer in captivity, based on the cognitive literature, and concluded that chimpanzees deserve special consideration due to their cognitive capacity. Researchers have identified that Great Apes well-being can be impaired if their behaviour is affected by the lack of a stimulating environment to meet their physical and psychological needs (Jane Goodall Institute; 1998; NRC/ILAR, 1998).

In 1999 New Zealand took a major step and protected Great Apes held in facilities in the country through an amendment to the Animal Welfare Act (New Zealand Government, 1999). Section 80 (1) (c) of the Act states that the section referring to Great Apes ...

“reflects Parliament's view that these animals merit special consideration. This followed Parliament's assessment of research and information that shows that great apes share similar qualities with humans including ‘the ability to communicate symbolically, the

ability to solve problems through reasoning, self awareness and emotional complexity.”

Therefore, if these animals are identified to have ‘emotional complexity’ or ‘merit special consideration’ in regards to their well-being as a result this would suggest that they must also merit special consideration as to what conditions provide for their well-being. Given this necessity, Great Ape well-being, or more specifically, chimpanzee’s psychological well-being, in the captive zoo environment will be the focus of this present research.

Promoting Psychological Well-Being

As outlined, there are varying views on exactly what psychological well-being looks like behaviourally in captive animals, both qualitatively and quantitatively. However, the promotion of forms of behaviour shown by wild conspecifics is highlighted as being a worthy objective in maintaining captive animals, such as the provision for tool use for captive chimpanzees (Jane Goodall, 1998). Dittrich (1990, cited in Robinson, 1998) used the term ‘functional substitution’ to describe the replacement of an element of the natural environment with something that may serve the same function for a captive animal. The provision of such items may allow for the animal to perform behaviour similar in form to that of its wild counterparts, arguably ‘natural’ behaviour.

Enrichment

Environmental enrichment has been developed as an attempt to provide for the needs of captive animals. In Swaisgood’s (2007) opinion enrichment is ‘the key concept for those interested in maintaining wild animals in captivity, a fundamental need on par with food and water’. By definition, enrichment is the act or process of increasing intellectual or spiritual resources (Markowitz, 1982). To enrich refers to the act of making something better (richer) by the addition or increase of some desirable quality, attribute, or ingredient (Markowitz, 1982). The word is usually qualified adjectivally, for example as: environmental-, habitat-, or behavioural-enrichment. The ultimate purpose and goal of enrichment, is evidence that the provision of interesting or challenging activities or resources improve an animal’s quality of life and psychological well-being (Mench, 1998, Shepherdson, 1998). Enrichment has come to mean a variety of things from increased environmental

complexity (Robinson, 1998), to improved biological functioning (Newberry, 1995) resulting from modifications made to the environment. Shepherdson (1998) defines enrichment as “an animal husbandry principle that seeks to enhance the quality of captive animal care by identifying and providing the environmental stimuli necessary for optimal psychological and physiological well-being”. At its simplest, Dittrich (1990) suggests enrichment involves identifying characteristics of the wild environment that are necessary for optimal psychological well-being and functionally recreating them in captivity.

Development of enrichment procedure. In the face of the debate surrounding animals' needs and the interpretation of their behaviour, people began developing ideas for enriching animals' environments to change their behaviour, and potentially improve their well-being (Shepherdson, 1998). As early as 1925, Yerkes wrote “the greatest possibility for improvement in our provision for captive primates lies with the invention and installation of apparatus which can be used for play or work” (p. 242). A fundamental dichotomy in past approaches to behavioural enrichment has been recognised (Tudge, 1992; Young, 2003). One, attributed to Hagenbeck, is the creation of the ‘naturalistic’ looking habitats, and has been termed the ‘naturalistic approach’ (Forthman-Quick, 1984; Young, 2003). The other, attributed to Yerkes, is the approach solely concerned with the well-being of the animals and not the environment’s appearance, which has been termed ‘behavioural engineering’ (Forthman-Quick, 1984; Young, 2003). The first tradition produced what might be called a human-viewpoint-based ‘naturalism’, and an emphasis on the promotion of natural, ‘wild-type’ behaviour. The other produced solutions based on apparatus – very much in the style continued by Markowitz, which placed an emphasis on the function of the behaviour being exhibited.

Markowitz was one of the first to adopt a systematic approach to improving zoo animal environments - designing and constructing complex pieces of equipment in an attempt to show active, interesting animals (Markowitz, 1979; 1982; Shepherdson, 1998). However, Markowitz’s work was criticised for having devices that were impracticable, for being artificial in nature, for the time required to develop the animal's behaviour, and for encouraging animals to exhibit ‘abnormal’ behaviours (Hutchins, Hancocks & Calip, 1978, 1979; Shepherdson, 1998; Veasey et al., 1996). Poole (1998) dismisses criticisms of Markowitz's ‘artificial’ designs

because they have proved successful in stimulating the animals concerned and, he argues, demonstrating to the public the adaptability of mammalian behaviour. Despite any reservations such designs have been adopted widely and have influenced the design of zoos. While others prefer a more naturalistic style (e.g., Irven, 1997; Snowden, 1991), most now appreciate that the two approaches are not necessarily incompatible and that a combination perhaps delivers the best results (e.g., Forthman-Quick, 1984).

Methods of enrichment. Researchers have identified many methods to enrich captive animal environments, from both the ‘natural’ and ‘functional’ perspectives, and agree that acceptable enrichment programmes should stimulate a variety of normal activities and meet all major areas of behavioural need in a species-typical manner, rather than concentrate on a few limited aspects of behaviour (Olfert et al., 1993; NRC/ILAR, 1998; Poole, 1991; United States Department of Agriculture, Animal and Plant Health Inspection Service, USDA/APHIS, 1999; Vivian, 2001). However, the application of enrichments in captive animal facilities is constrained by practical considerations such as the cost of providing the enrichment and the time involved in providing enrichments. Health and safety risks to the animal (and related humans), in the laboratory environment - the impact on experimental protocol, and in the zoo environment - the impact on the enclosure in terms of visitor experience, also impact on the provision of enrichments (Young, 2003). Taking these considerations into account, provision of enrichment should also be based on priority, of animal need, suffering and current behaviour (Mason, 1991a; Young, 2003).

One aim of the current research was to explore the provision of enrichment items for captive chimpanzees and Experiment 2 discusses methods of enrichment related to this present research further.

Systematic vs. Ad Hoc Provision and Evaluation of Enrichments

We do not know what components are essential for the psychological well-being for most species. We guess at these things or adjust them by trial and error; we seldom study them logically or systematically (Robinson, 1998; Schapiro & Lambeth, 2007; Swaisgood & Shepherdson, 2005). All too often management practices and legislative changes pertaining to the well-being of captive animals have been made on the basis of subjective opinions rather than scientific data (National

Research Council/Institute for Laboratory Animal Research, NRC/ILAR, 1998; Savage-Rumbaugh et al., 2007). Appleby (1995) cites one of the major problems encountered in enrichment studies is the lack of rigorous scientific method and achievable goals. Many argue that while using intuition as a method of approaching issues of well-being may occasionally be rewarding, it is generally risky and they advocate the use of empirical testing (Bekoff, 1994; Bloomsith, Brent & Schapiro, 1991; Crockett, 1998; Forthman & Ogden, 1992; Maple & Finlay, 1989; Morgan, Line & Markowitz, 1998; Newberry, 1995; NRC/ILAR, 1998; Robinson, 1998; Shepherdson, 1989a, b; Swaisgood & Shepherdson, 2005; Woolverton et al., 1989; Young, 2003). Mellen, Shepherdson and Hutchins (1998) cite the scarcity of empirical data for the lack of progress in enrichment techniques. In addition to assessing whether an enrichment has given rise to an increase in beneficial behaviour and a decrease in detrimental behaviour, there is also the question as to whether specific items are necessary for an animal's well-being. Savage-Rumbaugh et al. (2007) note that we rarely, if ever, directly assess the preferences of apes for any enrichments.

Robinson (1998) points out that many zoos employ 'tinkering' in attempting ecological/behavioural enrichment for captive animals. He defines tinkering to be repairing in a makeshift way and states that many zoos with knowledge and budget constraints simply 'tinker' in an attempt to improve things. To end tinkering, he suggests that fundamental research that systematically investigates the importance of various environmental factors is crucial. The primary purpose of such investigations would be to advance understanding of which environmental factors animals actually attend to, and how they react to them. Hosey (1997) also notes the fact that the majority of studies on captive populations have been done by zoo staff rather than by academic researchers. In Hosey's view, this limits the growth of knowledge in the area. Maple (2007) bemoans the lack of empirical and philosophical foundation of personnel working with captive animals. He suggests that all zoos should employ a doctoral-level animal behaviourist or collaborate with behavioural scientists from available academic institutions in order to monitor captive animal behaviour on a systematic basis in order to identify and solve problems related to animal well-being before such problems develop.

Morgan et al. (1998) provide a critical assessment of zoo animal environmental enrichment. They argue that only empiricism will allow conclusions

to be drawn about the relative effectiveness of enrichment methods and that while, for example, some ideas for improving well-being in non-primates have been shown to be effective, others have not. When effectiveness must be maximised or when the costs or risks of failure are particularly high, empirical assessment is required. In Schapiro and Lambeth's (2007) opinion assessments of the value of specific management strategies of captive non-human primates could, and should, employ consumer-demand analysis methods. Also, Young (2003) states that in his opinion 'far too much time, effort and money has gone into quantifying animal problems and not enough into solutions'.

Given the identified need for more systematic study to be undertaken in this field, this present research sought to examine chimpanzees' preference and demand for various enrichment items quantitatively.

Asking Captive Animals What They Want

In an effort to provide solutions to problems and answer questions relating to captive animal's psychological well-being, researchers have investigated the possibility of asking animals what it is that they want. As Dawkins (2004) suggested by asking two questions "Are the animals healthy?" and "Do the animals have what they want?" the dilemma is simplified as the ambiguity of what humans perceive to be an animal's 'need' is avoided.

For animals 'asking' the question of what they want is not straightforward. In an attempt to identify and rectify problems pertaining to animal well-being, a number of researchers have tried asking the animals what they want and what they prefer. The implication being that if the preferred alternative is used the animals' well-being will be improved or they will use the environment in a more appropriate way (Dawkins, 2006). In this way, animal well-being may be able to be enhanced proactively, rather than reactively (Young, 2003).

Choice/Preference

A source of data into what animals prefer can be derived from the use of procedures that are drawn from the methodology of experimental psychology. Two major procedures, choice tests and operant conditioning have been widely used in preference testing with farm and laboratory animals. These have been reviewed by Dawkins (1990) and advocated and/or used by her (e.g., Dawkins, 1977). In choice

tests, animals are given a choice between two or more environments and the time spent with each is recorded.

Choice tests have been criticised, in that there can be problems interpreting the test results (e.g., Bateson, 2004; Fritz, Nash, Alford & Bowen, 1992; Dawkins, 1977; Dawkins, 1990; Duncan, 1991). (These criticisms will be discussed further in Experiment 3). However, Dawkins (1996) suggested that, in spite of this, preference testing has the potential to indicate what elements may be important to captive animals. One aim of this current research was to explore the preference of captive chimpanzees for a variety of different enrichment items. Experiment 3 of this current research discusses preference testing further.

Work/Demand

Dawkins (1983; 1990) outlined a theory that describes the process of obtaining detailed information on what an animal regards as priorities. She proposed using operant conditioning and applying consumer demand theory to assessing animal needs. Commodities, such as food, mates, etc., could be used in a situation where an animal was given the opportunity to work for access to them. Commodities that the animal showed an inelastic demand for - that is kept working for in the face of increasing price - could then be described as a necessity, a need. On the other hand, commodities that the animal showed an elastic demand for in the face of price increases could be described as a luxury. Dawkins argues that by using this approach, an animal's needs could be ranked.

Operant conditioning techniques have been used by researchers to investigate a variety of natural behaviours (Markowitz, 1982). Laule and Desmond (1998) report that rhesus monkey (*Macaca mulatta*) infants that were given the opportunity to work for their food showed less fearfulness when exposed to threatening stimuli, and demonstrated better coping responses when separated from cage mates than did monkeys that received food items ad libitum. Working for food was shown to be associated with behaviour change suggestive of improved well-being.

The potential application of demand testing with captive chimpanzees and enrichment items has not been previously explored by researchers and this current research endeavoured to do so. These demand procedures and previous research, relating to that, will be discussed further in Experiment 5 of this current research.

Tustin (1994) suggested that both preference procedures and demand

procedures measure the relative reinforcer ‘value’ of the consequence of being selected or worked for and that they should be expected to give equivalent measures of reinforcer ‘value’. A comparison of the findings from conducting both preference testing (with a free access procedure), and demand testing, with the group of captive chimpanzees in this present research will allow for this proposition to be explored.

Research Setting

Much of the research on animal behaviour and methods of promoting psychological well-being of captive animals has taken place in laboratory environments (Logue, 2002). However, questions have been raised as to the validity of the application of such research findings to environments that differ physically and socially, and to individuals that have a different rearing history and social experience from the laboratory housed individuals. Webster’s (2003) view is that if research is to have relevance for captive animals, then there is a need to develop meaningful ways of assigning welfare in the environments the animals actually live in.

Animals held in laboratory environments have unique care and management requirements. Housing conditions can range from small enclosures that severely restrict the animal’s range of movement and cage single subjects, to large enclosures that hold multiple subjects so that it can be difficult to access individuals. Research protocols can dictate or restrict an animal’s amount and type of food, type of physical activity, ability to socialize, and access enrichment. In addition to this, the animals held by these facilities have varying degrees of handling experience and different rearing histories (NRC/ILAR, 1998).

Logue (2002) reviewed quantitative analysis research that has been conducted outside of the laboratory, in the ‘wide world’, citing it to have been a rare occurrence. The observation was made that such research is not able to control conditions as well as in the laboratory. However, the point was made that the results from studies conducted in more natural settings strengthen the validity of models of behaviour. Logue issued a challenge to researchers to find new and creative ways to investigate models of behaviour outside of the laboratory. Swaisgood and Shepherdson (2005) conducted a review of the environmental enrichment literature and noted that much zoo research lacks the strong theoretical framework evident in farm and laboratory research. They recommended that zoo researchers ‘take up the

challenge' to test theoretical models within these facilities.

This current research looked to explore and address this challenge via the application of preference and demand procedures with zoo-held chimpanzees.

Demand and Preference Out of the Lab

Demand and preference procedures have been used with a variety of animal species in laboratory environments. The efficacy of these procedures has not been demonstrated to a large extent in more naturalistic settings. Researchers such as Markowitz (1982) and Patterson-Kane (1999) suggest that such procedures, or a modification of them, have much to offer in such settings, and that they could allow us to assess and rank the importance (and enrichment benefits) of various commodities to captive animals. Markowitz (1982) and Patterson-Kane (1999) also suggest that the “work” alone would be enriching for animal subjects.

Researchers have pointed out that zoos represent an excellent but largely unexplored setting for the application of behaviour-analytic (operant) principles (Hutchins & Conway, 1995; Gibbons, Wyers, Waters & Manzel, 1994; Hutchins, Paul & Bowdoin, 1996; Kleiman, 1992; Patterson-Kane, 1999; Lukas, Marr & Maple, 1998; Ryder & Feister, 1995; Saudargas & Drummer, 1996; Thompson, 1993). Dawkins (2004) stated it is very important to develop ways of assessing preference that can be used for ‘at-the-zoo’ welfare assessment. Much of the provision of resources for captive animals in the zoo environment has its basis on findings from laboratory research. However, as Bateson (2004) states, to maximise the external validity of choice experiments, the context should be as similar as possible to the environment in which the subjects whose welfare it is the aim to improve, are housed.

This current research proposes to develop methods and techniques to enable such research to be performed in more naturalistic settings and, ultimately, to be utilized in scientific research as well as for general captive animal management.

Social Setting

Preference and demand studies have tended to employ single subject methodology, as will be discussed further in Experiment 3 and 5 of this current research. This is firstly due to difficulties in identifying individuals in a social setting, and also since animals are likely to affect the behaviour of other group

members (Olsson & Westlund, 2007). Social interaction can be in the form of social facilitation, which can lead to an over-estimation of the value of a resource for group-housed animals relative to individually-housed animals. In contrast, Olsson & Keeling (2002) suggest that social competition may lead to under-estimation of an animal's demand for a resource, as animals may avoid using a resource to avoid the risk of antagonistic encounters. However, as Cooper (2004) points out, it is important to 'investigate' behavioural priorities in group situations given the fact that many captive animals are housed in groups so the value an individual may place on a resource maybe of little relevance. Previous studies have indicated that the social environment in which an animal is tested in does have implications for findings (e.g., Pedersen, Jensen, Hansen, Munksgaard, Ladewig & Matthews, 2002). Jensen, Pedersen, and Ladewig (2004) suggest that it may be advisable to avoid isolation during demand testing for social species, as the social isolation may affect results.

Olsson and Westlund (2007) identify that both behaviour development and behaviour expression in social species of animals are greatly affected by the social conditions in which they are housed. They observe that whilst this has been explored, very little attention has been given to the effects social conditions have during behaviour tests. They suggest that group composition, stability, rank and previous social experience need to be taken into account when planning research and interpreting results. The presence of a compatible social partner may buffer stress reactions for animals in behavioural testing, such as it did for baboons in a study by Visalberghi and Anderson (1993). Alternatively a subject's performance may be improved by testing in the presence of a companion (Washburn & Rumbaugh, 1991).

Social needs of non-human primates. In the wild, factors that influence primate social behaviour include the mating system, migration, age at sexual maturity, parental care, communication and the type of dominance structure (Goodall, 1971; NRC/ILAR, 1998). Social contact is thought to be one of the most important influences on the psychological well-being of non-human primates (de Waal, 1991; Fritz & Howell, 1993; Harlow & Harlow, 1962; Novak, 1989; Novak & Derwsen, 1989; Novak & Suomi, 1988; NRC/ILAR, 1998; Olsson & Westlund, 2007; Pazol & Bloomsmith, 1993; Reinhardt, 1990a; Schapiro, Bloomsmith, Suarez & Porter, 1995; Schapiro et al., 1996 ; Snowdon & Savage, 1989, Young, 2003). Appropriate social contact can provide novelty, and sensory stimulation, opportunities for control, and

facilitate social communication (Bayne, 1989; Fitch, Merhalski & Blooms Smith, 1989; Goodall, 1986; NRC/ILAR, 1998). In captivity spatial density has been shown to have an impact on social behaviour (Videan & Fritz, 2006).

Social housing has potential detrimental effects such as competition for food or disease transmission (Elton, 1979; Erwin & Deni, 1979; Line, Markowitz, Morgan & Strong, 1989; Novak, 1989; Reinhardt, 1990a; Woolverton et al., 1989). Nevertheless, many consider the benefits of social housing outweigh any potential detrimental effects (Erwin & Deni, 1979; Reinhardt, 1990a; Visalberghi & Anderson, 1993). Of course, in the captive setting social structures are based on facility's management needs. Olsson and Westlund (2007) suggest that knowledge of a species' natural history is fundamental in achieving successful management of captive primates.

As has been suggested for research to maximise the external validity of choice experiments (Bateson, 2004), if animals are housed socially then testing should be conducting within social settings. This study sought to carry out such research, conducting demand and preference procedures with a social group of zoo chimpanzees. Chimpanzees' natural history was taken into consideration in the design and construction of the enrichment items used in the procedures.

This Research

Facilities housing captive animals have been given legislative mandate to provide for the psychological well-being of animals. However, they have not been given specific guidelines as to how this should be done.

Whilst there has been much debate with regards to the needs of captive animals and the components required to provide for their psychological well-being, the procedures of preference and demand testing have been identified as potentially valuable for providing information to enhance captive animal well-being. However, these procedures have had little application outside of the laboratory environment, in more naturalistic settings, both physically and socially. This is the case even though many have emphasised the need for testing environments to be similar to those in which recommendations are to be utilised in.

In addition to this, Great Apes have been identified as requiring 'special consideration' in regards to their needs and psychological well-being. Yet little research has been completed to quantitatively assess their needs, and none in more

natural environments outside of laboratory conditions, within complex social structures. This had been outlined here and will be discussed more fully in Experiment 3 and 5 of this thesis.

At the same time, environmental enrichment devices have been identified as potentially beneficial to the enhancement of captive animal well-being, yet there is a lack of empirical and systematic testing of the benefit and ‘need’ of the enrichment items for captive animals.

Kirkden and Pajor (2006), whilst using the term ‘motivated’ to express an animal’s interaction with a resource, suggested four distinct questions that could be asked in assessing animals’ motivation for access to a commodity.

- Whether an animal is motivated to obtain or avoid a resource;
- Whether it has a preference amongst alternative resources;
- How strong is its motivation or preference;
- Whether its preference, or the strength of its preference, is altered by changes in its internal or external environment.

Schapiro and Lambeth (2007) state that it is “up to primate welfare researchers to design studies and/or obstacles that will help measure the relative value of resources to captive primates without compromising the welfare they are attempting to evaluate and enhance”. This current research aimed to help measure such values in precisely such a way.

There are a number of areas relating to captive animal well-being that have not previously been explored and are in need of further investigation. Exploration of the use of operant methodology outside of the laboratory environment, with a social group, would maximise the validity of the research. Given that chimpanzees have been identified as being exceptional in their propensity to suffer in captivity, preference and demand testing of resources related to their well-being would be a valuable exercise. Utilizing enrichment items for the commodities under study in preference and demand research would provide quantitative information for the area and aid in the selection and provision of enrichment items that could enhance the well-being of captive chimpanzees. To enable an exploration into the influence of the setting of demand research on results, the chimpanzees’ demand for an enrichment item was tested whilst housed in a social situation, and then whilst alone. In addition, this would add to the discussion of the validity of applying research findings to

animals held in settings that differ socially to those the research was conducted in.

Goals

Overall, this current research set out to establish:

1) Whether demand and preference procedures could be conducted within a zoological facility, within an enclosure that enabled the subjects to freely interact with the experimental equipment and move away from the experimental equipment and elsewhere within their enclosure.

2) Whether and how this could be done with chimpanzees, as a species and in a social group setting (with a group consisting of multiple members of each sex and a variety of ages and sizes), and then individually.

3) Whether the information collected could indicate chimpanzees' ranked demand for selected enrichment items. Also, whether the results were the same for individuals and the group, and thus, if the social setting for the testing of demand had an impact on behaviour. It was anticipated that the results of this study could be used as a quantitative assessment of the chimpanzees' demand for enrichment items, and that by providing items that the chimpanzees showed greater demand for, problems such as the lack or decreased use of items could be reduced.

Specific Objectives of This Research

- To determine the activity time of the chimpanzee group within the indoor section of their enclosure during their 'off exhibit time'. The purpose of this was to determine the best time to perform the operant research. (Experiment 1).
- To design and construct enrichment items for use in a series of experiments to attempt to assess chimpanzees' preference and demand for commodities in a group setting. Equipment was required to be suitable for the subjects, the social setting, the facility and the purpose of the research. (Experiment 2).
- To shape and train the chimpanzees to use the operant equipment to gain access to reinforcers and access to the enrichment items. (Experiment 4).
- To use the results of the experiments to assess:
 - Whether the chimpanzees interact with or avoid the commodities, in this case enrichment items, and to what level they do so. (Experiments

2, 3, 5 and 6).

- Whether the chimpanzee group would spend a differential amount of time using the enrichment items and if the group had a preference for particular enrichment items, and if so what they were. (Experiment 3).
- Whether the chimpanzee group would work for the enrichment items differentially. (Experiment 5).
- How the amount of time the chimpanzee group spent using the enrichment items related to the amount of work the chimpanzees did to obtain access to the enrichment items. (Whether it is possible to rank the chimpanzees' demand for the commodities). (Experiment 5).
- To replicate the demand work with a sub-set of the chimpanzees, tested in isolation, to assess how the results relate to those for the group (i.e., how the demand for the commodities is altered by changes in the external environment of the chimpanzees). (Experiment 6).

EXPERIMENT 1: CHIMPANZEES' INDOOR ENCLOSURE ACTIVITY

The goal of the initial experiment of this research was to determine the timing of activity for a chimpanzee group whilst they were contained within their indoor enclosure during “off exhibit time”. The purpose was to assess the best time of the day to conduct the sessions for the remainder of the research.

Conducting Research in Zoos

This current research was conducted within a fully functioning zoological facility. Full consideration of the requirements and restrictions of working within such a captive animal environment was necessary to undertake this current research.

Changing Role of Zoos

In Victorian times, there was a dramatic increase in the number of zoos around the world (Seidensticker & Forthman, 1998). At that time people were only interested in seeing the new, unusual animals that were being discovered from different parts of the globe. In an effort to prevent disease, captive wild animals were kept in sterile tile and concrete enclosures to allow for easy cleaning (Seidensticker & Forthman, 1998; Young, 2003). As more zoos were developed worldwide, the criteria for good management of these animals changed to include considerations of breeding success. Then with the development of psychology and biology as academic disciplines, people began studying these animals (Schapiro et al., 1995; Shepherdson, 1998). Through this, it was discovered that animals needed a wide variety of experiences for their ‘normal’ development. The way zoos kept animals was influenced by research which helped determine what was required to produce specific behaviour patterns and seemingly healthy animals (Maple 2007; Seidensticker & Forthman, 1998; Shepherdson, 1998). There were not one or two things, which if applied, would produce a ‘normal’ animal. There were different early experiences, or early conditions, which were necessary for the development of different types of behaviour (Schapiro et al., 1995). As a result of such findings the role of zoos, which was once primarily entertainment, has over the years developed a focus on conservation and having animals which show people elements of what these animals are like in the wild (Young, 2003). The modern zoo is meant to be a ‘snapshot of the wild’, and to provide this, as Mench and Kreger (1996) suggest, we

need to discover what is important for these animals to behave ‘normally’ and have an optimal level of well-being.

Constraints on the Provision of Enrichment in the Zoo Environment

Unfortunately, animal well-being is not always the highest priority in the design and management of zoos. Many researchers are concerned that visitor perception may be being valued above the best interests of the animals in regards to the provision of enrichment (Poole, 1998; Robinson, 1998; Rosenblum & Andrews, 1995; Shepherdson, 1998). Robinson (1998) and Poole (1998) suggest that visitor considerations may limit the application of some unnatural objects with more ‘acceptable’ substitutes and suggest that zoos should not be afraid to include artificial components in animals’ enclosures if they benefit the animals. Poole (1998) goes further and suggests that zoo enclosures risk being sanitised versions of reality. The reluctance to provide carcasses for carnivores is, in his view, an example of sanitation taken too far. While many would agree that what is purely beneficial for the animals must be weighed against what is acceptable for the situation (Markowitz & Aday, 1998; Robinson, 1998), some suggest that what is regarded to be ‘acceptable’ needs to be considered carefully (Poole, 1998, Robinson, 1998, Shepherdson, 1998).

Practical Constraints

Adoption of enrichment practices may be inhibited if they are impractical, deemed to be unsafe to the animals or the humans the animals are in contact with, or if obtaining supplies is difficult or costly (Kreger, Hutchins & Fascione, 1998). With a limit on time, money or resources, zoos are often not able to cater for all the needs of their animals under charge. In such cases, enrichment priority decisions must be made (Kreger et al., 1998). These decisions can be complex and involve a number of overlapping contexts and ethical considerations (Chamove, 1989; Chamove & Anderson, 1989; Kreger et al., 1998). Markowitz and Aday (1998) suggest that where resources are lacking, ‘band-aid’ solutions are possible and should be applied. Shepherdson (1989a) recommends that successful enrichments projects must be evidenced as improving behaviour, and as being practical, effective over time and compatible with zoo aims.

Constraints on Conducting Research in Zoos

Many have suggested the need for research to be conducted in environments that more closely resemble those in which animal welfare recommendations are provided for (Bateson, 2004; Dawkins, 2004; Gibbons et al., 1994; Hutchins et al., 1996; Kleiman, 1992; Patterson-Kane, 1999; Ryder & Feister, 1995; Saudargas & Drummer, 1996; Thompson, 1993; Webster, 2003). However, while this may be the ideal scenario there are practical considerations that need to be factored into studies in these settings. Zoological facilities have many priorities impacting on their existence and functioning. These may include revenue earning, entertainment, education, animal welfare, and breeding (Reade & Waran, 1996). Any research that is conducted within the zoo setting must adjust its methodology to fit around these considerations. In addition it is also inevitable that such studies will be less controlled than those conducted in laboratory settings as many factors can vary and are out of experimental control within these external settings. Melfi (2005) found that most primatologists do not conduct their research in zoos. Hosey (1997) suggested that this may be due to the methodological difficulties of working within the zoo environments.

Practical Constraints on Conducting This Research

This current research was conducted within a fully functioning zoological facility, Wellington Zoo in New Zealand. The zoo's main objectives included visitor entertainment and education, animal welfare and management, national and international breeding and conservation programmes, and revenue earning. As a result the chimpanzee group utilized as subjects for this current research were managed in relation to these factors. In general, the group was held socially for the majority of the day, were on public display during the zoo's hours of operation, were managed under a schedule of standard husbandry protocol and maintained within the Facility's operational and animal welfare guidelines (details to follow).

The studies conducted for this current research were required to have methodology that fulfilled ethical considerations for the subjects, species, facility, Researcher's governing body (University of Waikato) and the Country's governing body for animal welfare (New Zealand Ministry of Agriculture and Forestry) (details to follow). In addition to this, the research had to have as little impact as possible on the chimpanzee group's standard husbandry. Practically the research had to be as

unobtrusive as possible to zoo staff and their daily functioning. This included ensuring equipment, computers and cables were out of the way. Minimal disruption through construction of experimental equipment was also required. Consideration was given to the presence of rodents in the facility, so that equipment would not harbour these and also that equipment that utilised food items had to be able to restrict access. Also considered was the maintenance of the area, including daily cleaning regimes, cables and equipment that could withstand this for the entire length of the research. Access to research subjects was restricted and was based on facility operating hours and procedures. There were periods of disruption for the subject group including injury, illness, medical procedures and death (unrelated to this current research). In addition to these considerations, impact on the zoo visitor experience was required to be minimal. At the same time the methodology including equipment had to take into consideration the practical implications of the species that were utilised as subjects while attempting to investigate the research subject matter. Prior studies conducted by the researcher within the facilities assisted in decisions regarding methodology for this current research (Vivian, 2001) as well as assisting in familiarities between the researcher and the subjects and zoo staff and protocols.

Where the Research was Conducted

Taking these factors into consideration, it was decided the Indoor Area of the chimpanzee enclosure (as seen in Figure 1.1) was the best location in which to conduct the research. Here, equipment could be housed and experimental sessions conducted so that they were semi-accessible to the chimpanzees, easily accessible to the researcher, impacted as little as possible on zoo staff activities. Weather-proof areas were available in the area, the public were not impacted in terms of the equipment and research inhibiting their visitor experience (in fact some of the research was visible to the public and therefore may have enhanced their experience) and impact on standard husbandry for the chimpanzees was minimised.

When the Research was Conducted

The chimpanzee group was held within the Indoor Area outside of zoo operating hours and overnight (details to follow). During this time the group engaged in activities including foraging, social interaction and rest. In order to ascertain the exact period in which sessions for future experiments in this research should be

conducted this first study sought to establish the group's general hours of activity and conversely inactivity (sleep) while within the indoor enclosure.

Chimpanzees' Nocturnal Sleep Period

Few studies have explored the nocturnal sleep period for apes. Studies of wild chimpanzees, which base their estimates on retiring and rising times for individuals, suggest they sleep around 12 hours per night (Lodwick, Borries, Pusey, Goodall & McGrew, 2004). Early studies of laboratory chimpanzees found the duration of sleep to range between 10-12 hours per night (Freemon, McNew & Adey, 1970; McNew, Howe & Adey, 1971). However, Videan (2006) undertook an examination of the factors that impact on captive chimpanzee sleep behaviour and found subject chimpanzees slept an average of 8.81 hours per night (similar to the human average of seven to nine hours). It was found that the period of sleep was interspersed with frequent awakenings, rather than being one continuous period of sleep. Individual differences were found with older chimpanzees sleeping longer and with fewer night time disturbances. The structures of a chimpanzee eye are reported to be identical to that of humans (Lythgoe, 1938) so they have similar abilities to humans to sense light and objects.

Aim

This study was conducted in order to determine how much of the time the chimpanzee group were awake and active during the time in which they were held within the Indoor Area of their enclosure, and when the period of activity/inactivity was. The purpose of this was to determine the best possible time to run the subsequent experiments for this current research.

Method

Subjects

The study group consisted of 14 chimpanzees: 8 males and 6 females. Their backgrounds were collected from zoo records and personal communication with zoo staff. Table 1.1 gives details for each chimpanzee.

The family tree is given in detail in Appendix A. A summary of the biological relationships is:

- Cara mother of Chima and Alexis
- Samantha mother of Temba and Keza
- Sally mother of Mahinga and Bahati

The paternity of the chimpanzees was established in 2004 and determined:

- Boyd father of Gombe, Chima, Keza and Bahati
- Sam father of Temba, and Alexis

Table 1.1

Chimpanzee's sex, age, place of birth and date of transfer (where applicable or NA if born at Wellington Zoological Gardens, Wgtn.), related age category, and physical characteristics.

| Name | Sex | Birth date | Age at Nov 2006 | Place and Date of Transfer to Wgtn. | Age category (Fritz, & Howell, 1993) | Physical Notes | Weight at Nov 2006 (kg) |
|----------|-----|------------|-----------------|-------------------------------------|--------------------------------------|---------------------------|-------------------------|
| Sam | M | 22/08/77 | 29 | NA | Adult (mature) | Largest, hairiest male | 73.0 |
| Jessie | F | 10/07/78 | 28 | NA | Adult (mature) | Baldest, largest female | 83.5 |
| Boyd | M | 29/10/78 | 28 | NA | Adult (mature) | Baldest male, brow scar | 58.5 |
| Cara | F | 10/09/81 | 23 | Sydney, '92 | Adult (prime) | Left ear droop | 53.0 |
| Samantha | F | 25/12/83 | 22 | Sydney, '92 | Adult (prime) | Right ear droop | 56.5 |
| Sally | F | 13/01/85 | 21 | Sydney, '92 | Adult (prime) | Bald back patches | 60.0 |
| Marty | M | 28/01/87 | 19 | NA | Adult (young) | Bald, protruding ears | 64.0 |
| Gombe | M | 4/02/93 | 13 | NA | Adolescent | | 52.0 |
| Chima | F | 24/05/94 | 12 | NA | Adolescent | Bald chest, and arms | 48.2 |
| Temba | M | 27/08/94 | 12 | NA | Adolescent | Large build, pinkish tone | 68.0 |
| Mahinga | M | 24/03/96 | NA | NA | Juvenile | | NA |
| Keza | F | 6/07/98 | 8 | NA | Juvenile | Receding hair line | 46.0 |
| Alexis | M | 20/08/98 | 8 | NA | Juvenile | Drop on ear lobe | 45.2 |
| Bahati | M | 23/12/01 | NA | NA | Kindergarten | White baby tuft | NA |

During prior research (Vivian, 2001) the researcher became familiar with each chimpanzee in the group and was able to identify each individual. This familiarization assisted in the identification of individuals during the data analysis of this current research. Also, during the earlier research the dominance hierarchy within the chimpanzee group was assessed through informal observation and discussion with the zoo staff. During the course of this current research the status of dominant male and highest ranking individuals fluctuated, being shared by adult

males Boyd and Marty. All others showed submissive gestures towards them, such as during greetings, times of aggression or when food sharing. The hierarchical dominance in the females was not obvious; although Jessie did exhibit more dominant behaviours, and conversely other chimpanzees exhibited more submissive behaviours to her, than any of the other females in the group. Goodall (1971) noted that in the wild female chimpanzees generally rank below adult male individuals. Jessie was hand-reared for the first few years of her life by zoo keepers, after her mother was unable to nurse her. All of the other chimpanzees were reared by their natural mothers in captivity.

Enclosures

The chimpanzee's housing consisted of both an indoor enclosure, originally constructed in 1954, and a large outdoor enclosure. The outdoor enclosure, opened in 1991, was 150 m long and 50 m wide and was surrounded by a 4-m high concrete wall. The enclosure would fall into the category of 'soft' and 'naturalistic' in appearance (Maple & Finlay, 1989). The indoor portion of the chimpanzee enclosure was used to house the chimpanzees overnight, on days when inclement weather precluded the use of the outdoor enclosure and on other days when the chimpanzees would not leave the Indoor Area. Figure 1.1 shows a diagram of the chimpanzees' indoor enclosure. Experiments were conducted within the indoor section of the chimpanzees' exhibit. This was the most favourable place for the chimpanzees to access the experimental equipment, from the Researcher's point of view as it was convenient to access, large enough to house all the equipment, and out of the way of general keeper management needs. The enclosure was divided into three areas, two of which were truly indoors and partitioned from each other by bars. These two areas included smooth concrete floors and furniture such as sleeping platforms, ropes and hammocks. These areas are shown in Figure 1.2, on the left. The indoor enclosure was heated with a central heating system and the sleeping platforms had 'under floor' heating. The third section contained one glass-panelled wall and one with open bars, and was therefore, both semi-indoors (or indoor/outdoor) and visible to the public. The floor area for this section was 3 m wide and 6 m long, the ceiling was 4 m high and consisted of bars covered by corrugated plastic roofing (the bars blocking the chimpanzees' access to the roofing). This section contained a large wooden climbing frame, ropes, hammocks and textured concrete flooring. This part of the enclosure is

shown in Figure 1.2 on the right. The area was referred to as the ‘Covered Area’ by zoo staff and from hence forth will be referred to as such for this current research.

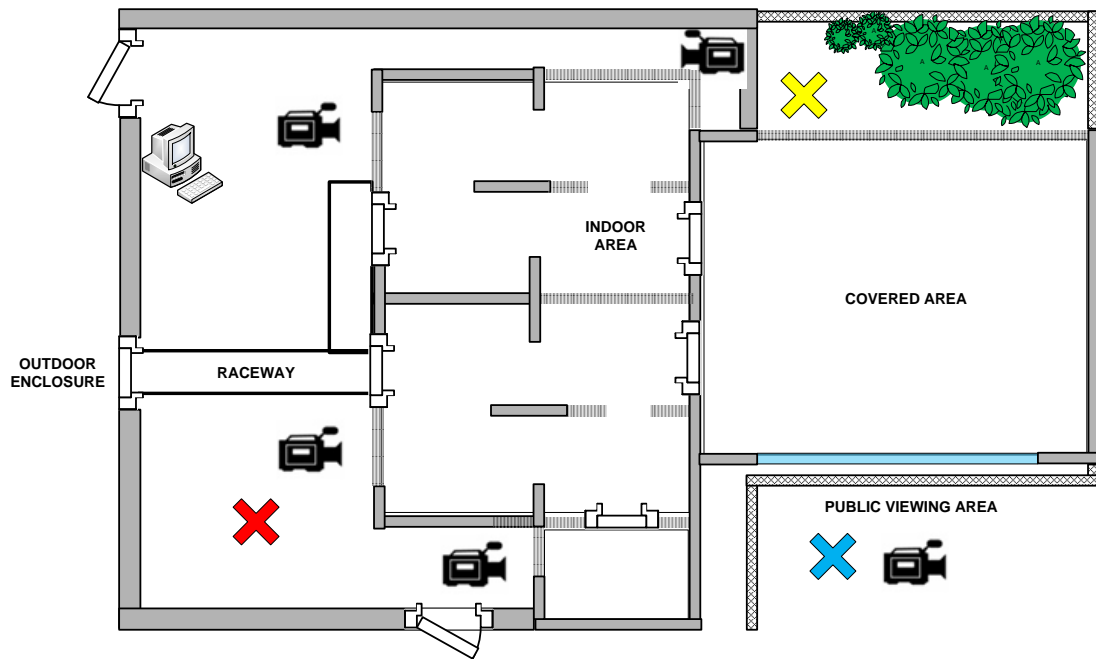


Figure 1.1. Floor plan of the chimpanzee Indoor Enclosure including the Indoor Area and Covered Area. The location of each camera for Experiment 1 is indicated by a symbol. The red cross indicates where the picture on the left in Figure 1.2 was taken from, and the blue cross indicates where the picture on the right in Figure 1.2 was taken from. The internally housed computer equipment is indicated by a computer symbol. The location of the experimental equipment for Experiments 2 to 6 is indicated by the yellow cross.



Figure 1.2. Chimpanzee Indoor Enclosure including the Indoor Area and

Covered Area.

Standard Husbandry Protocol

Initially, each day the outdoor enclosure was cleaned and fruit (oranges and carrots) and bread was scattered around it. Burlap sacks were deposited in the enclosure and log feeders and balls were baited with molasses or peanut butter. The log feeders were foraging puzzle feeders that the researcher constructed for use in previous research (Vivian, 2001). The feeders consisted of metal boxes secured into cavities in dead tree trunks. Partial walls were included within the boxes and a clear acrylic sheet with holes cut in it was secured on the face of the box. Peanuts were placed inside the box at one end and the chimpanzees were able to move the nuts, using tools, through the feeder to an access shoot. At approximately 0830 hours the chimpanzees were let through a caged raceway into the outdoor enclosure.

At 1315 hours the Keepers gave a public talk about the chimpanzees and during this time, the chimpanzees were provided with a, primarily fruit, snack. Enrichment items such as stuffed bottles (filled with fruit and water and frozen), and treat tubes (stuffed with a rice/porridge/raisin mix) were given to the chimpanzees at approximately 1430. At 1630 hours the chimpanzees were allowed access to the indoor enclosure. As each chimpanzee entered in through the raceway, the zoo keepers used this time to examine the chimpanzees more closely, and to administer any necessary medication and contraception to selected females. Within the Indoor Area they were provided with their main meal for the day of fruit and vegetables. Once a week, the chimpanzees were provided with a meal that included cooked chicken.

On inclement days, the chimpanzees were held indoors and moved around the various internal enclosures to allow for general maintenance work to be done by the Keepers.

Apart from these fixed procedures a number of things were provided for the chimpanzees on an ad-hoc basis. These included providing molasses in holes drilled in the trees in the outdoor enclosure, frozen juice in the afternoon on hot days and the provision of browse (branches and leaves) some afternoons. Indoors, the chimpanzees were also intermittently given used clothing or feeder balls or logs as enrichment items - but none during the periods of testing of this current research, i.e. Experiments 2, 3, 5 and 6.

Study's Impact on Standard Husbandry Protocol

During this current research the chimpanzees continued to receive their standard food, water and enrichment supplies. The enrichments they received during the experimental phases were additional to this. Thus, water was available to the group ad lib, at all times, and they were fed three times each day.

Ethical Consent

In 1999 New Zealand enacted legislation to protect Great Apes held within the country (as previously discussed). As such, this current research in general and the procedures it employed were required to gain the approval of the Director-General of the Ministry of Agriculture and Forestry (MAF), via consultation with the National Animal Ethics Advisory Committee. The research had to ultimately be in the best interests of the chimpanzees involved or the species in general. A partial requirement of the consent meant that MAF monitored the research throughout the experimental period. Ethical consent was also sought and gained from the University of Waikato Animal Ethics Committee overall and for specific components of the research. In addition, Wellington Zoological Gardens were required to give their consent for the research to be conducted within their facility and to the specific details of the research. Throughout the data collection period zoo staff were consulted about the procedure that was going to be undertaken and informed of any results that were found. All the procedures were approved by the Director-General of MAF via the National Animal Ethics Advisory Committee in accordance with the Animal Welfare Act 1999 concerning restrictions on the use of non-human hominids, the University of Waikato Animal Ethics Committee and the Wellington Zoo.

Procedure

The study was conducted during August 2003. Within the indoor enclosure (all three sections) five cameras were set in place so as to allow viewing of as much of the area as possible. The location of the cameras are indicated in Figure 1.1 These cameras were linked to video recording equipment via a quad system and then to monitors. The cameras were set to record between the hours of 1630 and 0800 as the chimpanzees came in at 1630 each night and were released into the outdoor enclosure at 0830 each morning.

Four sessions were run, covering four night/morning periods. This period was decided on as a reasonable basis for a judgment on the general activity that occurred with the chimpanzees overnight. Also there were constraints on the number of days the experimental equipment was able to be in place within the animals' enclosure (as the associated cameras and cords etc were somewhat in the way of the daily functioning of the zoo staff) and there was also a constraint on the time the equipment used was available to this current research.

For this experiment activity included any physical action or movement made by the chimpanzees. Thus in this context any behaviour by the chimpanzees that was not sleeping. Activity "stopped" at night when the last movement was seen to occur (that was not sleeping, or involved with sleeping, such as rolling over whilst sleeping). In the morning the chimpanzees first observed behaviour not associated with sleeping was when activity "began again".

The video recordings from each night were analysed to assess the time at which the chimpanzees' activity stopped, and whereabouts the last activity took place (visible to the cameras) and the time of the first activity the next morning and the location of this activity (as visible to the cameras) and the time and location at which most of the chimpanzee group was active in the morning.

For the night on day three and day four artificial lighting was left on in the indoor enclosure to try to enhance the ability to view the chimpanzees' movements in the recorded footage.

Results

Table 1.2 shows the time at which the sun set for each session; the time at which chimpanzee activity was last seen, and where it was seen for each session. It also shows the sunrise time; the time and place of the first chimpanzee activity for each session; and the time and place of the main group activity (more than three individuals active). The data show that the chimpanzees were not active during the time shortly after sunset until the time shortly before sunrise. Once the sun was down (and it was dark) the chimpanzees were either resting in one place or grooming but not moving around the enclosure. The majority of the chimpanzee group was active just before sunrise and the bulk of the activity took place in the Covered Area. The type of activity was not the focus in this study, rather it was the timing of activity. However, the majority of activity that took place in the main morning activity was

young individuals playing within the enclosure. It was also noted that the majority of the food for the chimpanzees' meals provided at night was consumed within half an hour of the chimpanzees gaining access to it.

During the two nights when artificial lights were left on in the indoor enclosure (day three and four) the time of last movement was the same as the two nights that artificial lighting was not left on (day one and two).

Over the period in which the study was conducted the chimpanzees were held within their indoor enclosures both day and night as the weather prevented them being able to be let outdoors. This being the case the results across days for the chimpanzees' time of activity were similar so this could be judged to have had little effect on the chimpanzees' overnight activity time.

Table 1.2
Chimpanzee group's activity time and location during Experiment 1 and the
sunrise and sunset times for sessions.

| Session | Sunset Time | Time last movement night | Place last movement night | Sunrise Time | Time first movement morning | Place first movement morning | Time main movement morning | Place main movement morning |
|---------|-------------|--------------------------|---------------------------|--------------|-----------------------------|------------------------------|----------------------------|-----------------------------|
| 1 | 1735 | 1756 | Covered Area | 0717 | 0559 | Indoor platform | 0708 | Covered Area |
| 2 | 1736 | 1816 | Indoor raceway | 0715 | 0655 | Covered Area | 0704 | Covered Area |
| 3 | 1737 | 1816 | Covered Area | 0714 | 0643 | Indoor raceway | 0647 | Covered Area |
| 4 | 1738 | 1812 | Covered Area | 0713 | 0606 | Covered Area | 0645 | Indoor raceway |

Discussion

This study showed that in general during the hours between sunset and sunrise the chimpanzees were inactive. The total hours of sleep varied from 12 hrs and 31 min to 13 hrs and 12 min. This was also the case even when artificial lighting was left on during two of the nights of the study.

The total sleep time for the chimpanzee group was similar to previous studies of wild and captive chimpanzees (Freemon et al., 1970; Lodwick et al., 2004; McNew et al., 1971). However, the period was greater than found recently by Videan

(2006) for captive chimpanzees, where the average night sleep time period was 8.81 hours. This difference may have been due to the fact that this current study sought to gauge a general time for activity for a later purpose. Exactly what behaviour the chimpanzees were performing after they had settled was not examined, similar to the 'inactivity' basis used in the wild sleep time studies. Individuals may have been interacting socially, including such things as grooming during this period but this was not explored (just as Lodwick et al., 2004 simply used retiring and rising times for estimates of sleep periods). For the purpose of this study a general guide to the groups' period of inactivity was what was sought. It should also be noted that Videan's (2006) study was conducted during the American summer time in an indoor-outdoor enclosure, which may have lead to the shorter sleep time comparison as the present study was conducted in the winter (with shorter day light hours).

These results showed that the longest time of activity for the chimpanzees during the hours in which they were within the indoor components of their enclosures was the time from when they came in at night until they retired to sleep. They also showed that artificial lighting would be unlikely to result in extending their activity time indoors overnight.

Conclusion

On the basis of these results the decision was made to conduct the next experimental sessions in this current research during the period after the chimpanzees had come in to the indoor enclosure at night. It was decided to allow half an hour for them to consume the bulk of their main daily meal before a session was started. It was also decided to conduct the experimental sessions for a maximum of three hours each night. It was also decided that the Free Access study and the Demand studies of this current research (Experiments 3, 5 and 6) were to be conducted during New Zealand Daylight Savings periods (but in different years) so that the change in day light hours would be relatively minimal. In general this period was during the summer months in New Zealand, occurring from the end of September until the beginning of April each year. (The present study was not conducted during the Daylight Savings period). The whole research was on a set deadline as the chimpanzees were moving to a new indoor facility. The area in which the research was based was therefore no longer going to be used. The deadline for this move was October 2006. A decision was also made to include artificial lighting in the research

area during the duration of each session of experimentation. This would provide more light for the researcher to be able to identify individual chimpanzees within the experimental area and operating the equipment and the chimpanzees to view the equipment. However, as suggested by findings of this study, the inclusion of this light should have little effect on the chimpanzees' normal activity time.

EXPERIMENT 2: INTRODUCTION AND TRIAL OF ENRICHMENT EQUIPMENT

PART 1

This current study sought to introduce a number of novel, specifically designed, enrichment items to a socially-housed chimpanzee group and trial the equipment to see whether the group would interact with the items and to what level they would do so. The aim was to also assess the suitability of the items for the research, including issues of durability and application.

Enrichment for Non-human Primates

Environmental or behavioural enrichment has developed as a means of improving the well-being of captive animals, including Great Apes (NRC/ILAR, 1998, Shepherdson, 1998; Young, 2003). The United States Amendments to their Animal Welfare Act of 1985 incorporated the need for facilities to have ‘an environmental enhancement plan for primates’ (USDA/APHIS, Sec 3.81). The regulations promoted discussion and resulted in an abundance of scientific and anecdotal information on enrichment. Worldwide similar provisions have been developed in an attempt to specify captive primates’ requirements (Poole, 1997, USDA/APHIS, 1999). In a report produced by the Australasian Regional Association of Zoological Parks and Aquaria (ARAZPA) in 1998, *Recommendations for the Management of Great Apes in Australasia*, the recommendations for their future management included the ‘need to recognise the importance of social structures and normal behavioural repertoires’ and to explore fully ‘behavioural and environmental enrichment’ (Section I.A.4).

Factors Effecting Enrichment Use

A variety of factors have been shown to influence the effectiveness of enrichment techniques. These include novelty, complexity and control, habituation, and individual differences.

Novelty, Complexity and Control

Novel objects are defined as “those which have a relatively high degree of

unpredictability to the animal in that many, if not all, of the properties are unknown to it...The more properties of an object that are known to the animal (predictable by it), the less novelty is inherent in the object” (Animal Care, 1999). Non-human primates have been shown to use objects more when they are novel (Menzel, 1971). Novel objects have been shown to increase activity, and decrease abnormal behaviour in captive chimpanzees (Line et al., 1989; Paquette and Prescott, 1988).

By definition complexity is “the quantity of information required to describe a system” (Chaitin, 1970), or, in the case of this research, to describe an object, i.e., an enrichment item. An enrichment items’ complexity can include both its visual complexity: (i.e., colours, shapes and movement included on or with the item), and the complexity of interactions that it affords a subject. Thus the number of “features” an item has can serve as an index of its complexity but, as Sambrook and Buchanan-Smith (1997) suggest, a subjective estimate of the complexity of an item maybe sufficient.

Objects provided for primates do not have to be complex for the animals to show interest in them. However, primates have been shown to prefer complex items (Humphrey, 1972). Increased cage complexities have been shown to be beneficial in reducing aggression and inactivity among primates (Chamove & Anderson, 1989; McKenzie, Chamove & Feistner, 1986, Perkins, 1992; Tripp, 1985). Videan, Fritz, Schwandt, Smith, and Howell (2005) suggest that novelty and complexity are key elements of an enrichment program for captive chimpanzees.

A critical factor influencing the effectiveness of enrichment in improving psychological well-being has been found to be the degree of control the animal has with respect to interacting with, or conversely avoiding, novel stimulation (Mench, 1998; Sambrook & Buchanan-Smith, 1997; Videan et al., 2005). Controllability is operationally defined to be the difference in likelihood of an event occurring depending on an animal’s behaviour. If the animal’s behaviour does not influence the likelihood of the event then the event is deemed uncontrollable (Overmeir, Oaterson, & Wielkiewicz, 1980). One hypothesis is that giving a primate the opportunity to change its environment whenever it chooses to do so is a form of enrichment (Novak & Drewsen, 1989) - ‘achievement’ as Poole (1998) describes it. Sambrook and Buchanan-Smith (1997) consider control to be highly attractive for animals because it is an adaptive aspect of behaviour. Studies have shown that control over enrichment events can improve animal welfare. The ability to exercise some control

over stimuli within the caged environment has been shown to reduce stress in captive animals (Hanson et al., 2002). Young rhesus monkeys, given the opportunity to control food and water by manipulating devices, showed less self-directed behaviour and more exploration than monkeys who had no control (Mineka, Gunnar & Champoux, 1986). However, the same study also showed that once an animal has been given control, the consequences of removing it could be worse than if the animal had never had it.

Enrichment devices that allow individuals the opportunity to control their environment have been utilized by a larger number of animals and for longer periods of time than nonresponsive objects (Markowitz & Line, 1989). Videan et al. (2005) conducted research with a large group of subjects (75) to assess if there was a correlation between chimpanzees' use of an object and degree of controllability. They found that the chimpanzees used the most controllable items (those that were destructible) significantly more than those that were fixed, movable or malleable. They also found that individual factors, such as age, sex, rearing and social group composition had minimal effects on enrichment item use. Sambrook and Buchanan-Smith (1997) proposed a ranking model of controllability, with those objects that are interactive (i.e., mechanically or electronically manipulable) as the most controllable, followed by malleable items, moveable items and then fixed items. Sambrook and Buchannan-Smith (1997) also state that, whilst it is increasingly suggested that an animal having some control over its environment may be an essential feature of a good captive setting, there remains a paucity of experimental work aimed at directly testing this hypothesis.

Habituation

Habituation is defined by McFarland (1981) as a decline, over repeated experiences, in the probability of responses to a stimulus that were initially present. Many studies have shown that while animals may initially show interest in objects, use can decrease over time (e.g., Brent, Lee & Eichberg, 1989; Cardinal & Kent, 1998; Paquette & Prescott, 1988; Pruetz & Bloomsmit, 1992; Taylor, Brown, Davis & Laudenslage, 1997; Vivian, 2001). Line, Morgan, and Markowitz, (1991) suggest that simple toys are ineffective enrichments, because animals lose interest in them quickly. Many argue that rotation of enrichment items can increase their use (Cardinal & Kent, 1998; Hienz et al., 2000; Markowitz, 1982; NRC/ILAR, 1998;

Paquette & Prescott, 1988; Sanz et al., 1999; Shefferly, Fritz & Howell, 1993). That an object can be picked up and carried has also been cited as adding to their value (Wilson, 1982). Tarou, Kuhar, Adcock, Bloomsmith and Maple (2004) designed a computer-joystick item of enrichment, anticipated to increase complexity, and decrease the rate of habituation when provided to zoo-housed orang-utans (*Pongo pygmaeus*). Their results did indeed show little habituation. However, the subjects displayed a significant increase in the level of aggression. Their recommendation was that the enrichment item was more suitable for singly-housed animals, or multiple apparatuses should be provided at once. Perhaps through measuring animals' demand for selected enrichment items, habituation could be reduced. By conducting research which investigated both chimpanzees' demand for enrichment items and their demand for the items this current research aimed to explore if this suggestion is valid.

Individual Differences

A number of studies have suggested individual differences between group member's preferences for enrichment items (Hienz, Zarcone, Turkkan, Pyle & Adams, 1998; Perkins, Burnett, Rice, Staley & Weick, 1992; Vivian, 2001; Watson, Houston & Macallum, 1989). Individual's age, sex, rank or state of housing, have been found to affect the outcome of the presentation of manipulanda, suggesting the need to consider their influence when designing enrichment programmes. Bloomsmith, Finley, Merhalski and Maple's (1990a) results indicated that age and housing differences for chimpanzees affected behaviour changes, with younger animals housed in more barren environments exhibiting higher levels of object use. In Pruett and Bloomsmith's (1992) study, male chimpanzees exhibited the greatest level of solitary play with objects.

Novak, Musante, Munroe, O'Neill, Price, and Suomi (1993) found that old, female rhesus monkeys manipulated objects more than male monkeys did and that subordinate monkeys avoided manipulating the objects. These findings suggested that the failure to manipulate objects was more a function of individual housing than of old age. Schapiro et al. (1996) found singly-housed rhesus macaques used inanimate enrichment more than macaques living in social groups. As previously discussed, Videan et al. (2005) had a very large sample size (75) and they found no significant individual effects of age, sex, rearing, or social group on enrichment use

by chimpanzees. Although they did observe that younger chimpanzees tended to use the destructible items more than adult individuals. Older, particularly female chimpanzees were shown to use the fixed items more but the researchers suggested this finding may have been due to the adults being less active and spending more time resting on the fixed benches provided.

Methods of Environmental Enrichment

Researchers have identified many methods for enriching captive animal environments (NRC/ILAR, 1998). Enrichment strategies have been categorised in various ways. However, many follow a similar theme (e.g., USDA/ APHIS, 1999; Bloomsmith et al., 1991; Newberry, 1995; Olfert et al., 1993; Poole, 1992 & 1998; Rosenblum & Andrews, 1995; Schapiro & Bloomsmith, 1995). The USDA/APHIS (1999) report states that for environments to promote the psychological well-being of non-human primates they must attend to five critical elements. These include: social grouping; social needs of infants; structure and substrate; foraging opportunities, and manipulanda. In addition, consideration should be given to sensory stimulation and providing an animal with control over of its environment (USDA/APHIS, 1999). A given strategy may simultaneously address more than one element. It is suggested by Tarou and Bashaw (2007) and Young (2003) that it is important to identify what you are trying to achieve – increasing the occurrence of a certain type of behaviour for example – before designing or deciding on an enrichment item so that the likelihood of achieving the goal is increased.

Research with Enrichment Elements Employed in This Research

The preference and demand procedures used in this current research proposed to utilize a variety of enrichment devices encompassing foraging apparatus and audiovisual and auditory enrichment. The basis for their use and the origin of the final design of the items was from previous research with enrichment items with a variety of animal species, including chimpanzees. The design of the items reflected consideration for elements of novelty, complexity and control for the subjects. Previous research by the researcher with this subject group (Vivian, 2001) and knowledge of the Facility's protocol for providing enrichment and ethical constraints also impacted on the inclusion and design of enrichment items.

Overall, the research sought to establish the application of the items with the

socially held zoo group, the group's use of the items, the level of habituation of the group to the items and whether this habituation was effected by the subjects working for the items and if there were individual differences in subject's use of items.

Visual and Audiovisual Enrichment

Primates convey a wide variety of information through facial expressions and body postures (Goodall, 1971). In captivity visual stimulation can be provided by motion on television or video games and several studies have evaluated the capacity of audiovisual media as enrichment (e.g., Newberry, 1995; Platt and Novak 1997; Rumbaugh, Washburn & Savage-Rumbaugh, 1989). A number of studies have shown primates communicating individual preferences for the content of television programs (Mahoney, 1992). Chimpanzees, previously frightened by the sound of a chainsaw operating out of sight, displayed less behaviour indicative of stress when they were able to watch the activity associated with the noise on closed-circuit television (Rumbaugh, Washburn & Savage-Rumbaugh, 1989).

Enrichment through visual stimulation has been investigated by a number of researchers using videotape and television presentation. Bloomsith, Keeling, and Lambeth (1990b) showed a variety of video content to socially and then individually segregated chimpanzees. The chimpanzees watched the videos for 42% of the time they were available and only the socially housed animals showed any habituation. The chimpanzees' preference for content was ranked from the most watched being the tapes depicting agonistic behaviour, chimpanzees performing other activities, familiar human caregivers and then tapes of other species. Brent et al. (1989) also found individually housed chimpanzees watched television and showed no evidence of habituation. However, in contrast Schapiro and Bloomsith (1995) found that singly-housed yearling rhesus monkeys presented with videotapes depicting primates engaging in normal activities showed little interest, watching for less than two minutes per hour of the presentation. Platt and Novak (1997) investigated the reaction of socially- and individually-housed rhesus monkeys to videotapes and a video game. They found both devices were substantially attended to, the videotapes more so. Little habituation to either device was shown by the females in the study. However, the males did show some habituation to the videotapes. Exposure to the video also affected other behaviour with lower levels of social contact and higher rates of locomotion. Individually-housed monkeys also slept less and engaged in

more agonistic behaviour. These subjects watched unfamiliar monkeys and humans (including soap operas) significantly more often than videotapes of familiar ones; the soap opera videos were noted to have the highest frequency of scene changes. The enriching effect of videotape presentation as a reward for rhesus macaques was demonstrated by Washburn and Hopkins (1994). Andrews and Rosenblum (1993) demonstrated a similar effect with the presentation of live-social-video reward for joystick task performance by bonnet macaques (*Macaca radiata*). Menzel, Premack and Woodruff (1978) concluded that chimpanzees have the ability to apply information they see on television monitors to solving problems in their immediate environment. Maple and Hoff (1982) suggested that “if television stimuli are made meaningful to an ape, attention should vastly be improved”. Bloomsmit and Lambeth (2000) followed this suggestion with a group of socially housed, but individually tested, chimpanzees but found that videotapes with varying content did not affect behaviour differentially as hypothesized, and the subjects did not respond more strongly to videotapes depicting conspecifics than to those of standard television programming or other animals. Neither the chimpanzees’ sex nor social housing situation affected their behavioural response. However, individually-housed subjects did watch the monitors more often. While some evidence of habituation was shown across the study, the level of attention to the videotapes remained substantial. Researchers agree that visual stimulation in the form of videotapes should be fully exploited and explored for their enriching potential for captive primates (Andrews & Rosenblum, 1994; Bloomsmit & Lambeth, 2000; Washburn & Rumbaugh, 1991).

As shown by previous research, the provision of visual and audiovisual enrichment to primates has impacted on the behaviour of primate subjects in a variety of different ways. Many, but not all, studies have shown behaviour change, associated with the provision of the enrichments, suggestive of the items being of benefit to captive primate psychological well-being. Studies have shown variation in findings as to the amount of time subjects have spent engaging with the enrichments, the level of habituation to the enrichment items and different correlations between use and age, sex and housing factors. There has been a suggestion that use of the items would be increased if the content of audiovisual enrichments is ‘meaningful’ to apes (Maple & Hoff, 1982).

Chimpanzee Self Awareness

Maple and Hoff (1982) suggested that the use of visual enrichments is increased if the subject matter of the items is 'meaningful' to individual animals. As such, a case could be made that a form of meaningful visual enrichment would be images of the subject animals themselves. Of course for this to be applicable it is important to discuss chimpanzees' capacity to be 'self' aware.

Recognition of self in a mirror image has received much attention as an experimental method of assessing self-awareness in animals. Gallop (1970) and Gallop, Povinelli, Suarez, Anderson, Lethmate, and Menzel (1995) reported that when most animals see their images in mirrors they react as though seeing another animal and even after prolonged exposure do not recognise the image as themselves. However, this was not the case for chimpanzees and orang-utans. Gallop went onto explore this recognition in chimpanzees. To do so four, wild born, chimpanzees, with no previous experience of mirrors, were placed in separate cages with full-length mirrors. On seeing their reflection each chimpanzee was observed to head-bob, vocalise and threaten the image. However, after an average of three days, they began to utilise the mirror to perform self-directed grooming, and manipulated wads of food on their lips. After ten days of exposure to the mirror, the chimpanzees were anaesthetised and had red dye applied to an eyebrow ridge and the top of the opposite eye. Upon waking, without the mirror present, the number of times the animals touched the spots of dye was recorded over a thirty minute interval. Then the mirror was returned and the same behaviour scored again. The behaviour was observed to occur seven times more frequently while looking in the mirror. From this Gallop concluded that these chimpanzees were able to recognise themselves in the mirror and were therefore self-aware. It should be noted that Gallop (1970) applied the dye portion of the experiment to chimpanzees that were not given any opportunity to experience a mirror and found that they only reacted as if confronted by another chimpanzee and failed to locate the marks on their faces.

Epstein, Lanza, and Skinner (1981) reported that three pigeons, following training to reinforce pecking at spots applied to their bodies, used a mirror to locate a spot on its body with which they could not directly see. However, Epstein et al. were reluctant to attribute this behaviour to self-awareness or claim that a pigeon has 'self-concept.' Instead they accounted for the behaviour in terms of environmental history and suggested that because Gallop (1970) was able to produce positive results only

for chimpanzees given the prior experience with their reflection; his results could also be attributed to environmental events. Notions such as self-awareness were, in their opinion, ‘constructs which impede the search for the controlling variables of the behaviour they are said to produce’ (p.696).

Gallup (1998) and Povinelli (1998) agree that passing the mirror test reveals the presence of a kind of self-concept, but they differ on the scope of that concept. Gallup believes that chimpanzees possess a psychological understanding of themselves. In contrast, Povinelli contends that when chimpanzees and orang-utans see their reflections they form an equivalence relation between the actions they see in the mirror and their own behaviour. He believes they possess an explicit mental representation of the position of their own bodies, what he refers to as a ‘kinesthetic self-concept’. He argues that chimpanzees and orang-utans require it to plan movements in their arboreal environment; however, this does not explain the fact that other arboreal living primates have not shown positive results on the mirror test. Povinelli disagreed that the chimpanzees were aware of their own internal, psychological state. These findings have implications as to the content of ‘meaningful’ visual enrichment items that employ images of animals who are also the audience.

Foraging Enrichment

In the wild, chimpanzees spend 43-62% of their day foraging and feeding, totalling around six to eight hours (Bloomsmith, 1989). Not only does foraging occupy a large proportion of time for wild apes but it may also be a source of intellectual stimulation as various studies of tool use by wild chimpanzees would suggest (Boesch & Boesch-Achermann, 1998; Goodall, 1971; Shepherdson, 1988). In the wild, chimpanzees were discovered to use tools to ‘fish’ for termites. Taking a stick or a long piece of grass or bamboo or foliage and breaking off the side branches, they strip it so it's a single rod and then insert it into a termite mound, waiting for the worker termites to attack the branch. They then remove it, eating the attached termites (Goodall, 1971). In captivity artificial termite mounds are constructed and some sticky, often sweet, substance is placed at the bottom of the holes (Shepherdson, 1998). A variety of results have been reported in regards to captive chimpanzees’ use of these artificial mounds but they are a widely employed in zoos (Markowitz, 1982). Boesch and Boesch-Achermann (1998) observed

chimpanzees in the wild use selected stone hammers to crack hard-shelled nuts against a stone anvil. A sex difference in this practice was observed, with markedly more females cracking nuts than males.

Unfortunately, due to practical constraints, most facilities have predictable schedules and food menus (Brent, 1995; Lindberg, 1998; Markowitz & Aday, 1998). Many suggest that the highly predictable delivery and type of food contributes to the development of certain forms of stereotyped behaviour, for example coprophagy and increased aggression (Anderson and Chamove, 1984; Appleby, 1997; Rooney & Sleeman, 1998). Offering a wider selection of food can stimulate food searching and handling behaviour, thereby improving physical condition (Lindberg, 1998). Other studies have used methods directed towards reducing food-related stereotypes and include providing smaller, more frequent meals, scattering and hiding food in unpredictable locations, increasing the time and skill required to catch or extract food (Appleby, 1995). Studies directed towards reducing food-related stereotypes have shown animals prefer to work for their food rather than simply receive it (Markowitz, 1982; Kreger et al., 1998). However, increasing the level of difficulty associated with a foraging enrichment has been shown to cause some distress (as evidenced by animals' behaviour) and will not necessarily increase foraging behaviour (Novak, Kinsey, Jorgensen, Hazen, 1998). Novak et al. (1998) suggest that foraging opportunities must be sufficiently time-consuming, but not too difficult, to have a sustained effect. Manipulable objects have proved to be more interesting and effective as enrichments if they include food (Crockett, Bielitzki, Carey & Velez, 1989; Phillippi-Falkenstein, 1993; Rooney & Sleeman, 1998). Different devices have been shown to elicit different responses depending on how challenging they are to use and how portable they are (Schapiro et al., 1996). Most primates are manually dexterous and as Lindburg (1998) and Young (2003) suggest, have a variety of specialized foraging adaptations that should be considered when employing foraging enrichments. Placing too much emphasis on foraging enrichment can cause nutritional imbalances or other challenges such as dominant animals obtaining all the preferred items. Markowitz (1992) and Shepherdson (1998) suggest that proper planning and research is needed to ensure that the potential benefits of providing foraging enrichments are maximised.

Foraging devices can present primate food in novel ways and many have been observed to encourage primates' species typical behaviour, increasing activity and

decreasing stereotypic behaviour thereby contributing to their well-being (e.g., Maki et al., 1989; Murchison, 1992; Phillippi-Falkenstein, 1992; Pyle, Bennett, Zarcone, Turkkan, Adams & Hienz, 1996; Pyle, Bennett, Zarcone, Turkkan, Adams & Hienz, 1996; Wood, 1997). Pyle et al. (1996) found this effect for baboons (*Papio hamadryas*), even when their device contained no food. The device was used more by those exhibiting a higher frequency of stereotypic behaviour but used less by those exhibiting higher frequency of self-directed behaviour. These observations were considered to be important for providing enrichments for addressing behavioural issues. Holmes, Riley, Juneau, Pyne and Hofing (1995) found a foraging device presented to singly-housed cynomologous macaques (*Macaca fascicularis*) was preferred to the standard feeder, and self-directed behaviours were significantly reduced. Using the device with novel foods and as part of a rotation programme renewed interest in it. Many researchers have found that even in the presence of 'free' food animals often prefer to work for access, such as the chimpanzees in Menzels' study (1991). This event is referred to as contrafreeloading (Inglis, Forkman & Lazarus, 1997), and this behaviour will be discussed more fully later in this document.

'Puzzle feeders' are designed to require primates to use manipulative and cognitive skills to gain access to food. The manipulation can sometimes require the use of a tool (Young, McNaught & Richardson, 1994). The effect of puzzle feeders on behaviour has been varied. Many have highlighted differences in individual animal subjects' techniques for using puzzle feeders (e.g., Gilloux, Gurnell & Shepherdson, 1992, Nash, 1982), increased foraging time and species-typical behaviour and a decrease in negative behaviours (e.g., Bloomstrand, Riddle, Alford & Maple, 1986; Brent and Eichberg, 1991; Gilloux et al., 1992; Murchison, 1991; Young et al., 1994), or feeder use (e.g., Gilloux et al., 1992; Reinhardt, 1993). Reinhardt (1993) found that a few pairs of rhesus macaques did not use a foraging puzzle, and in most cases, these were identified as animals that were older or had dental problems. Brent and Eichberg (1991) found that female rhesus macaques used a foraging puzzle box more often but that there was no correlation between age and use. Murchison (1991) found that male singly-caged cynomologous macaques were slower to learn to operate a PVC food pipe puzzle than socially-housed macaques. Bloomstrand et al. (1986) found significant behavioural changes after the introduction of a food puzzle with chimpanzees at the extreme ends of the dominance

hierarchy.

Other feeders have resulted in less positive results. Watson (1992) found a puzzle feeder presented to two singly caged macaques eliminated only some stereotypic or abnormal behaviour and there was, in fact, an increase in pacing and rocking when the device was filled. She suggested that other monkeys may have intimidated other subjects when treats were added to the device or that they may have responded to the presence of the observer, anticipating the addition of treats. Brent and Eichberg (1991) observed a reduction in social behaviour when a puzzle-board foraging enrichment was presented to captive chimpanzees. Moazed and Wolff (1988) suggested that the result of having several species of singly-housed monkeys too afraid to approach a device could have been attributed to the monkeys' rearing - the hand-reared animals being less apprehensive.

Much of the research with foraging enrichment items has shown them to have been successful in providing primates with opportunities to express wild-type behaviour related to foraging. Behaviour associated with the provision of these types of enrichment has largely been suggestive of the items being of benefit to the primate psychological well-being. Previous research with this form of enrichment has given a range of findings with differences in the amount of time subjects have spent engaging with the foraging enrichments and in the levels of habituation to the items and also there have been different correlations between use and age, sex, hierarchy and housing factors. These factors will be considered in relation to the results of this present research.

Contrafreeloading

Research, using a variety of species, has shown that animals trained to 'work' for their food continue to do so even when 'free' food is available, as previously mentioned. Hal Markowitz's (1982) first enrichment device showed just this result. A group of white handed gibbons (*Hylobates lar*) were trained to use an apparatus with stimulus lights and levers to encourage brachiation and leaping to gain food. After stable behaviour was maintained, the animals were given free access to identical food, as had previously been their experience. The gibbons, however, continued to use the apparatus and work for their food. This behaviour is referred to as contrafreeloading as it seems to contradict the predictions of two different theoretical frameworks: learning and motivation theory, and optimal foraging theory.

According to both frameworks, animals are predicted to maximise the ratio of benefit to cost (Inglis et al., 1997). While the cause of contrafreeloading is debated in the literature, a number of factors have been found to affect the level of contrafreeloading animals perform. These include: prior training; deprivation level; required effort; stimulus change; environmental uncertainty; rearing conditions; manipulation of the environment and the nature of the foraging task.

Prior training. Jensen (1963) reported that when presented with a choice between bar pressing for food pellets or eating the same pellets from a dish, all but one of the 200 rats (*Rattus rattus*) tested left the dish and worked for food at some time during the experimental trial. Furthermore, the percentage of pellets eaten that were earned by pressing was positively correlated with the number of rewarded presses made during training before the experimental trial. The preference for earned food therefore seemed to be a function of the habit strength formed during the training period. One explanation for the effect of training on subsequent levels of contrafreeloading is neophobia towards the free-food container, since in many of the early contrafreeloading experiments, animals received operant training before the test but had no prior experience of the free-food container (Inglis et al., 1997). However, evidence that contrafreeloading is not solely a function of prior training comes from the many studies showing that such behaviour can be acquired and maintained in the absence of training in the response required (Osbourne, 1977). In addition, animals' contrafreeload despite equal training on both free food and response-dependant food sources (Inglis & Ferguson, 1986).

Deprivation level. Evidence suggests that contrafreeloading decreases with increasing food deprivation. Inglis and Ferguson (1986) found that by increasing the hunger level of starlings (*Sturnus vulgaris*) the subsequent level of contrafreeloading performed by the birds decreased. What's more, as most free feeding takes place at the beginning of a trial with a subsequent increase in contrafreeloading and since hunger declines throughout the trial, within-trial changes in the proportion of food obtained by contrafreeloading also support the notion of hunger levels affecting contrafreeloading activities.

Required effort. The relative effort involved in obtaining earned and free food

is important in determining the level of contrafreeloading. Carder and Berkowitz (1970) found that rats' preference for earned food decreased from over 80% when two presses per reinforcer (FR 2) were required to less than 30% when 10 presses per reinforcer (FR 10) were needed. They concluded that 'as long as the work demands are not too high rats prefer earned food rather than free food' (p.1274). However, it is not just the effort involved in obtaining the earned food that is important because 'free' food is not always free. Effort required to obtain free food, such as climbing a tall food container, can affect (increase) the occurrence of freeloaded (Kleinman, McLaughlin, Gerard, Bosza & Clipper, 1976).

Stimulus change. Contrafreeloading has been found to be strongly affected by stimulus changes correlated with the presentation of earned food (Inglis et al., 1997). Contrafreeloading by a group of rats was shown to be dependent upon the operation of a food-hopper light. When key-pecking had no effect on the hopper light, contrafreeloading fell to a low level; it recovered when the hopper light contingency was reinstated (Osborne, 1977). Such studies demonstrate that working for earned food without associated stimulus changes is not sufficient to maintain contrafreeloading in an operant situation. Two explanations, which are not mutually exclusive, have been proposed to explain the way in which contingent stimulus change affects contrafreeloading (Osborne, 1977). The first argues that the stimulus change becomes a secondary reinforcer after repeated pairing with food presentation during training. This explanation cannot account for the experiments showing contrafreeloading without training. The second explanation is that stimulus change is reinforcing in its own right so that contrafreeloading is not working for food alone, but for food plus sensory reinforcement. The combined reinforcement is thought to be sufficient to maintain responses for earned food in the presence of free food (Inglis et al., 1997; Osborne, 1977).

Environmental uncertainty. There is evidence that a high degree of environmental uncertainty can reduce contrafreeloading. In a study by Forkman (1993) gerbils (*Gerbillus perpallidus*) were allowed to forage between three bowls: one with sand, the second with 30 sunflower seeds mixed with sand and the third with 250 seeds mixed with sand. The animals preferred to gather seeds from the 30-seed bowl until the relative positions of the bowls in the test cage were shifted. After

this, foraging on the 30-seed bowl fell markedly and the animals increased feeding from the 250-seed bowl. Forkman (1993) reported that gerbils are very sensitive to the spatial relationships between objects therefore moving the food bowls constituted a large environmental change. Environmental uncertainty can be induced not only by moving the food sources but also by hiding the food (Inglis & Ferguson, 1986), or by changing the food itself, for example, adding saccharin occasionally to water (Davidson, 1971).

Rearing conditions. In general, animals reared under sensory deprivation explore more when faced with novel stimuli than do animals reared under sensory-enrichment conditions (Inglis et al., 1997). These results can be explained on the basis that satiation to the response-dependant stimuli takes longer for sensory deprived animals than for sensory enriched animals (Osborne, 1977). Sensory deprived animals have been shown to perform more contrafreeloading than sensory enriched animals. Nau, Elias and Bell (1981) reared three groups of rats under different sensory conditions and then tested them in a novel maze as well as under the contrafreeloading paradigm. The sensory enriched group showed the least contrafreeloading. The animals reared in under sensory deprived conditions showed the most stimulation-seeking in the maze also exhibited the highest level of contrafreeloading.

Manipulation of the environment. White (1959) argued that behaviour is primarily directed towards controlling and modifying the environment and that such behaviour is 'self'-reinforcing. Contrafreeloading might be explained on this basis since lever pressing for earned food involves greater environmental manipulation than freely taking food from a continuously available source. This hypothesis has been supported by findings that animals prefer to work for response-dependent food rather than take response-independent food delivered at the same rate (Morgan, 1974).

The nature of the foraging task. It has been suggested that contrafreeloading occurs because the performance of the operant response required to obtain earned food is reinforcing in its own right (Jensen, 1963). However, there is no evidence to support an intrinsic appeal of the behaviour itself. A preference for earned food over

free food has been found when animals have been required to make operant responses that were unusual behaviours that had to be learned (e.g., Neuringer, 1969). Contrafreeloading occurs even though the same behaviour is required to obtain food from both food sources (e.g., Forkman, 1993). And lastly, when animals are given the choice between free food and making a response that no longer produces earned food, they take the free food (e.g., Neuringer, 1969).

Osborne (1977) and Inglis et al. (1997) argue that contrafreeloading, rather than being viewed as contradicting the basic tenets of prevailing theory, can instead be viewed as gaining access to more than just food. Some maintain that animals work for earned food partly for the food itself, and partly because of the reinforcing effects of the stimuli associated with the food (Osborne, 1977). Alternatively, animals act to improve and update their estimate of the profitability of an uncertain food source that may unpredictably become the optimal place to feed (Inglis, Forkman & Lazarus, 1997). While the cause of contrafreeloading is disputed, the factors which affect its occurrence are well documented. Such factors could impact on the provision of foraging enrichments to captive animals.

Manipulanda

Objects for non-human primates can be natural or man-made items, which may be destructible or durable. However, as with most enrichment items, there is much debate about the use of unnatural objects (Wemelsfelder, 1997). Maple and Perkins (1996) suggest that some objects are likely to be of greater functional value to animals than others. As such Shefferly et al. (1993) recommend that the presentation of objects should be monitored to assess their effect and ensure their safety. The benefits to the animals must be weighed against the costs and potential risks (NRC/ILAR, 1998). The advantage of many inanimate objects is their low cost, and little added effort associated with providing them (Reinhardt, 1997; Shefferly et al., 1993). Increasing environmental complexity for captive primates has often involved providing cost effective, manipulable objects such as telephone directories or toys. Chimpanzees' use of temporary (e.g., books, straws, pipes etc.) and semi-permanent (e.g., cargo nets, climbing structures etc.) enrichment objects were observed in a study by Sanz et al. (1999). Individual differences were apparent but generally from the 50 objects presented a preference was shown for certain objects. Fire hoses and cargo nets were the preferred semi-permanent objects and clothing, containers and

paper were the preferred temporary objects. Frequent rotation of objects was shown to have a significant effect on the interest shown in objects, but it was also noted that it was important to also have objects that were available for a longer time. Leaving objects in the enclosure overnight greatly reduced the interest animals showed in them. Sanz et al. (1997) cited a study that showed that for singly housed animals single object presentation was more effective than group object presentation. For the chimpanzees in their study, however, they preferred to use multiple objects at once. It is also noted that great care must be taken in the selection of objects to avoid injuries.

Manipulable objects have been effective in achieving many of the aims of enrichment - increasing species-appropriate behaviour and decreasing abnormal behaviour in many instances. Decreases in inactivity have been found with the provision of destructible objects (e.g., Pruetz & Bloomsmith, 1992; Shefferly et al., 1993) while some individuals have shown reductions in behavioural pathologies after the introduction of inanimate objects (e.g., Anderson & Stoppa, 1991; Bayne et al., 1993; Brent & Belik, 1993). Providing suitable inanimate objects can encourage the species-appropriate primate behaviour of tool use. Takeshita and van Hooff (1996) introduced novel and familiar objects into a chimpanzee enclosure and found that all were used for different purposes. The repertoires of tool use behaviour appeared to vary as a function of age.

Auditory Enrichment

Vocal communication is reported to be most important for primates in the wild (Bayne, 1995; Goodall, 1971). Auditory stimulation in a captive environment can include natural sounds such as vocalizations or man-made sounds such as recorded music. Humans talking to animals has been shown to be beneficial for captive animals (NRC/ILAR, 1998). Certain animals appear to be stimulated by verbal interaction, tone and intensity levels are important as some species may respond as if challenged (NRC/ILAR, 1998). Providing music and naturalistic sounds throughout the day have been shown to reduce aberrant behaviours in captive animals (NRC/ILAR, 1998). A rhesus macaque given auditory stimulation showed an increase in affiliative behaviour and a decrease in self-directed behaviours. The study also showed that the music had a calming effect during conditions of heightened arousal, such as the introduction of a novel objects (Novak & Drewson, 1989).

Captive environments are often extremely noisy and have been reported to contribute to abnormal behavioural and physiological effects (NRC/ILAR, 1998; Markowitz & Aday, 1998). Mahoney (1992) suggested that there is potential for auditory stimuli associated with husbandry practices and visitor noise to cause stress to captive primates. As such efforts can be made to design enclosures to restrict noise or low-level sound played to ‘mask’ unwanted noise (Mahoney, 1992; Tromberg, 1994).

Ogden, Lindburg, and Maple (1994) found the effect of a variety of recordings of ecologically relevant sounds on the behaviour of a group of captive lowland gorillas (*Gorilla gorilla gorilla*) was variable and influenced by the subject’s age. While the rain forest sounds were associated with increased arousal for the adults the effect was the opposite for infants. However, the authors did caution interpretation of the results due to the small sample size. O’Neill (1989) provided one of the few systematic evaluations of the effect of auditory stimulation with captive primates and determined that musical stimulation resulted in a significant decrease in abnormal behaviour. Several studies have combined the effects of music/sounds with the construct of environmental control (such as turning on and off items) with primates, with positive effects (Mineka et al., 1986; Markowitz & Line, 1989; Novak & Drewsen, 1989). Biologically relevant sounds have been shown to promote increased species typical behaviour in gibbons (Shepherdson, Bemment, Carman & Reynolds, 1989), while stereo music was shown to reduce aggression and increase social affiliations in chimpanzees in a laboratory environment (Howell, Schwandt, Fritz, Roeder & Nelson, 2003). Wells, Coleman, and Challis (2006) found that ‘ecologically non-relevant’ sounds (classical music) and ‘ecologically relevant sounds (rainforest sounds) produced fewer behaviours associated with stress and more behaviours associated with relaxation than when no auditory stimulation was provide for a group of captive gorillas.

Research with audio enrichment devices has shown the items to have been associated with behaviour change suggestive of the items being of benefit to primate psychological well-being. This form of enrichment has been recommended for inclusion for primates housed within captive environments.

Enrichment Items Employed in This Research

Visual and Audiovisual Enrichment in This Research

Given previous research on the potential of visual and audiovisual equipment as enrichment this current research sought to examine the use of such an item with a social group of chimpanzees held within a zoo. The use of this enrichment item was designed to combine a number of elements found to be enriching in previous research, such as control, complexity and ‘meaningful’ content. Given that similar items have been used in previous research a comparison could be made with the use of the form of enrichment by this group. As such items have been utilised by subjects, particularly primates and apes, in previous research it was anticipated the chimpanzees in would attend to an enrichment item of this type. Also, as habituation to such items has been shown previously, whether working for the item would affect this could also be explored.

A television monitor showing video footage was selected as the medium because it was relatively low in cost and easy to provide. The unit could also be housed externally and so was safe from destruction by the subjects. It could be seen and heard by the group from within the proposed experimental setting. The volume of the audio and the setting of the unit were such that it would not disturb visiting members of the public, zoo staff or other animals in the facility. The video selected to play contained footage of the chimpanzees themselves, of zoo keepers they were familiar with and of scenes of other animal species and other humans that were not familiar to the chimpanzees.

Foraging Enrichment in This Research

Not only have foraging devices been shown to be utilised by animals but they have been shown to have enriching effects on animals’ behaviour and well-being. As foraging devices have been shown to be utilised by a number of animal species and specifically apes and chimpanzees, they were identified for inclusion in this current research. Although many enrichment items utilised in zoos include food, the selection of the majority of these items is either ad hoc or based on research carried out in laboratories. This current research sought to explore if such enrichment items would be used by a social group of chimpanzees and whether, and to what level, these chimpanzees would work for access to these items.

A 'Marbleroll' unit had the basis for its design in visual interest, control for the subjects, complexity and a foraging element. The unit could be physically semi-accessible to the chimpanzees, but fully visually accessible. Items, both edible and not could be assisted in their movement by the chimpanzees. They could view the travel of the items. They could gain access to the food item and food delivery could be controlled. The Marbleroll unit was relatively low in cost and time to construct. Utilisation of the item had little to no impact on the visiting public, staff members or other animals held at the facility.

A 'Dipper' unit was designed on the model of a chimpanzee's natural feeding behaviour. The use of a tool or dipping stick has been shown in both wild and captive animals, as previously discussed. In previous research with this subject group (Vivian, 2001), the researcher had utilised this behaviour in a form of enrichment for the group, so was familiar with their skill in tool construction and use. The Dipper enrichment unit was designed to allow the chimpanzees to access a food reinforcer but also to restrict this access. The unit was partially accessible to the subjects and afforded the subjects control. A tool was provided for the chimpanzees to ensure a standard tool was permanently and uniformly available for all individuals. The Dipper unit was relatively low in cost and time to construct. Utilisation of the item had little to no impact on the visiting public, staff members or other animals held at the facility.

Auditory Enrichment in This Research

As auditory stimulation has been shown to be an effective enrichment in previous research, it was chosen to be included as an element in this current research so that a comparison could be made for a zoo-held social group of chimpanzees. To explore the animals use of the item when freely available and when a cost was associated with access to the item. A 'Musicbox' unit was based on auditory stimulation, complexity and control for the subjects. The chimpanzees could press different buttons to produce a musical tone, or a series to produce music. Or one button was provided which produced playback of a partial song. The Musicbox unit was robust, semi accessible to the chimpanzee group, relatively low in cost and time to construct. Utilisation of the item had little to no impact on the visiting public, staff members or other animals held at the facility.

Aim

Having established the best place and time to conduct experimental sessions for this current research and with these subjects (in Experiment 1), the next phase of the research was the introduction of the enrichment items to the chimpanzees. The purpose of this study was to check that the overall experimental set-up and the enrichment items were suitably robust and to explore the chimpanzees' initial interest in the enrichment items.

Method: Part 1

Subjects

The full chimpanzee group as shown in Table 1.1, with the exception of Mahinga, was utilised in this experiment. The juvenile Mahinga died of kidney failure on 10/3/2005. An infant was born in between Experiment 1 and 2 of this current research (15/10/03) to Cara, and the researcher gave this chimpanzee the name Hasani. Unfortunately this infant suffered physical injuries during its first few months of life and in the best interests of its welfare the decision was made by zoo staff to euthanize the animal. Paternity for this infant was not established.

Study's Impact on Standard Husbandry Protocol

The procedures applied in this experiment had no impact on standard husbandry protocol for the chimpanzees as outlined in Experiment 1.

Ethical Consent

The procedure and equipment used within this experiment were approved by the Director-General of MAF via the National Animal Ethics Advisory Committee in accordance with the Animal Welfare Act 1999 concerning restrictions on the use of non-human hominids, the University of Waikato Animal Ethics Committee and the Wellington Zoo.

Apparatus and Setting

The area in which the equipment was set up was one that was primarily utilised by the chimpanzees as a corridor area. It was not particularly 'comfortable' - containing primarily concrete flooring, an artificial termite mound and some ropes; it

was a link between the Indoor Area and the furniture in the rest of the Covered Area that the chimpanzees spent most of their time on when in the section. The Covered Area of the chimpanzee enclosure and floor plan are shown in Figures 1.1 and 1.2.

The research equipment was mounted on the bars of one section of the Covered Area in such a way that the chimpanzees had minimal access to the equipment and so that there was a ‘chimpanzee side’ and ‘researcher side’ in terms of where the different parts of the equipment were situated. The location of the experimental equipment is indicated in Figure 1.1. The researcher side of the experimental area was restricted to use only by the researcher and occasionally by zoo staff to gain access to the chimpanzees when inside the Covered Area. The area was ‘out of bounds’ for the general public. This being the case, the experimental equipment was less likely to be tampered with. Figure 2.1 shows the barred panels on the Covered Area in which the research equipment was later mounted.



Figure 2.1. Research area prior to equipment being put in place (with a view into the Covered Area of the chimpanzees’ Indoor Enclosure).

Research Area

At the outset of the research the barred panel in which the enrichments were to be placed was partially covered with chain mesh, as seen in Figure 2.2. This chain blocked the entire width of the panel (1.12 m wide) and was 1 m high. An additional access hole that was present in the panel was blocked off with timber. It was

anticipated that these measures would provide the enrichment items a sufficient level of protection from the chimpanzees. The video camera was placed on a tripod directly behind the area. During the testing phase of the enrichment items it became immediately apparent that this form of protection was not adequate enough to prevent the chimpanzees from damaging the enrichment items.



Figure 2.2. Experimental area with chainmail and the Musicbox enrichment in place, as viewed from within the Covered Area of the chimpanzee enclosure.

The overall set-up for the experimental area was redesigned in order to provide more protection for the enrichment items and the researcher and to allow greater ease of equipment manipulation. The overall set up can be seen in Figures 2.3 to 2.5. The area in which the research equipment was placed is indicated in the floor plan in Figure 1.1 and was predominantly in one panel of the barred wall of the chimpanzees Indoor Enclosure Covered Area. To protect the equipment from the chimpanzees the barred panel, measuring 112cm x 240cm, was entirely covered by a 5mm thick acrylic sheet, with 1.5cm thick plywood surrounds and support structure. Within the chimpanzee area coach bolts with flush heads were used to secure the structure so that the chimpanzees had no way of undoing the construction. Part of the adjacent panel also had an acrylic sheet mounted to restrict the chimpanzees' access to the equipment from the side. The chimpanzees' access to the other side of the barred panel was blocked by a concrete wall. On the panel where the enrichments were to

be mounted holes were cut in the acrylic sheet relating to the position of enrichment items button, slides and food openings to allow for the chimpanzees to later gain access to the items. There were 7, 3cm diameter round holes; 3, 4.5 x 2 cm holes; 1, 7cm x 3cm hole and 1, 5 x 5cm hole. A separate acrylic sheet, measuring 37.5cm x 56cm was mounted over this area to protect and strengthen the cut out area when no enrichment was in place. The access holes can be seen in Figure 2.3. When an enrichment was in place two other pieces of acrylic sheet panelling, with the same corresponding holes cut in them, were also placed over the main acrylic sheet piece to give added strength.



Figure 2.3. Access holes in the acrylic sheet panels on experimental panel.

On the researcher side of the experimental area a shelf was put in place on which the enrichment items were positioned. The items were held securely in position by strapping with ratchet connections (threaded through steel handles fixed to the plywood surround) which ensured the items had no movement once in place. This design also meant that the enrichment items could be put in place and removed when chimpanzees were within the enclosure at the time. As seen in Figure 2.4, a plywood roof was constructed over the experimental panel, on the researcher side, to partially protect the equipment from rain damage. Figure 2.5 shows the overall experimental set up from the chimpanzee side, within the Covered Area.



Figure 2.4. Experimental area from the researcher side of the Covered Area enclosure, showing the acrylic sheet panels (with cut out portions), plywood support, enrichment shelf, weather protective roof and operant equipment (with the back of the weighted lever).

A storage shed was constructed behind the experimental area which housed the equipment when not in use and was utilised to mount the video camera for behaviour recordings. This is shown in Figure 2.6. Figure 2.6 also shows the video camera which was placed on a tripod and the unit secured to a bracket on the concrete wall to ensure movement was limited. The camera had a plastic weather proof container placed over it. The computer which ran the enrichment and operant equipment programs was housed within the zoo keeper section of the chimpanzees' indoor enclosure, the position of which is indicated in Figure 1.2. Wires were run from the internally-housed computer out to the experimental area, as were power cords. This can be seen in Figure 2.7.



Figure 2.5. Experimental area from the chimpanzees' side of the Covered Area enclosure. Shows the structures within the chimpanzee enclosure, the chimpanzees' view through to the enrichments and research area in general and their access to the operant lever.



Figure 2.6. Experimental area from the researcher side, showing the equipment set up for the operant equipment, the storage shed and the video camera in position (with weather proof container).



Figure 2.7. Computer equipment, including the computer components, the interface cabinet and power supplies for unit and some of the enrichments. This was housed in the indoor component of the chimpanzee enclosure, within the Keepers section.

Tarpaulin. A tarpaulin erected on the researcher side of the experimental area to protect the equipment from the weather flapped when the wind was strong and may have affected the amount of time the chimpanzees spent in the area. However, the tarpaulin stayed in place over the course of the whole research so if it did have an impact on the chimpanzees' behaviour, or the time they spent in the Covered Area, it would have been uniform across the research.

Operant Equipment

Although not utilised until Experiment 4 of this current research, the demand equipment was in place prior to Experiment 2. The demand equipment employed a weighted lever and is shown in Figures 2.4 to 2.6 and 2.8 and 2.9. The unit consisted of a lever - a hollow steel handle - which was extremely robust. On the researcher side the base of the lever was mounted on metal brackets and via a number of shackles and chain, weights were hung. A light was visible on the chimpanzee side of the unit and this light was lit when the lever was 'operational'. An effective push down on the lever, when it was operational, resulted in a short 'beep'. The beep operated for 50 ms and was produced by a miniature piezo-electric audible warning device mounted in the lever unit. Sensors (Reed switches) mounted either side of the lever arm (on the researcher side) allowed recording of the arm

movement. An automatic door closer was fitted to the lever arm to act as a damper. The entire lever unit was fitted onto a plywood support which was secured onto the enclosure bars in such a way to limit all vertical movement and most horizontal movement. The operant lever unit had a weatherproof container mounted over it on the researcher side for added protection from the elements. The chimpanzees' access to the experimental equipment was restricted physically (by the acrylic sheet panels and holes provided) but their visual access to the equipment was not restricted as the acrylic sheet was clear so they were able to see the enrichments and all of the experimental set-up (and the researcher when present).

During Experiment 2 the lever had 62.37 kg of weight hung on it (the weights were in blocks of 5.67 kg each so this represented 11 blocks) which made it effectively inoperable for the chimpanzees. This weight was selected after trialling different weights with the chimpanzees to find the weight at which they were unable to move the lever. The trialling was done on a day prior to the experimental sessions of Experiment 2 taking place, on which the weather was inclement so the chimpanzee group was housed within the indoor enclosure. The lever was initially loaded with 68 kg of weight (12 blocks). From next to the lever, the researcher offered dried banana chips to the chimpanzees and tapped the handle of the lever (from the researcher side). When the chimpanzees pushed down on the handle the researcher gave the individual a chip. The researcher kept the same weight on the lever until numerous members of the group had pressed down on the lever (or tried to given the weight). These individuals had to include the smallest and youngest (Bahati, Keza and Alexis), an adult female and an adult male and adult female Jess (as she was the largest individual in the chimpanzee group). The group was unable to press the lever down with 68 kg on it. However, there was pressure placed on the lever (on the weighted side) at this weight so the weight was reduced to 62.37 kg - a weight at which the group was still unable to press the lever down.

Enrichment Items

The chimpanzees had limited physical access to the enrichment items (through the holes in the acrylic sheet panels) and they were secured so that the chimpanzees could not take them away from the experimental area, damage them or harm themselves.

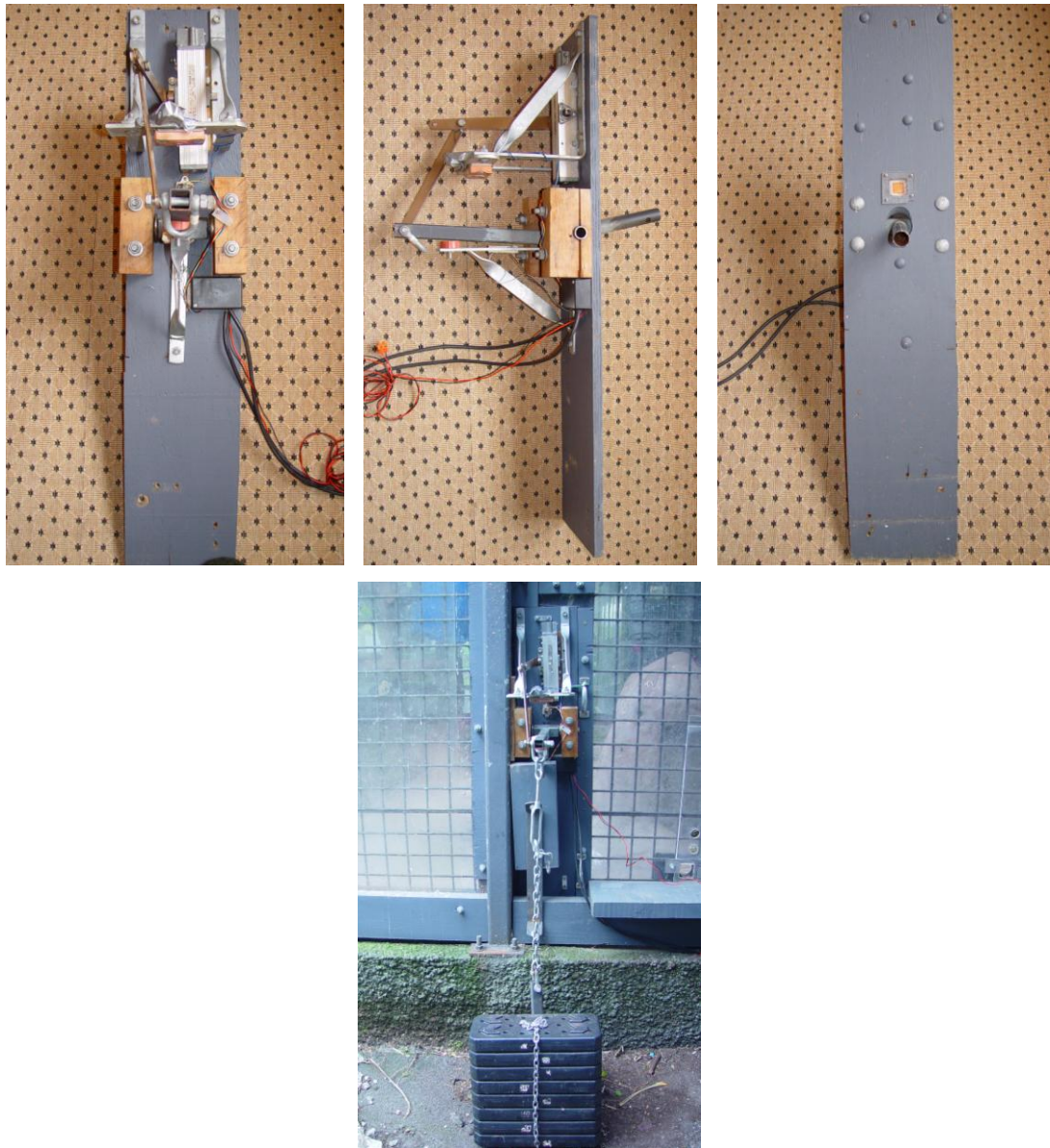


Figure 2.8. Demand equipment is shown from the researcher side (top, left), the side of the lever (top, middle) and the front of the lever (which faced the chimpanzees during the research) (top, right). The unit set in place within the experimental area, and with the weights attached is shown below.

The enrichments included a: Musicbox - a musical board (pushing different keys produced different musical notes); Dipper - food dipper (container of soft food (i.e. honey porridge) that could be accessed with a fixed tool when an internal barrier was open); Marbleroll - a feeder puzzle (whereby the chimpanzees were required to interact to assist a marble or round sweet to roll through the puzzle and further gain physical access to the sweet); TV/Video - television showing video of the

chimpanzees themselves, Keepers that the chimpanzees were familiar with, other animals in the zoo (set to turn on for a fixed period).

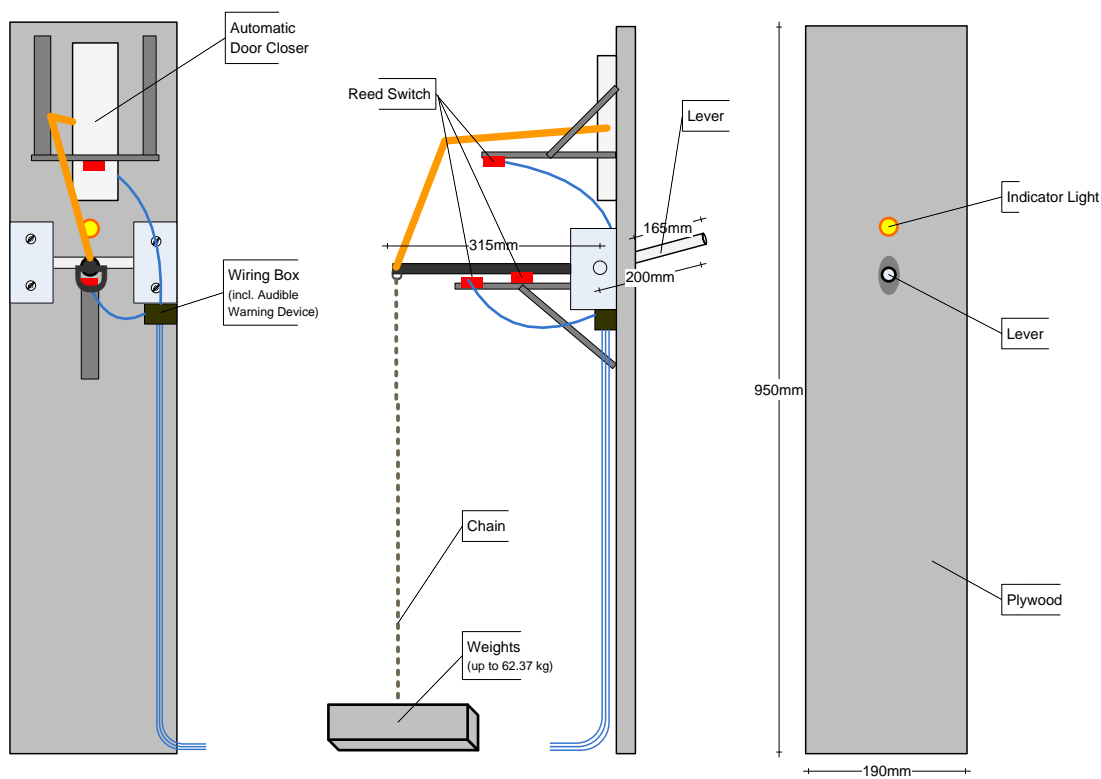


Figure 2.9. Diagram of demand equipment, with dimensions and components indicated, from back (left), the side of the lever (middle) and the front of the lever (right).

Musicbox enrichment. Figure 2.10 and 2.11 show the Musicbox. It was constructed by using the shell of a plastic tool box. Flush spring-return pushbuttons were wired into an electronic musical keyboard (a child's toy). These buttons were mounted on the top of the box within 5mm thick acrylic sheet. Plywood supports were mounted on the sides and a speaker (external to the keyboard) wired in and attached to one side. A light was mounted on the base of the unit and this was lit when the Musicbox was operational. The chimpanzees had physical access only to the buttons but could hear the notes produced via the speaker on the side of the Musicbox and see the operation light through the clear acrylic sheet barrier. Each of the buttons produced a different musical tone. However, when pressed, the green button played pop group Wham's 'Wake Me Up Before You Go Go'. To stop the

song playing the button had to be pressed again.

The visual complexity of the Musicbox included a variety of shapes and colours, in particular each of the pushbuttons was a different colour. The complexity of the interactions that this enrichment afforded the subjects included the option to push any one of the buttons and (when the unit was “on”) cause a different musical tone, or a song, to be produced. Thus, when the unit was “on” the chimpanzees had control over how they interacted with this device and what sounds they produced with it.

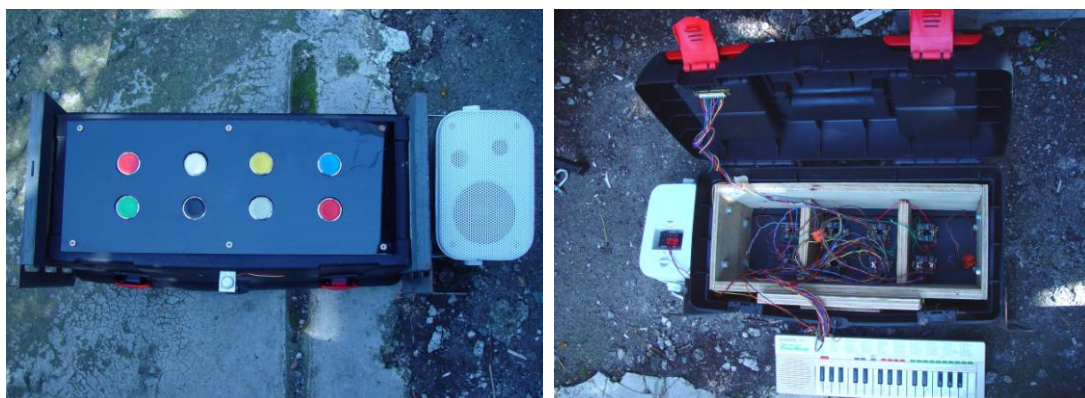


Figure 2.10. Musicbox enrichment, from the front (left) and from the back with the unit open and the keyboard out of the case (right).

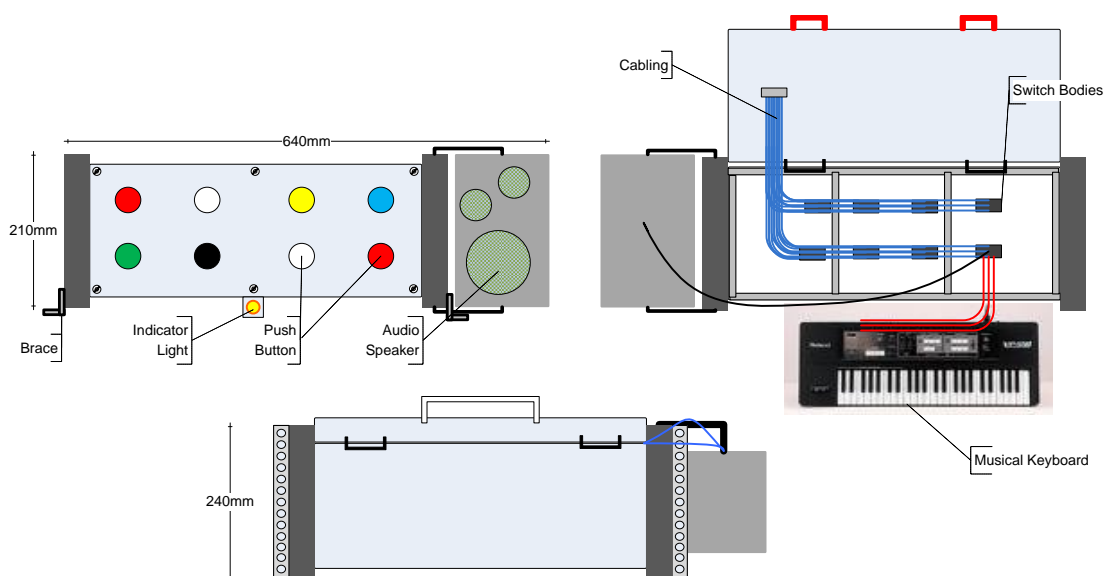


Figure 2.11. Diagram of Musicbox enrichment, with dimensions and components indicated, from the front (top, left), the back with the unit open and the

keyboard out of the case (top, right) and from the back (bottom).

Dipper enrichment. Figure 2.12 and 2.13 show the Dipper and the dipper tool. The Dipper apparatus consisted of a plywood box with an acrylic sheet front and a roof that was able to be opened by the researcher to allow access to the interior of the unit. Dexion was placed on two sides of the unit to help stabilize it when it was set in position during sessions. The front acrylic sheet had a hole where a piece of metal tubing lead down towards a trough, constructed of acrylic sheet, which held the honey porridge mix. A light was mounted within the unit visible to the chimpanzees, which was lit when the Dipper was operational. A barrier, which was used to limit access to food, was mounted at the base of the internal end of the metal tube. It lifted by a chain pulling it up which was operated by a solenoid. Plastic coated wire was secured outside the enclosure with the end protruded into the enclosure for the chimpanzees to have access to for use as a tool; it was 0.5cm in diameter. The chimpanzees had access to the opening of the dipper unit but the distance to the food within and the size of the opening precluded them from using their hands and required them to use the tool of the coated wire. The food within the unit was only accessible when the internal barrier of the unit was up. The chimpanzees could see the operation light through the acrylic sheet. They could also see the porridge in the holding container within the unit as this too was made of clear acrylic sheet.

The visual complexity of the Dipper enrichment included many different shapes and items for the chimpanzees to view, including the food held within the unit. The chimpanzees could also see (and hear) the movement of the internal barrier of the Dipper when it operated. The complexity of interactions that the Dipper enrichment afforded the chimpanzees, and the control they had over the item, included the use of the dipper tool to access the food within the unit when the enrichment was operating and the barrier was up.

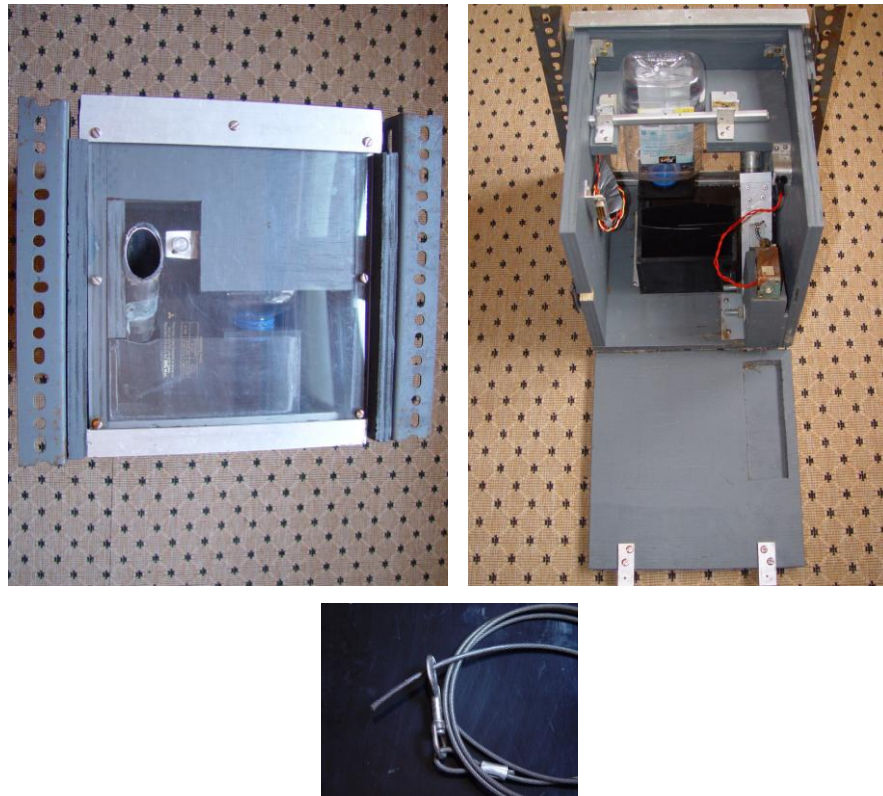


Figure 2.12. Dipper enrichment from the front (top, left), and from the back with the unit open (top, right), and the dipper tool (bottom).

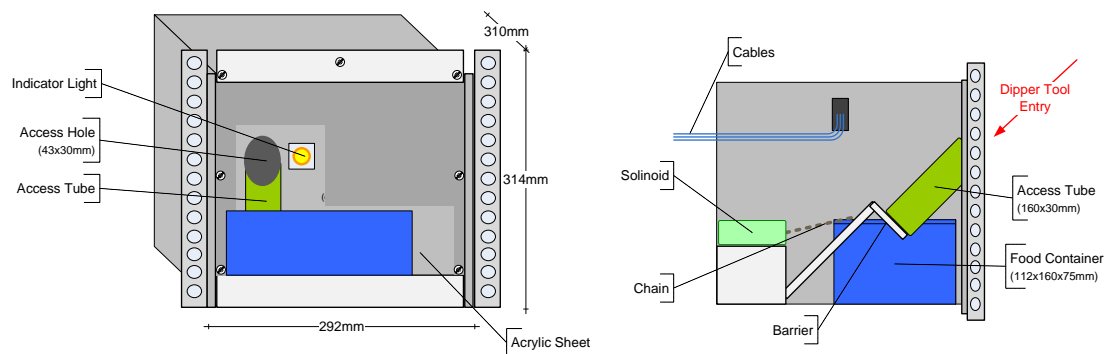


Figure 2.13. Diagram of Dipper enrichment, with dimensions and components indicated, from the front (left), from the back (right).

TV/Video enrichment. Figure 2.14 and 2.15 show the TV/Video set-up. It was constructed by making a plywood unit to house the television and video player. The unit had an acrylic sheet front to protect the electrical items from the weather. The video used for this enrichment was made from footage taken by the researcher of the

chimpanzee subjects, during times they were in both their internal and external enclosures and when they were being manipulated by zoo keepers. Images also included footage taken of other animals within the zoo, Keepers familiar to the chimpanzees, pets and human infants (both with no association to the chimpanzees). The volume of the television whilst in use was low in consideration of members of the public visiting the zoo.

The complexity of the TV/Video enrichment included the variety of sights and sounds that the chimpanzees could experience when the unit was “on” and the video was playing. This enrichment item lacked any complexity in terms of the interactions or control it afforded the chimpanzees as they could not operate anything on this enrichment and in fact they could not psychically touch this unit. (This was the only enrichment item that they could not touch in any way).



Figure 2.14. TV/Video enrichment from the front (top left) and from the back (top, right) and from the back with the video access door open (bottom).

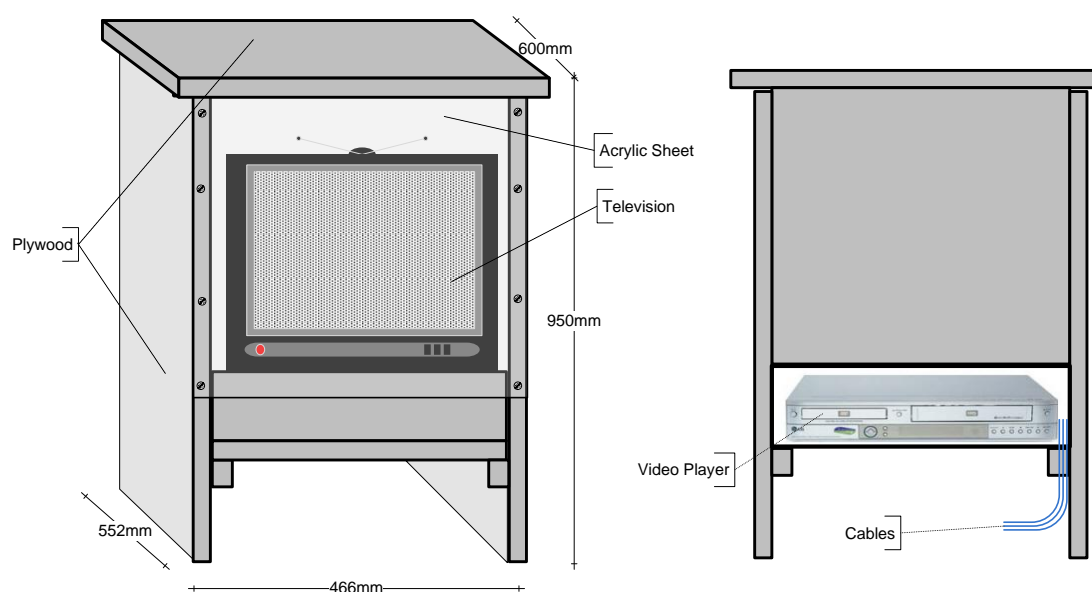


Figure 2.15. Diagram of TV/Video enrichment, with dimensions and components indicated, from the front (left) and from the back with the video access door open (right).

Marbleroll enrichment. Figure 2.16 and 2.17 show the Marbleroll and the Jaffas™ that were used in the unit. This unit was constructed by assembling two parallel raceways (each 1.5 cm wide), in a zigzag design and encasing them within a wooden frame and the overall unit being housed in a plywood structure with an acrylic sheet front (0.5 cm thick). The full unit was 76 cm high, 45 cm wide and 14 cm deep. The design was such that one raceway was specifically for marbles to travel through and the other was specifically for the Jaffas™. (Jaffas™ are a spherical chocolate sweet covered in a hard orange flavoured sugar coat). Once a marble reached the end of its raceway it dropped into a lift. The weight of the marble in the lift triggered a switch at the base of the lift, which operated a planetary gearbox motor at the top of the lift shaft. The lift was suspended on braided fishing line and when the lift reached the top of the shaft, the marble rolled back into cue, and the lift operated a switch which reversed the motor which acted to return the lift to the bottom of the shaft. At the end of the Jaffa™ raceway was an angled metal pipe (4.8 cm in diameter) which allowed the Jaffa™ to be delivered into the chimpanzees' enclosure. At the mid section of the four sections of both raceways a slide was located. These slides were made of acrylic sheet and had a protruding grip which allowed the slides to be pushed up, thereby allowing any marble or Jaffa™ in the

raceway to proceed down the unit. A clean-up mechanism was located behind the raceway which when operated (via solenoid) allowed any marbles that had not made their way down the entire unit to drop down behind the raceway and into the lift and again return to the top of the unit. The delivery of the marbles and Jaffa™ was controlled by the operation of solenoids (one at the entrance to the marble raceway and another at the entrance to the Jaffa™ raceway) which lifted small barriers that had been constructed out of acrylic sheet and until such time blocked the entrance of the raceways. The lifting of these barriers was controlled by a computer program written to deliver the marbles and Jaffas™ at different set periods of time during different phases of the research.

Both marbles and Jaffa™ were included in this enrichment item for two purposes: Firstly, to restrict the maximum number of Jaffas™ that the chimpanzees could potentially access during a session for dietary reasons (in consultation with the zoo veterinarian). Secondly, having by both Jaffas™ and marbles increased the complexity of the item: there was uncertainty provided by the variable ratio at which either of the items was delivered into the Marbleroll; and there was increased visual complexity (two different items and if a marble was utilised in the enrichment the lift operated – which was also able to be seen by the chimpanzees).

The Marbleroll enrichment was very visually complex as it included many different colours and shapes for the chimpanzees to see, including two different items that could appear at random in the raceways. When “on” the chimpanzees could view the lift moving up and down and see the clear-up in operation. Both of these mechanisms also had associated noises. Furthermore the chimpanzees could see the marbles and Jaffas™ rolling down the raceways of the unit. To add complexity through interactions, and control, the chimpanzees could operate the slides on the Marbleroll when they were included.

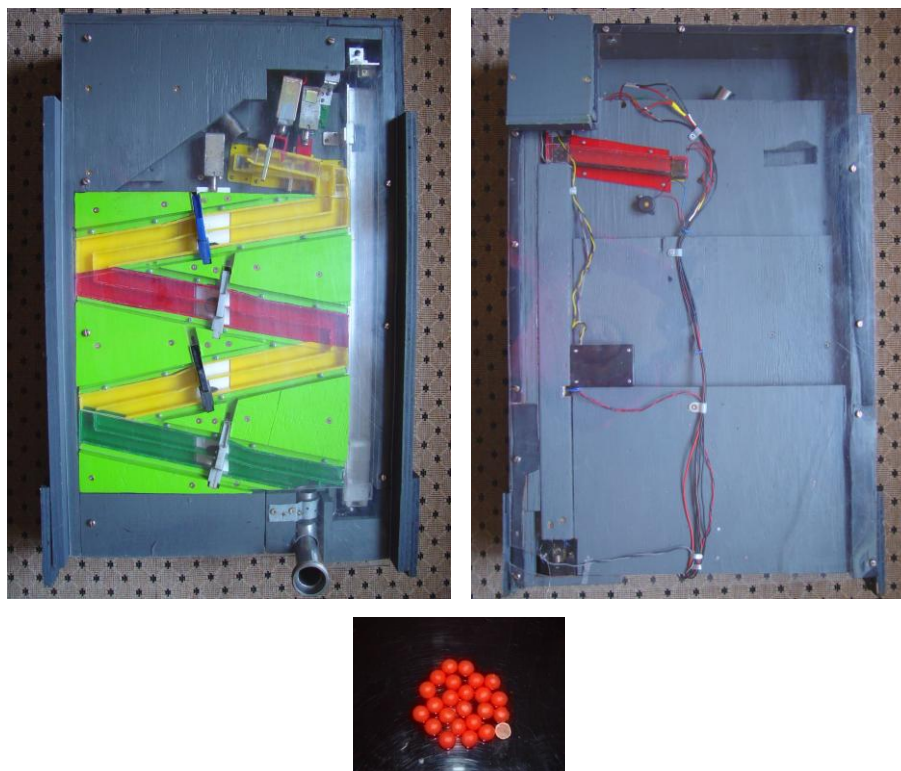


Figure 2.16. Marbleroll enrichment from the front (top, left) and from the back (top, right) and Jaffas™ (the full sweets and one split in half) (bottom).

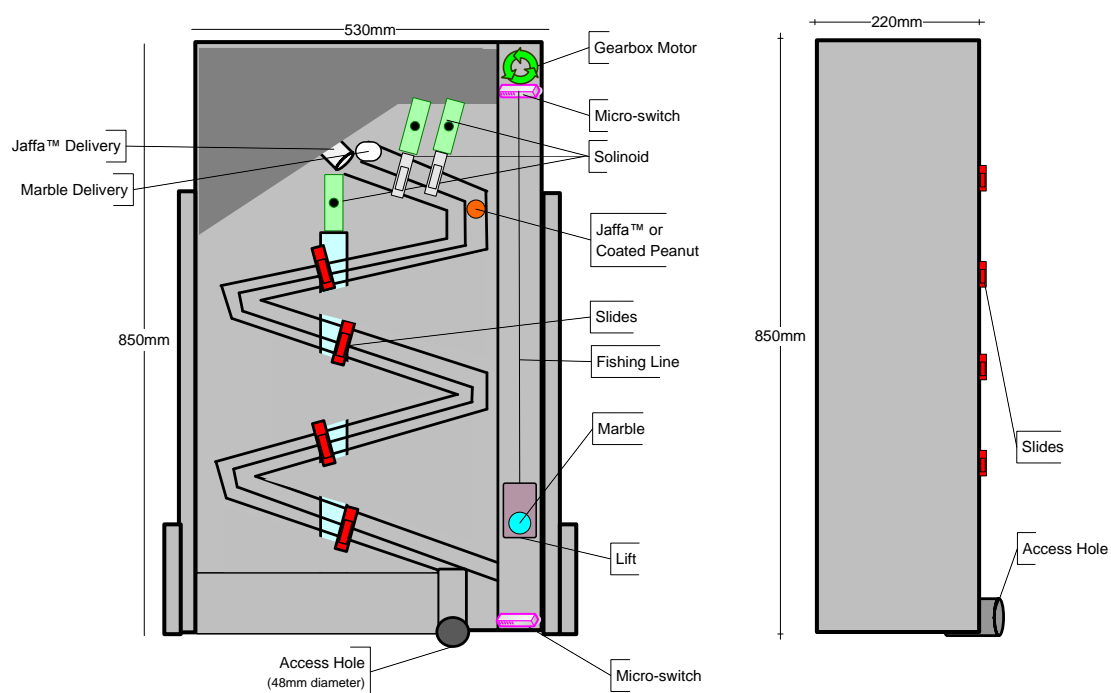


Figure 2.17. Diagram of Marbleroll enrichment, with dimensions and components indicated, from the front (left) and from the back (middle) and from the

side (right).

Procedure

The study was conducted from April 2005 until October 2005. A video camera was positioned above where the enrichments were to be placed later. Sessions ran for three hours - beginning at 1700 and terminating at 2000 (as the chimpanzees come in at approximately 1630 and it gave some time for dinner consumption). A flood light, operated by a timer, was on in the research area during the experimental sessions.

Four sessions of baseline were conducted initially. A Baseline session involved recording video footage for the three hour session. Under baseline conditions there were no enrichments in place on the experimental panel. The lever was present but had 62.37 kg of weight hung on it which made it effectively inoperable for the chimpanzees (as previously discussed). The operation light on the lever unit stayed off the entire time during Experiment 2. After the first session of baseline some damage was noted from excessive lateral movement of the lever by the chimpanzees so a wooden support block was placed beside the lever unit to minimise this movement.

After the baseline period one enrichment item was provided per session (put in place during the day while the chimpanzees were out of the indoor enclosure). The experimental equipment was mounted on the wall of bars in Covered Area section of the chimpanzees' enclosure: accessible to the chimpanzees from within their enclosure and to the researcher from outside of the entire enclosure. Again, the lever was present but had 62.37 kg of weight hung on it which made it effectively inoperable for the chimpanzees (as previously discussed).

The enrichment items (as seen in Figures 2.10 to 2.17) were provided in the order shown in Table 2.1, which also shows the detail of the operation of the enrichment item during this experiment. Each enrichment item stayed in place for two three hour sessions and on completion of those the next enrichment was put in place until all of the enrichment items had been trialled for a two sessions each.

Operation of Enrichments

During Experiment 2: Part 1 experimental events within the sessions were controlled by a computer programme and the internally housed computer unit. The computer and enrichments were controlled by MEDPC-IV software and interfaces.

Programmes were written for the experimental phase and for each particular enrichment item during that phase.

Access to enrichment items

The research was conducted in a closed economy so none of the components of the enrichment items were available from other sources outside of the research.

Table 2.1
Enrichment items in order of use for Experiment 2: Part 1 and enrichment item operation details.

| Enrichment Item | Operation Details |
|-----------------|---|
| Musicbox | Able to produce notes for three hours. |
| Dipper | Had the internal barrier removed for free access to the food. |
| TV/Video | Remained on for three hours playing a continuous video (no repeats). |
| Marbleroll | Released a marble or occasionally a Jaffa™, set at variable intervals of between 1 and 11 minutes at a rate of 10 Jaffas™ per hour. The slides on the Marbleroll were removed so the chimpanzees had nothing to operate. |
| Marbleroll | Released a marble or occasionally a Jaffa™ every 150 seconds (set so that no more than 10 Jaffas™ an hour were released). The slides on the Marbleroll were in place so the chimpanzees were able to control the progress of the items. Automatic cleanup operated to move any marbles that may have been left. |

Data Collection

Video Recordings and Behavioural Definitions

During the Experiment 2: Part 1 each experimental session was recorded on VHS video. Operational definitions, as shown in Table 2.2, were used to analyse the chimpanzees' behaviours across each session. These operational definitions were developed by the researcher after periods of initial observation of the chimpanzees

(prior to Experiment 2 being undertaken) and were included to allow for a comparison of behaviour across all the researches experiments to be made. When a chimpanzee was in view the length of time the individual was seen exhibiting a particular behaviour (as categorized in Table 2.2) was recorded. When a chimpanzee was seen to be behaving in the categories of use of an enrichment item (including: Using – alone; Using – others watch; Using – together), the time at which the behaviour was seen to start at and the time at which the behaviour was seen to stop at were recorded. Behaviours of particular note by individuals were also recorded. The area within view of the video recording was 5 m deep, 2 m across and 2 m in height.

Reliability. Within-observer reliability was assessed by the researcher viewing two videotaped sessions taped during Experiment 2 (one from the beginning of the study – and Part 1; and one from the near the end – and Part 2; both comprising of sessions in which enrichment items were included rather than being Baseline sessions) and recording the chimpanzees' behaviour (based on the behavioural definitions shown in Table 2.2). Each videotape was viewed and analysed twice. The video from the beginning of the study was viewed and analysed at the beginning of the data analysis for Experiment 2 and the video from the end was viewed and analysed near the end of the data analysis for the Experiment. Group totals for each behaviour category were compared between the two analyses of each tape. The index of concordance or proportion of all occurrences about which the two observations agreed i.e., $A/(A + D)$, where A is agreements and D is disagreements, is expressed by a percentage agreement. At the beginning of Experiment 2 within-observer reliability was 93.55%. Near the end of Experiment 2 within-observer reliability was 96.06%.

Data Analysis

Analysis of Video Data

The video recordings collected during Experiment 2: Part 1 were analysed and provided data of group behaviour and individuals' behaviour within the chimpanzee group.

Table 2.2
List of operational definitions of exclusive behavioural classes.

| Behaviour | Definition |
|-------------------------|---|
| Just in area | Animal in the vicinity of the research equipment. Within camera range. Animal is not orientated towards the equipment. Maybe passing through and glimpse at the equipment but not looking at it for any substantial length of time. |
| Attending – alone | Animal orientated towards the research equipment. Within camera range. At such a distance from the equipment not to be considered interacting. No other animals within the camera view are orientated towards the equipment (maybe present though). No other animals are using the equipment. |
| Attending - accompanied | Animal orientated towards the research equipment. Within camera range. Other animals within the camera view are also orientated towards the equipment. At such a distance from the equipment not to be considered interacting with it. No other animals are using the equipment. |
| Watching other use | Animal orientated towards the research equipment. Within camera range. At such a distance from the equipment not to be considered interacting with it. Whilst another or other animals in use of the equipment. |
| Using – alone | Animal either physically manipulating the equipment (including consuming food items sourced from the equipment) or within close enough proximity to be considered interacting with the equipment. No other animals are attending to the equipment within the camera view. |
| Using - others watch | Animal either physically manipulating the equipment (including consuming food items sourced from the equipment) or within close enough proximity to be considered interacting with the equipment. Another or other animals are attending to the equipment within the camera view. |
| Using – together | Two animals either physically manipulating the equipment (including consuming food items sourced from the equipment) or within close proximity to be considered interacting with the equipment. |

Behavioural definition notes:

- Use of the Dipper unit included time spent making tools.
- Attending included time staring into the Dipper.
- Attending required no movement (i.e., sitting watching). If walking, etc. this was not classed as attending.
- Watching was only those chimpanzees in frame – many could be watching further out (i.e., watching at close quarters).
- Attending alone for the Marbleroll included chimpanzees watching till something dropped. This was not recorded as using.

Results: Part 1

The data analysed here were based on the time any chimpanzee was within the observation area and recorded to be so. Definitions for the recorded behaviour are described in Table 2.2. The data are presented as behavioural category totals for each experimental condition. Details of data for each experimental session are presented in Appendix B. When a chimpanzee was observed to be present in the experimental area but their identity could not be ascertained their behaviour was recorded and classed under “Unknown” individual. As this did not occur often (less than 1% of behavioural recordings) the results are not shown in the figures. Scales on the Figures in this and other experiments in this current research are the same to allow for comparisons.

Throughout the results of this study figures utilise symbols where: B (no l) is Baseline, without the lever; B (l) is Baseline, with the lever; B (l+sup) is Baseline, with the lever and support; MB is Musicbox enrichment; D is Dipper enrichment; TV is TV/Video enrichment; MR (no s) is Marbleroll enrichment - delivering marbles and Jaffas™, without slides; MR (+s) is Marbleroll enrichment - delivering marbles and Jaffas™, with slides.

Group Behaviour

The chimpanzee group's overall behavioural data totals for each experimental session in Part 1 of Experiment 2 are shown in Table 2.3 and Figure 2.18. Table 2.3 and Figure 2.18 show that across sessions when an enrichment item was present and

those in which one was not (Baseline sessions) the total amount of time the group spent in the experimental area simply present but not interacting in any way with an enrichment item (including long periods of orientation towards the equipment) ‘Just in area’ remained at a similar level across all sessions.

Group Behaviour Related to Enrichment Items

Table 2.3 and Figure 2.18 show the entire chimpanzee group’s total time spent in each behaviour relating to each enrichment item across all sessions for Part 1 of Experiment 2. Table 2.3 and Figure 2.18 show that the Marbleroll unit, when presented with no slides present in the unit, was Used-alone for the greatest amount of time by the chimpanzee group. Members of the group used the item individually (Used-alone) more during the second session with it than they had during the first. The most the group used an enrichment item (the Marbleroll with no slides present, during the second session with the item) was 94.72 min in a session of 180 min. In a comparison between sessions in which a foraging item was available (sessions with the Dipper, Marbleroll, with slides present and Marbleroll, without slides) the group spent a lot less time with the other enrichments than they did with the Marbleroll, with no slides present. The group spent the least amount of time using the Musicbox and TV/Video enrichment items. The least amount of time the group used an enrichment item (the Musicbox, on the second session with the item) was 2.45 min in a session of 180 min.

Of all of the behavioural classes that the chimpanzees’ behaviour could be recorded as the behaviour Use-alone was performed considerably more by the group. The group spent a similar amount of time using an enrichment item while another individual observed this (Using-others watch), watching another individual using an item (Watching other use), using an item at the same time (Using-together) and orientated towards an item but not interacting (Attending-alone). Time in which multiple animals were oriented towards and item but not interacting with it (Attending-accompanied) was minimal.

Table 2.3

Chimpanzee group behaviour (as defined in Table 2.2) during Experiment 2: Part 1. The amount of time (min) in each session the group was performing each behaviour.

| Session Condition | Time Spent Exhibiting Class of Behaviour (min) | | | | | | |
|------------------------------|--|--------------|------------------|-------------------|-------------------------|--------------------|--------------|
| | Using - | | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in Area |
| | Using - alone | others watch | | | | | |
| Baseline (no lever) | NA | NA | NA | NA | NA | NA | 2.33 |
| Baseline (lever) | NA | NA | NA | NA | NA | NA | 2.15 |
| Baseline (lever + support) 1 | NA | NA | NA | NA | NA | NA | 3.93 |
| Baseline (lever + support) 2 | NA | NA | NA | NA | NA | NA | 3.77 |
| Musicbox 1 | 7.35 | 0.12 | 0.20 | 0.30 | 0.00 | 0.12 | 2.28 |
| Musicbox 2 | 2.45 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 2.10 |
| Dipper 1 | 28.17 | 0.45 | 0.50 | 0.00 | 0.00 | 0.45 | 2.17 |
| Dipper2 | 26.60 | 1.00 | 0.47 | 0.07 | 0.10 | 1.00 | 3.53 |
| TV 1 | 7.12 | 0.00 | 2.27 | 0.00 | 0.00 | 0.00 | 2.37 |
| TV 2 | 3.25 | 0.00 | 0.60 | 0.00 | 0.00 | 0.00 | 2.02 |
| Marbelroll (no slides) 1 | 77.73 | 1.03 | 2.20 | 1.32 | 0.13 | 1.03 | 3.33 |
| Marbleroll (no slides) 2 | 94.72 | 1.50 | 2.40 | 0.90 | 0.00 | 1.50 | 2.48 |
| Marbleroll (slides) 1 | 12.32 | 0.98 | 0.17 | 0.57 | 0.00 | 0.98 | 1.72 |
| Marbleroll (slides) 2 | 27.20 | 0.62 | 0.00 | 0.00 | 0.00 | 0.62 | 3.25 |

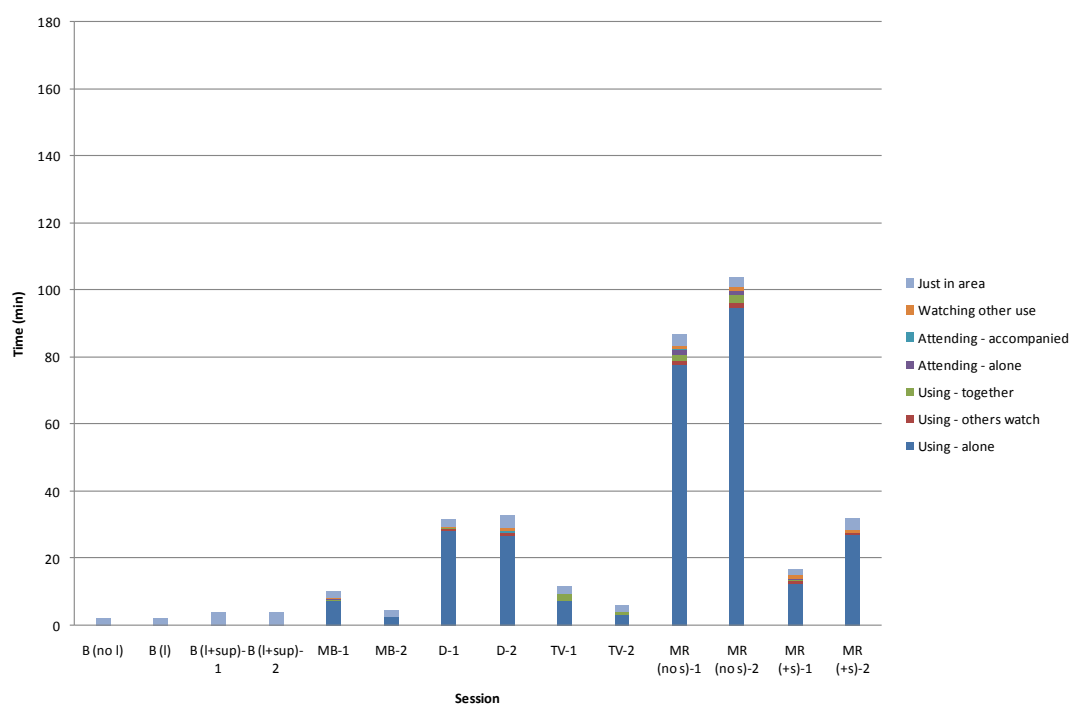


Figure 2.18. Total time that the chimpanzee group exhibited defined behaviours in experimental sessions of Experiment 2: Part 1.

Group Use Event Records

Data for the chimpanzee group were analysed to examine individual usage behaviour associated with the enrichment items (including behavioural classes: Using-alone, Using-others watch, Using-together). The event records that follow (here and elsewhere in this current research) were constructed based on the start and stop times for defined behaviours related to the group's use of the each enrichment item, during each session. A marker is first placed at the initial start time of use and a line goes between this and the eventual stop time of use, which is again indicated by a marker. Short periods of use may appear as one marker, when the time was so brief that the start and stop markers are actually on top of each other. Or two markers, without a line, as the length of time between the starting and stopping of use was not long enough to see the line in-between the markers. This use time is indicated for each individual chimpanzee in the group and for any use over the entire session length.

Musicbox enrichment. Figure 2.19a and 2.19b show that the use of this item occurred mainly at the beginning of both sessions with the item. The periods of use of the item were brief, typically lasting for less than one minute. The item was used for less time in the second session. Of the 13 individual chimpanzees, 3 used this enrichment item when it was present. Female juvenile Keza interacted with the Musicbox for the greatest length of time, while male adolescent Temba and kindergarten male Bahati were the other individuals to spend time using the Musicbox (but on only a few occasions).

Behaviour of note was that on the morning after the first session with this enrichment item hessian sacks were found piled in front of it indicating a chimpanzee or chimpanzees had constructed a nest in front of the item. This had not occurred during the session so was not recorded on video tape. However, as the chimpanzees had never been seen to sleep on the floor this was an interesting observation.

Dipper enrichment. Figure 2.20a and 2.20b show that the Dipper enrichment was used sporadically for the first two hours of both sessions the chimpanzees had with it (until sunset). The group initially took some time before interacting with the item. Periods of use of the item varied from a few seconds up to almost eight minutes. The enrichment item was used for around the same amount of time during

both sessions. All of the members of the chimpanzee group used this enrichment item when it was present. Some individuals (adult males - Sam, Marty, Gombe; kindergarten male Bahati; adult females – Samantha, Sally) used the item for only a short period. Female juvenile Keza used the enrichment item the greatest number of times but adult female Jess used the enrichment item for the greatest amount of time, her periods of use were the longest of all of the members of the group. Keza's use of the item increased during the second hour of the sessions.

TV/Video enrichment. During both sessions with the TV/Video enrichment, the chimpanzees used the item for a very brief time at the beginning of each session (during the first hour), as shown in Figures 2.21a and 2.21b. All of the interactions lasted less than a minute. The use of the item decreased in the second session. Over both sessions five members of the group used the TV/Video enrichment. All five of these subjects were adolescent or kindergarten age. Adolescent male Temba and juvenile female Keza used the item the same number of times. However, Temba used the item for a longer time.

Marbleroll enrichment - delivering marbles and Jaffas™. As Figures 2.22a and 2.22b show, all but one member of the chimpanzee group used the Marbleroll unit, without the slides present. The group used the item from the very beginning of the sessions until into the third hour of the sessions (therefore after sunset). Most of the interactions lasted for less than a minute, however, the adult female Jess used the item for longer periods, the longest spanning almost 10 min. Adult males Sam and Boyd, adolescent males Temba and Gombe and juvenile female Keza also used the item for periods lasting longer than three minutes. For the two individuals that used the item the most, Jess and Keza, Jess used the item predominantly at the beginning of the session whereas Keza used the item the more towards the end of the period of use of the item in the sessions. The chimpanzee group used the Marbleroll (without slides) more during the second session with it. Keza was noted to continually make her way to the Indoor Area, where the rest of the group were resting, but each time an item was released within the Marbleroll unit she came back to the item.

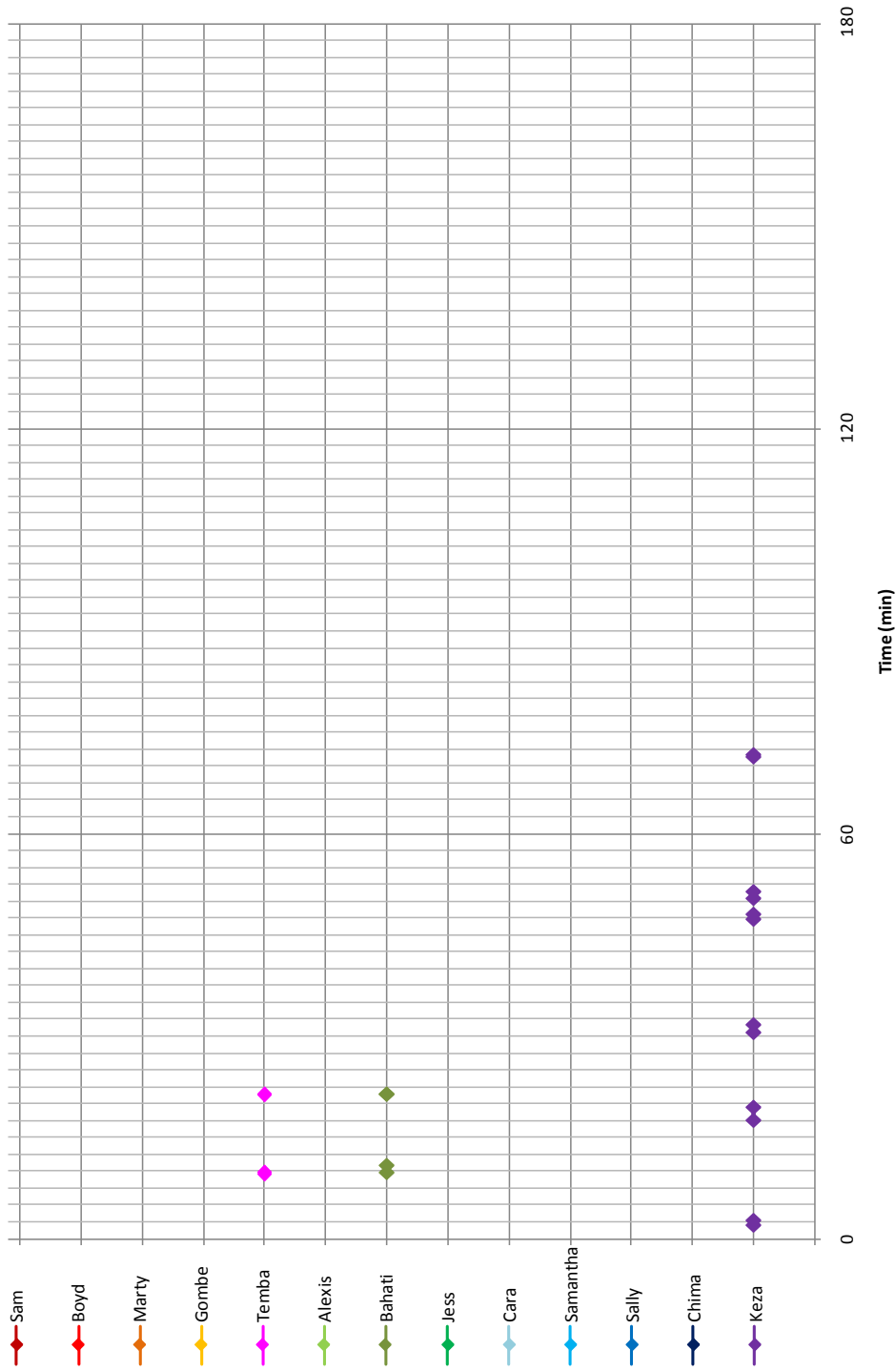


Figure 2.19a. Start and stop times for defined behaviours related to the group’s use of the Musicbox enrichment item during the first session within Experiment 2: Part 1. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

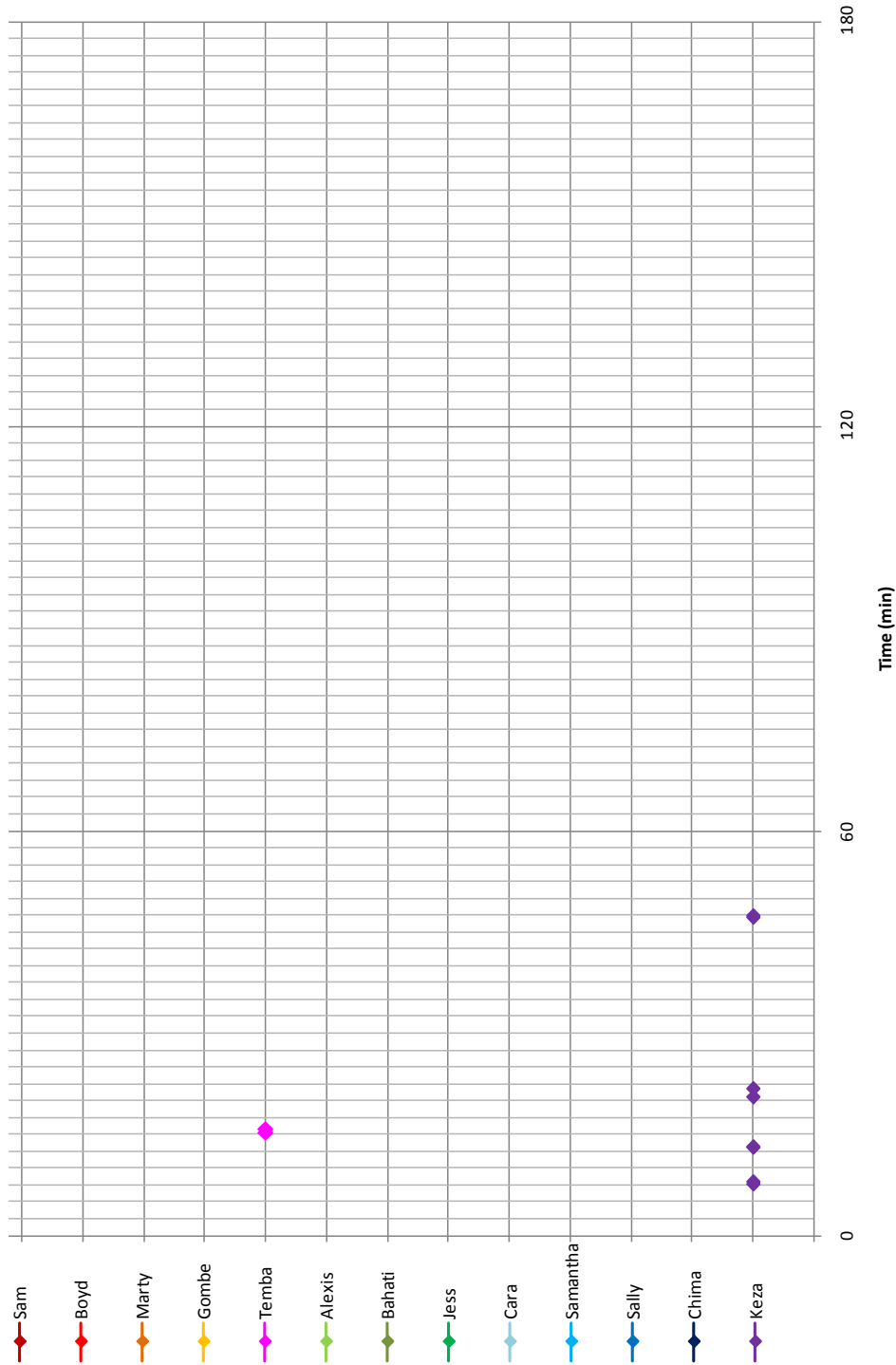
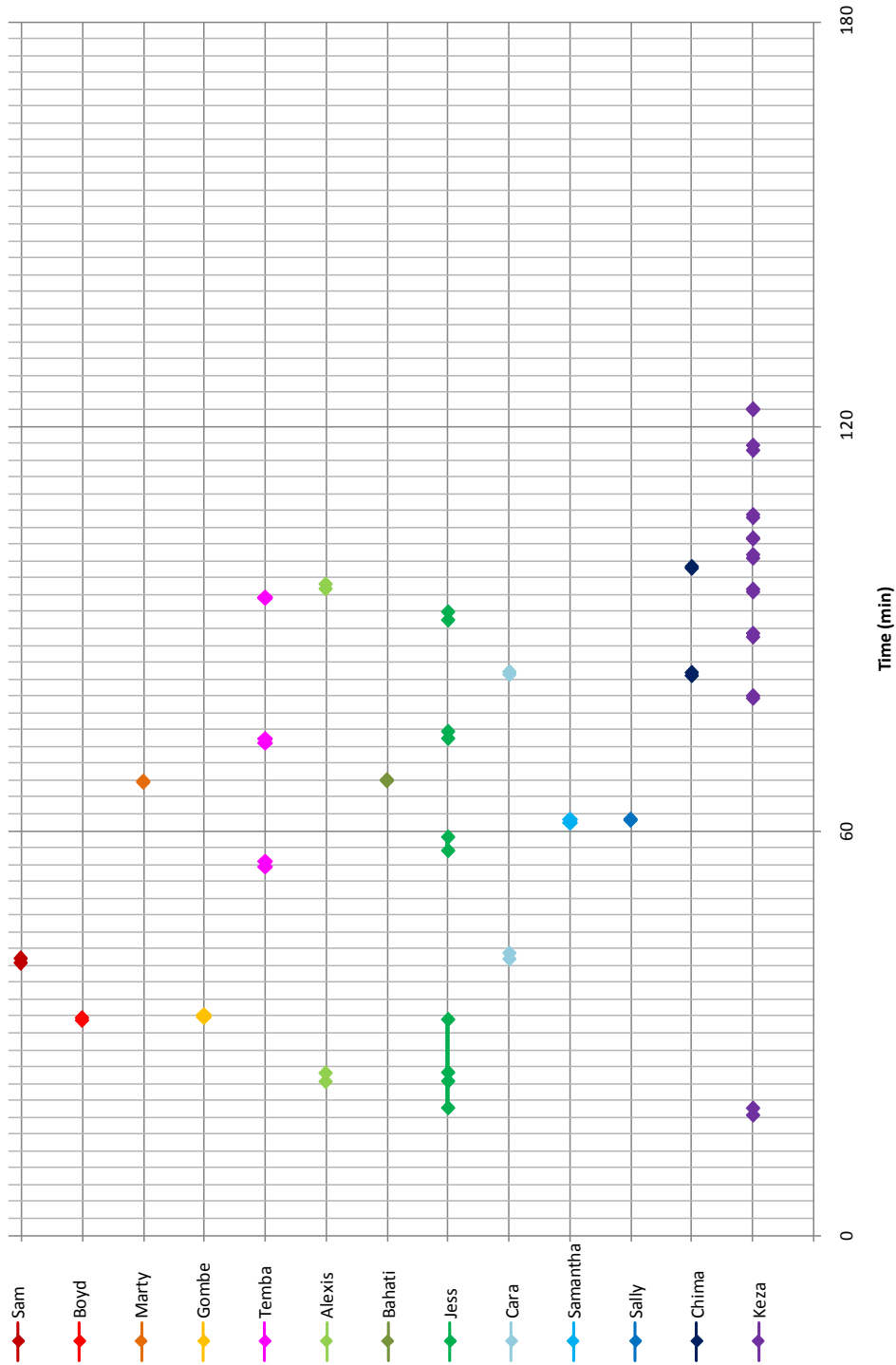


Figure 2.19b. Start and stop times for defined behaviours related to the group’s use of the Musicbox enrichment item during the second session within Experiment 2: Part 1. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.



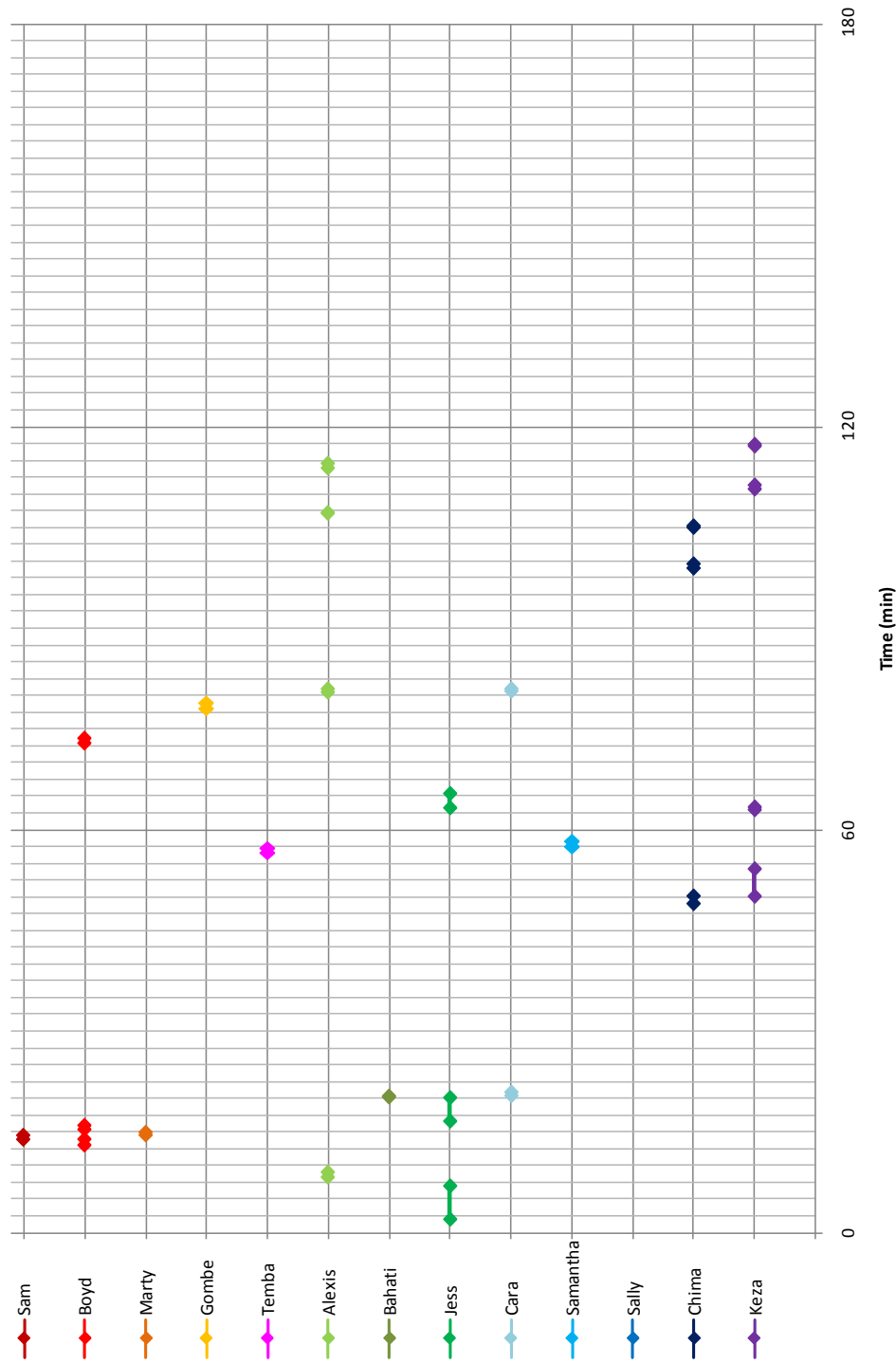
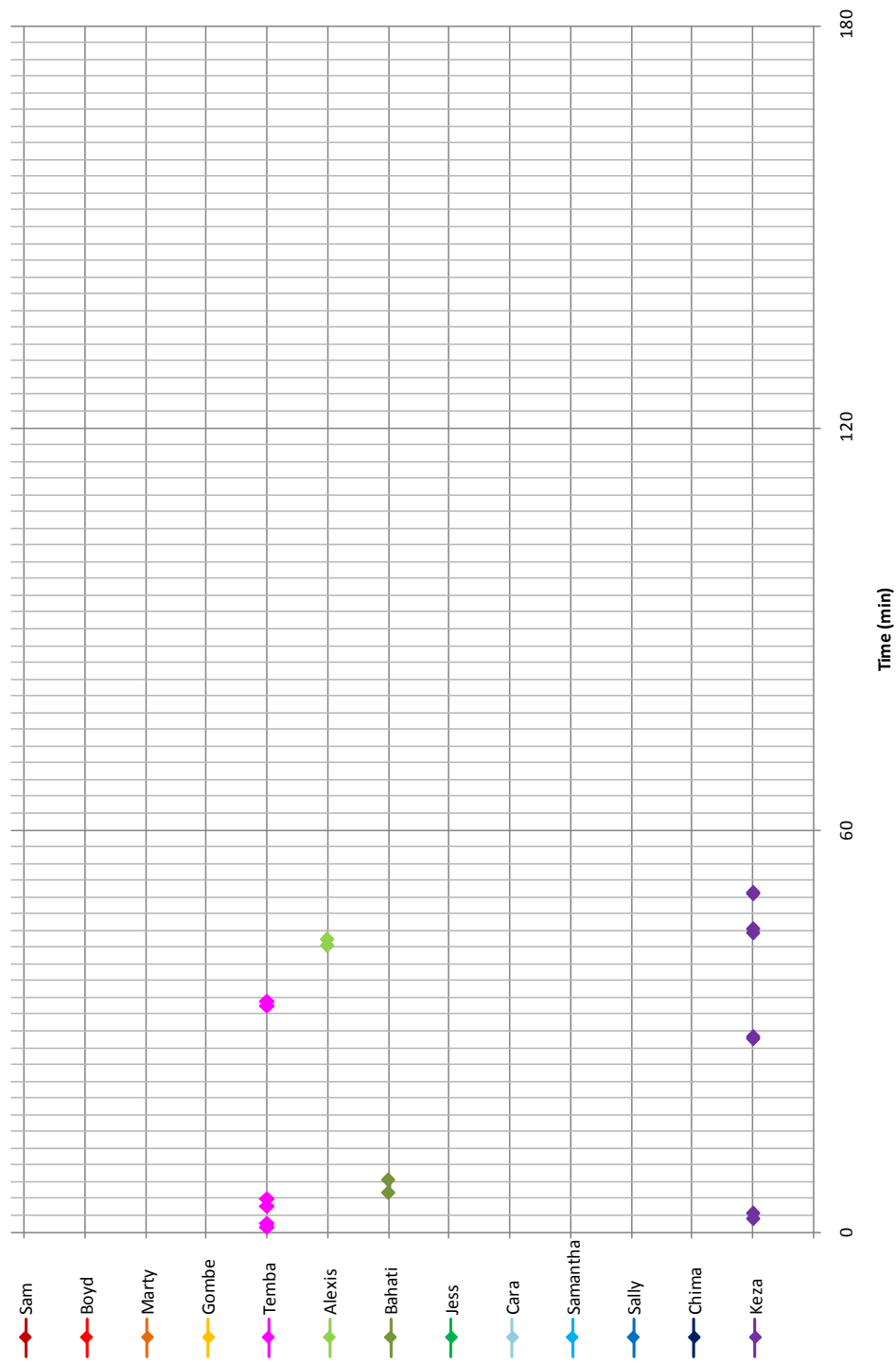
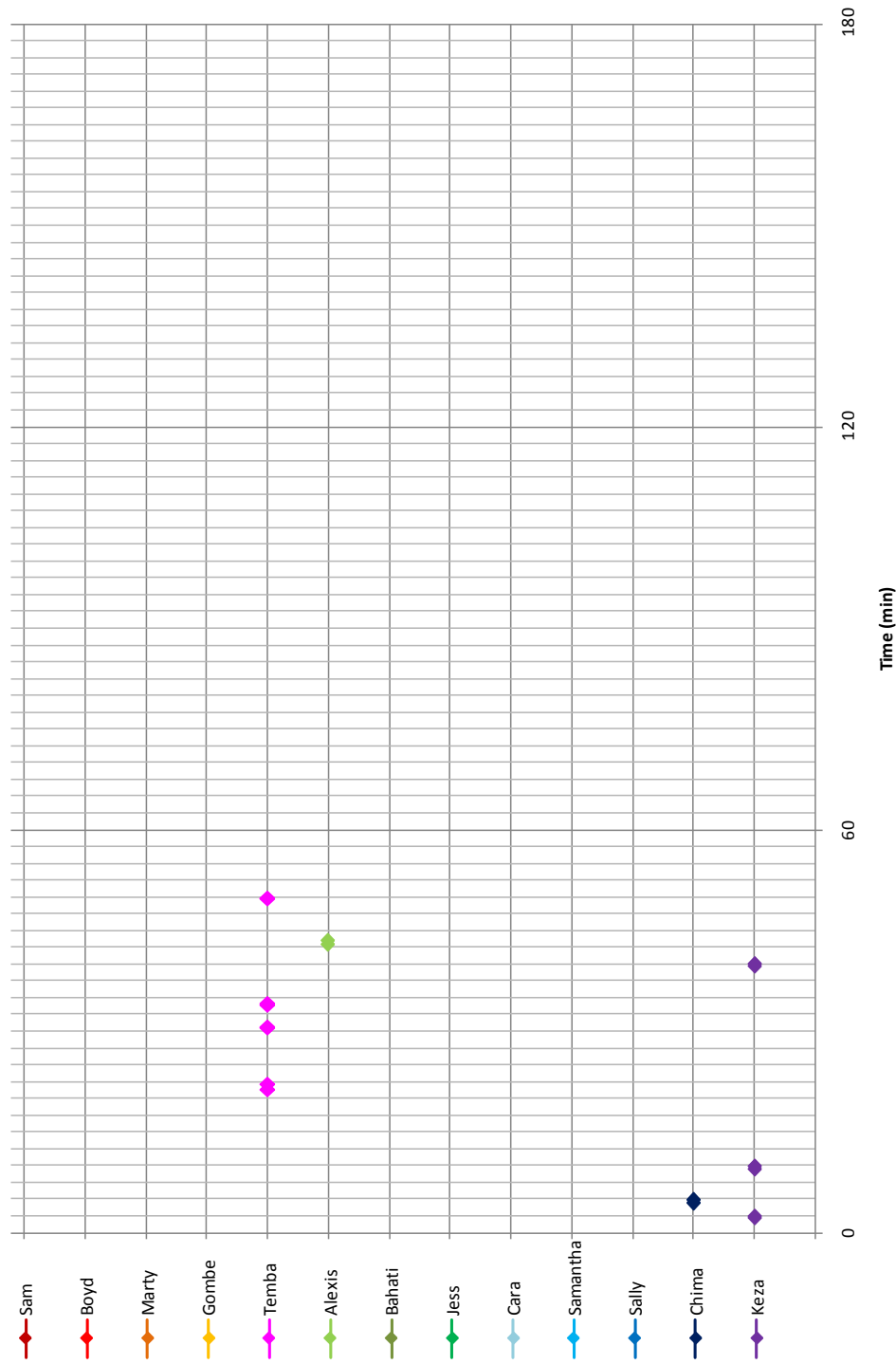


Figure 2.20b. Start and stop times for defined behaviours related to the group's use of the Dipper enrichment item during the second session within Experiment 2: Part 1. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.





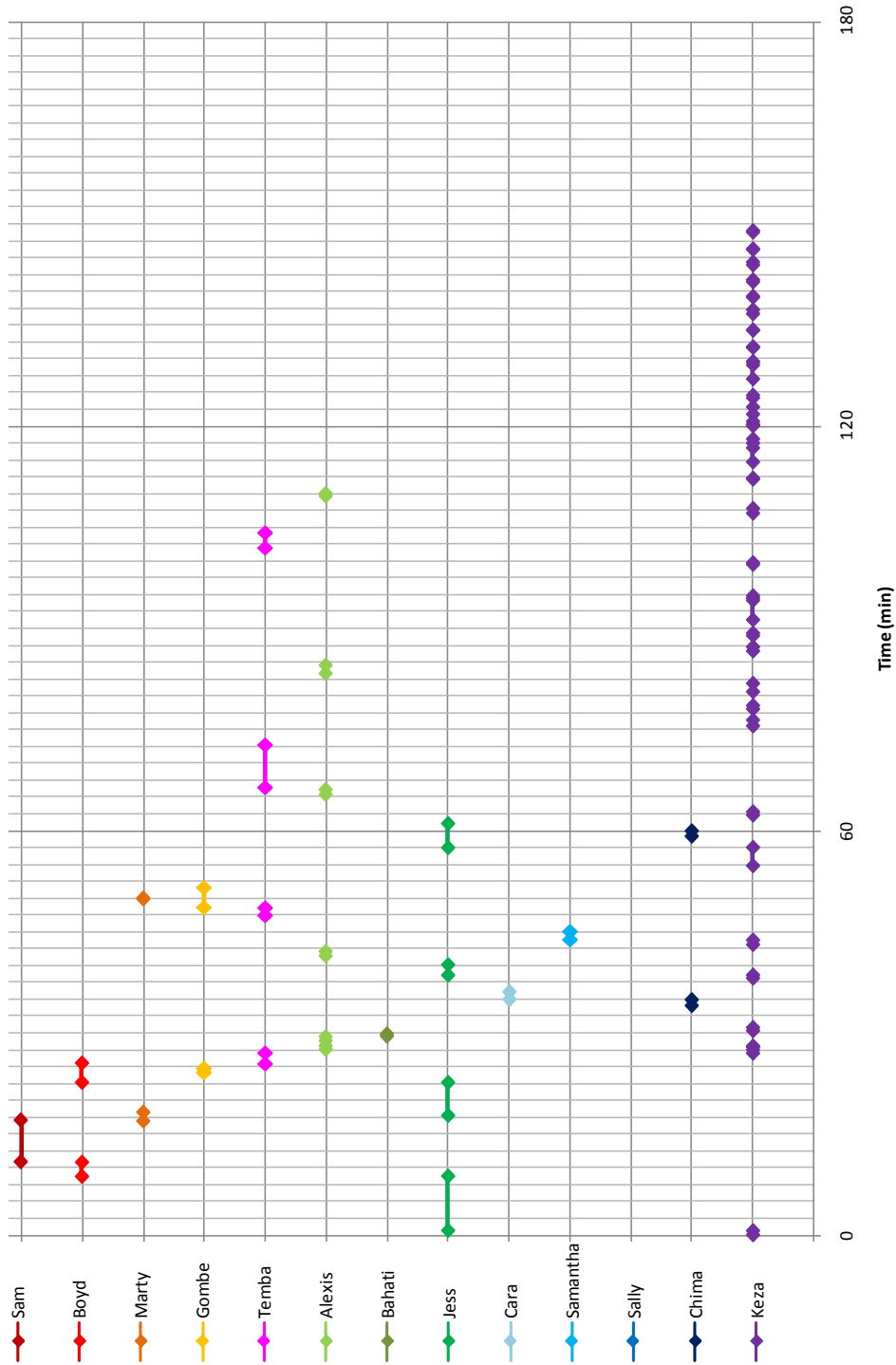


Figure 2.22a. Start and stop times for defined behaviours related to the group’s use of the Marbleroll enrichment item (with no slides present in the unit) during the first session within Experiment 2: Part 1. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

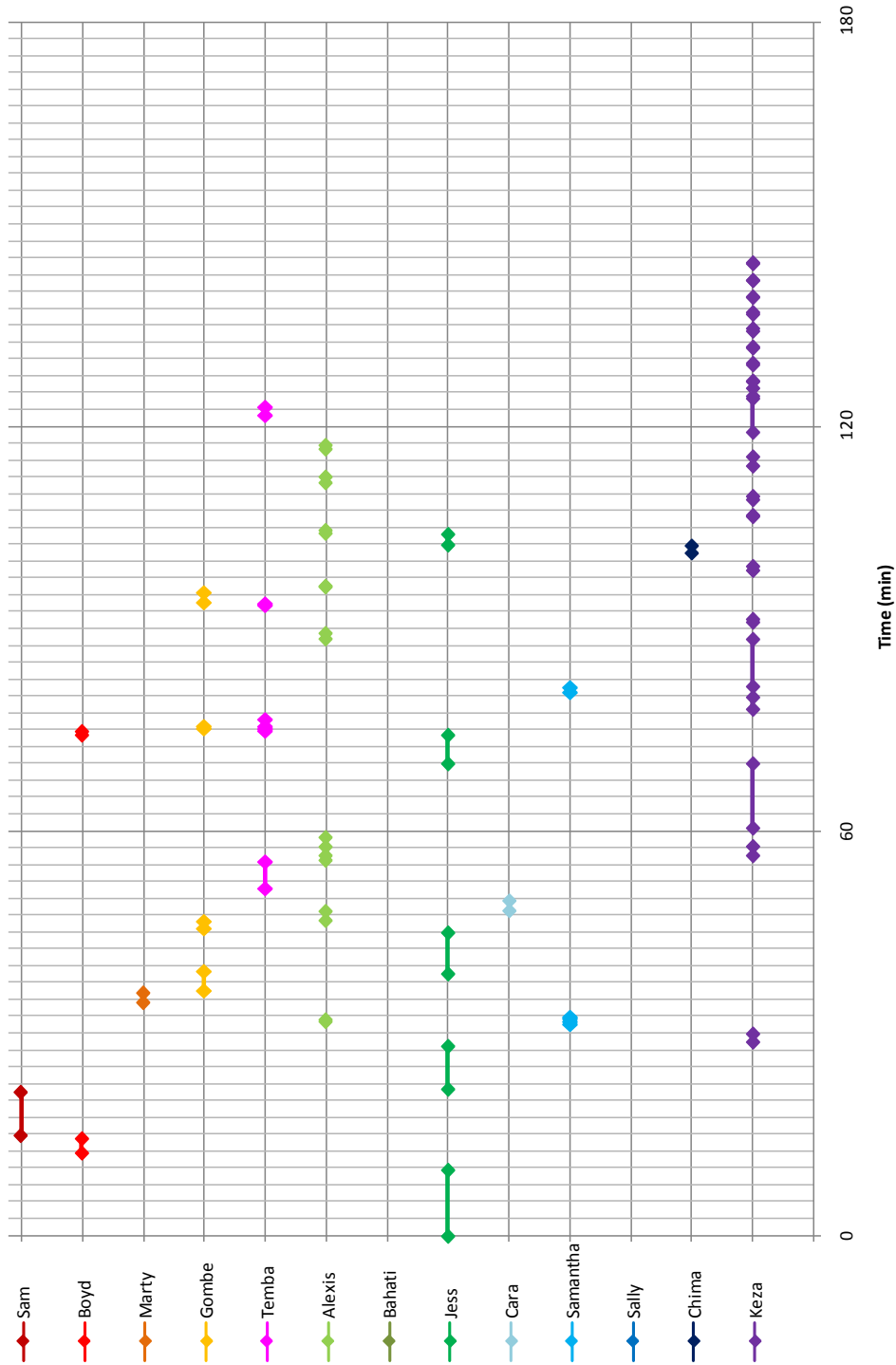


Figure 2.22b. Start and stop times for defined behaviours related to the group’s use of the Marbleroll enrichment item (with no slides present in the unit) during the second session within Experiment 2: Part 1. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

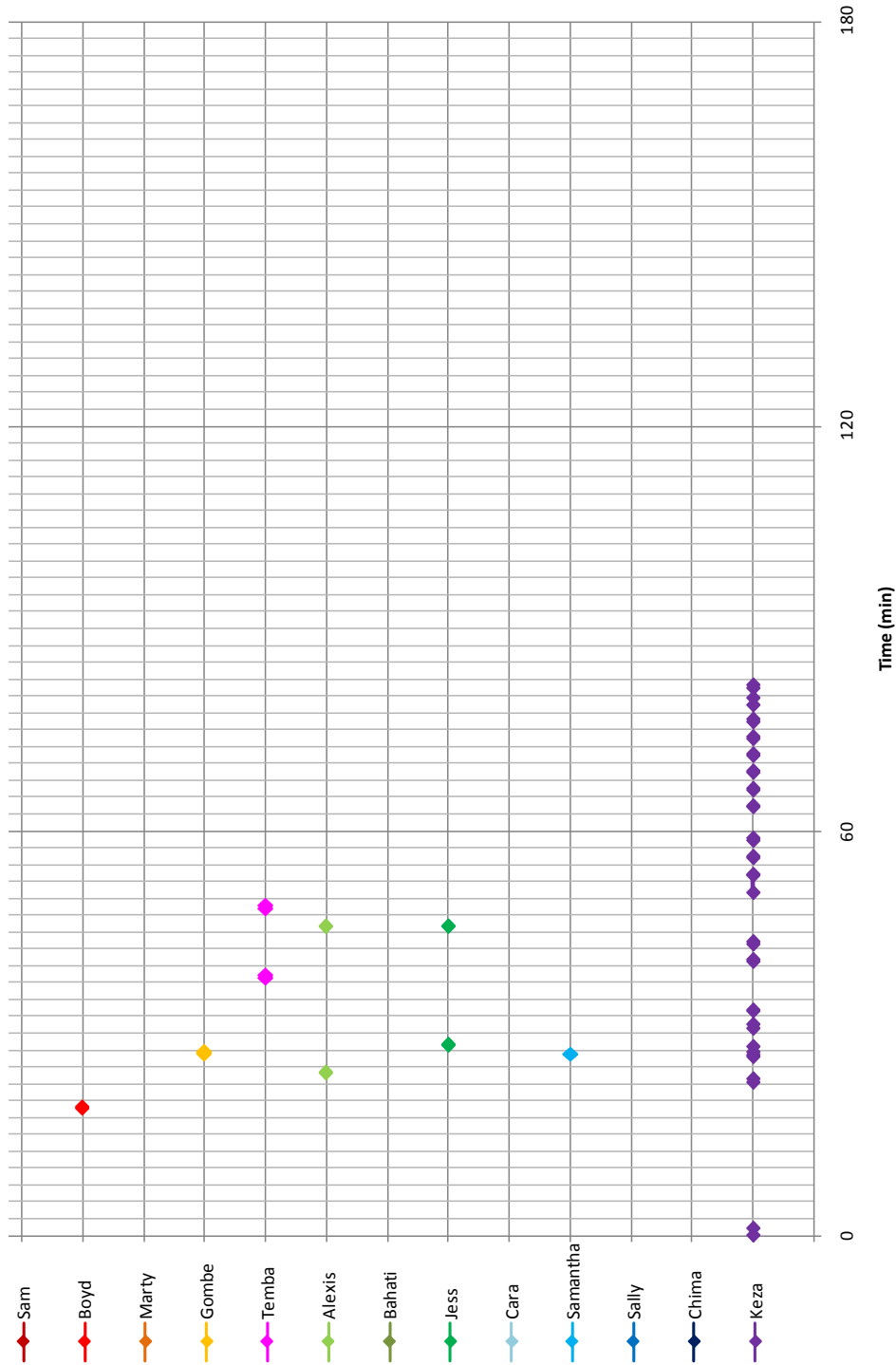


Figure 2.23a. Start and stop times for defined behaviours related to the group’s use of the Marbleroll enrichment item (with slides present in the unit) during the first session within Experiment 2: Part 1. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

When the slides were added to the Marbleroll the time the chimpanzees used the item dropped, as shown in Figures 2.23a and 2.23b. During these sessions 10 members of the group used the item, more members doing so during the second session with the item. Six of these individuals used the item for two periods or less in a session. All periods of use were under four minutes and most lasted less than a minute. The Marbleroll (with slides) was used by the majority of the group in the first hour of the sessions. Keza, however, was the only individual to use the item during the second hour, and more than half an hour after any other member of the group had. Keza was the first subject to use the item in both sessions, and the last.

Behaviour of note was that after some time Keza was able to operate the slides effectively (so that a marble or Jaffa™ was able to continue down the raceway) but when Boyd (a dominant male) approached she stopped interacting with the Marbleroll and sometimes moved away from the item. As Keza had stopped operating the slides in Boyd's presence he did not see this behaviour. Boyd did not operate the slides. Alexis, however, was seen to observe Keza operating the slides and subsequently operated the slides himself.

On a practical note with the slides included in the Marbleroll there wasn't the same loud noise as a Jaffa™ made its way down the raceway so this noise was not present as another cue to the chimpanzees that the item was active and that the food items were available.

Individual Behaviour Related to Enrichments

Figures 2.24a to 2.24e show the behaviour (as defined in Table 2.2) of individuals within the chimpanzee group during sessions of Experiment 2. The scale for all of the figures are the same for each figure and for the entire session length to allow for comparisons to be made.

Across all the individual chimpanzees juvenile female Keza used the enrichment items the most. Adolescent male Temba was the next highest user of the items. Adult female Jess was the second highest user of the Marbleroll (with no slides). However, she used the Musicbox, TV/Video and Marbleroll, when the slides were present, very little. Adolescent male Temba and juvenile female Keza spent the most time watching other individuals using the items. Adult female Sally used the items the least during these sessions, and was the only individual that did not use some items at all.

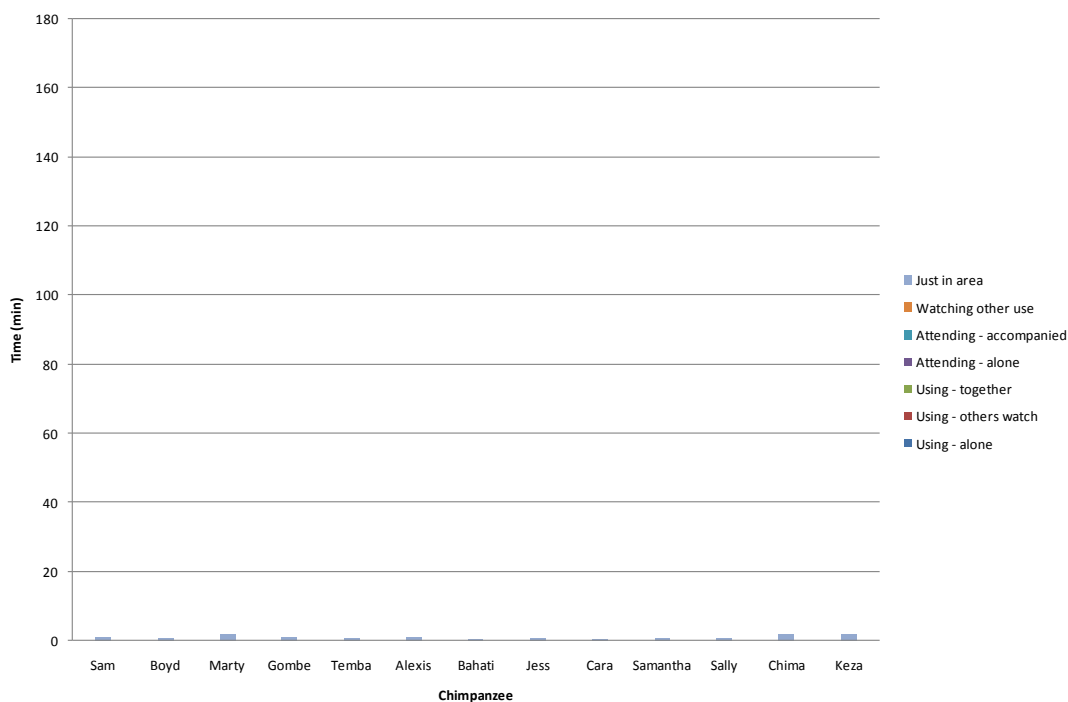


Figure 2.24a. Total time that the individuals of the chimpanzee group exhibited defined behaviours during Baseline sessions of Experiment 2: Part 1. Individual chimpanzees data are arranged in order of sex, males on the left and then age within each sex group, oldest on the left.

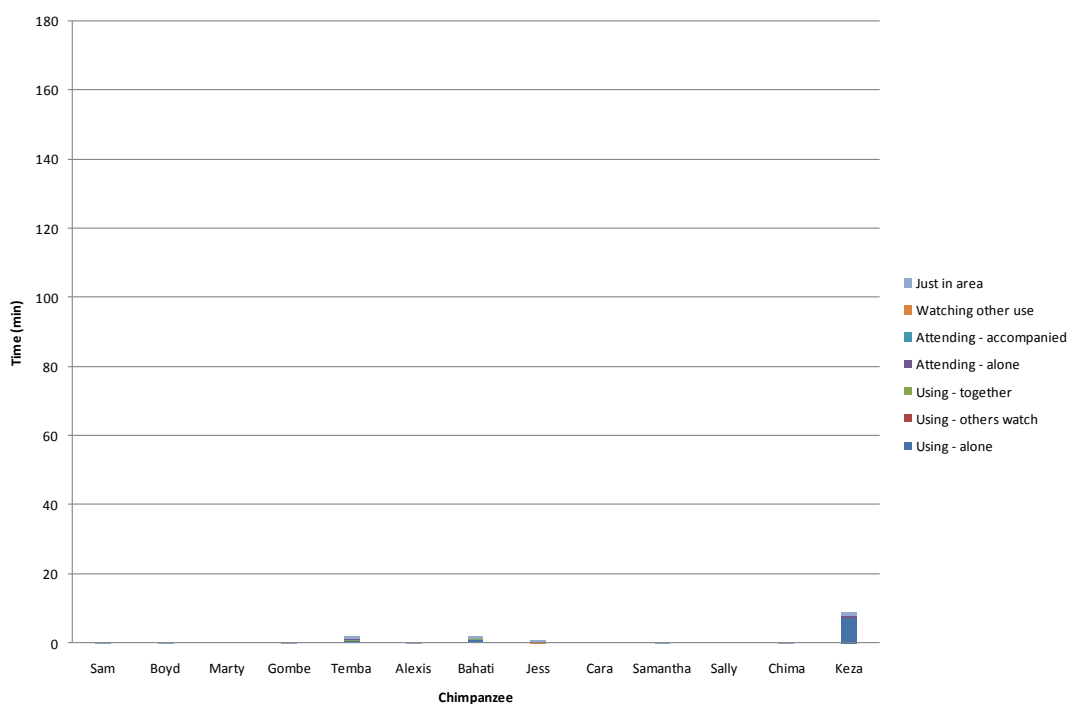


Figure 2.24b. Total time that the individuals of the chimpanzee group

exhibited defined behaviours during sessions with the Musicbox enrichment in Experiment 2: Part 1. Individual chimpanzees data are arranged in order of sex, males on the left and then age within each sex group, oldest on the left.

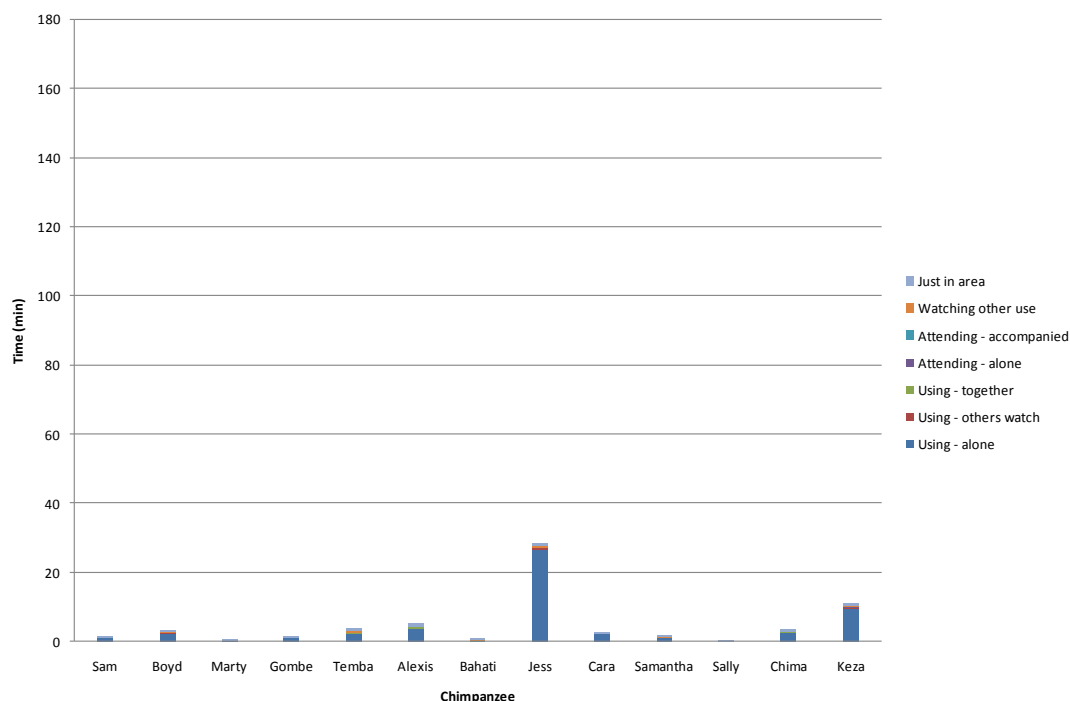


Figure 2.24c. Total time that the individuals of the chimpanzee group exhibited defined behaviours during sessions with the Dipper enrichment in Experiment 2: Part 1. Individual chimpanzees data are arranged in order of sex, males on the left and then age within each sex group, oldest on the left.

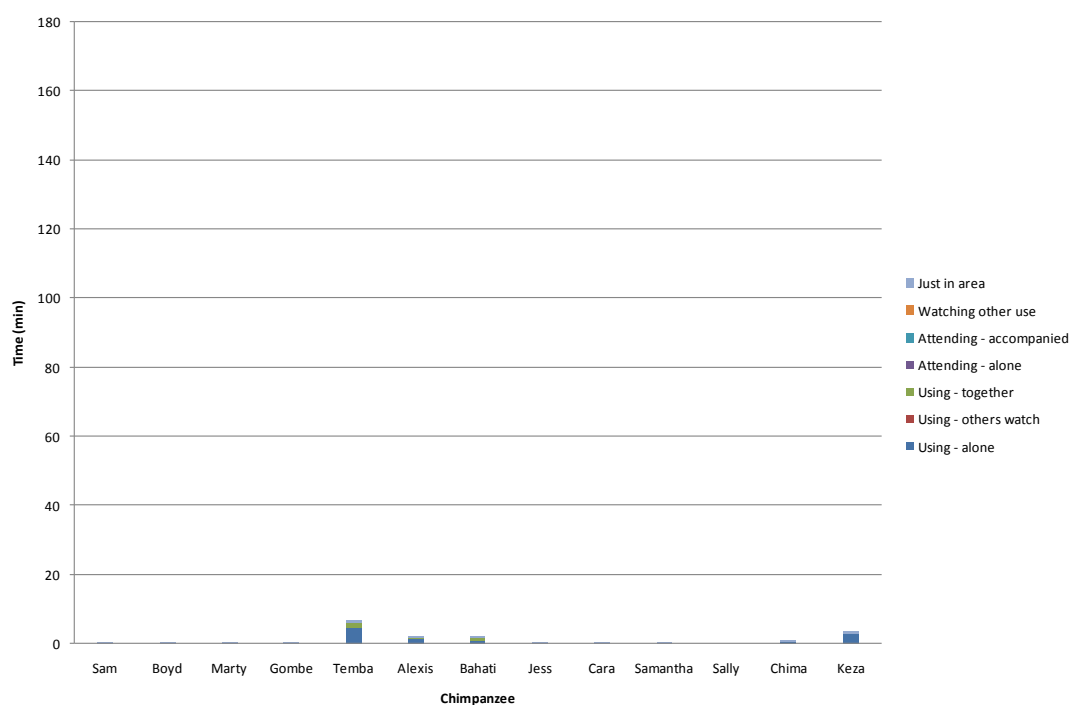


Figure 2.24d. Total time that the individuals of the chimpanzee group exhibited defined behaviours during sessions with the TV/Video enrichment in Experiment 2: Part 1. Individual chimpanzees data are arranged in order of sex, males on the left and then age within each sex group, oldest on the left.

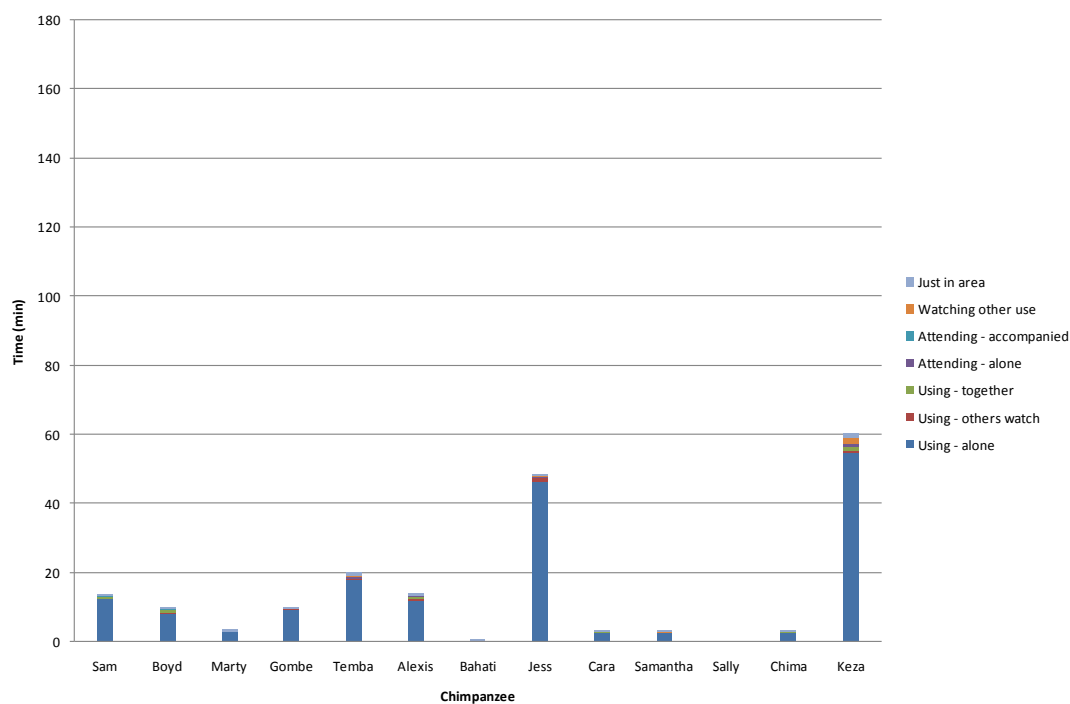


Figure 2.24e. Total time that the individuals of the chimpanzee group exhibited

defined behaviours during sessions with the Marbleroll enrichment (with no slides present) in Experiment 2: Part 1. Individual chimpanzees data are arranged in order of sex, males on the left and then age within each sex group, oldest on the left.

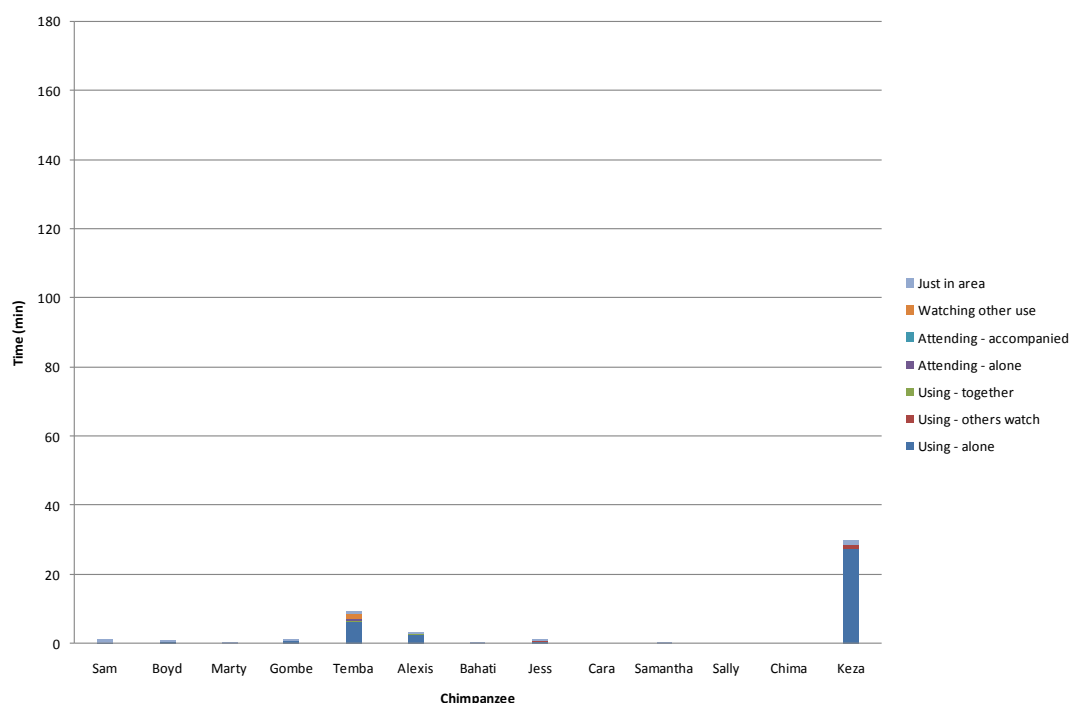


Figure 2.24f. Total time that the individuals of the chimpanzee group exhibited defined behaviours during sessions with the Marbleroll enrichment (with slides) in Experiment 2: Part 1. Individual chimpanzees data are arranged in order of sex, males on the left and then age within each sex group, oldest on the left.

Discussion

Following the completion of Part 1 of this experiment a brief analysis of the data was carried out to establish totals for time of use of the enrichment items. As only two of the four enrichment items were used for more than 30 min in a session a decision was made to include further enrichment items. This was done to attempt to establish another item which the group would use for more than 30 min in a session. Having an item that was used for more than this time in a session was anticipated as being important for the remainder of this current research. This gave rise to a second part of this experiment - Experiment 2: Part 2. As this was the case, a discussion of the results of Part 1 (and Part 2) will follow at the end of Part 2.

EXPERIMENT 2: INTRODUCTION AND TRIAL OF ENRICHMENT EQUIPMENT

PART 2

Following the results for the amount of time the enrichment items were used by the chimpanzee group during the introduction period (Experiment 2: Part 1) it was decided to design and trial two further enrichment items. The goal was to find if either of these items were used for a longer time during sessions than those trialled previously and to test their durability and suitability for the research.

Enrichment Items Employed in This Research

Foraging Enrichment in This Research

As previously discussed, many foraging devices have been found to be used by many animal species and with enriching effects. This use has been shown to be preferred over access to other items (Holmes, Riley, Juneau, Pyne & Hofing, 1995; Menzel, 1991). In Part 1 of Experiment 2, lower levels of use was shown by the chimpanzee group for items that did not contain a food element. As such, a decision was made to include two further foraging devices in this research.

A Screwfeeder unit was selected as a foraging device for this current research as it was robust and food delivery was easily controllable. The unit was relatively low in cost and time to construct. Utilisation of the Screwfeeder unit had little to no impact on the visiting public, staff members or other animals held at the facility.

The Marbleroll unit previously used was utilised in a different way to provide another form of reinforcement. The unit remained visually interesting, control could be provided to the subjects and a foraging element was included. The unit was again physically semi-accessible to the chimpanzees but fully visually accessible. Items could be assisted in their movement by the chimpanzees. They could view the travel of the items and gain access to a food reinforcer. This reinforcer delivery could be controlled. Utilisation of the modified Marbleroll unit had little to no impact on the visiting public, staff members or other animals held at the facility.

Aim

Based on the results from the initial introduction and trial of the enrichment items (Experiment 2: Part 1), the purpose of this study was to introduce further enrichment items to the chimpanzee group and ensure the overall experimental set-up and the enrichment items were suitably robust and to explore the chimpanzees' initial interest in the enrichment items.

Method: Part 2

Subjects

The subjects utilized in Experiment 2: Part 2 were the same as those in Part 1.

Study's Impact on Standard Husbandry Protocol

The impact on standard husbandry protocol for the chimpanzees was the same as in Part 1.

Ethical Consent

The approval was just as it was for Part 1.

Apparatus and Setting

The area and experimental equipment were as that described in Part 1.

Enrichment Items

Screwfeeder enrichment. Figure 2.25 to 2.27 show the Screwfeeder unit and Figure 3.14 the unit in position for use by the chimpanzees in the experiment. The base unit, a PPP Animal Feeder, was originally manufactured for the delivery of feed to pigs (*Sus scrofa*). The unit included a 12V motor which turned a shaft that had at its base a large metal screw shaped shaft (which when turned delivered feed that was held within the unit). The unit was mounted in a plywood frame and secured within by shaped metal supports. A funnel was fixed to the base of the unit and fed into a curved metal pipe which was the final delivery section to the chimpanzees. The pipe opening was 4.8 cm in diameter. When mounted in place in the operant area the unit was filled with sunflower seeds and taped over to prevent rain and vermin entering the unit. To make the quarter turn utilised in this current research the Screwfeeder

took 0.2 seconds and delivered approximately 20g of seeds.

The Screwfeeder operated automatically via a computer program. During the trailing and Free Access studies (Experiment 2 and 3) food delivery was entirely automatic, on the basis of time.

The visual complexity of the Screwfeeder enrichment item included the variety of shapes and colours. The chimpanzees were also able to see the sunflower seeds. Although the turning of the metal shaft could not be seen by the chimpanzees they could hear it and see the seeds move. This enrichment item lacked complexity in terms of the interactions or control it afforded the chimpanzees as, although they could touch the funnel of the unit they could not control the enrichment.



Figure 2.25. Screwfeeder, from the front (top, left) and back view (top, right), and sunflower seeds (bottom).

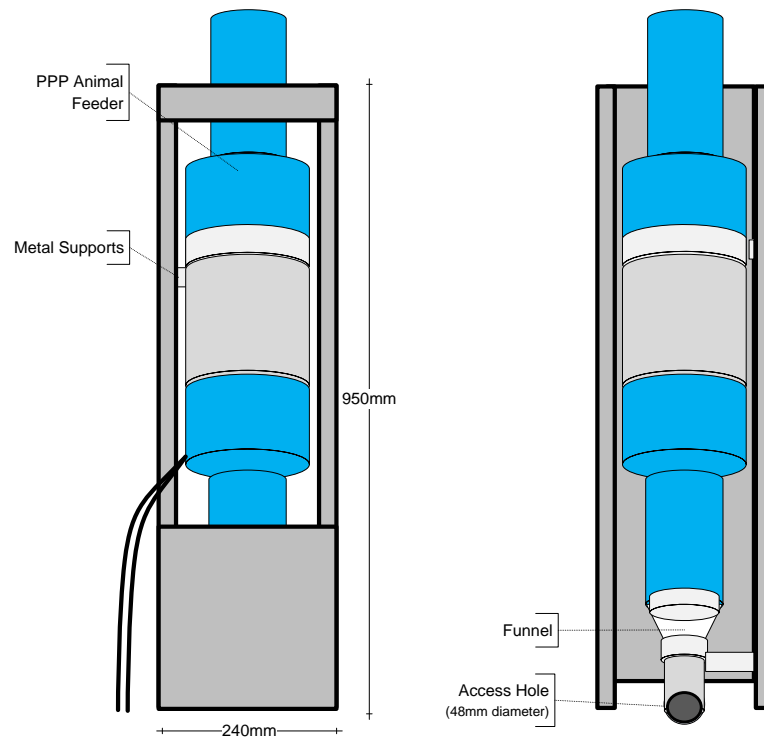


Figure 2.26. Diagram of Screwfeeder enrichment, with dimensions and components indicated, from the back (left), and from the front (right).

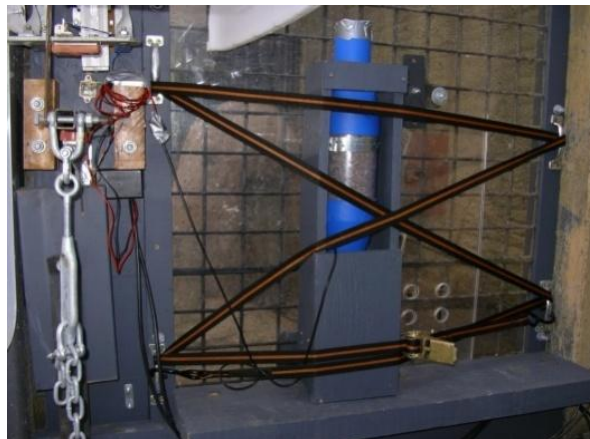


Figure 2.27. Research equipment is shown with the Screwfeeder enrichment strapped in place for use in the research.

Marbleroll enrichment - delivering coated peanuts. The Marbleroll as seen in Figure 2.16 and 2.17 was used in this experiment to delivered coated peanuts (as seen in Figure 2. 28) down the Jaffa™ raceway. In this form the operation of the item did not include any marbles.

As previously discussed the Marbleroll enrichment was visually complex with many different colours, shapes and moving parts. Both of these devices had associated noises.



Figure 2.28. Coated peanuts, whole and with one split in half.

Procedure

The study was conducted from April 2005 until October 2005. A video camera was positioned above where the enrichments were to be placed later. One enrichment was put in place, during the day (while the chimpanzees were out), per session. The experimental equipment was mounted on the wall of bars in the Covered Area section of the chimpanzees' enclosure: accessible to the chimpanzees from within their enclosure and to the researcher from outside of the entire enclosure. An outdoor flood light was on during the three hour sessions. The location of the experimental equipment is indicated in Figure 1.1.

The chimpanzees were given access to one enrichment item per session (as seen in Figures 2.16, 2.17, and 2.25 to 2.28) the order of which is shown below in Table 2.4, which also shows detail of the operation of the enrichment item during this experiment. Each enrichment item stayed in place for two three hour sessions and on completion of those the next enrichment was put in place until all of the enrichment items had been trialled for two sessions each.

Table 2.4
Enrichment items in order of use for Experiment 2: Part 2 and enrichment item operation details.

| Enrichment Item | Operation Details |
|-----------------|--|
| Screwfeeder | Turned every 2 minutes for 2 seconds (approximately a quarter turn) and delivered sunflower seeds (approximately 20g). |
| Marbleroll | Released a coated peanut (down the Jaffa™ raceway) every 150 seconds. The slides on the Marbleroll were removed so the chimpanzees had nothing to operate. |

Operation of Enrichments

During Experiment 2: Part 2 experimental events within the sessions were controlled by a computer programme and the internally housed computer unit. The computer and enrichments were controlled by MEDPC-IV software and interfaces. Programmes were written for the experimental phase and for each particular enrichment item during that phase.

Access to Enrichment Items

The research was conducted in a closed economy so none of the components of the enrichment items were available from other sources outside of the research.

Data Collection

Video Recordings and Behavioural Definitions

As in Part 1 of Experiment 2, during Part 2 each experimental session was recorded on VHS video. Each experimental session was recorded as described in Part 1 and individual chimpanzee's behaviour (as categorized in Table 2.2) recorded as described in Experiment 2. The area within view of the video recording was 5 m deep, 2 m across and 2 m in height.

Reliability. Within-observer reliability was assessed by the researcher and this

can be seen in Part 1 of this experiment, as the assessment methodology was the same for Part 2 of Experiment 2.

Data Analysis

Analysis of Video Data

The video recordings collected during Experiment 2: Part 2 were analysed and provided group and individual behavioural data within the chimpanzee group.

Results: Part 2

The data analysed here were based on the time any chimpanzee was within the observation area and recorded to be so. Definitions for the recorded behaviour are described in Table 2.2. The data are presented as behavioural category totals for each experimental condition. Details of data for each experimental session are presented in Appendix B.

Throughout the results of this study Figures will utilise symbols where: SF is Screwfeeder enrichment; MR (p) is Marbleroll enrichment, delivering coated peanuts.

Group Behaviour Related to Enrichment Items

The chimpanzee group's overall behavioural data totals for each experimental session in Part 1 of Experiment 2 are shown in Table 2.5 and Figure 2.29. These show that the Screwfeeder enrichment and the Marbleroll unit, delivering coated peanuts, were both used for more than 80 min in all the experimental sessions. The Screwfeeder was used for longer and both enrichment items were used less by the group during the second session with them.

Of all of the behavioural classes that the chimpanzees' behaviour could be recorded as, the behaviour Use-alone was performed considerably more by the group. The group spent more time using an enrichment item while another individual observed this (Using – others watch) or watching another individual using an item (Watching other use) during sessions with the Screwfeeder than with the Marbleroll delivering coated peanuts. Multiple chimpanzees spent time using the enrichment items at the same time (Using-together) for a similar duration with the exception of the first session with the Marbleroll unit when more time was spent Using-together.

Time in which multiple subjects and lone subjects were oriented towards and item but not interacting with it (Attending – accompanied, Attending-alone) was minimal.

Table 2.5

Chimpanzee group behaviour (as defined in Table 2.2) during Experiment 2: Part 2. The amount of time (min) in each session the group was performing each behaviour.

| Session Condition | Time Spent Exhibiting Class of Behaviour (min) | | | | | | |
|-----------------------|--|----------------------|------------------|-------------------|-------------------------|--------------------|--------------|
| | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in Area |
| Screwfeeder 1 | 126.08 | 5.72 | 2.30 | 0.00 | 0.00 | 5.72 | 3.40 |
| Screwfeeder 2 | 102.77 | 4.28 | 2.07 | 0.23 | 0.00 | 4.28 | 2.63 |
| Marbleroll (peanut) 1 | 93.50 | 2.00 | 6.68 | 1.30 | 0.27 | 2.00 | 3.98 |
| Marbleroll (peanut) 2 | 83.65 | 0.87 | 3.57 | 0.08 | 0.00 | 0.87 | 2.52 |

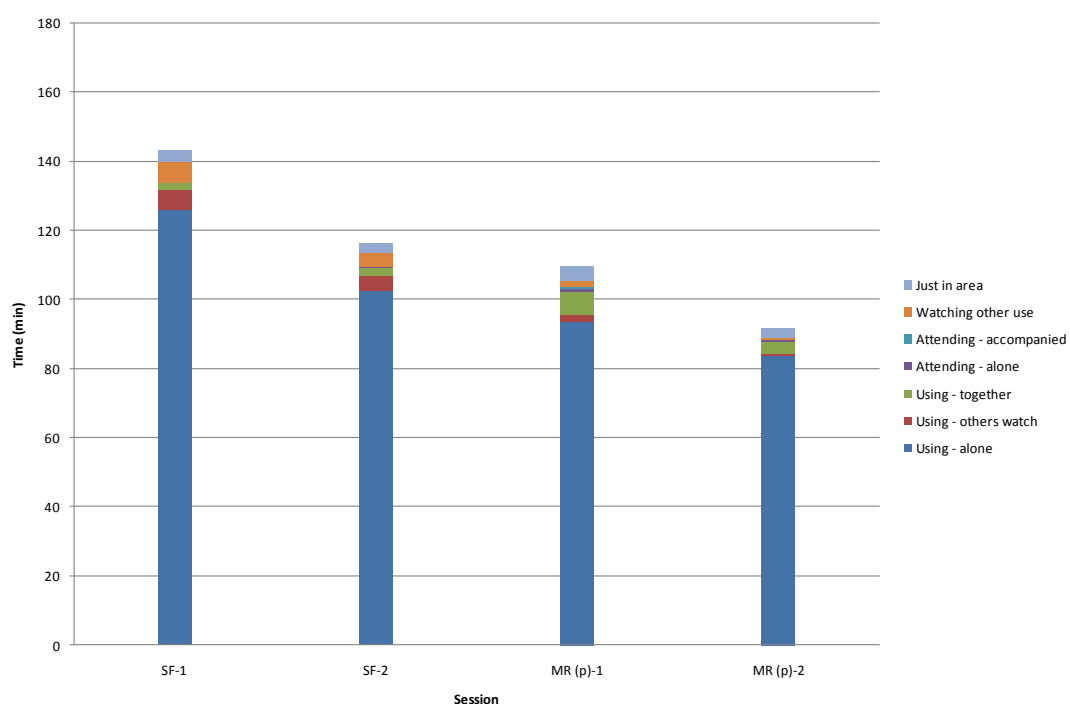


Figure 2.29. Total time chimpanzee group exhibited defined behaviours in experimental sessions of Experiment 2: Part 2.

Group Use Event Records

Screwfeeder enrichment. Figures 2.30a and 2.30b show that the Screwfeeder enrichment was used by the chimpanzee group from the very beginning of the

sessions until into the third hour (after sun set). The item was used slightly less during the second session. All of the members of the group were recorded using the item. Periods of use varied from a few seconds to almost 11 min (by adult female Jess). Adult females Jess and Sally, adult males Boyd and Marty, adolescent males Gombe and Temba and adolescent female Chima and juvenile male Alexis and female Keza all used the item for periods greater than three minutes. Jess was the individual to use the item for the most time. Keza used the item the most number of times. Jess used the item more towards the beginning of the sessions and Keza sporadically throughout. The kindergarten age male Bahati used the item the least. The adult males used the item mainly in the first half hour of the sessions.

Marbleroll enrichment - delivering coated peanuts. All of the members of the chimpanzee group used the Marbleroll when it was delivering coated peanuts, as shown in Figures 2.31a and 2.31b, most on multiple occasions. The item was used from the time the sessions started until early in the third hour (after sun set). The item was used slightly less during the second session the group had with it. Jess, an adult female, used the item for the longest bout, being almost eight minutes. Most periods of use were brief lasting a couple of minutes. The adolescent and then adult males used the item initially during the first session. However, in the second session an adult female (Jess) was the first to use the item. Jess used the item for the most time, followed by adolescent male Temba. The kindergarten age male Bahati used the item the least.

Individual Behaviour

Figures 2.32a and 2.32b show the behaviour of the individual chimpanzees (as defined in Table 2.2) during sessions with enrichment items. Out of the entire chimpanzee group adult female Jess used the enrichment items the most, followed by juvenile female Keza. Adolescent Temba was the male subject to use the items the most. Kindergarten male Bahati was the subject to use the items the least. There was no obvious pattern of use between the individuals of different age or sex. Adolescent male Temba and juvenile female Keza were the subjects that spent the most time watching other individuals using the items. Keza and adult female Samantha were the subjects to spend the most time using the item with another individual.

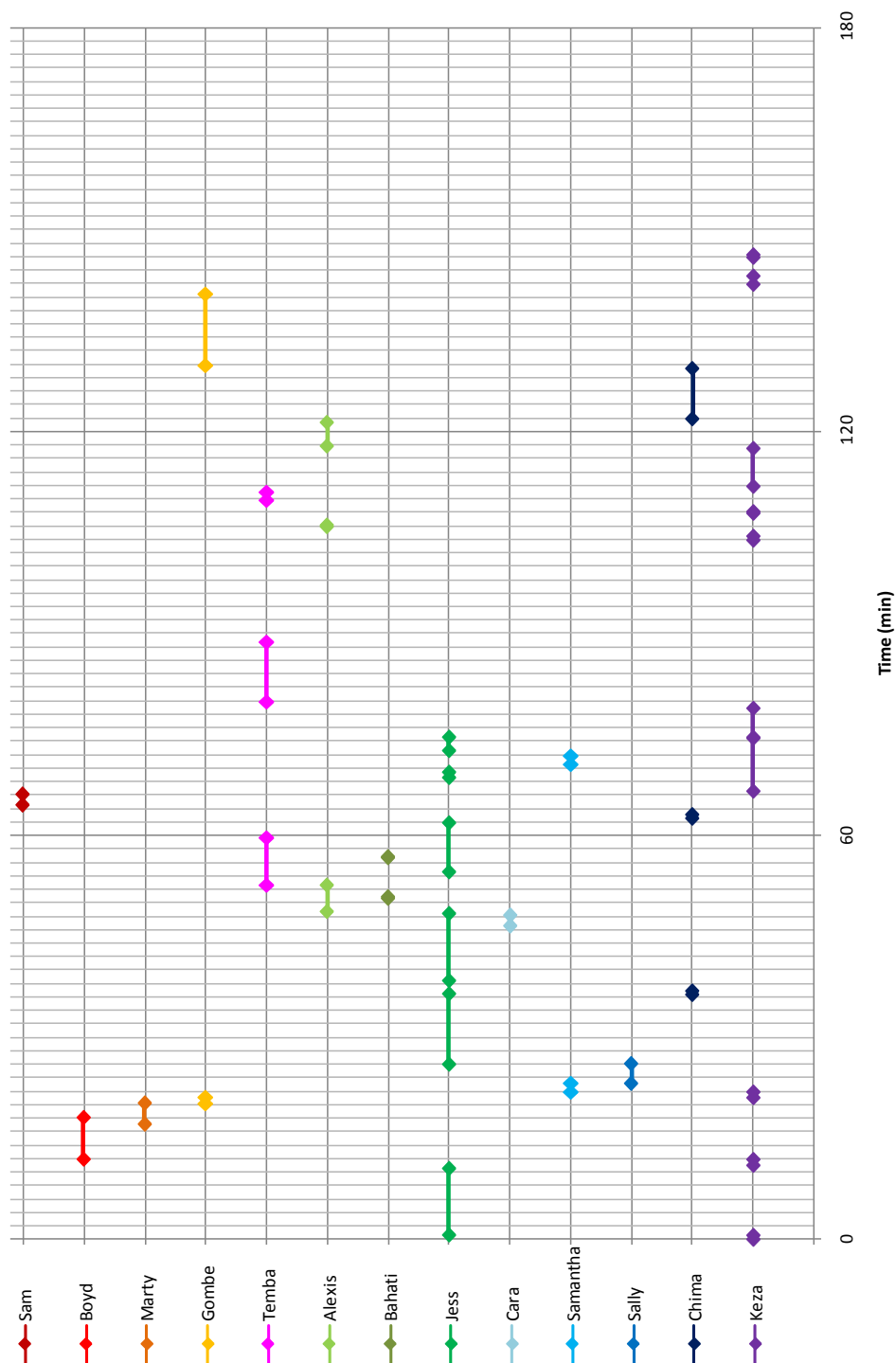


Figure 2.30a. Start and stop times for defined behaviours related to the group's use of the Screwfeeder enrichment item during the first session within Experiment 2: Part 2. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

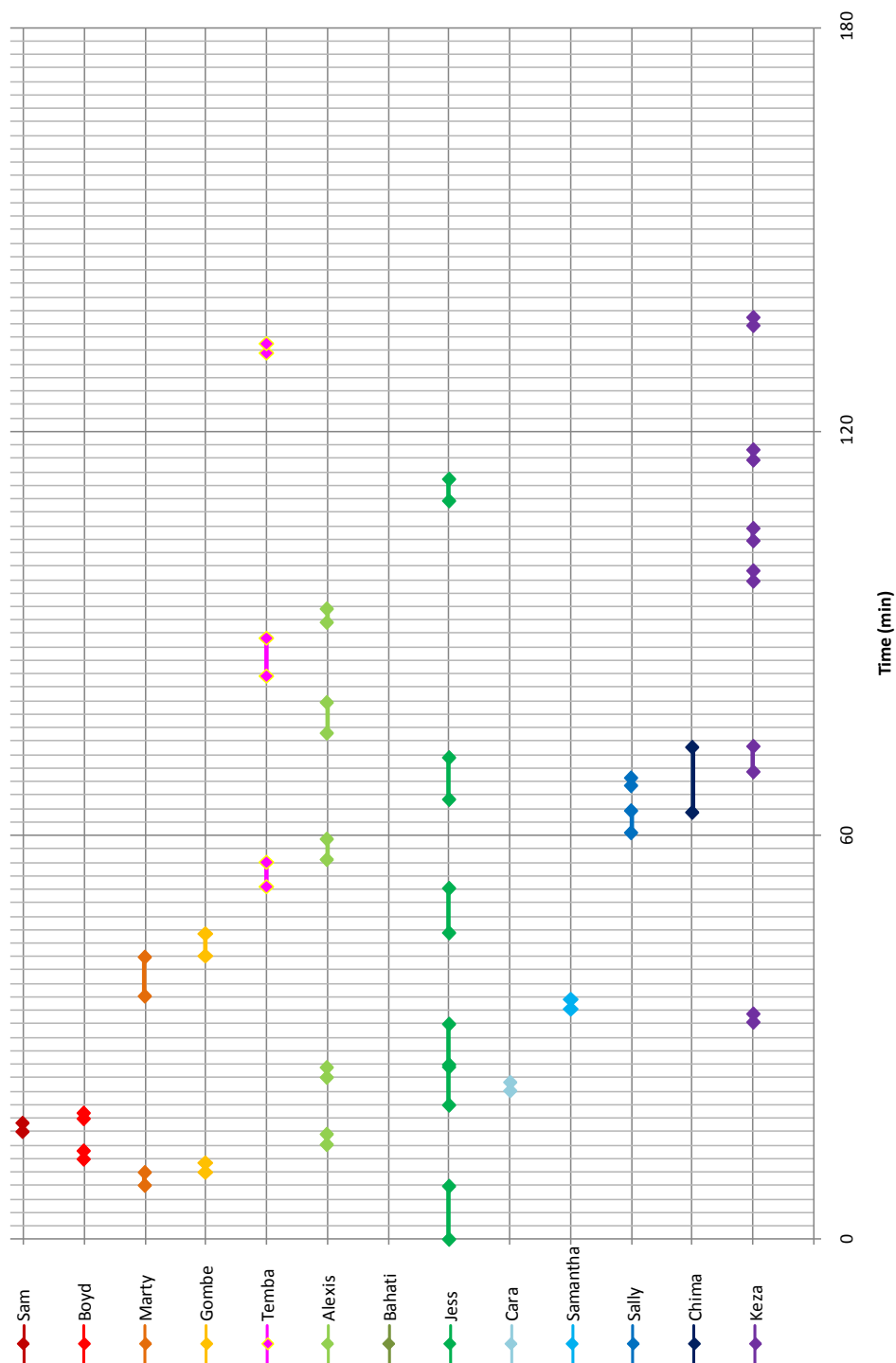


Figure 2.30b. Start and stop times for defined behaviours related to the group's use of the Screwfeeder enrichment item during the second session within Experiment 2: Part 2. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

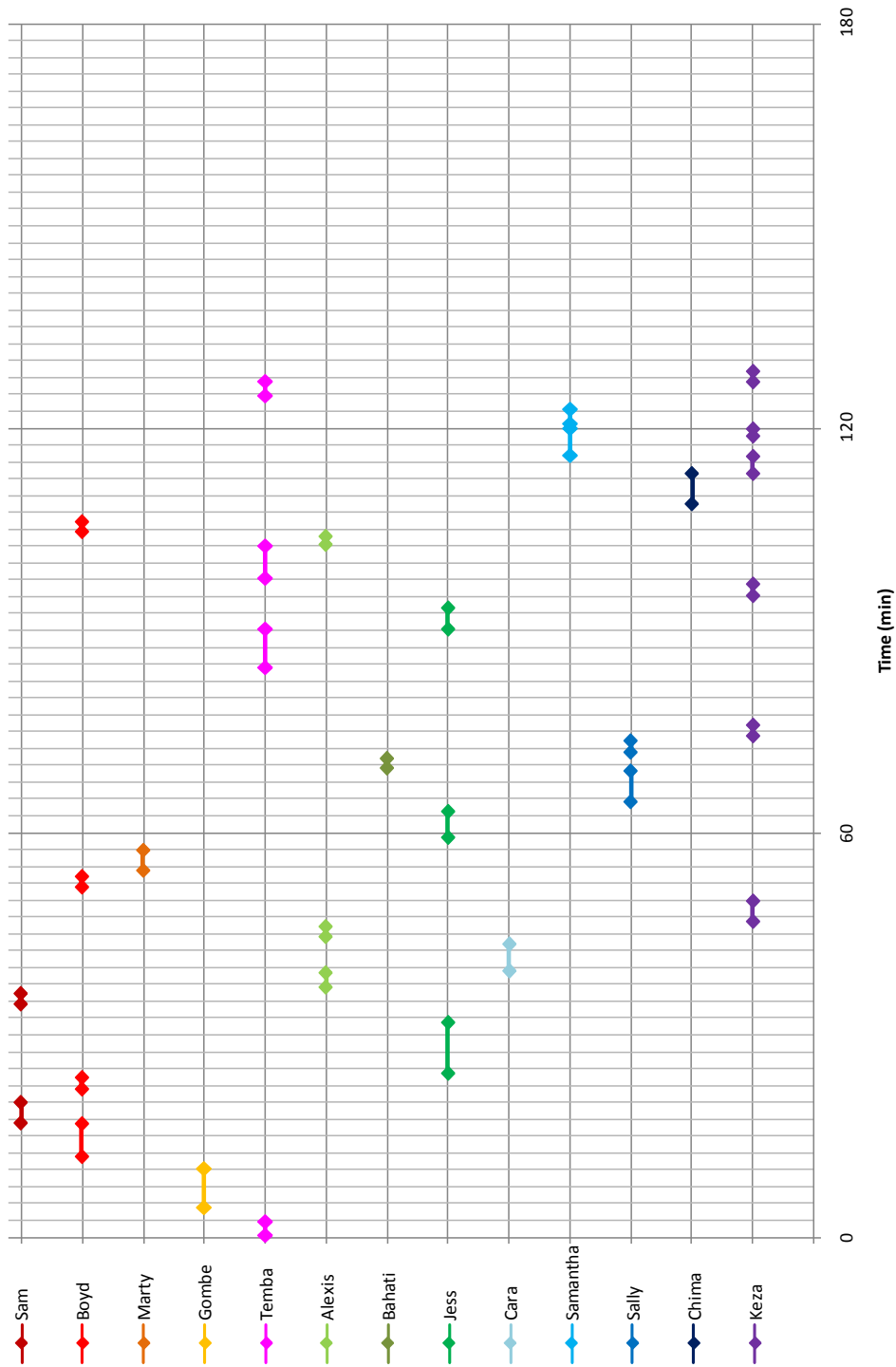


Figure 2.31a. Start and stop times for defined behaviours related to the group’s use of the Marbleroll enrichment item (delivering coated peanuts) during the first session within Experiment 2: Part 2. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

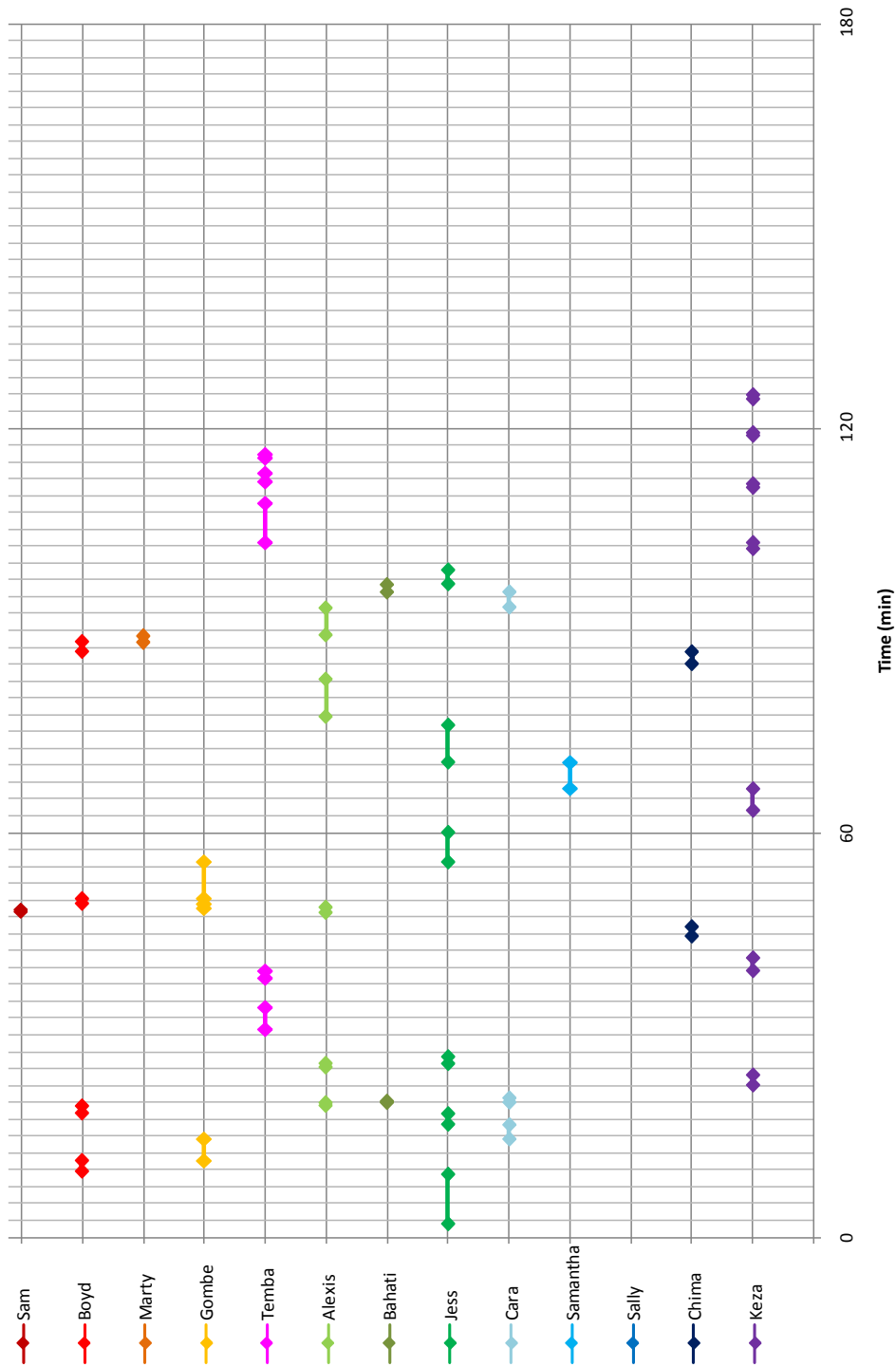


Figure 2.31b. Start and stop times for defined behaviours related to the group's use of the Marbleroll enrichment item (delivering coated peanuts) during the second session within Experiment 2: Part 2. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

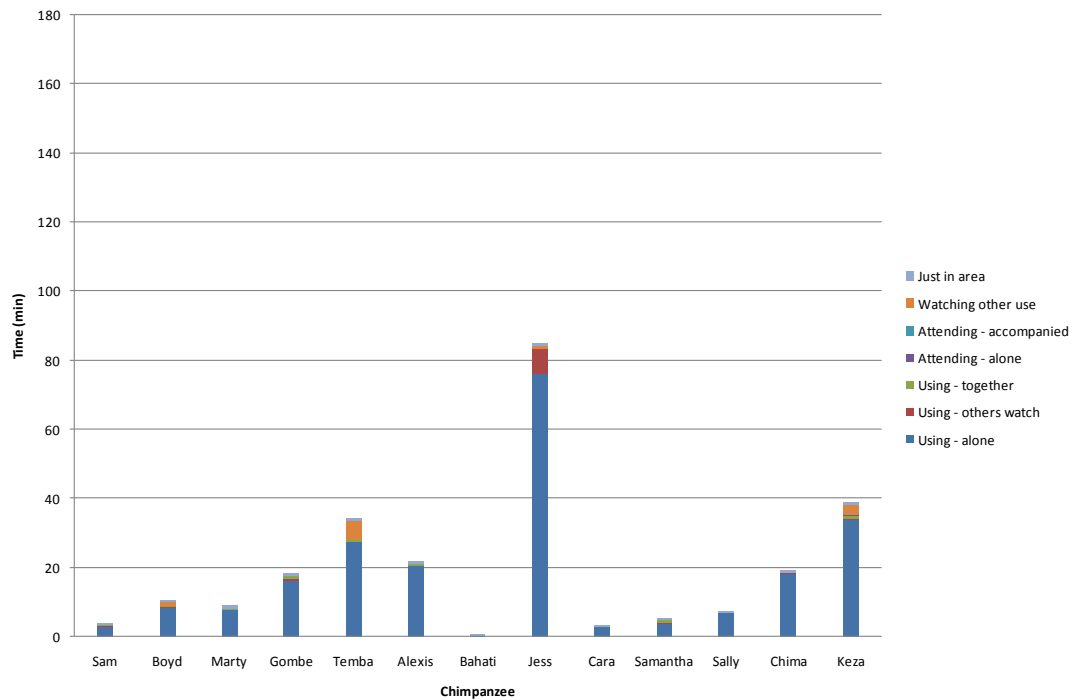


Figure 2.32a. Total time that the individuals of the chimpanzee group exhibited defined behaviours during sessions with the Screwfeeder enrichment in Experiment 2: Part 2. Individual chimpanzees are arranged in order of sex, males on the left and then age within each sex group, oldest on the left.

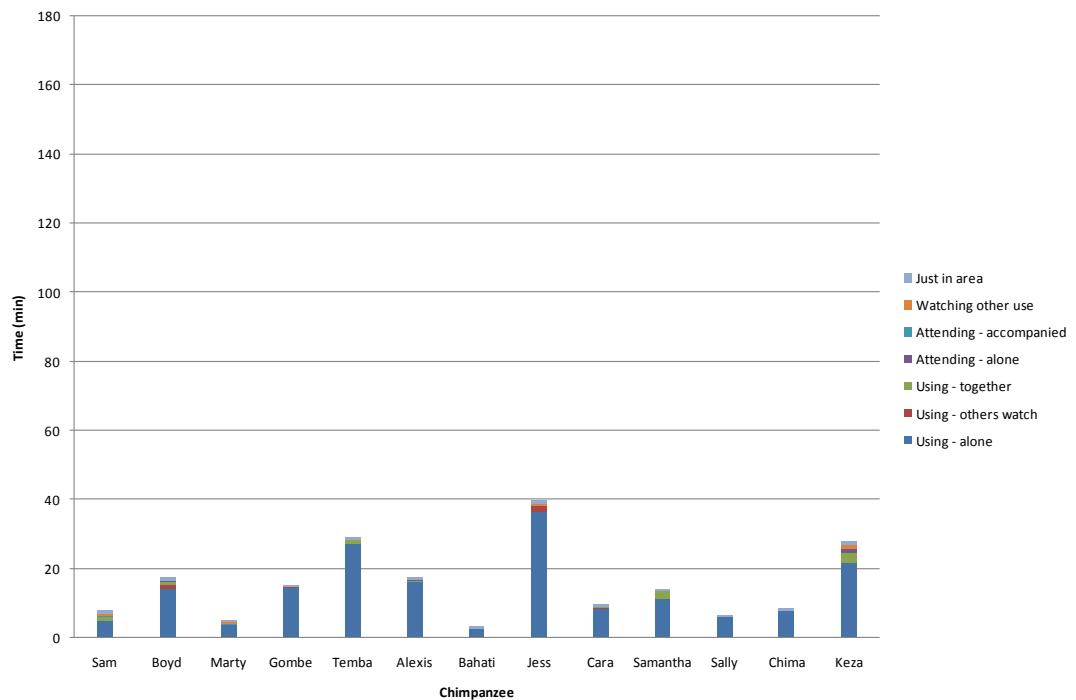


Figure 2.32b. Total time that the individuals of the chimpanzee group

exhibited defined behaviours during sessions with the Marbleroll enrichment-delivering coated peanuts, in Experiment 2: Part 2.

Discussion

This initial trial of the enrichment items with the entire chimpanzee group, Experiment 2, Part 1 and 2, showed the overall level of the chimpanzees' interest in the enrichment items, the durability of the items and the way in which the chimpanzees behaved in their presence. Overall, the experimental set-up functioned well when including considerations for research needs, animal well-being and researcher safety. The enrichment items were shown to function as successfully. All of the items were found to be robust and suitable for use in this current research.

exhibited defined behaviours during sessions with the Marbleroll enrichment - delivering coated peanuts, in Experiment 2: Part 2. Individual chimpanzees are arranged in order of sex, males on the left and then age within each sex group, oldest on the left.

Group Behaviour During Sessions

The group spent a similar amount of time in the experimental area simply present (but not interacting in any way with any enrichment item that may have been present) during all the sessions. Therefore having the enrichment items present did not change the amount of time the chimpanzees spent in the area. The vast majority of the time the group was visible was spent with an individual using the enrichment item independently. Access to the items was not restricted to prevent subjects using the items simultaneously. However, this group of chimpanzees did not often use the items together. The group spent little time simply observing the items or others using them.

Use of Enrichment Items

The majority of bouts of use were typically brief lasting less than a couple of minutes. All of the enrichment items were used for some time by the chimpanzee group but those that contained some form of food were used for the greatest amount of time, and those items that did not include food for the least amount of time. Other research has shown foraging enrichment items to be preferred over access to other items that contained no foraging component (Holmes et al., 1995; Menzel, 1991). In

the majority of sessions, items use decreased as a session progressed, both in terms of length of time of use and number of individuals using the item. Little use was made by the group during the third hour of the sessions. Of the seven different enrichment conditions, the use of five decreased in the second session with that item. This habituation to the objects is similar to that seen in other research (Brent et al., 1989; Cardinal & Kent, 1998; Pruetz & Bloomsmith, 1992; Taylor et al., 1997; Vivian, 2001). However, this is a difficult judgement to make using only two sessions with items. Assessing such habituation was not the purpose of this Experiment.

Individual Differences

All the individual chimpanzees used each enrichment item. The level of use varied greatly between individuals, as seen in other research comparing group member's preference for enrichment items (Hienz et al., 1998; Perkins et al., 1992; Vivian, 2001; Watson et al., 1989). Contrary to some research findings, however, (Bloomsmith et al., 1990a; Pruetz & Bloomsmith, 1992; Novak et al., 1993) there was no apparent pattern in terms of age and sex of the subjects relating to use of the enrichment items. The two subjects that used the items more than the rest of the group were both female however, one an adult and the other a juvenile. The other three adult females showed similar levels of use to each other. An adolescent used the enrichment items the most between the all the male subjects. The youngest member of the group, and a male, was the individual to use the items the least.

Conclusion

As the aim of this study was to introduce and trial the enrichment items a further exploration of the data, such as habituation to enrichments etc. is not discussed further here. The research showed that the chimpanzee group interacted with the enrichment items and that the commodities were successful in their design and construction. Based on the findings of this experiment the experimental set-up and the enrichment items were judged to be suitable and appropriate to use for the remainder of this current research.

EXPERIMENT 3: FREE ACCESS STUDY

Preference

There are a range of methods that have been utilized to explore the preference of animals for environmental resources. This current research sought to conduct preference testing with a socially-housed captive chimpanzees for a variety of enrichment items and to explore if the findings for the group reflected the preferences of individual members of the group.

Free Access

Perhaps the simplest method of accessing choice and/or preference is free access. In this procedure the animal is given free access to two or more environmental events and the proportion of time it spends with each option is taken as the measure of preference. The alternative the animal chooses to spend more time in/with is concluded to be the preferred option. The free access procedure has been successfully employed to assess preference for a range of environmental events such as: increased space (e.g., Dawkins, 1977, with hens; Patterson-Kane, 2002, with rats), social companions (e.g., Matthews & Ladewig, 1994, using pigs; Sherwin & Nicol, 1996, with mice), different floor types (e.g., Hughes & Black, 1973 with hens), and enrichment items or enriched environments (e.g., Pruetz & Bloomsmit, 1992; Bayne et al., 1992, with primates). Hughes and Black (1973) utilised this method to assess the preference of hens for different types of cage floor. Hens were presented with battery cage floors divided into two different types of base. Four different types of flooring were presented in all the different possible pair combinations. Individual hens were placed in a cage and the total time spent on each type of flooring recorded. The results of this study were significant particularly because the hen's preference of flooring appeared to contradict previous recommendations of a welfare committee. The committee was the Brambell Committee. Specifically the Technical Committee to Enquire into the Welfare of Animals kept under Intensive Livestock Husbandry Systems (1965) under the chairmanship of F. W. R. Brambell. The committee recommended the flooring of laying hens should include metal mesh no finer than No 10. In order to provide more secure and comfortable footing for the birds. However Hughes and Black's (1973) experiment found the hens preferred thinner mesh flooring, that had been criticised

by the Brambell committee, and that an increase in the gauge of the wire of the flooring did not increase the birds preference for it.

T-maze

The T-maze preference procedure requires an animal to make a simple response (e.g., turn left or right) in a T structure in order to make its choice. At either arm of the T are different environmental variables and the animal is required to remain in the situation for a set period of time. Preference is assessed by the number of occasions one arm is chosen over the other or by the amount of time it takes for the animal to make a choice. This procedure has been utilised to explore preference for cage size (e.g., Patterson-Kane, 2002, using rats; Hughes, 1975, using hens). Bradshaw and Poling (1991) utilized T-maze procedures to assess rat preference for standard cages versus those enriched with platforms, woodchip and paper towels.

Concurrents

A concurrent-schedule procedure provides a subject with two or more simultaneously available response alternatives (e.g., keys which can be pressed) each associated with its own reinforcement schedule (Ferster & Skinner, 1957). A reinforcement schedule is a rule that states under which conditions a reinforcer will be delivered (e.g., after a set amount of time or set number of responses); the schedules determining the rate of reinforcement for each response. Under a variable-interval (VI) schedule a reinforcer becomes available for the first response that is made after a variable amount of time has elapsed since the previous reinforcement. The measure of preference comes from the ratios of times and responses made on each alternative.

The schedule for each alternative response can operate independently or dependently. If independently arranged, then each schedule runs separately, regardless of the responses and reinforcement associated with another alternative. If dependently arranged, then the imminent delivery of a reinforcer on an alternative will pause the operation of the other alternative. Dependent scheduling has the advantage that it prevents exclusive responding, and therefore provides a more reliable measure of the degree of preference for one alternative over another (Ferster & Skinner, 1957).

A form of superstitious behaviour has been associated with concurrent VI VI

schedules (Herrnstein, 1961). Typically, animals switch rapidly between alternatives, referred to as ‘adventitious switching behaviour’. This is a result of reinforcement for changing over from one alternative to another. To minimise this behaviour in animals within these experimental settings, a changeover-delay (COD) can be included in the experimental design. This delay, typically one to three seconds depending on the species, means that a reinforcer can’t immediately follow a change between responses on the two manipulanda. The delay is (usually) from the first response to one alternative until reinforcement can be delivered.

Ferster (1959) identified that non-human primates were ‘convenient’ subjects for two-key experiments investigating concurrent schedules of reinforcement, as the two components of the concurrent schedule can be maximally independent of each other. It was noted that in this experiment, the subject chimpanzees operated the left key with their left hand and the right key with their right hand. The suggestion being that the switching behaviour seen with pigeons and rats, for example, during studies with concurrently available response keys, would be reduced with animals such as chimpanzees.

Generalized Matching Law (GML)

One of the characteristics of the behaviour of animals in choice situations is its orderliness and predictability. Specifically, the allocation of responses to an alternative, expressed in terms of the proportion of time or responses that are made to any one option, are made by the subject so as to match (approximately) the proportion of reinforcers that the experimenter arranges to come for that alternative. This event, strict matching, was described in a mathematical expression known as the matching law by Herrnstein (1961). However, further research showed the law to be an oversimplification. Baum (1979) found three ways that the results of choice experiments deviated from strict matching. When a regression line is fitted to log ratio data in the case of perfect matching relative rates of responding match relative reinforcement frequencies and yield a line with a slope (a) of 1 and a y-intercept ($\log c$) of 0. The slope of the line, a , is interpreted as the sensitivity of relative responding to relative reinforcement. Undermatching occurs when response proportions are consistently less extreme than reinforcement proportions (i.e. less responding to the alternative with the greater reinforcement frequency than predicted by strict matching). When a is less than 1.0 undermatching has occurred. When a is greater

than 1.0 then overmatching has occurred which indicates that more responding to the alternative with the greater reinforcement frequency than predicted has occurred, but this is rare. The third type of deviation from matching is bias. This is where a subject consistently spends more time or allocates more responses to one alternative, over and above any reinforcement-rate differences. This can be due to the subject favouring one response over the other or perhaps the quality of one reinforcer over the other. Once again using a regression line for analysis, if bias is present the line intercepts $y \neq 0$ and shows which response is preferred. This bias can be inherent (log b) such as in the case of a side preference for example, or an experimentally arranged bias, (log q) such as when qualitatively or quantitatively different reinforcers are arranged on two alternatives (Matthews & Temple, 1979).

To take into consideration these deviations, the generalized matching law (GML) incorporates values of sensitivity and bias into the linear equation (Baum, 1979). The equation relates the logarithm of response ratio B_1/B_2 as a function of reinforcement ratio r_1/r_2 . Based on natural logarithms, a line fitted to such data has the equation -

$$\ln (B_1 / B_2) = a \ln (r_1 / r_2) + \ln c \quad (1)$$

where B represents the behaviour (responses or time allocation) devoted to alternatives, r represents the rate of reinforcement obtained on each alternative, and a , the sensitivity of reinforcement, is the slope and $\log c$, the bias, is the intercept, which are arrived at empirically. Experimental data have been found to conform to this equation and typical values for sensitivity to changes in reinforcement rate, a , have been shown to be around 0.8 (Baum, 1979).

Through the application of concurrent schedules and the GML, animals' preferences for various commodities have been able to be quantitatively measured, and further to this, ranked. Since its formulation the GML has been shown to describe preference across a variety of species, responses and reinforcers. Studies have successfully demonstrated how amount, delay, and probability of reinforcement in concurrent contingencies affect preference.

Quantitative assessment of preferences of a range of species for a range of variables has been possible. Such as with rats (e.g., Baum, 1976), pigeons (e.g., Hunter & Davison, 1978), domestic hens (e.g., Sumpter, Temple & Foster, 1998; Temple, Scown & Foster, 1995), cows (e.g., Foster, Temple, Robertson, Nair & Poling, 1996; Matthews & Temple, 1979), horses (Krawczel, Friend & Johnson &

2006) and primates (e.g., Iglauer & Woods, 1974). Preferences have been assessed with different response types such as lever pressing, (e.g., Iglauer & Woods, 1974), key pecking (e.g., Hutton, Gardner & Lewis, 1978), and button pressing (e.g., (nose plate) Matthews & Temple, 1979). (Response topography will be discussed more fully further on in this document). Studies have utilized different reinforcers such as food (e.g., Matthews & Temple, 1979), shock avoidance (e.g., Hutton, Gardner & Lewis, 1978) drugs (e.g., Iglauer & Woods, 1974) and between drugs and food (Anderson, Velkey & Woolverton, 2002).

Benefits and Limitations of Preference Procedures

Previous research utilizing preference procedures has been able to provide some useful information about animal preferences for environmental resources. However, preference procedures do have both positive and negative aspects in regard to both their implementation and to the information they provide. These should be considered in undertaking research utilizing the procedures and interpreting data from such research.

Both the free access and T-maze preference procedures have the advantage of being relatively easy to undertake, they require relatively simple responses from subjects (such as moving to one environment) and assessment of the animal's choice is seemingly straightforward. However, free access and T-maze procedures also have disadvantages. With free access the proportion of time a subject spends in an environment or with an item is not necessarily a good measure of its importance. It is possible for it to be valuable but require little associated time allocation. With a T-maze procedure the latencies are often too variable to be able to interpret concisely. Also the procedure is often used to give group measures of preference which do not necessarily represent individual preferences.

In general, preference procedures have been criticised because they may present the animal with a choice between sub-optimal conditions with the lesser of the evils being chosen (Duncan, 1991). They provide only relative information and not anything about what would be ideal for the animal under assessment. A different criticism of preference procedures is that forced-choice tests may reflect only short term needs (Duncan, 1991) and are context specific (Bateson, 2004). Animal's preferences are not static but vary according to the specific internal and external conditions that each individual is exposed to over time. As Dawkins (1990) states

“short-term choices made in response to an immediate need may not reflect the animal’s long-term preference” (p60). In addition, what is preferred is also not always what is in the animal’s best long-term welfare interests (Bateson, 2004; Fritz, Nash, Alford & Bowen, 1992). Chimpanzees, for example, prefer to eat fruit over any other food but if they were to eat a diet solely based on fruit they may get chronic diarrhoea and die (as has happened) (Appleby, 1997). In addition to this, an animal’s previous experience can affect their preference and lead them to choose an alternative that is not in the best interests of their welfare. If you raise a chicken in a tiny, barren cage, it may initially choose an environment similar to that cage when allowed to choose. That situation is what it is used to and has come to accept (Dawkins, 1977). The novelty of a new enclosure may affect animals positively or negatively on their first encounter.

Research which undertakes to employ these preference procedures clearly needs to take into consideration these criticisms and limitations in the interpretation of resulting data. The interpretation of the results for the preference study in this present research will do just that.

Preference Testing with Non-Human Primates

Primates have been used as subjects in preference testing and many studies have used enrichment items as the environmental resources for the animals to choose between. Different primate groups have shown preference for particular types of enrichment items when given free access to them when the items were presented simultaneously. The combination of a manipulable object with food was shown to lead to increased object use and preference for the enrichment item (Crockett et al., 1989; Tripp, 1985). Sanz et al. (1999) found that presenting a variety of temporary and semi permanent objects into a chimpanzee enclosure revealed their preference for two semi-permanent objects, both of which increased the vertical complexity of the enclosure. Others studies have shown chimpanzees’ preferences for destructible items (e.g., Brent & Stone, 1998; Pruetz and Bloomsmith, 1992; Shefferly et al., 1993). An explanation for this preference is that animals are more responsive to novel stimuli and because as destructible items constantly change, they remain novel (Reinhardt, 1997). Conducting preference testing via the simultaneous presentation of items has been cautioned by researchers such as Kirkden and Pajors (2006). They observed that presenting resources concurrently is often inadvisable as the

availability of one resource may influence the value of another. As will be discussed, this present research considered such a view and during the preference procedure presented the items independently, rather than simultaneously, to the chimpanzee group.

Preference Testing in Social Housing

Although most preference testing has employed single-subject design animal choice, in the form of free access, has been used in settings in which animals have been housed collectively. Patterson-Kane (2002) used a T-maze to test rats' preference for cage size in a laboratory setting. They were tested once alone and then again when they shared the test with four other familiar conspecifics. Therefore an assessment of a rat's preference for a larger cage could be made as well as assessing if this preference was altered by social contact. The results were that the rats showed a preference for a larger cage and that this preference was of similar strength in the presence of cage mates. Fernandez, Dorey, and Rosales-Ruiz (2004) also tested preference for a number of different foods in a social group of five cotton-top tamarins (*Saguinus Oedipus*). Although there was a food preference shown by the group data, individual preference showed great variance.

Although during sessions, subjects were not socially housed (or an exploration of preference), Hare and Tomasello (2004) found that chimpanzees learn to perform cognitive tasks - object choice and discrimination - better in a socially competitive setting than in a socially cooperative environment. In this experiment a human 'informant' either acted as a 'competitor' or a 'cooperator'. As a competitor the experimenter also had access to a food reinforcer and used intimidating behaviour towards the chimpanzee. However, as the co-operator the experimenter made encouraging noises and did not consume the food reward. The experiment was repeated but with another chimpanzee as the 'competitor' or 'cooperator'. It was shown that when the competition was with a conspecific the discrimination task was further facilitated. These findings would suggest that the interpretation of the results of preference testing conducted in a social setting with chimpanzees, such as was the case for this current research, need to take into consideration social facilitation of behaviour.

Preference Testing Out of the Lab and with Groups

Baum (1974) reported that choice studies conducted in laboratory conditions had produced very different findings from animals behaving in natural situations. To explore if the matching law could be applied to behaviour outside of the specific and highly artificial conditions found in laboratories, he explored choice with a flock of free-ranging pigeons. Therefore this study also utilised group behaviour rather than isolated individuals. The flock of birds came and went freely from a house's attic space, in which the experimental equipment was set up. The birds were trained to peck response keys and their behaviour was reinforced by the delivery of a hopper of grain. Only one pigeon at a time could operate the equipment. This was controlled by restricting the size of the perch in front of the response keys. Baum did not include any changeover delay contingency in the procedure, preventing reinforcement for a period following a change of keys, noting that this increased the natural nature of the research. The group results showed the ratio of pecks approximately equalled the ratio of reinforcements, in accordance with the matching law. A small bias was shown in favour of one key (the left). Baum noted that, due to the amount of grain that was consumed, multiple pigeons must have contributed to the results (10-20 pigeons). Baum concluded that these results from a natural environment strengthened the argument for a basic property of behaviour.

Group choice has also been explored in research pertaining to ideal free distribution theory, with free-ranging flocks of pigeons (e.g., Baum & Kraft 1998) and sparrows (*Passer domesticus*) (e.g., Grey, 1994). Similar to the matching law, this theory predicts that the equilibrium ratio of animals distributed between foraging sites will match the food input ratio. Rather than responses, behaviour was examined by the distribution of animals between different areas containing food reinforcement. Grey (1994) utilized a flock of six sparrows and found their behaviour showed undermatching between group choice and overall reinforcement, and similar undermatching between individual choice and relative reinforcement. However, the results did show a difference in the results for individuals' choices. Grey noted that a high level of agonistic interactions occurred between members of the group and this may have contributed to the undermatching and stressed the importance of social constraints in such research. Baum and Kraft's (1998) research, with a flock of around 30 pigeons, did not show any consistency in preference, either across or within individual birds' behaviour suggesting that the group results were an

‘emergent phenomenon’. Although they did observe that individual subject participation was constant between sessions. They also suggested that perhaps the relatively small number of subjects in Gray’s study allowed for the individual preferences to be expressed.

The preference research that has employed social-group testing has shown that although multiple subjects have contributed to the results the data have been interpretable and provided useful information. Some data have revealed differences in responding for individual members of the group. These findings are of relevance to this current research as it undertook to test preferences of a group of chimpanzees for different enrichment items and also to explore how preferences of individuals within the group for enrichment items related to the findings for the group.

Application for This Research

Much preference research with animals has employed a design based on simultaneously available commodities. This form was considered for this current research. However, a decision was made to provide the commodities independently within sessions, gather information for use across these sessions and then to compare the group’s preference for items. The enrichment items intended to be included in this current research were vastly different in their form and the form of reinforcement they presented the chimpanzees. Having two items concurrently available that were so different was judged to be less than optimal. As shown in Experiment 2, the group used the items that contained a foraging component far more than those that did not. Having each enrichment item available independently was judged to be preferable. This decision was supported by Kirkden and Pajor’s (2006) view that presenting resources concurrently may influence the apparent value of multiple items. As the chimpanzees in this current research were tested within their usual housing environment the group’s preference for the enrichment items presented singly was judged in comparison with activities and resources that the chimpanzees normally had available.

Also, given that this testing was to be done in a group setting, there was the possibility that the more dominant animals would use the more preferred item, while the more subordinate animals accessed the item that was preferred less when two items were presented concurrently. This would have shown a difference in use, in terms of individuals using items, but in general the results of use would have been

confounded. In addition to these points, if the enrichment items were to be presented concurrently there would have been practical implications. The experimental area would have needed to have been increased in size with a further barred panel being used. This would have required that half of one of the walls of the Covered Area would have been covered in experimental equipment. This was not desirable for the facility, as it would have: hampered access to the chimpanzees while they were in this area, increased hygiene issues and been far more noticeable to the visiting public of the zoo (the public viewing area directly faced the experimental area). Taking these issues into consideration formed the basis for the decision to present the enrichment items independently in experimental sessions with the chimpanzee group.

Aim

The experimenter had previously established the suitability of the experimental set-up and enrichment items' design and construction and that the chimpanzee group interacted with the items (i.e., previous experiments of this current research). The purpose of this study was to assess the chimpanzee group's behaviour when given free access to the enrichment items. Specifically the amount and type of activity the chimpanzees exhibited when the enrichment items were available freely (no work required to gain access to enrichments) over the entire three hour session was assessed.

Method

Subjects

The full chimpanzee group as shown in Table 1.1 was utilised, with the exception of Mahinga (d. 20/3/05) and Bahati (d. 22/10/05) and the infant born (15/10/03) to Cara which was euthanized prior the second experiment of this current research. Sally gave birth to a baby in between Experiment 2 and 3 of this current research (16/7/05) but she suffered a prolapsed uterus during the birth and rejected the infant over the following days. Due to the zoo policy not to hand raise any Great Apes this infant was euthanized. Paternity for this infant was not established.

Study's Impact on Standard Husbandry Protocol

The procedures applied in this experiment had no impact on standard

husbandry protocol for the chimpanzees as outlined in Experiment 1.

Ethical Consent

The procedure and equipment used within this experiment were approved by the Director-General of MAF via the National Animal Ethics Advisory Committee in accordance with the Animal Welfare Act 1999 concerning restrictions on the use of non-human hominids, the University of Waikato Animal Ethics Committee and the Wellington Zoo.

Apparatus and Setting

The apparatus used in Experiment 3 is described in Experiment 2 and shown in Figures 2.8 to 2.17 and 2.25 to 2.28. The setting for Experiment 3 is indicated in Figure 1.1 and described in Experiment 2 and shown in Figures 2.4 to 2.6.

Procedure

The study was conducted from October 2005 until May 2006. The Free Access study and the Demand studies of this current research (Experiment 3, 5 and 6) were run during New Zealand Daylight Savings periods (but in different years) so that the change in day light hours would be relatively minimal. The whole research was on a set deadline as the chimpanzees were scheduled to move to a new indoor facility. The area in which the research was based was therefore no longer going to be used. The deadline for this move was October 2006.

A video camera was positioned above where the enrichments were to be placed later. Sessions ran for three hours - beginning at 1700 and terminating at 2000 (as the chimpanzees came in at about 1630 and it gave some time for dinner consumption). A flood light, operated by a timer, was on in the research area during the experimental sessions.

A Baseline session was conducted before a series of sessions with each different enrichment item. A Baseline session involved recording video footage for the three hour session. Under baseline conditions there were no enrichments in place on the experimental panel. The lever was present but had 62.37 kg of weight hung on it which made it effectively inoperable for the chimpanzees (as previously discussed). The operation light on the lever unit stayed off the entire time during Experiment 3.

After the baseline period one enrichment item was provided per session (put in place during the day while the chimpanzees were out of the indoor enclosure). The experimental equipment was mounted on the wall of bars in the Covered Area section of the chimpanzees' enclosure and was accessible to the chimpanzees from within their enclosure and to the researcher from outside of the entire enclosure. Again, the lever was present but had 62.37 kg of weight hung on it which made it effectively inoperable for the chimpanzees (as previously discussed).

Table 3.1

Enrichment items in order of use for Experiment 3 and enrichment item operation details.

| Enrichment Item | Operation Details |
|--|---|
| Musicbox | Able to produce notes for 3 hours. |
| Dipper | Had the internal barrier removed for free access to the food. |
| TV/Video | TV and video remained on for 3 hours playing a continuous video (no repeats). |
| Marbleroll Delivering Coated Peanuts | Released a coated peanut every 150 seconds. The slides on the Marbleroll were removed so the chimpanzees had nothing to operate. |
| Screwfeeder | Turned every 2 minutes for 2 seconds (approximately a quarter turn) and delivered a small amount of sunflower seeds (approximately 20g). |
| Marbleroll | Released a marble or occasionally a Jaffa™ every 150 seconds (set so that no more than 10 Jaffas™ an hour were released). The slides on the Marbleroll were removed so the chimpanzees had nothing to operate. |
| Marbleroll | Released a marble or occasionally a Jaffa™ every 150 seconds (set so that no more than 10 Jaffas™ an hour were released). The slides on the Marbleroll were in place so the chimpanzees were able to control the progress of the items. Automatic cleanup operated to move any marbles that may have been left. |

The enrichment items (as seen in Figures 2.10 to 2.17 and 2.25 to 2.28) were provided in the order shown in Table 3.1, which also shows detail of the operation of the enrichment item during this experiment. Each enrichment item stayed in place for five three hour sessions, and on completion of those, a Baseline session was conducted and then the next enrichment was put in place and so on, until all of the enrichment items had been offered to the chimpanzees on a free access basis.

Operation of Enrichments

During Experiment 3 experimental events within the sessions were controlled by a computer programme and the internally housed computer unit. The computer and enrichments were controlled by MEDPC-IV software and interfaces. Programmes were written for the experimental phase and for each particular enrichment item during that phase.

Access to Enrichment Items

The research was conducted in a closed economy so none of the components of the enrichment items were available from other sources outside of the research.

Data Collection

Video Recordings and Behavioural Definitions

During the Experiment 3 each experimental session was recorded as described in Experiment 2 and individual chimpanzee's behaviour (as categorized in Table 2.2) recorded as described in Experiment 2. Behaviours of particular note by individuals were also recorded. The area within view of the video recording was 5 m deep, 2 m across and 2 m in height. The time at which there ceased to be any day light (sunset time) and the general weather conditions for the day were also noted.

Reliability. Within-observer reliability was assessed for Experiment 3 in the same way it was described in Experiment 2. At the beginning of Experiment 3, within-observer reliability was 96.17%. Near the end of Experiment 3 within-observer reliability was 97.46%.

Data Analysis

Analysis of Video Data

The video recordings collected during Experiments 3 were analysed and provided data on total time of group behaviour and then for details of total time of individuals' behaviour, thereby enabling comparisons across conditions and across enrichments.

Results

The data analysed here were based on the time any chimpanzee was within the observation area and recorded to be so. Definitions for the recorded behaviour are described in Table 2.2. The data are presented as behavioural category totals for each experimental condition. Details of data for each experimental session are presented in Appendix C. When a chimpanzee was observed to be present in the experimental area but their identity could not be ascertained their behaviour was recorded and classed under "Unknown" individual. As this did not occur often (less than 1% of behavioural recordings the results are not shown in the figures. Scales on the Figures in this and other experiments are the same to allow for comparisons.

Throughout the results of this study Figures will utilise symbols where: B is Baseline; MB is Musicbox enrichment; D is Dipper enrichment; SF is Screwfeeder enrichment; TV is TV/Video enrichment; MR (no s) is Marbleroll enrichment - delivering marbles and Jaffas™, without slides; MR (+s) is Marbleroll enrichment - delivering marbles and Jaffas™, with slides; MR (p) is Marbleroll enrichment, delivering coated peanuts.

Group Behaviour

The chimpanzee group's overall behavioural data totals for each experimental session in Experiment 3 are presented in Table 3.2 and Figures 3.1 to 3.15. As shown across sessions, when an enrichment item was present and those in which one was not (Baseline sessions) the total amount of time the group spent in the experimental area simply present but not interacting in any way 'Just in area' remained at a similar level across all sessions. Temperature and seasonal changes in the behaviour of apes has previously been evidenced both in captivity and the wild (Stoinski et. al., 2004; Vivian, 2001). However, during this experiment behaviour was not shown to vary greatly in association with weather conditions. This may have been due in part to the

indoor/outdoor nature of the experimental setting.

Group Behaviour Related to Enrichment Items

Table 3.2 and Figures 3.1 to 3.15 show the chimpanzee group's total time spent in each behaviour relating to each enrichment item across sessions for Experiment 3.

Table 3.2

Chimpanzee group behaviour (as defined in Table 2.2) during Free Access study. The amount of time (min) in each session the group exhibited each behaviour and the sun set time, temperature and general weather conditions during each session.

| Session Condition | Time Spent Exhibiting Class of Behaviour (min) | | | | | | | Time of First Interaction (min) | Subject First Interacted | Sunset Time | Weather | Temp at 1700hrs |
|-----------------------------|--|----------------------|------------------|-------------------|-------------------------|--------------------|--------------|---------------------------------|--------------------------|-------------|---------|-----------------|
| | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in Area | | | | | |
| | | | | | | | | | | | | |
| Baseline | NA | NA | NA | NA | NA | NA | 8.52 | NA | NA | 1945 | Fine | 15 |
| Musicbox | 14.05 | 0.38 | 0.30 | 0.00 | 0.00 | 0.72 | 21.12 | 1.03 | Keza | 1946 | Fine | 16 |
| Musicbox | 1.05 | 0.00 | 0.00 | 0.42 | 0.00 | 0.00 | 17.08 | 43.00 | Temba | 1947 | Rain | 14 |
| Musicbox | 0.35 | 0.10 | 0.00 | 0.00 | 0.00 | 0.10 | 11.20 | 15.43 | Keza | 1948 | Rain | 11 |
| Musicbox | 0.00 | 0.00 | 0.00 | 0.05 | 0.00 | 0.00 | 2.23 | NA | NA | 1949 | Rain | 12 |
| Musicbox | 1.58 | 0.00 | 0.00 | 0.03 | 0.00 | 0.00 | 25.07 | 8.27 | Keza | 1950 | Fine | 15 |
| Baseline | NA | NA | NA | NA | NA | NA | 10.50 | NA | NA | 1951 | Rain | 15 |
| Dipper | 90.25 | 26.15 | 13.67 | 0.17 | 0.05 | 29.18 | 10.43 | 2.43 | Jess | 1953 | Fine | 16 |
| Dipper | 9.78 | 3.47 | 0.00 | 4.70 | 0.25 | 1.80 | 20.23 | 6.23 | Chima | 1954 | Fine | 17 |
| Dipper | 33.47 | 6.32 | 7.37 | 1.47 | 0.20 | 7.37 | 11.55 | 23.27 | Chima | 1955 | Fine | 18 |
| Dipper | 12.72 | 2.82 | 0.00 | 0.22 | 0.00 | 2.82 | 5.72 | 6.35 | Keza | 1956 | Fine | 18 |
| Dipper | 4.42 | 0.00 | 0.00 | 0.15 | 0.00 | 0.00 | 27.15 | 8.28 | Temba | 1957 | Fine | 19 |
| Baseline | NA | NA | NA | NA | NA | NA | 29.87 | NA | NA | 2024 | Cloudy | 17 |
| Screwfeeder | 12.67 | 0.00 | 0.00 | 0.32 | 0.00 | 0.00 | 13.70 | 4.55 | Samantha | 2026 | Rain | 18 |
| Screwfeeder | 59.80 | 0.77 | 27.40 | 0.42 | 0.00 | 0.77 | 3.67 | 0.00 | Jess | 2027 | Rain | 13 |
| Screwfeeder | 98.87 | 4.47 | 53.63 | 0.00 | 0.00 | 8.78 | 22.80 | 0.10 | Jess | 2028 | Rain | 18 |
| Screwfeeder | 57.87 | 1.53 | 1.53 | 0.13 | 0.00 | 1.53 | 11.37 | 4.10 | Keza | 2029 | Rain | 14 |
| Screwfeeder | 55.73 | 0.23 | 24.15 | 0.37 | 0.00 | 0.23 | 30.17 | 4.20 | Keza | 2030 | Rain | 13 |
| Baseline | NA | NA | NA | NA | NA | NA | 7.83 | NA | NA | 2031 | Rain | 12 |
| TV | 12.63 | 0.00 | 3.93 | 0.00 | 0.00 | 0.00 | 6.62 | 0.00 | Temba | 2033 | Rain | 13 |
| TV | 2.75 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 5.75 | 1.22 | Marty | 2034 | Rain | 13 |
| TV | 3.73 | 0.00 | 1.57 | 0.00 | 0.00 | 0.00 | 8.55 | 12.12 | Chima | 2035 | Cloudy | 13 |
| TV | 6.08 | 0.00 | 0.40 | 0.00 | 0.00 | 0.00 | 9.13 | 8.30 | Temba | 2036 | Fine | 15 |
| TV | 4.22 | 0.00 | 3.10 | 0.00 | 0.00 | 0.00 | 9.65 | 10.43 | Keza | 2037 | Fine | 16 |
| Baseline | NA | NA | NA | NA | NA | NA | 7.22 | NA | NA | 2041 | Rain | 21 |
| Marbleroll (without slides) | 32.28 | 6.72 | 18.03 | 12.80 | 7.03 | 6.77 | 92.15 | 0.40 | Boyd | 2042 | Rain | 19 |
| Marbleroll (without slides) | 20.60 | 1.93 | 1.93 | 4.82 | 0.00 | 1.93 | 6.13 | 0.82 | Keza | 2043 | Cloudy | 17 |
| Marbleroll (without slides) | 26.98 | 1.37 | 9.77 | 14.73 | 0.90 | 1.37 | 17.67 | 3.28 | Keza | 2044 | Fine | 18 |
| Marbleroll (without slides) | 24.63 | 0.38 | 5.43 | 7.88 | 0.43 | 0.38 | 7.80 | 2.07 | Temba | 2045 | Rain | 19 |
| Marbleroll (without slides) | 19.78 | 0.23 | 4.07 | 5.97 | 0.63 | 0.23 | 4.78 | 3.63 | Keza | 2046 | Rain | 17 |
| Baseline | NA | NA | NA | NA | NA | NA | 1.68 | NA | NA | 1808 | Rain | 19 |
| Marbleroll (with slides) | 9.95 | 6.07 | 22.73 | 1.13 | 0.23 | 6.07 | 2.82 | 0.10 | Keza | 1807 | Rain | 19 |
| Marbleroll (with slides) | 12.70 | 4.30 | 7.80 | 2.88 | 0.50 | 4.30 | 6.28 | 7.97 | Chima | 1806 | Cloudy | 17 |
| Marbleroll (with slides) | 10.82 | 1.22 | 5.63 | 1.55 | 0.13 | 1.22 | 9.87 | 4.05 | Keza | 1805 | Fine | 15 |
| Marbleroll (with slides) | 9.03 | 0.87 | 2.10 | 0.68 | 1.97 | 0.87 | 4.48 | 4.48 | Keza | 1803 | Rain | 18 |
| Marbleroll (with slides) | 6.72 | 0.72 | 1.03 | 1.37 | 0.73 | 0.72 | 3.85 | 1.95 | Jess | 1801 | Rain | 17 |
| Baseline | NA | NA | NA | NA | NA | NA | 2.77 | NA | NA | 1727 | Rain | 14 |
| Marbleroll (peanut) | 13.55 | 1.07 | 24.60 | 0.62 | 0.00 | 1.07 | 13.15 | 0.62 | Jess | 1726 | Cloudy | 14 |
| Marbleroll (peanut) | 6.43 | 1.32 | 16.47 | 0.82 | 0.00 | 1.32 | 6.43 | 1.13 | Keza | 1725 | Rain | 13 |
| Marbleroll (peanut) | 16.40 | 2.13 | 20.38 | 0.27 | 0.13 | 2.13 | 10.73 | 2.47 | Chima | 1724 | Cloudy | 14 |
| Marbleroll (peanut) | 7.88 | 0.72 | 8.87 | 0.97 | 0.00 | 0.72 | 4.02 | 1.43 | Temba | 1723 | Rain | 13 |
| Marbleroll (peanut) | 9.25 | 2.80 | 11.95 | 0.57 | 0.00 | 0.47 | 8.87 | 0.80 | Keza | 1721 | Cloudy | 14 |

Musicbox Enrichment

As shown in Table 3.2 and Figure 3.1 the maximum amount of time the Musicbox was used in a session by the chimpanzee group (including using the item alone, using it when another member of the group was watching and using the item with another member of the group) was 14.73 min during the first session with this item. This total amount of usage time dropped dramatically after the first session with this enrichment. Over the following four sessions with this enrichment total usage was under two minutes. There was no interaction with the item in the fourth session.

The time the chimpanzee group spent within the experimental area (within view of the video camera) simply present but not interacting in any way with an enrichment item (Just in area) was greatly increased from the baseline session that preceded the sessions with the Musicbox enrichment. The exception to this was the fourth session with this item in which the chimpanzees spent very little time in the area (2.23min). The group spent a similar and minimal amount of time using this enrichment item while another individual observed this (Using – others watch), watching another individual using the item (Watching other use), using the item at the same time (Using-together) and orientated towards an item but not interacting both while alone (Attending-alone) and with another subject (Attending – accompanied).

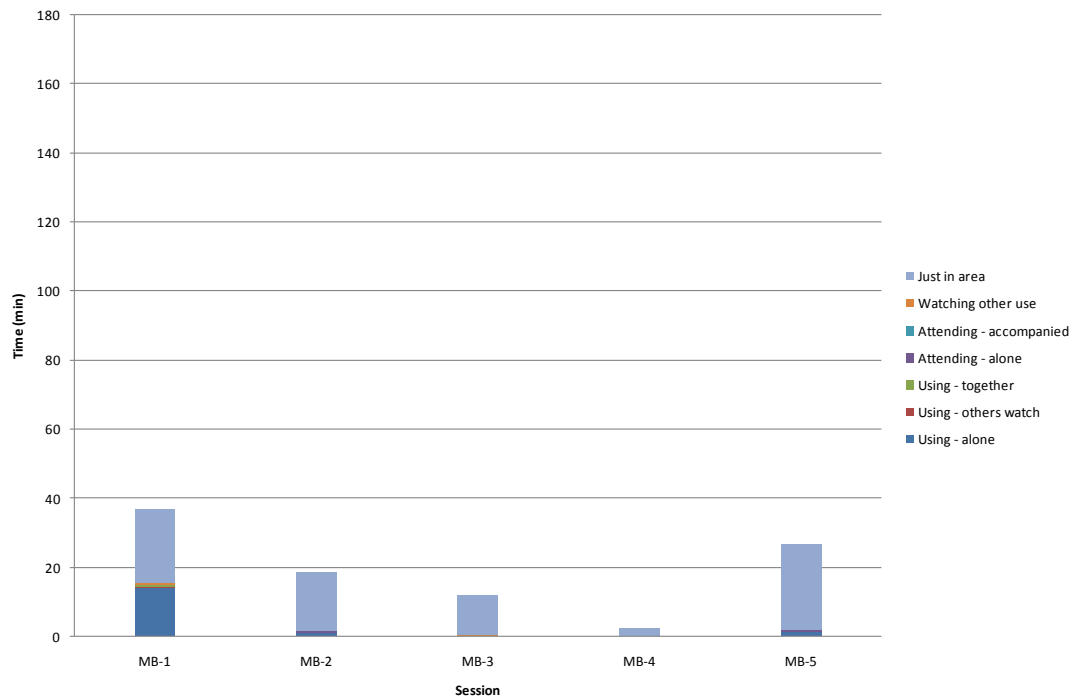


Figure 3.1. Total time that the chimpanzee group exhibited defined behaviours in experimental sessions of Experiment 3 with the Musicbox enrichment.

Dipper Enrichment

Table 3.2 and Figure 3.2 show that the Dipper enrichment was used for the most amount of time in a session by the chimpanzee group during the first session and for a total of 130.07min. The following four session saw a large drop in the total usage time to 13.15, 47.15 and 0.53 min, respectively. While the behaviour that the group exhibited most was using the enrichment item while alone, the other behaviour classes related to the enrichment item were observed. During the first session with the enrichment item, the individuals watched others use the item (and conversely used the item while others watched) and multiple subjects used the enrichment device together for substantial amounts of time. The total times for these behaviour classes dropped markedly in the following sessions.

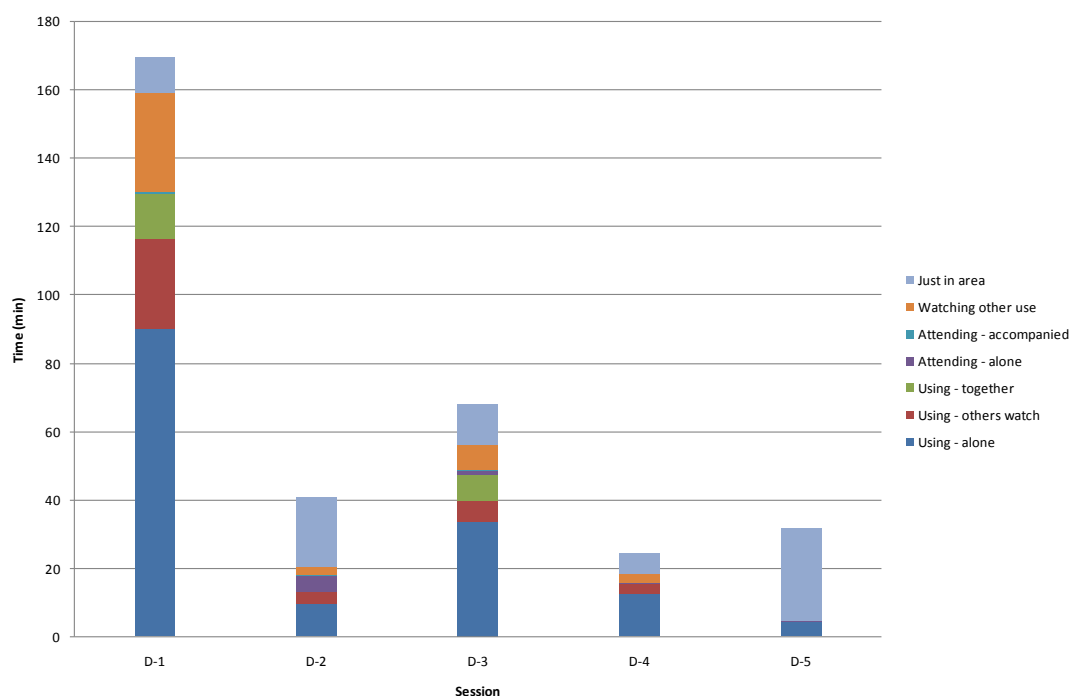


Figure 3.2. Total time that the chimpanzee group exhibited defined behaviours in experimental sessions of Experiment 3 with the Dipper enrichment.

Screwfeeder Enrichment

Table 3.2 and Figure 3.3 show that the first of the five sessions with the Screwfeeder was the one in which the group used the item the least (12.67 min). Usage of the item peaked during the third session, the total amount of time it was used on this day was 157 min (from a total session time of 180 min) and the fifth session saw the second highest level of use of the item. The majority of time spent using the item was an individual using the item while alone. However, during the third session, especially, the item was used by simultaneously by members of the group for a considerable amount of time (53.63 min).

TV/Video Enrichment

The chimpanzee group used the TV and video enrichment for a maximum total amount of time during the first session for 16.57 min, as shown in Table 3.2 and Figure 3.4. The total amount of time the item was used dropped away for the following four sessions and remained under ten minutes for all of these. Subjects' time interacting with this enrichment was predominantly spent using the item alone.

Given the nature of this enrichment it was never attended to alone or accompanied, nor used while others watched or another individual watched while they used it, as watching or attending was an interaction in its self.

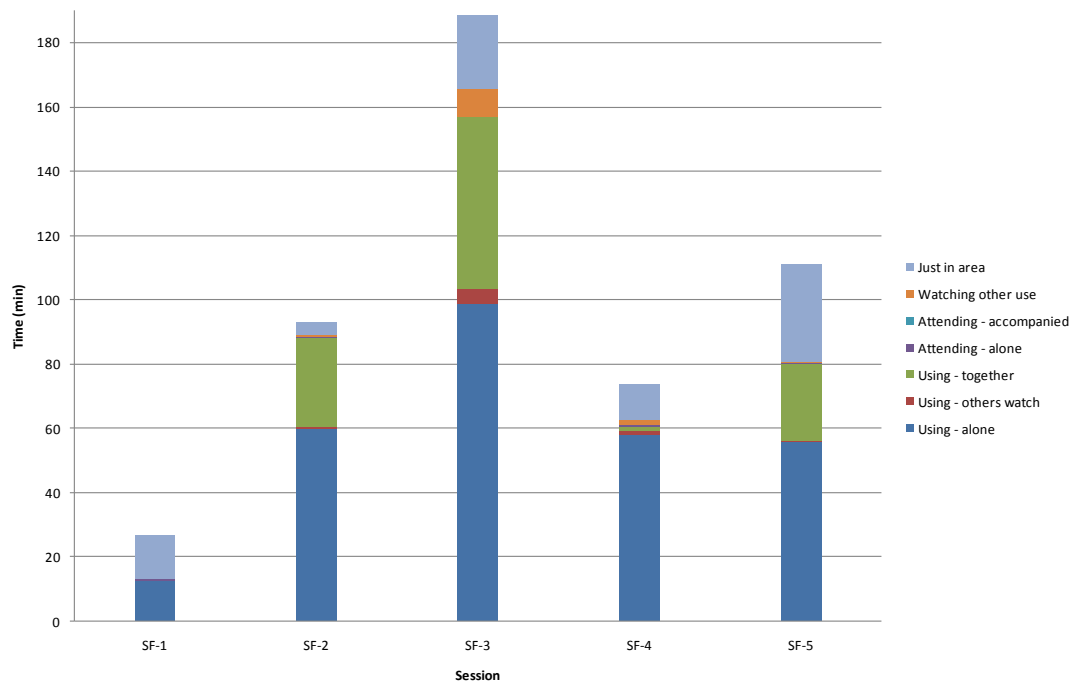


Figure 3.3. Total time that the chimpanzee group exhibited defined behaviours in experimental sessions of Experiment 3 with the Screwfeeder enrichment.

Marbleroll Enrichment - Delivering Marble and Jaffas™ (Without Slides)

The Marbleroll unit was initially set to deliver both Jaffas™ and marbles over the three hour sessions and no slides were in the unit. As Table 3.2 and Figure 3.5 show the enrichment item was used for 57.03 min in total (including using it alone, using it while others watched and using it with another member of the chimpanzee group) during the first session. This was the maximum the enrichment was used in a single session during the Free Access study. During this session, the chimpanzee group spent an exceptional amount of time in the experimental area not interacting with the enrichment item in any way. Usage time decreased in the following sessions and to 24.08 min in total at the fifth session. The time multiple members of the group spent using the enrichment item together decreased markedly from the first session.

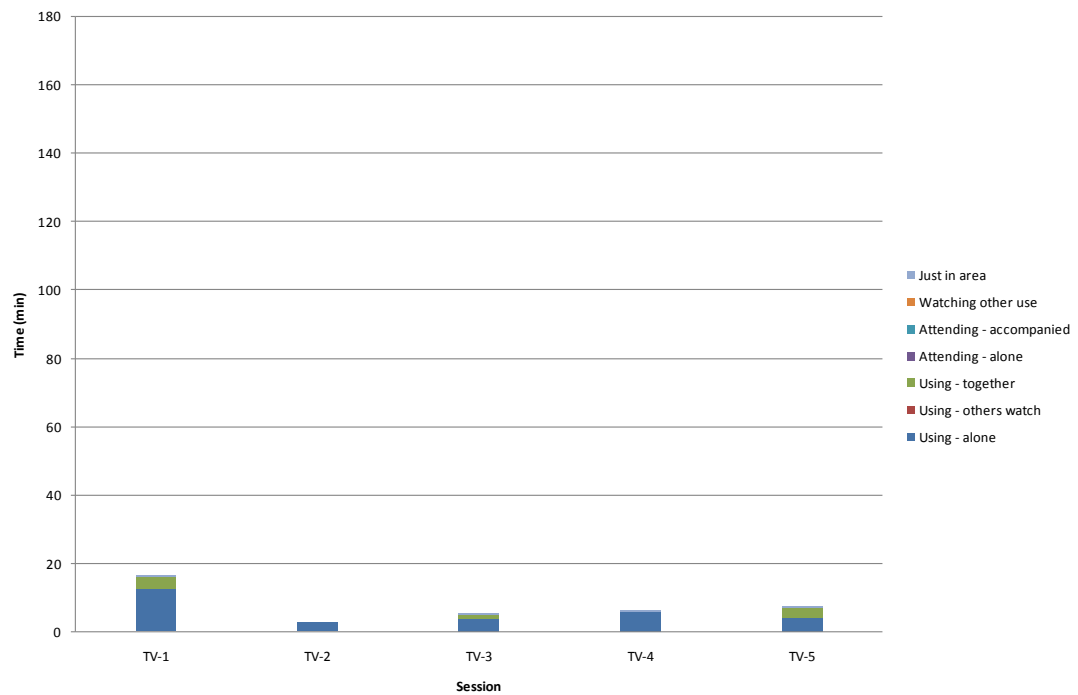


Figure 3.4. Total time that the chimpanzee group exhibited defined behaviours in experimental sessions of Experiment 3 with the TV/Video enrichment.

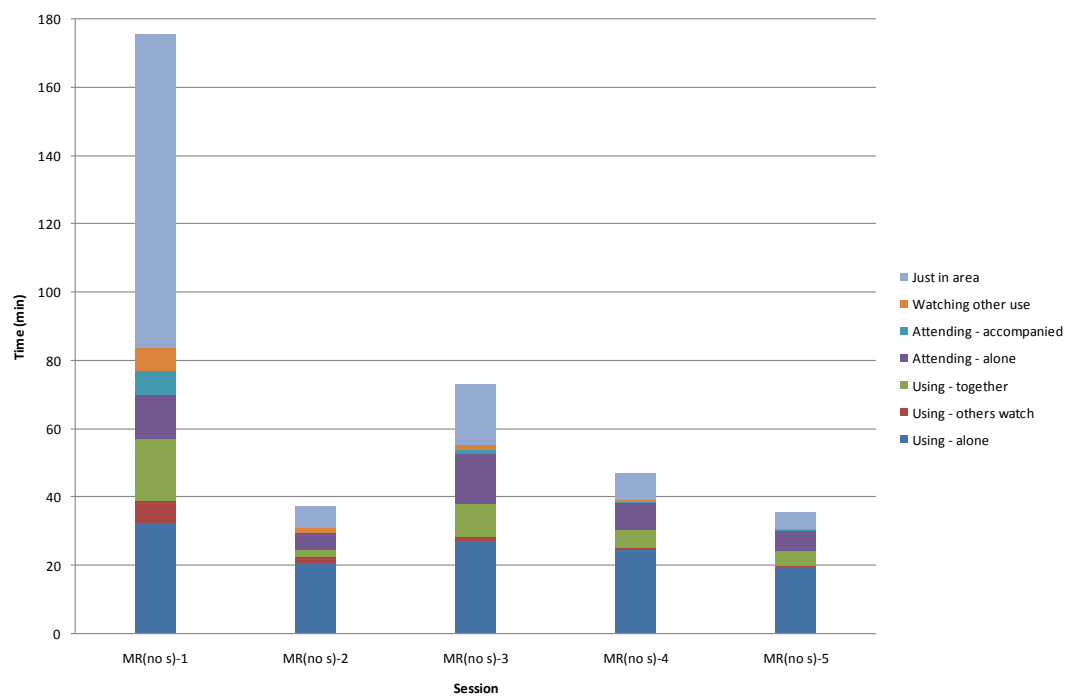


Figure 3.5. Total time that the chimpanzee group exhibited defined behaviours in experimental sessions of Experiment 3 with the Marbleroll enrichment, when no slides were present.

Marbleroll Enrichment - Delivering Marble and Jaffas™ (With Slides)

As Table 3.2 and Figure 3.6 show, the maximum length of time the Marbleroll unit was used in a session when the slides were put in place and the unit was delivering Jaffas™ and marbles was 38.75 min. This was during the first session. The total usage time decreased consecutively across the sessions to a low of 8.47 min by the fifth session. The amount of time members of the group spent using the enrichment item at the same time decreased markedly across the sessions.

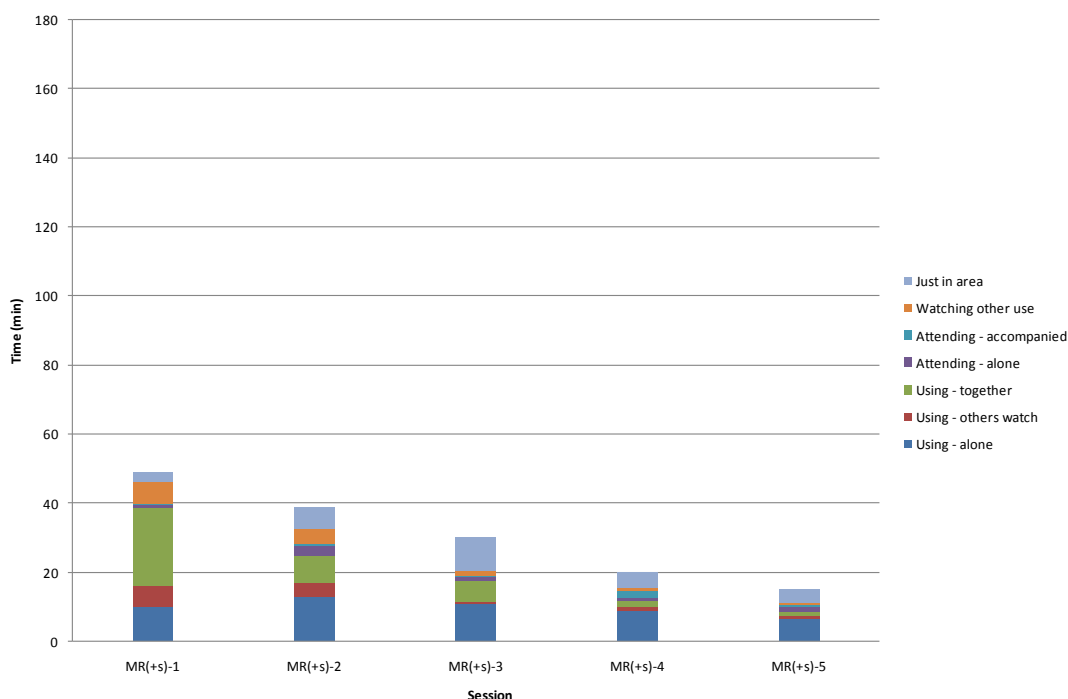


Figure 3.6. Total time that the chimpanzee group exhibited defined behaviours in experimental sessions of Experiment 3 with the Marbleroll enrichment when slides were present.

Marbleroll Enrichment – Delivering Coated Peanuts

When the Marbleroll enrichment was set to deliver covered peanuts the maximum total usage time occurred during the third session and was 38.92 min, as shown in Table 3.2 and Figure 3.7. The least amount of total usage time was during the fourth session and was 17.47 min. Members of the group spent more time using the enrichment item together than they did using it individually.

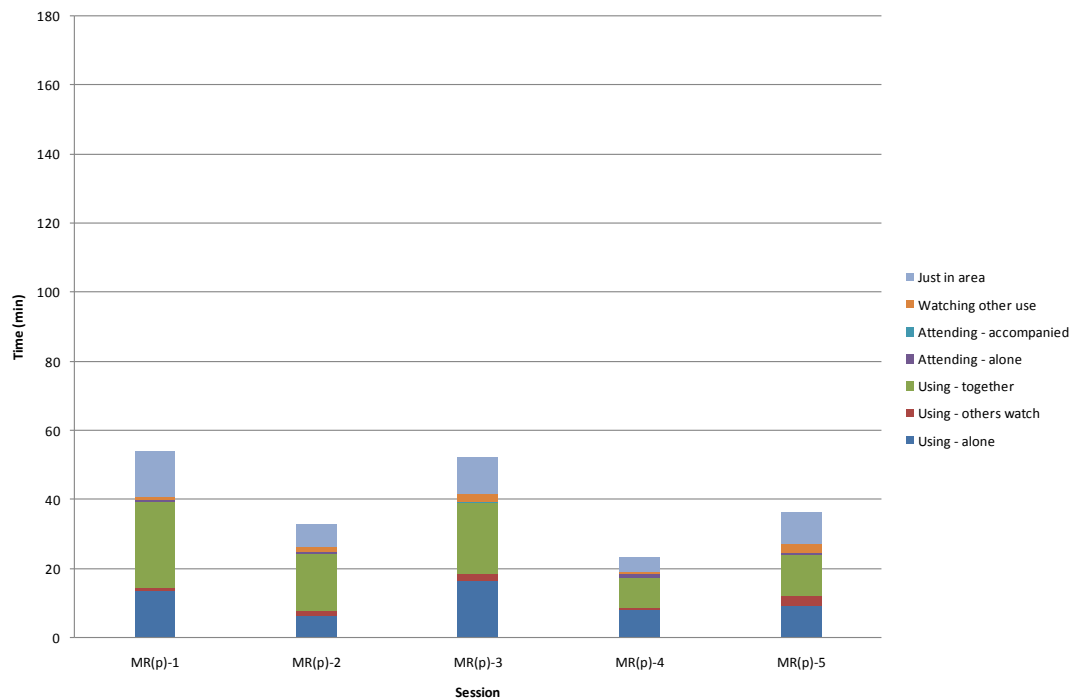


Figure 3.7. Total time that the chimpanzee group exhibited defined behaviours in experimental sessions of Experiment 3 with the Marbleroll enrichment when it was delivering coated peanuts.

Group Behaviour Between Enrichments

Overall, of the seven enrichment item conditions with the chimpanzee group the greatest amount of total time the group spent interacting with an item (using alone, using with another member or using while another member watched) was 157 min spent with the Screwfeeder (during the third session with this enrichment). When total usage was added across all the sessions the Screwfeeder was used most often of all of the enrichments (398.65 min). The Musicbox enrichment was used the least in total (17.82 min) across all the sessions.

Group Use Event Records

Data for the chimpanzee group were analysed to examine each individual's use behaviour associated with the enrichment items (including behavioural classes: Using-alone, Using-others watch, Using-together). The event records were constructed as described in Experiment 2: Part 1. In this experiment the time of

delivery of a reinforcer is also indicated on the figures.

Musicbox enrichment. Figures 3.8a to 3.8e show the earliest first interaction time with this enrichment item was during the first session. Also, during this session the chimpanzee group used the item the most frequently, for the greatest amount of time and it was used by the greatest number of individuals in the group. The periods of use of the item were brief, typically lasting for less than one minute. Adult females Cara and Sally were the only members of the group not to use the item for some time during the sessions. However, many members of the group used the item only during the first session. During subsequent sessions the subjects that did use the item did so on only a few occasions. Female juvenile Keza interacted with the Musicbox for the greatest length of time. Keza and adolescent male Temba were the individuals, in all sessions in which the Musicbox was used, to have the first interaction with it. No apparent pattern of use was obvious relating to each individual's age and sex. The item was used by the group into the second hour of the first session. However, in two of the other three sessions in which the item was used, this use occurred only during the first hour of the sessions.

Dipper enrichment. Figures 3.9a to 3.9e show that the first interaction with the Dipper was earliest in the first session the group had with the Dipper enrichment. Jess, Chima, Keza and Temba were all first to use the item during these sessions. The item was used by the group into the third hour of the first session with it. However, for three of the other four sessions the group used the item only during the first hour of the sessions. Periods of use of the item varied from a few seconds up to 12.08 min, which was by adult female Jess. This subject used the item for the longest periods during all the sessions. Jess and juvenile male Alexis used the item almost continuously across the first session, up until the first half of the third hour of the session. They were the individuals to use the item the most frequently and with the highest frequency. However, aside from the first session, juvenile female Keza used the item the most. Adult female Cara was the only individual not to use the item during any of the sessions. Adult male Boyd and adult female Sally used the item for only a short period during the experimental sessions. More individuals used the item during the first session. Adult male subjects used the item only during the first hour of sessions.

Screwfeeder enrichment. Figures 3.10a to 3.10e show that adult females Samantha and Jess and juvenile female Keza were the first to interact with the Screwfeeder enrichment during the sessions. The enrichment was used from the very beginning of the sessions, the earliest interactions were during session two (0 seconds) and session three (6 seconds) each time by Jess. The group's use continued in the second hour of all the sessions and during two sessions, into the third hour of the session. Periods of use varied from a few seconds to 15.85 min (by adult female Jess). Adult females Jess and Samantha, adult males Boyd and Marty, adolescent male Temba and adolescent female Chima and juvenile male Alexis and female Keza all used the item for periods greater than three minutes. All of the members of the chimpanzee group used the Screwfeeder during the Free Access sessions. Jess was the individual to use the item for the longest duration. Adult male Sam and adolescent male Gombe used the Screwfeeder the least across all sessions. No pattern of use was apparent in relation to age and sex of individuals.

TV/Video enrichment. The TV/Video enrichment was used by the chimpanzee group sporadically, mainly during the first hour of sessions, as shown in Figures 3.11a to 3.11e. All of the interactions lasted less than a minute. All of the individuals within the group interacted with the TV/Video enrichment at some time during these sessions. Adolescent male Temba, adult male Marty, adolescent female Chima and juvenile female Keza were first to interact with the item across sessions. Temba used the item the most frequently and for a longest time.

Behaviour of note was that Temba spent time watching the video footage of kittens, Alexis, Samantha and Keza all watched footage of a Sun Bear (*Helarctos malayanus*) (also held at Wellington Zoo), Samantha spent time watching a previous keeper of the chimpanzees, and Keza also spent time watching footage of a young child playing.

Marbleroll enrichment – Delivering marble and Jaffas™ (without slides). As Figures 3.12a to 3.12e show every member of the chimpanzee group interacted with the Marbleroll enrichment during all these sessions. The majority of the group used the item during the first half of the session. The exception to this was juvenile female Keza and male Alexis who continued to use the enrichment during the second half

(and after sunset). In fact, Keza used the item for almost the entire session length during the first session with it. Adult male Boyd, Keza, and adolescent male Temba were the first to interact with the item during these sessions. Keza was the individual to use the item the most frequently and for the greatest time, followed by Alexis. The others members of the group used the item considerably less than these two individuals. Most of the interactions lasted for less than a minute.

It was noted that this item was attended to frequently by individuals that sat a distance away and watched the marble or Jaffas™ come down the channels within the unit. Keza spent more time than most watching the marble ascend in the lift of the unit. When less dominant individuals such as Keza, Alexis, Temba and Chima received a Jaffa™ from the Marbleroll unit they moved away from the unit to consume the Jaffa™, in a very slow, deliberate fashion, splitting the sweet and looking inside and slowly sucking it.

Marbleroll enrichment – Delivering marble and Jaffas™ (with slides). In the sessions with Marbleroll, when the slides were present, all the members of the group used the item for some period, as shown in Figures 3.13a to 3.13e. Juvenile female Keza, adolescent female Chima and adult female Jess were the individuals to interact first in a session with this item. Keza was also the individual who used the item the most (both in frequency and duration) and who used it considerably more than the other members. Most use by the group occurred during the first half of each session. Most of the interactions lasted for less than a minute. Keza was the individual that was the last user in all of the sessions.

Marbleroll enrichment - delivering coated peanuts. All of the members of the chimpanzee group used the Marbleroll when it was delivering coated peanuts, as shown in Figures 3.14a to 3.14e, most on multiple occasions. Adult female Jess, juvenile female Keza, adolescent female Chima and adolescent male Temba were the individuals to first interact with this item during these sessions. Keza used the item for the longest time and on the most occasions. Temba and juvenile male Alexis were the individuals to spend the next greatest amount of time using the item. The majority of use by the group occurred during the first half of each session. Most of the interactions lasted for less than a minute. Keza was the individual that was the last user in all of the sessions.

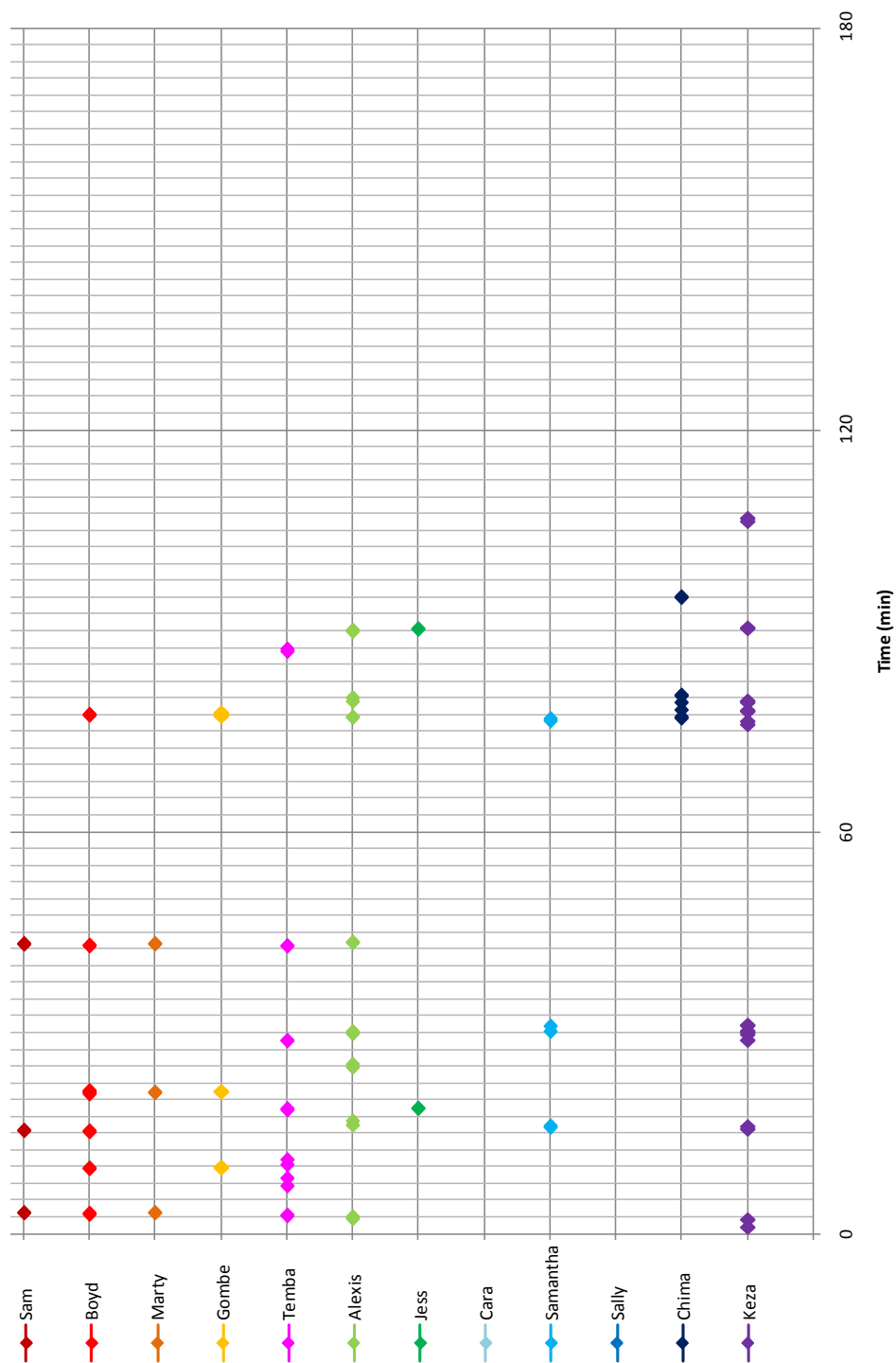


Figure 3.8a. Start and stop times for defined behaviours related to the group's use of the Musicbox enrichment item during the first session within Experiment 3. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

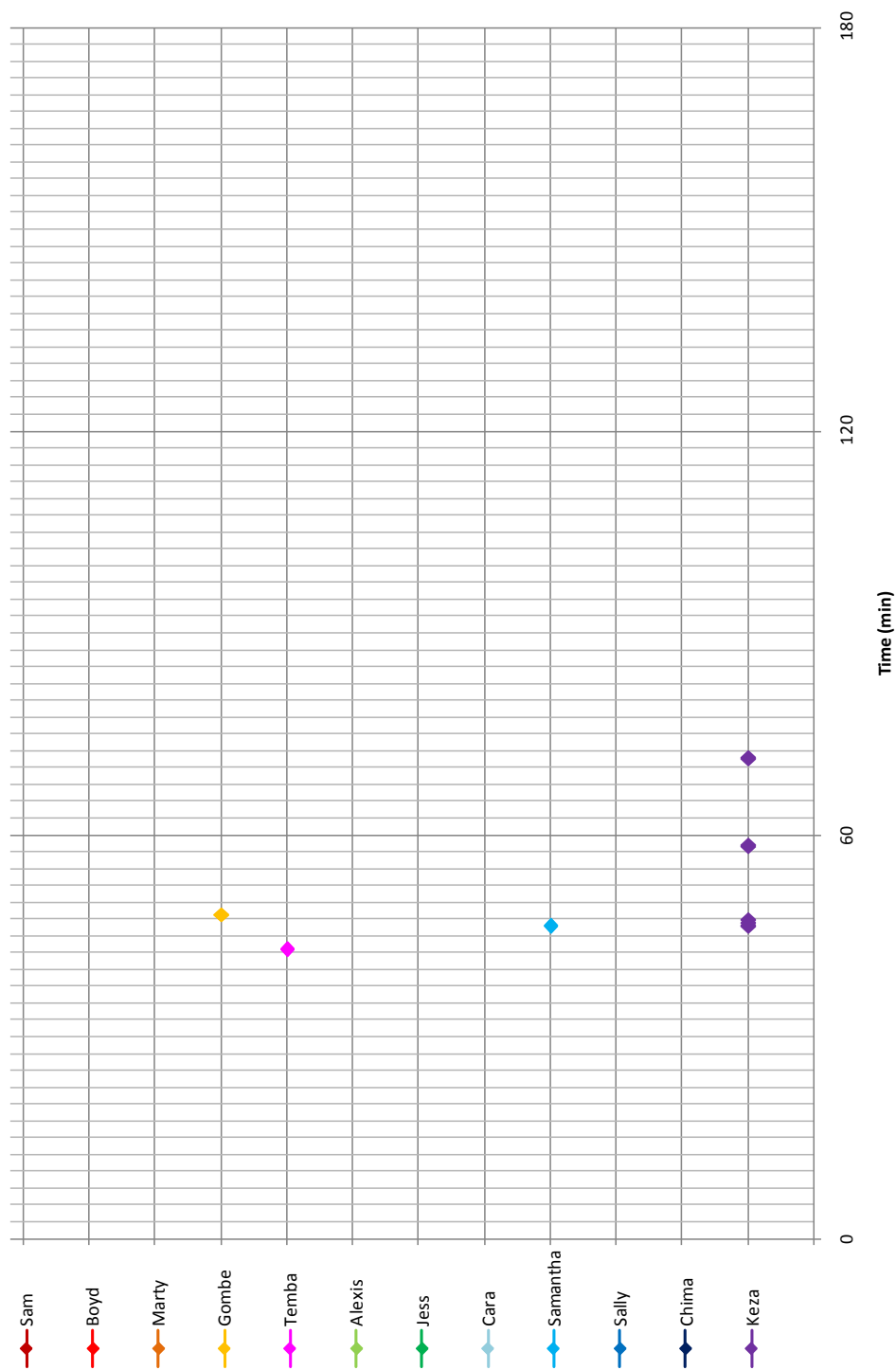


Figure 3.8b. Start and stop times for defined behaviours related to the group's use of the Musicbox enrichment item during the second session within Experiment 3. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

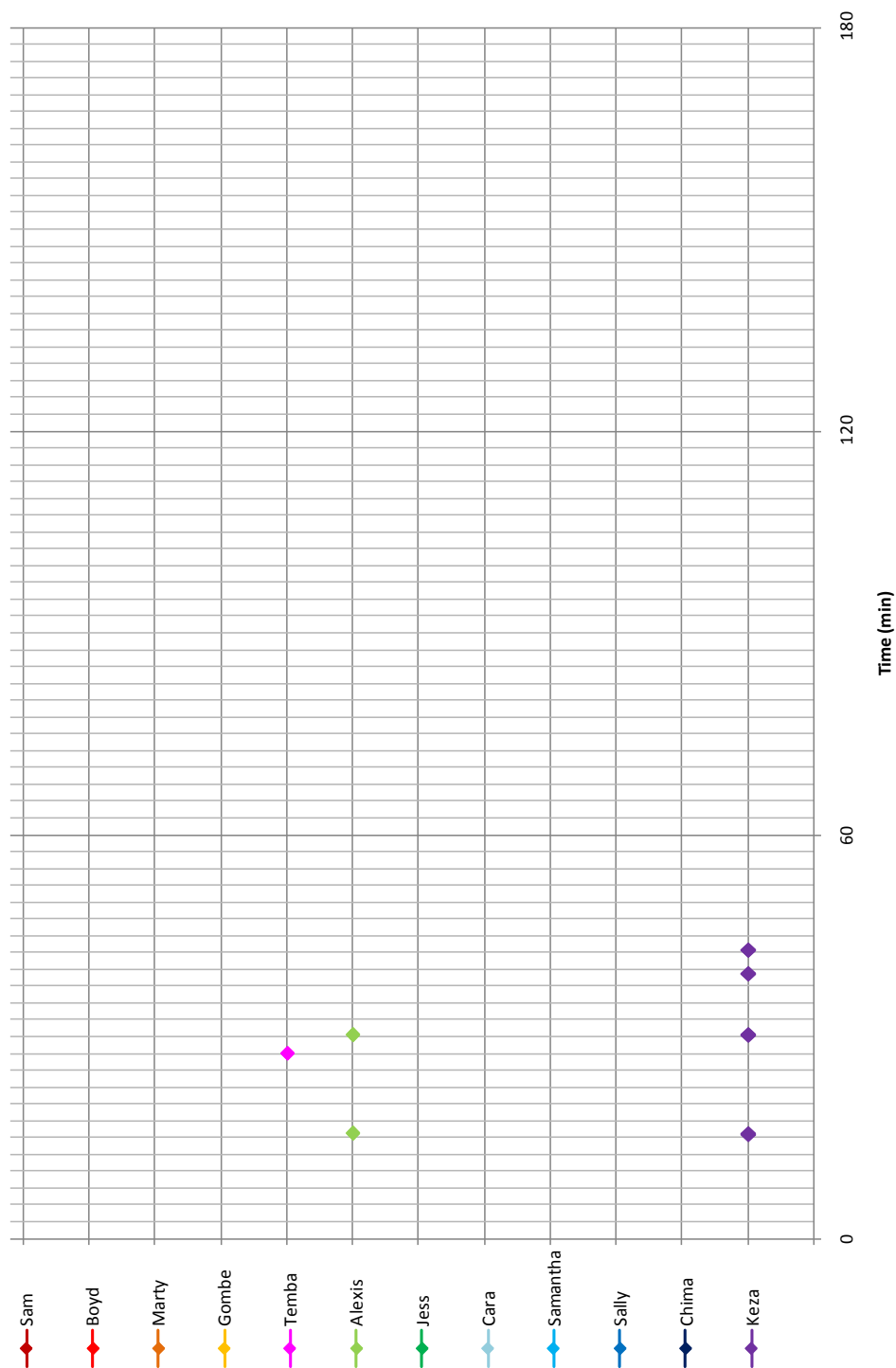


Figure 3.8c. Start and stop times for defined behaviours related to the group's use of the Musicbox enrichment item during the third session within Experiment 3. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

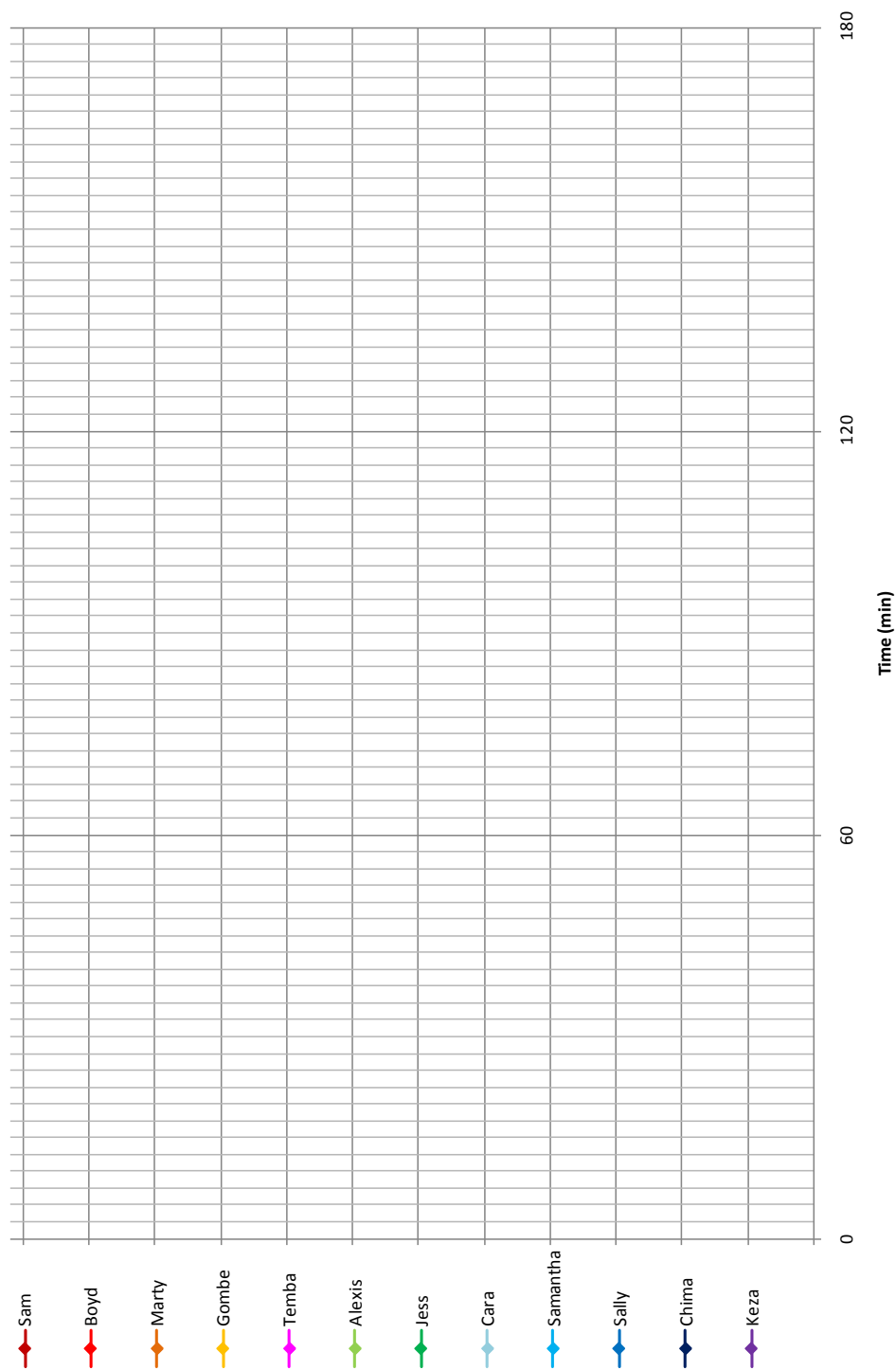


Figure 3.8d. Start and stop times for defined behaviours related to the group's use of the Musicbox enrichment item across during the fourth session within Experiment 3. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

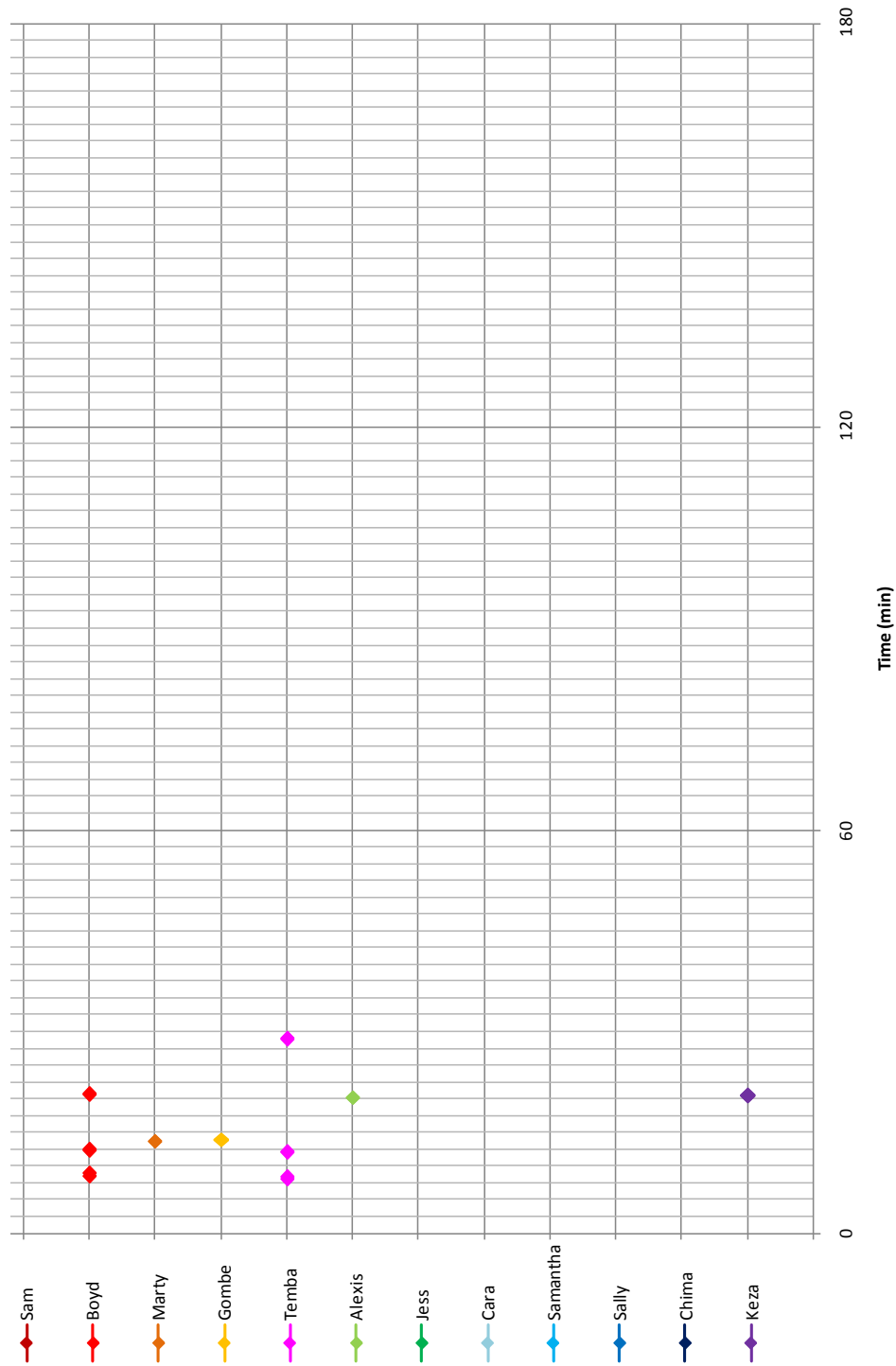


Figure 3.8e. Start and stop times for defined behaviours related to the group's use of the Musicbox enrichment item during the fifth session within Experiment 3. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

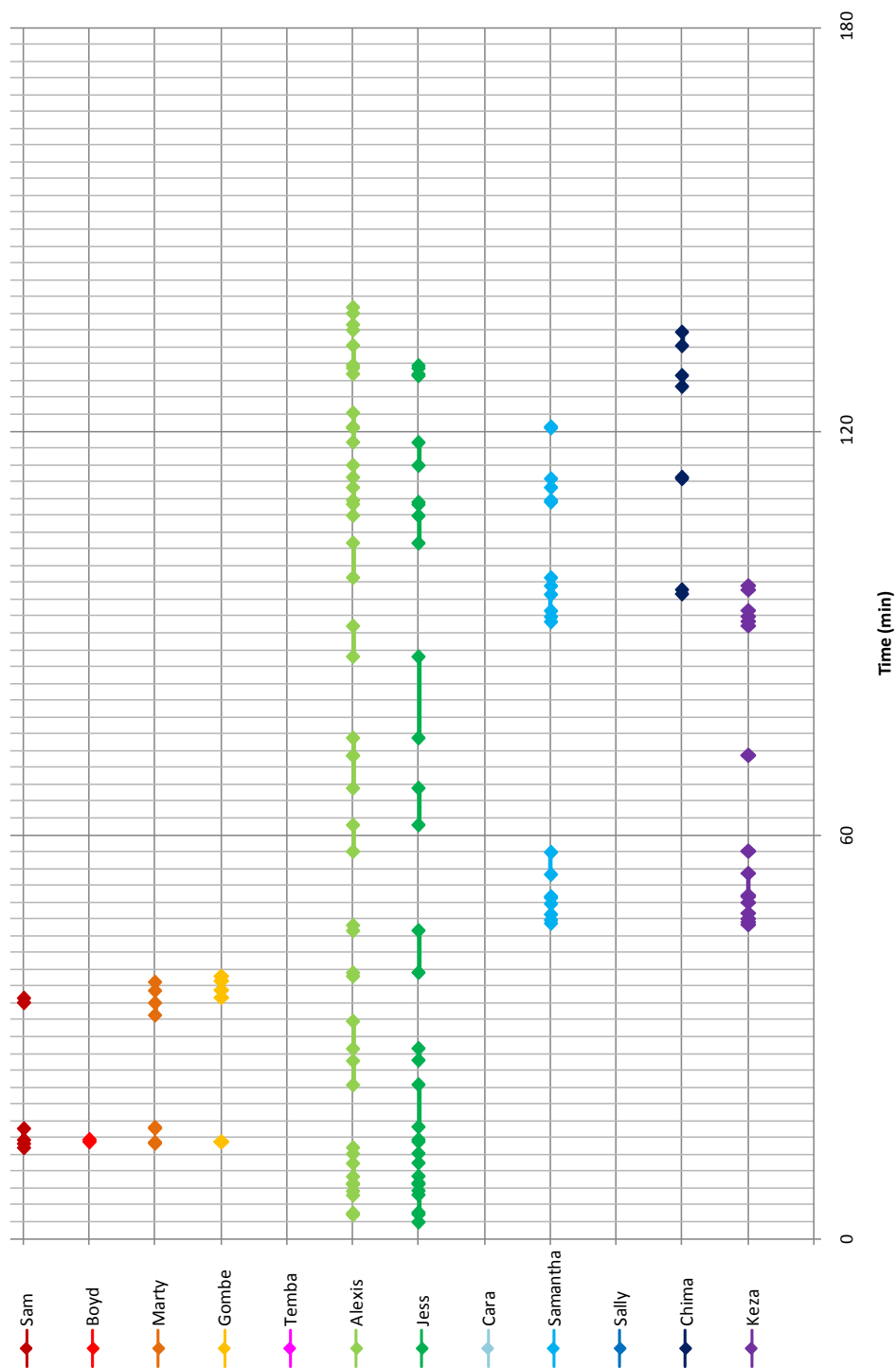


Figure 3.9a. Start and stop times for defined behaviours related to the group's use of the Dipper enrichment item during the first session within Experiment 3. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

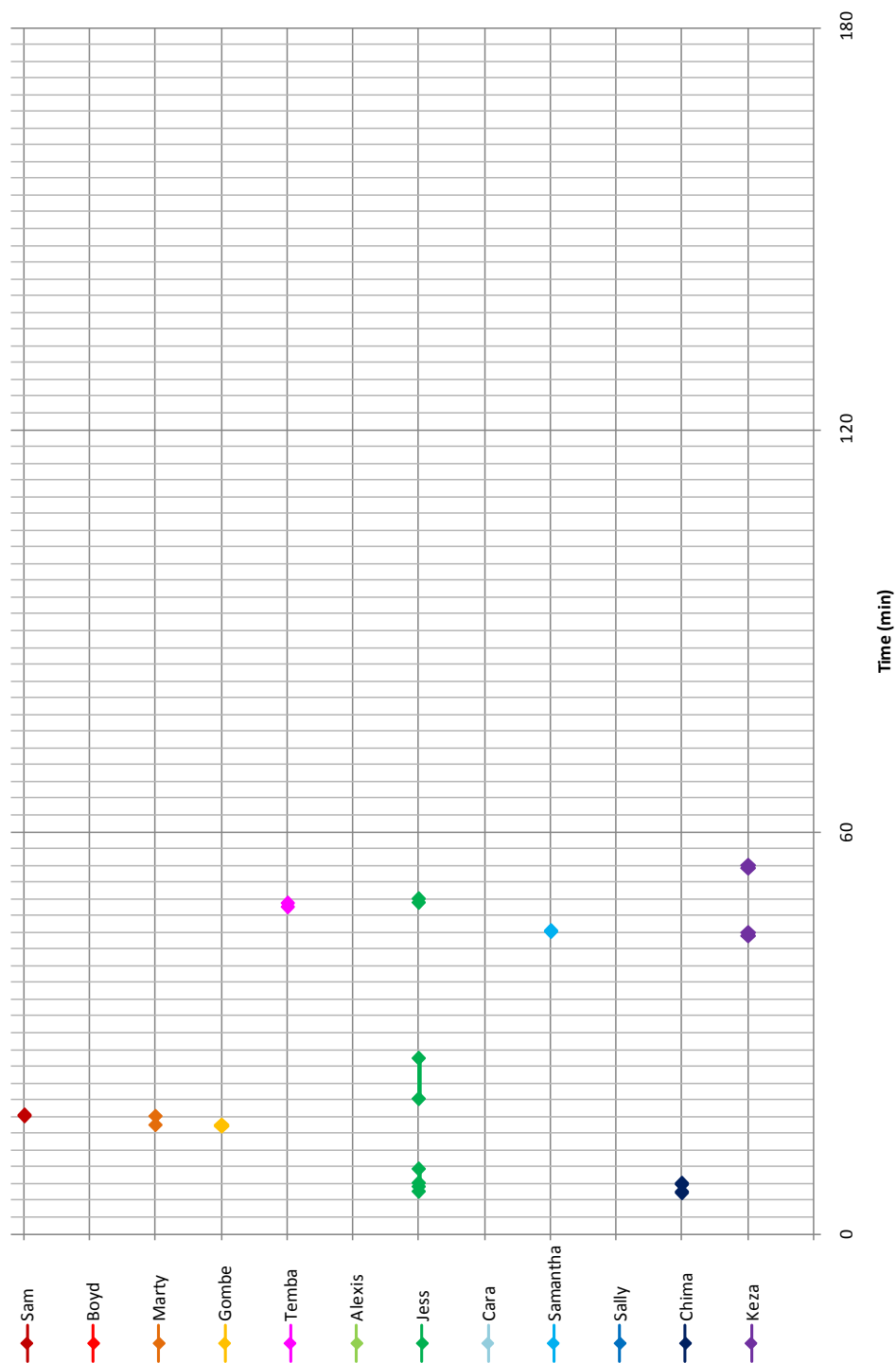


Figure 3.9b. Start and stop times for defined behaviours related to the group's use of the Dipper enrichment item across during the second session within Experiment 3. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

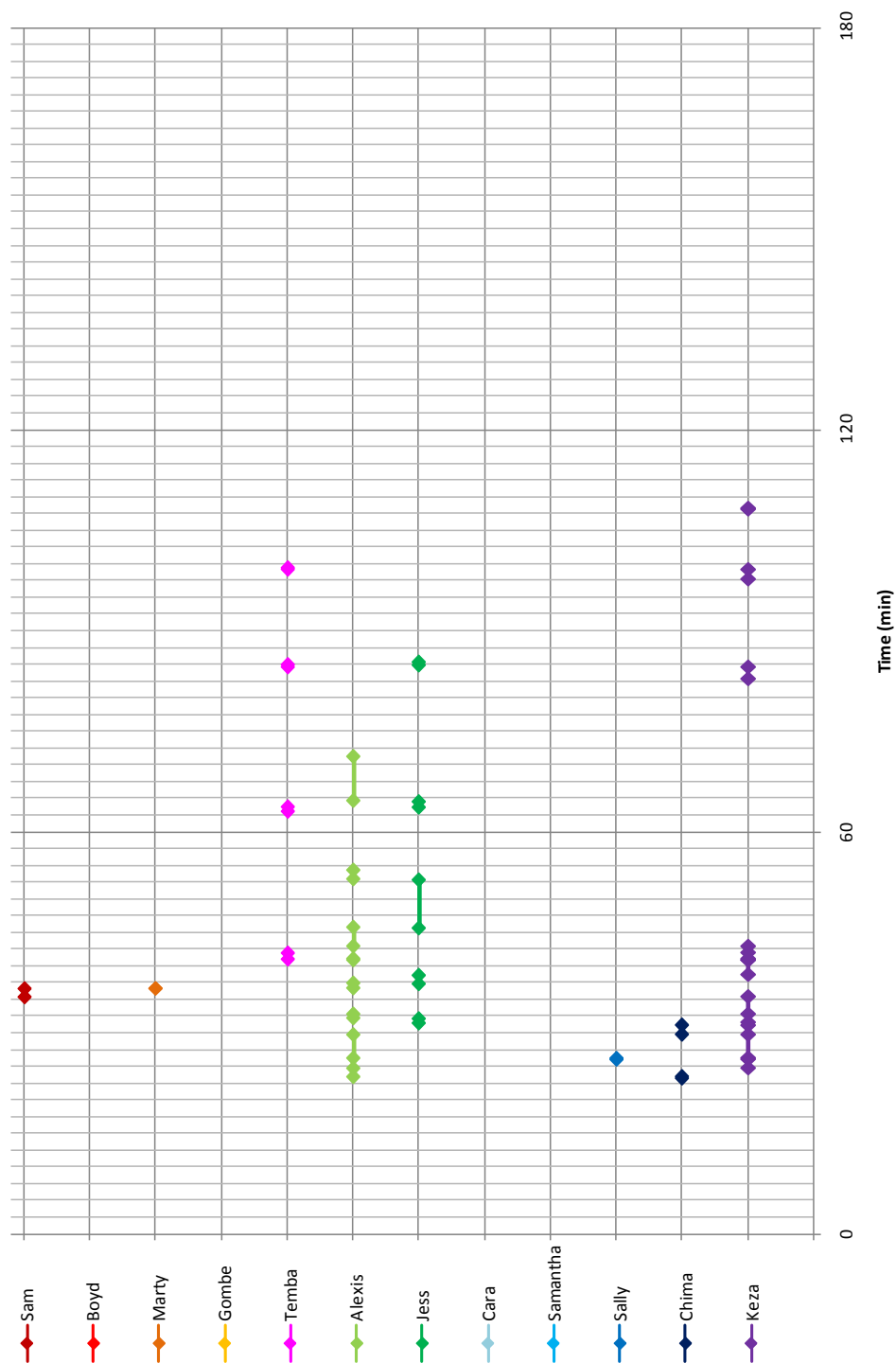


Figure 3.9c. Start and stop times for defined behaviours related to the group's use of the Dipper enrichment item during the third session within Experiment 3. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

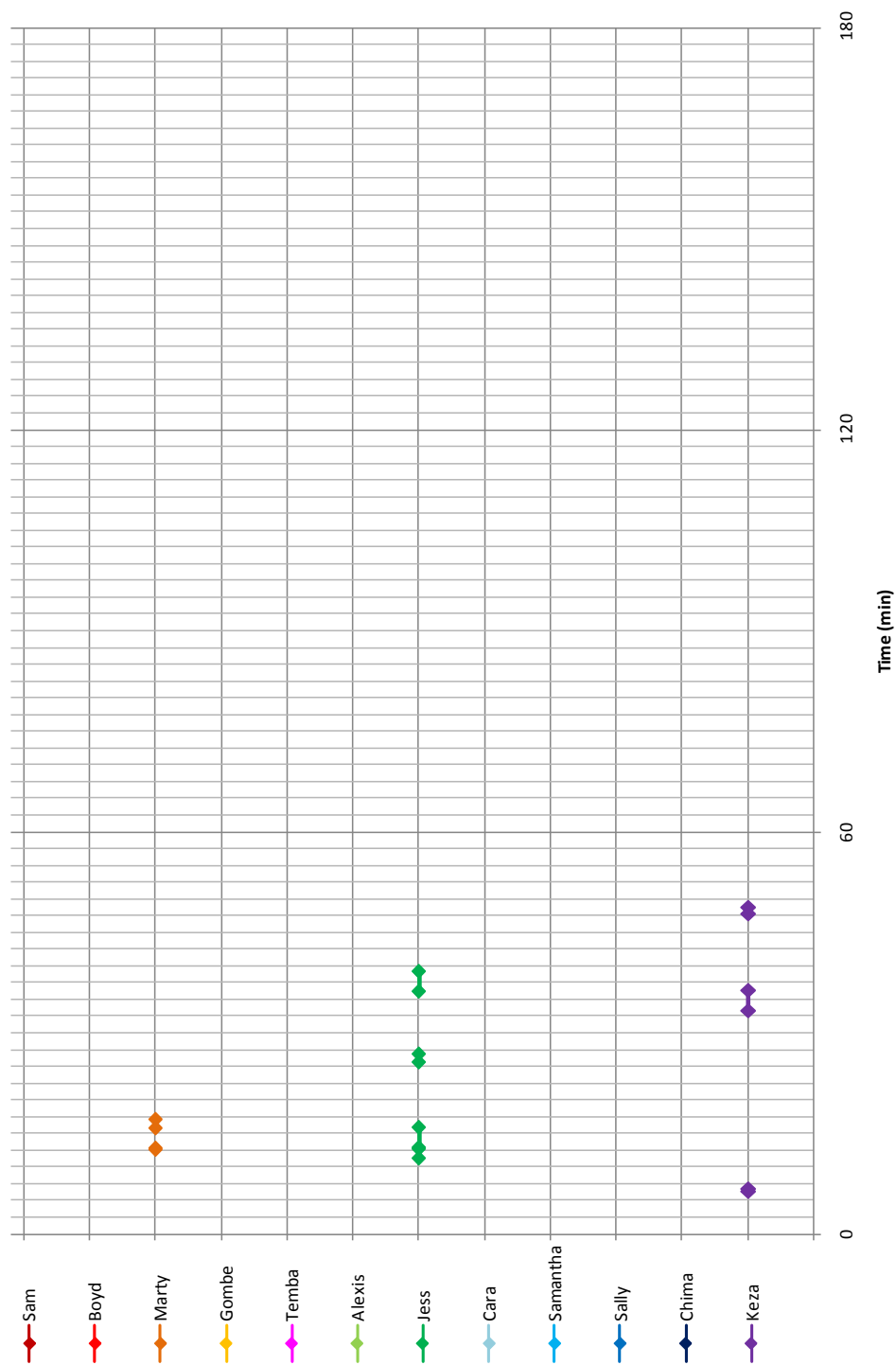


Figure 3.9d. Start and stop times for defined behaviours related to the group's use of the Dipper enrichment item during the fourth session within Experiment 3. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

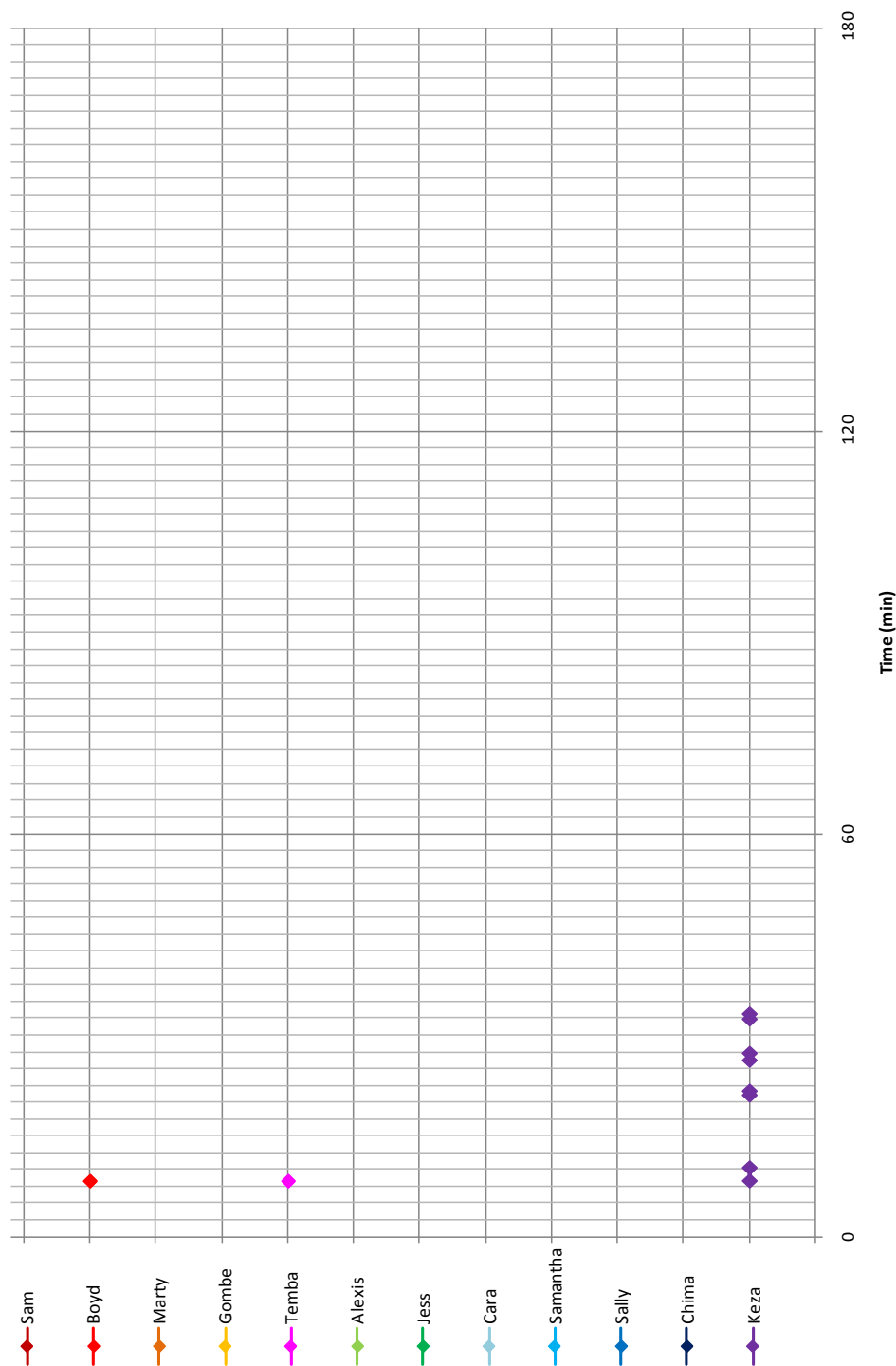


Figure 3.9e. Start and stop times for defined behaviours related to the group's use of the Dipper enrichment item during the fifth session within Experiment 3. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

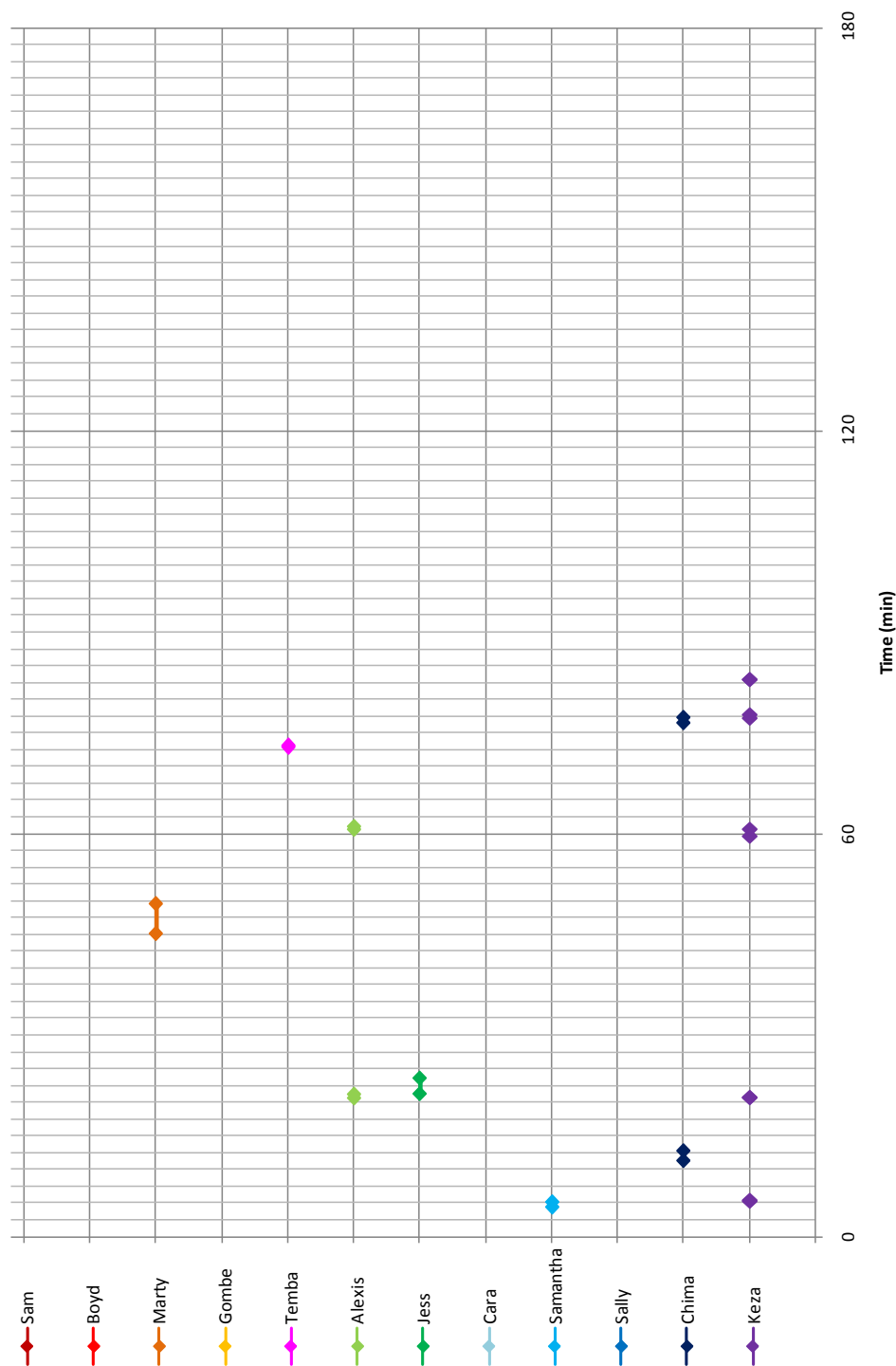


Figure 3.10a. Start and stop times for defined behaviours related to the group's use of the Screwfeeder enrichment item during the first session within Experiment 3. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

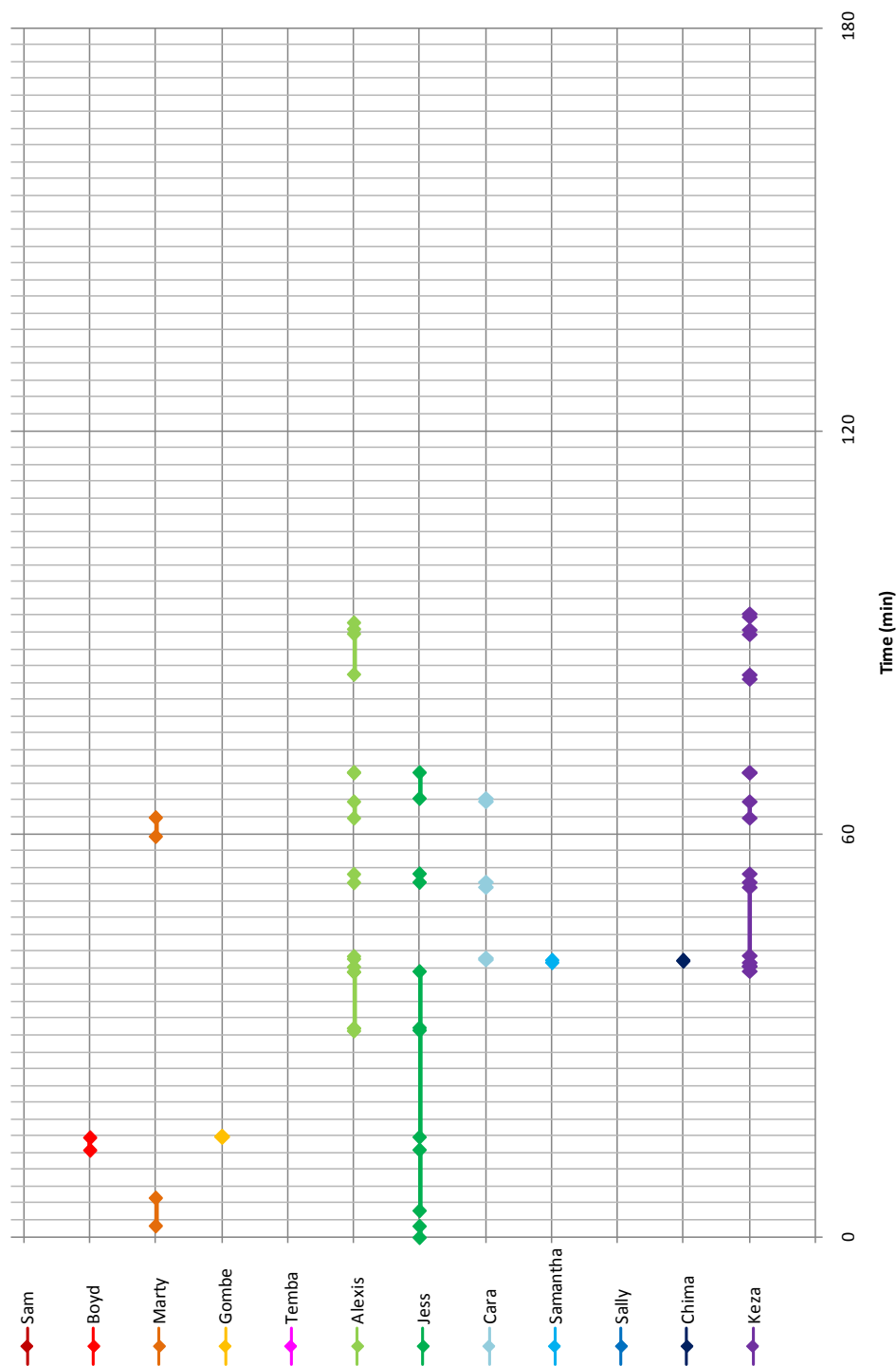


Figure 3.10b. Start and stop times for defined behaviours related to the group's use of the Screwfeeder enrichment item during the second session within Experiment 3. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

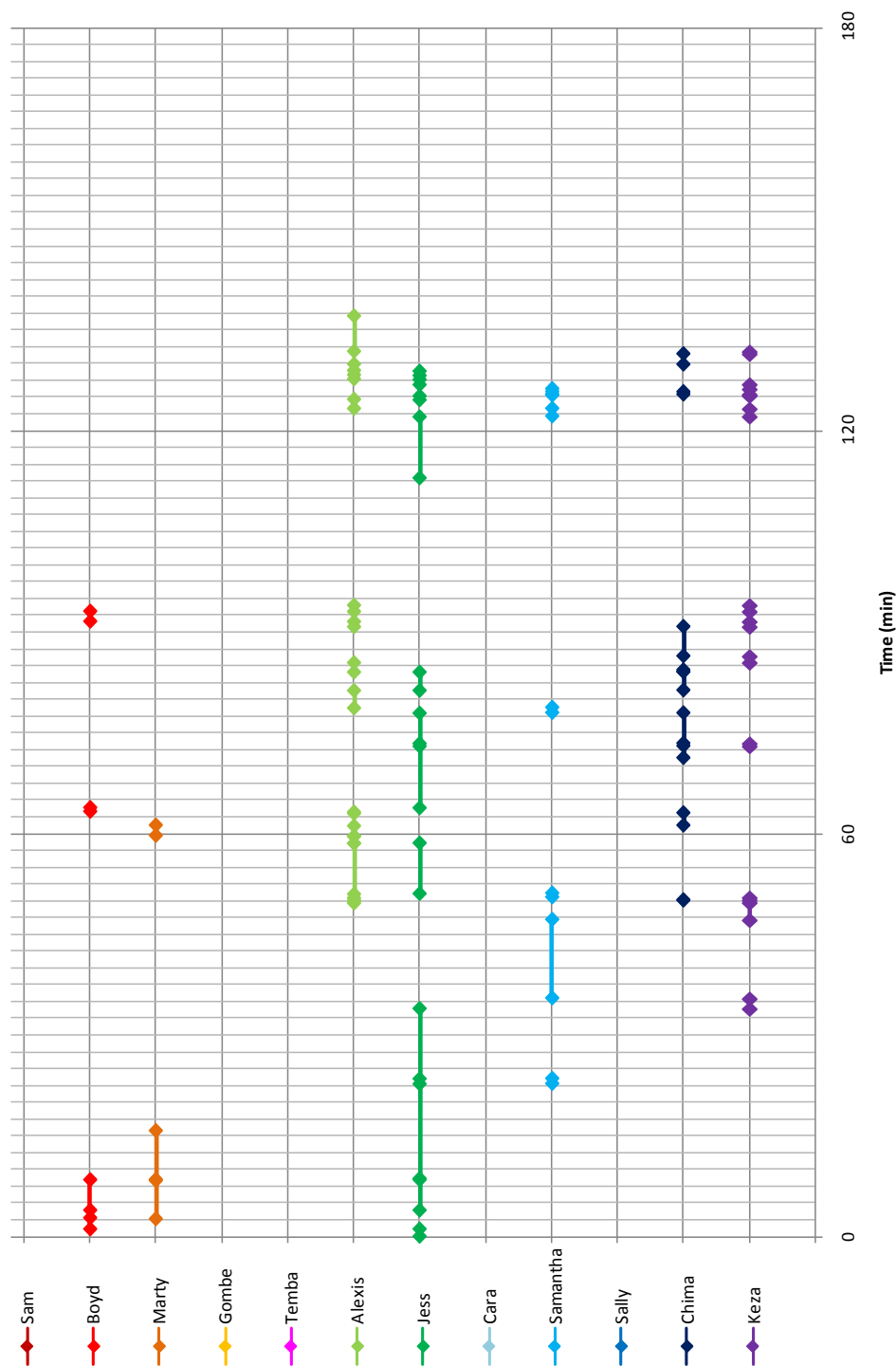


Figure 3.10c. Start and stop times for defined behaviours related to the group's use of the Screwfeeder enrichment item during the third session with it in Experiment 3. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

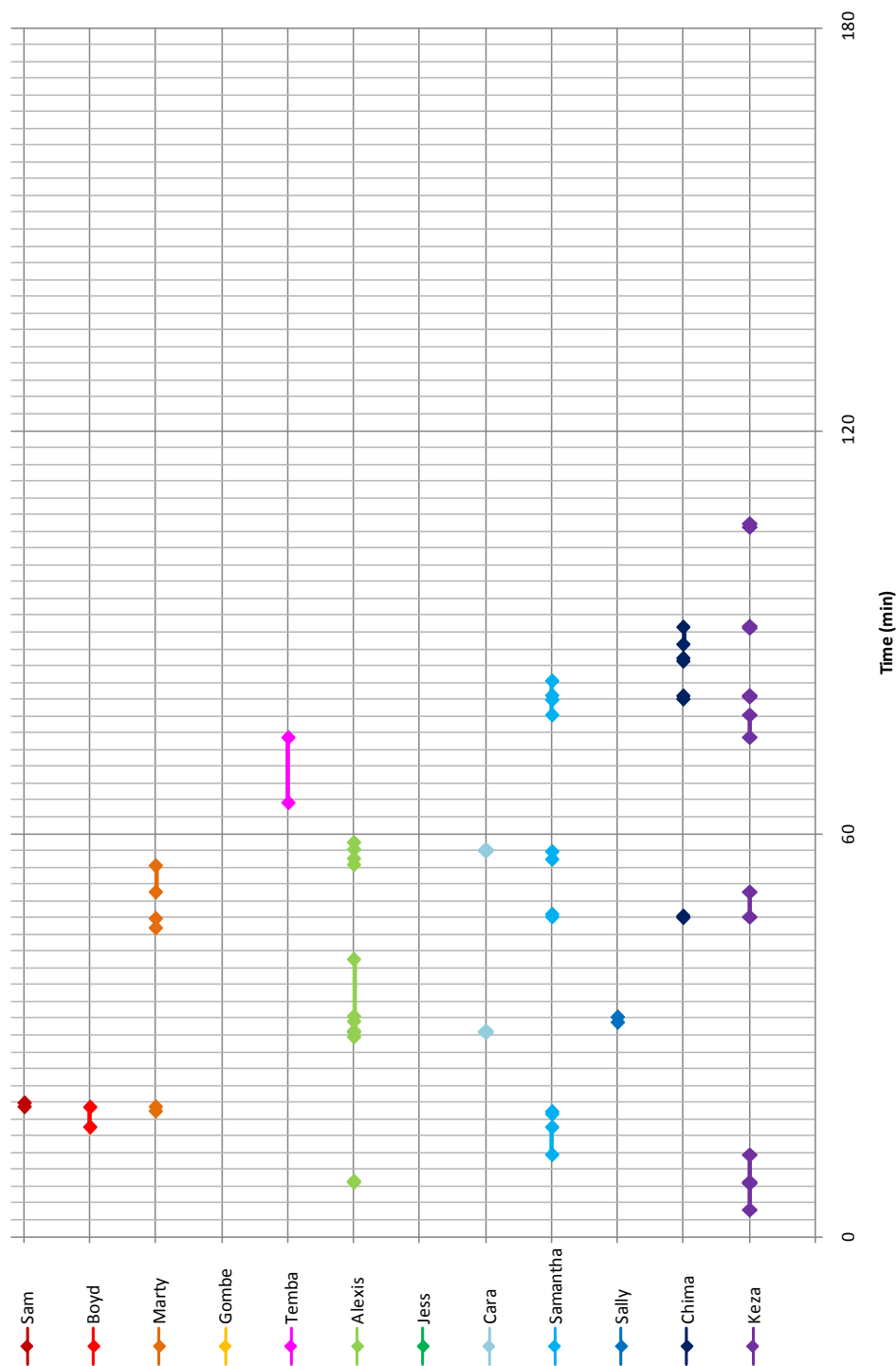


Figure 3.10d. Start and stop times for defined behaviours related to the group's use of the Screwfeeder enrichment item during the fourth session within Experiment 3. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

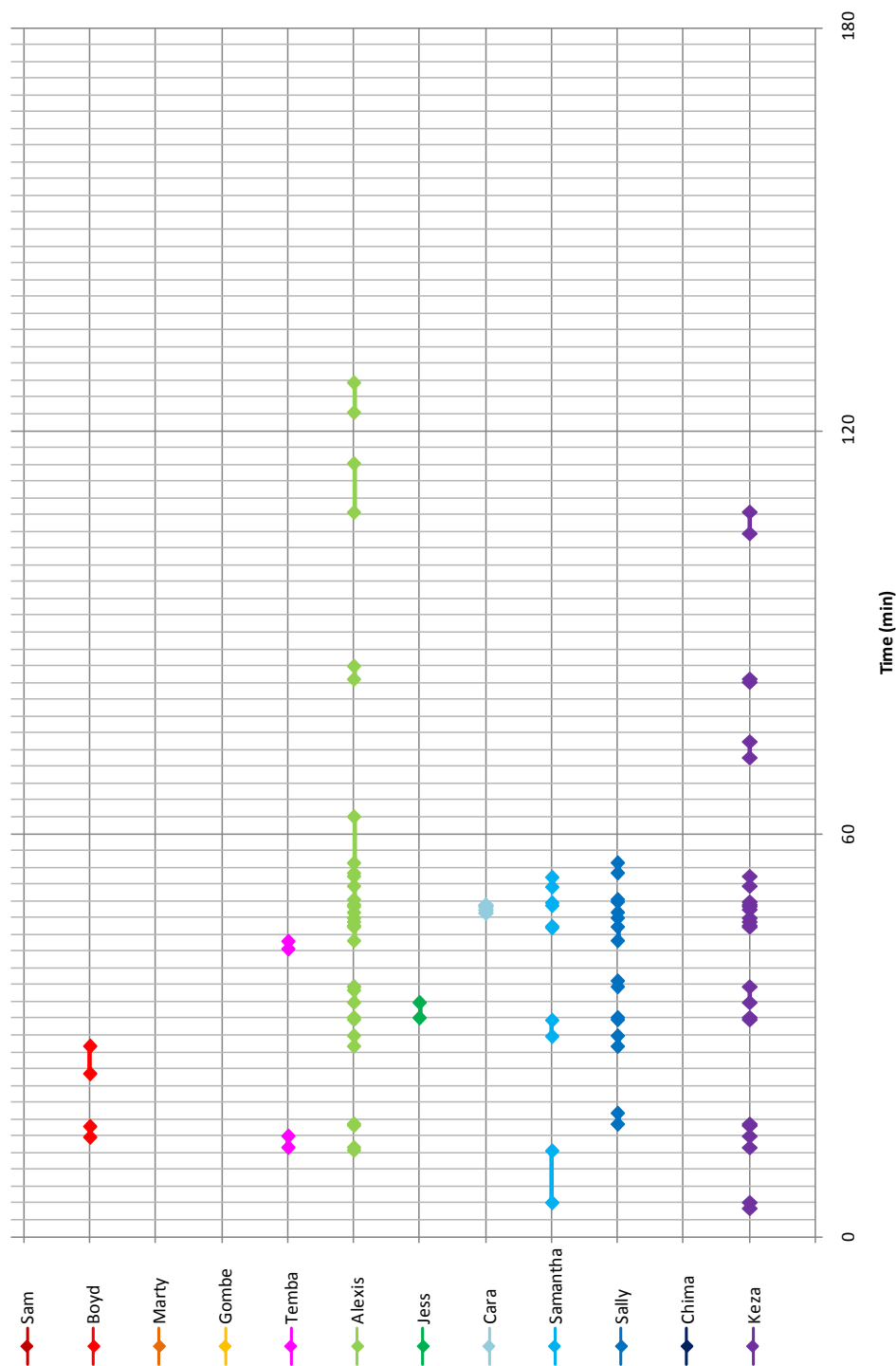


Figure 3.10e. Start and stop times for defined behaviours related to the group's use of the Screwfeeder enrichment item during the fifth session within Experiment 3. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

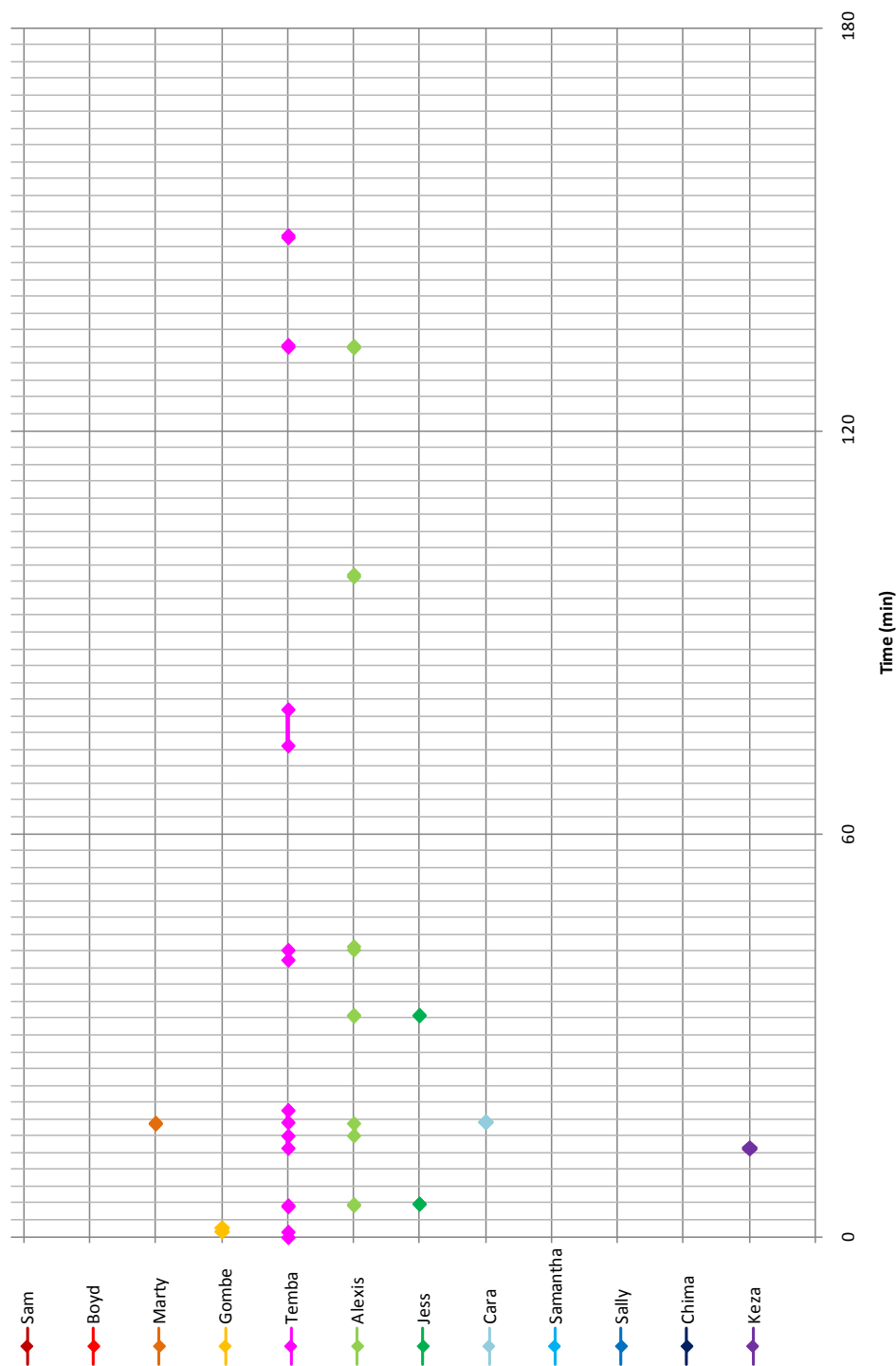


Figure 3.11a. Start and stop times for defined behaviours related to the group's use of the TV/Video enrichment item during the first session within Experiment 3. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

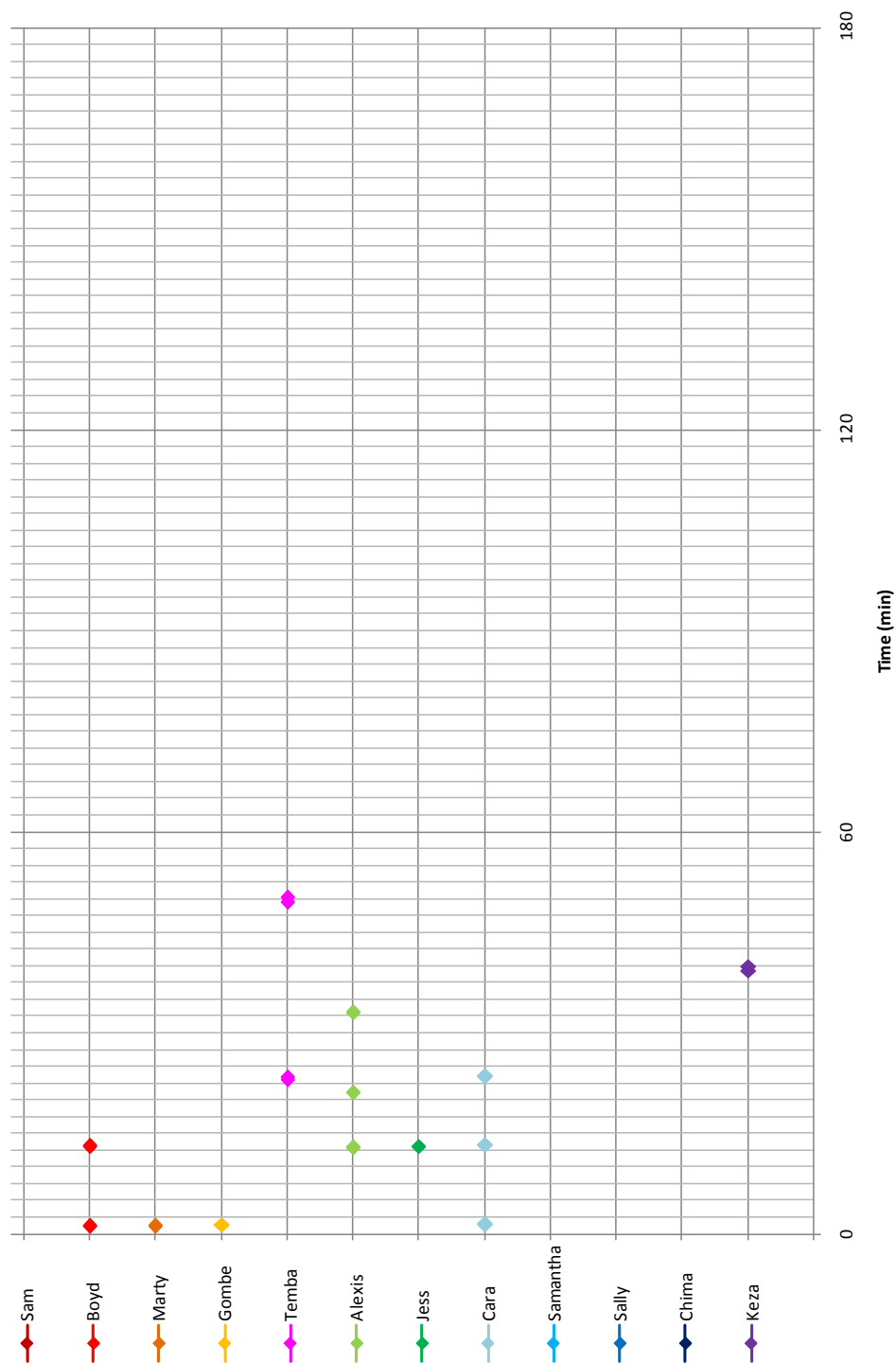


Figure 3.11b. Start and stop times for defined behaviours related to the group's use of the TV/Video enrichment item during the second session within Experiment 3. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

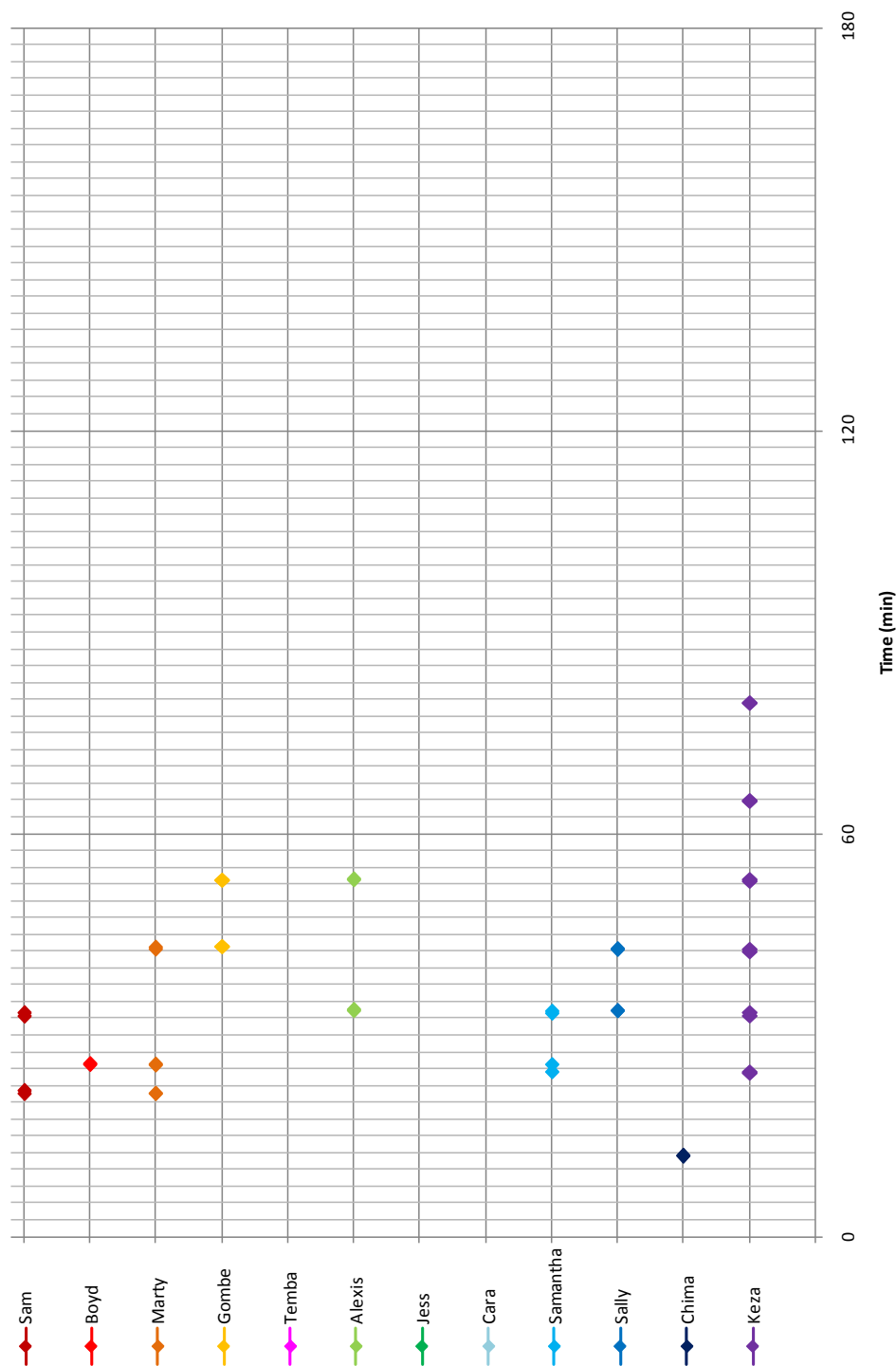


Figure 3.11c. Start and stop times for defined behaviours related to the group's use of the TV/Video enrichment item during the third session within Experiment 3. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

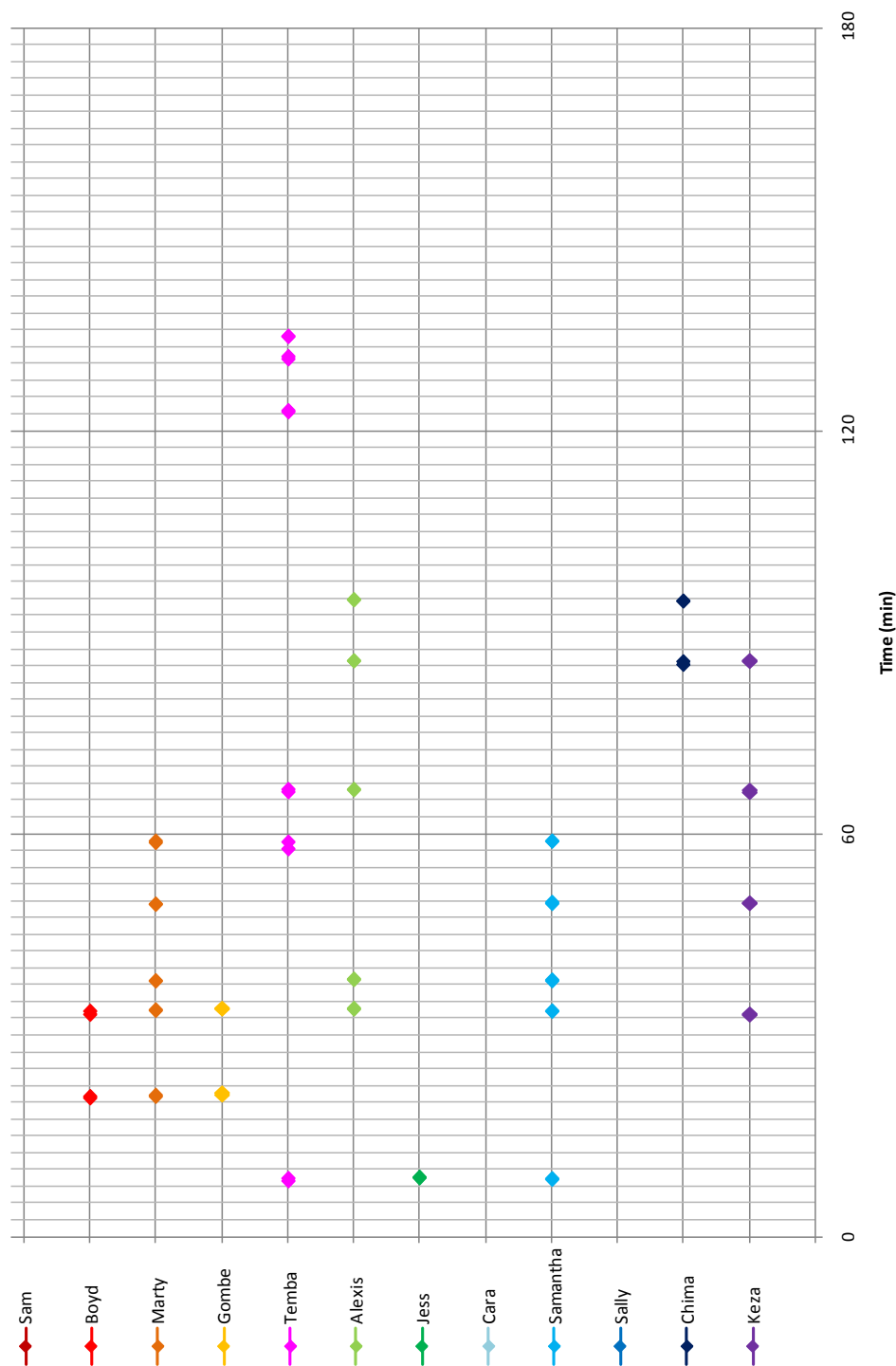


Figure 3.11d. Start and stop times for defined behaviours related to the group's use of the TV/Video enrichment item across during the fourth session within Experiment 3. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

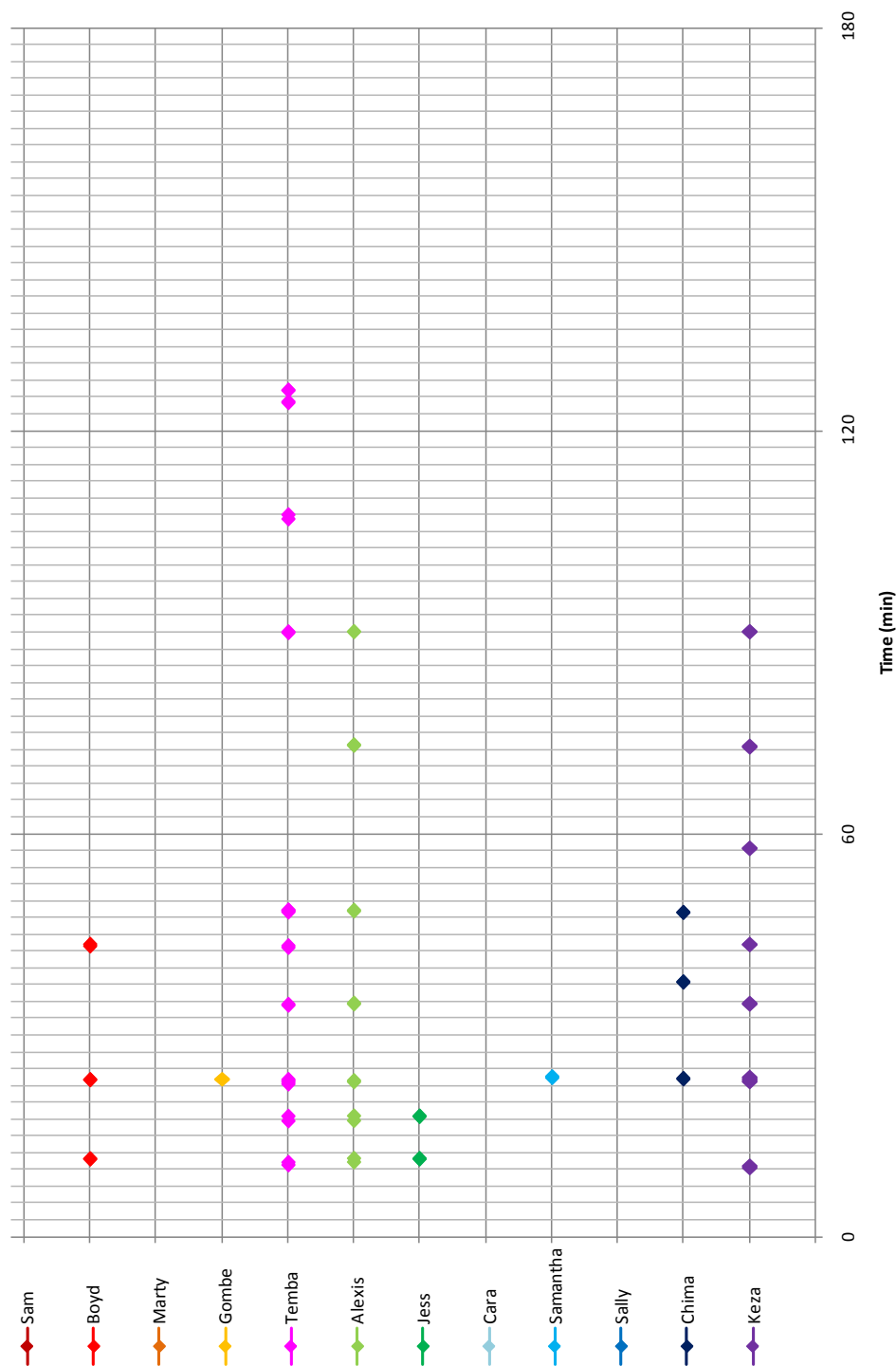


Figure 3.11e. Start and stop times for defined behaviours related to the group's use of the TV/Video enrichment item during the fifth session within Experiment 3. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

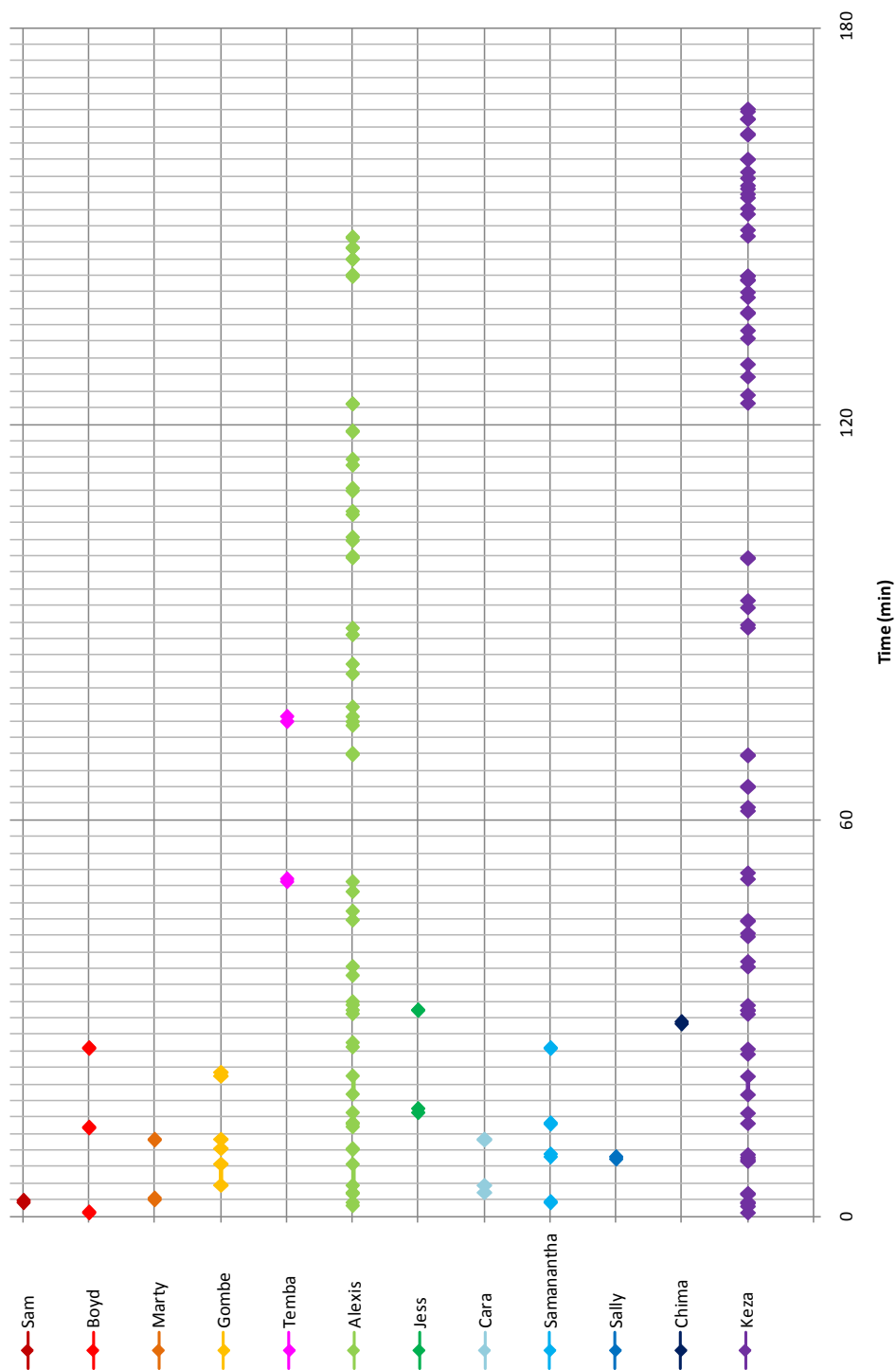


Figure 3.12a. Start and stop times for defined behaviours related to the group's use of the Marbleroll enrichment item, without slides present, during the first session within Experiment 3. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

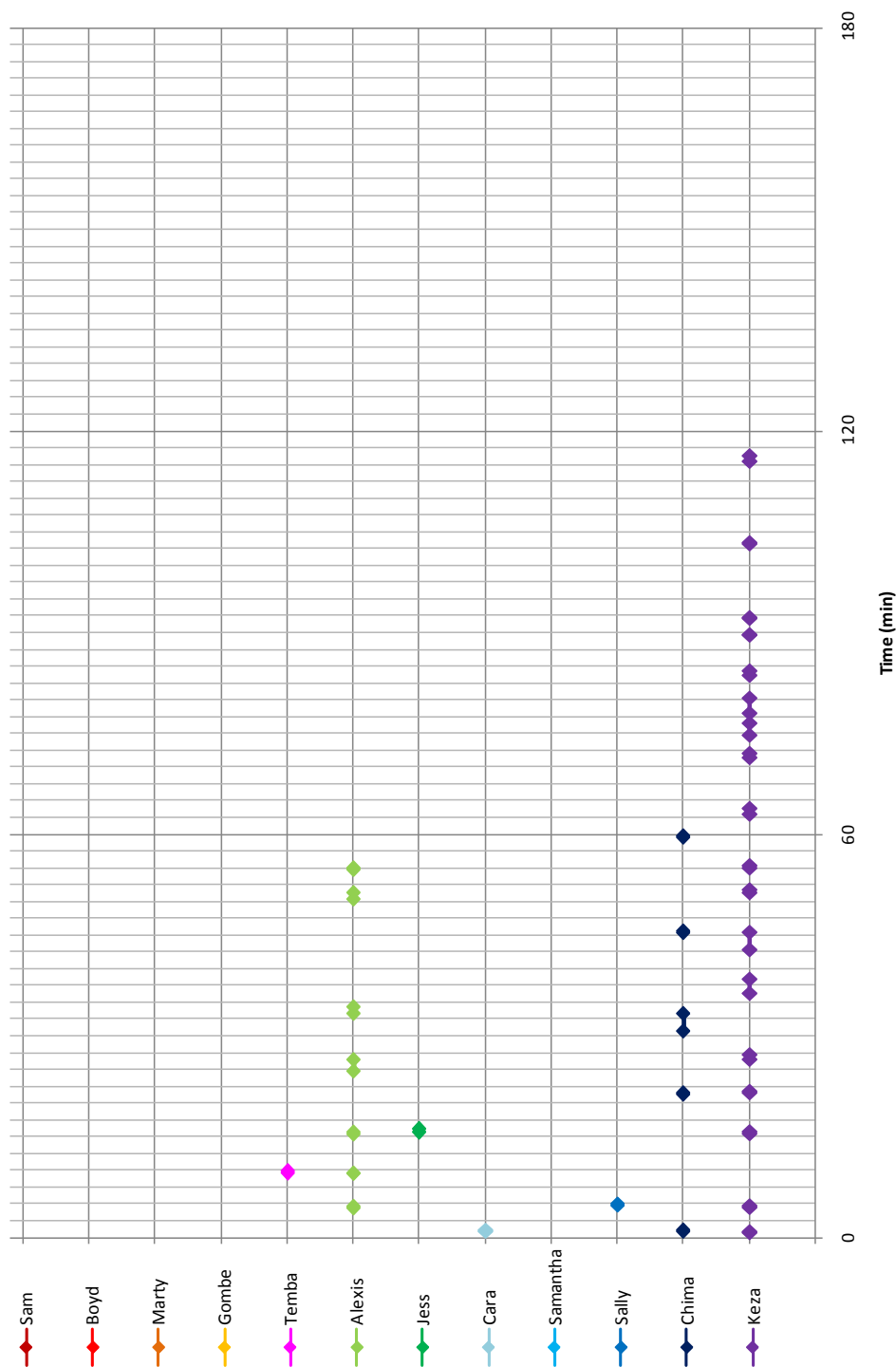


Figure 3.12b. Start and stop times for defined behaviours related to the group's use of the Marbleroll enrichment item, without slides present, during the second session within Experiment 3. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

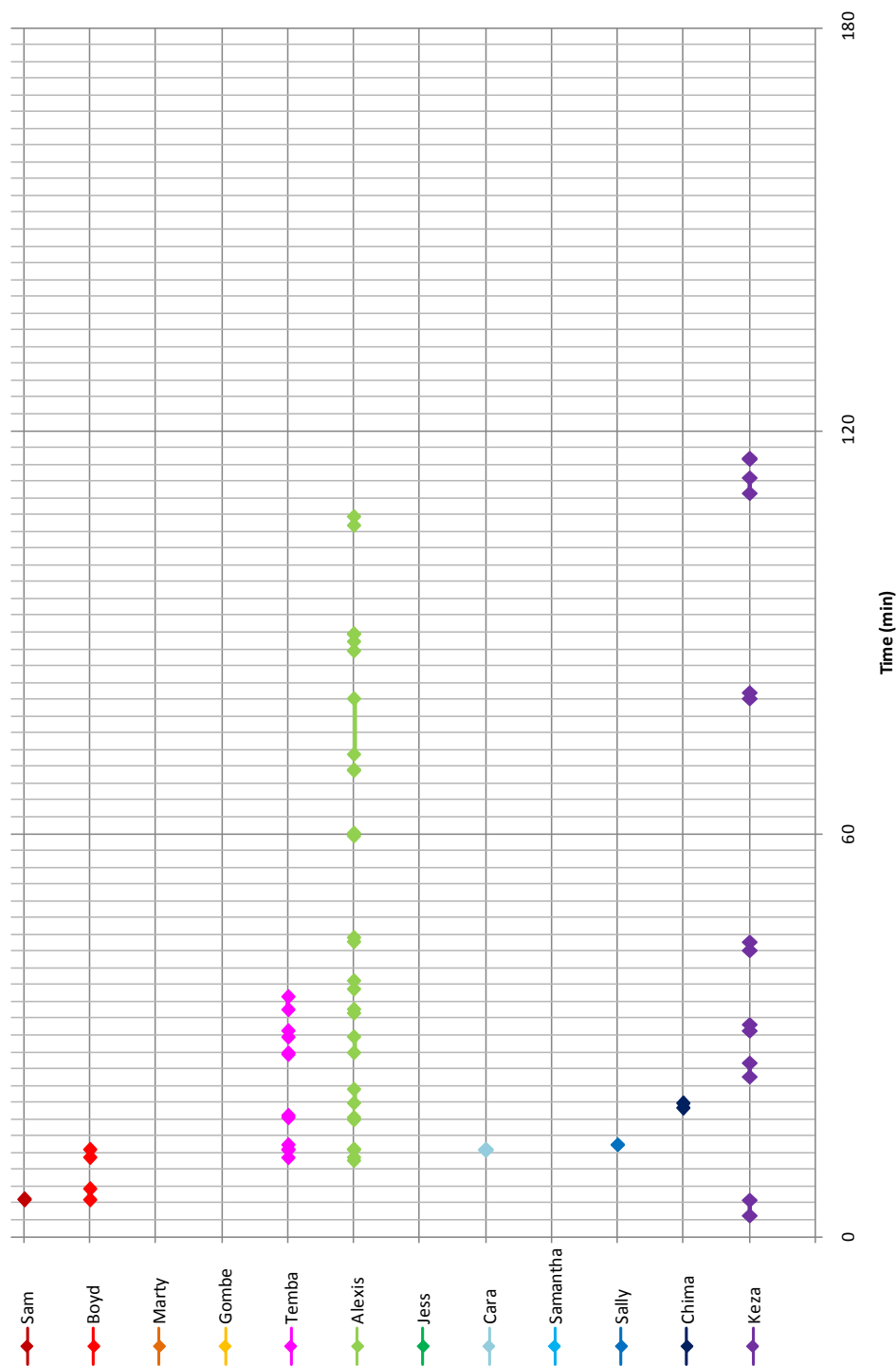


Figure 3.12c. Start and stop times for defined behaviours related to the group's use of the Marbleroll enrichment item, without slides present, during the third session within Experiment 3. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

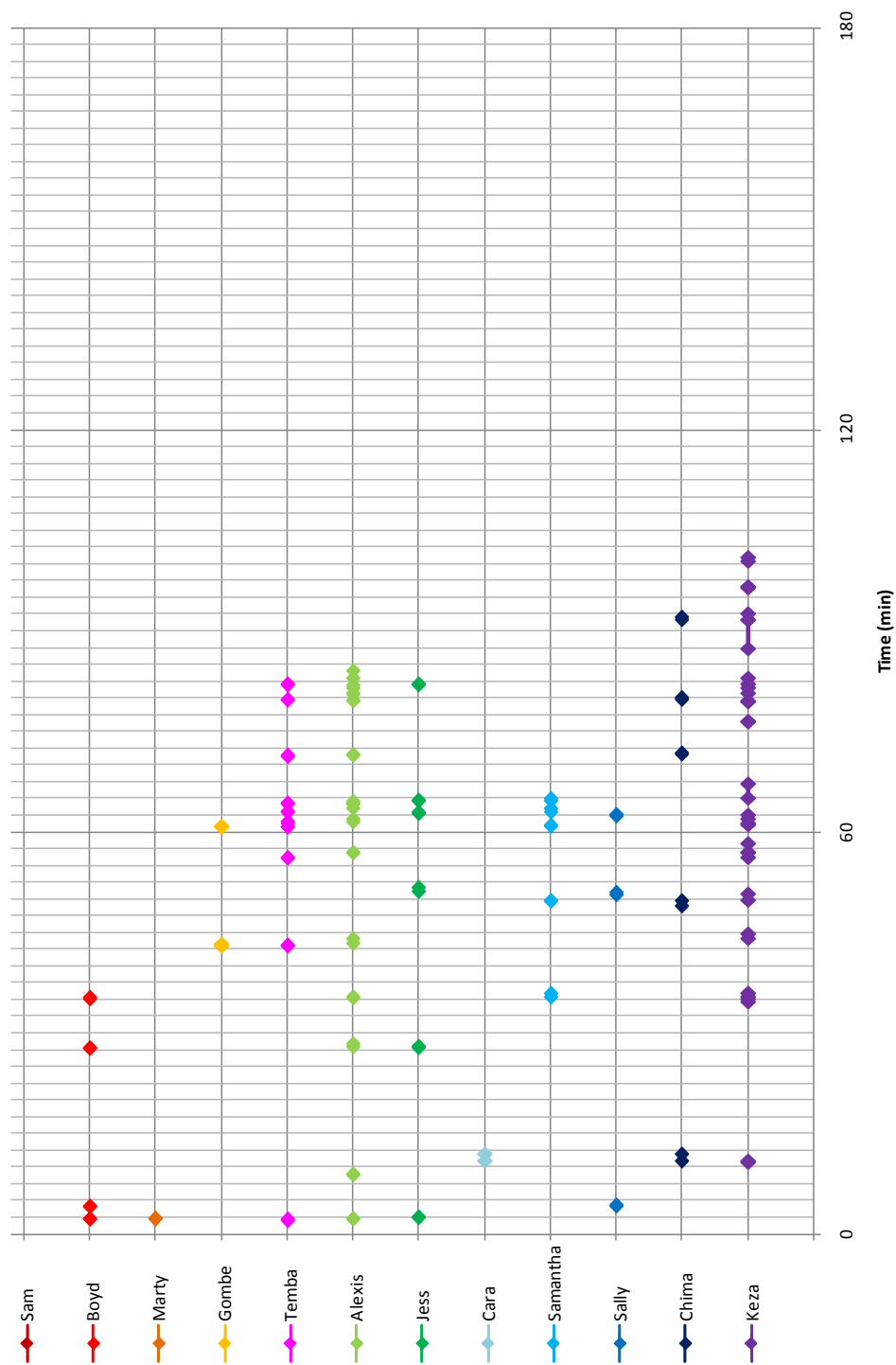


Figure 3.12d. Start and stop times for defined behaviours related to the group's use of the Marbleroll enrichment item, without slides present, during the fourth session within Experiment 3. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

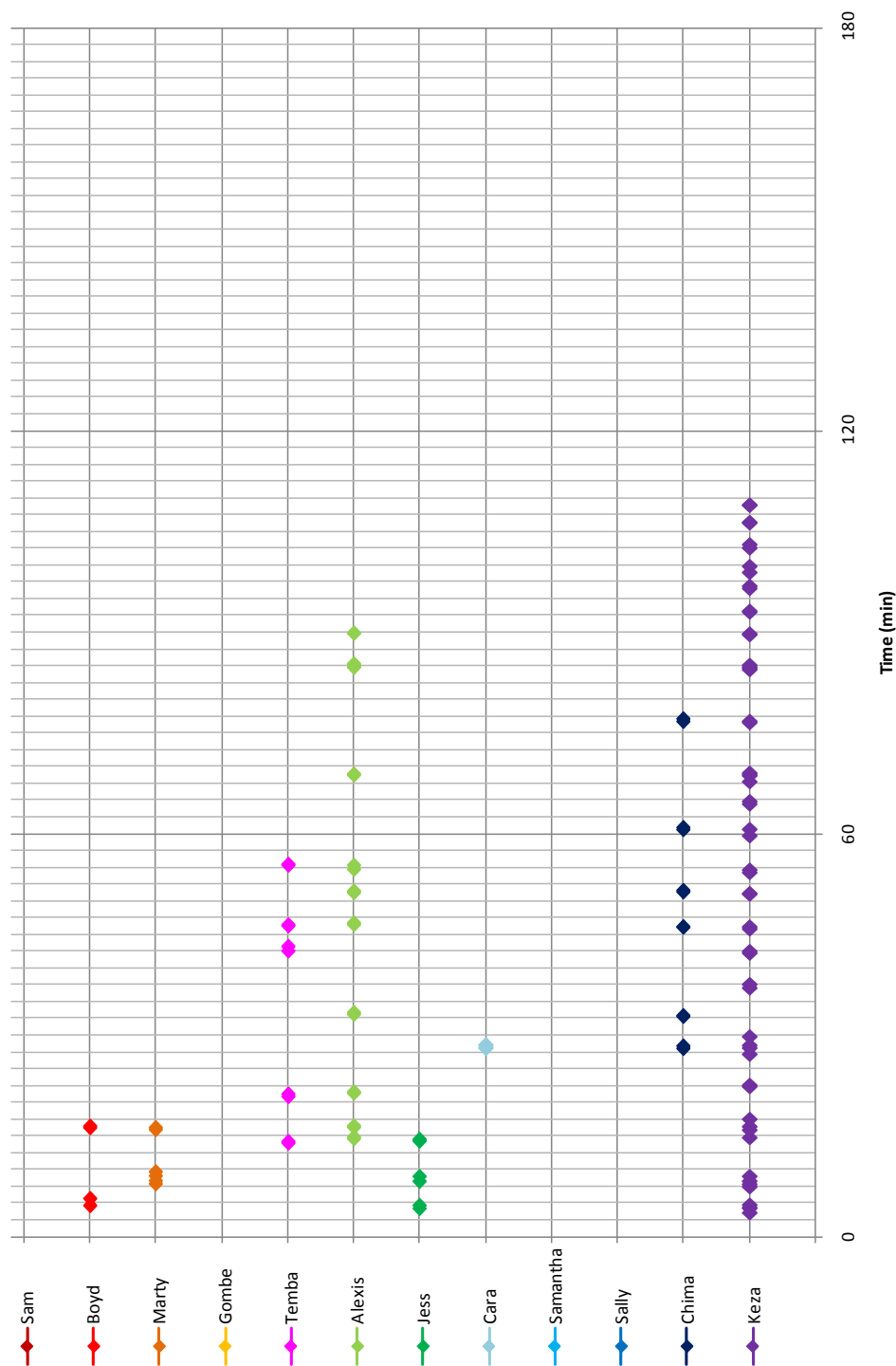


Figure 3.12e. Start and stop times for defined behaviours related to the group's use of the Marbleroll enrichment item, without slides present, during the fifth session within Experiment 3. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

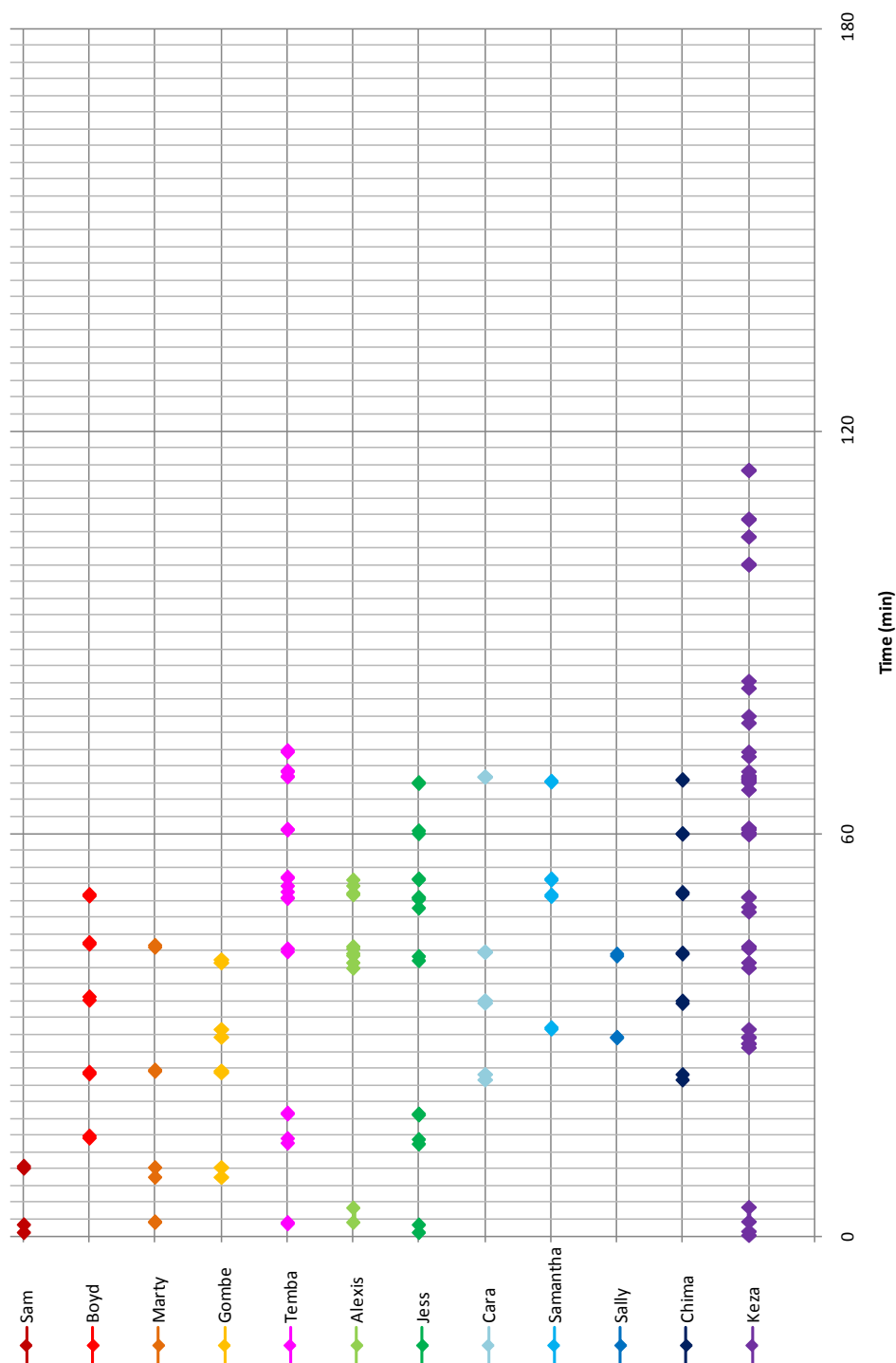


Figure 3.13a. Start and stop times for defined behaviours related to the group's use of the Marbleroll enrichment item, with slides present, during the first session within Experiment 3. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

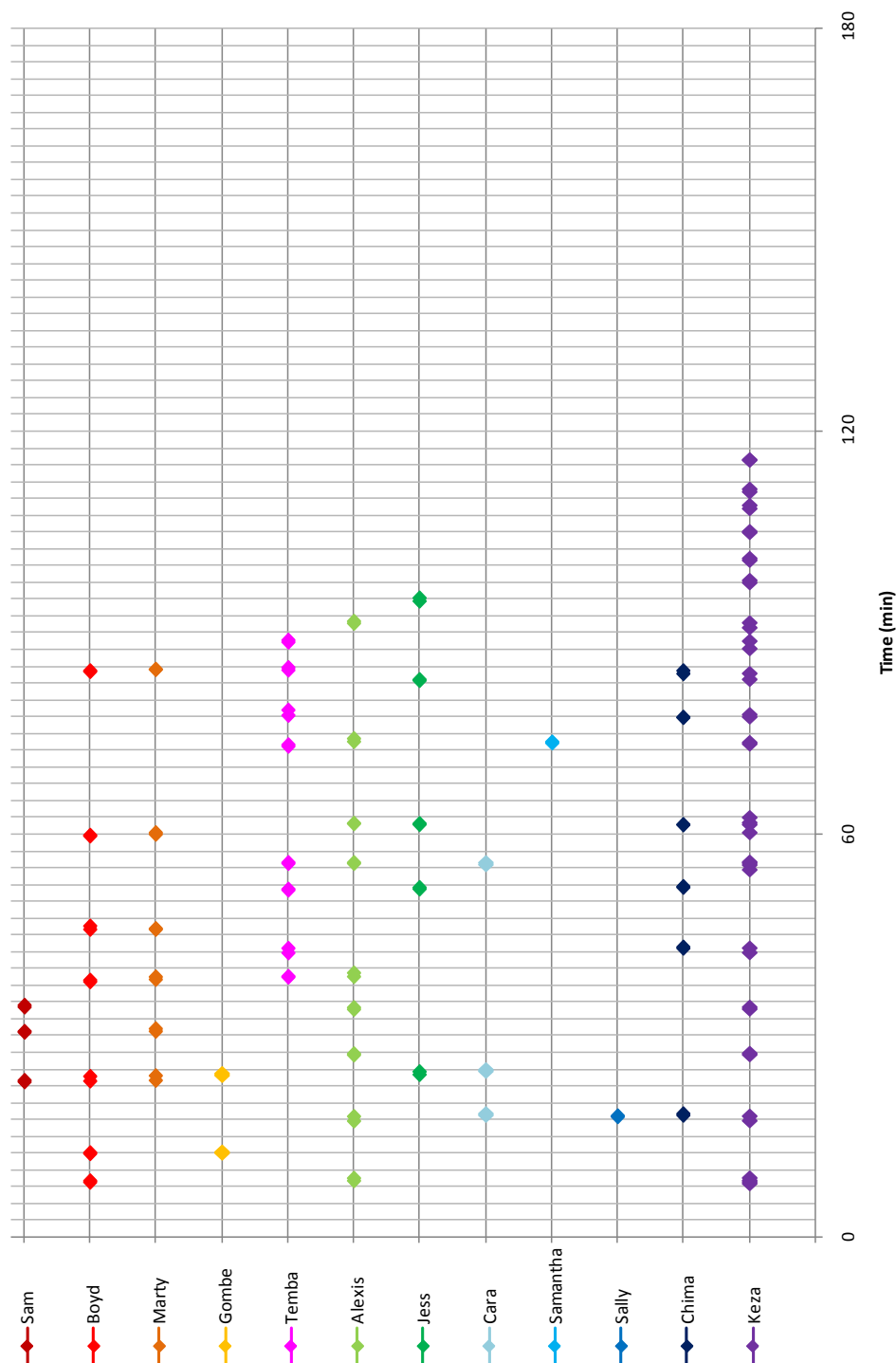


Figure 3.13b. Start and stop times for defined behaviours related to the group's use of the Marbleroll enrichment item, with slides present, during the second session within Experiment 3. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

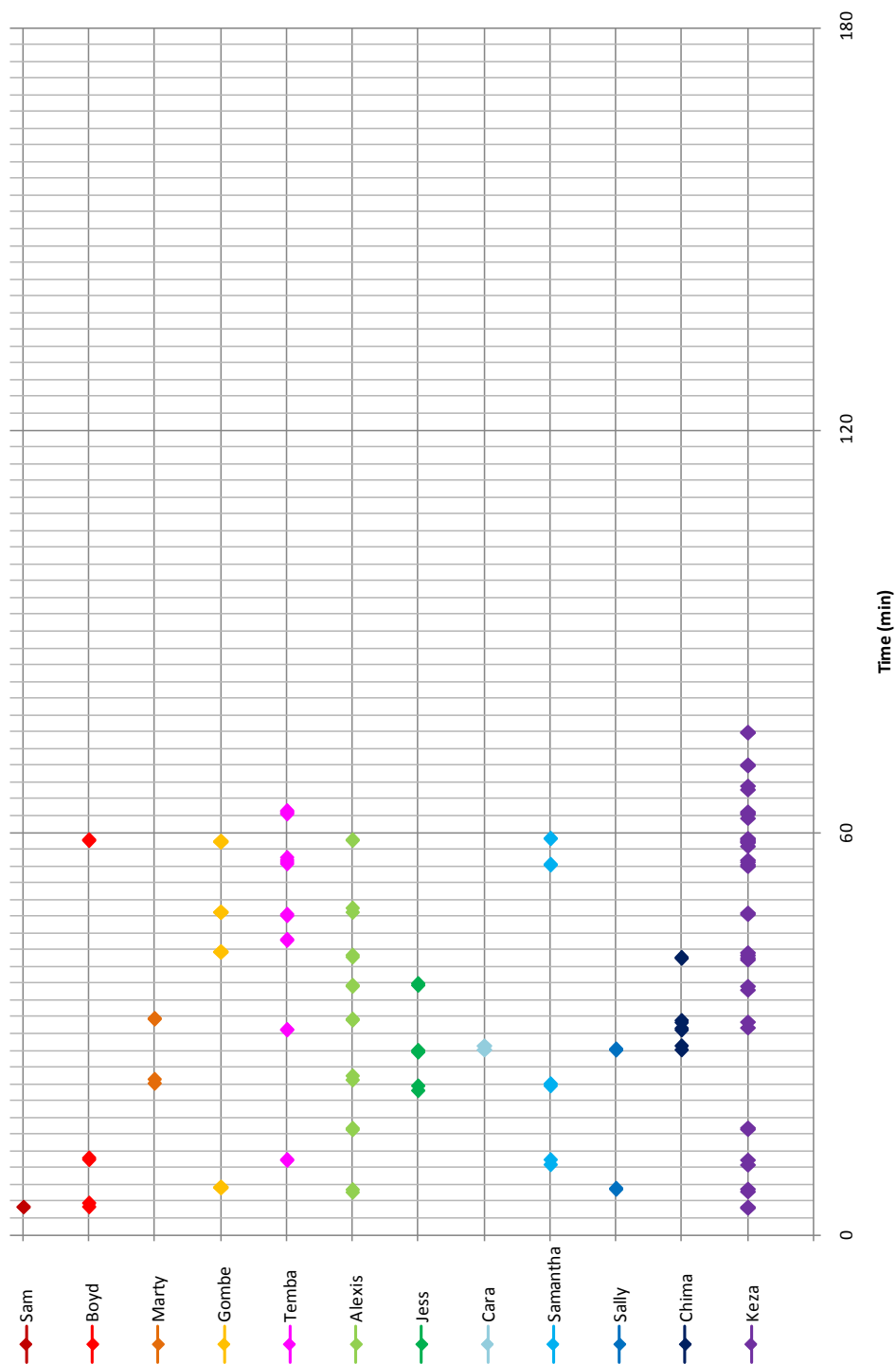


Figure 3.13c. Start and stop times for defined behaviours related to the group's use of the Marbleroll enrichment item, with slides present, during the third session within Experiment 3. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

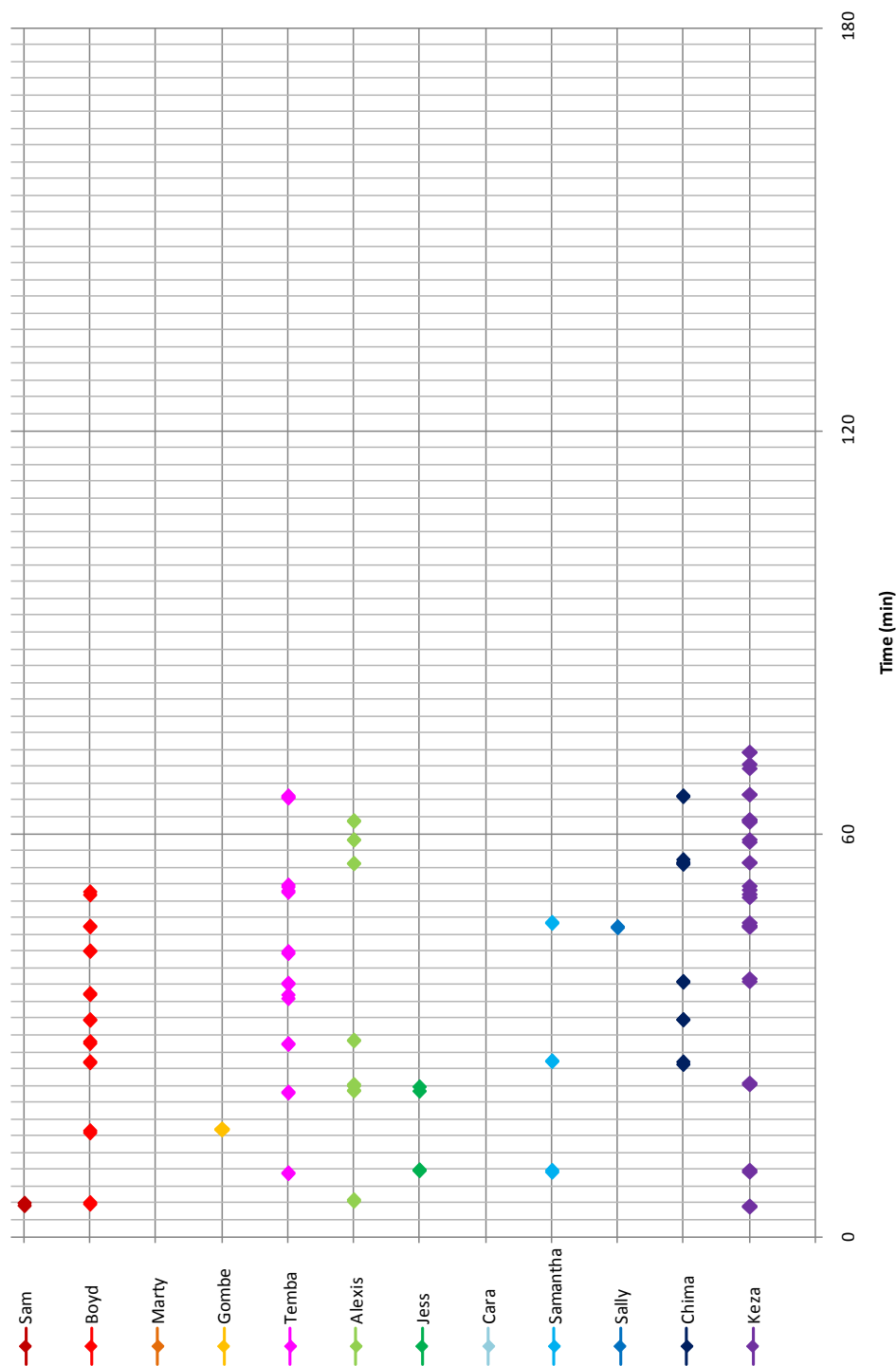
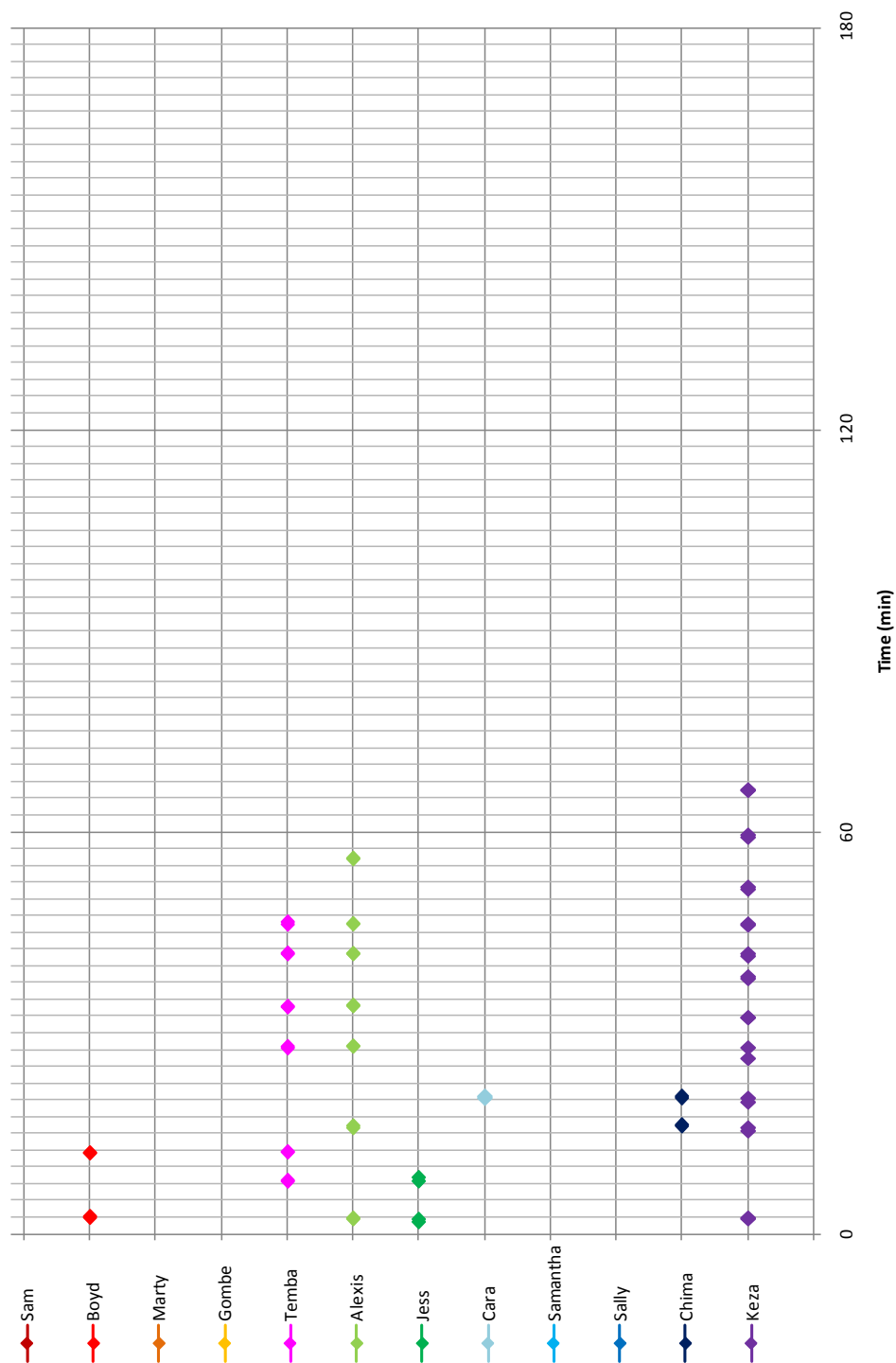


Figure 3.13d. Start and stop times for defined behaviours related to the group's use of the Marbleroll enrichment item, with slides present, during the fourth session within Experiment 3. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.



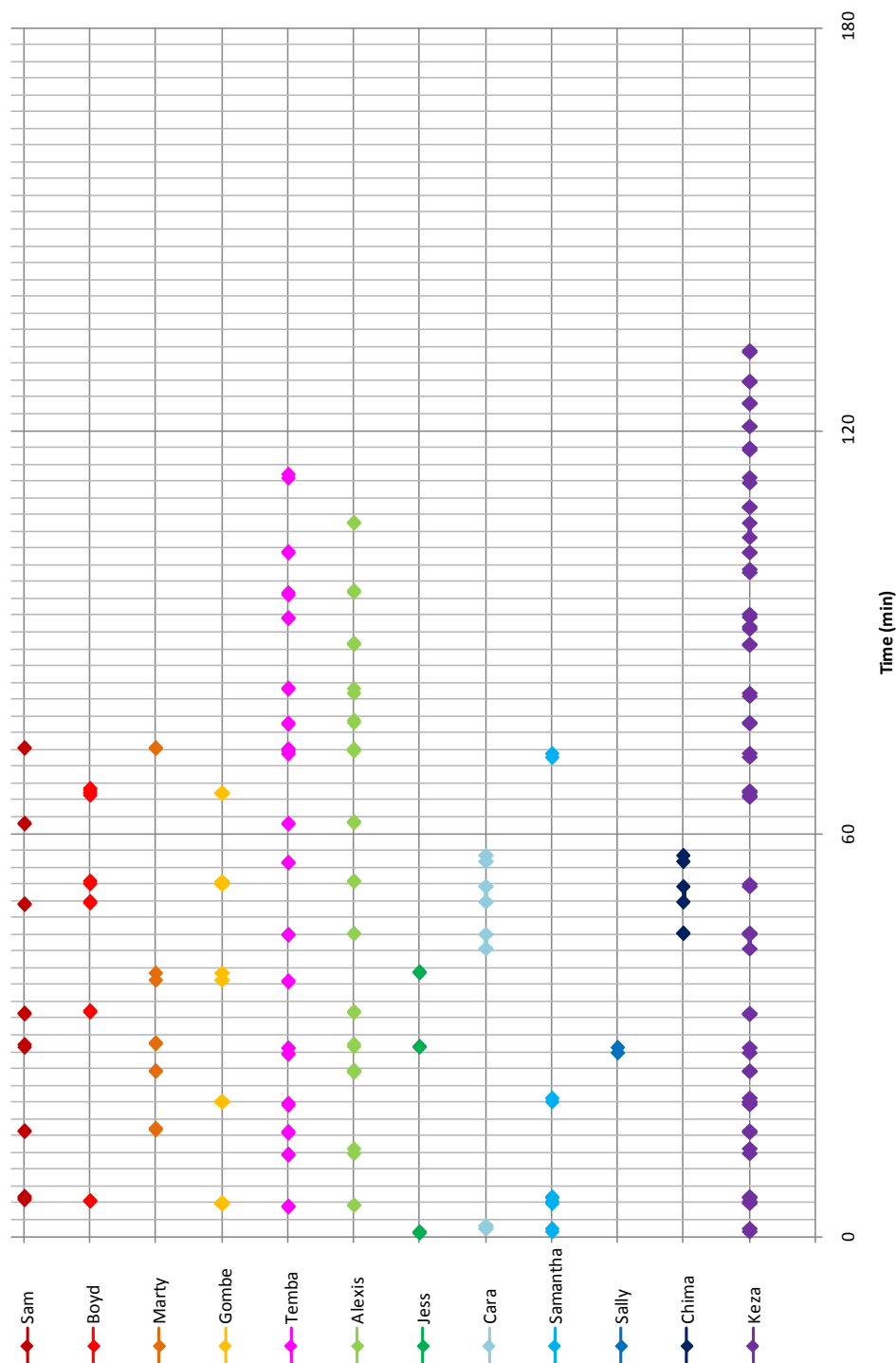


Figure 3.14a. Start and stop times for defined behaviours related to the group's use of the Marbleroll enrichment item, delivering coated peanuts, during the first session within Experiment 3. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

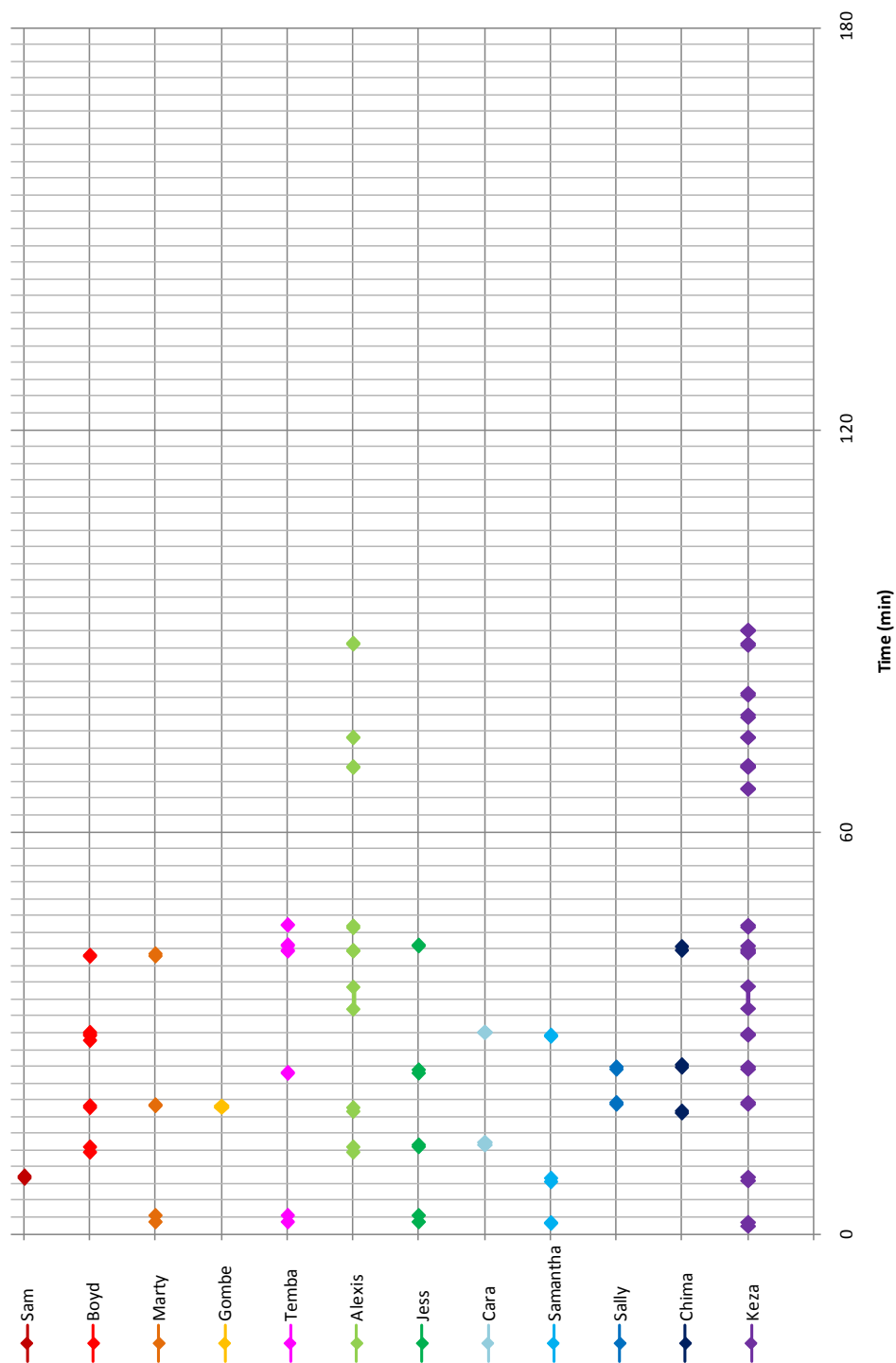


Figure 3.14b. Start and stop times for defined behaviours related to the group's use of the Marbleroll enrichment item, delivering coated peanuts, during the second session within Experiment 3. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

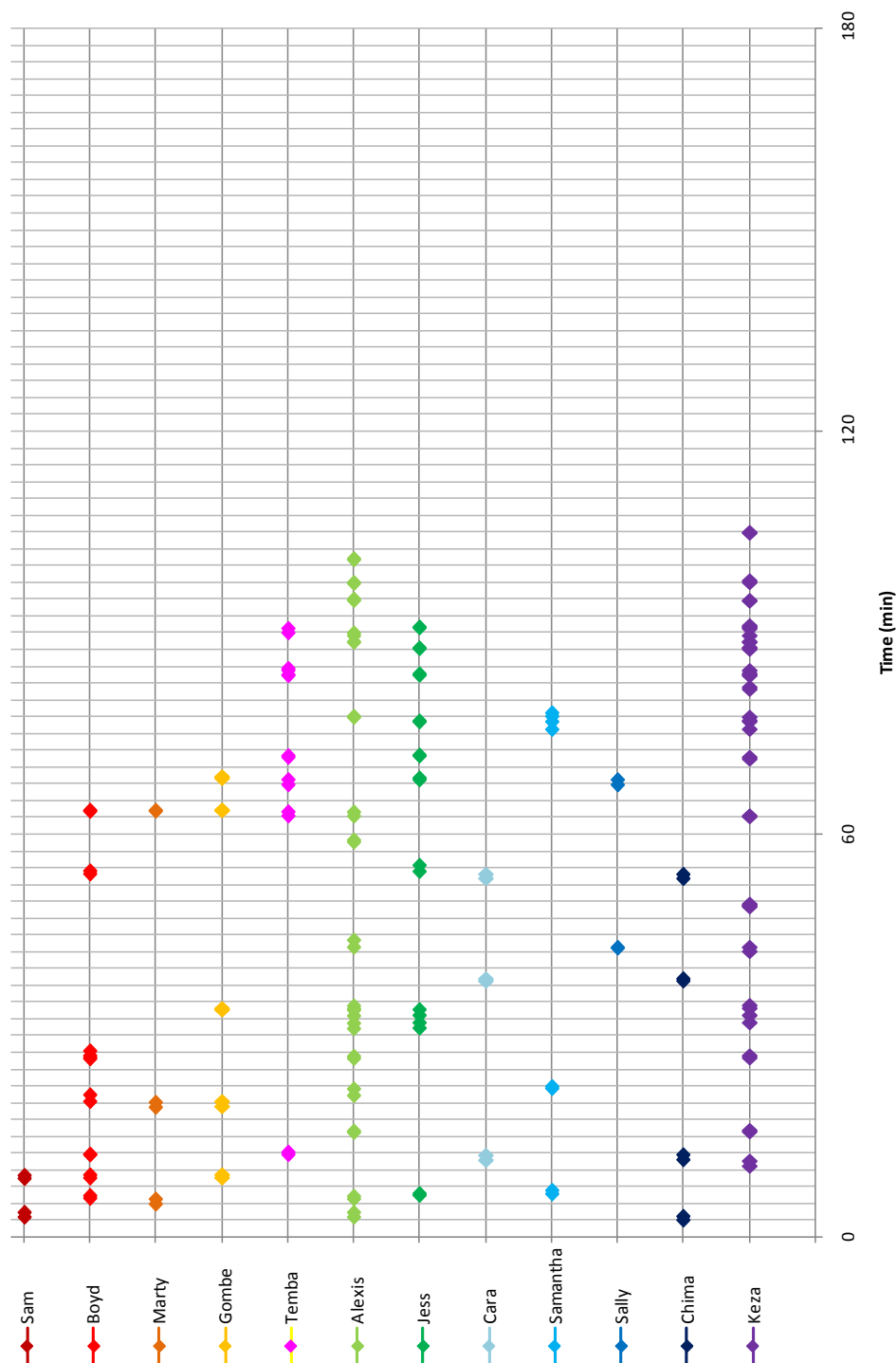


Figure 3.14c. Start and stop times for defined behaviours related to the group's use of the Marbleroll enrichment item, delivering coated peanuts, during the third session within Experiment 3. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

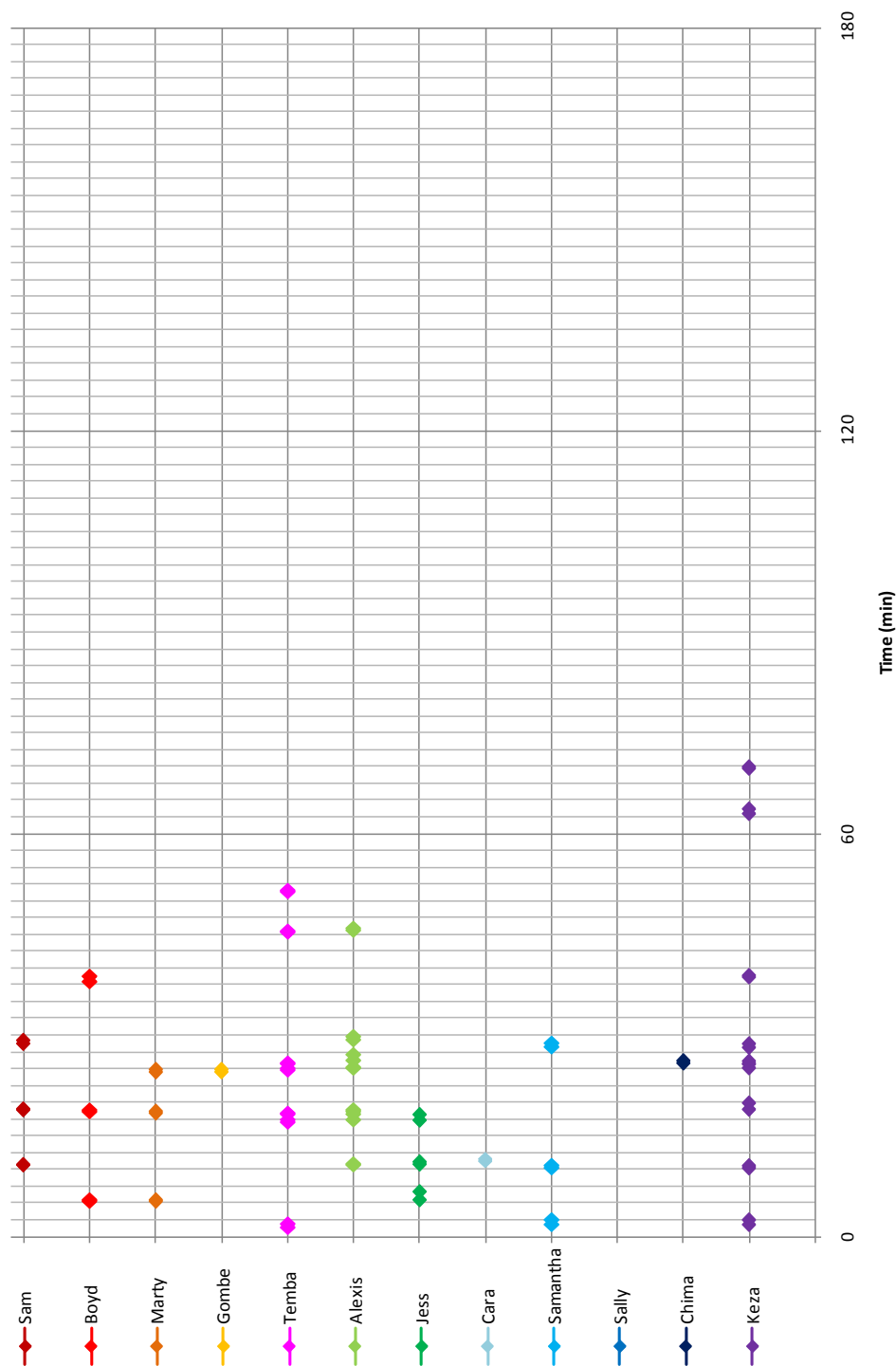


Figure 3.14d. Start and stop times for defined behaviours related to the group's use of the Marbleroll enrichment item, delivering coated peanuts, during the fourth session within Experiment 3. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

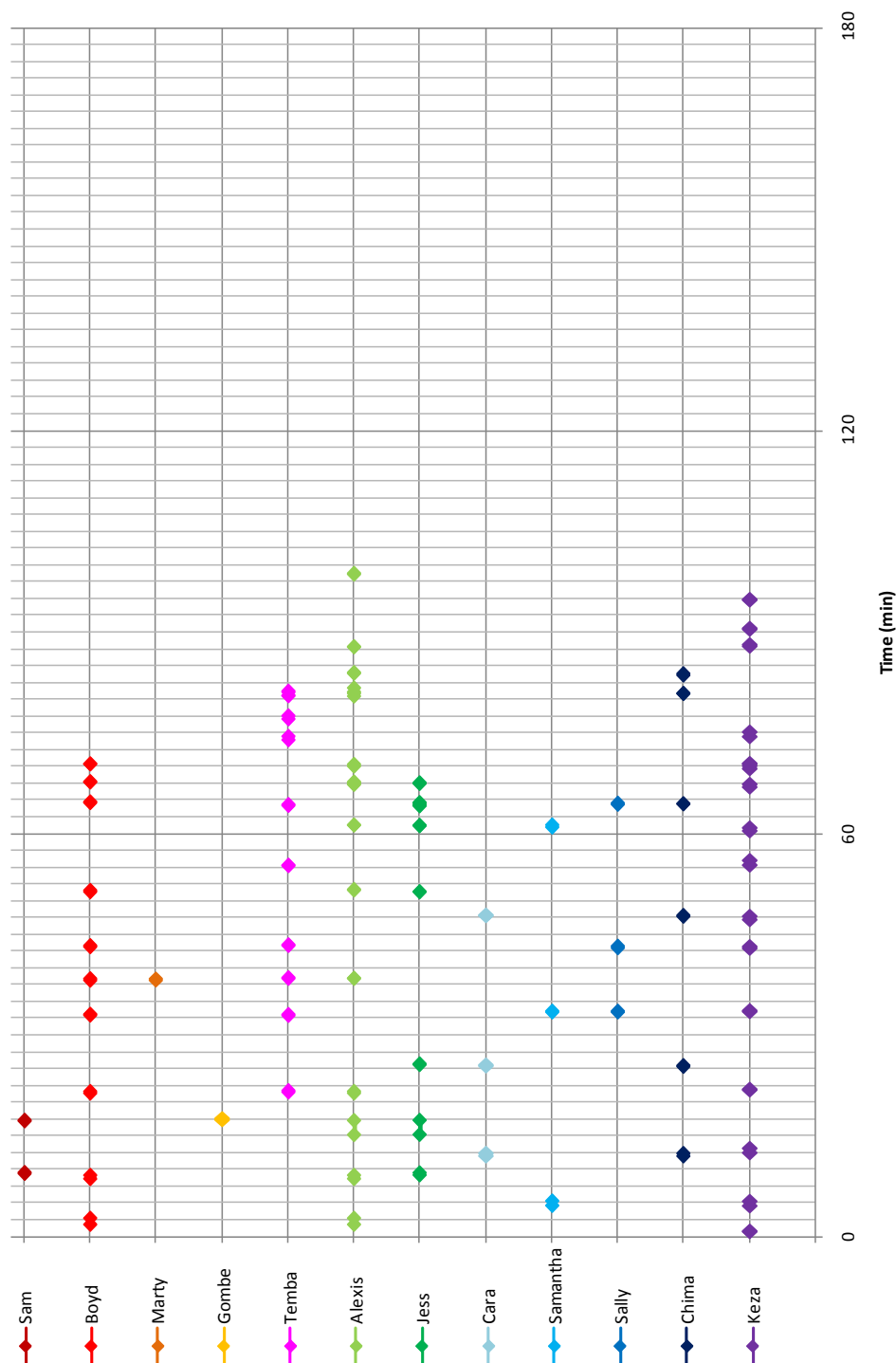


Figure 3.14e. Start and stop times for defined behaviours related to the group's use of the Marbleroll enrichment item, delivering coated peanuts, during the fifth session within Experiment 3. Figure. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

Individual Behaviour Related to Enrichments

Figures 3.15a to 3.15h show the behaviour (as defined in Table 2.2) of individual chimpanzees. Within the entire chimpanzee group juvenile female Keza was the individual to interact the most with the enrichment items overall. However, adult female Jess and juvenile male Alexis used the Dipper and the Screwfeeder more than Keza and adult female Samantha interacted with the TV/Video more. Adult females Cara and Sally spent very little time interacting with the enrichment items and the time they did was mainly with the Screwfeeder. Adult male Sam used the items very little and spent the most of his use time with the Dipper enrichment.

Jess was the individual to be observed the most of the entire group using an enrichment item, this occurred mainly with the Screwfeeder enrichment. Alexis and Jess were the individuals that most spent time using an enrichment item at the same time another subject was. Alexis spent the most amount of time in the experimental area simply present, and not interacting in any way with an enrichment item.

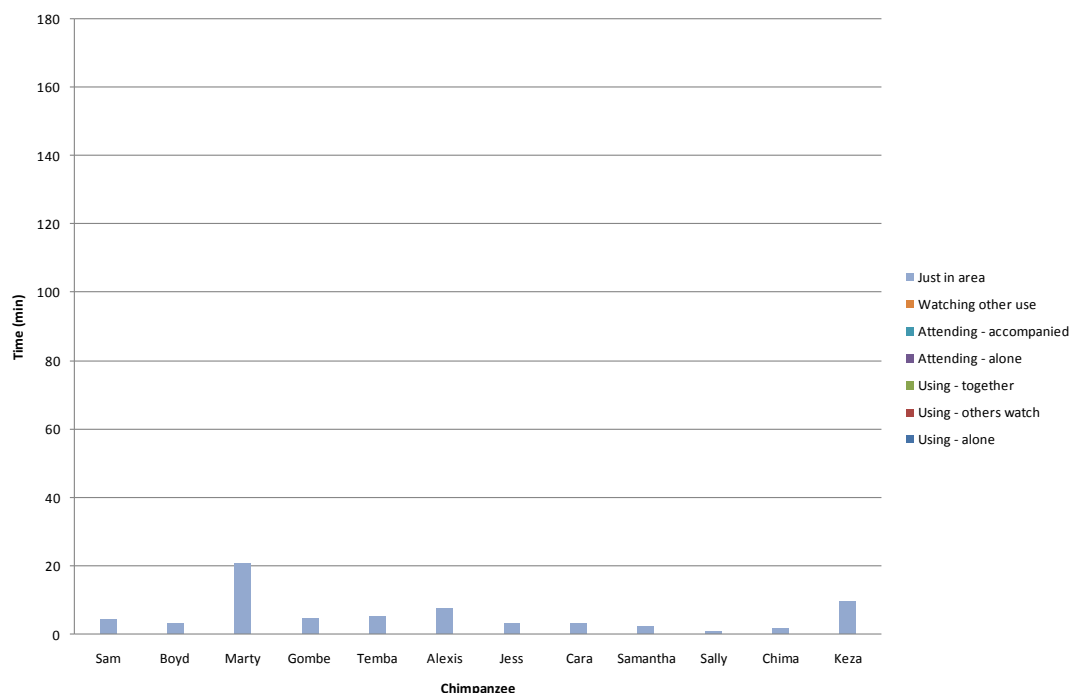


Figure 3.15a. Total time that the individuals of the chimpanzee group exhibited defined behaviours during Baseline sessions in Experiment 3. Individual chimpanzees are arranged in order of sex, males on the left and then age within each sex group, oldest on the left.

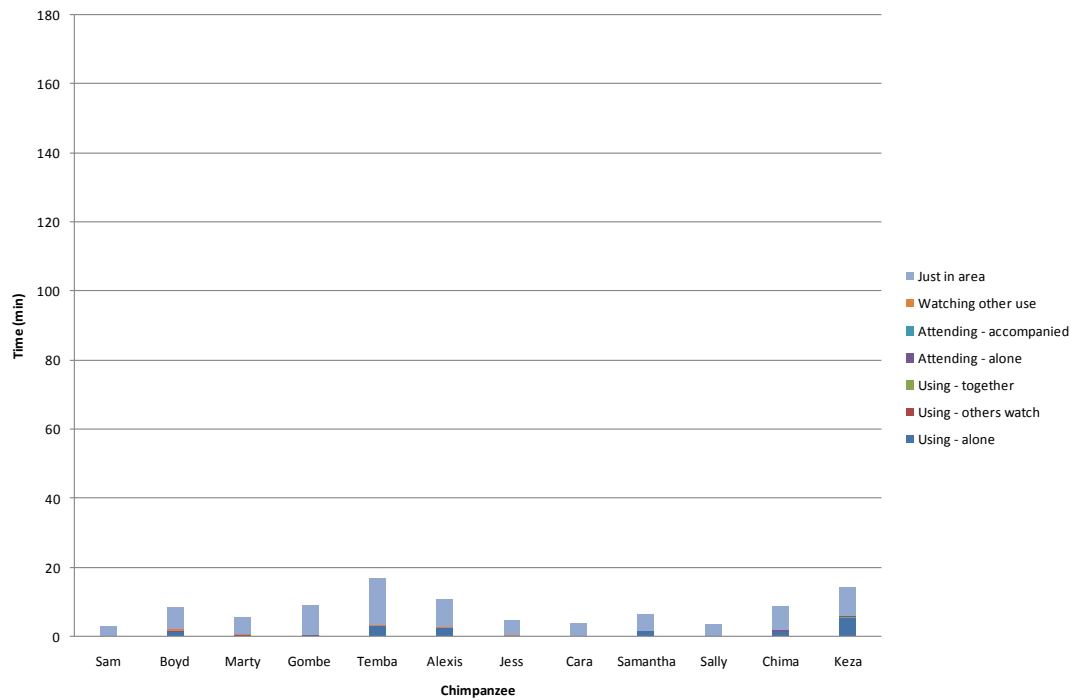


Figure 3.15b. Total time that the individuals of the chimpanzee group exhibited defined behaviours during sessions with the Musicbox enrichment in Experiment 3. Individual chimpanzees are arranged in order of sex, males on the left and then age within each sex group, oldest on the left.

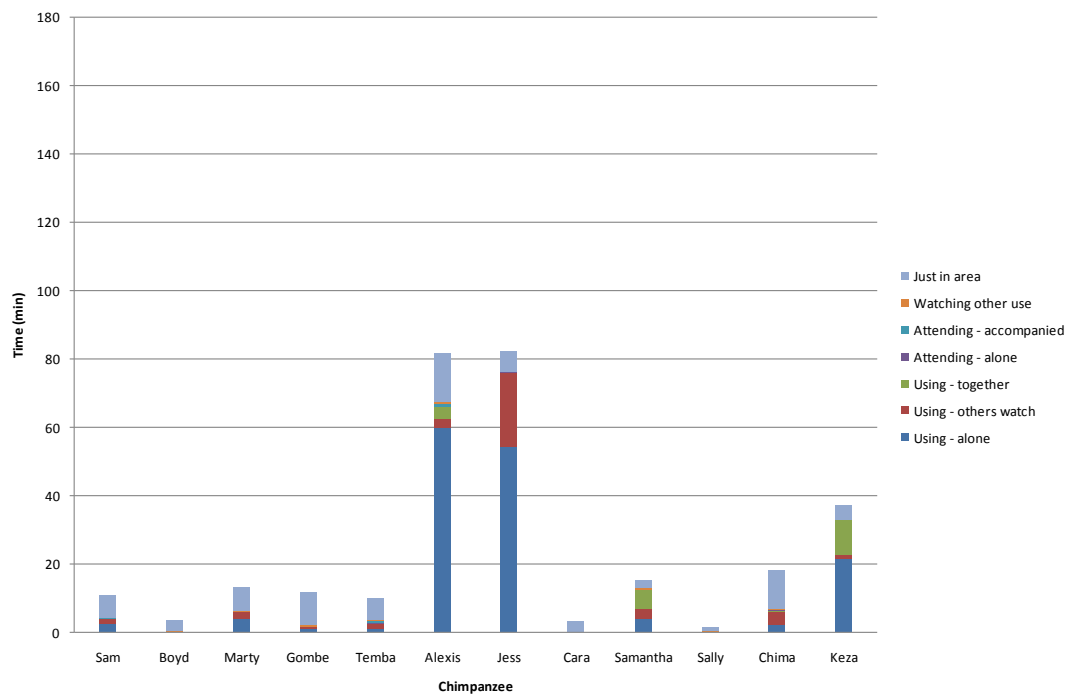


Figure 3.15c. Total time that the individuals of the chimpanzee group exhibited

defined behaviours during sessions with the Dipper enrichment in Experiment 3. Individual chimpanzees are arranged in order of sex, males on the left and then age within each sex group, oldest on the left.

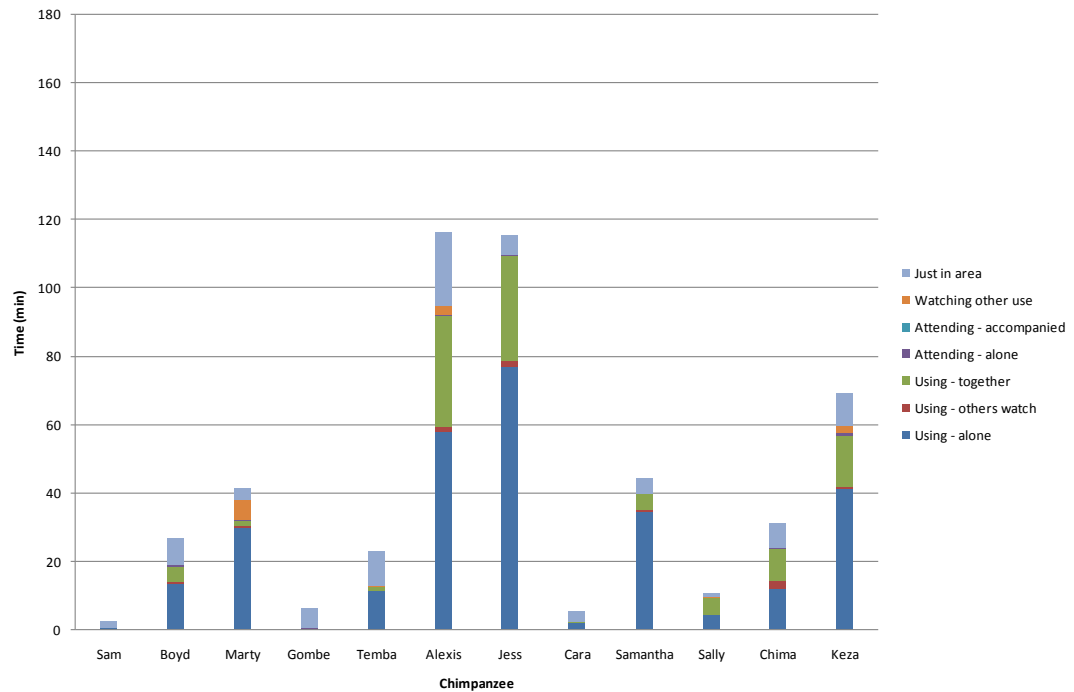


Figure 3.15d. Total time that the individuals of the chimpanzee group exhibited defined behaviours during sessions with the Screwfeeder enrichment in Experiment 3. Individual chimpanzees are arranged in order of sex, males on the left and then age within each sex group, oldest on the left.

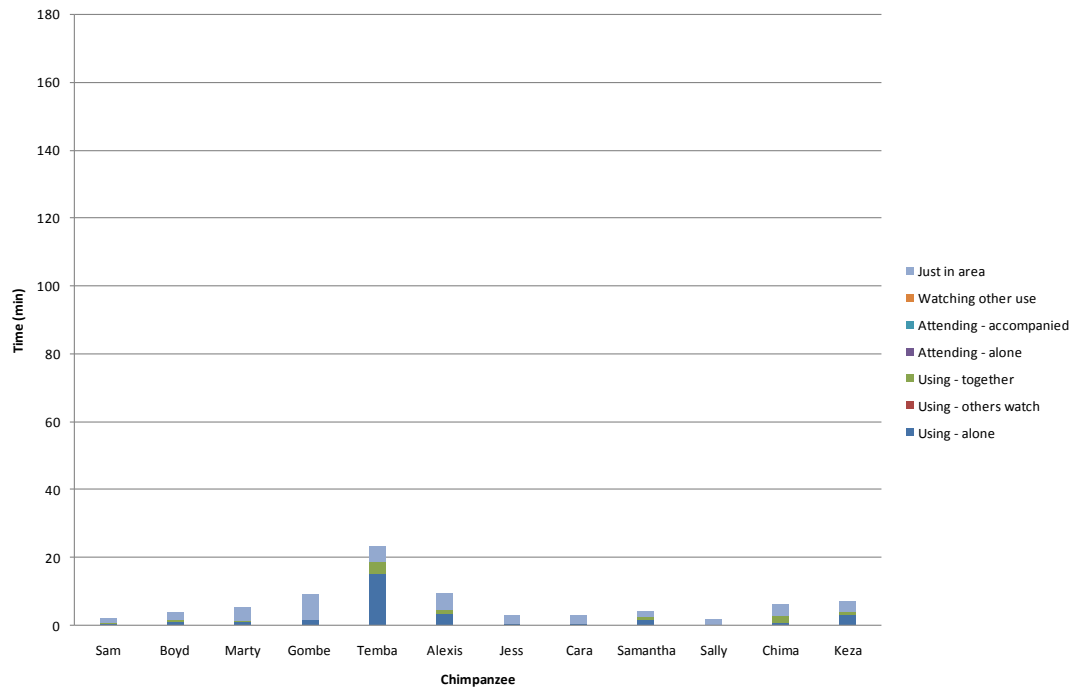


Figure 3.15e. Total time that the individuals of the chimpanzee group exhibited defined behaviours during sessions with the TV/Video enrichment in Experiment 3. Individual chimpanzees are arranged in order of sex, males on the left and then age within each sex group, oldest on the left.

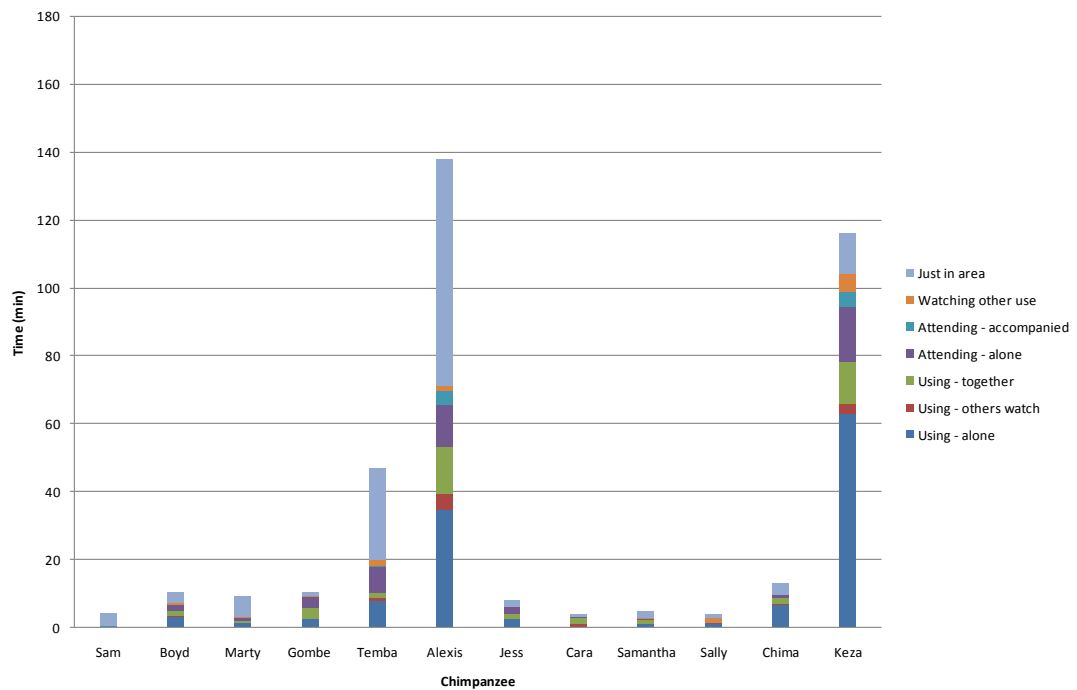


Figure 3.15f. Total time that the individuals of the chimpanzee group exhibited

defined behaviours during sessions with the Marbleroll enrichment - delivering marbles and Jaffas™ (without slides), in Experiment 3. Individual chimpanzees are arranged in order of sex, males on the left and then age within each sex group, oldest on the left.

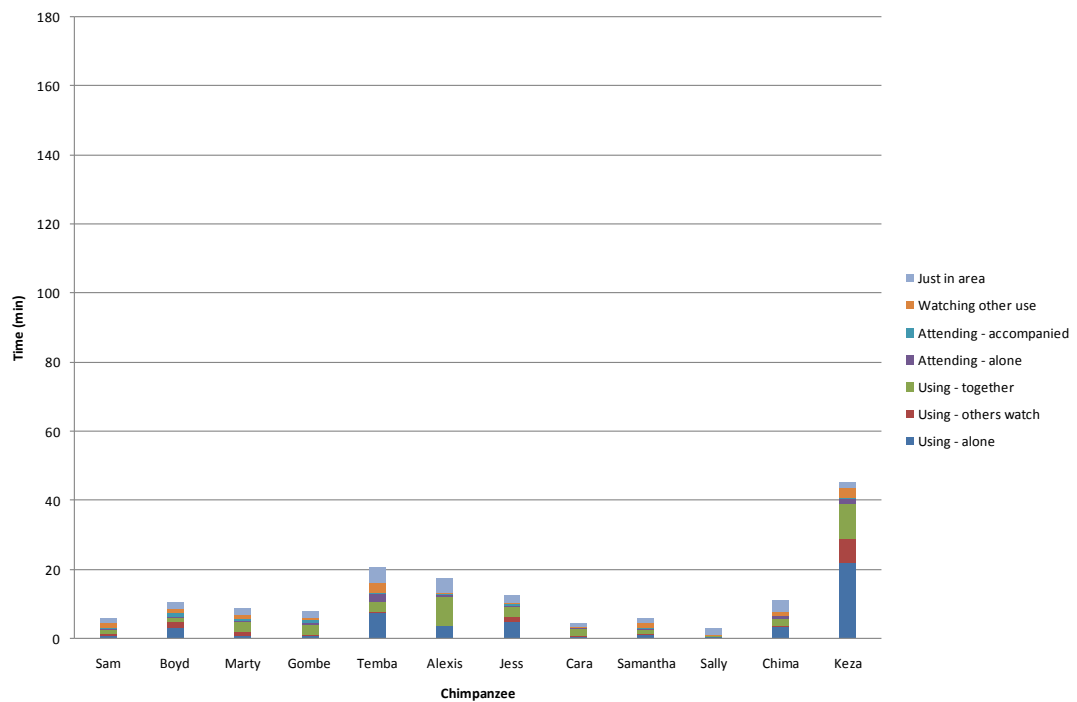


Figure 3.15g. Total time that the individuals of the chimpanzee group exhibited defined behaviours during sessions with the Marbleroll enrichment - delivering marbles and Jaffas™ (with slides), in Experiment 3. Individual chimpanzees are arranged in order of sex, males on the left and then age within each sex group, oldest on the left.

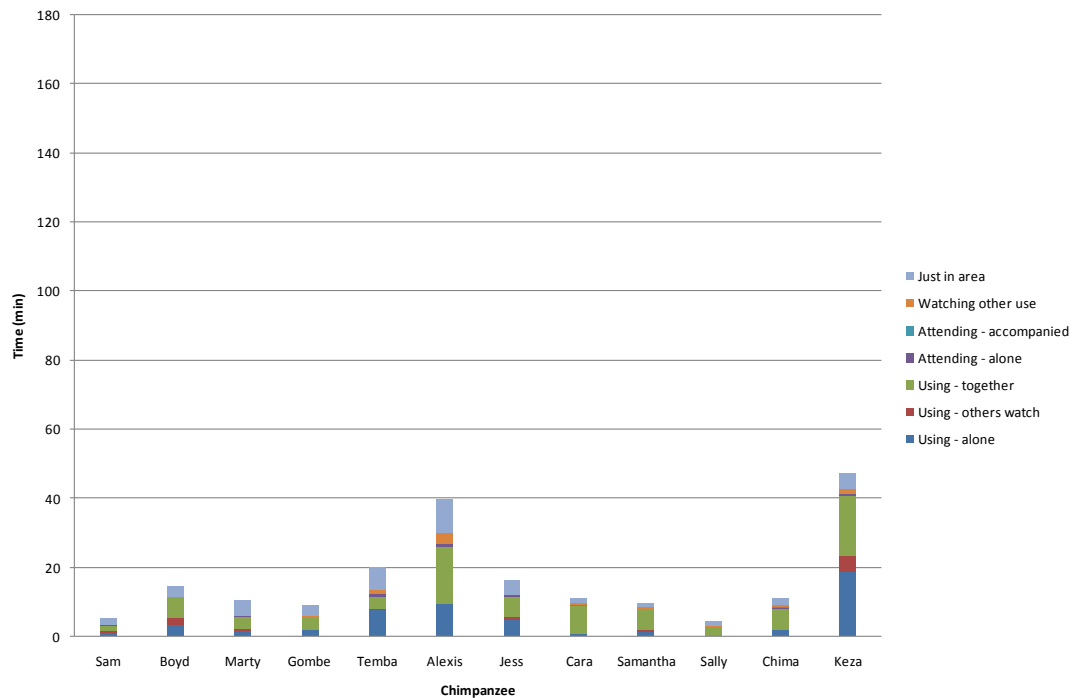


Figure 3.15h. Total time that the individuals of the chimpanzee group exhibited defined behaviours during sessions with the Marbleroll enrichment - delivering coated peanuts, in Experiment 3. Individual chimpanzees are arranged in order of sex, males on the left and then age within each sex group, oldest on the left.

Discussion

This study showed the chimpanzee group's overall interest for the enrichment items when they were presented freely, without any work required to gain access to them. The type of behaviour exhibited and the quantity of this behaviour was examined.

Group Behaviour During Sessions When Given Free Access to Enrichment Items

Across all of the sessions during this study the chimpanzee group (when within the visible area) spent most of their time using the enrichment items individually. Of the studies that have explored object use in a group or social setting none have examined the time spent in activities (associated with the objects) related to participation in the activity with multiple subjects at one time. Given this is the case no comparison with prior research can be made.

In general, the group – multiple subjects - spent a small proportion of the time

in the sessions within the experimental area (within view of the video camera), simply present but not interacting in any way with an enrichment item (Just in area). Also, little time was spent using an enrichment item while another individual observed this (Using – others watch), or watching another individual using an item (Watching other use). Only a short amount of time was spent by the group using an item at the same time another subject was (Using-together) and orientated towards an item but not interacting both while alone (Attending-alone) and with another subject (Attending – accompanied). Some sessions did show the chimpanzees exhibiting these behaviours more (in particular ‘Just in area’, and the other use categories). These results would suggest that the presence of the items did cause the group to spend more time within the experimental area, even if they were not directly interacting with the enrichment item. This finding may have been due to the social pressures evident in a hierarchal group. For example, individuals lower in the hierarchy may have been present in the area but waiting for the right time to interact with the enrichment item, such as when higher ranking individuals had left the area.

When the Screwfeeder was available, individuals spent a considerable amount of time using the item at the same time another member was (Using-together). Members also used the Marbleroll together for a large proportion of the time that they used the item when it was available and delivering coated peanuts. These findings would suggest that although the enrichment items, and the way in which they were provided, afforded multiple subject the opportunity to use the items at once, the vast majority of users choose to use the items independently. Findings also show that when the enrichment items were provided very little behaviour other than ‘use’ was evident in association with their provision (such as looking at them). If the chimpanzees chose to be in the experimental area then it would seem that they did so primarily to use the enrichment items.

Use of Enrichment Items

The majority of the time enrichment items were used within the first five minutes of the sessions. In general, the enrichment items were used more earlier in the sessions than in the latter part of the sessions. Very little use of the enrichment items took place during the third hour of any session. This finding would be supported by research that suggests object use is increased for novel items (Menzel, 1971). However, the time of day the sessions of this current research were conducted

may have contributed to this finding related to the use in the third hour (in terms of the change of day light). A full discussion of this will occur in the General Discussion of this thesis.

Juvenile female Keza was the chimpanzee from the group that most often interacted with an enrichment item first within the sessions. Adult members of the group were the subgroup that interacted with an enrichment item earliest the least. In this study, although the adult and more dominant members of the group did not interact first with the enrichment items, the adults used the enrichment items more during the earlier portion of the sessions. This finding was similar to that of Bloomstrand et al. (1986), who also found that adult chimpanzees used a commodity earlier in sessions. A possible explanation for the findings of this current research may be that younger members of the chimpanzee group were more responsive to novel stimuli within their environment. However, once these individuals had begun using the enrichment items the older, and more dominant, members of the group took over. Rather than it being the case that adult members use the items earlier in sessions and younger members later, instead it could be viewed that given their status the adult members used the items when they wanted to. However, the younger members were required to wait until the item was free, or at least being used by an individual they could safely interrupt (such as another young subject).

The vast majority of the periods of use of the enrichment items were brief (a couple of minutes) even though the enrichment items were freely available throughout every session. However, longer periods of use did occur, the longest was with the Screwfeeder and was 15.85 min long (by the adult female Jess). The highest frequency use occurred with the Screwfeeder. The Dipper enrichment also resulted in some longer periods of use. The impact of other social behaviour or restrictions related to the presence of other group members may have contributed to the number of brief periods of use. For example, individual chimpanzees that held lower rankings in the social hierarchy may have been under social pressure and as such kept the time they interacted with the commodities to a minimum. However, for items that individuals preferred this time was extended. A full discussion of the findings of this current research in regards to bouts of use will occur in the discussion of Experiment 6.

Habituation

Much research with non-human primates has shown that objects are used more when they are novel (e.g., Brent, Lee & Eichberg, 1989; Cardinal & Kent, 1998; Paquette & Prescott, 1988; Pruetz & Bloomsmith, 1992; Taylor, Brown, Davis & Laudenslage, 1997; Vivian, 2001). In this current research the use of the Musicbox, the auditory enrichment device, declined markedly across the sessions with it. Between the various foraging enrichment items the degree of habituation differed. The group showed very little habituation with the Screwfeeder enrichment, using it for more time during the last session with the item than in the first session with it (with peak use occurring on the third session). However, the Dipper enrichment was used by the chimpanzee group for a lot less time in the sessions after the first session with it. Previous research with this group of chimpanzees (Vivian, 2001) found that the subjects reduced the amount of time they spent using a variety of foraging enrichments. Items in that study included such things as puzzle feeders and stuffed feeding tubes. This finding was the same for all of the enrichment items, regardless of their relative degree of complexity. In research such as conducted by Tarou et al. (2004) increased complexity was identified as reducing object habituation. In this current study the Screwfeeder enrichment was not the most complex object. However, other studies have also found that objects have proved to be more interesting if they include food (Crockett, Bielitzki, Carey & Velez, 1989; Phillippi-Falkenstein, 1993; Rooney & Sleeman, 1998). This current study would support this finding. The fact that the group showed little habituation to the Screwfeeder may have related to combined factors of complexity, the chimpanzees' food preference, and the frequency of food delivery associated with this enrichment.

In this current study, the group used the TV/Video item for 16.56 min in the first session with the item and 7.32 min in the last (fifth) session with it. Research has showed various results in regards to habituation to audiovisual enrichments. Bloomsmith et al. (1990b) found that the habituation to the videotape enrichment provided in their study only occurred with the socially housed subjects, and not with the singly-housed subjects. Brent et al. (1989) also found individually housed chimpanzees showed no evidence of habituation to watching television. While Platt and Novak (1997) also found that both socially- and individually-housed monkeys showed little habituation to watching videotapes. Bloomsmith and Lambeth (2000) found the socially housed yet individually-tested chimpanzees showed some

habituation to the videotapes but viewing time was still substantial. The findings of this current study concur with the research which has shown habituation to audiovisual enrichment devices in a social setting with primates. This habituation may be due to the availability of other activities in a social setting, rather than using the experimental equipment.

Group Preference for Enrichment Items When Given Free Access

The judgement of preference for items in this study was made via a comparison of the time the group spent using each enrichment item, when each enrichment item was presented independently. If a comparison of total time of use is used as a measure of preference then the chimpanzee group showed a preference for the Screwfeeder enrichment when the items were provided freely. The order of preference from most preferred to least was Screwfeeder; Dipper; Marbleroll, delivering marbles and Jaffas™ without slides present; Marbleroll, delivering coated peanuts; Marbleroll, delivering marbles and Jaffas™ with slides present; TV/Video enrichment and the Musicbox was the least preferred. The fact that the foraging enrichments were preferred over the non-foraging enrichments supports the findings of other research (Holmes et al., 1995; Menzel, 1991; Vivian, 2001).

The order of preference based on each item's intrinsic effort required to use the item or access a food component, and the control afforded by the item and complexity of the item did not appear to be consistent with the ranking of the items. The Musicbox was the only enrichment item that needed to be manipulated by the chimpanzees for them to extract an active enriching effect (separate to visual complexity etc). All of the items that included a foraging component required the chimpanzees to manipulate the food item in order to consume it. The Screwfeeder, for example, during the Free Access experiment (Experiment 2) was automatically operated (via a computer programme). The chimpanzees were not required to manipulate it for it to operate. However, even during Experiment 2 the chimpanzees spent more time with the Screwfeeder than the Musicbox. In addition to this, with the Marbleroll enrichment when the slides were included in the unit (and therefore there was more potential for the chimpanzees to manipulate the item) (such as in Experiment 3) the chimpanzees spent less time using the item than when the slides were not included.

Preference Related to Intrinsic Effort, Control and Complexity

Each of the enrichment items employed in this current research afforded the chimpanzees varying degrees of control and varied in complexity. Although during this experiment no work was required for the chimpanzees to gain access to operable enrichments (in terms of an initial response), some of the enrichment devices intrinsically had some effort required to gain access to reinforcement. The element of intrinsic effort was part of the qualities of the enrichment devices and the degree of effort required varied between the enrichment items.

Of all of the foraging enrichment devices the Marbleroll, without slides present, allowed the chimpanzee group to access food reinforcers with the least required effort. This was the case when it was in this form and delivering marbles and Jaffas™ and when it was delivering coated peanuts. A single unit of food was delivered, most times, into the hand of a subject, and if not, was picked up off the floor. When the slides were present and delivering marbles and Jaffas™ the subjects needed to manipulate the slides on the unit to allow the food items to eventually be available. For subjects to gain access to the food within the Dipper enrichment they were required to use the tool provided.

The Screwfeeder enrichment delivered sunflower seeds, which were scattered in a small area on the ground in front of the unit, and the chimpanzees would then forage these seeds. Although the seeds were not scattered over a large area, in comparison to some of the other enrichment items the Screwfeeder was not the item that required the least effort to access a food item - even though it was the item used the most of all of the enrichment items.

The Marbleroll unit delivered only one edible item, Jaffa™, occasionally and no more than 10 every hour. But when the Marbleroll unit was delivering coated peanuts a food item was delivered each time, just as it was when the Screwfeeder operated. In addition to this, the Marbleroll (without the slides present) and delivering marbles and Jaffas™, was used more by the group than when the Marbleroll was delivering coated peanuts. This was the case even though a coated peanut was delivered each time the unit operated, and the edible Jaffa™ was only delivered occasionally and no more than 10 every hour. This would indicate that the Jaffa™ food item was preferred over the coated peanuts. There is no current data relating to chimpanzees' preference between chocolate and nuts. However, in this current study the subjects were seen to consume the items in different ways, the

coated peanuts almost immediately and the Jaffa™ after a longer period of time and inspection. This may suggest that the Jaffas™ were preferred over the coated peanuts. A preference test with simply the food items, without the enrichment item delivery, being presented would perhaps confirm this. However, as a comparison of enrichment devices can be based on more than just a comparison of method of food delivery, it may have been the case that the marble component of the Marbleroll unit (i.e., the travel down the tracks and the operation and travel of the lift) contributed to the fact the unit was used more when the enrichment delivered marbles and Jaffas™ than when it delivered coated peanuts.

Control and complexity have been identified as key factors in the provision of enrichment items to captive animals (Mench, 1998; Sambrook & Buchanan-Smith, 1997; Videan et al., 2005). Poole (1998) suggested that ‘achievement’ is key component of enrichment items. Yet in this current research a ranking of items based on use would not mirror a ranking based on giving subjects the ability to ‘achieve’ or effort or ‘work’ required. As previously discussed research on the topic of contrafreeloading suggests that prior training, deprivation level, required effort, stimulus change, environmental uncertainty, rearing conditions, manipulation of the environment and the nature of the foraging task impact on the level at which animals work for food in the presence of free food. It would seem the application of such findings would be of importance in the assessment of effective (in terms of use) enrichment items as some items require more ‘work’ than others. The findings of this study would suggest that judgement of the control an item affords an animal and the inherent complexity of the item may require further investigation.

Food vs. Non-food Enrichments

The enrichment items that had a food component were used far more than those that did not. This finding was similar to other studies that have compared use between the two different categories of enrichment items (Holmes et al., 1995; Menzel, 1991; Vivian, 2001). A previous study conducted by the researcher (Vivian, 2001) explored this same chimpanzee group’s use and behavioural responses to various categories of enrichment, occupational-foraging, occupational-structural and a combination of these enrichment types. The items were provided freely. However, some items were available simultaneously to other items, while some were provided at a time in the day when the other items may have already been used. Taking this

into account, during the study when non-food enrichment items were compared to enrichments that contained a food component (foraging enrichments) the foraging items were used for more time.

The audiovisual (TV/Video enrichment) and audio (Musicbox) enrichment devices, or sensory stimulation devices (the only enrichments that did not include any food component) were used by the group for a very small amount of the time available during the sessions of this study. The Musicbox enrichment included the feature of control, in terms of the fact that subjects could choose which buttons to push, which sounds to hear, whether to hear anything at all, or whether to play a small piece of music, however, the group did not use the item for more than 15 min in a session. Control has been a factor recognised by researchers as being critical for the effectiveness of environmental enrichment items (e.g., Mineka et al., 1986; Novak & Drewson, 1989; Poole, 1998; Sambrook & Buchanan-Smith, 1997). However, even though control was a feature of the Musicbox enrichment it was not used by the chimpanzee group for a substantial amount of time during sessions with it, nor in comparison to use of the other enrichment items.

Many researchers have shown behavioural changes related to the provision of auditory stimulation. These have included increased species typical behaviour (e.g., Drewsen, 1989), a decrease in stress (e.g., Drewsen et al., 2006) and aggression (Howell et al., 2003), both a decrease and increase in arousal (dependant on age) (e.g., Ogden et al., 1994) and a decrease in abnormal behaviour (e.g., O'Neill, 1989). Even though these behaviour changes have been reported after time with some form of audio enrichment device, none have reported any form of preference for the presence of these devices. Whether the audio enrichment device presented here, the Musicbox, had a beneficial effect for the chimpanzee behaviour (although not a focus of this current research) may be a moot point as the members of the group choose not spend much time using the item, even though they were free to do so. Although it should be noted they it is not clear how much time spent with an audio enrichment device is needed to have a positive impact on well-being. These findings may have been related to the chimpanzee group's preference for the type of audio stimulation they had access to. The musical notes and the pop song included with this device may not have been of interest to the group. This suggestion could be explored by presenting different types of audio enrichment to the group and assessing group preference for these.

Enrichment through visual and audiovisual stimulation have been advocated by researchers (e.g. Andrews & Rosenblum, 1994; Bloomsmith & Lambeth, 2000; Washburn & Rumbaugh, 1991) and have been shown to have positive impacts on the behaviour of animals, including primates (e.g., Andrews & Rosenblum, 1993; Washburn & Hopkins, 1994). Bloomsmith et al. (1990b) found that chimpanzees, given the opportunity to view video content, socially and then individually, watched the videos for 42% of the total time they were available. This is a lot less than the maximum time this group of chimpanzees watched the TV/Video enrichment item in any one session, which was 9.20% of the time. This was even though, as Maple and Hoff (1982) suggested, the information that was presented in the TV/Video enrichment was ‘meaningful’ to the individuals (it included footage of themselves and humans that they were familiar with). Although it should be acknowledged that ‘familiar’ may not have equated to being ‘meaningful’ enough for the chimpanzees to spend time using the enrichment. Bloomsmith and Lambeth (2000) found that the chimpanzees in their study responded no stronger to videos of conspecifics than they did to those containing images from standard television programming so perhaps what is ‘meaningful’ to chimpanzees in terms of audiovisual content needs to be explored further in other studies.

Much of the research conducted with animals and audiovisual enrichments has been in the laboratory environment utilising laboratory raised animals, many of which have been singly-housed and tested. Therefore, given that this group of socially-housed and tested individuals used the audiovisual item for very little time could suggest that it was the fact that this group of subjects were held in a social group in a zoo setting that was the reason for the relatively low interaction with the item. However, Schapiro and Bloomsmith (1995) also found that singly-housed yearling rhesus monkeys watched videotapes, with footage of other primates, for less than two minutes per hour of the presentations. While Platt and Novak (1997) found that socially- and individually-housed rhesus monkeys spent a substantial amount of their time attending to video content. The videotape content they used in their research included footage of unfamiliar and familiar conspecifics and unfamiliar humans (from a soap opera TV programme) and familiar humans. These studies do not seem to show any relation between the number of companions and level of use of audiovisual enrichments. It may be that the number of companions that are present is not the factor that impacts on the level of use of these enrichments. But rather that it

is the quality of the interactions of subjects with companions or other resources in their environment that impacts on the interactions an animal has with audiovisual enrichments. In this current study the chimpanzees had a variety of other activities they could do rather than using the enrichment items. These including solitary activities such as use of toys or objects in the enclosure and social activities such as grooming and social play.

Individual Differences in Preference for Enrichments

In this study the highest user of the enrichment items was the juvenile female Keza. Keza used the items for the longest duration for four of the seven forms of enrichment item and used five of the items most frequently. Adult female Jess, however, used a single enrichment item for the longest duration, this was the Screwfeeder enrichment. Adult females Cara and Sally interacted the least with the enrichment items the least out of all members of the chimpanzee group and, other than the Dipper enrichment, adult male Sam also used the enrichment items very little.

Reinhardt (1997) found sub-adult singly-housed rhesus macaques spent more time using an enrichment item than the adults. Videan et al. (2005) also reported that the younger chimpanzees in their study used the destructible items more. These findings would be supported by this current study. In general, the younger members of the group used the enrichment items more during this current research than the adults did. Jess, however, was the exception to this. Brent and Eichberg (1991), who found that the more dominant chimpanzees in their study were not the biggest users, suggested that this may have been due to in part to their large fingers and the lessened dexterity of the large adults. However, this suggested cause would not be supported by the findings here as Jess, one of the largest chimpanzees in this study, was one of the biggest users of the enrichments. Bloomstrand et al. (1986) found that the most dominant individual chimpanzees in their research had the highest level of overall use of an enrichment item (puzzle feeder). However, dominance did not directly correspond in many cases and they suggested that other factors may have been of influence. These were suggested to be prior experience, individuals' response to novel stimuli, and individual deprivation. These factors may have also been the influence in this present research.

A possible cause of the adults, and the more dominant individuals within the

group, using the enrichment items less during this study may relate to the other behaviours that occurred during the period when the animals were brought into and maintained in the Indoor Area. In coming into the Indoor Area at night the chimpanzee group was not only changing settings but was coming into an enclosure markedly smaller than that in which they had been in for the day. As the chimpanzee group has a hierarchical social structure, this change of environments can have impacts on the dynamics between individuals. The more dominant members of the hierarchy, predominantly the adult males Boyd, Marty, Gombe and Sam, spent time walking around the area, 'patrolling', in affiliative behaviour (grooming each other) and exerting their dominance (predominantly seen in aggressive behaviour directed towards individuals lower in the dominance hierarchy). This possible explanation would be supported by Fitch et al.'s (1989) suggestion that the frequent interactions among adult male members of chimpanzee groups in the wild are critical for group cohesion.

Conclusion

This study was successful in employing a free access choice test to explore the preference of the chimpanzee group for the various enrichment items. Bouts of use of the items were generally brief and this may have been due to social influences of the group environment and the testing taking place in a setting that allowed for many other activities. The results showed the group's preference for the enrichment items and based on the proportion of time the group spent using each item the items were able to be ranked in terms of the group's preference for them. The ranking showed a preference for the foraging enrichments over the non-foraging enrichments. This ranking was not consistent with consideration of the relative complexity of enrichments or the intrinsic effort involved in using them or the degree of control they afforded the chimps. Through this testing individuals' preferences were also able to be explored separate to the findings for the group and individual differences in preference for the enrichment items was established. Individual differences in the use of the items was evident, such as the younger individuals used the items more. Older individuals used the items earlier in the sessions, this may have been due to more dominant individuals having freer access to the items.

EXPERIMENT 4: SHAPING AND TRAINING WITH THE GROUP

In order to conduct the demand studies in this current research it was essential to first train the individual members of a socially-housed chimpanzee group to operate an operant lever to gain reinforcement and access to the enrichment items.

Positive Reinforcement Training with Animals in a Captive Environment

Previously the treatment or monitoring of animals' physical well-being has relied on the physical (e.g., in a crush) or chemical (e.g., anaesthetised) restraint of the animals. However, both of these methods can cause stress for the subject and increased risk to their health (Grandin, Rooney, Phillips, Cambre, Irlbeck & Graffam, 1995). Numerous studies have addressed how positive reinforcement training can be used to manipulate animal management-related behaviours, facilitating husbandry and veterinary care (Laule & Desmond, 1998; Prescott & Buchanan-Smith, 2003; Young & Cipreste, 2004). Non-human primates have been trained to present for blood pressure measurement (e.g., Segal, 1989; Turkkan, 1990); the application of topical drugs (e.g., Reinhardt, 1990b); offer urine, blood, or faecal samples for collection (e.g., Moseley & Davis, 1989; Phillipi-Falkenstein & Clarke, 1992); tolerate handling and restraint (e.g., Aarons, 1973; Heath, 1989), and move into a restraining device (e.g., Knowles, Fourrier & Eisele, 1995; Moseley and Davis, 1989; Reinhardt, 1990b) or portable transport cages (e.g., Heath, 1989; Kessel-Davenport and Gutierrez, 1994). Hoffmeister (1979) Carroll and Rodefer (1993) and English, Rowlett & Woolverton (1995) trained rhesus monkeys to self-administer opioids to conduct unit-price analysis.

Positive reinforcement training can be used to address issues unrelated to routine or specialised animal handling (Schapiro, Perlman & Boudreau, 2001). Training programs utilizing positive reinforcement techniques have been successful in reducing abnormal behaviour of captive animals, reducing aggression, improving socialization, reducing the stress that normally accompanies human manipulations while enhancing voluntary movement of captive primates and has potential to improve psychological well-being (Bloomsmith, Laule, Alford & Thurston, 1994; Bloomsmith, Stone & Laule, 1998; Laule, 1993b; Laule & Desmond, 1998; NRC/ILAR, 1998). Laule and Desmond (1998) illustrated that training has been proven to be useful in reducing abnormal behaviour. A bottlenose dolphin (*Tursiops*

truncatus) exhibited two behaviours – swallowing foreign objects and regurgitation – at a rate and frequency that indicated an abnormal behaviour pattern. The animal was trained to retrieve objects for a reward (a behaviour incompatible with swallowing the objects) and reinforcement occurred during times when regurgitation usually occurred. Subsequently the dolphin ceased swallowing objects and dramatically decreased its rate of regurgitation. Bloomsmith et al. (1994) were able to reduce aggression within a group of captive chimpanzees by using positive reinforcement to modify a dominant male response during feeding periods. Schapiro et al. (2001) utilised positive reinforcement training to alter the levels of affiliative interactions between members of group-housed rhesus macaques. They assert that higher levels of affiliation are associated with enhanced immune responses, thus successive training to increase this behaviour has a direct effect on animals' well-being.

Schapiro, Bloomsmith, and Laule (2003) suggest that two specific measures of effectiveness should provide custodians of primates in captivity the information needed to assess the value of implementing positive reinforcement training programmes. They are: a) the amount of time required to train particular behaviours, and b) the behavioural changes resulting from the training. It has been suggested that training itself can greatly increase the stimulation of an animal and be enriching for a captive animal (Laule, 1993a; Prescott & Buchanan-Smith, 2003) and present greater choice and control over events (Mineka et al., 1986). Poole (1998) expressed that caution should be taken to ensure that the training undertaken with captive animals is in the best interests of the animal and not for frivolous reasons (e.g. chimpanzee tea parties). Desmond and Laule (1994) and Young and Cipreste (2004) recommended that training should be well planned and conducted by skilled personnel.

Individual Differences

Although primates can be trained for participation in a wide variety of tasks, all primates cannot necessarily be trained for the same task or to the same level of competency. This may be due to aptitudes of different species (Schapiro et al., 2003), sex, age or individual differences (Bloomsmith et al., 1998; Schapiro et al., 2003). Characteristics of the species such as social hierarchy, may also affect individual outcomes (Schapiro et al., 2003). However, individual primates can be more relaxed in a social group (suffer less stress) than when isolated and can learn through observation of their conspecifics (Prescott & Buchanan-Smith, 1999). Factors such

as species and social and environmental factors would impact on this. Lonsdorf, Eberly and Pusey (2004) found that within a group of wild chimpanzees the females learnt how to fish for termites at a younger age than the males (younger by an average of 27 months); that they were more proficient than the males once they had acquired the skill; and that their technique was similar to that of their mothers, whereas the males was not.

Bloomsmith et al. (1998) utilised positive reinforcement procedures to train groups of captive chimpanzees to move between areas of their enclosure on request and be briefly restricted within those areas. They found significant age-by-sex interaction in the subjects' performance. Female subjects in their research required significantly fewer training sessions to reach reliable performance than the male subjects did. Adult males showing the lowest level of compliance during each phase of the study. Schapiro et al. (2003) described research to quantify the amount of time required to train rhesus monkeys living in small groups (one male to five to seven females) to perform certain target/control behaviours. One of their findings was that the lower ranking individuals in the group required little training to stay on their targets. Higher ranking individuals took longer and would typically leave their target to steal the reinforcers intended for another animal. They point out that training time will not be evenly distributed amongst members of a group. They also point out that an individual may have learned a behaviour but be unwilling to perform it within the social context of a group. Some may benefit from the proximity of conspecifics or from increased access to desirable food items. However, others may find new circumstances stressful.

Shaping

The systematic and differential reinforcement of successive approximations to a goal behaviour is termed 'behavioural shaping'. Rather than waiting for a new behaviour to occur in its final form, minor improvements or steps towards that behaviour are reinforced (Panyon, 1980). The intermediate behaviours are either prerequisite components of the final behaviour or a higher order member of the same response topography as that of the goal behaviour. Behaviour shaping is a positive procedure as reinforcement is consistently delivered. However, it can be time-consuming and a subject's progress is not always linear.

When undertaking a behavioural shaping procedure, it is advantageous to first

determine the criteria for success, analyse the response class and establish the steps that need to be undertaken and the order in which they should occur. The behaviour that will first be reinforced should be identified and the length of time that reinforcement at each step should occur needs to be determined. Subjects' behaviour may determine the size of the steps between behaviours or if some steps may be skipped. As Mellen and Ellis (1996) point out, the reinforcer should be biologically pertinent to the subject for maximum effectiveness. Young and Cipreste (2004) note that food, toys, physical or social contact can all act as reinforcers for a captive animal but their application should take into consideration the health and safety of the animal/s and the trainer and the restrictions of the facility or research protocol. The efficiency of the shaping procedure can be increased by maintaining close and consistent monitoring to detect subtle indications that the next step in the sequence has been performed. Also, using a discriminative stimulus, a physical prompt or an imitative prompt, should be considered.

Imitation

Thorpe (1963) proposed three categories of observational learning. The simplest is social facilitation in which the behaviour of one individual prompts a similar behaviour from another individual, where the behaviour is one that is already in the repertoire of the imitator. For example, Wyrwicka (1978) trained mother cats to eat some unusual foods (bananas and mashed potatoes), and their kittens also began to eat these foods. Thorpe's second category is local enhancement, in which the behaviour of a demonstrator directs the attention of the learner to a particular object or place in the environment. As a result, a response that might otherwise have been learned through trial and error is acquired more rapidly. For instance, Warden, Fjeld, and Koch (1940) trained monkeys to earn food reinforcers by making responses such as pulling a chain. After observing the demonstrator monkey make the required response, an untrained monkey immediately imitated it. The suggestion was that the untrained monkey would probably, eventually, have learned the responses by trial and error but their learning was accelerated by the demonstration from the experienced monkey. Thorpe's third category of observational learning is that of 'true imitation', which he defined as 'the copying of a novel or otherwise improbable act or utterance, or some act for which there is clearly no instinctive tendency'. Therefore behaviour patterns that are very unusual or improbable for the

species, so they would seldom be learned through trial and error. Some researchers have dissented from Thorpe's view of true imitation (McLean, 1995) preferring Thorndike's (1898) definition that imitation is 'learning to do an act from seeing it done'. In this view Thorpe's acts of social facilitation and local enhancement would be included as evidence of imitation. Whichever definition is employed animals have been shown to learn through imitation. There has been the suggestion that the concept of animals learning through imitation can be applied to animal well-being (Nicol, 1995).

Evidence of Learning Through True Imitation in Non-Human Primates

Imitation by chimpanzees was studied experimentally by Whiten (1998) through the use of specially-designed artificial fruit. The fruit could only be penetrated by removing a series of defence mechanisms in a sequential order. Each chimpanzee was able to observe one of two alternative methods for removing the defences and opening the fruit. What followed was imitation by these observer chimpanzees of the particular method that they had viewed. This was true imitation because no amount of trial and error with this object would have resulted in the chimpanzees working out the novel, sequential organisation techniques that made up the particular sequence they observed. Kawai (1965) described several examples of true imitation observed in a troop of monkeys living on an island off the coast of Japan. One described how the monkeys were initially observed to pick grains of wheat out of the sand to eat, however, one monkey was observed to throw a handful of sand and wheat into the ocean. The sand sunk and the wheat floated and was collected easily. Soon many other members of the troop were imitating this behaviour. The imitation of this novel act made the gathering of food a much less laborious process for the members of the troop that employed it. Byrne and Russon (1998) studied African mountain gorilla's food preparation behaviour. Similarly to Whiten's (1998) study, the gorillas were shown to acquire an elaborate sequence of co-ordinated actions to convert previously inedible nettle plants into nutritious meals. The novelty of these actions lay in their arrangement, and the skill was to arrange some basic repertoire of behaviours into novel and complex patterns that resulted in available food. The capacity of primates, and specifically of chimpanzees, to imitate has implication for shaping and training subjects in social groups and for the individuals utilized in this current research.

Aim

In order to eventually measure the chimpanzee group's demand for commodities, in this current research, the subjects had to learn to operate the experimental lever to access the reinforcements. Initially shaping was proposed to teach the chimpanzees to operate the lever on the operant equipment (seen in Figure 2.8) to gain reinforcement. Once a suitable number of chimpanzees were proficient in the operation of the lever to gain reinforcement training was planned to teach the chimpanzees to operate the lever to gain reinforcement from each of the different enrichment items.

Constraints of Undertaking Shaping and Training for This Research

As previously discussed there are practical limitations in undertaking research within a zoological facility. Those specific factors previously mentioned were again a factor during Experiment 4. However, these constraints were particularly central given the aim of this study. Given the number of subjects within the group and its dominance hierarchy, it was uncertain if all, especially the lower ranking individuals would get the opportunity to access reinforcement and the equipment enough to enable shaping and training to be completed successfully. Schapiro et al. (2003) point out the challenges inherent in attempting to train intelligent, socially-oriented animals such as primates without separating them from their social groups. As the separation can be time consuming and stressful during and due to the separation, Schapiro et al. prefer to work with intact social groups, even when the experimental objective is single subject training. The subjects utilised in this current research were not confined to the experimental area in any way. However, they were of course constrained to stay within their enclosure. They were free to move away from the equipment and free to interact with it at any level. During the rest of this current research this fact only added to considerations of how much the chimpanzee valued the commodities on offer. However, for shaping and training of behaviours this fact presented a potential challenge as the time the group spent with the experimental equipment was out of the control of the researcher.

Method

Subjects

The full chimpanzee group as shown in Table 1.1 was utilised, with the exception of Mahinga (d. 20/3/2005) and Bahati (d. 22/10/05) and the infants born to Cara (15/10/03) and Sally (16/7/05) but euthanized before Experiment 2 and 3 respectively.

Impact on Standard Husbandry Protocol

The procedures applied in this experiment had no impact on standard husbandry protocol for the chimpanzees as outlined in Experiment 1.

Ethical Consent

The procedure and equipment used within this experiment were approved by the Director-General of MAF via the National Animal Ethics Advisory Committee in accordance with the Animal Welfare Act 1999 concerning restrictions on the use of non-human hominids, the University of Waikato Animal Ethics Committee and the Wellington Zoo.

Apparatus and Setting

The apparatus used in Experiment 4 is described in Experiment 2 and shown in Figures 2.8 to 2.17 and 2.25 to 2.28. The setting for Experiment 3 is indicated in Figure 1.1 and described in Experiment 2 and shown in Figures 2.4 to 2.6.

Procedure

The study was conducted during March 2006. The trials took place on two days when the weather was inclement therefore the chimpanzee group was held within the indoor enclosure for the sessions in question. The location of the experimental equipment is indicated in Figure 1.1.

Part I – Shaping to Operate Lever to Access Reinforcement

The shaping of the chimpanzee group to operate the lever was done in two stages. The first was shaping to establish the weight required to be attached to the lever to render it operable for the group. The second was refined shaping to enable the chimpanzee group to operate the lever fully when it was indicated to be operable by a operation light.

Establishing operable lever weight. As the group comprised of individuals of different size, weight, age and strength the final weight chosen was one that was generally the best for the entire group. It was important to find a weight which was light enough for all the members of the chimpanzee group to press the lever down but heavy enough so that the stronger members of the group were not able to operate the lever too easily (and damage the lever). These trials followed the similar procedure used in Experiment 2 to establish the weight that would be placed on the lever to render it inoperable. The operant lever is shown in Figure 2.8 and 2.9.

With an initial 62.37 kg attached to the lever (the weight which rendered the lever inoperable, as used in Experiment 2 and 3) one block of weight was taken off the stack attached to the lever (each block being 5.67 kg) and the lever with the attached stack of weight was left in place. The researcher stood next to the lever and offered dried banana chips to the chimpanzees and tapped the handle of the lever (from the researcher side). When the chimpanzees successfully pushed down on the handle, the researcher gave the individual a banana chip. The researcher kept the same weight on the lever until numerous members of the group had pressed down on the lever (or tried to, given the weight). At each weight the researcher required that several members of the group press down the lever (or attempt to). These individuals had to include the smallest and youngest (Bahati, Keza and Alexis), an adult female and an adult male and Jess (as she was the largest individual in the chimpanzee group). If the group members could not press the lever down far enough to trigger Reed switches on the lever then another block of weight was removed and a trial run again as described. This continued until a weight was on the lever that all the members of the group could press the lever down far enough with (including the smallest individuals). This weight, 17 kg (3 blocks) was selected to be used for future experimental sessions in which the chimpanzees were operating the lever. Wolfe (1936) used a 5.44 kg of weight in his research with chimpanzees. However, this may have been due to the relative size, age and strength of the subjects his work utilised (the subjects utilised by Wolfe were between the ages of two and six years).

Shaping group lever operation. Shaping was conducted with the chimpanzees using successive approximations to operate the lever when the lever was in an operable state. Operable state was when the weight on the lever was light enough to

allow movement, the light was on and a lever press produced access to reinforcement. The light above the lever indicated that the lever was operable. The chimpanzees were required to press the lever down, at which time the indicator light went off, a response beep sounded and reinforcement was delivered.

During the first stage of training, the reinforcer delivered was dried slices of banana, delivered by hand by the researcher. Successive approximations to the lever operation were rewarded. Initially, the banana chips were delivered to the chimpanzees if they made any contact with the lever and this progressed to the point whereby the chimpanzees were required to press the lever down far enough for the response beep to sound before a banana chip was delivered (i.e. until they pulled down the lever and expected food). The shaping procedure continued for a maximum of five hours, or until more than half of the group were proficient. The criterion for learning was based on the animals addressing the lever and pressing it at a sufficient force to trigger the response light to go off and beep to sound once.

Operable/non-operable lever operation. After more than half of the individuals (in this case, it was after 9 of the 12 subjects) were successfully trained to operate the lever for reinforcement (of a banana chip), a check was made for discriminated control of lever use. This was accomplished by checking the level at which the chimpanzees used the operable lever (the lever with 17 kg on it) when the lever ‘on’ light was on and when it was not. This behaviour was compared between periods when the signalling stimulus was ‘on’ with that from periods when the stimulus was ‘off’. The periods lasted for 15 min and two of each condition were run alternately.

Part II – Training to Operate Enrichments

The Screwfeeder was used to train the chimpanzees initially so this enrichment item was put in place for the first sessions. A light above the lever showed that the lever was operative. During a training session when a chimpanzee pressed the lever down the indicator light went off, a response beep sounded and the Screwfeeder (as seen in Figure 2.21) rotated and sent out a small amount of sunflower seeds (approximately 20g). The Screwfeeder was set on a fixed ratio programme of one (FR 1). Therefore the sunflower seeds were delivered each time the lever was operated fully by the chimpanzees. When the period of access to each enrichment ended the light was illuminated again and the lever had to be pressed by the

chimpanzees again to gain access to an operable enrichment.

Each enrichment stayed in place until training on each reached proficiency for as many subjects that could be training during the experimental period (but it was required to be more than half the group). (If less than half of the group were able to be trained during the initial training period another training period would have been required). The maximum amount of time an enrichment was in place was two hours. Following the Screwfeeder training sessions training continued with the other enrichments, all utilising FR 1 programmes specifically written for each enrichment. (A fixed-ratio (FR) schedule of reinforcement is one in which the number of responses necessary to produce a reinforcer remain fixed throughout a session, this will be discussed in more detail in Experiment 5). The order in which the enrichment items were provided is shown in Table 4.1, which also shows detail of the operation of the enrichment item during this experiment.

Table 4.1.

Enrichment items in order of presentation in Experiment 4 (after Screwfeeder enrichment use) and their operation details.

| Enrichment Item | Operation Details |
|-----------------|--|
| Musicbox | Able to produce notes for 30 seconds. |
| Dipper | The internal barrier was in place and lifted for 60 seconds to allow access to the food. |
| TV/Video | Turned on and remained on for a 25 seconds showing a continuous video (no repeats). |
| Marbleroll | Released a marble or occasionally a Jaffa™, set at a random 4:1 ratio (marbles/Jaffas™). The slides on the Marbleroll were in place so the chimpanzees were able to control the progress of the items. Automatic cleanup operated to move any marbles that may have been left. |

Operation of Enrichments

Experimental events were controlled by a computer programme and the internally housed computer unit. The computer and enrichments were controlled by

MEDPC-IV software and interfaces. Programmes were written for the experimental phase and for each particular enrichment item during that phase.

Access Times to Enrichment Items

The length of time an enrichment item was operated for when they were not on throughout the session (such as in Experiments 2 and 3) but were turned on by a response, was based on educated assumptions as to what seemed reasonable and on initial trialling of the items during the design phase. This applied to items that needed to be turned on and off (such as the TV and Musicbox), rather than those that had discreet operation (such as the Marbleroll). Initially, during the design of the item (and the preparation of the computer programmes which operated the items) consideration was given to how long an access time should be to allow “adequate” time for the chimpanzees to see the item was “on” (such as with the Musicbox having the lit operation light). Taking into account the size of the enclosure the animals were housed in and the time for them to physically interact with an item (such as push the Musicbox buttons several times).

Access to Enrichment Items

The research was conducted in a closed economy so none of the components of the enrichment items were available from other sources outside of the research.

Data Collection

Data were monitored to check individual chimpanzee’s mastery of the shaping to operate the lever and operate the lever for access to an operable enrichment item.

Results

The outcomes of the shaping and training of individuals within the chimpanzee group are shown in Table 4.2. Shaping the subjects behaviour so that they operated the lever was successfully completed with all members of the group except adult male Marty and adult females Cara and Sally. Temba was the individual to be shaped to operate the lever fully and receive a reinforcer soonest (after ten minutes). The entire shaping trial took three hours. The training to access operable/non-operable lever operation resulting in the group operating the lever a total of 112 times while the operation light was on and a total of 14 times when the operation light was off.

Training of all of the individuals to operate all of the enrichment items was successfully completed for almost all members of the chimpanzee group. However, adult male Boyd did not operate the lever to gain access to the Musicbox and adult Marty did not operate the lever for any enrichments other than the Screwfeeder and the Marbleroll. Adult females Cara and Sally never operated the lever when the Musicbox or TV/Video enrichment item was being used for training.

Table 4.2.
Individual chimpanzee's success in shaping and training procedures.

| Chimpanzee | Shaping Successful | Training on Enrichment Item Successful | | | | |
|------------|-----------------------|--|----------|--------|----------|------------|
| | | Screwfeeder | Musicbox | Dipper | TV/Video | Marbleroll |
| Sam | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Boyd | ✓ | ✓ | • | ✓ | ✓ | ✓ |
| Marty | • | ✓ | • | • | • | ✓ |
| Gombe | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Temba | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Alexis | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Jess | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Cara | • | ✓ | • | ✓ | • | ✓ |
| Samantha | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Sally | • | ✓ | • | ✓ | • | ✓ |
| Chima | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Keza | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |

Discussion

This study was successful in shaping the behaviour of the majority of the chimpanzee group to enable operation of the operant lever, when an operation light was lit, to receive reinforcers. It was also successful in training the majority of the group members to operate the lever to gain access to each of the enrichment items. And also to operate the lever more when doing so was associated with the consequence of access to a commodity.

Shaping a complex 'goal behaviour' such as operating a lever to gain access to operate an enrichment device requires many steps. All subjects were initially taught the connection between a secondary reinforcer (the lever operation light) and the primary reinforcer (rewards of dried banana chip) using a continuous schedule of

reinforcement. Successive approximations were reinforced as the subjects touched the lever and pressed it down and eventually subjects lever presses were reinforced only when they pressed the lever down far enough to trigger the reinforcement 'beep' to sound (triggered by an automated switch).

The fact that the chimpanzee group was shown to operate the lever more often when the lever light was on rather than when it was off may have been partly due to the setting of the testing. The experimental sessions were conducted in the same area in which the chimpanzees were housed daily. The experimental equipment, including the lever had been in place within their enclosure for many weeks prior to these sessions being run. During this time the lever was inoperable (due to the weight that was attached to it) and the lever light off. The chimpanzees would have had experience with the lever in this state. Of course, during the discrimination testing, the lever was operable in that the weight was light enough to enable the chimpanzees to press the lever down, which it was not during the time outside of the experimental sessions. But the light stimulus was the visual signal that was novel to the situation.

All of the individuals that did not successfully complete the shaping to operate the lever during this initial trial were successful in operating the lever in the later training sessions. This may have been due to the fact that subjects had had more sessions in which to experience the lever/reinforcer association. Another possibility may have been that the banana chip was not an effective reinforcer for this behaviour for these individuals. The enrichment items (the items that the subject successfully achieved training on) may have been more effective reinforcers for the lever operation behaviour for these individuals. A further possibility is that these individuals benefited from social facilitation related to the performance of the behaviour of lever pressing to receive reinforcement (Thorndike, 1989). Social facilitation may have influenced the behaviour of all of the members of the group, during shaping and training, as discussed there is evidence that primates do learn through imitation (e.g., Kawai, 1965; Whiten, 1998).

The fact that the individual chimpanzees that did not initially successfully complete shaping to operate the lever went on to perform the behaviour successfully is noteworthy as it suggests that all animal subjects in a group setting may not need to have their behaviour shaped in order for them to learn to operate switches, such as the lever. However, it does raise questions such as the proportion of animals or which individuals need to have their behaviour successfully shaped (e.g., does it need

to be high ranking animals) for others to learn.

The four individuals that were not successfully shaped to operate the lever were all adult chimpanzees - two females and two males. This finding is similar to that of Bloomsmith et al. (1998) who found that the adult male chimpanzees within their subject group had the lowest level of successful training. However, they also found that in general the females in the group took the least number of sessions to reach reliable performance. This study did not find a correlation between the sex of an individual and the outcome of shaping and training.

Schapiro et al. (2003) found that lower ranking rhesus monkeys required less training to achieve successful performance in their task. Of the four individuals in this study that either did not achieve successful shaping of behaviour in the initial trial or were not trained to successfully operate the lever to receive reinforcement of access to all of the enrichment items, two of these were high ranking members of the group, and the other two individuals (adult females) were not.

Conclusion

This study was successful in shaping and training a sufficient number of individual members of the chimpanzee group to operate the lever and to operate the lever for access to the enrichment items. Individual differences were evident in the proficiency at earning the task. Particularly, younger members of the chimpanzee group learnt to press the lever for reinforcement earlier than the adult members. However, all of the individual chimpanzees were able to operate the lever for access to an enrichment by the end of the study. Based on these findings, the research was able to progress to testing the demand of the group for the enrichment items.

EXPERIMENT 5: CHIMPANZEE DEMAND WITH INDIVIDUALS HOUSED SOCIALLY

A goal of this next study was to assess the demand of a socially-housed and tested group of captive chimpanzees, for the enrichment items used in the previous experiment. The chimpanzees' demand was to be assessed as a group, and then analysed at the level both of the group and of the individuals in the group.

Demand

One approach proposed to assess the value of a commodity or event to an animal is behavioural economics, and this method has been suggested as being useful in the assessment of animals' needs (Allison, 1983; Dawkins, 1983; Hursh, 1980, 1984; Mason, McFarland & Garner, 1998b; Sherwin & Nicol, 1997). These procedures involve training an animal to make a particular response (e.g., press a lever) for an environmental event or commodity (e.g., food, mates, enrichment items), and then increasing the amount of work required to obtain that event or commodity. In animal research this is typically achieved by increasing the number of responses (i.e., a fixed-ratio (FR) schedule) or the force required to obtain that commodity (Kirkden & Pajor, 2006). The relationship between the number of reinforcers and the work required to obtain them is described by the demand function. Based on natural logarithms, the equation is as follows:

$$\ln(Q) = \ln(L) + b [\ln(P)] \quad (2)$$

where Q is the consumption (reinforcement rate or, when sessions are of fixed length, number of reinforcers) and P is the price (response requirement, e.g., FR size). The parameter L represents the intensity of demand and is the point at which the demand curve cuts the consumption (Y) axis. Parameter b is the slope of the demand curve or elasticity (Hursh, 1984). Examination of the rate of consumption of that event or commodity across price increases, allows an assessment of the degree of the animal's apparent 'need' for that event. For example, if the animal increases responding across price increases, then consumption rate will remain relatively constant across price increases. In such cases, demand for the commodity is said to be inelastic and the commodity being worked for is assumed to be a 'need' (Dawkins, 1983; Hursh, 1984), since the animal is prepared to work harder across price increases to maintain a relatively constant level of consumption. Conversely,

commodities that the animal shows an elastic demand for could be described as a 'luxury' (Dawkins, 1983; Hursh, 1984). Dawkins (1983) suggested that changes in consumption across price increasing result in demand functions with steeper slopes (greater than -1.0) and indicate inelastic demand. As the animals' response rate increases as the price increases so consumption remains relatively stable across price increases. While demand functions with shallower slopes (less than -1.0) would be indicative of an elastic demand for a commodity. Elastic because the animal does not increase its response rate across price increases, and so consumption decreases across price.

Studies, such as Matthews and Ladewig's (1994), have shown that highly reinforcing commodities (such as food) result in demand function slopes close to zero. Hursh and Winger (1995) also suggest that as such commodities result in small negative of near zero b values that changes in elasticity can be seen in changes in values of a . Linear demand functions, based on Equation 2, have been shown to represent data based on animal demand well. Matthews and Ladewig (1994) utilized linear functions to describe data obtained for domestic pigs demand for food, conspecific social contact, and a stimulus change (door opening). They found the slope of the demand functions for food were the shallowest (indicating inelastic demand) and the slopes for the door opening were the steepest (indicating more elastic demand).

The relation between price and consumption rate when plotted, are generally well fitted by straight lines. However, some data, even when plotted logarithmically, appear curvilinear, representative of mixed elasticity. Hursh, Raslear, Shurtleff, Bauman, and Simmons (1988) developed an equation for generating a curved line to describe nonlinear demand functions. A demand curve is expressed on a log-log plot, with price as the independent variable and amount consumed as the dependant variable. Based on natural logarithms, the equation is as follows:

$$\ln(Q) = \ln(L) + b [\ln(P)] - a(P) \quad (3)$$

where Q is the consumption (reinforcement rate or, when sessions are of fixed length, number of reinforcers) and P is the price (response requirement). The parameter L represents the initial level of demand at minimal price and is the point at which the demand curve cuts the consumption (Y) axis. Parameter b is the initial slope of the demand curve at minimal price. Parameter a represents the increase in slope of the demand curve with increases in price (i.e., the sensitivity of consumption

to increases in price) and generally determines the shape of the demand curve. These form of demand functions describe demand for a commodity which (usually) changes from being relatively inelastic at a lower price to being elastic at higher prices. The point at which demand changes from being inelastic to elastic [i.e., the price yielding maximal response output (P_{\max})] can be determined by the free parameters (Hursh et al., 1988). This price can be found with the equation:

$$P_{\max} = (1+b) / a \quad (4)$$

where b and a represent as previously described. The P_{\max} value is reduced when elasticity of demand increases or the level of demand decreases. A larger P_{\max} would indicate an increase in reinforcing efficacy (Hursh et al., 1988). Many studies of animals' demand for commodities have shown data to be well described by demand functions based on Equation 3.

As previously mentioned an FR schedule is one in which the number of responses necessary to produce reinforcement remain fixed throughout a session. For example, an FR 16 schedule would deliver a reinforcer after every 16th response was made, and this would remain the case for an entire session (Ferster & Skinner, 1957). Such a schedule would also be considered to have a price of 16. Just as in Foltin's (1991) research testing baboons' demand for food, many demand studies have used increasing FR schedule requirements as being analogous to increases in price. Foltin (1991), for example, doubled the ratio values between sessions, i.e., 2, 4, 8, 16, ... 128. In a progressive-ratio (PR) schedule, however, the number of responses necessary to produce reinforcement increases within a session. This current research employed FR schedules to increase the price of access to the enrichment items, details of this will follow.

Behaviour on a FR Schedule of Reinforcement

A distinctive pattern of responding by an animal performing on an FR schedule of reinforcement is that after each reinforcement is delivered there is a pause in responding and after some time responding then continues. This is referred to as the 'post-reinforcement pause' (PRP) (Ferster & Skinner, 1957). The cause of the occurrence of the PRP has been suggested to be due to several different possibilities. These include fatigue, satiation or remaining-responses (given that at that time the subject is required to make the most number of responses to receive reinforcement) (Ferster & Skinner, 1957). Studies have shown that this pattern of responding

produces a distinct pattern of cumulative responses. The average size of a PRP during an FR schedule increases as the size of the ratio increases. In addition, the subject's rate of responding after the post-reinforcement pause decreases gradually as the size of the ratio increases (Ferster & Skinner, 1957).

Changes in the consumption rate as price increases on an FR schedule of reinforcement can sometimes show mixed elasticity. At lower FR values, when the price is low, demand is relatively inelastic, with the animal increasing response rate to maintain consumption rate. At larger FR values, when the price is higher, the animal's consumption rate shows a decrease and demand becomes elastic. Functions which show this mixed elasticity are referred to as 'bitonic' functions (Hursh, 1980). This type of data may be represented by a curved demand function that, based on Equation 3, has a positive b value, showing highly inelastic demand. Bitonic functions have mainly been shown in testing animals' demand for food. For example, the resulting demand functions for Foltin's (1991) research showed the baboons to have an inelastic demand for food until the subjects food intake decreased to be 15% to 55% of that of baseline conditions (i.e., at higher FR values). The researcher concluded that demand functions are "appropriate for the study of food intake in baboons".

Changes in Intensity and Elasticity of Demand

As Hursh (1980) points out demand is not an intrinsic property of a commodity, but a result of the 'economic context' as well. Intensity of demand ($\log L$) appears to be affected by variables such as level of deprivation and magnitude of reinforcement (e.g., size of the food pellet, caloric density of the food) (Hursh, 1984). Elasticity of demand has been shown to be altered by a number of different factors (Hursh, 1984). These include the nature of the commodity being worked for, the species of the subject (or consumer), the availability of substitutes for the commodity, the type of operant task, the social context (as discussed later) and the economic context the experiment is being conducted in (Kirkden & Pajor, 2006; Matthews & Chandler, 1996; Jensen et al., 2004; Sumpter et al., 1999).

Lea and Roper (1977) showed how demand for food pellets changed from being fairly inelastic to very elastic when a perfect substitute could be earned. A 'substitute' refers to the something that is concurrently available in a setting; this can include an item, a type of food, or an activity, for example. In Lea and Ropers'

(1997) research that substitute was a concurrently available identical type of food pellet. In this current research a substitute for the chimpanzees to working for access to the commodities (enrichment items) could have been engaging in another activity within their enclosure, such as a grooming another member of the group, for example.

It has also been suggested that the response type required to gain access to a commodity (Hursh, 1980) and the type of price manipulation employed (Sumpter, Temple & Foster, 1999) can influence elasticity of demand. Response topography and the effect of using different responses on the elasticity of demand will be discussed further in this thesis.

A number of studies have found animals can compensate for increased cost of access to a commodity with longer visit lengths, and furthermore, it has been shown that resource interaction is more intense having overcome higher costs on access (Cooper & Mason, 2000). Not all demand testing allows for an animal to control the amount of time they spend with a resource (this current research did not, as will be detailed in the Method section of this study). However, in Cooper and Masons' (2000) study they tested the demand of mink for a variety of resources and the animals were able to control the amount of time they spent with each of the resources. This was done by having the commodities within separate compartments and allowing the mink to work to gain access to the compartments (via a door which was increasingly weighted, to increase price). Having gained access the animals were free to remain in the compartment. However, a consequence of demand measures based on time with a resource is that they may underestimate resource consumption at higher access costs and demand curves derived from these measures may not be a true reflection of the value of different resources. An alternative approach to demand curves is 'reservation price' or the maximum price individuals are prepared to pay to gain access to resources (Kirkden & Pajor, 2006), P_{\max} as previously discussed. Cooper and Mason (2000) suggest that this maximum price provides a valid means of assessing resource value. Also that it is simpler to use and less prone to artefacts created by the animal's abilities to alter rates and bout lengths than measures based on elasticity, and whose findings are supported by independent measures of animal well-being (Cooper & Mason, 2000).

Hurshs' (1978) study illustrated that another aspect of the situation that can affect the shape of the demand curve is the degree of openness of the experimental

economy. In an experiment conducted with a closed economy, subjects obtain their entire consumption of the commodity in the experimental situation. In an open economy, however, subjects have access to the commodity outside experimental sessions (Mason, Garner & McFarland, 1998a). In closed economies, the subject's consumption of the commodity is a direct result of the equilibrium of its demand (Mason et al., 1998a). Hursh (1978) explored the differences in demand for food and water with rhesus monkeys working under open and then closed economic conditions. The animals were found to increase responding as price increased under a closed economy and decrease responding slightly as the price of food increased under an open economy. Thus the nature of the economy in which the demand procedure is performed in can affect the results. However, it has also been argued that it is session length and not the nature of the economy that influences results (Foster, Blackman & Temple, 1997). These results serve to caution researchers about relying strongly on a single determinate of demand. Some commodities that truly are important to an animal can be overlooked by this reliance (Dawkins, 1990).

Demand procedures have been utilised to explore a variety of animals' responses to increases in the effort required to gain access to a variety of commodities. These have included mice (*Mus musculus*) for increased space (Sherwin & Nicol, 1997) and rabbits for cage size (Jezierski, Scheffler, Bessei & Schumacher, 2005); pregnant sows (*Sus scrofa*) for straw bedding and food (Arey, 1992) and pigs for rooting material (Pedersen, Holm, Jensen & Jorgensen, 2005); laying hens (*Gallus gallus domesticus*) for nest building (Cooper & Appleby, 1995) and food (Petherick & Rutter, 1990); calves for social contact (Holm, Jensen & Jeppesen, 2002) and locomotor behaviour (Jensen, Tuomisto & Pedersen, 2004); foxes (*Vulpes vulpes*) for social contact (Hovland, Mason, Boe, Steinheim & Bakken, 2005), pigeons (*Columba livia*) for food (McSweeney & Swindell, 1999); pigs for food, conspecific social contact and door opening (Matthews & Ladewig, 1994); rats (*Rattus rattus*) for food (Elsmore, Kant & Bauman, 1991; Hursh et al., 1988; Raslear, Bauman, Hursh & Shurtleff, 1988) and water (Ladewig, Sørensen, Nielsen & Matthews, 2002; Sørensen, Ladewig, Ersboll & Matthews, 2004); baboons for access to food (Foltin, 1991); and mink (*Mustela vison*) for swimming water and running wheels (Hansen & Jensen, 2006).

Demand testing has been shown to provide useful information about a variety of species of animals' responses to increases in the effort required to gain access to a

variety of commodities. Details regarding the manner in which demand testing has been carried out, and the relative success (or otherwise), of specific research will be discussed further using examples of demand research with non-human primates.

Comparison of Demand Functions for Preference Judgements

Demand testing can include concurrent schedules whereby two commodities are available to an animal at the same time (e.g., Sørensen, Ladewig, Matthews & Ersboll, 2001; Sørensen et al., 2004). However, Kirkden and Pajor (2006) suggest there has been no clear merit shown for this procedure versus providing the commodities singly. It has been argued that a comparison of demand functions for commodities presented independently may allow for the relative importance of the commodities to be assessed (Matthews and Ladewig, 1994). Hansen and Jensen (2006) found when the demand of mink for different resources (swimming water and running wheel) were assessed the demand curves for when the resources were presented separately were similar to when they were presented simultaneously. Supported by these findings and Kirkden and Pajors' (2006) view, this current research did not employ concurrently available commodities and a discussion of this will follow.

Limitations of Operant Tests

Comparison of demand function parameters and fitted lines is not entirely straightforward. Research has shown that it is important that demand for a resource be viewed as situation and circumstance specific. Kirkden and Pajor (2006) advise that an animals' demand for a certain commodity will be directly influenced by its environment and experience. For example, an animal's demand for a food source may be influenced by the amount of other food it has access to. Caution must be exercised in generalising the findings of demand for a commodity as in situations where the resource is unavailable it may be a case of, as Kirkden and Pajor (2006) suggest, 'out of sight, out of mind'. Hansen and Jensen (2006) also caution that the findings from operant research are often interpreted as a measure of the strength of a behavioural need. They question whether it would impact negatively on an animal if it lacked a resource that, were it not for the research, it would have had no experience of. Also, animals may work more for an 'unhealthy' resource rather than for a 'healthy' one. Such was the case when monkeys were shown to perform operant

tasks to earn drugs at the exclusion of earning food (Paronis, Gasior & Bergman, 2002).

It has been argued that some operant tasks are easier to learn if the association with the resource is familiar (Kirkden & Pajor, 2006). For example pecking a key to gain access to a food resource (Dawkins & Beardsley, 1986). By using a response that does not resemble an associated behaviour, such as the lever press used in this present research, any bias may be avoided.

Another difficulty with demand tests is that the demand for the commodity could change across the testing days as deprivation of the commodity may change across sessions (e.g., the animals hadn't had any seeds for weeks then had them yesterday). So at different points on the demand curve the level of deprivation for the commodity would be different (Kirkden & Pajor, 2006). Satiation of deprivation is less of an issue if the FR value is increased each consecutive session rather than during a session. Reinforcers must be delivered in a consistent quantity across sessions to produce a valid demand curve.

When demand functions are used to rank the importance of different commodities or behaviours, primarily the elasticity, rather than the intensity, of the functions are considered. This is based on the assumption that variables such as level of deprivation and reward duration influence intensity, but not elasticity, of the demand function (Hursh, 1984). There is some support for this assumption (e.g. Hursh & Natelson, 1981) but further testing with a variety of animals, commodities and behaviours would aid in accepting this to be generally valid. Jensen, Munksgaard, Pedersen, Ladwig, and Matthews (2004) found that prior deprivation (of rest for cows) and reward duration affected the intercept and the elasticity of the demand functions in their study.

The limitations that these researchers have cautioned about in regards to demand testing were taken into consideration in planning the methodology of this current research. The point that Kirkden and Pajor's (2006) made, of demand being situation specific, was one that was central to this present research. For example, as discussed, recommendations that the provision of enrichment items to captive animals in zoo facilities not be based on findings from demand tests in laboratory environments (with restricted options for other activities and lab raised animals). By exploring whether demand testing could be conducting in the zoo environment, and how this could be done, it was anticipated that the validity of the findings from

demanding testing could be increased. Also, following recommendations, this current research had FR values which increased each session, rather than within a session, and an operant task that was not associated with any of the resources available to the chimpanzees.

However, the caution that the demand for commodities be considered on the basis that the animal's would not have access to them if it were not for the research (Hansen & Jensen, 2006; Kirkden & Pajor, 2006) was not considered a factor in this present research. As enrichment is regarded to be a potential method of enhancing the psychological well-being of captive animals, exploration of the items that animal's 'want' can only seem to aid in the effective enhancement of well-being. Even though the animal's had no prior experience with the enrichment items before this current research being conducted, and as such were, as Kirkden and Pajor (2006) described, essentially 'out of sight, out of mind'.

While operant tests do have limitations they are able to provide more valuable information, as to the demand an animal may have for an item or commodity, than by providing commodities via trial and error. As a method of quantifying behavioural priorities Hansen and Jensen (2006) suggest that they should be used with caution in regards to the interpretation of results. In this current research the caution regarding animals' working for access to commodities that may negatively impact their well-being (Paronis, Gasior & Bergman, 2002) will be taken into consideration in the interpretation of the results. As will the satiation of demand (Kirkden & Pajor, 2006; Mason et al., 1998a). Both the intensity of demand and elasticity of demand shown by the chimpanzee group for the enrichment items will be discussed in the findings of this present research.

Demand Testing with Non-Human Primates

Very little demand research has been done with non-human primates and almost all of the research that has been done has been conducted within the laboratory setting. As previously discussed, Foltin (1991) explored laboratory housed baboons' demand for food. In this research the baboons responded by pressing a lever on an increasing FR schedule, with sessions lasting 22 hours and with no additional food available outside the experimental conditions (closed economy). The results showed an inelastic demand with response rate increasing with increasing FR values as the animals maintained consumption levels. Foltin (1991) judged the use of

demand testing to be useful in providing information on primates' demand for commodities.

Hoffmeister (1979), Carroll and Rodefer (1993) and English, Rowlett and Woolverton (1995) explored demand for opioids with rhesus monkeys. Monkeys have also been utilised in studies on demand for alcohol (Williams & Woods, 2000). Bauman, Raslear, Hursh, Shurtleff and Simmons (1996) found increases in the FR, but not the presence of concurrently available saccharin solution, affected the slope of the demand curves for food with rhesus monkeys (*Macaca mulatta*). Hodos and Trumbule (1967) explored chimpanzees' preference for schedules of reinforcement (fixed ratio and progressive ratio) with two highly experienced subjects (singly-housed) responding on response panel switches. Belleville, Rohles, Grunzke and Clark (1963) conducted research utilising four chimpanzees, two of which were used in the suborbital space flights, their trials being conducted during the space travel. The different operant procedures and the responses required included: concurrent discriminated avoidance, responding on a lever; fixed ratio performance for food, responding on a response chain; differential reinforcement, responding on a chain; and symbol discrimination, responding on three levers. All of these studies have provided useful information about behaviour, and more specially primate behaviour and given examples of how to conduct such research with primates.

Wolf (1936) conducted experiments with six juvenile chimpanzees to explore the effectiveness of tokens as reinforcers. He found that when the subjects responded on a weighted lever for access to food, an exchangeable poker chip, or a non-exchangeable poker chip, that the valuable-token rewards were almost as effective as food rewards. The subjects utilised in his research were held in 'restraining cages' the largest measuring 148cm in diameter and 103cm in height. Therefore the subjects had very little opportunity to move away from the experimental equipment and limited options of other activities to engage in. Other studies have utilised similarly aged chimpanzee subjects to Wolf (1936) (two to five years) held in similar housing working in this way to explore responding for access to token reinforcement (Cowles & Nissen, 1937; Cowles, 1937a & b; Kelleher, 1956,1958; Sousa & Matsuzawa, 2001). Kelleher (1956,1958) trained chimpanzees to press a key to obtain tokens (poker chips) to be exchanged for food. The number of responses required to obtain reinforcement were increased via an FR schedule and results were compared with those obtained through food reinforcement. Kelleher found results for both token and

food response behaviour to be similar, and observed highly stable rates of responding for both types of reinforcement. However, when tokens were the reinforcement prolonged pauses were observed at the beginning of sessions with higher FR values. Sousa, Matsuzawa (2001) sought to explore the effectiveness of token rewards in maintaining a chimpanzee responding to an ‘intellectually costly’ task. They argued that many past studies had required a response related to a physical act from the animals. They conducted a matching to sample task in which the chimpanzees responded via a touch screen and tokens were given for correct responses, which could then be exchanged for food. They found subjects maintained high levels of accuracy with tokens as reinforcers and also observed chimpanzees saving tokens before exchanging them for food. They termed the tokens to be ‘tools’ as the chimpanzees used the tool to obtain a specific goal (food). Cowles (1937a) concluded that chimpanzees would work for tokens (that could be exchanged for food items) and also found that the subjects would sometimes accumulate several tokens before exchanging them (10 to 30 tokens). However, there were individual differences in the length of these bouts of accumulation.

Schapiro and Lambeth (2007) suggest that systematic use of demand studies has been absent in testing primates demand for resources. They suggest that none of the early studies (during the 1960’s and 1970’s) meet all the conditions for effective demand research (the specifics of which will be discussed).

It can be seen from the studies cited that it is possible to undertake demand testing with captive primates. However, very little demand testing with primates has taken place outside of the laboratory environment. In addition to this, most studies have employed young (two to six years old) laboratory-raised animals. Most testing of subjects has taken place within restricted housing (restraining cages caging around the size of 1m x 1m x 1m) whereby interaction with the demand experiment was unavoidable and very few other activity options were available. The environment in which this demand testing has been conducted would lead to questions as to the validity of utilizing the findings of such research in more ‘natural’ settings, physically and socially.

This current research was conducted in a setting that allowed for the chimpanzees to engage in many other activities, both independently and socially. Chimpanzees given the opportunity to work for a token in a setting which afforded the subjects more choice of activities may not have the same demand as those in

Wolf's (1936) study, for example. In addition to this, findings based on young chimpanzee subjects and demand for the tokens may be different to those for older subjects. In this present research the subject group ranged in age which allowed for an exploration of any correlation of demand for commodities with age.

Demand Testing with Non-Human Primates Out of the Lab

A very limited amount of demand research has been conducted with non-human primates out of the laboratory environment. An example of a study that has occurred out of the laboratory with primates (and in a social group) was conducted by Markowitz (1982; Markowitz & Aday, 1998). Utilizing diana monkeys (*Cercopithecus diana*) the animals were given control of their own schedules and could choose to exchange tokens for food immediately, hoard them, steal them from each other, or give them away, etc. One individual was observed to 'deceive' his mother (who had taken to stealing his food) by clanging his tokens as if inserting them for the delivery of food, but not actually doing so until his mother reportedly got tired of jumping over to the food delivery slot to steal his food. This behaviour resembles instances of 'tactical deception' recorded in wild populations, and is in a sense naturalistic. However, as Markowitz and Aday observed (1998) there are no token-dispensing apparatus in the wild. Therefore this device, although artificial, allowed for the expression of 'natural' behaviour. This relates directly to the enrichment devices that were utilized in this present research as they were artificial. However, they were designed based on the natural history of the primates and on the basis that they allowed for the potential for 'natural' behaviour to be expressed.

Demand Testing in Social Housing

Very little exploration of demand in group settings has been undertaken. Several studies by Sherwin (2003, 2004) have been successful in testing individual demand in a group context. Sherwin (2003) explored an individual's demand while held in a social situation by training a single subject to perform an operant task that would not be performed randomly nor learnt by the other, non-trained, members of the group. The trained mice were housed in a start cage with the group of non-trained mice and able to enter a resource cage which provided either additional space or a running wheel. They found that the mice were less likely to work for access to a running wheel when this access meant time away from a cage mate. The presence of

a cage mate did not affect their demand for access to additional space. Although subjects were not housed socially Pederson, Jensen, Hansen, Munksgaard, Ladewig and Matthews (2002) found that pigs' demand for a resource, in this case food and straw, was affected by social isolation. They also found also that isolation may affect demand in a different way for different resources. The researchers used linear demand functions to describe the data for this study, whereby the intensity of demand is equal to the intercept of the demand function through the Y axis (as previously discussed). An exploration of the effects of a change in the social setting of demand testing will occur in this present research. This will be done via the comparison of findings from demand testing in the social group (Experiment 5) to those from demand testing of isolated individuals (Experiment 6).

Effective Conditions for Demand Testing

According to Mason et al. (1998a) and Matthews (1998) it is an important precondition for the construction of the demand curve that a) the reward duration is sufficiently long enough to be meaningful to the animal b) closed economies should be used in the preference to open economies, and, c) the price and the amount of the resource used must co-vary. Schapiro and Lambeth (2007) suggest that while demand studies undertaken with farm animals or mice, for example, may easily satisfy all the conditions required to ensure compelling results, satisfying all the criteria in research with primates may be difficult. They suggest a partial list of conditions, which include, a) a closed economy, b) validity, and c) adversity. Closed economies have been discussed previously in this thesis. Validity, Schapiro and Lambeth argue, is relatively easy to achieve internally. External validity is more difficult, especially for animals that live socially but undergo testing individually. Schapiro and Lambeth (2007) suggest that the greater the amount of adversity an animal is willing to experience the stronger their 'desire' for that resource. However, they do distinguish the ethical issues of this approach in research with primates.

This current research undertook to conduct testing with methodology that reflected these recommended conditions, as will be discussed. The ethical issues of testing socially-housed subjects individually, that Schapiro and Lambeth (2007) address, were of consideration in this current research, particularly in Experiment 6. How these issues were addressed will be discussed further in Experiment 6.

Response Topography

Operant research with animals has employed a variety of different response requirements with a variety of different animals. Lever pressing has been utilised with mink (e.g., Hansen & Jensen, 2006), rabbits (e.g., Jezierski et al., 2005), rats (e.g., Ladewig et al., 2002) and baboons (Foltin, 1991). Pressure pads presses have been used with pigs (e.g., Arey, 1992; Matthews & Ladewig, 1994; Pedersen et al., 2005), cows (e.g., Matthews & Temple, 1979) and calves (e.g., Jensen et al., 2004). Key pecking had been used with hens (e.g., Dawkins & Beardsley, 1986) and pigeons (e.g., Tsunematsu, 2000). Pushing weighted doors has been used for testing demand with hens (e.g., Cooper & Appleby, 1995) and mink (e.g., Cooper & Mason, 2000). Switch operation has been explored with mice (e.g., Sherwin & Nicol, 1997) and pulling chain was used with foxes (e.g., Hovland et al., 2005).

The appropriateness of the response that is used in demand research has also been explored. As previously mentioned, animals responding according to price has been suggested to be affected by the type of response utilised to explore the behaviour and the price manipulation that is used (Hursh, 1980; Sumpter, Temple & Foster, 1999). Dawkins and Beardsley (1986) found that hens were able to learn to break a photo beam to attain access to litter but did not learn to peck a key for the same commodity. They suggest that certain forms of responding may therefore be inappropriate when working for certain types of commodities. Hansen et al. (2002) explored the effect of the type of operant response on the demand functions of mink for food. They found that the demand curves for food were steeper when the animals were required to pull a chain than they were when the response requirement was pressing a lever. They also found that the mink learned to pull the chain faster than they did to press the lever. An appropriate match of response to animal must also be made. It is species-appropriate for a hen to peck a key but requiring a hen to pull a chain may prove a challenge for the animal to complete. Cooper (2004) suggests that where possible naturalistic tasks should be used in place of abstract operant tasks as they require less training of subjects to associate the task with a reinforcement and appear less prone to operant bias than artificial tasks. They can also provide valid measures of reinforcer values in terms of the maximum price an individual will pay for access to a resource. However, it is suggested that the use of operant responses that do not resemble a particular appetitive behaviour (such as lever pressing rather than key pecking) are best, as they do not bias in any way a resource that may have

elements related to the response (such as a food reinforcer) (Kirkden & Pajor, 2006).

Given that changes in response type have been associated with changes in the elasticity of demand for a commodity this current research employed one form of response, details of what this was follow.

Operant Response in This Research

Several factors were taken into consideration in the selection of the response requirements used in this current research. The first was the setting in which the research was to take place. The subjects were able to move freely within their Indoor Enclosure. They were not, as in some other research, contained within a small experimental area. In addition to this, the subjects were maintained in a social group in an enclosure allowing for various forms of activity, including social interactions, and these activities occupied much of their time. This meant that a response requirement was needed to be obvious so that the subjects could easily see it within their enclosure.

The next consideration was the strength and destructive nature of the species. Any response manipulandum needed to be robust and indestructible. As the group consisted of animals of different ages, sizes and strengths the response had to be operable by all of the members. Given all of these factors, a weighted lever was selected to be the best option to use as the response requirement for the group of chimpanzees in this current research. The lever was large and protruded into the enclosure so was highly visible. It was solid and indestructible. The weight placed on the lever was able to be adjusted, which was crucial as it was not known at the beginning of this current research what weight would be suitable both for the group to be able to operate the lever, and to prevent them from being able to operate the lever if required. Also a suitable weight could be found at which all members of the group could operate the lever. (The method for establishing the weight is described in Experiment 4). The lever was also able to be built in such a way that it did not risk the subjects' safety.

Aim

During this next phase of the research the strength of the chimpanzees' preferences – demand - for the different enrichment items was assessed in the group setting. To do this, the 'price' the chimpanzees had to pay in order to access a single

enrichment item was increased by increasing the number of responses required. The number of access events for each item across price increases was then assessed.

The research was conducted in a closed economy in that access to the enrichments (and components of the enrichments, including food items) was not available when outside of the experimental periods. In terms of validity, the research was conducted with a social-housed group of chimpanzees, maintained in their normal captive environment. The ‘sufficiency’ of the reward durations (Mason et al., 1998a) was based on educated assumptions, and a previous study conducted in this present research (Experiment 2).

Enrichment items that were not used to a large degree by the chimpanzee group during the Free Access study (Experiment 3) were still included in this experiment to assess whether requiring the chimpanzees to work for access to the item altered the amount the item was used.

Method

Subjects

The full chimpanzee group as shown in Table 1.1 was utilised, with the exception of Mahinga (d. 20/3/2005) and Bahati (d. 22/10/05) and the infants born to Cara (15/10/03) and Sally (16/7/05) respectively but euthanized before Experiment 2 and 3 respectively.

Study's Impact on Standard Husbandry Protocol

The procedures applied in this experiment had no impact on standard husbandry protocol for the chimpanzees as outlined in Experiment 1.

Ethical Consent

The procedure and equipment used within this experiment were approved by the Director-General of MAF via the National Animal Ethics Advisory Committee in accordance with the Animal Welfare Act 1999 concerning restrictions on the use of non-human hominids, the University of Waikato Animal Ethics Committee and the Wellington Zoo.

Apparatus and Setting

The apparatus used in Experiment 5 is described in Experiment 2 and shown in Figures 2.8 to 2.17 and 2.25 to 2.28. The setting for Experiment 3 is indicated in Figure 1.1 and described in Experiment 2 and shown in Figures 2.4 to 2.6.

Procedure

The study was conducted from the July 2006 until September 2006. The Free Access study and the Demand studies of this current research (Experiment 3, 5 and 6) were originally scheduled to be run during New Zealand Daylight Savings periods (but in different years) so that the change in day light hours would be relatively minimal. However, the whole research was on a set deadline as the chimpanzees were to move to a new indoor facility. The area in which the research was based was therefore no longer going to be used. The deadline for this move was October 2006. Given technical delays in conducting this current research and zoo management issues with the chimpanzee group, this study needed to be conducted when it was in order for it to be completed before the chimpanzees scheduled move.

A video camera was positioned above where the enrichments were to be placed later. Sessions ran for three hours - beginning at 1700 and terminating at 2000 (as the chimpanzees come in at about 1630 and it gave some time for dinner consumption). A flood light, operated by a timer, was on in the research area during the experimental sessions.

A session of baseline was conducted before a series with each different enrichment item. A baseline session involved recording video footage for the three hour session. Under baseline conditions there were no enrichments in place on the experimental panel. The lever was present but had 62.37 kg of weight hung on it which made it effectively inoperable for the chimpanzees (as previously discussed). The operation light on the lever unit stayed off during the baseline sessions of Experiment 5.

After a baseline period, one enrichment item was provided per session (put in place during the day while the chimpanzees were out of the indoor enclosure). The experimental equipment was mounted on the wall of bars in Covered Area section of the chimpanzees' enclosure: accessible to the chimpanzees from within their enclosure and to the researcher from outside of the entire enclosure.

The lever was present and had a 17 kg weight placed on it to allow the lever to

be operable by the group. How this weight was selected is described in Experiment 4. A light above the lever showed that the lever was 'on'. Once the lever had been pressed down, a set number of times (depending on the FR schedule the item was operating on at during that session), the indicator light went off for a defined time (depending on the item in use), a response beep sounded and the enrichment item 'operated' for a defined period (depending on the item). Following this, the light was re-illuminated and the lever needed to be pressed the appropriate amount of times to once more gain access to the enrichment item. Each enrichment item stayed in place between sessions with the light off. In each subsequent session, the number of responses required to produce a reinforcement doubled from the number required in the previous session i.e. 1, 2, 4, 8, 16, 32, 64, 128 ... This series was run through until breakpoint was reached (i.e. zero reinforcements were delivered for two consecutive experimental sessions). This procedure was completed twice with each enrichment item. After two series with an enrichment item, a session of baseline (as described previously) was then conducted and then the next enrichment item was put in place and so on until all of the enrichment items had been offered to the chimpanzees.

The enrichment items (as seen in Figures 2.9 to 2.12, 2.21 and 2.23) were provided in the order shown in Table 5.1, which also shows detail of the operation of the enrichment item during this experiment.

Operation of Enrichments

During Experiment 5, experimental events within the sessions were controlled by a computer programme and the internally housed computer unit. The computer and enrichments were controlled by MEDPC-IV software and interfaces. Programmes were written for the experimental phase and for each particular enrichment item during that phase.

Access Times to Enrichments

The access times to enrichment item reinforcement was based initially on educated assumptions as to what seemed reasonable and then through testing and observation with the chimpanzees during the initial trialling of the enrichment items (as described in Experiment 4).

Access to Enrichment Items

The research was conducted in a closed economy so none of the components of the enrichment items were available from other sources outside of the research.

Table 5.1

Enrichment items in order of use for Experiment 5 and enrichment item operation details.

| Enrichment Item | Operation Details |
|--|--|
| Screwfeeder | Rotated for 2 seconds (approximately a quarter turn) and delivered a small amount of sunflower seeds (approximately 20g). |
| Marbleroll Delivering Coated Peanuts | Released a coated peanut. The slides on the Marbleroll were removed so the chimpanzees had nothing to operate. |
| Musicbox | Able to produce notes for 30 seconds. |
| Dipper | The internal barrier was in place and lifted for 60 seconds to allow access to the food. |
| TV/Video | Turned on and remained on for a 25 seconds showing a continuous video (no repeats). |
| Marbleroll | Released a marble or occasionally a Jaffa™, set at a random 4:1 ratio (marbles/Jaffas™). The slides on the Marbleroll were in place so the chimpanzees were able to control the progress of the items. Automatic cleanup operated to move any marbles that may have been left. |

Data Collection

Video Recordings and Behavioural Definitions

During the Experiment 5, each experimental session was recorded as described in Experiment 2 and individual chimpanzee's behaviour (as categorized in Table 2.2) recorded as described in Experiment 2. Behaviours of particular note by individuals were also recorded. The area within view of the video recording was 5 m deep, 2 m across and 2 m in height. The amount of time that there was day light (sunset time)

and the general weather conditions for the day were also noted.

Reliability. Within-observer reliability was assessed for Experiment 5 in the same way it was described in Experiment 2. At the beginning of Experiment 5, within-observer reliability was 99.14%. Near the end of Experiment 5 within-observer reliability was 98.29%.

Computer Recorded Behaviour

During the demand study each experimental session was run and recorded by computer programmes run from the internally housed computer unit. The computer was controlled by a programmable interface cabinet and this operated MEDPC_IV software. Programmes were written for each experimental phase of the research and for each particular enrichment item during that phase.

- The computer recorded summary events including:
- Day, month, year on which the session was being run
- FR. The schedule that the enrichment was on for that particular session.
- First response. The time from when the experiment started (light on lever ready to press) until the first response is completed (being triggered off the top switch on the operant equipment). Recorded in seconds
- Responses. The number of lever presses made. This is a top switch closure after a bottom switch closure on the operant equipment. Note two 'ups' in a row did not count as the lever needed to be released/bottom switch triggered before a second up was counted.
- Reinforcements (Rfts). The number of feeds etc/per completed FRs.
- Post reinforcement pause (PRP). The amount of time from the reinforcement to the first response of the next FR. This was counted cumulatively over the session so the average PRP is the total PRP divided by the number of reinforcements (average inter-reward interval). Recorded in seconds.
- Runtime. In session running an FR greater than one the average time between responses (within reinforcement). Average inter-response interval. Recorded in seconds.
- Keytime. The amount of time the lever was available for responding during the session. Essentially the time the light on the lever indicated the lever was

active and ‘on’. Therefore the total time minus whatever the length of the reinforcement times the number of reinforcements. Recorded in seconds.

- Total time. Total length of the session, measured in seconds.
- For the Marbleroll enrichment, summary data also included the number of marbles and Jaffas™ delivered.

All of these data were automatically recorded in separate data files on the computer at the completion of each experimental session. Event data were recorded automatically as the session was taking place. This recorded all of the summary data as above and additionally recorded any movement of the lever or reinforcement delivery from an enrichment item. Each event was recorded with a corresponding time of occurrence.

Data Analysis

Analysis of Video Data

The video recordings collected during Experiment 5 were analysed and provided data of total time of group behaviour and then for details of total time of individuals behaviour.

Analysis of Computer Recorded Behaviour

The data for demand functions were log transformed (using natural logs) to assess the relation between the consumption rate per session (assessed as obtained reinforcer delivery rate) and the FR size (price).

Results

The data analysed here were based on the time any chimpanzee was within the observation area and recorded to be so. Definitions for the recorded behaviour are described in Table 2.2. The data are presented as behavioural category totals for each experimental condition. Details of data for each experimental session are presented in Appendix D. When a chimpanzee was observed to be present in the experimental area but their identity could not be ascertained their behaviour was recorded and classed under “Unknown” individual. As this did not occur often (less than 1% of behavioural recordings the results are not shown in the figures. Scales on the Figures in this and other experiments are the same to allow for comparisons.

Throughout the results of this study figures will utilise symbols where: B is Baseline; MB is Musicbox enrichment; D is Dipper enrichment; SF is Screwfeeder enrichment; TV is TV/Video enrichment; MR (no s) is Marbleroll enrichment - delivering marbles and Jaffas™, without slides; MR (+s) is Marbleroll enrichment - delivering marbles and Jaffas™, with slides; MR (p) is Marbleroll enrichment, delivering coated peanuts.

Group Behaviour

The chimpanzee group's overall behavioural data totals for each experimental session of Experiment 5 are shown in Table 5.2 and Figures 5.1 to 5.6. Across all of the sessions of Experiment 5, those when enrichment items were present and those in which one was not (Baseline sessions) the total amount of time the group spent in the experimental area simply present but not interacting in any way (Just in area) was the greatest during the Baseline sessions. However, the maximum total time for this behaviour was only 6.88 min in a session (during the Baseline session prior to the Dipper enrichment item sessions). Temperature and seasonal changes in the behaviour of apes has previously been evidenced both in captivity and the wild (Stoinski et. al., 2004; Vivian, 2001). However, during this experiment, as in Experiment 3, behaviour was not shown to vary greatly in association with weather conditions. This may have been due in part to the indoor/outdoor nature of the experimental setting.

Group Behaviour Related to Enrichment Items Whilst Housed Socially

Table 5.2 and Figures 5.1 to 5.6 show the chimpanzee group's total time spent in each behaviour relating to each enrichment item across sessions for Experiment 5.

Screwfeeder Enrichment

As shown in Table 5.2 and Figure 5.1 the maximum amount of time the Screwfeeder was used in a session by the chimpanzee group (including using the item alone, using it when another member of the group was watching and using the item with another member of the group) was 114.24 min, during FR 2 of Series B. Across both Series, the level of use by the group followed a similar pattern as during FR 1. The group used the item for the second greatest amount of time, use peaked during FR 2 sessions and then sequentially dropped right down as the FR size

increased (FR 4 use time being less than FR 1 use time). The least amount of overall use occurred during FR 64, Series B (2.99 min).

Table 5.2

Chimpanzee group behaviour (as defined in Table 2.2) during Demand study. The amount of time (min) in each session the group exhibited each behaviour and the sun set time, temperature and general weather conditions during each session.

| Session Condition | Time Spent Exhibiting Class of Behaviour (min) | | | | | | | Time of First Interaction (min) | Subject First Interacted | Sunset Time | Weather | Temp at 1700hrs |
|-------------------|--|----------------------|------------------|-------------------|-------------------------|--------------------|--------------|---------------------------------|--------------------------|-------------|---------|-----------------|
| | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in Area | | | | | |
| Baseline | NA | NA | NA | NA | NA | NA | 5.02 | NA | NA | 1702 | Cloudy | 7 |
| Screwfeeder-1A | 93.67 | 1.15 | 10.33 | 0.00 | 0.00 | 1.15 | 1.28 | 0.52 | Jess | 1702 | Fine | 11 |
| Screwfeeder-2A | 74.33 | 17.92 | 15.87 | 0.00 | 0.00 | 17.92 | 1.28 | 1.20 | Keza | 1702 | Fine | 12 |
| Screwfeeder-4A | 68.05 | 1.17 | 2.23 | 0.00 | 0.00 | 1.17 | 1.75 | 2.67 | Temba | 1703 | Rain | 9 |
| Screwfeeder-8A | 17.03 | 0.22 | 2.95 | 0.62 | 0.00 | 0.22 | 1.55 | 0.63 | Jess | 1704 | Rain | 8 |
| Screwfeeder-16A | 13.45 | 0.32 | 0.10 | 1.03 | 0.00 | 0.32 | 1.63 | 1.20 | Boyd | 1704 | Rain | 11 |
| Screwfeeder-32A | 7.77 | 0.20 | 0.00 | 0.00 | 0.00 | 0.20 | 1.42 | 1.62 | Keza | 1705 | Rain | 10 |
| Screwfeeder-1B | 94.10 | 1.83 | 3.27 | 0.13 | 0.00 | 1.83 | 2.12 | 1.63 | Jess | 1706 | Fine | 13 |
| Screwfeeder-2B | 96.37 | 0.77 | 17.10 | 0.00 | 0.00 | 0.77 | 1.78 | 2.52 | Jess | 1706 | Fine | 12 |
| Screwfeeder-4B | 74.53 | 0.77 | 1.20 | 0.00 | 0.13 | 0.77 | 1.42 | 5.92 | Keza | 1707 | Fine | 12 |
| Screwfeeder-8B | 70.03 | 1.97 | 2.87 | 0.00 | 0.00 | 1.97 | 1.38 | 5.03 | Jess | 1708 | Showers | 12 |
| Screwfeeder-16B | 8.23 | 0.68 | 2.17 | 0.23 | 0.00 | 0.68 | 1.48 | 0.92 | Temba | 1708 | Showers | 12 |
| Screwfeeder-32B | 7.82 | 0.10 | 0.13 | 0.00 | 0.00 | 0.10 | 1.75 | 2.75 | Keza | 1709 | Fine | 11 |
| Screwfeeder-64B | 2.62 | 0.00 | 0.37 | 0.00 | 0.00 | 0.00 | 1.30 | 2.13 | Gombe | 1710 | Showers | 12 |
| Baseline | NA | NA | NA | NA | NA | NA | 2.85 | NA | NA | 1711 | Rain | 10 |
| Baseline | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 4.55 | NA | NA | 1740 | Fine | 10 |
| Marbleroll(p)-1A | 103.90 | 1.05 | 4.70 | 0.00 | 0.00 | 1.05 | 1.98 | 3.13 | Keza | 1741 | Fine | 11 |
| Marbleroll(p)-2A | 102.23 | 0.87 | 0.90 | 0.12 | 0.07 | 0.87 | 1.95 | 0.88 | Jess | 1741 | Fine | 12 |
| Marbleroll(p)-4A | 6.20 | 0.07 | 0.20 | 0.00 | 0.00 | 0.07 | 1.48 | 1.17 | Jess | 1743 | Rain | 13 |
| Marbleroll(p)-8A | 4.20 | 0.00 | 0.00 | 0.03 | 0.00 | 0.00 | 1.75 | 13.90 | Keza | 1744 | Fine | 14 |
| Marbleroll(p)-1B | 62.65 | 1.15 | 2.20 | 0.00 | 0.00 | 1.15 | 2.37 | 1.50 | Keza | 1745 | Rain | 11 |
| Marbleroll(p)-2B | 90.35 | 1.43 | 6.40 | 0.08 | 0.00 | 1.43 | 2.88 | 4.02 | Jess | 1746 | Rain | 9 |
| Marbleroll(p)-4B | 23.03 | 0.10 | 0.37 | 0.00 | 0.00 | 0.10 | 1.50 | 3.40 | Jess | 1747 | Fine | 9 |
| Marbleroll(p)-8B | 0.57 | 0.05 | 0.00 | 0.15 | 0.00 | 0.05 | 0.80 | 7.28 | Temba | 1748 | Showers | 10 |
| Baseline | NA | NA | NA | NA | NA | NA | 2.90 | NA | NA | 1749 | Rain | 13 |
| Musicbox-1A | 8.45 | 0.03 | 0.10 | 0.00 | 0.00 | 0.03 | 4.78 | 3.75 | Keza | 1750 | Rain | 9 |
| Musicbox-2A | 10.57 | 0.10 | 0.00 | 0.15 | 0.00 | 0.10 | 0.97 | 6.87 | Keza | 1751 | Rain | 10 |
| Musicbox-4A | 0.85 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.43 | 14.17 | Keza | 1752 | Fine | 12 |
| Musicbox-1B | 4.40 | 0.20 | 0.00 | 0.00 | 0.00 | 0.20 | 1.65 | 11.18 | Keza | 1753 | Fine | 13 |
| Musicbox-2B | 1.72 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.43 | 7.13 | Temba | 1754 | Fine | 15 |
| Musicbox-4B | 0.37 | 0.07 | 0.00 | 0.00 | 0.00 | 0.07 | 1.27 | 12.35 | Temba | 1755 | Fine | 13 |
| Baseline | NA | NA | NA | NA | NA | NA | 5.57 | NA | NA | 1756 | Fine | 13 |
| Baseline | NA | NA | NA | NA | NA | NA | 6.88 | NA | NA | 1757 | Cloudy | 14 |
| Dipper 1A | 77.88 | 2.02 | 3.48 | 0.00 | 0.00 | 2.02 | 2.43 | 5.22 | Jess | 1758 | Fine | 15 |
| Dipper 2A | 15.52 | 0.17 | 0.00 | 0.35 | 0.23 | 0.17 | 1.33 | 7.40 | Jess | 1759 | Cloudy | 14 |
| Dipper 4A | 0.85 | 0.00 | 0.00 | 0.38 | 0.00 | 0.00 | 1.62 | 2.45 | Temba | 1800 | Showers | 15 |
| Dipper 1B | 110.48 | 1.13 | 1.03 | 0.00 | 0.00 | 1.13 | 1.07 | 2.35 | Temba | 1801 | Rain | 13 |
| Dipper 2B | 2.38 | 0.23 | 0.00 | 0.52 | 0.00 | 0.23 | 1.00 | 5.15 | Jess | 1802 | Rain | 12 |
| Dipper 4B | 0.58 | 0.00 | 0.00 | 0.23 | 0.00 | 0.00 | 1.27 | 8.93 | Jess | 1803 | Fine | 11 |
| Baseline | NA | NA | NA | NA | NA | NA | 4.67 | NA | NA | 1804 | Fine | 13 |
| TV/Video-1A | 8.08 | 0.00 | 1.70 | 0.30 | 0.13 | 0.00 | 1.92 | 2.40 | Keza | 1806 | Cloudy | 10 |
| TV/Video-2A | 0.15 | 0.00 | 0.00 | 0.12 | 0.00 | 0.00 | 0.95 | 12.20 | Keza | 1806 | Fine | 11 |
| TV/Video-1B | 3.08 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.78 | 18.30 | Keza | 1807 | Fine | 13 |
| TV/Video-2B | 0.70 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.93 | 7.53 | Alexis | 1808 | Fine | 10 |
| Baseline | NA | NA | NA | NA | NA | NA | 4.02 | NA | NA | 1809 | Fine | 13 |
| Marbleroll-1A | 91.82 | 0.30 | 10.20 | 1.22 | 1.33 | 0.30 | 3.93 | 0.63 | Jess | 1810 | Fine | 13 |
| Marbleroll-2A | 37.35 | 0.53 | 2.07 | 0.32 | 0.00 | 0.53 | 2.75 | 0.50 | Jess | 1811 | Cloudy | 14 |
| Marbleroll-4A | 0.68 | 0.03 | 0.00 | 0.00 | 0.00 | 0.03 | 2.93 | 2.48 | Jess | 1812 | Fine | 15 |
| Marbleroll-8A | 3.50 | 0.00 | 0.00 | 1.58 | 0.00 | 0.00 | 1.57 | 3.25 | Keza | 1813 | Fine | 14 |
| Marbleroll-1B | 61.07 | 0.37 | 2.47 | 0.00 | 0.00 | 0.37 | 2.85 | 1.70 | Jess | 1814 | Rain | 13 |
| Marbleroll-2B | 32.60 | 1.90 | 1.30 | 0.07 | 0.10 | 1.90 | 2.13 | 0.95 | Jess | 1815 | Fine | 13 |
| Marbleroll-4B | 0.35 | 0.00 | 0.00 | 0.63 | 0.00 | 0.00 | 1.12 | 11.22 | Keza | 1816 | Cloudy | 15 |
| Baseline | NA | NA | NA | NA | NA | NA | 4.88 | NA | NA | 1817 | Rain | 16 |

Of all of the behavioural classes (as defined in Table 2.2) the chimpanzee group used the Screwfeeder enrichment while unaccompanied (Used-alone) for by far the greatest amount of time of all the enrichment item across all sessions with it. Although a lot less than the time the group spent using the enrichment item alone, the time they spent using an item at the same time as another subject was (Using-together) considerable. During FR 2 of Series A, the group spent a substantial amount of time using an enrichment item while another individual observed this (Using – others watch) and conversely watching another individual using an item (Watching other use). With the exception of FR 2, Series A, the group spent a minimal amount of time using an enrichment item while another individual observed this (Using – others watch), watching another individual using an item (Watching other use), orientated towards an item but not interacting (Attending-alone), multiple animals oriented towards and item but not interacting with it (Attending – accompanied) and within the experimental area simply present but not interacting in any way with an enrichment item (Just in area).

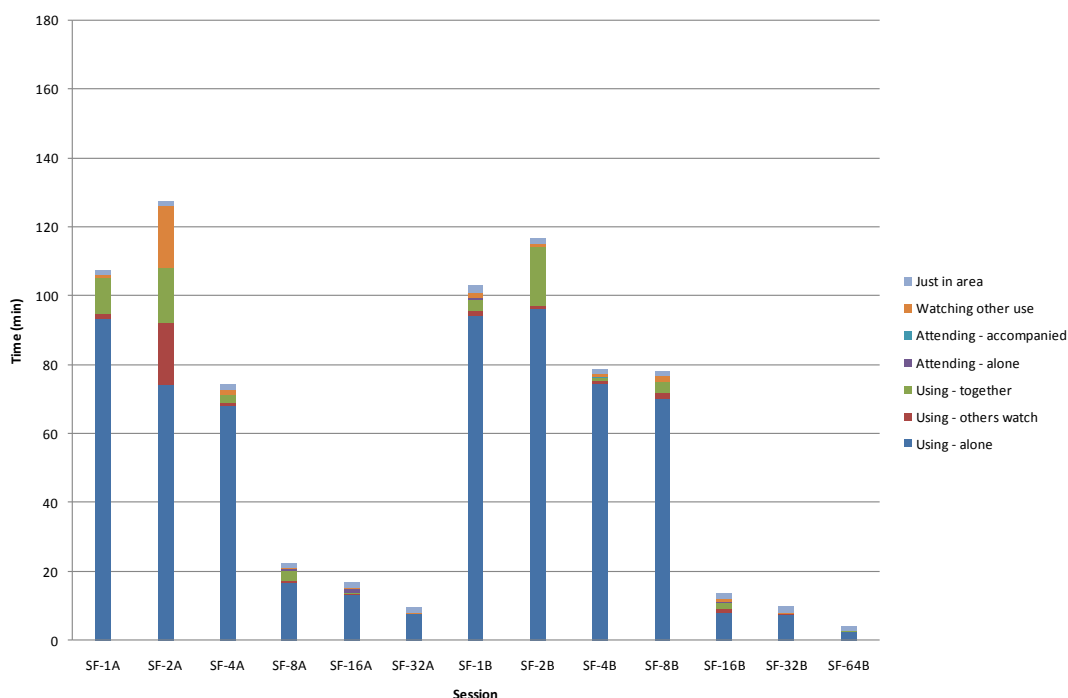


Figure 5.1. Total time that the chimpanzee group exhibited defined behaviours in experimental sessions of Experiment 5 with the Screwfeeder enrichment.

Marbleroll Enrichment Delivering Coated Peanuts

Overall use of the Marbleroll enrichment by the chimpanzee group (combining Using-alone, Using-others watch and Using-together), when it delivered coated peanuts, peaked during FR 1 of Series A at 109.65 min, as shown in Figure 5.2. The pattern of use across the two series differed. During the first series, A, when the FR increased to FR 2 the use dropped slightly and with further FR increased dropped off markedly. However, during Series B, use peaked at FR 2 from FR 1 and then dropped right down with further FR size increases. The least amount of overall use was 0.62 min and occurred during FR 8 of Series B.

Of all of the behavioural classes (as defined in Table 2.2), the chimpanzee group used the Marbleroll enrichment, when delivering coated peanuts, while unaccompanied (Used-alone) for by far the greatest amount of time across all sessions with the item. The time they spent using an enrichment item at the same time as another subject was (Using-together) was considerable, although this was a lot less than the time than spent in using the item alone. The group spent a minimal amount of time using the Marbleroll (with peanuts) while another individual observed this (Using – others watch), watching another individual using the item (Watching other use), orientated towards the item but not interacting (Attending-alone), multiple animals oriented towards the item but not interacting with it (Attending – accompanied) and within the experimental area simply present but not interacting in any way with the item (Just in area).

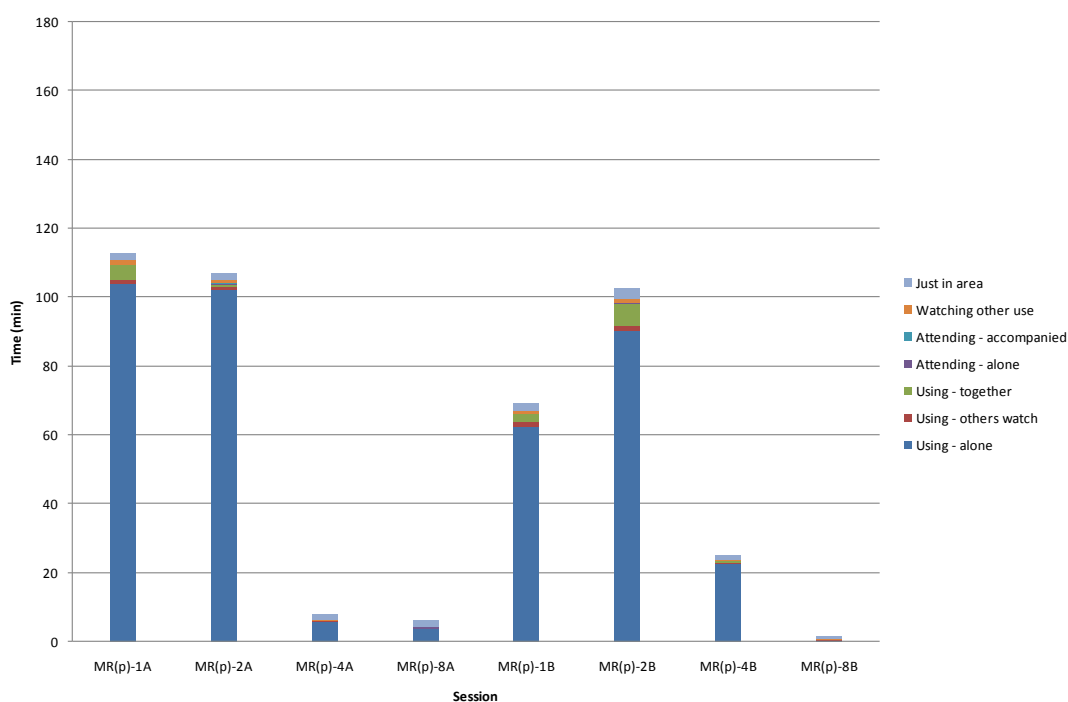


Figure 5.2. Total time that the chimpanzee group exhibited defined behaviours in experimental sessions of Experiment 5 with the Marbleroll enrichment when it was delivering coated peanuts.

Musicbox Enrichment

Figure 5.3 shows that overall use of the Musicbox enrichment (combining Using-alone, Using-others watch and Using-together) by the entire chimpanzee group remained low across all sessions but did peak during FR 2 of Series A at 8.58 min. The least time of use occurred during Series B at FR 4 and was 0.44 min. The pattern of use across the two series differed as during the first series (Series A) as the FR size increased from FR 1 to FR 2, the use increased and then dropped right down with sessions of increasing FR. However, during Series B total use time dropped each time the FR size was increased.

Of all of the behavioural classes (as defined in Table 2.2) the chimpanzee group used the Musicbox enrichment while unaccompanied (Used-alone) for the greatest amount of time across all sessions with the item. The group spent a minimal amount of time using the enrichment item while another individual observed this (Using – others watch), using the item at the same time as another subject was (Using-together), watching another individual using the item (Watching other use),

orientated towards the item but not interacting (Attending-alone), multiple animals oriented towards the item but not interacting with it (Attending – accompanied) and within the experimental area simply present but not interacting in any way with the item (Just in area).

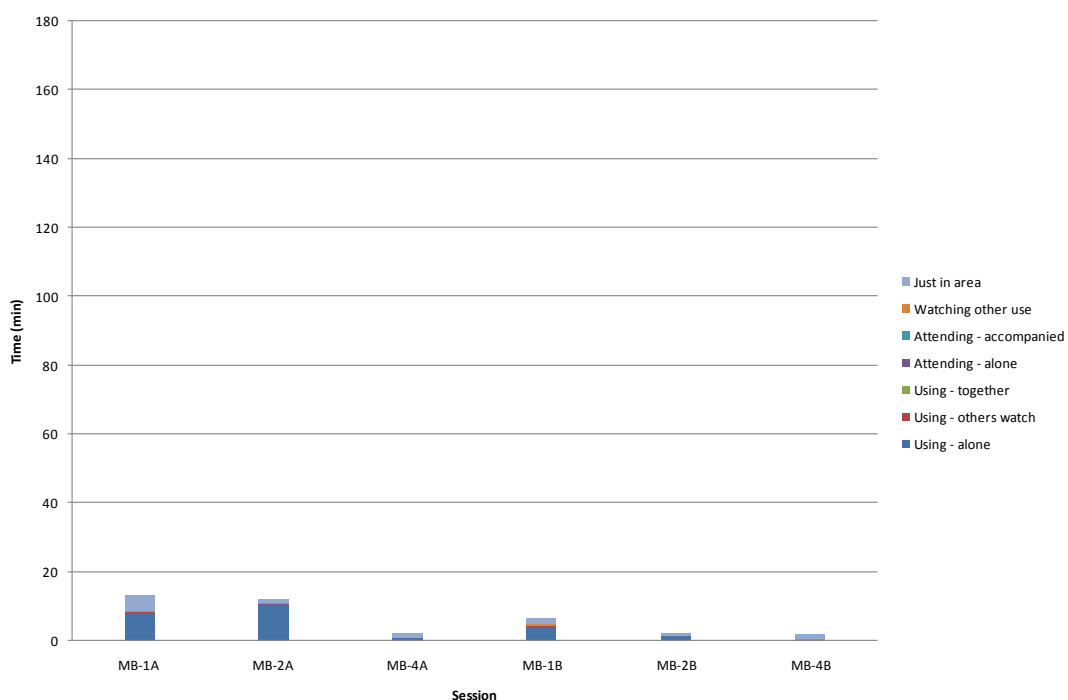


Figure 5.3. Total time that the chimpanzee group exhibited defined behaviours in experimental sessions of Experiment 5 with the Musicbox enrichment.

Dipper Enrichment

The time that the chimpanzee group spent using the Dipper enrichment (combining Using-alone, Using-others watch and Using-together) was at its maximum during FR 1 of Series B at 112.64 min, as shown in Figure 5.4. The pattern of use across the two series was similar as total use time dropped when the FR size was increased, dropping markedly from FR 1 to FR 2. The least amount of time the group spent using the Dipper enrichment across all sessions was 0.58 min during FR 4 of Series B.

Of all of the behavioural classes (as defined in Table 2.2) the chimpanzee group used the Dipper enrichment while unaccompanied (Used-alone) for the greatest amount of time across all sessions with the item. The group spent a minimal

amount of time using the item while another individual observed this (Using – others watch), using the item at the same time as another subject was (Using-together), watching another individual using the item (Watching other use), orientated towards the item but not interacting (Attending-alone), multiple animals oriented towards the item but not interacting with it (Attending – accompanied) and within the experimental area simply present but not interacting in any way with the item (Just in area).

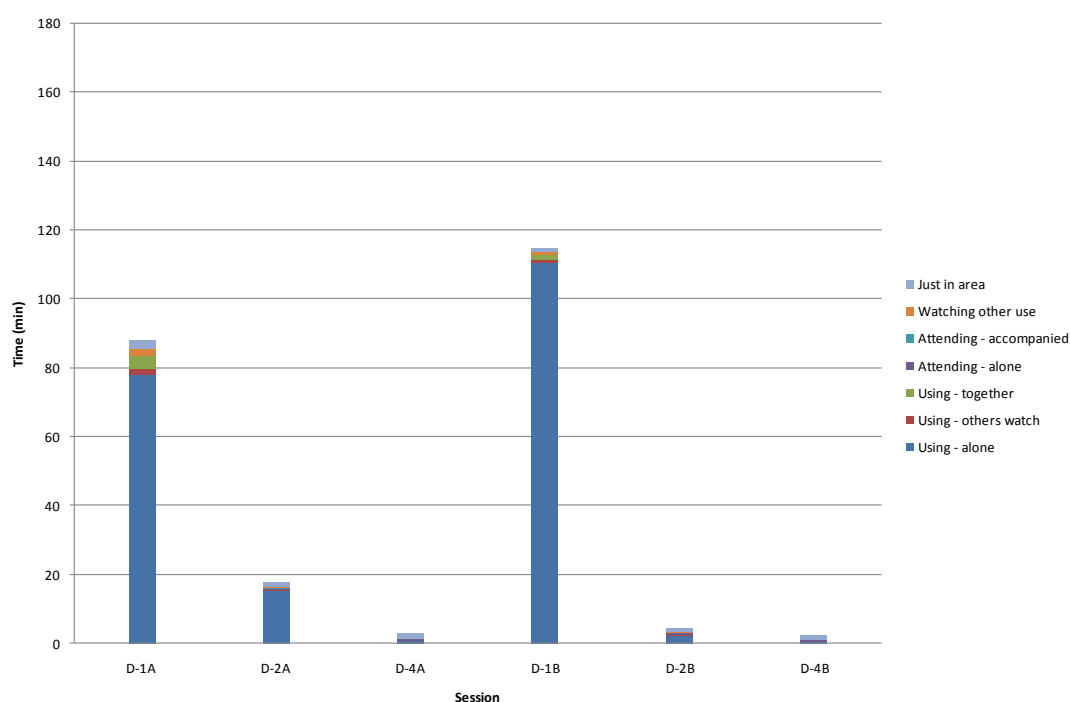


Figure 5.4. Total time that the chimpanzee group exhibited defined behaviours in experimental sessions of Experiment 5 with the Dipper enrichment.

TV/Video Enrichment

Figure 5.5 shows that overall use of the TV/Video enrichment (combining Using-alone, Using-others watch and Using-together) by the chimpanzee group remained low across all sessions but did peak during FR 1 of Series A at 9.78 min. The least time of use occurred during Series A at FR 2 and was 0.15 min. The pattern of use across the two series was similar as total use time dropped when the FR size increased.

Of all of the behavioural classes (as defined in Table 2.2) the chimpanzee group used the TV/Video enrichment while unaccompanied (Used-alone) for the greatest amount of time across all sessions with the item. The group spent a minimal amount of time using the item while another individual observed this (Using – others watch), using the item at the same time as another subject was (Using-together), watching another individual using the item (Watching other use), orientated towards an item but not interacting (Attending-alone), multiple animals oriented towards the item but not interacting with it (Attending – accompanied) and within the experimental area simply present but not interacting in any way with an enrichment item (Just in area).

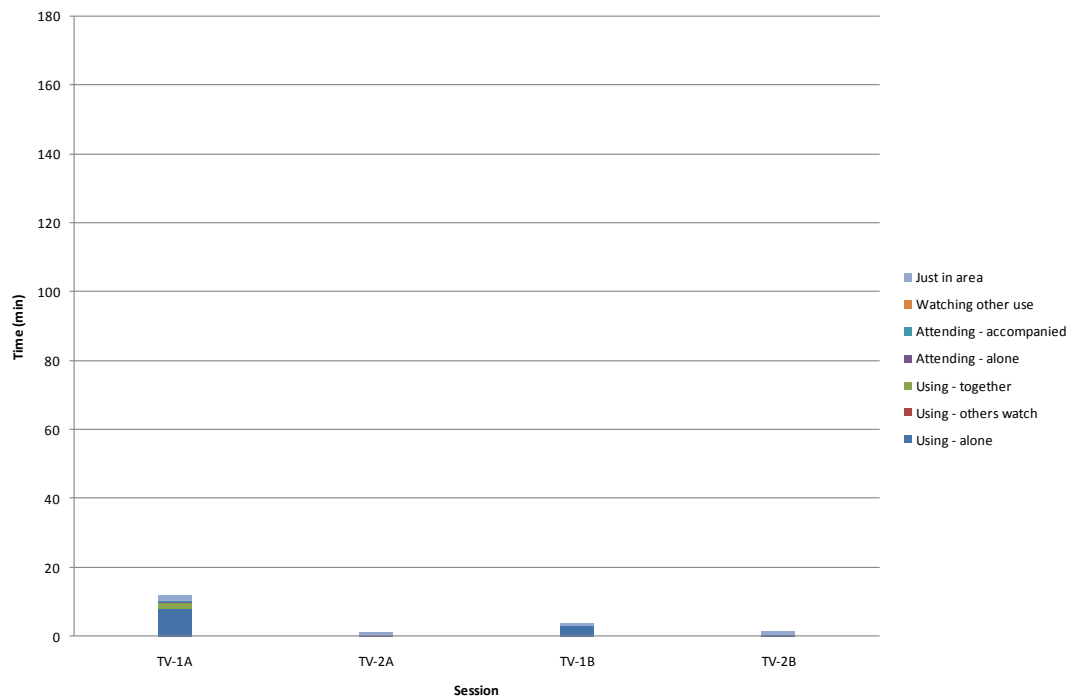


Figure 5.5. Total time that the chimpanzee group exhibited defined behaviours in experimental sessions of Experiment 5 with the TV/Video enrichment.

Marbleroll Enrichment

The chimpanzee group as a whole used the Marbleroll enrichment (combining Using-alone, Using-others watch and Using-together) the most during FR 1 of Series A, using the item for 102.32 min, as shown in Figure 5.6. The pattern of use across

the two series was similar as total use time dropped when the FR was increased. There was, however, an exception as use was higher during FR 8 of Series A than in FR 4. The least amount of time the group spent using the Marbleroll enrichment across all sessions was 0.35 min during FR 4 of Series B.

Of all of the behavioural classes (as defined in Table 2.2) the chimpanzee group used the Marbleroll enrichment while unaccompanied (Used-alone) for the greatest amount of time across all sessions with the item. The group spent a minimal amount of time using the item while another individual observed this (Using – others watch), using the item at the same time as another subject was (Using-together), watching another individual using the item (Watching other use), orientated towards an item but not interacting (Attending-alone), multiple animals oriented towards the item but not interacting with it (Attending – accompanied) and within the experimental area simply present but not interacting in any way with the item (Just in area). However, they did spend an increased amount of time using the item jointly (Using-together) during FR 1 of the Series A.

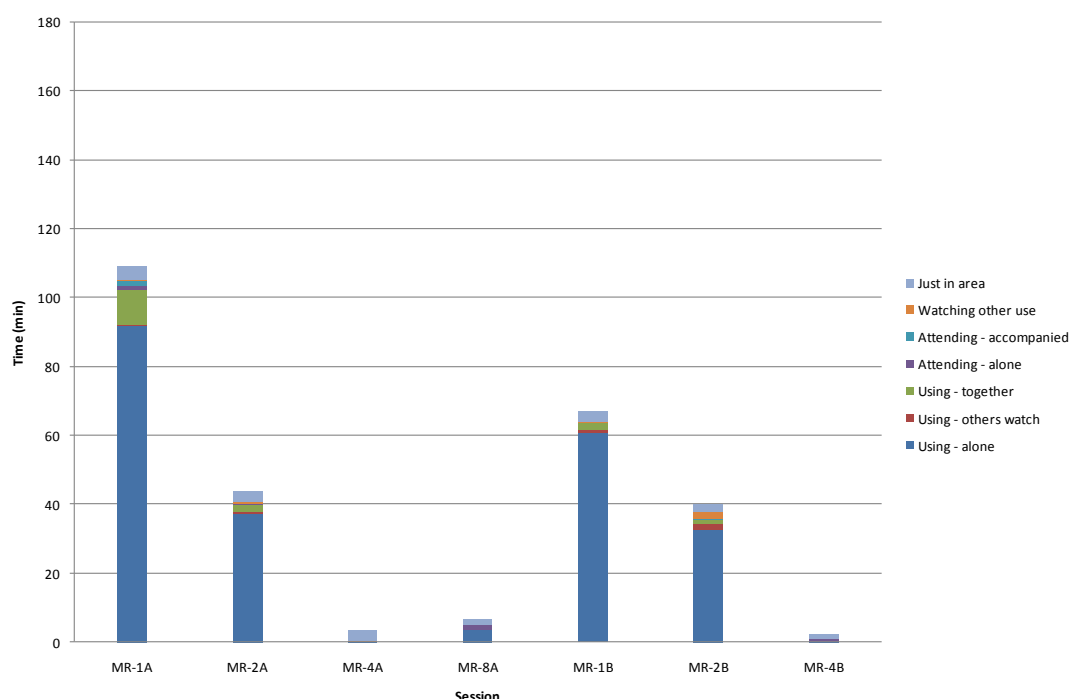


Figure 5.6. Total time that the chimpanzee group exhibited defined behaviours in experimental sessions of Experiment 3 with the Marbleroll enrichment.

Group Behaviour Between Enrichments

Across all sessions the chimpanzee group had with an enrichment item the item that was used for the greatest amount of time (combining Using-alone, Using-others watch and Using-together) was the Screwfeeder. As shown in Table 5.2 and Figures 5.1 to 5.6, the Dipper and the Marbleroll enrichment (when it delivered coated peanuts) were used in several sessions for a greater amount of time by an individual subject (Using-alone). However, the Screwfeeder was used for a considerable amount of time by multiple individuals at once (Using-together). The TV/Video enrichment item was used the least by the chimpanzee group across the sessions of Experiment 5. The Musicbox enrichment was used for the second least amount of time.

Group Use Event Records Whilst Housed Socially

Data for the chimpanzee group was analysed to examine individuals' use of the enrichment items (including behavioural classes: Using-alone, Using-others watch, Using-together). The event records were constructed as described in Experiment 2: Part 1. The time of delivery of a reinforcer is also indicated on the figures.

Screwfeeder enrichment. Figures 5.7a to 5.7m show all use of the Screwfeeder enrichment in the sessions in which it was available to the chimpanzee group during Experiment 5. Regardless of the FR size, all of the use of the item took place towards the start of the sessions. The vast majority of the bouts of use were brief, typically lasting less than one minute. However, occasionally they were longer - the longest being 12 min by juvenile female Keza during FR 32 of Series A. All members of the chimpanzee group used the enrichment item at some time during Experiment 5. Adolescent male Temba used the enrichment item with the greatest frequency and for the longest duration. The next highest user was juvenile female Keza. Temba, Keza, and adult female Jess, adult male Boyd and adolescent Gombe, were the individuals to first use the item during these sessions. In general adolescent and juvenile members of the group were the only subjects using the item in the latter period of its use, and the last user was always either Temba or Keza. Of all of the age and sex categories the adult females used the Screwfeeder the least.

Figure 5.7 shows that some bouts of use of the Screwfeeder enrichment by individuals in the group occurred without the delivery of reinforcement at the end of

a bout. Sometimes a bout of use by one individual was followed by use by another individual in the group and delivery of a reinforcer early in their period of use. This occurred more so as FR size increased in both series. As FR size increased the use of item by the adult members of group decreased, most markedly during and after FR 4 in both series.

Marbleroll enrichment - delivering coated peanuts. As shown in Figures 5.8a to 5.8h, all members of the chimpanzee group, except adult female Sally, used the enrichment item at some time during Experiment 5. Adult females Cara and Samantha used the item on only one and two occasions respectively. Whatever the FR size, all of the use of the item took place towards the start of the sessions. The vast majority of the use was brief, typically lasting less than one minute. However, occasionally bouts of use did go for longer, the longest being 6.12 min by adult female Jess during FR 1 of Series B. Adolescent male Temba used the enrichment the greatest number of times and for the largest amount of time. The next highest user was juvenile female Keza. Individuals Keza, Jess and Temba all the members of the group to first use the item during these sessions. In general adolescent and juvenile members of the group were the only subjects using the item in the latter period of its use, and the last user was always either Temba or Keza. Of all of the age and sex categories the adult females used the Marbleroll, when it was delivering coated peanuts, the least. Some use of the Marbleroll, when it was delivering coated peanuts, was unrelated to the delivery of reinforcement at larger FRs. As the FR values increased the use of the enrichment item by the adult members of group decreased, most markedly during and after FR 4 in both series.

Musicbox enrichment. Figures 5.9a to 5.9h show that adolescent male Temba, juvenile male Alexis, adult female Jess, adolescent female Chima and juvenile female Keza were the only members of the chimpanzee group to use the Musicbox when it was available. Further, Temba and Keza were the only individuals to use the item multiple times during a session. All but one of the episodes of use by the group occurred in the first hour of the sessions. The majority of the bouts of use were brief, typically lasting less than one minute. However, occasionally bouts of use were longer, the longest being 9.58 min by adolescent Temba during FR 2 of Series A. Adolescent male Temba used the enrichment the greatest number of times and for the

largest amount of time. The next highest user was Keza. Both of these subjects were the first individuals to first use the item during these sessions. Minimal use of the Musicbox occurred without an individual obtaining reinforcement.

Dipper enrichment. All members of the chimpanzee group, except adult male Marty and adult female Sally, used the Dipper enrichment in the sessions within which it was available during Experiment 5, as shown in Figures 5.10a to 5.10f. However, when the FR increased from FR 1 to FR 2 the number of individuals using the item dropped to include only adolescent male Temba, adult female Jess and juvenile female Keza. Regardless of the FR all of the use of the item took place towards the start of the sessions, and at FRs larger than 1 all interactions took place within the first hour of the sessions. The majority of the bouts of use were brief, typically lasting less than one minute. However, many bouts of use did go for longer, the longest being 20.8 min by adolescent female Chima during FR 1 of Series B. Jess used the enrichment the greatest amount of time and Temba used the item the most occasions (and was the highest user in terms of time). With the exception of Jess the adults of the group used the item the least. Individuals Temba and Jess were all the individuals to first use the item during these sessions. Some use of the Dipper occurred without association to obtaining reinforcement.

TV/Video enrichment. Figures 5.11a to 5.11d show that adolescent male Temba, juvenile male Alexis and juvenile female Keza were the only members of the chimpanzee group to use the TV/Video item in sessions of Experiment 5 within which it was available. Further to this in all but one session (FR 1, Series A) the individuals used the item only once in a session. All of use by the group occurred in the first half hour of the sessions. The majority of the bouts of use were brief, typically lasting less than one minute. However, some bouts of use did go for longer, the longest being 4.19 min by adolescent male Temba during FR 1 of Series A. Adolescent male Temba used the enrichment the greatest number of times and for the largest amount of time. The next highest user was Keza. Keza and Alexis were the first individuals to use the item during these sessions. Minimal use of the TV/Video item occurred without an individual obtaining reinforcement.

Marbleroll enrichment. Figures 5.12a to 5.12g show that all members of the

chimpanzee group used the Marbleroll at some time when it was available, except for adult male Marty, and adult females Cara and Sally. Regardless of the FR size, all of the use of the item took place towards the start of the sessions. Much of the use occurred as bouts of multiple minutes, the longest being 28.52 min by juvenile female Keza during FR 1 of Series A. Keza used the enrichment the greatest number of times and for the largest amount of time. The next highest user was adolescent male Temba. Individuals Keza and adult female Jess were the subjects to first use the item during these sessions. In general adolescent and juvenile members of the group used the item far more than the adult members, with the exception of Jess. Keza was the last subject to use the item in all of the Marbleroll enrichment sessions. A lot of use of this item occurred without the association of delivering of a reinforcement. However, this use was generally by an individual that had received a reinforcer close in time to the present bout of use.

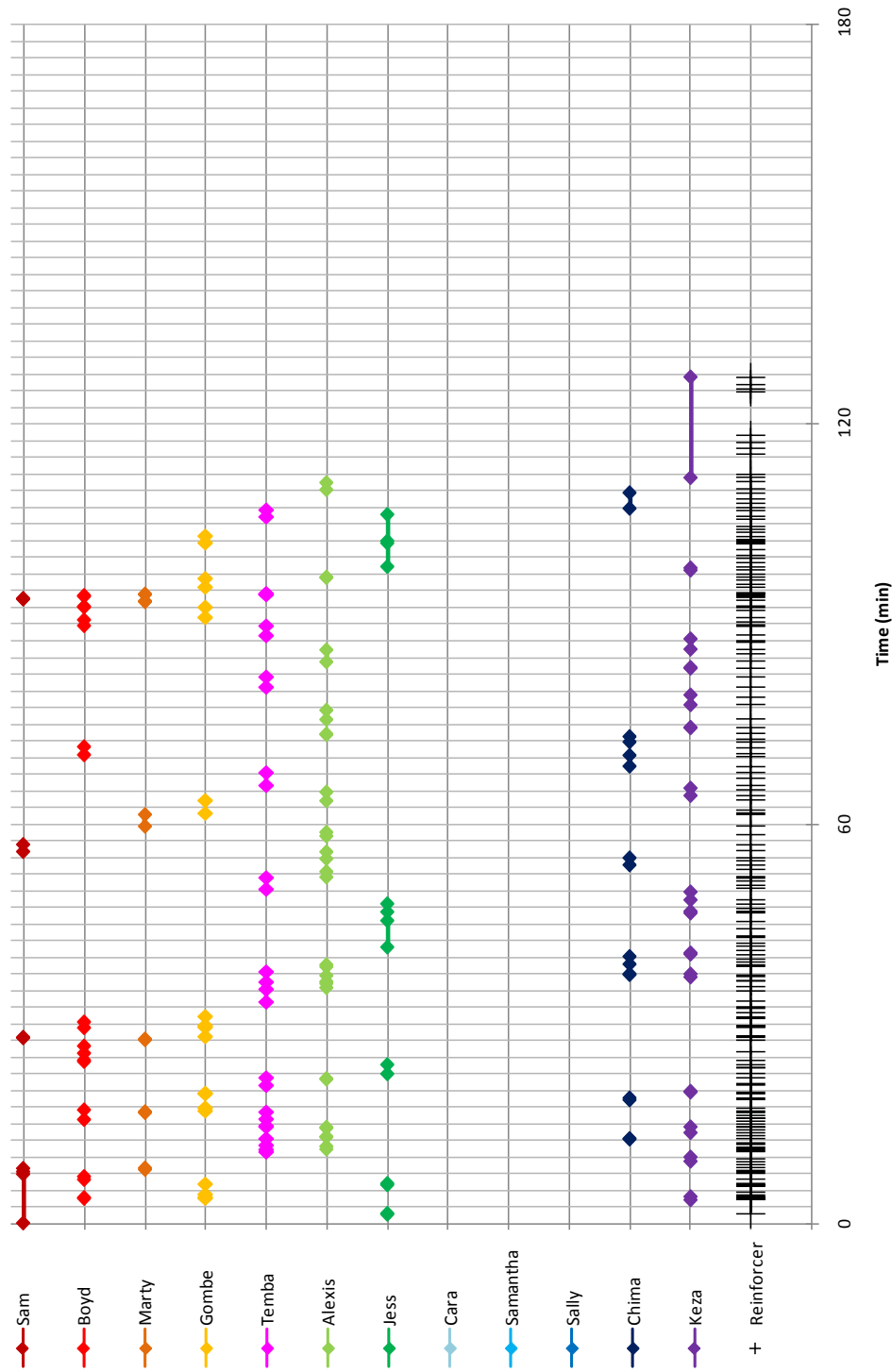


Figure 5.7a. Start and stop times for defined behaviours related to the group's use of the Screwfeeder enrichment item and time any reinforcements were delivered during the FR 1 session of, Series A, during Experiment 5. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

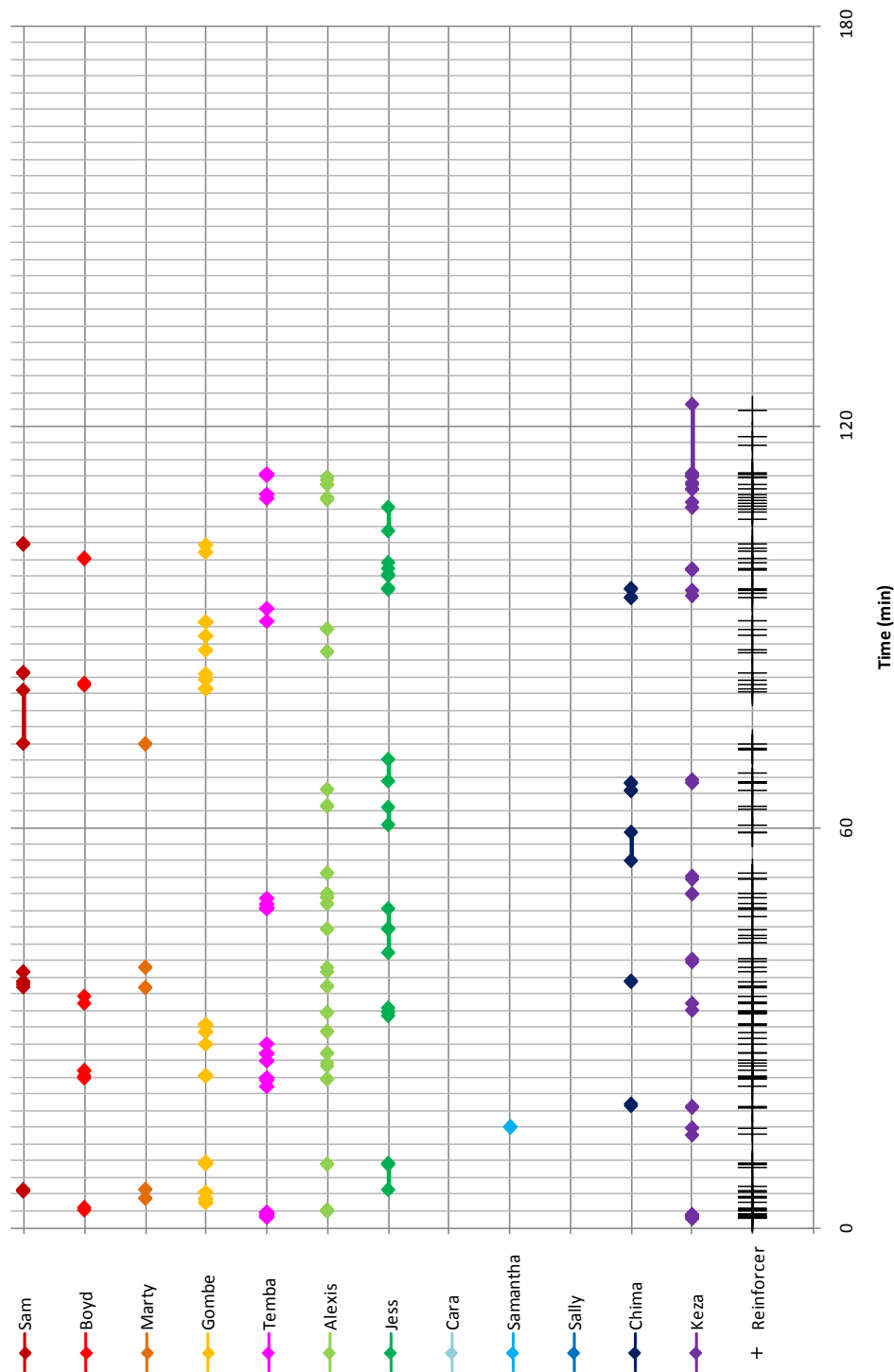


Figure 5.7*b*. Start and stop times for defined behaviours related to the group’s use of the Screwfeeder enrichment item and time any reinforcements were delivered during the FR 2 session of, Series A, during Experiment 5. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

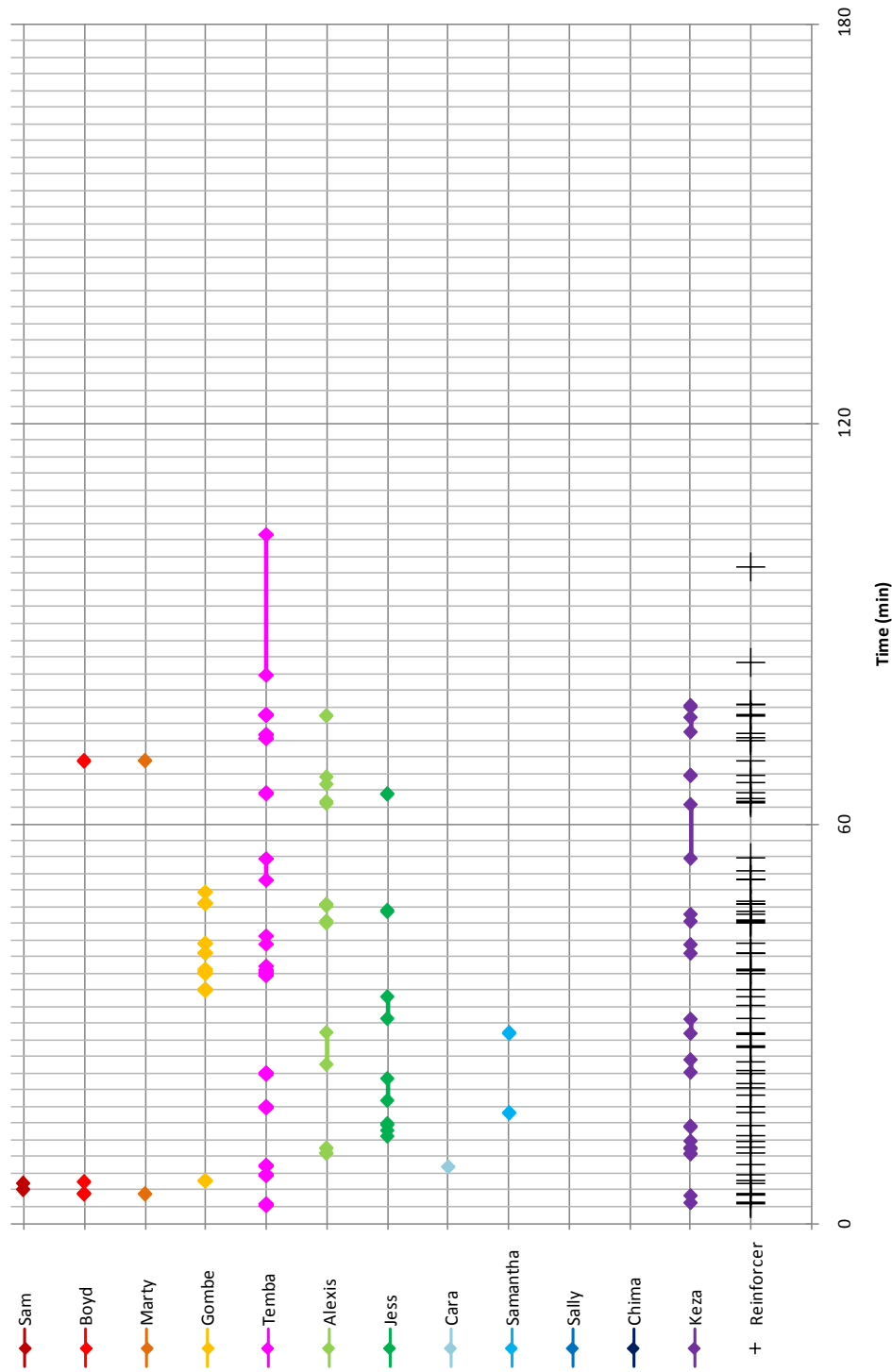
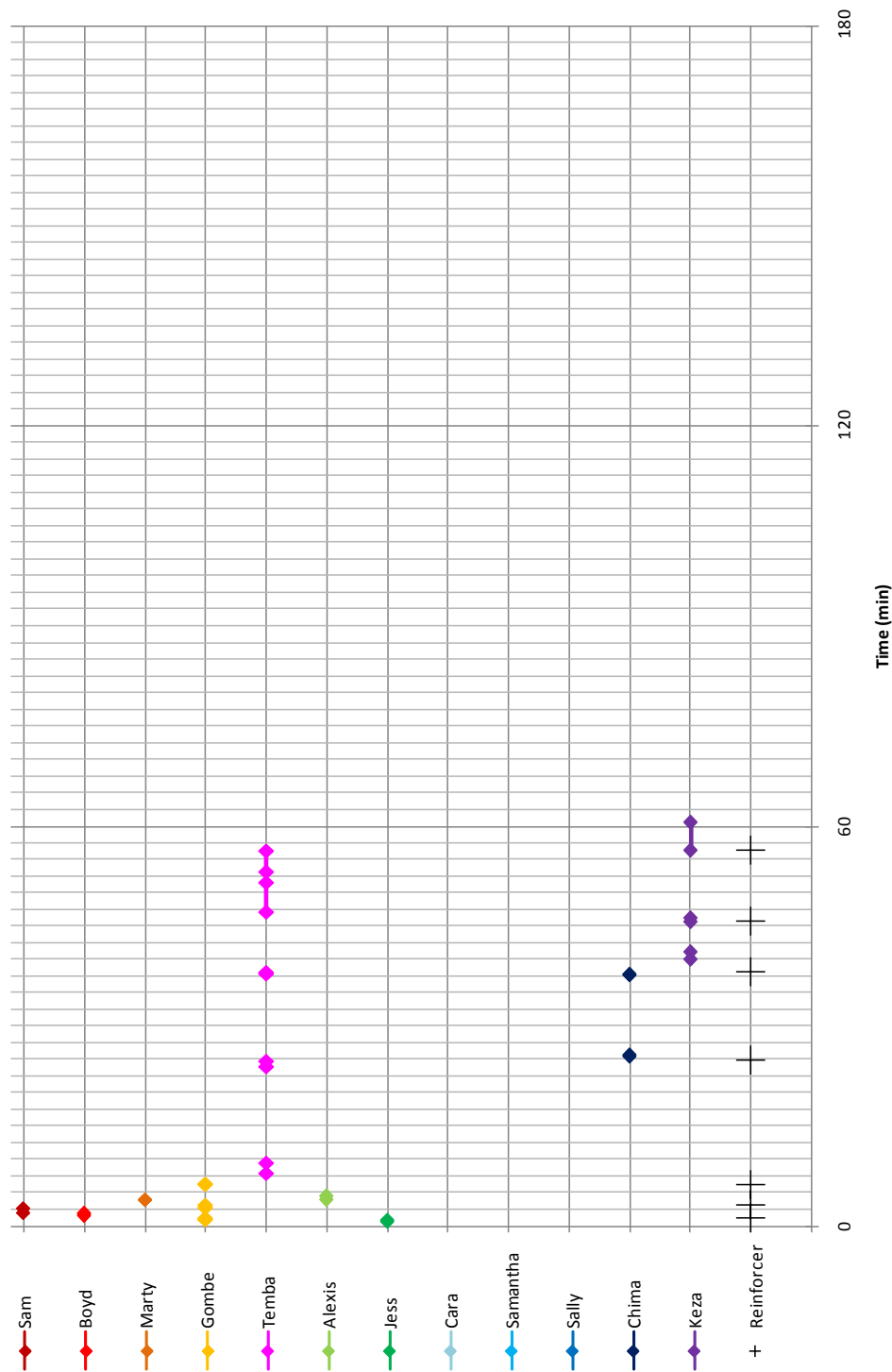


Figure 5.7c. Start and stop times for defined behaviours related to the group's use of the Screwfeeder enrichment item and time any reinforcements were delivered during the FR 4 session of, Series A, during Experiment 5. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.



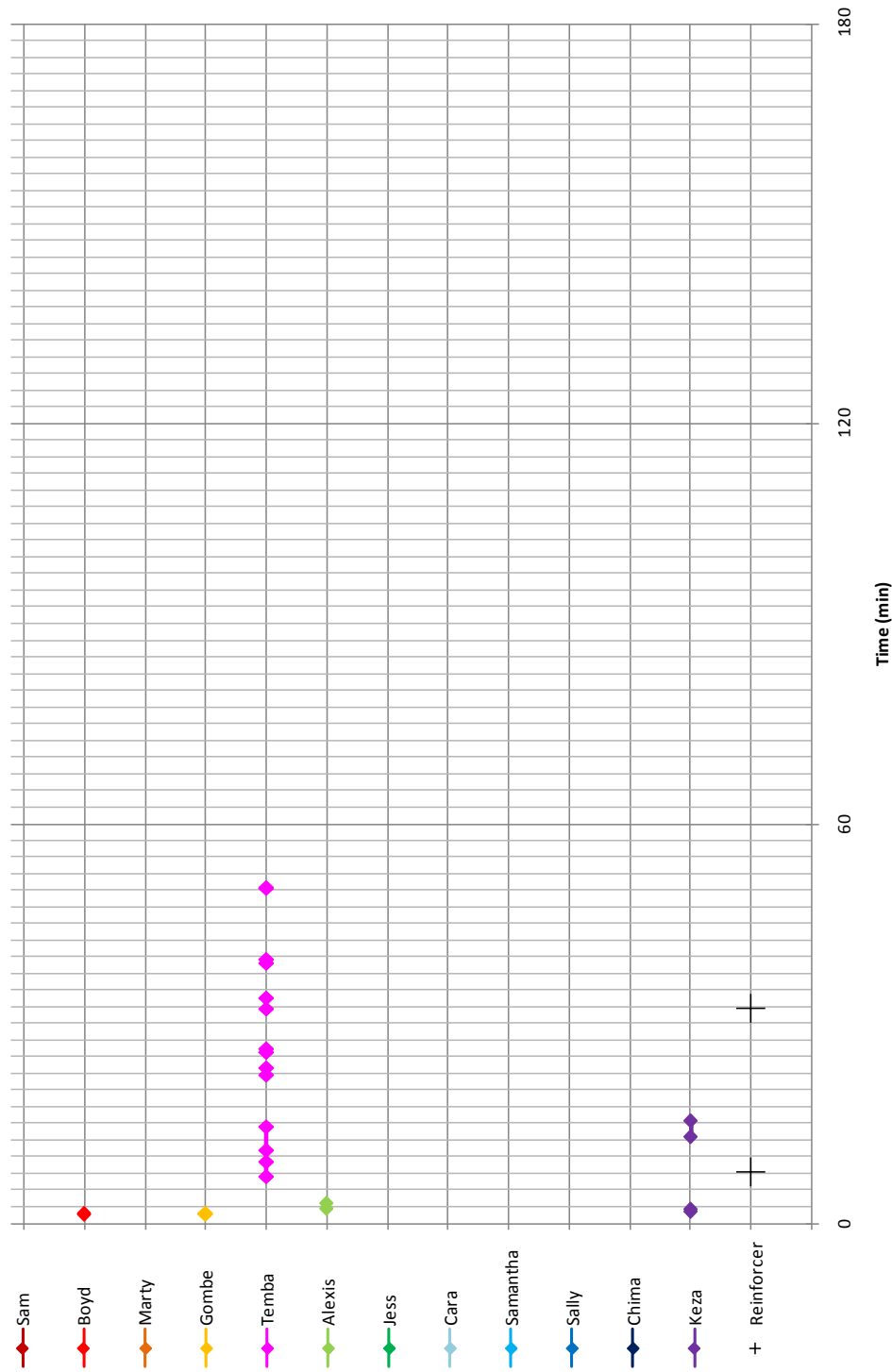


Figure 5.7e. Start and stop times for defined behaviours related to the group's use of the Screwfeeder enrichment item and time any reinforcements were delivered during the FR 16 session of, Series A, during Experiment 5. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

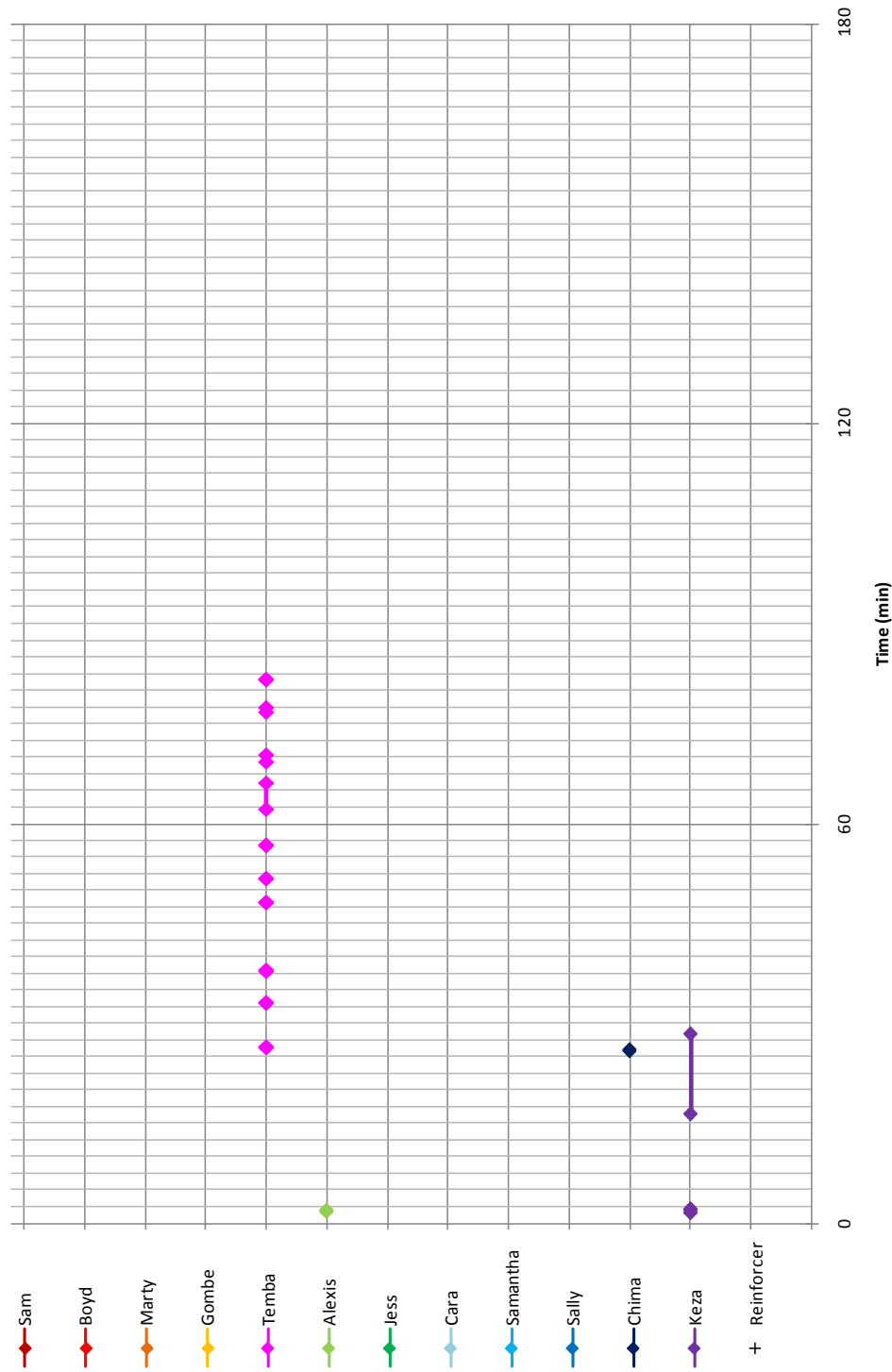


Figure 5.7f. Start and stop times for defined behaviours related to the group's use of the Screwfeeder enrichment item and time any reinforcements were delivered during the FR 32 session of, Series A, during Experiment 5. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

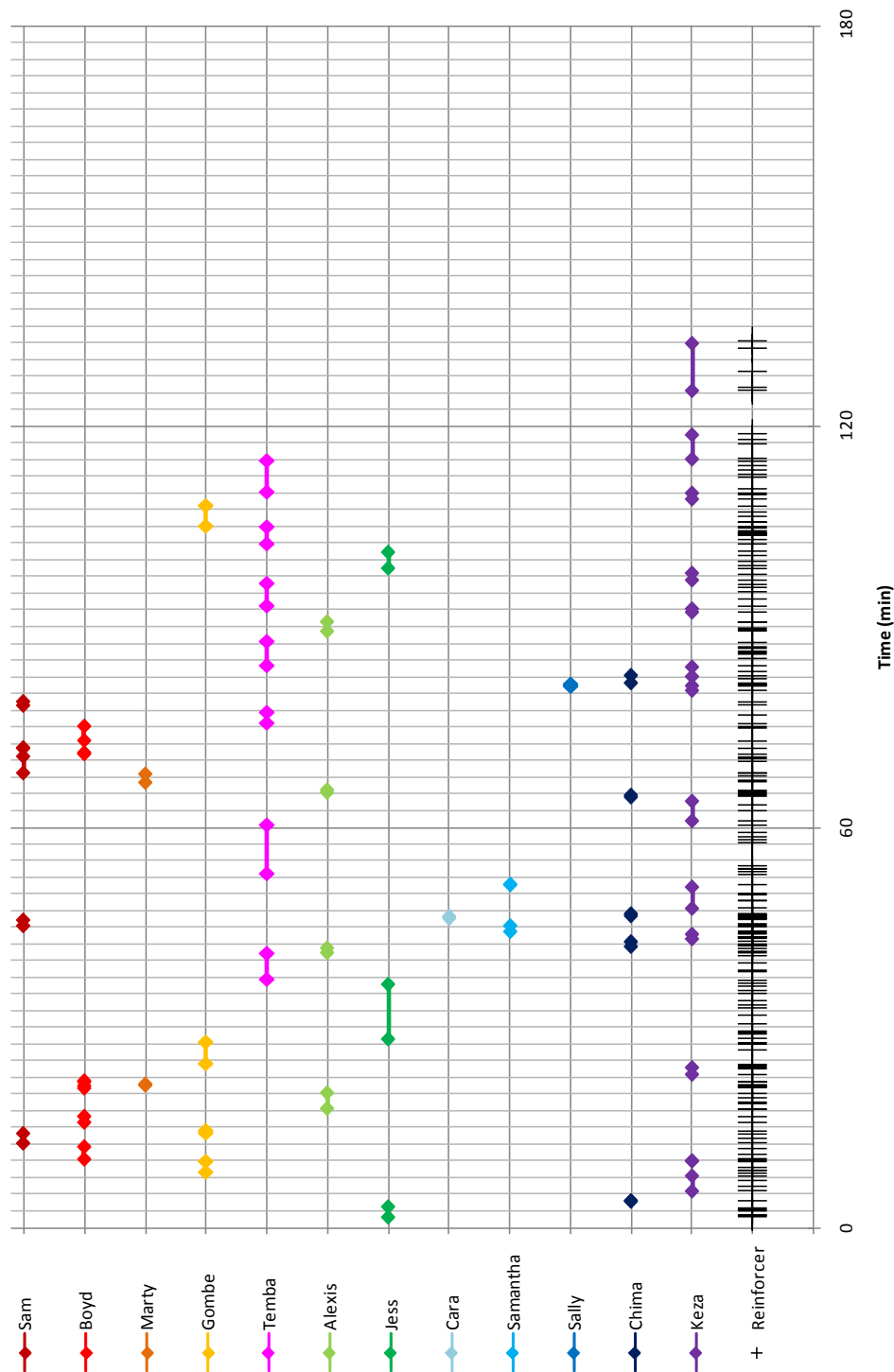


Figure 5.7g. Start and stop times for defined behaviours related to the group's use of the Screwfeeder enrichment item and time any reinforcements were delivered during the FR 1 session of, Series B, during Experiment 5. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

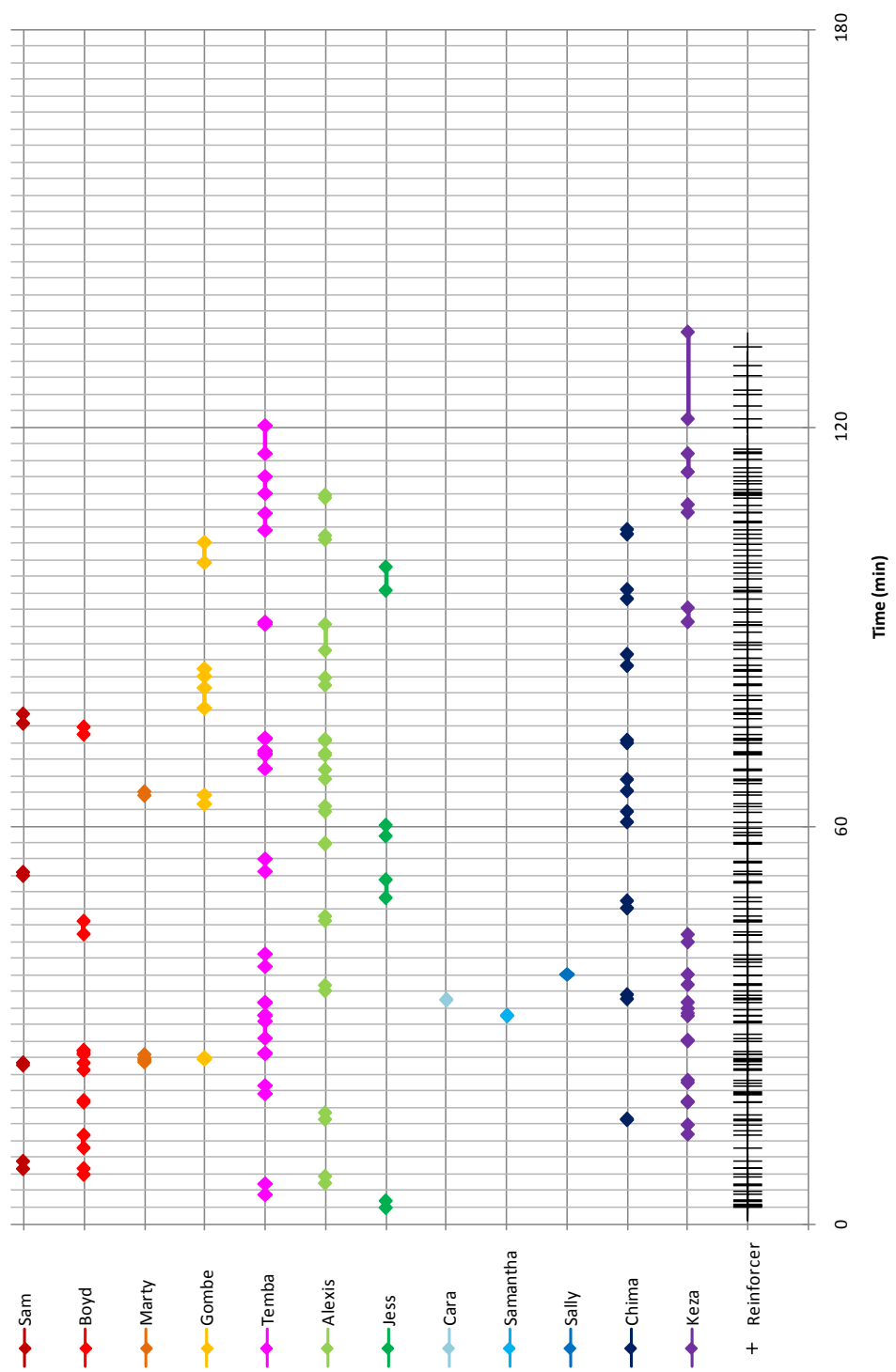


Figure 5.7h. Start and stop times for defined behaviours related to the group's use of the Screwfeeder enrichment item and time any reinforcements were delivered during the FR 2 session of, Series B, during Experiment 5. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

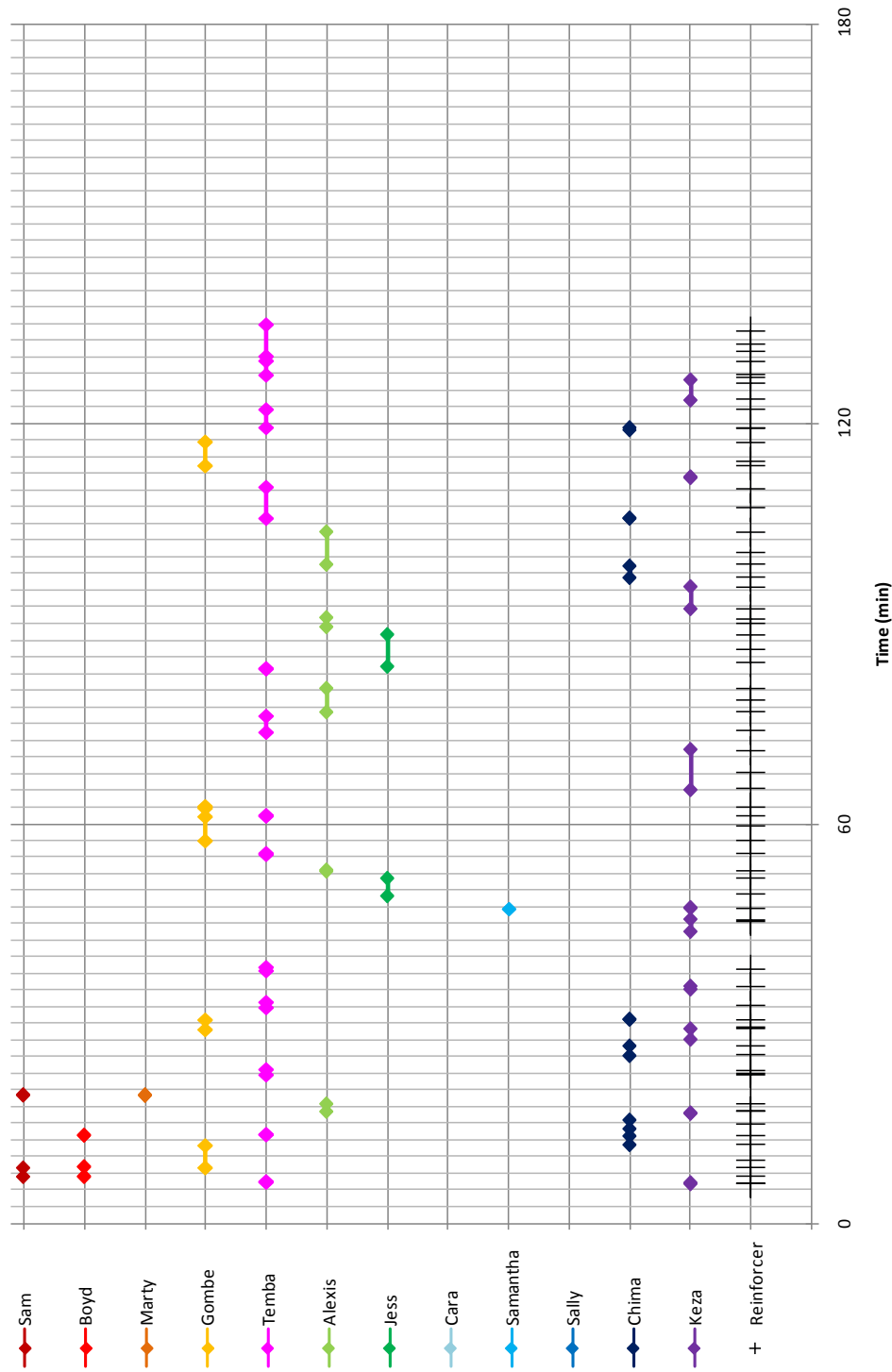


Figure 5.7*i*. Start and stop times for defined behaviours related to the group's use of the Screwfeeder enrichment item and time any reinforcements were delivered during the FR 4 session of, Series B, during Experiment 5. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

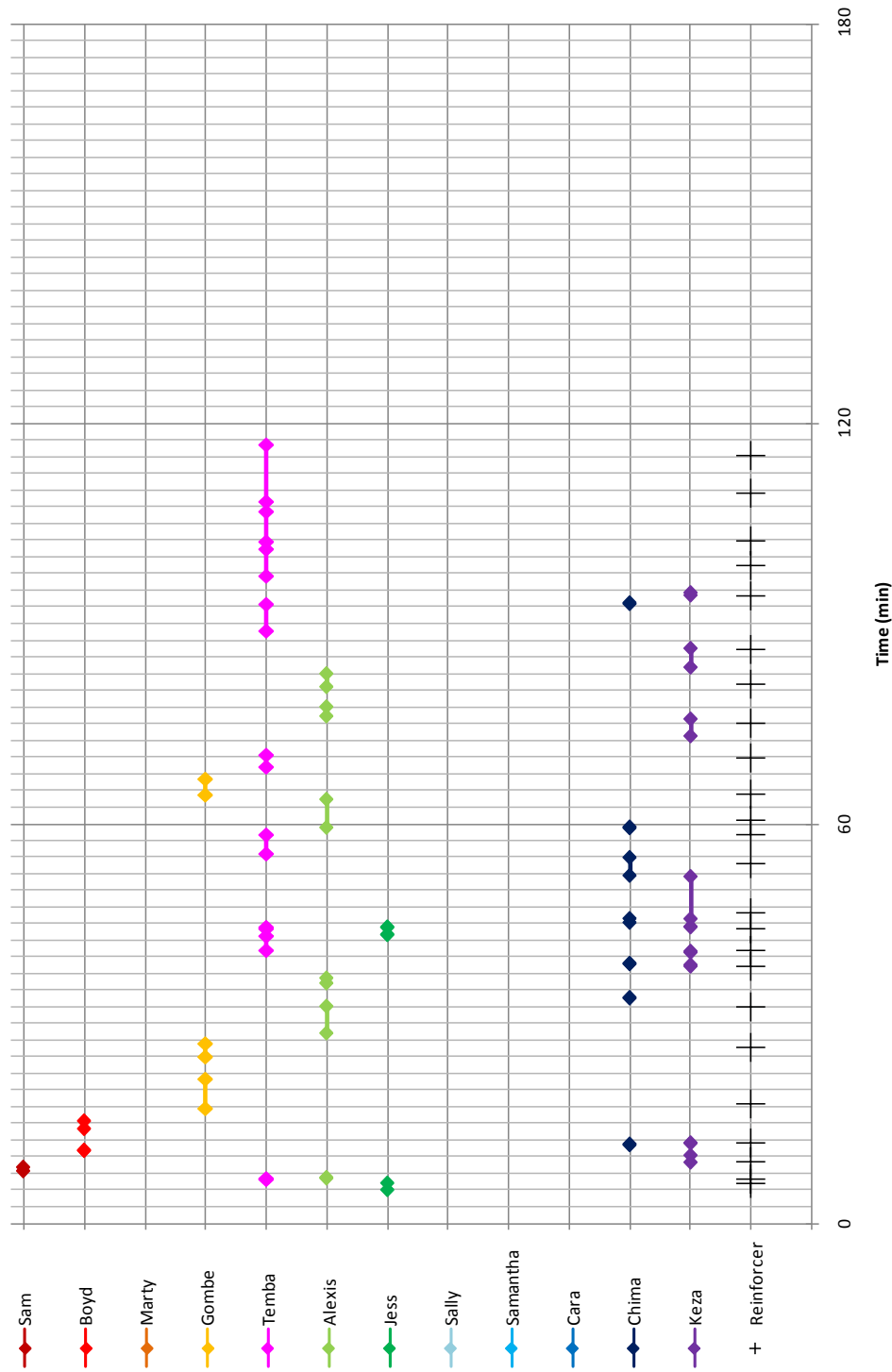


Figure 5.7j. Start and stop times for defined behaviours related to the group's use of the Screwfeeder enrichment item and time any reinforcements were delivered during the FR 8 session of, Series B, during Experiment 5. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

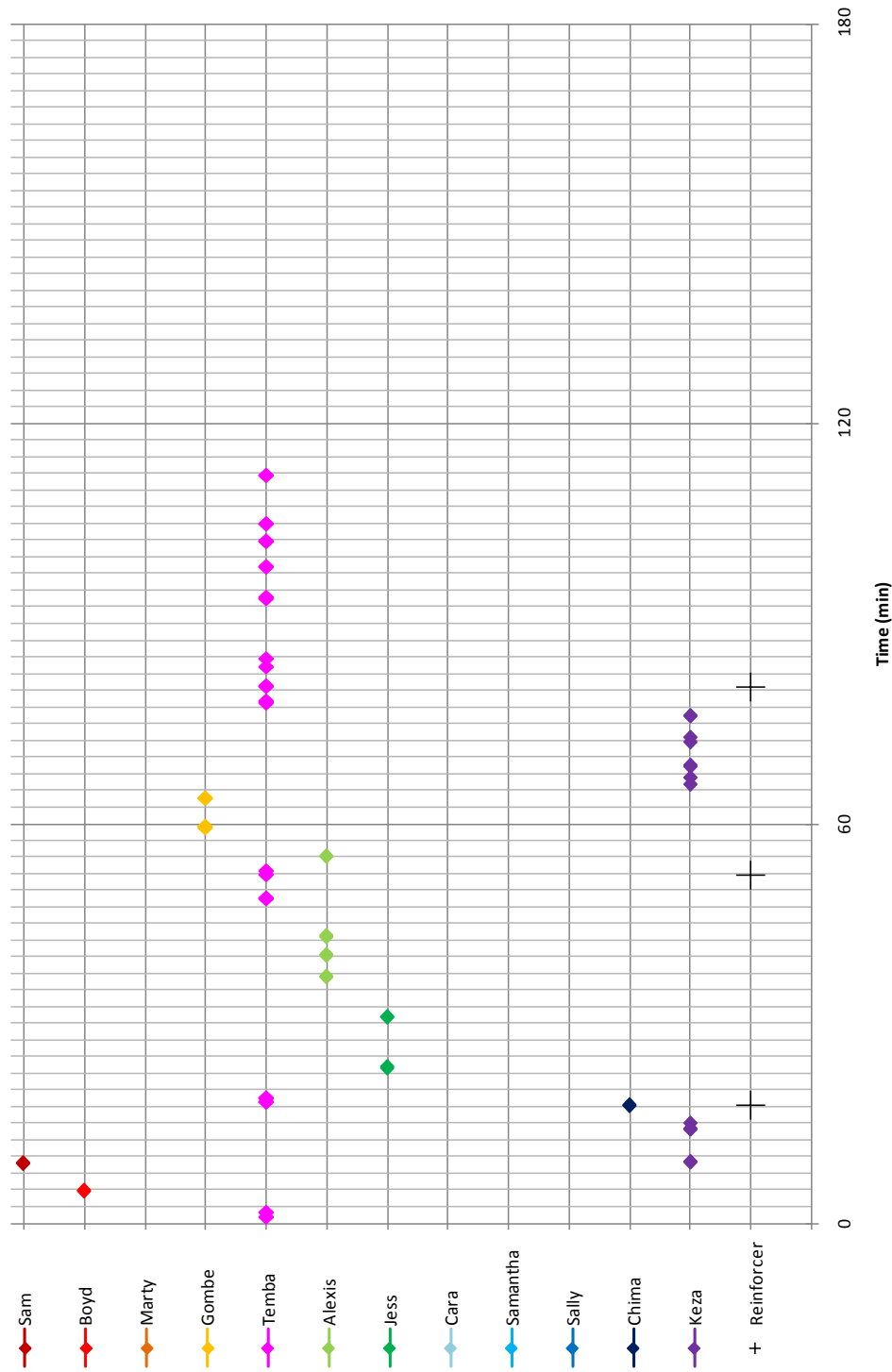


Figure 5.7k. Start and stop times for defined behaviours related to the group's use of the Screwfeeder enrichment item and time any reinforcements were delivered during the FR 16 session of, Series B, during Experiment 5. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

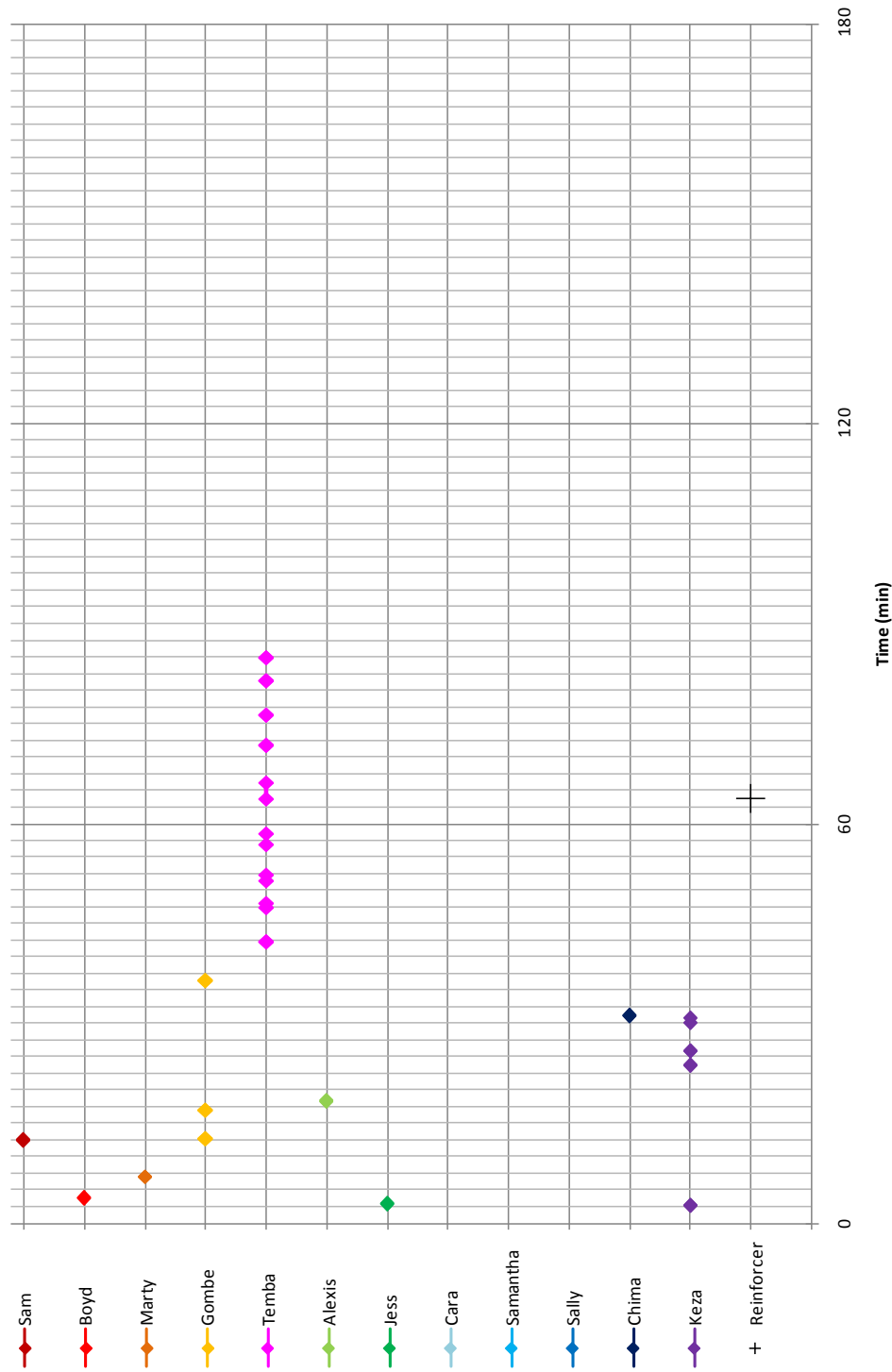


Figure 5.7l. Start and stop times for defined behaviours related to the group's use of the Screwfeeder enrichment item and time any reinforcements were delivered during the FR 32 session of, Series B, during Experiment 5. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

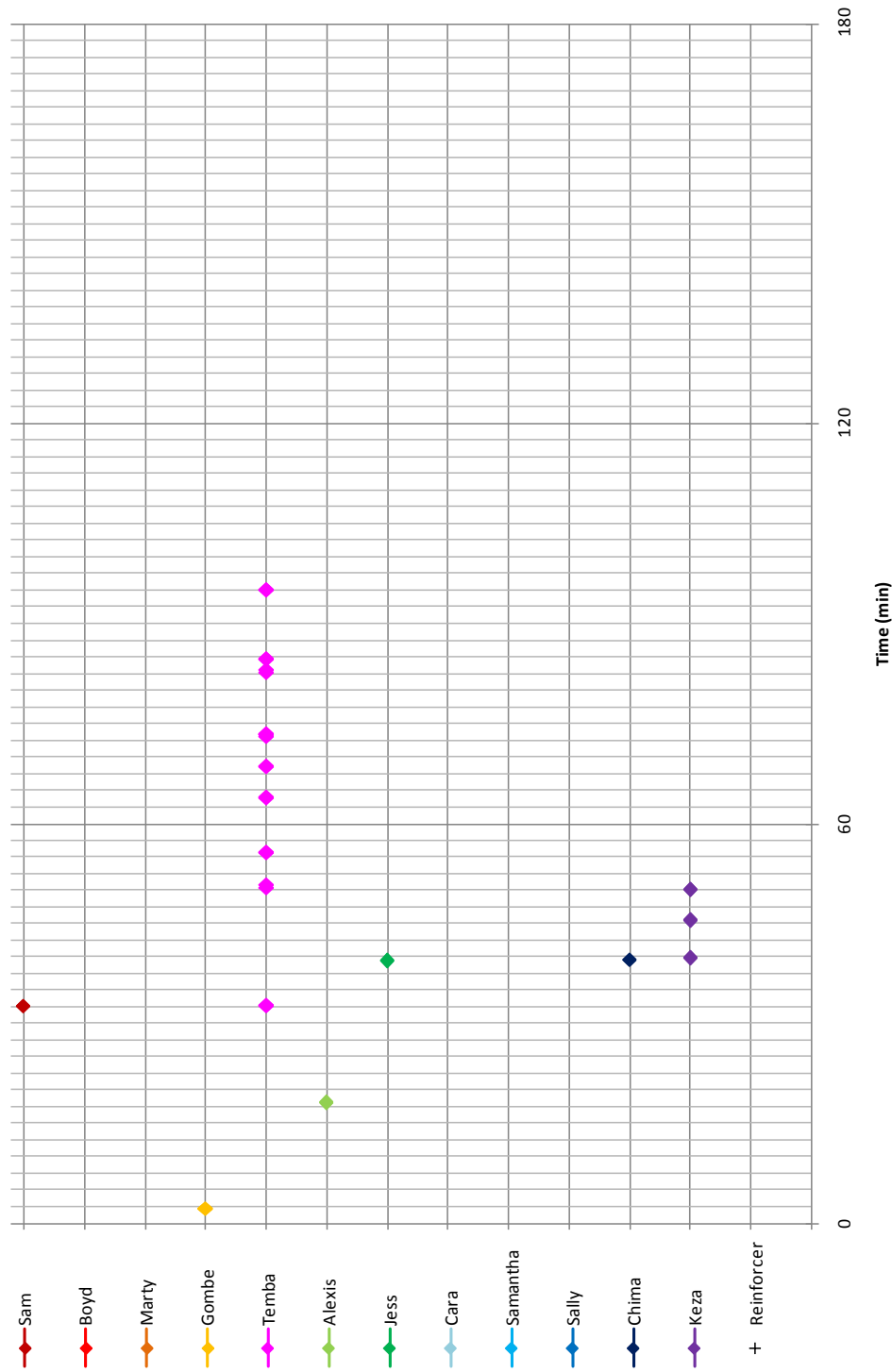


Figure 5.7m. Start and stop times for defined behaviours related to the group's use of the Screwfeeder enrichment item and time any reinforcements were delivered during the FR 64 session of, Series B, during Experiment 5. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

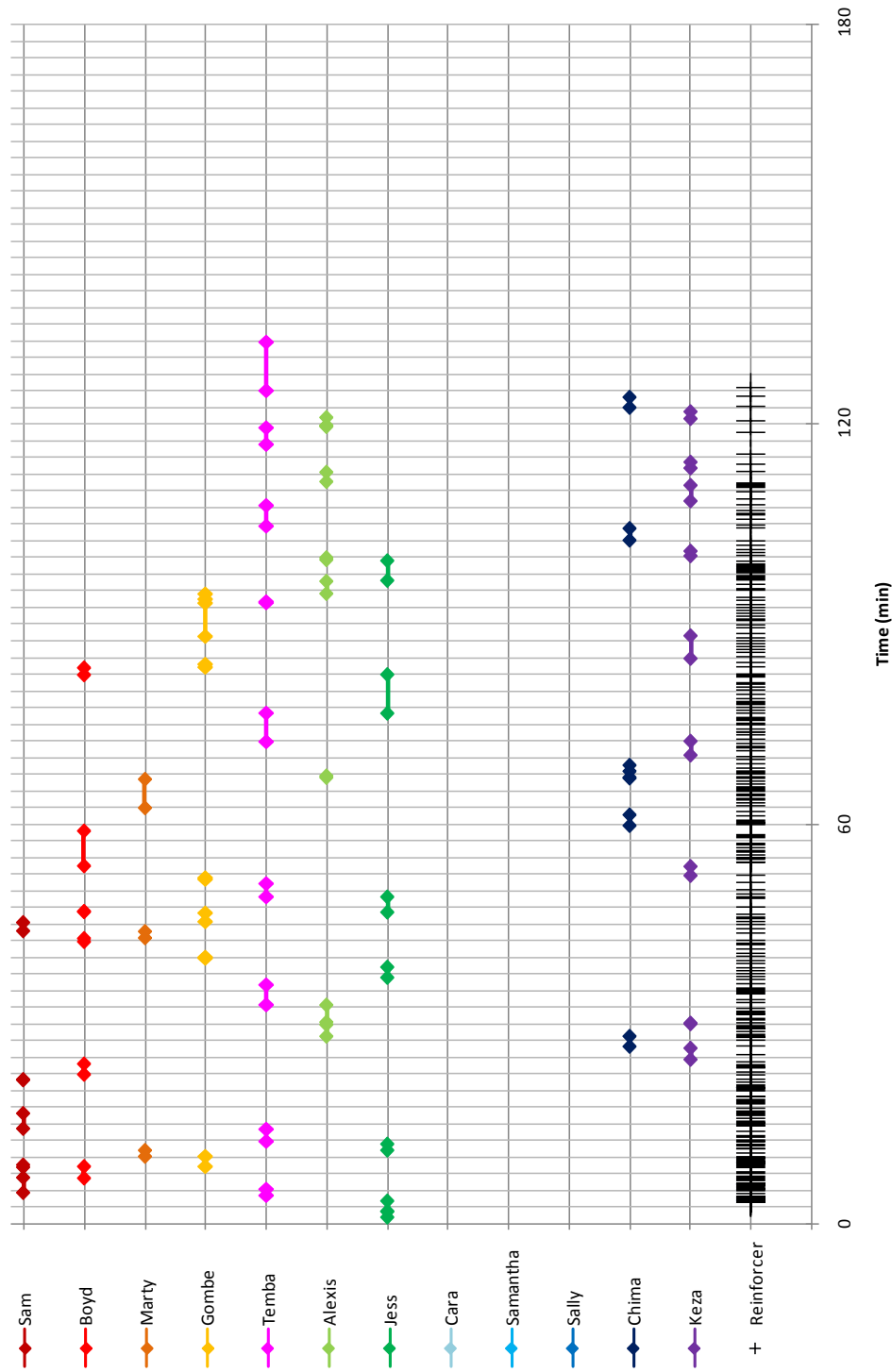


Figure 5.8a. Start and stop times for defined behaviours related to the group's use of the Marbleroll enrichment item, delivering coated peanuts, and time any reinforcements were delivered during the FR 1 session of, Series A, during Experiment 5. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

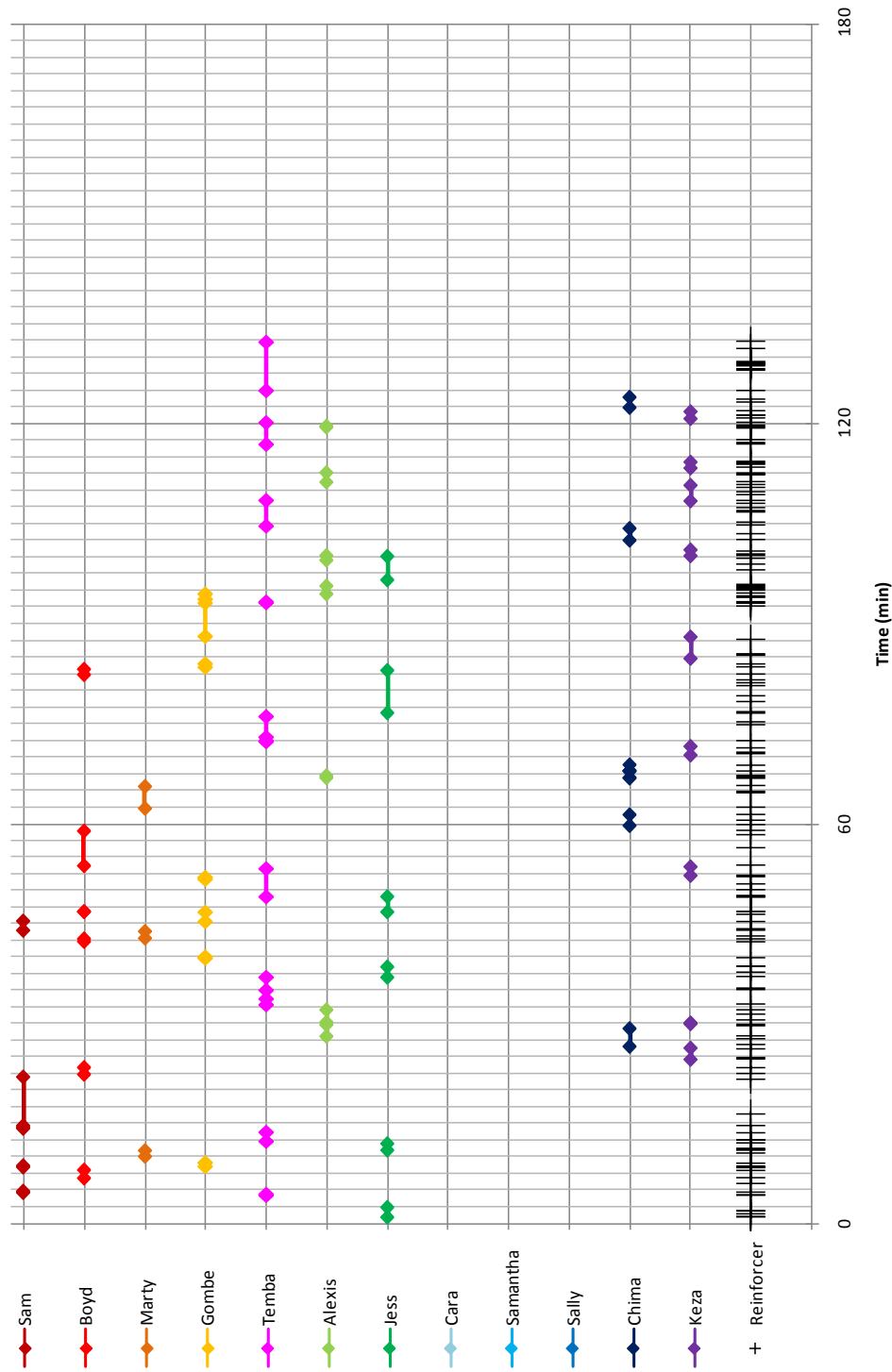
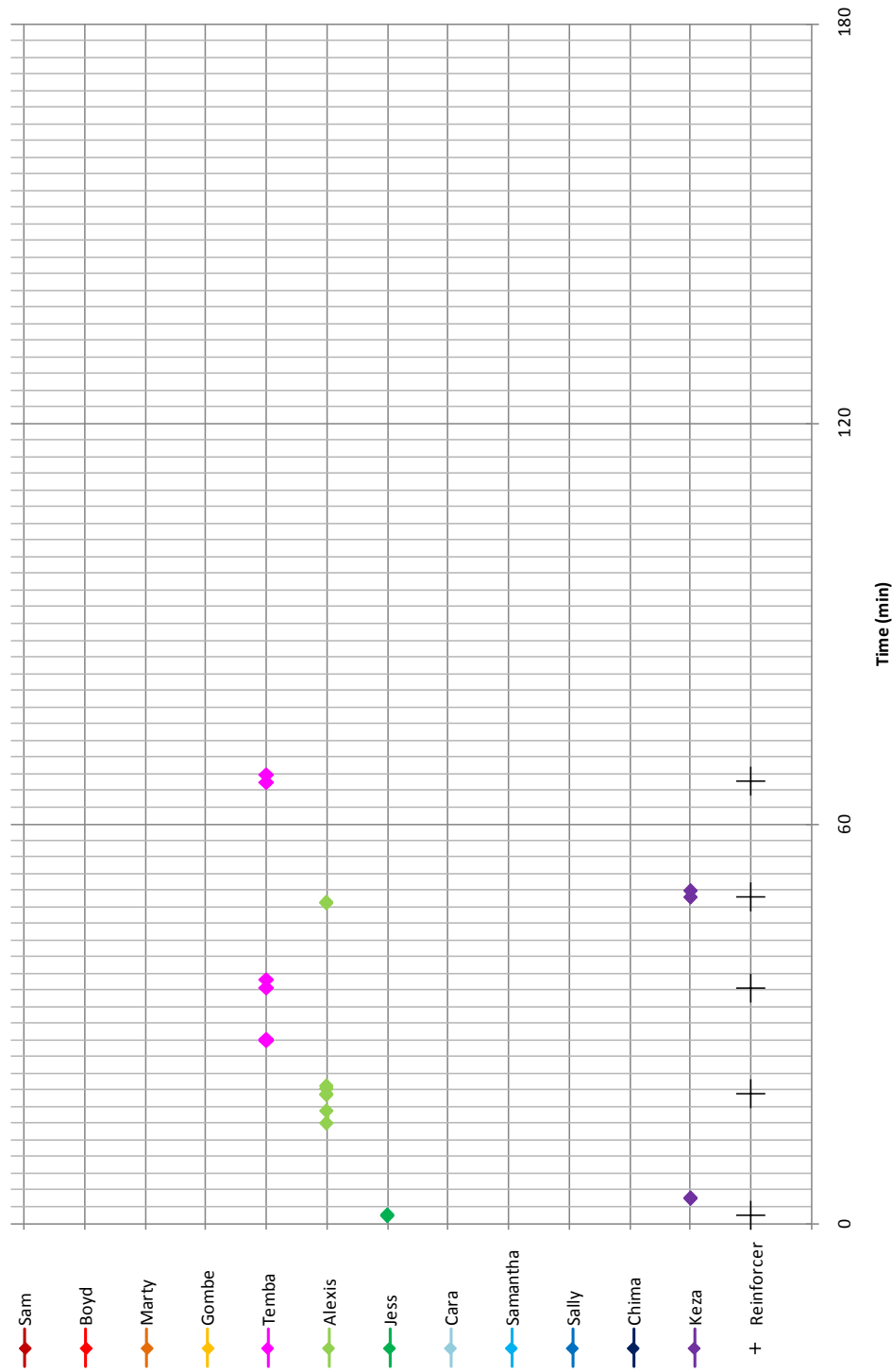


Figure 5.8b. Start and stop times for defined behaviours related to the group's use of the Marbleroll enrichment item, delivering coated peanuts, and time any reinforcements were delivered during the FR 2 session of, Series A, during Experiment 5. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.



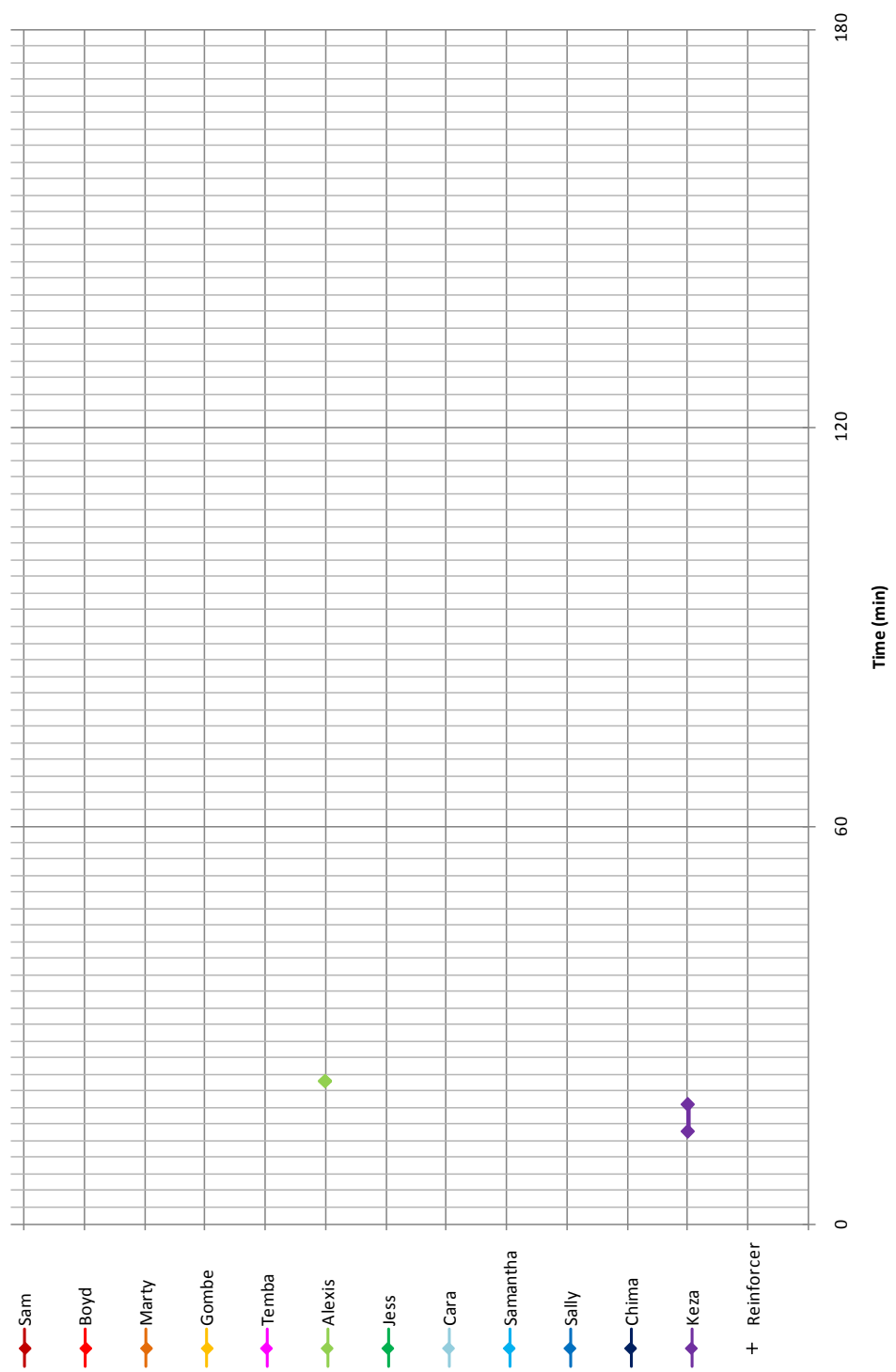


Figure 5.8d. Start and stop times for defined behaviours related to the group's use of the Marbleroll enrichment item, delivering coated peanuts, and time any reinforcements were delivered during the FR 8 session of, Series A, during Experiment 5. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

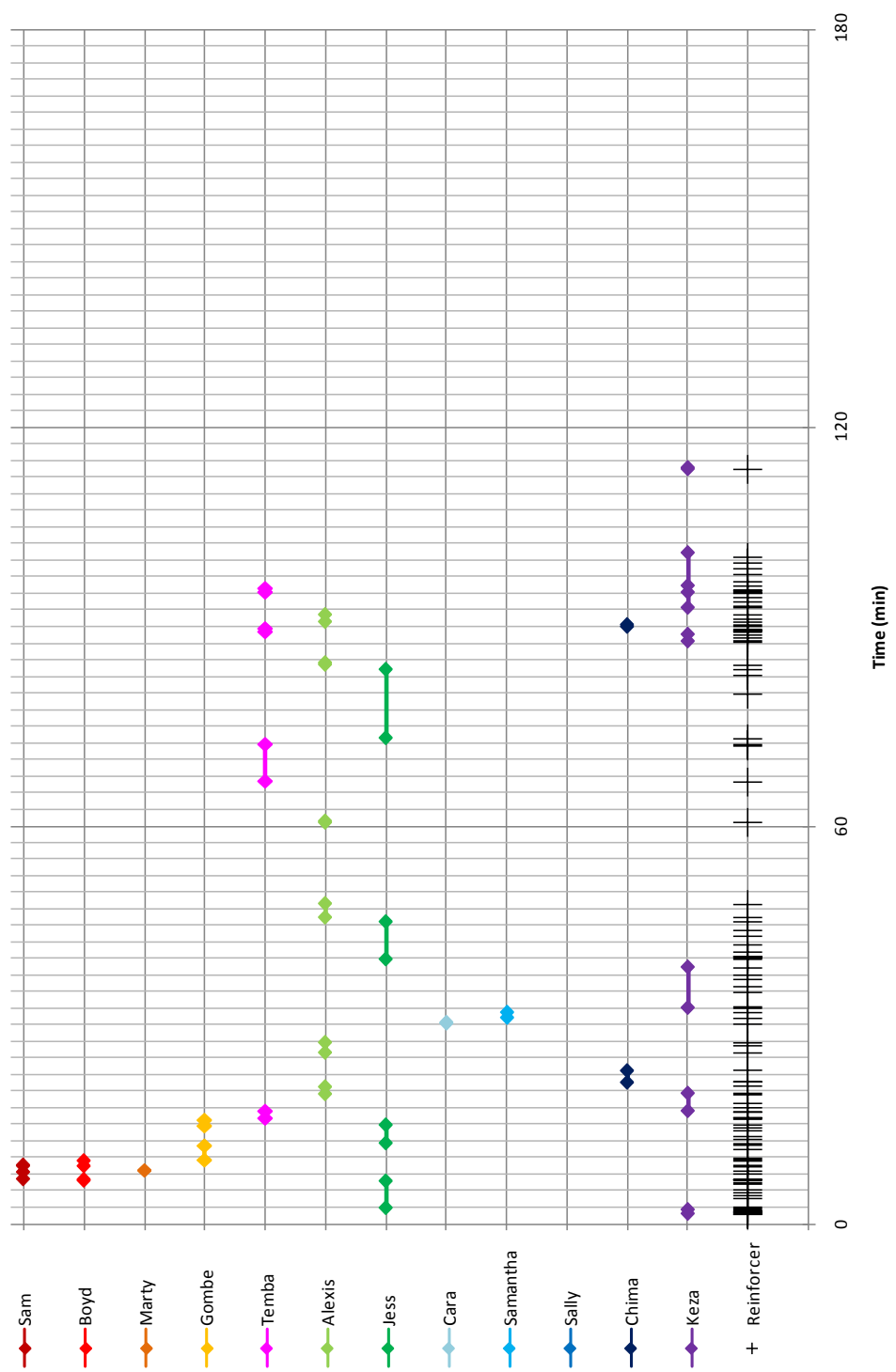


Figure 5.8e. Start and stop times for defined behaviours related to the group's use of the Marbleroll enrichment item, delivering coated peanuts, and time any reinforcements were delivered during the FR 1 session of, Series B, during Experiment 5. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

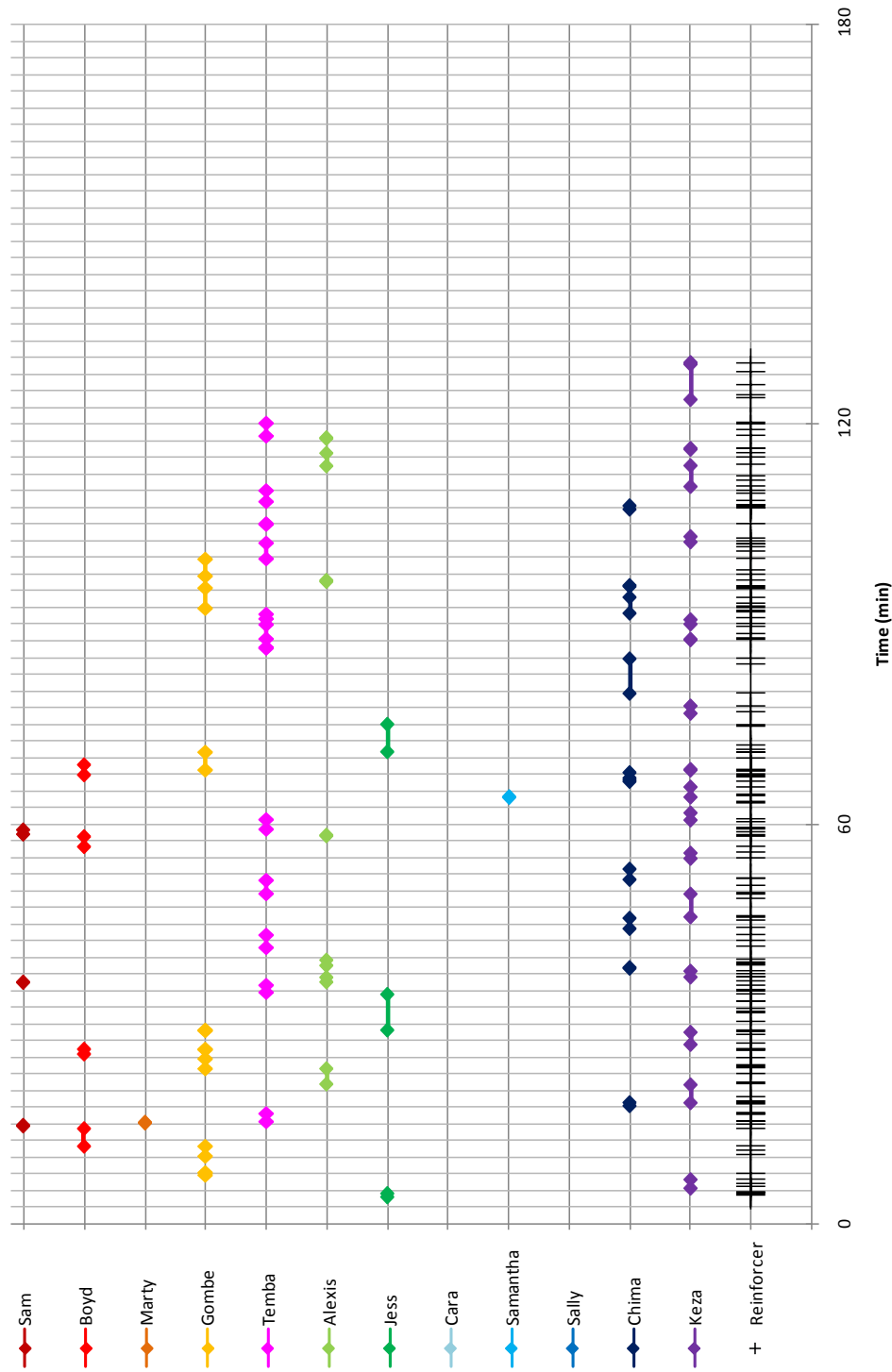


Figure 5.8f. Start and stop times for defined behaviours related to the group's use of the Marbleroll enrichment item, delivering coated peanuts, and time any reinforcements were delivered during the FR 2 session of, Series B, during Experiment 5. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

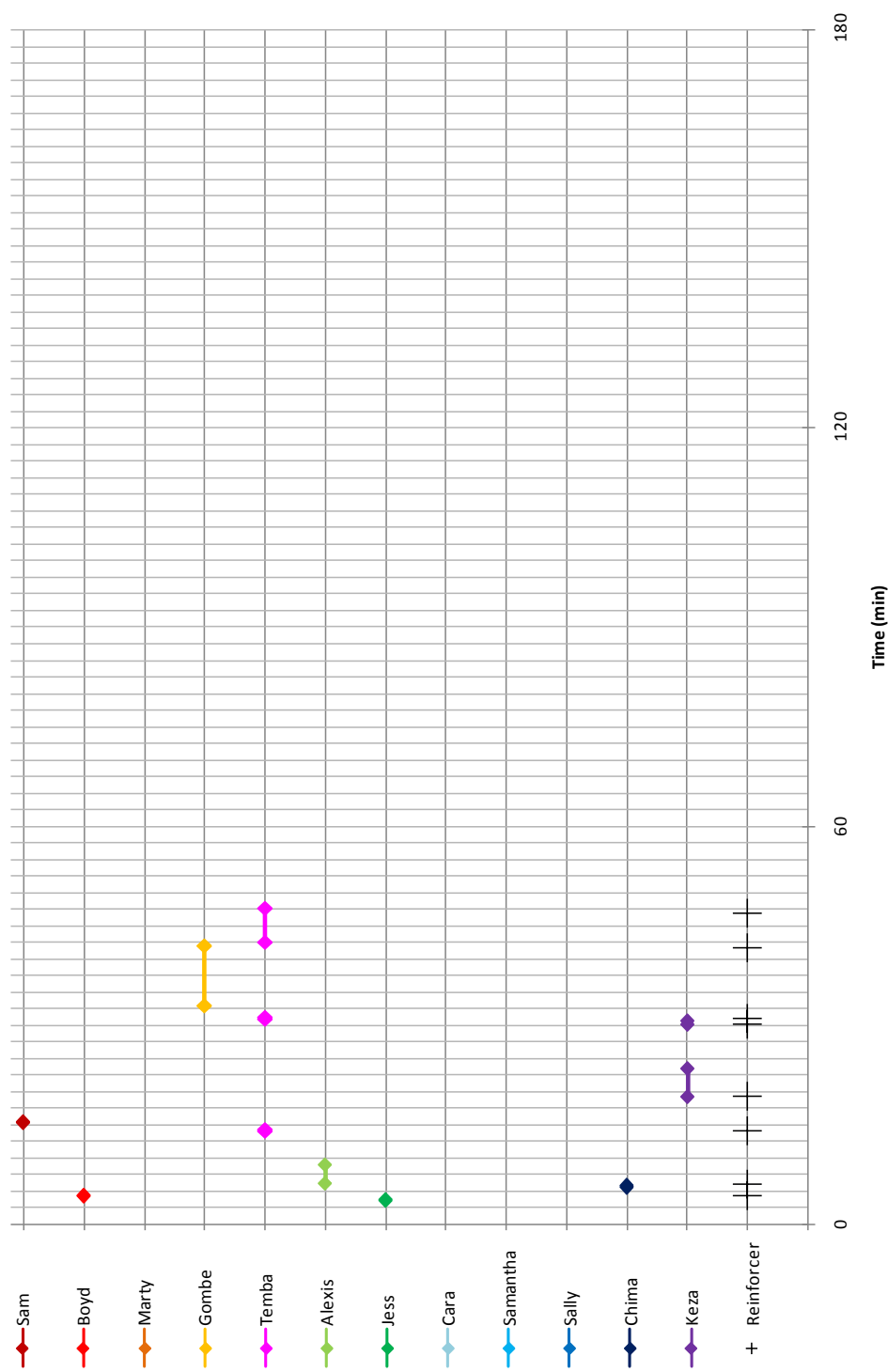


Figure 5.8g. Start and stop times for defined behaviours related to the group's use of the Marbleroll enrichment item, delivering coated peanuts, and time any reinforcements were delivered during the FR 4 session of, Series B, during Experiment 5. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

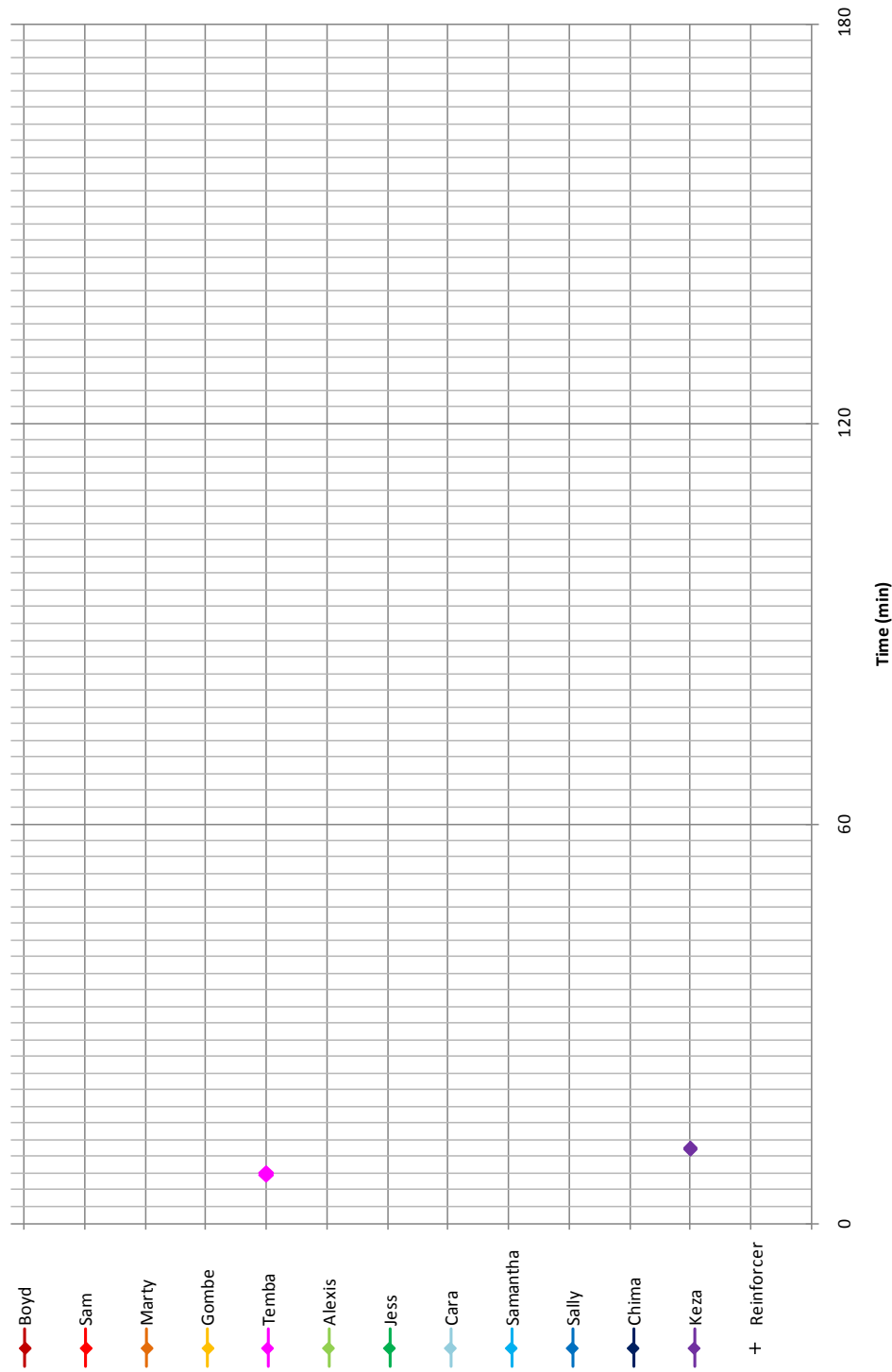


Figure 5.8h. Start and stop times for defined behaviours related to the group's use of the Marbleroll enrichment item, delivering coated peanuts, and time any reinforcements were delivered during the FR 8 session of, Series B, during Experiment 5. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

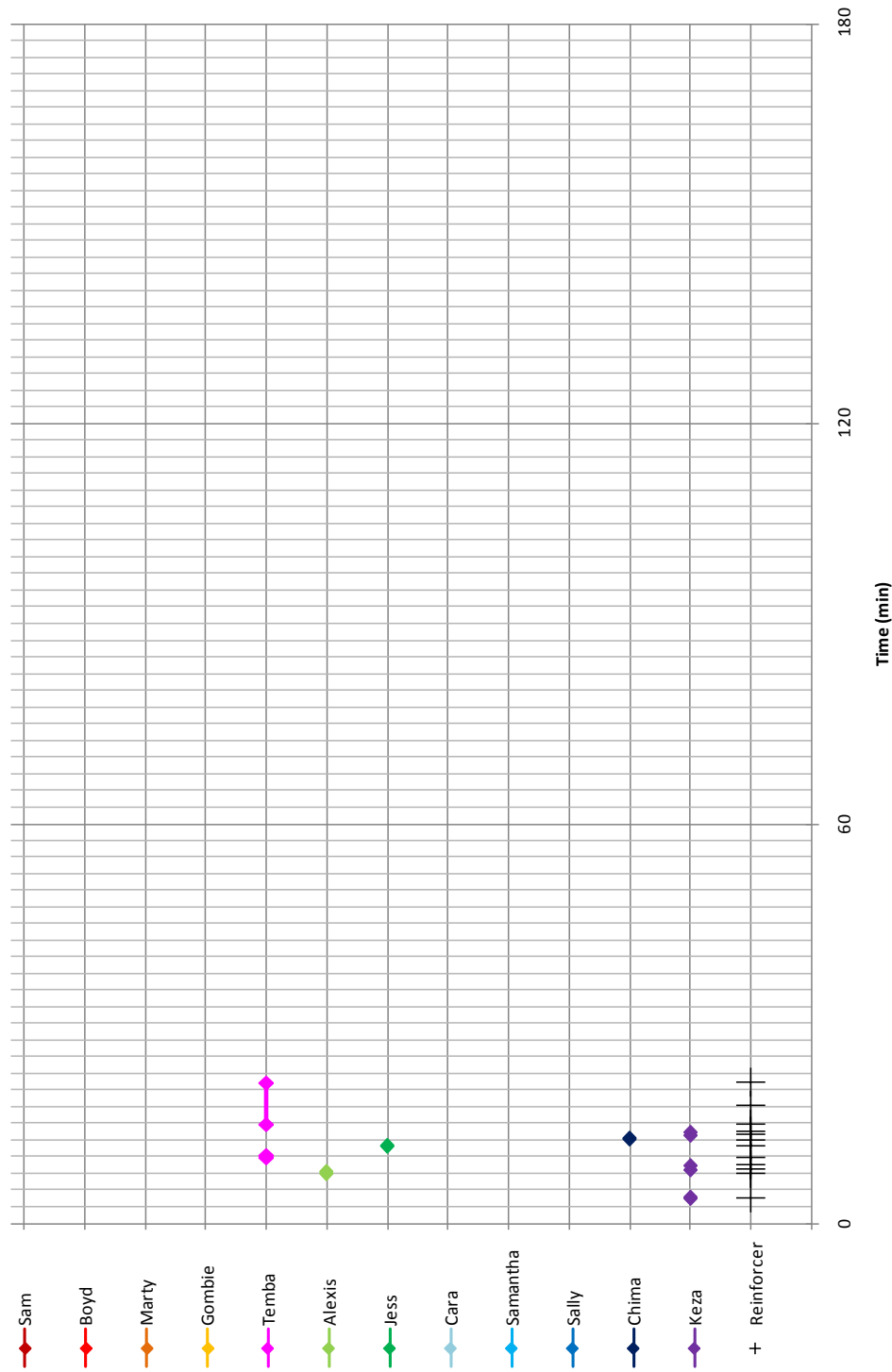


Figure 5.9a. Start and stop times for defined behaviours related to the group's use of the Musicbox enrichment item and time any reinforcements were delivered during the FR 1 session of, Series A, during Experiment 5. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

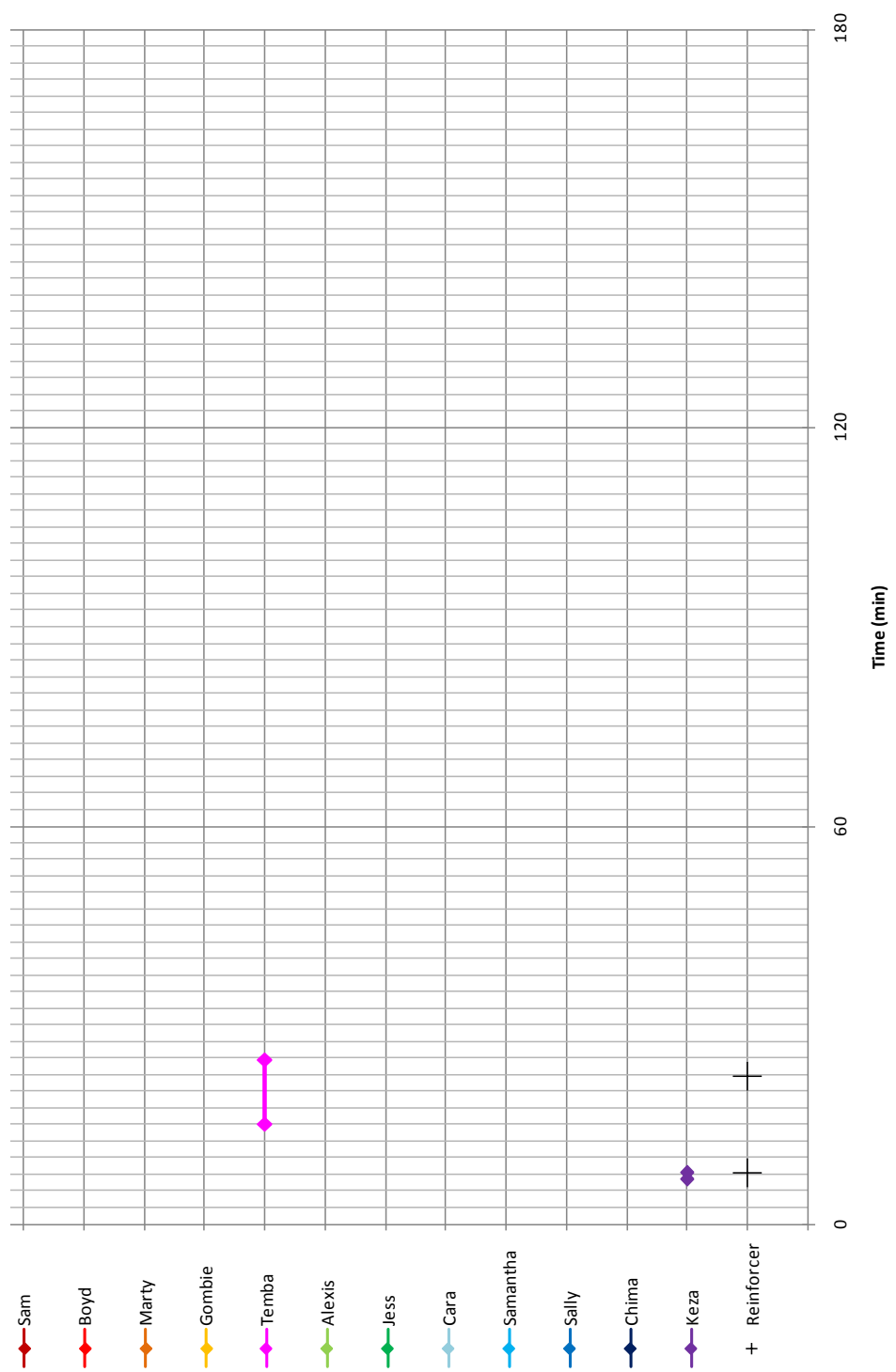


Figure 5.9b. Start and stop times for defined behaviours related to the group’s use of the Musicbox enrichment item and time any reinforcements were delivered during the FR 2 session of, Series A, during Experiment 5. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

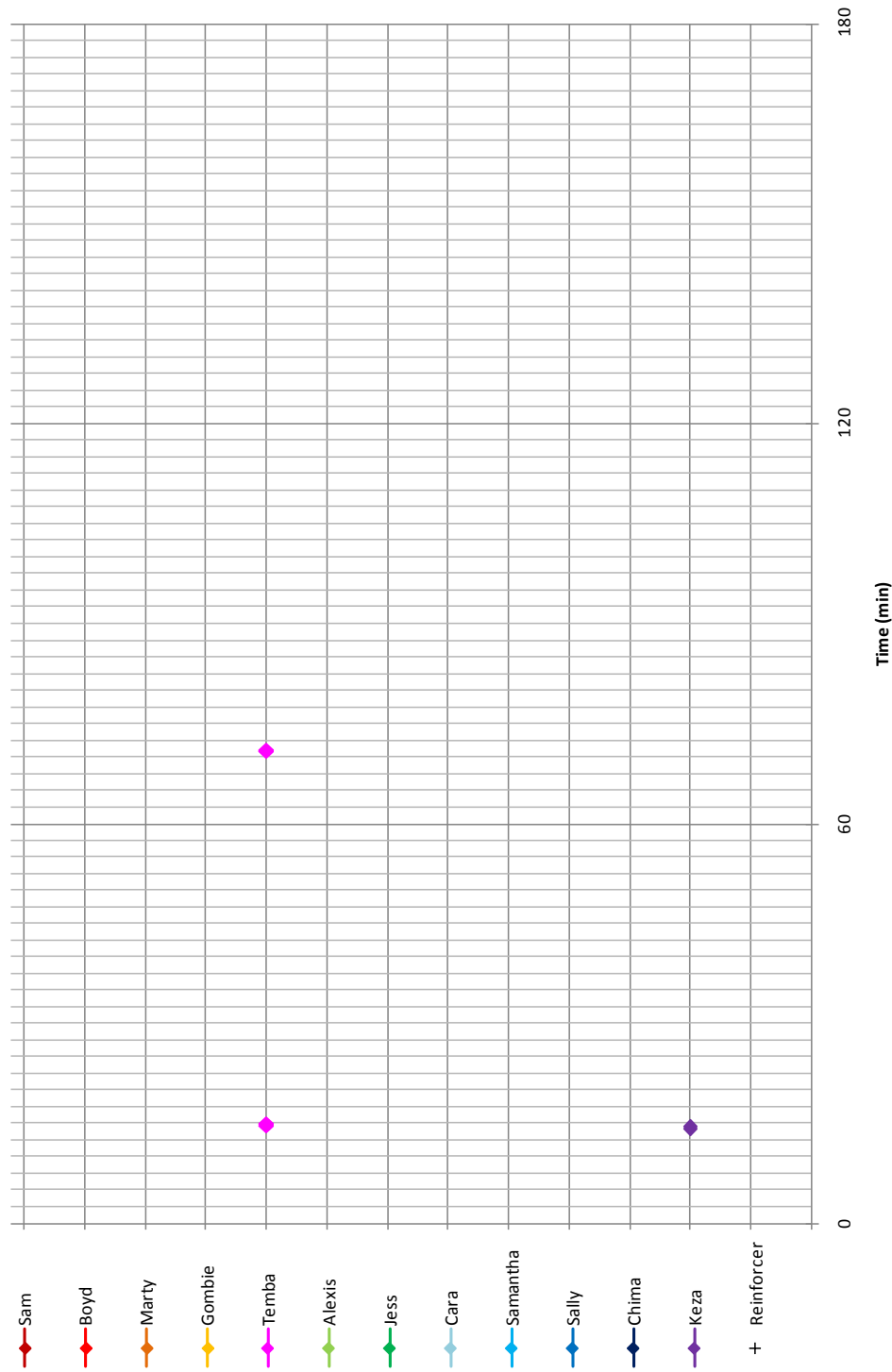


Figure 5.9c. Start and stop times for defined behaviours related to the group's use of the Musicbox enrichment item and time any reinforcements were delivered during the FR 4 session of, Series A, during Experiment 5. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

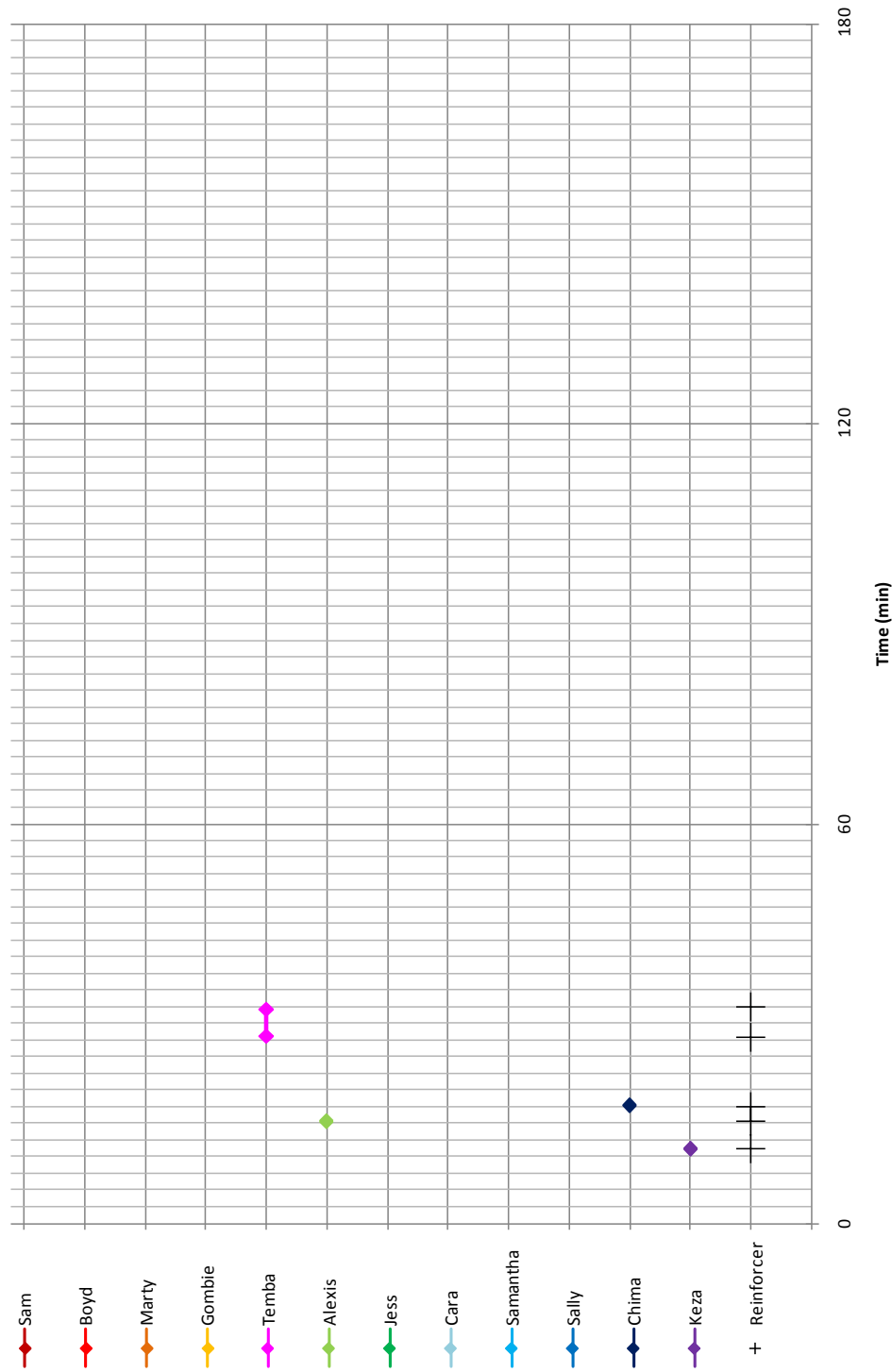


Figure 5.9d. Start and stop times for defined behaviours related to the group’s use of the Musicbox enrichment item and time any reinforcements were delivered during the FR 1 session of, Series B, during Experiment 5. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

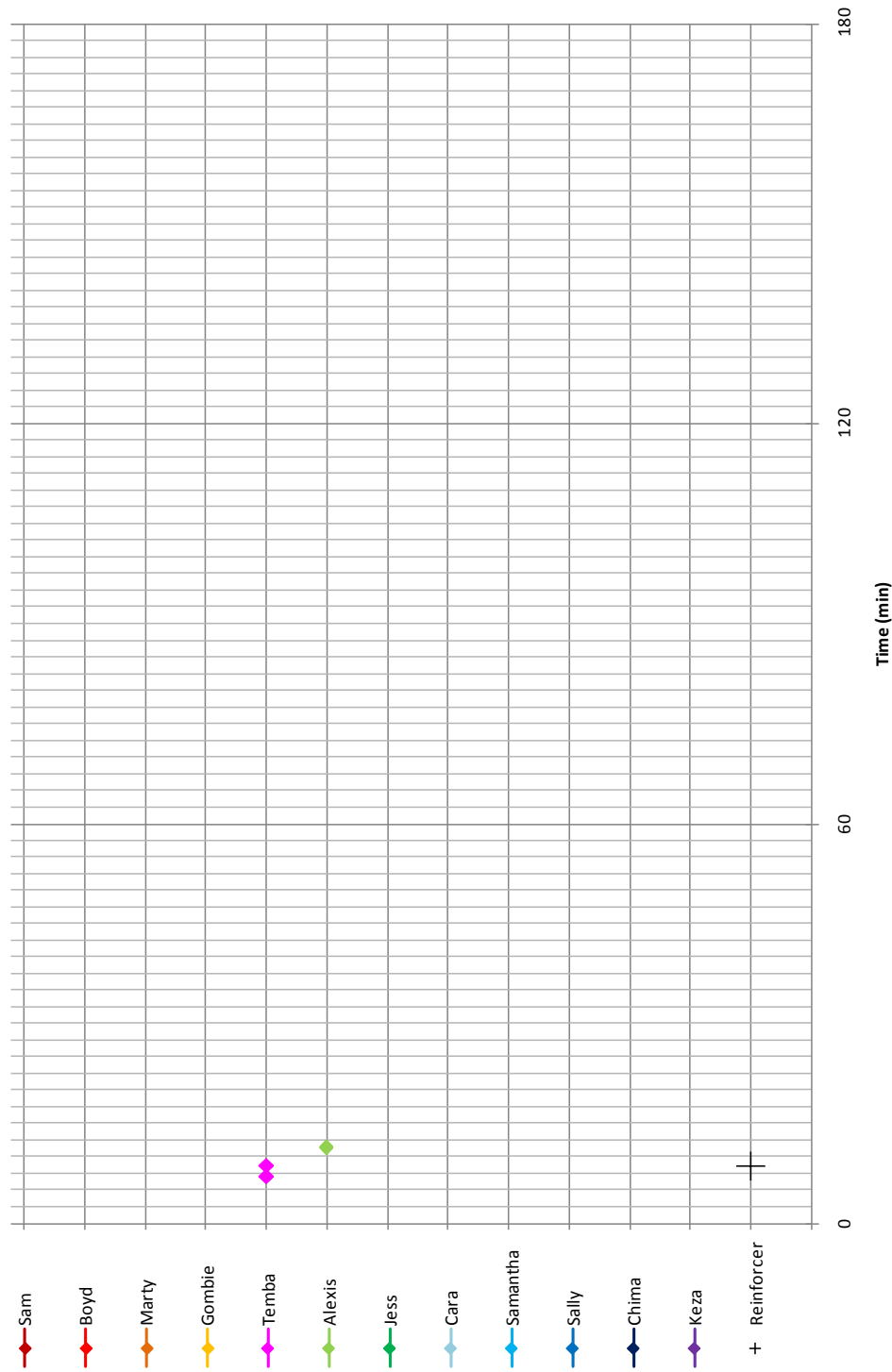


Figure 5.9e. Start and stop times for defined behaviours related to the group's use of the Musicbox enrichment item and time any reinforcements were delivered during the FR 2 session of, Series B, during Experiment 5. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

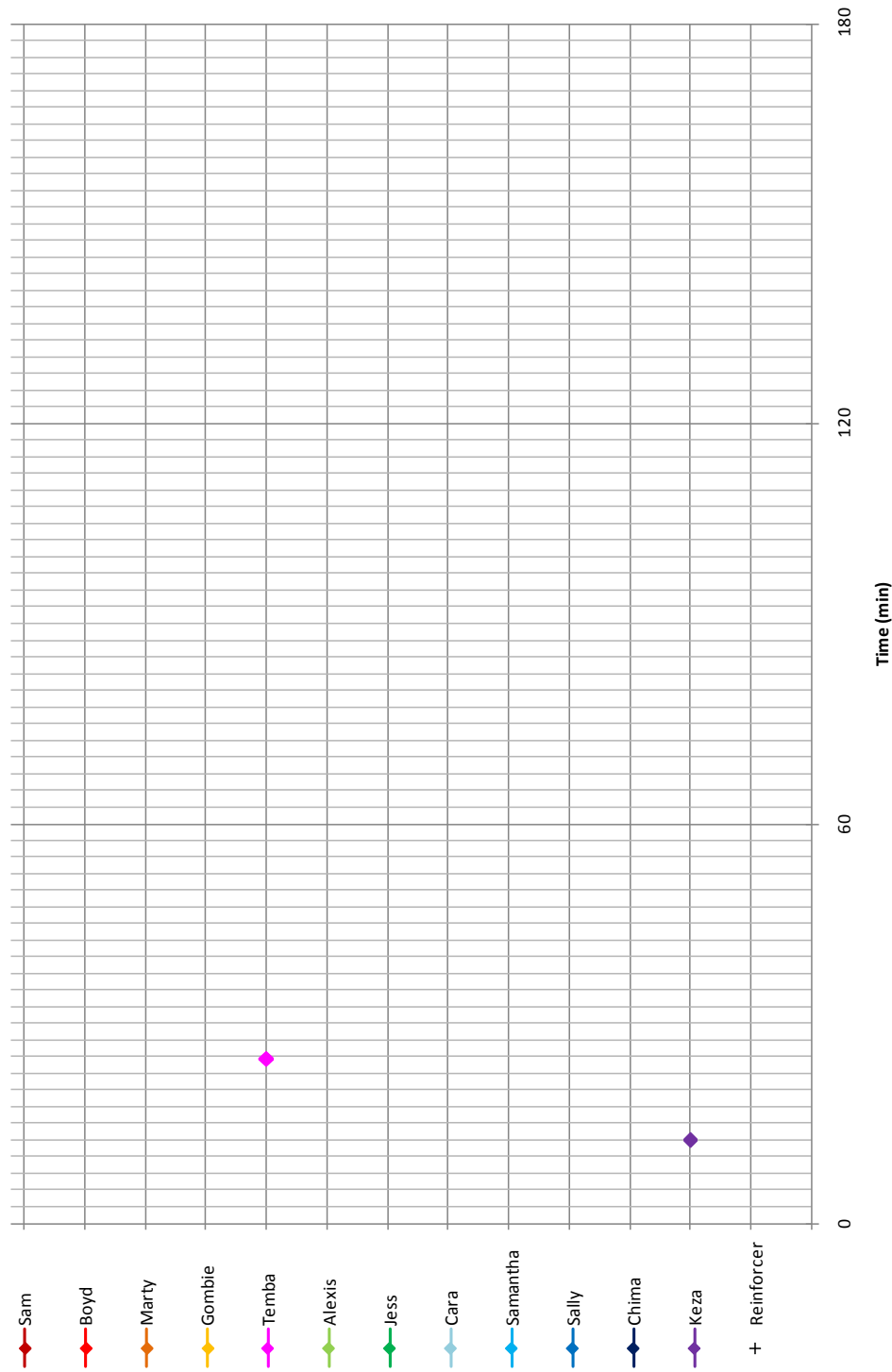


Figure 5.9f. Start and stop times for defined behaviours related to the group's use of the Musicbox enrichment item and time any reinforcements were delivered during the FR 4 session of, Series B, during Experiment 5. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

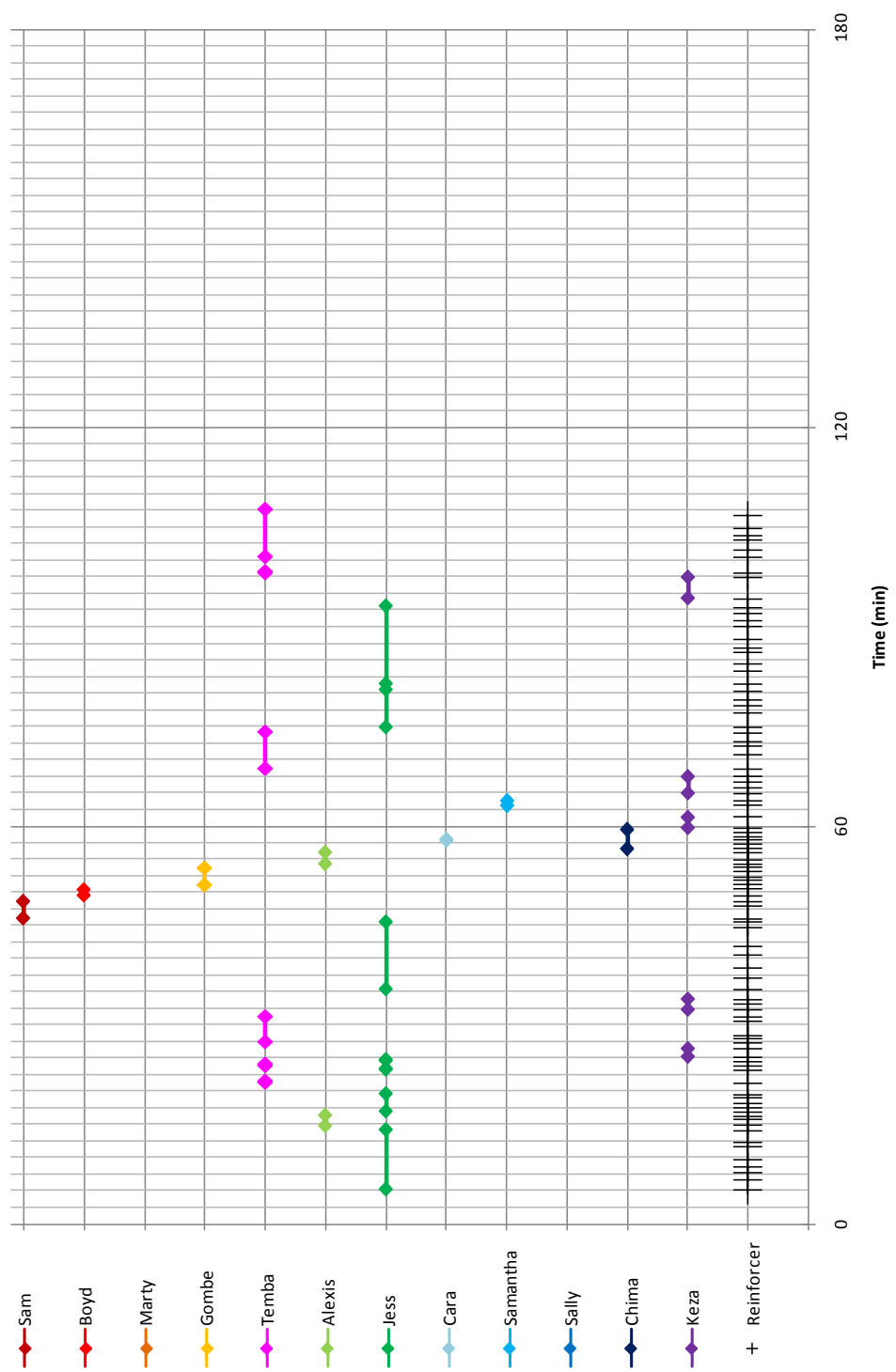
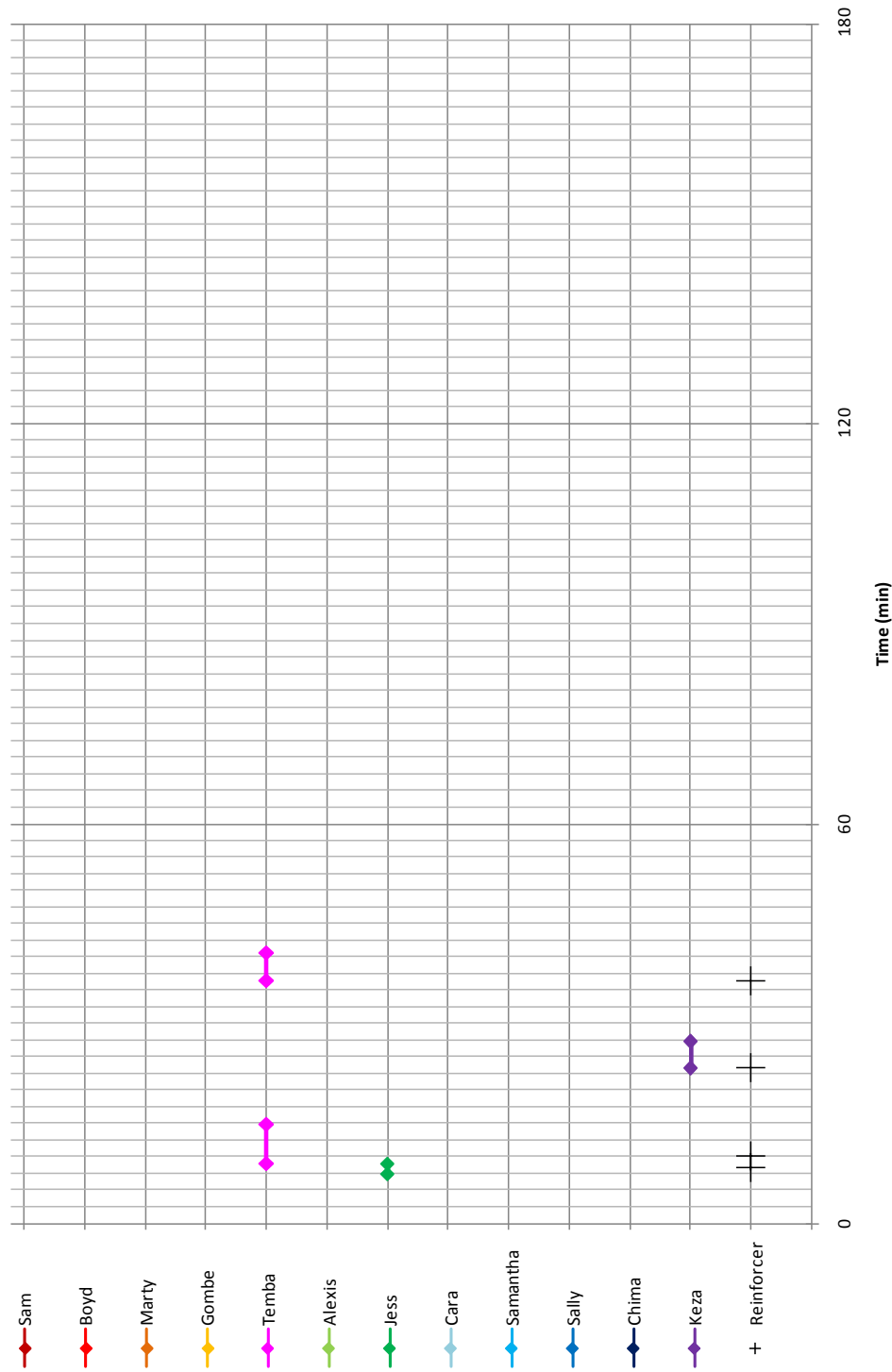


Figure 5.10a. Start and stop times for defined behaviours related to the group's use of the Dipper enrichment item and time any reinforcements were delivered during the FR 1 session of, Series A, during Experiment 5. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.



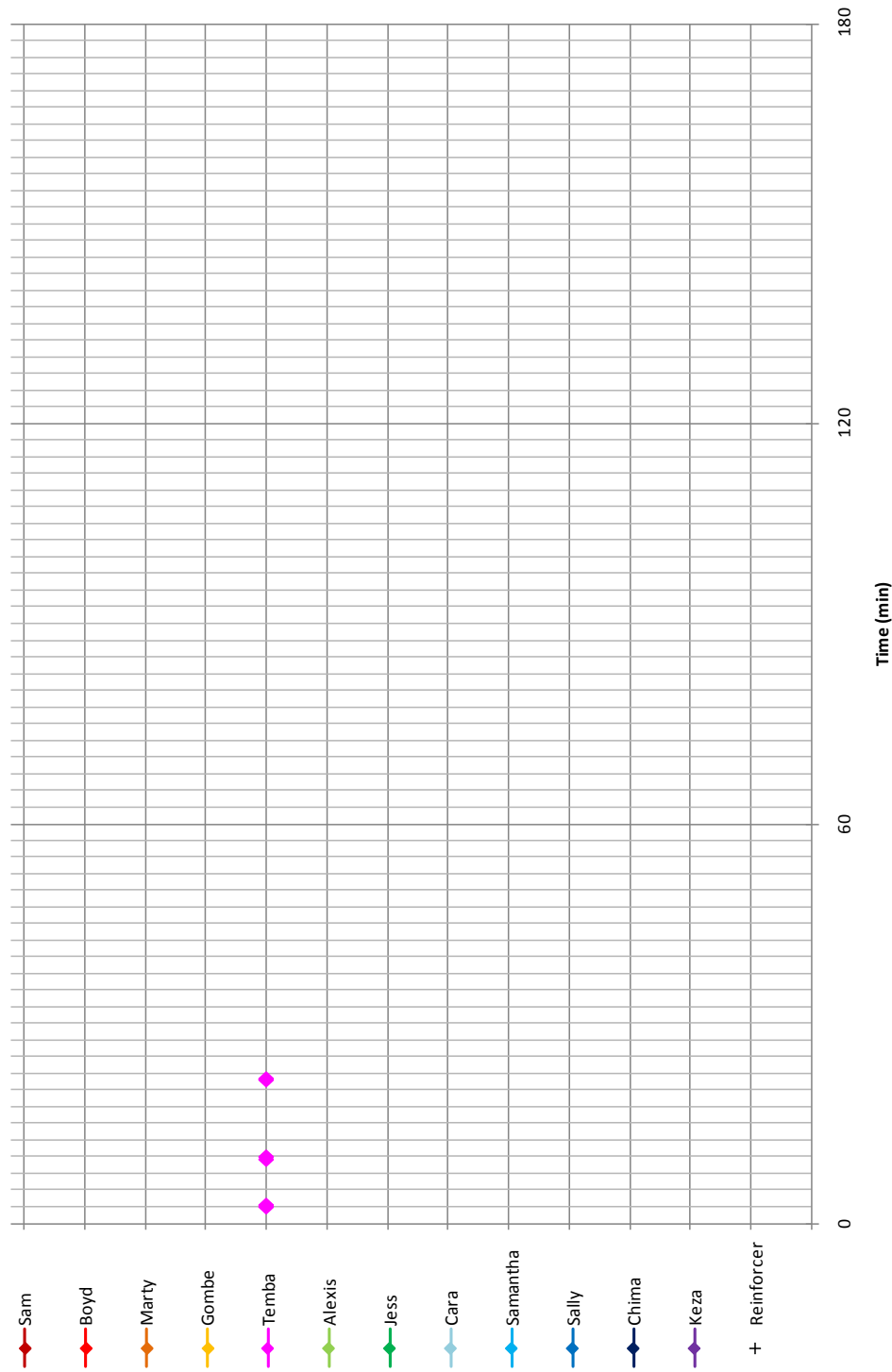


Figure 5.10c. Start and stop times for defined behaviours related to the group’s use of the Dipper enrichment item and time any reinforcements were delivered during the FR 4 session of, Series A, during Experiment 5. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

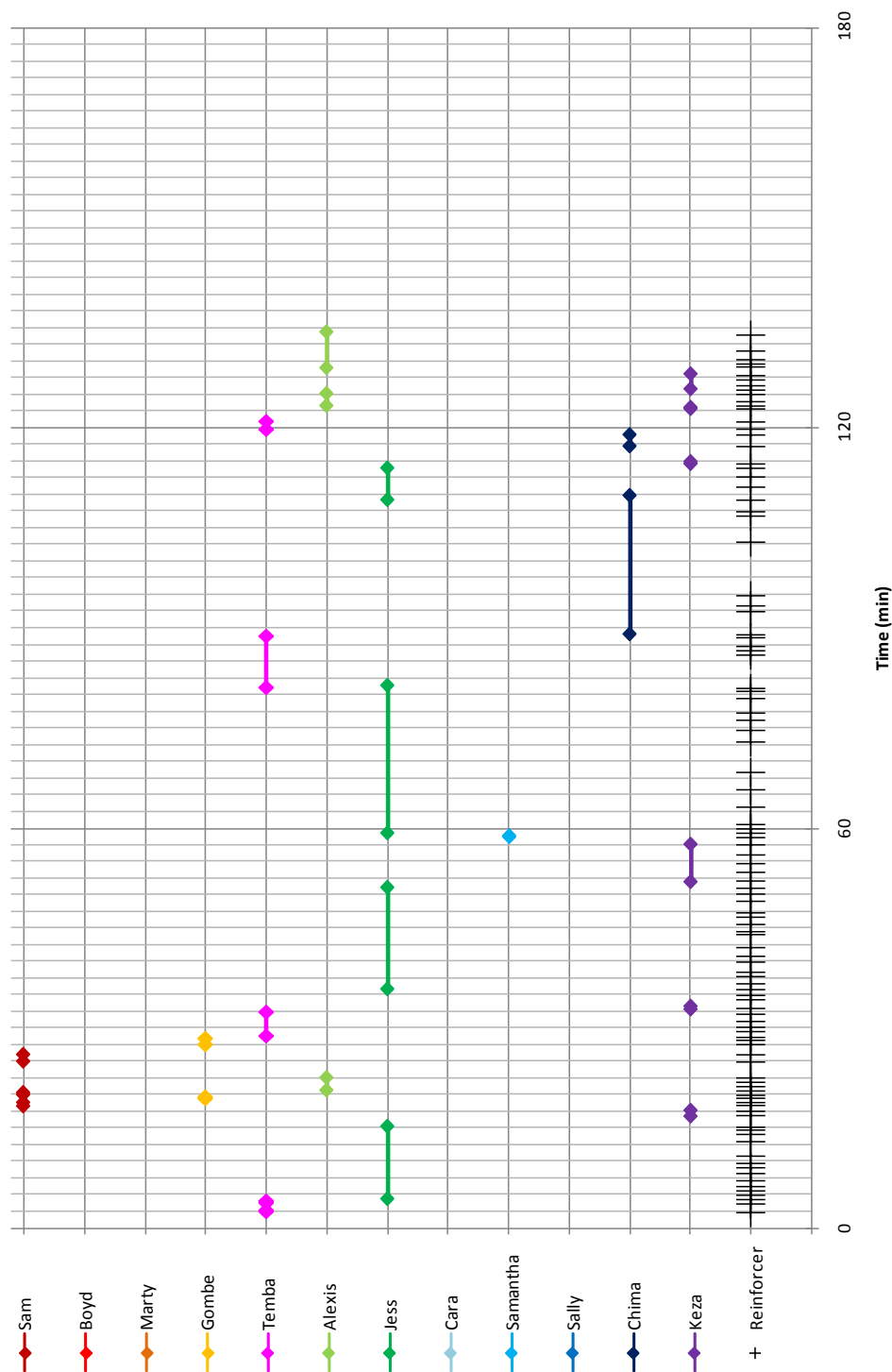


Figure 5.10d. Start and stop times for defined behaviours related to the group's use of the Dipper enrichment item and time any reinforcements were delivered during the FR 1 session of, Series B, during Experiment 5. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

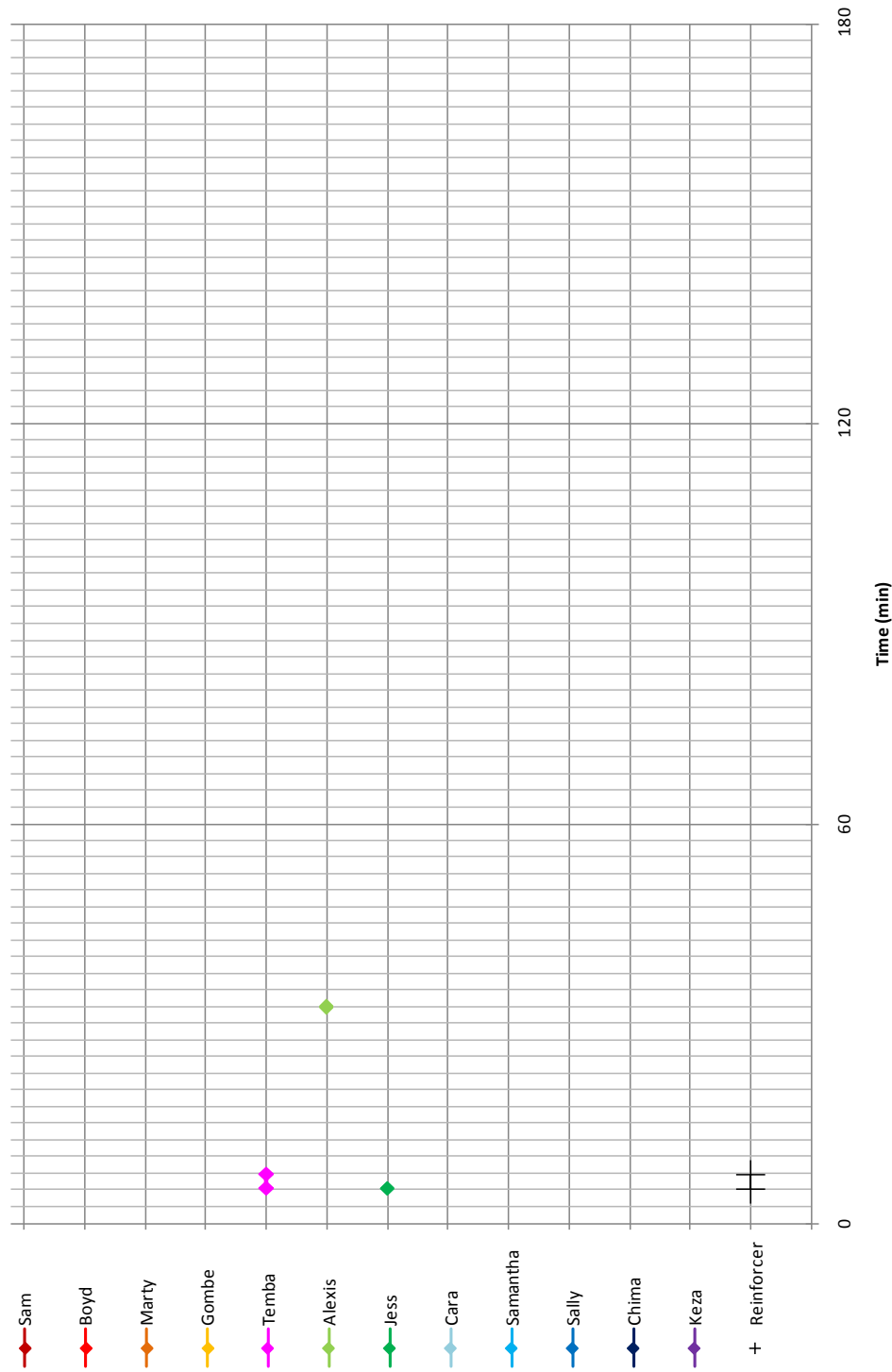


Figure 5.10e. Start and stop times for defined behaviours related to the group’s use of the Dipper enrichment item and time any reinforcements were delivered during the FR 2 session of, Series B, during Experiment 5. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

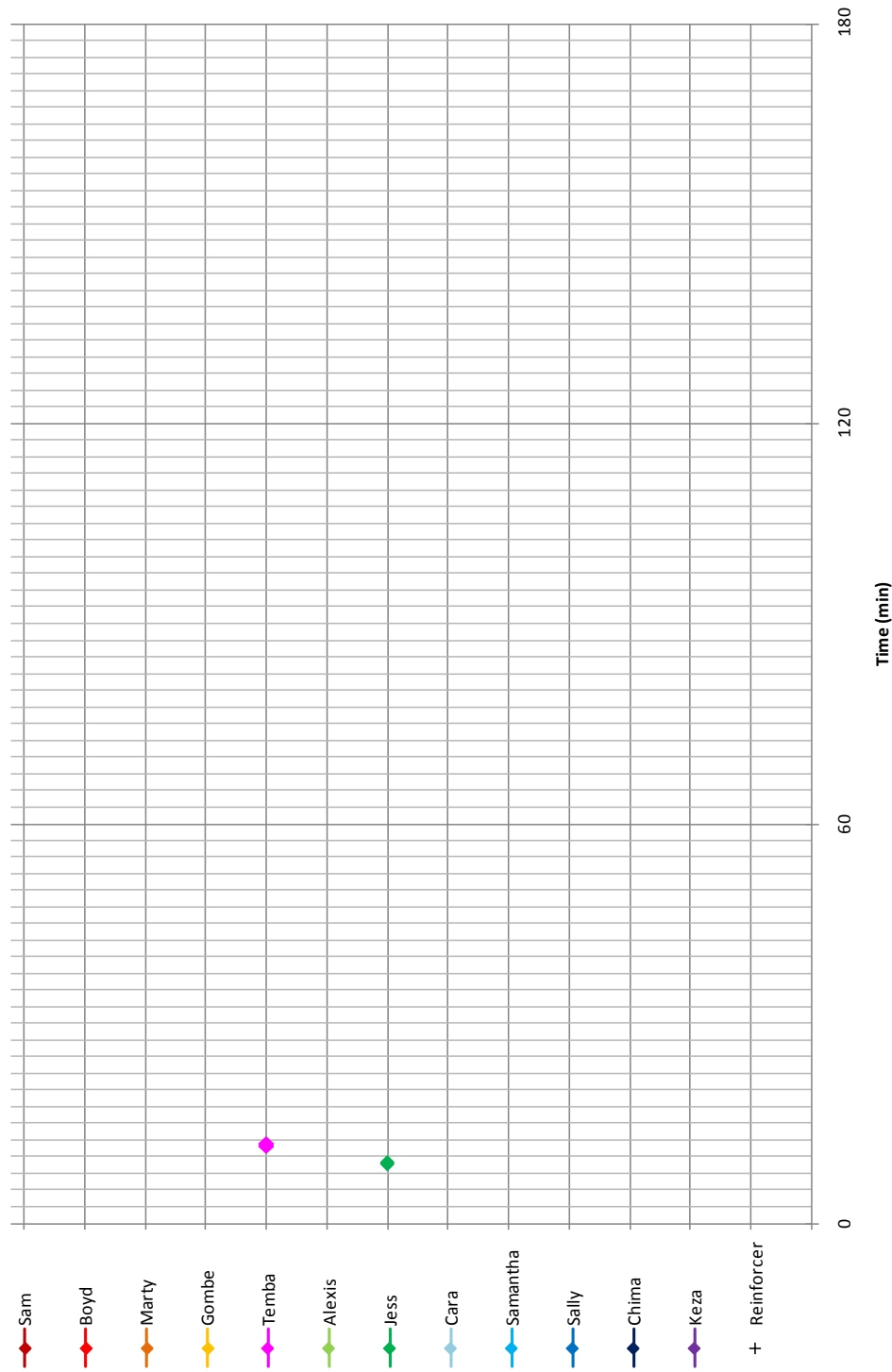
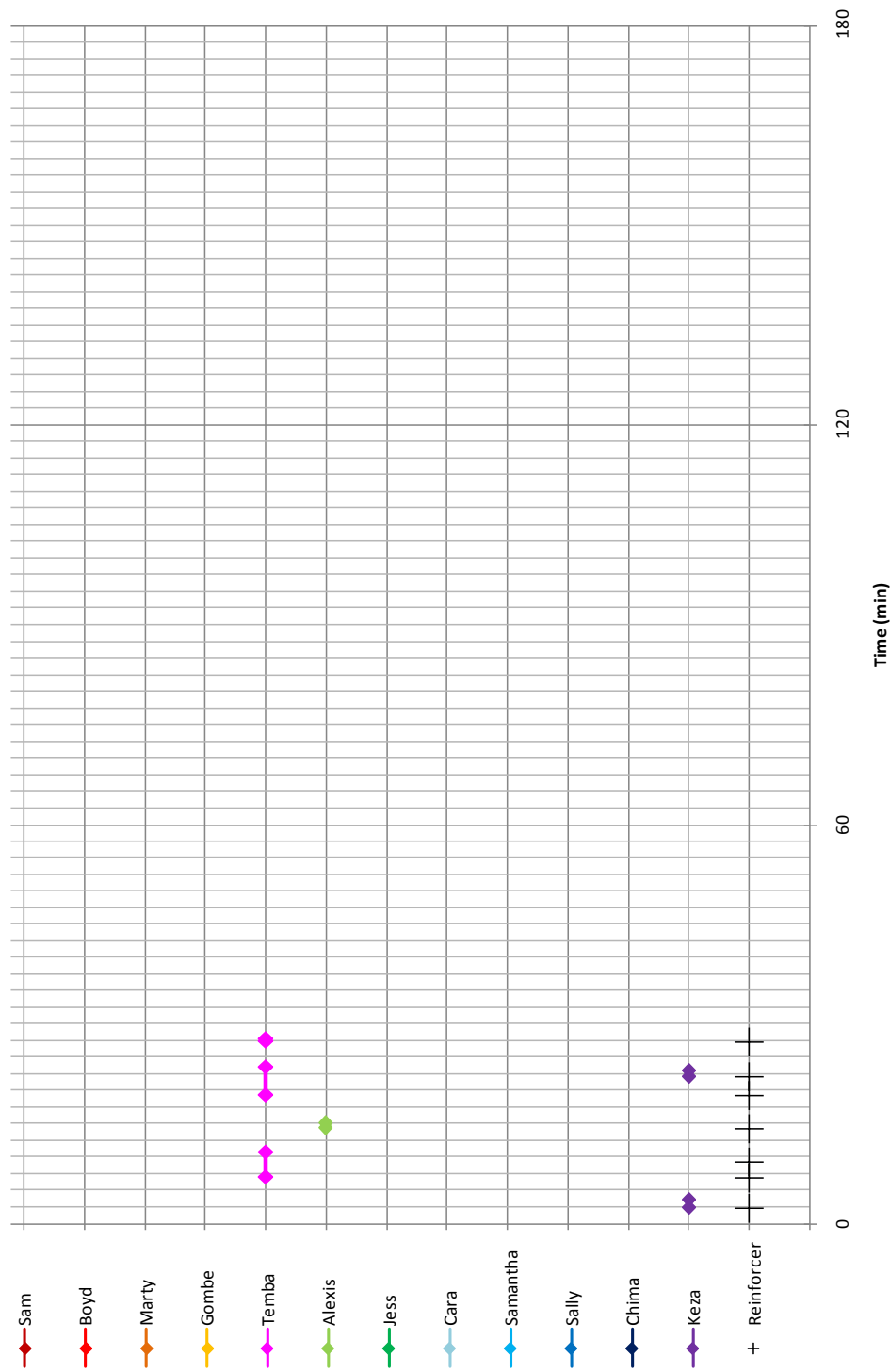


Figure 5.10f. Start and stop times for defined behaviours related to the group's use of the Dipper enrichment item and time any reinforcements were delivered during the FR 4 session of, Series B, during Experiment 5. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.



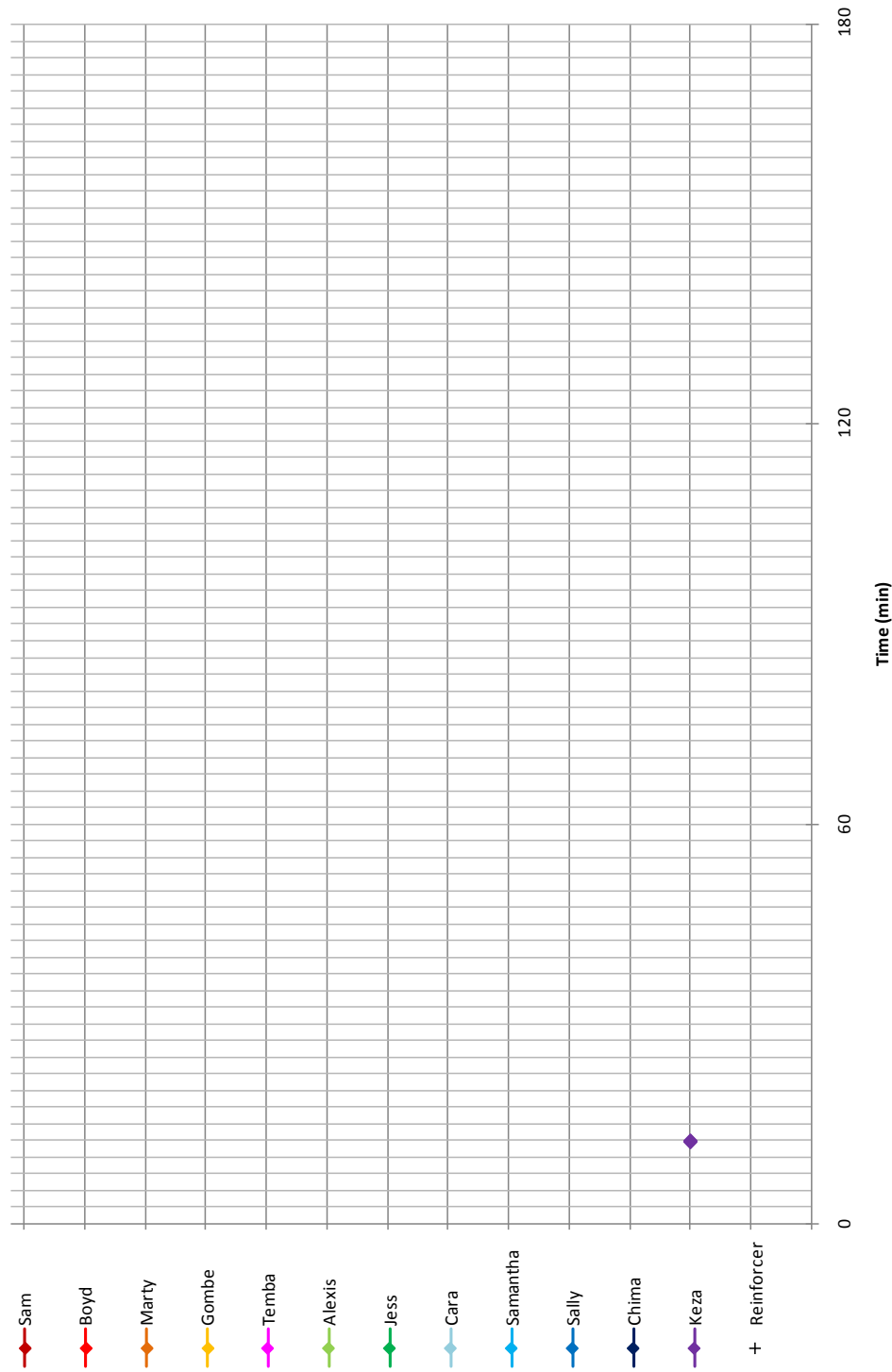


Figure 5.11b. Start and stop times for defined behaviours related to the group's use of the TV/Video enrichment item and time any reinforcements were delivered during the FR 2 session of, Series A, during Experiment 5. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

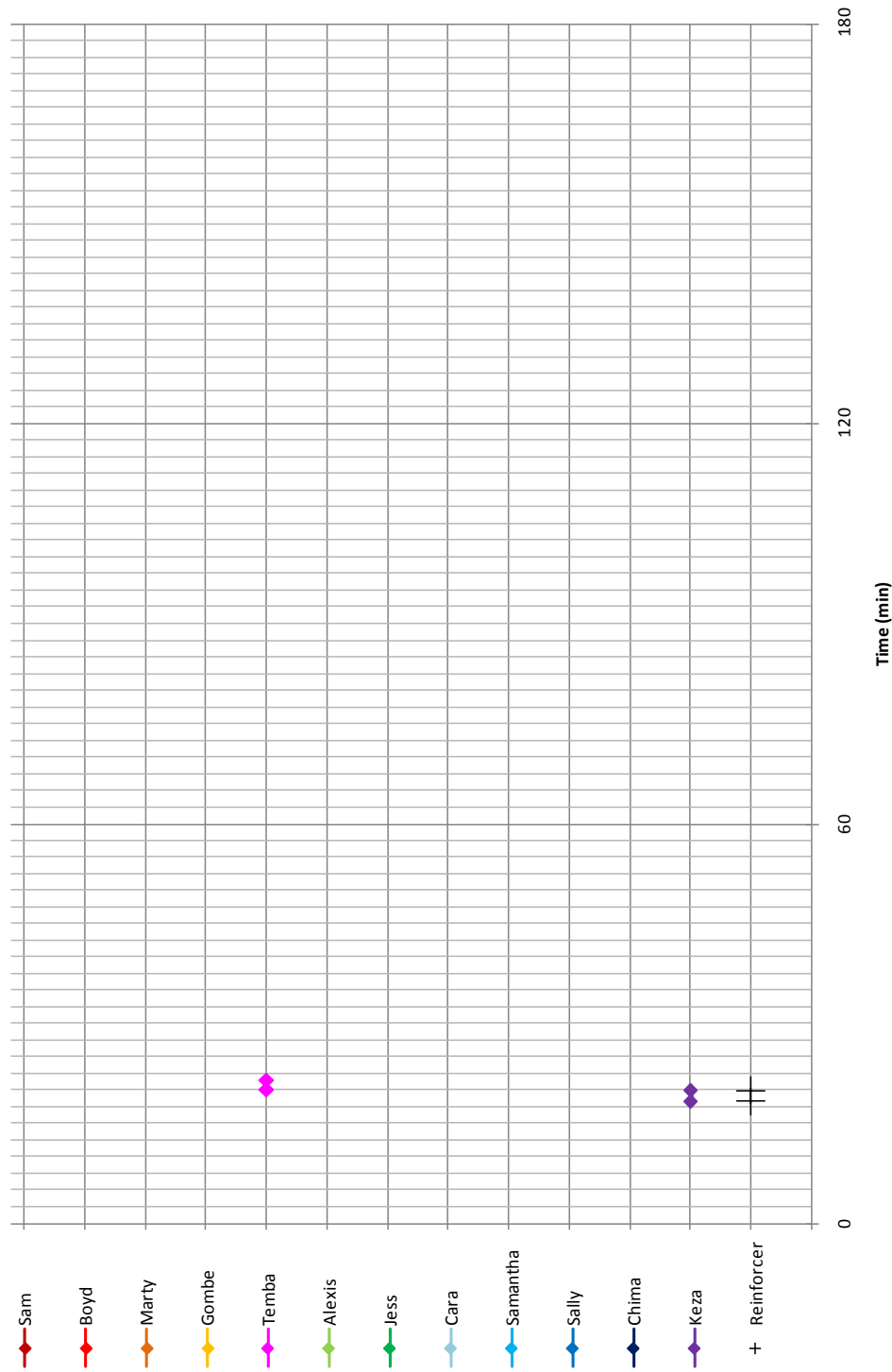


Figure 5.11c. Start and stop times for defined behaviours related to the group's use of the TV/Video enrichment item and time any reinforcements were delivered during the FR 1 session of, Series B, during Experiment 5. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

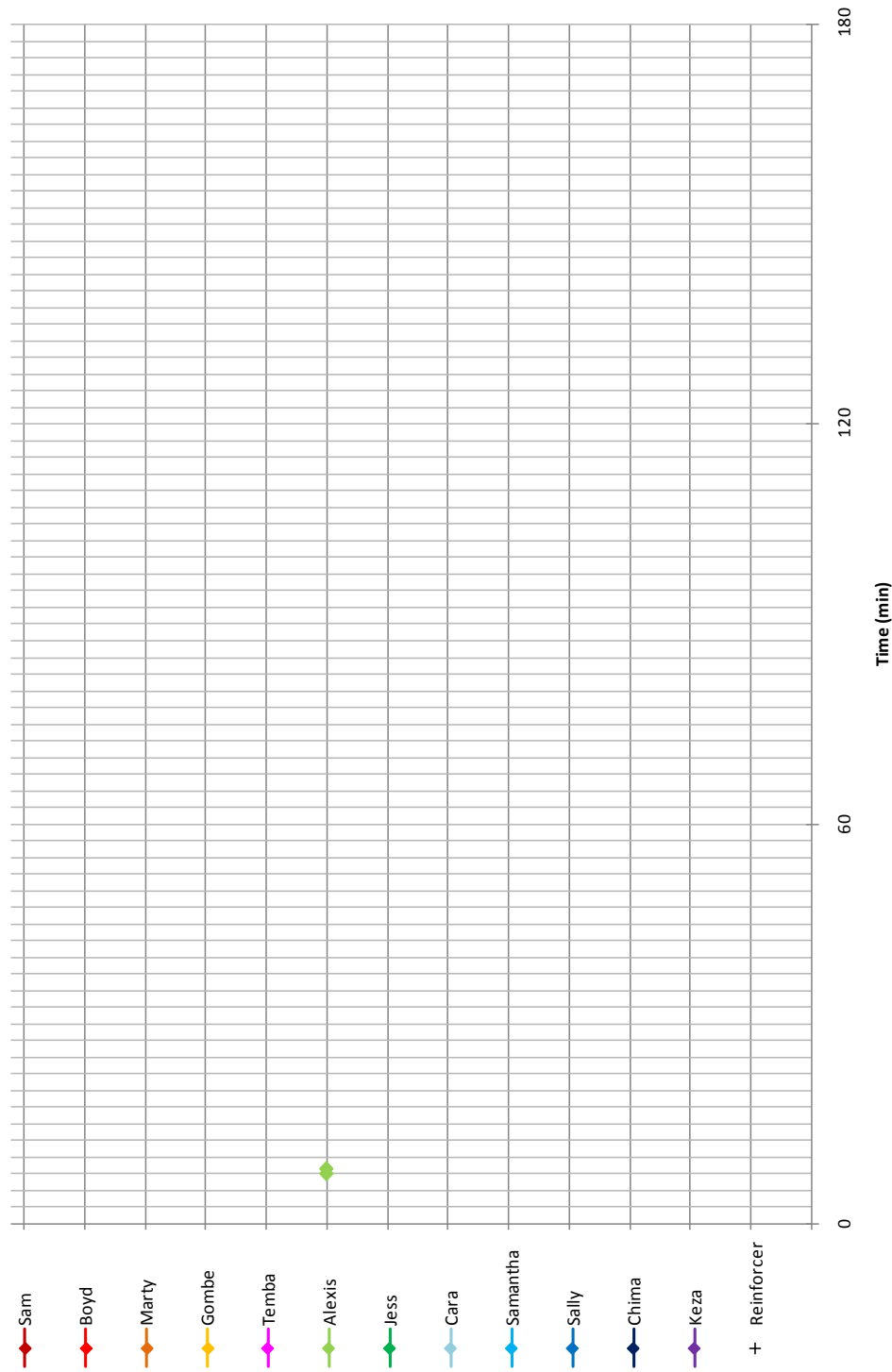


Figure 5.11d. Start and stop times for defined behaviours related to the group's use of the TV/Video enrichment item and time any reinforcements were delivered during the FR 2 session of, Series B, during Experiment 5. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

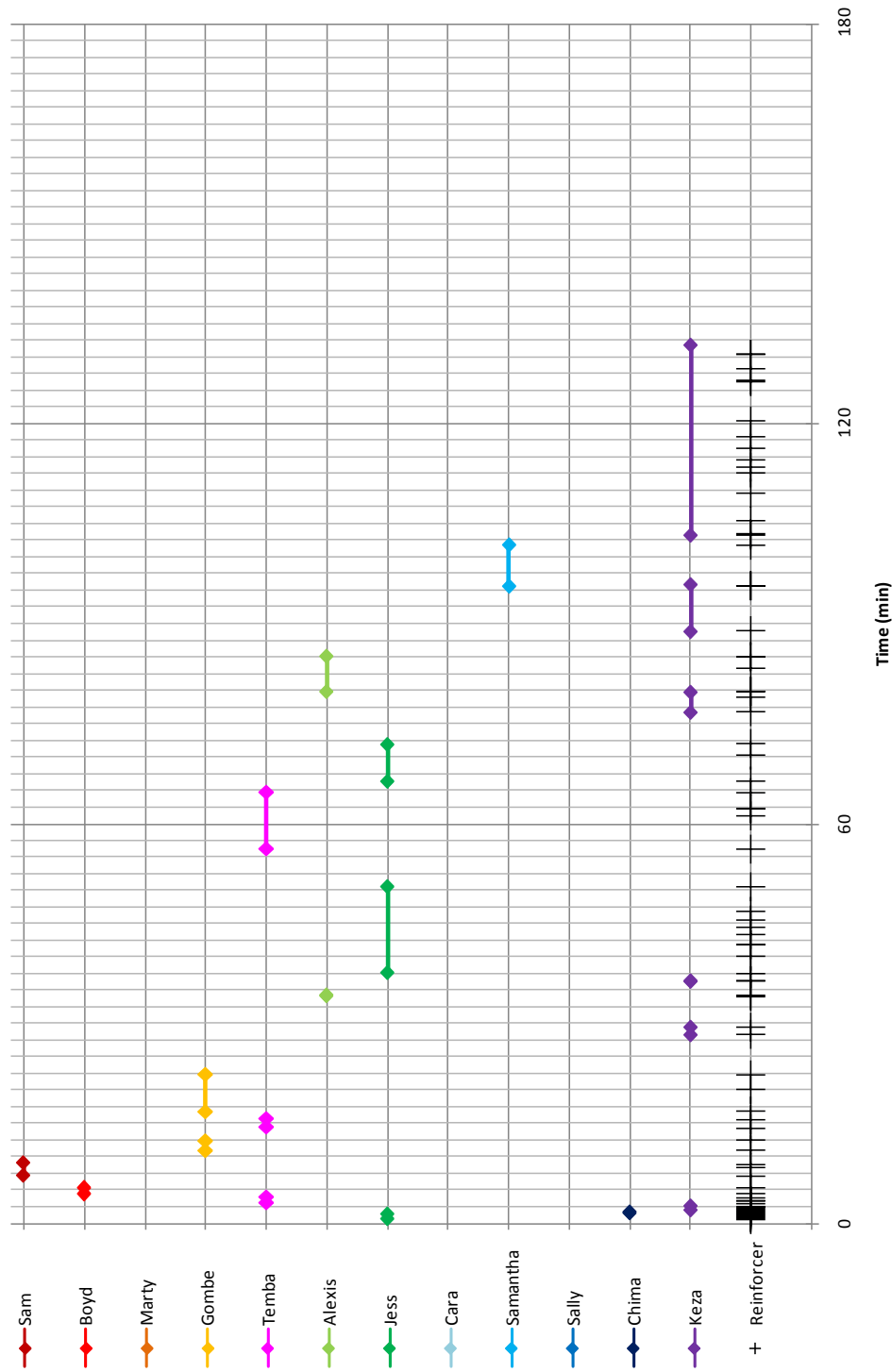


Figure 5.12a. Start and stop times for defined behaviours related to the group's use of the Marbleroll enrichment item and time any reinforcements were delivered during the FR 1 session of, Series A, during Experiment 5. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

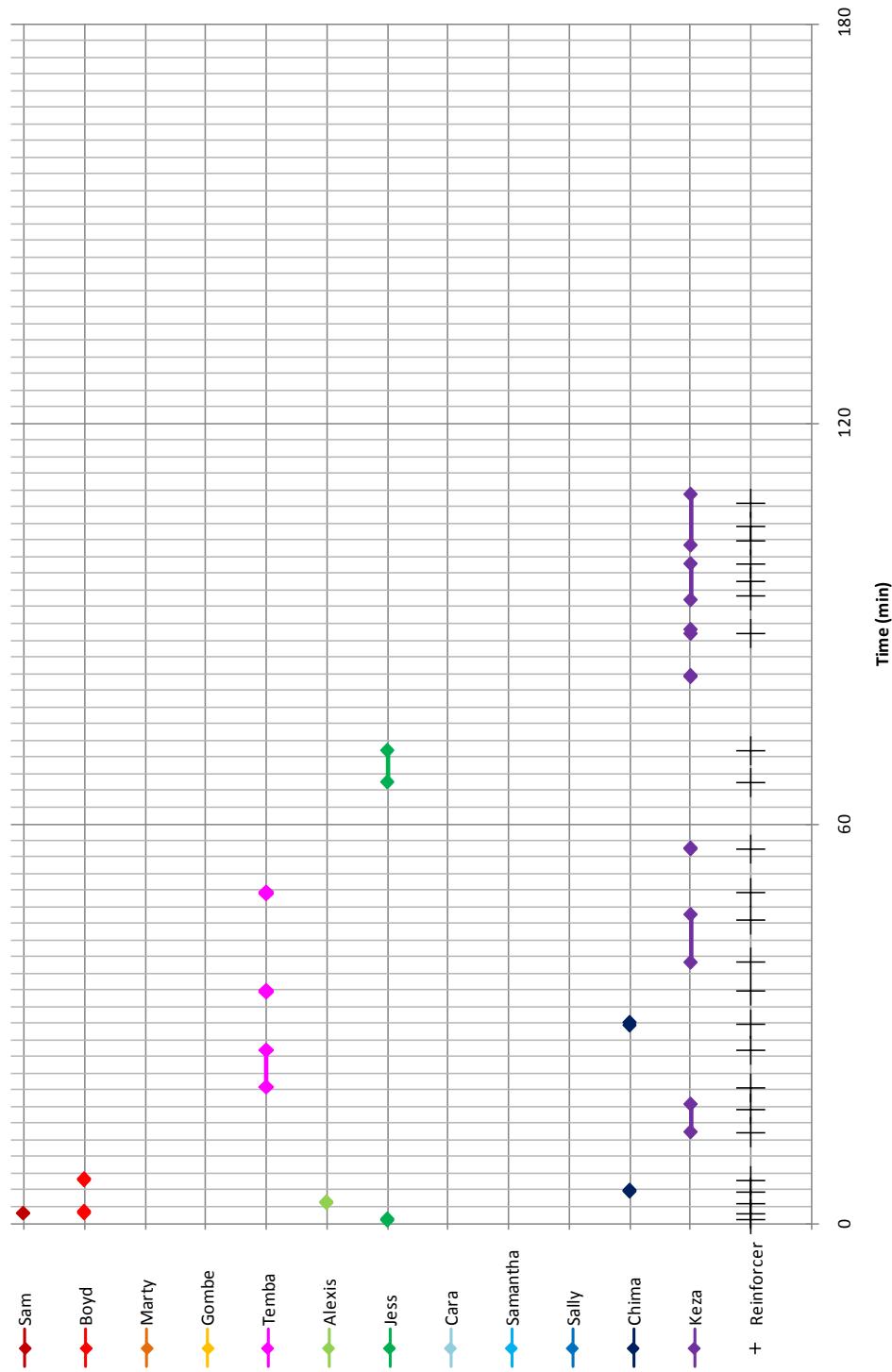


Figure 5.12b. Start and stop times for defined behaviours related to the group's use of the Marbleroll enrichment item and time any reinforcements were delivered during the FR 2 session of, Series A, during Experiment 5. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

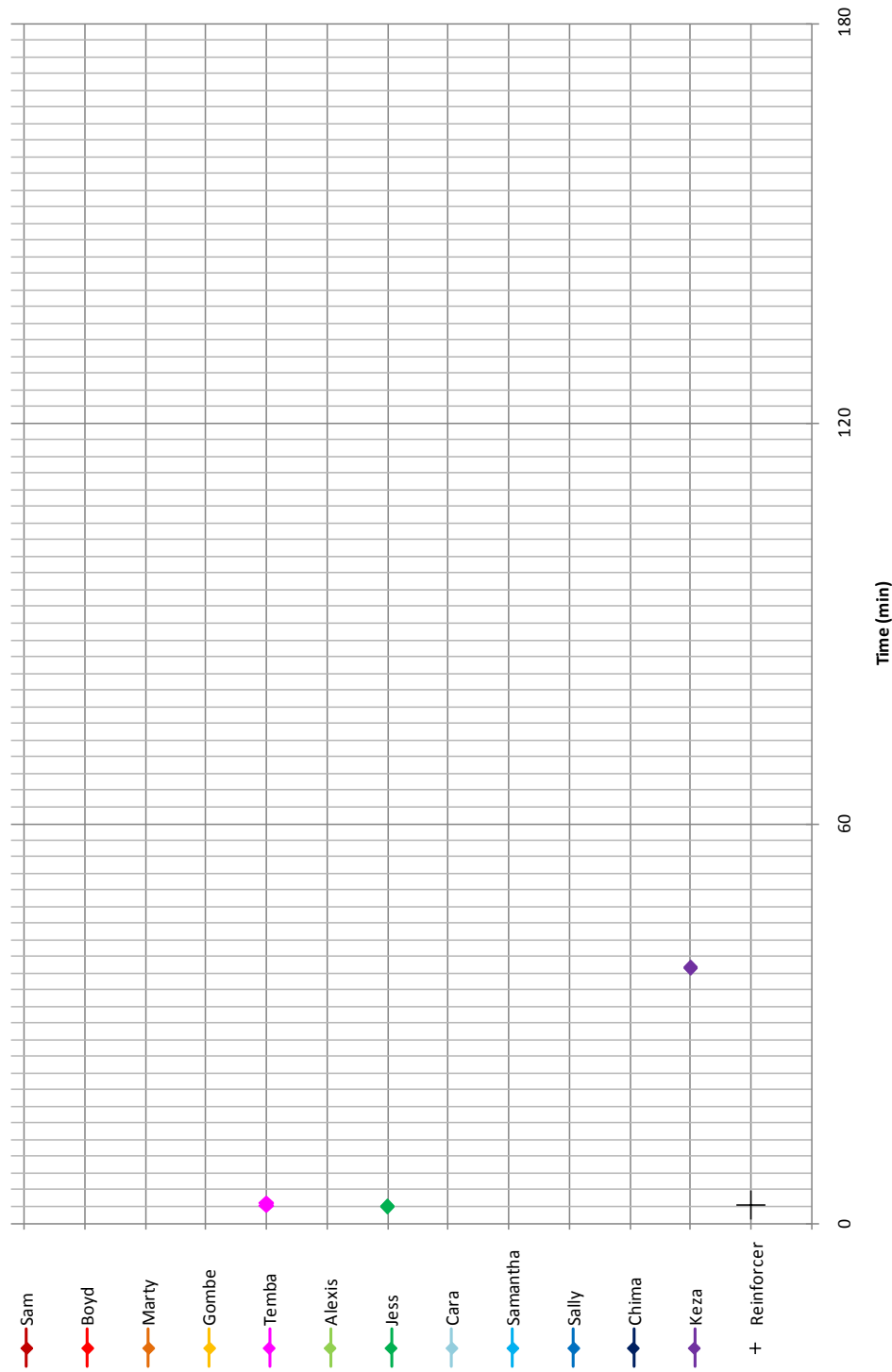


Figure 5.12c. Start and stop times for defined behaviours related to the group's use of the Marbleroll enrichment item and time any reinforcements were delivered during the FR 4 session of, Series A, during Experiment 5. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

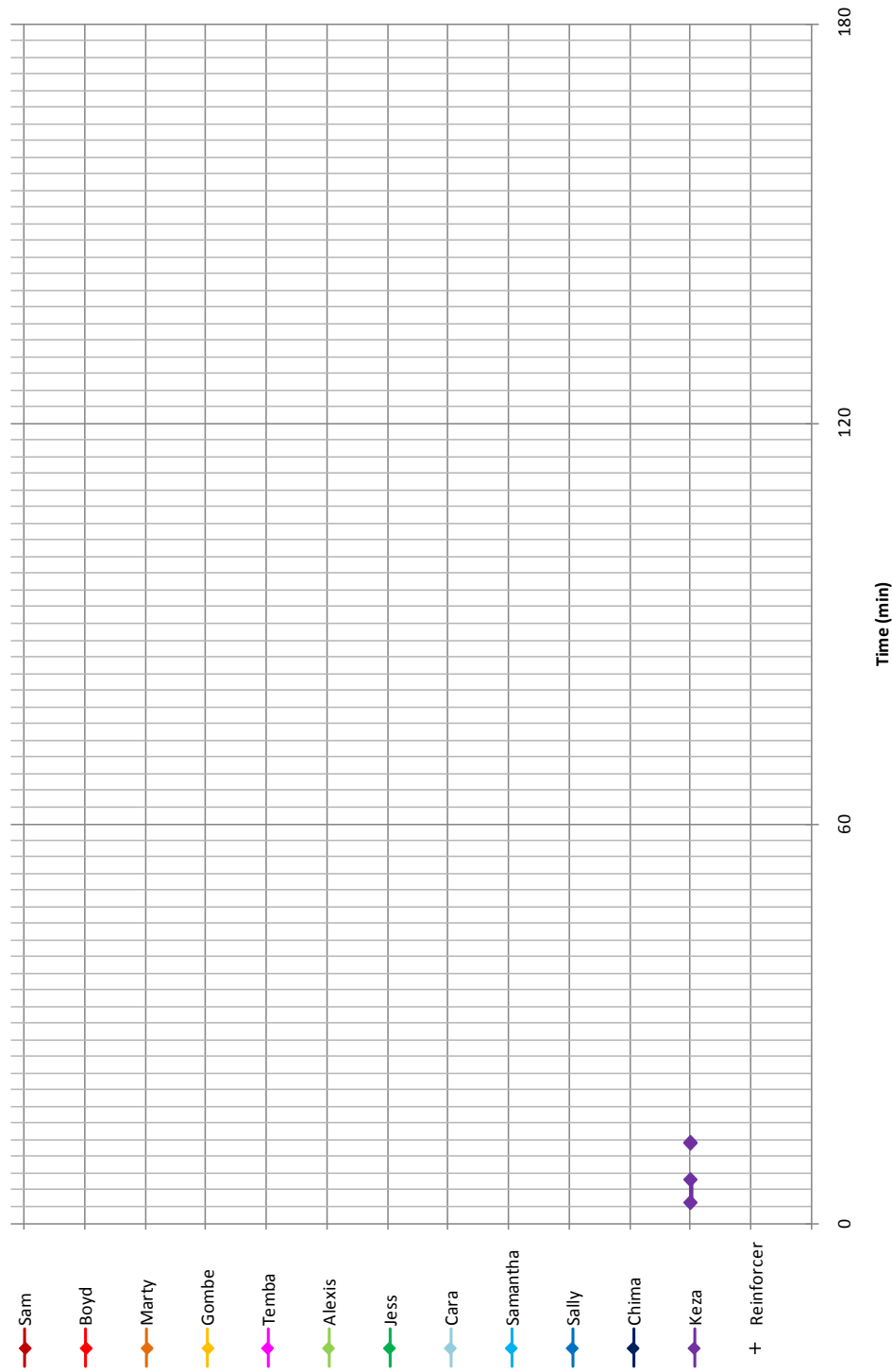


Figure 5.12d. Start and stop times for defined behaviours related to the group's use of the Marbleroll enrichment item and time any reinforcements were delivered during the FR 8 session of, Series A, during Experiment 5. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

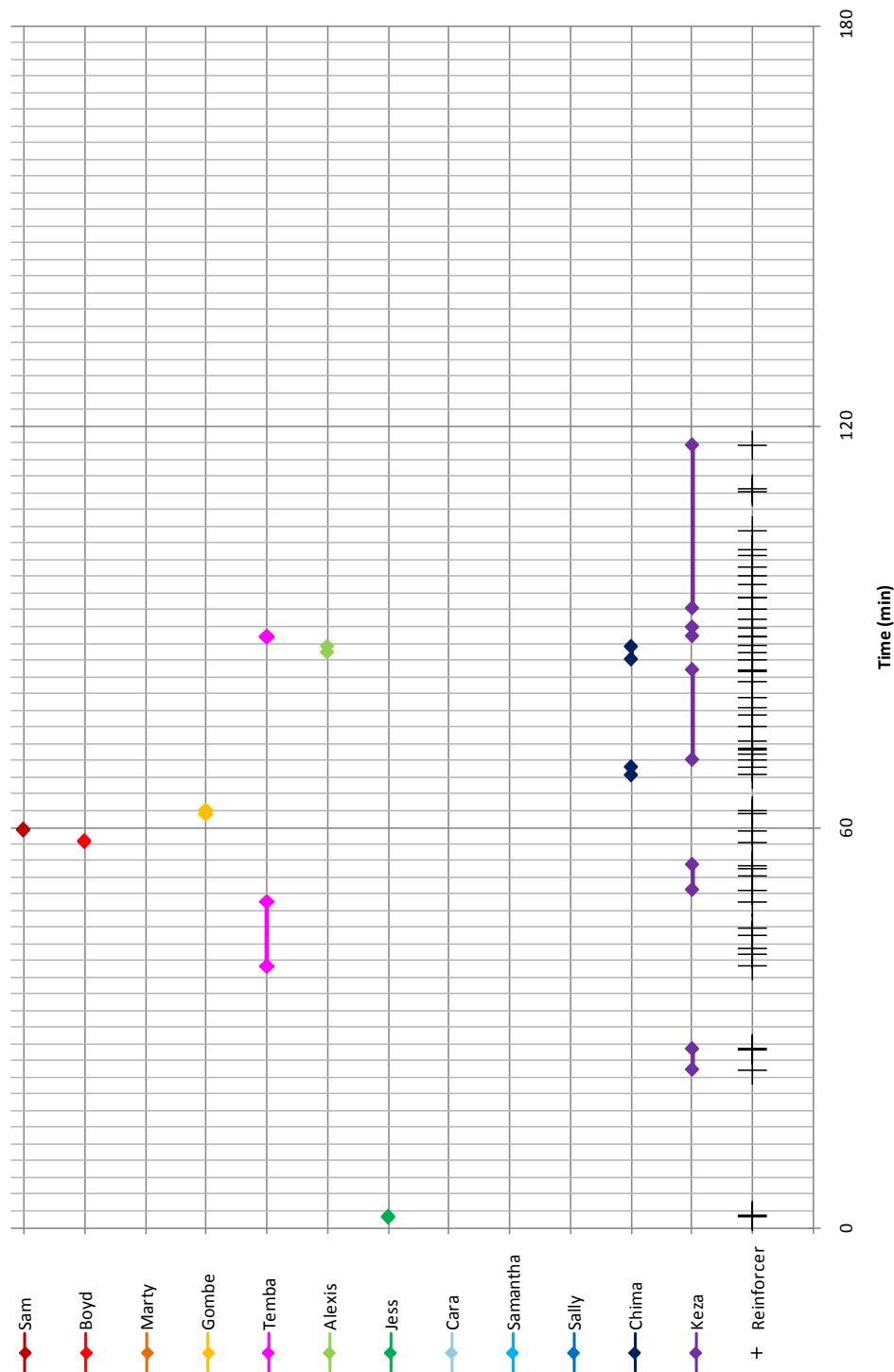


Figure 5.12e. Start and stop times for defined behaviours related to the group's use of the Marbleroll enrichment item and time any reinforcements were delivered during the FR 1 session of, Series B, during Experiment 5. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

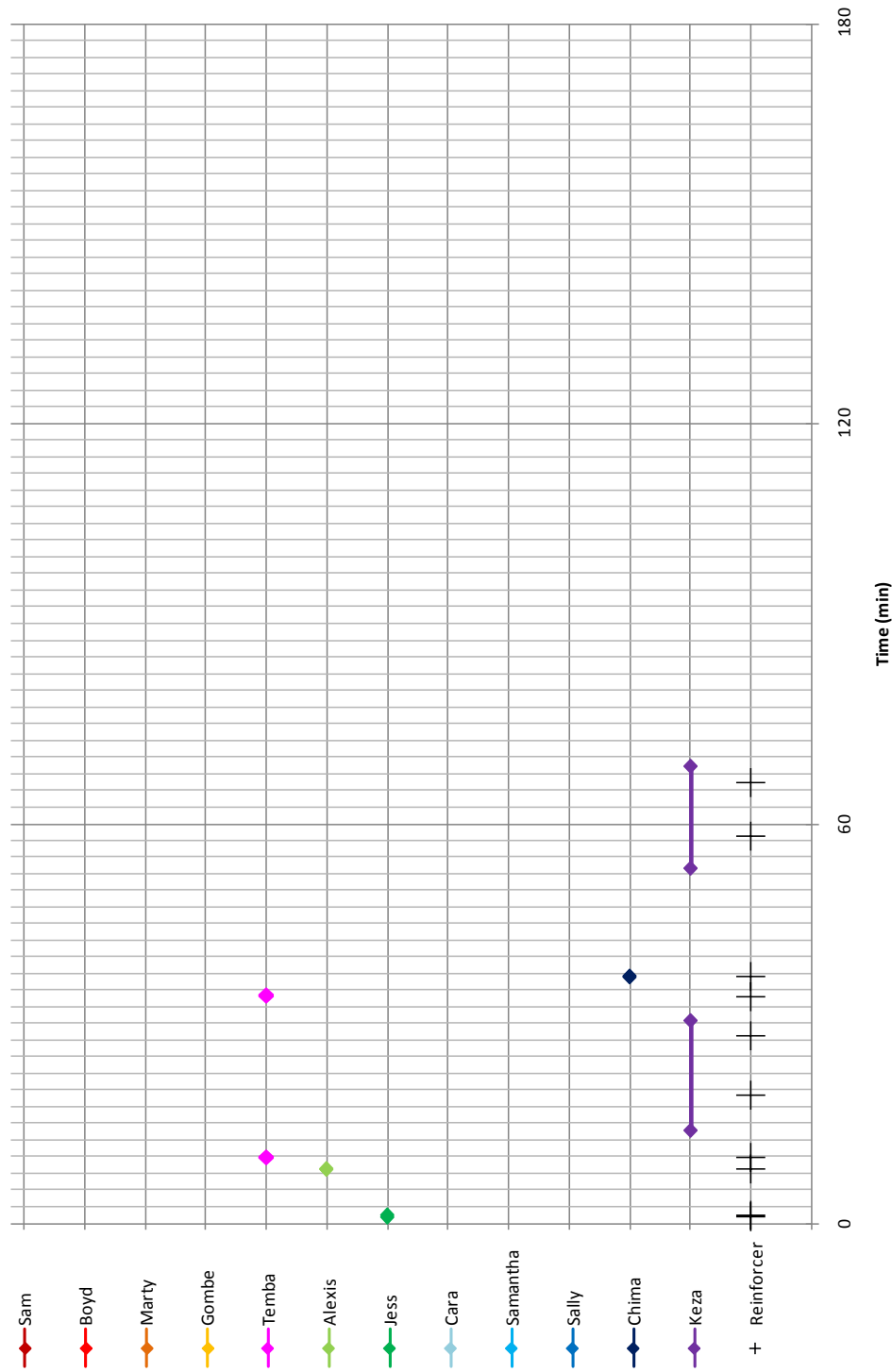


Figure 5.12f. Start and stop times for defined behaviours related to the group's use of the Marbleroll enrichment item and time any reinforcements were delivered during the FR 2 session of, Series B, during Experiment 5. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

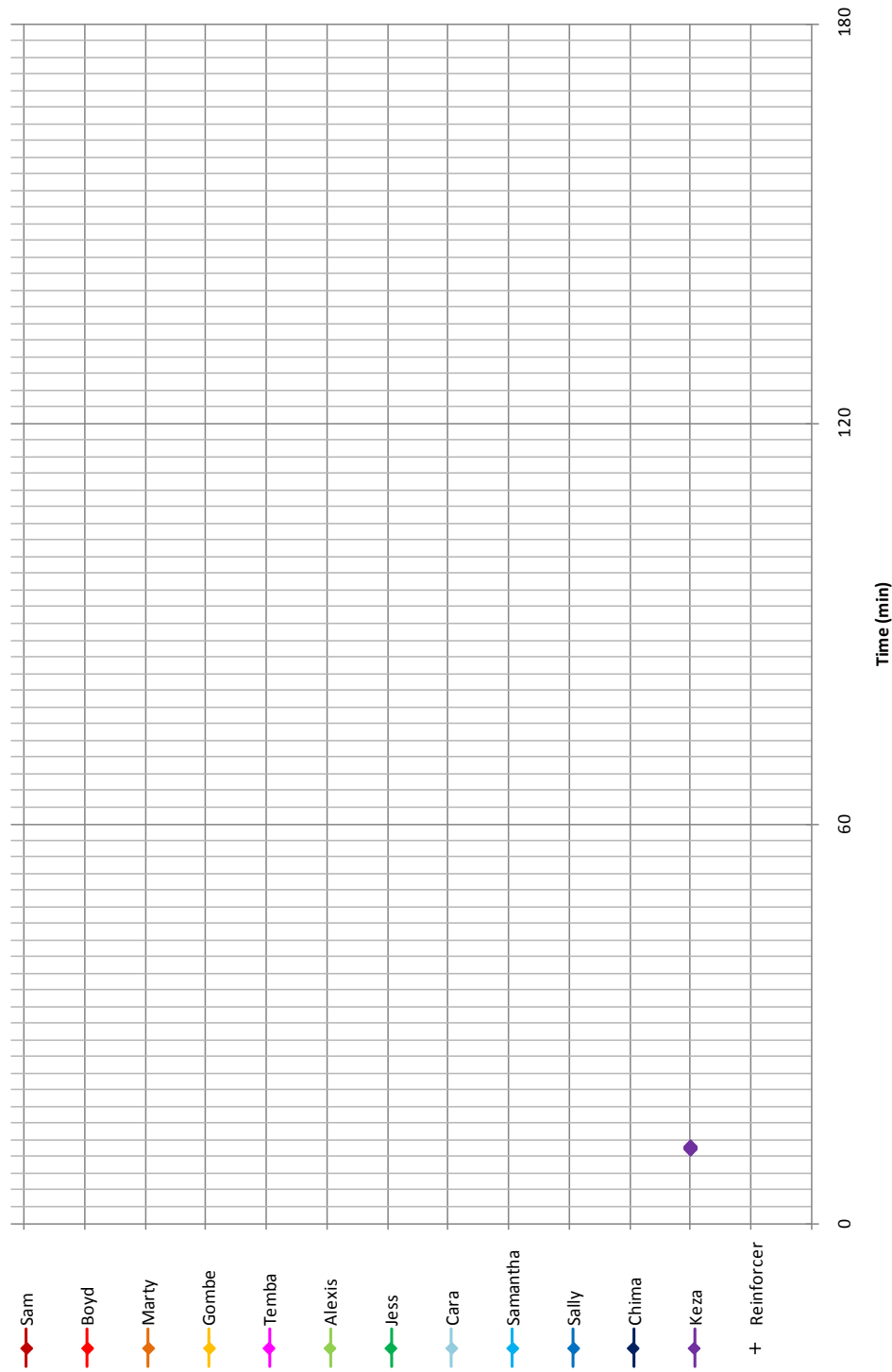


Figure 5.12g. Start and stop times for defined behaviours related to the group's use of the Marbleroll enrichment item and time any reinforcements were delivered during the FR 4 session of, Series B, during Experiment 5. Individual chimpanzees are arranged via sex (males above females) and within each sex arranged in order of age, oldest down to youngest.

Individual Chimpanzee Behaviour Whilst Housed Socially

Figure 5.13a to 5.13g show the behaviour (as defined in Table 2.2) of individuals of the chimpanzee group during sessions of Experiment 5. Juvenile female Keza was the individual to use the items the most across all the sessions of the experiment. Adolescent male Temba was the next highest user of the items, and the highest user of the Screwfeeder, Marbleroll (delivering coated peanuts), Musicbox, and TV/Video enrichment. Adult female Jess was the third highest user and the highest for the Dipper enrichment. Keza's time using the Marbleroll enrichment was markedly higher than the rest of the group. Minimal time was spent by the group using an enrichment item while another individual observed this (Using – others watch), using the item at the same time as another subject was (Using-together), or watching another individual using the item (Watching other use). They also spent little time in sessions orientated towards an item but not interacting (Attending-alone), multiple animals oriented towards an item but not interacting with it (Attending – accompanied) and within the experimental area simply present but not interacting in any way with an enrichment item (Just in area) (if one was present). The time spent in exhibiting each of these behaviour categories was similar across the individuals of the chimpanzee group. However, individuals, including adult male Boyd, juvenile male Alexis, Jess and Keza, did spend more time than the rest of the group using an enrichment item while another individual observed this (Using – others watch), using the item at the same time as another subject was (Using-together) or watching another individual using an item (Watching other use).

It was noted that when the Screwfeeder was included juvenile female Keza and adolescent male Temba often used it whenever it was free. However, if adult males Sam, Boyd, or Marty, or adult female Jess approached the Screwfeeder, and Keza, Temba, or juvenile male Alexis or adolescent female Chima were currently using it, they would move away from the item. Jess continued to use the Screwfeeder when any of the group approached her while doing so. These observations were similar for sessions with the other enrichment items but not as pronounced as they were during the sessions with the Screwfeeder.

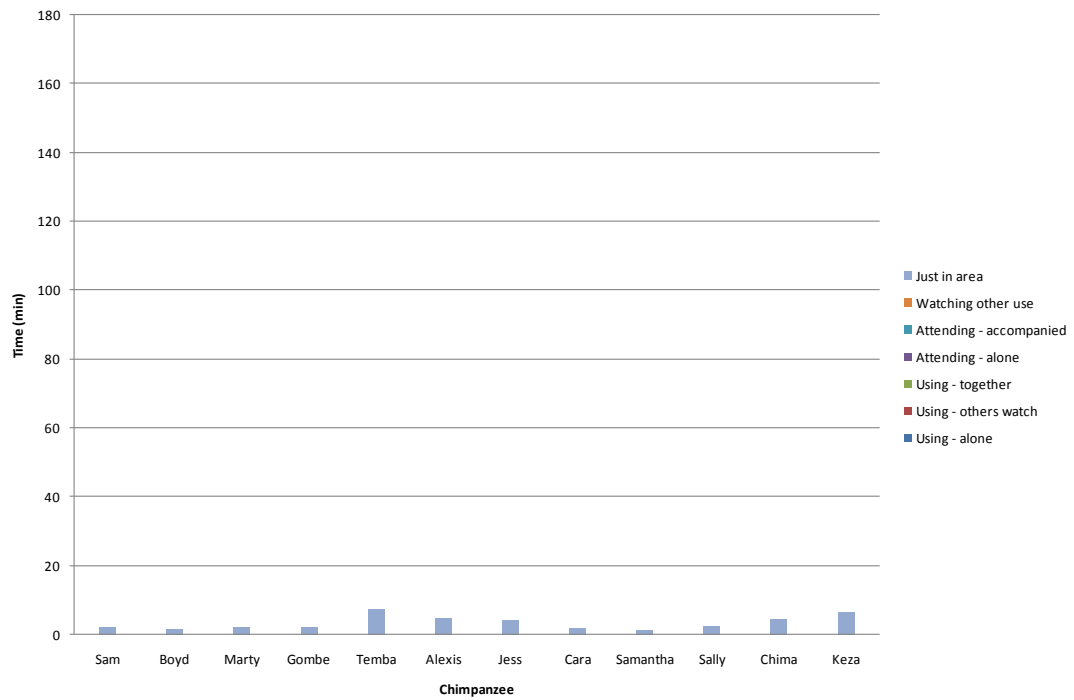


Figure 5.13a. Total time that the individuals of the chimpanzee group exhibited defined behaviours during Baseline sessions of Experiment 5. Individual chimpanzees are arranged in order of sex, males on the left and then age within each sex group, oldest on the left.

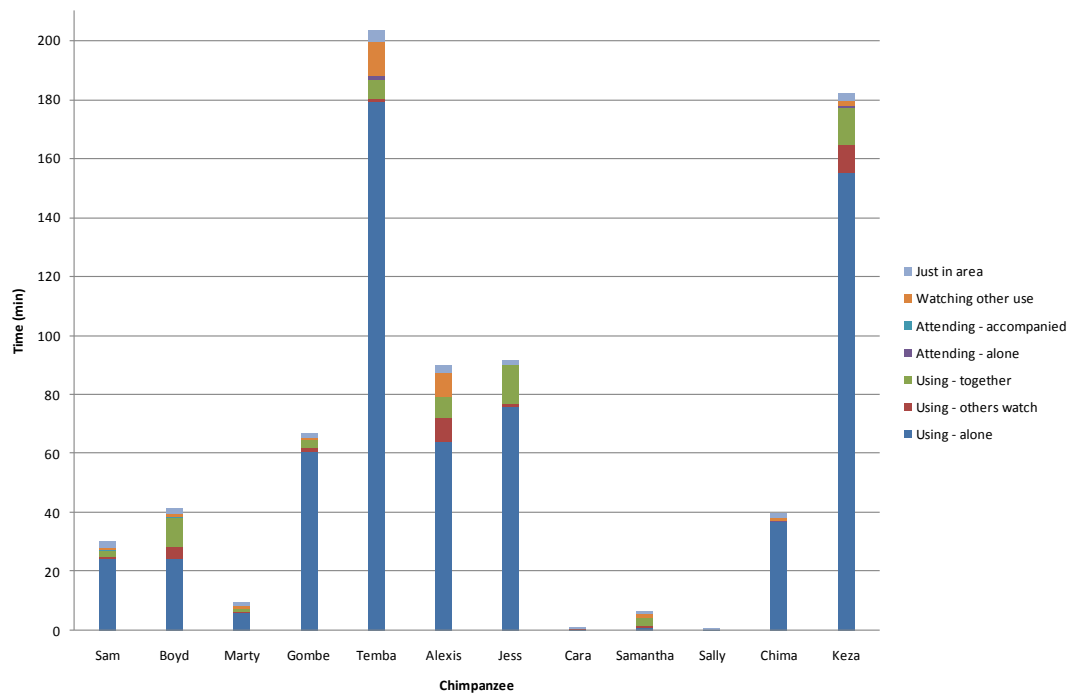


Figure 5.13b. Total time that the individuals of the chimpanzee group

exhibited defined behaviours during sessions with the Screwfeeder enrichment in Experiment 5. Individual chimpanzees are arranged in order of sex, males on the left and then age within each sex group, oldest on the left.

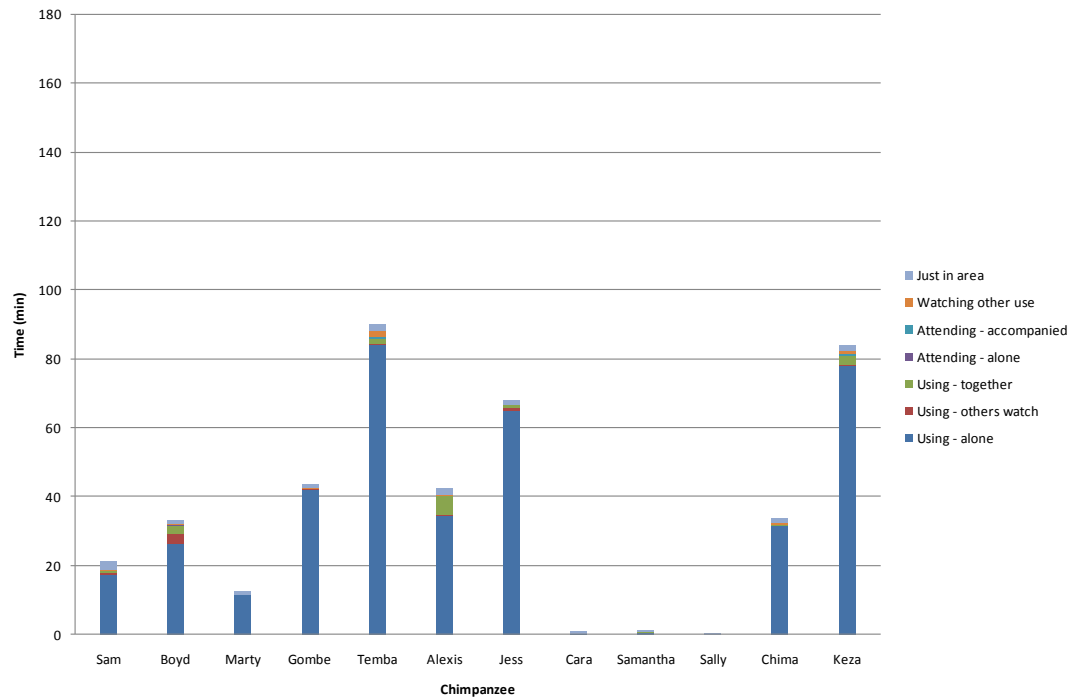


Figure 5.13c. Total time that the individuals of the chimpanzee group exhibited defined behaviours during sessions with the Marbleroll enrichment - delivering coated peanuts, in Experiment 5. Individual chimpanzees are arranged in order of sex, males on the left and then age within each sex group, oldest on the left.

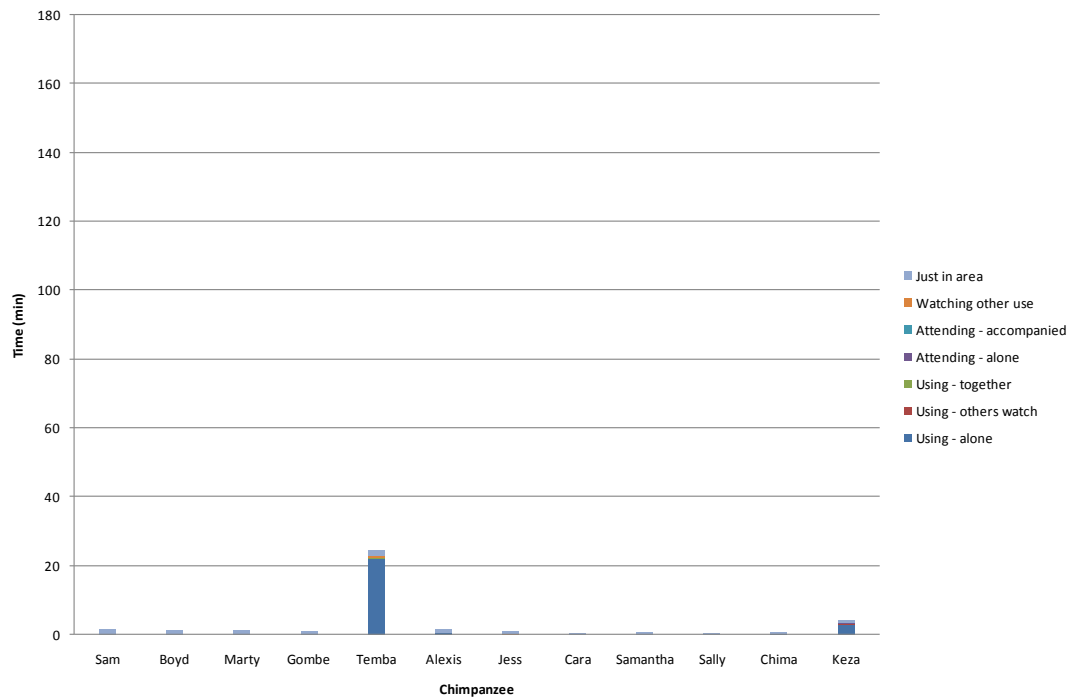


Figure 5.13d. Total time that the individuals of the chimpanzee group exhibited defined behaviours during sessions with the Musicbox enrichment in Experiment 5. Individual chimpanzees are arranged in order of sex, males on the left and then age within each sex group, oldest on the left.

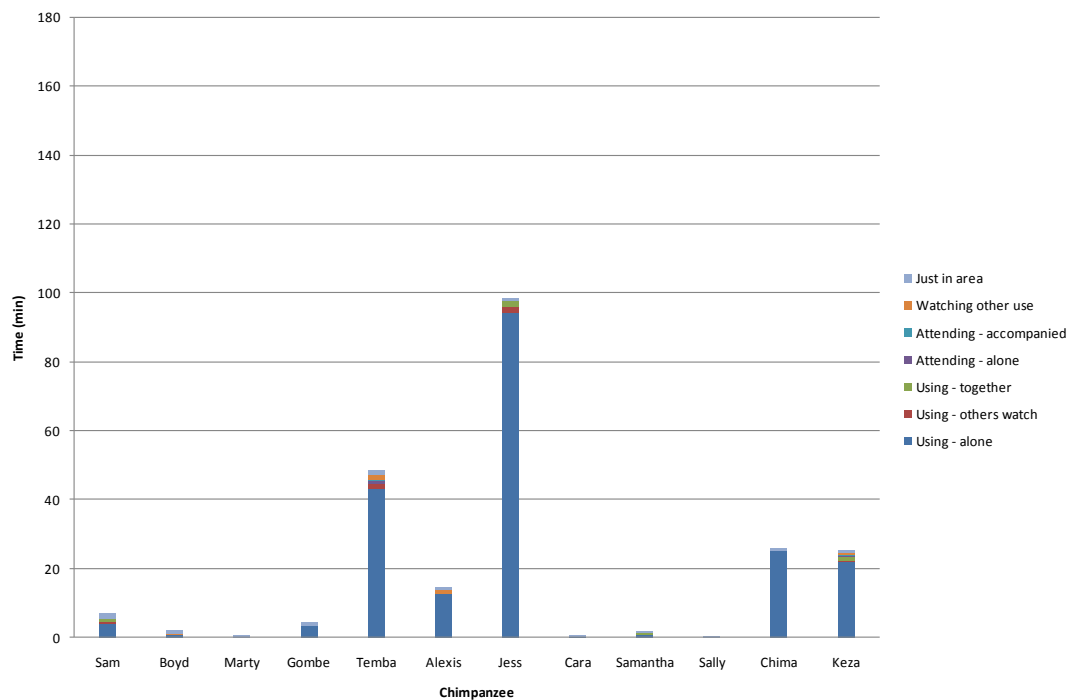


Figure 5.13e. Total time that the individuals of the chimpanzee group exhibited

defined behaviours during sessions with the Dipper enrichment in Experiment 5. Individual chimpanzees are arranged in order of sex, males on the left and then age within each sex group, oldest on the left.

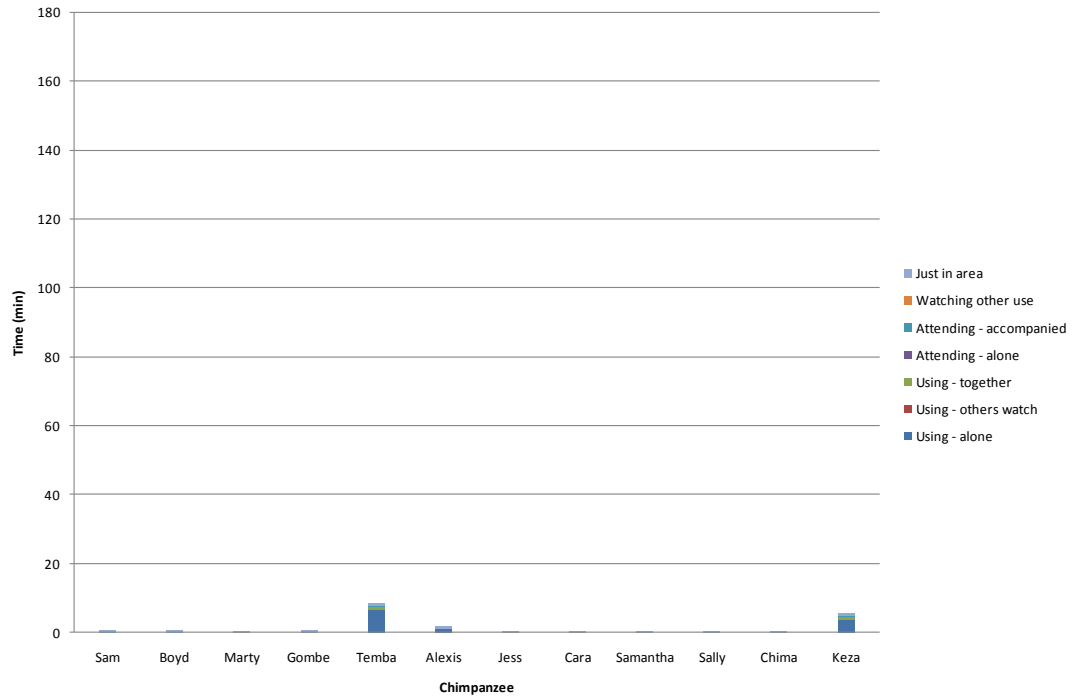


Figure 5.13f. Total time that the individuals of the chimpanzee group exhibited defined behaviours during sessions with the TV/Video enrichment in Experiment 5. Individual chimpanzees are arranged in order of sex, males on the left and then age within each sex group, oldest on the left.

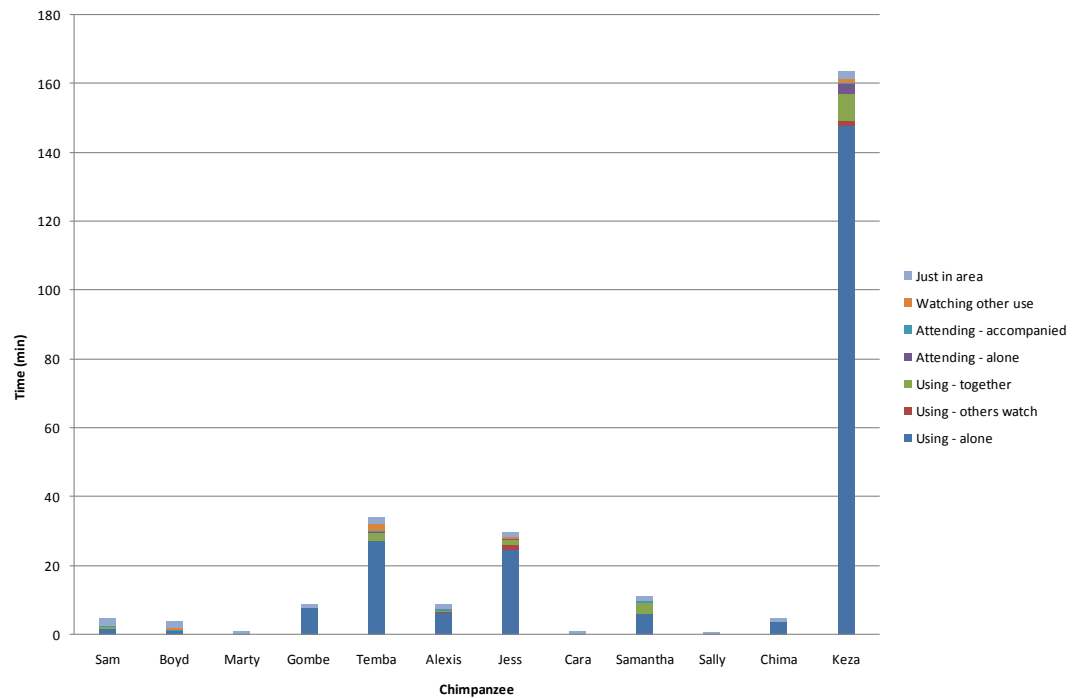


Figure 5.13g. Total time that the individuals of the chimpanzee group exhibited defined behaviours during sessions with the Marbleroll enrichment—delivering marbles and Jaffas™, in Experiment 5. Individual chimpanzees are arranged in order of sex, males on the left and then age within each sex group, oldest on the left.

Chimpanzee Demand Whilst Housed Socially

The chimpanzee group's behavioural data as recorded by the computer (as discussed and defined previously) for each experimental session of Experiment 5 are shown in Table 5.3 and 5.4 and Figure 5.14 to 5.30. PRP times will not be discussed for the group as too many factors impact on this aspect of the data when the animals were working for a commodity in a social environment, these will be discussed further.

Group Responses with Enrichment Items Across FRs

Overall response rate was calculated as the total number of responses made on the lever by the group divided by total session time excluding the time the enrichment items were operative.

Computer recorded behaviour of chimpanzee group during Demand study.

| Session Condition | Computer Recorded Event | | | | | | | | |
|-------------------|-------------------------|-----------------|----------------------|-----------------|------------------------------|-----------|----------------|----------------|------------------|
| | First response (min) | Total responses | Total reinforcements | Lever Down | Lever Up When Should Be Down | PRP (min) | Run time (min) | Key time (min) | Total time (min) |
| | | | | Failed Response | | | | | |
| Baseline | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| Screwfeeder-1A | 1.43 | 184 | 184 | 13 | 14 | 171.15 | • | 173.87 | 180.00 |
| Screwfeeder-2A | 1.47 | 226 | 113 | 29 | 14 | 144.77 | 2.96 | 176.24 | 180.00 |
| Screwfeeder-4A | 2.75 | 253 | 63 | 16 | 14 | 56.97 | 11.84 | 177.90 | 180.00 |
| Screwfeeder-8A | 0.73 | 59 | 7 | 5 | 4 | 10.84 | 16.83 | 179.77 | 180.00 |
| Screwfeeder-16A | 1.32 | 38 | 2 | 6 | 1 | 0.73 | 17.80 | 179.94 | 180.00 |
| Screwfeeder-32A | 1.65 | 25 | 0 | 7 | 0 | • | 17.84 | 180.00 | 180.00 |
| Screwfeeder-1B | 1.72 | 199 | 199 | 23 | 17 | 170.56 | • | 173.37 | 180.00 |
| Screwfeeder-2B | 2.53 | 337 | 168 | 33 | 56 | 99.89 | 7.16 | 174.40 | 180.00 |
| Screwfeeder-4B | 5.92 | 271 | 67 | 22 | 11 | 91.07 | 8.11 | 177.77 | 180.00 |
| Screwfeeder-8B | 5.08 | 193 | 24 | 16 | 9 | 26.53 | 14.80 | 179.20 | 180.00 |
| Screwfeeder-16B | 0.92 | 56 | 3 | 4 | 1 | 3.61 | 17.55 | 179.90 | 180.00 |
| Screwfeeder-32B | 2.77 | 39 | 1 | 9 | 1 | 0.27 | 17.70 | 179.97 | 180.00 |
| Screwfeeder-64B | 2.22 | 27 | 0 | 5 | 1 | • | 17.79 | 180.00 | 180.00 |
| Baseline | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| Baseline | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| Marbleroll(p)-1A | 3.15 | 277 | 277 | 11 | 5 | 172.48 | • | 177.70 | 180.00 |
| Marbleroll(p)-2A | 0.93 | 322 | 161 | 20 | 14 | 147.05 | 3.02 | 178.66 | 180.00 |
| Marbleroll(p)-4A | 1.17 | 22 | 5 | 1 | 0 | 5.80 | 17.30 | 179.96 | 180.00 |
| Marbleroll(p)-8A | 13.92 | 5 | 0 | 1 | 0 | • | 16.61 | 180.00 | 180.00 |
| Marbleroll(p)-1B | 1.52 | 110 | 110 | 11 | 7 | 176.94 | • | 179.09 | 180.00 |
| Marbleroll(p)-2B | 4.08 | 307 | 153 | 14 | 14 | 115.23 | 5.92 | 178.73 | 180.00 |
| Marbleroll(p)-4B | 3.58 | 34 | 8 | 4 | 0 | 12.53 | 16.39 | 179.94 | 180.00 |
| Marbleroll(p)-8B | 7.30 | 7 | 0 | 0 | 0 | • | 17.27 | 180.00 | 180.00 |
| Baseline | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| Musicbox-1A | 3.82 | 12 | 12 | 15 | 14 | 170.12 | • | 174.00 | 180.00 |
| Musicbox-2A | 6.90 | 5 | 2 | 3 | 0 | 8.52 | 16.36 | 179.00 | 180.00 |
| Musicbox-4A | 14.18 | 3 | 0 | 0 | 0 | • | 16.58 | 180.00 | 180.00 |
| Musicbox-1B | 11.22 | 5 | 5 | 0 | 0 | 166.25 | • | 177.50 | 180.00 |
| Musicbox-2B | 7.15 | 3 | 1 | 0 | 0 | 2.39 | 17.00 | 179.50 | 180.00 |
| Musicbox-4B | 12.37 | 2 | 0 | 0 | 0 | • | 16.76 | 180.00 | 180.00 |
| Baseline | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| Baseline | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| Dipper 1A | 5.25 | 92 | 92 | 12 | 5 | 128.29 | • | 134.00 | 180.00 |
| Dipper 2A | 3.63 | 9 | 4 | 0 | 0 | 17.83 | 15.65 | 178.00 | 180.00 |
| Dipper 4A | 2.43 | 3 | 0 | 1 | 0 | • | 17.76 | 180.00 | 180.00 |
| Dipper 1B | 2.38 | 104 | 104 | 12 | 12 | 125.09 | • | 128.00 | 180.00 |
| Dipper 2B | 5.23 | 5 | 2 | 0 | 0 | 26.15 | 14.76 | 179.00 | 180.00 |
| Dipper 4B | 8.97 | 3 | 0 | 0 | 0 | • | 17.10 | 180.00 | 180.00 |
| Baseline | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| TV/Video-1A | 2.42 | 7 | 7 | 0 | 0 | 173.97 | • | 179.97 | 180.00 |
| TV/Video-2A | 12.23 | 1 | 0 | 0 | 0 | • | 16.78 | 180.00 | 180.00 |
| TV/Video-1B | 18.35 | 2 | 2 | 0 | 0 | 160.62 | • | 179.99 | 180.00 |
| TV/Video-2B | 7.58 | 1 | 0 | 0 | 0 | • | 17.24 | 180.00 | 180.00 |
| Baseline | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| Marbleroll-1A | 0.65 | 77 | 77 | 2 | 1 | 178.32 | • | 179.36 | 180.00 |
| Marbleroll-2A | 0.53 | 49 | 24 | 1 | 0 | 96.22 | 8.30 | 179.80 | 180.00 |
| Marbleroll-4A | 2.50 | 6 | 1 | 0 | 0 | 35.59 | 14.19 | 179.99 | 180.00 |
| Marbleroll-8A | 3.23 | 5 | 0 | 0 | 0 | • | 17.68 | 180.00 | 180.00 |
| Marbleroll-1B | 1.73 | 52 | 52 | 2 | 0 | 177.57 | • | 179.57 | 180.00 |
| Marbleroll-2B | 0.98 | 21 | 10 | 0 | 0 | 46.32 | 13.26 | 179.92 | 180.00 |
| Marbleroll-4B | 11.20 | 2 | 0 | 0 | 0 | • | 16.88 | 180.00 | 180.00 |
| Baseline | NA | NA | NA | NA | NA | NA | NA | NA | NA |

Group responses with Screwfeeder enrichment. As seen in Table 5.3 the first response on the lever, in sessions with the Screwfeeder, occurred very early in each session. In general the group lifted the lever up when it should have been down or had the lever down after a failed response very few times during each session with the most occurring with FR 2. Table 5.3 shows the number of responses made by the chimpanzee group with the Screwfeeder peaked during FR 2 of Series B at 337.

Overall group response rate with Screwfeeder enrichment. Figure 5.14 shows that the overall rate of responding for the enrichment peaked during FR 2 for Series B and FR 4 for Series A. With further increases in FR size the rate of responding dropped to levels lower than those at smaller FR values. The chimpanzees continued to respond for access to the Screwfeeder up to FR 32 in Series A and FR 64 in Series B, but they gained no food in these two sessions.

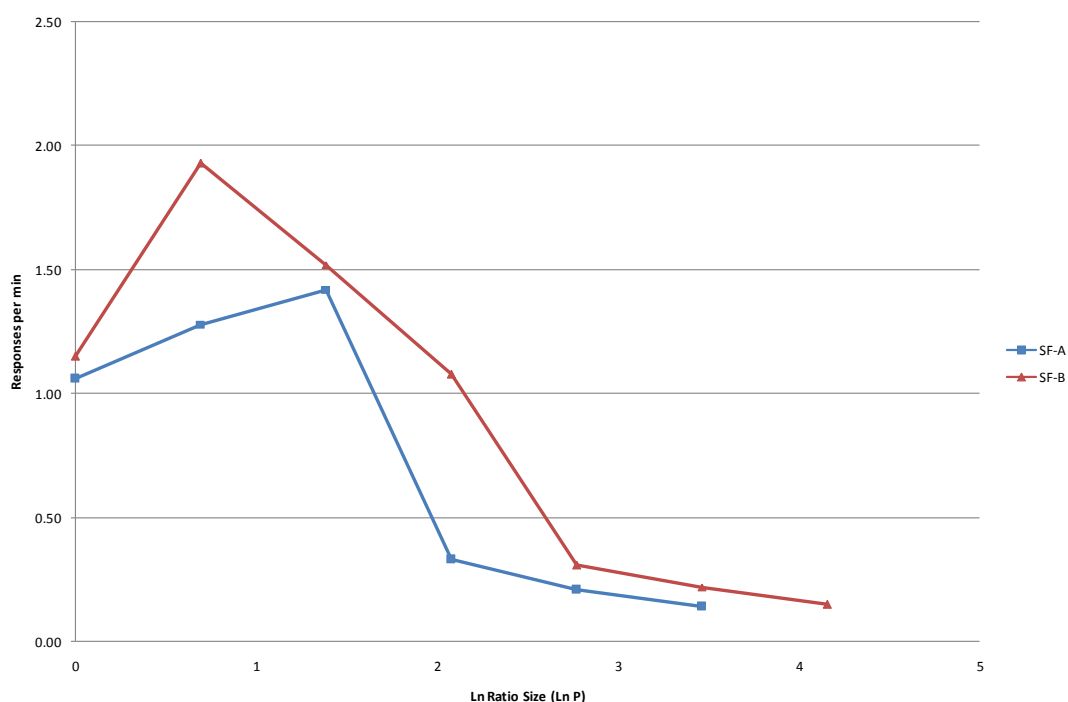


Figure 5.14. Overall response rates (responses per minute excluding enrichment operation time) plotted against the logarithms (ln) of the ratio requirements for the chimpanzee group during sessions in Experiment 5 with the Screwfeeder enrichment.

Group responses with Marbleroll enrichment - delivering coated peanuts. The first response on the lever occurred very early in sessions with the Marbleroll enrichment, as it delivered coated peanuts, although during FR 8 of Series A the first response was 13.92 min into the session (Table 5.3). In general the group lifted the lever up when it should have been down, or had the lever down after a failed response, only a few times each session but did so most with FR 2. Table 5.3 shows the number of responses made by the group in a single session with the Marbleroll enrichment (delivering coated peanuts) was highest with FR 2 in Series A at 322.

Overall group response rate with Marbleroll enrichment - delivering coated peanuts. Figure 5.15 shows the peak overall response rate occurred during FR 2 and then the rate decreased as FR size increased during both series. The group responded during FR 8 but not enough to obtain any peanuts.

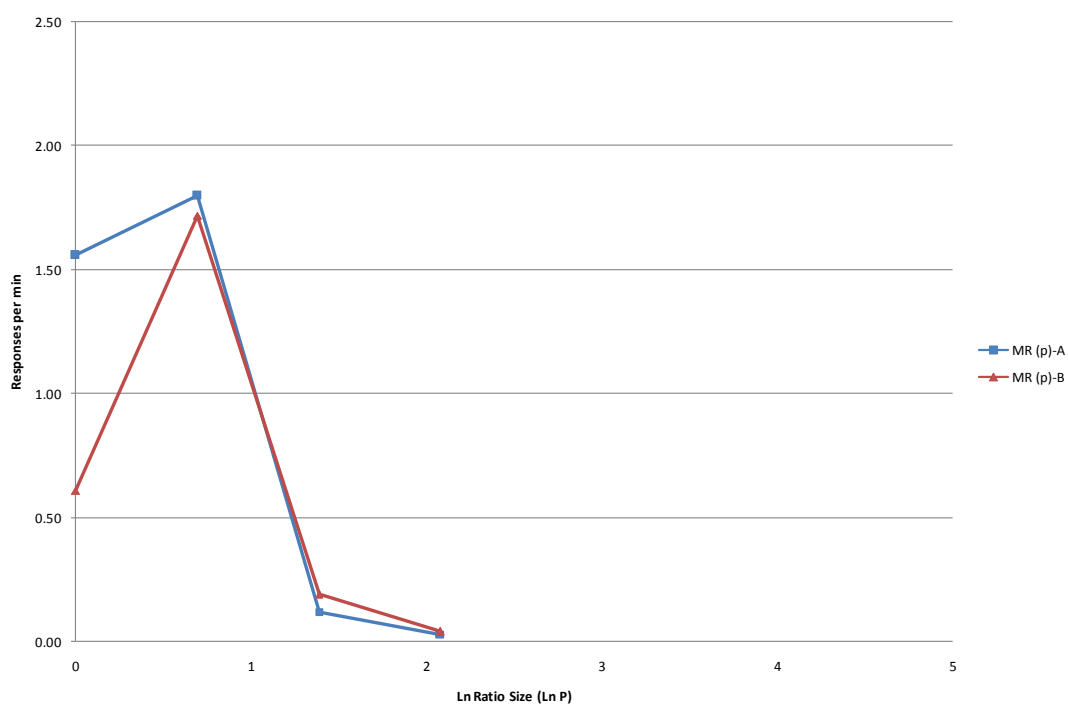


Figure 5.15. Overall response rates (responses per minute excluding enrichment operation time) plotted against the logarithms (ln) of the ratio requirements for the chimpanzee group during sessions in Experiment 5 with the Marbleroll enrichment - delivering coated peanuts.

Group responses with Musicbox enrichment. The first response on the lever occurred early in sessions with the Musicbox enrichment, with 14.18 min into the FR 4 session in Series A being the longest latency (Table 5.3). The group lifted the lever up when it should have been down or had the lever down after a failed response very few times, the most occurring during the FR 1 of Series A. FR 1, Series A, had the most responding but with only 12 response being made (Table 5.3).

Overall group response rate with Musicbox enrichment. Figure 5.16 shows that the overall rate of responding by the group was highest during FR 1 and then decreased with increases in FR size. The group did not respond enough to gain any reinforcement once the FR schedule reached 4.

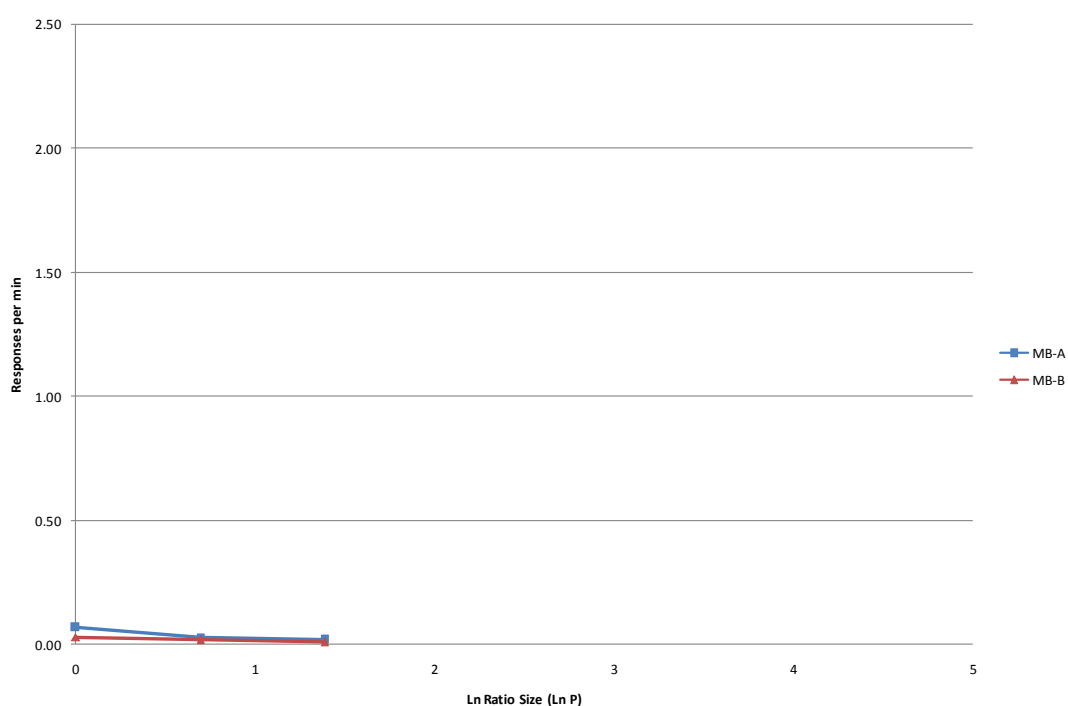


Figure 5.16. Overall response rates (responses per minute excluding enrichment operation time) plotted against the logarithms (ln) of the ratio requirements for the chimpanzee group during sessions in Experiment 5 with the Musicbox enrichment.

Group responses with Dipper enrichment. With the Dipper enrichment, the first response on the lever occurred very early in a session, the longest latency of 8.97 min was with FR 4 in Series B (Table 5.3). The chimpanzee group lifted the lever up when it should have been down or had the lever down after a failed response very few times, the highest number was with FR 1. Table 5.3 shows that the chimpanzee group made 104 responses during FR 1 in Series B, the most during a session with the Dipper enrichment.

Overall group response rate with Dipper enrichment. Figure 5.17 shows that the overall rate of responding for Dipper was maximum with FR 1 and decreased with further increases in FR size. The group did not respond enough during either session at FR 4 to gain reinforcement.

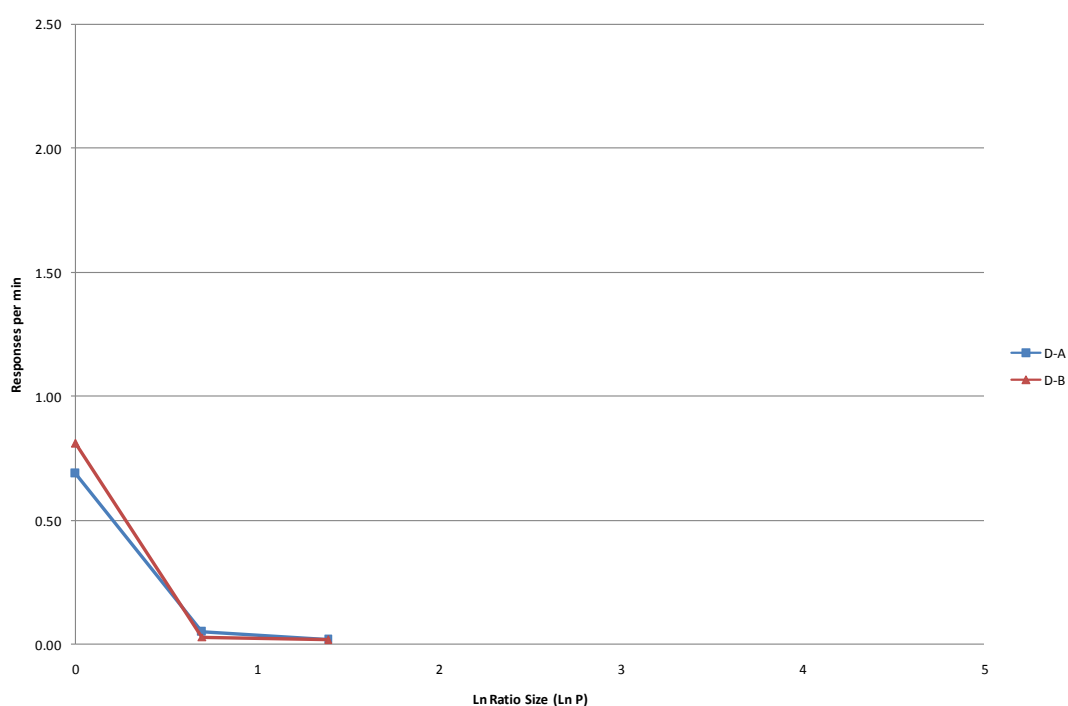


Figure 5.17. Overall response rates (responses per minute excluding enrichment operation time) plotted against the logarithms (ln) of the ratio requirements for the chimpanzee group during sessions in Experiment 5 with the Dipper enrichment.

Group responses with TV/Video enrichment. The latency to the first response

on the lever was reasonably short with the TV/Video, the longest being 18.35 with FR 1 of Series B (Table 5.3). The group never lifted the lever up when it should have been down or had the lever down after a failed response during any of the sessions. Table 5.3 shows there were very few responses for access to the TV/Video in any session with the most being 7 during FR 1 in Series A. The group did not respond enough to gain any reinforcements during FR 2 in both series.

Overall group response rate with TV/Video enrichment. Figure 5.18 shows that the overall rate of responding for the TV/Video was very low but was highest with FR 1.

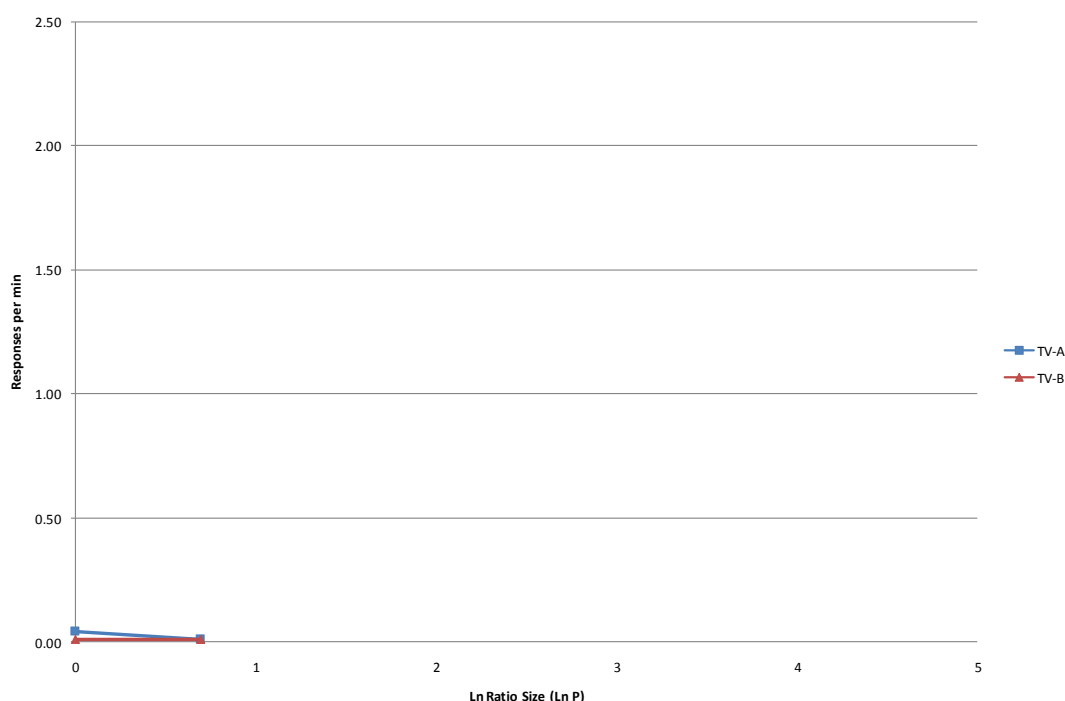


Figure 5.18. Overall response rates (responses per minute excluding enrichment operation time) plotted against the logarithms (ln) of the ratio requirements for the chimpanzee group during sessions in Experiment 5 with the TV/Video enrichment.

Group responses with Marbleroll enrichment - delivering marbles and Jaffas™. When the Marbleroll enrichment delivered marbles and Jaffas™ the time to the first response on the lever was short, it was longest (11.20 min) with FR 4 of Series B (Table 5.3). The group lifted the lever up when it should have been down or

had the lever down after a failed response on only four occasions. Table 5.3 shows responding was highest at 77 during FR 1 in Series A.

Overall group response rate with Marbleroll enrichment - delivering marbles and Jaffas™. Figure 5.19 shows that during both series, the group's response rate was the highest during FR 1 and decreased as FR size increased until FR 8 in series A and FR 4 in series B, in these sessions they did not received any reinforcement.

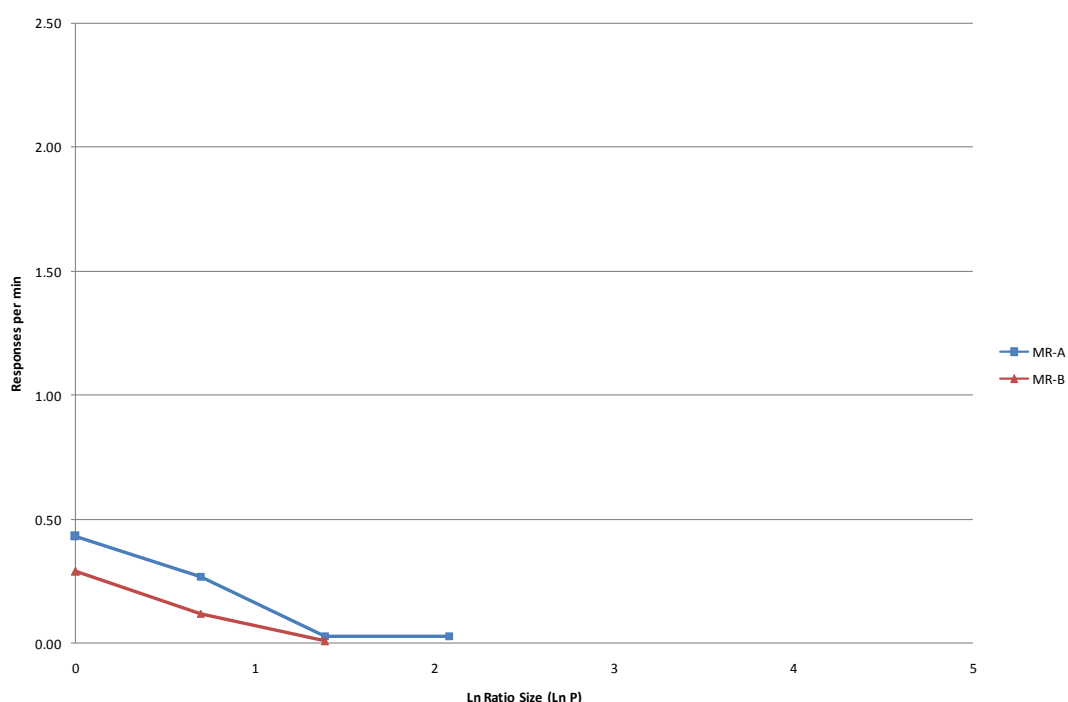


Figure 5.19. Overall response rates (responses per minute excluding enrichment operation time) plotted against the logarithms (ln) of the ratio requirements for the chimpanzee group during sessions in Experiment 5 with the Marbleroll enrichment delivered marbles and Jaffas™.

Comparison of Group Responses for Enrichment Items

The chimpanzee group responded the most (and gained the most access to the reinforcer) with the Screwfeeder enrichment. The Marbleroll (delivering coated peanuts) had the next highest number of responses and the Marbleroll (delivering marbles and Jaffas™), the third highest. There was considerably less responding for access to the Dipper, Musicbox and TV/Video.

Group Response Rate with Enrichments Across Sessions With Each FR

Figures 5.20 - 5.24 show the cumulative responding of the chimpanzee group during sessions with the enrichment items during Experiment 5. On these figures each symbol denotes a response made by an individual (rather than a reinforcer).

Group cumulative records for Screwfeeder enrichment. Figure 5.20 shows that once the chimpanzee group started responding in a session with the Screwfeeder item and with FR 1, FR 2 and FR 4 they responded steadily with few pauses until the point they stopped, 1.5 to over 2 hours into the session. At the larger FR sizes they paused between responses from the very start of the session and stopped responding earlier, but still generally responded for the first hour or more of the session. The response rates with the different FRs over the period of the session the group was responding show similar relations to the overall response rates shown earlier. This is a result of the steady responding and the fact that, generally, the higher the response rate the longer the response period. Given the amount of information shown on Figure 5.20 separate figures for each session are shown in Appendix F.

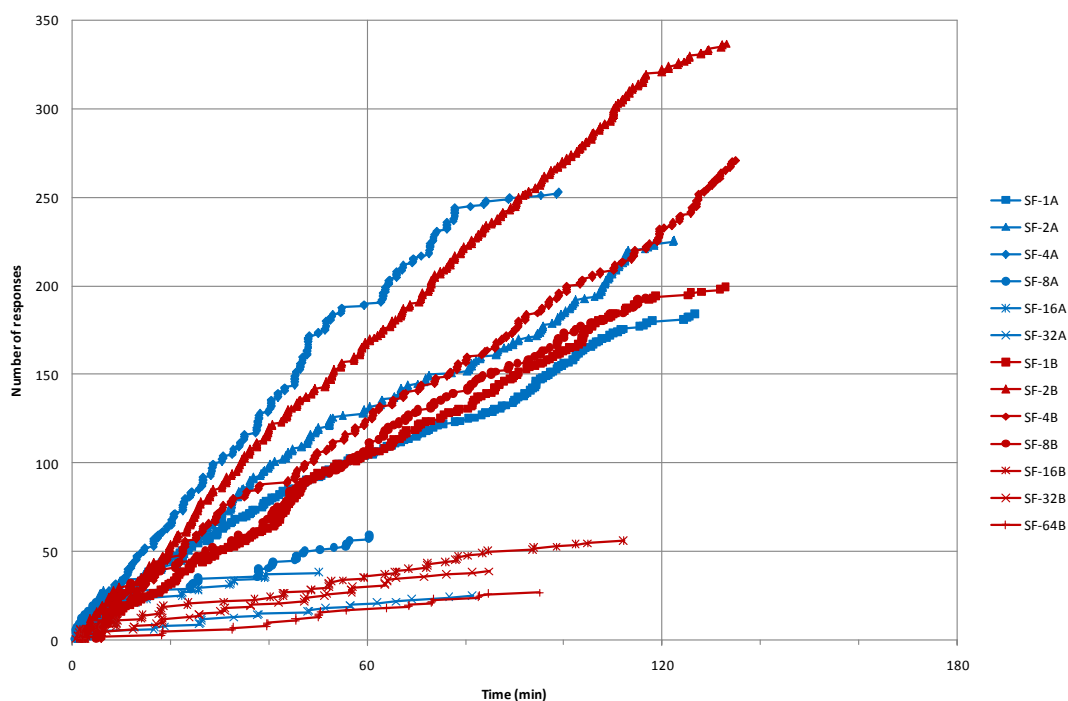


Figure 5.20. Cumulative rate of responding by chimpanzee group during sessions of Experiment 5 with the Screwfeeder enrichment.

Group cumulative records for Marbleroll enrichment delivering coated peanuts. During the sessions with the Marbleroll delivering coated peanuts the chimpanzee group responded steadily during the FR 2 sessions and FR 1 of Series A with few pauses until the point at which they stopped responding, as shown in Figure 5.21. During the rest of the sessions with this item the group paused between responding and stopped responding earlier in the sessions. In general, the higher the FR the sooner the group stopped responding in a session.

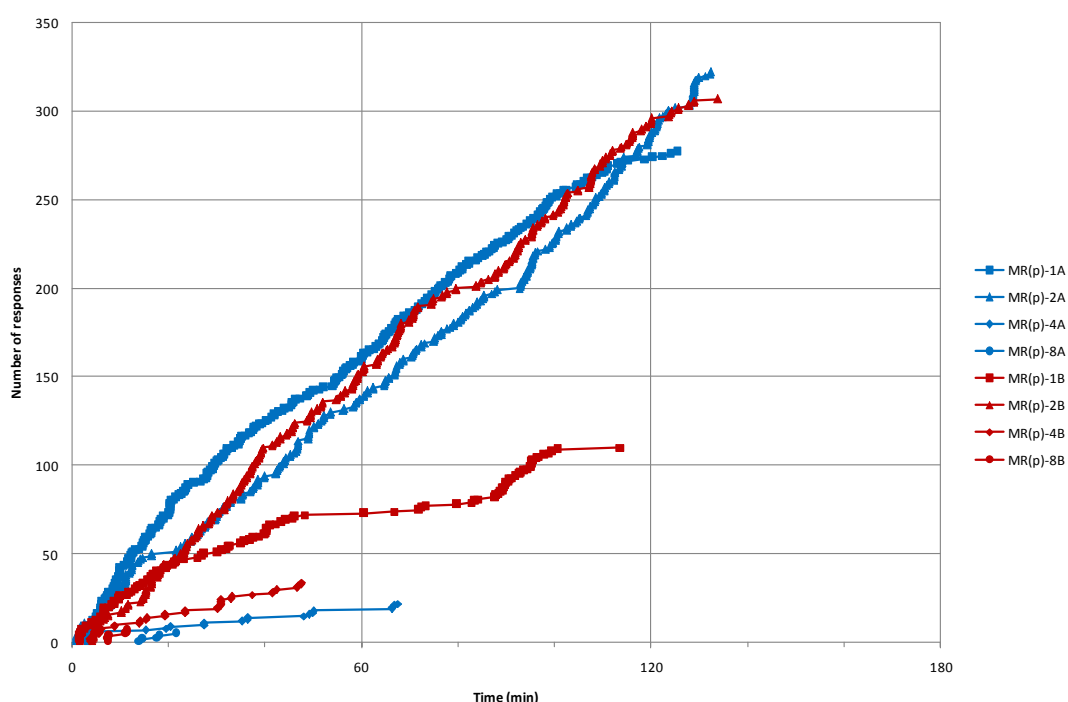


Figure 5.21. Cumulative rate of responding by chimpanzee group during sessions of Experiment 5 with the Marbleroll enrichment delivering coated peanuts.

Group cumulative records for Musicbox enrichment. As shown in Figure 5.22 the chimpanzee group responded at a very low rate for the Musicbox enrichment over all sessions. FR 1 during Series A was the greatest rate but as there was very little responding for access to this enrichment, the rates were very low.

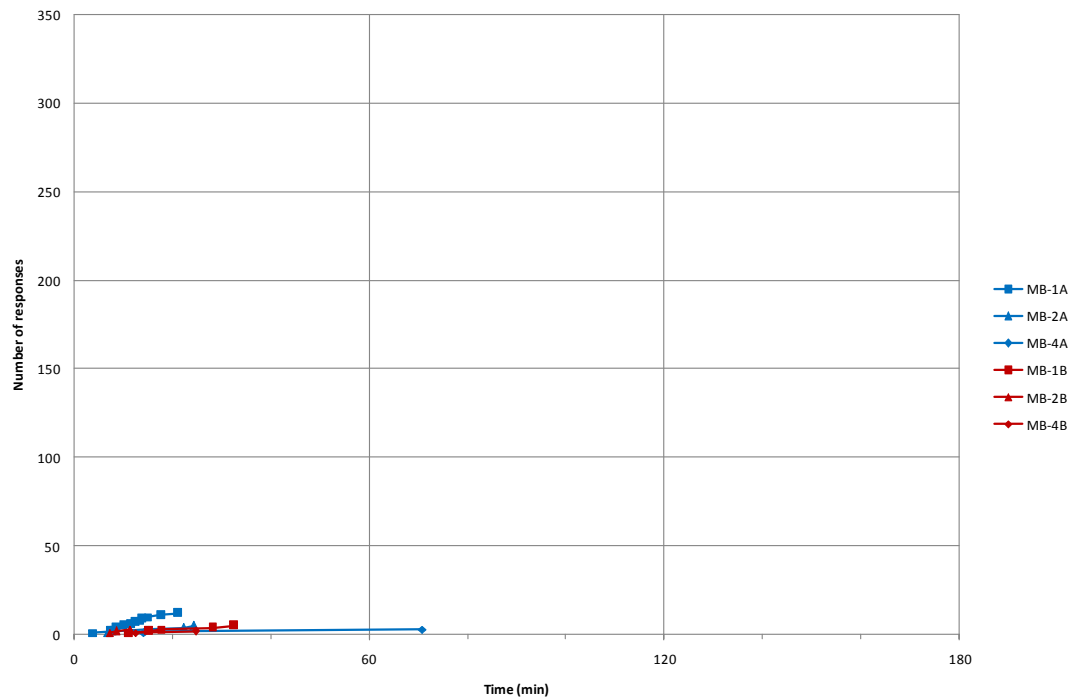


Figure 5.22. Cumulative rate of responding by chimpanzee group during sessions of Experiment 5 with the Musicbox enrichment.

Group cumulative records for Dipper enrichment. The chimpanzee group responded relatively steadily during the FR 1 sessions with the Dipper enrichment item and continued responding for more than half the entire session length (as shown in Figure 5.23). During the sessions with larger FR sizes the group stopped responding much earlier in the sessions.

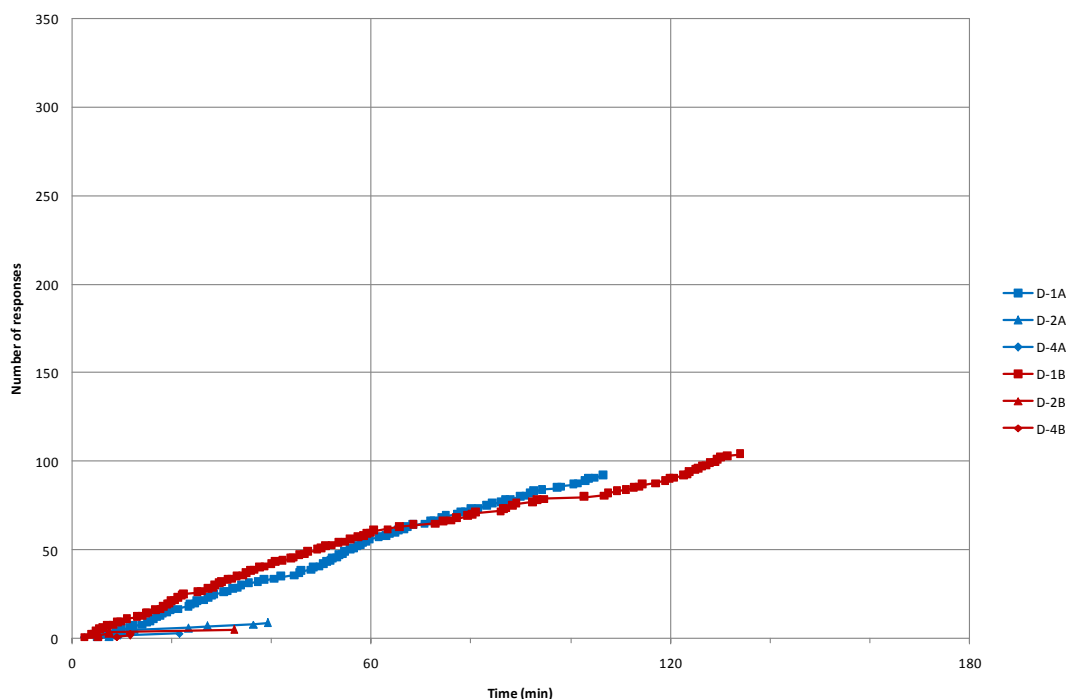


Figure 5.23. Cumulative rate of responding by chimpanzee group during sessions of Experiment 5 with the Dipper enrichment.

Group cumulative records for TV/Video enrichment. Very little responding was done by the chimpanzee group for the TV/Video enrichment, as such the rate of responding was very low throughout all the sessions.

Group cumulative records for Marbleroll enrichment - delivering marbles and Jaffas™. Figure 5.24 shows that the chimpanzee group paused between responding in all of the sessions with this item, and that this pausing increased as the FR size increased. The group also responded longer in sessions the smaller the FR size.

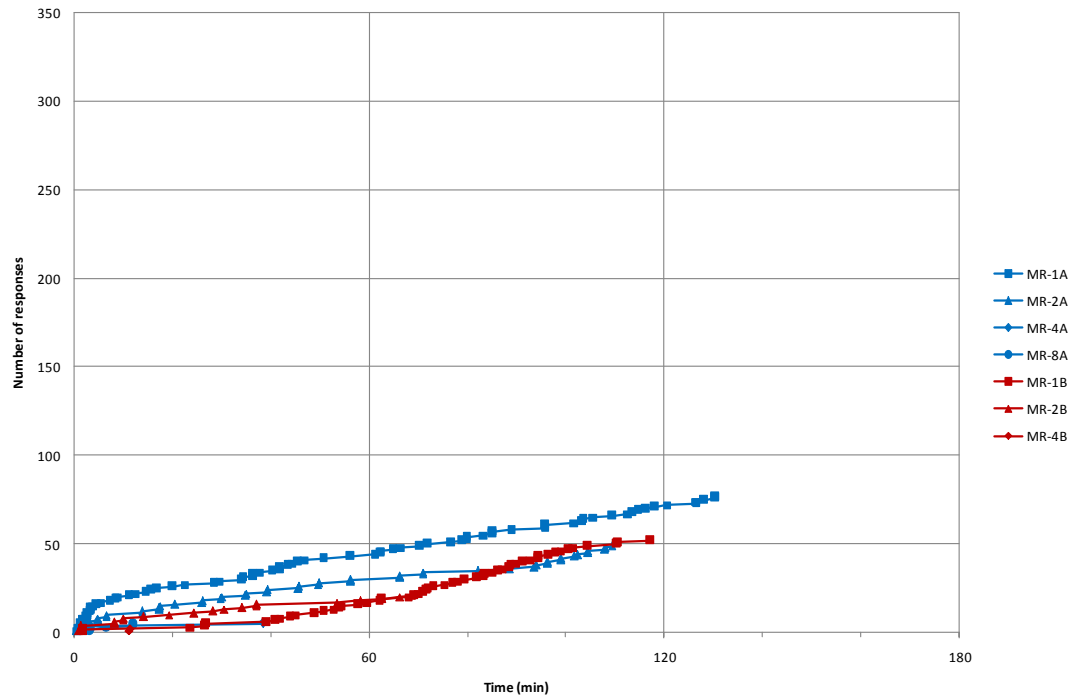


Figure 5.24. Cumulative rate of responding by chimpanzee group during sessions of Experiment 5 with the Marbleroll enrichment.

Group Response Rates Between Enrichment Items

When comparing sessions in which the enrichment items were available the chimpanzee group responded the most steadily, and for the longest time in sessions, for the Screwfeeder enrichment. This was followed by the Marbleroll delivering coated peanuts. With very little responding in general by the group for the Musicbox and TV/Video, enrichments rates of responding were very low.

Group Demand for Enrichment Items

Curvilinear demand functions. Figure 5.25 shows the natural logarithm of the reinforcement rates (Q in Equation 3) as functions of the natural logarithms of the FR size (P in Equation 3). Equation 3 was fitted to the data iteratively through nonlinear regression, and the resulting demand functions are shown on the graphs [(the parameters, the percentages of the data variance the functions account for (% VAC), and the standard errors of the fits are given in Table 5.4].

These demand functions describe the data well, with both high % VAC and low

standard errors (as there are few data points). The standard error value was greater than 0 only with the Screwfeeder. There were not enough data points to fit this function for either of the series with the TV/Video enrichment item.

The Y intercept, or consumption rate at a price of 1.0, is equal to $\ln(L)$ minus a . Thus, when a , the rate of change of elasticity, is small $\ln(L)$ is approximately equal to the Y intercept and thus to the consumption rate at this point. However, in this study a values were large for some conditions (the greatest value being 3.29, occurring during the B series with the Marbleroll delivering coated peanuts). As such the Y intercepts for the demand graphs were not represented by the $\ln(L)$ values. For sessions with other enrichment items, however, the values of a , were small, in that data paths were almost linear.

Positive values of a indicate that the rate of decline in consumption increased with successive increases in FR size. This was evident for all condition data for which a demand function could be fitted except during Series B with the Dipper enrichment. The data for chimpanzee group with the Screwfeeder, the Marbleroll, delivering coated peanuts and delivering marbles and Jaffas™, appear curvilinear, such that the rate of decline in consumption tended to increase with successive increases in FR size and then decreased as FR values increased further.

The initial slopes, b , varied from -6.20 to 5.23, with 3 more negative than -1.0. For half of the condition data that lines were able to be fitted to the b parameters were negative in sign, indicating that the demand functions decreased with initial price increases. This was the case for both series with the Screwfeeder and Dipper and Series B with the Marbleroll.

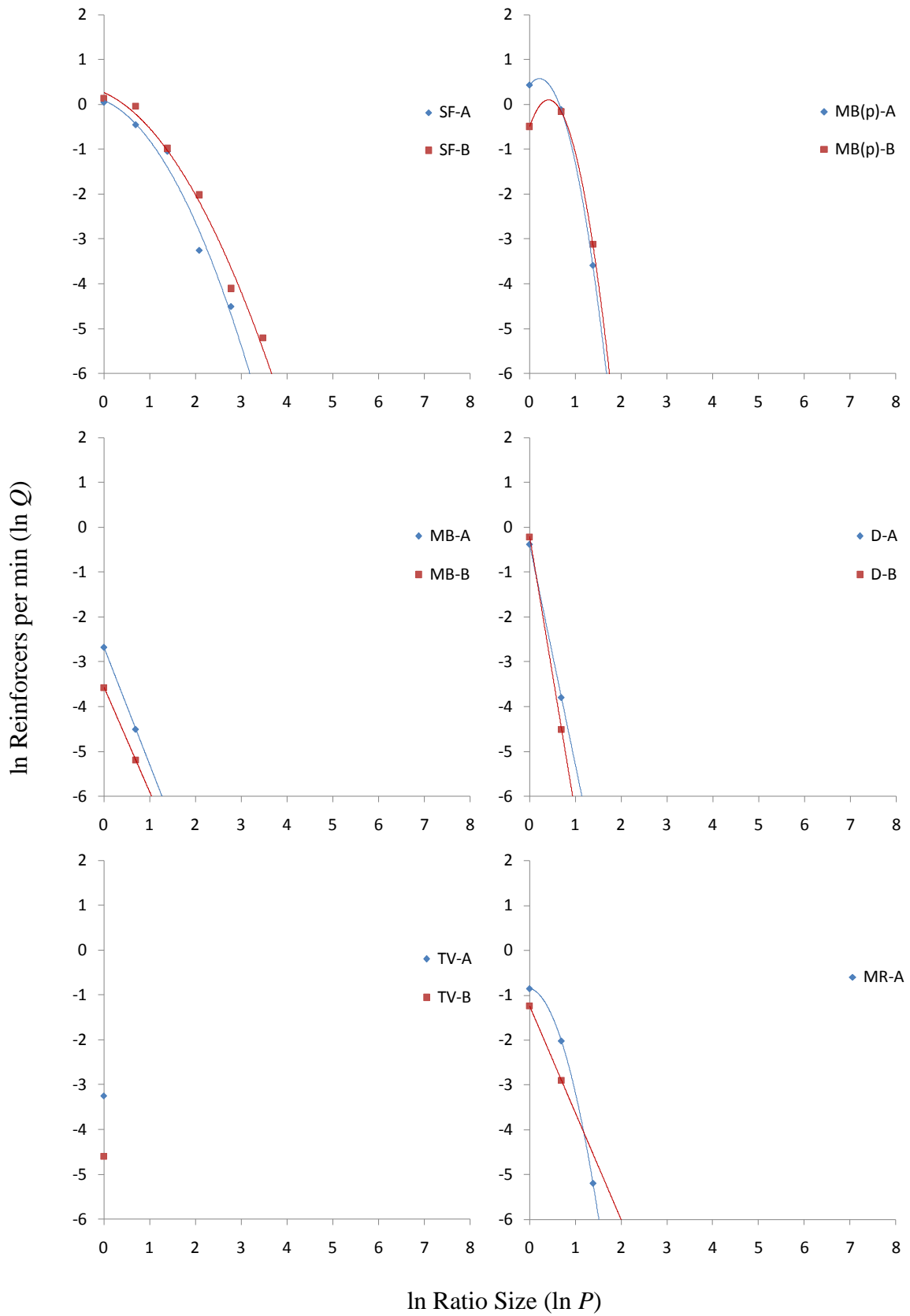


Figure 5.25. The natural logarithms of obtained reinforcement rates plotted against the natural logarithms of FR schedules size for the chimpanzee group for

each condition in Experiment 5. The demand functions, shown by the lines, were obtained by fitting Equation 3 to the data.

Table 5.4

The parameters $\ln(L)$, a , and b of the lines fitted by Hursh et al.'s (1988) Total consumption equation (Equation 3) to the log consumption rate versus log FR data for the sessions of Experiment 5. The percentage of variance accounted for by lines (% VAC) and the standard errors of the estimates (se) are also shown.

| Condition (Item/Series) | Parameters | | | | |
|----------------------------|------------|-------|-------|------|--------|
| | $\ln(L)$ | b | a | se | % VAC |
| Screwfeeder -A | 0.38 | -0.86 | 0.17 | 0.32 | 96.60 |
| Screwfeeder-B | 0.53 | -1.03 | 0.07 | 0.33 | 97.30 |
| Marbleroll (p)-A | 3.38 | 3.44 | 2.93 | 0.00 | 100.00 |
| Marbleroll (p)-B | 2.80 | 5.23 | 3.29 | 0.00 | 100.00 |
| Musicbox-A | -0.71 | 0.20 | 1.96 | 0.00 | 100.00 |
| Musicbox-B | -1.15 | 1.15 | 2.42 | 0.00 | 100.00 |
| Dipper-A | 1.79 | -1.81 | 2.16 | 0.00 | 100.00 |
| Dipper-B | -0.22 | -6.20 | -0.01 | 0.00 | 100.00 |
| TV-A | NA | NA | NA | NA | NA |
| TV-B | NA | NA | NA | NA | NA |
| Marbleroll-A | 1.17 | 1.22 | 2.01 | 0.00 | 100.00 |
| Marbleroll-B | 0.19 | -0.33 | 1.43 | 0.00 | 100.00 |

Linear demand functions. Equation 2 was fitted to the same data shown in Figure 5.25 by the method of least squares. The resulting linear demand functions are shown in Figure 5.26 [the parameters, the percentages of the data variance the functions account for (% VAC), and the standard errors of the fits are given in Table 5.5]. The demand functions describe the data well (with high % VAC values and low standard error values).

The initial intensity of demand for the enrichment items, $\ln(L)$, varied from 0.93 (Series A, with the Marbleroll delivering coated peanuts) to -3.57 (Series B, Musicbox).

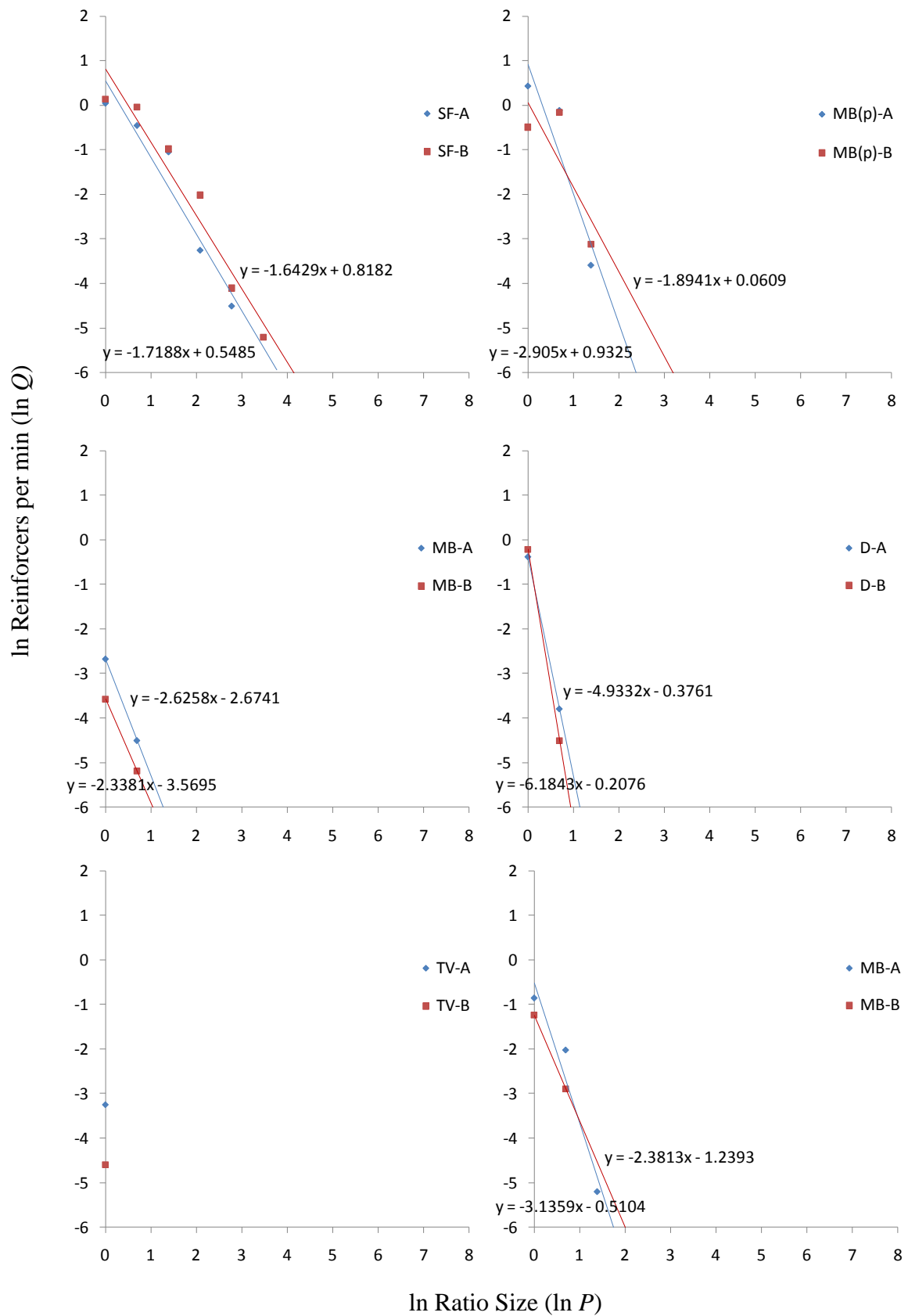


Figure 5.26. The natural logarithms of obtained reinforcement rates plotted against the natural logarithms of FR schedules size for the chimpanzee group for

each condition in Experiment 5. The demand functions, shown by the lines, were obtained by fitting Equation 2 to the data.

Negative values of b , the slope of the graph, were evident for all of the conditions to which a demand function could be fitted. Thus, the number of reinforcers obtained by the chimpanzee group declined steadily as the FR values increased during all conditions. The slope of the functions was steeper for some functions than others. The functions fitted to the Screwfeeder Series data were the shallowest (slope of -1.72 and -1.64), while the Dipper functions were the steepest (slope of -4.93 and -6.18). All of the demand functions had slopes (values of b) less than -1.0.

Table 5.5

The parameters $\ln(L)$, and b of the lines fitted by Hursh et al.'s (1988) Total consumption equation (Equation 2) to the log consumption rate versus log FR data for the sessions of Experiment 5. The percentage of variance accounted for by lines (% VAC) and the standard errors of the estimates (se) are also shown.

| Condition (Item/Series) | Parameters | | | |
|----------------------------|------------|-------|------|--------|
| | $\ln(L)$ | b | se | % VAC |
| Screwfeeder-A | 0.55 | -1.72 | 0.46 | 93.15 |
| Screwfeeder-B | 0.82 | -1.64 | 0.47 | 94.39 |
| Marbleroll (p)-A | 0.93 | -2.91 | 0.69 | 84.99 |
| Marbleroll (p)-B | 0.06 | -1.89 | 0.78 | 65.65 |
| Musicbox-A | -2.67 | -2.63 | 0.00 | 100.00 |
| Musicbox-B | -3.57 | -2.34 | 0.00 | 100.00 |
| Dipper-A | -0.38 | -4.93 | 0.00 | 100.00 |
| Dipper-B | -0.21 | -6.18 | 0.00 | 100.00 |
| TV-A | NA | NA | NA | NA |
| TV-B | NA | NA | NA | NA |
| Marbleroll-A | -0.51 | -3.14 | 0.47 | 93.34 |
| Marbleroll-B | -1.24 | -2.38 | 0.00 | 100.00 |

Individual Chimpanzee's Responses and Reinforcements with Enrichment Items

Screwfeeder enrichment. Figure 5.27 shows that adolescent male Temba was the individual that made the greatest number of responses on the lever to gain access to the Screwfeeder enrichment, responding a total of 494 times over all the sessions. He was also the individual to receive the greatest number of reinforcers (178). The next highest responder was juvenile female Keza with 377 responses. With the exception of female Jess, all of the other adult members of the group made fewer than 100 responses while the Screwfeeder enrichment was in place and received fewer than 50 reinforcers.

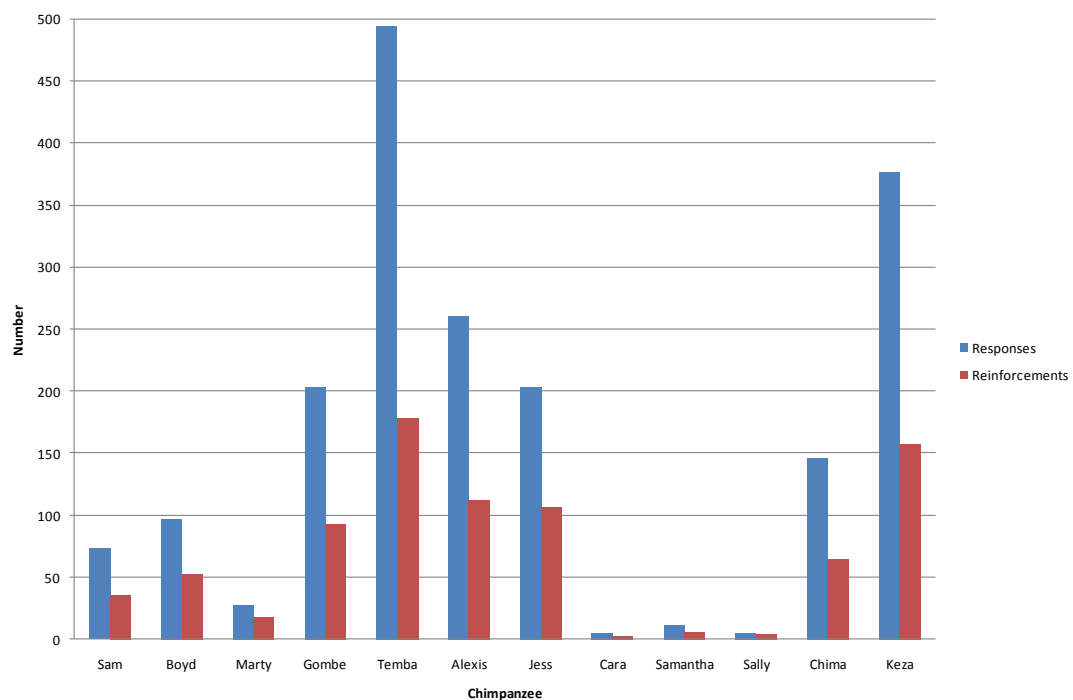


Figure 5.27. Total number of responses made and reinforcers gained by each individuals of the chimpanzee group in experimental sessions of Experiment 5 with the Screwfeeder enrichment. Individual chimpanzees are arranged in order of sex, males on the left and then age within each sex group, oldest on the left.

Marbleroll enrichment - delivering coated peanuts. Figure 5.28 shows that juvenile female Keza made the most responses of all the chimpanzees when the

Marbleroll enrichment was in place and delivering coated peanuts, making 249 responses in total. Keza also received the most reinforcers at 169 in total. Adolescent male Temba made the second highest number of responses (225), however, adult female Jess received the second highest number of reinforcers (142). Juvenile male Alexis was the only other individual to make more than 100 responses (122) and to gain more than 50 reinforcements (83). All the rest of the individuals of the group responded fewer than 100 times and received fewer than 50 reinforcers.

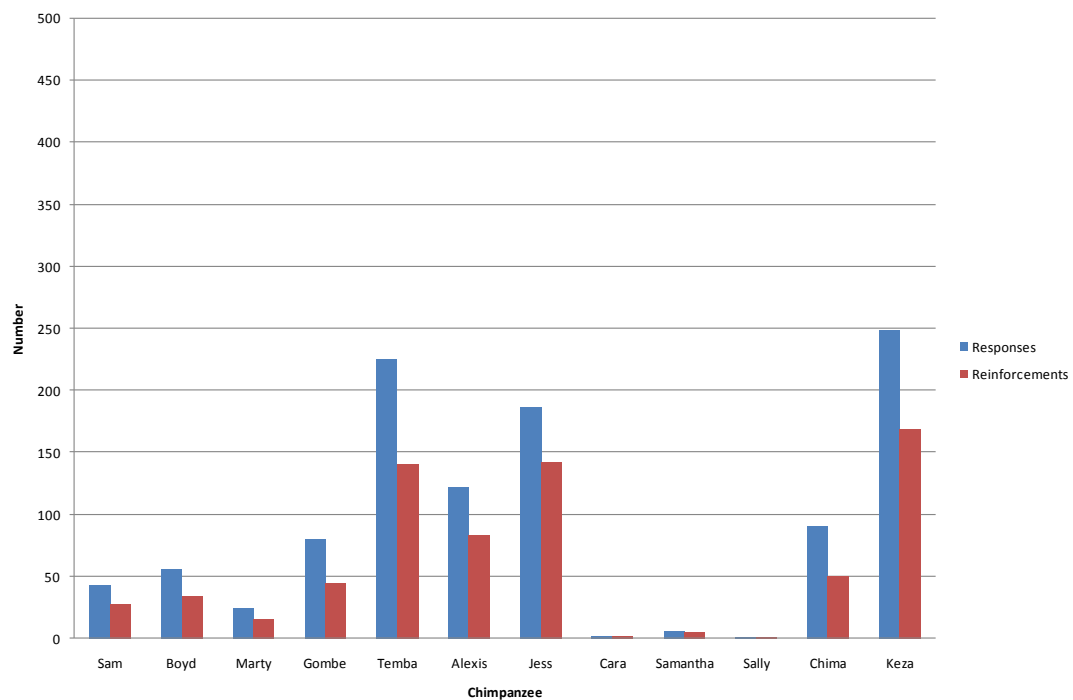


Figure 5.28. Total number of responses made and reinforcers gained by each individuals of the chimpanzee group in experimental sessions of Experiment 5 with the Marbleroll enrichment, delivering coated peanuts. Individual chimpanzees are arranged in order of sex, males on the left and then age within each sex group, oldest on the left.

Musicbox enrichment. Adolescent male Temba made the most responses and gained the most reinforcers with the Musicbox, making 14 responses and obtaining 8 reinforcers. Juvenile female Keza was the only other individual to respond 10 times or more and to receive more than 5 reinforcements. With the exception of female Jess, none of the other adults in the group made any responses on the lever when the

Musicbox was present.

Dipper enrichment. Adult female Jess made the most responses (85) to gain access to the Dipper enrichment and received 82 reinforcers (Figure 5.29). Adolescent male Temba made 46 responses and received 37 reinforcers. With the exception of Jess, Temba and adolescent female Chima and juvenile female Keza the rest of the chimpanzee group responded fewer than 15 times with this item (two adults: male Marty and female Sally made no responses in total).

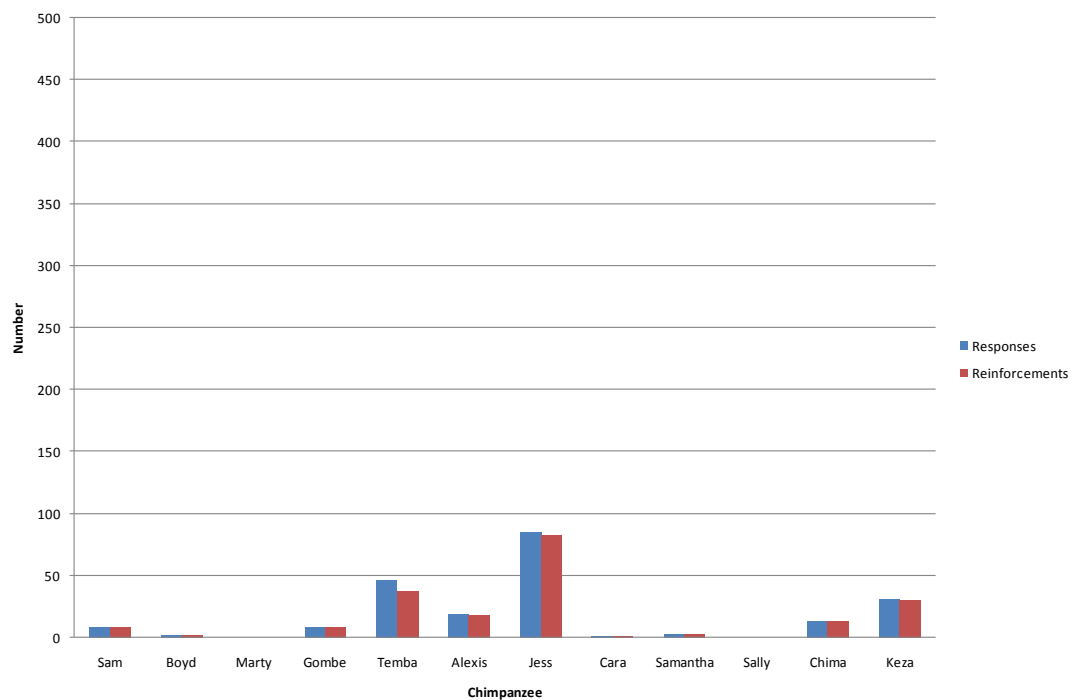


Figure 5.29. Total number of responses made and reinforcers gained by each individuals of the chimpanzee group in experimental sessions of Experiment 5 with the Dipper enrichment. Individual chimpanzees are arranged in order of sex, males on the left and then age within each sex group, oldest on the left.

TV/Video enrichment. Adolescent male Temba made 5, Keza made 4 and Alexis made 2 responses for this item. These were the only individuals to respond on the lever and turn on the TV/Video enrichment.

Marbleroll enrichment - delivering marbles and Jaffas™. Juvenile female

Keza made a total of 106 responses, and received a total of 77 reinforcers when the Marble roll was in place and delivering marbles and Jaffas™ (Figure 5.30). Both adolescent male Temba and adult female Jess made 31 responses and both also received 25 reinforcers. The rest of the individuals made fewer than 15 responses in total and adult female Sally and adult male Marty did not make any responses when the Marble roll was delivering marbles and Jaffas™.

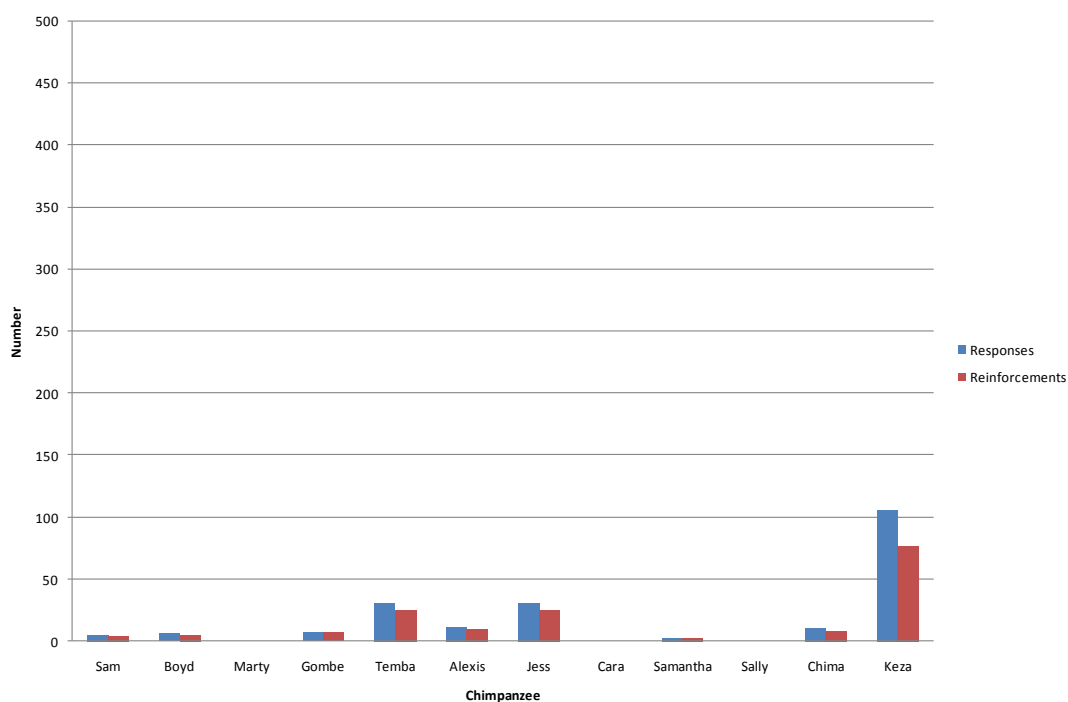


Figure 5.30. Total number of responses made and reinforcers gained by each individuals of the chimpanzee group in experimental sessions of Experiment 5 with the Marbleroll enrichment. Individual chimpanzees are arranged in order of sex, males on the left and then age within each sex group, oldest on the left.

Individual Responses Across Enrichment Items

The individual chimpanzees within the group responded at a different level for different enrichment items. Adolescent male Temba made the highest number of responses during the sessions, making 815 responses in total. Temba responded the most when the Screwfeeder was in place and available to be accessed (494 responses). Juvenile female Keza made the next highest number of responses in total with 777. Adult female Sally with just 6 responses in total across all of the demand

sessions was the chimpanzee who responded the least, closely followed by adult female Cara who made 8 responses on the lever during these sessions. The order of individuals from the one that made the greatest total number of responses to the one that made the least, was: Temba, Keza, Jess, Alexis, Gombe, Chima, Boyd, Sam, Marty, Samantha, Cara and Sally.

All of the members of the chimpanzee group made their largest number of responses with the Screwfeeder enrichment. The order of enrichment items from the one that received the greatest total number of responses to the one that received the least, from most to least, was: Screwfeeder, Marbleroll (delivering coated peanuts), Dipper, Marbleroll (delivering marbles and Jaffas), Musicbox and then the TV/Video.

Discussion

This study describes the zoo-held chimpanzee group's behaviour when provided with the enrichment items and had to operate a lever to turn these items on. The number of lever operations required was increased to assess the group's demand for the items. The amount and type of behaviour exhibited by the group with each item was examined.

Group Behaviour During Sessions When Work Required for Access to Enrichment Items

During the sessions of the demand study with the entire chimpanzee group the members of the group spent most of the time within the visual area of the experimental area individually using the enrichment items that were provided. The amount of time the chimpanzees spent using the enrichment items reduced as FR values increased. Pederson et al. (2002) found that pigs given access to straw during demand testing spent an average of 72% of session time in activities directed towards the straw. However, Pederson et al. also found that the pigs spent more time manipulating the straw as the FR increased. As previously discussed, the time spent with the items may have been reduced as they were provided in an area with other options for activities. The chimpanzees had the option of either participating in those activities or in the activities related to the enrichment items at any time. However, the increase in the required lever operations (price of access to the enrichments) would seem to have resulted in decreases the amount of time the chimpanzees spent

in activities related to enrichment items.

The chimpanzee group spent only a small proportion of the time they were within the experimental area exhibiting behaviours fitting any of the other behaviour categories other than 'use'. When the Screwfeeder was available the group spent a larger proportion of their time using the item together, this was more apparent at smaller FR values. Although sessions with the other enrichments did not show the same level of group members using the enrichment items together, this behaviour was seen more often during sessions with lower FR values. This result reflects the individual demand for items. As the response requirement increased the number of subjects willing to pay that price reduced and hence there were fewer opportunities for subjects to be sharing in the use of the enrichment items. This was shown by the reduced number of subjects using the enrichment items at higher FR values. Pederson et al. (2002) also found that the level of FR affected several results regarding the percentage of time spent performing some behaviours. However, no other studies have explored demand in a social setting and the associated social behaviour thus no comparison with other research can be made.

Individual Chimpanzee Behaviour

Although the group spent a relatively small amount of time engaging in behaviour relating to the other behaviour categories, adult male Boyd, adult female Jess, juvenile male Alexis and juvenile female Keza did spend the most time of the group members using enrichment items while another member of the group was also using the item. Typically the pairing of these interactions was an adult chimpanzee with a younger individual, or the two juvenile members using an item at once. These four individuals also spent the most time of all the group members watching another individual use an item – this was most often a less dominant individual watching a more dominant individual that was using the enrichment item; and using an item while another individual watched – whereby the more dominant subject was most often the user. These findings were similar to those from the Free Access study (Experiment 3) of this current research and thus the discussion of the finding there would apply to the results of this experiment, whereby an individual's ranking had implications on the access they had to the enrichment devices.

Use of Enrichment Items

Adult female Jess was the individual that most often interacted with an item first, closely followed by juvenile female Keza. Six other members of the group were the first to interact, and they were from a cross-section of sex-age groups. All the enrichment items were interacted with before the first twenty minutes of the sessions in which they were included, and most before the first ten minutes. Across all the sessions, most of the use of the enrichment items took place earlier in each session, and the chimpanzee group used the items very little during the third hour of the sessions. In addition to this, the less an item was used by the chimpanzee group, the earlier in the session the use of the item ended. As in Experiment 3, this may relate to findings regarding the increased use of novel items (Menzel, 1971). On the other hand this may have been a result of the timing of the experimental sessions as suggested previously. That is, that the experimental sessions were run late in the day and as the session progressed members of the chimpanzee group settled down to rest for the night (and more individuals did this as time progressed) and there were active fewer chimpanzees to use the enrichment items.

The majority of bouts of use of the enrichments during these sessions were brief, lasting less than a couple of minutes. Some longer bouts did occur. For each of the different enrichments the longest bout of use ranged in length from 4.19 min with the TV/Video enrichment to 28.52 min with the Marbleroll enrichment. The bout of use with the Marbleroll enrichment was by juvenile female Keza and it occurred as the last period of use with this item during FR 1 of Series A. This finding was similar that that of the Free Access study (Experiment 3) and thus the discussion had there is applicable here with regards to the affect of the social group behaviour on use. With regards to the social implications for behaviour this would support the finding regarding the long use time by Keza with the Marbleroll enrichment. This bout occurred as the last bout of use in the session, and at a time when the rest of the group were not sighted within the experimental area (or thereafter). Keza (a low ranking individual) was therefore able to use the enrichment item essentially without any influence on her behaviour from other members of the group.

Habituation. The reduction of use of all the enrichment items by the group was correlated with the relative increase in the FR requirements of the sessions. As the

FR values increased, use decreased. A full discussion in Experiment 3 of habituation related to these enrichments would again apply here. A broader discussion of the habituation across procedures will occur in the discussion of Experiment 6.

Individual Chimpanzee Use

When effort was associated with access to the enrichment items adolescent male Temba was the individual to use the most enrichment items the greatest amount out of the entire group. Juvenile female Keza was the individual that used the enrichment items the most overall. This difference was mainly due to the high level of use Keza showed with the Marbleroll item, when it was delivering marbles and Jaffas™. Adult male Marty and adult females Sally and Cara were the individuals that used the enrichment items the least. In terms of association between age and sex categories and use of the enrichment items, the younger members of the group, of both sexes, used the items the most and the adult members, of both sexes, the least. Although an adult female, and the only hand-reared individual, Jess was an exception to this, being a high user with several of the enrichment items. The reduction of use by the adult members of the group also increased as the value of the FRs increased across sessions. Other demand research has also shown the time spent using commodities has been different for different individuals related to age, e.g., Bloomstrand et al. (1986). As in the Free Access study (Experiment 3), during this experiment the adult and more dominant members of the group used the enrichment items earlier in the sessions. As such the discussion of this finding had in the Free Access study is applicable here also with regards to more dominant members of the group gaining access to the items when they sought to and younger, less dominant individuals having to wait until the enrichments were available.

Use Without Reinforcement

Individuals' use of the enrichment items without it being associated with the delivery of a reinforcer occurred at different level with the different enrichment items. With the items that the group used the least (the Musicbox and the TV/Video enrichments) very little use was not associated with the delivery of a reinforcer. However, whilst the items that were used the most showed the highest level of individuals using an item without any associated reinforcement, the item which had the highest level of this was not the item that was used the most. The Screwfeeder

enrichment item was used by the chimpanzee group the most but the Marbleroll enrichment, when delivering marbles and Jaffas™, had the greatest level of use not associated with the delivery of a reinforcer. A possible explanation for this may have been that during the operation of the Marbleroll, a food reinforcer (Jaffa™) was delivered only occasionally and never more than 10 times in an hour. However, the Screwfeeder, Marbleroll – delivering coated peanuts, and the Dipper enrichment item made a food component available each time the item was operated. Also, when the group did use the Marbleroll and the use was not associated with the delivery of a reinforcer, the individual that had been using the item was usually the subject that eventually received the reinforcer. This suggests that the individual remained using the item until they received a reinforcer. Whereas with the other two enrichment items that were used the most, individuals did not stay using the item when they did not receive reinforcement or, alternatively, another individual took over using the enrichment item, as shown in the event record data.

Group Preference for Enrichment Items When Work Required for Access

If comparison of total time of use is used as a measure of preference then the chimpanzee group showed a preference for the Screwfeeder enrichment when work was required to access enrichment items. The order of preference from most preferred to least was Screwfeeder; Marbleroll, delivering coated peanuts; Marbleroll, delivering marbles and Jaffas™; Dipper; Musicbox; and the TV/Video enrichment was the least preferred. This ranked preference showed that the foraging enrichments were preferred over the non-foraging enrichments, as in Experiment 3, a finding which is supported by other research . A further discussion of the comparison between the chimpanzee group ranked preference will follow.

Preference Related to Intrinsic Effort, Control and Complexity

Similar to the findings during the Free Access component of this current research (Experiment 3) the chimpanzee group's preference for the enrichment items did not completely reflect the control afforded to the chimpanzee or the inherent complexity of the items. As such the discussion had for that study is equally applicable here.

Group Demand for Enrichment Items

Responses. The chimpanzee group responded the greatest number of times in sessions which included the Screwfeeder enrichment and this enrichment maintained responding to the highest FR values. The group responded the least during the sessions with the TV/Video enrichment item, and this maintained responding to only FR 2. The highest ratio reached has been suggested as a good measure of demand and the findings of this study show that ranking the enrichments via highest ratio would support the free access data.

The first lever operation was within the first 20 min of the session across all sessions, and it was most often within the first 10 min. Again this is supported by other findings related to the use of novel items (Menzel, 1971). At no time in the study did multiple members of the chimpanzee group operate the lever at one time, even though it was possible for them to have done so. This finding is of interest given that a concern in conducting research in a group may be the simultaneous response of subjects and also aggression related to multiple subjects making a response at one time. (These concerns which were considered in undertaking this present research). In this current research neither of these factors were evident. This may be of interest to other researchers planning to undertake demand studies in group settings.

Overall response rates. For the two enrichment items that were used the most, the Screwfeeder and the Marbleroll unit, when delivering coated peanuts, the responding on the response lever peaked during FR 2 sessions (or FR 4 during Series A with the Screwfeeder). The responding that occurred in sessions with the other four enrichment items decreased as the FR values increased. This finding is supported by other research that shows responding to increase as FR values increase and then to decrease with further increases of FR value. Such as Foltin (1991) found in assessing baboons' demand for food. Demand research, such as Foltin's (1991) has explored individual responding, whilst this current research examined the response behaviour of a group of subjects. From these results it could be suggested that group responding was similar to the responding shown in research with single subjects.

Cumulative response rates. As a group the chimpanzees responded at the greatest rate and the most steadily during sessions with the Screwfeeder enrichment. The highest cumulative response rate of the entire study occurred during the FR 4 session of Series A with this enrichment item. In general, the cumulative response rates increased with initial increases in FR values and then dropped markedly down at even higher increases in FR values, and dropped further with each increase in FR value. Also, the lower the FR size the more steadily the group responded and also the longer the group continued to respond in a session. During the sessions with the TV/Video and Musicbox enrichments the cumulative response rate of the group was the lowest at any time during the study. These findings again relate to the preference of foraging items of non-foraging ones. In addition to the results support other research showing an initial increase in response rate and then decrease in response rate for food related commodities.

Differences in Demand for Enrichment Items. In this experiment, the FR values were increased until the chimpanzee group failed to obtain reinforcement in a session, at which time the next series was started at the lowest FR value, and the FR was increased again until no reinforcers were obtained in a session.

When curvilinear demand functions were fitted to the data some of the values of the rate of change of elasticity (parameter a in Equation 3) were large. As a result the initial intensity of demand for these functions (the intercept of the demand function through the y axis) were not close to $\ln(L)$. As there were so few data points for many of the conditions, the demand functions gave high %VAC values, however, the data were not always well described by the curvilinear functions. The curvilinear demand function for the Screwfeeder sessions describe the data well (this item resulted in the most data points) but other data were not so well described. Given that most of the curvilinear demand functions did not provide ‘sensible’ information, P_{\max} values were not useful.

The demand data were better described by Equation 2 (linear functions). The absolute values of the slopes of these functions provided quantitative indices of the demand elasticities. The linear demand function for all the enrichment items had slopes less than -1.0 and so demand for all items was elastic. Studies such as Jensen et al.’s (2004) suggest that both elasticity and intensity of demand functions can be affected by prior deprivation levels and reward durations. Given this, rather than

simply considering the elasticity of demand functions when ranking the importance, intensity of demand may also need to be considered. The rank ordering of the enrichment items (from the most to the least essential) using the demand function slopes gives a sequence - Screwfeeder, Marbleroll-delivering coated peanuts, Musicbox, Marbleroll-delivering marbles and Jaffas™, Dipper. While demand functions could not be fitted for the TV/Video enrichment data as there were too few data points. However, the initial intensity of demand for the items ranks the enrichment in a slightly different order – Screwfeeder, Marbleroll-delivering coated peanuts, Dipper, Marbleroll-delivering marbles and Jaffas™, Musicbox. Of particular note in the comparison of these ranking is that the Musicbox was ranked third to top in the elasticity ranking yet last in the intensity ranking (taking into consideration that a demand function could not be produced for the data for the TV/Video unit). Using this ranking based on elasticity alone as a basis for judgement of the demand for this item would seem counter-intuitive given the relatively low level of responding for access to it by the chimpanzee group.

The slope of the linear demand functions for the data for the chimpanzee group working for access to the enrichment items were similar to those found for commodities in other research. (e.g., pigs for social contact and stimulus change – door opening, Matthews & Ladewig, 1994; pigs for straw, Pedersen et al., 2002). Other studies have shown demand function slopes for food close to zero (Matthews & Ladewig, 1994). Although some of the enrichment items in this study included a food element none of the enrichment items gave demand functions with coefficient values close to zero. A complete comparison of the demand function cannot be made as there were only two enrichments that did not include food, and demand functions could be fitted to the data of only one of these. On the one hand, the linear demand function elasticity from the Musicbox data suggests that this enrichment item was preferred over several of the other food enrichments. On the other hand, the intensity of demand for this enrichment item was the lowest of all the items for which demand functions could be fitted to session data.

The linear demand functions fitted the data for all of the enrichment items well, given the lack of data points. Thus, to enable comparison between conditions, linear demand functions will be fitted to data from sessions in subsequent demand analysis in this thesis.

Individual Differences in Responding for Enrichments. Over the entire chimpanzee group, adolescent male Temba made the greatest number of responses on the operant lever. Most of these responses were made during the sessions with the Screwfeeder enrichment. Juvenile female Keza was second highest operator of the lever. However, Keza received the greatest number of reinforcers over the entire study. This difference was due to the fact the Temba made many more responses during sessions with higher FR values than Keza did. The adult females, Sally and Cara, were the individuals that operated the lever the least during the study. Again, these the findings of this study with regard to individual differences related to age, sex and dominance are supported by other research and discussed more fully in the discussion of the findings of the Free Access study (Experiment 3).

Post-Reinforcement Pauses

As mentioned earlier, in the group setting, the measure of PRP was not valid due to factors relating to the social setting. It was not a reliable measure as breaks in responding on the equipment may have been due to other factors rather than being a reflection of the interest level of the chimpanzees with the enrichment items. Responding or use of items may have been impacted by aggression in the group, or other social group interactions. Also, different enrichment items resulted in different time-consuming behaviour. For example, when a chimpanzee received a Jaffa™ they were observed to move away from the enrichment device and consume the item in a slow and deliberate way - often putting it out in the front of their lower lip so they could see it, and opening the sweet to look at its centre. In contrast, the coated peanut were opened and inspected but the chimpanzees consumed them quickly thereafter. In other research, commodities are similar so direct comparisons can be made of PRPs. In this case, items were totally different – some took longer to eat or to access, so direct comparisons are difficult.

Comparison of Group Behaviour When Given Free Access to Enrichment Items vs. When Work Required for Access

The habituation seen when the enrichment items were provided freely was generally evidenced by a drop in use across sessions with a particular item. Of course the extent of the decrease was different with the different enrichment items.

However, when the items were only available when work was required to access them the level of use of the items decreased in relation to the increase in the FR value. When the second series of FRs was run with each item (Series B) the level of use went back up. With the Screwfeeder, for example this occurred even though the first session in Series B was the seventh session with the item and during the eighth session (FR 2, Series B) the level of use was the second highest total time across all sessions with the item. This finding could suggest that the degree of habituation to the items was reduced by working for them. This suggestion is supported by findings such as that increased complexity of a task decreases the level of habituation shown (Tarou et al., 2004), perhaps working for an item has similar effects to increasing complexity.

*Individual Use of Enrichment Items When Given Free Access vs. When Work
Required for Access*

When no work was required to gain access to the enrichment items the highest user of the items was the juvenile female Keza, followed by the adult female Jess. Of all the members of the group, adult females Cara and Sally used the items the least. Adult females Sally and Cara, along with adult male Marty, were again the lowest users of the enrichment items when work was required to gain access to the enrichment items. When work was required to gain access to the enrichment items the highest user of the items was the adolescent male Temba, who was the eighth highest user (out of a group of twelve) when the items were offered freely. This finding again relates to individual age, sex, hierarchy differences discussed and this specific finding will be discussed more fully in the general discussion of this document.

*Group Preference for Enrichment Items When Given Free Access vs. When Work
Required for Access*

Across all of the sessions during the Free Access study (Experiment 3) and the demand study (Experiment 5) the chimpanzee group (when within the visual area of experiments) spent the majority of the time using the enrichment items individually. Of the few studies that have explored demand testing in a group or social setting, none have examined the time spent in activities, such studies have not allowed for the potential of multiple subjects to respond at one time whilst at the same time

collecting data relating to individual responding for reinforcement. Given this is the case, no comparison with prior research can be made. However, as previously discussed in the Free Access study this finding may suggest that even though the chimpanzees were able to use the items in a social sense their preference was to use them alone. This finding may again be of interest for other researchers contemplating preference or demand research in groups.

As Tustin (1994) suggested, preference and demand measure reinforcer ‘value’ and as such they should be expected to give equivalent measures of reinforcer ‘value’. The order of preference from most preferred to the least preferred during the Free Access study (based on a comparison of the time spent with the items) was Screwfeeder; Dipper; Marbleroll, delivering marbles and Jaffas™ without slides present; Marbleroll, delivering coated peanuts; Marbleroll, delivering marbles and Jaffas™ with slides present; TV/Video enrichment and the Musicbox was the least preferred. The order of preference during the group demand study from most preferred to least (based on a comparison of demand elasticity) was Screwfeeder; Marbleroll, delivering coated peanuts; Marbleroll, delivering marbles and Jaffas™; Dipper; Musicbox; and the TV/Video enrichment was the least preferred. In general the most preferred item, and the least preferred items, in both the Free Access and the demand testing with the group study remained the same. However, there was some change in order of the preference for the foraging items in between. This difference may suggest inherent qualities of the enrichment items impacted on the chimpanzees’ preference for them. That working for the items impacted on the groups’ preference for them. The results of this study would seem to support Tustin’s (1994) view in a general sense (i.e., the rank order of preference for the items and the order of demand for the items was broadly the same), however, some differences were shown with regards to reinforcer ‘value’. As research has suggested (Jensen, 1963) the nature of a foraging task can impact on work for it and this would be supported by the finding of this study. This can be seen in the difference in preference ranking between when the enrichment items were freely available and when work was required to access them.

Enrichment Items in Preference and Demand Procedures: Factors Effecting Enrichment Use

Although the enrichment items utilized in this current research were drawn

from a variety of enrichment classes they broadly fall into the two categories: non-foraging enrichments and foraging enrichments. Such classification is also supported by the chimpanzees' behaviour with the different items.

Non-foraging enrichments. Both the audiovisual enrichment item (TV/Video) and the auditory enrichment item (Musicbox) utilised in this current research were used to a very small degree by the chimpanzee group. This was the case when the items were available at a cost, and also when they were freely available. Previous research has shown high use of such items by captive primates (e.g., Bloomsmith et al, 1990b). Much of the previous research with these enrichment items has been conducted with singly-held individuals (e.g., Brent et al., 1989). This would suggest that the results found in this current research have may their basis in fact that this group of subjects were tested within a social environment - that perhaps in a group the social interactions take up time an animal would spend with an animate object if it were alone. Bloomsmith et al.'s (1990b) testing of an audiovisual enrichment device was conducted within a social group setting and a high level of use was shown. The study, however, was conducted within a laboratory setting. Therefore, this may suggest that it is not only the social setting but the general environment that can influence an animal's behaviour with enrichment items. If not for the restriction on the amount of time individual members were able to be separated from the group and general time constraints in this present research, testing individuals demand for a non-foraging item in isolation may have added to an exploration these findings.

Of course, there may have been qualitative features of these enrichment items which were the reason for the group's lack of interest in them. The TV/Video enrichment was the only item that was not physically assessable (interactive) in any way to the chimpanzees. Previous research has suggested that control and complexity - most often in the form of destructibility - are highly preferable attributes of enrichment items (Mench, 1998; Sambrook & Buchanan-Smith, 1997; Videan et al., 2005). However, the TV/Video enrichment lacked these features - other than the control of its operation afforded during the demand testing sessions. As discussed, it may have also been that the videotape content was not 'meaningful' for the chimpanzees. This may have also been true for the Musicbox enrichment. This enrichment did include elements of control and complexity (although not destructibility). However, the different musical tones and choice of music (pop group

Wham's "Wake Me Up Before You Go Go") may not have been preferable to the chimpanzees in this current research. Preference testing of similar devices with different types of auditory stimulation, or video tape content, would add to the judgement of the demand for these types of enrichment. This would clarify whether it is the content of the enrichments or the devices themselves which is related to the 'value' of the item to animals.

Foraging enrichments. The preference found for the foraging enrichments over the non-foraging enrichment items for the chimpanzee group supports the findings in other research. This has included primate preference for foraging devices over simple food presentation (e.g., Holmes et al., 1995) and for food enrichments over other forms of enrichment (e.g., Vivian, 2001).

Contrafreeloading, as discussed, has been described as a behaviour whereby an animal works for food even though there is free food present (Inglis et al., 1997). Some of the behaviour evident in this current research suggests the presence of contrafreeloading. Although the sessions of group testing, both Free Access and Demand, were begun after the group had had half an hour to consume the bulk of their regular evening meal, there was often many food items from this meal still available at the time the sessions were begun. The results of this study show that in most sessions, use of the enrichment items took place more towards the beginning of the sessions, at a time when 'free food' was available. This was the case even when the enrichment devices were only available at a cost. This would suggest that working for the food may have been rewarding for the chimpanzees in this research.

In exploring the influence of the established factors which affect the level of contrafreeloading performed by animals, prior training would have had little influence on this behaviour. The chimpanzees had had experience with all of the items during the introduction and training periods of this current research, prior to testing. In terms of food deprivation, the chimpanzees had no reduction in their daily diets to partake in this current research. In terms of required effort, the foraging items that required the least effort, in terms of work required to operate the enrichment to generate a food item, were not the most preferred (as previously discussed). The effect of stimulus change and environmental uncertainty were not a factor in this present research. Inglis et al. (1997) suggested that rearing animals in sensory deprived conditions show increased levels of contrafreeloading. In terms of sensory

experiences, all members of the chimpanzee group were reared and held in a relatively sensory-rich setting.

White's (1959) suggestion that contrafreeloading is a form of controlling and modifying of the environment by an animal, that is in itself reinforcing, may have been evident in this current research. This suggestion is strengthened by the research that shows enrichment items that afford control are often preferred. Of course the nature of the foraging task may have been reinforcing itself, as suggested by Jensen (1963). The preference for different enrichment items, the level of use of the items and the level of work to gain access to the items may have had their basis in the inherent qualities of the foraging enrichment items - whether that was operating the slides on the Marbleroll or using a tool in the Dipper enrichment.

To ascertain exactly what features were the basis for certain enrichment items to be preferred over other items, used more, more contrafreeloading behaviour to occur, more work to be done to gain access to an item, further research would need to be conducted. Each variable of each item would need to be explored, adjusted and tested to further understand the nature of the preference. However, as the aims in the provision of enrichment items to captive animals are the supply of items that are of interest and benefit to the animals, efforts may be better placed in empirically assessing what these are rather than 'why' initially.

As Bateson (2004) suggested, what animals prefer may not always be in their best long-term welfare interests. This relates to the findings of Free Access study in this current research which showed that the chimpanzee group preferred the Screwfeeder enrichment above the other available enrichment items. However, during the group demand study of this current research, while this item was still the most preferred (based on a ranking of the demand functions for the items), the demand for this enrichment was shown to be elastic, and as such could be seen to be as a luxury. This finding is supported by the association of increased intake of seeds in primates' diet and the increased level of coprophagy (Fritz et al., 1992). Therefore, it could be suggested that the assessment of animals' demand for items may be a better basis for the provision of commodities than simple judgments of preference. Although, as some demand research has shown, even these results need to be carefully considered with regards to animals overall well-being (Paronis et al., 2002).

Novelty was not a factor in the use or preference of the chimpanzee group between the different enrichment items as the group had experience of all of the

items prior to testing. However, in terms of the enrichment items in general being novel to the chimpanzees this would depend on when an item loses the novel quality. The items were the newest features in the chimpanzees' enclosure (other than fresh food and everyday enrichments). However, they had had previous experience of the items in testing and training. The operant lever was in place for more than a year prior to the demand portion of this current research. During this time, the chimpanzees had gone from trying to manipulate it often (although fully weighted when first present in the enclosure), to barely ever touching it when nothing else was introduced into the experimental area. At the beginning of each session it could be argued that having an enrichment item available was novel.

In terms of control and complexity, the Marbleroll and the Dipper enrichment items offered a large degree of these factors. However, they were not the items most preferred by the chimpanzee group. The Screwfeeder was both the most preferred item (in terms of the time spent using it) and the item the group and individual subjects (while in the group setting) had the highest demand for. This item included a food element, previously found to be more preferable and food being the commodity for which animals show the greatest demand for. However, three of the other enrichment items also included a food element and in the context of control and complexity as enrichment characteristics, the Screwfeeder was not the item which provided the greatest level of these. Other research has shown that enrichment items that were more controllable were preferred over items that were not by macaques (Markowitz & Line, 1989; Sambrook & Buchanan-Smith, 1997) and chimpanzees (Videan et al., 2005). These findings may again have been due to the setting in which the research was conducted, and the species of subjects the research was conducted with.

Conclusion

This study was successful in testing the demand of chimpanzees for enrichment items while socially-housed. The results showed that as the price increased for the access to the commodities the consumption decreased. The chimpanzees showed elastic demand for all of the enrichment devices, but to varying degrees between items. The enrichment items could be ranked in terms of the chimpanzees' demand for them. This ranking differed slightly depending on whether the elasticity of demand was considered alone or the intensity of demand was also considered. The

amount of use of the enrichments without the delivery of a reinforcer was shown to increase as the value of the FRs increased. This may have related to the social setting of the testing. PRP times were shown to be a poor measure of demand in a group setting given the impact of a variety of factors on the measure.

The findings suggest that individual members within the chimpanzee group had different levels of demand for different enrichment items, and that individual demand differed from those of the group in general. Some of these differences related to age and social hierarchy factors, such as younger members of the group using, and having a higher demand, for the enrichment items. A comparison with findings from other research would suggest that the setting (both physical and social) of demand testing has an impact on animals' demand for resources. This finding is supported by other research on demand testing with animals.

In the comparison of the chimpanzee group's preference for the enrichment items and their demand for the items the ranking of both were very similar, with some difference in the order of some of the mid-ranked foraging enrichments. Some of these differences may relate to the nature of the enrichment task altering the animals' demand for it.

Foraging enrichments were both the most preferred items and the items the group had the highest demand for in comparison to the non-foraging enrichments. This 'value' of these items, as shown in the ranking of them, did not appear to relate to considerations of intrinsic effort, complexity or control. A further exploration of the features of the enrichment items would be needed to provide more information as to the grounds of rankings found in this research.

When the items were available both freely and at a cost to the group the members of the group were shown to spend by far the most time using the items alone. This was the case even though they were free (in terms of the experimental set-up) to use the items together. This may suggest social, especially hierarchal, influences on behaviour in this present research. The majority of the use in both procedures was in brief bouts, which may have also been related to social pressures within the group, or the availability of other alternative activities in the setting. The items were used more during the earlier portion of the sessions in both procedures; this may have been due to the novel aspect of the item or the timing of the sessions.

While the preference procedure was able to provide information as to the basic ranking of the items the demand testing showed the chimpanzee group to have elastic

demand for the enrichment items. Therefore, this could lead to a judgement that the items were 'luxury' items for the chimpanzees, rather than needs. This finding has support based on the role of enrichments in the life of captive animals and on the basis of health and well-being (i.e., too many seeds being associated with coprophagy).

The level of habituation for items was changed when access to the items came at a cost to when they were freely available. This findings could have implications for the provision of enrichment devices. Contrafreeloading was evident in this present research and may have been related to the work itself being reinforcing.

EXPERIMENT 6: CHIMPANZEE DEMAND WITH INDIVIDUALS HOUSED ALONE

This current research sought to explore some individual chimpanzee's demand when this was assessed in the absence of the other members of the group (i.e., in isolation). The intention to compare individuals' responding when in isolation with their responding when they were with the group (extracted from the previous experiments data set) and with the responding of the chimpanzee group as a whole from the previous experiment.

Individual Testing of Demand

As previously discussed (in Experiment 5) almost all operant research with non-human primates has been conducted with singly-housed subjects (within laboratory facilities). It was also pointed out that the social setting can influence behaviour: for example, social facilitation can change behaviour as can competition for resources (Olsson & Keeling, 2002; Olsson & Westlund, 2007). Several studies have shown that animals react differently in behaviour tests when tested in groups than when tested individually (e.g., Visalberghi & Anderson, 1993; Washburn & Rumbaugh, 1991). In an editorial, Dunlap (2002) expressed the opinion that research into animal psychology needed to do away with the 'mythical average animal' and that research should include detail data on an individual's behaviour so that findings are not generalized for animals as a whole. Of course the aim of much research is to establish relationships and rules relevant to wider populations however, individual differences do need to be taken into consideration both for patterns of behaviour and for other measures (e.g., preferences) etc. This current research aimed to explore details of individual behaviour.

Foxall and Schrezenmaier (2006) showed that a measure of demand from a group generally reflected the trend in the data from individual members of that group. They explored demand elasticity and analysed results for the group and for individuals within the group. Their research involved humans and consumer brand choice was the behaviour investigated. The findings included that, when comparing demand elasticities of different product categories, group and individual behaviour showed similar trends and that individual differences in demand elasticities were relatively consistent across time, but not across products.

Pedersen et al. (2002) showed that demand functions obtained from socially isolated animals are not necessarily the same as those from the same animals when not socially isolated. They explored socially housed and socially isolated pigs' demand for food and straw. They found that demand curves for food had steeper slopes when the pigs were tested in isolation, reflecting greater elasticity. They postulated that the isolation may have caused stress to the subjects which caused the pigs' 'motivation' to eat to decrease. Another possible reason, they suggested, was that the social facilitation related to the behaviour was lacking when the companion animal was absent. When testing the demand for straw, the results showed demand functions with similar slopes but the intensity of demand was higher. The pigs obtained more reinforcement at all FR values when tested with the companion animal. The researchers had expected the demand for straw to increase in the absence of social contact. They suggested that the results may have been due to the fact that the social contact the pigs had during sessions was restricted (subjects were in separate pens and could not manipulate each other a great deal). Thus it is not clear whether or not the demand functions found in the previous experiment would be similar if each animal had been tested in isolation.

Practical Constraints on Conducting This Research

As previously discussed, this current research was conducted within a fully functioning zoological facility. Also the subjects utilized were part of a socially-housed multi-male chimpanzee group, thus there were special considerations to be addressed in conducting this experiment. This posed problems for testing the individual chimpanzees.

The exclusion and introduction of individual chimpanzees to and from a social group requires careful control and management to limit negative consequences such as increased aggression (NRC/ILAR, 1998). The researcher was familiar with the subject chimpanzee group's response to such social manipulations. As such, the time for which any individual was to be removed from the group, to partake in any individual testing in this current research, needed to be kept as brief as possible. This was to limit disruption to the social structure and potential aggressive consequences, and disruption to the management of the group by the facility. Also, given that the individuals utilized for this study were to be accessing food reinforcers during sessions of the experiment, consideration to the dietary implications were made when

deciding on the length of the sessions and the nature of the experiment.

Taking these factors into consideration, it was decided that the individual sessions would be conducted with three members of the group. The members chosen would be individuals that reflected high levels of use from the previous experiments, and also individuals that the researcher considered to be at less risk of being targets of aggression upon returning to the group. [Through observation the researcher judged that the adult females (other than Jess) were the individuals at greatest risk of this behaviour]. The sessions for each subject would be conducted over two days for each individual chimpanzee and each session would be one hour long so that the demand research could fit within this time period. Also, given concerns regarding the amount of food individuals could potentially receive over the course of the individual sessions a decision was made to begin the series at FR 2 rather than FR 1. This decision was made in consultation with the zoo staff.

Aim

Following on from testing the chimpanzees' demand for commodities, in this case different enrichment items, whilst held as a group, the aim was to measure the strength of individual chimpanzee's demand for a commodity while the rest of the group was not present but within the same environment in which the group testing was conducted. Individual demand was analysed and the results compared to those found for the group and for the same individuals whilst they were in the group-housed environment.

Method

Subjects

The dynamics of this group of chimpanzees had to be considered carefully in designing for this component of the research. Individual chimpanzees were not able to be separated from the group without careful management and for a restricted period, mainly due to the multi-male structure of the group. Any individual separated from the group for a period could expect to receive particular negative attention on reintroduction to the group. The longer the period the more risk that the individual could be at risk of harm, and as such this time was kept to a minimum.

The individuals selected to take part in this study were those that had been

shown to operate the equipment during previous studies. Proficient users– Temba and Keza and Jess, were all chosen to take part. Details of these chimpanzees are given in Table 1.1. Physically Temba was a particularly strong member of the group with a very muscular build. Jess was also one of the strongest members of the group being the largest individual. Keza was one of the youngest members and hence one of the least strong. However, even though some of the chimpanzees were smaller, all of the chimpanzees were exceptionally strong (when compared to human strength).

The management practice of the zoo was that if any chimpanzee stayed inside the indoor enclosure for the day (i.e., did not go outside with the group in the morning) they were not given any food throughout the day. However, as during the group testing of demand the chimpanzees had had their breakfast meal of the day, during this individual demand testing the individuals they were given breakfast.

Impact on Standard Husbandry Protocol

The procedures applied in this experiment had no impact on standard husbandry protocol for the chimpanzees as outlined in Experiment 1.

Ethical Consent

The procedure and equipment used within this experiment were approved by the Director-General of MAF via the National Animal Ethics Advisory Committee in accordance with the Animal Welfare Act 1999 concerning restrictions on the use of non-human hominids, the University of Waikato Animal Ethics Committee and the Wellington Zoo.

Apparatus and Setting

The apparatus used in Experiment 6 was as shown in Figures 2.8, 2.9 and 2.25 to 2.27. The enrichment item used was the Screwfeeder (Figure 2. 25) The setting was that described in Experiment 2 (Figures 2.4 to 2.6) and indicated in Figure 1.1.

Procedure

The study was conducted during July and August 2006. The Free Access study and the Demand studies of this current research (Experiment 3, 5 and 6) were originally scheduled to be run during New Zealand Daylight Savings periods (but in different years). Given technical delays in conducting this current research, and

management issues with the chimpanzee group, this study needed to be conducted when it was in order to be completed before the chimpanzees' scheduled move. However, as these sessions were conducted during the day the reduced day light periods did not affect this experiment.

Each session ran for one hour (starting at 1000 each day) and the number of responses required doubled each session, i.e., 1, 2, 4, 8, 16, 32, 64, 128 ... The requirement was increased until the breakpoint was reached (i.e., zero reinforcements for two consecutive experimental sessions). The impact on group dynamics and safety concerns were behind the decision to run one hour sessions for this portion of the research.

The lever had a weight placed on it to allow the lever to be operable - 17 kg. Experiment 4 describes how this weight was selected. One enrichment item was put in place. The Screwfeeder (Figure 2.21) was chosen for use in this study due to the group's high level of use of the item while in the group setting during Experiment 3. As previously, a session started by the light above the lever coming on indicating the lever was 'on'. When a chimpanzee pressed the lever down, a set number of times (depending on the session), the indicator light went off, a response beep sounded and the Screwfeeder rotated for two seconds (approximately a quarter turn) and sent out a small amount of sunflower seeds (approximately 20g). Following this, the light was re-illuminated and the lever needed to be pressed the appropriate amount to again gain access to the enrichment item.

Operation of Enrichment

Experimental events were controlled by a computer programme and the internally housed computer unit. The computer and enrichment item were controlled by MEDPC_IV software and interfaces. Programmes were written for the experimental phase.

Access Time to the Enrichment Item

The access time to the enrichment item reinforcement was based initially on educated assumptions as to what seemed reasonable and then through testing and observation with the chimpanzees during the initial trialling of the enrichment items (as described in Experiment 4).

Access to Enrichment Item

The research was conducted in a closed economy so none of the components of the enrichment items were available from other sources outside of the research.

Data Collection

Video Recordings and Behavioural Definitions

A portable Sony Handicam was used to record each experimental session. The operational definitions used to analyse the chimpanzees' behaviours across each session were as described in Experiment 2 and shown in Table 2.2. Behaviours of particular note by individuals were also recorded. The amount of time that there was day light (sunset time) and the general weather conditions for the day were also noted.

Computer Recorded Behaviour

Each experimental session conducted during Experiment 6 was run and recorded by computer programmes run from the internally housed computer unit. The computer was controlled by a programmable interface cabinet and this operated MEDPC_IV software. The programme utilised for the enrichment item (the Screwfeeder) utilised in Experiment 6 was written for the item. The computer recorded events (as defined in Experiment 5) including: session date; FR schedule; first response; responses; reinforcement, PRP, Runtime; Keytime; Total time. The time of any lever movement, response and reinforcement were also recorded.

Data Analysis

Analysis of Video Data

The video recordings were analysed and this provided a measure of the total time the individual interacted with the enrichment as in the previous experiments.

Analysis of Computer Recorded Behaviour

The data for demand functions were log transformed to obtain a linear relation between the number of reinforcers per session and the FR level. Comparison was made between individuals whilst housed alone.

Results

The data analysed here were based on the time any chimpanzee was within the observation area and recorded to be so. Definitions for the recorded behaviour are described in Table 2.2. As the individuals were housed alone categories of Using-together, Using – others watch, Watching other use and Attending – accompanied were not applicable. The data are presented as behavioural category totals for each experimental condition. Details of data for each experimental session are presented in Appendix E. Scales on the figures are the same as in the previous experiments to allow comparisons.

Individual Chimpanzee Behaviour Whilst Housed Alone

The individual chimpanzee's behavioural data for each experimental session are shown in Table 6.1 and Figures 6.1 to 6.23.

Table 6.1

Individual chimpanzee's behaviour (as defined in Table 2.2) during all sessions of Experiment 6. The amount of time (min) in each session an individual was performing each behaviour and the sunset time, temperature and general weather conditions during each session.

| Chimpanzee/ Session Condition | Time Spent Exhibiting Class of Behaviour (min) | | | | | | | Time of First Interaction (min) | Subject First Interacted | Sunset Time | Weather | Temp at 1700hrs |
|----------------------------------|--|----------------------------|---------------------|----------------------|----------------------------|-----------------------|-----------------|--|--------------------------------|----------------|---------|--------------------|
| | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in Area | | | | | |
| | | | | | | | | | | | | |
| Temba | | | | | | | | | | | | |
| Screwfeeder2A | 32.10 | NA | NA | 0.00 | NA | NA | 0.12 | 1.08 | Temba | NA | Fine | 14 |
| Screwfeeder4A | 16.37 | NA | NA | 0.03 | NA | NA | 0.22 | 0.20 | Temba | NA | Fine | 14 |
| Screwfeeder8A | 5.75 | NA | NA | 0.15 | NA | NA | 0.38 | 0.48 | Temba | NA | Fine | 14 |
| Screwfeeder16A | 5.87 | NA | NA | 0.40 | NA | NA | 0.13 | 2.00 | Temba | NA | Fine | 14 |
| Screwfeeder32A | 1.15 | NA | NA | 0.08 | NA | NA | 0.42 | 1.90 | Temba | NA | Fine | 14 |
| Screwfeeder2B | 30.93 | NA | NA | 0.03 | NA | NA | 0.13 | 0.82 | Temba | NA | Fine | 12 |
| Screwfeeder4B | 19.48 | NA | NA | 0.37 | NA | NA | 0.27 | 0.58 | Temba | NA | Fine | 12 |
| Screwfeeder8B | 3.60 | NA | NA | 0.00 | NA | NA | 0.08 | 0.85 | Temba | NA | Fine | 12 |
| Screwfeeder16B | 1.83 | NA | NA | 0.00 | NA | NA | 0.05 | 1.03 | Temba | NA | Fine | 12 |
| Screwfeeder32B | 1.55 | NA | NA | 0.00 | NA | NA | 0.10 | 2.08 | Temba | NA | Fine | 12 |
| Keza | | | | | | | | | | | | |
| Screwfeeder2A | 15.53 | NA | NA | 0.00 | NA | NA | 0.03 | 0.93 | Keza | NA | Cloudy | 11 |
| Screwfeeder4A | 3.53 | NA | NA | 0.20 | NA | NA | 0.08 | 2.85 | Keza | NA | Cloudy | 11 |
| Screwfeeder8A | 0.32 | NA | NA | 0.03 | NA | NA | 0.15 | 2.30 | Keza | NA | Cloudy | 11 |
| Screwfeeder2B | 21.27 | NA | NA | 0.07 | NA | NA | 0.07 | 0.58 | Keza | NA | Cloudy | 12 |
| Screwfeeder4B | 0.47 | NA | NA | 0.00 | NA | NA | 0.40 | 1.02 | Keza | NA | Cloudy | 12 |
| Screwfeeder8B | 0.10 | NA | NA | 0.00 | NA | NA | 0.08 | 1.77 | Keza | NA | Cloudy | 12 |
| Jess | | | | | | | | | | | | |
| Screwfeeder2A | 4.87 | NA | NA | 0.15 | NA | NA | 0.32 | 0.92 | Jess | NA | Drizzle | 11 |
| Screwfeeder4A | 0.18 | NA | NA | 0.00 | NA | NA | 0.03 | 0.62 | Jess | NA | Drizzle | 11 |
| Screwfeeder2B | 0.50 | NA | NA | 0.00 | NA | NA | 0.00 | 3.28 | Jess | NA | Cloudy | 10 |
| Screwfeeder4B | 0.12 | NA | NA | 0.00 | NA | NA | 0.08 | 7.62 | Jess | NA | Cloudy | 10 |

Temba

As shown in Table 6.1 and Figure 6.1 adolescent male Temba used the Screwfeeder the most during FR 2 of Series A, using it for 32.10 min. Across both series use sequentially reduced as the FR increased. Temba spent very little time during the sessions within the experimental area simply present but not interacting in any way with an enrichment item (Just in area). The first interaction with the Screwfeeder by Temba took place very early on in each session (i.e. within one or two minutes).

It was noted that during FR 2 and FR 4 sessions Temba sat by the equipment during the whole sessions, the only breaks away from the equipment were to go to the roof. During FR 8, 16 and 32 session he often sat further away but still looked at the equipment.

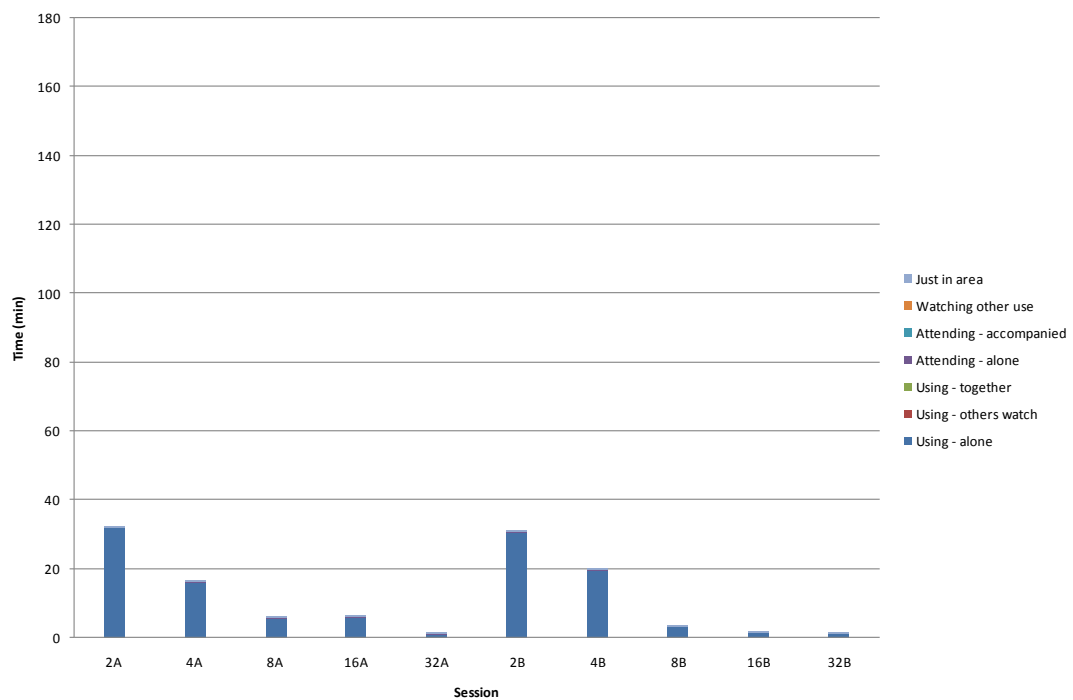


Figure 6.1. Total time that Temba exhibited defined behaviours in experimental sessions of Experiment 6 with the Screwfeeder enrichment.

Keza

Juvenile female Keza used the Screwfeeder the most during FR 2 of Series B,

using it for 21.27 min, as shown in Table 6.1 and Figure 6.1. Across both series use sequentially reduced as the FR increased. Keza spent very little time during the sessions within the experimental area simply present but not interacting in any way with an enrichment item (Just in area). The first interaction with the Screwfeeder by Keza took place with a couple of minutes of the start of a session.

It was noted that during FR 4 and 8 sessions Keza tried using tools on the Screwfeeder. Stuffing paper in the shoot and pulling it out for example. Initially during sessions Keza was seen to spend time walking between the enclosure entrances (which were closed at the time) trying to push them open.

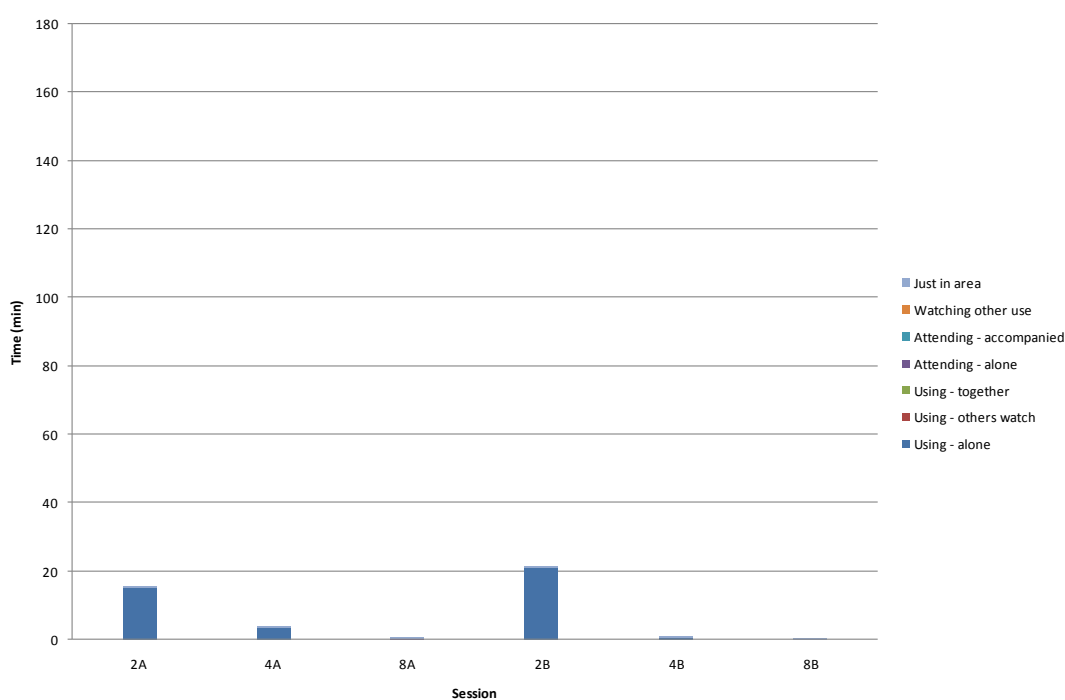


Figure 6.2. Total time that Keza exhibited defined behaviours in experimental sessions of Experiment 6 with the Screwfeeder enrichment.

Jess

Adult female Jess used the Screwfeeder most during FR 2 of Series A, using it for 4.87 min, as shown in Table 6.1. Jess used the Screwfeeder very little in the other sessions although, across both series, use sequentially reduced as the FR value increased. Jess spent very little time during the sessions within the experimental area simply present but not interacting in any way with an enrichment item (Just in area).

The first interaction with the Screwfeeder by Jess was very early in each session.

It was noted that Jess spent most of the session time away from the equipment hunched over, only occasionally looking up.

Individual Use Event Records Whilst Housed Alone

The event records were constructed as described in Experiment 2 :Part 1, However, as the chimps were alone the use behaviour included only the Use-alone category. The times of delivery of reinforcers are also indicated on the figures.

Temba. Figure 6.3 shows Temba's use behaviour for each session over all FR sizes. During FR 2 and 4 sessions Temba used the Screwfeeder continuously throughout the session, and so received frequent reinforcers. Many of Temba's bouts of use lasted longer than a couple of minutes, the longest being 5.82 min. During sessions with FR 8 and above use occurred across the session with long pauses, bouts of use finished without a reinforcer delivery. Temba received three and eight reinforcers with FR 8, one and two with FR 16 and none with FR 32.

Keza. Figure 6.4 shows the use data for Keza. During FR 2 sessions Keza used the Screwfeeder continuously throughout the sessions. However, during sessions with increased FR values, use occurred infrequently and sporadically across the sessions. Most of Keza's bouts of use were brief, lasting less than a minute, however, several longer periods of use occurred, the longest being 7.63 min. Bout length decreased at FR 4, some use was completed without reinforcer delivery, and he received four and two reinforcers with FR 4 and none with FR 8.

Jess. Figure 6.5 show the event records for Jess. Jess used the Screwfeeder infrequently and sporadically even at FR 2. The longest bout Jess used the item was 3.12 min, during FR 2, Series A, but most use was brief. She received five and two reinforcers with FR 2 and none with FR 4.

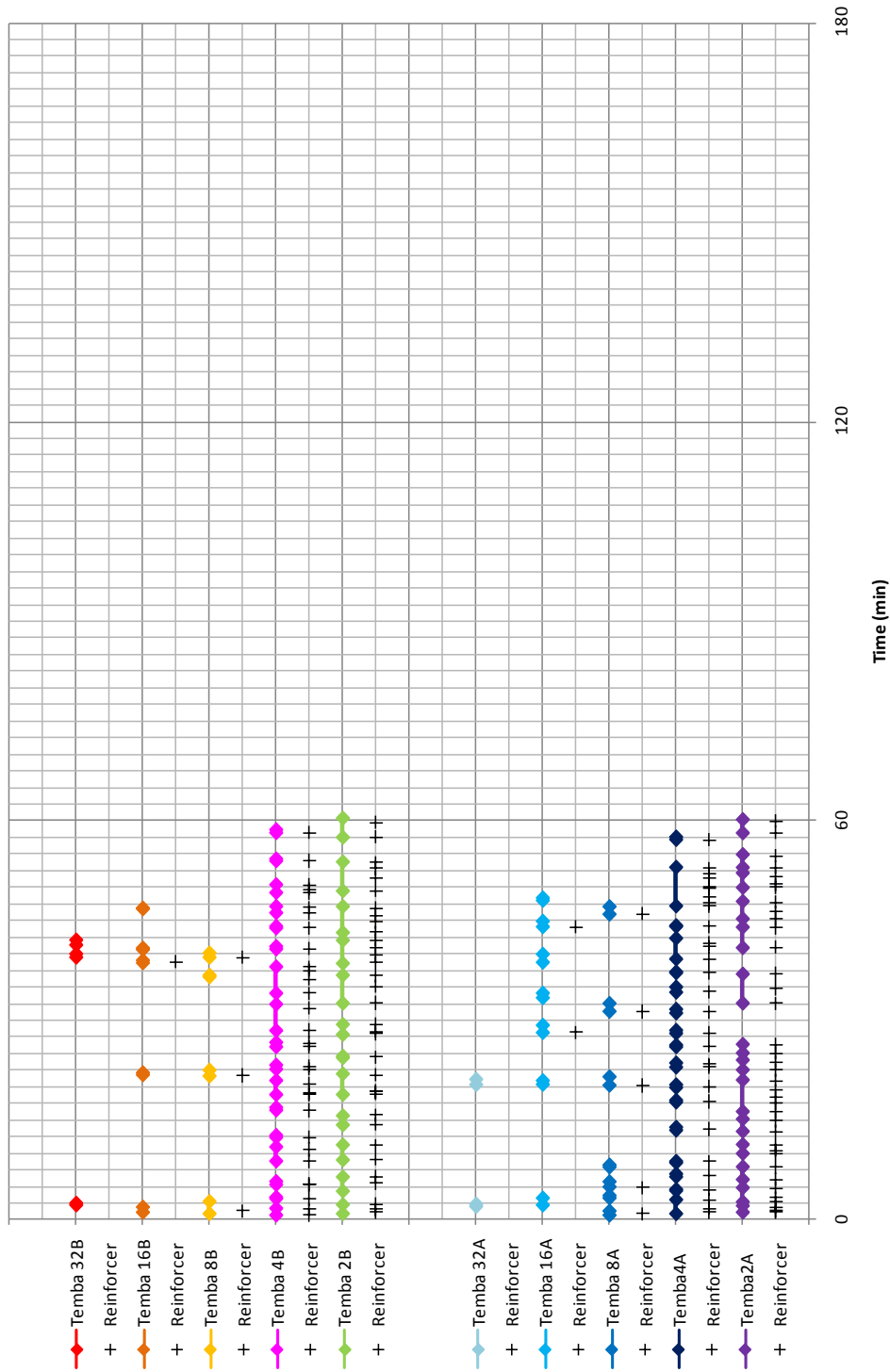


Figure 6.3. Start and stop times for defined behaviours related to Temba's use of the Screwfeeder enrichment item and time any reinforcements delivered across experimental sessions of Experiment 6. Sessions shown on graph of 180 min although sessions only 60 min in length.

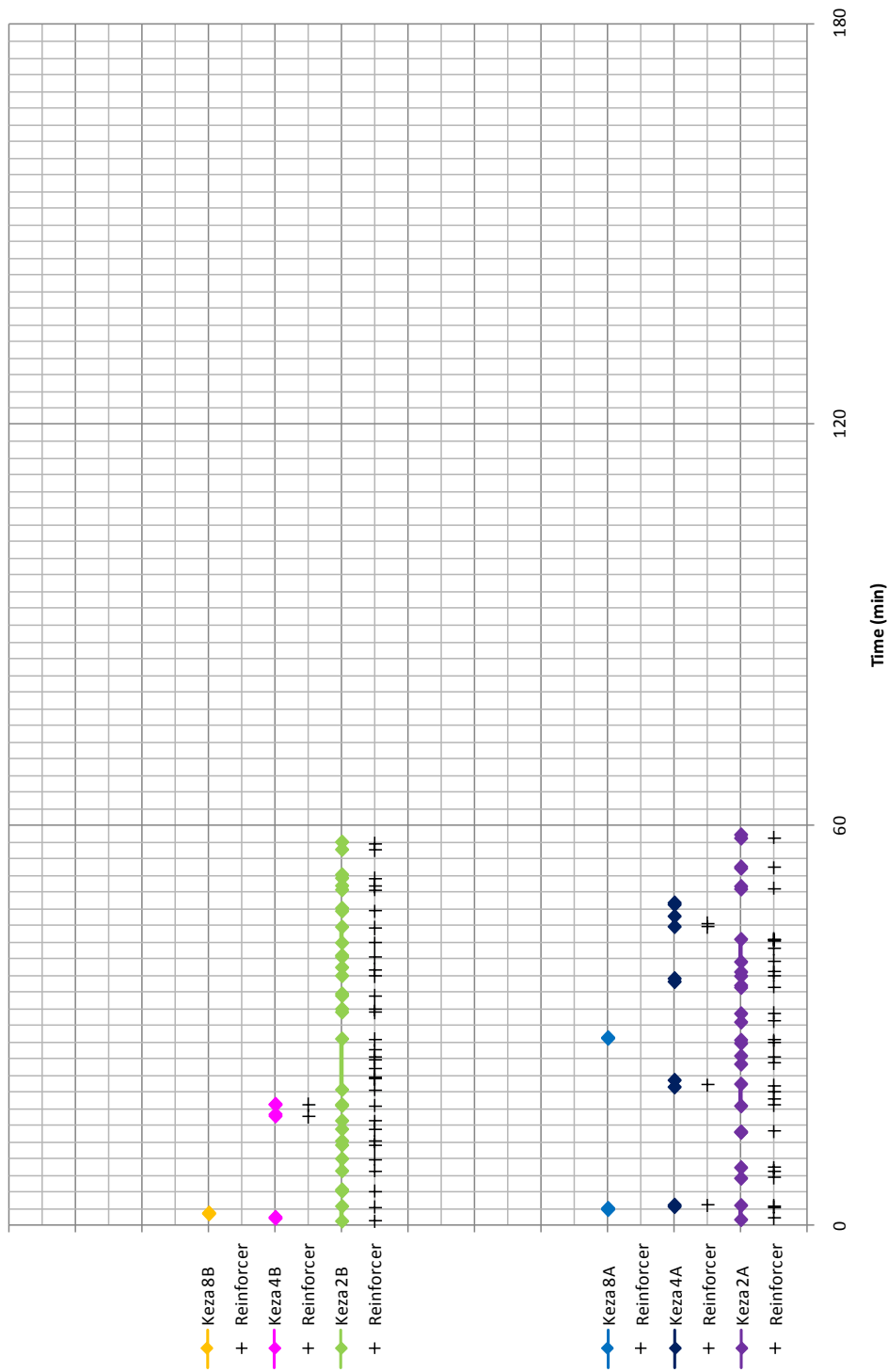


Figure 6.4. Start and stop times for defined behaviours related to Keza's use of the Screwfeeder enrichment item and time any reinforcements delivered across experimental sessions of Experiment 6. Sessions shown on graph of 180 min although sessions only 60 min in length.

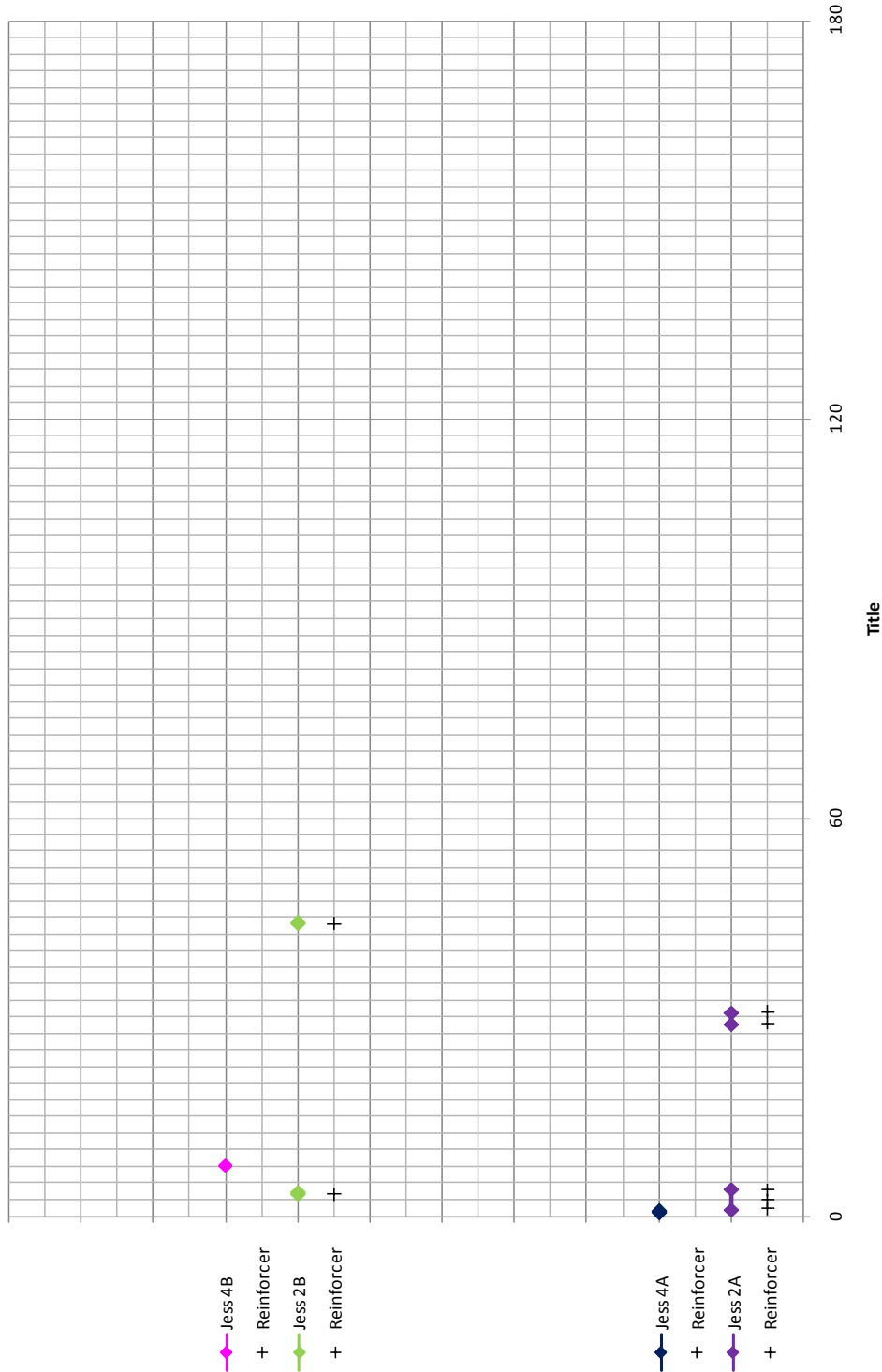


Figure 6.5. Start and stop times for defined behaviours related to Jess's use of the Screwfeeder enrichment item and time any reinforcements delivered across experimental sessions of Experiment 6. Sessions shown on graph of 180 min although sessions only 60 min in length.

Chimpanzee Demand Whilst Housed Alone

The individual chimpanzee's lever use as recorded by the computer (as discussed and defined previously) for each experimental session are shown in Table 6.2 and 6.3 and Figure 6.6 to 6.10.

Table 6.2

Computer recorded lever use of the individual chimpanzees for each session during the Individual Demand study.

| Chimpanzee/ Session Condition | Computer Recorded Event | | | | | | | | |
|-------------------------------------|----------------------------|--------------------|----------------------------|---|---------------------------------------|-----------|-------------------|-------------------|---------------------|
| | First response (min) | Total responses | Total reinforcme nts | Lever Down After Failed Response | Lever Up When Should Be Down | PRP (min) | Run time (min) | Key time (min) | Total time (min) |
| Temba | | | | | | | | | |
| Screwfeeder2A | 1.08 | 74 | 37 | 11 | 5 | 56.33 | 0.13 | 58.78 | 60.00 |
| Screwfeeder4A | 0.90 | 116 | 29 | 9 | 5 | 56.40 | 0.19 | 59.03 | 60.00 |
| Screwfeeder8A | 0.48 | 42 | 5 | 5 | 3 | 6.63 | 5.28 | 59.83 | 60.00 |
| Screwfeeder16A | 2.00 | 38 | 2 | 2 | 6 | 0.11 | 5.79 | 59.93 | 60.00 |
| Screwfeeder32A | 1.90 | 11 | 0 | 0 | 1 | • | 5.81 | 60.00 | 60.00 |
| Screwfeeder2B | 0.82 | 68 | 34 | 5 | 2 | 54.63 | 0.34 | 58.87 | 60.00 |
| Screwfeeder4B | 0.58 | 124 | 31 | 4 | 8 | 56.62 | 0.19 | 58.97 | 60.00 |
| Screwfeeder8B | 0.85 | 27 | 3 | 1 | 0 | 2.28 | 5.68 | 59.90 | 60.00 |
| Screwfeeder16B | 1.03 | 22 | 1 | 0 | 0 | 1.88 | 5.71 | 59.97 | 60.00 |
| Screwfeeder32B | 2.08 | 17 | 0 | 2 | 1 | • | 5.80 | 60.00 | 60.00 |
| Keza | | | | | | | | | |
| Screwfeeder2A | 0.93 | 56 | 28 | 4 | 3 | 57.43 | 0.06 | 59.07 | 60.00 |
| Screwfeeder4A | 2.85 | 18 | 4 | 3 | 0 | 36.16 | 2.09 | 59.87 | 60.00 |
| Screwfeeder8A | 2.30 | 5 | 0 | 0 | 0 | • | 5.77 | 60.00 | 60.00 |
| Screwfeeder2B | 0.58 | 64 | 32 | 2 | 0 | 57.60 | 0.07 | 58.93 | 60.00 |
| Screwfeeder4B | 1.02 | 8 | 2 | 1 | 0 | 41.86 | 1.71 | 59.93 | 60.00 |
| Screwfeeder8B | 1.77 | 2 | 0 | 1 | 0 | • | 5.82 | 60.00 | 60.00 |
| Jess | | | | | | | | | |
| Screwfeeder2A | 0.92 | 10 | 5 | 0 | 0 | 58.60 | 0.03 | 59.83 | 60.00 |
| Screwfeeder4A | 0.62 | 2 | 0 | 0 | 0 | • | 5.94 | 60.00 | 60.00 |
| Screwfeeder2B | 3.28 | 4 | 2 | 0 | 0 | 56.54 | 0.01 | 59.93 | 60.00 |
| Screwfeeder4B | 7.62 | 2 | 0 | 0 | 0 | • | 5.24 | 60.00 | 60.00 |

Individual Responses with Enrichment Item Across FRs

Overall response rate was calculated as the total number of responses made on the lever by each individual chimpanzee divided by total session time excluding the time the Screwfeeder was operative.

Temba. Table 6.2 shows that Temba started responding within two minutes of the start of each session. Temba made his greatest number of number of responses during FR 4 in Series B (124) and the table show there was very little inappropriate

lever use.

Figure 6.6 shows that Temba's overall rate of responding peaked during FR 4 in both series. Rate of responding decreased across further increases in FR. With FR 32 Temba did not respond enough in either series to receive a reinforcer.

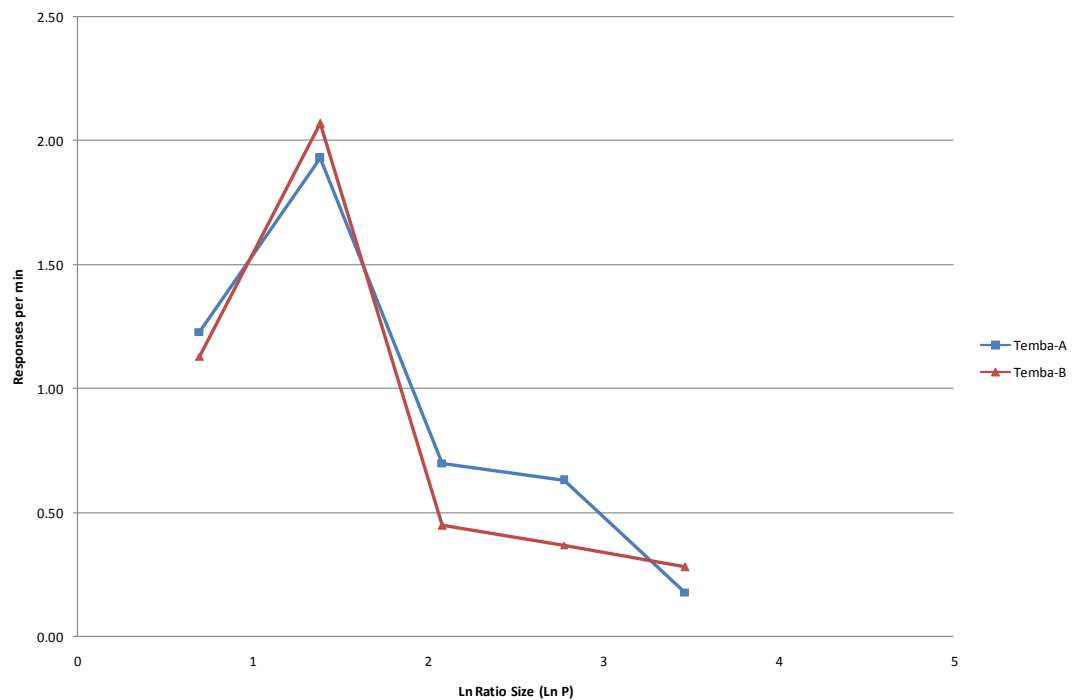


Figure 6.6. Overall response rates (responses per minute) plotted against the logarithms (ln) of the ratio requirements for Temba during sessions in Experiment 6 with the Screwfeeder enrichment.

Keza. Table 6.2 shows that Keza started responding within three minutes of the start of a session. Keza did little responding above FR 2 and there was also very little inappropriate lever use.

Figure 6.7 and Table 6.2 show that Keza responded most at FR 2, 64 responses during series B was her maximum, and her response rate decreased with further increase in FR size.

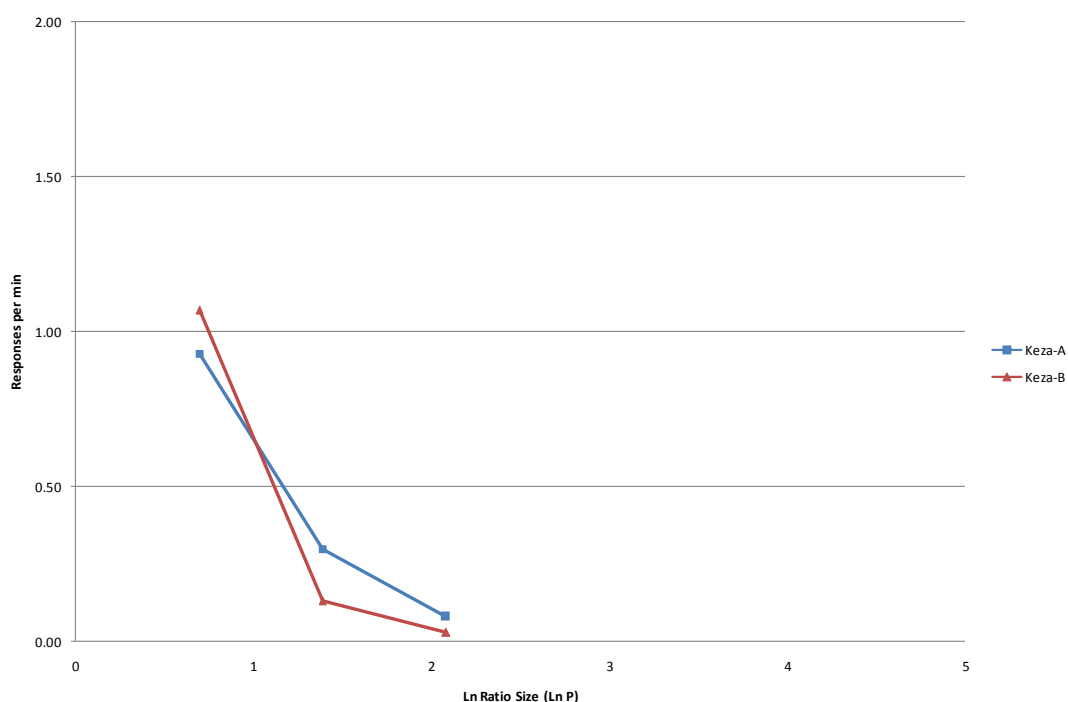


Figure 6.7. Overall response rates (responses per minute) plotted against the logarithms (ln) of the ratio requirements for Keza during sessions in Experiment 6 with the Screwfeeder enrichment.

Jess. Table 6.2 show that although Jess responded on the lever within the first ten minutes of a session, she did very little other appropriate responding and no inappropriate responding. She made more responses during FR 2 in both series than in FR 4. Jess' rates of responding are not plotted, but her response rate was greatest during FR 2 of the first series (A) (with ten responses).

Individual Post-Reinforcement Pauses

As shown in Table 6.2 Temba's PRPs were short at the low FR values and increased greatly during FR 8 of both series, and increased further during the sessions with greater FR values. Keza's PRPs were larger with FR 4 than with FR 2. Jess did not respond enough to establish PRP time changes associated with FR value changes.

Individuals Response Rate with Enrichment Across Sessions With Each FR

Figure 6.8 and 6.9 give the cumulative number of responses as in Figure 5.20 to 5.24. The X-axis is extended to 180 minutes for comparison with those earlier graphs.

Cumulative records for Temba. As seen in Figure 6.8 Temba responded steadily with few pauses in sessions with the Screwfeeder item at FR 2 and FR 4 and continued to respond for the entire length of these sessions. At larger FR sizes Temba paused more between responses and stopped responding before the end of the sessions. This effect was more exaggerated the larger the size of the FR.

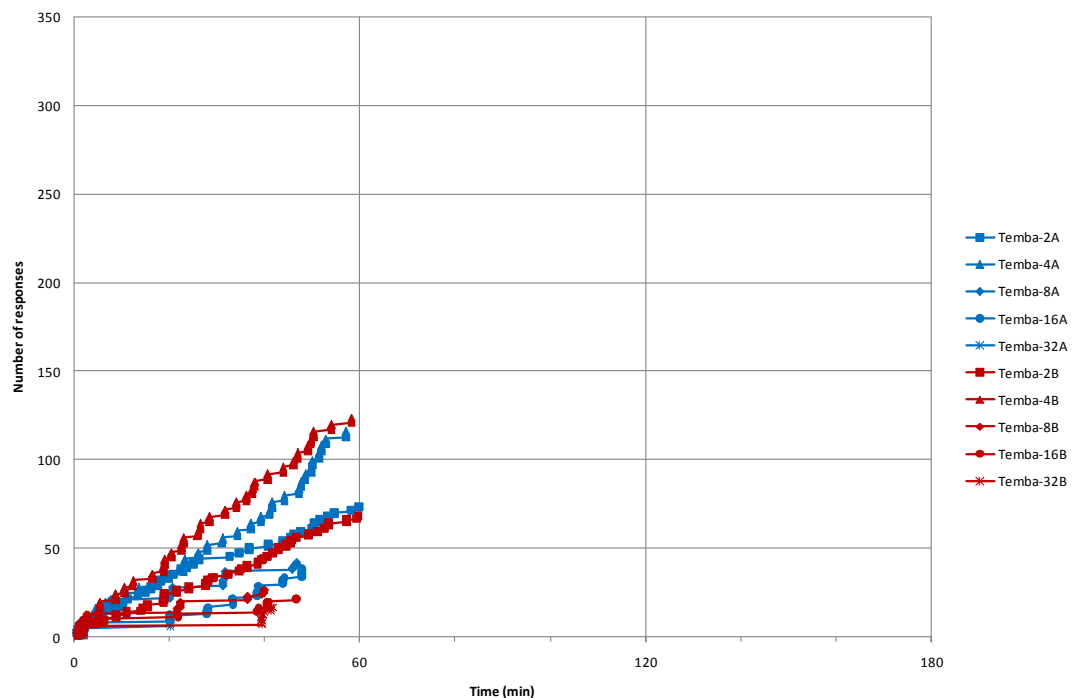


Figure 6.8. Cumulative rate of responding by Temba during sessions of Experiment 6 with the Screwfeeder enrichment.

Cumulative records for Keza. Keza responded steadily during sessions at FR 2 and continued responding for almost the entire length of these sessions. During sessions with larger FR sizes Keza greatly increased pauses between responses and stopped responding earlier in the sessions.

Cumulative records for Jess. Jess did not respond a great deal during the sessions with the Screwfeeder whilst held alone, as such her rate of response was very low and only registered for FR 2.

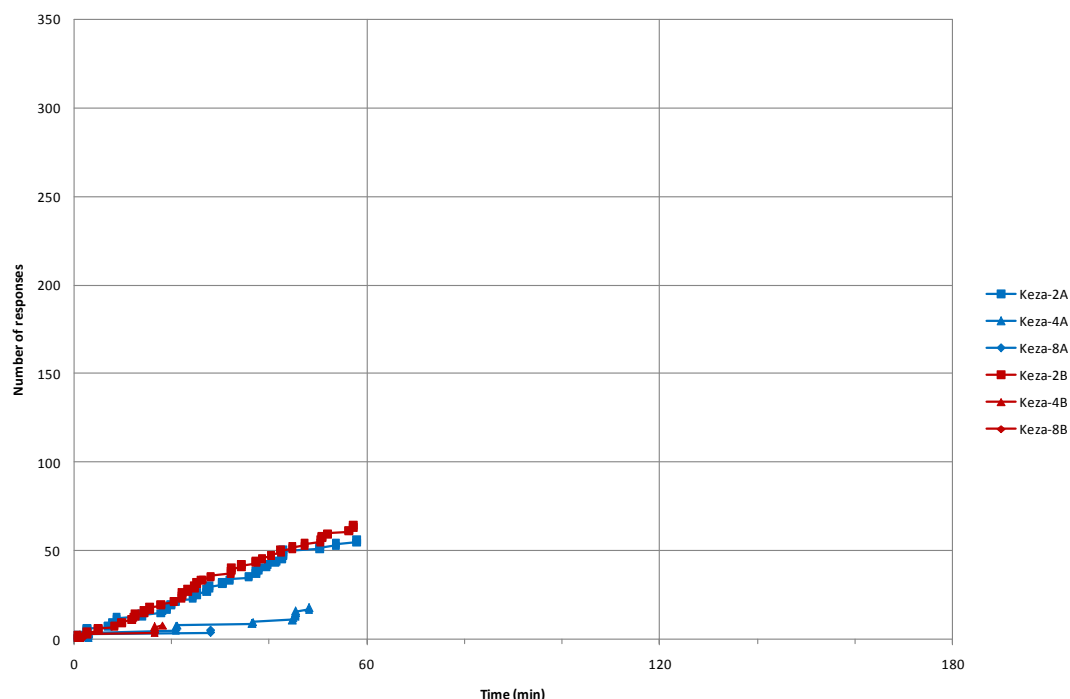


Figure 6.9. Cumulative rate of responding by Keza during sessions of Experiment 6 with the Screwfeeder enrichment.

Individual Demand for Enrichment Item

Figure 6.10 shows the consumption rate plotted against FR size as in Figure 5.26. Linear demand functions (Equation 2), fitted to the data by the method of least squares, are shown. There were two few data point for Jess to fit demand functions. For Temba and Keza the parameters, the percentages of the data variance the functions account for [% VAC], and the standard errors of the fits are given in Table 6.3. The demand functions describe the data well (with high % VAC values and low standard error values).

The four demand functions had negative slopes (b values). Those fitted to Temba's data were shallower than those from Keza's. The intensity of demand varied from 0.88 (Series B, Temba) to 2.18 (Series B, Keza).

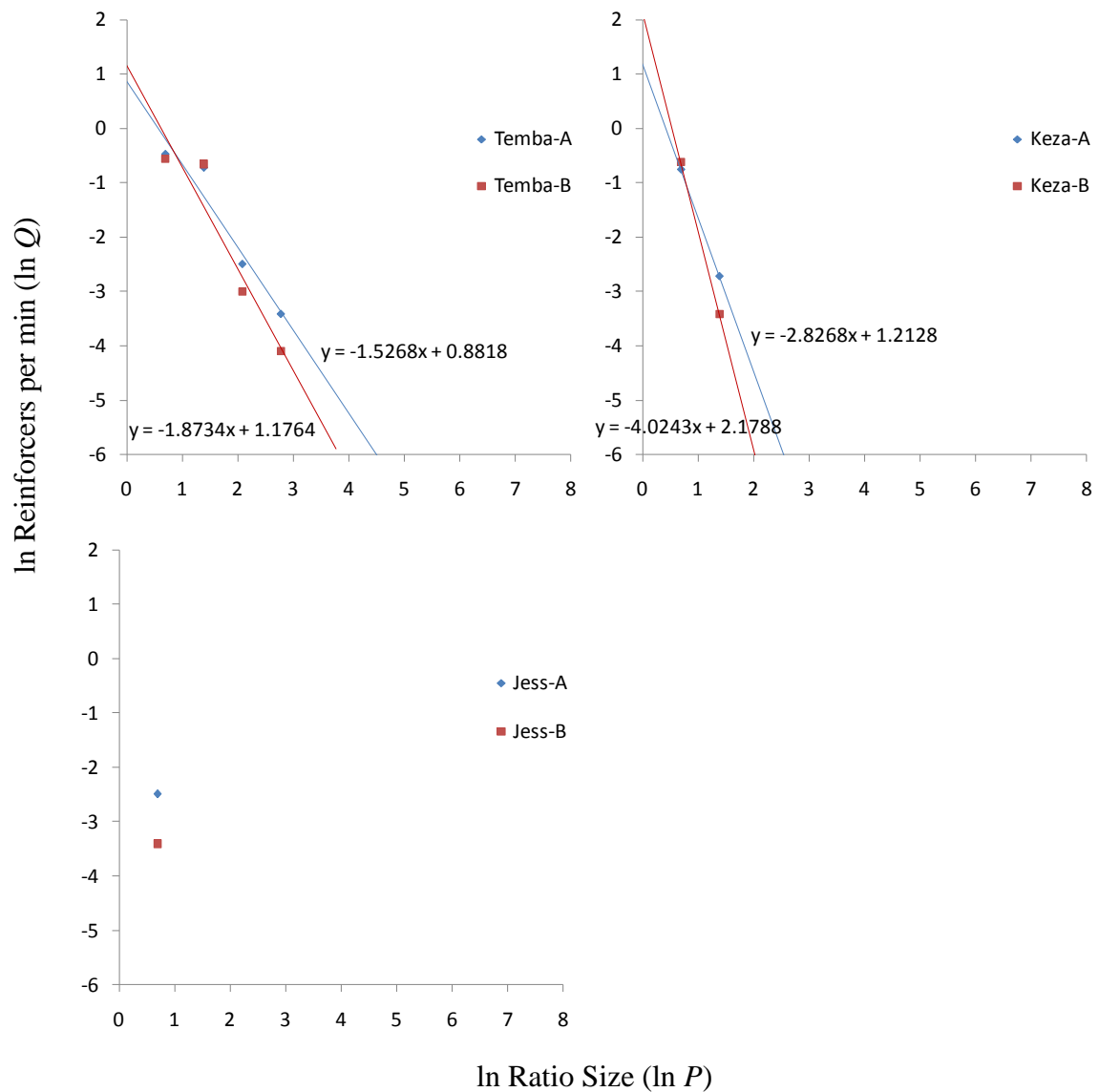


Figure 6.10. The natural logarithms of obtained reinforcement rates plotted against the natural logarithms of FR schedules for individuals Temba, Keza and Jess for each condition in Experiment 6. The demand functions, shown by the lines, were obtained by fitting Equation 2 to the data.

Individual Chimpanzee's Responses and Reinforcements with Enrichment Item

As shown in Figure 6.11 adolescent male Temba was the individual that responded the most on the lever to gain access to the Screwfeeder enrichment whilst housed alone. Temba responded a total of 539 times over all the sessions. He was also the individual to receive reinforcers on the greatest number of occasions (142). Jess made the fewest responses and received the fewest reinforcements while housed alone.

Table 6.3

The parameters $\ln(L)$, and b of the lines fitted by Hursh et al.'s (1988) Total consumption equation (Equation 2) to the log consumption rate versus log FR data for the sessions of Experiment 5. The percentage of variance accounted for by lines (% VAC) and the standard errors of the estimates (se) are also shown.

| Condition (Subject/Series) | Parameters | | | |
|-------------------------------|------------|-------|------|--------|
| | $\ln(L)$ | b | se | % VAC |
| Temba-A | 1.18 | -1.87 | 0.47 | 93.40 |
| Temba-B | 0.88 | -1.53 | 0.45 | 90.60 |
| Keza-A | 1.21 | -2.83 | 0.00 | 100.00 |
| Keza-B | 2.18 | -4.02 | 0.00 | 100.00 |
| Jess-A | NA | NA | NA | NA |
| Jess-B | NA | NA | NA | NA |

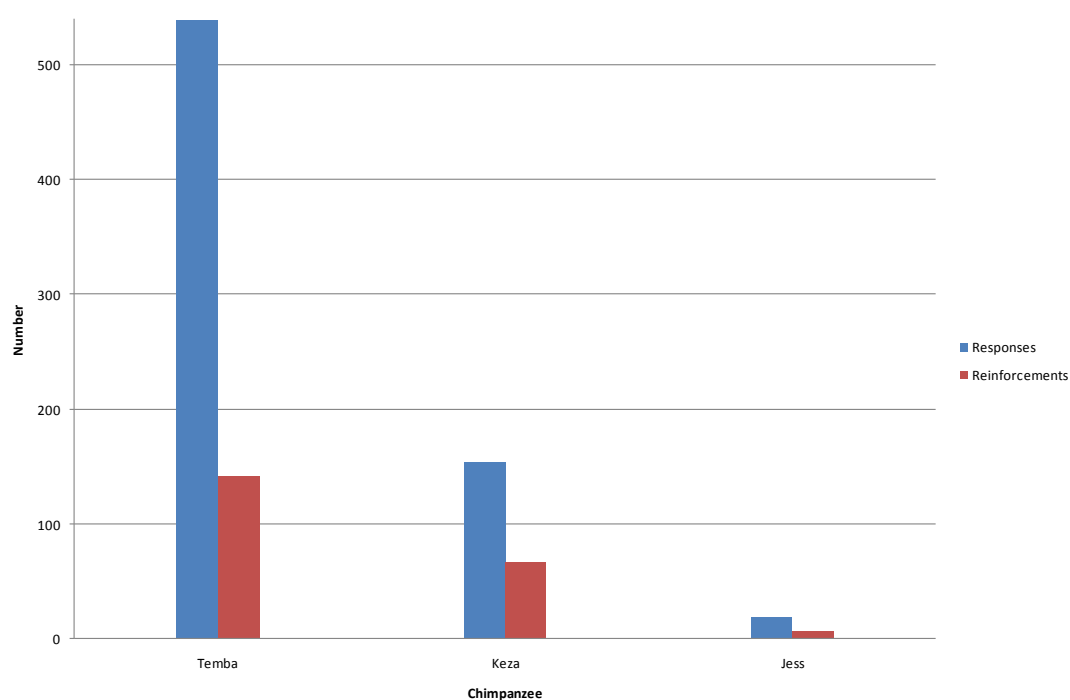


Figure 6.11. Total number of responses made and reinforcers gained by each individual in experimental sessions of Experiment 6 with the Screwfeeder enrichment.

Discussion

This study examined the behaviour of three socially-housed but individually tested zoo-held chimpanzees when they were held separately from the group and provided access to an enrichment item (the Screwfeeder) and required operate a lever for access the item. The work requirement was increased to determine each animal's demand for the enrichment item.

Individual Behaviour During Sessions When Work was Required for Access to Enrichment Items

Since the three chimpanzees were tested whilst held alone only three of the categories of behaviour used in the previous experiment applied here. Each of the chimpanzees spent most of their time in sessions using the Screwfeeder. Very little time was spent by the individual chimpanzees simply present in the area (not interacting in any way with the enrichment item) therefore having the items present did not result in a change in this behaviour.

Use of Enrichment Item

During all of the sessions of Experiment 6, the individual subjects interacted with the Screwfeeder within the first five minutes of the session, again reflecting findings related to animals use of novel objects (Menzel 1971). Temba used the Screwfeeder for the largest amount of time of the three chimpanzees. For each chimpanzee, the FR 2 sessions were when the greatest amount of use of the enrichment item occurred, the lowest FR value in the isolated demand testing. The level of use of the item by Keza during the FR 2 to FR 8 sessions was similar to Temba's use in the FR 4 to FR 32 sessions. Jess's use of the item was minimal across all sessions of this experiment. For all of the individual chimpanzees tested in isolation, as the price of the access to the enrichments increased their consumption decreased.

Temba's use of the Screwfeeder was continuous during the entire sessions with FR values of 2 and 4 and Keza for FR 2. During the other sessions (and for sessions in which Jess was the subject) the use occurred sporadically throughout the length of the sessions, but slightly more towards the start of the sessions. Most of the bouts of use were brief in all the sessions of this experiment. However, many of Temba's bouts of use lasted longer (the longest being 5.82 min). These longer bouts occurred

more at smaller FR values. Keza also had some longer bouts (the longest being 7.63 min) and again this was during the smaller FR value. Jess used the Screwfeeder very infrequently during Experiment 6 but the long bouts of use she did have were again during the lower FR sessions. That bouts of use were brief even though the rest of the social group was not present during testing was of note. However, for a social animal which is normally housed-socially the impact of being apart from the group may be evident in their behaviour, as supported by other research (Jensen, Pedersen & Ladewig, 2004; Schapiro et al., 2003). In this current research the effect of the separation from the group would seem to have been different for different individuals.

Habituation

The reduced use of the enrichment item by individual chimpanzees was correlated with the relative increase in the FR requirements of the sessions, as the FR values increased, use decreased. However, Jess showed a minimal increase in use when the FR value was again at two during Series B. A discussion of the reduction of use of foraging items in this current research had in Experiment 3 is equally applicable here.

Use without Reinforcement

A minimal amount of use was completed in this experiment without a reinforcer being delivered. When it did occur, it was during sessions with higher FR values. Given that the subjects were tested in isolation there was no opportunity in this study that another individual would be able to receive reinforcement that they had not worked at all, or mainly, for. This finding would support the suggestion that the occurrence of use without the delivery of reinforcement shown in the demand testing in the group (Experiment 5) was related to testing in social environment, as discussed.

Individual Demand for Enrichment Item

Responses. Temba responded enough to increase the FR value of sessions to 32 (for both series). However, Keza only responded enough to result in the FR sessions increasing to 8 and Jess only responded enough to result in the FR sessions

increasing to 4. As discussed previously, the highest ratio reached can be used as a measure of demand. In this case Temba would appear to have had a much greater demand for the Screwfeeder enrichment than the other individuals used in isolated testing. The lever was lifted for the first time within the first eight minutes of each session of Experiment 6, and for sessions with Temba and Keza, within the first three minutes. This again is supported by other research regarding the use of novel objects.

Overall response rates. For Temba overall response peaked during the FR 4 sessions and then decreased in subsequent increases in FR values. This finding is supported by other research that shows responding to increase as FR values increase and then to decrease with further increases of FR value (Hursh, 1984). However, both Keza and Jess reduced their rate of responding through each increase of FR value.

Individual Post Reinforcement Pauses. Just in other research (Ferster & Skinner, 1957), the PRP time, shown during Temba and Keza's responding during FR schedule of reinforcement, increased as the size of the ratio increased and the their rate of responding after the post-reinforcement pause decreased as the size of the ratio increased.

Cumulative response rates. Temba and Keza responded steadily across the entire length of the FR 2 sessions with the Screwfeeder. Temba continued this during the FR 4 sessions. During sessions with larger FR sizes both increases pauses between responses and stopped responding earlier in the sessions. Jess's responding was too low to make a judgement on her cumulative rate of responding. Therefore, overall the cumulative response rate pattern was similar to the groups with the Screwfeeder item, however the effect was shown to be slightly different with each individual.

Individual differences in demand for the enrichment item. In this experiment, the FR values were increased until each individual chimpanzee (being singly-tested) failed to obtain reinforcement in a session, at which time the next series was run starting at the lowest FR value and again increasing this level until no reinforcement was obtained in a session. The demand functions fitted to the data of sessions for

individuals tested in this experiment differed between the different individual chimpanzee subjects. The functions for both Temba and Keza showed elastic demand for the Screwfeeder during testing in isolation. However, the slope of the demand functions differed. The slopes for Temba's sessions were shallower than Keza's were. Keza showed stronger intensity of demand during testing in isolation than Temba. The level of responding by Jess during testing in this experiment was not enough to enable demand functions to be fitted to the data. These findings will be discussed further in a comparison of demand between procedures, which follows.

*Comparison of Individual Behaviour When Enrichment Item Freely Available vs.
When Work was Required for Access to the Enrichment Item When Tested Alone vs.
When Tested In Social Group*

Each individual chimpanzee's behaviour differed across each of the different procedures of this current research, as shown by Figure 6.12. The figure is based on data from Experiments 3, 5, and 6, and reproduced here to allow for comparison. Temba spent less time using the Screwfeeder when the item was freely available (FA) in a social setting than when work was required to gain access to it in a social setting (FR(G)). Temba's total use time was largest when the work to gain access to the enrichment was done in isolation (FR(I)). Of the time Temba spent using the Screwfeeder, the highest proportion was spent using the item alone across all the settings. Keza used the Screwfeeder enrichment for the most time when work was required to gain access to it in a social setting (FR(G)) and spent the least time using the Screwfeeder when the item was freely available (FA). Keza spent the highest proportion of her time using the item alone across all the settings. Jess used the Screwfeeder for the least time when tested alone and working for access to it (FR(I)). Jess spent almost the same amount of time using it when in the social group and when it was freely available (FA) and when work was required to access the item (FR(G)). However, Jess did spend proportionally more time using the item simultaneous to the use of other subjects when it was freely available.

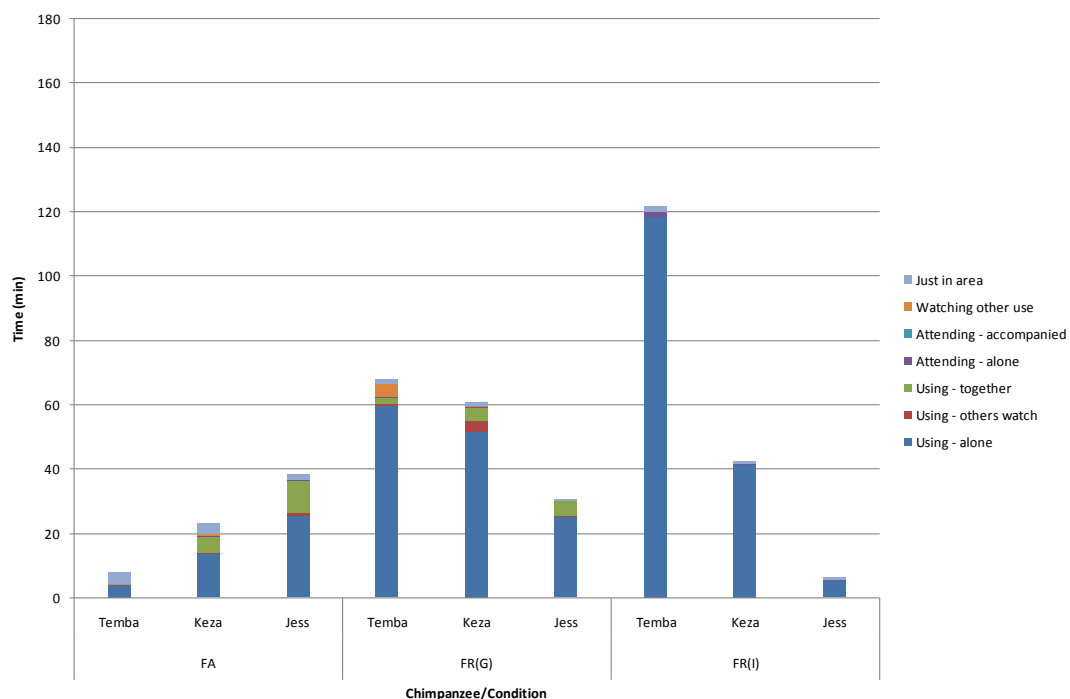


Figure 6.12. Total time that the individual chimpanzees exhibited defined behaviours in first hour of experimental sessions of Experiment 3 and 5 and the hour long sessions of Experiment 6 with the Screwfeeder enrichment.

Individual Use of Enrichment Item

It is also possible to compare the use patterns across the three studies for these chimpanzees. Figure 6.13 shows each of the three individual chimpanzee's use of the Screwfeeder during the sessions of when the subjects had free access to it in a social situation (Experiment 3). Figures 6.14 to 6.16 show the same data from the sessions where work was required in a social situation (Experiment 5) These data are represented here to allow for comparisons to those from Experiment 6.

Temba. Figure 6.13 shows that adolescent male Temba used the Screwfeeder on very few occasions during the first hour of the sessions of Experiment 3, when it was freely available. As Temba performed so few bouts of use during Free Access, no pattern of use can be seen. A comparison of Figure 6.3 (Temba's use during individual testing) and Figure 6.13 (Temba's use during Free Access) and Figure 6.14 (Temba's use during group testing) show that Temba used the Screwfeeder far more when work was required to gain access to the item, both in the social and

isolated setting. Figure 6.3 and Figure 6.14 show Temba used the Screwfeeder when in the group much less frequently and far more sporadically in the first hour of the session than in the hour-long sessions with the enrichment whilst alone. Temba's use occurred at a similar level during this period as the FR value increased during Series A rather than decreasing as it had in both series when housed alone (in fact, using the item the least during that series during FR 2). Temba used the enrichment item more towards the end of the session when housed with the group. Most of Temba's bouts of use were brief, however, some longer bouts did occur, the longest being during FR 8 of Series B of 4.42 min in length. Many instances of Temba's use were completed without receiving reinforcement, more so as FR increased, whilst housed with the group. When housed alone, much less of Temba's use was not associated with delivery of reinforcement.

Keza. Figure 6.13 shows that in general, juvenile female Keza used the Screwfeeder towards the end of the first hour during the sessions of Experiment 3. Most of Keza's bouts of use were brief, but some much longer periods of use did occur during this first hour. Comparisons of Figure 6.4 (Kea's use during individual testing), Figure 6.13 (Keza's use during Free Access) and Figure 6.17 (Keza's use during group testing), show Keza's bouts of use of the Screwfeeder when in the group occurred far more frequently in the first hour of the session than they did in the hour long sessions whilst alone. The exception to this was the FR 2 sessions in which Keza used the item more often and continuously when housed alone. Keza's bouts of use while in the group were balanced between occurring during the beginning of the period or the end of the period. Most bouts were brief, however, some bouts lasted a lot longer, the longest being 12 min during FR 32 of Series A (Keza received no reinforcement during that long bout). As was the case when housed alone, some use was completed without receiving reinforcement, more so as FR increased.

Jess. Figure 6.13 shows no real pattern in the use of the Screwfeeder by adult female Jess during the first hour of the sessions of Experiment 3. During some sessions, Jess used the Screwfeeder very little, however, during one session Jess used it almost continually for the first hour. Comparison of Figure 6.5 (Jess's use during individual testing), Figure 6.13 (Jess's use during Free Access) and Figure 6.18 (Jess's use during group testing), shows that Jess's bouts of use of the Screwfeeder

when in the group were far more frequent in the first hour of the session than in the hour long sessions the subject had with the enrichment whilst housed alone. Jess's bouts of use while in the group were balanced between occurring during the beginning of the period or the end of the period. Most bouts were brief, however, some bouts lasted a lot longer, many occurring during Series A, the longest being 3.6 min during FR 2 of Series A. Little of Jess's use of the Screwfeeder in sessions with low FR values, while in the group, was completed without receiving reinforcement. During sessions with higher FR values some use was not associated with reinforcement. This was also the case when Jess used the enrichment whilst housed alone, although only two different FR values were used utilized during these sessions.

Comparison of Use Across Procedures

Throughout this current research, the majority of the interactions that the chimpanzees had with the Screwfeeder were brief, lasting just a few minutes. This finding is of interest as it was the case across all experimental procedures: when the item was freely available, when work was required both in a social environment and with the subject isolated. If the bouts of use of the item had been brief only in the group testing (both when the item was available freely and at a cost), then it could have been that the social interactions were influencing the time animals chose to spend with the enrichment items. However, given that this pattern of behaviour was also evident during individual testing, the group testing situation was not the cause.

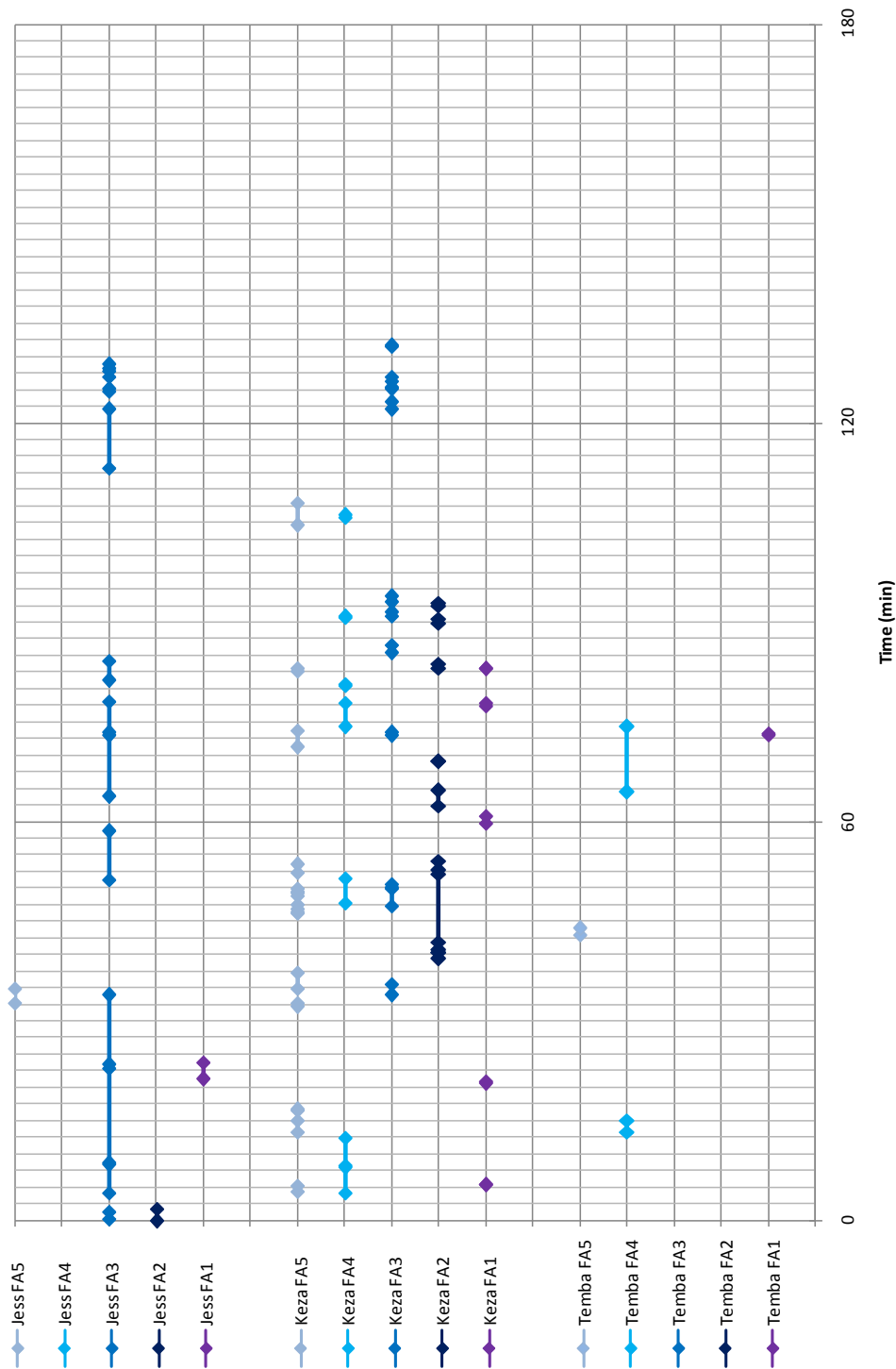


Figure 6.13. Start and stop times for defined behaviours related to Temba, Keza and Jess's use of the Screwfeeder enrichment item across experimental sessions of Experiment 3. No reinforcements are shown, as the Screwfeeder was available throughout the sessions.

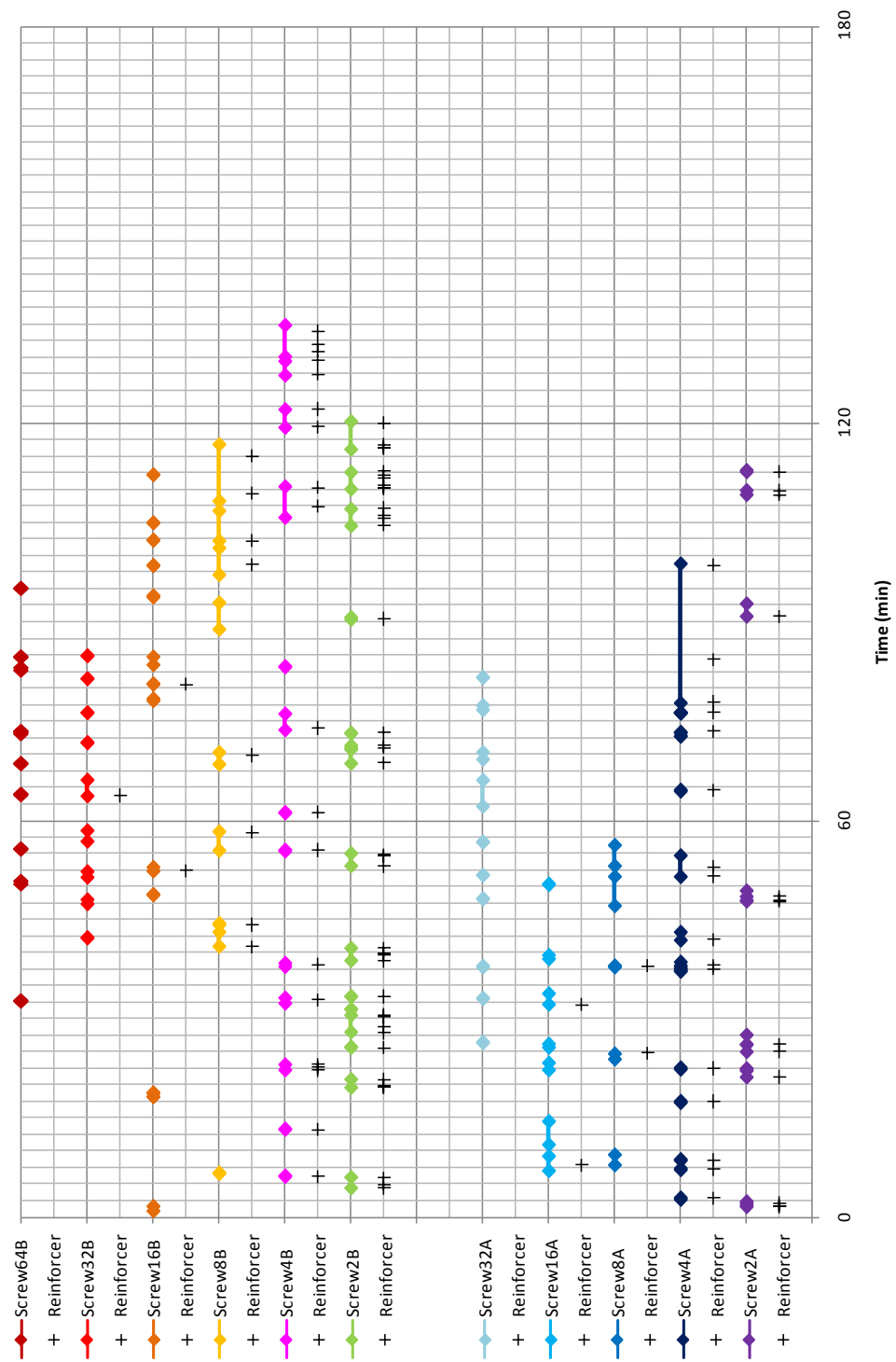


Figure 6.14. Start and stop times for defined behaviours related to Temba's use of the Screwfeeder enrichment item and time any reinforcements delivered across experimental sessions of Experiment 5, whilst with entire chimpanzee group.

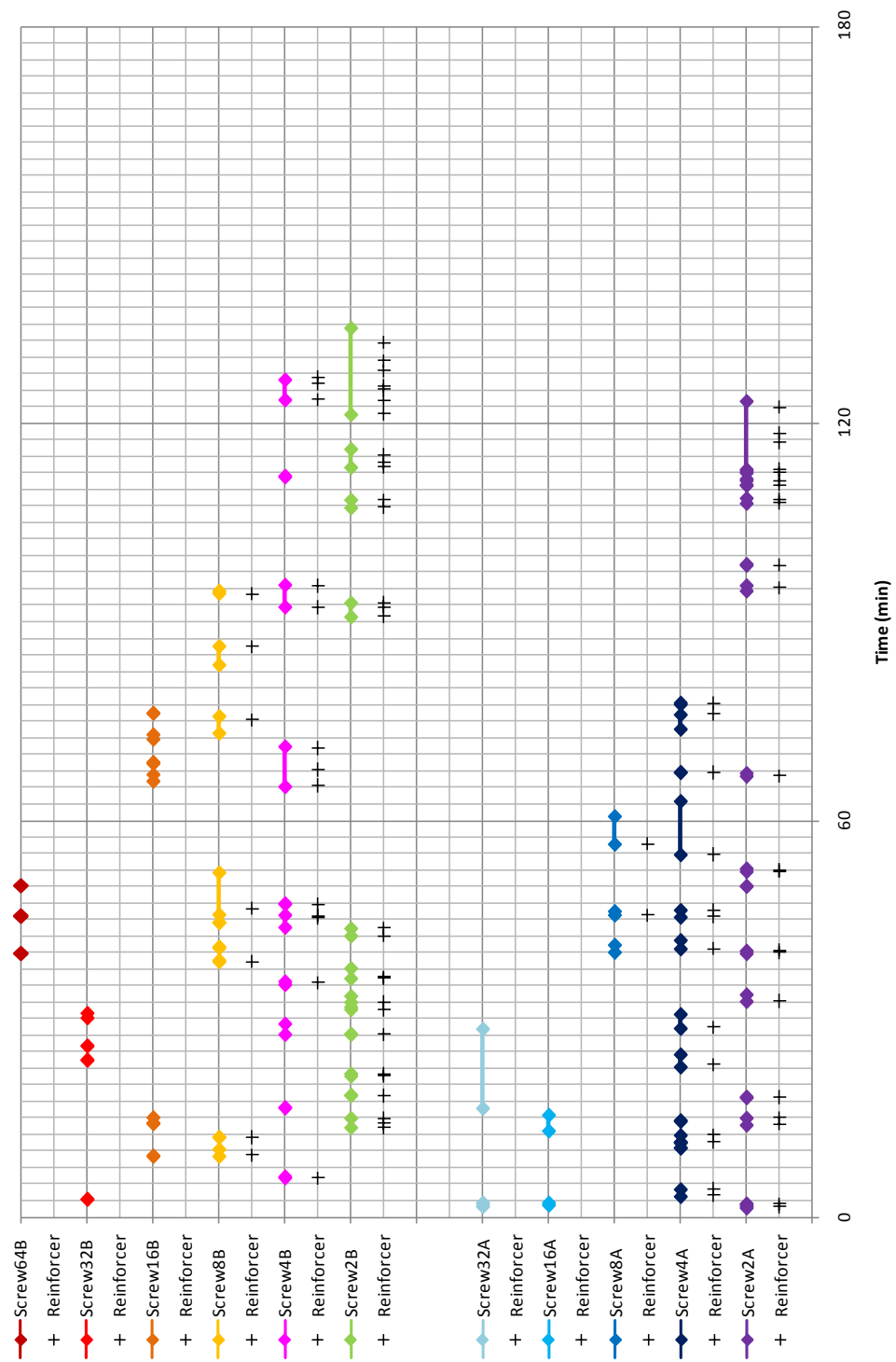


Figure 6.15. Start and stop times for defined behaviours related to Keza's use of the Screwfeeder enrichment item and time any reinforcements delivered across experimental sessions of Experiment 5, whilst with entire chimpanzee group.

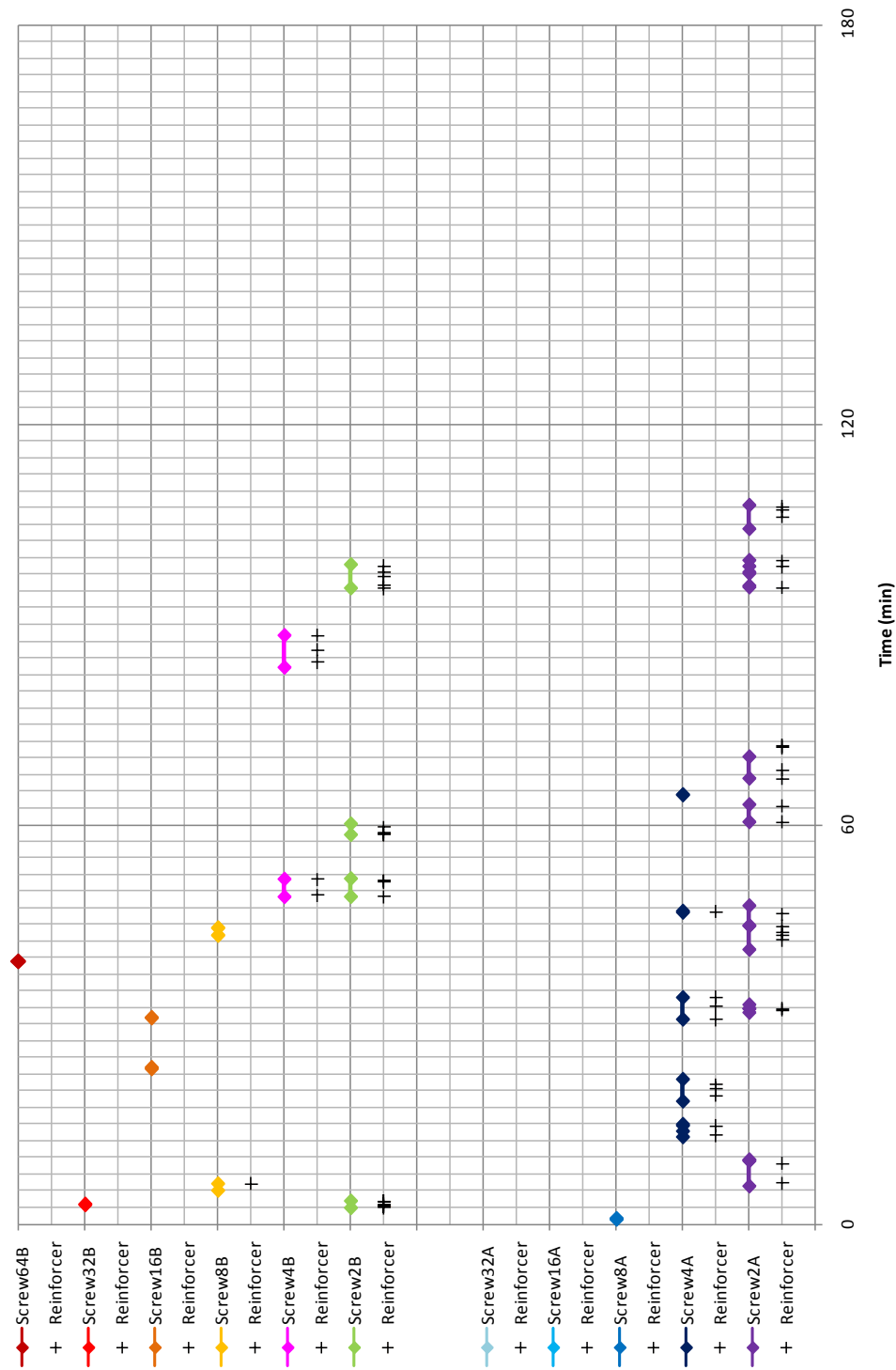


Figure 6.16. Start and stop times for defined behaviours related to Jess's use of the Screwfeeder enrichment item and time any reinforcements delivered across experimental sessions of Experiment 5, whilst with entire chimpanzee group.

Previous research has shown an effect on behaviour of testing social species individually (e.g., Pedersen et al., 2002) and recommendations have been made about conducting individual testing with social species (Jensen et al., 2004; Olsson & Westlund, 2007). Therefore, given that the subjects in this current research were usually members of a social group, when they were separated for testing temporarily the social effect of the group was a factor. Specifically in this research, the subjects that were individually tested were observed to spend time during the experimental sessions communicating or attempting to communicate with the rest of the chimpanzee group (which was being held outside of the experimental area) or, as was the case with Jess, doing very little at all. This behaviour was evident at different levels for the different individuals. Therefore, this research would suggest that individual testing of an animal that is normally socially-housed does not provide accurate information about the individuals demand for a commodity. As such, this research would support the recommendation that animals normally maintained in a social group should not be tested individually, unless the findings are viewed on the basis that they only relate to the circumstances in which the testing was conducted.

The results of this current research show that the social group had a different effect on each individual's level of use of the enrichment item. This is shown by comparing adolescent male Temba's use of the Screwfeeder across procedures to that of adult female Jess. Temba was shown to use and respond more for access to the Screwfeeder enrichment when tested in isolation. However, Jess spent less time using the item when tested in isolation. Previous research has shown that social companions can have influence behaviour via social facilitation, competition or related stress responses (Olsson & Keeling, 2002; Pedersen et al., 2002). Such factors could have been present in this current research. Temba was a lower ranking individual in the chimpanzee group. He could have been under social pressures from the hierarchy and as a result unable to spend more time with the enrichment item when in the group situation. This suggestion is supported by the finding that more dominant chimpanzees spend more time using enrichment items (e.g., Bloomstrand et al., 1986). Schapiro et al. (2003) also suggested that animals may be unwilling to perform certain behaviours in a social situation, and this may have been the case for Temba when accessing the enrichment items in the group setting.

The increase in Temba's use from when the enrichment was available freely to when it was available at a cost may have also related to the fact that Temba was the

most proficient operator of the lever apparatus (taking only ten minutes to be shaped in its use). Other members of the group who were less proficient or less willing to work for the items (had less demand for the items) may have allowed Temba access to the enrichment item that he would not have had if the item had of been freely available. This suggestion is supported by the finding that the level of work for access to food can be related to prior training and proficiency (Jensen (1963). Jess, on the other hand, was a relatively high ranking individual - therefore access to the enrichment item in the group setting was easier. It should be noted that Jess was also the only individual subject to have been 'hand-reared' and she did have noticeably different behaviour from the other chimpanzees in the group (as seen in her interaction with humans and response to events). It may also have been that the facilitation of the social group was important for Jess to choose to interact with activities related to this current research. The present findings would appear to support other research in that individuals' prior training, deprivation level, rearing history, and the required effort, environmental uncertainty, and the nature of the foraging task all have an impact on the use and demand for commodities.

Habituation. Habituation to the Screwfeeder was evident in this current research as it has been in others (e.g., Bloomsmith et al., 1990b). The pattern of habituation was different depending on the procedure and the individual subjects. In terms of individuals, the adults showed a higher level of habituation than the younger members of the group (with Jess again being an exception to this). When the enrichment items were freely available to the chimpanzee group, the reduction of use, in general, was across subsequent sessions with an item. In the group demand sessions, the reduction in use was related to the FR value of the session rather than the position of the session. This finding could imply that having the chimpanzees work for access to the enrichment items limited the degree of habituation they showed to the items. However, this effect was different for individual chimpanzees, some of which showed habituation to the items overall, some failing to work for access to some items at all (e.g. adult female Sally). Perhaps working for access to enrichments may limit item habituation, but it would need to be explored for individual subjects and items in subsequent research. Also, the value of the FR of the demand schedules would need to vary or similar habituation may be shown as was the case during the free access sessions.

*Comparison of Individual Demand When Work was Required for Access to
Enrichment Item When Tested Alone vs. When Tested In Social Group*

Individual Demand for Enrichment Item

Data from Experiment 5 for the three chimpanzees and some of the group data are shown in Figures 6.17 to 6.19 to allow for comparisons to be made.

Responses. Comparison of Figures 6.11 and 6.17 shows that adolescent male Temba made far more responses to access the Screwfeeder enrichment whilst tested in isolation than he did in the first hour of sessions when tested with the chimpanzee group. Juvenile female Keza made around the same number of responses when working for access alone and in the group (first the first hour of the sessions). Adult female Jess made more responses on the lever to access the Screwfeeder when tested in the social setting (in the first hour of the sessions) than when tested in isolation.

Overall rate of responding. Figure 6.18 shows the overall response rate for the whole group during the first hour of sessions with the Screwfeeder enrichment item. The first hour of the sessions was used to allow comparison with the individual data from this present study. The group's overall response rate reached a higher peak rate (3.5 during Series A, FR 4). than any of the three the individuals tested in isolation (Figure 6.6 and 6.7). However, the pattern of change in the group response rate was similar to Temba's rate when tested alone. Response rates in both cases rose with increasing FR values, peaked and then dropped markedly with further increases in FR. This finding differed from both Keza's and Jess's response rates when tested in isolation, their rate decreased with each increase in FR - although Jess's made so few responses a true judgment of response rate changes is not possible.

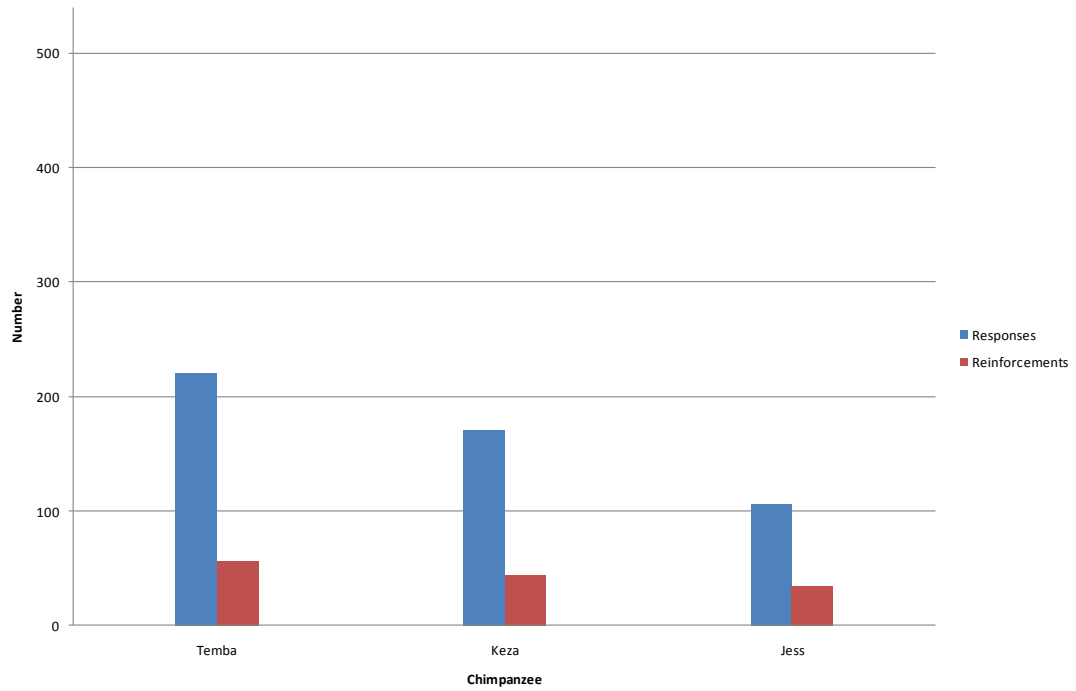


Figure 6.17. Total number of responses made and reinforcers gained by each individual in the first hour of experimental sessions of Experiment 5 with the Screwfeeder enrichment.

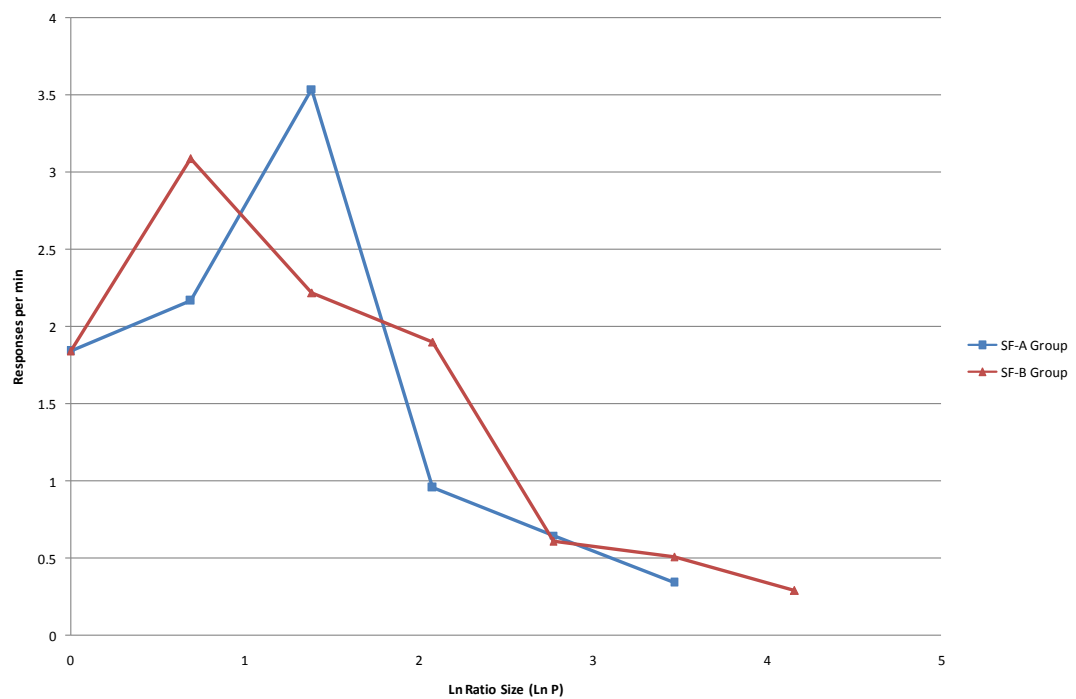


Figure 6.18. Overall response rates (responses per minute) plotted against the logarithms (ln) of the ratio requirements for the chimpanzee group during the first

hour of sessions in Experiment 5 with the Screwfeeder enrichment.

Demand functions. In order to compare the demand functions the data from Experiment 5 was reanalysed to extract those for the three individual in this experiment and for the whole group from just the first hour for sessions with the Screwfeeder. The extracted data related to the responding by each individual and to each time that individual received a reinforcer, in the first hour of the sessions. This allowed a comparison to the individual results when tested alone, as these sessions were one hour in duration. Linear demand functions were fitted to the data by the method of least squares. The resulting lines are shown in Figure 6.19 (the parameters, the percentages of the data variance the functions account for [% VAC], and the standard errors of the fits are given in Table 6.4).

With one exception, all of the demand functions had negative slopes. During Series A when the group were responding for access to the Screwfeeder, the slope of the demand function fitted to Jess's data was 0. However, only two data points were available for the construction of this function. The intensity of demand was stronger for the entire group during the first hour with the Screwfeeder. The slope average of series data for Keza were the shallowest of all of the demand functions, although very similar to those produced from data of Temba's responding. There was also more variance in the data from Keza's responding.

The results of the individual testing whilst alone can be compared to the individual demand found when in the group through Figure 6.10 to Figure 6.19. This shows that the demand functions for both Temba and Keza were steeper when they were alone. However, Temba's function was only slightly steeper while Keza's was much steeper. As Jess responded at such a low level while held alone a demand function was not possible. The intensity of demand for both Temba and Keza was greatest when tested alone. Pederson et al. (2002) also found that the slopes of the demand function for access to commodities (food and straw) were steeper when their subjects were tested in isolation compared to when they were tested in a social situation.

In this current research the intensity of demand for the Screwfeeder was higher when the individual chimpanzees were tested alone. Pederson et al. (2002) simply compared the findings of testing with the group with those of the testing with individuals, without comparing the individuals demand when within the group. The

results of this current research are similar to their findings that the intensity of demand for the group for the Screwfeeder was greater than the individual demand. However, no comparison can be made regarding the finding of individuals demand whilst in the group environment.

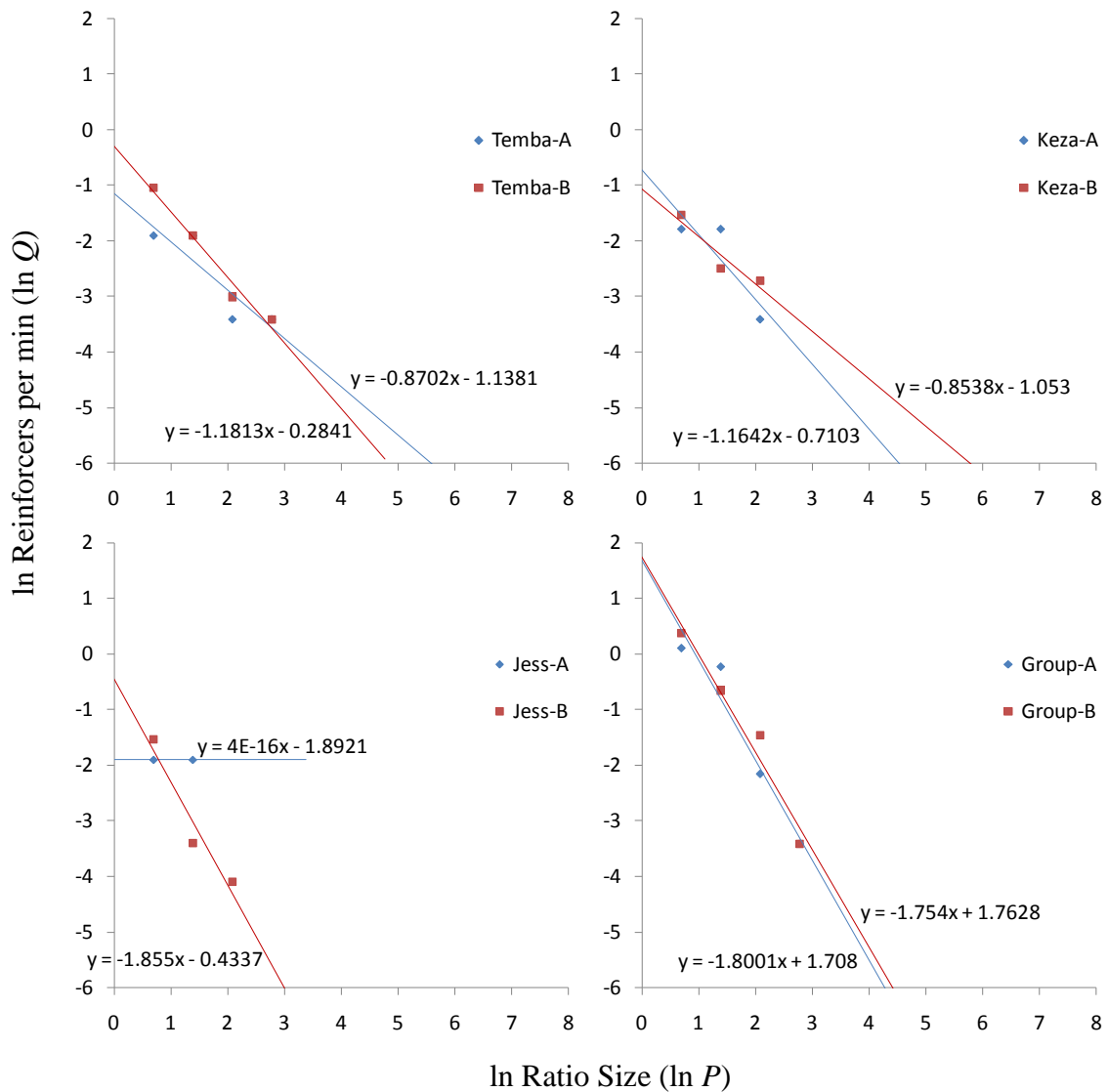


Figure 6.19. The natural logarithms of obtained reinforcement rates plotted against the natural logarithms of FR schedules size for individuals Temba, Keza and Jess for the first hour of sessions with the Screwfeeder enrichment in Experiment 5 (whilst tested with the group) and group data for the first hour of these sessions. The demand functions, shown by the lines, were obtained by fitting Equation 2 to the data.

Table 6.4

The parameters $\ln(L)$, and b of the lines fitted by Hursh et al.'s (1988) Total consumption equation (Equation 2) to the log consumption rate versus log FR data for the sessions of Experiment 5. The percentage of variance accounted for by lines (% VAC) and the standard errors of the estimates (se) are also shown.

| Condition (Subjects/Series) | Parameters | | | |
|--------------------------------|------------|-------|------|-------|
| | $\ln(L)$ | b | se | % VAC |
| Temba-A | -1.14 | -0.87 | 0.40 | 80.00 |
| Temba-B | -2.84 | -1.18 | 0.49 | 97.20 |
| Keza-A | -0.71 | -1.16 | 0.73 | 75.00 |
| Keza-B | -1.05 | -0.85 | 0.64 | 88.50 |
| Jess-A | -1.89 | 0.00 | NA | NA |
| Jess-B | -1.86 | -1.86 | 0.47 | 93.40 |
| Group-A | 1.71 | -1.80 | 0.47 | 94.30 |
| Group-B | 1.76 | -1.75 | 0.48 | 96.00 |

Comparison of Demand Across Procedures

For each of the individual chimpanzees utilized as subjects in the isolation testing of demand the effect of the social setting resulted in different behaviour being exhibited. Adolescent male Temba was shown to have a higher intensity of demand and use the enrichment item more when tested in isolation. However, adult female Jess was shown to have a higher intensity of demand and use the item more when tested in the social environment (in fact she worked so little for access to the commodity during isolation testing that a demand function could not be fitted to the data).

The reason for the effect of isolation on demand and use of the enrichment item may have been the stressor of being with the socially barren environment (particularly in reference to the behaviour shown by the adult female Jess). Social contact has been shown to be an important feature for captive chimpanzees (de Waal, 1991; Fritz & Menkhous Howell, 1993; Goodall, 1971; Novak, 1989; Novak & Drewson, 1989; Novak & Suomi, 1988; NRC/ILAR, 1998; Olsson & Westlund, 2007; Reinhardt, 1990a; Schapiro et al., 1993). Another possibility for the reduction of use and demand when tested in isolation may have been the lack of social

facilitation.

Pederson et al. (2002) found that the social context in which their subjects (pigs) were tested affected the demand functions, but the effects differed for each of the resources being investigated. The pigs demand for food, as indicated by the elasticity of the demand function, was lower when subjects were tested in isolation. The presence of a companion did not affect the elasticity of the subjects demand for straw, but it did increase the intensity of the demand. Sherwin (2003) also found that mice worked less for access to a running wheel when access implied moving away from cage mates, while the presence of cage mates did not affect their tendency to work for access to additional space. These findings and the findings of this current research indicated that isolation during testing may affect the demand for a resource, especially for social species and/or animals normally held in a social environment.

As previously mentioned the increase in responding for the Screwfeeder between procedures shown by Temba may have been due to the social structure of the chimpanzee group. Temba was a lower ranking individual in the group. When testing occurred in the social situation his behaviour was impacted on by the presence of the other members of the group, especially the higher ranking individuals. When tested in isolation, however, Temba was free to respond for access to the enrichment item free of this social impact. Jess, however, was a high ranking individual in the group and as this type of social pressure had little implications on her access to the enrichment items. That dominance may have influenced responding suggestion is supported by other studies which have shown the strength of social facilitation between individuals to be influenced by the social dominance relation (e.g., Bloomstrand et al., 1986). It would seem from the findings of the current study that the effect of the presence or absence of the social group is different for individuals depending on their status in the dominance structure.

Conclusion

The aim of this study was to investigate if behaviour related to provision of an enrichment item (Screwfeeder) and the demand functions generated using operant conditioning techniques were affected by testing chimpanzees, normally socially-held, in isolation. The results indicated that this was the case and that the effect of testing in isolation may vary depending on the individual and their status in the dominance structure of the social group. These findings are supported by other

research related to the impact of social settings on animal behaviour.

As these results would suggest, it would not be meaningful to assess behavioural priorities of animals in social situations different to those in which recommendations for the provision of environmental commodities are being made for. Or that consideration should be given to the social setting in which the testing occurred.

GENERAL DISCUSSION

Summary of Research Findings

The zoo-held chimpanzee group utilized in this present research was found to be inactive for around 12 to 14 hours a night, as discussed in Experiment 1. This time of inactivity was directly related to the change in natural light and was unaffected by the presence of an artificial light source.

A variety of original enrichment devices were specifically designed and built for application in this present research. The designs were based on the natural history of the subjects (as previously discussed taking into consideration their physical capabilities and patterns of behaviour in the wild, such as tool use) and the requirements of the research, as discussed in Experiment 2. The enrichments were shown to be effective as commodities on offer in preference (Experiment 3) in that all were interacted with to some degree, albeit to a small degree for some of the selected items. The enrichment items were also shown to be practical in that they were suitably durable for the chimpanzees' interactions.

In Experiment 3 the chimpanzee group's preference for the different enrichment items was explored based on free access to each enrichment, when independently provided. The items were ranked in order of the group's preference when assessed by the relative amount of time spent using each item. The order was: Screwfeeder; Dipper; Marbleroll, delivering marbles and Jaffas™ without slides present; Marbleroll, delivering coated peanuts; Marbleroll, delivering marbles and Jaffas™ with slides present; TV/Video enrichment and the Musicbox was the least preferred.

In general, for the group as a whole, the foraging enrichment items were preferred over the non-foraging enrichments. The ranking was not consistent with the relative complexity of the enrichments or with the intrinsic effort involved in using them or with the degree of control they afforded the chimpanzees. Individual preferences of group members for the different enrichment devices were evident in that differences in the level of use of the items by different members of the group were shown. In particular, younger members of the group used the items more than the adult members and the older (higher ranking) members of the group used the items earlier in the sessions.

An operant methodology has not been used previously with chimpanzees in a

zoo setting, and the response manipulanda had to be designed for use in this research. The lever design was shown to be practical in that it could be adjusted so that all the chimpanzees could operate it, and it was robust enough to withstand the chimpanzees handling it. Being able to weight the lever was also important as this allowed the force needed to operate it to be adjusted and it could be made inoperable when not required.

The members of the chimpanzee group were successfully trained by the method of successive approximations to operate the response lever for access to a food reinforcer. This was extended to operating the lever to give access to the operable enrichment items, as discussed in Experiment 4. There were individual differences in the proficiency at this task. Particularly, it was noted that the younger members of the group learnt the task earlier than did the older members of the group. All members of the group were trained to be able to operate the lever to obtain access to an enrichment item.

After training to operate the lever to activate the items all chimps operated it a few times for most of the items in the demand assessment with the group (Experiment 5). One item (the Screwfeeder) was also used in demand assessment with each of three chimps when isolated from the rest of the group (Experiment 6).

Demand functions were obtained for each enrichment item when access was available at a price in a social situation, as discussed in Experiment 5. Linear demand functions described the data well. The slopes of the functions from the group testing of demand were shallowest for the Screwfeeder enrichment item and were steepest (more elastic demand) for the Musicbox enrichment item. Ranking the enrichment items (from the most to the least essential) based on the elasticity measures (the slopes of the lines) gave the order: Screwfeeder, Marbleroll-delivering coated peanuts, Musicbox, Marbleroll-delivering marbles and Jaffas™, Dipper. (Demand functions could not be derived for the TV/Video enrichment data as there were too few data points). On the other hand, the initial intensity of demand for the items (the intercepts of the lines) ranked the enrichments in a different order: Screwfeeder, Marbleroll-delivering coated peanuts, Dipper, Marbleroll-delivering marbles and Jaffas™, Musicbox. As suggested in Experiment 5, both elasticity and intensity of demand functions can be affected by prior deprivation levels and reward durations and thus it was suggested that both should be considered in ranking overall demand.

As discussed in Experiment 5, the demand function slopes for all the

enrichment devices indicated the chimpanzees had elastic demand for the commodities. The slopes of the demand functions for enrichment items that included food items were closer to zero (more inelastic) than those for the items that did not. The result of the rank ordering of the enrichment items highlights the sensitivity of the demand procedure in identifying the environmental requirements of captive animals.

Individual members of the chimpanzee group were shown to have different levels of demand for the enrichment items (Experiment 5). Differences related to age and social hierarchy factors; younger members of the group having a higher demand for the enrichment items and older, more dominant members using the items earlier in the sessions. The setting, both physical and social, had an impact on the demand the individuals had for the enrichment items.

Demand testing of three individual chimpanzees in isolation from the rest of the group, gave different results for each individual and these also differed from those of the group as a whole, as discussed in Experiment 6. Demand functions for access to the Screwfeeder were steeper when subjects were tested in isolation compared to that from the group as a whole – a finding similar to that from other research (Pederson et al., 2002). The intensity of demand for the Screwfeeder was higher for each individual chimpanzee when the chimpanzee was tested alone as compared to when it was tested in the social environment.

The results suggested that the effect of testing in isolation may vary depending on the individual and their status in the dominance structure of the social group. The finding that having other animals present and that testing animals normally socially-housed in isolation affects the results is supported by other research, and this was discussed in Experiment 6. These findings suggest that future demand research may need to take individual differences into account.

Research into environmental enrichments has suggested the importance of specific features of items, such as control and complexity. However, the rank ordering of the items from neither the free access procedure nor the demand analysis correlated with the ranking of items with regards to these features. A further exploration of the contribution of various features of the enrichment items to their ranking is needed to provide more information as to what is important.

Comparing the groups' preference for the enrichment items with their demand for them, showed the rankings of both were very similar, with some differences in

the mid-ranked items. In both cases, the enrichment item that was the most preferred was the same - it was the Screwfeeder enrichment. The least preferred items were the non-foraging items; the Musicbox and the TV/Video unit. The foraging items in-between these extremes were ranked in a different order by the two procedures, with the Dipper enrichment being less preferred by the group when work was required to access it than when it was available freely. Some of these differences may have been related to the nature of the task included with the enrichment altering the animals' demand for it. Such as the tool use required with the Dipper enrichment.

The majority of bouts of use of the enrichment items were brief, even when the items were freely available. This finding may suggest that social, especially hierarchical, influences on behaviour were present in this research or that there were impacts of the availability of other activities in the research setting. Habituation to the items varied depending on the procedure.

PRP times for the group were suggested to be a poor measure of demand in a group setting given the influence of other factors on the measure. The amount of use not related to the delivery of a reinforcer increased as the price of the commodities increased. This finding may have related to the social setting of the testing. This was not the case in the demand testing in isolation, indicating that the social influence on the group needs to be taken into consideration in the setting of procedures.

The preference procedure was able to provide information on the basic ranking of the commodities in terms of time spent using each, whilst, the demand procedure was able to show that the chimpanzee group had an elastic demand for the commodities. This finding of the items being 'luxury' commodities (i.e., having elastic demand) is supported by other considerations of well-being, as discussed in the Introduction and Experiment 5.

The results overall suggest that it would not be meaningful to assess behavioural priorities of animals in social situations different from those for which recommendations for the provision of environmental commodities are to be made. Rather, recommendations should take into consideration the social and physical setting in which the testing occurred in, as discussed in Experiment 6.

Summary of Research Related to General Aims

The aims of this current research included the examination of the level at which a group of zoo-held captive chimpanzees interacted with the commodities

(enrichment items) when they were freely accessible and presented independently. This was achieved and enabled judgement of the chimpanzees' preference for the items. Another aim was to examine the chimpanzee group's demand for the different commodities to assess the group's preference for the items when available at a cost. Again this was achieved and showed it was possible to study behaviour of the chimpanzees under the FR schedules in a group setting. This procedure generated the demand functions and allowed ranking of the items based on the elasticity of the demand or based on the intensity of the demand. Comparison of the findings related to the preference and demand assessment allowed an exploration of the relation between these measures, and found the results to be similar. It was argued that both elasticity and intensity should be considered when ranking items. A further aim was to assess the demand of three chimpanzees, that were isolated from the group for testing purposes, for one of commodities that had been used in the group situation. These demand function were compared to the demand in the group situation. This comparison showed that demand changed depending on the social environment.

Operant Methodology Out of the Lab - Zoo Research

A focus of this research was the attempt to use an operant (normally laboratory-based) methodology effectively in a working zoo. The chimpanzees in this current research were not constrained and could avoid the experimental equipment in that they had control over their interaction and environment. The equipment was not presented in close quarters or with few alternatives for other activities – such is the case in many other preference and demand studies. The subjects were in their normal environment and had their normal behavioural options open to them within their group setting. The benefits of these features are that the recommendations or findings from this current research are truly applicable for this group and for chimpanzee groups in similar situations. Animals tested in barren environments (physically and socially) may simply provide results on the basis of 'nothing else to do'. While the findings of such research would be useful for animals in similar circumstances, the transfer for application to richer environments could potentially be inappropriate, a waste of time, effort and money and of little benefit to the animals involved.

However, there are many constraints on conducting research in a zoo setting, and these constraints were apparent in this research, as previously detailed and

discussed. As a result, such studies will never have perfect methodology as there are many factors that can vary and are outside of experimental control.

Lack of Data

One problem with conducting this research was the difficulty in arranging data collection in this setting. Although enough data was produced in this current research to enable the analysis of demand for the chimpanzee group and individuals chimpanzees it would have been good to have been able to obtain more data. There was not enough responding in the session for the animals to gain access to an enrichment item for some enrichments, and this impeded the data analysis, particularly the fitting of the curvilinear functions. A possible solution to this may be to have longer sessions during testing, to allow more responding to occur. Of course, as shown in the results of this current research, the timing of sessions would be critical. The chimpanzee group were shown to use the enrichment items very little during the third hour of availability. This could be because the sessions continued past the time of sunset and the animals were resting or asleep rather than interacting with the enrichments. Therefore, if longer sessions were to be conducted, they would need to be in daylight hours. Having longer sessions during daylight hours would not have been possible in the setting in which this current research was conducted. The chimpanzees were held for a maximum of 16 hours (during which the chimpanzees spent most of the time sleeping) over the evening/night in the area in which the experimental equipment was located. The alternative of keeping the group within the Indoor Enclosure over the whole of a day on which a research session was conducted was also not possible given the needs of the zoo facility and the welfare requirements of the chimpanzees. Another possibility would have been to locate the experimental equipment so that it was accessible to the subjects in the area within which they spent the main portion of their day – the Outdoor Enclosure. This was considered during the planning of this current research, however, the experimental site was chosen based on considerations of cost, impact to enclosures, zoo-visitors, subject well-being and ease of conducting the research. In addition to this, the current research sought to explore the chimpanzees' preference and demand for the enrichment items in the area which was most lacking in such resources – the chimpanzees' Indoor Enclosure. For research in the future, considerations may need to focus on locating the equipment where it affords the longest experimental sessions in day light hours

possible in order to acquire the greatest amount of data possible.

Operant Methodology Applied with a Group

A further focus of this research was the use of the methodologies with the social group of animals, rather than one animal at a time. These findings contribute to the little existing research that has used an operant methodology with an entire social group.

Group Influence on Behaviour in Research

Both competition and cooperation were evident during sessions with the whole chimpanzee group in this current research. Observational learning (Thorpe, 1963) was evident during both assessment and shaping and training components of this study. The level of competition was different with each of the enrichment items - dependent on individuals' preference or demand for the item (or for access to it or to the operant lever). Hare and Tomasello's (2004) findings suggested that chimpanzee task performance was enhanced in a socially competitive setting. This may have been an influence in the performance of the chimpanzee in this current research. Social facilitation by learning to perform a task through imitation has also been shown in research with primates (e.g., Kawai, 1965; Whiten, 1998) and was also evident in this current research. Social species have been shown to be greatly affected by the presence or absence of conspecifics (Olsson & Westlund, 2007; Schapiro et al., 2003). The findings of this research would support this.

Individual Differences Within Group Members for Enrichment Items

Different members of the chimpanzee group showed different responses to the enrichment items during the group testing, both when items were freely available and when they were available at a cost. In general, while the group showed preference for the foraging items over the non-foraging ones the preference was not uniform across the chimpanzees. Some individuals showed little use of the enrichments no matter what the item was, such as adult female Sally, while other chimpanzees responded and used the foraging items at a high level throughout, such as Temba.

Some individual preference for particular enrichment items was evident and there appeared to be a correlation between the age of the chimpanzees and the use of the enrichment items. In general, the younger members of the group both used and

worked for access to the enrichment items more than the adult members did, this is similar to findings from other research (e.g., Reinhardt, 1997). There was an exception to this in the case of Jess. Her rearing history may have been the cause of this difference, being the only hand-reared individual. There appeared to be little correlation between the sex of an individual and the use of or work for enrichment items.

This current research was successful in assessing behaviour beyond that of the ‘mythical average animal’ that Dunlap (2002) refers to. Of course, this research relied on the fact that the researcher could identify individual chimpanzees easily and realisably. This would need to be a consideration before attempting to conduct other research in a social setting to establish individual differences.

Shared labour. Although multiple subjects contributed to the results it is argued here that the findings are still interpretable. As pointed out previously, when conducting the group demand portion of this current research, the performance at higher FR values (higher than one) was truly a group effort. Many times different individuals contributed work effort to gain a reinforcer. In this way, the work was shared between the individuals of the chimpanzee group. Because of this fact, one chimpanzee may have started responding on the FR schedule and another may have continued (done less work than the full requirement for that reinforcement schedule but have received reinforcement). For such a chimpanzee, the FR is essentially small, until this same chimpanzee tries the same number of responses and does not receive reinforcement. Therefore, for the individual chimpanzees, the schedules will be more like a variable ratio than a fixed ratio schedule.

This issue could be addressed by a change in the methodology to include housing the experimental equipment in a restricted entry area. Here only one chimpanzee would be able to access the area and would be required to leave before another could enter. However, this could lead to a safety concern if used with this species, as a less dominant chimpanzee could be attacked when it re-entered the group having received its ‘private’ food reinforcers. Attempts to limit the reward solely to the individual working (but still in a group setting), could potentially decrease the amount of work done for access and the use of the items as the less dominant individuals, under pressure from the more dominant individuals (increased by them receiving the rewards) may stop working (been intimidated or driven off).

This is a general problem (or a consideration) in a group setting when testing demand with social animals, but this study gives the general view of the true importance of the commodities to the group.

Factors effecting chimpanzees participating in research. As previously pointed out, a large number of parameters need to be carefully controlled to generate valid data (Jezierski et al., 2005). In an uncontrollable setting - such as zoo - this is particularly difficult. One factor over which there was no control was the degree and type of social interactions. This group had rich collective interactions and some of these social interactions had implications for the participation of individuals. For example, there was no control over the day's events involving various individuals (including fights), or over female members of the group being in season (this having implications for male behaviour in terms of proximity to the females and female behaviour in terms of mood). Several members of the chimpanzee group died (unrelated to the research) during the course of this study and the effects of this on the rest of the group in terms of behaviour were out of the control of the researcher. Also, in this group setting, the amount of food each chimpanzee got throughout the day (from sources outside of this current research) varied between individuals. In general, those individuals at lower end of the hierarchy were likely to be receiving less food in a group setting, while infants and adolescents often obtained food relinquished by their mothers. Such uncontrolled variation may have had an impact on the results where food was a factor.

Although these factors may have impacted on the chimpanzees and their level of participation in this current research, this may not be of central concern to this current research. The present research focused on captive zoo-held chimpanzees, their preference and demand for commodities in the setting in which they were housed and tested, and so the results may, in fact, be more relevant and valid because of these factors.

Operant Methodology Applied with Chimpanzees

Physical and Mental Capabilities

Great Apes pose a considerable challenge to those who manage their care in captivity due to their physical and intellectual capabilities (Byrne, 1999; NRC/ILAR,

1998). Although research on temporary environmental enrichment strategies has flourished in recent years, very little presentation of enrichment items has been based on empirical data relating to the relative importance of the items to the animals. Ferster (1959) suggested that although chimpanzees presented as ‘convenient’ subjects, the species’ mental and physical capabilities do pose a challenge in the undertaking research with them. This was the case in this study, as the attributes of the target species had implications for the design and construction of the equipment and on the methodology. Although the species capabilities did prove to add to the difficulty in conducting this current research, it also meant that the design and procedures were carefully tailored to this species of animal.

Hierarchical Structure

Chimpanzees are a hierarchical species and so the effect of the group on each individual’s behaviour can vary. Individuals that are lower in the hierarchy are cautious at all times. As Schapiro et al. (2003) pointed out, such individuals may be unwilling to perform a behaviour in a social setting given the associated pressure. Individuals that are high in the hierarchy have other behaviours that they need to be undertaking, including the maintenance of group structure and their own standing within it (Goodall, 1971; Fitch et al., 1989). In previous research with this group (Vivian, 2001), adult male Sam was one of the highest users of the enrichment devices on offer (whereas he was not in this current research). However, the earlier research was conducted within the chimpanzees’ Outdoor Enclosure. It may be that different behaviours occupy the time of individuals at different levels of the hierarchical structure in different settings. In some cases an individual may have been engaging in behaviour that precluded another individual from using the equipment. For example, when a female was in oestrous a dominate male would be continually pursuing her and occupying her time by grooming her and having sexual interactions. Such factors may have contributed to the resulting difference in findings for different individuals. Such factors may also have contributed to the different results that were evident when individual demand was tested in isolation, such as was the case for Temba who responded more whilst tested in isolation.

Other Session Behaviour

During the demand testing in this current research some chimpanzees were

observed to hit the Screwfeeder unit, primarily at higher FR values. This behaviour was only related to the research, and did not happen during sessions with low FR values, with any of the other enrichment items or outside experimental sessions. The occurrence of this behaviour may have been related to what has been described as ratio strain as the price of the access to the enrichment items increased. Ratio strain is seen when the size of the FR schedule is increased rapidly, and responding on the schedule deteriorates as if the behaviour is in extinction (Ferster, & Skinner, 1957). Alternatively, the hitting may have been what is termed extinction induced aggression, which has been described in several studies inferring the animals become ‘frustrated’ during extinction (Azrin, Hutchinson, & Hake, 1966). However, there is another explanation possible, the researcher observed that hitting of the Screwfeeder unit occasionally resulted in stray sunflower seeds falling out of the unit. This observation would indicate that when the price of access to the commodity was low the chimpanzees would work for access to the Screwfeeder, and as the price increased, they would hit the unit and this could result in getting some of the sunflower seeds.

Very little aggressive behaviour was seen, either associated with the inclusion of the enrichment items or with this current research in general. Some aggressive interactions did take place, generally over a food item (such as a Jaffa™). These incidents were generally infrequent and brief. However, observations were that general bouts of aggression (unrelated to this research) did peak when the chimpanzees entered into the Indoor Enclosure and early in their time within this area (returning from the Outdoor Enclosure). The chimpanzees’ Indoor Enclosure was around a fourth of the size of their Outdoor Enclosure. Thus, entering into the Indoor enclosure in the afternoons, just prior to this research, greatly reduced the amount of space available to the chimpanzee group. Results regarding the effect of spatial density on social behaviour have been mixed (Videan & Fritz, 2006). Whilst there are no empirical data available, in this current research the chimpanzees were not seen to interact with the operant equipment during such periods of aggression.

Enrichment Devices in Demand Procedures

Kirkden and Pajor (2006) and Hansen and Jensen (2006) warn of the “out of sight, out of mind” component to demand testing. In the case of enrichment items, Keepers of animals in captivity have the obligation of providing stimulation through

enrichment. Therefore, some form of demand or preference testing prior to full scale provision of an enrichment item could save a facility time, money and effort which would be wasted if an item was deemed to be of little value to an animal.

As previously discussed, there were many differences between the enrichment devices and in the behaviour that was related to them. Different enrichment items afforded the chimpanzee group different cues as to their availability. For instance, the Dipper made an audible click when the barrier lifted which indicated that it was open and available. There were also audible sounds when a marble, Jaffa™ or coated peanut was released within the Marbleroll unit. The more the group used the Dipper enrichment, the more excess porridge was left smeared around the opening of the access hole of the item and on the dipper tool, indicating that the item had food available. As Kirkden and Pajor (2006) point out, comparing behaviour in demand tests between multidimensional commodities is not simple. Different ‘motivations’ (as they call them) may be satiated at different rates and may require different quantities of their respective resource. In this current research, for example, it may have taken many more sunflower seeds to satisfy any hunger need the chimpanzees had than it did Jaffas™. These factors may have influenced the level of use and work for each item by the chimpanzee group.

Limitations of this Research

Access to Enrichments

The order of presentation of the enrichment items during both the Free Access (Experiment 3) and group demand experiments (Experiment 5) may have had an effect on the preference and behaviour of the chimpanzee group. However, Matthews and Ladewig (1994) found that the order of exposure to different reinforcers appeared to have had no effect in their study.

The access times to reinforcement of the enrichments were carefully selected but since they were not varied it is not possible to know if they were the ‘best’ times or not. It is possible, for example, that the 20 s access to the TV/Video may have been too short a period. Further research is needed to explore how variations in these times affect demand and to enable more valid access times to be employed.

The constraints on this current research meant that the item being used in a condition was present even when not operative. Thus the chimpanzees experienced

more and more time with the enrichment items present in the experimental area but not operating as the days (sessions) went on (i.e., in the mornings before they went out into the Outdoor Enclosure). No solution was found to avoid this given the constraint and setting of this current research.

Timing of Research (Year/Day)

One factor that was outside of the control of the researcher was that on some days the chimpanzees spent their daytime hours (those which they would normally spend within the Outdoor Enclosure) indoors. This happened as a result of adverse weather conditions or of zoo management requirements. Being held inside may have had an impact on the data for experimental sessions conducted on such a day.

Seasonal changes in weather and hours of daylight may also have had an effect. In the original planning for this entire research project, it was decided to conduct the Free Access study (Experiment 3) and the group demand study (Experiment 5) during the same time of year, in different years. However, difficulties and constraints in setting up the experiment and zoo management requirements meant that delays were experienced. The chimpanzees were scheduled to move to a new Indoor Enclosure (and hence the area in which the experimental equipment was housed would no longer be in use) and this meant the demand study had to be completed as soon as possible. Temperature and seasonal changes in the behaviour of apes is evidenced both in captivity and the wild (Stoinski et al., 2004; Vivian, 2001). No strong relations between behaviour change during the experimental sessions and temperature or weather conditions were seen in this study. However, the reduced day light in the sessions of the demand study compared to that in the Free Access may have had an effect on the results, possibly seen as reduced response time.

Session Length for Individual and Group Demand

Given the practical and ethical constraints on this current research, assessing demand with the individuals when isolated, required sessions shorter than in the group assessment. It would have been preferable, here, to have been able to have used sessions of the same length. However, given this was not possible, the data from the individual's sessions were compared to those from the first hour of the group demand sessions. The issue is whether or not this comparison is valid. If animals respond in the first part of a long session similarly to the way they respond in a short

session of that length, then the comparison would be valid. There are data that suggest this could be the case with demand assessed in this way (e.g., Foster, Blackman, and Temple (1997)) which suggest the comparison could be valid. To establish this more clearly requires further research on the effects of session length on demand for items such as those used here.

Response Topography

The decision to use a lever as the response mechanism in this current research was based on previous research and a judgment of what was best for the circumstances (as previously discussed). However, given that the response required force and given that different members of the group were of varying ages and sizes, this response form had a potential limitation. A response button may have served to address this limitation. However, given the setting, a button may have lacked the visual cue that was evident with the lever. Nevertheless, despite the potential concern that the size of the chimpanzees may have an impact on their use of the lever, juvenile female Keza, one of the youngest members of the group, was one of the highest users of the response lever during the demand study. Therefore, strength alone was unlikely to be a factor in the results for the demand testing.

At the outset of this current research, it was anticipated that it would be possible to vary the weight on the lever across sessions as a form of increasing the work required. It was decided not to proceed with this procedure. If the group had consisted of individuals of similar size and strength then this could have been done. However, this group included chimpanzees of varying age, size and strength. Increasing the weight on the lever would have introduced an element of attrition as the weaker members became unable to operate the lever, thus the resulting demand would not have reflected their interest in an enrichment item but rather just their relative strength.

Contributions of the Research

Schapiro and Lambeth (2007) suggest that demand research with primates should satisfy a list of conditions which include, a) a closed economy, b) validity, and c) adversity. This current research was conducted within a closed economy as the enrichments, and the food reinforcements that some items included, were available only during the experimental sessions. In terms of validity, the research

was conducted with a social-housed group of chimpanzees, maintained in their normal captive environment. In terms of adversity, there was an adversity factor in that having a hierarchical structure, for members of the group that were not at the top of the hierarchy, interacting with the commodities was likely to have included an element of stress (Schapiro, 2003). Whilst there are limitations in this current research, it has been successful in testing the preference and demand of captive chimpanzees for enrichment items, in a social setting and outside a laboratory environment.

Schapiro and Lambeth (2007) state that it is “up to primate welfare researchers to design studies and/or obstacles that will help measure the relative value of resources to captive primates without compromising the welfare they are attempting to evaluate and enhance”. This present research sought to, and succeeded in, accomplishing this if you consider value to be “time spent” (preference) and effort (demand) exerted.

This research provided data on a comparison of group animal preference and group animal demand, which had not previously been explored. The research found that the rankings of the enrichment items based on the amount of time the group used them was very similar to the rankings based on the degree the group would work to gain access to them as the amount of work required was increased. The group were shown to have the greatest preference for a foraging enrichment item (Screwfeeder) and the least preference for an audiovisual enrichment item (TV/Video). When the group were able to access to the commodities at a price the slopes of linear demand functions were shallowest for the Screwfeeder enrichment and steepest for the Musicbox. A function could not be fitted to the data for the TV/Video enrichment (due to the lack of data points) so demand for this could be considered lower than that for the Musicbox.

This research provided data on group demand, and no research has previously examined a group of animals responding under FR schedules. Findings were that the behaviour of the group was influenced by the FR value and that the resulting response rate changes were very similar to behaviour shown by individual subjects in other FR studies, i.e., group response rates initially increased and then decreased as the FR was increased (a bitonic function) and, also as FR increased, the consumption of a commodity decreased. Although the members of the group were able to access and work for the items together, the vast majority of the access and work was done

independently. However, even though the individuals worked in bouts and did not experience simple FR schedules the overall pattern of behaviour was as seen previously under increasing FR schedules with individual animals.

It is argued that both intensity of demand and elasticity of demand need to be considered in overall judgments of subject demand. As in this research ranking the items based on each of these gave a different outcome and intensity can be impacted by other factors.

The research found that during both the demand and preference studies all of the subjects' use of enrichment items was done in short bouts (most under a couple of minutes, even at times in the research when the enrichment items were constantly available). Arguably this was due to the social structure of the group and other influential social behaviours that were evident in the setting.

This research compared the demand of a group with that of some individuals in the group and also compared the demand of these individuals when they were alone and when they were in the group, such comparisons have not been explored before. The results showed that the linear demand functions were steeper for the individual chimpanzees, when alone, than those for the group or those for the individuals whilst in the group. Thus, it is argued that an individual's demand for an enrichment item can be impacted by the social setting in which they are tested. The change of social setting was shown to have a different impact on the behaviour of each of the individual chimpanzees. This finding supports the argument that the experimental environment impacts the outcome of demand testing and that testing and application environments should be similar.

This research provided data on the comparison of the value of enrichment items via subjects' demand for the items. Whilst enrichment items have been compared via measures of preference previously, the use of demand for this purpose has not been studied before. Recommendations for enrichment design (both for increased use and increased benefit to welfare) have included providing items with greater degrees of complexity and affording animals more control. However, this research showed that the ranking of the enrichment items based on the amount of time the chimpanzee group used the items or ranking the items based on the groups demand for the items did not relate to ranking of enrichment items based on:

- complexity,
- intrinsic effort, or

- the degree of control they afforded the chimpanzees (e.g., the Screwfeeder vs. the Musicbox or Dipper or Marbleroll with slides).

This research argued that previous findings about enrichment items is context dependent and cannot be generalised. For example, what may be used by an animal in a laboratory setting may be used very little by an animal in a social setting. For example, previous research in laboratories has found television to be of value to chimpanzees (e.g. Platt & Novak, 1997) but this was not the case for these chimpanzees in this setting.

This research strengthens the call that individual differences need to be taken into consideration in interpreting future research results. This is based on the fact that individual preferences for the enrichment items were evident, differences in individual's demand within the group were evident and the effects of the hierarchal structure were evident (included access to items).

In addition to these contributions to knowledge the research provided a variety of new practical contributions. The practical contributions include:

- a methodology for shaping and training individuals of the species in a group setting to operate a lever that can be used in operant research,
- apparatus that can be use for studying schedule control, including demand, in such a setting, and
- some new forms of enrichment devices for use in testing.

This research also demonstrates a method by which demand testing can be conducted in a zoo facility and with a group. No research has done this previously.

The research provides the first reported data on an effective means of shaping behaviour in a group setting. It showed that although not all of the subjects successfully completed shaping to operate the lever they all went on to successfully operate the lever. Thus when shaping a behaviour (such as the operation of the response lever) with chimpanzees not all members of a group need to have their behaviour successfully shaped. This still leaves the question as to what number of chimpanzees need to have completed shaping and which individuals need to have their behaviour shaped (such as individuals of particular hierarchical ranking etc) for this to happen as areas for further research.

Researchers have called for studies to be conducted in more natural environments and environments more closely related to those in which animals are

actually housed. This research highlighted the constraints around conducting research:

- in a captive environment such as a zoo,
- with subjects in a social setting, and
- with Great Apes.

This research is, at the time of writing, the only research to have been conducted and managed under the constraints of new Great Ape legislation in New Zealand.

Conclusion

Many have suggested the need for research to be conducted in environments that more closely resemble those in which recommendations for animal well-being are provided for (Bateson, 2004; Dawkins, 2004; Gibbon et al., 1994; Hutchins et al., 1996; Kleiman, 1992; Patterson-Kane, 1999; Ryder & Feistner, 1995; Saudargas & Drummer, 1996; Thompson, 1993; Webster, 2003). This research contributes to this both through highlighting some of the issues such research raises and through its results.

Baum (1974) suggested the need for more research carried out in more complex environments so that the research is relevant to the animals and so that the principles of behaviour can be established to hold beyond the laboratory and in more natural settings. These results contribute to establishing the generality of behaviour principles by showing the effects of FR changes on group behaviour and the relations of these to the behaviour of individuals.

If research regarding animal preference and demand is to be truly useful for improving animal well-being, rather than simply theoretical exploration, this research would suggest that the environment in which testing is conducted, physically and socially, should match as closely as possible the environment in which the recommendations are to be implemented. As discussed, of the few demand studies that have been done with primates most have been conducted in the laboratory setting. Most often the animals have been young, lab-raised, singly-housed, in small cages, with very little alternatives available other than participation in the experiment. This current research has shown that while there are constraints in undertaking research in environments outside of the laboratory, it is possible and that such research can produce valid findings. These findings can aid in assessments of what elements are important to animals in captive environments outside of the lab.

As Dawkins (2006) says “We now have a wide range of methods for ‘asking’ animals what they want and we should have the humility to use this evidence and ask the animals rather than automatically assuming that we know from our human standpoint” (p. 10). The present research shows that using demand and preference procedures can provide measures of the value of environmental features to animals. However, it also shows that there are a number of issues that make these measures difficult to interpret. However, as Dawkins (1983) points out, these can be taken into consideration and the approach can provide a means of obtaining measures for making comparisons between resources and that allow animals’ needs to be assessed and ranked. Such information can be used to improve captive animal well-being and this present research provides information relevant to this and demonstrates a means by which such information can be obtained.

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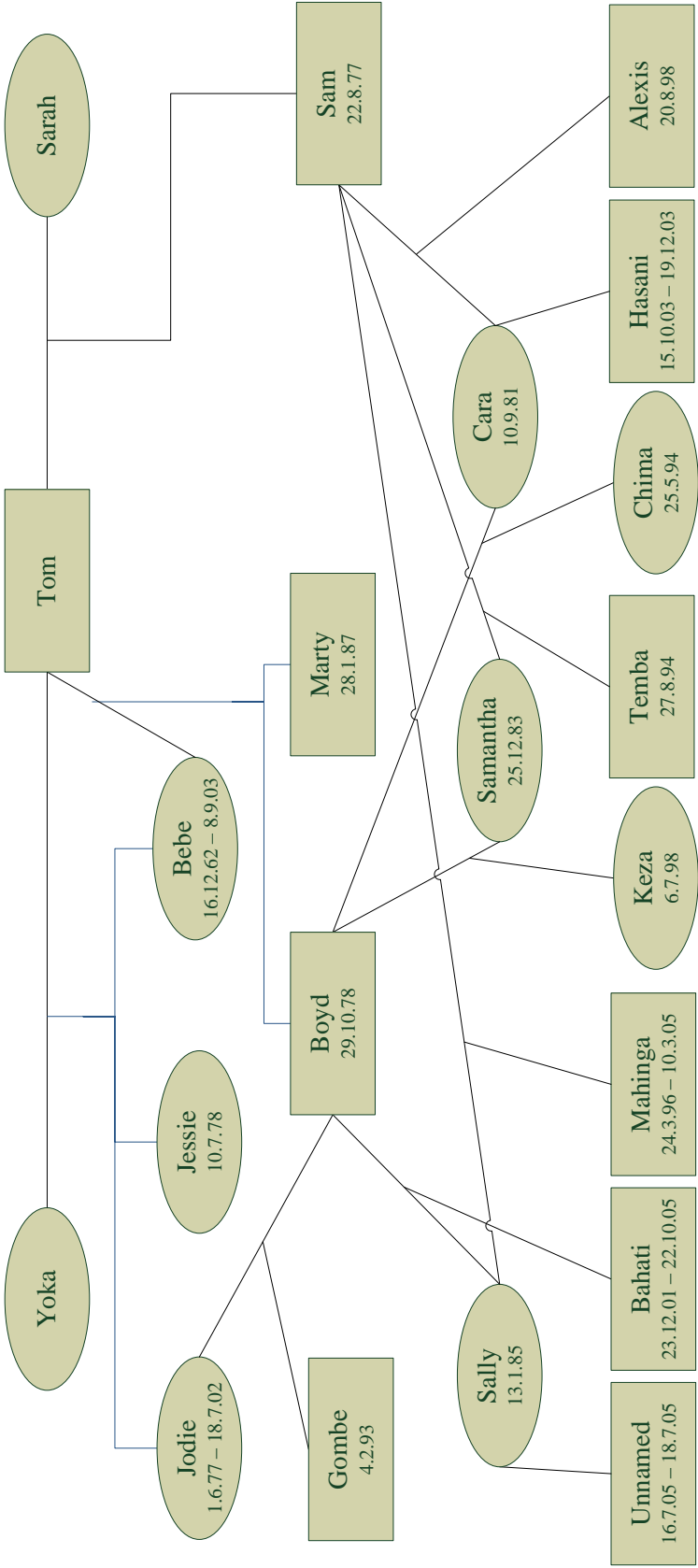
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APPENDIX A

Wellington Zoo chimpanzee group family tree.



APPENDIX B

Raw behavioural observation data from Experiment 2. Based on the behavioural classes in Table 2.2.

| Baseline 1 | | | | | | | |
|------------|---------------|----------------------|------------------|-------------------|-------------------------|--------------------|----------------------------|
| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
| Sam | NA | NA | NA | NA | NA | NA | 5,27 = 32 |
| Boyd | NA | NA | NA | NA | NA | NA | 0 |
| Marty | NA | NA | NA | NA | NA | NA | 1,2,120 = 123 |
| Gombe | NA | NA | NA | NA | NA | NA | 1,10,6,5 = 22 |
| Temba | NA | NA | NA | NA | NA | NA | 6,4,7,20 = 37 |
| Alexis | NA | NA | NA | NA | NA | NA | 1,2,1,66,13 = 83 |
| Jess | NA | NA | NA | NA | NA | NA | 2,1,3,1,10 = 17 |
| Cara | NA | NA | NA | NA | NA | NA | 1 |
| Samantha | NA | NA | NA | NA | NA | NA | 10 |
| Sally | NA | NA | NA | NA | NA | NA | 2,15 = 17 |
| Chima | NA | NA | NA | NA | NA | NA | 26 |
| Keza | NA | NA | NA | NA | NA | NA | 2,1,6,3,10,20,3,7,70 = 122 |
| Unknown | NA | NA | NA | NA | NA | NA | 8,3,10 = 21 |

| Baseline 2 | | | | | | | |
|------------|---------------|----------------------|------------------|-------------------|-------------------------|--------------------|--|
| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
| Sam | NA | NA | NA | NA | NA | NA | 16,12 = 28 |
| Boyd | NA | NA | NA | NA | NA | NA | 36,7,3,2,5 = 53 |
| Marty | NA | NA | NA | NA | NA | NA | 24,12,16,9,6,44,8,17 = 136 |
| Gombe | NA | NA | NA | NA | NA | NA | 17,6,12,4,7 = 46 |
| Temba | NA | NA | NA | NA | NA | NA | 5,8,14,6,22 = 55 |
| Alexis | NA | NA | NA | NA | NA | NA | 7,8,2,4,6,3,4 = 34 |
| Jess | NA | NA | NA | NA | NA | NA | 3,6,7 = 16 |
| Cara | NA | NA | NA | NA | NA | NA | 15,7,5 = 27 |
| Samantha | NA | NA | NA | NA | NA | NA | 3,6,9,31 = 49 |
| Sally | NA | NA | NA | NA | NA | NA | 4,8 = 12 |
| Chima | NA | NA | NA | NA | NA | NA | 26,3 = 29 |
| Keza | NA | NA | NA | NA | NA | NA | 16,7,8,4,18,24,4,6,3,3,12,26,9,4 = 144 |
| Unknown | NA | NA | NA | NA | NA | NA | 1 |

| Baseline 3 | | | | | | | |
|------------|---------------|----------------------|------------------|-------------------|-------------------------|--------------------|---|
| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
| Sam | NA | NA | NA | NA | NA | NA | 6,55,29,21,4,2,2,54 = 173 |
| Boyd | NA | NA | NA | NA | NA | NA | 53,2,3,3,1,2,2,6,2 = 21 6,3,2,3,82,7,2,5,43,4,2,4,3,4,17,4,3,2,2,19,156,3,2,397,7,NA |
| Marty | NA | NA | NA | NA | NA | NA | 58,29 = 869 |
| Gombe | NA | NA | NA | NA | NA | NA | 4,3,3,3,2,9,18,7,3,2,1,2,4,2,1,8,21 = 102 |
| Temba | NA | NA | NA | NA | NA | NA | 133,29,35,7,9 = 213 |
| Alexis | NA | NA | NA | NA | NA | NA | 4,34,63,14,1,29,2 = 147 |
| Jess | NA | NA | NA | NA | NA | NA | 8,2,18,2,7,12,2,19,5,2,2,2,2,3,4,2,4,2,3 = 101 |
| Cara | NA | NA | NA | NA | NA | NA | 3,2,5,14,3,2,3,3,1,2,1,3,4,1,2 = 25 |
| Samantha | NA | NA | NA | NA | NA | NA | 14,16,16,4,8 = 58 |
| Sally | NA | NA | NA | NA | NA | NA | 0 |
| Chima | NA | NA | NA | NA | NA | NA | 7,2,5,4 = 18 |
| Keza | NA | NA | NA | NA | NA | NA | 0 |
| Unknown | NA | NA | NA | NA | NA | NA | 9,2,21,15,2,1,2,1,1,2,3,1,1,2,2 = 65 |

| Baseline 4 | | | | | | | |
|------------|---------------|----------------------|------------------|-------------------|-------------------------|--------------------|--------------------|
| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
| Sam | NA | NA | NA | NA | NA | NA | 0 |
| Boyd | NA | NA | NA | NA | NA | NA | 88,11 = 99 |
| Marty | NA | NA | NA | NA | NA | NA | 32,3 = 35 |
| Gombe | NA | NA | NA | NA | NA | NA | 16,4,35 = 55 |
| Temba | NA | NA | NA | NA | NA | NA | 14 |
| Alexis | NA | NA | NA | NA | NA | NA | 4,12,42,22,13 = 93 |
| Jess | NA | NA | NA | NA | NA | NA | 2,2,3,6,2,8 = 23 |
| Cara | NA | NA | NA | NA | NA | NA | 90,3 = 93 |
| Samantha | NA | NA | NA | NA | NA | NA | 2,2,3 = 7 |
| Sally | NA | NA | NA | NA | NA | NA | 3 |
| Chima | NA | NA | NA | NA | NA | NA | 6,4 = 10 |
| Keza | NA | NA | NA | NA | NA | NA | 4,8,20 = 32 |
| Unknown | NA | NA | NA | NA | NA | NA | 4,2 = 6 |

TV/Video 1

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|-------------------|----------------------|------------------|-------------------|-------------------------|--------------------|-----------------|
| Sam | | | | | | | 8,3,6 = 17 |
| Boyd | | | | | | | 5,2,4 = 11 |
| Marty | | | | | | | 4,3 = 7 |
| Gombe | | | | | | | 4,3,3,9,3 = 22 |
| Temba | 35,124,42 = 201 | | 68/2 | | | | 2,3,24,8,3 = 40 |
| Alexis | 53 | | | | | | 6,7 = 13 |
| Bahati | 59 | | 68/2 | | | | 2,4 = 6 |
| Jess | | | | | | | 3 |
| Cara | | | | | | | |
| Samantha | | | | | | | |
| Sally | | | | | | | |
| Chima | | | | | | | 4,3 = 7 |
| Keza | 49,18,36,11 = 114 | | | | | | 6,3,2,5 = 16 |
| Unknown | | | | | | | |

TV/Video 2

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|----------------|----------------------|------------------|-------------------|-------------------------|--------------------|------------------|
| Sam | | | | | | | |
| Boyd | | | | | | | |
| Marty | | | | | | | |
| Gombe | | | | | | | |
| Temba | 48,7,14,5 = 74 | | 18/2 | | | | 6,5,3 = 14 |
| Alexis | 34 | | 18/2 | | | | 4,6,3,3,2 = 18 |
| Bahati | | | | | | | 3 |
| Jess | | | | | | | 6 |
| Cara | | | | | | | 3,8 = 11 |
| Samantha | | | | | | | 2,6,5,7 = 20 |
| Sally | | | | | | | 3 |
| Chima | 26 | | | | | | 18,3,4 = 25 |
| Keza | 14,26,21 = 61 | | | | | | 3,4,2,5,4,3 = 21 |
| Unknown | | | | | | | |

Marbleroll (no slides) 1

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---|----------------------|----------------------------|-------------------|-------------------------|---|-----------------|
| Sam | 363 | | 3/2 | | 4 | | 4,7,3,2,7, = 23 |
| Boyd | 126,172 = 298 | 4,7 = 11 | 18/2,3/2 = 21 | | 4 | 7,2 = 9 | 2,3,2 = 7 |
| Marty | 78,8 = 86 | | | | | | 3,4,2,5 = 14 |
| Gombe | 38,177 = 215 | | | | | | 9,6 = 15 |
| Temba | 97,68,379,135 = 679 | 2 | | 2,5,3,9,6,7 = 32 | | | 8,7,7,13,2 = 37 |
| Alexis | 78,82,38,43,73,22 = 336 | | 18/2,4/2,6/2 = 28 | 3 | | | 4,2,1,2 = 9 |
| Bahati | 18 | | | | | 6 | 3,2,2 = 7 |
| Jess | 485,294,93,215 = 1087 | 23,7 = 30 | 6/2 | | | 9,4,7 = 20 | 4 |
| Cara | 63 | | 18/2 | | | | 5,8 = 13 |
| Samantha | 72 | | 11/2 | | | 4 | 3,3,1,2 = 9 |
| Sally | | | | | | | |
| Chima | 52,47 = 99 | | | | | | 4,2,3,2 = 11 |
| | 37,31,9,28,40,163,29,52,31, 74,37,23,173,21,15,42,9,125 ,37,8,25,64,24,123,8,8,4,36, 9,18,26,6,13 = 1348 | | | | | | |
| Keza | | 9,4,6 = 19 | 6/2,18/2,4/2,11/2,6/2 = 45 | 4,5,32,3 = 44 | | 2,2,1,4,3,5,2,1,1,7,32,3,4,2 = 23 51 | |
| Unknown | | | | | | | |

Marbleroll (no slides) 2

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|--|----------------------|------------------|-------------------|-------------------------|--------------------|----------------------|
| Sam | 384 | | 42/2 | | | | 1,5,2 = 8 |
| Boyd | 128,32,42 = 202 | | 42/2 | | | 7 | 6,2,3 = 11 |
| Marty | 84 | | | | | | 3,15 = 18 |
| Gombe | 172,63,20,88 = 343 | 17 | | | | | 4,3,2,4 = 13 |
| Temba | 238,18,63,14,73 = 406 | | | 15,4,8 = 27 | | 7 | 2,2,9,1 = 14 |
| Alexis | 17,82,42,84,50,7,27,52,34 = 395 | 7,3 = 10 | 23/2 | 5 | | | 4,3,7,1,1,4 = 20 |
| Bahati | | | | | | | |
| Jess | 588,382,366,254,95 = 1685 | 52,7 = 59 | | 8 | | 3 | 3,2,2,4,1,2 = 14 |
| Cara | 91 | | | | | | 5,2 = 7 |
| Samantha | 24,15,44 = 83 | | | | | 4 | 2,2,2 = 6 |
| Sally | | | | | | | |
| Chima | 68 | | 7/2 | | | | 4 |
| | 72,81,573,107,421,26,36,11, 30,82,392,21,7,15,10,23,17, 6,3,9 = 1942 | | | | | | |
| Keza | | 4 | 7/2,23/2 = 30 | 5,6,3 = 14 | | 52,17 = 69 | 3,2,6,2,4,8,4,5 = 34 |
| Unknown | | | | | | | |

Marbleroll (slides) 1

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---|----------------------|------------------|-------------------|-------------------------|--------------------|--------------------------|
| Sam | | | | | | | 6,1 = 7 |
| Boyd | 15 | | | | | | 3,4,2 = 9 |
| Marty | | | | | | | |
| Gombe | 18 | | | | | | 4 |
| Temba | 25,28 = 53 | | 5/2 | 34 | | 14,9,36 = 59 | 4,2,2,3 = 11 |
| Alexis | 8,5 = 13 | | 5/2 | | | | 3,1,5,5,2 = 16 |
| Bahati | | | | | | | |
| Jess | 9,3 = 12 | 9 | | | | | 3,2,3,3 = 11 |
| Cara | | | | | | | |
| Samantha | 3 | | | | | | 7 |
| Sally | | | | | | | |
| Chima | 62,31,15,48,36,8,17,22,161, 6,13,21,9,15,13,15,18,24,63, 28 = 625 | | | | | | |
| Keza | | 14,36 = 50 | | | | | 9,5,3,6,2,4,2,3,1,3 = 38 |
| Unknown | | | | | | | |

Marbleroll (slides) 2

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---|----------------------|------------------|-------------------|-------------------------|--------------------|-----------------------|
| Sam | 9 | | | | | | 3,56,2 = 61 |
| Boyd | 9,8 = 17 | | | | | | 3,6,5 = 14 |
| Marty | 17 | | | | | | 6 |
| Gombe | 21,14 = 35 | | | | | | 2,4,5,4 = 15 |
| Temba | 135,76,132 = 343 | | | | | 32,5, = 37 | 5,6,7,3,3,4 = 28 |
| Alexis | 36,42,15,57 = 150 | 5 | | | | | 1,3,2,1 = 7 |
| Bahati | 4 | | | | | | 5 |
| Jess | 18,7,7 = 32 | | | | | | 4,3,6,3 = 16 |
| Cara | | | | | | | |
| Samantha | 9 | | | | | | 3 |
| Sally | | | | | | | |
| Chima | | | | | | | |
| Keza | 42,63,99,187,33,42,35,48,23 ,9,25,26,52,164,35,18,8,7,14 ,24,17,14,8,13,10 = 1016 | | 32 | | | | 8,14,7,2,3,1,1,4 = 40 |
| Unknown | | | | | | | |

Screwfeeder 1

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---|----------------------|------------------|-------------------|-------------------------|--------------------|----------------------|
| Sam | 91 | 5 | 4/2,33/2 = 37 | | | | 7 |
| Boyd | 372 | 4,3,5 = 12 | 33/2 | | | 16 | 5,8 = 13 |
| Marty | 182 | 7 | | | | 4 | 6,9,3 = 18 |
| Gombe | 57,637 = 694 | | 3/2 | | | | 3,4,11,5 = 23 |
| Temba | 423,534,72 = 1029 | 16 | 3/2 | | | 54,22,71 = 147 | 2,7,8,4 = 21 |
| Alexis | 236,14,211 = 461 | | 10/2,4/2 = 14 | | | | 3,2,1,4 = 10 |
| Bahati | 14,9 = 23 | | | | | | 3 |
| Jess | 593,628,598,437,48,120 = 2424 | 128,54,71 = 253 | | | | 7,3,5,8 = 23 | 4,2,1,1,3 = 11 |
| Cara | 90 | | | | | | 8,3,4 = 15 |
| Samantha | 79,76 = 155 | 2,8 | 19/2 | | | | 3,3,4,2 = 12 |
| Sally | 174 | | | | | | 5,4 = 9 |
| Chima | 32,33,448 = 513 | 18 | | | | | 1,3,4,2,17,2 = 29 |
| Keza | 36,53,51,472,259,36,15,338, 74,23 = 1357 | 22 | 10/2,19/2 = 29 | | | 128,5,18,2 = 153 | 3,4,4,2,5,7,2,3 = 30 |
| Unknown | | | | | | | 3 |

Marbleroll (slides) 2

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---|----------------------|------------------|-------------------|-------------------------|--------------------|--------------------------|
| Sam | | | | | | | 6,1 = 8 |
| Boyd | 21 | | | | | | 3,4,2 = 10 |
| Marty | | | | | | | |
| Gombe | 24 | | | | | | 4 |
| Temba | 25,28 = 54 | | 5/2 | 35 | | 14,9,36 = 60 | 4,2,2,3 = 12 |
| Alexis | 8,5 = 14 | | 5/2 | | | | 3,1,5,5,2 = 17 |
| Bahati | | | | | | | |
| Jess | 9,3 = 13 | 10 | | | | | 3,2,3,3 = 12 |
| Cara | | | | | | | |
| Samantha | 3 | | | | | | 7 |
| Sally | | | | | | | |
| Chima | | | | | | | |
| Keza | 62,31,15,48,36,8,17,22,161, 6,13,21,9,15,13,15,18,24,63, | 14,36 = 51 | | | | | 9,5,3,6,2,4,2,3,1,3 = 39 |
| Unknown | | | | | | | |

Marbleroll (delivering peanuts) 1

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|----------------------------|----------------------|------------------|-------------------|-------------------------|--------------------|--------------------|
| Sam | 182,93 = 275 | | 84/2 | | 8 | 48 | 5,4,3,7,15,3 = 37 |
| Boyd | 293,103,94,88 = 578 | 48 | 84/2 | 3 | | | 4,3,22,4 = 33 |
| Marty | 183 | | | | 8 | | 2,5 = 7 |
| Gombe | 342 | | | | | | 4 |
| Temba | 121,342,287,127 = 877 | | 63/3 | | | | 3,2,5 = 10 |
| Alexis | 128,90,72 = 290 | | 5/2,17/2 = 22 | 5,3,2,8 = 18 | | | 1,8,3,5 = 17 |
| Bahati | 83 | | | | | | 2,7,3,1 = 13 |
| Jess | 452,231,188 = 871 | 72 | | 3,2,1 = 6 | | | 4,3,5,7,7,3,2 = 31 |
| Cara | 231 | | 17/2 | | | | 7,4,5 = 16 |
| Samantha | 281,170 = 451 | | 63/3 | | | | 3,6,2,4 = 15 |
| Sally | 277,103 = 380 | | | | | | 3,2 = 5 |
| Chima | 275 | | | | | | 9,7 = 16 |
| Keza | 182,96,184,153,64,95 = 774 | | 63/3,5/2 = 68 | 4,2,6,33,6 = 51 | | 72 | 4,3,12,5,7,3 = 34 |
| Unknown | | | | | | | 1 |

Marbleroll (delivering peanuts) 2

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|------------------------------|----------------------|--------------------------|-------------------|-------------------------|--------------------|--------------------------|
| Sam | 19 | | | | | | 5,4 = 9 |
| Boyd | 95,63,42,88 = 288 | | | | | 44,5 = 49 | 4,3,2,1,3 = 13 |
| Marty | 53 | 5 | | | | | 2,3 = 5 |
| Gombe | 193,38,325 = 556 | | | 3,2 = 5 | | | 7,2,1,3 = 13 |
| Temba | 194,63,348,75,31,53 = 764 | | | | | | 3,6,3,2,5 = 19 |
| Alexis | 25,33,47,332,240 = 677 | | 13/2 | | | | 3,1,2,1 = 7 |
| Bahati | 12,66 = 78 | | | | | | 6,3 = 9 |
| Jess | 441,94,61,263,329,123 = 1311 | 44 | 4/2,21/2 = 25 | | | 3 | 4,3,2,1,1,3 = 14 |
| Cara | 127,38,135 = 300 | 3 | | | | | 8,4,4 = 16 |
| Samantha | 234 | | 69/2 | | | | 2,2 = 4 |
| Sally | | | | | | | |
| Chima | 83,106 = 199 | | | | | | 3,4,3,5 = 15 |
| Keza | 89,113,191,54,32,24,37 = 540 | | 69/2,13/2,4/2,21/2 = 107 | | | | 2,2,3,1,3,2,4,2,3,5 = 27 |
| Unknown | | | | | | | |

APPENDIX C

Raw behavioural observation data from Experiment 3. Based on the behavioural classes in Table 2.2.

| Baseline 1 | | | | | | | |
|------------|---------------|----------------------|------------------|-------------------|-------------------------|--------------------|----------------------------|
| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
| Sam | NA | NA | NA | NA | NA | NA | 5,27 = 32 |
| Boyd | NA | NA | NA | NA | NA | NA | 0 |
| Marty | NA | NA | NA | NA | NA | NA | 1,2,120 = 123 |
| Gombe | NA | NA | NA | NA | NA | NA | 1,10,6,5 = 22 |
| Temba | NA | NA | NA | NA | NA | NA | 6,4,7,20 = 37 |
| Alexis | NA | NA | NA | NA | NA | NA | 1,2,1,66,13 = 83 |
| Jess | NA | NA | NA | NA | NA | NA | 2,1,3,1,10 = 17 |
| Cara | NA | NA | NA | NA | NA | NA | 1 |
| Samantha | NA | NA | NA | NA | NA | NA | 10 |
| Sally | NA | NA | NA | NA | NA | NA | 2,15 = 17 |
| Chima | NA | NA | NA | NA | NA | NA | 26 |
| Keza | NA | NA | NA | NA | NA | NA | 2,1,6,3,10,20,3,7,70 = 122 |
| Unknown | NA | NA | NA | NA | NA | NA | 8,3,10 = 21 |

| Baseline 2 | | | | | | | |
|------------|---------------|----------------------|------------------|-------------------|-------------------------|--------------------|--|
| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
| Sam | NA | NA | NA | NA | NA | NA | 16,12 = 28 |
| Boyd | NA | NA | NA | NA | NA | NA | 36,7,3,2,5 = 53 |
| Marty | NA | NA | NA | NA | NA | NA | 24,12,16,9,6,44,8,17 = 136 |
| Gombe | NA | NA | NA | NA | NA | NA | 17,6,12,4,7 = 46 |
| Temba | NA | NA | NA | NA | NA | NA | 5,8,14,6,22 = 55 |
| Alexis | NA | NA | NA | NA | NA | NA | 7,8,2,4,6,3,4 = 34 |
| Jess | NA | NA | NA | NA | NA | NA | 3,6,7 = 16 |
| Cara | NA | NA | NA | NA | NA | NA | 15,7,5 = 27 |
| Samantha | NA | NA | NA | NA | NA | NA | 3,6,9,31 = 49 |
| Sally | NA | NA | NA | NA | NA | NA | 4,8 = 12 |
| Chima | NA | NA | NA | NA | NA | NA | 26,3 = 29 |
| Keza | NA | NA | NA | NA | NA | NA | 16,7,8,4,18,24,4,6,3,3,12,26,9,4 = 144 |
| Unknown | NA | NA | NA | NA | NA | NA | 1 |

| Baseline 3 | | | | | | | |
|------------|---------------|----------------------|------------------|-------------------|-------------------------|--------------------|---|
| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
| Sam | NA | NA | NA | NA | NA | NA | 6,55,29,21,4,2,2,54 = 173 |
| Boyd | NA | NA | NA | NA | NA | NA | 53,2,3,3,1,2,2,6,2 = 21 6,3,2,3,82,7,2,5,43,4,2,4,3,4, 17,4,3,2,2,19,156,3,2,397,7, |
| Marty | NA | NA | NA | NA | NA | NA | 58,29 = 869 |
| Gombe | NA | NA | NA | NA | NA | NA | 4,3,3,3,2,9,18,7,3,2,1,2,4,2,1 8,21 = 102 |
| Temba | NA | NA | NA | NA | NA | NA | 133,29,35,7,9 = 213 |
| Alexis | NA | NA | NA | NA | NA | NA | 4,34,63,14,1,29,2 = 147 8,2,18,2,7,12,2,19,5,2,2,2,2, |
| Jess | NA | NA | NA | NA | NA | NA | 3,4,2,4,2,3 = 101 |
| Cara | NA | NA | NA | NA | NA | NA | 3,2,5,14,3,2,3,3,1,2,1,3,4,1,2 = 25 |
| Samantha | NA | NA | NA | NA | NA | NA | 14,16,16,4,8 = 58 |
| Sally | NA | NA | NA | NA | NA | NA | 0 |
| Chima | NA | NA | NA | NA | NA | NA | 7,2,5,4 = 18 |
| Keza | NA | NA | NA | NA | NA | NA | 0 |
| Unknown | NA | NA | NA | NA | NA | NA | 9,2,21,15,2,1,2,1,1,2,3,1,1,2, 2 = 65 |

| Baseline 4 | | | | | | | |
|------------|---------------|----------------------|------------------|-------------------|-------------------------|--------------------|--------------------|
| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
| Sam | NA | NA | NA | NA | NA | NA | 0 |
| Boyd | NA | NA | NA | NA | NA | NA | 88,11 = 99 |
| Marty | NA | NA | NA | NA | NA | NA | 32,3 = 35 |
| Gombe | NA | NA | NA | NA | NA | NA | 16,4,35 = 55 |
| Temba | NA | NA | NA | NA | NA | NA | 14 |
| Alexis | NA | NA | NA | NA | NA | NA | 4,12,42,22,13 = 93 |
| Jess | NA | NA | NA | NA | NA | NA | 2,2,3,6,2,8 = 23 |
| Cara | NA | NA | NA | NA | NA | NA | 90,3 = 93 |
| Samantha | NA | NA | NA | NA | NA | NA | 2,2,3 = 7 |
| Sally | NA | NA | NA | NA | NA | NA | 3 |
| Chima | NA | NA | NA | NA | NA | NA | 6,4 = 10 |
| Keza | NA | NA | NA | NA | NA | NA | 4,8,20 = 32 |
| Unknown | NA | NA | NA | NA | NA | NA | 4,2 = 6 |

Baseline 5

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---------------|----------------------|------------------|-------------------|-------------------------|--------------------|---------------------------|
| Sam | NA | NA | NA | NA | NA | NA | 20,4 = 24 |
| Boyd | NA | NA | NA | NA | NA | NA | 0 |
| Marty | NA | NA | NA | NA | NA | NA | 23,6 = 29 |
| Gombe | NA | NA | NA | NA | NA | NA | 4,17 = 21 |
| Temba | NA | NA | NA | NA | NA | NA | 0 |
| Alexis | NA | NA | NA | NA | NA | NA | 8,12,3,35,2,5,6 = 71 |
| Jess | NA | NA | NA | NA | NA | NA | 3,2,3,6,7 = 21 |
| Cara | NA | NA | NA | NA | NA | NA | 8,3 = 11 |
| Samantha | NA | NA | NA | NA | NA | NA | 5,1 = 6 |
| Sally | NA | NA | NA | NA | NA | NA | 5 |
| Chima | NA | NA | NA | NA | NA | NA | 2,6,4 = 12 |
| Keza | NA | NA | NA | NA | NA | NA | 11,12,76,20,50,51,7 = 227 |
| Unknown | NA | NA | NA | NA | NA | NA | 6 |

Baseline 6

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---------------|----------------------|------------------|-------------------|-------------------------|--------------------|--------------|
| Sam | NA | NA | NA | NA | NA | NA | 6 |
| Boyd | NA | NA | NA | NA | NA | NA | 0 |
| Marty | NA | NA | NA | NA | NA | NA | 13,3 = 16 |
| Gombe | NA | NA | NA | NA | NA | NA | 0 |
| Temba | NA | NA | NA | NA | NA | NA | 7 |
| Alexis | NA | NA | NA | NA | NA | NA | 14 |
| Jess | NA | NA | NA | NA | NA | NA | 0 |
| Cara | NA | NA | NA | NA | NA | NA | 7,4,5,1 = 17 |
| Samantha | NA | NA | NA | NA | NA | NA | 3,2 = 5 |
| Sally | NA | NA | NA | NA | NA | NA | 4,6 = 10 |
| Chima | NA | NA | NA | NA | NA | NA | 2 |
| Keza | NA | NA | NA | NA | NA | NA | 24 |
| Unknown | NA | NA | NA | NA | NA | NA | 0 |

Baseline 7

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---------------|----------------------|------------------|-------------------|-------------------------|--------------------|--------------|
| Sam | NA | NA | NA | NA | NA | NA | 6,4 = 10 |
| Boyd | NA | NA | NA | NA | NA | NA | 4 |
| Marty | NA | NA | NA | NA | NA | NA | 6,28 = 34 |
| Gombe | NA | NA | NA | NA | NA | NA | 3,3,22 = 28 |
| Temba | NA | NA | NA | NA | NA | NA | 3 |
| Alexis | NA | NA | NA | NA | NA | NA | 2,2,22 = 26 |
| Jess | NA | NA | NA | NA | NA | NA | 5,7 = 12 |
| Cara | NA | NA | NA | NA | NA | NA | 6,4 = 10 |
| Samantha | NA | NA | NA | NA | NA | NA | 8 |
| Sally | NA | NA | NA | NA | NA | NA | 0 |
| Chima | NA | NA | NA | NA | NA | NA | 3 |
| Keza | NA | NA | NA | NA | NA | NA | 12,16 = 28 |
| Unknown | NA | NA | NA | NA | NA | NA | 0 |

Musicbox 1

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|----------------------------------|----------------------|------------------|-------------------|-------------------------|--------------------|--|
| Sam | 2,4,6 = 12 | | | | | | 4,3,48 = 55 |
| Boyd | 10,7,9,12,6,7,9 = 60 | 3 | | | | 4,5,2,5 = 14 | 6,4,3,26,4,15,38 = 96 |
| Marty | 3,5,4 = 12 | | | | | 6,9,2 = 17 | 14,7,3,4,5,3,9,4,22,17 = 88 9,6,6,19,4,5,37,12,21,3 = 122 |
| Gombe | 5,4,7,8 = 24 | | | | | | 8,49,6,3,2,9,21,18,40,8,29 = 193 |
| Temba | 7,69,45,12,3,4,22 = 162 | 3,2 = 5 | | | | | 6,8,4,9,9,3,5,7,2,8,52,6,3,2,5,12,8 = 149 |
| Alexis | 17,37,26,19,5,4,33,12 = 153 | | 9/2 = 9 | | | | |
| Jess | 2,5 = 7 | | | | | 6,2,4 = 12 | 7,5,7,4,12,28,19,16,4 = 95 |
| Cara | | | | | | | 16,6,2,5,7 = 36 |
| Samantha | 12,47,19 = 78 | | | | | | 7,16,5,3,22,7 = 60 |
| Sally | | | | | | | 22,4 = 27 |
| Chima | 12,67,8,7 = 94 | | | | | | 7,3,2,1,3,6,4,2,18,14,5,69 = 134 |
| Keza | 68,23,48,12,4,29,8,14,7,28 = 241 | 4,3,2,2,4 = 15 | 9/2 = 9 | | | | 67,43,2,36,48,2,5,3 = 206 |
| Unknown | | | | | | | 2,1,3 = 6 |

Dipper 1

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|--|---|------------------------------------|-------------------|-------------------------|---|--|
| Sam | 36,101 = 137 | 41 | | | | 25 | 7,2,4,2 = 15 |
| Boyd | | | 19/2 | | | 19 | |
| Marty | 10,9,110 = 129 | 77 | | | | 7 | 7,3,7,2,3,5,9,2,2,9 = 49 |
| Gombe | 2,64 = 66 | 3,42 = 45 | | | | 29,48,15,23,9,38,42 = 204 | 4,7,8,8,4,49 = 80 |
| Temba | | | | | | 106,17,78 = 201 | 11,15,6,1,5,2,15 = 55 |
| Alexis | 15,37,8,118,13,134,68,10,21 8,31,48,236,214,49,63,157,2 68,83,222,101,115,108,127, 86,15,137,49,54 = 2784 70,28,8,24,13,12,200,117,33 ,58,87,84,3,308,10,7,89,364, 13,164,198 = 1890 | 43,15,17,26,4,39 = 144 158,30,29,55,60,14,34,56,33 ,78,10,207,58,53,14,20,7,12, 24 = 952 | | | 10 | 24,14,18,10,12,78,10,207,58 ,53,14,20,24,29,41,13,122 = 747 | 2,3,10,4,4,9,10,19,26,5,4,2,1 ,3,6,8,26,7,1,9,2,9,2,19,2,6,5 = 204 |
| Jess | | | 19/2 | | 3 | | 3,9,2,3,4,3,4,3 = 31 |
| Cara | | | | | | 4 | 4,4,7,14 = 29 |
| Samantha | 22,11,44,93,73 = 243 | 29,45,14,78,9 = 175 | 50/2,53/2,197/2,53/2 = 353 | | | 60,40 = 100 | 7,8,4 = 19 |
| Sally | | | | | | | 2 |
| China | 98 | 13,122 = 135 | 38/2 | | | 24,85,102,24,26 = 261 | 3,7,2,3,15,56 = 86 |
| Keza | 24,2,2,40 = 68 | | 50/2,53/2,197/2,53/2,38/2 = 391 | | | 48,4,29,45,14,4,39 = 183 | 2,3,4,12,3,4,26 = 54 |
| Unknown | | | | | | | 1,1 = 2 |

Dipper 2

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|-------------------|----------------------|------------------|-------------------|-------------------------|--------------------|--|
| Sam | 8 | | | | | | 8,27 = 35 |
| Boyd | | | | | | | |
| Marty | 9 | 74 | | | 12 | 6 | 5,4,9,9,10,128,14 = 179 |
| Gombe | | 11 | | | | 25 | 3,50 = 53 |
| Temba | 34 | | | 12,14 = 26 | | | 17 |
| Alexis | | | | 4,8 = 12 | | 74 | 12,2,4,29,2,4,5,4,2,61,116 = 241 |
| Jess | 43,2,362,34 = 441 | 123 | | 71 | | | 4,2,4,8,68,2,22,5,9,20,3,25,4 = 176 |
| Cara | | | | | | | 4,5 = 9 |
| Samantha | 9 | | | | | | 5,26,16 = 47 |
| Sally | | | | | 3 | | |
| China | 11,11 = 22 | | | 159,11 = 170 | | | 85,91,13,4,45,68 = 306 |
| Keza | 10,29,25 = 64 | | | 3 | | 18,11,10 = 39 | 10,41,20,35,10,2,10 = 126 |
| Unknown | | | | | | | 13,5,4,1,1,1 = 25 |

Dipper 3

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|----------------------------------|----------------------|------------------|-------------------|-------------------------|------------------------------------|-----------------------------|
| Sam | | 75 | | | | 4 | 22,58,7,7 = 94 |
| Boyd | | | | | | | |
| Marty | 2 | | | | | | 5,3,5,3,9,7,9 = 41 |
| Gombe | | | | 7 | | | 10,3,58 = 71 |
| Temba | 25 | 55,15,21 = 91 | | 10 | | | 5,4,13,159,4,10 = 195 |
| Alexis | 76,35,44,169,79,394,14 = 811 | | 209/2,12/2 = 221 | 8 | | 23,13,27,28,9,15,75,12,29 = 231 | 14,2,3,8,3,25,18,7,4,4 = 88 |
| Jess | 39,72,431 = 542 | 4,50,27 = 81 | | 5 | | | 4,2,2,3,6,9 = 26 |
| Cara | | | | | | | 4,3,2,8 = 17 |
| Samantha | | | | | 6 | 26 | 3,9,15,4,21 = 52 |
| Sally | | 12 | | | | | 2,2,33 = 37 |
| China | 15 | 83 | | 42 | | | 16,5,26 = 47 |
| Keza | 79,27,156,130,57,106,58 = 613 | 28,9 = 37 | 209/2,12/2 = 221 | 16 | 6 | 83,26,55,21 = 185 | 3,2,4,12 = 21 |
| Unknown | | | | | | | 1,3 = 4 |

Dipper 4

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|------------------|----------------------|------------------|-------------------|-------------------------|--------------------|------------------------|
| Sam | | | | | 5 | | 4,6,3,6 = 19 |
| Boyd | | | | | | | |
| Marty | 13,79 = 92 | | | | | | 3,4,5,16,5 = 33 |
| Gombe | | | | | | | 8,3,27,8,10 = 56 |
| Temba | | | | | | | 5,6,5 = 16 |
| Alexis | | | | | | 34,21,73 = 128 | 2,2,2,7,2,3,33,15 = 66 |
| Jess | 84,147,159 = 390 | 34,21,73 = 128 | | | | | 2,3,5 = 10 |
| Cara | | | | | | | 5,7 = 12 |
| Samantha | | | | | | | 6 |
| Sally | | | | | | | 3 |
| China | | | | 3 | | 41 | 3,15,5,43,4,21,4 = 95 |
| Keza | 23,142,116 = 281 | 41 | | 5 | | | 5 |
| Unknown | | | | | | | 1,5,3,13 = 22 |

Dipper 5

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|--------------------|----------------------|------------------|-------------------|-------------------------|--------------------|---|
| Sam | | | | | | | 112,31,3,4,72,2 = 224 |
| Boyd | 3 | | | | | | 53,3,51,46,2,16,4 = 175 |
| Marty | | | | | | | 24,26, 26,4,15,2,11,2 = 110 17,4,52,43,5,3,4,5,3,7,43,6,6, 14,6,13,7,6,15 = 304 |
| Gombe | | | | | 3 | | 55,14,7 = 76 |
| Temba | 2 | | | | 6 | | 2,21,12,4,4,18,62,21,16,40,1 2,37,12,36,4,9,2 = 263 33,37,3,2,24,4,2,4,1,6,3 = 119 |
| Alexis | | | | | | | 30,9,11,14,2,28,21 = 115 |
| Jess | | | | | | | 2,17 = 19 |
| Cara | | | | | | | 26 |
| Samantha | | | | | | | 108,2,14,11 = 135 |
| Sally | | | | | | | 10,13,3,9,4,3 = 42 |
| China | | | | | | | 2,8,1,6,3,1 = 21 |
| Keza | 117,36,63,46 = 262 | | | | | | |
| Unknown | | | | | | | |

Screwfeeder 1

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|-------------------|----------------------|------------------|-------------------|-------------------------|--------------------|------------------------|
| Sam | | | | | | | 8 |
| Boyd | | | | | | | 6,16 = 62 |
| Marty | 262 | | | | 2 | | 46,12,24 = 82 |
| Gombe | | | | | 6,3,1 = 10 | | 6,82,47 = 135 |
| Temba | 12 | | | | | | 2,87 = 89 |
| Alexis | 34,26 = 60 | | | | 2 | | 46,122,6,20,2 = 196 |
| Jess | 141 | | | | 2 | | 9,2,2,3,12,5 = 33 |
| Cara | | | | | | | 3,4,35 = 42 |
| Samantha | 44 | | | | | | 4,3,7,8,2 = 24 |
| Sally | | | | | | | 9 |
| China | 83,49 = 132 | | | | 3 | | 11,6,45,25,6 = 93 |
| Keza | 9,4,63,31,2 = 109 | | | | | | 2,3,3,2,2,12,4,15 = 43 |
| Unknown | | | | | | | 3,3 = 6 |

Screwfeeder 2

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|------------------------|----------------------|------------------------------------|-------------------|-------------------------|--------------------|-----------------------------|
| Sam | | | | | | | 1,3 = 4 |
| Boyd | 112 | | | | | | 2,3,2,3 = 10 |
| Marty | 239,168 = 407 | | 10/2 = 10 | | | | 3,17,3 = 23 |
| Gombe | 2 | | | | | | 4,3,4 = 11 |
| Temba | | | | | | | |
| Alexis | 23,330,58 = 411 | | 45/2,502/2,76/3,146/2,5/2 = 774 | | | 15 | 5,4,4,11,6,2,7,3,2,3,4 = 38 |
| Jess | 101,532,951,213 = 1797 | 15 | 10/2,502/2,76/3 = 588 | | | | 1,2,3,33,2,5,16 = 62 |
| Cara | 14,45,26 = 85 | | | | | | 3,1,2,4,2 = 12 |
| Samantha | 21 | | | | | | 4,2,3,4 = 13 |
| Sally | | | | | | | |
| China | 4 | | | | | | 2,2,1,5 = 10 |
| Keza | 32,611,38,41,27 = 749 | | 45/2,76/3,146/2,5/2 = 272 | 25 | | 31 | 2,2,5,5,4,19 = 37 |
| Unknown | | | | | | | |

Screwfeeder 3

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|--|----------------------|--|-------------------|-------------------------|-------------------------|---|
| Sam | | | | | | | |
| Boyd | 100,34,90 = 224 | | 272/2 | | | | 3,45,48,4,3,161 = 264 1,2,2,9,3,10,3,4,3,2,2,10,8 = 55 |
| Marty | 785 | 11 | 92/2 | | | 262,94 = 356 | 4,8,9,7 = 26 10,9 = 19 |
| Gombe | | | | | | | 4,15,2,30,2,92,9,9,10,2,7,2,3 5,9,20,91,9,5,21,20,4,10,1,1, 2,16 = 426 |
| Temba | 18,64,13,156,67,82,37,57,31 5 = 805 | | 23/2,453/2,92/2,17/2,46/2,5 6/2 = 687 | | | 35,45,23,14,11,10 = 136 | 6,110,1,14,2,2,1,20,4,8 = 166 |
| Alexis | 65,845,628,444,546 = 2526 | 35,45,39 = 115 | 272/2,453/2,106/2,271/2,16 4/2 = 1266 | | | | 1,4,3,3,5 = 16 |
| Jess | | | | | | | 2,4,2,14,15,19,10,8 = 74 |
| Cara | | | | | | | 4 |
| Samantha | 46,702,35,47 = 830 | 25 | 30/2,69/2,11/2 = 110 | | | | 3,2,12,9,2,6,54,4,6,3 = 101 3,4,4,14,4,5,18,15,37,2,3,1,1 3,1,1,5,4,2,5,3,9,2,47,4,2,1,2 = 211 |
| Sally | | | | | | | 4,2 = 6 |
| China | 4,111,263 = 376 | 23,94 = 117 | 106/2,271/2,164/2,17/2,30/2 = 586 | | | | |
| Keza | 90,155,24,57,42,20 = 386 | | 23/2,46/2,56/2,69/2,11/2 = 205 | | | 10,25 = 35 | |
| Unknown | | | | | | | |

Screwfeeder 4

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|-----------------------------|----------------------|------------------|-------------------|-------------------------|--------------------|--|
| Sam | 33 | | | | | | 82,2,4,7 = 95 |
| Boyd | 156 | | 22/2 | | | | 11,5,5,22 = 43 |
| Marty | 39,84,236 = 359 | | | | | 13 | 2,2,7,8,3 = 22 |
| Gombe | | | | | | | 17 |
| Temba | 591 | | | | | | 4,4,2 = 10 |
| Alexis | 10,41,29,508,41,62,54 = 745 | 57,14 = 71 | | 8 | | 8 | 2,6,2,19,2,3,13,36,38,3,7,3,2 3,3,2,2,7,3,4 = 160 |
| Jess | | | | | | | 8,19,5,6 = 38 |
| Cara | 12,13 = 25 | | | | | | 2,2,3,4 = 11 |
| Samantha | 246,61,135,130 = 572 | 8 | 22/2,24/2 = 46 | | | | 3,6,4 = 13 |
| Sally | 46 | | | | | | 10,3,2,12 = 27 |
| Chima | 14,15,26,154 = 209 | 13 | | | | | 8,5,10,25,22,5,9,5,2,27 = 118 |
| Keza | 238,243,199,11,15,30 = 736 | | 24/2 | | | 57,14 = 71 | 4,4,5,2,13,11,61,2,2,3,2,4,11 .2 = 126 |
| Unknown | | | | | | | 1,1 = 2 |

Screwfeeder 5

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---|----------------------|--|-------------------|-------------------------|--------------------|--|
| Sam | | | | | | | 3,3 = 6 |
| Boyd | 86,243 = 329 | 8 | | 2 | | | 57,11,22,2 = 92 |
| Marty | | | | | | | 5,2 = 7 |
| Gombe | | | | 12 | | | 6,37,106 = 149 |
| Temba | 69 | | 102/2 | | | 6 | 8,42,358,37,27,4 = 476 |
| Alexis | 26,34,121,29,414,117,437,2 67 = 1445 | | 15/2,94/2,19/3,141/2,32/2,1 23/2,49/2,16/2 = 489 | 2 | | | 2,92,1,2,3,2,18,30,9,213,7,4, 2,58,8,20,3,2,2 = 478 |
| Jess | 134 | | | | | | 4,4,4,11,5,13,2 = 43 |
| Cara | 26 | | 16/2 | | | | 41,9,2,2,36 = 90 |
| Samantha | 464,144 = 608 | | 12/2,25/2,87/2 = 124 94/2, 19/3,32/2,123/2,49/2 = 317 | | | | 107,5,28,5,5,8 = 158 |
| Sally | 98,20,91 = 209 | | | | | 8 | 3,3,11,7 = 24 |
| Chima | | | | | | | 35,10,39,9,19 = 112 |
| Keza | 53,46,34,28,143,28,192 = 524 | 6 | 102/2,15/2,19/3,141/2,12/2, 25/2,87/2 = 401 | 6 | | | 4,6,13,11,2,5,4,8,3,3,8,8,17, 22,42 = 156 |
| Unknown | | | | | | | 19 |

TV/Video 1

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---------------------------|----------------------|------------------|-------------------|-------------------------|--------------------|---------------------|
| Sam | | | | | | | 8 |
| Boyd | | | | | | | 5 |
| Marty | 8 | | | | | | 1,29,78 = 108 |
| Gombe | 34,20 = 54 | | | | | | 86,4 = 90 |
| Temba | 48,108,88,323,15,17 = 599 | | 9/2,109/2 = 118 | | | | 5,81,2 = 88 |
| Alexis | 9,29,19,15 = 72 | | 9/2, | | | | 2,1,2,5,2,6,10 = 28 |
| Jess | 1,2,4 = 7 | | | | | | 2,8,4,2,4,4,5 = 25 |
| Cara | 3 | | | | | | 2,3,21,3 = 29 |
| Samantha | | | | | | | 4 |
| Sally | | | | | | | |
| Chima | | | 109/2, | | | | 3 |
| Keza | 15 | | | | | | 2,4 = 6 |
| Unknown | | | | | | | 3 |

TV/Video 2

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---------------|----------------------|------------------|-------------------|-------------------------|--------------------|---------------------------------------|
| Sam | | | | | | | 1,2 = 3 |
| Boyd | 6,9 = 15 | | | | | | 2,4,2,2,3 = 13 |
| Marty | 7 | | | | | | 2,3 = 5 |
| Gombe | 2 | | | | | | 6,10 = 16 |
| Temba | 23,44 = 67 | | | | | | 1,2,4,4,10 = 21 |
| Alexis | 9,2,8 = 19 | | | | | | 2,1,2,1,3,10,2,2,6,2,4,12,2,2 = 51 |
| Jess | 1 | | | | | | 2,3,2,7,6,2,3,10,3 = 38 |
| Cara | 10,2,8 = 20 | | | | | | 3,3,2,14,4,21 = 47 |
| Samantha | | | | | | | 3,3,2 = 8 |
| Sally | | | | | | | 3,2,2,3,3,2,2,3,2,11,7,2 = 42 |
| Chima | | | | | | | 2,2,1,3,4,4,13 = 29 |
| Keza | 41 | | | | | | 6,12,6,3,2,4,5,5,5,4,5,6,6 = 69 |
| Unknown | | | | | | | 1,1,1 = 3 |

TV/Video 3

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|------------------|----------------------|------------------|-------------------|-------------------------|--------------------|--|
| Sam | 27 | | 30/2, | | | | 3,6,3,11,3,5 = 31 |
| Boyd | | | 9/2, | | | | 2,2,6,2,2,3,3,3 = 23 |
| Marty | 3,17 = 20 | | 9/2, | | | | 4,6,2,3,2,6 = 23 |
| Gombe | 2,1 = 3 | | | | | | 2,2,2,8,9,2,2,4,3,10,5,60,2,3, 4,54,3,3,4 = 182 |
| Temba | 10 | | | | | | 2,3,4,3 = 12 |
| Alexis | 12,9 = 21 | | | | | | 4,52 = 56 |
| Jess | | | | | | | |
| Cara | | | | | | | 2,6,52,3 = 63 |
| Samantha | 59,20 = 79 | | 8/2, | | | | 3,5,4,4 = 16 |
| Sally | 1,7 = 8 | | | | | | 36,3,6 = 45 |
| Chima | 2 | | | | | | 2,3,4,1,14,2,2,3 = 31 |
| Keza | 3,22,16,8,5 = 54 | | 8/2,30/2 = 38 | | | | 5,3,2,8,2,1,3,5,2 = 31 |
| Unknown | | | | | | | |

TV/Video 4

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---------------------|----------------------|------------------|-------------------|-------------------------|--------------------|---|
| Sam | | | | | | | 5 |
| Boyd | 14,29 = 43 | | | | | | 2,5,8,2 = 17 |
| Marty | 12,7,4,15 = 48 | | | | | | 2,2 = 4 |
| Gombe | 18,6 = 24 | | | | | | 3,6,5,7,8,4,4,23,12,4,5 = 81 |
| Temba | 23,62,12,23,4 = 124 | | 12/2 = 12 | | | | 3,6,17,23,33,6,4,3,8,10 = |
| Alexis | 9,7,6,3,4 = 29 | | | | | | 3,6,7,4,2,2,9,8,15,6,4,6,3,7,6 9,9,2 = 102 |
| Jess | 5 | | | | | | 3,5,7,3,8,23,5 = 31 |
| Cara | | | | | | | 1,6,8,3 = 18 |
| Samantha | 8,5,9,12,3 = 37 | | | | | | 3,5,7,42,4 = 61 |
| Sally | | | | | | | 3 |
| Chima | 28,4 = 32 | | | | | | 3,4,12,23,9,7,8,3 = 69 |
| Keza | 9,6,8 = 23 | | 12/2 = 12 | | | | 3,6,5,8,3,6,2,7,4 = 44 |
| Unknown | | | | | | | |

TV/Video 5

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|--------------------------|----------------------|-------------------------|-------------------|-------------------------|--------------------|---------------------------|
| Sam | | | | | | | 7,8,4,5 = 24 |
| Boyd | 4,3 = 7 | | 16/2 = 16 | | | | 1,2,3,7,3,9,17,38,4 = 83 |
| Marty | | | | | | | 3,35,9,4,6,19,8,7 = 91 |
| Gombe | 4 | | | | | | 33,8,6,3,9,5,7,3,9,2 = 85 |
| Temba | 23,17,7,3,8,38,9,4 = 109 | | 42/2,12/2,9/2,16/2 = 79 | | | | 5,8,4,9,3,6,7 = 42 |
| Alexis | 33,12,9,7,3 = 64 | | 42/2,9/2 = 51 | | | | 5,8,4,6,7,3,9,4,7,8 = 61 |
| Jess | 5,4 = 9 | | | | | | 23,42,9 = 74 |
| Cara | | | | | | | |
| Samantha | | | 14/2 = 14 | | | | 3,6,8,4,3 = 24 |
| Sally | | | | | | | 4 |
| Chima | 7,5,2 = 14 | | | | | | 28,9,16,4,6 = 63 |
| Keza | 16,8,4,5,9,4 = 46 | | 12/2,14/2 = 26 | | | | 2,5,7,8 = 22 |
| Unknown | | | | | | | 4,2 = 6 |

Marbleroll delivering Jaffas and Marbles 1

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|--|----------------------------|---|--|-------------------------|---|--|
| Sam | 18 | | | | | | 2,136,4 = 142 |
| Boyd | 9,4 = 13 | 4,7 = 11 | | | | 26 | 5,2,89 = 96 |
| Marty | | 17 | 8/3, | 1 | | | 2,238 = 240 |
| Gombe | 85,34 = 119 | | 193/2 | 28 | | | 2,3,2 = 7 |
| Temba | 25 | 46 | | 50,11,33 = 94 | | 17,66 = 83 | 5,673,66,42,5 = 791 |
| Alexis | 28,9,25,26,6,55,68,29,12,34, 50,89,2,14,32,29,25,55,8,3,1 6,4,5,10 = 634 | 14,23,26,14,62,38,59 = 236 | 9/2,193/2,93/2,166/2,33/2 = 494 | 10,7,26,91,15,68,32,39,95,4 3,4 = 430 | 31/2,143/2,37/2 = 211 | 7,5,25 = 37 | 3,25,2,4,3,3,1,2,3710,21,4,5, 1,24,2,1 = 3811 |
| Jess | 37,4 = 41 | | | | | | 4,2,8,4 = 18 |
| Cara | | 66 | 8/3, | | | | 3,2 = 5 |
| Samantha | 11,7 = 18 | | 10/2,25/2 = 35 | 2 | | | 2,2,3 = 7 |
| Sally | 21 | | | | | | 2,18 = 20 |
| Chima | 18 | | | | | | 60,2,31 = 93 |
| Keza | 58,15,47,39,49,5,8,57,34,10, 9,28,65,4,6,74,114,72,9,48,8 | 5,25 = 27 | 10/2,9/2,25/2,93/2,8/3,166/2 ,33/2 = 344 | 8,34,6,23,73,69 = 213 | 31/2,143/2,37/2 = 211 | 4,14,23,14,62,46,38,59 = 3,8,4,2,4,1,4,137,34,3,4,37,1 260 | 9,8,6,3,2,1,2,5,3 = 290 |
| Unknown | | | | | | | 4,5 = 9 |

Marbleroll delivering Jaffas and Marbles 2

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|--|----------------------|---------------------|----------------------------|-------------------------|--------------------|--------------------------|
| Sam | | | | | | | 6 |
| Boyd | | | | | | | |
| Marty | | | | 10 | | | 4,5 = 9 |
| Gombe | | | | | | 4 | 5,4,5 = 14 |
| Temba | 14 | 3 | | 2 | | | 17,2,4,48 = 71 |
| Alexis | 3,102,59,58,15 = 237 | | 15/2,18/2 = 33 | 17 | | 16,3 = 19 | 2,2,1,1,8,22,9,37 = 82 |
| Jess | 27 | | | 2 | | | 3,6,2,8,4,5,2,2 = 32 |
| Cara | | | 12/2, | | | | 13,8 = 21 |
| Samantha | | | | | | | 22,4 = 26 |
| Sally | 18 | | | | | 73 | 5,3 = 8 |
| Chima | 157,2,5 = 164 | 13,7 = 20 | 12/2,13/2 = 25 | 5 | | | 4,44,7,2,3,4 = 64 |
| Keza | 9,42,127,156,26,22,36,34,76 .135,40,4,8,11,50 = 776 | 16,4,73 = 93 | 15/2,18/2,13/2 = 46 | 3,126,8,25,6,41,6,38 = 253 | | 13,7 = 20 | 4,2,2,1,1,2,3,2,7,2 = 26 |
| Unknown | | | | | | | 2,7 = 9 |

Marbleroll delivering Jaffas and Marbles 3

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|--------------------------------------|----------------------|---------------------------|--------------------|-------------------------|--------------------|-----------------------|
| Sam | 4 | | | | | | 14 |
| Boyd | 96 | | 69/2, | 56 | | | 1,2 = 3 |
| Marty | | | | | | | |
| Gombe | | | | 7,116 = 123 | | | 2 |
| Temba | 34,13,57,116 = 220 | 7 | 69/2,21/2 = 90 | 88,262 = 350 | | | 2,194,458 = 654 |
| Alexis | 5,142,6,34,25,7,498,83,4,79 = 883 | 22,29,4 = 55 | 5/2,21/2,123/2,75/2 = 224 | 176 | 27/2, | 20 | 6,2,23 = 31 |
| Jess | | | | | | | 4 |
| Cara | | | | | | | |
| Samantha | | | 5/2, | | | | 17 |
| Sally | 2 | | | | | | 3,4,1 = 8 |
| Chima | 40 | | | | | | 4 |
| Keza | 138,36,53,138,9 = 374 | 20 | 123/2,75/2 = 198 | 19,28,23,109 = 179 | 27/2, | 22,7,29,4 = 62 | 4,3,296,5,2,4,4 = 318 |
| Unknown | | | | | | | 5 |

Marbleroll delivering Jaffas and Marbles 4

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|--|----------------------|-----------------------|---|-------------------------|--------------------|--------------------------|
| Sam | | | | 2 | | | 6,4,7,2 = 19 |
| Boyd | 3,5,4,12 = 24 | | | 4,12,8 = 24 | | 4,7 = 11 | 3,7,5,4,9 = 28 |
| Marty | 3 | | | 7,3,9,2,7,4 = 32 | | 6 | 4,7,3,8,2,3 = 27 |
| Gombe | 16,8 = 24 | | | 23,14,6,18,8,4 = 56 | | | 5,3,3,7,4 = 22 |
| Temba | 13,9,6,4,16,7,9,12,6,9 = 91 | | | 6,3,2,2,6,5,4,8 = 36 | 13/2 = 13 | 3 | 4,6,5,7,35,5,3,2,6 = 73 |
| Alexis | 6,8,8,4,23,36,17,9,5,8,26,66 = 216 | | 26/2,43/2 = 69 | 3,16,3,4,7,3 = 38 | 13/2 = 13 | 3 | 3,6,5,2,19,15,6,9,4 = 69 |
| Jess | 7,12,35,12,8,9 = 83 | | | 4,12,7,3,4,5,15,2 = 52 | | | 4,23,4,6,7 = 44 |
| Cara | | | 62/2 = 62 | 2,10 = 12 | | | 3,6,4,8,3,2 = 26 |
| Samantha | 6,9,31 = 46 | | 32/2 = 32 | 3,2,3 = 8 | | | 3,6,2,6,24,7 = 48 |
| Sally | 9,21,19 = 49 | | | 3 | | | 12,9 = 21 |
| Chima | 46,12,9,16,23 = 106 | | 62/2 = 62 | 6,8 = 14 | | | 8,5,14,3,6 = 36 |
| Keza | 12,56,43,78,12,36,128,6,5,4 7,53,258,56,12,34 = 836 | 4,7,6,3,3 = 23 | 26/2,32/2, 43/2 = 101 | 7,9,12,16,5,8,9,12,10,6,5,32 5,8,9,6,4,3,6,4,7 = 196 | | | 5,7,4,8,3,3,4,7,8 = 49 |
| Unknown | | | | | | | 3,3 = 6 |

Marbleroll delivering Jaffas and Marbles 5

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|--|----------------------|---------------------|-------------------------|-------------------------|--------------------|-------------------------------|
| Sam | | | | | 5/2 = 5 | | 3,6,9,24 = 42 |
| Boyd | 62 | | 13/2 = 13 | 9,12,7 = 28 | | 8 | 5,7,4,8,3,1,3,8,7 = 55 |
| Marty | 28,37,18 = 83 | | | 23 | 5/2 = 5 | | 6,3,4,8,4,3,7,8,9,4,12,8 = 76 |
| Gombe | | | | 4,7 = 11 | | | 7,8,4,6 = 25 |
| Temba | 14,23,41,9,16,8 = 111 | | | | | | 6,15,7,4 = 32 |
| Alexis | 12,17,16,37,10,8,3 = 103 | | 16/2,13/2 = 29 | 6,22,19,5 = 52 | 14/2 = 14 | | |
| Jess | | | 27/2,43/2,16/2 = 86 | 13,18,8,9,27,6 = 81 | | | 3,2,5,8 = 18 |
| Cara | | | 23/2 = 23 | | | | |
| Samantha | | | | 14,5 = 19 | | 6 | 3,4 = 7 |
| Sally | | | | | | | |
| Chima | 8,5,14,19,24 = 70 | | 23/2 = 23 | 16,13 = 29 | | | 4,7 = 11 |
| Keza | 43,23,68,52,13,56,78,32,16, 19,7,23,58,23,54,14,12,15,1 7,8,9,21,55,31,6,5 = 758 | 14 | 27/2,43/2 = 70 | 23,46,16,3,6,17,4 = 115 | 14/2 = 14 | | 3,6,4,8 = 21 |
| Unknown | | | | | | | |

Marbleroll delivering Jaffas and Marbles (with slides) 1

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---|-------------------------------------|---|-------------------|-------------------------|--------------------|----------------------|
| Sam | | 17 | 69/2 = 69 | | | 49 | 3,6,8 = 17 |
| Boyd | 5,7,14 = 26 | 14,23 = 37 | 15/2,14/2 = 19 | 4 | | 10,32,9 = 51 | 4,6,3 = 13 |
| Marty | 6,9 = 15 | 3,18 = 21 | 87/2 = 87 | | | 5,7 = 12 | 6,8 = 14 |
| Gombe | 8 | 19 | 87/2,15/2,69/2 = 171 | | | 6,17 = 23 | 2,2 = 4 |
| Temba | 12,26,9,7,7,9,14 = 84 | | 41/2,9/2,6/2,53/2 = 109 129/2,48/2,18/2,20/2,53/2,1 5/2 = 283 | 6,12 = 18 | | 23,18,8,15 = 64 | 5,2,7,6,6,3,8,9 = 46 |
| Alexis | | | | | | | 3,5,2,5,6,7,12 = 40 |
| Jess | 29,6 = 35 | 9,73,5,7,8 = 102 | 69/2,41/2,9/2,26/2 = 145 | | 7/2 = 7 | 3 | 2 |
| Cara | 7,5 = 13 | | 49/2, 22/2 = 71 | | | | |
| Samantha | 5,4,8 = 17 | 9,7 = 16 | 13/2 = 13 | | | 8,7,3,14 = 32 | 2,3 = 5 |
| Sally | 6 | | 18/2 = 18 | | | | |
| China | 9,13,6,5 = 33 | | 49/2,22/2 = 71 | | | 19,3,5 = 29 | 3 |
| Keza | 35,27,44,12,7,64,7,9,25,38,1 2,49,10,3,8,6 = 356 | 8,10,32,7,3,6,3,14,5,49,15 = 152 | 129/2,69/2, 48/2,20/2,6/2,26/2 = 298 | 5,8,4,7,14,8 = 46 | 7/2 = 7 | 14,73,9,7 = 103 | 3,6,8,5,3 = 25 |
| Unknown | 4 | | | | | | |

Marbleroll delivering Jaffas and Marbles (with slides) 2

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|--|-----------------------------------|--|----------------------|-------------------------|--------------------|------------------------|
| Sam | 4,8,16 = 28 | 7 | | 23,12 = 35 | | 9 | 17,12 = 29 |
| Boyd | 8,7,16 = 29 | 5,7,14,7,8 = 41 | 9/2,42/2 = 51 | | | 7,9 = 16 | 5,7,3,9 = 24 |
| Marty | 17 | 5,23,8,15,3,7 = 61 | 42/2 = 42 | 2,17 = 19 | 15/2 = 15 | 7 | 4,6 = 11 |
| Gombe | 7 | 9 | 9/2 = 9 | | 15/2 = 15 | 5,14 = 19 | 7,9,4,3 = 23 |
| Temba | 7,9,14,48,23,18 = 119 | | 9/3,41/2 = 50 23/2,41/2,12/2,17/3, 9/3 = 102 | 28,17,6,4,3,6,9 = 73 | | 34,21,8,7,14 = 84 | 2,8,3,16,6,8,3,15 = 61 |
| Alexis | 33,5,27,19 = 84 | | | 3,6,4 = 13 | | 7,8 = 15 | 3,5,4,4,4,7 = 27 |
| Jess | 26,14,9,9,28 = 86 | | 17/3 = 17 | | | 9,7 = 16 | 4,7,4,9,6,3,8,5 = 46 |
| Cara | 7,14 = 21 | 6,3 = 9 | 14/2 = 14 | 6 | | 15 | 8 |
| Samantha | | | 13/2 = 13 | | | 8,2,7 = 17 | 6,8,4,5,6,3 = 32 |
| Sally | 9 | | | 4 | | 5 | 22,6 = 28 |
| China | 6,8,3,27 = 44 | 5 | 14/2 = 14 | 12,7,4 = 23 | | 6,3 = 9 | 9,6,8,4,9,25,8 = 69 |
| Keza | 15,9,63,25,17,44,59,37,14,9, 7,15,4 = 318 | 34,9,21,7,9,8,7,7,8,2,14 = 126 | 23/2,41/2,12/2,17/3,41/2,9/3 ,13/2 = 156 | | | 5,23,8,3,7 = 46 | 5,3,7 = 15 |
| Unknown | | | | | | | 3,1 = 4 |

Marbleroll delivering Jaffas and Marbles (with slides) 3

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|--|----------------------|--------------------------|-------------------|-------------------------|--------------------|-------------------------------|
| Sam | 5 | | | | 2 | 5,7 = 12 | 12 |
| Boyd | 28,6 = 34 | 5,9,7 = 2 | | 5,4 = 9 | 2,2 = 4 | | 3,8,4,6,9,4,5 = 39 |
| Marty | 7 | | 37/2 = 37 | | | 9,8 = 17 | 7,5,9,4,7,7,4,6 = 49 |
| Gombe | 7,5,4,8 = 24 | | | | 2 | | 8,6,3,9,12 = 38 |
| Temba | 6,3,8,12,17,22,9,8 = 85 | | | 9,7 = 16 | | 7,5,7 = 19 | 27,37,9,6,17 = 96 |
| Alexis | 9,9,17,38,6 = 79 | | 23/2, 13/2,37/2 = 73 | 7,5 = 12 | | | 6,9,4,7,3,8,4,17,8,9,3,9 = 87 |
| Jess | 42,16 = 58 | | 16/2 = 16 | 6 | | | 6,7,16,22,5 = 56 |
| Cara | 2 | | 36/2 = 36 | | | | 14, 5 = 19 |
| Samantha | 19,7,4 = 30 | | 44/2 = 44 | 3 | | 9,7 = 16 | 3,5,2 = 10 |
| Sally | 9,10 = 19 | | | | | | 5,7,2,8,32,7 = 61 |
| China | 15,18,8,2,6 = 49 | | 36/2 = 36 | 8 | | 9 | 6,8,4,8,8,9,3,6,7,2,4,5 = 70 |
| Keza | 9,45,27,14,6,8,9,24,8,9,37,1 2,33,9,7 = 257 | 7,5,9,7,7,8,9 = 52 | 23/2,44/2,13/2,16/2 = 96 | 23,16 = 39 | | | 5,3,7,6,4,6,4,8,3 = 46 |
| Unknown | | | | | | | 2,3,1,3 = 9 |

Marbleroll delivering Jaffas and Marbles (with slides) 4

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|--------------------------------------|----------------------|------------------------|-------------------|-------------------------|--------------------|-------------------------|
| Sam | 23 | | | | | | 4,5 = 9 |
| Boyd | 19,8,7,5,9,3,5,27 = 83 | 9 | 14/2 = 14 | 4 | 28/3,9/2 = 37 | 2 | 5,3 = 8 |
| Marty | | | | | 28/3 = 28 | 9 | 2,7,3,3 = 15 |
| Gombe | | | 8/2 = 8 | 2 | 28/3 = 28 | | 9,2,3,2,8 = 26 |
| Temba | 7,7,33,8,15,12,18,3,9 = 112 | 2 | 8/2 = 8 | 5,6 = 11 | 9/2 = 9 | 9,6 = 15 | 5,8,3,9,4,6 = 35 |
| Alexis | 6,7,4,8 = 25 | | 14/2,4/2,14/2 = 32 | | | | 19,6,8,4,7,2,9,6,3 = 64 |
| Jess | 8,39 = 47 | | | 3 | | 2 | 3 |
| Cara | | | | | | | 7,8,6,5 = 26 |
| Samantha | 6,8 = 14 | | 16/2 = 16 | | 8/2 = 8 | 12 | 14 |
| Sally | | | 9/2 = 9 | | | | 5,8,3,2 = 18 |
| China | 23,3,7,9,24,7 = 73 | | | | | 8,4 = 12 | 7,16,7,3 = 33 |
| Keza | 9,13,17,22,27,18,9,4,5,38,3 = 165 | 12,9,6,8,4,2 = 41 | 16/2,14/2,9/2,4/2 = 39 | 7,6,8 = 21 | 8/2 = 8 | | 6,9 = 15 |
| Unknown | | | | | | | 3 |

Marbleroll delivering Jaffas and Marbles (with slides) 5

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|-------------------------------|----------------------|------------------|-------------------|-------------------------|--------------------|------------------|
| Sam | | | | 6 | | | 5,9 = 14 |
| Boyd | 12 | | 4/2 = 4 | 9 | 15/2 = 15 | 3 | 9,5,7,4,3 = 28 |
| Marty | | | | | | 9 | 6,4,2,8 = 20 |
| Gombe | | | | 9 | 15/2 = 15 | | 3,6,9,3 = 21 |
| Temba | 9,14,7,9,22 = 61 | | | 22,4 = 26 | | 12 | 7,9,8,3 = 27 |
| Alexis | 19,8,5,5,8 = 45 | | 9/2,4/2,4/2 = 17 | | 1/2 = 1 | 6,8 = 14 | 7,5,8,4,9,3 = 36 |
| Jess | 24,33 = 57 | | | 6 | 1/2 = 1 | 5 | 2,23 = 25 |
| Cara | | | 14/2 = 14 | | | | 11,3 = 14 |
| Samantha | | | | 5,3 = 8 | 6/2 = 6 | | 7,8 = 15 |
| Sally | | | | | | | 3 |
| Chima | 10 | | 14/2 = 14 | 7,11 = 18 | | | 4,3,9 = 16 |
| Keza | 29,36,87,12,14,6,8,19,7 = 218 | 9,6,8,5,12,3 = 43 | 9/2,4/2 = 13 | | 6/2 = 6 | | 3,4 = 7 |
| Unknown | | | | | | | 2,3 = 5 |

Marbleroll, delivering Coated Peanuts 1

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---|----------------------|--|-------------------|-------------------------|--------------------|--|
| Sam | 4,9,7,8,5,6,3 = 42 | | 23/2 = 23 | | | | 6,3,15,23,6,4 = 57 |
| Boyd | 5,12,23,17 = 57 | 6 | 11/3,24/2 = 35 | 3 | | | 8,7,5,7,3,3,4,8,3,9,6,7 = 70 9,6,8,5,8,3,5,4,8,9,21,11 = 97 |
| Marty | 14 | 6 | 7/2,9/2,63/2 = 79 | 6 | | | 4,8,7,6,9,6,3,4,2,15,8,7,4 = 83 |
| Gombe | 12,9,6 = 27 | | 63/2,16/2,24/2 = 103 | | | 6 | 7,8,6,4,8,6,4,8,3,9,7,3,23,7 = 103 |
| Temba | 4,8,6,3,9,7,6,23,4,7,19,11,34 = 141 | 4 | 14/2,17/2,9/2,11/3 = 51 | 5 | | 19 | 5,9,8,4,6,12,8,9,5,3,8 = 77 7,9,5,3,8,7,6,3,6,4,12,16 = 86 |
| Alexis | 6,5,7,3,8,11,18,20,42,12,16,8 = 156 | | 43/2,23/2,11/3 = 77 | | | 6,6 = 12 | 4,9,4,3,5,2,6,5,3,4,2,5,3,7,6,8,9,3,6,3 = 97 |
| Jess | 12,7,9 = 28 | | | 5,6 = 11 | | | 3,1,1 = 5 |
| Cara | | | 26/3,128/2,137/2,54/2 = 345 26/3,16/2,9/2,32/2,34/2 = 117 | | | 9 | 4,5,4,5,6,8 = 32 |
| Samantha | | | | | | 14 | 4,3,2 = 9 |
| Sally | | | 47/2 = 47 | | | | 4,8 = 12 |
| Chima | | | 3/2,137/2,54/2 = 194 26/3,16/2,9/2,43/2,14/2,17/2,32/2,7/47/2,2,9/2,128/2,3/2,34/2,11/3,9/2 = 405 | 3 | | | 5,6,8,7,5,8,4,9,7 = 61 |
| Keza | 8,7,5,9,22,26,28,3,129,7,48,18,3,8,9,14 = 344 | 14,6,9,19 = 48 | | 2,3,4 = 9 | | 4 | |
| Unknown | | | | | | | |

Marbleroll, delivering Coated Peanuts 2

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|-------------------------------|----------------------|---|-------------------|-------------------------|--------------------|--------------------------------------|
| Sam | 14 | | | | | | 4,7,16 = 37 |
| Boyd | 6,8,3 = 17 | 38,9,6 = 53 | 47/2,16/2 = 63 | | | | 4,7,9,5,7 = 42 |
| Marty | 9,14 = 23 | 6 | 58/3 = 58 | | | | 2,3,8,12 = 25 |
| Gombe | 35 | | 16/2 = 16 | | | 9,6 = 15 | 4,7,8 = 19 |
| Temba | 8,6,9,3 = 26 | | 58/3 = 58 | 8 | | 6 | 6,4,7,3,5 = 25 |
| Alexis | 7,8,6,9 = 39 | | 34/3,47/2,198/2,17/2 = 294 | 16,24 = 30 | | 38,3 = 41 | 14,43,9 = 66 |
| Jess | 17,29 = 46 | 5,3 = 8 | 58/3 = 58 | 4,7 = 11 | | | 2,4,3,9 = 18 |
| Cara | 23,4 = 27 | | | | | | 12,12 = 24 |
| Samantha | 6 | | 32/2,11/2 = 43 | | | 5 | 5,7 = 13 |
| Sally | | | 16/2,20/2 = 36 | | | | 19 |
| Chima | 23,18 = 41 | | 34/3 = 34 | | | 7 | 3,6 = 9 |
| Keza | 34,8,7,4,6,5,22,17,16,8 = 112 | 7,5 = 12 | 32/2,16/2,20/2,11/2,198/2,34/3,17/2 = 328 | | | 5 | 9,8,5,7,4,7,3,7,8,3,8,6,3,4,2,5 = 89 |
| Unknown | | | | | | | |

Marbleroll, delivering Coated Peanuts 3

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|--|----------------------|--|-------------------|-------------------------|--------------------|--|
| Sam | | | 42/2,27/3 = 69 | | | | 7 |
| Boyd | 6,9,18,27,8 = 68 | 23 | 23/2,27/3,59/2 = 109 | | | 17 | 4,5,2,3 = 14 |
| Marty | 38 | 6,7 = 13 | 44/2 = 44 | | | | 16,8,4,9,14,7 = 58 |
| Gombe | 12,6,14 = 32 | | 27/3,44/2 = 71 | | | 9 | 14 |
| Temba | 22,14,7,18,38 = 99 | | 36/2,45/2 = 81 | 6,2 = 8 | | 7,5 = 12 | 28,31,13,5,9,17,8,6,9,48,7 = 181 |
| Alexis | 63,18,9,4,25,13,8,10 = 150 | | 42/2,23/2,12/2,59/2,19/2,48/2,51/2,16/2,36/2 = 306 | | | 28,5 = 33 | 17,8,9,25,8,5,9,10,93,44,27,18,3 = 276 |
| Jess | 16,55,17,8,12,6,7 = 121 | | 48/2,51/2 = 99 | | | | 6,8,3,9,10 = 36 |
| Cara | 15 | | 44/2,20/2,38/2 = 102 | | 4/2 = 4 | | 2,4 = 6 |
| Samantha | 23,17,31 = 71 | 8 | 69/2 = 69 | | | 8 | 5,7,2 = 14 |
| Sally | | 5 | 45/2 = 45 | | | 5 | 5 |
| Chima | 33 | | 44/2,20/2,38/2 = 102 | 5 | 4/2 = 4 | 7,8 = 15 | 4,8 = 12 |
| Keza | 28,57,9,6,5,3,9,31,18,7,27,9,48,54,11,8,5,16,6 = 357 | 17,9,28,5,8,5,7 = 79 | 12/2,19/2,26/2,69/2 = 126 | 3 | | 23,6 = 29 | 3,5,2,6,5 = 21 |
| Unknown | | | | | | | |

Marbleroll, delivering Coated Peanuts 4

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|-------------------------|----------------------|---------------------------|-------------------|-------------------------|--------------------|--------------------------|
| Sam | 4,9 = 13 | | 29/2 = 29 | | | | 3,3 = 6 |
| Boyd | 39,15 = 54 | 8 | 12/2,14/2 = 26 | 4 | | | 4,5 = 9 |
| Marty | 16 | | 12/2,22/2 = 34 | 2 | | | 6,12 = 18 |
| Gombe | | | 22/2 = 22 | | | | 2,3 = 5 |
| Temba | 32,21,8,15,7,9,12 = 104 | | | 5,3,7 = 15 | | 8 | 7,5,5,8,13,8 = 46 |
| Alexis | 9,8,52,18 = 87 | | 51/2,14/2, 29/2 = 94 | 9,3 = 12 | | 21,6 = 27 | 12,9,3,7,8,8,4,15,9 = 75 |
| Jess | 73 | | 21/2,51/2 = 72 | | | | 4,5 = 9 |
| Cara | | | 21/2 = 21 | | | | 4,8 = 12 |
| Samantha | | | 42/2,21/2,33/2 = 96 | | | | 2,2,6 = 10 |
| Sally | | | | | | | 3,6,8 = 17 |
| Chima | | | 21/2 = 21 | | | | 4,7 = 11 |
| Keza | 57,12,8,35,14 = 126 | 21,6,8 = 35 | 42/2,21/2,21/2,33/2 = 117 | 12,4,3,1,5 = 25 | | 8 | 3,5,3,8,2 = 21 |
| Unknown | | | | | | | 2 |

Marbleroll, delivering Coated Peanuts 5

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---------------------------------------|-------------------------|-------------------------------|-------------------|-------------------------|--------------------|---------------------------|
| Sam | 5,7 = 13 | 5 | | | 4 | | 3,4 = 7 |
| Boyd | 7,5 = 12 | 4,8,5,2 = 19 | 56/2,31/2,16/2,9/2,15/2 = 127 | | 2 | | 6,6,3,7 = 22 |
| Marty | 7 | | 15/2 = 15 | | | | 14,6,8,7,6,2,8,9,13 = 73 |
| Gombe | 15 | | | | | 2 | 36,9,5,7,3,7,4 = 71 |
| Temba | 13,7,7,5,9,31,28,4,9 = 113 | | 9/2 = 9 | 11,5 = 16 | | 9,7,5,12 = 33 | 16,13 = 29 |
| Alexis | 3,7,2,2,9,7,17,25,36,8,3,9 = 128 | | 56/2,31/2,128/2,16/2 = 231 | | | 5,4,8,32,4,17 = 70 | 6,14,18,5,3,5,8,31,4 = 94 |
| Jess | 6,8,3 = 17 | 14,6,9,7,8 = 44 | 128/2 = 128 | 5 | | | 7,26,9,18,5,4,16,4 = 89 |
| Cara | 5 | | 24/2,9/2 = 33 | | | 9 | 12,7 = 19 |
| Samantha | 14 | 6 | 41/2,9/3 = 50 | | | 9,6 = 15 | 5,4 = 9 |
| Sally | 12 | | 16/2,9/3 = 25 | | | 5 | 14,3,9 = 31 |
| Chima | 9,9,4,14 = 36 | | 24/2,9/2 = 33 | 3 | | 8 | 6,4,8,4,2,3 = 27 |
| Keza | 5,8,3,18,33,21,8,16,5,37,14,9,6 = 183 | 32,4,12,9,6,17,9,5 = 94 | 41/2,16/2,9/3 = 66 | 4 | | 14,6,6 = 26 | 3,5,2,6,4,8,6,12,2,9 = 57 |
| Unknown | | | | | | | 1,3 = 4 |

APPENDIX D

Raw behavioural observation data from Experiment 5. Based on the behavioural classes in Table 2.2.

| Baseline 1 | | | | | | | |
|------------|---------------|----------------------|------------------|-------------------|-------------------------|--------------------|---------------------|
| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
| Sam | NA | NA | NA | NA | NA | NA | 12,6,3 = 21 |
| Boyd | NA | NA | NA | NA | NA | NA | 3 |
| Marty | NA | NA | NA | NA | NA | NA | 3 |
| Gombe | NA | NA | NA | NA | NA | NA | 4,9,3 = 16 |
| Temba | NA | NA | NA | NA | NA | NA | 32,2,5 = 39 |
| Alexis | NA | NA | NA | NA | NA | NA | 11,7,4,8,3 = 33 |
| Jess | NA | NA | NA | NA | NA | NA | 4,7,2,9,27,4,8 = 61 |
| Cara | NA | NA | NA | NA | NA | NA | 7,9,4,7 = 27 |
| Samantha | NA | NA | NA | NA | NA | NA | 5,4,3 = 12 |
| Sally | NA | NA | NA | NA | NA | NA | 6,8 = 14 |
| Chimu | NA | NA | NA | NA | NA | NA | 33,9,4,6 = 52 |
| Keza | NA | NA | NA | NA | NA | NA | 8,3,2,2,5 = 20 |
| Unknown | NA | NA | NA | NA | NA | NA | |

| Baseline 2 | | | | | | | |
|------------|---------------|----------------------|------------------|-------------------|-------------------------|--------------------|----------------|
| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
| Sam | NA | NA | NA | NA | NA | NA | 7,7 = 14 |
| Boyd | NA | NA | NA | NA | NA | NA | |
| Marty | NA | NA | NA | NA | NA | NA | 6,3,6 = 15 |
| Gombe | NA | NA | NA | NA | NA | NA | 8,4 = 12 |
| Temba | NA | NA | NA | NA | NA | NA | 5,3,28 = 35 |
| Alexis | NA | NA | NA | NA | NA | NA | 17 |
| Jess | NA | NA | NA | NA | NA | NA | 6,8,8,3 = 25 |
| Cara | NA | NA | NA | NA | NA | NA | 4 |
| Samantha | NA | NA | NA | NA | NA | NA | 9 |
| Sally | NA | NA | NA | NA | NA | NA | 2,1 = 3 |
| Chimu | NA | NA | NA | NA | NA | NA | 6,8,3 = 17 |
| Keza | NA | NA | NA | NA | NA | NA | 8,3,6,1,2 = 20 |
| Unknown | NA | NA | NA | NA | NA | NA | |

| Baseline 3 | | | | | | | |
|------------|---------------|----------------------|------------------|-------------------|-------------------------|--------------------|-----------------------|
| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
| Sam | NA | NA | NA | NA | NA | NA | 5,8,3,9 = 25 |
| Boyd | NA | NA | NA | NA | NA | NA | 11,3 = 14 |
| Marty | NA | NA | NA | NA | NA | NA | 4,4 = 8 |
| Gombe | NA | NA | NA | NA | NA | NA | 7,3,14,3 = 27 |
| Temba | NA | NA | NA | NA | NA | NA | 3,8,2 = 13 |
| Alexis | NA | NA | NA | NA | NA | NA | 7,3,8,8,5,4,12,7 = 54 |
| Jess | NA | NA | NA | NA | NA | NA | 4,3,1,1 = 9 |
| Cara | NA | NA | NA | NA | NA | NA | 16,2,8 = 26 |
| Samantha | NA | NA | NA | NA | NA | NA | 5,9 = 14 |
| Sally | NA | NA | NA | NA | NA | NA | 3,2,7,7,2 = 21 |
| Chimu | NA | NA | NA | NA | NA | NA | 7 |
| Keza | NA | NA | NA | NA | NA | NA | 12,7,25,9 = 53 |
| Unknown | NA | NA | NA | NA | NA | NA | 2 |

| Baseline 4 | | | | | | | |
|------------|---------------|----------------------|------------------|-------------------|-------------------------|--------------------|-----------------|
| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
| Sam | NA | NA | NA | NA | NA | NA | |
| Boyd | NA | NA | NA | NA | NA | NA | 3 |
| Marty | NA | NA | NA | NA | NA | NA | |
| Gombe | NA | NA | NA | NA | NA | NA | |
| Temba | NA | NA | NA | NA | NA | NA | 18,3,6 = 27 |
| Alexis | NA | NA | NA | NA | NA | NA | 7,18,4,9 = 38 |
| Jess | NA | NA | NA | NA | NA | NA | 3,5,8,17,4 = 37 |
| Cara | NA | NA | NA | NA | NA | NA | |
| Samantha | NA | NA | NA | NA | NA | NA | 7 |
| Sally | NA | NA | NA | NA | NA | NA | |
| Chimu | NA | NA | NA | NA | NA | NA | 11 |
| Keza | NA | NA | NA | NA | NA | NA | 7,34,8,2 = 51 |
| Unknown | NA | NA | NA | NA | NA | NA | |

Baseline 5

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---------------|----------------------|------------------|-------------------|-------------------------|--------------------|---------------|
| Sam | NA | NA | NA | NA | NA | NA | 5,8,4,9 = 26 |
| Boyd | NA | NA | NA | NA | NA | NA | 3,3,3 = 9 |
| Marty | NA | NA | NA | NA | NA | NA | 4,3 = 7 |
| Gombe | NA | NA | NA | NA | NA | NA | 4,3 = 7 |
| Temba | NA | NA | NA | NA | NA | NA | 34,3,8,5 = 50 |
| Alexis | NA | NA | NA | NA | NA | NA | 39,2,1,4 = 46 |
| Jess | NA | NA | NA | NA | NA | NA | 6,7,8 = 21 |
| Cara | NA | NA | NA | NA | NA | NA | 13,8,3,5 = 29 |
| Samantha | NA | NA | NA | NA | NA | NA | 7,6 = 13 |
| Sally | NA | NA | NA | NA | NA | NA | 8,62 = 70 |
| Chima | NA | NA | NA | NA | NA | NA | 7,22,5 = 34 |
| Keza | NA | NA | NA | NA | NA | NA | 1,18 = 19 |
| Unknown | NA | NA | NA | NA | NA | NA | 2,1 = 3 |

Baseline 6

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---------------|----------------------|------------------|-------------------|-------------------------|--------------------|------------------|
| Sam | NA | NA | NA | NA | NA | NA | 32,2,4 = 38 |
| Boyd | NA | NA | NA | NA | NA | NA | 3 |
| Marty | NA | NA | NA | NA | NA | NA | 45 |
| Gombe | NA | NA | NA | NA | NA | NA | 17,4 = 21 |
| Temba | NA | NA | NA | NA | NA | NA | 94,3 = 97 |
| Alexis | NA | NA | NA | NA | NA | NA | 6,7,7,22 = 42 |
| Jess | NA | NA | NA | NA | NA | NA | 6,8,3 = 17 |
| Cara | NA | NA | NA | NA | NA | NA | 1 |
| Samantha | NA | NA | NA | NA | NA | NA | |
| Sally | NA | NA | NA | NA | NA | NA | |
| Chima | NA | NA | NA | NA | NA | NA | 5,8,10,25,3 = 51 |
| Keza | NA | NA | NA | NA | NA | NA | 5,9,3,78,3 = 98 |
| Unknown | NA | NA | NA | NA | NA | NA | |

Baseline 7

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---------------|----------------------|------------------|-------------------|-------------------------|--------------------|--------------------|
| Sam | NA | NA | NA | NA | NA | NA | |
| Boyd | NA | NA | NA | NA | NA | NA | 4,10,9 = 23 |
| Marty | NA | NA | NA | NA | NA | NA | 3,14,8 = 25 |
| Gombe | NA | NA | NA | NA | NA | NA | |
| Temba | NA | NA | NA | NA | NA | NA | 26,42,78,3,6 = 155 |
| Alexis | NA | NA | NA | NA | NA | NA | 6 |
| Jess | NA | NA | NA | NA | NA | NA | 3 |
| Cara | NA | NA | NA | NA | NA | NA | |
| Samantha | NA | NA | NA | NA | NA | NA | |
| Sally | NA | NA | NA | NA | NA | NA | |
| Chima | NA | NA | NA | NA | NA | NA | 8,5 = 13 |
| Keza | NA | NA | NA | NA | NA | NA | 16,7,32 = 55 |
| Unknown | NA | NA | NA | NA | NA | NA | |

Baseline 8

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---------------|----------------------|------------------|-------------------|-------------------------|--------------------|--------------|
| Sam | NA | NA | NA | NA | NA | NA | 6,3,8 = 17 |
| Boyd | NA | NA | NA | NA | NA | NA | 2,2,7,1 = 12 |
| Marty | NA | NA | NA | NA | NA | NA | 5,5,8 = 18 |
| Gombe | NA | NA | NA | NA | NA | NA | 34 |
| Temba | NA | NA | NA | NA | NA | NA | 7 |
| Alexis | NA | NA | NA | NA | NA | NA | 4,8,6,2 = 20 |
| Jess | NA | NA | NA | NA | NA | NA | 14,3,8 = 25 |
| Cara | NA | NA | NA | NA | NA | NA | 6,8 = 14 |
| Samantha | NA | NA | NA | NA | NA | NA | 7,2,8 = 17 |
| Sally | NA | NA | NA | NA | NA | NA | 3,3,8 = 14 |
| Chima | NA | NA | NA | NA | NA | NA | 57,2 = 59 |
| Keza | NA | NA | NA | NA | NA | NA | 3,1 = 4 |
| Unknown | NA | NA | NA | NA | NA | NA | |

Baseline 9

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---------------|----------------------|------------------|-------------------|-------------------------|--------------------|------------------------|
| Sam | NA | NA | NA | NA | NA | NA | |
| Boyd | NA | NA | NA | NA | NA | NA | 27 |
| Marty | NA | NA | NA | NA | NA | NA | 3 |
| Gombe | NA | NA | NA | NA | NA | NA | 7 |
| Temba | NA | NA | NA | NA | NA | NA | 8,4,7,2,9 = 26 |
| Alexis | NA | NA | NA | NA | NA | NA | 21,8,1 = 30 |
| Jess | NA | NA | NA | NA | NA | NA | 52 |
| Cara | NA | NA | NA | NA | NA | NA | 8,8 = 16 |
| Samantha | NA | NA | NA | NA | NA | NA | 7 |
| Sally | NA | NA | NA | NA | NA | NA | 4,24 = 28 |
| Chima | NA | NA | NA | NA | NA | NA | 4,8,2,9,4,2,2,1,4 = 36 |
| Keza | NA | NA | NA | NA | NA | NA | 5,7,2,9,29,4,2,2 = 60 |
| Unknown | NA | NA | NA | NA | NA | NA | 1 |

Screwfeeder - FR1 Series A

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---|----------------------|----------------------|-------------------|-------------------------|--------------------|----------------|
| Sam | 23,52,6,64,7=152 8,27,87,12,65,52,73,52,6,8=390 | 2,9 = 11 | 25/2 | | | | 3,2,8 = 13 |
| Boyd | | 5,8,11,4,4 = 32 | 25/2,78/2 = 103 | | | 2 | 2,2,1,4 = 9 |
| Marty | 14,9,7,106,6,5=147 9,93,27,4,84,82,115,92,78,6 | 2,3,3 = 8 | 56/2 | | | 2,3,1,5 = 11 | 4,1 = 5 |
| Gombe | 2=646 21,51,7,64,69,115,92,104,11 | 3,2 = 5 | 56/2 | | | | 7,2 = 9 |
| Temba | 5,92,87,3,5,62=887 26,4,8,5,37,54,18,49,62,34,7 | 4 | | | | 3,4 = 7 | 5 |
| Alexis | 9,6,84,108,5,64=643 9,13,73,238,83,211,238=86 | 5 | 12/2,78/2 = 90 | | | 5,8,3,9,11,2 = 38 | 3,2,4,1,2 = 12 |
| Jess | 5 | | 136/2 | | | | 2,3,3,5 = 13 |
| Cara | | | | | | | |
| Samantha | | | | | | | |
| Sally | | | | | | | |
| Chima | 5,18,7,69,63,98,48,141=449 29,38,52,7,27,12,16,72,67,5 | | 3/2 | | | 4 | 3,4,2 = 9 |
| Keza | 89,7,93,21,906=1441 | 4 | 12/2,3/2,136/2 = 151 | | | 3,4 = 7 | 2 |
| Unknown | | | | | | | |

Screwfeeder - FR2 Series A

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---|----------------------|-----------------------|-------------------|-------------------------|--------------------|----------------|
| Sam | 15,23,5,1,479,8,8 = 539 | | 63/2,29/2 = 92 | | | 34,6 = 40 | 5,4,2 = 11 |
| Boyd | 23,17,4,64,18,8=134 | 82 | 49/2 | | | 12 | 3,2 = 5 |
| Marty | 4,3,2,4,6=19 | 12 | | | | 13,6 = 19 | 2,2,1 = 5 |
| Gombe | 5,58,15,6,111,8,5,52,129,4,6 6 = 459 | 6 | 12/2,38/2,29/2 = 79 | | | | 2 |
| Temba | 14,14,58,2,64,85,9,53,115,3 9,14 = 467 | 13,6 = 19 | 12/2,38/2 = 50 | | | 126,82,347 = 555 | 3,5,6 = 14 |
| Alexis | 16,5,8,27,3,6,5,5,39,3,3,3,3, 7,10,4,5,3,19,4,28 = 206 | | 63/2,49/2 = 112 | | | 391 | 2,4,3,1,2 = 14 |
| Jess | 226,3,34,34,216,182,156,19 5,12,12,54,212 = 1336 | 126,347 = 473 | 259/2 | | | | 2,1,3,2 = 8 |
| Cara | | | | | | | |
| Samantha | 3 | 16 | 11/2,15/2 = 26 | | | 42 | |
| Sally | | | | | | | |
| Chima | 15,6,256,6,4,4,6 = 297 15,8,64,9,62,25,2,27,27,49,1 | | | | | | 2,3,1 = 6 |
| Keza | 0,47,6,15,16,618 = 1000 | 34,391,42 = 467 | 11/2,259/2,15/2 = 285 | | | 16 | 2,1,3,4,2 = 12 |
| Unknown | | | | | | | |

Screwfeeder - FR4 Series A

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|--|----------------------|-------------------|-------------------|-------------------------|--------------------|--------------|
| Sam | 52 | | | | | 2,6 = 8 | 2,1,1 = 4 |
| Boyd | 3,4,4,8=19 | 10 | 19/2,5/2,3/2 = 27 | | | 9 | 2,6 = 8 |
| Marty | 3,3=6 | | | | | 10 | 3,4,6 = 13 |
| Gombe | 6,14,10,18,6,4,2,97=157 16,12,10,13,15,4,13,33,73,1 | | | | | 9,5 = 14 | 8,7 = 15 |
| Temba | 92,12,2,8,4,6,1264=1677 | 9 | | | | | 9,15,2 = 26 |
| Alexis | 6,4,288,19,9,3,17,67,2=355 | 5 | 19/2,3/2 = 22 | | | 24 | 4,2 = 6 |
| Jess | 52,12,198,197,12,4=475 | 2,24 = 26 | 5/2,35/2 = 40 | | | | 2,3,1,9 = 15 |
| Cara | 2 | | | | | | 3,1 = 4 |
| Samantha | 4,10=14 | 3 | 5/2 | | | | 3,5 = 8 |
| Sally | | | | | | | |
| Chima | 7,4,42,102,6=161 | | | | | | 3,1 = 4 |
| Keza | 64,4,8,63,9,113,128,78,64,4 85,4,131,14=1165 | 2,6,9 = 17 | 35/2,5/2 = 40 | | | 3,2 = 5 | 2 |
| Unknown | | | | | | | |

Screwfeeder - FR8 Series A

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|----------------------|----------------------|------------------|-------------------|-------------------------|--------------------|--------------|
| Sam | 42 | | | | | | 4,17 = 21 |
| Boyd | 19 | 4 | | | | | 7 |
| Marty | 2 | | | | | | 2 |
| Gombe | 13,22,2=37 | 3 | | | | | 3,2,4 = 9 |
| Temba | 93,49,13,265,188=508 | | 21/2,15/2 = 36 | | | 3 | 2,29 = 31 |
| Alexis | 31 | | 21/2,24/2 = 45 | | | | 4,2,5 = 11 |
| Jess | 14 | 6 | 36/2 | | | | 2,1 = 3 |
| Cara | | | | | | | |
| Samantha | | | | | | | |
| Sally | | | | | | | |
| Chima | 12,6=18 | | | | | | 2,4 = 6 |
| Keza | 66,34,251=351 | | 24/2,36/2 = 60 | 4,6,8,2,17 = 37 | | 4,6 = 10 | 3 |
| Unknown | | | | | | | |

Screwfeeder - FR16 Series A

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---------------------------|----------------------|------------------|-------------------|-------------------------|--------------------|----------------------|
| Sam | | | | | | | 4,2 = 6 |
| Boyd | 9 | | 3/2 | | | 2,2 = 4 | 1,3,5,2 = 11 |
| Marty | | | | | | | |
| Gombe | 6 | | | | | 3 | 6,3 = 9 |
| Temba | 133,212,64,31,98,34,6=578 | 2,5,7,2,3 = 19 | 3/2 | 62 | | | 2,2,2,5,1 = 12 |
| Alexis | 49 | | | | | 5 | 7,4,7,1 = 19 |
| Jess | | | | | | | |
| Cara | | | | | | | |
| Samantha | | | | | | | 2,4 = 6 |
| Sally | | | | | | | |
| Chima | | | | | | | 3,1 = 4 |
| Keza | 21,144=165 | | | 4,2,6,3,3,22 = 37 | | 7 | 6,2,5,2,1,2,9,4 = 31 |
| Unknown | | | | | | | |

Screwfeeder - FR32 Series A

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|-----------------------------|----------------------|------------------|-------------------|-------------------------|--------------------|-------------------------|
| Sam | | | | | | | |
| Boyd | | | | | | | 4,3,12 = 19 |
| Marty | | | | | | | |
| Gombe | | | | | | | 2,4 = 6 |
| Temba | 8,7,12,6,4,6,236,63,41,5=38 | | | | | 4,3 = 7 | 2,5,1,2,3,4,2,6,2, = 27 |
| Alexis | 18 | | | | | | 4,3,2 = 9 |
| Jess | | | | | | | 2,1,1 = 4 |
| Cara | | | | | | | 3 |
| Samantha | | | | | | | 4 |
| Sally | | | | | | | |
| Chima | 11 | | | | | 5 | 2,1 = 3 |
| Keza | 7,6,36=49 | 4,5,3 = 12 | | | | | 3,2,1,1,3 = 10 |
| Unknown | | | | | | | |

Screwfeeder - FR1 Series B

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---|----------------------|------------------|-------------------|-------------------------|--------------------|---------------------|
| Sam | 88,53,149,6,35=331 | 3 | 12/2 | | | 2,3 = 5 | 6,2,1,2,1 = 12 |
| Boyd | 112,54,22,9,12,129=338 | 3,12,5,39 = 59 | 32/2,13/2 = 45 | | | 4,6 = 10 | 2,1 = 3 |
| Marty | 11,76=87 | 6,6 = 12 | | | | 3 | 1 |
| Gombe | 97,23,194,184=498 | | | | | 12,6 = 18 | 4,4 = 8 |
| Temba | 233,438,6,7,217,202,153,28 2=1538 | 2,4 = 6 | 32/2 | 2,1 = 3 | | 39 | 2,4,2,17,2,1 = 28 |
| Alexis | 141,42,23,85=291 | | 12/2,13/2 = 25 | | | 16,5 = 21 | 5,4 = 9 |
| Jess | 94,492,144=790 | | | | | | 2,2 = 4 |
| Cara | 14 | | | | | | 2 |
| Samantha | 53,6=59 | | 41/2 | | | 3,4,2 = 9 | 2,3 = 5 |
| Sally | 18 | | | | | | 3,6 = 9 |
| Chima | 5,43,18,16,67=149 | | | | | 4,1 = 5 | 3,2,5,7, = 17 |
| Keza | 137,4,62,42,192,177,43,86,3 0,63,54,218,425=1533 | 4,3,16,4,1,2 = 30 | 41/2 | 3,2 = 5 | | | 2,1,3,4,5,12,2 = 29 |
| Unknown | | | | | | | |

Screwfeeder - FR2 Series B

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|--|----------------------|--------------------|-------------------|-------------------------|--------------------|--------------------|
| Sam | 68,21,30,86=205 | | 9/2 | | | | 5,3,3,2 = 13 |
| Boyd | 55,115,16,64,12,6,117,67=452 | 21 | 322/2,33/2 = 355 | | | 3 | 2,1,2,4,8,3,2 = 22 |
| Marty | 20,31,34=85 | | 14/2 | | | | 12,2,1 = 14 |
| Gombe | 14,81,183,68,183=529 | | | | | | 3,1,2,4,1 = 11 |
| Temba | 98,74,7,153,4,4,113,127,23,6,20,153,153,255=1190 | 3,4 = 7 | 53/2,61/2 = 114 | | | | 2,9,3 = 14 |
| Alexis | 63,61,50,41,9,49,84,18,14,68,237,57,27=758 | | 14/2,53/2,9/2 = 76 | | | 4 | 2,1 = 3 |
| Jess | 62,163,98,212=535 | | 322/2 | | | | 3,2,2 = 7 |
| Cara | 3 | | | | | | 1 |
| Samantha | 6,3=9 | | 21/2,61/2 = 82 | | | 12 | 3 |
| Sally | 4 | | | | | | |
| Chima | 7,39,66,95,103,25,103,84,42=504 | | | | | 6,21 = 27 | 2,4,2 = 8 |
| Keza | 85,6,21,6,23,57,92,68,127,71,166,786=1508 | 6,12 = 18 | 33/2,21/2 = 54 | | | | 2,1,3,5 = 11 |
| Unknown | | | | | | | |

Screwfeeder - FR4 Series B

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|--|----------------------|------------------|-------------------|-------------------------|--------------------|------------------|
| Sam | 80,6=86 | 9,7 = 16 | 4/2 | | 4 | | 5,8 = 13 |
| Boyd | 4,3=7 | 2 | 4/2,9/2 = 13 | | 4 | 9 | 2 |
| Marty | 4 | | | | | | 3,6 =9 |
| Gombe | 200,88,217,16,215=736 | 28 | 9/2 | | | | 3,2,1= 6 |
| Temba | 7,5,49,49,31,11,8,147,6,281,163,128,286=1122 | | | | | 28,7 = 35 | 3,2,1,1,1,4 = 12 |
| Alexis | 69,12,214,84,294=673 | | | | | | 4,2,1,2 = 9 |
| Jess | 160,289=449 | | | | | | 4 |
| Cara | | | | | | | |
| Samantha | 4 | | 23/2 | | | | 1 |
| Sally | | | | | | | 1,2 =3 |
| Chima | 79,79,88,2,105,4,21=378 | | | | | | 4,3,7 = 14 |
| Keza | 11,6,96,28,111,6,363,200,9,183=1013 | | 23/2 | | | 2 | 2,4,2,3,1 = 12 |
| Unknown | | | | | | | |

Screwfeeder - FR8 Series B

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---------------------------------------|----------------------|------------------|-------------------|-------------------------|--------------------|-------------------|
| Sam | 33 | | | | | | 3,3 = 6 |
| Boyd | 4,69=73 | 39 | | | | | 2,8,1 = 11 |
| Marty | | | | | | | 3 |
| Gombe | 265,119,143=527 | 45 | 15/2 | | | | 3,6 = 9 |
| Temba | 8,129,14,171,107,240,242,271,512=1694 | | 58/2,13/2 = 71 | | | 13,39 = 52 | 3,2,4 = 9 |
| Alexis | 7,242,46,254,84,118=751 | 13 | 58/2 | | | 14 | 5,1,6,3,3 = 18 |
| Jess | 61,5,3=69 | 14,7 = 21 | | | | | 3,1,1 = 5 |
| Cara | | | | | | | |
| Samantha | | | | | | | |
| Sally | | | | | | | |
| Chima | 8,6,36,4,162,9,9=234 | | 13/2 | | | | 6,2 = 8 |
| Keza | 63,4,13,11,4,380,153,170,23=821 | | 15/2 | | | 45,7 = 52 | 3,4,2,2,2,1, = 14 |
| Unknown | | | | | | | |

Screwfeeder - FR16 Series B

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|------------------------------------|----------------------|------------------|-------------------|-------------------------|--------------------|------------------|
| Sam | 7 | | | | | | 2 |
| Boyd | 5 | 7 | 3/2 | | | | 2,4 = 6 |
| Marty | | | | | | | 3 |
| Gombe | 13,4=17 | | | | | | 2,5,2 = 9 |
| Temba | 43,3,6,8,35,19,7,73,14,6,6,4,2=226 | | 3/2,62 = 65 | 7,5 = 12 | | 7 | 2,3,1,4,5,3 = 18 |
| Alexis | 7,9,12,4=32 | | | | | | 3,4,1,2,4 = 14 |
| Jess | 14,6=20 | | | | | | 6,2 =8 |
| Cara | | | | | | | 4,3 = 7 |
| Samantha | | | | | | | 6,2,2 = 10 |
| Sally | | | | | | | 2 |
| Chima | 5 | | | 2 | | 34 | 1 |
| Keza | 6,6,51,60,13,42,4=182 | 34 | 62/2 | | | | 2,5,2 = 9 |
| Unknown | | | | | | | |

Screwfeeder - FR32 Series B

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|----------------------------|----------------------|------------------|-------------------|-------------------------|--------------------|--------------------|
| Sam | 11 | | | | | | 8,2,3 = 13 |
| Boyd | 5 | 6 | | | | | 4,2,3 = 9 |
| Marty | 3 | | | | | | 4,2 = 6 |
| Gombe | 4,3,5=12 | | 4/2 | | | | 1,6,3,2 = 12 |
| Temba | 6,39,53,98,146,6,4,4,3=359 | | | | | | 4,7,2,4,2,3,1 = 23 |
| Alexis | 12 | | 4/2 | | | | 5,3,4,2,2,6 = 22 |
| Jess | 6 | | | | | | 2 |
| Cara | | | | | | | 5,3,4 = 12 |
| Samantha | | | | | | | |
| Sally | | | | | | | |
| Chima | 4 | | | | | | 1 |
| Keza | 4,6,4,43=57 | | | | | 6 | 2,3 = 5 |
| Unknown | | | | | | | |

Screwfeeder - FR64 Series B

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|----------------------------|----------------------|------------------|-------------------|-------------------------|--------------------|--------------|
| Sam | 4 | | | | | | 7,4 = 11 |
| Boyd | | | | | | | 4 |
| Marty | | | | | | | 4 |
| Gombe | 4 | | | | | | 3 |
| Temba | 6,27,6,9,7,17,6,24,7,5=114 | | 11/2 | | | | 2,4,3,1 = 10 |
| Alexis | 7 | | | | | | 3,5 = 8 |
| Jess | 5 | | | | | | 2,7 = 9 |
| Cara | | | | | | | |
| Samantha | | | | | | | 5,1 = 6 |
| Sally | | | | | | | |
| Chima | 4 | | | | | | 8 |
| Keza | 6,9,4=19 | | 11/2 | | | | 4,8,3 = 15 |
| Unknown | | | | | | | |

Marbleroll, delivering Coated Peanuts - FR1 Series A

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|--|----------------------|----------------------|-------------------|-------------------------|--------------------|------------------|
| Sam | 136,21,137,5,76=375 | 7 | 46/2 | | | 2,7 = 9 | 5,3,4,2,2 = 16 |
| Boyd | 105,95,29,5,315,64=613 | 2,23 = 25 | 21/2 | | | 4 | 6,2,1,4 = 13 |
| Marty | 55,58,258=371 | | | | | | 3,6,4,7 = 20 |
| Gombe | 91,9,78,14,29,300,47=568 56,110,180,119,258,9,186,1 | 7,5 = 12 | | | | 23 | 5,3,3 = 11 |
| Temba | 50,437=1505 105,154,15,111,19,85,9,72= | | | | | | 3,2,2,4,1 = 12 |
| Alexis | 570 51,93,56,94,138,349,178=9 | | 46/2,21,2,68/2 = 135 | | | 7 | 3,2,1,2 = 8 |
| Jess | 59 | 4,15 = 19 | | | | | 1,2,2 = 5 |
| Cara | | | | | | | 3 |
| Samantha | | | | | | | 2 |
| Sally | | | | | | | |
| Chima | 92,97,7,54,107,93=450 102,7,82,126,205,43,141,54, | | 6/2 | | | | 3,2,4 = 9 |
| Keza | 63=823 | | 6/2,68/2 = 74 | | | 5,15 = 20 | 2,3,2,5,4,2 = 18 |
| Unknown | | | | | | | 2 |

Marbleroll, delivering Coated Peanuts - FR2 Series A

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|--|----------------------|------------------|-------------------|-------------------------|--------------------|--------------|
| Sam | 13,13,9,438,84=557 | | | | | | 4,3,7 = 14 |
| Boyd | 73,64,25,2,313,49=526 | 16,24 = 40 | 16/2 | | | | 3,5,5,2 = 15 |
| Marty | 53,62,198=313 | | | | | | 7,2 = 9 |
| Gombe | 34,12,85,18,31,300,47=527 11,82,53,117,253,6,186,7,23 | | | | | | 2,4,3,2 = 11 |
| Temba | 1,196,437=1579 | 4 | 16/2,7/2 = 23 | 3,4 = 7 | 2 | 16 | 2,1,3,1 = 7 |
| Alexis | 104,111,19,72,42,85,9=442 | | | | | | 12,6,3 = 21 |
| Jess | 89,59,94,138,382,212=970 | 8 | | | | | 3,2,5,2 = 12 |
| Cara | | | | | | | 3,2 = 5 |
| Samantha | | | | | | | |
| Sally | | | | | | | |
| Chima | 161,98,5,5,54,107,93=523 103,9,79,79,194,54,141,54,6 | | 4/2 | | | 8,4 = 12 | 4,6,2,2 = 14 |
| Keza | 3=697 | | 7/2,4/2 = 11 | | 2 | 24 | 3,2,3,1 = 9 |
| Unknown | | | | | | | |

Marbleroll, delivering Coated Peanuts - FR4 Series A

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|----------------|----------------------|------------------|-------------------|-------------------------|--------------------|------------------|
| Sam | | | | | | | 18,2,4,3,7 = 34 |
| Boyd | | | | | | | 2,4 = 6 |
| Marty | | | | | | | 4 |
| Gombe | | | | | | | 4 |
| Temba | 12,74,69=155 | 4 | 6/2 | | | | 2,3,4,3,9,2 = 23 |
| Alexis | 110,6,23,6=145 | | | | | 4 | 2,1,2,1= 6 |
| Jess | 9 | | | | | | 2,5 = 7 |
| Cara | | | | | | | |
| Samantha | | | | | | | |
| Sally | | | | | | | |
| Chima | | | | | | | |
| Keza | 5,58=63 | | 6/2 | | | | 3,2 = 5 |
| Unknown | | | | | | | |

Marbleroll, delivering Coated Peanuts - FR1 Series B

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---------------|----------------------|------------------|-------------------|-------------------------|--------------------|----------------|
| Sam | | | | | | | 4,3,8,2 = 17 |
| Boyd | | | | 2 | | | 6,4,2,3,1 = 16 |
| Marty | | | | | | | 1,2,1,1 = 5 |
| Gombe | | | | | | | 5,4,3,4 = 16 |
| Temba | | | | | | | 3,2,6,8 = 19 |
| Alexis | 7 | | | | | | 4,3 = 7 |
| Jess | | | | | | | 3,1,1 = 5 |
| Cara | | | | | | | 2 |
| Samantha | | | | | | | |
| Sally | | | | | | | 2 |
| Chima | | | | | | | 4,3 = 7 |
| Keza | 245 | | | | | | 4,3,2 = 9 |
| Unknown | | | | | | | |

Marbleroll, delivering Coated Peanuts - FR8 Series A

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|-------------------------------|----------------------|------------------|-------------------|-------------------------|--------------------|------------------|
| Sam | 62,7=69 | 8,4 = 12 | 7/2 | | | | 6,4,2,8,5 = 25 |
| Boyd | 9,48=57 | 6,32,2 = 40 | | | | | 5 |
| Marty | 6 | | | | | | 4,2 = 6 |
| Gombe | 130,53=183 | 7 | | | | | 4,3,2 = 9 |
| Temba | 64,333,29,34=460 | | | | | 32,4,7 = 43 | 4,3,2,4 = 13 |
| Alexis | 64,91,124,12,16,64=371 | 7 | 7/2 | | | 3,7 = 10 | 3,2,3,1,1,3 = 13 |
| Jess | 242,164,338,619=1363 | | 59/2 | | | | 2,7,4,5,2 = 20 |
| Cara | 8 | | | | | | 3 |
| Samantha | 48 | | | | | | 3,4,5 = 12 |
| Sally | | | | | | | 5 |
| Chima | 106,17=123 | | | | | | 14 |
| Keza | 36,159,367,62,138,297,12=1071 | 3 | 59/2 | | | 6,8,2 = 16 | 2,5,3,7 = 17 |
| Unknown | | | | | | | |

Marbleroll, delivering Coated Peanuts - FR2 Series B

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|--|----------------------|-----------------------|-------------------|-------------------------|--------------------|----------------------|
| Sam | 7,4,39=50 | | | | | | 6,3,8,2 = 19 |
| Boyd | 159,44,95,91=389 | 62 | 121/2 | | | | 2 |
| Marty | 7 | | | | | | 1 |
| Gombe | 23,89,87,5,6,160,183,152=705 | | | | | | 2,9 = 11 |
| Temba | 72,64,113,121,87,8,129,41,142,7,99,116=999 | | 53/2 | | | 62 | 3,2,6,2,8,2,6,3 = 32 |
| Alexis | 139,42,49,7,12,115,8=372 | | 121/2,53/2,16/2 = 190 | | | | 4,8,5,2,8,17,2 = 46 |
| Jess | 31,321,247=599 | 17 | | | | | 4,2,6 = 12 |
| Cara | | | | | | | 4 |
| Samantha | 6 | | 2/2 | | | | 2,1 = 3 |
| Sally | | | | | | | |
| Chima | 29,7,94,96,15,49,312,144,9,32=787 | | 16/2 | | | 4,17,3 = 24 | 3,6,8,3,2,2 = 24 |
| Keza | 7,67,6,40,49,188,10,316,9=1507 | 4,3 = 7 | 2/2 | 3,2 = 5 | | | 4,3,3,4,2 = 16 |
| Unknown | | | | | | | 3 |

Marbleroll, delivering Coated Peanuts - FR4 Series B

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---------------|----------------------|------------------|-------------------|-------------------------|--------------------|---------------|
| Sam | 7 | | | | | | 12,5,4,3 = 24 |
| Boyd | 4 | 4,2 = 6 | | | | | 6,2 = 8 |
| Marty | | | | | | | 3,2,5 = 10 |
| Gombe | 534 | | | | | | 3 |
| Temba | 15,17,307=339 | | 11/2 | | | 2 | 2,8,3 = 13 |
| Alexis | 173 | | | | | | 4,2,1,2 = 9 |
| Jess | 9 | | | | | | 2 |
| Cara | 17 | | | | | | 2,1,3,2 = 8 |
| Samantha | | | | | | | |
| Sally | | | | | | | |
| Chima | 13 | | | | | | 2,4 = 6 |
| Keza | 254,32=286 | | 11/2 | | | 4 | 3,2,2 = 7 |
| Unknown | | | | | | | |

Marbleroll, delivering Coated Peanuts - FR8 Series B

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---------------|----------------------|------------------|-------------------|-------------------------|--------------------|--------------|
| Sam | | | | | | | 5 |
| Boyd | | | | | | | 4,2,3,1 = 10 |
| Marty | | | | | | | 3,6 = 9 |
| Gombe | | | | | | | |
| Temba | 21 | | | 3,6 = 9 | | 3 | 1,2 = 3 |
| Alexis | | | | | | | |
| Jess | | | | | | | 2,5,1 = 8 |
| Cara | | | | | | | 6 |
| Samantha | | | | | | | |
| Sally | | | | | | | 2,3 = 5 |
| Chima | | | | | | | |
| Keza | 13 | 3 | | | | | 2 |
| Unknown | | | | | | | |

Musicbox - FR1 Series A

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---------------|----------------------|------------------|-------------------|-------------------------|--------------------|-------------------|
| Sam | | | | | | | 5,3,7,2,8,12 = 37 |
| Boyd | | | | | | | 3,9,4,3,2 = 21 |
| Marty | | | | | | | 8,6,18,4 = 36 |
| Gombe | | | | | | | 28,4,7 = 39 |
| Temba | 21,374=395 | | | | | 2 | 7,13,6,26 = 52 |
| Alexis | 18 | | 3/2 | | | | 3,7,18 = 28 |
| Jess | 6 | | | | | | 3,7,2 = 12 |
| Cara | | | | | | | 7,12 = 19 |
| Samantha | | | | | | | 24,3,1 = 28 |
| Sally | | | | | | | 4 |
| Chima | 9 | | | | | | 4,3 = 7 |
| Keza | 12,39,28=79 | 2 | 3/2 | | | | 2 |
| Unknown | | | | | | | 2 |

Musicbox - FR2 Series A

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---------------|----------------------|------------------|-------------------|-------------------------|--------------------|--------------|
| Sam | | | | | | | |
| Boyd | | | | | | | 2,1 = 3 |
| Marty | | | | | | | |
| Gombe | | | | | | | |
| Temba | 575 | 6 | | | | | 2,1,5,4 = 12 |
| Alexis | | | | | | | 3,6,2 = 11 |
| Jess | | | | | | 6 | 8,7 = 15 |
| Cara | | | | | | | 2 |
| Samantha | | | | 3 | | | 4 |
| Sally | | | | | | | |
| Chima | | | | | | | |
| Keza | 59 | | | 4,2 = 6 | | | 2,5,4 = 11 |
| Unknown | | | | | | | |

Musicbox - FR4 Series A

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---------------|----------------------|------------------|-------------------|-------------------------|--------------------|--------------|
| Sam | | | | | | | 6,3,7,2 = 18 |
| Boyd | | | | | | | 2,4,1,4 = 11 |
| Marty | | | | | | | 16 |
| Gombe | | | | | | | 3 |
| Temba | 19,11=30 | | | | | | 4,6=10 |
| Alexis | | | | | | | |
| Jess | | | | | | | 4,7=11 |
| Cara | | | | | | | |
| Samantha | | | | | | | 2 |
| Sally | | | | | | | |
| Chima | | | | | | | |
| Keza | 21 | | | | | | 3,5,7 = 15 |
| Unknown | | | | | | | |

Musicbox - FR1 Series B

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---------------|----------------------|------------------|-------------------|-------------------------|--------------------|----------------|
| Sam | | | | | | | 8,3,5,5,4 = 25 |
| Boyd | | | | | | | 6,3,4 = 13 |
| Marty | | | | | | | 3 |
| Gombe | | | | | | | 3,4 = 7 |
| Temba | 237 | | | | | 12 | 3,5 = 8 |
| Alexis | 12 | | | | | | 3 |
| Jess | | | | | | | 2 |
| Cara | | | | | | | 2 |
| Samantha | | | | | | | 4 |
| Sally | | | | | | | 4,5 = 9 |
| Chima | 6 | | | | | | 3,12 = 15 |
| Keza | 9 | 12 | | | | | 3,5 = 8 |
| Unknown | | | | | | | |

Musicbox - FR2 Series B

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---------------|----------------------|------------------|-------------------|-------------------------|--------------------|--------------|
| Sam | | | | | | | |
| Boyd | | | | | | | |
| Marty | | | | | | | |
| Gombe | | | | | | | 2 |
| Temba | 95 | | | | | | 5,8,1 = 14 |
| Alexis | 8 | | | | | | 2,1 = 3 |
| Jess | | | | | | | |
| Cara | | | | | | | |
| Samantha | | | | | | | 2 |
| Sally | | | | | | | |
| Chima | | | | | | | 5 |
| Keza | | | | | | | |
| Unknown | | | | | | | |

Musicbox - FR4 Series B

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---------------|----------------------|------------------|-------------------|-------------------------|--------------------|--------------|
| Sam | | | | | | | 3,6 = 9 |
| Boyd | | | | | | | 4,5,9 = 18 |
| Marty | | | | | | | 2,15 = 17 |
| Gombe | | | | | | | 6 |
| Temba | 9 | | | | | 4 | 2,4 = 6 |
| Alexis | | | | | | | 2 |
| Jess | | | | | | | |
| Cara | | | | | | | 2 |
| Samantha | | | | | | | |
| Sally | | | | | | | 5 |
| Chima | | | | | | | |
| Keza | 13 | 4 | | | | | 4,7 = 11 |
| Unknown | | | | | | | |

Dipper - FR1 Series A

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|------------------------------|----------------------|------------------|-------------------|-------------------------|--------------------|-----------------|
| Sam | 151 | 12 | 62/2 | | | | 7,5,9,4 = 25 |
| Boyd | 53 | | | | | 12 | 4,3,12,5 = 24 |
| Marty | | | | | | | 4,3 = 7 |
| Gombe | 153 | | | | | | 6,3,3,2 = 14 |
| Temba | 12,14,228,331,12,428=1025 | 63 | | | | | 2,7,4,16,2 = 31 |
| Alexis | 94,103=197 | | | | | 63 | 5,3,3 = 11 |
| Jess | 538,158,9,9,607,339,702=2362 | 46 | 62/2 | | | | 3,2,1,1 = 7 |
| Cara | 12 | | | | | | 3,2 = 5 |
| Samantha | 40 | | 42/2 | | | | 3 |
| Sally | | | | | | | 3 |
| Chima | 167 | | | | | | 2,2 = 4 |
| Keza | 72,94,9,149,189=513 | | 42/2 | | | 46 | 3,2,2,1,4 = 12 |
| Unknown | | | | | | | |

Dipper - FR2 Series A

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---------------|----------------------|------------------|-------------------|-------------------------|--------------------|--------------|
| Sam | | | | | | | 5,7 = 12 |
| Boyd | | | | | | | 4,2,2 = 8 |
| Marty | | | | | | | 3,1 = 4 |
| Gombe | | | | | | | 6 |
| Temba | 352,249=601 | | | | 7 | 10 | 3,5,6 = 14 |
| Alexis | | | | | | | 2 |
| Jess | 96 | | | | | | 2,1,2 = 5 |
| Cara | | | | | | | |
| Samantha | | | | | | | |
| Sally | | | | | | | 3,1 = 4 |
| Chima | | | | | | | 6 |
| Keza | 234 | 10 | | 21 | 7 | | 3,2,14 = 19 |
| Unknown | | | | | | | |

Dipper - FR4 Series A

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---------------|----------------------|------------------|-------------------|-------------------------|--------------------|--------------|
| Sam | | | | | | | 4,6,3,8 = 21 |
| Boyd | | | | | | | 4,7,2 = 13 |
| Marty | | | | | | | 4,4,3 = 11 |
| Gombe | | | | | | | 3,2,4 = 9 |
| Temba | 17,23,11=51 | | | 23 | | | 2,3,2 = 7 |
| Alexis | | | | | | | 3,7 = 10 |
| Jess | | | | | | | 1 |
| Cara | | | | | | | 4,8 = 12 |
| Samantha | | | | | | | 2,2 = 4 |
| Sally | | | | | | | 3 |
| Chima | | | | | | | 6 |
| Keza | | | | | | | |
| Unknown | | | | | | | |

Dipper - FR1 Series B

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|-------------------------|----------------------|------------------|-------------------|-------------------------|--------------------|--------------|
| Sam | 32,19,61=112 | | | | | | 3,2,2 = 7 |
| Boyd | | | | | | | |
| Marty | | | | | | | |
| Gombe | 14,54=68 | | | | | | 3,2 = 5 |
| Temba | 12,17,215,463,72=779 | | | | | 62 | 3,5,2,2 = 12 |
| Alexis | 113,109,324=546 | | | | | | 4,1,1 = 6 |
| Jess | 652,914,1328,286=3180 | 62,6 = 68 | 31/2 | | | | 3,2,4 = 9 |
| Cara | | | | | | | |
| Samantha | 10 | | | | | | 2,3 = 5 |
| Sally | | | | | | | |
| Chima | 1248,103=1351 | | | | | | 4,3,5 = 12 |
| Keza | 53,27,337,19,12,135=583 | | 31/2 | | | 6 | 2,4,1,1 = 8 |
| Unknown | | | | | | | |

Dipper - FR2 Series B

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---------------|----------------------|------------------|-------------------|-------------------------|--------------------|--------------|
| Sam | | | | | | | 4,6,3,8 = 21 |
| Boyd | | | | | | | 4,7,3 = 14 |
| Marty | | | | | | | |
| Gombe | | | | | | | |
| Temba | 127 | 14 | | 31 | | | 2,4 = 6 |
| Alexis | 12 | | | | | 14 | 3,4 = 7 |
| Jess | 4 | | | | | | 2,3,1,6 = 12 |
| Cara | | | | | | | |
| Samantha | | | | | | | |
| Sally | | | | | | | |
| Chima | | | | | | | |
| Keza | | | | | | | |
| Unknown | | | | | | | |

Dipper - FR4 Series B

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---------------|----------------------|------------------|-------------------|-------------------------|--------------------|--------------|
| Sam | | | | | | | 2,5 = 7 |
| Boyd | | | | | | | 4,6 = 10 |
| Marty | | | | | | | 3,3 = 6 |
| Gombe | | | | | | | 4,9 = 13 |
| Temba | 21 | | | 14 | | | 2,5,7,2 = 16 |
| Alexis | | | | | | | |
| Jess | 14 | | | | | | 2,6,2 = 10 |
| Cara | | | | | | | |
| Samantha | | | | | | | 2 |
| Sally | | | | | | | 4 |
| Chima | | | | | | | 8 |
| Keza | | | | | | | |
| Unknown | | | | | | | |

TV/Video - FR1 Series A

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---------------|----------------------|------------------|-------------------|-------------------------|--------------------|--------------|
| Sam | | | | | | | 4,3,2,2 = 11 |
| Boyd | | | | | | | 4,8,3,1 = 16 |
| Marty | | | | | | | 3,2,2,2 = 9 |
| Gombe | | | | | | | 2,2,1,3 = 8 |
| Temba | 224,73,21=318 | | 51/2 | 18 | 4 | | 2,5,2 = 9 |
| Alexis | 42 | | | | | | 3,2 = 5 |
| Jess | | | | | | | 2,2,6,2 = 12 |
| Cara | | | | | | | 4,3,6 = 13 |
| Samantha | | | | | | | 3,5,2 = 10 |
| Sally | | | | | | | 3,2 = 5 |
| Chima | | | | | | | 4 |
| Keza | 71,54=125 | | 51/2 | | 4 | | 3,2,8 = 13 |
| Unknown | | | | | | | |

TV/Video - FR2 Series A

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---------------|----------------------|------------------|-------------------|-------------------------|--------------------|--------------|
| Sam | | | | | | | 6,2 = 8 |
| Boyd | | | | | | | 4,3,3,2 = 12 |
| Marty | | | | | | | 2,2 = 4 |
| Gombe | | | | | | | 5,1,3 = 18 |
| Temba | | | | | | | |
| Alexis | | | | | | | 3 |
| Jess | | | | | | | 2 |
| Cara | | | | | | | |
| Samantha | | | | | | | |
| Sally | | | | | | | |
| Chima | | | | | | | 2 |
| Keza | 9 | | | 7 | | | 4,3,1 = 8 |
| Unknown | | | | | | | |

TV/Video - FR1 Series B

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---------------|----------------------|------------------|-------------------|-------------------------|--------------------|--------------|
| Sam | | | | | | | 5,1 = 6 |
| Boyd | | | | | | | |
| Marty | | | | | | | |
| Gombe | | | | | | | 2 |
| Temba | 84 | | | | | | 2,6,9,1 = 18 |
| Alexis | | | | | | | 5 |
| Jess | | | | | | | |
| Cara | | | | | | | |
| Samantha | | | | | | | |
| Sally | | | | | | | |
| Chima | | | | | | | |
| Keza | 101 | | | | | | 3,8,5 = 16 |
| Unknown | | | | | | | |

TV/Video - FR2 Series B

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---------------|----------------------|------------------|-------------------|-------------------------|--------------------|--------------|
| Sam | | | | | | | 5,4,8 = 17 |
| Boyd | | | | | | | |
| Marty | | | | | | | |
| Gombe | | | | | | | 4 |
| Temba | | | | | | | |
| Alexis | 42 | | | | | | 2,13 = 15 |
| Jess | | | | | | | 3,5 = 8 |
| Cara | | | | | | | |
| Samantha | | | | | | | |
| Sally | | | | | | | 2 |
| Chima | | | | | | | 6 |
| Keza | | | | | | | 4 |
| Unknown | | | | | | | |

Marbleroll, delivering Jaffas and Marbles - FR1 Series A

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---------------------------|----------------------|------------------|-------------------|-------------------------|--------------------|-----------------|
| Sam | 114 | | 21/2 | | 8 | | 4,7,5,9 = 25 |
| Boyd | 51 | 9 | | | 8 | 6,3 = 9 | 12,3,7 = 22 |
| Marty | | | | | 11 | | 4,2 = 6 |
| Gombe | 87,334=421 | | | | | | 5,8,3,5 = 21 |
| Temba | 52,76,510=638 | | | 21 | 17 | 9 | 5,7,8,3 = 23 |
| Alexis | 8,319=327 | 3 | 21/2 | | 8,11 = 19 | | 6,4,8,3 = 21 |
| Jess | 43,776,332=1151 | 6 | 73/2 | 4,7 = 11 | | | 4,8,3,6,12 = 33 |
| Cara | | | | | | | 4 |
| Samantha | 369 | | 212/2 | | | | 3,7,8,4 = 22 |
| Sally | | | | | | | 4,8 = 12 |
| Chima | 10 | | | | | | 4,7,5 = 16 |
| Keza | 37,69,5,182,423,1712=2428 | | 73/2,212/2 = 285 | 4,6,3,3,6,19 = 41 | 17 | | 2,2,2,2,21 = 29 |
| Unknown | | | | | | | 2 |

Marbleroll, delivering Jaffas and Marbles - FR2 Series A

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|----------------------------------|----------------------|------------------|-------------------|-------------------------|--------------------|------------------|
| Sam | 2 | | | | | | 5,4,5 = 14 |
| Boyd | 13,9=22 | | | | | | 3,3,6,7 = 19 |
| Marty | | | | | | | 2,2 = 4 |
| Gombe | | | | | | | 5,3,1,2 = 11 |
| Temba | 332,14,15=361 | | 62/2 | 5,7,3 = 15 | | 21 | 7,3,3 = 13 |
| Alexis | 9 | | | | | | 6,8,17 = 31 |
| Jess | 11,284=295 | | | | | 11 | 9,2,3 = 14 |
| Cara | | | | | | | 5,2 = 7 |
| Samantha | | | | | | | 3,3 = 6 |
| Sally | | | | | | | 9 |
| Chima | 9,25=34 | | | | | | 3,8 = 11 |
| Keza | 250,430,8,10,37,325,458=1 518 | 21,11 = 32 | 62/2 | 4 | | | 2,3,7,7,5,2 = 26 |
| Unknown | | | | | | | |

Marbleroll, delivering Jaffas and Marbles - FR4 Series A

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---------------|----------------------|------------------|-------------------|-------------------------|--------------------|------------------|
| Sam | | | | | | | 22,6 = 28 |
| Boyd | | | | | | | 5,17,5 = 27 |
| Marty | | | | | | | 5,6 = 11 |
| Gombe | | | | | | | 8,3 = 11 |
| Temba | 25 | | | | | 2 | 3,7,32 = 42 |
| Alexis | | | | | | | |
| Jess | 7 | | | | | | 3,5 = 8 |
| Cara | | | | | | | 7,7,5 = 19 |
| Samantha | | | | | | | |
| Sally | | | | | | | 3,3,2,2,2,7 = 19 |
| Chima | | | | | | | 8 |
| Keza | 9 | 2 | | | | | 3 |
| Unknown | | | | | | | |

Marbleroll, delivering Jaffas and Marbles - FR8 Series A

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---------------|----------------------|------------------|-------------------|-------------------------|--------------------|----------------|
| Sam | | | | | | | 22 |
| Boyd | | | | | | | 3,5 = 8 |
| Marty | | | | | | | 18 |
| Gombe | | | | | | | 12 |
| Temba | | | | | | | |
| Alexis | | | | | | | 4,3 = 7 |
| Jess | | | | | | | 5,3,3 = 11 |
| Cara | | | | | | | |
| Samantha | | | | | | | |
| Sally | | | | | | | |
| Chima | | | | | | | |
| Keza | 204,6 = 210 | | | 3,5,64,23 = 95 | | | 4,2,5,3,2 = 16 |
| Unknown | | | | | | | |

Marbleroll, delivering Jaffas and Marbles - FR1 Series B

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|--------------------------|----------------------|------------------|-------------------|-------------------------|--------------------|------------------|
| Sam | 6 | | | | | | 2,18,5 = 25 |
| Boyd | 9 | | | | | | 9,1,9 = 19 |
| Marty | | | | | | | |
| Gombe | 37 | | | | | | 3,2,4 = 9 |
| Temba | 580,8=588 | | 74/2 | | | | 5,2,2,3 = 12 |
| Alexis | 57 | | | | | | 3,1 = 4 |
| Jess | 7,12=19 | 22 | | | | | 3,3,2,1,2 = 11 |
| Cara | | | | | | | 4,4,2,3,6 = 19 |
| Samantha | | | | | | | 32 |
| Sally | | | | | | | |
| Chima | 72,112=184 | | | | | | 14,5 = 19 |
| Keza | 186,226,807,80,1465=2764 | | 74/2 | | | 22 | 3,9,2,1,4,3 = 21 |
| Unknown | | | | | | | |

Marbleroll, delivering Jaffas and Marbles - FR2 Series B

| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
|------------|---------------|----------------------|------------------|-------------------|-------------------------|--------------------|----------------|
| Sam | | | | | | | 4,7,3,2 = 16 |
| Boyd | | | | | | | 6,7,3,4,3 = 25 |
| Marty | | | | | | | 2,9 = 11 |
| Gombe | | | | | | | |
| Temba | 8,12=20 | | | | | 73 | 3,5,21 = 29 |
| Alexis | 5 | | | | | | 7 |
| Jess | 18 | 41 | 39/2 | 4 | | | 6,3 = 9 |
| Cara | | | | | | | |
| Samantha | | | | | 3 | | 2,4 = 6 |
| Sally | | | | | | | |
| Chima | 9 | | | | | | |
| Keza | 987,917=1904 | 73 | 39/2 | | 3 | 41 | 5,13,7 = 25 |
| Unknown | | | | | | | |

| Marbleroll - delivering Jaffas and Marbles - FR4 Series B | | | | | | | |
|---|---------------|----------------------|------------------|-------------------|-------------------------|--------------------|--------------|
| Chimpanzee | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
| Sam | | | | | | | 4 |
| Boyd | | | | | | | |
| Marty | | | | | | | |
| Gombe | | | | | | | 2,3 = 5 |
| Temba | | | | | | | |
| Alexis | | | | | | | 7 |
| Jess | | | | | | | |
| Cara | | | | | | | 4,7 = 11 |
| Samantha | | | | | | | 5,3,8 = 16 |
| Sally | | | | | | | |
| China | | | | | | | 5 |
| Keza | 9,12=21 | | | 38 | | | 3,6,8,2 = 19 |
| Unknown | | | | | | | |

APPENDIX E

Raw behavioural observation data from Experiment 6. Based on the behavioural classes in Table 2.2.

| Temba | | | | | | | |
|---------------|--|----------------------|------------------|-------------------|-------------------------|--------------------|--------------|
| | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
| FR2 Series A | 59,128,115,82,111,285,89,79,2 64,186,158,132,117,121 = 1926 | NA | NA | 0 | NA | NA | 4,3 = 7 |
| FR4 Series A | 126,12,26,13,27,17,25,38,16,2 7,34,47,9,187,8,347,23 = 982 | NA | NA | 2 | NA | NA | 3,8,2 = 13 |
| FR8 Series A | 38,23,47,19,77,72,69 = 345 | NA | NA | 2,4,3 = 9 | NA | NA | 5,3,7,8 = 23 |
| FR16 Series A | 63,34,67,42,73,50,23 = 352 | NA | NA | 4,7,9,4 = 24 | NA | NA | 3,5 = 8 |
| FR2 Series B | 82,128,136,83,187,15,92,254,2 08,236,262,173 = 1856 | NA | NA | 2 | NA | NA | 3,5 = 8 |
| FR4 Series B | 62,13,28,128,18,24,128,37,40, 238,239,23,16,58,72,18,27 = 1169 | NA | NA | 4,18 = 22 | NA | NA | 6,7,3 = 16 |
| FR8 Series B | 110,53,15,38 = 216 | NA | NA | 0 | NA | NA | 5 |
| FR16 Series B | 47,19,23,14,7 = 110 | NA | NA | 0 | NA | NA | 3 |
| FR32 Series B | 17,31,45 = 93 | NA | NA | 0 | NA | NA | 4,2 = 6 |
| Keza | | | | | | | |
| | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
| FR2 Series A | 128,96,5,197,74,29,77,18,37,2 03,24,13,31 = 932 | NA | NA | 0 | NA | NA | 2 |
| FR4 Series A | 14,61,28,93,16 = 212 | NA | NA | 4,8 = 12 | NA | NA | 3,2 = 5 |
| FR8 Series A | 12,7 = 19 | NA | NA | 2 | NA | NA | 4,3,2 = 9 |
| FR2 Series B | 134,13,109,37,76,9,458,27,18, 75,14,144,26,37,31,68 = 1276 | NA | NA | 1,3 = 4 | NA | NA | 4 |
| FR4 Series B | 9,15,4 = 28 | NA | NA | 0 | NA | NA | 6,18 = 24 |
| FR8 Series B | 6 | NA | NA | 0 | NA | NA | 5 |
| Jess | | | | | | | |
| | Using - alone | Using - others watch | Using - together | Attending - alone | Attending - accompanied | Watching other use | Just in area |
| FR2 Series A | 187,105 = 292 | NA | NA | 2,3,1,5 = 9 | NA | NA | 5,9,5 = 19 |
| FR4 Series A | 11 | NA | NA | 0 | NA | NA | 2 |
| FR2 Series B | 17,13 = 30 | NA | NA | 0 | NA | NA | 0 |
| FR4 Series B | 7 | NA | NA | 0 | NA | NA | 5 |

APPENDIX F

Cumulative rate of responding by chimpanzee group during sessions of Experiment 5
with the Screwfeeder enrichment, for each FR session.

