THE RELATION BETWEEN PREFERENCE AND DEMAND FOR LITTER SUBSTRATES IN THE DOMESTIC HEN

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ABSTRACT

Six hen's preferences between 5-min access to each of two litter substrates, sand and sawdust, were measured using dependent concurrent VI 60-s VI 60-s schedules of reinforcement. The obtained preferences were small and idiosyncratic. Demand functions were generated separately for each of the two substrates by requiring the hens to perform under increasing FR schedules. The demand functions were disorderly, some were linear, some were of mixed elasticity, and others curved upwards. No clear relation between the individual hens' preference and demand measures was found. The overall response rates, running response rates and average post-reinforcement pause durations were atypical compared to previous demand research, possibly due to low levels of reinforcer collection, but were similar for individual subjects in both demand conditions. During the demand assessment, dustbathing took place in a similar proportion of reinforcers for each substrate. During the preference assessment, a greater proportion of dustbathing took place during sand reinforcers. Individual hens did not consistently dustbathe more in their preferred substrate. It was argued that the inconclusive results were a product of the substrates used. The atypical demand functions, response rates and average PRP durations may have been due to behaviour that was not schedule related occurring during key time (i.e., the subjects may have been continuing a dustbathing bout). It is possible, that the two substrates were too similar, and thus the subjects did not have a clear preference for one over the other. In future research preference should be assessed prior to demand, to ensure a clear preference can be obtained, with reinforcers that are qualitatively more different than those used in the present experiment.

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DEDICATION

This thesis is dedicated in loving memory to my Oma, Johanna Mesman, who sadly passed away just weeks before it was to be completed. Oma, your constant kindness, encouragement and support throughout my time at university, even while you were sick, has meant everything to me. By simply remembering the person you were, every day I strive to better myself. I love you.

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The welfare and living conditions of animals under intensive farming systems are increasingly of concern to the public. One such system is the battery cage system, which is the most physically restrictive poultry production method (Appleby, Mench, & Hughes, 2004). In New Zealand, typically between five and seven birds are confined to a single battery cage, composing just one unit of a multi-layer style caging system. Each bird within the cage is entitled to a minimum space allowance of 450 cm^2, an area smaller than an A4 piece of paper (National Animal Welfare Advisory Committee, 2004). Welfare concerns include the barren environment of the battery cage (Appleby et al., 2004), and the prevention of many ‘normal’ behaviours, seen in less constrained species members, such as roosting, ground scratching and dustbathing (Dawkins, 1977). As well as the prevention of behaviour, the restriction of barren environments, such as battery cages, is thought to encourage the development of problem behaviours such as feather pecking and cannibalism (Hughes & Duncan, 1972).

One behaviour that is generally not available to hens in battery cages is dustbathing. Concern over the effects of not being able to perform this behaviour has led to the function of dustbathing being widely studied to determine its importance for hens (Appleby et al., 2004). According to van Liere (1992), dustbathing is a maintenance behaviour that removes stale feather lipids (fatty deposits), and as a result increases the quality, fluffiness, and insulation of feathers. It has been found that when hens are given access to a suitable substrate (e.g., peat), dustbathing occurs for approximately 20 minutes every two days, most commonly in the afternoon (van Liere, Kooijman, & Wiepkema, 1990; Vestergaard, 1982), and in warm temperatures (Duncan, Widowski, Malleau, Lindberg & Petherick, 1998). In an early study, Vestergaard (1982) deprived hens of suitable dustbathing substrates from 24 to 101 hours. He found that as the duration of deprivation increased, longer and more frequent bouts of dustbathing were performed when the hens were given the opportunity. After 32 days of deprivation van Liere and Bokma (1987) observed that, when compared with a control group of hens with free access to sand, the feathers of hens deprived of access to suitable dustbathing substrates had excess lipids, were less fluffy and therefore had less insulation capacity. These deprived birds performed ‘sham’ or ‘vacuum’ dustbathing (the performance of dustbathing behaviour in the absence of a dustbathing substrate; Lindberg & Nicol, 1997), and when given access to sand at the conclusion of the deprivation period, they performed dustbathing behaviour more often and for longer periods than the control group.

More recent studies have explored the link between deprivation of dustbathing substrates and the development of feather pecking, a major problem in intensive poultry systems (Blokhuis & Arkes, 1984). Vestergaard, Hogan and Kruijt (1990) and Vestergaard, Kruijt and Hogan (1993) compared the behaviour of two groups of hens. One group was raised with free-access to sand, grass and perches, and the other group was raised in a plain wire cage. The ‘wire’ birds performed ‘vacuum’ dustbathing, showed higher rates of damaging feather pecking, and appeared to use the feathers as a substrate for dustbathing. Johnsen, Vestergaard and Norgaard-Nielsen (1998) explored this link further, by raising three groups of hens on sand and straw, straw, or wire for the first four weeks of life. From weeks five to 17, all birds had access to both sand and straw, and at 18 weeks the birds were moved to an egg laying facility with a straw covered floor, and observed until 45 weeks of age. Across all substrates, birds initially reared on wire displayed the highest rates of feather pecking, the highest mortality rates due to cannibalism, the lowest instances of dustbathing, a reduced plumage condition, showed the most fear in tonic immobility tests, and they laid the fewest eggs.

The above results detailing the consequences of the deprivation of access to suitable dustbathing substrates suggests that dustbathing may be a behavioural need, essential for the wellbeing of domestic hens. As Dawkins (1977) points out, physiology and productivity were, in the past, widely supported indicators of animal suffering. Such measures included poor physical health indicated by a slow growth rate in broiler hens, and an inferior quality or number of eggs produced in laying hens. These measures may be of use if an animal is suffering from an injury, disease, or food deprivation, but do not necessarily indicate whether an animal is suffering from the deprivation of the performance of a behaviour such as dustbathing (Dawkins, 1983). Behavioural indicators of such deprivation must be identified and observed to assess and address the welfare of animals living in such conditions (Dawkins, 1988).

Animals can tell us about their welfare needs by their behaviour. According to Dawkins (1983), the behavioural assessment of an animal’s welfare should involve both an assessment of what an animal likes and dislikes, also known as preference assessment, and an assessment of their needs, which may be achieved with demand assessment.

There are three main ways in which to assess the preferences of animals; free-access, T-maze, and the concurrent schedules of reinforcement procedure (Sumpter, Foster, & Temple, 2002). In a free-access procedure, the animal is given unrestricted access to at least two simultaneously available but incompatible options. The time spent in or interacting with each option (known as dwell time) is taken as the measure of preference (Sumpter et al., 2002). This procedure has been successfully used to assess preferences of hens, including their preference between wire floor types (Hughes & Black, 1973), wire verses litter floors (Hughes, 1976), cage size (Dawkins, 1977), and dustbathing substrates (Santroa, Vestergaard, Agger, & Lawson, 1995).

The second preference procedure, the T-maze, requires the animal to turn left or right in a T-maze in order to enter one of two environments for a predetermined period of time (Sumpter et al., 2002). Preference is measured by the number of times each alternative is selected and/or the latency to choose the alternative. For example, using latencies, Dawkins (1977) found a preference for an outside run over an inside cage in hens with the use of a T-maze.

Free-access and T-maze procedures are easy to implement and require simple responses from the animal (Sumpter et al., 2002). However, they also have several limitations. Firstly, the use of dwell time as an indicator of preference can be problematic. As explained by Duncan (1978, 1981), the time spent in an activity/environment is not necessarily indicative of the value of that activity/environment. An animal may only spend 10% of the time available in one environment, but this environment may be just as important for the welfare of the animal as the environment in which the animal spends 90% of its time. For example, while laying is a behaviour that only occupies a small proportion of the day, it has been suggested that access to a nesting site is important for hens (as it has been observed that hens will develop methods in which to gain access to such a site by opening a one-way door; Smith, Appleby & Hughes, 1990), and therefore dwell time as a measure may undermine the importance of access to a nesting site for hens.

Another limitation is bias due to choice alternatives that differ in size. If the animal does not prefer one of the alternatives to the other, an apparent, but false preference for the larger environment may be suggested by a time spent measure, simply because it is more likely that the animal will spend more time in the larger environment if they are randomly wandering (Sumpter et al., 2002). For example, Dawkins (1977) assessed hens' preference between a battery cage (38 × 43m) and pen floored with wood shavings (260 × 82 cm) using the Free-access method, and found no apparent preference for either environment. Given the differing sizes of the two environments, a preference for the larger environment might be expected, but in this case, as no clear preference for either environment was found, the data was difficult to interpret.

A third problem in free-access and T-maze procedures is that preferences may vary depending on the procedure used. In his 1976 preference assessment of floor type in the domestic hen, Hughes found that during a free-access procedure in which the subjects had continuous access to both litter and wire, no preference was evident. However, a preference for a litter floor over a wire floor was obtained using a second procedure, which required the birds, after making a choice, to remain in the environment for several hours.

Most importantly, a problem often encountered when using free-access and T-maze procedures is exclusivity of choice. This means that if one option is highly preferred, it is likely that the animal will choose that option on most or all trials. Exclusivity of choice means that it is difficult to get a quantitative measure of preference (how much one alternative is preferred over the other) from either the free-access or T-maze procedures (Sumpter et al., 2002).

The third preference assessment procedure, the concurrent schedules of reinforcement procedure, provides a quantitative measure of preference. The concurrent schedules procedure involves the simultaneous presentation of two or more incompatible response manipulanda (e.g., two keys which can be pecked; Sumpter et al., 2002). The animal is required to respond (e.g., key peck) on the manipulanda, each of which is associated with a different intermittent schedule of reinforcement, and/or consequence (e.g., different foods; Matthews & Temple, 1979). Access to the consequence is achieved when the schedule requirements are met for the particular option. The measure of preference for one alternative over another is derived from the relative amount of time spent and/or responses made by the animal on each alternative to gain access to each outcome (McAdie, Foster, Temple & Matthews, 1993). The requirement may be time-based or response-based, but typically time-based schedules are used, the most common being concurrent variable-interval (VI) schedules (Davison & McCarthy, 1987; Sumpter et al., 2002). Under VI schedules, reinforcement is provided following the first response made on an alternative after an average period of time has elapsed since the previous reinforcer (Martin & Pear, 2003). For example, on a VI 30-s schedule, the first response made after an average of 30 s has elapsed since the previous reinforcer was received will produce reinforcement. Concurrent VI VI schedules of reinforcement are commonly used because, under such time-based schedules, the subject will tend to sample both alternatives, thereby increasing their reinforcement rate (Sumpter et al., 2002).

Concurrent VI VI schedules may be arranged independently or dependently. When the schedules are independent, the delivery of a reinforcer for responding on one alternative is not affected by the arrangement of the reinforcer for the other alternative (Herrnstein, 1961). When a reinforcer becomes available on one alternative, the other alternative continues timing; meaning that at any one time both alternatives may have a reinforcer available (Davison & McCarthy, 1987). In contrast, when the schedule pair is arranged dependently, both alternatives stop timing when a reinforcer is available on either of the alternatives (Stubbs & Plisskoff, 1969). When the reinforcer has been collected, both schedules continue timing (Davison & McCarthy, 1987). Dependent scheduling means that the subject must sample both alternatives (Sumpter et al., 2002). If a subject has a choice between two alternatives, one highly preferred, and one non-preferred, responding will tend toward the preferred alternative. However, the preferred alternative will be indefinitely unavailable unless the non-preferred alternative is selected, because the timing of both alternatives stops when a non-preferred reinforcer is available. This means that exclusivity of choice is prevented under dependent scheduling, ensuring that the preference measures are quantifiable. By contrast, exclusivity of choice is a problem faced with independent schedules when the preferences are extreme (i.e., the relative frequency of responding on the highly preferred alternative is 1.0, and on the non-preferred alternative is 0.0), making quantification of the preference impossible (Stubbs & Pliskoff, 1969).

Dependent scheduling also ensures that the subject experiences the reinforcement ratios as arranged by the experimenter (Davison & McCarthy, 1987). However, Matthews and Temple (1979) found that this does mean that the observed preferences may be less than the ‘actual’ preferences. This is because in order to obtain a highly preferred alternative, the less preferred alternative must be sampled occasionally.

Subjects tend to switch between alternatives under concurrent VI VI schedules to maximise the rate of reinforcement (Catania, 1966). Switching between alternatives may be inadvertently reinforced, which may encourage further switching and thus produce inaccurate measures of preference (Herrnstein, 1961). This alternation between options may be reduced with the introduction of a changeover delay (COD; Herrnstein, 1961). A COD specifies a minimum amount of time that must pass between the changing of alternatives and the possibility of a reinforcer. This period of time is usually between 1 and 3 s depending on the species of the subject (Sumpter et al., 2002).

Herrnstein (1961) compared concurrent VI VI schedules with and without a COD, and reported that a COD was essential for behaviour to be sensitive to the rate of reinforcement. Temple, Scown and Foster (1995) established that (using hens as subjects) behaviour was least sensitive to the reinforcement rate when no COD was programmed, and became more sensitive as the COD increased up to 2 s. However, additional increases in the length of the COD beyond 2 s did not appear to further increase the sensitivity of the hens' behaviour to the reinforcement rate.

In an early choice study using concurrent VI VI schedules and pigeons, Herrnstein (1961) found that the relative behaviour allocated to each alternative was proportional to the relative reinforcement rate provided on each alternative. This matching relation is known as the Strict Matching Law (SML; Herrnstein, 1961), and may be quantified by the equation;

$$B_1 \,/\, (B_1 + B_2) \;=\; R_1 \,/\, (R_1 / R_2) \qquad (1),$$

where B reflects the number of responses or times spent, R reflects the number of reinforcers obtained on each alternative, and the subscripts 1 and 2 represent the two alternatives (Baum, 1974, 1979).

Matching data may be graphed by plotting the log ratios of the responses made or times allocated (y axis), against the log ratios of the reinforcers obtained (x axis). When strict matching has occurred, a regression line fitted to these data has a slope of 1.0, and a y-intercept of 0.0 (Davison & McCarthy, 1987). However, in more recent studies (i.e., since Herrnstein) it has been found that behaviour under concurrent schedules of reinforcement typically does not result in strict matching.

In order to account for deviations from strict matching, Baum (1974) formally introduced the Generalised Matching Law (GML), now the most common way in which to quantify behaviour under concurrent schedules (Davison & McCarthy, 1987). Expressed logarithmically the GML is;

$$\log (B_1 / B_2) = a \log (r_1 / r_2) + \log c \qquad (2),$$

where B reflects the behaviour allocated (number of responses made or the times spent) to each of the alternatives (subscripts 1 and 2), and r represents the number of reinforcers received on the two alternatives. The parameter a (slope) measures how sensitive the organism's behaviour is to any changes in the relative reinforcement rate, and the parameter $\log c$ (y intercept) is a measure of bias, or 'preference', for one alternative over another irrespective of the reinforcement rates on the two alternatives (Davison & McCarthy, 1987).

The GML accounts for three main types of deviation from perfect matching; overmatching, undermatching, and bias. Baum (1974) used the term overmatching to describe values of a greater than 1.0. This occurs when more behaviour than is predicted by the SML is allocated to the richer schedule of reinforcement.

More commonly under concurrent schedules (Baum, 1974), *a* values are found to be less than 1.0, an occurrence known as undermatching (Baum, 1974). Typically, *a* values are found to be around 0.8 (Baum, 1979; Myers & Myers, 1977). Undermatching occurs when less behaviour than would be predicted by the relative reinforcement rate or the SML is allocated to the richer schedule. Baum (1974) suggested that undermatching results from the subject responding under the concurrent schedules procedure having poor discrimination between the alternatives, or from the use of a COD that is too short in length.

The third deviation from strict matching described by Baum (1974, 1979) is bias. Bias is evident when more behaviour than predicted by strict matching is allocated to one alternative across all relative rates of reinforcement. On a regression line, bias is shown when the y-intercept (log *c*) is not equal to 0.0.

When the concurrent alternatives are the same, bias is thought to be inherent (Baum, 1979). For example, the subject may prefer one key to the other due to the colour or force required to emit a response, or due to a positional preference (Baum, 1974). Another type of bias noted by Baum (1979) can be experimentally arranged. For example, different reinforcers may be deliberately arranged on each alternative, such as different foods (e.g., wheat and puffed wheat), in order to measure the degree of preference for one food over the other. In order to obtain a true measure of preference for these experimentally arranged variables, inherent bias must be measured and then deducted from the total bias measure. Matthews and Temple (1979) proposed the following equation to separate the two forms of bias;

$$\log (B_1 / B_2) = a \log (r_1 / r_2) + \log b + \log q \qquad (3),$$

where log b is the inherent bias, log q is the bias due to deliberate experimentally arranged differences to the alternatives (e.g., food quality), and B, r, and the subscripts 1 and 2 are as previously defined. log b + log q is equal to log c in Equation 2.

In order to assess preference assuming the GML and using equal schedules and different reinforcers, a minimum of two conditions (one being an experimental condition) are required to account for inherent bias (Davison & McCarthy, 1987). Inherent bias may be removed by either using the same reinforcer on both alternatives (e.g., Foster, Temple, Robertson, Nair & Poling, 1996; Matthews & Temple, 1979; Tannahill, 2004) or by reversing the reinforcer alternatives (Davison & McCarthy, 1987).

The concurrent schedules procedure together with the GML has been successfully used to assess the food and environmental preferences of many species. Examples include the assessment of food preferences in possums, hens and cows (Bron, Sumpter, Foster & Temple, 2003; Flevill, 2002; Foster et al., 1996), the assessment of sound preferences in hens (McAdie et al., 1993), and the assessment of social preferences in hens (Walker, 1996; Tannahill, 2004).

While valuable information has and can be obtained from preference testing procedures, there are some limitations with preference measures however they are obtained. Firstly, preference measures are only ever relative to the testing situation, and as such do not provide any information about the absolute properties of the alternatives (Duncan, 1978). For example, a subject indicating a preference towards one alternative may dislike both alternatives on offer (Duncan, 1978). Additionally, Duncan (1978) notes that experimental subjects may not make choices in the interest of their long-term welfare, giving the example of hens at the time of oviposition choosing nest boxes in which to lay, resulting in deprivation of food, water and social contact for hours.

In order to address these problems and to assess and quantify the needs of animals, Dawkins (1983) suggested using operant methods derived from consumer demand theory (known as behavioural economics). Dawkins (1988) went on to propose that the importance of different commodities/environments to a subject may be measured by comparing the demand (how hard the animal will work), or the way in which consumption changes with price for each commodity.

In economics, demand refers to how much the consumers' consumption of a commodity changes across increases in price. In behavioural economics, the subject is the consumer, and typically the number of responses made to gain access to the reinforcer (the commodity) is taken as the price (Green & Freed, 1998). Ratio schedules are most directly analogous to price in consumer economics (Green & Freed, 1998), and fixed ratio (FR) schedules of reinforcement are most commonly used in behavioural economic procedures, although other manipulations such as force required and type of response may also be used to change the price of the commodity (Sumpter, Temple & Foster, 1999). Under an FR schedule, a reinforcer is obtained after a specified number of responses have been emitted. Thus, the price of the reinforcer may be increased by increasing the FR schedule and therefore the number of responses required (Lea, 1978).

A small initial FR value is typically increased by a base percentage each session in behavioural economic experiments (Hursh, 1984). The number of reinforcers obtained each session (consumption) may then be graphed logarithmically as a function of the log schedule size (Lea, 1978). This is known as a demand function.

Demand Theory maintains that the curve of the demand function should slope downwards from left to right for most goods, demonstrating a decrease in consumption as price increases (Hursh, Raslear, Bauman & Black, 1989). Hursh (1980) suggested the importance of different reinforcers may be determined by the slope or elasticity of the demand function. A shallow demand function or one with a slope less steep than -1, reflects inelastic demand (Hursh, 1980). Reinforcers that demonstrate inelastic demand are said to be 'necessities' because the demand for these commodities is relatively unaffected by changes in price (Dawkins, 1983). This means that as the price of the commodity increases, the subject will increase their response rate in order to maintain a relatively steady level of consumption (Hursh, 1980; Hursh & Winger, 1995).

When the demand function shows a slope steeper than -1, demand is said to be elastic (Hursh, 1980). Reinforcers demonstrating elastic demand are said to be 'luxuries', because when the price (FR) increases, the demand for these commodities decreases (Dawkins, 1983). This decrease occurs because the subject does not increase their response rate in order to maintain a constant level of the commodity across increases in price. In such cases the response rate decreases rapidly with increases in price (Hursh, 1980, 1984).

A demand function with a slope of exactly -1 is said to reflect unit elasticity (Hursh, 1980). Unit elasticity occurs when responding for a commodity remains constant across changes in price, meaning that consumption decreases proportionally to price increases (Foster, Blackman & Temple, 1997).

The demand function for a commodity may be either elastic, inelastic or of unit elasticity, however, the elasticity for a commodity does not always remain the same across all prices (Green & Freed, 1998). That is, a demand function may change from inelastic to elastic demand as the price increases (Hursh, 1984). The demand for a commodity demonstrating a curvilinear demand function such as this is said to be mixed (Hursh, 1980); a common finding in many animal experiments (Sumpter, Temple & Foster, 2004). Hursh, Raslear, Shurtleff, Bauman and Simmonds (1988) proposed an equation that allows the quantitative description of curvilinear demand functions showing mixed elasticity. In natural logarithms the equation is:

$$\ln Q = \ln L + b\,(\ln P) - a\,P \qquad (4).$$

In this equation, Q reflects the total consumption per session (e.g., reinforcers obtained or amount consumed), L estimates the level of consumption at the minimal price (e.g., FR 1), b is the initial elasticity of the demand function at the minimal price, P reflects the price in terms of the response requirement (FR size), and a represents the rate of change of the elasticity of the demand function across increases in price (Hursh et al., 1989). The point at which demand changes from inelastic to elastic, or the price (FR value) generating the maximal response output, is known as P_{max} (Hursh et al., 1989), and may be determined by the equation;

$$P_{max} = (1 + b) / a \qquad (5),$$

where the parameters a and b are the same as defined in Equation 4.

There are many variables that may affect the elasticity of demand functions. Hursh (1984) has shown that these variables include the type of economic system, and the commodity itself.

An economic system may be open or closed. A closed economy is one in which the subject has access to the commodity within the experimental sessions only (Hursh, 1980). By contrast, in an open economy the subject has access to the commodity outside the experimental session (Hursh, 1980). Generally, demand for food has been found to be inelastic under closed economic conditions, and elastic under open economic conditions (Hursh, 1980). However, experimental sessions in closed economies are typically long in order for the subject to obtain all of the food that it requires, while open economy sessions are usually short and therefore the subject often requires supplementary food (Foster et al., 1997). Foster et al. (1997) investigated demand for food by hens in closed and open economies varying the session length in the closed economies. The subjects had to obtain their entire daily food intake in the closed economy sessions, but received supplementary food outside of the experimental sessions in the open economy in order to maintain their 80% of free-feeding body weights. Demand for food was inelastic during long (24-hr) closed economy sessions, and elastic during open economy sessions, in concurrence with previous findings, but demand for food was also elastic during the short (40-min) closed-economy sessions. Foster et al. (1997) argued that these findings indicate that the length of the session may be more important in determining demand than the type of economic system per se.

Another variable affecting the elasticity of demand is the commodity itself. Typically, it is expected that if the commodity is essential to the survival of the subject (a necessity), demand for that commodity will be inelastic, while if that commodity is not essential for survival (a luxury), demand will be elastic (Dawkins, 1983). For example, in a study investigating the environmental requirements of pigs, Matthews and Ladewig (1994) compared the demand functions for food, social contact, and simple stimulus changes in the environment, finding that demand for food was highly inelastic, while demand for social contact and stimulus changes were more elastic. Matthews, Temple, Foster and McAdie (1993) compared hens' demand for access peat litter with a study investigating hens' demand for food (Blackman, 1990). Matthews et al. (1993) found that the demand for peat was inelastic and not significantly different from the demand for food, suggesting that access to peat litter is important to hens.

When the price of a commodity is manipulated by increasing FR schedules, behaviour under these schedules is characterised by a high, steady rate of responding following a pause after receiving a reinforcer (post reinforcement pause, PRP; Ferster & Skinner, 1957). The length of the PRP is affected by the response requirement. It has been found that as the size of the ratio increases, so too does the PRP (Felton & Lyon, 1966; Barofsky & Hurwitz, 1968; Mazur, 1983; Foster et al., 1997).

In animal experiments, the length of the PRP is recorded, along with the overall response rate, and the running response rate. These measures are the three most common measures of performance under ratio schedules (Mazur, 1983). The overall response rate refers to the number of responses per minute excluding the reinforcement time, and the running response rate is the number of responses per minute, excluding both the PRP and reinforcement time (Mazur, 1983). Results of studies exploring the relation between response rates and ratio requirements have been mixed (Crossman, Bonem & Phelps, 1987), but typically, the running response rate decreases as the FR increases (e.g., Felton and Lyon, 1966; Foster et al., 1997; Mazur, 1983).

Some studies have reported that overall response rates initially increase over low FRs and then decrease as the FR increases further (Barofsky & Hurwitz, 1968; Mazur, 1983; Crossman et al., 1987), producing bitonic overall response rate functions. While investigating open economies and short-session closed economies, Foster et al. (1997) also found the overall response rates showed an initial increase over low FRs. However, in contrast to previous findings, the overall response rates did not change markedly with additional increases in FR, and the functions were not clearly bitonic as in previous research (e.g., Barofsky & Hurwitz, 1968). Foster et al. (1997) explained that this finding may be due to the method of calculating response rates. In their 1968 study, Barofsky and Hurwitz included the time in which the food was available (eat time) in the calculation of the overall response rate. This methodology means that during low FRs, the eat time takes up a larger proportion of the total time than at the higher FRs. As the FR increases, the eat time decreases, and therefore there is more time within the session available for responding, resulting in an overall response rate that initially increases. Foster et al. (1997) did not include eat time in their calculations of overall response rate, and recalculated Barofsky and Hurwitz's (1968) rats' overall response rates excluding eat time, resulting in functions that were less bitonic and more like the functions obtained by Foster et al. (1997).

Additionally, Foster et al. (1997) found that the overall response rates increased with increases in the FR size during the long-session closed economies. They explain that the response rate differences between the long and short-session closed economies may be due to the consumption time available within the different session lengths. During a 40-min session, much of that time is likely to be allocated to schedule-related behaviour, even during exposure to low FRs.

This means that the animal may be less able to increase their response rate during a short session as the FR increases. In contrast, it is unlikely that all of a 24-hr session will be allocated to schedule-related behaviour, and as the FR increases, the animal has the capacity to allocate more time to schedule-related behaviour.

In summary, both preference and demand measures have been extensively used in the assessment of animals' likes, dislikes and welfare needs respectively. However, to this author's knowledge, there is no published research investigating whether preferences influence the shape of the demand function. The aim of the current experiment was to investigate the possibility of a relation between preference, as assessed using concurrent schedules of reinforcement, and demand, as assessed using increasing FR schedules, for two litter substrates in domestic hens. One would expect that animals would work harder for commodities that are preferred as opposed to commodities that are less preferred.

Only three previous unpublished studies known to this author have been conducted examining the relation between preference and demand measures. Flevill (2002) used concurrent Random Interval (RI) schedules of reinforcement and increasing FR schedules to investigate hens' preference and demand respectively for three different foods in open economic conditions. The preference assessment indicated that the most preferred food was wheat, followed by honey-puffed wheat, and then puffed wheat. It was found during the assessment of demand that all foods generated demand functions of mixed elasticity, with the most preferred food, wheat, producing functions with the smallest rates of change of elasticity, and the most inelastic initial slopes, indicating less elastic demand. The P_{max} values for wheat were also larger than for the two less preferred foods. However, it was also observed that initial levels of demand were lowest for the most preferred food, wheat, and highest for the least preferred food, puffed wheat. It would be intuitive to assume that a preferred food would yield higher consumption rates across all response requirements, and thus these findings were unexpected. Flevill (2002) suggested that this may be due to the different sizes of the foods used, honey-puffed and puffed wheat being larger than wheat, meaning that more wheat, or calories from wheat may have been obtained by the subjects during each food delivery.

It was later found that the different natures of the foods used by Flevill (2002) did not influence the relation between preference and demand. Following on from Flevill (2002), Grant (2005) had very similar findings, investigating hens' preference (using concurrent RI RI schedules of reinforcement) and demand (using increasing FR schedules) for three different reinforcer access periods (2 s, 8 s, and 12 s) to wheat. It was found that the preferred reinforcer, the longest reinforcer access duration (12 s), generated demand functions with lower initial demand, more inelastic initial demand, slower rates of change of elasticity, and higher P_{max} values, similar to the results found by Flevill (2002).

A study investigating preference and demand for food in possums produced similar findings. Osugi (2003) compared demand for three foods with the results from a previous preference assessment of the same foods by Martin (2002) using the same possums. Using concurrent RI RI schedules of reinforcement, Martin (2002) found barley with sunflower seeds to be most preferred, followed by rolled oats, and then San Bran™. Osugi's (2003) demand assessment, using increasing FR schedules, resulted in demand functions of mixed elasticity. The most preferred food, barley with sunflower seeds had the smallest rate of change in elasticity, indicating more inelastic demand. The opposite was found for the least preferred food, San Bran™. The initial slopes of the demand functions were, on average, more inelastic for the most preferred food, but differed across individual subjects. Like Flevill (2002) and Grant's (2005) counterintuitive findings, it was reported that initial levels of demand were lowest for the most preferred food, and highest for the least preferred food. In contrast with Flevill (2002) and Grant's (2005) findings however, Osugi (2003) found that, on average, the P_{max} values were largest for San Bran™, the least preferred food, and smallest for barley with sunflower seeds, the most preferred food.

Flevill (2002), Grant (2005) and Osugi's (2003) experiments involved the comparison of preference and demand for food in an open economy. In order to determine whether these counterintuitive results are specific to experiments utilising food as a reinforcer, and because litter has been found to be important to the welfare of hens, the assessment of preference and demand for litter in hens was chosen to extend this research with a different commodity. To date, there are no published data comparing preference and demand for litter substrates in hens.

One major methodological problem in the assessment of preference and demand for litter substrates in hens has been the inability to provide multiple reinforcer deliveries within a single experimental session. In order to assess preference using concurrent schedules of reinforcement and demand using increasing FR schedules, multiple deliveries of any reinforcer are required (Davison & McCarthy, 1987). When food is the reinforcer, it is straightforward to deliver small amounts and remove the magazine after (for example) a 3 s period of access. With dustbathing as a reinforcer, it is not so easy to present and remove small periods of access. A typical dustbath lasts for approximately 20 minutes (Vestergaard, 1982), and this activity must be broken up in order for multiple reinforcer deliveries to be administered. To do this the hen must be removed from the litter mid-dustbath without human handling or some other aversive means.

As a result of such methodological problems, demand research for litter substrates in hens is very contradictory. Some researchers have reported that hens will not pay a price or perform a task to gain access to litter (Widowski & Duncan, 2000). For example, in order to assess whether access to litter was reinforcing to hens, Dawkins and Beardsley (1986) required hens to peck a key in a ‘choice-chamber’ for access to a ‘goal box’ with a litter floor. After 100 seconds of access to the litter, an air blower blew air into the goal box, forcing the hen to return to the choice-chamber, ready for another trial. Dawkins and Beardsley (1986) noted that the air blower was aversive to the hens, and then concluded that access to litter was not reinforcing for hens when the operant response was a key peck.

To overcome this problem, Matthews et al. (1993) developed an apparatus consisting of a cage that could be moved over various floors, with response keys on each side. This equipment allowed the hens to be given access to a substrate, following pecking, and then to be removed from the substrate without human intervention or the need for anything more aversive than simple cage movement. Research using the equipment has established that hens will work to access litter by pecking a key, and indicates that there are several different litter substrates that are important to hens (Gunnarsson, Matthews, Foster & Temple, 1997; Gunnarsson, Matthews, Foster & Temple 2000; Matthews et al., 1993; Matthews, Temple, Foster, Walker, & McAdie, 1995).

With this equipment, Matthews et al. (1993) used increasing FR schedules to assess hens’ demand for 5-min access to peat. The resulting demand functions were inelastic, with demand for dustbathing in peat being more inelastic than demand for pecking and scratching in that substrate. The average slope of the demand functions for access to litter was similar to hens' demand for food in a previous experiment (Blackman, 1990). Using the same equipment, Matthews et al. (1995) observed that demand was inelastic for peat, as well as sand and woodshavings, when hens were required to peck a key to gain access to the different substrates on the same increasing FR schedules. The importance (as indicated by the elasticity of demand) of each substrate appeared to differ according to the type of activity performed. For dustbathing, sand was most valued (as shown by the most inelastic demand), and woodshavings least valued (as shown by the least inelastic demand). However, for pecking and scratching, the three substrates were similarly valued (all demonstrating relatively inelastic demand). Additionally, also using the same equipment, Gunnarsson et al. (2000) found that hens would peck a key on the same series of increasing FR schedules for access to feathers and straw. Demand for feathers was found to be inelastic for the three subjects who worked for feathers, as was demand for straw for all subjects. These findings indicate that access to litter substrates that are not suitable for dustbathing may also be important to hens.

Research conducted to examine hens' preferences for litter substrates is even more restricted than the demand research, being limited to the free-access and T-maze methods. The data indicate that substrates made up of fine particles, such as peat and sand are preferred by hens, as these particles are most effective in reducing feather lipids during dustbathing bouts (van Liere, 1992). Van Liere et al. (1990) presented hens with sand and woodshavings simultaneously (using the free-access method), and found that the hens preferred sand to woodshavings.

They observed, during bouts of dustbathing, that the fine sand particles reached the skin of the birds, while the larger and lighter woodshavings were barely able to reach between the feathers.

In light of the limited findings of hens' preferences and demand for litter substrates, sand and sawdust were the chosen substrates for the current experiment in the expectation of finding a clear preference for one of the substrates (sand) over the other (sawdust), thus allowing the examination of any possible relation between preference and demand for litter substrates. The non-aversive apparatus utilised by Matthews et al., (1993) was used for the current experiment. In previous experiments using this equipment, and given the typical length of a dustbath (approximately 20 min), 5-min access was judged to be a suitable period of access to the litter (Gunnarsson et al., 1997; Gunnarsson et al., 2000; Matthews et al., 1993; Matthews et al., 1995). This period of time permits the hen to commence, but not finish a dustbath, allowing multiple choices and deliveries of the reinforcer within a session.

Bias measures from behaviour under concurrent VI VI schedules of reinforcement with access to a short period (5-min) of both sand and sawdust were compared with demand functions for the same two substrates under closed-economic conditions. Demand was assessed first in order to ensure the subjects had experience with both substrates before the commencement of the preference assessment. The expected results of a possible relation between preference and demand for litter substrates are uncertain. Intuitively, it would be expected that the preferred substrate would yield higher initial levels of demand, more inelastic demand, and larger P_{max} values. However, based on Flevill (2002), Grant (2005) and Osugi's (2003) findings with food, the preferred substrate may yield initial levels of demand that are lower than the non-preferred substrate, and more inelastic demand. Based on the findings of Flevill (2002) and Grant (2005), it is expected that P_{max} values will be higher for the preferred litter substrate.

METHOD

Subjects

Six Shaver-Starcross domestic hens (*Gallus domesticus*), numbered 331 through 336, served as subjects. All hens were one year old at the start of the experiment and had been reared in a pen with a sawdust-covered floor. They had had some previous experience with simple schedules of reinforcement, pecking a single key for a food consequence, but no experience with the current experimental apparatus or procedure. When not in the experimental apparatus, the hens were housed individually in home cages (450-mm long × 300-mm wide × 430-mm high) with free access to water. Grit and vitamins were provided weekly.

Each hen was weighed every second day, (i.e., the days on which their experimental session took place) and they were maintained at 90% (+/-5%) of their free-feeding body weights through feeding of commercial layer pellets. Throughout the experiment, all hens laid eggs regularly.

Every day the hens had a 12-h period of light in their home room, from 3 am to 3 pm, provided by two white 23-W PL-Electronic-U energy saving light bulbs. Throughout the experiment it was attempted to maintain the home and experimental rooms between 20-25°C. The minimum and maximum temperatures of the home room were recorded every day, immediately before the first experimental session, as were the maximum and current temperatures of the experimental room.

Apparatus

The experimental apparatus was located in a room (2800-mm long × 2280-mm wide), separate from, but close to, the hens' home room. The room was lit with one white 23-W PL-Electronic-U energy saving light bulb, positioned directly above the experimental apparatus. The experimental apparatus consisted of a mechanically moveable wire cage (450-mm long × 460-mm wide × 420-mm high) attached to an aluminium rectangular frame (2000-mm long × 650-mm wide × 1340-mm high). The top of the cage was attached to the frame and the cage could move between three different positions (named 'left floor', 'home floor', and 'right floor'). At each floor position, placed so as to lie approximately 20 mm below the lower edge of the moveable cage, was a removable metal tray (450-mm long × 400-mm high). There was a plywood false floor placed inside the tray, making each tray 45-mm deep. The home tray had a piece of wire mesh (35 mm^2) placed over the top throughout the experiment. Figure 1 shows a photo of the apparatus as seen from the door of the experimental room.

At the start of the session, the cage was suspended over the wire home floor. The cage was made of wire mesh (20 mm^2), and therefore the hens could see the trays and litter (if present) inside the trays on either side of the home floor. There were two transparent plastic response keys (30 mm in diameter) on the left and right wire mesh walls of the cage, which, when operational, were lit red with an 80-millicandela (mcd) light bar. The response keys were 350 mm above the wire floor, and key operation required a minimum response force of 0.2 N, resulting in an audible beep. During the delivery of a reinforcer (a 5-min period of access to the litter substrate, called a 'trip'), the cage (with the hen inside) moved to one of the outer trays (a distance of 510 mm), over a period of 29 s. When the reinforcer time of 5 min had elapsed, the cage (and hen) moved back to the wire floor.

Figure 1. Side view of the experimental apparatus. In the centre is the moveable cage, above the home (central wire) position, attached to the frame. The back of the left response key is visible in the upper left of the picture, and the right response key is partially concealed by the cage door. The left tray contains sand and the right tray contains sawdust. To the left of the cage is the web cam that moved with the cage during trips to each substrate. The manual controls are shown in the upper right corner of the picture.

The apparatus had several safety features, including sensitive flaps on the moving edges of the cage which, when triggered, sounded an alarm and reversed the movement of the cage to ensure that the hens did not become stuck. On the occasions that the alarm did sound, it alerted the individual running the experiment to check on the hen. An emergency stop string, which stopped the movement of the cage, was suspended above the equipment, and a manual control, from which the cage could be moved right or left, was mounted on the top right edge of the frame. There was also a shear pin in the cage drive, which would break if the forces involved became too severe.

A web camera was attached by an aluminium bracket to the side of the cage opposite the cage door. In all experimental conditions, the camera moved with the cage, and was programmed by the computer to turn on and record the behaviour of the hen while on a litter substrate. When the cage returned to the home (central wire) position, the camera stopped recording. After each session, the videos were analysed, and the behaviour (dustbathing, pecking and scratching, and other; see page 34 for definitions) of the subject during each trip was recorded manually in a data book.

A Dell PC computer (1.59GHz, P4, 256mb, Windows XP Service Pak 2), located in a separate room and using Med-PC® IV software recorded and controlled experimental events. The data were also recorded manually into a data book at the end of each session.

Reinforcers consisted of access to two substrates, sand and sawdust. The fine sand was purchased in a 30-kg bag from Firth Industries Ltd, a building supplies company. The sand, intended for the production of concrete, was made up of particles that were small and uniform in both colour and size. The sawdust was untreated pinus radiata, ranging in size from approximately less than 1 mm^3 to 10 mm × 8 mm × 2 mm, with most of the dust being approximately 1 mm^3. From the third series of the first condition (the sand condition) onwards, the moisture content (Volumetric Water Content; VWC) of the sand (straight out of the bag) was measured with the use of a HydroSense probe, and then both substrates were maintained at this moisture level for the remainder of the experiment.

Procedure

Demand Assessment

In both demand conditions, the hens were exposed to increasing FR schedules, and responded to gain access to either sand (Condition 1) or sawdust (Condition 2). Experimental sessions were conducted for each set of 3 hens every other day, and in relation to the lighting regime, these sessions took place in the afternoon. Occasionally, during the low FRs or due to equipment problems, sessions for each hen were not conducted every second day, but every third. All subjects were weighed and fed approximately 20 min before the first hen's experimental session to reduce the amount of litter ingested during the session.

Training. During the first session of training, the birds were individually placed in the experimental cage, over one of the litter substrates for 30 min, with the keys and cage inoperable, in order to habituate the birds to the novel equipment and the litter substrates.

During the second part of training, the birds were trained to operate the moveable cage by pecking the response keys. The three trays of the experimental apparatus had plywood lids placed over them, making them level, and a 20-mm thick line of food (wheat or commercial layer pellets, depending on the subject) was positioned across the middle of the trays. The birds were individually placed in the moveable cage positioned to the right of the apparatus, with the left key light illuminated. When the key was pecked, the cage was slowly moved with the manual controls across to the left of the apparatus, giving the bird access to approximately 100 mm of the line of food. When the cage reached the left side of the equipment, more food was positioned across the trays, and the birds worked back to the right side of the apparatus by pecking the right key, thus gaining experience working on both response keys. Each of these training sessions lasted for approximately 20 min. Five of the hens were reliably pecking both keys (with enough force to produce the audible beep), and moving the length of the equipment both left and right after two such training sessions working for wheat. Hen 335 was pecking and moving reliably only after the food was changed to commercial layer pellets during her third training session.

Finally, the hens were placed in the experimental cage over the home floor on alternative days and were exposed to a FR 5 schedule of reinforcement which resulted in 5-min access to sand. During sand training, only the left key was lit, the left tray was filled with sand and the right tray was empty. After at least 3 sessions in which at least one reinforcer was delivered, this training was also conducted for sawdust (i.e., the right key only was lit, the right tray was filled with sawdust and the left tray was empty). Upon the completion of each FR, the subjects received 5-min access (excluding the move time of the cage) to the substrate and the key light was extinguished. Each of these final training sessions lasted for 40 min, excluding the reinforcer time and move time of the cage (keytime).

Condition 1 (Sand). During the sand condition (Condition 1), the hens responded on a series of increasing FR schedules, every other day, for 5-min access to sand. Only the left key was operative, and the left tray was filled with sand. The first FR schedule in a series was FR 1 and the ratio requirement was then doubled each session until no reinforcers were received within that session (i.e., no trips were made). The same FR (under which no reinforcers had been obtained) was then presented in a second session, and if the subject did not obtain a single reinforcer in this session, the series was ended. Three series of FR increases were conducted in the sand condition, the procedure used in each being an exact replication of the procedure used in Series 1. Table 1 presents the sequence of conditions and the highest FR values at which each subject completed a series (i.e., the last FR at which at least one reinforcer was obtained). Between the three series of the sand condition, the subjects were exposed to small FRs. Ideally, between each series, the subjects would have been exposed to a FR 5 schedule for at least three sessions, but due to experimental error, between Series 1 and 2, the subjects were exposed to a FR 1 schedule for one session. This problem was addressed between Series 2 and 3, and subjects were exposed to an FR 5 schedule for at least one session, but due to equipment problems, this sometimes increased to an FR 10 schedule.

Each experimental session lasted for a total of 30-min keytime. The training keytime of 40 min was reduced to the 30-min experimental keytime, because the total session time on some occasions, especially during the small FRs, exceeded six hours in length. With sessions of such length, only one experimental session could take place per day, which was impractical due to time constraints. The reduced experimental keytime ensured that at least two, and more commonly,

Table 1.

The order of experimental conditions, together with the highest FR schedule completed in each series of Conditions 1 and 2 (for each hen).

		Hen					
Condition	Series	331	332	333	334	335	336
Condition 1: Demand Assessment Sand (Increasing FRs)							
	1	16	64	2	32	64	64
	2	16	64	4	8	32	64
	3	32	128	8	8	64	64
Condition 2: Demand Assessment Sawdust (Increasing FRs)							
	1	16	32	32	32	32	64
	2	16	128	16	32	16	64
Condition 3: Preference Assessment Sand and Sawdust (Concurrent VI 60-s VI 60-s Schedules)							

three experimental sessions could take place each day (i.e., two or three hens could be run per day).

In the first series of the sand condition, when the first bag of sand was opened, it was noted that the sand was damp. As Series 1 and Series 2 continued, the sand slowly dried out, and it appeared during the observation videos that less dustbathing behaviour was taking place in the dry sand. For the third series of the sand condition, a new bag was opened and the VWC (Volumetric Water Content) of this sand was measured using the Hydrosense probe, and found to be 10%. The VWCs of the substrates were then maintained at 10% for the entire third sand demand series, for the two demand series for sawdust (Condition 2), and for both substrates during the concurrent preference assessment (Condition 3).

Condition 2 (Sawdust). In this condition, the right key only was operative and the right tray was filled with sawdust. The procedure was the same as that used in the sand condition. However, only two series of FR increases were conducted using sawdust as the litter substrate (Condition 2). The FR values reached at the end of each series for each subject are shown in Table 1. Between the end of the sand condition and the commencement of the sawdust condition, all subjects responded on a FR 5 schedule working for sawdust for at least three sessions. Between the two series of this condition, subjects were again exposed to a FR 5 schedule for at least three sessions.

Data collected and recorded in the data book during each experimental session in the sand (Condition 1) and sawdust (Condition 2) conditions included the time at which the experiment was started, FR size, PRP time, and keytime. Also recorded were the number of pecks made, number of trips (reinforcers obtained), total session time (from beginning to end of session), and the total move time of the cage.

Following each experimental session, the video recordings of the hens' behaviour while in the substrate were analysed. Behaviour during each 5-min trip was classified as dustbathing, pecking and scratching, or other, using a partial interval method of recording.

The following definition of dustbathing is adapted from descriptions of the behaviour by van Liere (1992) and van Liere and Wiepkema (1992). Dustbathing behaviour was recorded when, during trips, the subject lay in the litter, on her breast and/or side, with her feathers fluffed and wings extended, scratching at the litter with her feet, and thereby tossing litter upwards onto and between her feathers. Dustbathing behaviour also included bill raking, where the hen moved her bill through the litter towards her body, and head rubbing, in which the hen lay on her side and moved her head and neck across the litter. Concluding the dustbathing process is a body/wing shake in which the litter is removed from the feathers (van Liere, 1992; van Liere & Wiepkema, 1992).

Pecking and scratching were recorded when the subject remained standing for the entire 5-min period of access, scratching with both feet at the litter and bill raking. In trips where both pecking and scratching and dustbathing took place, the behaviour was recorded as dustbathing, because pecking and scratching behaviour sometimes precedes dustbathing (van Liere, 1992).

Behaviour was recorded as 'other' when no dustbathing or pecking and scratching behaviours were observed for the entire trip. For example, standing, walking and lying in the litter.

Due to equipment problems, the webcam occasionally (during eight of all presented sessions) failed to record the behaviour of the subjects while in the litter. This problem tended to occur more often for one particular subject (Hen 336). On such occasions, each trip that could not be observed was recorded as ‘other’.

Preference Assessment

Throughout the preference assessment, both of the trays of the apparatus were filled with litter and both response keys were illuminated red. The two substrates were organised as in the demand assessment with sand in the left tray and sawdust in the right.

Training. As the subjects had never experienced concurrent schedules of reinforcement, the dependent concurrent VI VI schedules of reinforcement initially had a short average interval, and a short COD. As the subjects became more experienced with the concurrent schedules, both the VI interval and COD were slowly increased.

During the first two training sessions, the hens were exposed to dependent concurrent VI 15-s VI 15-s schedules of reinforcement with a 0-s COD. During these sessions, only 2 of the 6 subjects responded on both keys and sampled both alternatives.

In order to encourage the subjects to respond on both keys, the programme was adjusted to give the hens 5-s access to food as opposed to 5-min access to a litter substrate. The left and right trays were covered with plywood lids, a pile of food (commercial layer pellets) was placed on each side of the moveable wire cage, and both key lights were illuminated. Each subject was individually placed in the moveable cage, and worked on a dependent concurrent VI 15-s VI 15-s schedules of reinforcement training programme with a 0-s COD. When the response requirement had been met, the cage moved to the right or left floor. After 5-s access to the food-covered floor, the cage and subject returned to the home floor. After one session with food, all birds were reliably responding on both keys and sampling both alternatives.

Following food training, the reinforcer-access period and reinforcers were changed so that the subjects were again working on dependent concurrent VI 15-s VI 15-s schedules of reinforcement with a 0-s COD for 5-min access to the litter substrates. Over the next 25 training sessions, the COD and VI were both slowly increased, in increments of 0.5 s and 15 s respectively, until the COD reached 2.5 s and the VI schedules reached 60 s.

Condition 3 (Concurrent Sand and Sawdust). In Condition 3 proper, the hens were exposed to dependent concurrent VI 60-s VI 60-s schedules of reinforcement with a 2.5-s COD. At the start of each session, both keys were lit red, and the trays were organised as in the demand assessment. During reinforcement, both key lights were extinguished, and the keys were inoperative.

All concurrent sessions ended after eight reinforcers had been received or 30-min keytime had elapsed (whichever occurred first). The 30-min keytime was the same as in the demand condition, and the maximum of eight reinforcers was chosen to allow three experimental sessions to take place daily.

Stability of performance was determined statistically by calculating the median of the proportion of responses (made to the left key) over the last five sessions. This median was then compared with the median obtained for the previous 5-session period. Statistical stability was achieved when five (not necessarily consecutive) pairs of medians differed by no more than 0.05. When statistical stability was obtained, visual stability was then sought. Visual stability was attained graphically by plotting the log ratio of responses made to and times spent on, the left key across sessions. When the graphs were judged as visually stable (i.e., not trending) by at least two laboratory members, visual stability was achieved.

The data collected and recorded in the data book during each experimental session of Condition 3 included the time at which the session began, the number of responses made on each alternative (left and right), the relative numbers of responses (proportion) on each key, the times spent on each alternative (left and right), the numbers of trips to the left side (sand), the numbers of trips to the right side (sawdust), keytime, the move time of the cage, and the total session time (including keytime, move time, and reinforcement time). As in the sand and sawdust demand conditions, videos of trips made were analysed and categorised (dustbathing, pecking and scratching, or other) after each experimental session. In addition, the order in which the trips took place was also recorded, along with which substrate(s) dustbathing behaviour took place in.

RESULTS

Demand Assessment

All data from all FR series and each condition are presented in Appendix A. As there were no consistent differences between the three series of FR increases conducted in the sand condition (Condition 1), only the data from Series 2 and 3 were analysed and are presented here. The data from both Series 1 and 2 of the sawdust condition (Condition 2) were analysed and are presented here.

Condition 1 (Sand). Figure 2 presents, for all hens, the overall response rates (left panel), the running response rates (middle panel) and the average post-reinforcement pause (PRP) durations (right panel), plotted against the natural logarithms of the FR size for Series 2 (circles) and 3 (stars) of the sand condition. The y-axes for each of the three graphs are different. The overall response rates (per min) were calculated as the total numbers of responses divided by the keytime, which excluded both the move time of the cage and the reinforcer-access time. The running response rates (per min) were calculated by dividing the total numbers of responses by the run time (keytime). It was not possible to calculate running response rates for FR 1. Average PRP durations (s) were calculated by dividing the total PRP time (the time taken to respond following a reinforcer) by the total number of reinforcers obtained.

Figure 2 shows that there were no consistent differences across hens or series in the overall response rates, running response rates or average PRP durations. The left-hand panel of Figure 2 shows that for both Series 2 and 3 of the sand condition, the overall response rates were generally low (ranging from 0 to 7 responses per minute) and tended to increase for all hens, albeit slowly, as the FR size increased. In most cases, the running response rates (middle panel) in

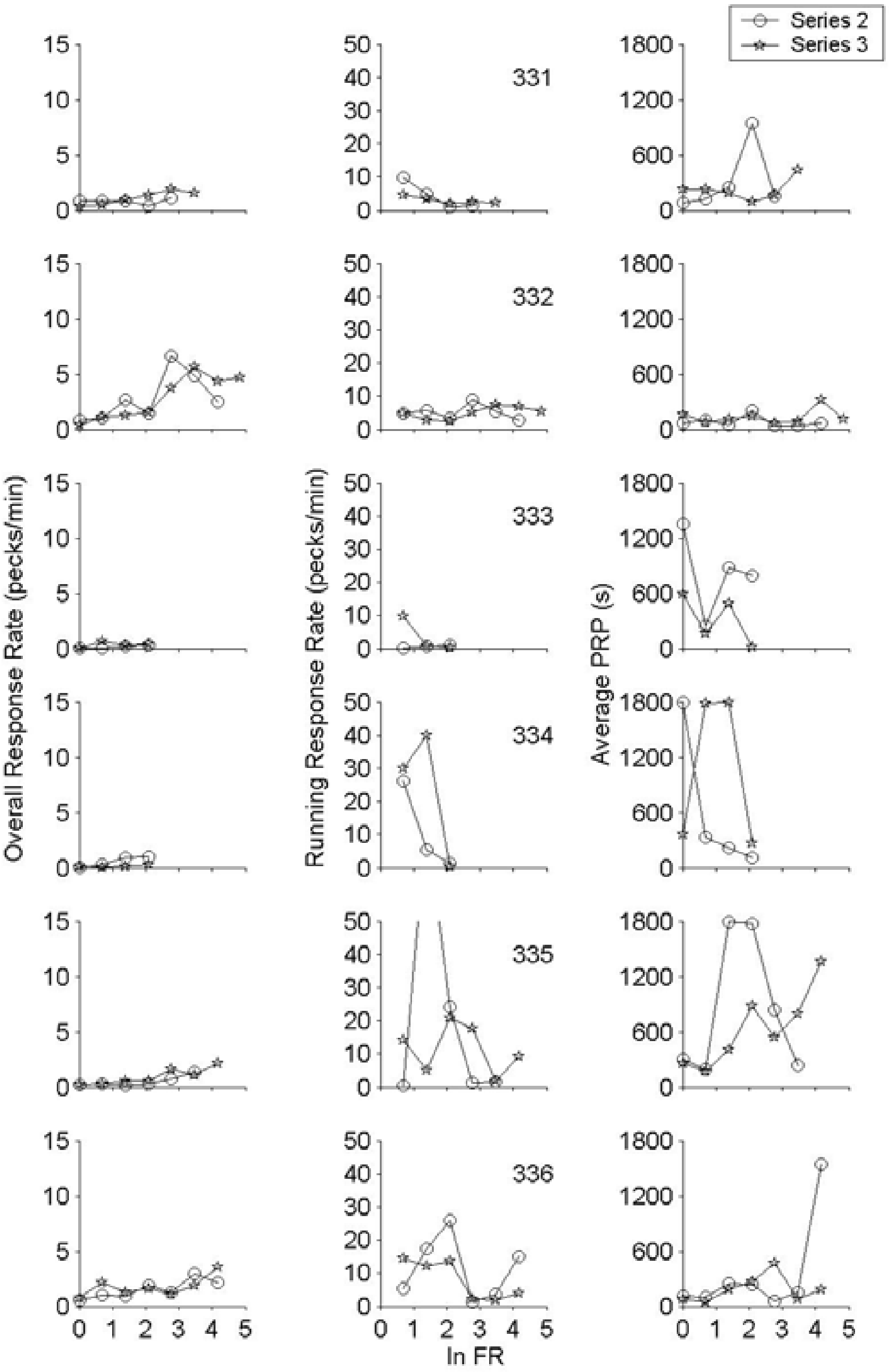

Figure 2. Overall response rates (left panel), running response rates (middle panel), and post-reinforcement pause durations (right panel), plotted against the ln FR schedule size for each subject for Series 2 and 3 of the sand condition.

Series 2 and 3 of the sand condition were low (i.e., between 0 and 25 responses per min), however, in several cases the running response rates were high (one data point for Hen 335 is off the scale at 80 responses per min) and were not representative of typical running response rate patterns. These aberrant running response rates typically occurred when only one reinforcer was obtained during the session (the numbers of reinforcers obtained during each session will be presented later in the results). The average PRP durations observed in Series 2 and 3 of the sand condition (right-hand panel) were relatively short (between 0 and 300 s), but in several cases some of the PRP durations were very long (over 800 s), and so the patterns were not representative of normal PRP durations. These long PRPs also tended to occur when the numbers of reinforcers obtained during the session were very few (i.e., only one or two).

The natural logarithms of the consumption data (i.e., number of reinforcers obtained at each FR) for Series 2 and 3 of FR increases conducted during the sand condition are plotted as functions of the ln FR size in the left-hand and middle panels of Figure 3, respectively. The lines shown were fitted to the data using Hursh et al.'s (1988) nonlinear equation (Equation 4) and the parameters of the lines are displayed in Table 2, along with the variances accounted for by the lines (%VAC), the standard errors of the estimates (*se*) and the FR value predicted to generate maximum responding (P_{max}), as calculated by Equation 5. The lines fitted to the consumption data from the sand condition accounted for over 80% of the data variance in 11 of the 12 cases, with the *se* measures ranging between 0 and 0.54.

Figure 3 shows that in Series 2 and 3 of the sand condition, there were no consistent differences in the demand functions for each subject across the two

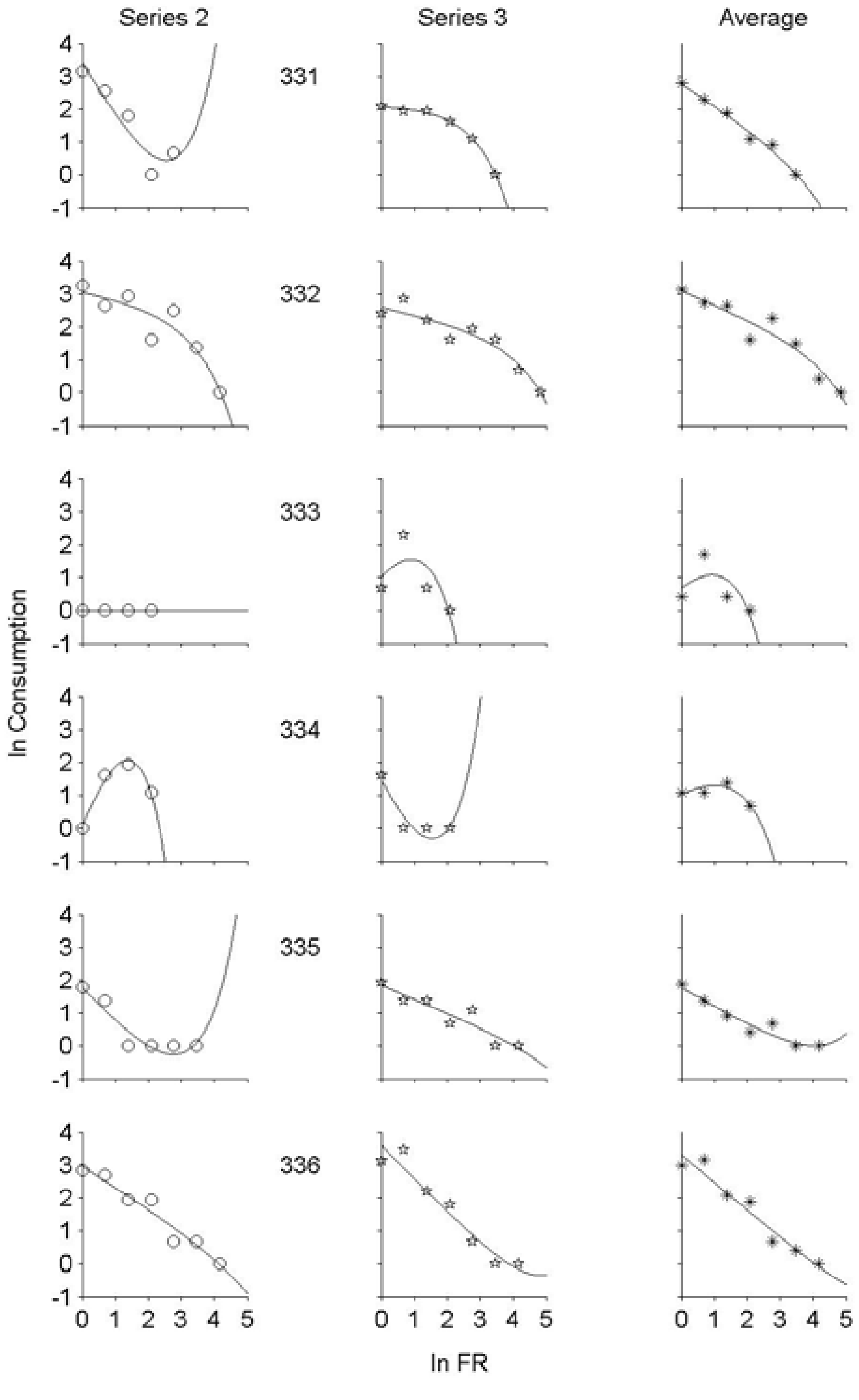

Figure 3. The natural logarithms of consumption plotted against the ln FR schedule size for each hen for Series 2 (left panel), Series 3 (middle panel), and the averaged data points from Series 2 and 3 combined (right panel) of the sand condition.

Table 2.

The parameters a, b, and ln L for Hursh et al.'s (1988) equation (Equation 4) fitted to the ln consumption verses ln FR data from Series 2, Series 3, and the averaged data of Series 2 and 3, of the sand condition (Condition 1). Also shown are the standard errors of the estimates (se), the percentages of variance accounted for by the lines (%VAC) and the FR value at which the fitted functions predict maximal responding (P_{max}). Asterisks indicate cases in which P_{max} was not meaningful due to negative a values.

Hen	Series	*a*	*b*	ln *L*	$P_{\max}$	*se*	%VAC
331	2	-0.1395	-1.81	3.29	*	0.39	88.59
	3	0.0697	0.03	2.13	14.78	0.04	99.74
	Average	0.0144	-0.66	2.78	23.95	0.12	98.43
332	2	0.0329	-0.21	3.09	23.90	0.39	86.18
	3	0.0118	-0.24	2.61	65.01	0.25	91.86
	Average	0.0089	-0.43	3.11	64.54	0.30	92.07
333	2	0.0000	0.00	0.00	*	0.00	Inf
	3	0.6609	1.66	1.67	4.03	0.54	58.90
	Average	0.4800	1.23	1.15	4.65	0.45	51.20
334	2	0.7992	3.18	0.86	5.23	0.10	98.14
	3	-0.4898	-2.32	0.98	*	0.24	88.41
	Average	0.2536	0.71	1.28	6.73	0.11	78.40
335	2	-0.0701	-1.12	1.74	*	0.25	89.30
	3	0.0025	-0.43	1.86	232.67	0.25	86.80
	Average	-0.0100	-0.58	1.77	*	0.18	92.62
336	2	0.0041	-0.66	2.98	84.49	0.23	94.76
	3	-0.0081	-1.03	3.60	*	0.33	93.79
	Average	-0.0020	-0.84	3.32	*	0.26	94.94

series. Consumption generally decreased as the FR size increased. The initial levels of demand (ln *L* values) ranged between 0 and 3.60 across subjects and series, but were very similar across the two series for each individual subject. The initial slopes (*b* values) ranged between -2.32 and 3.18 across subjects and series, and no consistent differences were apparent across subjects or series. Some of the demand functions showed curvilinear demand with positive *a* values (ranging between 0.0025 and 0.7792) indicating that demand became more elastic as the FR size increased. Other demand functions were approximately linear, and some curved upwards due to negative *a* values (ranging from 0.00 to –0.4898). In these cases, the curving upwards of the demand functions typically occurred beyond the last data point, and these values were not a good indicator of the change in elasticity. Negative *a* values also resulted in the calculation of P_{max} values that were meaningless (hence the asterisks in Table 2). In cases where the calculation of P_{max} was meaningful (7 of 12 instances), the values ranged between 4.03 and 232.67. Across subjects and series, breaking points (as previously presented in Table 1) ranged between FR 4 and FR 128, however for each individual hen, the difference in the breaking points between both series was within one FR value.

As there were no consistent differences for each hen across Series 2 and 3 of the sand condition, the individual data were averaged and presented in the right-hand panel of Figure 3. The averaged consumption data were calculated by adding together the numbers of reinforcers obtained at each FR value in the two series, and then dividing this number by two. In cases where the breaking point was different across the two series, the numbers of reinforcers obtained at the highest FR value were taken and used as the averaged value. Again, lines of best fit were fitted to the averaged data, using Hursh et al.'s (1988) nonlinear

Equation (Equation 4). The fitted lines and other parameters accounted for over 80% of the data variance in 4 of the 6 cases, and the *se* measures ranged between 0.11 and 0.45, which are also presented in Table 2.

The averaged demand functions retained the overall shape of the functions in Series 2 and 3 of the sand condition for most, but not all, hens. The averaged demand functions of Hens 333 and 334 did not retain the same overall shape, but these hens worked only to very small FR values and therefore the demand functions were based on few data points. These demand functions were averaged to compare the demand for sand and sawdust.

When the demand functions obtained in the sand condition were averaged, ln L values ranged between 1.15 and 3.32, and consumption generally decreased as the FR increased. The demand functions for most subjects were curvilinear, although in some cases appeared approximately linear (Hen 336) or curved upwards (Hen 335). The b values of the fitted lines of the averaged consumption data for two hens (Hens 333 and 334) were positive, indicating initial increases in consumption across small FRs, and the b values of the fitted lines of the consumption data for the remaining four hens were less negative than -1 (ranging between -0.43 and -0.84) also indicating inelastic initial demand. The a values of lines fitted to the data were positive in four of the six cases (ranging between 0.0089 and 0.4800), and negative in the remaining two cases (Hens 335 and 336). This means the P_{max} values were meaningful in four of the six cases, ranging between 4.65 and 64.54.

Condition 2 (Sawdust). Presented in Figure 4 are the overall response rates (left-hand panel), running response rates (middle panel) and average PRP durations (right-hand panel), all plotted against the natural logarithms of the FR

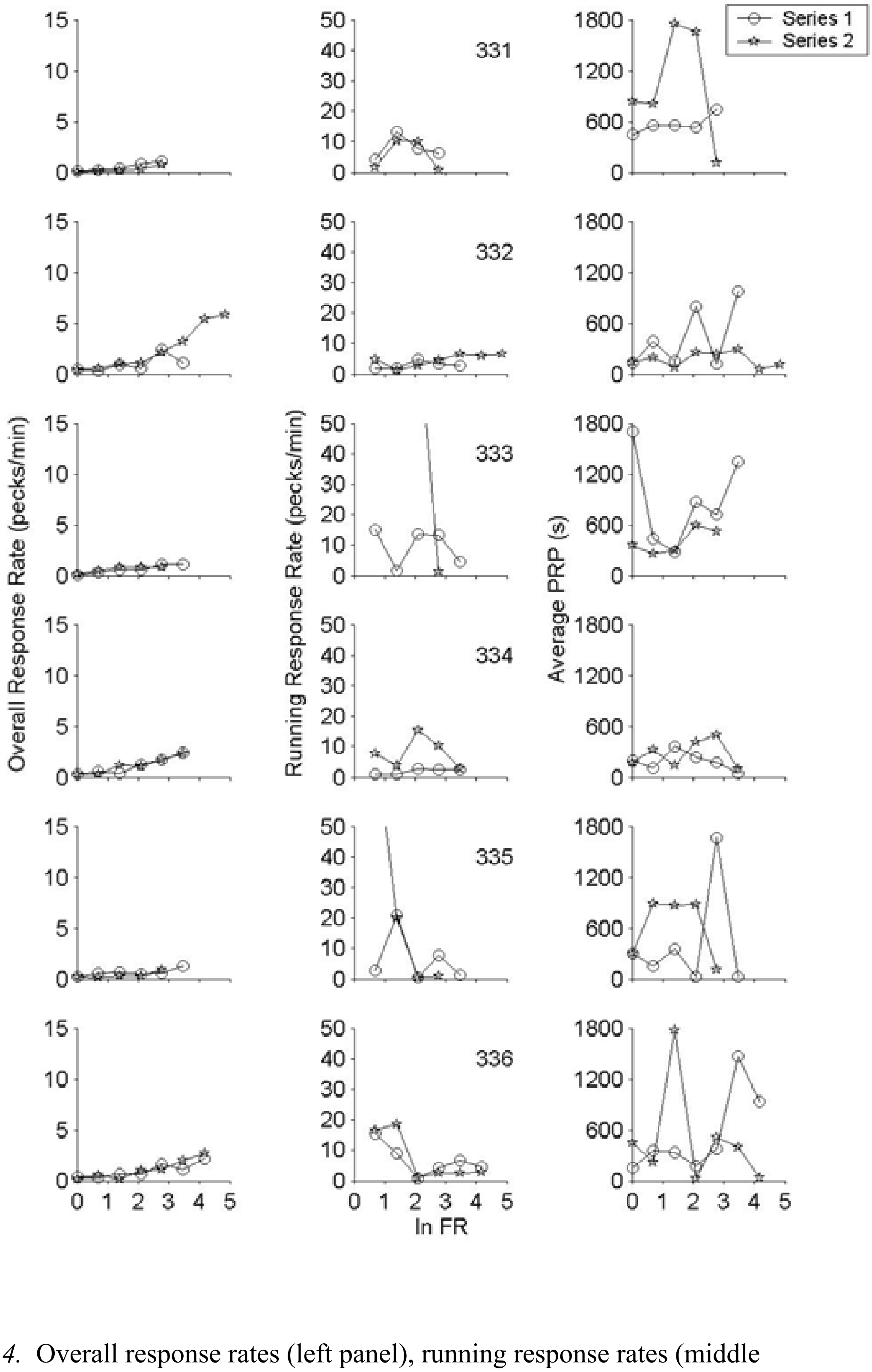

Figure 4. Overall response rates (left panel), running response rates (middle panel), and post reinforcement pause durations (right panel), plotted against the ln FR schedule size for each subject and series of the sawdust condition.

size for Series 1 (circles) and 2 (stars) of the sawdust condition. As in Figure 2, the y-axes for each of the three graphs are different.

As shown in Figure 4, there were no consistent differences across hens or series for the overall response rates, running response rates or average PRP durations. The overall response rates (left-hand panel) in Series 1 and 2 of the sawdust condition were orderly and generally low (ranging from 0 to 6 responses per min) and tended to increase as the FR size increased for all hens.

The running response rates (middle panel) were also generally low (i.e., between 0 and 25 responses per min) but in several cases they were high (several data points for Hens 333 and 335 are off the scale; up to 105 responses per min) and therefore were not representative of typical running response rate patterns. These very high running response rates were related to the average PRP durations (Figure 4; right-hand panel), occurring when the number of reinforcers received was low (i.e., typically less than two reinforcers were obtained each session in these cases), or the PRP duration per reinforcer was very high.

In most cases, the average PRP durations were shorter than 600 s, but in some cases (several times each for all subjects excluding Hen 334), they were very long (over 800 s), and as a consequence the PRP patterns were not representative of those normally found. Like the high running response rates, the long PRP durations tended to occur when the number of reinforcers obtained during the session was very few.

Figure 5 presents the natural logarithms of the consumption data obtained for each hen in Series 1 (left-hand panel) and 2 (middle panel) of FR increases in the sawdust condition, plotted as functions of the ln FR size. The lines shown were fitted to the data using Hursh et al.'s (1988) nonlinear equation (Equation 4).

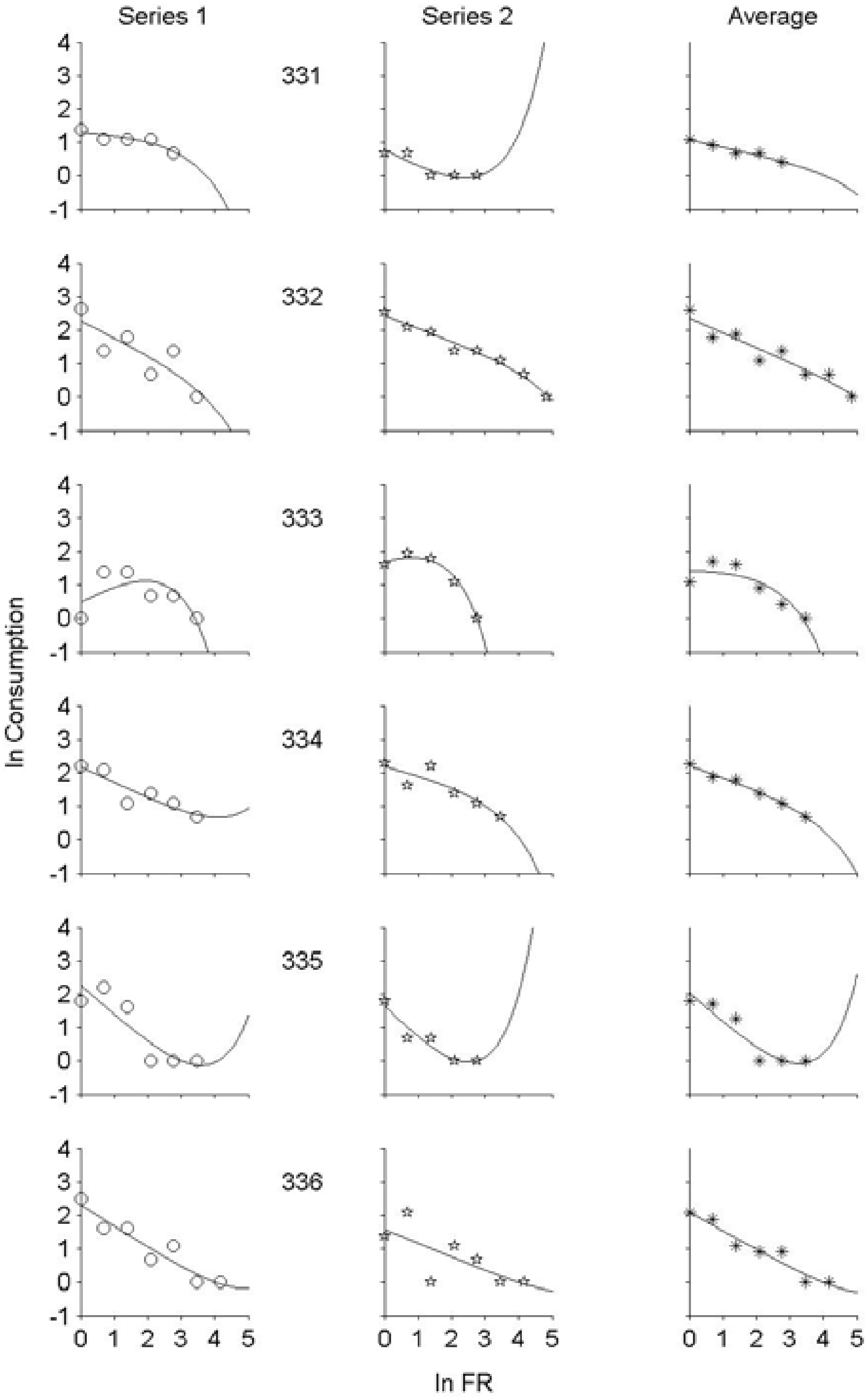

Figure 5. The natural logarithms of consumption plotted against the ln FR schedule size for each hen for Series 1 (left panel), Series 2 (middle panel), and the averaged data points from Series 1 and 2 (right panel) of the sawdust condition.

The parameters of the lines are displayed in Table 3, together with the variances accounted for by the lines (%VAC), the standard errors of the estimates (*se*) and the FR value predicted to generate maximum responding (P_{max}), as calculated by Equation 5. The lines fitted to the consumption data from the sawdust condition accounted for over 80% of the data variance in 8 of the 12 cases, with the *se* measures ranging from 0.09 to 0.52.

As shown in Figure 5, there were no consistent differences in the demand functions of each individual subject across the two series of FR increases in the sawdust condition. Consumption tended to decrease as the FR size increased in both series of FR increases. The initial levels of demand (ln *L* values) were very similar for each subject across the two series, and ranged between 0.56 and 2.44 across subjects and series. The initial slopes (*b* values) ranged between -1.06 and 0.59 across subjects and series, but again were similar across the two series for each individual subject. Some of the demand functions showed curvilinear demand (with positive *a* values ranging from 0.0046 to 0.2015), while other demand functions were approximately linear, and some curved upwards beyond the last data point due to negative *a* values (ranging from -0.0015 to -0.0856), and therefore these values were not a good indicator of the change of elasticity. In cases (6 of 12) where the calculation of P_{max} was meaningful (i.e., when the *a* values were positive) the P_{max} values ranged from 7.25 to 136.89. Across subjects and series, the breaking points (Table 1) ranged between FR 16 and FR 128, however for each individual hen, the difference in the breaking points across the two series was within one or two FR values.

Because there were no consistent differences for each hen across both series of FR increases in the sawdust condition, each individual hen's

Table 3.

The parameters a, b, and ln L for Hursh et al.'s (1988) equation (Equation 4) fitted to the ln consumption verses ln FR data from Series 1, Series 2, and the averaged data of Series 1 and 2, of the sawdust condition (Condition 2). Also shown are the standard errors of the estimates (se), the percentages of variance accounted for by the lines (%VAC) and the FR value at which the fitted functions predict maximal responding (P_{max}). Asterisks indicate cases in which P_{max} was not meaningful due to negative a values.

Hen	Series	*a*	*b*	ln *L*	$P_{\max}$	*se*	%VAC
331	1	0.0250	-0.07	1.33	37.26	0.09	83.53
	2	-0.0505	-0.56	0.74	*	0.14	83.51
	Average	0.0037	-0.21	1.08	212.71	0.05	94.73
332	1	0.0124	-0.49	2.29	41.44	0.44	71.55
	2	0.0046	-0.37	2.44	136.89	0.12	97.66
	Average	0.0013	-0.44	2.36	448.26	0.22	91.57
333	1	0.0851	0.59	0.56	18.69	0.39	53.34
	2	0.2015	0.46	1.90	7.25	0.10	97.90
	Average	0.0514	0.01	1.48	19.65	0.27	80.24
334	1	-0.0080	-0.49	2.18	*	0.22	83.79
	2	0.0200	-0.26	2.21	36.94	0.25	81.52
	Average	0.0101	-0.35	2.23	64.66	0.06	98.82
335	1	-0.0246	-0.91	2.25	*	0.43	79.25
	2	-0.0856	-1.06	1.58	*	0.19	91.56
	Average	-0.0345	-0.92	2.02	*	0.27	89.26
336	1	-0.0049	-0.64	2.32	*	0.28	89.40
	2	-0.0015	-0.41	1.58	*	0.52	52.16
	Average	-0.0029	-0.56	2.10	*	0.19	93.63

consumption data was averaged and presented in the right-hand panel of Figure 5. Lines of best fit were fitted to the averaged data, using Hursh et al.'s (1988) nonlinear equation (Equation 4), and the parameters of these lines are presented in Table 3. The fitted lines accounted for over 80% of the data variance in all six cases, and the *se* measures ranged from 0.05 to 0.27.

The averaged demand functions retained the shape of the functions in Series 1 and 2 of the sawdust condition for all hens. The ln *L* values ranged between 1.08 and 2.36, and consumption generally decreased as the FR increased. Some of the demand functions were curvilinear, and some appeared approximately linear (Hens 332 and 336) or curved upwards (Hen 335). Inelastic initial demand was indicated in five of the six cases by *b* values that were less negative than -1 (ranging between -0.21 and -0.92). In the remaining case (333), the *b* value fitted to the demand function was positive. The *a* values of lines fitted to the data were positive in four of the six cases (ranging between 0.0013 and 0.0514), and negative in the two remaining cases (Hens 335 and 336), where fitted lines curved upwards beyond the data points. Therefore, P_{max} was meaningful in only four of the six cases, ranging between 19.65 and 448.26.

Conditions 1 and 2 (Sand and Sawdust). The averaged consumption data from both the sand (circles and unbroken line) and sawdust (stars and broken line) conditions are represented, for all hens, in Figure 6 for ease of comparison. The parameters of Hursh et al.'s (1988) nonlinear equation (Equation 4) for the averaged demand functions of the sand (Series 2 & 3) and sawdust (Series 1 & 2) conditions, for all hens are represented in Table 4 together with the variances accounted for by the lines (%VAC), the standard errors of the estimates (*se*) and

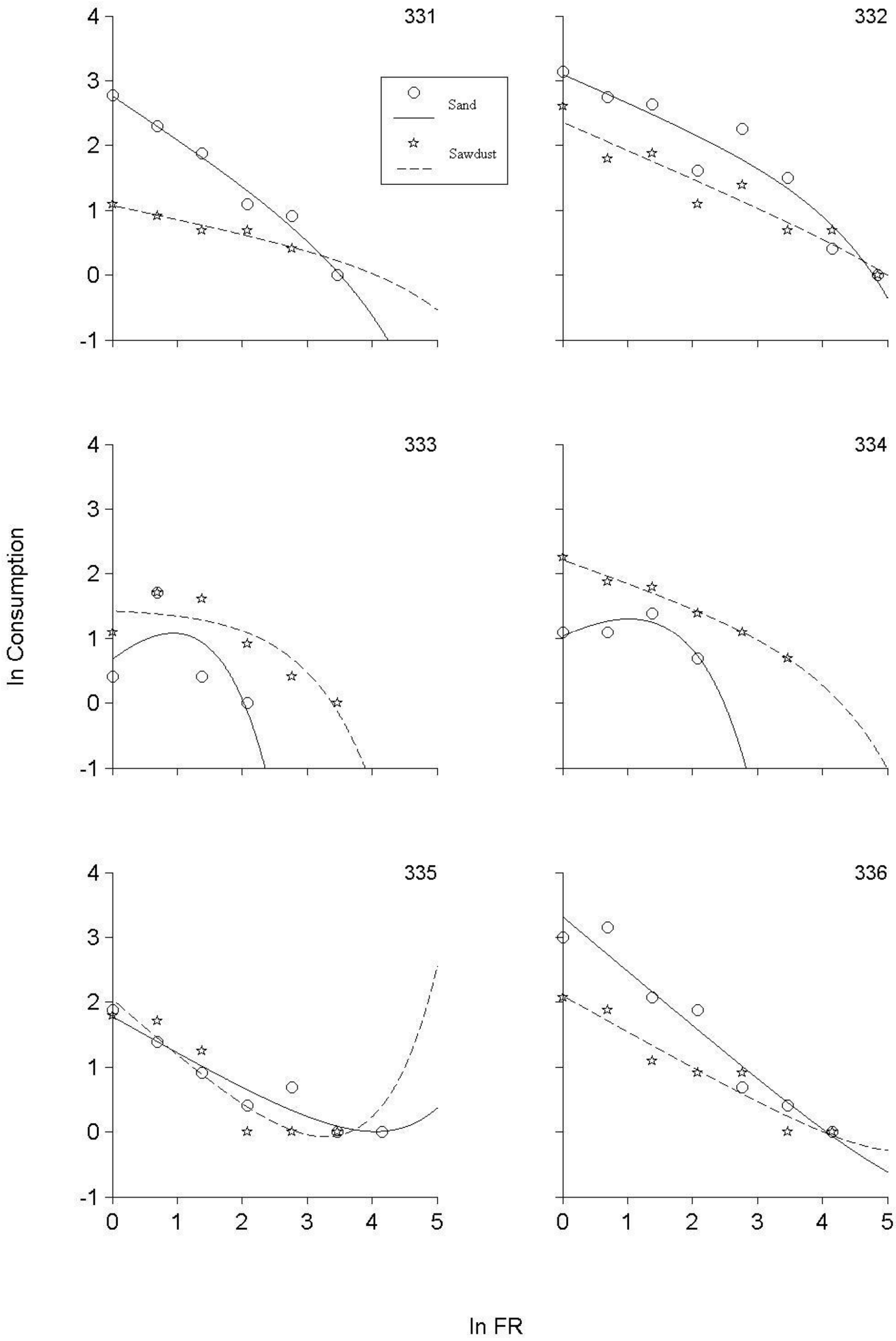

Figure 6. The natural logarithms of consumption plotted against the ln FR schedule size for each hen for the averaged data from Series 2 and 3 of the sand condition (circles, unbroken line), and the averaged data from Series 1 and 2 of the sawdust condition (stars, dotted line).

Table 4.

The parameters a, b, and ln L for Hursh et al.'s (1988) equation (Equation 4) fitted to the ln consumption plotted against the ln FR data averaged across the two series of the sand and sawdust conditions (Conditions 1 and 2). Also shown are the standard errors of the estimates (se), the percentages of variance accounted for by the lines (%VAC) and the FR value at which the fitted functions predicts maximal responding (P_{max}). Asterisks indicate cases in which P_{max} was not meaningful due to negative a values.

Hen	Series	*a*	*b*	ln *L*	$P_{\max}$	*Se*	%VAC
331	Sand	0.0144	-0.66	2.78	23.95	0.12	98.43
	Sawdust	0.0037	-0.21	1.08	212.71	0.05	94.73
332	Sand	0.0089	-0.43	3.11	64.54	0.30	92.07
	Sawdust	0.0013	-0.44	2.36	448.26	0.22	91.57
333	Sand	0.4800	1.23	1.15	4.65	0.45	51.20
	Sawdust	0.0514	0.01	1.48	19.65	0.27	80.24
334	Sand	0.2536	0.71	1.28	6.73	0.11	78.40
	Sawdust	0.0101	-0.35	2.23	64.66	0.06	98.82
335	Sand	-0.0100	-0.58	1.77	*	0.18	92.62
	Sawdust	-0.0345	-0.92	2.02	*	0.27	89.26
336	Sand	-0.0020	-0.84	3.32	*	0.26	94.94
	Sawdust	-0.0029	-0.56	2.10	*	0.19	93.63

the FR value predicted to generate maximum responding (P_{max}), as calculated by Equation 5, also for ease of comparison.

In three cases (Hens 331, 332 and 336), the initial consumption levels (ln *L*) were higher in the sand condition, while in the remaining three cases (Hens 333, 334, and 335), the ln *L* levels were higher in the sawdust condition. In one case (Hen 332) the initial slopes of the demand functions (*b* values) were almost the same, but slightly less elastic (a smaller negative number) for the sand condition. In another case (Hen 335) *b* values were less elastic for the sand condition than for the sawdust condition. The reverse was true for two hens (Hens 331 and 336). In one of the remaining cases (Hen 334), the initial slope of the demand function was positive in the sand condition, and relatively inelastic in the sawdust condition. In the final case (Hen 333), the initial slopes of the demand functions from both conditions were positive. In this case, the *b* value of the demand function for the sand condition was more inelastic (a larger positive number). The rates of change in elasticity (*a* values) of the fitted lines were, for four of the six subjects (Hens 331, 332, 333 and 334), positive in both the sand and sawdust conditions, suggesting that demand became increasingly more elastic as the FR size increased. In each of these cases, the rates of change of elasticity (*a* values) were greater for the sand condition, indicating that consumption decreased faster over FR increases during this condition than during the sawdust condition. The *a* values of the fitted lines for Hens 335 and 336 were negative for both the sand and sawdust conditions, and therefore, the resulting P_{max} values were meaningless. In the remaining cases (Hens 331 to 334) in which P_{max} was meaningful, the estimated points of maximal responding were, for all subjects, higher in the sawdust condition. The break points (presented in Table 1) varied between hens and were higher in the sand condition in two cases (Hens 331 and 335), higher in the sawdust condition in two cases (Hens 333 and 334), and were the same for both conditions in the remaining two cases (Hens 332 and 336).

Preference Assessment

The raw data from all sessions of Condition 3 for each hen are presented in Appendix B. Figure 7 shows the logarithms of the ratios of responses (circles) and times (crosses) plotted for all sessions of Condition 3 for each hen. All ratios were taken to the left key (sand). In each panel, the horizontal dotted line at zero indicates where the preferences would be likely to fall had no biases been shown in the hens' behaviour (i.e., no preference for either substrate). Data points above this line suggest a bias toward the left substrate (sand), and points below the line suggest a bias toward the right substrate (sawdust). As can be seen in Figure 7, on a session-by-session basis, the individual log response and time ratios are generally similar. However, they vary both between hens, and across sessions within individual hen data. In some cases (Hens 334 and 336), preference is still unclear despite each subject continuing for a minimum of 55 sessions. In cases in which a bias is apparent (Hens 331, 332, 333, and 335), a considerable amount of variation from session to session is still evident. Due to the variation, trends in the data are difficult to see. Across sessions, the behaviour of Hen 331 appears to have changed from indifference at the beginning of the condition, to indicating a preference for sand, while the behaviour of Hen 332 appears to have changed from indifference to a preference for sawdust. From the beginning of the experiment, preferences for sawdust and sand are apparent for Hens 333 and 335 respectively. No obvious trends in behaviour are apparent for Hens 334 and 336

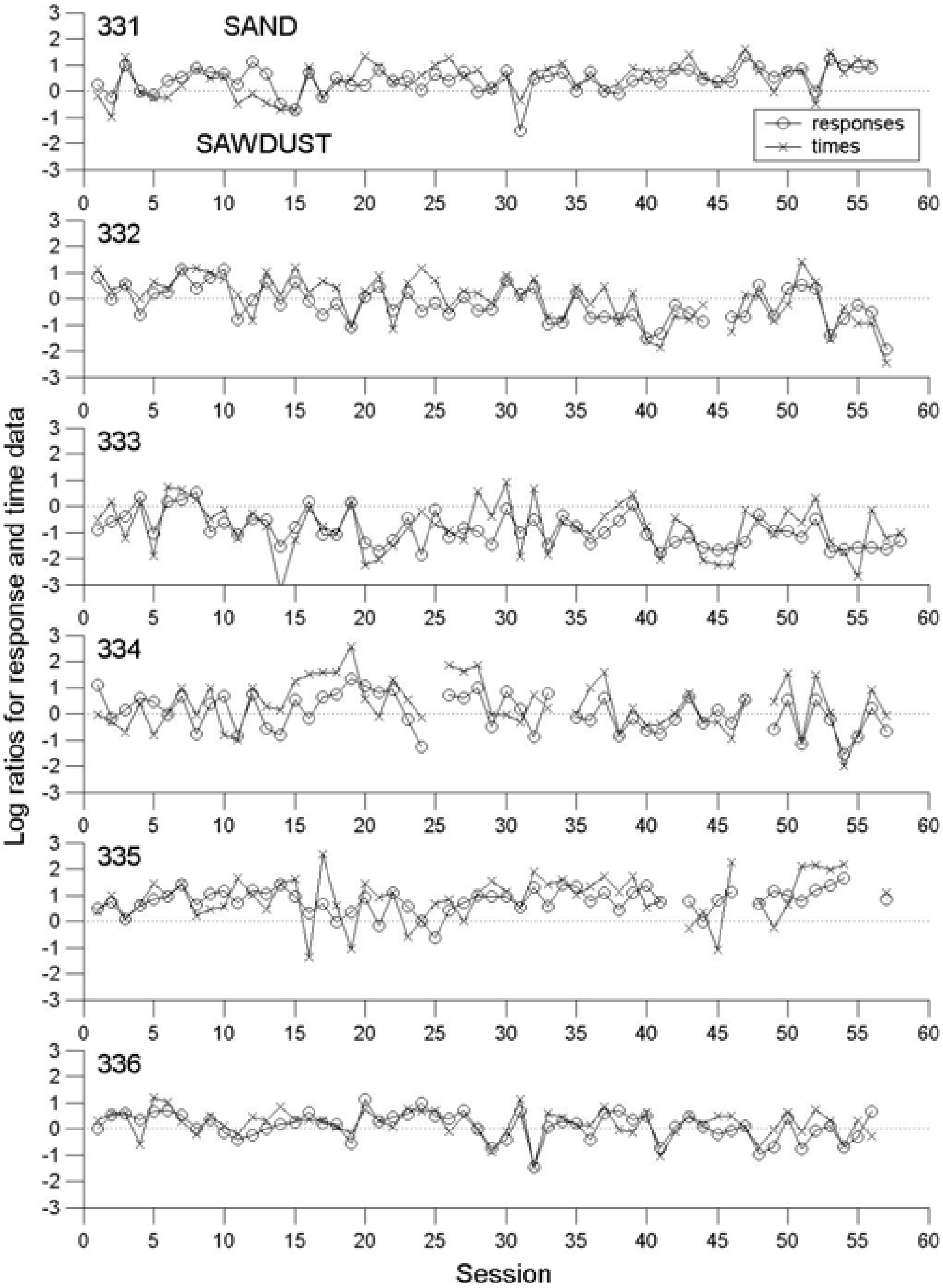

Figure 7. The logarithms of the ratios of responses (circles) and times (crosses) plotted against session, for all sessions of Condition 3 and all hens. The horizontal dotted line at zero indicates where the ratios would be likely to fall had no biases been shown in the hens' behaviour. Gaps in the data indicate sessions in which responding was exclusive to one key only.

(i.e., indifference is indicated across sessions). Overall, no clear bias towards one substrate is apparent across all subjects.

In order to make any trends more obvious, Figure 8 shows both the medians and averages of the response and time data from every second five-session period of Condition 3 for each hen on a logarithmic scale. These log ratios are point estimates of log c (Equation 2) and show the overall bias, including any inherent bias as well as any experimental bias due to the different litter substrates. The point estimates were calculated in two ways. The first (left-hand panel) was by summing the data from each five-session period, and the second (right-hand panel) was by taking the median of each five-session period. Trends in the data are similar even though the methods of calculation differ. The values of the log c point estimates are also shown in Table 5. As can be seen in Table 5 and Figure 8, the response and time ratios, again, are variable, although the data from three hens (331, 335 and 336) generally show a bias towards sand, while the response and time ratios for the remaining three hens (332, 333 and 334) generally show a bias towards sawdust.

Summary

A summary of the preference and demand findings is presented in Table 6. Table 6 specifies, for each subject, the substrate for which a preference was found, and the substrate for which the demand function parameters were found to be lower or higher and/or more inelastic. As can be seen in Table 6, preferences and demand function parameters varied across all six subjects, and also within individual findings. In previous research using food as a reinforcer (Flevill, 2002; Grant, 2005), the preferred reinforcer generated demand functions with lower initial levels of demand, the most inelastic initial slopes, the smallest rate of

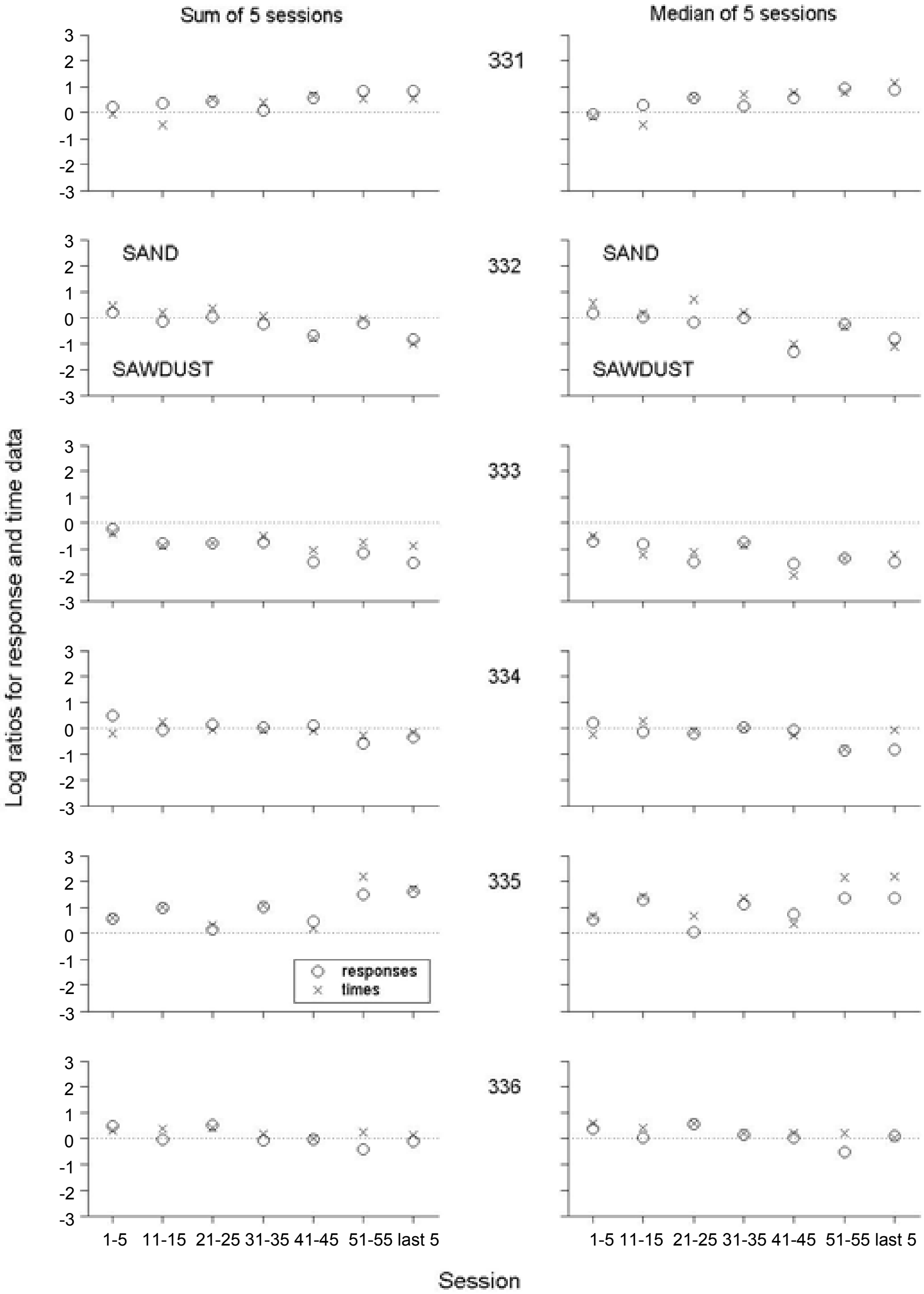

Figure 8. The summed (left panel) and median (right panel) point estimates of log *c* (Equation 2) for responses (circles) and times (crosses) for every second five-session period of Condition 3, for all hens.

Table 5.

Estimates of log c (overall bias) for response and time data for, all hens, for every second five-session period throughout Condition 3. The estimates were calculated by summing the data from the five-session period (sum), and by taking the median of the five-day period (median).

Hen	Sessions	Overall Bias (log c) Sum		Overall Bias (log c) Median	
		Responses	Times	Responses	Times
331	1-5	0.21	-0.08	-0.07	-0.19
	11-15	0.34	-0.48	0.28	-0.49
	21-25	0.41	0.54	0.54	0.61
	31-35	0.09	0.39	0.23	0.71
	41-45	0.56	0.66	0.56	0.78
	51-55	0.81	0.48	0.96	0.77
	last 5	0.85	0.54	0.88	1.15
332	1-5	0.21	0.44	0.18	0.56
	11-15	-0.13	0.23	0.03	0.17
	21-25	0.04	0.37	-0.17	0.70
	31-35	-0.25	0.07	0.00	0.23
	41-45	-0.71	-0.80	-1.35	-1.00
	51-55	-0.22	-0.03	-0.26	-0.37
	last 5	-0.84	-1.02	-0.82	-1.11
333	1-5	-0.25	-0.38	-0.70	-0.52
	11-15	-0.76	-0.87	-0.82	-1.23
	21-25	-0.76	-0.77	-1.50	-1.11
	31-35	-0.73	-0.52	-0.74	-0.83
	41-45	-1.52	-1.06	-1.57	-2.05
	51-55	-1.16	-0.75	-1.37	-1.37
	last 5	-1.56	-0.88	-1.51	-1.24

Table 5. *(Continued)*

Hen	Sessions	Responses	Times	Responses	Times
	1-5	0.49	-0.22	0.22	-0.25
334	11-15	-0.06	0.25	-0.12	0.29
	21-25	0.13	-0.06	-0.21	-0.12
	31-35	0.02	-0.08	0.03	0.02
	41-45	0.10	-0.09	-0.06	-0.29
	51-55	-0.58	-0.28	-0.86	-0.82
	last 5	-0.35	-0.19	-0.84	-0.08
	1-5	0.55	0.59	0.52	0.68
335	11-15	1.00	1.02	1.30	1.45
	21-25	0.13	0.31	0.03	0.68
	31-35	1.02	1.07	1.14	1.38
	41-45	0.45	0.17	0.73	0.36
	51-55	1.50	2.19	1.38	2.14
	last 5	1.60	1.72	1.38	2.17
	1-5	0.48	0.33	0.39	0.60
336	11-15	-0.02	0.37	0.03	0.42
	21-25	0.52	0.44	0.58	0.59
	31-35	-0.08	0.17	0.14	0.22
	41-45	-0.04	-0.01	0.05	0.20
	51-55	-0.42	0.25	-0.51	0.19
	last 5	-0.11	0.15	0.10	0.03

Table 6.

Summary of the concurrent preference assessment and demand function parameters. Asterisks indicate cases in which values were meaningless.

Measure	Subject					
	331	332	333	334	335	336
Preferences Towards	Sand	Sawdust	Sawdust	Sawdust	Sand	Sand
Lower *ln* L	Sawdust	Sawdust	Sand	Sand	Sand	Sawdust
More inelastic *b* values	Sawdust	Sand	Sand	Sand	Sand	Sawdust
More inelastic *a* values	Sawdust	Sawdust	Sawdust	Sawdust	*	*
Higher P_{max}	Sawdust	Sawdust	Sawdust	Sawdust	*	*
Higher Break point	Sand	Same	Sawdust	Sawdust	Sand	Same

change of elasticity, and larger P_{max} values. This relation was found in the present experiment for only one subject (Hen 335). A somewhat similar relation was found for two other subjects in the present study (Hens 333 and 334), however, the initial levels of demand were lower and initial slopes more inelastic for the non-preferred reinforcer.

Dustbathing

During the Demand Assessment (Condition 1 and 2). Table 7 presents the numbers of trips (reinforcers), the numbers of dustbathing trips (trips during which a dustbathing bout took place), and the proportions of trips spent dustbathing in each substrate (numbers of trips dustbathing in sand divided by trips made to sand, and numbers of trips dustbathing in sawdust divided by trips made to sawdust, for each subject), and summed across all subjects (group total) during the sand and sawdust conditions. Table 7 shows that, although a larger overall (group total) number of trips and dustbathing trips took place during the sand condition, a slightly larger overall (group total) proportion of dustbathing trips occurred in the sawdust condition. Individually, the results were very idiosyncratic, however. While in four of the six cases, a larger number of trips were made in the sand condition (Hens 331, 332, 335 and 336), in only two of the six cases (Hens 335 and 336) was a larger number of dustbathing trips made during the sand condition. One subject (Hen 331) made the same number of dustbathing trips in each condition. Four of the six subjects (Hens 331, 332, 333, and 336) spent a larger proportion of trips dustbathing in the sawdust condition, while the remaining two subjects (Hens 334 and 335) spent a larger proportion of trips dustbathing in the sand. Also presented are the combined totals (the summed data from both the sand and sawdust) of the numbers of trips, dustbathing trips,

Table 7.

The number of 5-min trips to a litter substrate (sand or sawdust) together with the number of trips spent dustbathing, and the proportion of trips spent dustbathing, for each hen, in the sand and sawdust demand conditions (Conditions 1 and 2). Also presented are the numbers of trips, numbers of dustbathing trips, and dustbathing proportions for the demand assessment combined (sand and sawdust together; Combined Total), and summed across all subjects (Group Total).

	Sand Condition			Sawdust Condition			Combined Total		
Hen	Trips	Dustbathing Trips	Dustbathing Proportion of Trips	Trips	Dustbathing Trips	Dustbathing Proportion of Trips	Total Trips	Dustbathing Trips	Dustbathing Proportion of Total Trips
331	77	6	0.08	22	6	0.27	99	12	0.12
332	138	4	0.03	73	6	0.08	211	10	0.05
333	19	1	0.05	36	4	0.11	55	5	0.09
334	24	3	0.13	62	4	0.07	86	7	0.08
335	36	12	0.33	35	8	0.23	71	20	0.28
336	125	34	0.27	49	15	0.31	174	49	0.28
Group Total	419	60	0.14	277	43	0.16	696	103	0.15

and proportions (summed sand and sawdust numbers of dustbathing trips divided by summed sand and sawdust trips, for each subject) that occurred during the preference assessment. The summed proportion (combined total) of dustbathing trips that occurred in the sand and sawdust conditions ranged from 0.05 to 0.28.

Figure 9 shows the total numbers of trips and numbers of trips in which dustbathing took place (white bars) for each subject at each FR during the demand assessment, in order to assess dustbathing behaviour across changes in price. The two bars at each FR represent the two series conducted in each condition (Series 2 and 3 of the sand condition, and Series 1 and 2 of the sawdust condition). Trips in which the hen performed dustbathing behaviour are indicated in white. The left-hand panel of Figure 9 presents the total numbers of trips and the numbers of dustbathing trips for each hen in the sand condition. The right-hand panel of Figure 9 presents the total numbers of trips and the numbers of dustbathing trips for each hen in the sawdust condition.

Figure 9 shows that the total number of trips tended to decrease as the FR size increased, across both conditions and for most subjects. In only one case (Hen 336) did the number of dustbathing trips (white bars) tend to systematically decrease along with an increase in the FR size. In the other five cases, the numbers of dustbathing trips were small, even during low FRs, and there were no systematic differences across changes in the FR size. However, because the total number of trips decreased along with increases in the FR size, trips in which dustbathing occurred tended to take up an increasing proportion of the total number of trips across most hens and conditions.

Dustbathing during the Preference Assessment (Condition 3). Presented in Table 8 are the numbers of trips, the numbers of dustbathing trips, and the

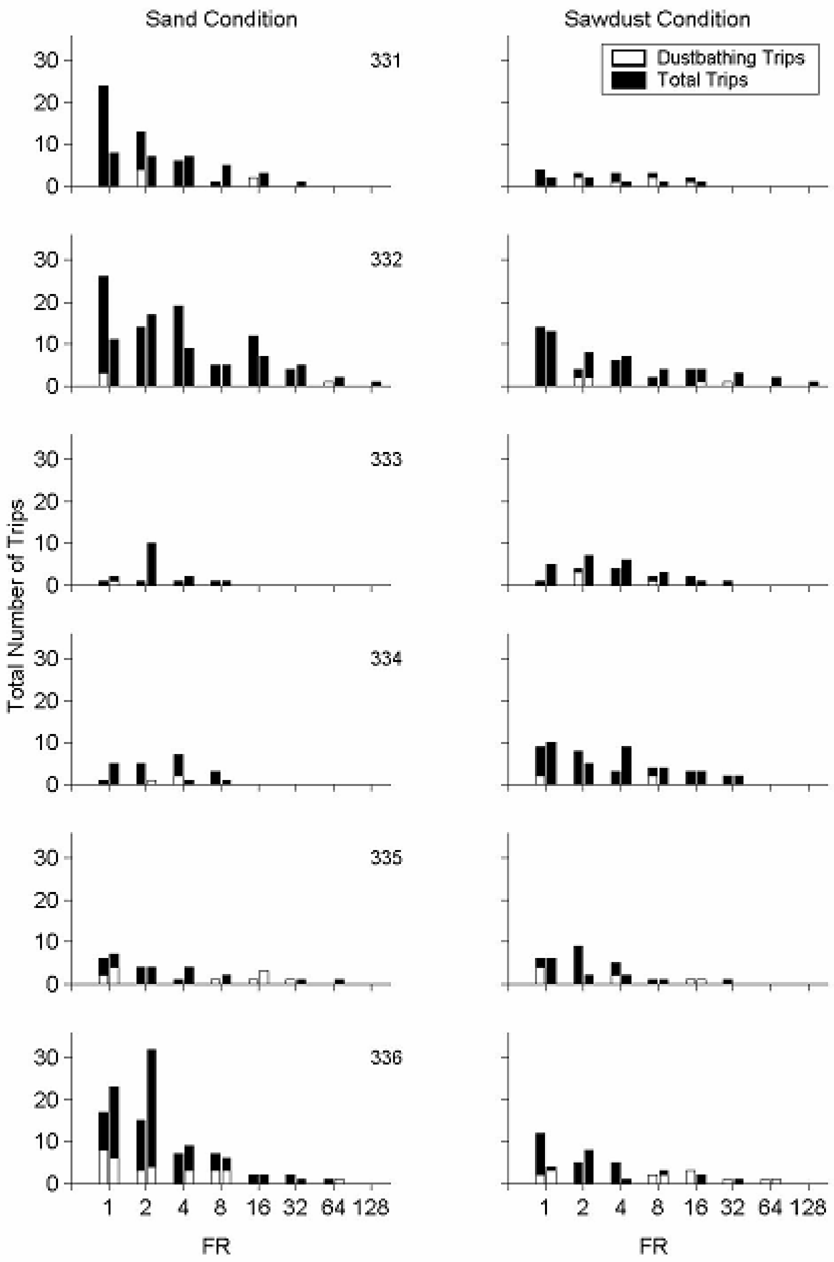

Figure 9. The total number of 5-min trips made to a litter substrate (sand or sawdust) together with the number of trips spent dustbathing (white bars), for each hen, plotted against FR schedule size for Series 2 and 3 of the sand condition (left panel) and Series 1 and 2 of the sawdust condition (right panel). Bars that are all white indicate sessions in which dustbathing occurred on all trips.

Table 8.

The number of 5-min trips to a litter substrate (sand or sawdust) together with the number of trips spent dustbathing, and the proportion of trips spent dustbathing, for each hen, in the preference assessment (Condition 3). Also presented are the numbers of trips, numbers of dustbathing trips, and dustbathing proportions for the preference assessment combined (sand and sawdust together; Combined Total), and summed across all subjects (Group Total).

	Sand			Sawdust			Combined Total		
Hen	Trips	Dustbathing Trips	Dustbathing Proportion of Trips	Trips	Dustbathing Trips	Dustbathing Proportion of Trips	Total Trips	Total Dustbathing Trips	Dustbathing Proportion of Total Trips
331	156	25	0.16	140	3	0.02	296	28	0.09
332	176	46	0.26	174	3	0.02	350	49	0.14
333	141	36	0.26	153	14	0.09	294	50	0.17
334	145	69	0.48	141	17	0.12	286	86	0.30
335	109	23	0.21	69	28	0.41	178	51	0.29
336	192	105	0.55	191	14	0.07	383	119	0.31
Group Total	919	304	0.33	868	79	0.09	1787	383	0.21

proportions of trips in which dustbathing occurred in each substrate, during the preference assessment, for each subject and summed across all subjects (group total), along with the combined totals (the summed data of both sand and sawdust) from the entire preference assessment. As shown in Table 8, the overall (group total) numbers of trips, dustbathing trips and dustbathing proportions were all higher for sand. Individually, most subjects obtained a similar number of trips to each substrate, except for Hen 335, who obtained a greater number of trips to the sand. For all subjects except Hen 335, a greater total number of dustbathing trips and a greater proportion of dustbathing trips took place in the sand. The summed (combined total) proportion of trips in which dustbathing occurred during Condition 3 ranged from 0.09 to 0.31.

Comparison of dustbathing during preference and demand conditions. Presented in Tables 7 and 8 are the numbers of trips, dustbathing trips, and proportions of dustbathing trips, that occurred in both substrates during both the demand and preference assessments. Comparing the total proportions (combined total and group total) of dustbathing trips that occurred for all subjects, in both substrates during the preference and demand assessments, it is evident that a greater total proportion of dustbathing occurred during the preference assessment.

When comparing the summed data of both substrates (combined total) from the preference and demand assessments, it can be seen that three subjects (Hens 331, 335 and 336) spent a similar proportion of trips dustbathing during both the preference and demand assessments, while the remaining three subjects (Hens 332, 333 and 334) dustbathed during a greater proportion of trips in the preference assessment. Comparing the overall (group total) proportions of dustbathing that occurred for all subjects in each substrate during the preference and demand assessments, it can be seen that during the demand assessment, the proportion of dustbathing that took place in each substrate was similar, while during the preference assessment, a much greater proportion of dustbathing took place in the sand.

Comparing the individual data from each substrate, it is apparent that during the preference assessment, four subjects (Hens 331, 332, 333, and 336) dustbathed in a greater proportion of trips to the sand, and a lesser proportion of trips to the sawdust, compared to the demand assessment. The opposite was true for one subject (Hen 335) who, during the preference assessment, dustbathed during a greater proportion of trips to the sawdust, but during a lesser proportion of trips to the sand. The remaining subject (Hen 334) dustbathed during a greater proportion of trips to both the sand and the sawdust during the preference assessment.

During eight of the presented sessions, across all subjects and conditions, the webcam failed to record the behaviour of the subjects while in the litter, a problem that tended to occur more often for one particular subject (336). On such occasions, each trip that could not be observed was recorded as a non-dustbathing trip.

Room Temperatures

Table 9 presents the average minimum and maximum temperatures in degrees Celsius for the home room, and the average minimum and current (temperature at the start of the first experimental session of the day) temperatures of the experimental room for all experimental conditions. Ideally, the temperature would have been maintained within 20 to 25ºC, but this was not always the case. In the sawdust condition, the average temperatures of both rooms increased

Table 9.

Average home (minimum and maximum) and experimental room (maximum and current; room temperature at the start of the first experimental session of the day) temperatures in degrees Celsius for each experimental condition.

Condition	Series	Home Room		Experimental Room	
		Min	Max	Max	Current
Sand	2 and 3	18.8	19.7	20.9	19.1
Sawdust	1 and 2	19.4	20.3	21.1	18.9
Preference Assessment		21.3	23.1	24.6	21.1

slightly in all but one case compared to the sand condition. During the preference assessment, the average temperatures were warmer (by between 1.9 and 3.7ºC), in all cases, than during the demand assessment.

DISCUSSION

The aim of the current experiment was to compare preference and demand measures for two different litter substrates, using concurrent schedules of reinforcement and increasing FR schedules of reinforcement, respectively. Based on previous research, a clear preference was expected to be found for one substrate (sand) over the other (sawdust), as it is considered to be a more effective substrate for dustbathing (e.g., van Liere, 1992; van Liere et al. 1990), a behaviour that is considered to be important to hens (Matthews et al., 1993). However, no clear preference for either substrate was obtained across all subjects. In the hope of extending previous research conducted with food reinforcers examining the relation between preference and demand (Flevill, 2002; Grant, 2005; Osugi, 2003), the individual obtained measures of preference were then compared to measures of demand for the same substrates. No obvious relation was found between the obtained preference and demand measures.

In the present experiment, no clear preference for sand or sawdust was found across all subjects (i.e., the obtained preferences, if any, were idiosyncratic). A preference for sand was obtained in three of the six cases (Hens 331, 335 and 336), and a preference for sawdust was found in the remaining three cases. However, in most cases, the obtained preferences were not large, and in all cases, these preferences were variable across sessions. Based on previous research (van Liere, 1992; van Liere et al. 1990) it was expected that sand would be preferred to sawdust, however this was not found in the present experiment. There are several possible reasons as to why no clear preference for sand was found.

One possible reason that sand was not clearly preferred over sawdust in the present experiment may be due to the experimental subjects being raised on sawdust for approximately the first six months of their lives. It has been found in previous research that the preference of hens for different litter substrates and other floor types may be influenced by previous experience and that the birds are likely to choose the floor or substrate that is familiar to them (Petherick, Duncan, & Waddington, 1990; Vestergaard & Lisborg, 1993). However, as hens gain more experience with substrates that are more appropriate for dustbathing, preference tends to change to favour that substrate (Santroa et al., 1995; Vestergaard & Lisborg, 1993). Thus, it could be expected in the current experiment that, initially, sawdust would be preferred, but this preference would change to sand as the subjects gained more experience with the substrate. However, during the preference assessment, the subjects had had previous experience with both substrates (during the demand assessment), and therefore it was not expected that the subjects would initially prefer sawdust. At the beginning of the preference assessment, only one subject (Hen 333) appeared to show a preference for sawdust, and this preference remained throughout the entire preference condition. Additionally, in opposition to the findings of Vestergaard and Lisborg (1993) and Santroa et al. (1995), another subject (Hen 332) appeared to initially prefer sand, but exhibited a bias towards sawdust by the conclusion of the preference assessment. In order to ensure that the familiarity of the substrate does not influence the findings of an experiment, the subjects should have experience with both substrates before any preference or demand assessment takes place. In the present study, the demand assessment was conducted first, so that the subjects did have extensive experience with both sand and sawdust prior to the preference assessment. Therefore, the lack of a clear preference for sand in the present experiment was unlikely to be due to a lack of prior experience with the substrates used.

Another possible reason for the lack of finding a preference for sand in the present study pertains to the commodities used and the duration of the reinforcer-access period. In any preference assessment, the obtained measure of preference is only ever relative to the testing environment (Duncan, 1978). It is possible that the lack of finding a clear preference in the present experiment may be due to the 5-min period of access being much shorter than the duration of a typical dustbathing bout, which is reported to be approximately 20 minutes (Vestergaard, 1982). By replicating the present experiment with different reinforcer-access periods, a preference assessment may yield different results. In addition, it has been suggested in previous research, that when using economic techniques and the opportunity to dustbath as a reinforcer, the subjects should be able to schedule the length of their dustbathing bout because an interruption (e.g., allowing only a short period of access to the litter substrate), may devalue the activity to the subject (Mason, McFarland, & Garner, 1998; Widowski & Duncan, 2000).

If an interruption to a dustbathing bout devalues the activity to the subject, five minutes of access to sand might not be equivalent to five minutes of access to sawdust. Van Liere et al. (1990) observed that when hens were given free access to woodshavings, shorter and incomplete dustbathing bouts were performed, while when given access to sand, longer complete bouts were performed. If, like woodshavings, sawdust is a less effective substrate for dustbathing, shorter dustbathing bouts may be performed in sawdust than in sand. This was observed in the present experiment. Typically, as observed by the author, dustbathing bouts in the sand occurred across several reinforcer-access periods within a session, even when the trips (reinforcers) to the sand were not consecutive (i.e., due to the dependent concurrent schedules, a trip to the sawdust occurred in-between). Conversely, a dustbathing bout in the sawdust typically only lasted the duration of one 5-min period of reinforcement, even if further trips to the sawdust were obtained. Thus, a greater proportion of a dustbathing bout in the sawdust might be expected to be completed within the 5-min reinforcer access period used in the current experiment, compared to a sand dustbath, meaning that dustbathing in the sawdust was less interrupted. This implies that, when given only five minutes of access, dustbathing in the sand may be of lesser value to the subjects than dustbathing in the sawdust, and it would be expected that sawdust would be the more preferred substrate. However, this was not the case for all hens, and it is unlikely that the period of access and interruption in dustbathing influenced the present findings. It was found that during the preference assessment, a far greater proportion of dustbathing bouts took place in the sand than in the sawdust, even though the same reinforcer-access period as in the demand assessment was used during this condition. In addition, as previously mentioned, dustbathing bouts that took place in the sand often occurred across several periods of access to the sand, even when a trip to the sawdust occurred in-between.

Previous demand research has successfully established that hens will work for a 5-min period of access to various litter substrates (Gunnarsson et al., 1997; Gunnarsson et al., 2000; Matthews et al., 1993; Matthews et al., 1995). Furthermore, Matthews, Walker, Foster and Temple (1998) examined the effect of three different reinforcer periods (150, 300 and 450 s) on the elasticity of demand for access to peat. Across the three reinforcer-access periods, the mean elasticities did not differ significantly for all obtained reinforcers (regardless of what behaviour occurred in the litter), or for the reinforcers in which only dustbathing behaviour occurred. It was concluded that reward magnitude has no effect on the elasticity of demand for access to litter.

The previous experience of the subjects with sand and sawdust and the reinforcer-access period are unlikely to have influenced the results in the present study because the results of the preference assessment were highly idiosyncratic, and a bias towards the sawdust was shown by only three subjects. It is more plausible, given the preference findings, that the subjects simply did not have a clear preference for sand or sawdust. The expectation of a preference for sand was based on previous research indicating that hens prefer sand to woodshavings when given simultaneous access to the two substrates (van Liere, et al., 1990). Woodshaving particles are larger and lighter than sand, and therefore are less effective in reducing feather lipids (van Liere, 1992). Sawdust particles, the alternative substrate used in the current experiment, are closer in size to sand particles, and, as the sawdust was maintained at a VWC (Volumetric Water Content) of 10% throughout the experiment, it is possible that this sawdust was a more effective dustbathing substrate than typical woodshavings, as they were heavier and more adhesive. Given the similar demand assessment results and dustbathing percentages for each substrate, the two substrates used may have been too similar, hence the lack of a clear preference across all subjects. However, this lack of preference could not have been predicted, and was not discovered until the main experiment had been completed.

It is common practice, when assessing animals' preferences, to continue experimental conditions until their behaviour is judged to be stable. Such practice implies initial preference estimates will shift with time and experience to a more stable estimate of ‘true’ preference. This was attempted in the present experiment, but the biases did not appear to stabilise with time, suggesting no clear preference was to be found. Because the findings of the preference assessment in the present study were so idiosyncratic, it is unlikely that these results could have been predicted. If anything, indifference to either substrate might have been predicted at the start of the preference assessment, because both schedules were equal throughout the condition, and the subjects were familiar both with the equipment and substrates (due to the demand assessment being conducted first). In the present experiment, indifference followed by a clear preference occurred in only two of six cases (Hens 331 and 332).

Due to the lack of a clear preference, the interpretation of the preference results was difficult. One major problem in the current experiment was that on a session-by-session basis, the obtained preferences were variable, even for those subjects whose behaviour demonstrated a clear bias towards one of the substrates (i.e., Hens 333 and 335). For all subjects, sessions continued long after statistical stability was obtained in the expectation of obtaining visual stability. However, behaviour remained variable, even after a minimum of 55 sessions, and it was agreed that the response and time ratio graphs were ‘stably unstable’ (i.e., behaviour was still variable, but did not appear to be trending).

Another problem was that due to the visual instability, preference was difficult to interpret in some individual cases. For example, Hen 336’s data (as presented in Figure 7) appeared to show indifference throughout the experiment, while the preference shown when the statistical stability criterion had been reached and the calculated point estimates both indicated a bias towards the sand.

For all of the other subjects, excepting Hen 334, measures at the time of statistical stability, the point estimates, and the graphical representations of the ratios of responses were all consistent. The preference of Hen 334, however, was the most difficult to interpret. In the present experiment, statistical stability was based on response biases, and determined by calculating the median of the proportion of responses (biases) of the last five sessions, which was then compared with the median obtained for the previous five-session period. The statistical stability criterion was achieved when five (not necessarily consecutive) medians differed by less than 0.05. Due to this method, and the long period of time in which it took to reach the statistical stability criterion, the first four medians of Hen 334 demonstrated a bias towards sand, while the final median demonstrated a bias towards sawdust. Because the graphical representation of Hen 334's ratios of responding suggested indifference, the only remaining way to obtain a measure of preference was to use the point estimates (estimates of overall bias). As the experimental subjects were experienced with both sand and sawdust, the equipment, and the experimental procedure, there is no reason why the first five sessions of Condition 3 should not be as good an estimate of 'true' preference as any five sessions. Because of this and the variability of the biases, point estimates were calculated for every second five-session period in order to clarify any trends and biases. Although the point estimates were still somewhat variable across sessions, the time and response estimates were similar for each five-session period. In addition, preferences that were initially unclear graphically and when using the statistical criterion (i.e., Hen 334), were more obvious when presented as point estimates.

Another possible explanation for the variable biases across sessions and lack of preference for one substrate across all subjects may be due to the methodology used in the present experiment. As previously mentioned, prior research investigating the preference of hens for different litter substrates has been conducted using a free-access method (e.g., van Liere et. al, 1990), while in the current study dependent concurrent schedules of reinforcement were used. In a free-access procedure, the subject is given unrestricted access to several different alternatives, and the measure is dwell time (Sumpter et al., 2002). Conversely, under dependent concurrent schedules of reinforcement, the subject must firstly work (e.g., peck a key) for access to each alternative under a specific schedule of reinforcement, and sometimes the alternative chosen is forced because of the dependent schedules, leading to obtained preferences that may be lower than 'actual' preference (Matthews & Temple, 1979). In addition, Dawkins and Beardsley (1986) suggested that access to litter was not reinforcing for hens when the operant response required to gain access to the litter was a key peck.

The methodology used in the current experiment is not likely to have influenced the preference results because, although the results were not as predicted, preferences toward one of the substrates were successfully obtained (the criterion for statistical stability had been reached for one substrate) in five of six cases. Furthermore, concurrent schedules have been found to be an effective measure of preference in hens for other commodities in previous research (e.g., foods, Flevill, 2002; sounds, McAdie et al., 1993; and social preferences, Walker, 1996). Therefore, there is no reason to assume that a preference for another commodity (i.e., litter substrates) would not be found if it were present, using dependent concurrent schedules of reinforcement. Contradictory to Dawkins and

Beardsley (1986), the operant response required is also unlikely to have influenced the lack of a clear preference in the current experiment as previous research has established that hens will work to access litter by pecking a key (Gunnarsson et al., 1997; Gunnarsson et al., 2000; Matthews et al., 1993; Matthews et al., 1995). As previously mentioned, it is more likely to be due to the substrates used in the current experiment that the obtained biases were variable across sessions, and that no clear preference for either substrate was found across subjects.

Although the methodology used is unlikely to be the cause of the lack of preference obtained in the present study, it would be interesting, in future research, to assess preference for the same litter substrates using the free-access method. By doing this, it would be possible to determine if hens' preferences for litter substrates are similar when using these different methodologies.

Due to time constraints, only one experimental condition could be conducted during the preference assessment. Ideally, more than one condition would have been conducted in order to assess preference. Such conditions might vary the relative reinforcement rates on the two keys to allow a matching line to be fitted using the GML (Generalised Matching Law) so that bias could be assessed more accurately. A reversal of the two litter substrates at equal reinforcement rates would also allow the assessment of inherent bias. Because only one condition was conducted during the preference assessment, this means that the preference measures that were obtained in the present experiment may not be as accurate as they could be because any inherent bias that was present could not be removed from the total bias. It is recommended that, in future research, more than one preference condition, as well as a reversal condition be undertaken in order to obtain ‘true’ measures of preference.

The demand functions obtained in the present experiment were also idiosyncratic, and the most salient finding was that the demand functions were not the typical orderly demand curves of mixed elasticity generally found in experiments using food as a reinforcer (e.g., Foster et al., 1997: Sumpter et al., 1999). Commonly, in food experiments, the demand functions generated for food reinforcers are similar across subjects (i.e., demand tends to be similar for all subjects). In the current experiment, the demand functions across the two demand conditions for individual subjects were similar, but between subjects the demand functions differed considerably. Additionally, the response rates during the present experiment were low, as were the breaking points when compared to data generated with food as the reinforcer (e.g., Flevill, 2002; Grant, 2005; Sumpter et al., 1999) and therefore the lines of best fit did not approximate the data as well as they typically do with food experiments. In some cases, the *a* values were negative, suggesting that demand became more inelastic as the FR size increased. These values commonly resulted from aberrant data points on the demand function. In these cases, both the *a* values and P_{max} values became meaningless, and results were difficult to compare. In several cases, the initial slopes of the demand functions were positive, giving these demand functions a bitonic appearance, also rarely reported in studies of demand for food. It is possible that the demand functions in the present study differed from those previously reported in studies using food as a reinforcer because the demand for sand and sawdust may be weaker than that for food.

Of the previous research investigating demand for litter substrates, demand functions are presented in only one study conducted by Gunnarsson et al. (2000). Gunnarsson et al.'s (2000) demand functions appear to approximate the data points somewhat better than those in the present experiment, a factor that is likely to be due to the substrates used in the study (straw and feathers), which differ from the substrates used in the present experiment. However, Gunnarsson et al.'s (2000) demand functions differ considerably between subjects, and do not fit as well as food demand functions, an outcome similar to the demand functions presented in the current study, and an outcome to be expected due to weak demand.

In the current experiment, the demand curves obtained during the sand condition generally appeared to closer approximate the demand functions of mixed elasticity obtained in food experiments than the functions obtained in the sawdust condition, but there were still many atypical points and curves. This finding, however, was not conclusive, as for some subjects (Hens 333 and 334), the demand functions were more regular during the sawdust condition than the sand condition. This is further evidence that the substrates used in the present study may have been too similar, and were perhaps not highly valued by the subjects, because, again no clear findings generalised across all hens.

The parameters of the demand functions showed that in three cases (Hens 331, 332 and 336), the initial levels of demand were higher in the sand condition, while the reverse was true in the other three cases. The initial slopes of the demand functions were more inelastic in the sand condition in four cases (Hens 332 through 335), and more inelastic for sawdust in the remaining two cases. Due to negative *a* values, the rates of change of elasticity parameters and P_{max} values were meaningful in only four cases (Hens 331 through 334). In each of these four cases, the rates of change of elasticity were more inelastic, and P_{max} values were higher in the sawdust condition. Finally, the breaking points were higher in the sand condition in two cases (Hens 331 and 335), higher in the sawdust condition in two cases (Hens 333 and 334), and in the remaining two cases (Hens 332 and 336) were the same in both conditions.

The demand parameters for each individual hen were also very disorderly, although in the three cases in which a pattern was found, the obtained preferences appeared to correspond to the demand function parameters. As presented in Table 6, in only one case (Hen 335) was an orderly pattern obtained for all of the meaningful demand parameters. For Hen 335, this pattern was predicted based on previous demand research with food. Grant (2005) and Flevill (2002) found that subjects worked harder, resulting in more inelastic demand, larger P_{max} values, and seemingly counterintuitively, lower initial levels of consumption, when working for a preferred food reinforcer. In this experiment Hen 335 showed a preference for sand. For this subject, the initial slopes of the demand functions were more inelastic for sand and the break points higher (the rate of change of elasticity and P_{max} values were meaningless due to negative a values). Like the previous data generated using food as a reinforcer, initial demand for this hen was found to be higher for the non-preferred substrate (sawdust). In the other two cases (Hens 333 and 334) in which a relation was found between preference and demand, the relation was not the seemingly counterintuitive relation found in prior food research. Hens 333 and 334 each demonstrated a bias towards sawdust. In both cases, the rates of change of elasticity were more inelastic for this substrate, and the P_{max} values and break points larger. However, unlike previous research, initial levels of demand were higher for this preferred substrate. One exception to this orderly pattern was that the initial slopes of the demand functions were, in both cases, more inelastic for the non-preferred substrate.

Because the findings in these three cases are contradictory, it is still unclear whether the relation between preference and demand for litter substrates is the same as the relation that has been found previously with food. Because no clear relation between preference and demand was found across subjects, the preferences and corresponding measures of demand in the present study must be individually analysed.

For only two of the six subjects (Hens 332 and 335) were the initial levels of demand lower for the preferred substrate, as predicted from previous research. The slope of the demand function for the preferred substrate was initially more inelastic for only one subject (Hen 335). The rates of change of elasticity of the demand functions were meaningful in four of the six cases (Hens 331 through 334), and the rates of change of elasticity for the preferred substrate were more inelastic in three of the four cases (Hens 332 though 334). Three of the four (Hens 332 through 334) meaningful P_{max} values were higher for the preferred substrate. Finally, in four cases (Hens 331, 335, 334 and 335) the breaking points were higher for the preferred substrate. These data obtained in the present experiment do not support previous research investigating the relation between preference and demand, which found that demand was more inelastic, P_{max} was higher and initial demand lower, for the preferred substrate.

Flevill (2002) suggested that the counterintuitive findings of her experiment comparing preference and demand for three different foods in hens might have been partially due to the different sizes of the foods used. Thus more calories may have been obtained for one food during the standard three seconds of access to the food hopper used in the assessment of all three foods. However, Grant (2005) obtained the same counterintuitive findings when the experiment was replicated using different periods of access to the same food, countering Flevill's explanation.

A problem in the present experiment was that no clear preference was found across all subjects, and the biases that were obtained were very variable. In addition, although the demand functions, their parameters, and response rates differed between individual subjects, for each subject these data were similar for both sand and sawdust. Based on these data, there is no suggestion that the two substrates differ considerably, indicating that the substrates were not different enough. This may be why, in the present study, a relation was not found between preference and demand for litter substrates. Further research is required to determine whether the previously established relation between preference and demand exists for litter substrates. A replication of the present study using litter substrates that are qualitatively more different than sand and sawdust may yield preferences that are more obvious.

As previously mentioned, in order to give the subjects experience with both substrates for the preference assessment, the demand conditions were conducted before the preference condition in the present experiment. In future research, it is recommended that the preference condition be conducted before the demand assessment. This is because data collection, especially during the demand condition, was lengthy. Previous research indicates that hens dustbathe every second day (Vestergaard, 1982, van Liere et al., 1990), and thus the subjects were exposed to experimental conditions, at most, on alternative days. By conducting the preference assessment first, it can be established whether a clear preference for either of the chosen substrates is evident before the lengthy demand assessment is undertaken.

Like the aforementioned preference and demand findings of the present study, the response rates and average PRP durations obtained in the present experiment were also idiosyncratic and dissimilar to those obtained in prior research. Commonly, in previous research, bitonic overall response rates have been obtained (Barofsky & Hurwitz, 1968; Crossman et al., 1987; Flevill, 2002; Mazur, 1983). The overall response rates obtained in the current study were slow (ranging between 0 and 7 responses per min), but increased consistently as the FR size increased across subjects in both conditions. Foster et al. (1997) investigated the behaviour of hens under open economies, and long and short-session (24-hr and 40-min sessions respectively) closed economies. They found that during long-session closed economy sessions, the overall response rate increased with increases in the FR size, however during the short-session closed economy sessions, overall response rates were obtained that initially increased over low FRs, but did not markedly change with further increases in the FR size. The authors explained that this difference is likely to be due to the differing consumption times available in the two session lengths. During a short session, even during low FRs, much of the session time is allocated to schedule-related behaviour, giving the subject no scope to increase their response rate as the FR size increases. In contrast, during long sessions, a small proportion of the total session time is likely to be allocated to schedule-related behaviour during low FRs, allowing the subject to allocate a greater proportion of the session time to schedule-related behaviour as the FR size increases. In these terms, the current experiment was conducted under short-session (30 min) closed economic conditions, and based on Foster et al.'s (1997) findings it would be expected that the overall response rates would approximate the short-session findings and show response rates that initially increased over low FRs, with no marked change as the FR increased further. However, this was not the case. The overall response rates obtained in the current study were similar to the rates and patterns found in Foster et al.'s (1997) long-session condition.

The different commodities used in the two studies may explain this inconsistency. Food is a need, which may explain why the overall response rates in the current experiment were so low when compared to overall response rates obtained in experiments using food as a reinforcer. These low overall response rates again suggest weak overall demand for the substrates used in the present study. Because the overall response rates in the present experiment were initially slow, clearly not all of the consumption time at FR 1 was being used for schedule-related behaviour, allowing the subjects to spend more time responding as the FR increased. In addition, when working for food, hens store food in their crops and do not satiate until approximately 50 3-s reinforcers have been obtained, but dustbathing is not a reinforcer that can be stored. Previous research suggests an average dustbath lasts for a duration of 20 minutes (van Liere et al., 1990; Vestergaard, 1982), and based on the 5-min reinforcer-access period used in the present experiment, a dustbathing bout is likely to be complete within approximately four to five trips. Based on this information, low overall response rates are to be expected when litter substrates are used as the reinforcer. However, in the present experiment, many trips obtained by the subjects were used to perform behaviours other than dustbathing, and during the low FRs, some subjects obtained up to 30 reinforcers. Furthermore, when comparing hens' demand for litter substrates with a study investigating hens' demand for food (Blackman, 1990), Matthews et al. (1993) found that hens' demand for peat was similar to their demand for food. This suggests that peat is a highly valued litter substrate and therefore it is possible that the investigation of a substrate such as peat may yield overall response rates that more closely resemble data obtained using food as a reinforcer.

Generally, in previous research, running response rates have been found to decrease as the FR size increases (Felton & Lyon, 1966; Flevill, 2002; Foster et al., 1997; Mazur, 1983). The most obvious feature of the running response rates in the present experiment was that in both demand conditions the running response rates were extremely variable. In most cases, the running response rates generally were slow, however in some cases, the running response rates were exceptionally fast, an unusual finding, especially because the overall response rates were so slow. These atypical running response rates occurred during sessions in which the number of reinforcers obtained was very small, or the PRP durations per reinforcer were large, or both.

These uncommon and inconsistent running response rates are likely to be due to the commodity used in the present experiment for two main reasons. Firstly, at each FR, generally a small number of reinforcers were obtained compared with consumption during food experiments (e.g., Foster et al., 1997; Sumpter et al., 1999). Because few reinforcers were obtained, the running response rates had more capacity to vary, depending on how soon the subject responded after receiving a reinforcer. If, for example, a subject performing under an FR 8 schedule met the response requirement relatively soon after the first response, and did not respond at all after receiving the reinforcer, the resulting running response rate will be high and the PRP duration very long (e.g., Hen 335 in Series 2 of the sand condition, at FR 4). This is because the two measures necessarily correspond as the calculation of the running response rates excludes PRP durations. However, if the same subject responded (not enough to meet the response requirement) reasonably soon after receiving the reinforcer, the running response rate would be very low, and the PRP duration short (e.g., Hen 334 in Series 2 of the sand condition, at FR 8).

A second reason for the inconsistent running response rates may be because behaviour that was not schedule-related occurred during the PRP time after the reinforcer was obtained. It is possible that, immediately after a trip spent dustbathing, the subjects returned to the central position of the apparatus and continued the process of dustbathing. The observation videos recorded only the behaviour of the subjects during trips to the litter, and thus behaviour during keytime was not observed. However, in all conditions, litter was commonly found in the central position of the apparatus, which indicates possible evidence of a wing or body shake, a concluding part of the dustbathing process necessary to remove the litter from the feathers (van Liere, 1992; van Liere & Wiepkema, 1992). Therefore, the atypical running response rates in the current experiment are likely to be due, at least in part, to the commodities used.

The PRP durations of the current experiment were dissimilar to the pattern described in previous research; an increase in the PRP duration as the FR size increases (Barofsky & Hurwitz, 1968; Felton & Lyon, 1966; Foster et al., 1997; Mazur, 1983). Most PRP durations were reasonably short across subjects and both demand conditions, but some were very long, meaning that the PRP durations in the present study were unrepresentative of typical PRP patterns. The exceptionally long average PRP durations generally occurred when two or fewer reinforcers were obtained during the session, indicating that after receiving a trip to the litter, the subject did not respond for the remainder of the session. Again, like the running response rates, these atypical results could be due to the occurrence of behaviours during the experimental session that were not schedule-related.

Dustbathing behaviour, like the preference and demand results, was also very idiosyncratic. The dustbathing findings of the demand assessment provide further evidence that when presented individually, the two substrates used in the present experiment are very similar to the subjects. During the demand assessment, the overall (group total) numbers of trips (reinforcers) and dustbathing trips (number of reinforcers in which dustbathing behaviour occurred) summed across all subjects, were higher in the sand condition than in the sawdust condition, yet, the overall (group total) proportion of dustbathing in sand was very similar to the proportion of dustbathing in sawdust. However, as in the previously reported comparison of demand function parameters, dustbathing behaviour was idiosyncratic, and no pattern was evident across all subjects. While in four of the six cases (Hens 331, 332, 335 and 336), a larger number of trips occurred in the sand condition, in only two of the six cases (Hens 335 and 336) did a larger number of dustbathing trips occur in the sand condition. One subject (Hen 331) made the same number of dustbathing trips in both conditions. Of the total number of trips made to each substrate, the proportion of trips in which dustbathing occurred was larger in four of the six cases (Hens 331, 332, 333 and 336) during the sawdust condition.

One problem that occurred during the present experiment was the occasional failure of the web cam to record behaviour during trips to the litter substrates. This problem tended to occur more often for one particular subject (Hen 336) during the demand assessment and, as a result, behaviour could not be observed and each trip was recorded as a non-dustbathing trip. The obtained dustbathing proportions of this subject may therefore be slightly lower than the 'actual' dustbathing proportions. However, this problem is unlikely to have influenced the overall findings of the present experiment, as the videos only failed to record behaviour during eight sessions, of a total number of 2483 sessions that occurred for all subjects and all presented conditions.

As with dustbathing behaviour during the demand assessment, and the previously discussed preference findings, no consistent pattern across subjects was found between the preferred substrate and the proportion of dustbathing in that substrate during the preference assessment (presented in Table 8). During this condition, only two of the six subjects (Hens 331 and 336) dustbathed more in their preferred substrate. In these two cases, the preferred substrate was sand. In the four remaining cases, a greater proportion of dustbathing took place in the non-preferred substrate. In three of these four cases (Hens 332 through 334), the preferred substrate was sawdust, but more dustbathing took place in the sand. The remaining subject (Hen 335), while showing a bias towards sand, performed a greater proportion of dustbathing bouts in the sawdust. Therefore, in four of the six cases, a considerably greater proportion of dustbathing took place in the non-preferred substrate. This means that a preference for one substrate, as measured in the present experiment, does not imply that more dustbathing will take place in that substrate, a finding that is seemingly counterintuitive. From the author's video observations, across all subjects, a greater amount of foraging behaviour (pecking and scratching) occurred during trips to the sawdust as opposed to trips to the sand. It is possible that the three subjects who showed a preference for sawdust may have preferred sawdust for this reason. This does not, however, explain the behaviour of Hen 335, who showed a bias towards sand, yet, on the majority of trips to the sand, appeared simply to stand on the substrate. In addition, Hen 335 was the only subject to spend a greater proportion of trips dustbathing in the sawdust during the preference assessment. It was noted that during trips to the sand in which the subjects were not dustbathing, some foraging behaviour occurred, but not as much as occurred in the sawdust, and often the subjects simply stood in the sand for the entire duration of the trip. It is unclear as to how these results should be interpreted. As mentioned by Gunnarsson et al. (2000), the development of methods to assess preference and demand for particular behaviours rather than for different environments would aid the interpretation of such findings.

No relation during the preference assessment was found between the preferred substrate and substrate in which a greater proportion of dustbathing trips occurred. Therefore, for each subject, the substrate yielding a greater proportion of dustbathing trips during the preference assessment was compared to the individual demand functions, obtained in the demand assessment, in the hope of finding a relation. For two of the six subjects (Hens 333 and 334), initial levels of demand were lower for the substrate yielding greater proportions of dustbathing trips. In three of the six cases (Hens 332 through 334), the initial slopes of the demand functions were more inelastic for this substrate, and in all four cases that were meaningful (Hens 331 through 334), the rates of change of elasticity were more elastic for this substrate, and P_{max} values smaller. Again, there is no clear pattern across all subjects, and the dustbathing findings are seemingly counterintuitive.

Dustbathing in the two substrates also differed for each subject during the preference and demand assessments. Overall, a considerably greater proportion of total dustbathing trips occurring during the preference assessment (0.21) than in the demand conditions (0.14 in the sand and 0.16 in the sawdust). This finding may be due to several factors. Firstly, previous research has indicated that sand may become unfamiliar to hens as a dustbathing substrate after long-term deprivation, displaying a fear response of fleeing the sand dustbath immediately following the deprivation (van Liere & Wiepkema, 1992). It is possible that deprivation of other dustbathing substrates may also make them unfamiliar to hens. The hens in the present study had never before had access to sand, and although they were raised on sawdust, were deprived of suitable dustbathing substrates for at least six months prior to the experiment. However, this is unlikely to have influenced the results of the current experiment, because the subjects were deprived of sand for 10 weeks between the conclusion of the sand condition and the commencement of the preference assessment, and during this condition, a comparable number of trips took place in the sand and the sawdust. In addition, the subjects were given six weeks of training immediately prior to the commencement of the first condition of the demand assessment in order to become habituated to the novel equipment and the litter substrates.

Another possible reason for the greater proportion of dustbathing in the concurrent condition may have been the procedure used. Under concurrent VI VI schedules of reinforcement with a COD, a minimum of two responses are required to gain access to a reinforcer. Conversely, under increasing FR schedules of reinforcement, the allocation of reinforcers depends entirely on the response rate of the subject. This means that under an FR schedule with a ratio greater than 2, the amount of work required to obtain just one reinforcer is larger than is required under concurrent schedules. However, it is unlikely, in the present experiment, that the different procedures influenced the proportion of dustbathing, because in most cases, the subjects made just as many or even more responses under the concurrent schedules than under the FR schedules during the two demand conditions. During the demand conditions, the number of responses ranged between zero and 199 within each session, while during the preference assessment, the number of responses ranged between zero and 272 within each session. Additionally, during the demand conditions, dustbathing did not typically occur more often under low FRs, but remained relatively stable across all FR values (Figure 9), so the response requirement did not appear to influence the likelihood of a dustbathing bout.

Another factor that may have affected the proportion of dustbathing that occurred under the concurrent conditions as opposed to the demand conditions is the temperature of the home and experimental rooms. In previous research, temperature has proven to be an important factor in the performance of dustbathing. In an investigation of the external factors influencing dustbathing in the domestic hen, Duncan et al. (1998) reported that dustbathing occurred approximately 50% more often when temperatures were maintained at 22ºC than when they were held at 10ºC. In the present experiment, the overall proportion of dustbathing that occurred during the demand assessment was 0.15, increasing approximately 40% to 0.21 in the preference assessment. Throughout the current experiment, it was attempted to maintain the temperature of both the home and experimental rooms between 20 and 25ºC, but this was not always possible due to the climate. The sand and sawdust demand conditions were both conducted during the winter season, and throughout both conditions the temperature was very similar (all average temperature measures ranging between 18.8 and 21.1 degrees Celsius), and the proportion of total trips in which dustbathing occurred was almost identical. However, the concurrent condition was conducted throughout the spring, summer and autumn months, and the average temperatures of both rooms were markedly warmer (all measures of temperature ranged between 2 and 3 degrees Celsius warmer) than during the demand conditions. Although the difference in temperatures was not as diverse as those used in the study by Duncan et al. (1998), the temperature increase may be a possible explanation as to why dustbathing occurred during a greater proportion of total trips in the concurrent condition.

Although the greater overall proportion of dustbathing (to both substrates) that occurred during the preference assessment may be explained by a slight increase in temperature, it does not explain the much greater incidence of dustbathing in the sand during the preference assessment. In general, the proportion of dustbathing in each substrate was very similar in the two demand conditions, but during the preference assessment, the proportion of dustbathing in the sand (0.33) was much higher than in the sawdust (0.09). This finding suggests that when only one substrate is available (as in the demand assessment), dustbathing will ensue, regardless of the quality of the substrate for the purpose of dustbathing. However, when two substrates are concurrently available (as in the preference assessment), one possibly being more effective for the purpose of dustbathing, more dustbathing takes place in that substrate in most cases.

These dustbathing trends apply to most, but not all, subjects. During the demand assessment Hens 331, 332, 333, and 336 each performed a larger proportion of dustbathing trips in the sawdust, but during the preference assessment these subjects spent a much greater proportion of dustbathing trips in the sand. During the demand assessment, Hen 335 spent a greater proportion of trips dustbathing in the sand, while in the preference assessment, performed a greater proportion of dustbathing trips in the sawdust. Finally, during both the preference and demand assessments, Hen 334 dustbathed during a greater proportion of trips to the sand. In sum, five of the six subjects, regardless of the preferred substrate, performed a greater proportion of dustbathing trips in the sand during the preference assessment. The one exception to this finding is Hen 335, who despite demonstrating a clear preference for sand, and performing a larger proportion of dustbathing trips in the sand during the demand assessment, performed a greater proportion of dustbathing trips in the sawdust during the preference assessment.

One possible explanation may be that during the start of the concurrent condition, the sawdust that was used in the sawdust condition of the demand assessment ran out, and new sawdust was used in the concurrent condition. This new sawdust was lighter in colour, as sawdust darkens with age, although appeared the same in texture and size. It has been discussed in previous research that resurgence in dustbathing following deprivation may be due to the novelty of the litter (McFarland, 1989; van Liere & Wiepkema, 1992). It may be possible that the novelty of the new substrate is the cause of this change of behaviour for

Hen 335. However, this explanation is unlikely because all subjects were exposed to the new sawdust at the same time, and this change occurred for only one subject. Therefore it is unclear how to interpret the behaviour of this subject. As previously mentioned, the assessment of preference and demand for particular behaviours may aid the interpretation of such findings (Gunnarsson et al., 2000).

In conclusion, the relation between preference and demand that has previously been established in food research was not obtained in the current experiment using litter substrates. No clear pattern was found within the demand function parameters, and the obtained preferences were variable, both across subjects and from session to session for individual subjects. Future research is required to determine whether the relation between preference and demand is specific to food reinforcers. The present experiment may be improved and repeated using reinforcers that are qualitatively more different. In future experiments, the preference assessment should be conducted before the demand assessment, to ensure that a clear preference is obtained, and a reversal of the substrates should be conducted in order to account for any inherent bias. Future research also requires a method for assessing preference and demand for different behaviours, as opposed to the different environments that were assessed in the present study.

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APPENDIX A

The raw data from each demand condition are presented for each hen. Series 1, 2 and 3 are presented for the sand condition (Condition 1), and Series 1 and 2 are presented for the sawdust condition (Condition 2). The hen number (Hen), the date (Day, Month and Year), the condition number (Cond), the series (Series), the average post reinforcement pause durations (PRP), the total number of responses (Resp), the number of reinforcers obtained (Trips), the runtime (RunT), the move time (MoveT), the total session time (TotT), the keytime (KeyT), the fixed ratio size (FR), the latency to the first response (First; where entered as necessary to calculate the average PRP), and the number of trips in which dustbathing took place (DB; asterisks indicate instances where the number of dustbathing trips was not recorded due to equipment problems) are all recorded. The measures are presented in seconds.

Hen	Day	Month	Year	Cond	Series	PRP	Resp	Trips	RunT	MoveT	Tot T	Key T	FR	First	DB
331	6	5	5	1	1	1800	6	6	0	336	3938	1800	1		0
331	10	5	5	1	1	1727	10	5	73	302	3604	1800	2		2
331	13	5	5	1	1	1534	32	8	266	429	4630	1800	4		0
331	16	5	5	1	1	1574	32	4	226	218	3219	1800	8		0
331	20	5	5	1	1	1482	32	2	318	106	2507	1800	16		0
331	22	5	5	1	1	1215	2	0	585	0	1800	1800	32		
332	6	5	5	1	1	1800	3	3	0	171	2872	1800	1		2
332	11	5	5	1	1	1222	66	33	578	1821	13530	1800	2		4
332	13	5	5	1	1	947	33	8	853	428	4630	1800	4		0
332	16	5	5	1	1	862	88	11	938	616	5720	1800	8		3
332	20	5	5	1	1	146	76	4	1654	243	3246	1800	16		1
332	22	5	5	1	1	213	98	3	1588	155	2857	1800	32		0
332	24	5	5	1	1	36	121	1	1764	106	2209	1800	64		1
332	27	5	5	1	1	5	118	0	1795	0	1801	1800	128		
333	6	5	5	1	1	1800	6	6	0	325	3926	1800	1		3
333	12	5	5	1	1	1794	2	1	6	58	2158	1800	2		0
333	14	5	5	1	1	1800	0	0	0	0	1800	1800	4		0
334	3	5	5	1	1	2400	9	9	0	0	5574	2400	1		0
334	9	5	5	1	1	1525	25	12	276	648	6051	1800	2		3
334	12	5	5	1	1	2121	20	5	52	276	3577	2173	4		0
334	14	5	5	1	1	1378	16	2	423	115	2516	1800	8		0
334	18	5	5	1	1	1050	34	2	751	103	2504	1800	16		1

334	21	5	5	1	1	1130	64	2	670	106	2508	1800	32		0
334	23	5	5	1	1	232	16	0	1568	0	1800	1800	64		
335	9	5	5	1	1	1800	17	17	0	896	7799	1800	1		3
335	12	5	5	1	1	1736	24	12	64	651	6054	1800	2		3
335	14	5	5	1	1	1089	57	14	711	750	6752	1800	4		0
335	18	5	5	1	1	1078	72	9	722	478	4981	1800	8		*
335	21	5	5	1	1	160	50	3	1640	155	2856	1800	16		0
335	23	5	5	1	1	132	78	2	1668	104	2505	1800	32		0
335	25	5	5	1	1	38	74	1	1763	57	2158	1800	64		1
335	28	5	5	1	1	1	90	0	1799	0	1801	1800	128		
336	4	5	5	1	1	2400	57	57	0	0	22526	2400	1		*
336	10	5	5	1	1	1774	20	10	26	540	5342	1800	2		1
336	15	5	5	1	1	1198	64	16	602	848	7451	1800	4		4
336	19	5	5	1	1	1335	32	4	465	213	3214	1800	8		*
336	21	5	5	1	1	303	44	2	1498	103	2504	1800	16		0
336	23	5	5	1	1	347	67	2	1454	103	2504	1800	32		2
336	25	5	5	1	1	1284	64	1	516	54	2155	1800	64		1
336	28	5	5	1	1	9	79	0	1792	0	1801	1800	128		
331	26	5	5	1	2	1800	24	24	0	1247	10251	1800	1	24.2	0
331	28	5	5	1	2	1641	26	13	160	704	6407	1800	2	47.2	4
331	5	6	5	1	2	1504	24	6	296	327	3928	1800	4	11.4	0
331	8	6	5	1	2	1046	13	1	754	59	2160	1800	8	102.6	0
331	10	6	5	1	2	378	33	2	1422	117	2518	1800	16	65.6	2
331	12	6	5	1	2	370	10	0	1430	0	1800	1800	32		
332	30	5	5	1	2	1800	26	26	0	1466	11072	1800	1	1.6	3
332	8	6	5	1	2	1445	29	14	355	810	6813	1800	2	8.5	0
332	12	6	5	1	2	957	79	19	843	1477	8981	1800	4	2.9	0
332	14	6	5	1	2	1040	44	5	760	284	3585	1800	8	2.7	0
332	16	6	5	1	2	456	199	12	1344	655	6060	1800	16	9.7	0
332	19	6	5	1	2	165	146	4	1636	212	3215	1800	32	4.4	0
332	21	6	5	1	2	94	75	1	1706	72	2174	1800	64	22.3	1
332	24	6	5	1	2	16	90	0	1785	0	1801	1800	128		
333	27	5	5	1	2	1800	1	1	0	58	2158	1800	1	449.4	0
333	31	5	5	1	2	665	2	1	1135	61	2161	1800	2	413.8	0
333	8	6	5	1	2	1261	7	1	539	59	2159	1800	4	380.8	0
333	13	6	5	1	2	1327	8	1	473	64	2165	1800	8	529.8	0
333	15	6	5	1	2	1579	3	0	221	0	1800	1800	16		
334	27	5	5	1	2	1800	1	1	0	56	2156	1800	1	4.3	0
334	31	5	5	1	2	1777	10	5	23	292	3593	1800	2	102.3	0
334	6	6	5	1	2	1493	28	7	307	443	4345	1800	4	19.3	2
334	9	6	5	1	2	342	31	3	1458	181	2882	1800	8	2.3	0
334	11	6	5	1	2	1800	0	0	0	0	1800	1800	16		
335	7	6	5	1	2	1800	6	6	0	378	3979	1800	1	5.8	2
335	9	6	5	1	2	774	8	4	1027	234	3235	1800	2	2	0
335	11	6	5	1	2	1797	4	1	3	304	2404	1800	4	1	0
335	13	6	5	1	2	1780	8	1	20	97	2199	1800	8	3.2	1
335	15	6	5	1	2	843	22	1	957	68	2169	1800	16	1	1
335	17	6	5	1	2	239	40	1	1561	56	2157	1800	32	2.3	1
335	20	6	5	1	2	9	27	0	1791	0	1800	1800	64		
336	7	6	5	1	2	1800	17	17	0	1063	7969	1800	1	1.7	8
336	10	6	5	1	2	1461	30	15	339	883	7186	1800	2	1.6	3
336	12	6	5	1	2	1703	28	7	97	388	4290	1800	4	1.9	0
336	16	6	5	1	2	1671	56	7	130	385	4286	1800	8	1.2	3
336	19	6	5	1	2	118	38	2	1682	107	2508	1800	16	2.2	3
336	20	6	5	1	2	314	87	2	1486	109	2510	1800	32	1.7	0
336	26	6	5	1	2	1543	64	1	257	52	2153	1800	64	3.9	0
336	28	6	5	1	2	19	86	0	1781	0	1801	1800	128		

331	3	7	5	1	3	1800	8	8	0	439	4641	1800	1	9.4	0
331	6	7	5	1	3	1613	14	7	187	383	4284	1800	2	5.9	0
331	8	7	5	1	3	1301	28	7	499	395	4296	1800	4	2.7	0
331	10	7	5	1	3	596	40	5	1204	273	3575	1800	8	140.8	0
331	12	7	5	1	3	500	56	3	1300	164	2866	1800	16	4.7	0
331	14	7	5	1	3	548	47	1	1253	57	2158	1800	32	106	0
331	17	7	5	1	3	72	15	0	1728	0	1800	1800	64		
332	3	7	5	1	3	1800	11	11	0	592	5694	1800	1	2.3	0
332	8	7	5	1	3	1378	34	17	423	911	7815	1800	2	14.2	0
332	10	7	5	1	3	978	37	9	822	493	4995	1800	4	3.9	0
332	12	7	5	1	3	728	46	5	1072	275	3577	1800	8	12.8	0
332	14	7	5	1	3	490	112	7	1310	384	4287	1800	16	47.6	0
332	17	7	5	1	3	454	170	5	1346	274	3576	1800	32	17.7	*
332	20	7	5	1	3	653	129	2	1147	111	2513	1800	64	20	0
332	22	7	5	1	3	204	142	1	1596	54	2156	1800	128	92.1	0
332	26	7	5	1	3	316	3	0	1485	0	1800	1800	256		
333	9	7	5	1	3	1800	2	2	0	118	2519	1800	1	605	1
333	11	7	5	1	3	1676	20	10	124	566	5368	1800	2	24.8	0
333	13	7	5	1	3	995	8	2	805	116	2517	1800	4	6.2	0
333	15	7	5	1	3	17	12	1	1783	57	2157	1800	8	2.6	0
333	18	7	5	1	3	492	15	0	1309	0	1800	1800	16		
334	4	7	5	1	3	1800	5	5	0	283	3584	1800	1	6.5	0
334	7	7	5	1	3	1796	2	1	4	56	2156	1800	2	8.8	1
334	9	7	5	1	3	1794	4	1	6	56	2156	1800	4	4.1	0
334	11	7	5	1	3	271	10	1	1529	56	2156	1800	8	1.4	0
334	13	7	5	1	3	4	4	0	1797	0	1800	1800	16		
335	7	7	5	1	3	1800	7	7	0	404	4306	1800	1	2.9	4
335	9	7	5	1	3	1766	8	4	34	222	3223	1800	2	1054.1	0
335	11	7	5	1	3	1617	16	4	183	227	3228	1800	4	0.9	0
335	13	7	5	1	3	1754	16	2	46	113	2514	1800	8	4	0
335	15	7	5	1	3	1637	48	3	164	273	2977	1800	16	0.9	3
335	21	7	5	1	3	793	32	1	1007	56	2157	1800	32	1.2	0
335	23	7	5	1	3	1384	64	1	416	56	2157	1800	64	22.9	0
335	25	7	5	1	3	4	113	0	1796	0	1801	1800	128		
336	5	7	5	1	3	1800	23	23	0	1585	10291	1800	1	24.6	6
336	7	7	5	1	3	1534	64	32	267	1704	13111	1800	2	87.4	4
336	10	7	5	1	3	1615	37	9	185	507	5010	1800	4	0.9	3
336	12	7	5	1	3	1587	48	6	213	374	3976	1800	8	4.2	3
336	14	7	5	1	3	942	32	2	858	114	2515	1800	16	5.1	*
336	17	7	5	1	3	83	56	1	1717	54	2155	1800	32	7.4	1
336	20	7	5	1	3	188	106	1	1612	84	2187	1800	64	1.9	0
336	22	7	5	1	3	4	68	0	1797	0	1801	1800	128		
331	15	8	5	2	1	1800	4	4	0	227	3228	1800	1	25.4	0
331	17	8	5	2	1	1714	6	3	86	184	2885	1800	2	63.1	2
331	21	8	5	2	1	1746	12	3	54	174	2875	1800	4	74.9	1
331	23	8	5	2	1	1611	24	3	189	195	2897	1800	8	6.9	2
331	25	8	5	2	1	1488	32	2	312	108	2509	1800	16	9.5	1
331	28	8	5	2	1	9	10	0	1791	0	1800	1800	32		
332	15	8	5	2	1	1800	14	14	0	751	6754	1800	1	3.8	0
332	19	8	5	2	1	1566	8	4	235	286	3289	1800	2	10.4	2
332	21	8	5	2	1	938	27	6	862	333	3935	1800	4	9.3	0
332	23	8	5	2	1	1603	16	2	197	108	2509	1800	8	8.8	0
332	25	8	5	2	1	519	73	4	1282	216	3218	1800	16	40.7	0
332	30	8	5	2	1	1099	32	1	701	59	2159	1800	32	128	1
332	1	9	5	2	1	39	46	0	1761	0	1801	1800	64		
333	16	8	5	2	1	1800	1	1	0	56	2156	1800	1	100.7	0
333	19	8	5	2	1	1768	8	4	32	288	3291	1800	2	1	3
333	21	8	5	2	1	1123	18	4	677	215	3216	1800	4	2	0

333	24	8	5	2	1	1730	16	2	70	113	2514	1800	8	1.5	1
333	26	8	5	2	1	1656	32	2	144	126	2527	1800	16	224	*
333	29	8	5	2	1	1363	32	1	437	76	2177	1800	32	21.6	0
333	31	8	5	2	1	39	53	0	1761	0	1801	1800	64		

334	16	8	5	2	1	1800	9	9	0	541	5044	1800	1	2.5	2
334	19	8	5	2	1	907	17	8	893	430	4631	1800	2	2.3	0
334	22	8	5	2	1	1109	12	3	692	171	2872	1800	4	4.8	0
334	24	8	5	2	1	954	39	4	847	258	3260	1800	8	1.5	2
334	26	8	5	2	1	527	52	3	1274	165	2866	1800	16	1.4	*
334	29	8	5	2	1	91	72	2	1710	174	2577	1800	32	1.9	0
334	31	8	5	2	1	2	44	0	1798	0	1801	1800	64		

335	16	8	5	2	1	1800	6	6	0	446	4051	1800	1	8.2	4
335	20	8	5	2	1	1402	18	9	399	498	5000	1800	2	1.1	0
335	24	8	5	2	1	1743	20	5	57	291	3593	1800	4	3.6	2
335	26	8	5	2	1	38	15	1	1762	55	2155	1800	8	6.5	*
335	29	8	5	2	1	1674	16	1	126	56	2156	1800	16	9	1
335	31	8	5	2	1	27	38	1	1773	58	2159	1800	32	2.4	0
335	2	9	5	2	1	47	24	0	1754	0	1800	1800	64		

336	17	8	5	2	1	1800	12	12	0	674	6077	1800	1	1.1	2
336	20	8	5	2	1	1761	10	5	39	329	3632	1800	2	1	0
336	23	8	5	2	1	1666	20	5	134	317	3620	1800	4	6.3	*
336	25	8	5	2	1	358	19	2	1442	131	2533	1800	8	3.3	2
336	28	8	5	2	1	1128	48	3	672	202	2904	1800	16	1.6	3
336	30	8	5	2	1	1513	32	1	287	85	2187	1800	32	40.2	1
336	1	9	5	2	1	930	64	1	870	57	2158	1800	64	3.2	1
336	4	9	5	2	1	1	89	0	1799	0	1801	1800	128		

331	17	9	5	2	2	1800	2	2	0	117	2518	1800	1	118.5	0
331	19	9	5	2	2	1636	4	2	164	145	2547	1800	2	24	0
331	21	9	5	2	2	1777	4	1	23	59	2159	1800	4	21	0
331	23	9	5	2	2	1752	8	1	48	60	2160	1800	8	95.9	0
331	25	9	5	2	2	181	22	1	1619	55	2155	1800	16	66.2	0
331	27	9	5	2	2	66	12	0	1734	0	1800	1800	32		

332	17	9	5	2	2	1800	13	13	0	696	6399	1800	1	7.1	0
332	19	9	5	2	2	1597	16	8	204	468	4670	1800	2	31.6	2
332	21	9	5	2	2	555	30	7	1245	405	4307	1800	4	4.4	0
332	23	9	5	2	2	1051	34	4	749	223	3224	1800	8	1.3	0
332	25	9	5	2	2	945	64	4	855	237	3239	1800	16	5.2	1
332	27	9	5	2	2	926	96	3	874	164	2866	1800	32	43	0
332	29	9	5	2	2	167	162	2	1633	107	2509	1800	64	49.6	0
332	1	10	5	2	2	190	174	1	1610	53	2155	1800	128	74.3	0
332	3	10	5	2	2	150	63	0	1651	0	1801	1800	256		

333	18	9	5	2	2	1800	5	5	0	264	3566	1800	1	0.1	0
333	20	9	5	2	2	1793	14	7	8	429	4330	1800	2	10.8	0
333	22	9	5	2	2	1785	24	6	15	357	3958	1800	4	2.4	0
333	24	9	5	2	2	1782	24	3	18	180	2881	1800	8	1.5	0
333	26	9	5	2	2	520	26	1	1280	58	2159	1800	16	3.7	0
333	28	9	5	2	2	18	26	0	1782	0	1800	1800	32		

334	18	9	5	2	2	1800	10	10	0	513	5315	1800	1	15.1	0
334	20	9	5	2	2	1722	10	5	78	296	3598	1800	2	91.3	0
334	22	9	5	2	2	1257	36	9	543	517	5019	1800	4	1.3	0
334	24	9	5	2	2	1675	32	4	125	232	3233	1800	8	1.6	0
334	26	9	5	2	2	1498	52	3	302	176	2877	1800	16	1.1	0
334	28	9	5	2	2	219	71	2	1581	110	2512	1800	32	14	0
334	30	9	5	2	2	4	15	0	1796	0	1800	1800	64		

335	18	9	5	2	2	1800	6	6	0	311	3912	1800	1	3.2	0
335	20	9	5	2	2	1797	4	2	3	116	2517	1800	2	11	0
335	22	9	5	2	2	1776	8	2	24	116	2517	1800	4	31.2	0
335	24	9	5	2	2	979	8	1	821	54	2155	1800	8	98.3	0

335	26	9	5	2	2	224	28	1	1576	81	2182	1800	16	116.4	1
335	28	9	5	2	2	37	2	0	1763	0	1800	1800	32		
336	19	9	5	2	2	1800	4	4	0	246	3248	1800	1	1.4	3
336	21	9	5	2	2	1742	16	8	58	475	4677	1800	2	13.7	0
336	23	9	5	2	2	1787	4	1	13	62	2162	1800	4	9.2	0
336	25	9	5	2	2	88	30	3	1712	271	2975	1800	8	2.7	2
336	27	9	5	2	2	1030	32	2	771	108	2509	1801	16	1.8	0
336	29	9	5	2	2	398	60	1	1402	54	2155	1800	32	2.5	0
336	1	10	5	2	2	42	80	1	1758	77	2179	1800	64	4.7	1
336	3	10	5	2	2	7	84	0	1793	0	1801	1800	128		

APPENDIX B

The raw data from all sessions of Condition 3 are presented for each hen. The hen number (Hen), the date (Day, Month and Year), the number of responses (Resp) to the left (L) and right (R) key, the times (Time) spent responding on the L and R key, the number of trips (Trips) to the L and R, the keytime (KeyT), the move time (MoveT), the total time (TotT), and the number of L and R trips in which dustbathing took place (DB; asterisks indicate instances where the number of dustbathing trips was not recorded due to equipment problems) are all recorded. The measures are presented in seconds.

Hen	Day	Month	Year	Responses		Time		Trips		MoveT	KeyT	TotT	Dustbathing	
				L	R	L	R	L	R				L	R
331	4	12	5	39	22	704	1094	3	4	482	1800	4383	1	0
331	6	12	5	11	20	173	1621	1	3	220	1800	3221	0	0
331	8	12	5	50	5	1715	84	1	1	126	1800	2527	1	0
331	10	12	5	4	4	837	956	0	1	49	1800	2150	0	0
331	12	12	5	17	24	640	1151	2	2	235	1800	3237	1	0
331	16	12	5	39	16	639	1142	2	2	221	1800	3222	1	0
331	18	12	5	51	15	1018	634	1	4	260	1800	3561	0	0
331	20	12	5	44	6	1555	242	3	2	257	1800	3558	1	0
331	23	12	5	56	11	1365	427	2	2	221	1800	3221	0	0
331	2	1	6	62	13	1377	419	4	3	375	1800	4277	3	2
331	4	1	6	36	21	439	1358	4	3	366	1800	4267	0	0
331	6	1	6	95	7	782	1017	1	2	171	1800	2871	0	0
331	8	1	6	89	19	469	1328	1	3	248	1800	3249	1	0
331	10	1	6	6	18	292	1498	2	1	182	1800	2883	2	0
331	12	1	6	8	41	269	1526	2	1	162	1800	2863	0	0
331	15	1	6	39	8	1603	193	3	2	347	1800	3650	1	0
331	17	1	6	18	29	623	1174	2	4	353	1800	3953	0	0
331	19	1	6	37	12	1216	583	2	2	300	1800	3303	2	0
331	21	1	6	47	30	1328	465	4	3	392	1800	4293	0	0
331	23	1	6	36	22	1715	80	2	1	168	1800	2868	0	0
331	25	1	6	31	5	1597	197	1	0	53	1800	2153	0	0
331	27	1	6	19	8	1182	553	2	2	268	1800	3270	2	0
331	30	1	6	25	7	1072	710	1	3	214	1800	3215	1	0
331	1	2	6	28	25	1439	357	3	3	373	1800	3975	2	0
331	3	2	6	34	8	1626	173	3	2	253	1800	3554	0	0
331	8	2	6	40	17	1699	92	4	2	309	1800	3910	0	0
331	11	2	6	60	11	1377	421	3	3	373	1800	3975	0	0
331	15	2	6	9	10	1529	242	5	2	357	1800	4258	1	0

331	17	2	6	19	15	978	803	4	2	309	1800	3910	0	0
331	20	2	6	70	12	1387	412	2	3	271	1800	3572	0	0
331	23	2	6	3	96	562	1236	3	1	198	1800	3199	2	0
331	25	2	6	76	26	1421	275	4	4	432	1698	4531	0	0
331	27	2	6	83	22	1567	231	4	3	389	1800	4290	0	0
331	1	3	6	31	6	1647	148	0	3	165	1800	2865	0	0
331	3	3	6	44	44	1095	671	3	5	427	1769	4597	0	0
331	6	3	6	100	19	1355	438	3	4	376	1800	4276	0	0
331	8	3	6	29	29	919	879	3	2	285	1800	3587	0	0
331	11	3	6	49	63	1175	619	5	1	320	1800	3921	1	1
331	13	3	6	45	18	1568	209	4	3	377	1800	4278	0	0
331	17	3	6	82	26	962	173	3	5	427	1143	3971	0	0
331	19	3	6	62	31	1542	254	4	3	358	1800	4258	0	0
331	21	3	6	117	17	1546	252	4	3	360	1800	4261	0	0
331	23	3	6	92	14	1725	69	1	2	163	1800	2863	0	0
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331	29	3	6	64	28	1538	260	4	3	354	1800	4255	0	0
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331	2	4	6	170	21	1532	261	3	3	299	1800	3900	0	0
331	4	4	6	84	25	863	919	2	3	241	1800	3542	1	0
331	7	4	6	64	12	1540	252	3	2	250	1800	3551	0	0
331	9	4	6	119	17	1537	261	4	3	372	1800	4273	1	0
331	11	4	6	20	21	441	1342	1	1	105	1800	2505	0	0
331	13	4	6	140	8	1735	57	3	2	275	1800	3576	0	0
331	15	4	6	120	13	1471	314	1	3	216	1800	3217	0	0
331	18	4	6	76	9	1698	100	4	3	349	1800	4250	0	0
331	21	4	6	75	10	1247	104	5	3	419	1353	4173	0	0

332	4	12	5	64	10	1383	102	6	2	519	1487	4410	3	0
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332	4	1	6	13	83	1037	760	3	2	259	1800	3560	0	0
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332	17	1	6	12	53	1476	322	4	2	334	1800	3935	0	0
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332	25	2	6	8	74	109	534	4	4	415	665	3481	0	0
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332	7	4	6	78	24	1730	69	2	2	201	1800	3202	2	0
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333	19	12	5	50	28	1459	336	2	2	240	1800	3242	1	1
333	21	12	5	62	19	1153	645	2	3	267	1800	3568	0	0
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333	10	1	6	1	36	1	1797	1	1	104	1800	2505	0	0
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333	15	1	6	26	18	791	1003	1	3	211	1800	3212	0	0
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333	19	1	6	4	49	148	1648	3	3	331	1800	3931	1	0
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333	27	1	6	2	39	53	1731	2	1	165	1800	2866	0	0
333	30	1	6	19	54	113	799	4	4	479	915	3797	4	2
333	1	2	6	2	143	680	1119	2	0	102	1800	2502	1	0
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333	6	2	6	4	62	176	1622	3	2	254	1800	3554	0	0
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333	15	2	6	4	116	514	1285	3	2	264	1800	3565	2	0
333	17	2	6	48	63	1519	180	2	3	270	1800	3572	2	2
333	20	2	6	4	40	21	1773	1	2	150	1800	2850	0	0
333	23	2	6	15	50	1475	323	2	2	216	1800	3218	2	0
333	25	2	6	3	91	25	1773	2	1	154	1800	2854	0	0
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333	8	3	6	14	50	955	826	3	3	308	1800	3909	1	0
333	11	3	6	44	37	1322	468	1	2	157	1800	2858	0	0
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333	17	3	6	4	97	455	1341	2	3	268	1800	3569	0	0
333	19	3	6	6	96	224	1568	2	2	202	1800	3202	0	0
333	21	3	6	3	111	15	1783	3	3	302	1800	3903	0	0
333	23	3	6	3	150	10	1783	3	2	256	1800	3557	0	0
333	25	3	6	2	83	10	1742	2	1	157	1800	2858	0	0
333	27	3	6	5	120	741	1048	2	2	206	1800	3207	0	0
333	29	3	6	51	104	215	945	4	4	456	1168	4026	1	2
333	31	3	6	11	94	51	613	4	4	403	674	3478	0	0
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333	9	4	6	3	168	73	1725	3	2	256	1800	3557	0	0
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333	13	4	6	2	74	4	1795	2	3	257	1800	3558	0	0
333	15	4	6	6	221	739	1055	5	2	368	1800	4269	0	0
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334	7	12	5	17	25	602	1196	4	3	358	1800	4259	0	0
334	9	12	5	40	29	218	1071	3	3	325	1800	3926	0	0
334	11	12	5	36	9	1264	534	3	2	325	1800	3627	2	0
334	15	12	5	67	24	242	1557	1	2	175	1800	2876	1	1
334	17	12	5	23	24	938	861	2	2	217	1800	3218	1	0
334	19	12	5	104	22	1629	168	3	4	385	1800	4286	3	0
334	21	12	5	7	43	728	761	3	5	413	1493	4306	1	0
334	30	12	5	76	31	1631	167	3	2	497	1800	3798	3	1
334	3	1	6	100	21	242	1556	2	4	354	1800	3956	2	0

334	5	1	6	4	28	172	1626	2	1	168	1800	2869	0	0
334	7	1	6	108	20	1623	174	4	3	397	1800	4299	3	0
334	9	1	6	21	75	1185	614	4	1	328	1800	3630	4	0
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334	13	1	6	41	12	1695	103	2	3	269	1800	3569	0	0
334	16	1	6	15	22	1743	56	2	1	212	1800	2913	2	0
334	18	1	6	70	17	1752	47	1	2	190	1800	2891	1	0
334	20	1	6	34	6	1581	42	2	2	239	1800	3240	1	0
334	22	1	6	85	4	1793	5	1	1	113	1800	2514	1	1
334	24	1	6	230	21	1227	334	4	4	429	1565	4395	3	0
334	26	1	6	169	26	775	1024	4	3	363	1800	4264	4	0
334	28	1	6	127	16	878	44	3	5	459	923	3784	3	0
334	31	1	6	18	29	1375	422	3	3	368	1800	3970	3	2
334	2	2	6	3	56	761	1038	3	2	256	1800	3556	0	0
334	4	2	6	0	107	0	1799	0	1	52	1800	2153	0	0
334	7	2	6	26	5	1767	25	1	1	121	1800	2522	1	1
334	10	2	6	46	12	1754	44	3	2	268	1800	3569	0	0
334	13	2	6	78	8	1774	25	3	1	241	1800	3242	3	0
334	16	2	6	16	50	263	289	4	4	414	555	3369	0	0
334	19	2	6	145	21	856	942	4	3	372	1800	4273	3	2
334	22	2	6	39	26	571	1227	3	3	297	1800	3897	0	0
334	24	2	6	3	22	1506	293	1	2	169	1800	2869	0	0
334	26	2	6	59	10	1115	684	2	2	267	1800	3269	2	1
334	28	2	6	0	25	0	1799	0	0	0	1800	1800	0	0
334	2	3	6	27	38	913	882	2	2	215	1800	3216	1	0
334	4	3	6	31	53	1634	165	3	1	244	1800	3245	2	0
334	7	3	6	66	17	1753	45	3	2	268	1800	3568	1	0
334	9	3	6	15	107	255	1543	3	4	370	1800	4270	0	0
334	12	3	6	33	50	1108	690	2	3	260	1800	3560	0	0
334	14	3	6	9	39	459	1331	3	2	295	1800	3597	2	0
334	16	3	6	10	58	528	1262	3	2	273	1800	3573	0	0
334	18	3	6	53	84	841	833	4	4	439	1680	4520	2	1
334	20	3	6	222	50	1264	208	3	5	412	1475	4287	2	2
334	22	3	6	28	61	607	1191	3	4	365	1800	4266	1	0
334	24	3	6	130	95	580	1218	3	4	390	1800	4292	2	1
334	26	3	6	47	105	189	1610	2	2	219	1800	3220	0	0
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334	30	3	6	0	89	0	1792	0	0	0	1800	1800	0	0
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334	5	4	6	6	89	147	1651	4	1	248	1800	3549	0	0
334	8	4	6	34	10	1734	58	1	3	206	1800	3207	0	0
334	10	4	6	30	48	935	864	3	3	369	1800	3971	3	1
334	12	4	6	3	106	18	1781	2	1	160	1800	2860	0	0
334	14	4	6	7	51	229	1509	2	1	165	1800	2866	0	0
334	17	4	6	77	46	1465	186	3	5	411	1653	4466	1	0
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335	24	1	6	25	3	1728	63	1	1	100	1800	2500	1	1
335	26	1	6	8	12	1602	191	5	1	302	1800	3903	0	1
335	28	1	6	48	4	1649	137	4	2	321	1800	3922	0	1
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335	7	2	6	18	7	1569	229	3	1	206	1800	3206	0	0
335	10	2	6	25	5	915	884	4	3	370	1800	4271	2	1
335	13	2	6	49	5	1646	149	3	1	232	1800	3234	2	1
335	16	2	6	53	6	1743	50	2	1	148	1800	2848	0	0
335	19	2	6	26	3	1659	121	2	1	144	1800	2844	0	1
335	22	2	6	20	6	1391	403	3	2	241	1800	3542	1	1
335	24	2	6	41	2	1772	22	1	1	106	1800	2507	0	0
335	26	2	6	30	8	1725	68	2	2	204	1800	3204	1	0
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335	4	3	6	18	3	1722	77	1	1	113	1800	2513	0	0
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335	9	3	6	19	7	1666	129	2	1	153	1800	2853	1	1
335	12	3	6	84	7	1763	34	1	2	153	1800	2853	0	0
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335	18	3	6	4	0	1763	0	2	0	102	1800	2502	0	0
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335	22	3	6	16	18	1250	545	3	0	150	1800	2851	1	0
335	24	3	6	20	3	140	1659	1	2	156	1800	2857	0	1
335	26	3	6	41	3	1788	10	1	1	108	1800	2508	0	0
335	28	3	6	21	0	1794	0	1	0	49	1800	2150	1	0
335	30	3	6	28	6	1545	254	1	1	104	1800	2505	0	0
335	1	4	6	133	9	642	1157	1	1	105	1800	2506	0	0
335	3	4	6	28	3	1466	332	0	1	87	1800	2189	0	1
335	5	4	6	12	2	1780	14	2	1	147	1800	2847	0	0
335	8	4	6	46	3	1786	13	2	1	159	1800	2860	0	0
335	10	4	6	48	2	1779	19	1	0	51	1800	2152	0	0
335	12	4	6	88	2	1780	12	1	1	103	1800	2504	1	0
335	14	4	6	92	0	1799	0	0	0	0	1800	1800	0	0
335	17	4	6	32	0	1798	0	0	0	0	1800	1800	0	0

335	19	4	6	21	3	1653	138	0	1	51	1800	2151	0	1
336	5	12	5	16	16	514	257	5	3	493	777	3673	3	1
336	7	12	5	39	12	1436	362	2	3	267	1800	3568	2	0
336	9	12	5	70	18	1427	370	3	3	305	1800	3906	3	0
336	11	12	5	29	13	352	1447	1	3	212	1800	3213	1	0
336	16	12	5	78	17	1691	106	3	2	265	1800	3566	3	2
336	18	12	5	26	5	653	61	6	2	498	716	3617	4	0
336	20	12	5	43	13	1176	623	2	4	336	1800	3938	1	0
336	22	12	5	29	28	414	699	4	4	409	1124	3934	0	0
336	30	12	5	61	27	1213	397	3	5	441	1615	4458	2	2
336	3	1	6	37	51	588	456	4	4	602	1049	4058	0	2
336	5	1	6	16	41	312	489	4	4	460	805	3667	3	0
336	9	1	6	16	29	1306	465	5	3	422	1773	4596	1	0
336	11	1	6	31	31	1217	575	2	3	269	1800	3570	2	1
336	13	1	6	31	21	1220	173	3	5	469	1416	4288	2	0
336	16	1	6	48	27	484	213	3	5	449	701	3551	2	0
336	18	1	6	52	12	1254	544	2	4	357	1800	3958	2	0
336	20	1	6	41	25	507	241	4	4	464	750	3615	2	0
336	22	1	6	85	59	446	390	3	5	435	839	3675	1	1
336	24	1	6	7	26	724	1066	4	2	363	1800	3965	3	0
336	26	1	6	118	9	1516	281	1	2	178	1800	2879	1	0
336	28	1	6	68	35	509	242	4	4	432	753	3586	3	0
336	31	1	6	43	15	954	844	4	3	384	1800	4285	1	1
336	2	2	6	81	22	946	157	4	4	460	1104	3967	4	0
336	4	2	6	77	8	1459	324	2	4	328	1800	3930	2	0
336	7	2	6	58	18	911	187	3	5	452	1101	3955	2	1
336	10	2	6	55	22	391	481	3	5	463	874	3739	3	0
336	13	2	6	59	12	1347	443	1	2	199	1800	2900	*	*
336	16	2	6	40	40	628	665	4	4	461	1300	4164	3	0
336	19	2	6	9	51	215	1581	3	2	249	1800	3550	2	0
336	22	2	6	11	28	777	1011	4	3	359	1800	4261	2	0
336	24	2	6	76	17	1669	129	2	2	216	1800	3216	2	1
336	26	2	6	6	177	61	1739	2	2	247	1800	3248	1	1
336	28	2	6	59	50	1425	373	3	4	389	1800	4290	2	0
336	2	3	6	44	24	394	145	5	3	423	547	3372	1	0
336	4	3	6	71	43	327	239	5	3	449	568	3419	2	0
336	7	3	6	9	24	1029	764	2	1	174	1800	2875	2	0
336	9	3	6	78	19	1325	197	4	4	476	1525	4404	2	0
336	12	3	6	54	11	848	951	1	2	155	1800	2856	1	0
336	14	3	6	86	38	554	741	3	5	462	1297	4161	2	0
336	16	3	6	122	38	641	148	3	5	431	792	3625	2	1
336	18	3	6	17	90	148	1647	3	3	337	1800	3939	1	0
336	20	3	6	60	52	579	746	4	4	469	1327	4198	1	0
336	22	3	6	84	29	904	267	4	4	439	1173	4013	3	0
336	24	3	6	58	51	495	333	4	4	466	833	3702	3	0
336	26	3	6	33	55	1134	362	4	4	444	1601	4447	1	0
336	28	3	6	49	58	560	183	4	4	421	745	3568	2	0
336	30	3	6	90	73	554	495	4	4	449	1051	3902	3	0
336	1	4	6	9	89	150	769	5	3	429	945	3775	2	0
336	3	4	6	17	86	424	474	5	3	537	912	3854	1	0
336	5	4	6	66	25	1089	255	5	3	441	1345	4188	2	0

336	8	4	6	20	118	312	384	5	3	414	700	3514	2	0
336	10	4	6	24	28	1515	283	3	2	274	1800	3575	2	0
336	12	4	6	35	27	599	297	5	3	408	896	3705	1	0
336	14	4	6	22	114	137	572	5	3	435	710	3547	1	0
336	17	4	6	39	78	1214	572	4	4	474	1791	4667	1	0
336	19	4	6	84	18	611	1184	2	3	283	1800	3584	2	0

APPENDIX C

The temperatures of the home and experimental rooms are presented for all conditions in degrees Celsius. The condition (Cond), the series (Series; where applicable), the date (Day, Month and Year), the minimum (Min) and maximum (Max) temperatures of the home room (Home Room), and the Max and current (Current; temperature at the start of the first session) temperatures of the experimental room (Expt Room) are recorded. Asterisks indicate days in which sessions did not take place, or temperatures were not recorded.

					Home Room		Expt Room	
Cond	Series	Day	Month	Year	Min	Max	Max	Current
1	2	26	5	5	19	20	25	22
1	2	27	5	5	20	21	21	21
1	2	28	5	5	19	20	23	21
1	2	29	5	5	*	*	*	*
1	2	30	5	5	19	20	23	20
1	2	31	5	5	23	24	22	20
1	2	1	6	5	19	19	*	*
1	2	2	6	5	19	19	22	19
1	2	3	6	5	19	19	*	*
1	2	4	6	5	*	*	*	*
1	2	5	6	5	*	*	*	*
1	2	6	6	5	19	19	21	18
1	2	7	6	5	17	17	20	19
1	2	8	6	5	*	*	*	*
1	2	9	6	5	17	19	21	18
1	2	10	6	5	21	23	19	19
1	2	11	6	5	18	18	20	19
1	2	12	6	5	21	18	20	19
1	2	13	6	5	17	18	21	19
1	2	14	6	5	18	18	21	20
1	2	15	6	5	*	*	*	*
1	2	16	6	5	19	19	21	19
1	2	17	6	5	21	22	21	19
1	2	18	6	5	*	*	*	*
1	2	19	6	5	20	19	20	20
1	2	20	6	5	18	20	22	18
1	2	21	6	5	19	19	19	18
1	2	22	6	5	*	*	*	*
1	2	23	6	5	*	*	*	*
1	2	24	6	5	19	20	21	18
1	2	25	6	5	*	*	*	*
1	2	26	6	5	19	20	21	19
1	2	27	6	5	16	19	21	16
1	2	28	6	5	17	17	19	18
1	2	29	6	5	*	*	*	*
1	2	30	6	5	19	19	21	19
1	2	30	6	5	19	19	21	19
1	3	3	7	5	16	22	20	20
1	3	4	7	5	16	18	20	16
1	3	5	7	5	18	18	20	19
1	3	6	7	5	*	*	*	*
1	3	7	7	5	20	20	22	20
1	3	8	7	5	20	22	20	20
1	3	9	7	5	20	20	21	20
1	3	10	7	5	20	21	19	19
1	3	11	7	5	16	20	21	18
1	3	12	7	5	18	18	20	19
1	3	13	7	5	*	*	*	*
1	3	14	7	5	19	20	21	20
1	3	15	7	5	19	20	21	19
1	3	16	7	5	*	*	*	*
1	3	17	7	5	20	20	21	20
1	3	18	7	5	18	19	22	20
1	3	19	7	5	19	20	*	*
1	3	20	7	5	*	*	*	*
1	3	21	7	5	18	19	22	19
1	3	22	7	5	17	19	21	21
1	3	23	7	5	20	21	20	19

1	3	24	7	5	19	21	20	18	2	2	10	10	5	20	20	21	15
1	3	25	7	5	20	20	20	18	3		4	12	5	19	23	24	19
1	3	26	7	5	19	20	21	19	3		5	12	5	21	25	24	20
1	3	27	7	5	*	*	*	*	3		6	12	5	21	26	26	20
1	3	28	7	5	19	20	22	20	3		7	12	5	16	21	25	19
2	1	16	8	5	16	16	19	18	3		8	12	5	24	26	25	20
2	1	17	8	5	20	20	21	20	3		9	12	5	25	26	26	21
2	1	18	8	5	18	19	21	20	3		10	12	5	26	25	26	21
2	1	19	8	5	18	20	22	19	3		11	12	5	25	26	25	20
2	1	20	8	5	19	19	21	20	3		12	12	5	26	26	27	21
2	1	21	8	5	*	*	*	*	3		13	12	5	26	26	*	*
2	1	22	8	5	18	20	23	20	3		14	12	5	*	*	*	*
2	1	23	8	5	19	20	22	20	3		15	12	5	25	28	27	23
2	1	24	8	5	*	*	*	*	3		16	12	5	25	26	27	22
2	1	25	8	5	20	20	23	20	3		17	12	5	*	*	*	*
2	1	26	8	5	20	20	22	20	3		18	12	5	24	24	*	*
2	1	27	8	5	20	20	*	*	3		19	12	5	24	24	26	22
2	1	28	8	5	20	20	21	19	3		20	12	5	24	26	26	22
2	1	29	8	5	18	18	21	17	3		21	12	5	21	25	26	21
2	1	30	8	5	19	20	21	17	3		22	12	5	24	26	25	25
2	1	31	8	5	*	*	*	*	3		23	12	5	23	26	25	20
2	1	1	9	5	19	20	21	18	3		24	12	5	*	*	*	*
2	1	2	9	5	20	20	21	20	3		25	12	5	*	*	*	*
2	1	3	9	5	20	19	*	*	3		26	12	5	*	*	*	*
2	1	4	9	5	19	19	20	20	3		27	12	5	*	*	*	*
2	1	5	9	5	19	19	21	19	3		28	12	5	*	*	*	*
2	1	6	9	5	20	20	21	20	3		29	12	5	*	*	*	*
2	1	7	9	5	*	*	*	*	3		30	12	5	21	26	26	20
2	1	8	9	5	18	19	22	21	3		31	12	5	25	27	*	*
2	1	9	9	5	20	20	21	20	3		1	1	5	25	27	*	*
2	2	18	9	5	21	22	21	19	3		2	1	5	25	26	26	23
2	2	19	9	5	19	23	19	19	3		3	1	5	21	26	21	27
2	2	20	9	5	21	25	19	18	3		4	1	5	21	26	26	22
2	2	21	9	5	*	*	*	*	3		5	1	5	21	26	26	21
2	2	22	9	5	19	20	20	14	3		6	1	5	22	26	25	19
2	2	23	9	5	19	20	20	19	3		7	1	5	21	25	25	20
2	2	24	9	5	19	21	21	16	3		8	1	5	18	20	26	21
2	2	25	9	5	20	20	20	19	3		9	1	5	21	25	26	21
2	2	26	9	5	19	20	21	19	3		10	1	5	25	26	25	21
2	2	27	9	5	21	21	21	20	3		11	1	5	22	27	28	22
2	2	28	9	5	*	*	*	*	3		12	1	5	24	26	27	22
2	2	29	9	5	20	20	22	17	3		13	1	5	24	26	26	22
2	2	30	9	5	20	22	21	19	3		14	1	5	*	*	*	*
2	2	1	10	5	21	22	21	21	3		15	1	5	21	28	28	22
2	2	2	10	5	19	22	22	20	3		16	1	5	25	26	27	23
2	2	3	10	5	18	21	23	18	3		17	1	5	22	25	27	21
2	2	4	10	5	20	21	21	20	3		18	1	5	17	26	28	23
2	2	5	10	5	*	*	*	*	3		19	1	5	22	26	26	22
2	2	6	10	5	20	20	22	16	3		20	1	5	22	26	26	20
2	2	7	10	5	20	21	21	19	3		21	1	5	20	27	26	20
2	2	8	10	5	20	21	21	20	3		22	1	5	24	27	27	22
2	2	9	10	5	*	*	*	*	3		23	1	5	25	26	27	22

3	24	1	5	26	27	27	23
3	25	1	5	25	26	28	25
3	26	1	5	26	27	27	23
3	27	1	5	25	27	27	22
3	28	1	5	22	27	27	23
3	29	1	5	23	28	*	*
3	30	1	5	28	27	28	23
3	31	1	5	28	27	29	25
3	1	2	5	27	28	31	26
3	2	2	5	28	27	29	25
3	3	2	5	27	27	29	26
3	4	2	5	24	27	28	25
3	5	2	5	20	26	*	*
3	6	2	5	23	26	28	24
3	7	2	5	22	26	28	22
3	8	2	5	21	23	27	22
3	9	2	5	20	20	*	*
3	10	2	5	20	20	28	22