AN INVESTIGATION INTO ESTABLISHING (MOTIVATING) OPERATIONS

A thesis
submitted in fulfilment
of the requirements for the degree
of

Doctor of Philosophy in Psychology

at the
University of Waikato
by

SURREY MERRYN KATE JACKSON

THE UNIVERSITY OF
WAIKATO
Te Whare Wānanga o Waikato

_____

2017

ABSTRACT

Motivating Operations (MOs) are a fundamental concept in behavioural psychology. Despite this, empirical research into MOs is lacking. The overall aim of this thesis is to contribute to the experimental literature base for MOs.

Experiment 2.1 used an already published video analysis methodology to assess the morphology of food motivated pecks made to a computer screen by hens, after the hens had been trained to emit the peck using either an autoshaping or handshaping procedure. The intention of this was to then be able to use the video analysis to assess the effect of altering two MOs related to two different reinforcers (e.g., food and water) at one time, on morphology. The study showed that both methods produced similarly formed pecks despite the variability inherent in the handshaping procedure. It was then concluded it is the nature of the reinforcer that gives rise to morphology not the autoshaping procedure *per se* which gives rise to a particular form of elicited responses.

The aim of Experiment 3.1 and 3.2 was to develop a procedure for restricting access to water in laying hens, in order to motivate them sufficiently to respond for water reinforcers. Experiment 3.1 assessed the effect that gradually decreasing time and amount of water access had on food-restricted hens' water consumption and health. It was found that hens could be restricted to one hr access of water (restricted to the maximum amount that hens would consume when access was ad libitum) without adverse effects to health being apparent. However, when the hens were subsequently exposed to FR schedules with a low response requirement in Experiment 3.2, they did not respond consistently. This indicated that the level of restriction was insufficient to motivate responding and this finding, combined with the difficulty of obtaining ethical approval, meant that the proposed experiments utilising water deprivation as an MO had to be abandoned.

Experiment 4.1 used the autoshaping paradigm to assess the acquisition of food motivated pecks to a stimulus, at two different levels of bodyweight (75% and 95%). An infra-red screen was used to analyse

performance separately from learning effects by examining activity levels (location and amount of pecks). It was found that that higher numbers of effective pecks were made by hens maintained at 75% free-feeding bodyweight than hens maintained at 95% (different MO conditions). There were also higher levels of ineffective pecks in the 75% group.

Experiment 5.1 investigated relative preference for stimuli correlated with different MO conditions: high deprivation (no pre-feeding), or low deprivation (pre-feeding), when subjects were maintained at either 75% or 95% of free-feeding bodyweight. The results showed that 6/10 hens demonstrated an increased preference for the stimulus paired with high deprivation conditions (no pre-feeding) when measured by log ratios of responses, and had faster response rates on this stimulus. Overall, the 75% bodyweight hens had faster response rates than the 95% hens (as in Experiment 4.1), and 8/10 hens responded faster on the stimulus that was paired with no pre-feeding. It was also found, as per Experiment 4.1, that higher numbers of effective pecks were made by hens maintained at 75% free-feeding bodyweight than hens maintained at 95% (different MO conditions).

Experiments 6.1 and 6.2 extended the findings of the thesis thus far in that concurrent VI VI schedules were used to assess the effect of bodyweight and pre-feeding as MOs on steady state responding. In total 16 conditions were run exposing hens to three different VI pairs: VI-12, VI-60 (5:1); VI-20, VI-20 (1:1); and VI-60, VI-12 (1:5). Bodyweight values of 85%, 95%, 100%, and 85% with pre-feeding of 40 cc wheat delivered 40 minutes prior to experimental sessions were manipulated between hens finishing a series of the three VI pairs. It was found that 4/6 hens had higher absolute and relative response rates when bodyweight was made lower. For 3/6 of these hens, increasing bodyweight increased sensitivity as measured by the parameter *a*; this was more distinct when the Generalised Matching Law was applied to response rather than time locations for these hens. Frequency distributions of IRTs showed that for the hens that tended to show increasing sensitivity as bodyweights increased there were more IRTs in bins greater than 0.4 s. This was

reflected on the log-survivor plots as the limbs were shallower when bodyweights were higher, indicating that more between-bout responses were occurring. It was also found that pre-feeding increased sensitivity as measured by the parameter *a* for all hens; this was more noticeable when the GML was applied to response rather than time allocations. Although overall response rates tended to resemble those for the 85% bodyweight condition and remain higher than the 95% and 100% bodyweight conditions, the distribution of left and right response rates showed that hens matched better to the prevailing reinforcer rates when they were pre-fed, than when they were not pre-fed.

Overall, the main findings were: (1) that reducing bodyweights increased amounts of species-specific behaviour; and (2) that reducing bodyweight causes increases in response rate. These findings could explain why changes in preference for stimuli paired with high levels of deprivation are observed during SDVL procedures, and why increased sensitivity to available reinforcement at lower levels of deprivation found in studies utilising the GML have been observed in previous studies. These findings contribute to the empirical data informing the behavioural treatment of motivation and have applied implications. Reinforcement and punishment procedures such as extinction or differential reinforcement of alternative behaviours may no longer be necessary when MOs are manipulated.

ACKNOWLEDGEMENTS

Firstly, I would like to thank my supervisors Mary Foster, Lewis Bizo, and James McEwan. I am very grateful for all the guidance, perseverance, and assistance throughout this process. I am especially grateful for the many wonderful opportunities granted to me during my time at the University of Waikato.

I am grateful for the technical support I received from Rob Bakker, Jennifer Chandler, and Allan Eaddy.

I am very grateful to the lab runners of Dairy No 3 who assisted me with data collection. There are too many people to name but much deserved thanks go to Haylee Ellis who watched and scored hours and hours of videos for my inter-observer reliability data. An enormous thank you is also owed to Clare Browne for her careful and efficient proofreading.

I would like to thank all my friends and fellow PhD students for being there at various points in time along the way; especially Helen, Clare, Kristie, Kathleen, Kitt, and Karen. The shared experience made this process enjoyable.

I gratefully acknowledge the financial support of the University of Waikato Doctoral Scholarship and the Claude McCarthy Foundation.

Finally, Darryl Turner, thank you so much for always being helpful, for keeping everything running, and for telling me that I had to get on with it. Thank you for writing programs to salvage my data when technical errors had occurred, I am very appreciative.

CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

Chapter 1 : GENERAL INTRODUCTION

A History of the Behavioural Treatment of Motivation

While behavioural concepts such as reinforcement, extinction, stimulus control and generalisation have been well examined, motivation, as a source of behavioural control, has not been given equal attention by researchers (Michael, 1993; Sundberg, 2004). Terminology related to the behavioural analytic treatment of motivation has changed over time. From Skinner's (1938) arguments against "drive" to Keller and Schoenfeld's (1950) proposal of "establishing operation" and Michael's (2000) proposal of "motivating operation", the changing terminology reflects the different conceptualisations of motivation.

Sundberg (2004) outlined the history of the behavioural analysis of motivation. He noted that Skinner (1938) argued against the term "drive" and the treatment of motivation that was common at that time. Skinner's argument was that "drive" is a hypothetical state and so is not required in a descriptive system. Skinner proposed that environmental variables should be the focus of the analysis. Skinner also made it clear that he thought motivation should be considered separately from other types of antecedent control over behaviour (created by discriminative, unconditioned, or conditioned stimuli).

The next significant contribution to the behavioural treatment of motivation was made by Keller and Schoenfeld (1950) who were the first to coin the term "establishing operation". They described the relation between deprivation and satiation, and response strength, by positing that depriving an animal of food is a way of strengthening a conditioned reflex (e.g., lever pressing) and with sufficient satiation these reflexes drop to zero. They concluded that this concept required a more specific term than "drive" and that the "establishing operation" could be considered a separate independent variable in behaviour analysis. They called for an experimental analysis of this variable.

Skinner (1953) expanded on his early analysis of motivational variables by considering deprivation and satiation, emotion and aversion, avoidance and anxiety. He defined motivational variables as consisting of

a functional relation between the level of deprivation, satiation, and aversive stimulation and its evocative effect on behaviour. He made it clear that a single motivational variable can affect a large class of behaviours (Sundberg, 2004). Holland and Skinner (1961) extended the concepts presented in *Science and Human Behavior* (Skinner, 1953). They presented a behavioural analysis of motivation as a functional relation between variables determining the *momentary* value of events functioning as reinforcement or punishment, and the frequency of the behaviour that has been reinforced or punished.

Millenson (1967) reviewed the emerging empirical literature related to motivation. He summarised the existing research as showing that behaviour varies in an orderly fashion with deprivation, satiation, and associated operations (e.g., Broadhurst, 1957; Clark, 1958). He stated that there appeared to be a set of behavioural measures which (within limits) covary with deprivation of the reinforcer.

The Motivating Operation

Despite the early interest in motivation, the topic received little attention in behaviour analysis textbooks published between 1970 and 1990 (Sundberg, 2004). Michael (1993) pointed out “in applied behaviour analysis or behavior modification, the concept of reinforcement has taken over much of the subject matter that was once considered part of the topic of motivation” (p. 191). Michael argued that the topic deserved separate attention as an antecedent principle of behaviour. Over a series of papers Michael elaborated on what he termed the Establishing (Motivating) Operation (MO) (1982; 1988; 1993; 2000) to describe an operation (defined as a change in the environment) that has two specific, momentary, effects. The first effect is that an MO alters reinforcer efficacy (the potency of the reinforcer) (Michael, 2000). The second effect is that an MO increases or decreases the rate of behaviour associated with obtaining the reinforcer (Michael, 2000). The first effect has been termed the “reinforcer-establishing effect” or the “value-altering effect”, the second has been termed “the evocative effect” or the “behaviour-altering” effect (Klatt & Morris, 2001). Also, important to note is that the MO encompasses two

variables: the establishing and the abolishing effects (Laraway, Snycerski, Olson, Becker, & Poling, 2014).

Since the work of Michael (1982; 1988; 1993; 2000) MOs have come to be described as a fundamental concept in behavioural psychology (Klatt & Morris, 2001). MOs exist in relation to a reinforcer (or another substitutable reinforcer). A simple example of an MO is food deprivation and a simple example of a reinforcer is food. Food is a reinforcer because it can increase behaviour that is associated with the outcome of food. Food deprivation is an MO because if an organism is deprived of food it is more likely to perform behaviour that has been associated with the outcome of food in the past (this is the behaviour-altering effect). The delivery of food strengthens the behaviour that was performed to gain food and that behaviour is then more likely to occur again in future when the organism is in a state of food deprivation (this is the value-altering effect). Figure 1 illustrates food deprivation as an example of an MO.

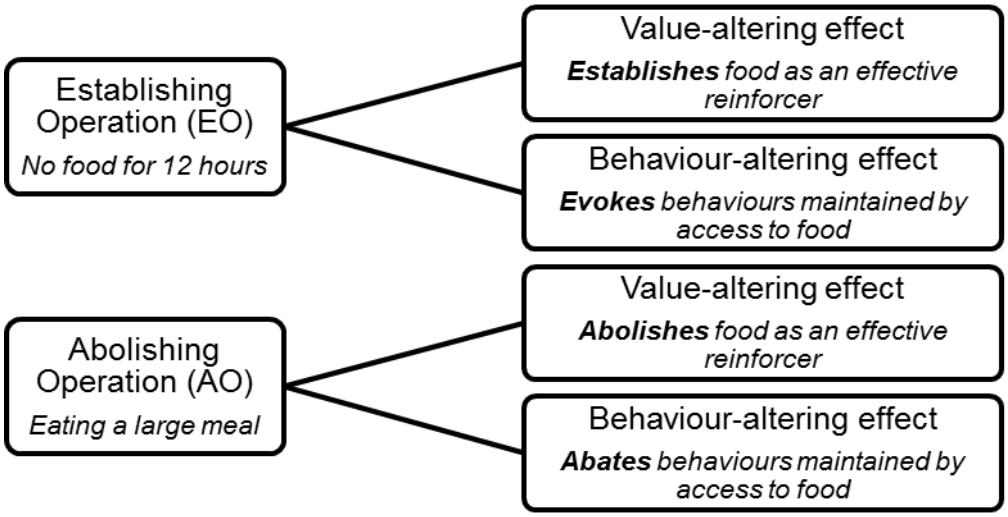

Figure 1.1. Illustration of the value- and behaviour-altering effects of the Motivating Operation.

It is important to note that for an MO to be evocative it must lead to increased behaviour that leads to a specific reinforcer with or without the presence of a discriminative stimulus (S^D; a stimulus that signals the availability of reinforcement). Thus, MOs act on all three elements of the three-term contingency (antecedent – behaviour – consequence) (Dougher & Hackbert, 2000). Behaviour that is maintained by positive

reinforcement has often been envisioned along a continuum in which the reinforcing effects of the stimulus are strongest in the presence of an MO (North & Iwata, 2005). As pointed out by Laraway et al. (2014) although previous writings on the MO have considered the effects to be “momentary” (Michael, 1993), the effects of MOs can be long-lasting, or even permanent. For example, hyperphagia (excessive appetite) associated with Prader-Willis syndrome is lifelong. Because of examples such as Prader-Willis, Laraway et al. (2014) state that they see no reason to restrict the time frame in which MOs can produce their effects, without empirical evidence rather than theoretical reasoning to make this restriction.

Unconditioned Motivating Operations

MOs can be either unconditioned (UMOs), that is, unlearned such as pain or the previous example of food deprivation; or conditioned (CMOs), that is, learned, meaning that the effect of the MO depends on the organism’s learning history (Michael, 1993). Although by definition they do not have to be, the MOs that have the most stable effects on behaviour are natural and they tend to come in pairs, thus deprivation and satiation are two terms commonly used to describe MOs (Michael, 2000), and deprivation and satiation are most commonly used when discussing unconditioned reinforcers. Examples of UMOs include deprivation and satiation of unconditioned reinforcers such as food, water, and sex. Other UMOs include hormonal changes, circadian rhythms, gene expression, brain damage, drugs, and other biological phenomena that change the effectiveness of operant consequences (Laraway et al., 2014).

Conditioned Motivating Operations

As stated above some MOs acquire their value-altering effects as a result of an organism’s learning history. These MOs are termed conditioned MOs (CMOs). Previously neutral events may acquire their MO properties by being paired with an unconditioned MO. Michael (1988) proposed three types of CMO: surrogate, transitive, and reflexive. Surrogate CMOs are formerly neutral stimuli that become effective by

being associated with an already effective MO, thereby acquiring the same motivational properties as that MO (Laraway et al., 2014). Transitive CMOs affect the conditioned reinforcing or punishing effectiveness of some other event, often occurring within a behaviour chain (e.g. Michael (1982) gave the example of an electrician working with his apprentice. The electrician moves to use his screwdriver but it does not fit. He asks the apprentice for another screwdriver. The screwdriver not fitting is the transitive CMO that causes obtaining a screwdriver that does fit to be reinforcing. Reflexive CMOs make their own removal or continued presence a reinforcer or punisher (e.g., due to their predictive relationship with appetitive or aversive stimuli) (Laraway et al., 2014). Langthorne and McGill (2009) provide a comprehensive tutorial on the usefulness of the concept of the CMO and its importance to application.

Applied and Clinical Significance of Motivating Operations

Researchers in experimental analysis of behaviour are interested in functions of behaviour. When functions of behaviour are understood, behaviour can be changed at the antecedent level. Reinforcement and punishment may no longer be necessary for changing behaviour when the motivation for performing behaviour is gone. Knowledge of MOs is commonly utilised by practitioners in applied settings when attempting to change socially significant behaviour. Iwata, Smith, and Michael (2000) summarised the research, at the time of publication, on the influence of MOs in applied settings. Iwata et al. (2000) state that use of MOs in applied settings falls into three main categories: general demonstrations of the effects of MOs on behaviour, the use of MOs to clarify the results of behavioural assessments, and incorporating MOs during behaviour manipulations when aiming to change behaviour.

Since 2000 MOs have continued to be utilised when changing human behaviour in applied settings. For example, Rispoli et al. (2011) identified, using functional analysis, MOs that increased the occurrence of problem behaviour in the classroom for two students with autism. Subsequent deliberate manipulation of the identified MOs resulted in a decrease of problem behaviour and an increase in academic engagement.

MOs have also been considered for use in organisational settings (Olson, Laraway, & Austin, 2001) and as a contributor to understanding consumer behaviour (Fagerstrøøm, Foxall, & Arntzen, 2010). MOs may also help in understanding variables that influence depression (Dougher & Hackbert, 2000).

Iwata et al. (2000) identified a methodological difficulty that arises when conducting applied research using MOs. That is, whether research conducted with MOs should be conducted in the presence or absence of the reinforcer. For an MO to truly be considered an MO then the presence of an MO should evoke behaviour regardless of the availability of reinforcement; for example, thirst promotes water seeking behaviour, regardless of whether water is present or not (Klatt & Morris, 2001). Though many applied studies with MOs have been conducted under conditions of extinction (when no reinforcer is available) if a participant is able to readily determine that there will be no reinforcer regardless of behaviour the extinction effect may override the MO effect. The same may also be true when using animal subjects. So, more research controlling for this possibility is needed.

Iwata et al. (2000) also suggested the applied use of MOs would benefit from more empirical data concerning the effects of MOs. They stated that more research is needed to determine how the MO acquires and maintains its reinforcer-establishing (value-altering) and evocative (behaviour-altering) properties. They also proposed that because most MOs that are studied in applied research have multidimensional characteristics (quality, duration, magnitude, rate), attempts to identify the influence of MOs might benefit from quantitative as well as qualitative analysis. Basic research using schedules of reinforcement could contribute to knowledge of MOs and their effects which could then be utilised in applied settings.

Basic Research using Animals and Motivating Operations

Although not always stated, every operant experiment that requires an animal to respond for a reinforcer involves an MO. Related to this is the Premack principle. The Premack principle emerged from Premack's (1959)

research on the "rate differential" or "probability differential" effect, wherein "any response A will reinforce any response B, if and only if, the independent rate of A is greater than that of B" (p. 220; see Premack, 1961, 1962,1963). As pointed out by Klatt and Morris (2001), the Premack principle, as originally stated, is an incomplete principle. It is not fundamental, but instead is explained by response deprivation. A contingent behaviour will serve to reinforce an instrumental behaviour if, and only if, by engaging in the baseline amount of the instrumental behaviour, a subject is thus deprived of the baseline amount of the contingent behaviour (Timberlake & Allison, 1974). In any operant experiment, the organism must be deprived of a reinforcer enough so that motivation for that reinforcer is consistent and stable. In order to appropriately reinforce and subsequently change behaviour it is vital to understand the effects that MOs have on both behaviour and reinforcer value.

Much basic research involves animals working under a schedule of reinforcement in order to obtain a food reinforcer with the focus of the research having little or no relation to studying eating or the effects of food deprivation. As stated above, when animals are working to obtain a food reinforcer some level of food deprivation, food restriction, or manipulation of bodyweight is required in nearly all cases in order to motivate animals to respond. Though most studies alter the availability of food in order to promote responding, few studies have specifically investigated either the effects of food deprivation as an MO on behaviour within the operant chamber or the interaction that food deprivation might have with other possible MOs.

Water restriction has proved to function robustly as an MO, as have types of food restriction such as manipulating bodyweight (e.g., Ferguson & Paule, 1995) and feeding outside of experimental sessions. Type of food fed to animals, time of day (time in the animal’s natural body cycle), and pain are also UMOs that have been less frequently manipulated in studies with animals. For example, Charlton (1984) investigated hoarding-induced lever pressing in golden hamsters and found that time of day can function

as an UMO to increase the motivation to hoard food pellets. Charlton (1984) therefore suggested that illumination could act as an alternative to deprivation for maintaining food reinforced behaviours.

Although UMOs are repeatedly manipulated (most commonly bodyweight, water restriction, and feeding outside experimental sessions), little research (e.g., McPherson & Osborne, 1988) can be found into CMOs with animals.

Water Restriction as a Motivating Operation in Basic Research

As stated above, water access has been manipulated in operant experiments. One early example, Fallon, Thompson and Schild (1965) assessed the effect of 22 hr food, water, and food plus water, deprivation cycles on the lever-pressing performance of rats using concurrent Variable Interval Variable Interval (VI VI) schedules. They found that when two levers were presented (one producing food-reinforcement and the other producing water-reinforcement) the distribution of responding between the two levers revealed substantial responding on the food lever under all deprivation conditions. The most responses were emitted under food deprivation, the next most under food plus water deprivation, and the least under water deprivation. They concluded that the consistency of food-lever responding can be taken as providing good support for the suggestion that the food-deprived rat is hungry, but not necessarily thirsty, whereas the water-deprived rat is both hungry and thirsty, indicating that manipulating one MO (food) can affect responding for another reinforcer (water).

As stated above MOs may not necessarily be independent and multiple MOs may be in effect at one time. Lucas, Timberlake, and Gawley (1989) investigated the effect of learning and meal associated drinking in rats. They restricted rats' access to water by not providing water for 10, 20 or 30 min delays after the rats were fed. The results showed that when the rats were returned to baseline and water access was given at the same time as food, they began drinking substantially more water than previously, indicating that eating the meal could be an MO for water. A second experiment, where the same procedure was followed but the rats were given five minutes water access before the 10, 20 or 30 min delays, found

that the rats increased water intake in the five-min period. They suggested meal-associated drinking may depend on the rats learning to anticipate water deficits (Lucas, Timberlake, & Gawley, 1988). These results also demonstrate the power that a past history of deprivation can have, which may be useful for understanding why human behaviour occurs in applied settings. Overall the results of these studies suggest that there is a relationship between eating and drinking behaviour in animals and humans, and manipulation of this relationship could provide us with further information about interactions between MOs and effects that occur when multiple MOs are active at one time.

Reduced Bodyweight as a Motivating Operation in Basic Research

Bodyweight is a commonly manipulated MO in basic animal research and it has been found that changes in bodyweight effects responding for food reinforcers. For example, Ferguson and Paule (1997) found that when rats were maintained between 75% and 100% of free-feeding bodyweight, there were significant differences in Progressive Ratio (PR) schedule performance relative to the percentage of free-feeding bodyweight the rats were maintained at. They found that Post Reinforcement Pause (PRP) times were higher and response rates and number of reinforcers earned were lower when the bodyweights of the rats were higher. This and a number of other studies (Belke & Pierce, 2008; Bradshaw, Szabadi, Ruddle, & Pears, 1983) attest to the strength of bodyweight as an MO that can change the value of food.

Some interesting results have been found when considering bodyweight as an MO for animals working for food reinforcers under Differential Reinforcement of Low Rate (DRL) and Variable Interval Omission (VRO) schedules. Lewis and Dougherty (1992) investigated whether pigeons' performance on a VRO schedule would be effected by maintaining the pigeons at differing bodyweights (therefore at different levels of food deprivation). They hypothesised that pigeons could either respond more as the severity of deprivation increased and omit more reinforcers, or pigeons could respond less as the severity of food deprivation increased and omit fewer reinforcers. They found that the

pigeons who were maintained at the lower weights responded more than the schedule required and therefore they obtained fewer reinforcers than the birds maintained at higher weights. The results of this study indicate that food deprivation resulted in the pigeons responding more (i.e., they increased their rate of responding); even though the consequence was that the deprived pigeons earned fewer reinforcers. Tanno, Kurashima, and Watanabe (2011), Ho, Wogar, Bradshaw, and Szabadi (1997), and Uslaner and Robinson (2006), all using rats, also found that increased level of food deprivation led to impaired performance on schedules that require an element of self-control or inhibition of a response, such as VRO and DRL schedules. These results have interesting implications for the earlier stated idea that food deprivation is a robust MO; in these situations, the behaviour-altering effect of the MO appeared to be greater but as more deprived animals failed to gain more reinforcers overall this was not efficient.

Feeding Outside Experimental Sessions as a Motivating Operation in Basic Research

Another way of manipulating MOs for food is feeding outside of an experimental session. Food is often available outside of the experimental session in order to meet nutritional requirements. Given that food deprivation functions as an MO, feeding animals before or after experimental sessions can have an effect on how the animals respond for reinforcers during sessions. Ladewig, Sørenson, Nielsen and Matthews (2002) found that rats worked harder to obtain water reinforcers, if water was only provided in the test situation. They concluded that the availability of a commodity, used as a reinforcer, outside of the test situation can significantly affect how fast animals respond for the reinforcer dependant on when access to the commodity is given.

Ferguson and Paule (1995) investigated the effect of pre-feeding on how rats, maintained below their free-feeding bodyweight, would respond on PR schedules of reinforcement. They found no significant effect of pre-feeding intervals ranging from 0.25 to 6 hours before they conducted the PR session. They concluded that this was related to the fact that the rats

were maintained below their free-feeding bodyweight which could have been causing an increase in value for food. Therefore, they supposed that the MO of a low bodyweight can mask the effects of pre-feeding, thus raising questions about how behaviour is affected when dual MOs are manipulated.

The Behaviour-Altering Effect in Basic Research

As stated earlier, MOs can have two behaviour-altering effects: (1) the establishing effect, and (2) the abolishing effect. Although the argument for more basic research is strong, as pointed out by Laraway et al. (2014) in many laboratory (particularly free-operant) situations researchers may have trouble disentangling the value-altering and behaviour-altering effects of a given MO in basic research. This is because consequences often occur while the MO functions effectively which confounds the two effects. Pure behaviour-altering effects can be seen most clearly in extinction because reinforcer delivery does not occur.

In studying extinction Skinner (1938) trained rats to press levers for food reinforcers and then pre-fed them varying amounts (0, 2, 4, or 6 g) of food prior to extinction sessions. Rats emitted fewer responses in the extinction sessions when they had been pre-fed with greater amounts of food, thereby demonstrating pre-feeding as an abolishing operation and showing evidence for the behaviour-altering effect. The role of the behaviour-altering effect has also been considered in understanding mands (verbal operants under the primary control of motivational variables) (Sundberg, 2004), and for understanding the effects of MOs on aversive stimuli (Laraway et al., 2014).

The Value-Altering Effect in Basic Research

The value-altering effects of MOs cause consequences to be more or less effective at changing the behaviours they follow (Laraway et al., 2014). For example, Lattal and Williams (1997) examined the role of bodyweight, in the acquisition and subsequent maintenance of responding with delayed reinforcement. They trained naïve rats deprived to either 70%, 80%, or 90% of free-feeding bodyweight to bar press and then

exposed them to tandem VI 15-s Differential Reinforcement of Other Behaviour (DRO) 30-s schedules. They found that in the first experiment, speed of magazine training, acquisition of lever pressing, and final rate of lever pressing were related to bodyweight. They concluded that bodyweight therefore seems to affect response acquisition because of the response-reinforcer relation (Lattal & Williams, 1997). In more detail, they posited that an animal placed in an operant chamber is likely to do at least an occasional response independent of bodyweight. If such a response is followed by a reinforcer further responding is determined by the animal's bodyweight. Therefore, the bodyweight of the animal acts as a function of the response-reinforcer dependency and determines the likelihood of the next response, the value-altering effect. The value-altering effect makes operant conditioning possible because, by definition, consequences must have an effective function to change or maintain behaviour (Laraway et al., 2014).

The Behaviour- and Value-Altering Effect in Basic Research

In much basic research pertaining to MOs researchers have not attempted to isolate the behaviour- and value-altering effects (Klatt & Morris, 2001). Some researchers have, however, attempted to investigate both. O'Reilly, Edrisinha, Sigafoos, Lancioni, and Andrews (2006) demonstrated both the behaviour-altering and value-altering effects of access to social attention with a man diagnosed with Autism Spectrum Disorder (ASD). A functional analysis revealed that attention served as a reinforcer for challenging behaviour. Preceding some sessions, the participant was given attention, but before other sessions he was not. When pre-session access to attention was restricted, and challenging behaviour was followed by attention, the challenging behaviour occurred at a frequency higher than when pre-session access to attention was available. Therefore, it was concluded that manipulation of pre-session attention changed the reinforcing value of attention delivered dependent on challenging behaviour (a value-altering effect). O'Reilly et al. (2006) also manipulated the MO prior to extinction sessions and measured behaviour in the absence of reinforcer delivery (i.e., in extinction), thereby

separating the behaviour-altering effect of the MO. The participant engaged in less challenging behaviour during extinction sessions when he received pre-session attention than when he did not receive pre-session attention.

Summary

Although behaviour analysis has a long history in its treatment of motivation, the research and theories on this subject have been sporadic. The clinical and applied significance of the MO cannot be understated. For some time now researchers have commented that while the MO has received little attention in basic research, there is room for a greater focus on this (Laraway et al., 2014). There has been suggestion made that MOs can inform understanding of extinction, behavioural contrast, Pavlovian-directed responses (e.g., response forms that vary with the deprived reinforcer), and adjunctive behaviour. In applied research MOs could be implicated in the efficacy of procedures such as time-out, functional communication training, and incidental teaching (Langthorne & McGill, 2009). There has also been the suggestion that MOs have clinical significance and that emotions should be considered as MOs (Dougher & Hackbert, 2000; Lewon & Hayes, 2015). A persisting definition of MOs is an environmental event that affects an organism by altering (1) the reinforcing effectiveness (value-altering) of other events, and (2) the frequency of occurrence (behaviour-altering) of that part of the organism's repertoire relevant to those events as consequences (Michael, 1993).

Although the argument for more basic research is strong, as pointed out by Laraway et al. (2014), in many laboratory (particularly free-operant) situations researchers may have trouble disentangling the value-altering and behaviour-altering effects of a given MO, because, in basic research, consequences often occur while the MO functions effectively which confounds the two effects. Pure behaviour-altering effects can be seen most clearly in extinction or before the first occurrence of the relevant consequences. Thus, research preparations might aim to control for these contingencies and processes, offering evidence that the value-altering and behaviour-altering effects occur independently of them.

In applied settings with human behaviour it can be reasonably assumed there are multiple MOs, for example, social (conditioned) as well as biological deprivation states such as food, sleep and water deprivation (unconditioned) at any one time. Given that MOs are now seen as important in the science of behaviour (Klatt & Morris, 2001), more research surrounding the interactions between multiple MOs is necessary.

Thesis Aim

The original aim of this thesis was to manipulate two MOs concurrently (food-deprivation and water-deprivation) and to use autoshaping and concurrent schedules to assess whether the effects of these MOs could be measured by analysing the conditioned responses using peck morphology. Therefore, it may have been possible to assess whether altering one MO, e.g. food-deprivation, effected responding for another reinforcer, e.g. water. When Experiments 3.1 and 3.2 were not successful at creating a methodology for motivating hens to respond for water reinforcers, the aim of the thesis changed. The revised aim of the thesis was to assess the effect of bodyweight and pre-feeding as MOs when manipulated individually and concurrently, therefore assessing not only the effects of bodyweight and pre-feeding as MOs, but also whether altering them simultaneously would have differential effects on responding.

Following this General Introduction, Chapter 2 comprises one study. Experiment 2.1 is presented where video analysis was used to (1) assess the morphology of food-reinforced pecks made to a computer screen by hens; and (2) to compare the morphology of these pecks after the hens had been trained to emit the peck using either an autoshaping or handshaping procedure (with hens held at the same level of motivation). If the food reinforcer was the main determinant of peck morphology then it would be expected that both methods would produce similarly formed pecks in spite of the variability in the handshaping procedure, therefore allowing response morphology to be utilised as a dependent measure for assessing the effect of altering MOs in future experiments, provided the reinforcer was the same. The intention was to use the analysis developed

in Experiment 2.1 to compare the morphology of food motivated and water motivated pecks in further studies.

Chapter 3 comprises two studies. Experiment 3.1 attempted to develop a procedure for restricting water access to hens. The aim of this study was to assess the effect that gradually decreasing time and amount of water access would have on water consumption and health of hens maintained at 85% ±5% of their free-feeding bodyweights, in order to develop a water restriction procedure that would obtain approval from animal ethics committees. Experiment 3.2 aimed to utilise the developed water restriction procedure in order to motivate hens to respond stably for water reinforcers. This procedure was ineffective at creating sufficient motivation to maintain responding and the proposed experiments comparing the effect of food and water deprivation as MOs on peck morphology were not undertaken.

Chapter 4 comprises two studies. Experiment 4.1 utilised an autoshaping procedure to shape screen-peck responses in 30 hens maintained at two different percentages of free-feeding bodyweights: 75% and 95%. The aim of this experiment was to use the autoshaping paradigm to assess the acquisition of food motivated pecks to a stimulus at two different levels of bodyweight; and then to use an infra-red screen to analyse activity and performance measures separately, thereby investigating the value-altering effect. Lewon and Hayes (2015) had shown that pre-feeding could give rise to preference for a stimulus associated with it. The next study, Experiment 5.1, aimed to see if bodyweight would affect this preference. Experiment 5.1 reports on whether preference for a stimulus assessed at a baseline and then paired with a period of low or high deprivation (pre-feeding or no pre-feeding) would be differentially effected during extinction, by having the hens maintained at two different free-feeding bodyweights, 75% and 95%. Therefore Experiment 5.1 assessed the effect that two interacting manipulations of MOs (pre-feeding and bodyweight) would have on the behaviour-altering effect. Given the findings in this experiment the next step was to assess whether increased activity levels shown at reduced

bodyweights would affect hens' ability to respond sensitively to contingencies of reinforcement, therefore investigating the value-altering effect.

Chapter 6 comprises two experiments, in Experiment 6.1 hens were exposed to concurrent VI VI schedules at three different levels of bodyweight and the Generalised Matching Law (GML) was applied to the data. Experiment 6.2 continued to use concurrent VI VI schedules to assess the value-altering effect of pre-feeding on sensitivity to contingencies. Across this diverse set of experiments, we come to better understand the effect the MO has on responding.

Chapter 2 : THE MORPHOLOGY OF THE HANDSHAPED VERSUS AUTOSHAPED FOOD MOTIVATED PECK IN HENS

Experiment 2.1: The Morphology of the Handshaped versus Autoshaped Food Motivated Peck in Hens

We cannot ask animals questions directly – we don't speak the same language. Animals can, however, be trained to indicate a choice between different potential outcomes by emitting responses that are specific in form and unambiguous from which we can infer the relative value of, or preference for, those outcomes (e.g., Sumpter, Foster, & Temple, 2002). For avian species, a key peck can be used to indicate a choice as it has a short duration, can be directed at a small area, looks much the same each time it is performed, and is easily shaped, reinforced, and recorded. These properties have made the key peck an important and useful object of study in operant conditioning (e.g., Ferster & Skinner, 1957). For these reasons, the key peck is the most common operant response trained in birds for behavioural experiments. Over a number of years, a variety of avian species, including pigeons (Jenkins & Moore, 1973), hens (Grant et al., 2014), bobwhite quail (Cloar & Melvin, 1968), Japanese quail (e.g., Cloar & Melvin, 1968; Lejeune & Nagy, 1986), and starlings (Swaddle & Ruff, 2004), have all been trained to peck keys in operant experiments.

Birds must be trained to emit pecks towards a key in the experimental chamber, either through handshaping: reinforcing closer approximations of the target response (Schwartz & Gamzu, 1977); or autoshaping: pairing the stimulus and the reinforcer, with no response contingency (Brown & Jenkins, 1968; Jenkins & Moore, 1973). Once trained, situations can then be devised to "ask" the bird a question, which they "answer" using this key peck response.

The process of handshaping by successive approximations has been described "as inexact as it [is] artful" (Schwartz & Gamzu, 1977, p. 54). The shaper reinforces successive behaviours that are closer to a key peck directed at the key. Effective decisions on the timing and size of a

shaping step are a result of experience and “intuition” as much as stringently defined criteria. Shaping can alter a behaviour along several dimensions, including location, force, and duration (Gleeson, 1991). Conversely Galbicka (1994) argued that shaping does not have to be an inexact science and proposed the use of percentile schedules in applied settings. In a percentile schedule the eligibility of a response to produce a reinforcer depends on its location within a response distribution. Because its criteria for differential reinforcement are relative rather than absolute, it operates consistently over a range of changes in performance and therefore makes automated shaping possible.

In a standard autoshaping procedure, after an inter-trial interval (ITI) a keylight immediately precedes the delivery of reinforcement. No response is required by the animal to gain the reinforcer, but if one is made to the lit key the reinforcer is delivered immediately, and the ITI begins again. While a response is not necessary to obtain a reinforcer, most birds will nonetheless begin to peck the lit key (Gamzu & Schwam, 1974).

The seminal work of Jenkins and Moore (1973) found that pigeons that were autoshaped to peck a key for food or for water directed ‘eating’ or ‘drinking’ like pecks to keys that delivered food and water reinforcers, respectively. This suggested that the motivation behind each key peck and its relationship to the obtained reinforcer could affect the motor pattern expressed. One suggestion is that these differences were the result of the elicited nature of the autoshaped response with the stimuli coming to elicit a response appropriate to the reinforcer type (LaMon & Zeigler, 1988). However, further work using more sophisticated technology carried out by LaMon and Zeigler (1988) and measuring more elements of the peck than topography (e.g., peck force and duration, gape, and eye closure) led to them concluding that the control of the conditioned response form involves the construction of the response from movements produced by different effector systems, that have potentially different sources of control.

As well as enabling the operation of an experimental key, the hen’s peck serves several functions, including foraging, aggression (e.g., feather

pecking), and grooming. Dixon, Duncan, and Mason (2008) quantified aspects of the morphology of hens' pecks at forages (objects with various foods attached) dustbathes (pans filled with various substrates), novel objects, and water. They used video analysis to record the durations of the head fixation before the peck, between the head fixation to beak contact with each stimulus, and of the whole peck sequence. They found that the motor patterns involved in pecks at forages, dustbathes, novel objects and water all varied significantly and that severe feather pecks resembled foraging pecks. Based on their results, and supporting Jenkins and Moore (1973), they suggested that the different forms of peck could be viewed as a motivationally distinct 'fixed-action pattern' and they suggested that finely examining fixed-action pattern morphology can help understand the motivational bases of perplexing abnormal behaviours in captive animals (Dixon et al., 2008).

These differences in peck morphology were found by measuring pecks that were elicited by the type of consequence involved. The form of the handshaped response may not depend on the character of the consequence but on the judgement made by the shaper. There are no data on the morphology of the handshaped response. The aim of this experiment was to (1), examine use of the Dixon et al. (2008) methods in assessing the morphology of food motivated pecks made to a computer screen by hens; and (2), to compare the morphology of these pecks after the hens had been trained to emit the peck using either an autoshaping or handshaping procedure. It was hypothesised that if the food reinforcer was the main determinant of peck morphology then it would be expected that both methods would produce similarly formed pecks in spite of the variability in the handshaping procedure.

Method

Subjects

Six experimentally naïve hens (*Gallus gallus domesticus*) numbered 25-1 - 25-6 were used as subjects. The hens were aged one-year old at the beginning of the experiment and two were of the breed Australorpe

and four were Orpington. Throughout the course of the experiment the hens were maintained at 85 ±5% of their 100% free-feeding bodyweights. To aid in the maintenance of the hens' weights, hens were fed NRM Peck'n'Lay commercial laying pellets outside of experimental sessions if necessary. Oyster grit and vitamins were given to the hens once weekly. Water was available ad libitum via nipple feeders located in the hens' cages. Hens were housed individually in custom built cages measuring 620-mm high by 790-mm wide by 610-mm deep. Each cage was fitted with a wooden door and wire sides and floor. A wooden perch situated 300-mm from the left edge of the cage and 100-mm off the floor ran the width of the cage. Lights were on a 12 hr light / dark cycle (06:00 – 18:00 hr). Ethical approval for this research was gained from the University of Waikato Animal Ethics Research Committee (protocol number 871).

Apparatus

The experimental chamber measured 600-mm high x 570-mm wide x 450-mm deep. A white house-light in the centre of the ceiling was activated at the beginning of each session and terminated at the end to facilitate filming. Two, 50-mm x 50-mm openings on the lower edge of the front wall, allowed access to laying pellets (NRM Peck'n'Lay) placed in a hopper. An infrared beam inside the magazine recorded movement of the hen's head in and out of the hopper. The front wall of the chamber housed a computer monitor (Dell 19" flat screen) onto which two white circles 30-mm in diameter (one on the left side of the screen and one on the right side) were illuminated against a black background. Pecks made to the white circles were categorised as effective pecks. When an effective peck was made the hopper operated. Pecks to the other parts of the screen were either recorded as a near miss, if it was made to an area of 20 mm near to any part of the white circle, or as a black peck if it was made to any other part of the black screen, both of which would not operate the hopper. The hopper could also be operated manually using a button located outside of the experimental chamber. Pecks of all types and their locations were recorded using a customised computer programme. The left side of the chamber was made of clear plastic, and a high-performance camera

(GoPro® Hero 3 Black) was fixed to the exterior. All sessions were filmed in the WVGA setting, which recorded in 240 fps. Black plastic covered the clear plastic side of the chamber to eliminate extraneous light.

Procedure

Autoshaping procedure

Three hens (25-1 - 25-3) were autoshaped using a procedure similar to Ploog and Zeigler (1996). Hens were placed in the experimental chamber and the door closed. After a variable ITI with a mean of 45 s, a white circle, the conditioned stimulus (CS), was activated on either the left or right side of the black screen. If there was no response to this circle, the circle disappeared off screen after 6 s and the 6-s unconditioned stimulus (US) period began, where the hopper was activated to allow access to pellets. If a peck occurred, the circle disappeared off screen immediately and the 6-s US period began. Sessions were terminated after 40 reinforcers had been delivered. The average session length was 321.59 s (*SD* = 256.19 s).

Handshaping procedure

Three hens (25-4 – 25-6) were shaped via the method of successive approximations, firstly to peck the left circle and then to peck the right circle. The chamber door was opened slightly to observe the hen, and a button was used to manually activate the hopper and deliver 6-s access to laying pellets. All handshaping was performed by the same experimenter, who had experience in shaping hens to peck keys. This was done by the experimenter using their judgement to reinforce successive approximations of the pecking response. Sessions were terminated after 40 reinforcers had been delivered or 2400 s, whichever was sooner. Training sessions continued until pecking was judged to be occurring reliably, i.e., hens were pecking at every circle presentation. Hens 25-4 – 25-6 required seven, five and four sessions respectively to peck the left key reliably and one, two and two sessions respectively to peck the right key reliably.

Continuous reinforcement sessions

Once pecking reliably, all hens were placed on a multiple continuous reinforcement schedule for four sessions. During these sessions, the white circle would appear randomly on either the left or right side of the black screen. A peck to this circle would activate the hopper giving 3-s access to laying pellets. Each session continued until either 40 reinforcers had been obtained, or 2400 s had elapsed, whichever occurred first.

Data analysis

All videos for the continuous reinforcement sessions were analysed using the methodology described by Dixon et al. (2008). Using this approach peck duration was divided into three measurable parts: (1) duration of head fixation: the length of time that the head is kept still before the peck; (2) duration from fixation to contact: duration from the end of head fixation to beak contact with the white circle; and (3) duration of beak contact back to no head movement. In addition to this, pecks that were effective (to the white circle) or ineffective (to the black screen) were coded separately to allow for individual analysis. The duration of the beak opening to closing, which could occur at any point during the entire peck, was also measured. Independent sample t-tests were used to calculate whether there were any significant differences between the component durations exhibited by autoshaped and handshaped hens.

All raw video footage was adjusted to be in 30 fps and analysed using Adobe Premier Pro CS4. An experimenter manually added coded markers to the relevant parts of the videos. These videos were then exported from Adobe Premier Pro CS4 using customised software to obtain CSV files containing the durations of the measured events. The same experimenter analysed all videos. Inter-observer reliability checks were carried out on 10% of each video by a second experimenter. The durations obtained from the first experimenter were correlated (using Spearman's correlation) with the relevant durations obtained by the second experimenter and a correlation coefficient of $r_s = .82$ was obtained, indicating good inter-observer reliability.

Results

Table 2.1 presents the duration of the components for hens that experienced either handshaping or autoshaping. Unfortunately, the videos for the first two continuous reinforcement sessions for Hen 25-5 could not be analysed due to a technical error.

Figure 2.1 presents the average durations of each component of handshaped and autoshaped pecks. As seen on Figure 2.1, independent sample t-tests showed that there was a significant difference with a large effect size between beginning fixation to end of fixation for autoshaped (M = 0.193, SD = 0.010) and handshaped (M = 0.218, SD = 0.004) conditions; $t(4)$= -4.318, p = 0.012; d = 3.53. There was no significant difference in time taken for fixation to contact for autoshaped (M = 0.061, SD = 0.002) and handshaped (M = 0.061, SD = 0.006) conditions; $t(4)$ = -0.1177, p = 0.912. There were also no significant differences in contact with screen times for autoshaped (M = 0.059, SD = 0.013) and handshaped (M = 0.053, SD = 0.010) conditions; $t(4)$= 0.7043, p =0.520. There was no significant difference in time taken from screen contact to no movement for autoshaped (M = 0.176, SD = 0.009) and handshaped (M = 0.172, SD = 0.002) conditions; $t(4)$ = 0.7977, p = 0.470. There was no significant difference for the time taken for fixation to no contact in autoshaped (M = 0.060, SD = 0.004) and handshaped (M = 0.060, SD = 0.003) conditions; $t(4)$ = 0.0842, p = 0.937.

Discussion

In this study, it was found that all components of the peck (excluding beginning to end of fixation) had similar durations, regardless of whether the peck was handshaped or autoshaped. It would appear that the morphology was not affected by the method of training except for fixation time.

Overall the peck morphology seen in this experiment replicated other findings (Dixon et al., 2008; Smith, 1974). The hens would hold their heads immobile with eyes facing the key, move their head and neck forward to contact the screen, and then move the head back to near the

Table 2.1

The durations (s) of each component of the peck for both the handshaped and autoshaped responses.

Hen	Beginning fixation to end fixation	Fixation to contact	Contact duration	Contact to no movement	Fixation to missed Peck
	CRF Session One				
251	0.189	0.065	0.044	0.178	0.054
252	0.182	0.057	0.049	0.187	0.065
253	0.189	0.057	0.077	0.178	0.052
254	0.221	0.067	0.079	0.176	0.062
255	*	*	*	*	*
256	0.229	0.053	0.048	0.158	0.047
	CRF Session Two				
251	0.171	0.056	0.045	0.177	0.063
252	0.183	0.061	0.047	0.193	0.060
253	0.191	0.047	0.074	0.175	0.051
254	0.235	0.074	0.063	0.169	0.070
255	*	*	*	*	*
256	0.216	0.052	0.046	0.174	0.058
	CRF Session Three				
251	0.180	0.061	0.049	0.173	0.064
252	0.180	0.058	0.061	0.191	0.061
253	0.235	0.074	0.063	0.169	0.070
254	0.199	0.056	0.050	0.170	0.054
255	0.224	0.059	0.041	0.167	0.060
256	0.204	0.053	0.054	0.163	0.056
	CRF Session Four				
251	0.248	0.063	0.067	0.149	0.058
252	0.181	0.077	0.054	0.175	0.073
253	0.182	0.056	0.082	0.172	0.051
254	0.230	0.070	0.060	0.178	0.063
255	0.215	0.065	0.045	0.180	0.061
256	0.208	0.064	0.061	0.184	0.067
Mean Autoshaped	0.193	0.061	0.059	0.176	0.060
Mean Handshaped	0.218	0.061	0.053	0.172	0.060
SE Autoshaped	0.006	0.001	0.007	0.005	0.003
SE Handshaped	0.002	0.003	0.006	0.001	0.002

* Missing data.

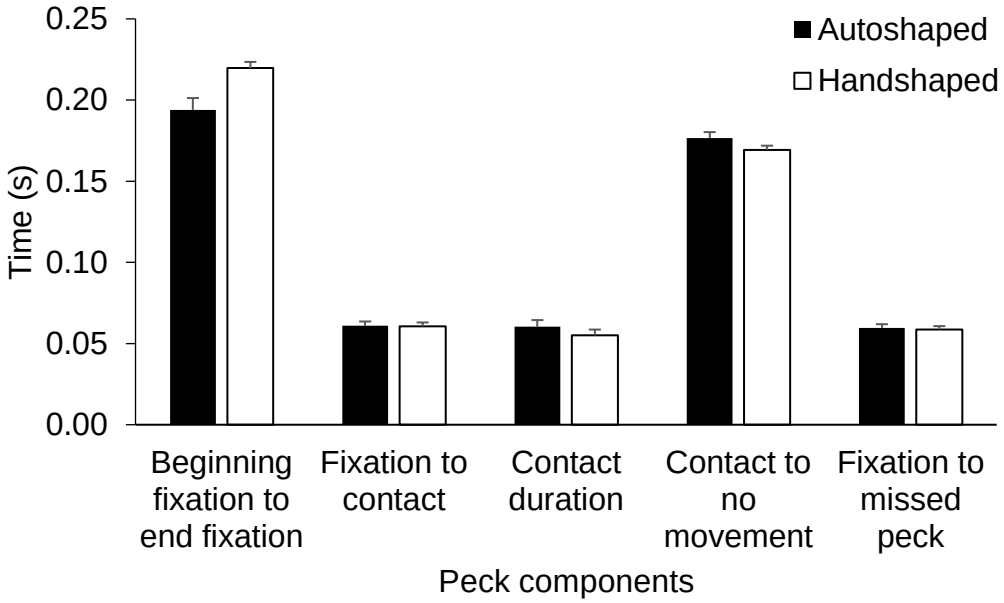

Figure 2.1. The average durations of each component of the peck for both the handshaped and autoshaped responses. The error bars represent ±SEM.

original position. The eyes were open at the beginning of the peck, but were closed during contact, as in Smith (1974). Also, similar to Smith (1974) the beak was usually fully open by the time it contacted the screen. In Jenkins and Moore's (1973) study pigeons made key pecks for food that were short, forceful, and characterised by a widely opened beak. Dixon et al. (2008) did not include pecks directed at food in their study so the duration components from this study are not able to be compared to any previous research.

The finding that the only difference between pecks that were handshaped or autoshaped was in the beginning to end fixation was interesting. It could be possible that time spent in between emitting pecks, such as the fixation, was effected by the variability in using hand shaping and the other components of the peck were not.

As cautioned by LaMon and Zeigler (1988) and Ploog and Zeigler (1997), contact topography can be influenced by the key type and

therefore contact duration can reflect a complex interaction between the physical properties of the key and the topographical features of the response. For this reason, a flat computer monitor was used to display the stimuli. There was no significant difference in contact duration between the handshaped and autoshaped hens.

As pointed out by Ploog and Zeigler (1997) units of topographical or morphological measures are not easily defined. It is important therefore to continue to develop and define measures of assessing topography and morphology as there are many applications for its use.

In conclusion, this study extended a fixed-action pattern morphology analysis to the operant chamber and offers an observational method for studying peck morphology in future studies. Given that handshaping and autoshaping gave rise to similar peck morphology, this suggests that it is the nature of the reinforcer that gives rise to morphology not that the autoshaping procedure *per se* gives rise to a particular form of elicited responses. Future studies could utilise concurrent schedules with different reinforcer types (e.g., food and water) and assess whether morphology changes depending on the MO employed.

Chapter 3 : RESTRICTING ACCESS TO WATER IN FOOD-RESTRICTED LAYING HENS

Experiment 3.1: A Procedure for Restricting Access to Water in Food-Restricted Laying Hens

Experiment 2.1 extended a fixed-action pattern morphology analysis to the operant chamber and offered an observational method for studying peck morphology. The findings of Experiment 2.1 suggest that it is the nature of the reinforcer that gives rise to morphology not that the autoshaping procedure *per se* gives rise to a particular form of elicited responses. However, the question remains of whether the elicited responses would be affected by MOs. It was planned to utilise concurrent schedules with different reinforcer types (e.g., food and water) and assess whether morphology changes depending on the MO employed. Therefore, the aim of Experiment 3.1 was to develop a procedure for restricting access to water in hens maintained at 85% of free-feeding bodyweights in order to allow future experiments to manipulate both food and water MOs during autoshaping and under concurrent schedules.

When motivating animals to respond for a reinforcer, most researchers use a level of restriction which produces stable performance. When food is used as a reinforcer animals are often maintained at 80 - 85% of their ad libitum or free-feeding bodyweights (Toth & Gardiner, 2000). This level of bodyweight restriction is frequently employed with pigeons (e.g. Kangas & Branch, 2006), mice and rats (e.g. Rowland, 2007), and has also been used with monkeys (e.g. Carroll & Stotz, 1984) and hens (e.g., Foster et al., 1997; Grant et al., 2014).

In contrast, when motivating animals to respond for water reinforcers there is not a generally agreed restriction level that applies across species. Some studies have contributed to knowledge about restriction procedures that can motivate stable responding in some species. For example, 21 hr of water restriction has been used to motivate rats to respond for water reinforcers (Hughes et al., 1994), and 46 hr has been used to motivate pigeons (Ploog & Zeigler, 1997). Typically, water

access has been restricted on a time basis, rather than quantity, with the quantities consumed during the access periods going unreported in papers. Thus, we are unsure of whether the animals are consuming a different amount of water in the restriction period to what they would when access is ad libitum.

Published overviews of laboratory food and water restriction protocols suggest that animals adapt well to a once daily water restriction schedule, but, this is mainly based on data from rats or mice and not avian species (Rowland, 2007; Toth & Gardiner, 2000). The overviews state that it is important to consider that total water intake does not necessarily represent need as it is affected by many factors (such as availability and palatability of fluids) and can be influenced by environmental, dietary, and learning factors (Toth & Gardiner, 2000). In addition, people are likely to overestimate animals' true water intake requirements, thus making adequate restriction difficult to obtain ethical approval for (Rowland, 2007; Toth & Gardiner, 2000). The laboratory protocol overviews by Rowland (2007) and Toth and Gardiner (2000) made a number of recommendations that researchers should consider when using water restriction. Consideration should be given to the amount of water intake during the period of availability, as well as the length of time given for adequate consumption, with food and water being made available concurrently. There should be established criteria for food intake and weight loss, and animals should be weighed regularly with provision made for supplemental access if needed.

One difficulty when developing a water restriction regimen for hens is that it is not possible to state precise requirements of daily water intake for this species as intake is affected by factors such as temperature, relative humidity, egg production, growth, and diet (National Research Council, 1994). Although published data on the amount of water hens consume each day are limited (particularly for caged laying hens) (National Research Council, 1994; Xin et al., 2002), estimates suggest adult laying hens drink around 150-200 ml per day or consume about 1.6-2.0 times as much water as food per day, by weight (Appleby, Mench &

Hughes, 2004; Savory, 2010). Additional data on water consumption has come from acclimation or pilot studies investigating the effect of other variables on laying hens' water intake. Two such studies found that adult hens drank 193-194 ml and 214.6 ml per day, with water to feed ratios being 1.8-2.0 and 2.0, respectively (Savory, 1978; Xin et al., 2002).

Hens' water consumption has also been measured by recording the time spent drinking over a day. Hens housed in pens have been reported to spend 1.35% of their available time drinking and 11.57% feeding (Mishra et al., 2005). Caged hens have higher percentages with data showing that hens spend between 11.2 and 12.5% of their available time drinking and 41.4 and 44.9% feeding (Roll, Briz & Levrino., 2008). Caged hens also show hourly patterns of water and food intake that covary throughout the day (Savory et al., 1978; Xin et al., 2002). Polydipsia (excessive drinking) has also been found to occur in caged hens (Savory; 2010; Yeomans, 1986).

Hens are a non-traditional laboratory animal but have been used in numerous studies for basic experimental behavioural research, psychophysical research, and welfare research (e.g., Grant et al., 2014; Gunnarsson, Matthews, Foster & Temple, 2000 & Railton et al., 2014), working for access to food, straw, and litter as reinforcers. If a water restriction procedure was developed for hens, this would allow future research to be undertaken where hens would work reliably for water reinforcers. This is of interest for assessing the value of water to hens and assessing the motivation of hens to obtain water if they are deprived in another way (e.g., restricted bodyweight). In addition, the effects of water restriction on hens' consumption is of interest for animal welfare and farming practices as controlling litter moisture is a priority for the poultry industry in order to avoid environmental and animal welfare problems (Collett, 2012; Francesch & Brufau, 2004).

The aim of the current experiment was to assess the effect that gradually decreasing time and amount of water access would have on food-restricted hens' water consumption and health. It was hypothesised

that restriction periods of less than 24 hr would have no observable effects on hen health.

Method

Subjects

Eleven Brown Shaver hens numbered 24-1 – 24-6 and 25-2 – 25-6 served as subjects. Hens 24-1 – 24-6 were approximately two years old; Hens 25-2 – 25-6 were approximately three years old. Throughout the course of the experiment the hens were maintained at 85 ±5% of their 100% free-feeding bodyweights. To calculate the 100% free-feeding bodyweights; hens numbered 24- had ad libitum access to their normal food, NRM Peck'n'Lay commercial laying pellets, for 68 days, and hens numbered 25- for 25 days. After the hens' weights had been judged visually stable (the weights were not trending up or downwards) the weights from the last 10 days of the free-feeding period were averaged and used as their 100% free-feeding bodyweights. Hens were housed individually in custom built cages measuring 620-mm high by 790-mm wide by 610-mm deep. Hens numbered 24- were housed in a room measuring 2000-mm high by 1850-mm wide by 2000-mm deep containing six cages stacked in two rows of three. Hens numbered 25- were housed in an identically sized room adjacent to the first room. All hens were housed under a 12 hr light / dark cycle (0600 hr – 1800 hr). One day a week the hens' food was enriched with vitamins and they were also given grit on a weekly basis. All hens had prior experimental experience responding for food reinforcers by pecking Perspex keys. Ethical approval for this research was gained from the University of Waikato Animal Ethics Research Committee (protocol number 847).

Apparatus

Water was delivered to the hens via Lubing™ (Dine-a-chook, Townsville, Australia) cups attached to 1.5 litre plastic bottles. The Lubing™ cups were designed to operate at low water pressures and maintain a constant water level of around 6-mm depth to minimise spillage.

The water apparatus was located on the left-hand side of each individual cage. Food was delivered via containers located on the door of the cage.

Procedure

Ad libitum access

The ad libitum access condition was in effect for 54 days. All 11 hens participated in this condition. During the ad libitum access condition, the amount of water used by the hens over a 24 hr period was measured. Hens were weighed daily just prior to 11:00 hr and at 11:00 hr the water apparatus was removed and weighed, and then cleaned, refilled, weighed, and returned to the hens' cages. The hens were then fed their daily allotment of food (commercial laying pellets). The amount of food was calculated depending on whether a hen was above or below their 85% target weight and was never less than 50 cc. For the last four days of the ad libitum access condition the amount of water used was measured at three times over each 24 hr period, 06:00 hr, 11:00 hr and 18:00 hr.

Restriction condition

Condition 2 was in effect for 10 days. Hens 24-1, 24-3, 24-5, 25-2, 25-4, and 25-6 (Group A, hereafter termed the restricted group) participated in this condition. Hens 24-2, 24-4, 24-6, 25-3, and 25-5 (Group B, hereafter termed the non-restricted group) served as control hens. This meant that their access to water was not restricted and the daily routine continued as per the ad libitum access condition throughout the duration of the experiment. All hens were weighed daily prior to 11:00 hr. Each water apparatus was removed from the cages at 11:00 hr and then weighed, cleaned, refilled, weighed, and then reattached to the cages. The hens were then fed their daily allotment of food (commercial laying pellets). At 18:00 hr the water devices were removed from the restricted group hens' cages. For both groups health checks (agreed upon by veterinary consultation and as a requirement of ethical approval) were carried out twice daily, once before 11:00 hr and once in the afternoon of the same day. The checks were designed to assess whether or not any of the hens were showing signs of dehydration. The observational health

checks were whether each hen's comb was red and fleshy, whether the hen was sitting and moving normally, whether the capillary refill of the combs/wattles when lightly pressed was fast (less than two seconds), whether the eyes were round, bright and full, whether the hen's mouth was moist when opened, whether egg production had changed, and whether their faeces had changed (either in colour, consistency, or if the amount of urine around faeces altered). The remaining conditions followed the exact same procedure as Condition 2 except the hours of access to water for the restricted group changed which are outlined in Table 3.1.

Table 3.1

The number of days in each condition and the number of hours of water access per condition, for the restricted group.

Condition	Days	Time of water access
1	54	1100 hr – 1100 hr (24 hr)
2	10	1100 hr – 1800 hr (7 hr)
3	8	1100 hr – 1600 hr (5 hr)
4	11	1100 hr – 1400 hr (3 hr)
5	9	1100 hr – 1300 hr (2 hr)
6	8	1100 hr – 1800 hr (7 hr)

Accelerated restriction condition

Hens 24-1, 24-2, 24-3, 24-4, 24-5, and 24-6 (hereafter termed the accelerated restriction group) participated in this condition. In this condition, the general procedure was the same as in the restriction condition, except the time to water access was decreased quickly, over seven days; this is outlined in Table 3.2.

Data analysis

Pearson's product-moment correlations *r,* were used to assess the correlations between daily water usage (ml), daily food intake (g), bodyweight (g), average daily relative humidity (ø), and average daily temperature (ºC) over Condition 1. Repeated measures ANOVA was used

Table 3.2

The number of days in each condition and the number of hours of water access per condition, and the average amount of water (ml) used for the accelerated restriction procedure.

Condition	Days	Time of water access	Water used (ml)
1	3	1100 hr – 1100 hr (24 hr)	446.1
2	1	1100 hr – 1700 hr (6 hr)	277.3
3	1	1100 hr – 1600 hr (5 hr)	298.3
4	1	1100 hr – 1500 hr (4 hr)	242.2
5	1	1100 hr – 1400 hr (3 hr)	215.7
6	1	1100 hr – 1300 hr (2 hr)	170.4
7	8	1100 hr – 1200 hr (1 hr)	155.5

to compare the effect of changing condition for the restricted, non-restricted, and accelerated restriction groups. IBM™ SPSS™ Statistics Version 21 was used to conduct all statistical analyses.

Results

Water usage

Tables 3.3 and 3.4 show the average amount of water used (ml), food consumed (g), bodyweight (g), and water to feed ratio (ml/g) for each individual hen across all conditions, as well as the averages across all hens, for each condition. For the ad libitum access condition, the average amount of water used across the 11 individual hens was 115.4 ml to 493.3 ml (M = 276.4, SD = 117.5).

For the last four days of Condition 1 the amount of water used by each hen overnight was measured. Figure 3.1 shows the amounts of water used in ml averaged over all 11 hens for each of the four days for three-time periods, 0600 hr - 1100 hr, 1100 hr - 1800 hr and 1800 hr -

Table 3.3

The hens' bodyweights (g), the average amount of water (ml), and the food (g) used over each condition for the hens in the non-restricted group.

Hen	Condition	Hours of water access	Bodyweight (g)	Water (ml)	Feed (g)
24-1	1	24	1672	449.2	105.0
	2	7	1674	363.3	107.4
	3	5	1628	332.9	100.5
	4	3	1667	290.0	115.6
	5	2	1680	210.8	124.7
	6	7	1642	404.7	120.0
24-3	1	24	1676	267.2	36.8
	2	7	1667	330.0	41.4
	3	5	1672	310.9	43.5
	4	3	1680	257.1	33.3
	5	2	1678	168.7	33.3
	6	7	1674	335.3	34.5
24-5	1	24	1722	280.6	40.1
	2	7	1722	284.1	35.4
	3	5	1721	339.1	42.0
	4	3	1724	266.4	31.6
	5	2	1721	148.0	36.7
	6	7	1731	288.5	30.8
25-2	1	24	1614	241.1	38.7
	2	7	1612	190.8	38.4
	3	5	1604	150.4	42.8
	4	3	1623	199.0	34.4
	5	2	1613	149.5	34.0
	6	7	1621	304.5	37.5
25-4	1	24	1757	225.9	38.9
	2	7	1756	180.3	39.0
	3	5	1754	151.7	32.3
	4	3	1750	116.3	36.0
	5	2	1761	105.5	30.7
	6	7	1750	228.8	33.8
25-6	1	24	1617	129.5	44.7
	2	7	1612	171.2	37.2
	3	5	1612	150.2	39.8
	4	3	1615	164.9	32.7
	5	2	1611	122.0	34.0
	6	7	1616	236.1	30.0
Means	1	24	1676.2	265.6	50.7
	2	7	1673.7	253.3	49.8
	3	5	1665.0	239.2	50.1
	4	3	1676.4	215.6	47.3
	5	2	1677.4	150.8	48.9
	6	7	1672.4	299.6	47.8

Table 3.4

The hens' bodyweights (g), the average amount of water (ml) and, the food (g) used over each condition for the hens in the restricted group.

Hen	Condition	Hours of water access	Bodyweight (g)	Water (ml)	Feed (g)
24-2	1	24	1626	355.7	42.8
	2	7	1619	515.0	39.0
	3	5	1615	401.4	45.0
	4	3	1623	482.9	37.1
	5	2	1624	520.9	42.0
	6	7	1624	637.9	37.5
24-4	1	24	1619	219.6	83.8
	2	7	1637	242.3	79.8
	3	5	1621	194.0	79.5
	4	3	1637	246.0	77.5
	5	2	1609	368.4	74.7
	6	7	1618	271.2	73.5
24-6	1	24	1523	493.3	41.1
	2	7	1521	809.8	38.4
	3	5	1517	689.1	42.0
	4	3	1525	593.1	38.7
	5	2	1521	920.8	37.3
	6	7	1522	630.1	42.0
25-3	1	24	1606	115.4	33.2
	2	7	1601	243.5	34.2
	3	5	1594	229.4	36.0
	4	3	1605	229.5	40.4
	5	2	1630	186.7	30.0
	6	7	1629	277.2	28.5
25-5	1	24	1649	263.0	44.7
	2	7	1624	380.8	53.4
	3	5	1621	259.8	57.0
	4	3	1619	181.6	89.5
	5	2	1643	127.1	106.7
	6	7	1688	204.1	88.5
Means	1	24	1604.7	289.4	49.1
	2	7	1600.3	438.3	49.0
	3	5	1593.4	354.7	51.9
	4	3	1601.8	346.6	56.6
	5	2	1605.5	424.8	58.1
	6	7	1616.4	404.1	54.0

0600 hr, as well as the total amount used over the entire 24 hr period. The majority of total water usage occurred between 1100 hr – 1800 hr, with a small proportion occurring between 0600 hr – 1100 hr, and a very small proportion when the lights were off between 1800 hr – 0600 hr.

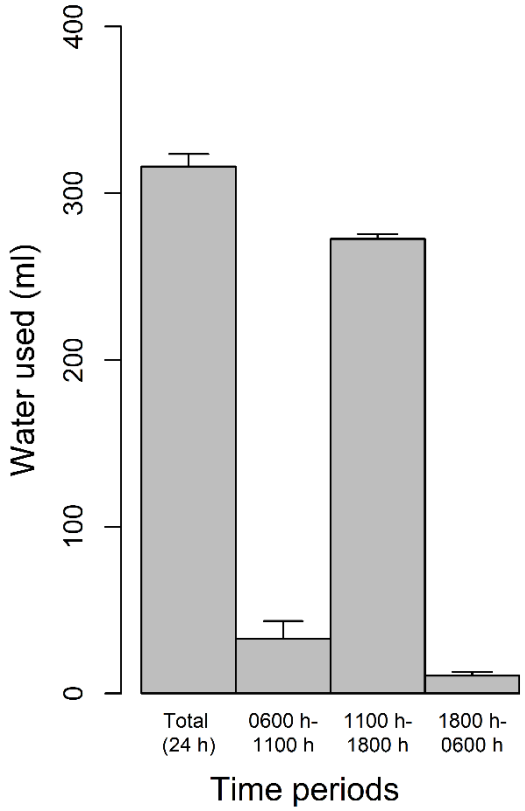

Figure 3.1. The average amount (ml) of water used averaged over all hens, for the four days at the end of Condition 1 where water usage was measured three times over each 24 hr period. Total usage, usage between 1100 hr - 1800 hr, 1800 hr - 0600 hr, and 0600 hr - 1100 hr is shown. The error bars represent ±SEM.

Figure 3.2 presents the average amount of water used and the standard error of these amounts for the restricted group (bars) and the non-restricted group (line) over all conditions. For the restricted group as the time of access to water decreased from seven to two hours (Conditions 2 through 5) water usage also decreased and the amount of variation in consumption amongst individual hens decreased; when time to

access was increased again in Condition 6, usage also increased. For the non-restricted group, whose access remained at 24 hr water usage was variable across conditions.

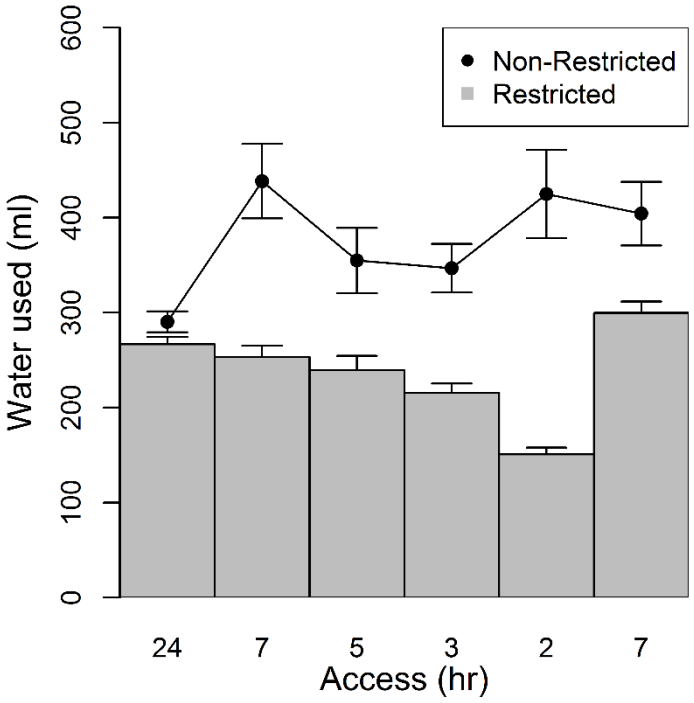

Figure 3.2. The bars represent the average amount (ml) of water used over each condition for the six hens in the restricted group. The line represents the average amount (ml) of water consumed by the non-restricted group of hens over the same time periods. The error bars represent ±SEM.

Figure 3.3 presents the average amount of water used and the standard error of these amounts for the accelerated restriction group. A similar pattern of water consumption to that of the restricted group was observed, with the amount used when access to water was one hour, being very similar to the amount used when access to water was two hours, as shown on Figure 3.3.

A repeated measures ANOVA determined that changing the time of access to water significantly affected water usage for the restricted group ($F(1,5) = 13.077$, $p < .001$, $\eta_p^2 = .766$). Posthoc tests using the Bonferroni correction showed that water usage between Condition 6 (water access

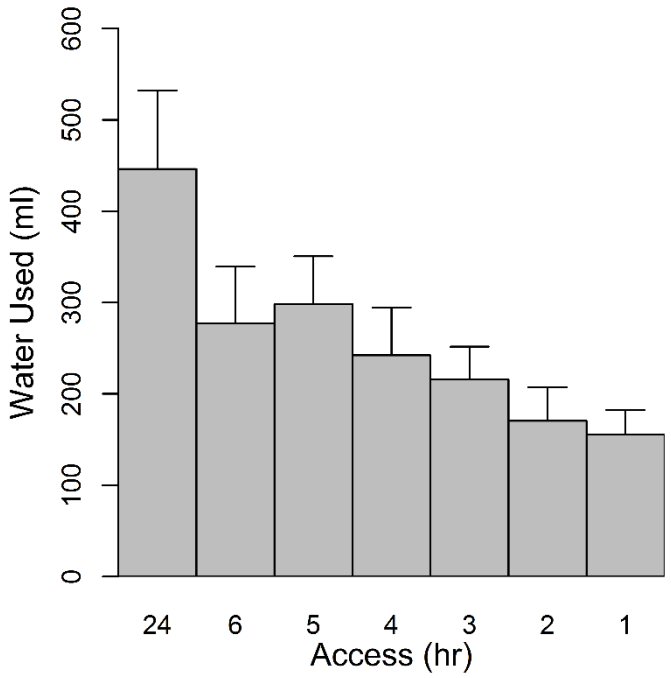

Figure 3.3. The average amount (ml) of water used over each condition for the six hens in the accelerated restricted group. The error bars represent ±SEM.

from 1100 hr – 1800 hr, 299.5 ±42.7 ml) differed from Condition 4 (water access from 1100 hr – 1400 hr, 215.5 ±27.4 ml) and Condition 5 (water access from 1100 hr – 1300 hr, 151 ±15.1 ml).

A repeated measures ANOVA also determined that water usage of the non-restricted group did not change significantly when measured concurrently with the conditions the restricted group were experiencing ($F(1,5) = 1.643$, $p = 0.209$, $\eta_p^2 = .354$).

A repeated measures ANOVA showed that when the hens were exposed to the accelerated restriction procedure water usage changed significantly across conditions ($F(1,6) = 18.793$, $p < .007$, $\eta_p^2 = .790$). Posthoc tests using the Bonferroni correction showed that water usage between Condition 4 (water access from 1100 hr – 1300 hr, 242.2 ±32.4 ml) differed from Condition 6 (water access from 1100 hr – 1300 hr, 170.4 ±36.7 ml) and Condition 7 (water access from 1100 hr – 1200 hr, 155.5 ±23.8 ml).

Temperature and relative humidity

Hens numbered 24- were housed in Room One, and hens numbered 25- were housed in Room Two. Temperature and relative humidity was similar between the two rooms. Over the duration of the experiment the temperature ranged from 15.7 to 17.2°C (average of the minimum and maximum temperatures, respectively), with an overall average of 16.4°C. The relative humidity ranged from 74.2% to 79.7%, with an overall average of 78.9%. For the ad libitum access condition, the correlation of water used per day with daily average temperature was calculated using the data from all hens, and the correlation was not significant, $r(567) = -.022$, $p = 0.603$. The correlation of water used with average daily relative humidity was also calculated, and was not significant, $r(567) = -.077$, $p = 0.067$.

Water used and bodyweight

For the ad libitum access condition, the correlation of water used per day with daily bodyweight was significant, $r(567) = -.144$, $p \leq .01$.

Water used and food consumed

The amount of food given to each hen was fixed, based on whether they were at, below, or above their target weight and it was never below 50 cc per day. All of the hens consumed their entire food ration each day during the experiment. For the ad libitum access condition, the correlation of water used per day with daily bodyweight was significant, $r(567) = -.248$, $p \leq .01$.

Health checks and egg laying

At no time throughout the procedures did any of the hens show any signs of being in poor health and none of the hens failed any of the health checks that were carried out twice daily. Only two hens that had been regularly laying eggs prior to commencing the experiment continued to lay during it. The other hens did not lay eggs during the experiment.

In summary, the results show that the amount of water hens used was reduced by restricting time of access to two hours per day (and later one hr per day), and these time restricted access hens showed no signs of

dehydration on twice daily health checks and no changes in bodyweight or egg production, although they had drier faeces then the non-restricted group. The non-restricted hens continued to drink more water, had wet faeces, and the amount of water used varied greatly across individual birds. When the procedure was repeated over an accelerated time frame, the same findings as stated above were replicated.

Discussion

In this experiment, the amount of water used by 11 food-restricted hens (with bodyweight held at 85% ±5%) was measured over 54 days. The time of access to water was then gradually reduced from 24 hr access to two hr access, for six of the hens. The procedure was then repeated, over an accelerated time frame of seven days, to restrict the water access to one hr per day for six of the hens,

It was found that when access to water was ad libitum some hens used a larger amount of water than reported in previous studies (e.g., National Research Council, 1994; Xin et al., 2002). As time of access to water was decreased the amount of water used also decreased with no observable effects on the hens' health. In addition, the hens that had previously been using large amounts of water now decreased their usage to amounts comparable to those reported in previous studies. The hens that continued to have ad libitum access continued to use large amounts of water and varied more in the amounts consumed from day to day.

The water restriction procedure followed in this study conformed to the guidelines suggested by laboratory protocol overviews that had been documented previously to adapt different species mainly rats and mice, to once daily water restriction schedules (Rowland, 2007; Toth & Gardiner, 2000). One recommendation was that food and water be made available concurrently, which they were in this study. Data recorded showed that when water was made available for 24 hr (with a 12 hr light, dark cycle), the hens used the largest proportion of water from when food was made available at 11:00 hr to when the lights were turned off at 18:00 hr. This finding is in line with previous research which also reported an increase in

drinking behaviour after hens were fed their daily food ration (Savory & Kostal, 1996).

Bodyweight and food intake were monitored closely as recommended by laboratory protocol overviews (Rowland, 2007; Toth & Gardiner, 2000). Hens were weighed daily and the amount of food provided was adjusted to keep the hens within the specified weight range of 85% ±5% of their free-feeding bodyweights.

Overall, the amount of water used per day when access was ad libitum was higher than reported in previous studies: 276.4 ml compared to 193-194 ml, 214.6 ml, and 254 ml (National Research Council, 1994; Savory 1978; Xin et al., 2002). There was also variability in the amount of water used by individual hens (e.g., for the ad libitum access condition amounts used ranged from 115.4 ml to 493.3 ml, M = 276.4, SD = 117.5). Savory (1978) found less variation in the amounts used when access was ad libitum over a three-week period, with mean intake for 10 hens ranging from 178.9 ml – 264.2 ml. It is important to note, however, that the hens in the studies reported above were not food-restricted.

Some studies have investigated what happens when hens' access to water is restricted and results have generally suggested that less than ad libitum access does not affect hens' welfare (Savory, 2010). Water restriction from 100% of ad libitum intake to 90% for 6 weeks resulted in no ill effects on hens' health, and egg production did not differ significantly between the restriction and ad libitum periods (Savory, 2010). However, higher restriction amounts can affect egg laying. Water restriction from 100% of ad libitum intake to 80% and 60% found that live weight of the hens declined for both the 80% and 60% group and for the 60% group egg production was negatively affected (Mishra et al., 2005). In contrast, Dun and Emmans (1973) as cited by the National Research Council (1994) found that when water was restricted from 100% of ad libitum intake to 60%, 40%, and 20% of ad libitum intake, only the 20% restriction had a negative effect on hens' laying.

The above studies investigated water restriction when food was available ad libitum. However, it has been reported that there is a close

relationship between hunger and thirst in hens with consumption of food and water tending to covary (Savory, 2010). It is also known that if dietary factors, such as the amount of protein contained in the food and whether the food is pelleted or crumbed, are altered, they can influence water intake (National Research Council, 1994). Food restriction (feeding less than ad libitum) can also have an effect on water usage and on drinking behaviour. One study investigated the behaviour of food and water-restricted broiler chickens housed in pens, and housed individually in cages, compared to ad libitum fed birds (Savory et al., 1994). They found that when observed at specific intervals, food and water-restricted birds (58 gm of food per bird per day and water access from 8:00 to 12:00 hr), spent a larger percentage of time drinking (29% compared to 2% drinking for non-food and water-restricted birds). They also reported greatly increased activity in the restricted birds and incidences of orally directed stereotyped behaviours (such as pecking walls and drinkers), and posited that the birds were showing excessive water drinking in response to polydipsia caused by the food restriction. Similar findings have been reported by other studies (Savory et al., 1994).

When access to water was un-restricted, there were no significant correlations of food intake with water intake on a daily basis, as has been reported previously (Savory, 1978). It is, however, important to note that bodyweight was held stable in this experiment meaning that food intake was fixed and could only change by a maximum of 10 cc per day. Previous research has reported an hourly correlation between eating and drinking amounts (Savory, 1978). Hourly data was not taken in this experiment as the hens were food-restricted, however, it was ascertained that hens were not drinking water in the 12 hr dark cycle. It was found that there was a peak in consumption in the morning when the lights were turned on, which is line with previous research (Savory, 2010); however, the majority of water usage occurred after the hens were fed at 11:00 hr.

One limitation of this experiment was that hens of two different ages (two and three years old) were used as subjects. These hens were older than those used traditionally used in commercial systems (less than one-

year old) so this could limit applicability of the findings. However, as induced molting is in use with some flocks to rejuvenate flocks for a second or third laying cycle (Bell, 2003) the age of these hens is still similar to those that may be used in some commercial systems.

Another limitation of this experiment, and other similar studies, is the consideration of whether water "usage" reflects water consumption. The water apparatus employed in this study was a Lubing™ cup drinker attached to a plastic bottle, and although it was designed to fill to a level that minimised spillage (6 ml) it was still possible that hens could peck at the water apparatus and spill water. It has been reported in previous studies that water restriction can cause an increase in stereotypic behaviour in general (Savory, Seawright & Watson, 1992; Savory et al., 1994; Savory, 2010) and it is possible that the hens pecked at the water apparatus without consuming water as has been previously reported (Savory & Kostal, 1996). Lubing™ cup drinkers were chosen for several reasons: one being they were straightforward to use; another that cup drinkers promote a more natural drinking behaviour then nipple drinkers. Hens depend on gravity to transfer water to the alimentary tract and when drinking from cup drinkers they dip their beaks in at an angle and raise the head between each drink; when drinking from nipple drinkers hens peck at the nipple drinkers and let water trickle down, which varies in efficiency between hens leading to more time being spent drinking from nipple drinkers (Savory, 2010).

Excessive drinking, as could said to have been shown by some of the hens in this study, has been hypothesised to be caused by environmental stress (Savory, 2010; Yeomans, 1986). One study has investigated the relationship between water intake and the production of wet droppings in the domestic fowl (Lintern-Moore, 1972). It was hypothesised that hens with wet droppings were experiencing polydipsia, and found that hens that produced wet droppings did have a significantly greater intake of water than hens that produced normal, dry, droppings. In some cases, the water consumption of the wet droppings hens per day was up to 40% of the hens' bodyweight (Lintern-Moore, 1972). There was

no relationship between hens with wet droppings and food intake, and no hens were found to have health issues that could cause excessive drinking (such as diabetes). After Lintern-Moore restricted the wet droppings hens to 250 ml of water per day (a comparable intake to the normal droppings hens), the wet droppings changed to be similar to the droppings of the dry hens and no dehydration effects were observed. The conclusion was that the over consumption of water and the wet droppings of some of the hens were a result of the behavioural problem of polydipsia (Lintern-Moore, 1972).

Overall, this study found that following previously documented water restriction recommendations worked well with a new species, hens. Hens adapted to the restriction procedure and were able to be restricted to one hr water access per day, whilst maintaining a stable bodyweight (85%) on a food-restriction regimen. When the hens were water-restricted the amount of variability in the amounts of water used decreased both within and between hens, perhaps giving a truer reflection of the amount of water that the hens “needed”, than when access is given ad libitum. The shortest time period allowed for the hens to consume their daily allotment of water in this study was one hr (as approved by the UOW Animal Ethics Committee). The hens were observed to consume the water in a shorter time then the allowed hr, leaving future studies to investigate how hens could adapt their drinking to even shorter time periods. Future studies could also assess the effects of both water and food restriction (dual MOs) on responding for water and food reinforcers.

Experiment 3.2: Hens Working for Water Reinforcers on Fixed-Ratio Schedules

Introduction

Experiment 3.1 investigated the effect that gradually decreasing time and amount of water access would have on food-restricted hens' water consumption and health. It was found that following previously documented water restriction recommendations worked well with a new species, hens. Hens adapted to the restriction procedure and were able to be restricted to one hr water access per day, whilst maintaining a stable bodyweight on a food-restriction regimen. A similar regimen has been used previously by Ploog (2014) to motivate hens to respond for water reinforcers. In this regimen hens experienced approximately 22.5 hr with no access to water, 1 hr with access to water earned during experimental sessions, and then, following each experimental session, 30 min with free access to water in their home cage.

The aim of this study was to expose hens maintained on the one hr water-restriction regimen described in Experiment 3.1 to FR schedules in order to see whether stable responding for water reinforcers would occur. It was hypothesised that hens would respond until they had earned 40 reinforcers, without reaching satiation and ceasing to respond.

Method

Subjects

Hens 24-1 – 24-6 from Experiment 3.1 served as subjects and were maintained using the same procedures outlined in Experiment 3.1. During this experiment, the hens were fed a base diet of NRM Peck'n'Lay commercial laying pellets via food containers in their home cages. The amount of food given was adjusted to maintain the hens at ±5 % of the 85 % free-feeding bodyweight but was always a minimum of 50 cc. The hens began Experiment 3.2 after the accelerated restriction procedure outlined above had been carried out. This meant that at the time of beginning this experiment all hens were receiving one hr access to water per day (with the amount being restricted to the average amount they would consume

when water was provided ad libitum). Ethical approval for this research was gained from the University of Waikato Animal Ethics Research Committee (protocol number 883).

Apparatus

The experimental chamber measured 600-mm high x 570-mm wide x 450-mm deep. A white house-light in the centre of the ceiling was activated at the beginning of each session and terminated at the end to facilitate filming. Two 50-mm x 50-mm openings on the lower edge of the front wall allowed access to water delivered via a hopper. The hopper was attached to a water reservoir and when activated the reservoir would raise causing the hopper to fill with water. Only the left hopper was active during this experiment. The hopper was placed on top of a Jadever Sky-3000 weighing scale to allow recording of water consumed. An infrared beam inside the magazine recorded movement of the hens' heads in and out of the hopper. The front wall of the chamber housed a computer monitor (Dell 19" flat screen) onto which a white circle 30-mm in diameter (on the left side of the screen) was illuminated against a black background. Pecks made to the white circles were categorized as effective pecks. When an effective peck was made the water, reservoir was raised and access to water reinforcers was given. Pecks to the other parts of the screen were either recorded as near misses, if they were made to an area within 20 mm to the white circle, or as ineffective pecks, if they were made to any part of the screen; these pecks would not operate the hopper. Pecks of all types and their locations were recorded by the computer. The left side of the chamber was made of clear plastic, and a high-performance camera (GoPro® Hero 3 Black) was fixed to the exterior, pointed at the screen. All sessions were filmed in the WVGA setting, which recorded in 240 fps Black plastic covered the clear plastic side of the chamber to eliminate extraneous light.

Procedure

As all hens had been shaped to peck keys for food reinforcers previously, no key peck training was necessary. Once per day all hens were exposed to FR schedules with response requirements of one or two. Hens responded for 1.5-s access to water. When a session started the stimulus (white circle) would appear on screen and remain there until an effective peck was made. Once the response requirement in effect was fulfilled the keylight went off and the magazine hopper was raised for 1.5 s. Sessions terminated when 20 reinforcers had been earned or 2400 s had elapsed. After experimental sessions had ceased hens were given one hr water access. Hens were exposed to six FR1 sessions and six FR2 sessions.

Results

Hens were exposed to six FR1 sessions and six FR2 sessions. During the first eight sessions, technical problems with the water magazine and hopper meant data were occasionally lost or rendered invalid therefore only the last four FR2 sessions, when technical issues had been addressed, are displayed here, for all six hens.

Figure 3.4 shows the number of reinforcers earned per session, along with the number of reinforcers not consumed, and the total number of reinforcers consumed for all hens. As can be seen on Figure 3.4 no hens worked consistently for, and consumed all 20 reinforcers, across all sessions. The only hen to earn all 20 water reinforcers and consume them was Hen 24-4. Hen 24-2 ceased responding during the last three sessions.

Figure 3.5 presents the amount of water (ml) consumed outside of the session and the amount of water (ml) consumed within session for all hens. The total number of water reinforcers earned per session is also shown. As can be seen on Figure 3.5 all hens consumed the vast majority of total daily consumption during the one hr access period. The only hen to work consistently on the FR schedules, Hen 24-4, also consumed up to four times more water while in the home cage, than compared to consumption in session.

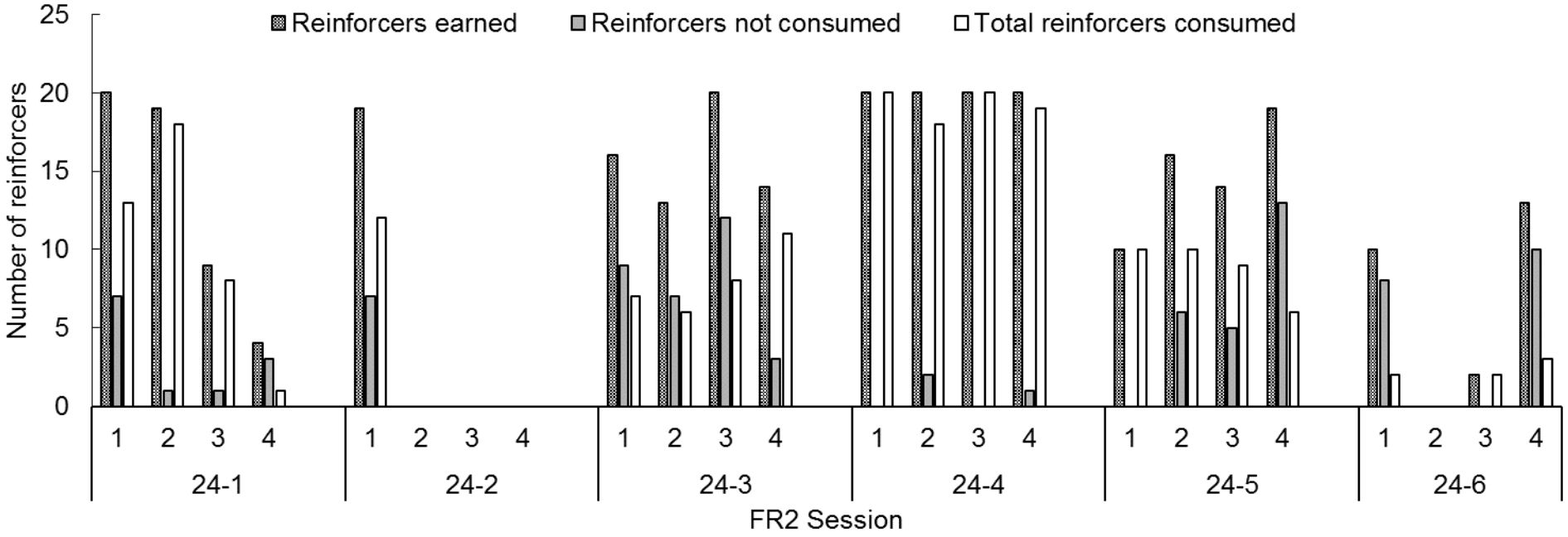

Figure 3.4. The number of reinforcers earned, along with the number of reinforcers not consumed and the total number of reinforcers consumed, over four FR2 sessions is shown for Hens 24.1 – 24.6.

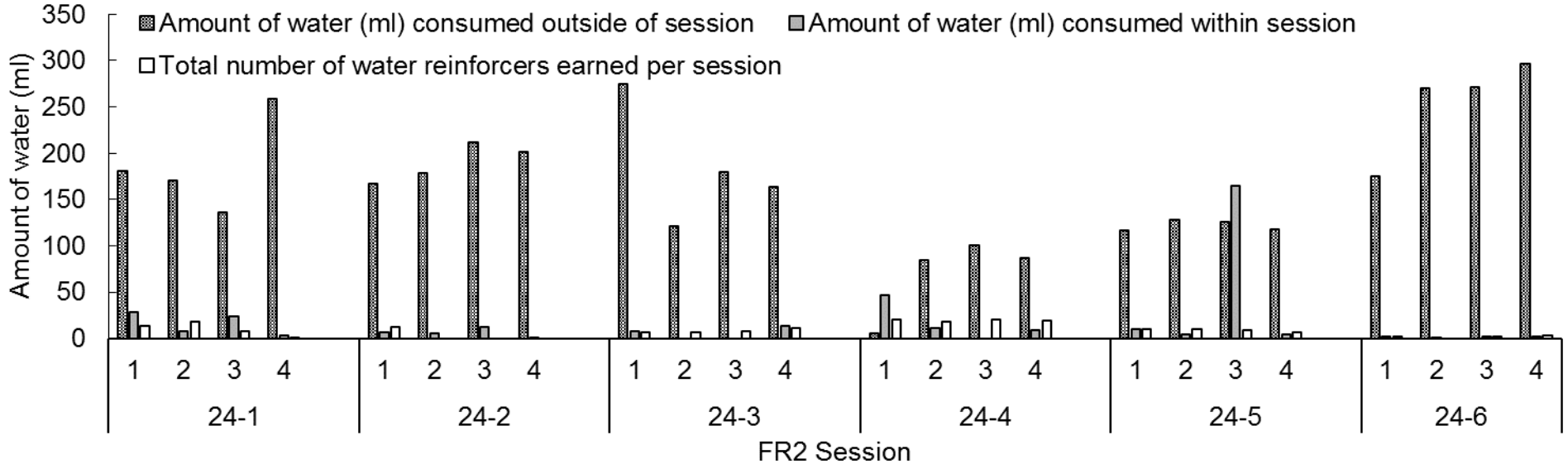

Figure 3.5. The amount of water (ml) consumed outside of the session and the amount of water (ml) consumed within session, over four FR2 sessions, for Hens 24.1 – 24.6. The total number of water reinforcers earned per session is also shown.

Discussion

The aim of this study was to expose hens maintained on the water-restriction regimen described in Experiment 1 to FR schedules in order to see whether stable responding for water reinforcers would occur. The hens in this study did not respond consistently for water reinforcers. In addition, they consumed the vast majority of their total daily intake outside of experimental sessions. The results of this experiment clearly show that the water restriction procedure outlined in Experiment 1 was insufficient at motivating the hens to respond for water reinforcers stably.

Only one other published study can be found that utilises water reinforcers with hens. This study by Ploog (2014) utilised a restriction procedure of approximately 22.5 hr with no access to water, 1 hr with access to water earned during experimental sessions, and then, following each experimental session, 30 min with free access to water in their home cage. Ploog notes that all birds in the experiment ceased working throughout sessions indicating that they had reached satiation.

As noted in Experiment 3.1, the hens were observed to consume their daily allotment of water in a shorter time then the allowed hr, leaving the possibility that hens could adapt to even shorter time periods of water access. A protocol proposing increased restriction to water was submitted to the University of Waikato Animal Ethics Committee, and the committee declined to give approval to the protocol. As a consequence, the planned experiments manipulating water restriction in this thesis as an MO were abandoned. As stated by both Rowland (2007) and Toth and Gardiner (2000) people are likely to overestimate animals' true water intake requirements, thus making adequate restriction difficult to obtain ethical approval for.

Chapter 4 : BODYWEIGHT AS A MOTIVATING OPERATION: EFFECTS ON ACQUISTION

Experiment 4.1: Bodyweight as a Motivating Operation for Screen Peck Responses in Autoshaped Hens

Experiment 2.1 extended a fixed-action pattern morphology analysis to the operant chamber which offers an observational method for studying peck morphology. The intention was to use this methodology to compare responses for food and water reinforcers when both food and water MOs were manipulated in order to assess the effects of two MOs operating at the same time. Ploog (2014) tested whether species-specific patterns observed between pigeons' and hens' drinking responses would be reflected in the form of conditioned (autoshaped) responses. Ploog found that the birds showed species-specific differences in their unconditioned responses which were reflected in different conditioned responses in the presence of the keylight. If different MOs affected species-specific behaviour this could be expected to be seen in the form of the conditioned response.

Experiments 3.1 and 3.2 investigated whether food-restricted hens (85% of free-feeding bodyweight) could be motivated to respond for water reinforcers. Although it was found that hens maintained at 85% of free-feeding bodyweight could be restricted to one hr water access per day, this was not sufficient to motivate stable responding for water reinforcers. Ethical approval to restrict water access further was not obtained and the planned experiments manipulating both water and food MOs during autoshaping and concurrent schedules had to be abandoned.

Due to the proposed experiments needing to be abandoned, Chapter 4 presents Experiment 4.1 that investigates the effect of manipulating bodyweight (75% or 95% of free-feeding bodyweight) on acquisition of responding. Nearly 50 years ago Brown and Jenkins (1968) reported on a novel procedure for training key pecking in pigeons, which was termed 'autoshaping' because the key peck was shaped

'automatically'. Gleeson (1991) states that autoshaping was more than just an addition to the operant conditioners' array of techniques for generating responding. He stated that the initial study subsequently generated a wealth of research on the phenomenon itself, its features and its implications for the distinction between classical and operant conditioning (for a review see, Gibbon, Lucurto, & Terrace, 1981).

In a standard autoshaping procedure, after an ITI averaging 60 s, a keylight immediately precedes the delivery of reinforcement. No response is required by the animal to gain the reinforcer, but if one is made to the lit key the reinforcer is delivered immediately, and the ITI begins again. While a response is not necessary to obtain a reinforcer, most birds will nonetheless begin to peck the lit key (Gamzu & Schwam, 1974).

There are a number of features critical to autoshaping. There must be a unique correlation between the keylight and food and the ratio of keylight duration to ITI duration. Explicitly, for autoshaped key pecking to occur reliably food must be correlated more with the keylight than any other stimuli (Hearst & Jenkins, 1974; Schwartz & Gamzu, 1977). In addition, CS duration must also be short relative to ITI duration (Gibbon, Baldock, Lucurto, Gold, & Terrace, 1977). Parameters can vary but CS periods of 6 – 8 s, reinforcer durations of 3 – 5 s and variable ITIs of 30 – 60 s with sessions terminating after 60 – 80 reinforcers are the most common (Gleeson, 1991). Under these conditions pigeons emit the first key peck after an average of 20 – 40 trials (Gleeson, 1991). Magazine training can precede autoshaping, however, some studies have shown that food presented independently of the CS can slow key peck acquisition (Balsam & Schwartz, 1981).

A wealth of research has been carried out on the phenomenon of autoshaping and the parameters under which it occurs; however, one important area, the effect motivational variables have on acquisition of autoshaped responses, has not been fully investigated.

Food restriction (achieved via keeping an animal at less than ad libitum bodyweight or by restricting access to food) has traditionally been considered as an MO. Michael (1982) suggested that an effect of food restriction is to evoke either increased general activity or increased

specific responses. Once these responses are evoked, they are more likely to persist because they are followed by food reinforcement.

Early research found that food deprivation leads to higher activity levels in initial training sessions (e.g., Baumeister, Hawkins and Cromwell, 1964; Campbell & Sheffield, 1953; Sheffield & Campbell, 1954) which could facilitate the acquisition of the response in shaping procedures. Campbell and Sheffield (1953) found that rats deprived of food showed higher activity levels, than when they were not deprived of food. However, the difference in activity levels was much more marked when the deprivation period was paired with a change in environment. They concluded that the slight rise in general activity during the deprivation period could be interpreted as due to their greater sensitivity to minimal stimulus changes in the environment. Hypothetically, increased deprivation could lead to an increased sensitivity to US-CS pairings and lead to faster acquisition of autoshaped key pecks. However, as stated above, Balsam (1985) reported that high activity levels that occur when a pigeon is placed in a context correlated with food (i.e., a chamber in which extensive magazine training has occurred) can inhibit response acquisition in autoshaping procedures.

Lattal and Williams (1997) examined the role of body weight in the acquisition and subsequent maintenance of responding with delayed reinforcement using rats as subjects. In their review of the literature they stated that previous research (e.g., Dickinson, Watt & Griffiths., 1992; Lattal & Gleeson, 1990; Skinner, 1938; van Haaren, 1992; Wilkenfield, Nickel, Blakely & Poling, 1992) has demonstrated response acquisition with delayed reinforcement by showing that: (1) response acquisition is more likely at bodyweight percentages lower than free-feeding; (2) response maintenance with delayed reinforcement is less reliably related to bodyweight; (3) reducing body weight during magazine training leads to faster acquisition; (4) magazine training is unnecessary in establishing behaviour with delayed reinforcement; and (5) acquisition proceeds more rapidly with magazine training and when such training occurs at lower, rather than higher, body weights.

Lattal and Williams (1997) extended these findings by examining the role of another MO, body weight, in the acquisition and subsequent

maintenance of responding with delayed reinforcement. They trained naïve rats deprived to 70%, 80%, or 90% of free-feeding bodyweight that were then exposed to tandem VI 15-s DRO 30-s schedules. They found that in the first experiment, speed of magazine training, acquisition of lever pressing, and final rate of lever pressing were related to body weight. They concluded that body weight therefore seems to affect response acquisition because of the response-reinforcer relation (Lattal & Williams, 1997). In more detail, they posited that an animal placed in an operant chamber is likely to emit at least an occasional response independent of bodyweight. If such a response is followed by a reinforcer, further responding is determined by the animal's bodyweight. Therefore, the bodyweight of the animal acts as a function of the response-reinforcer dependency and determines the likelihood of the next response.

The aim of this experiment was to use the autoshaping paradigm to assess the acquisition of food motivated pecks to a stimulus at two different levels of bodyweight, and then to use an infra-red screen to analyse performance separately from learning effects by examining activity levels. If increased activity levels lead to increased contact with the stimulus it would be expected that the more deprived birds (75% of free-feeding bodyweight) would acquire pecking responses more rapidly than less deprived birds (95% of free-feeding bodyweight).

Method

Subjects

Thirty experimentally naïve hens (*Gallus gallus domesticus*) numbered 1-1 – 1-15 and 2-1 – 2-15 were used as subjects. The hens were aged one-year old at the beginning of the experiment and were brown shavers. Throughout the course of the experiment Hens 1-1 – 1-15 were maintained at 75 ±5% of their 100% free-feeding body weights and Hens 2-1 – 2-15 were maintained at 95 ±5% of their 100% free-feeding body weights. To aid in the maintenance of the hens' weights, they were fed NRM Peck'n'Lay commercial laying pellets outside of experimental sessions if necessary. Oyster grit and vitamins were given to the hens once weekly. Water was available ad libitum via nipple feeders located in

the hens' cages. Hens were housed individually in custom built cages measuring 620-mm high by 790-mm wide by 610-mm deep. Each cage had wire sides and floor. Lights were on a 12 hr light/dark cycle (06:00 hr – 18:00 hr). Ethical approval for this research was gained from the University of Waikato Animal Ethics Research Committee (protocol number 924).

Apparatus

The experimental chamber measured 600-mm high x 570-mm wide x 450-mm deep. A white house-light in the centre of the ceiling was activated at the beginning of each session and terminated at the end to facilitate filming. Two 50-mm x 50-mm openings on the lower edge of the front wall allowed access to laying pellets (NRM Peck'n'Lay) placed in a hopper. An infrared beam inside the magazine recorded movement of the hens' heads in and out of the hopper. The front wall of the chamber housed a computer monitor (Dell 19" flat screen) onto which two white circles 30-mm in diameter (one on the left side of the screen and one on the right side) were illuminated against a black background. Pecks made to the white circles were categorised as effective pecks. When an effective peck was made the hopper operated. Pecks to the other parts of the screen were recorded as a near miss if made within 20 mm to the outside of the white circle, or as a black peck if it was made to any other part of the screen; these pecks would not operate the hopper. The hopper could also be operated manually using a button located outside of the experimental chamber. Pecks and their locations were recorded by a computer. The left side of the chamber was made of clear plastic, and a high-performance camera (GoPro® Hero 3 Black) was fixed to the exterior to allow filming of the hens' responses. All sessions were filmed in the WVGA setting, which recorded in 240 fps. Black plastic covered the clear plastic side of the chamber to eliminate extraneous light.

Procedure

All hens were autoshaped using a procedure similar to Ploog and Zeigler (1996). Hens were placed in the experimental chamber and the door closed. After a variable ITI with a mean of 45 s, a white circle, the conditioned stimulus (CS), was activated on either the left or right side of

the black screen. If there was no response to this circle, the circle disappeared off screen after 6 s and the 6-s unconditioned stimulus (US) period began, where the hopper was activated to allow access to laying pellets. If a peck occurred, the circle disappeared off screen immediately and the 6-s US period began. Sessions were terminated after 40 reinforcers had been delivered. The average session length was 2091 s (*SD* = 90.59 s).

Results

Raw data for all hens are presented in Appendix C. The mean data for the 75% bodyweight and 95% bodyweight groups is presented in the following analyses.

Figure 4.1 presents the mean percentage of stimulus presentations (the US) that resulted in a peck across sessions for both the 75% group (grey lines) and the 95% group (black lines) and for left and right stimuli. The error bars represent the standard error of the mean. As shown on Figure 4.1, the 75% group pecked slightly more presentations of the lit stimulus than the 95% group, for both the left and right stimuli. Overall both groups did not achieve a high degree of accuracy throughout the 10 autoshaping sessions and effectively pecked between 45 – 65% of stimulus presentations.

Figure 4.2 presents the mean latency to the stimulus across sessions for both the 75% group (grey lines) and the 95% group (black lines), for the left and right stimuli. The error bars represent the standard error of the mean. As shown on Figure 4.2 there were no clear differences between the 75% and 95% bodyweight groups or between the left and right stimuli.

Figure 4.3 presents the mean number of near miss pecks made across sessions for both the 75% group (grey lines) and the 95% group (black lines), for the left and right stimuli. The error bars represent the standard error of the mean. As shown on Figure 4.3 slightly more near miss pecks were observed for the 75% group, than the 95% group, on the right key only.

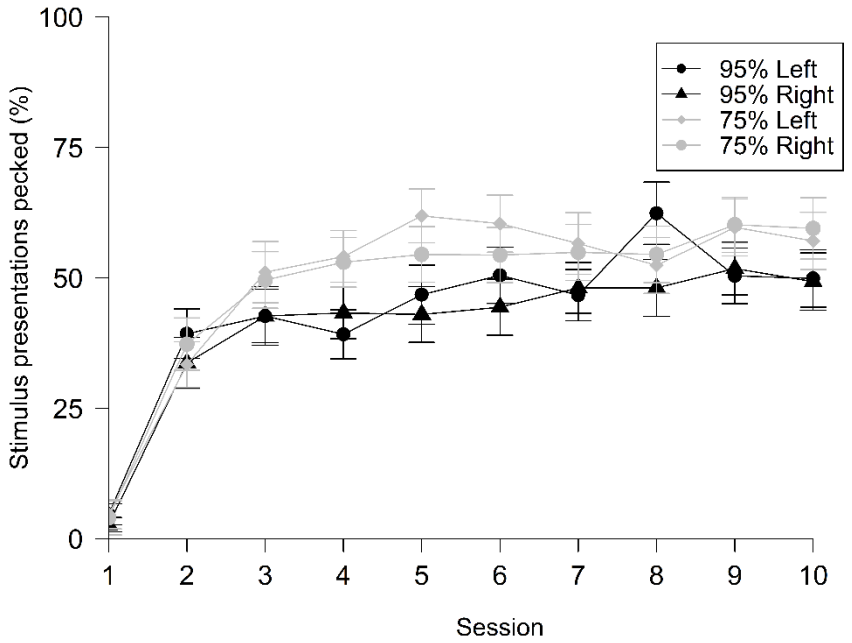

Figure 4.1. Mean percentage of stimulus presentations pecked across sessions for both the 75% group (grey lines) and the 95% group (black lines), for the left and right stimuli. The error bars represent ±SEM.

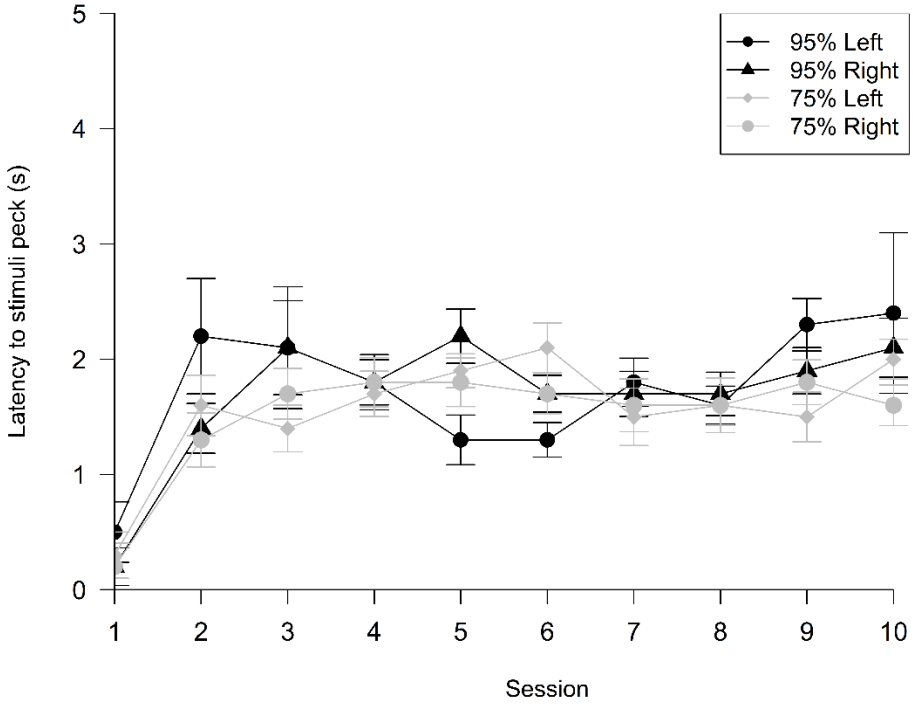

Figure 4.2. Mean latency to stimulus pecks across sessions for both the 75% group (grey lines) and the 95% group (black lines), for the left and right stimuli. The error bars represent ±SEM.

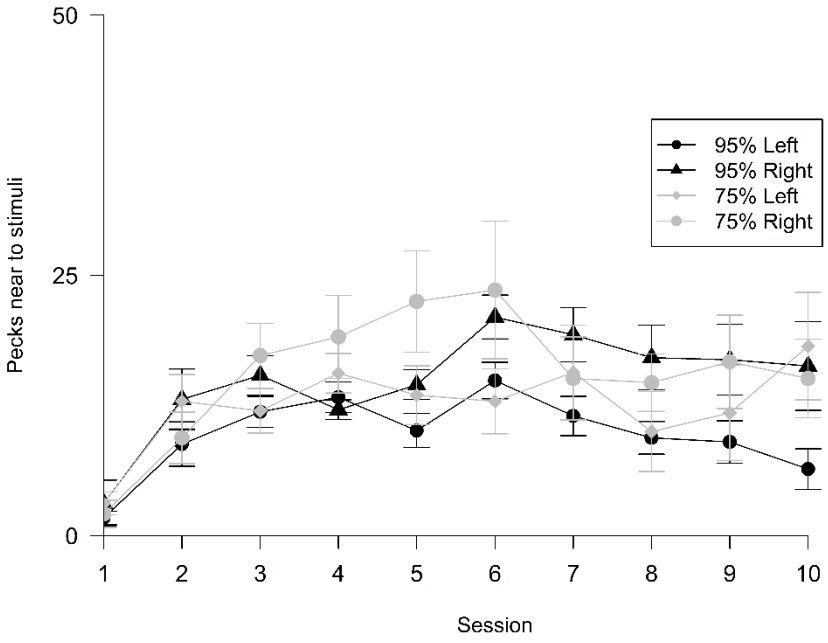

Figure 4.3. Mean number of near pecks made to the stimulus across sessions for both the 75% group (grey lines) and the 95% group (black lines), for the left and right stimuli. The error bars represent ±SEM.

Figure 4.4 presents the mean number of pecks made to the black screen across sessions for both the 75% group (grey lines) and the 95%

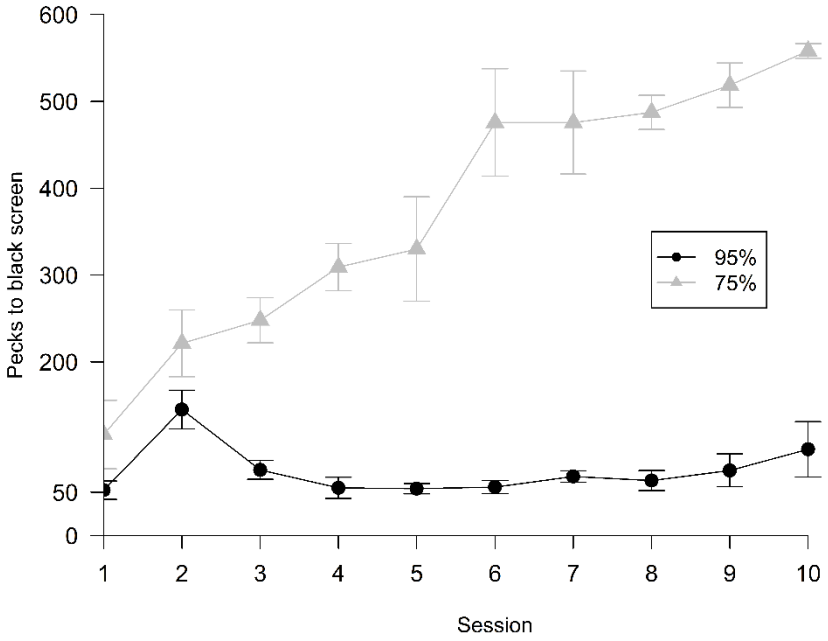

Figure 4.4. Mean number of pecks made to the black screen across sessions for both the 75% group (grey lines) and the 95% group (black lines), for the left and right stimuli. The error bars represent ±SEM.

group (black lines), for the left and right stimuli. The error bars represent the standard error of the mean. As shown on Figure 4.4 considerably more pecks were made to the black screen for the 75% group, than the 95% group.

Figure 4.5 presents the mean number of CS-US presentations required prior to the hens beginning to peck the white circle for both the 75% and the 95% groups. The error bars represent the standard error of the mean. As can be seen on Figure 4.6, both bodyweight groups required similar numbers of CS-US exposures (75% group: *M* = 69.7, *SD* = 56.56; 95% group: *M* = 63.3, *SD* = 48.62) before hens began to peck the stimulus.

Figure 4.6 presents the location of white circle pecks (grey), near miss pecks (light grey) and black screen pecks (black), across sessions 1, 3, 5, 7, and 9 for two representative birds: one from the 75% bodyweight group (Hen 1-1) and one from the 95% bodyweight group (Hen 2-1). As can be seen on Figure 5, Hen 1-1 made more near pecks and black pecks that were more spread out, than did Hen 2-1.

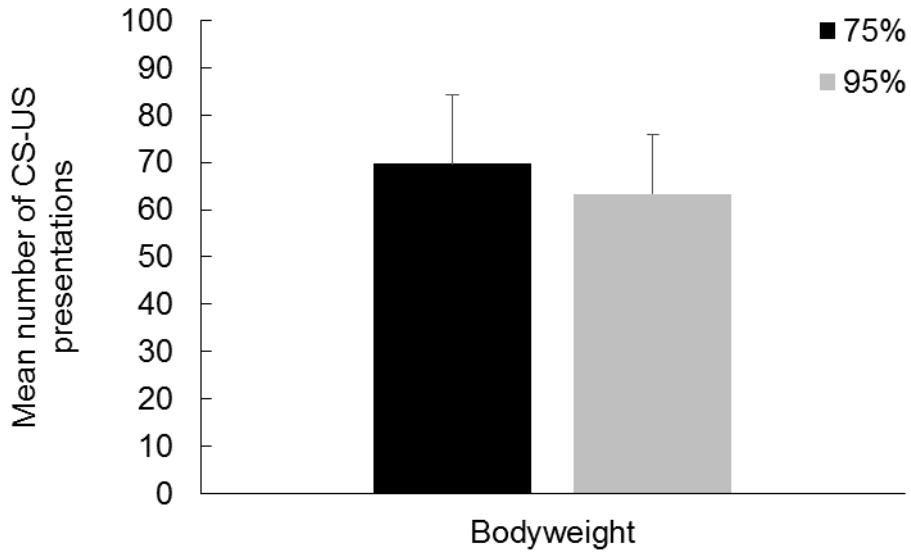

Figure 4.5. The mean number of CS-US presentations prior to the white circle being pecked. The error bars represent ±SEM.

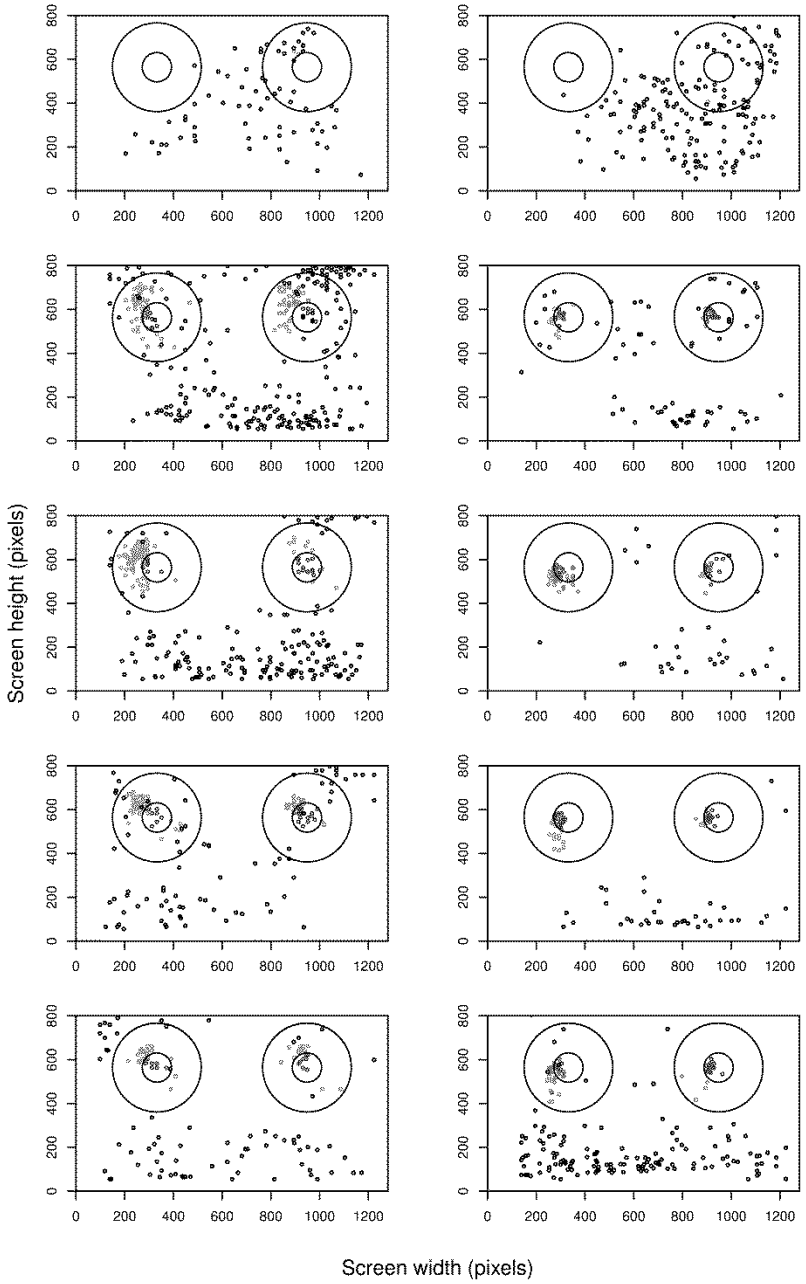

Figure 4.6. The location of white circle pecks (grey), near white circle pecks (light grey), and black screen pecks (black), across sessions 1, 3, 5, 7, and 9 (from top down). The left panel presents the first hen from the 75% group (Hen 1-1) and the right panel presents the first hen from the 95% group (Hen 2-1).

Discussion

This experiment used the autoshaping paradigm to assess the acquisition of food motivated pecks to a stimulus, at two different levels of bodyweight. Performance was analysed separately from learning effects by examining activity levels (location and number of pecks). Overall, it was found that the hens in the 75% of free-feeding bodyweight group exhibited higher number of pecks and made more pecks to the black screen and near to the stimuli, than those maintained at 95% of free-feeding body weight.

Contrary to the hypothesis that hens maintained at 75% would acquire the pecking response faster, the higher activity levels did not affect the number of CS-US presentations required to acquire the autoshaped pecking response. However, the 75% hens hit the stimuli at a higher percentage of accuracy, slightly more than the 95% hens, once the response was acquired. On average, the 30 subjects in this experiment required between 60 - 70 CS-US presentations prior to acquiring the autoshaped response. This is higher than the average of 20 – 40 trials reportedly taken by pigeons to acquire the first peck (Gleeson, 1991).

Overall these results were both similar to, and inconsistent with, previous studies. For example, several studies done with rats (Cleland & Davey, 1982; Sparber, Bollweg, & Messing, 1991) have found that changing the MO for the reinforcer (by changing either body weight or hours of food access) changed the rate at which rats learned to lever press using autoshaping, as well as changing the amount and type of lever directed behaviour of the rats.

Although time to acquisition of the first effective peck to the white stimulus did not differ with bodyweight, a main finding of this experiment is that the hens maintained at 75% of free-feeding bodyweight exhibited considerably more ineffective pecks (i.e., pecks to the black screen or pecks made near (but not activating) the stimuli) and slightly more effective pecks (pecks made to the lit stimulus), than those maintained at 95% of free-feeding bodyweight. Moran (1975) suggested that it is possible that a severely deprived subject is likely to acquire certain behaviours which probabilities are increased directly by hunger and the

presence of food. He also suggested that these behaviours appear different from others in that they are relevant or appropriate to the species-specific behavioural pattern or food acquisition. Timberlake (1993) stated that if we take seriously the idea that learning evolved as it produced a better fit with the environment, then we can assume that animals should come to a learning situation “equipped with” stimulus sensitivities, response components, and motivational states to facilitate learning.

Ploog (2014) tested whether species-specific patterns observed between pigeons’ and hens’ drinking responses would be reflected in the form of conditioned (autoshaped) responses. Ploog found that the birds showed species-specific differences in the unconditioned responses which were reflected in different conditioned responses in the presence of the keylight. It has been reported that main activities of free-range hens are grazing, ground pecking, ground scratching, and dust-bathing, with the exhibition of these being weather-dependent (Hughes & Dun, 1983). Semi-wild jungle fowl have been reported to spend up to 60% of their time actively pecking the ground, even when satiated, and domesticated free-range hens will spend time pecking for food even when feed is available ad libitum (Nicol & Dawkins, 1990). The increased deprivation could maybe enhance the species-specific behaviour of pecking when a screen is made available for the hens to peck on, regardless of the response-reinforcer contingency, and lead to the high activity levels seen within the experimental chamber.

Balsam (1985) reported that the high activity levels that occur when a pigeon is placed in an environmental context correlated with food (i.e., a chamber in which extensive feeder training has occurred) can interfere with autoshaping. In this experiment hens were not feeder-trained however they still displayed high numbers of ineffective pecks. It is possible that in addition to high levels of ineffective pecks shown in this experiment, the hens could have also been displaying other unrecorded species-specific behaviours such as ground pecking or scratching and this could explain why the 30 hens in this experiment required between 60 - 70 CS-US presentations prior to acquiring the autoshaped response, as opposed to the average of 20 – 40 CS-US presentations often reported in pigeon research (Gleeson, 1991).

Baumeister, Hawkins and Cromwell (1964) suggested that as more is learned about the role of learning with respect to activity, there will be less need to refer to drive concepts. The use of concepts such as “drive” to explain behaviour is inversely related to an understanding of the conditions under which the behaviour develops. He suggested that associative interpretations of activity level may be more meaningful than drive interpretations. He states that activity cannot be seen as a simple indicator of drive and is as complex a phenomenon as ever seen in the laboratory. As previously mentioned, Skinner (1938) also argued against the term “drive” and the treatment of motivation that was common at that time. Skinner’s argument was that “drive” is a hypothetical construct interpolated between operation and behaviour and not required in a descriptive system. Skinner proposed that environmental variables should be the focus of the analysis. Skinner made it clear that motivation should be considered separately from other types of antecedent control over behaviour (created by discriminative, unconditioned, or conditioned stimuli). The findings from these studies indicate that bodyweight as an MO may simply affect activity levels (the behaviour-altering effect) and not necessarily the efficacy of the reinforcer (the value-altering effect).

As highlighted in the General Introduction, Laraway et al. (2014) pointed out in many laboratory (particularly free-operant) situations researchers may have trouble disentangling the value-altering and behaviour-altering effects of a given MO in basic research, because consequences occur while the MO functions effectively which confounds the two effects. Pure-behaviour altering effects can be seen most clearly in extinction because reinforcer delivery does not occur, meaning that the behaviour-altering effect is assessed separately from learned behaviour. However, when behaviour is paired with a consequence it becomes possible to assess the value-altering effect. As this experiment was not conducted during extinction it is not possible to consider the behaviour-altering affects pure, e.g., unaffected by consequences. However, the higher levels of ineffective pecks in the 75% group, increased by decreased bodyweight, could also be argued to be evidence of the behaviour-altering effect, seen more clearly than the value-altering effect. The slightly higher number of effective pecks made by the 75% hens than

for the 95% group can be seen as evidence of the value-altering effect after the response has been acquired.

Chapter 5 : PRE-FEEDING AS AN MOTIVATING OPERATION AFFECTING PREFERENCE

Experiment 5.1: Bodyweight and Pre-Feeding as Motivating Operations Affecting State Dependent Valuation Learning

Experiment 4.1 used the autoshaping paradigm to assess the acquisition of food motivated pecks to a stimulus at two different levels of bodyweight. Performance was analysed by examining activity levels (location and number of pecks). Overall it was found that the hens in the 75% of free-feeding bodyweight group exhibited higher number of pecks and made more pecks to the black screen and near to the stimuli than those maintained at 95% of free-feeding body weight. However, both groups acquired the pecking response over a similar number of CS-US presentations. This increase in behaviour when hens were maintained at lower bodyweights could be indicative of MOs affecting the species-specific behaviour of pecking, regardless of the response-reinforcer contingency, providing evidence for the behaviour-altering, but not the value-altering effect. Experiment 5.1 proposed to investigate the value-altering effect by examining whether hens maintained at the same bodyweights as in Experiment 4.1 would show a differential preference for neutral stimuli paired with pre-feeding.

Recently researchers have examined the relationship between MOs and preference for basic stimuli. For example, Lewon and Hayes (2015) investigated the effect of the magnitude of the food deprivation MO on free-operant preference in mice. Lewon and Hayes found that the mice demonstrated a preference for a stimulus that had been correlated with high deprivation conditions over a stimulus that had been correlated with low deprivation conditions.

State Dependent Valuation Learning (SDVL) is a term used to describe such preferences (Aw, Holbrook, Perera, & Kacelnik, 2009). Aw et al. (2009) explain that the idea behind SDVL is that when a subject becomes acquainted with a novel reward, it acquires two forms of “knowledge”. The first knowledge refers to the physical properties (e.g., amount, quantity, location, temporal properties) of the reward. The second

knowledge refers to learning about the benefits accrued from these outcomes under the specific circumstances they occur. Aw et al. (2009) explain that when a subject is faced with a choice between alternatives both kinds of “knowledge” come into play, and both can strengthen and both can compete with each other. They state that this knowledge can lead to the violation of simple optimality predictions. For example, animals have preferred options that have been associated with greater effort in the past (e.g. Kacelnik & Marsh, 2002). Animals such as starlings and locusts have been shown to prefer an option leading to longer delays to food, if this option has a history of having been encountered under greater need (Pompilio & Kacelnik, 2005).

Lewon and Hayes (2015) state that while SDVL analysis offers an account of preference as a function of organismic energetic “states”, the “states” held to be responsible for preference are not the variables being measured in SDVL procedures. The preferences are dependent on MOs of varying magnitudes (e.g., varying food deprivation). They state that any such measurement of organismic “states” will be a function of the way in which food deprivation is imposed.

Lewon and Hayes (2015) posited that research further testing SDVL can be carried out by assessing preferences for stimuli correlated with reinforcers under differential MOs. This can be achieved in the laboratory by manipulating the water or food deprivation levels of subjects prior to training sessions and correlating one stimulus (e.g., lights, tones) with water or food delivery under low deprivation conditions and another stimulus with water or food delivery under high deprivation conditions. Preference testing is carried out after the procedure whereby response alternatives produce either stimulus that has been correlated with the reinforcer under either low or high deprivation conditions. The measure of preference taken is the proportion of total responses on the alternative that produces one of the stimuli relative to the proportion of responses on the other alternative.

Existing research using similar procedures has produced mixed results. For example, Brown (1956) studied the effects of high and low “drive” (high and low MOs) on three phases of the secondary reinforcement process: acquisition, instrumental learning, and extinction,

with rats. Brown found that altering “drive” (32 hr water restriction versus eight hr water restriction) during instrumental learning sessions, did not have an effect on subsequent responding (e.g., there was no effect on the number of responses made during extinction sessions). Hall (1956) also found that the strength of “drive” during the time a neutral stimulus acquired its reinforcing power had no effect on the strength of the secondary reinforcer. However, both studies found that the strength of “drive” affected performance. Rats with a “high drive” responded more than rats with a “low drive”.

Despite early studies not finding a consistent preference for a stimulus that had been correlated with reinforcers under high deprivation conditions, more recent studies have suggested that subjects do appear to prefer stimuli correlated with reinforcers under high deprivation conditions. Marsh (2004), Pompilio (2006), Vasconcelos and Urcuioli (2008) and Aw et al. (2009) have demonstrated this finding with starlings, locusts, pigeons and fish respectively.

Lewon and Hayes (2015) pointed out that although this published research exists there are some methodological issues that require further investigation. They state that Marsh (2004), Pompilio et al. (2006), and Aw et al. (2009) all utilised preference test procedures where reinforcement was delivered following each trial. Whilst avoiding extinction these procedures introduce a confounding variable in that whichever the choice the subject makes first becomes correlated with more reinforcement than the other. A second methodological issue is that studies published prior to Lewon and Hayes (2015) did not include a baseline measure of preference. This means inherent biases for the stimuli correlated with the high and low deprivation conditions have gone unmeasured. A third methodological issue is the discrete trial tests for preference used in the aforementioned experiments. Lewon and Hayes points out that by using a discrete trial test the responses are constrained in that subjects can only respond once per choice trial offered. Lewon and Hayes suggested that by using a free-operant preference test whereby both stimuli are made available simultaneously, this may reveal more about the extent to which organisms prefer stimuli correlated with reinforcement under high deprivation levels.

Lewon and Hayes (2015) expanded the SDVL literature by testing for preference under extinction, at baseline, and post stimulus deprivation/correlation sessions. As stated earlier, they found that mice demonstrated a preference for a stimulus that had been correlated with high deprivation conditions over a stimulus that had been correlated with low deprivation conditions. However, they also found that nearly all subjects engaged in higher rates of responding under high food deprivation conditions during deprivation/correlation sessions. The higher rates of responding translated into consistently shorter delays to reinforcement during high deprivation sessions for most subjects. They suggested that future studies should investigate controlling delay explicitly to determine if preference for high deprivation stimuli is due to shorter delays to reinforcement.

Lewon and Hayes (2015) suggested that as MOs are easily quantified and manipulated, that further study of the SDLV phenomenon could be pursued by studying functional relations between varying magnitude of MOs for reinforcers and preference for stimuli correlated with those reinforcers. Lewon and Hayes suggested that as all recent studies have utilised the same method for varying deprivation (depriving animals of food for a set period of time) that future research could examine SDVL by using different methods, e.g., reducing bodyweight.

The aim of the current study was to investigate whether relative preference for stimuli would change depending on being correlated with different MO conditions: high deprivation (no pre-feeding), and low deprivation (pre-feeding), when subjects were maintained at either 75% or 95% of free-feeding bodyweight. Therefore, this study will investigate whether the effects of manipulating two MOs will be additive. It was hypothesised that hens would demonstrate a preference for stimuli paired with high deprivation conditions (no pre-feeding), and that hens maintained at the lower bodyweight would demonstrate a greater preference. It was also expected that hens maintained at a lower bodyweight would have higher response rates, which may lead to pre-feeding having a greater effect at changing preference for a stimulus paired with high deprivation (no pre-feeding), if higher response rates

meant that reinforcers paired with no pre-feeding were earned faster for the 75% hens than for the 95% hens.

Method

Subjects

Ten hens (*Gallus gallus domesticus*) numbered 1-1 – 1-5 and 3-1 – 3-5 were used as subjects. These hens were randomly allocated to four groups for the purpose of counterbalancing experimental sessions. Group 1 consisted of Hens 1-2 & 1-4; group 2 consisted of Hens 3-1, 3-2, & 3-4; group 3 consisted of Hens 1-1, 1-3, and 1-5; and group 4 consisted of Hens 3-3 and 3-5.

The hens were aged one-year old at the beginning of the experiment and were brown shavers. The hens had been previously autoshaped to peck white stimuli presented on a screen. Throughout the course of the experiment Hens 1-1 – 1-5 were maintained at 75 ±5% of their 100% free-feeding body weights, and Hens 3-1-3-5 were maintained at 95 ±5% of their 100% free-feeding body weights. To aid in the maintenance of the hens' weights, hens were fed NRM Peck'n'Lay commercial laying pellets outside of experimental sessions if necessary. Oyster grit and vitamins were given to the hens once weekly. Water was available ad libitum via nipple feeders located in the hens' cages. Hens were housed individually in custom built cages measuring 620-mm high by 790-mm wide by 610-mm deep. Each cage had wire sides and floor. Lights were on a 12 hr light / dark cycle (06:00 hr – 18:00 hr). Ethical approval for this research was gained from the University of Waikato Animal Ethics Research Committee (protocol number 961).

Apparatus

The experimental chamber measured 600-mm high x 570-mm wide x 450-mm deep. A white house-light in the centre of the ceiling was activated at the beginning of each session and terminated at the end to facilitate filming. Two 50-mm x 50-mm openings on the lower edge of the front wall allowed access to laying pellets (NRM Peck'n'Lay) placed in a hopper. An infrared beam inside the magazine recorded movement of the hens' heads in and out of the hopper. The front wall of the chamber

housed a computer monitor (Dell 19” flat screen) onto which two white circles 30-mm in diameter (one on the left side of the screen and one on the right side) were illuminated against a black background. Pecks made to the white circles were categorised as effective pecks. When an effective peck was made the hopper operated. Pecks to the other parts of the screen were either recorded as a near miss, if it was made to an area of 20 mm near to any part of the white circle, or as a black peck, if it was made to any other part of the black screen; both of which would not operate the hopper. The hopper could also be operated manually using a button located outside the experimental chamber. Pecks of all types and their locations were recorded using a customised computer program. The left side of the chamber was made of clear plastic, and a high-performance camera (GoPro® Hero 3 Black) was fixed to the exterior. All sessions were filmed in the WVGA setting, which recorded in 240 fps. Black plastic covered the clear plastic side of the chamber to eliminate extraneous light.

Procedure

Pre-training

Prior to beginning the experiment proper, the hens were exposed to a training condition. As hens had already been trained to peck the white stimuli, shaping was not necessary. In this condition, the hens worked on a concurrent VR-10 VR-10 schedule. During these sessions, the two white stimuli would appear, one on the left and one on the right side of the black screen. For each alternative, the first peck to a white stimulus after an average of 10 pecks on that stimulus activated the hopper and produced 1.5-s access to the reinforcer. Reinforcers were programmed so that each VR counter ran independently of the other. Sessions lasted for up to 40 min had elapsed or 40 reinforcers had been delivered in total, whichever was sooner; at this point the white stimuli would vanish from the screen and the chamber would darken. The hens were exposed to 25 VR-10 sessions in total and each session was conducted under approximately 23 hours of food deprivation with hens at their respective bodyweights.

Baseline preference test

Following pre-training, a baseline preference test was conducted. The baseline preference test session was 5 min in duration and was conducted when subjects had been deprived of food for 23 hr. Both white stimuli were illuminated, and subjects were free to respond on either alternative. Responses on the left stimuli produced a 3-s presentation of a green stimulus on a VR-10 schedule. Responses on the right stimulus produced a 3-s presentation of a red stimulus on a VR-10 schedule. No reinforcers were delivered at any point during the test (i.e., the test was performed under extinction conditions). The number and proportion of responses on either white stimulus was recorded. Prior to this baseline preference test, the subjects had not been exposed to either the red or green stimulus.

Deprivation/correlation sessions

Following the baseline preference test, subjects were exposed to 20 deprivation and correlation sessions. Ten of these sessions were conducted when subjects were deprived of food for 23 hr (high deprivation sessions) and 10 were conducted when subjects were pre-fed 40 cc wheat, 10 minutes prior to experimental sessions (low deprivation sessions). During high deprivation sessions (no pre-feeding), one of the stimuli (either left or right depending on group, counterbalanced across the two groups) was illuminated white and responses on that apparatus produced a 3-s presentation of either the red or green stimulus (depending on group, counterbalanced across the two groups) followed by the delivery of food on a VR-10 schedule. During low deprivation sessions (pre-feeding), the stimuli associated with food delivery were switched (e.g., if a peck to the white stimulus on the left side illuminated green during high deprivation sessions, a peck to the white stimulus on the right side would illuminate red during low deprivation sessions). Each session was terminated following 40 food deliveries. Note, however, that for each subject, the side/stimulus correlated with food in high deprivation sessions and the side/stimulus correlated with food in low deprivation sessions remained the same throughout all deprivation and correlation sessions. The order of sessions (high versus low deprivation) was also

counterbalanced across groups and arranged in a pseudorandom fashion such that no more than two consecutive sessions of either type (either high or low deprivation) occurred in succession, as per Lewon (2015). The order of sessions for each group is listed in Table 5.1.

Table 5.1

Order of sessions for deprivation and correlation phases, side/stimulus assignments for low/high deprivation sessions.

Experimental phase	Group 1	Group 2	Group 3	Group 4
	75% 1-2 & 1-4	95% 3-1, 3-2 & 3-4	75% 1-1, 1-3 & 1-5	95% 3-3 & 3-5
	Stimulus Lit	Colour	Stimulus Lit	Colour
High deprivation (no-pre-feeding) (H)	Left	Green	Right	Red
	Right	Red	Left	Green
Low deprivation (pre-feeding) (L)				
Session order	LHHLHLLHLHHHLHLL HLH		HLLHLHHLHLHLLHLHH LHL	

Post-training preference test

Following 10 deprivation and correlation sessions, the subjects were exposed to a post-preference test that was identical to the baseline preference test described above. As with the baseline preference test, subjects were deprived of food for 23 hr prior to this test.

Data analysis

For all statistical analyses described below, the number of responses made for either alternative by a particular subject was divided by the total number of responses made by that subject during the test to obtain proportions of responses for either alternative. These proportions were analysed as quantitative data and t-tests were performed on all subjects' proportion data to determine if performance differed significantly from indifference. Table 5.2 shows the number of responses made to the white stimuli to produce the high and low deprivation stimuli in baseline

and post-preference tests for each subject, as well as totals, means, and proportions and log ratios for each preference test.

Results

Raw data from all conditions are presented in Appendix D.

Training

Response rates (per s) during pre-training sessions were calculated by dividing the number of responses per total session time in seconds. Figure 5.1 presents the response rates on both the left and right side for the last 10 VR pre-training sessions for the 75% hens. Response rates were relatively consistent over both sides, for all hens in the 75% group, indicating that the hens did not have a bias for a particular side.

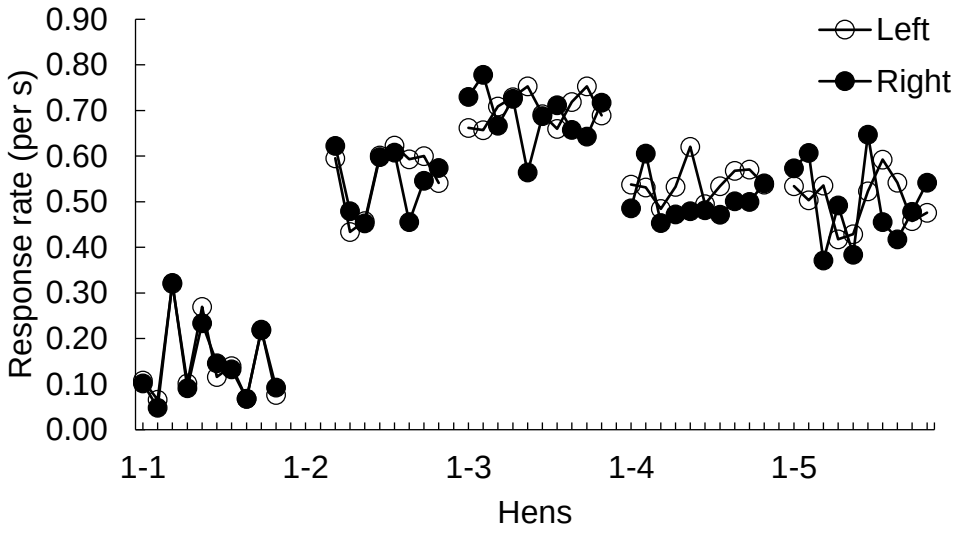

Figure 5.1. Response rates (per s) during the last 10 VR-10 VR-10 training sessions for both the left and right stimuli, for the 75% hens.

Figure 5.2 presents the response rates on both the left and right side for the last 10 VR pre-training sessions for the 95% hens. As can be seen on Figure 5.2, response rates were relatively consistent over both sides, for all hens, aside from Hen 3-4, in the 95% group, indicating that the hens did not have a bias for a particular side.

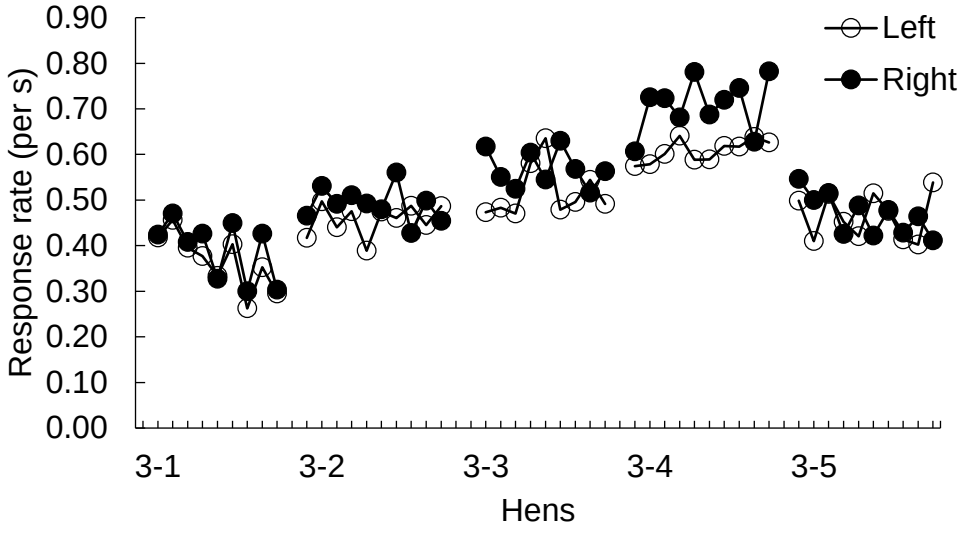

Figure 5.2. Response rates (per s) during the last 10 VR-10 VR-10 training sessions for both the left and right stimuli, for the 95% hens.

Baseline preference test

In baseline, a proportion of near .5 would be expected if there were no biases resulting from the different coloured stimuli. The proportion of responses, as well as the log ratios, made to produce the high deprivation stimulus by each subject in each preference test is shown in Table 5.2. As can be seen in Table 5.2, each hen had idiosyncratic proportions of responses made to these stimuli, aside from Hens 3-3 and 3-4 who both showed proportions of .5, indicating that they were indifferent between the two sides.

During the baseline preference test a mean proportion of .26 (*SD* = 0.21) of the 75% group's responses were made to the stimulus that would subsequently become the high deprivation stimulus. In order to compare results with Lewon and Hayes (2015), a t-test was carried out to determine if this proportion differed significantly from indifference. This proportion did not differ significantly from indifference $t(4)=-2.56$, $p = 0.06$. A log ratio of -.070 of the 75% group's responses were made to the stimulus that would subsequently become the high deprivation stimulus.

During the baseline preference test a mean proportion of .66 *SD* = 0.15) of the 95% group's responses were made to the stimulus that would subsequently become the high deprivation stimulus. In order to compare results with Lewon and Hayes (2015), a t-test was carried out to determine

if this proportion differed significantly from indifference. This proportion did not differ significantly from indifference $t(4)=-1.64$, $p = 0.20$. A log ratio of -.019 of the 95% group's responses were made to the stimulus that would subsequently become the high deprivation stimulus.

It was considered that preference shown during the baseline test may have been a function of a bias for either the left (green) alternative or the right (red) alternative. In order to compare results with Lewon and Hayes (2015), t-tests were carried out to assess whether there was a significant difference between indifference and either responding for the left (green) or right (red) alternative. The left (green) proportion $M = 0.40$, $SD = 0.31$ did not differ significantly from indifference ($t(9)=-1.25$, $p = 0.24$). The right (red) proportion $M = 0.60$, $SD = 0.21$ did not differ significantly from indifference ($t(9)=1.25$, $p = 0.24$).

Deprivation/correlation sessions

Figure 5.3 presents the mean response rates (calculated by dividing total session time by the number of responses) for all hens, to either the left or right stimuli during deprivation/correlation sessions. As can be seen on Figure 5.3 all of the 75% hens had higher response rates to the right stimuli (red) regardless of whether it was associated with high or low deprivation (no pre-feeding or pre-feeding conditions), and Hens 3-2, 3-3, and 3-5 (Group 2) of the 95% hens had higher response rates to the right stimuli.

Figure 5.4 presents the mean response rates (calculated by dividing total session time by the number of responses) for all hens to either the stimulus paired with pre-feeding or the stimulus paired with no-pre-feeding during deprivation/correlation sessions. As can be seen on Figure 5.4, the 75% hens had higher response rates overall than the 95% hens. Three out of five of the 75% hens had higher response rates to the stimulus paired with pre-feeding, and all of the 95% hens had higher response rates to the stimuli paired with pre-feeding, than for the stimuli not paired with pre-feeding.

Table 5.2

The responses to the white stimuli made in baseline and post-preference tests for each subject.

					Number of responses baseline preference test			Number of responses post-preference test			Proportion of high deprivation responses			Log ratios of high deprivation responses		
Weight	Group	Hen No	High	Low	High	Low	Total	High	Low	Total	Baseline	Post	Difference	Baseline	Post	Difference
75%	Group 3	1-1	Green	Red	10	45	55	5	55	60	0.18	0.08	-0.10	-0.74	-1.08	-0.34
75%	Group 1	1-2	Red	Green	43	28	71	37	19	56	0.61	0.66	0.06	-0.22	-0.18	0.04
75%	Group 3	1-3	Green	Red	20	48	68	6	33	39	0.29	0.15	-0.14	-0.53	-0.81	-0.28
75%	Group 1	1-4	Red	Green	7	79	86	79	8	87	0.08	0.91	0.83	-1.09	-0.04	1.05
75%	Group 3	1-5	Green	Red	9	69	78	31	43	74	0.12	0.42	0.30	-0.94	-0.38	0.56
95%	Group 2	3-1	Red	Green	54	11	65	54	19	73	0.83	0.74	-0.09	-0.08	-0.13	-0.05
95%	Group 2	3-2	Green	Red	52	26	78	55	13	68	0.67	0.81	0.14	-0.18	-0.09	0.08
95%	Group 4	3-3	Red	Green	42	42	84	67	5	72	0.50	0.93	0.43	-0.30	-0.03	0.27
95%	Group 2	3-4	Green	Red	45	40	85	75	8	83	0.50	0.90	0.40	-0.28	-0.04	0.23
95%	Group 4	3-5	Red	Green	47	13	60	34	17	51	0.78	0.67	-0.12	-0.11	-0.18	-0.07
	Totals				329	401	730	443	220	663	4.56	6.27	1.72	-4.46	-2.97	1.49
	Means				32.9	40.1	73.0	44.3	22.0	66.3	0.46	0.63	0.17	-0.45	-0.30	0.15
Means	75%				17.8	53.8	71.6	31.6	31.6	63.2	0.26	0.44	0.19	-0.70	-0.50	0.21
Means	95%				48.0	26.4	74.4	57.0	12.4	69.4	0.66	0.81	0.15	-0.19	-0.09	0.09

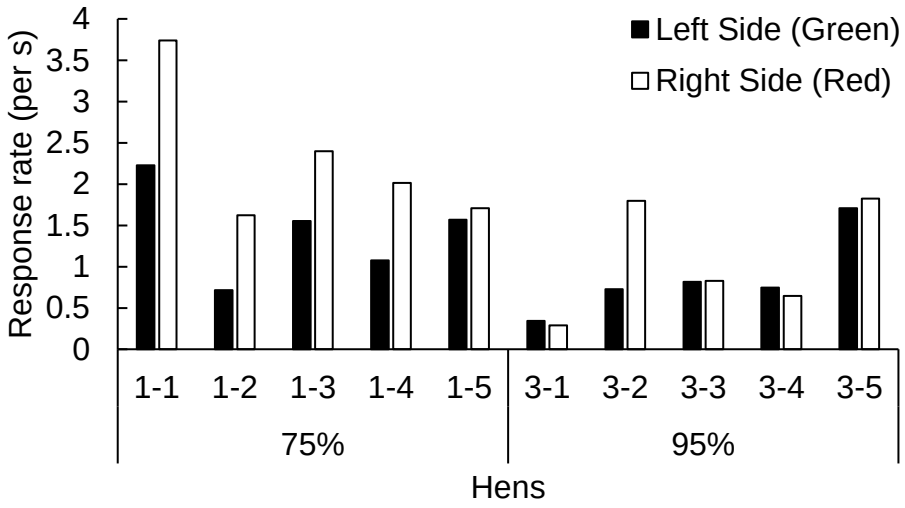

Figure 5.3. Mean response rates for all hens to the left and right stimuli during deprivation/correlation sessions.

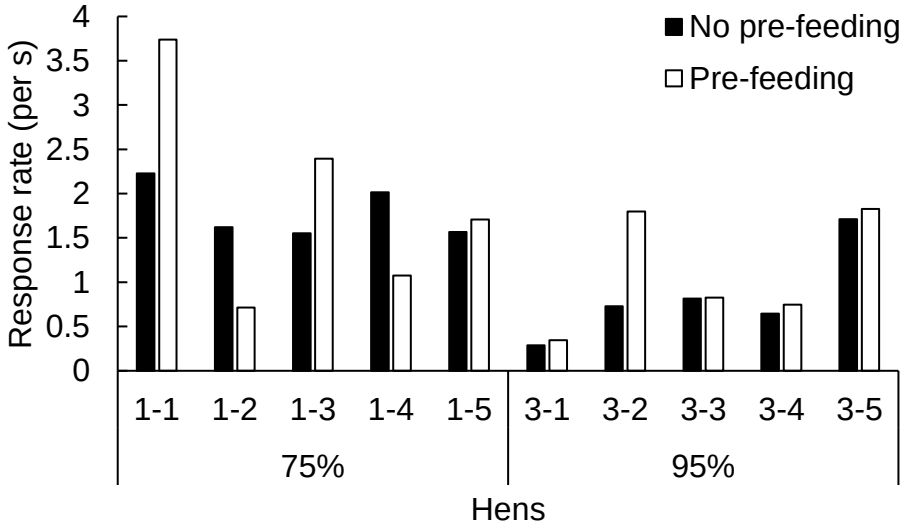

Figure 5.4. Mean response rates for all hens during no pre-feeding and pre-feeding conditions during deprivation/correlation sessions.

Figure 5.5 presents the location of the pecks during deprivation/correlation sessions for sessions 1-20 for Hen 1-1 (75% group). When the stimulus was on the left side, Hen 1-1 was not pre-fed (H); when the stimulus was on the right side, Hen 1-1 was pre-fed (L). The order of

the sessions was as follows: HLLHLHHLHLHLLHLHHLHL. As can be seen on Figure 5.5, when deprivation was high (no pre-feeding), the pecks tended to be scattered over both sides of the screen. Figure 5.6 presents the location of the pecks during deprivation/correlation sessions for sessions 1-20 for Hen 3-1 (95% group). When the stimulus was on the left side, Hen 3-1 was pre-fed (L); when the stimulus was on the right side, Hen 3-1 was not pre-fed (HR). The order of the sessions was as follows: LHHLHLLHLH LHHLHLLHLH. As can be seen on Figure 5.6, when deprivation was high (no pre-feeding), the pecks tended to be scattered slightly more than when deprivation was low (no pre-feeding). Overall, the pecks of Hen 3-1 were located closer to the stimulus and were less scattered than the pecks of Hen 1-1. Figures presenting the location of pecks during deprivation/correlation sessions for Hens 1-2 and 1-5 are shown in Appendix D. As can be seen on these figures, Hens 1-3 and 1-5 showed a similar pattern to Hen 1-1. Hens 1-3 and 1-4 had less scattered pecks. Hens 3-2 – 3-5 showed similar patterns of pecking to Hen 3-1 and only pecked on the side that the stimulus was active on.

Post-training preference test

As shown on Figure 5.7, during the post-training preference test a mean proportion of .44 (*SD* = 0.34) of the 75% group's responses were made to the high deprivation stimulus. A proportion of .81 (*SD* = 0.11) of the 95% group's responses were made to the high deprivation stimulus. These results showed a mean shift in proportions of responses of .19 and .15 respectively. The shift in proportions of each subject's responses on the high deprivation alternative from the expected shift of zero were analysed using t-tests. The shift in proportion from baseline was not statistically significant when compared the expected shift of zero for the 75% group ($t(4)=1.07$, $p = 0.34$), or the 95% group ($t(4)=1.30$, $p = 0.26$).

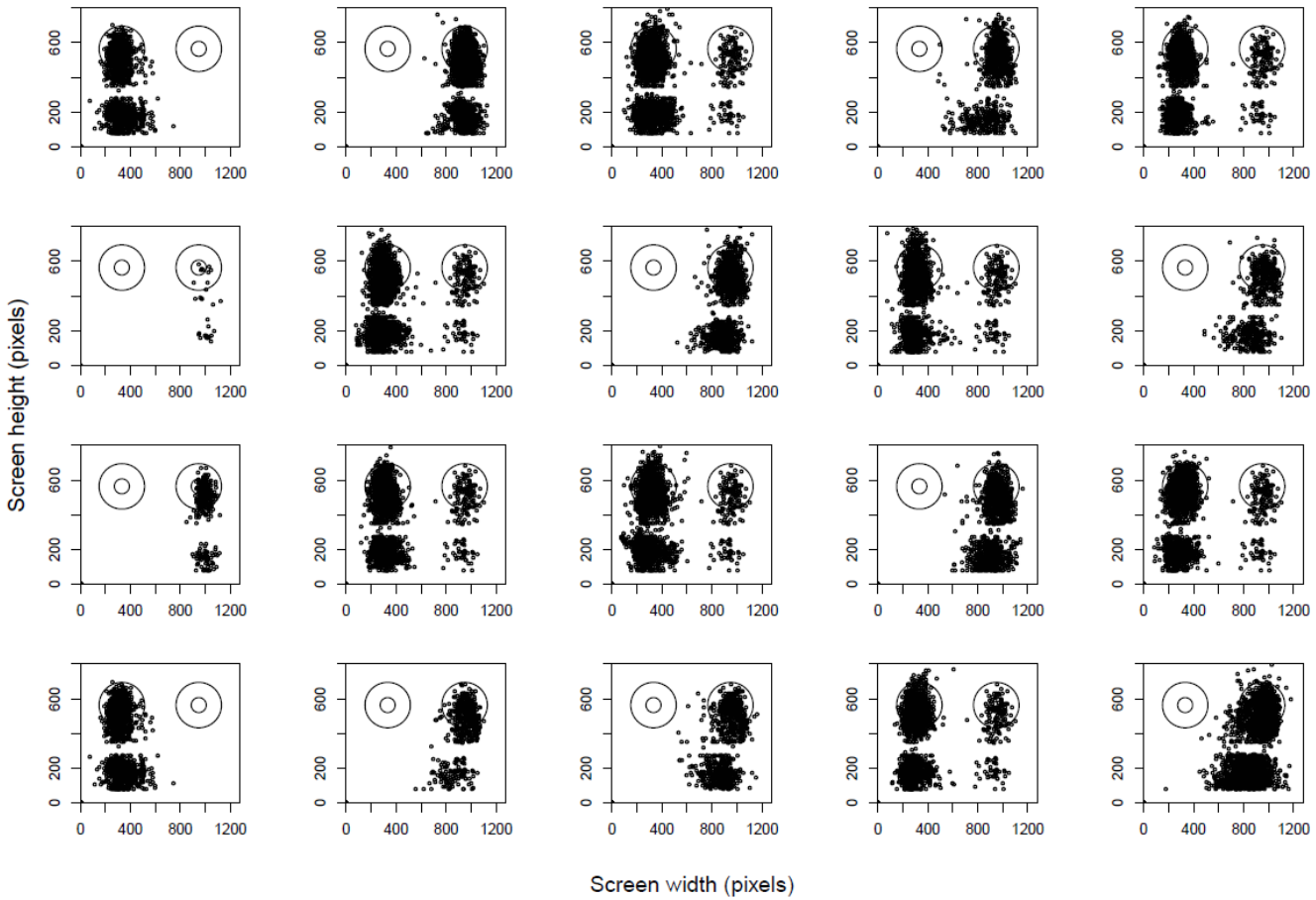

Figure 5.5. The location of the pecks during deprivation/correlation sessions for sessions 1-20 (left panel, 1 – 4, second from left panel 5 – 8, middle panel 10 – 12, second from right panel 13 – 16, and right panel 17 – 20) and sessions 6-10 for Hen 1-1.

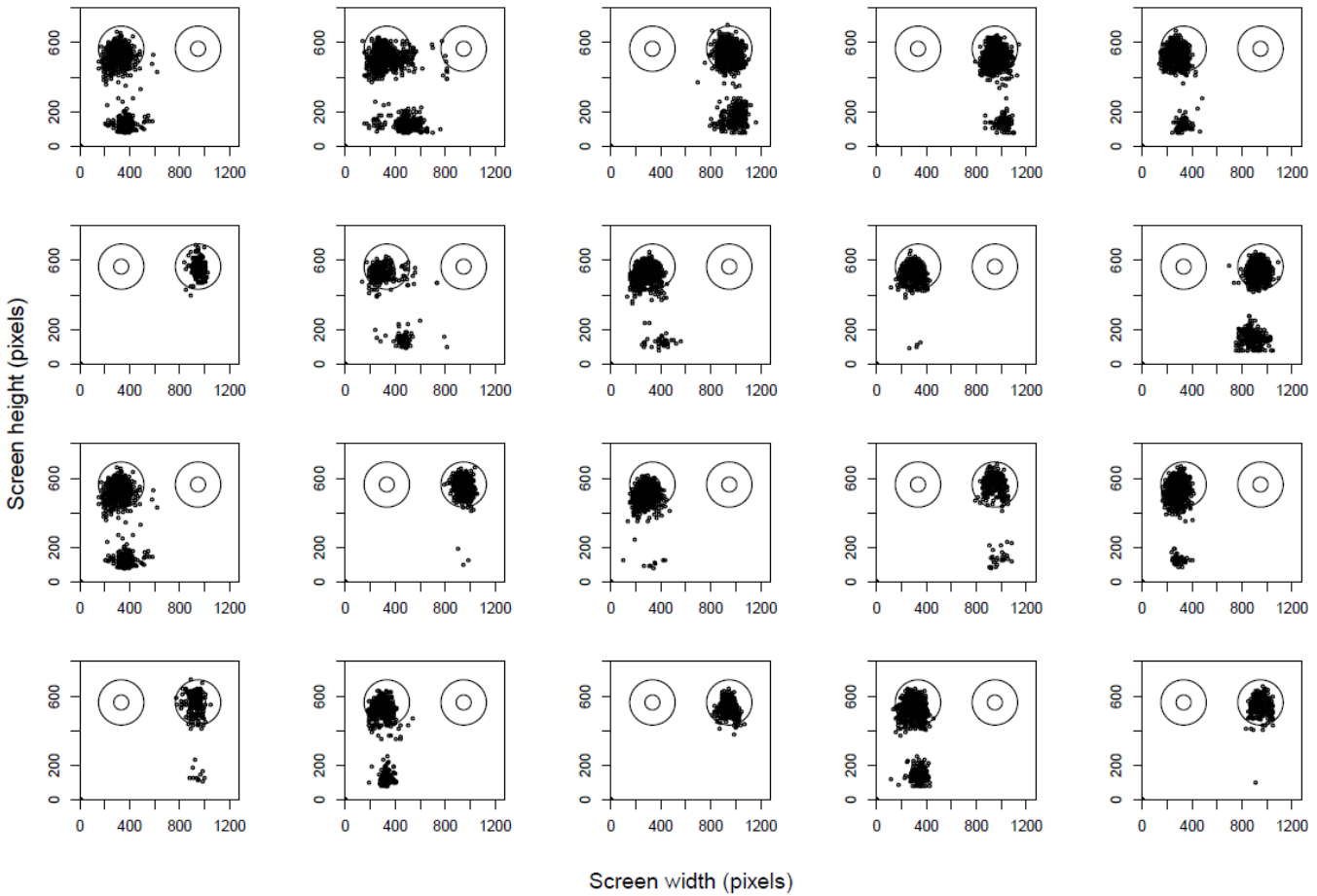

Figure 5.6. The location of the pecks during deprivation/correlation sessions for sessions 1-20 (left panel, 1 – 4, second from left panel 5 – 8, middle panel 10 – 12, second from right panel 13 – 16, and right panel 17 – 20) and sessions 6-10 for Hen 3-1.

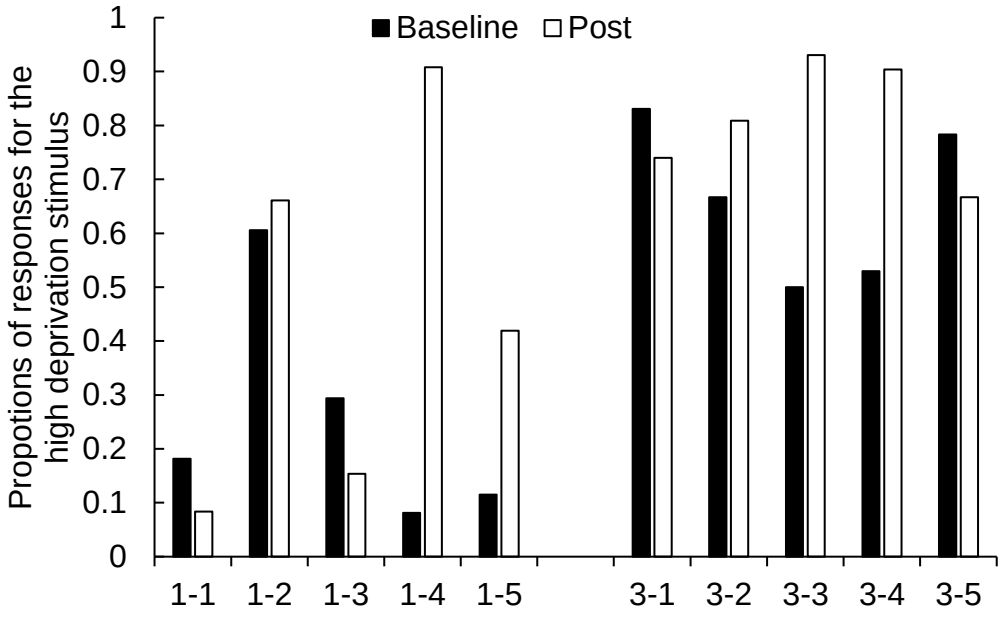

Figure 5.7. Proportions of responses for the high deprivation stimulus made during baseline and post-preference tests.

Figure 5.8 shows the log ratios of the responses made to the high deprivation stimulus during baseline and post-preference tests. As can be seen on Figure 5.8 the log ratios display a very similar pattern to the one shown on Figure 5.7, except the differences between baseline and post are less extreme. Hen 3-3 has a log zero for baseline so this is not shown on the figure.

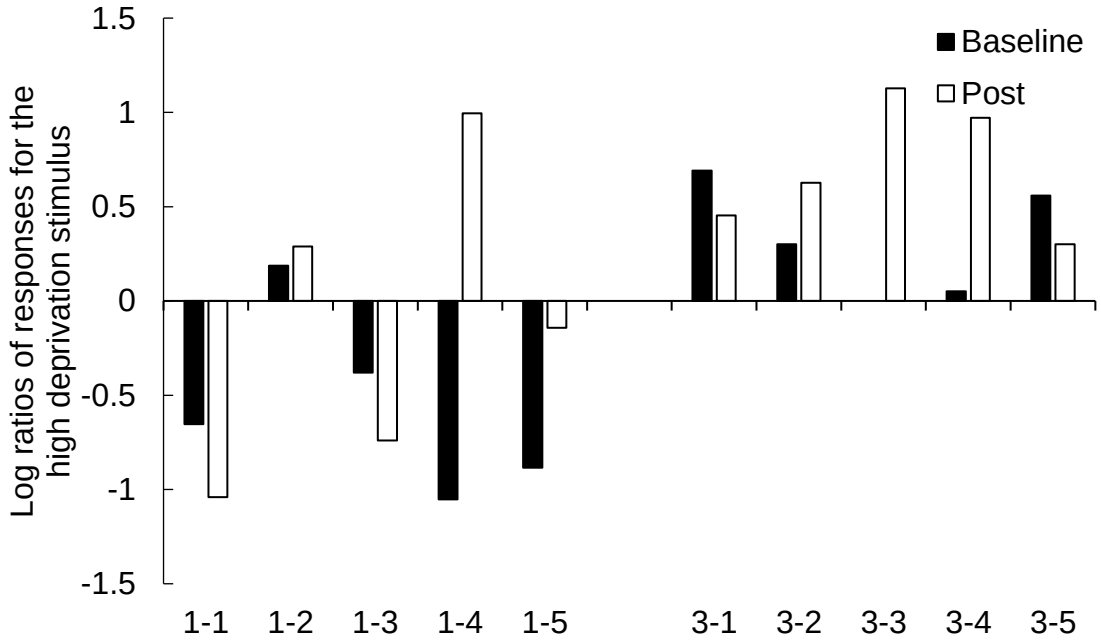

Figure 5.8. Log ratios of responses for the high deprivation stimulus made during baseline and post-preference tests.

Discussion

The purpose of the current study was to investigate relative preference for stimuli correlated with different MO conditions of high deprivation (no pre-feeding) and low deprivation (pre-feeding) when subjects were maintained at either 75% or 95% of free-feeding bodyweight (also MO conditions). Therefore, this study extended previous research in this area by investigating the interactions between manipulating two concurrent MOs, pertaining to the same reinforcer. It was expected that hens would demonstrate a preference for stimuli paired with high deprivation conditions (no pre-feeding), and that hens maintained at the lower bodyweight would demonstrate a greater preference. It was also expected that hens maintained at a lower bodyweight would have higher response rates, which may lead to pre-feeding having a greater effect at changing preference for a stimulus paired with high deprivation (no pre-feeding), if higher response rates meant that reinforcers paired with no pre-feeding were earned faster for the 75% hens than for the 95% hens.

It was also found that 6/10 hens demonstrated a greater proportion of responses for stimuli paired with high deprivation conditions, over stimuli paired with low deprivation conditions, than in baseline. These mixed results are in line with the previous literature cited in the introduction (Aw et al., 2009; Lewon & Hayes, 2015; Marsh, 2004; Pompilio et al., 2006, Vasconcelos & Urcuioli, 2008).

It is important to note that although 6/10 hens demonstrated a shift in proportions of responses to the high deprivation stimulus, 8/10 had proportions that varied widely during baseline, indicating that the preference for each side was idiosyncratic between hens and that there may be inherent biases individual to each hen. Lewon and Hayes (2015) also found idiosyncratic biases during baseline. Baum (1974) pointed out that the GML allowed assessment of bias in choices between two alternatives. Analyse of bias based on the GML use the log ratios of responses on the two alternatives. Response bias may occur when there are two alternatives that appear to be similar but are not. For example, responding on one side may require more effort than responding on another side, due to asymmetry in the organism’s musculature or nervous

system. Baum (1974) also suggested that inherent colour preferences may account for bias. Colour bias was ruled out in this experiment as when the proportions of responses for the left (green) and right (red) stimuli where subjected to t-tests no significant colour bias was found. However, proportions are bounded by 0 and 1 do not form an equal interval scale but log ratios are not bounded and the log of the ratio of X is equally far above 0 and the log of the ratio of 1/X is below 0. Thus, in addition to the proportions used by Lewon and Hayes (2015), log ratios were calculated in this experiment. The log ratios (Figure 5.8) show that the change in responding for the stimulus paired with high deprivation (no pre-feeding) between baseline and post-preference tests was less extreme for the 95% group, than for the 75% group. This indicates that the 75% group were possibly more prone to have an inherent bias at baseline, and therefore show a greater degree of change in preference at post-preference testing.

Similar to Experiment 4.1, hens that were maintained at 75% tended to have pecks more scattered across the screen than hens maintained at 95%; this was most evident for Hens 1-1, 1-3, and 1-5. In addition, when the hens were not pre-fed, the pecks for both bodyweights were more scattered than when the hens were pre-fed; this was true for both the 75% and 95% hens, however, it occurred to a greater degree for the 75% hens.

In an extension to previous research, it was found that the hens maintained at 75% of free-feeding bodyweight had a slightly larger shift in preference from baseline to post-preference test, than hens maintained at 95%. These data provide evidence that having more than one MO in place at the time of exposure to a reinforcer may have additive effects. However, 8/10 subjects had higher rates of responding under no pre-feeding conditions during deprivation/correlation sessions. Since VR schedules were employed, in which the delay to reinforcement depends on rate of response during the deprivation/correlation sessions, higher rates of responding translated into consistently shorter delays to reinforcement during no pre-feeding sessions. Lewon and Hayes (2015) found the same pattern evident in the response rates during deprivation/correlation sessions. Lewon and Hayes proposed that in their experiment it is

possible that the preference for the high deprivation stimulus observed was a function of the fact that, although the tones correlated with food delivery under high and low deprivation conditions signalled the same 3-s delay to the delivery of food, the illumination of one of the two nose poke apparatus (right or left, depending on group and counterbalanced across subjects) during high deprivation/correlation sessions was correlated with consistently shorter delays to reinforcement due to higher response rates, thereby arranging the conditions under which preference for that response alternative was established. In summary, these results provide further evidence that altering MOs can change species-specific behaviour that may offer explanations for observed phenomenon such as SDVL.

There are some limitations to the study. The free-operant baseline and post-preference tests were carried out over only one session, under extinction conditions. However, as stated in the introduction to this thesis, carrying out testing under extinction conditions is beneficial for investigating the behaviour-altering effect of the MO. In future studies other, established methods for assessing preference could be used, such as concurrent chains (e.g., Squire & Fantino, 1971) or concurrent schedules (e.g., Sumpter, Foster, and Temple, 2002). Another shortcoming is that as pointed out by Lewon and Hayes (2015), all prevailing research (and this study) have utilised food deprivation and food reinforcement to investigate this phenomenon. Future studies could utilise manipulations of MOs pertaining to different reinforcer types, such as water, drugs, or removal of aversive stimulation, and could utilise VI schedules and control rate (and average delay) more closely than using VR schedules.

Future investigations might consider measuring controlling delay explicitly to determine if preference for high deprivation stimuli is due to shorter delays to reinforcement. In summary, more research is needed to ascertain the generality of the phenomena and to confirm that obtained results are robust and not products of the procedures utilised.

Chapter 6 : BODYWEIGHT AND PRE-FEEDING AS MOTIVATING OPERATIONS EFFECTS ON CONCURRENT SCHEDULE PERFORMANCE

Experiment 6.1: Bodyweight as a Motivating Operation for Concurrent Schedule Responding

Experiment 4.1 investigated the effect of bodyweight on autoshaping and found that higher numbers of effective pecks were made by hens maintained at 75% free-feeding bodyweight than hens maintained at 95% (different MO conditions). There were also higher levels of ineffective pecks in the 75% group. These higher numbers of pecks overall could be argued to be evidence of the behaviour and value-altering effects. Experiment 5.1 investigated relative preference for stimuli correlated with different MO conditions, high deprivation (no pre-feeding) and low deprivation (pre-feeding), when subjects were maintained at either 75% or 95% of free-feeding bodyweight (also different MO conditions). The results showed that 6/10 hens demonstrated an increased preference for the stimulus paired with high deprivation conditions (no pre-feeding) when measured by log ratios of responses, and that they also had faster response rates on this stimulus. Overall, the 75% bodyweight hens had faster response rates than the 95% hens (as in Experiment 4.1), and 8/10 hens responded faster on the stimulus that was paired with no pre-feeding. Hens that were not pre-fed had more scattered pecks than when the hens were pre-fed; this was true for both the 75% and 95% hens, but this occurred to a greater degree in the 75% hens.

Experiment 6.1 proposed to investigate the relation between preference and bodyweight further, by examining the effect of altering bodyweight on stable concurrent schedule performance. One aim was to see how bodyweight affected both concurrent schedule response rates and the distribution of responding between the schedules when the reinforcer rates were varied.

Concurrent schedules and the Generalised Matching Law

Much research has been done on the subject of choice behaviour using concurrent schedules. This has shown that concurrent schedule performance can be quantified. One of the simplest analyses of the relation between the ratios of behaviour and the ratios of reinforcement rate has been termed the Generalised Matching Law (GML) (Baum, 1974). It is important to note that there are alternative models for explaining choice behaviour (e.g., the contingency discriminability model; Davison and Jenkins, 1985). The logarithmic transformation of the GML expressed mathematically is:

$$\log\left(\frac{B_1}{B_2}\right) = a\log\left(\frac{r_1}{r_2}\right) + \log c, \qquad (1)$$

where *B* is the measure of behaviour (i.e., the time spent responding or the number of responses) and *r* is the rate of obtained reinforcers on alternatives 1 and 2 (e.g., Davison & Jones, 1995; Sumpter et al., 2002). Two deviations from systematic matching can be assessed: sensitivity and bias. The parameter *a* is termed sensitivity to reinforcement and it measures the change in the behaviour ratio in relation to the change to the reinforcement rate ratio. A value of *a* less than 1.0 is termed undermatching and the response ratio is less extreme than predicted by strict matching. When *a* is more than 1.0 this is termed overmatching and the response ratio is more extreme than predicted by strict matching. The parameter log *c* is termed inherent bias and it represents the proportional preference for one alternative over the other alternative that is independent of reinforcement-rate changes. When log *c* = 0, no bias is evident. Figure 5.1 from Poling, Edwards, Weeden, and Foster (2011) shows what regression lines fitted to hypothetical data would look like when demonstrating matching, undermatching, overmatching, and bias.

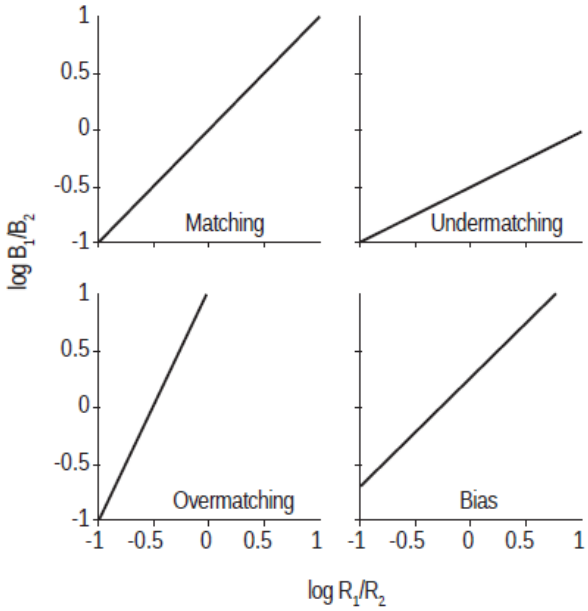

Figure 6.1. Regression lines demonstrating matching, undermatching, overmatching, and bias. These lines describe the relative allocation of responses or time to two alternatives (B1 and B2) as a function of the relative number of reinforcers earned under those alternatives (R1 and R2). Poling, A., Edwards, T. L., Weeden, M., & Foster, T. M. (2011). The matching law. *Psychological Record, 61*(2), 313-322. Reprinted with permission.

Baum (1979) inspected sensitivity parameters from large number of data sets produced by two researchers and found sensitivity differed systematically between the two sets (the values of *a* were near 0.8 for Davison and near 1.0 for Baum) (Baum, 1979; Davison & McCarthy, 1988). Baum proposed that procedural variables, such as the type of VI schedule, change of delay duration, and deprivation level of the subjects, may have contributed to these differences. Baum suggested several factors that could lead to sensitivity values less than 1.0 (undermatching). These included asymmetrical pausing (which would affect response allocation, but not time allocation as typically measured), idiosyncrasy of preference, and patterns of changeover responding.

Since Baum (1979) there have been a large number of papers published that address the subject of concurrent schedule choice behaviour (e.g., Boutros, et al., 2011; Davison & McCarthy, 1988). The result is an extensive body of research showing that the GML can be consistently and reliably applied to describe concurrent schedule data obtained across species (e.g., monkeys, Lau & Glimcher, 2005; rats,

MacDonall, 1988; humans, Horne & Lowe, 1993; and goats, Foster, Matthews, Temple & Poling, 1997), across response types (e.g., keys and levers, McSweeney, Weatherly, & Roll, 1995; running wheels, Belke & Belliveau, 2001), and across reinforcer types (e.g., cocaine and food, Anderson, Velkey & Woolverton, 2002). However, when reinforcer magnitude or delay of reinforcement has been manipulated, more inconsistent results have been obtained (e.g., Davison & Hogsden, 1984).

Inconsistent results have also been obtained when MOs related to the reinforcer have been manipulated. A common way to manipulate MOs in laboratory studies using pigeons and rats is to maintain them at 80% of their free-feeding bodyweights. Under these conditions the pigeons and rats may receive all of their food in a brief period of the day and are never allowed to satiate within an experimental session (Baum, 1972); this means that performance is stable. What happens when bodyweight is allowed to vary is less understood, however, several studies have investigated the effect of altering bodyweight on schedule performance using concurrent VI VI schedules and multiple VI VI schedules.

McSweeney (1974) found that manipulating bodyweight has an effect on variability of responding, under concurrent VI 1-min VI 4-min schedules, that is independent of its effect on mean rate of responding. Specifically, higher bodyweights produced more variability in Inter Response Times (IRTs). McSweeney (1975) examined the changes that variations in bodyweight produce in the absolute and relative rates of responding on several concurrent VI VI schedules (VI-1 min, VI-4 min; VI-2 min, VI-30 s; VI-1.5 min, VI-6 min; and VI-6 min, VI-8 min). She found that although absolute response rate varied according to the bodyweight as expected (overall rate was slower at higher bodyweights), relative rates of responding equalled the overall rates of reinforcers on all schedules at all bodyweights. Similarly, Wald and Cheyney (1975) also found that on concurrent VI VI schedules, as bodyweight increased relative response rate and relative time spent in the denser schedule remained constant, while post-reinforcement pauses increased.

Herrnstein and Loveland (1974) and Charman and Davison (1983) found that sensitivity approached strict matching (a = 1.0) as subjects working on multiple VI VI schedules were made less food deprived, and

that absolute response rates were higher at lower bodyweights. They suggested that decreasing food deprivation decreases the value of the food reinforcer rates and could change the amount of extraneous reinforcers. Extraneous reinforcers are said to be reinforcers available in the environment, uncontrolled by the experimenter, for example, an animal pressing a lever for food might pause for a drink of water.

Elliffe and Davison (1996) investigated the effects of deprivation and session duration on pigeons' multiple-schedule performance in a closed-economy. They found different results to Charman and Davison (1983) and Herrnstein and Loveland (1974) in that GML sensitivity decreased from overmatching (rather than strict matching) to undermatching values typical of conventional multiple schedules when food deprivation was increased by decreasing session duration, but not when deprivation was increased by decreasing overall reinforcer rate. Sensitivity also increased from undermatching to overmatching as session duration increased from 100 min to 24 hr, while deprivation was held constant by decreasing overall reinforcer rate. They suggested that the results could be understood in terms of increasing the value of extraneous reinforcers (as emphasised by models developed by Herrnstein, 1970 and McLean and White, 1983), relative to food reinforcers as deprivation decreases or as the economy for the extraneous reinforcers becomes closed.

Changes in sensitivity as measured by the GML have also been found with varying genetic phenotypes. Buckley and Rasmussen (2012) investigated behavioural allocation with different densities and types of food reinforcement in obese and lean Zucker rats. Obese Zucker rats have impaired leptin signalling and have been used as a genetic model of obesity to determine behavioural and physiological mechanisms that contribute to obesity-related health problems (Buckley & Rasmussen, 2012). In the study, obese and lean Zucker rats were placed under three concurrent VI VI schedules of sucrose and carrot reinforcement. The reinforcer ratios were 5:1, 1:1, and 1:5. Allocations of responses to the alternatives were characterised using the GML. All rats showed a bias towards sucrose, and obese Zucker rats presented higher sensitivity to reinforcement rates than lean Zucker rats. This resulted in obese Zucker

rats being closer to strict matching providing evidence for genetic differences in bodyweight as an MO having an effect on sensitivity. One aim of the present study was to assess how bodyweight would affect sensitivity and response rate under these same concurrent schedules.

Bouts of responding on concurrent schedules

As stated above, changes in bodyweight can cause changes in response rates and the pattern of responding. Of interest is how these changes in response rates and patterns might affect concurrent schedule performance. As mentioned previously, VI schedules of reinforcement are commonly used in concurrent schedules of reinforcement. A VI schedule of reinforcement is identified by the arithmetic mean of the individual time intervals of which it is composed (Herrnstein, 1961). For example, in a single VI-20 s schedule, a reinforcer will be delivered after the first response is made after an average of 20 s has elapsed. On a VI schedule, it is possible for an animal to earn a consistent number of reinforcers per min, but the exact moment that the reinforcer will be delivered is unpredictable (Buckley & Rasmussen, 2012). In a concurrent VI VI schedule, two or more VI schedules are made available simultaneously via incompatible response manipulanda, allowing animals to choose between two reinforcers (Sumpter, Foster, & Temple, 2002).

Response bouts are often observed in VI schedules of reinforcement, whether programmed alone (e.g., Brackney, Cheung, Neisewander, & Sanabria et al., 2011; Conover, Fulton, & Shizgal, 2001; Shull, 2004), or concurrently with another VI schedule (e.g., Shull, 2011; Smith et al., 2014). Response bouts can be described as periods of engagement (emitting the measured behaviour) and disengagement (emitting the unmeasured behaviour), and emerge spontaneously when behaviour is allowed to occur at its operant level, unreinforced by the experimenter (Cabrera, Sanabria, Jiménez, & Covarrubias, 2013).

Response bouts have multiple parameters, each differentially affected by various experimental manipulations. For example, the rate at which bouts occur (the initiation rate) is highly effected by MOs (Brackney, Cheung, Herbst, Hill, & Sanabria, 2012; Shull, 2004). In contrast, response rate during a bout (the within-bout response rate) and the number of

responses in a bout (the bout length), are relatively unaffected by motivating operations but are highly sensitive to response requirements (Brackney et al., 2011; Shull et al., 2001).

Shull (2001) describes an illustrative example, e.g., imagine a food-deprived rat has been obtaining food pellets intermittently by nose-poking a lit key and the rate of poking has stabilised at 20 responses per min. To increase response rate, one could: (1) increase food deprivation; (2) increase the rate of the reinforcer by decreasing the VI schedule; (3) increase the taste quality of the reinforcer; (4) reduce the availability of alternative reinforcers; or (5) add a small FR or VR schedule requirement at the end of the VI schedule. All five of these changes should increase response rate. But what is not known is whether the first four (variables related to motivation) would affect response rate in the same way that the last one would. Shull (2001) proposed that the motivational variables could alter the tendency to engage in the reinforced activity by altering the relative reinforcement of the designated response. He also proposed that the fifth variable could be regarded affecting what the rat learns to do to obtain the reinforcer (i.e., the form of the behavioural unit) rather than the inclination to emit that unit.

Shull (2004) investigated these concepts by studying the effects of deprivation level on bouts of responding of rats exposed to concurrent VI VI schedules. The purpose was to investigate whether deprivation level affected response rate similarly to the way that reinforcer rate and amount do. Shull used log-survivor plot analyses to conclude that decreased deprivation (as altered by pre-feeding prior to experimental sessions) operated in essentially the same way as increasing reinforcer amount and rate do, which is to alter the between-bout pauses which could be reflected in IRTs. A log survivor plot shows the proportion of IRTs (logarithmic scale) that are longer than any duration, *t*. IRTs are actually composed of two distributions, one representing within-bout IRTs (which are short) and the other representing between-bout pauses (which may also be short but which are, on average, relatively long). Characteristics of these component distributions — and thus characteristics of bouts — can sometimes be inferred from the shape of the log survivor plot (i.e., when more between-bout pauses are evident, this is often described as a

broken-stick appearance). Steeper limbs represent more within-bout responses and less steep limbs represent more between-bout responses. Given that MOs have been shown to effect response rates (e.g., Charman & Davison, 1983; Herrnstein & Loveland, 1974; and Experiment 4.2), log-survivor plots could be used to measure whether changes in response rates are due to changes in within-bout responses or between-bout responses.

As noted by Davison (2004), in a concurrent VI schedule the allocation of time comprises of both time spent emitting a response and time spent in between responses (IRTs). Inter-response Time RT distributions provide an additional way to characterise the temporal occurrence of behaviour. Typically, IRT distributions have been compared graphically using relative frequency histograms. Davison pointed out that much analysis focuses on observing and measuring changes in short-duration, easily repeatable responses, rather than observing or measuring the time between responses (IRTs). Davison (2004) suggested that the IRT represents time spent doing something other than pecking the key. He suggests there may be sets of IRTs (time spent emitting other behaviour) with consistent lengths. He posits that we need to know what controls the duration of an activity and what controls the relative probabilities of moving between activity states. It is possible that extraneous activities are associated activity states to pecking and are affected by MOs. Davison (2004) showed that ratios of frequencies of inter-response times in a series of temporal bins varied in their sensitivity to reinforcement under concurrent schedules. Sensitivity values were highest for IRTs greater than 0.4 s, followed by IRTs between 0 – 0.2 s and were the lowest around 0.2 – 0.4 s. Davison (2004) found that time allocation to alternatives was mostly determined by IRTs between .08 – 6.4 s, and least by IRTs less than 0.8 s. He hypothesised that time spent emitting unmeasured behaviour may be the main constituent of time allocation on concurrent schedules. As pointed out by Davison, key-operations or lever-presses are used as our main measure of behaviour under these types of investigations and extraneous behaviour goes unmeasured. He states that pecking responses may be a limiting case because of their short duration and that for generality, defined responses of a longer duration also need

investigation. Whether or not pecks are considered to have a short duration does depend on the definition of the peck being used. If the micro-switch closure is taken as the definition of a peck, this can be a short duration. However, if the peck included the time the animal is orientated and moving towards the key it could be seen as having a longer duration. Weiss and Gott (1972) found that responding in pigeons maintained under FR schedules could be divided into three (possibly functionally distinct) classes of IRTs: (1) very short IRTs, or "nibbles" that result from closing and opening the beak rapidly while it is in contact with the response key; (2) IRTs that terminate with "clean" pecks of the key; and (3) "harmonics" – IRTs that result "from intervening pecking motions which do not strike the key" (p. 196). They found that these distinct classes of responding were differentially affected by different drugs.

Morphology

As well as enabling the operation of an experimental key, a hen's peck serves several functions, including foraging, aggression (e.g., feather pecking), and grooming. Dixon et al. (2008) quantified aspects of the morphology of hens' pecks at forages, dustbathes, novel objects, and water. They used video analysis to record the durations of the head fixation before the peck, between the head fixation to beak contact with each stimulus, and of the whole peck sequence. They found that the motor patterns involved in pecks at forages, dustbathes, novel objects, and water all varied significantly and that severe feather pecks resembled foraging pecks. Based on their results, and supporting Jenkins and Moore (1973), they suggested that the different forms of peck could be viewed as a motivationally distinct "fixed-action pattern" and they suggested that finely examining fixed-action pattern morphology can help understand the motivational bases of perplexing abnormal behaviours in captive animals (Dixon et al., 2008). Experiment 2.1, here, extended the Dixon et al. (2008) fixed-action pattern morphology analysis to the operant chamber. The finding from Experiment 2.1, that handshaping and autoshaping gave rise to similar peck morphology, suggested that it could be the nature of the reinforcer that gives rise to morphology and not that the autoshaping procedure *per se* gives rise to a particular form of elicited responses. As

only one bodyweight (85%) was used in Experiment 2.1 the effect of altering MOs on bodyweight was not able to be assessed. However, as found in both Experiment 4.1 and 5.1, hens maintained at lower bodyweights (75% compared to 95%) tended to peck more, but also miss the stimuli more. What is unknown is how these missed pecks interact with reinforcement rate changes. As mentioned, IRTs typically count the time from key micro-switch closure to key micro-switch closure; however, peck durations can include the head fixation before the peck, which, although part of the peck, would be measured as part of the IRT. As stated above, Davison (2004) suggested that for generality, defined responses of a longer duration also need investigation. It is possible that components of the food-reinforced peck (e.g., head fixation) could be affected by MOs more or less than other components. Changes in IRTs could reflect morphology changes rather than time doing extraneous behaviours. An analysis of peck morphology alongside IRT analysis can help to analyse if slower response rates result from changes in peck morphology.

Summary

In summary, level of deprivation (an MO) has been found to have a systematic effect on rates of responding on single VI schedules (Clark, 1958; Ferster & Skinner, 1957; McSweeney, 1975; Revusky, 1963). As suggested by Baum (1979), deprivation level may be one variable that contributes to differences found in sensitivity values in concurrent VI schedules. As shown by Davison (2004), IRTs can show differential sensitivity values and, as demonstrated by Brackney, Cheung, Herbst, Hill, and Sanabria (2012) and Shull (2004), bout initiation (which will affect IRTs) can be affected by MOs. This means that MOs such as deprivation level can influence time allocation behaviour and sensitivity values in concurrent schedule, but exactly how this might occur is not clear.

The mixed results of the aforementioned studies provide justification for investigating the effect of deprivation level as an MO on concurrent VI VI schedule performance of hens and carrying out a micro analysis of the findings in addition to applying the GML. While no studies have specifically used hens to investigate the effect of altering MOs on concurrent schedule performance, hens have been shown to work reliably

on concurrent schedules and to produce data like other species (e.g., McAdie, Foster, & Temple, 1996; Sumpter, Foster, & Temple, 1995; Sumpter, Temple, & Foster, 1998; Temple, Scown, & Foster, 1995).

This next experiment aimed to systematically alter bodyweight for hens responding under concurrent VI VI schedules. Based on the findings from Experiments 4.1 and 5.1, it would be expected that species-specific behaviour (pecking) would be greater at lower bodyweights resulting in higher response rates. One aim of this experiment was to test whether altering bodyweight would differentially affect local response rates, therefore affecting bias and sensitivity as measured by the GML, or whether only overall rate would be affected. Log-survivor plots were created to assess whether responses were organised into bouts and whether any changes in response rates were due to changes between-bout or within-bout responding. Inter-response time distributions were used to assess the temporal distribution of responses and a video analysis of peck morphology was used to analyse if any changes in response rates due to changes in bodyweight resulted from changes in peck morphology.

Method

The six subjects, numbered 25-1 through 25-6, were domestic hens, two were Australorpe and four were Orpington. At the beginning of the experiment, the hens were one-year old and had previously been trained (either via autoshaping or via the method of shaping by successive approximations) to peck a white stimulus displayed on a computer screen. Hens were housed individually in custom built cages measuring 620-mm high by 790-mm wide by 610-mm deep. Each cage was fitted with a wooden door and wire sides and floor. A wooden perch situated 300-mm from the left edge of the cage and 100-mm off the floor ran the width of the cage. Lights were on a 12 hr light/ dark cycle (06:00 hr – 18:00 hr). Each hen was weighed every day an experimental session took place (seven days per week), and they only took part in the experimental session if they were in the specified weight range. They were maintained at the weight ranges (±5%) outlined in Table 6.1 though supplemental feeding of NRM Peck'n'Lay commercial laying pellets given at the end of experimental sessions. Oyster grit and vitamins were given to the hens once weekly.

Water was available ad libitum via nipple feeders located in the hens' cages.

Apparatus

The experimental chamber was made of particle board (600-mm high x 570-mm wide x 450-mm deep) and was in a room with one other experimental chamber. The interior of the chamber was painted matt black. The chamber floor was covered with a thick, black rubber mat. On the right-hand wall of the chamber a Dell E176FP 17" flat panel monitor with a display resolution of 1280 x 1024 pixels was located. Displayed on the monitor at were two white circles each measuring 60 pixels in diameter illuminated against a black background; the locations of the diameters of each stimulus were at 948 x 564 and 332 x 948 pixels, respectively. When the stimuli were pecked an audible beep was made. Immediately below this monitor were two openings (115-mm high x 100-mm wide). These openings allowed access to two food magazines. When operational, each food magazine was lit and allowed 1.5-s access to commercial laying pellets. Both magazines were placed on top of Jadever Sky-3000 precision weighing scales. The timing and location (in x and y pixel coordinates) were recorded for all pecks made to the white stimulus. The timing and location of pecks to the other parts of the screen were recorded as either a black peck, if it was made to the black screen, or a near miss, if it was made to an area of 182 pixels from the diameter of the white stimulus, both of which would not operate the hopper. A customised computer program written by Rob Bakker and Jennifer Chandler ran the experimental sessions and collected the data. The wall of the left side of the chamber was made of transparent plastic, and a high-performance camera (GoPro® Hero 3 Black) was fixed to the exterior. Black plastic covered the transparent plastic side of the chamber to eliminate extraneous light.

Procedure

Training

Prior to beginning the experiment proper, the hens were exposed to a training condition. As hens had already been trained to peck the white

stimuli, shaping was not necessary. In this condition, the hens worked on a concurrent VI 10-s VI 10-s schedule. During these sessions two white stimuli would appear on the left and right side of the black screen. For each alternative, the first peck to the white stimulus after an average of 10 s had passed activated the hopper and produced 1.5-s access to the reinforcer. The schedules were programmed dependently, meaning that when a reinforcer became available on one stimulus, the VI timer on the other stimulus stopped counting down until the hen obtained the due reinforcer. For example, if a reinforcer was due on the left stimulus, the time until a reinforcer was due on the right stimulus did not decrease until the reinforcer on the left stimulus had been obtained. Once the 1.5-s reinforcement had concluded, the right VI timer continued counting down the time until the next reinforcer was due on the right, and the next interval started on the left VI timer until a reinforcer was due on the left again. A 3-s changeover delay (COD) was then put into effect, meaning that after a reinforcer was delivered on one schedule, 3 s must have elapsed before responding on the alternate schedule could produce a reinforcer, ensuring the hen was not reinforced for simply switching stimuli. Sessions lasted for up to 40 min or 40 reinforcers had been delivered in total, whichever was sooner; at this point the white stimulus would vanish from the screen and the chamber would darken.

Experimental conditions

After all hens were responding reliably and stably on the training schedules, as judged by visual inspection of the plotted proportion of response to the left stimulus, concurrent VI VI schedules were arranged using the same procedure as training. The concurrent VI VI schedules (and programmed ratios of reinforcement) that were used were VI 20 s, VI 20 s (1:1); VI 12 s, VI 60 s (5:1); and VI 60 s, VI 12 s (1:5). Under these VI schedules the hens could earn an average of six accesses to reinforcers per min. The experimental conditions were changed when the behaviour of all subjects had reached a stability criterion five times, not necessarily consecutively. The criterion was that the median relative number of responses (i.e., total number of pecks on the left stimulus divided by the total number of responses made on both manipulanda) over the last five

sessions was within 0.05 of the median of the previous five sessions. Conditions were changed when the plots of the proportion of left responses were judged to be not trending over the last five sessions. Two sessions after the hens had reached the stability criterion were filmed using the GoPro Hero 3 camera in the WVGA setting, which recorded in 240 fps. In total 10 experimental conditions were run. The order of the experimental conditions, together with the bodyweight percentage and the number of days each condition was in effect for each hen are presented in Table 6.1.

Table 6.1.

The order of the experimental conditions, together with the bodyweight percentage, and the number of sessions each condition was in effect for each hen.

Condition	VI left	VI right	Bodyweight	Hen 25-1	Hen 25-2	Hen 25-3	Hen 25-4	Hen 25-5	Hen 25-6
1	20	20	85%	35	37	35	36	35	36
2	12	60	85%	20	19	20	20	20	19
3	60	12	85%	24	24	24	24	22	22
4	20	20	85%	31	27	27	25	28	29
5	20	20	95%	29	60	60	49	58	59
6	12	60	95%	40	19	38	36	42	39
7	60	12	95%	35	37	42	31	40	39
8	20	20	100%	42	40	38	39	50	36
9	12	60	100%	50	55	28	35	57	30
10	60	12	100%	39	37	32	20	41	23

Results

Raw data from all conditions are presented in Appendix E. The data from only the last five stable sessions of each condition have been analysed and presented here.

Overall response rates

The overall response rates were calculated by dividing the total session time by the total number of responses. Figure 6.2 presents the overall response rates for the 85% condition, the 95% condition, and the 100% condition, averaged over the last five stable sessions, for each condition and each bird. The error bars represent the standard error of the mean. The left panel presents the data from conditions where a VI 12-s, VI

60-s schedule was in effect (5:1 reinforcer ratio); the middle panel shows the data for the VI 20-s, VI 20 -s schedule (1:1 reinforcer ratio); and the right panel for the VI 60-s, VI 12 -s schedule (1:5 reinforcer ratio). For Hens 25-1 – 25-4 the overall response rate tended to show a decreasing trend as bodyweight increased. The conditions where the overall response rates were lower and bodyweight higher also showed more variability in responding, see the error bars. Hen 25-5 and 25-6 did not show these trends, with response rates staying relatively stable across all reinforcer ratios.

Left and right stimulus response rates

Response rates for the left and right stimuli were calculated separately by dividing the total response counts by the time the hens allocated to each stimulus. Figure 6.3 presents these response rates for each condition averaged over the last five stable sessions, for each condition and each bird. The error bars represent the standard error of the mean. The left panel presents the data from conditions where a VI 12-s, VI 60-s schedule was in effect (5:1 reinforcer ratio); the middle panel shows the data for the VI 20-s, VI 20-s schedule (1:1 reinforcer ratio); and the right panel for the VI 60-s, VI 12-s schedule (1:5 reinforcer ratio). Similar patterns were observed as in the overall response rates, with both left and right response rates slowing down as bodyweight increased for many hens. Again Hen 25-5 and 25-6 tended to show similar response rates on both the left and right side across all conditions. When the 5:1 schedule was in effect, the hens were faster on the rich (left) stimulus, than they were on the rich (right stimulus) when the 1:5 schedule was effect. This could be representative of a left stimulus bias. When the 1:1 schedule was in effect all hens were faster on the left stimulus, again showing a left stimulus bias.

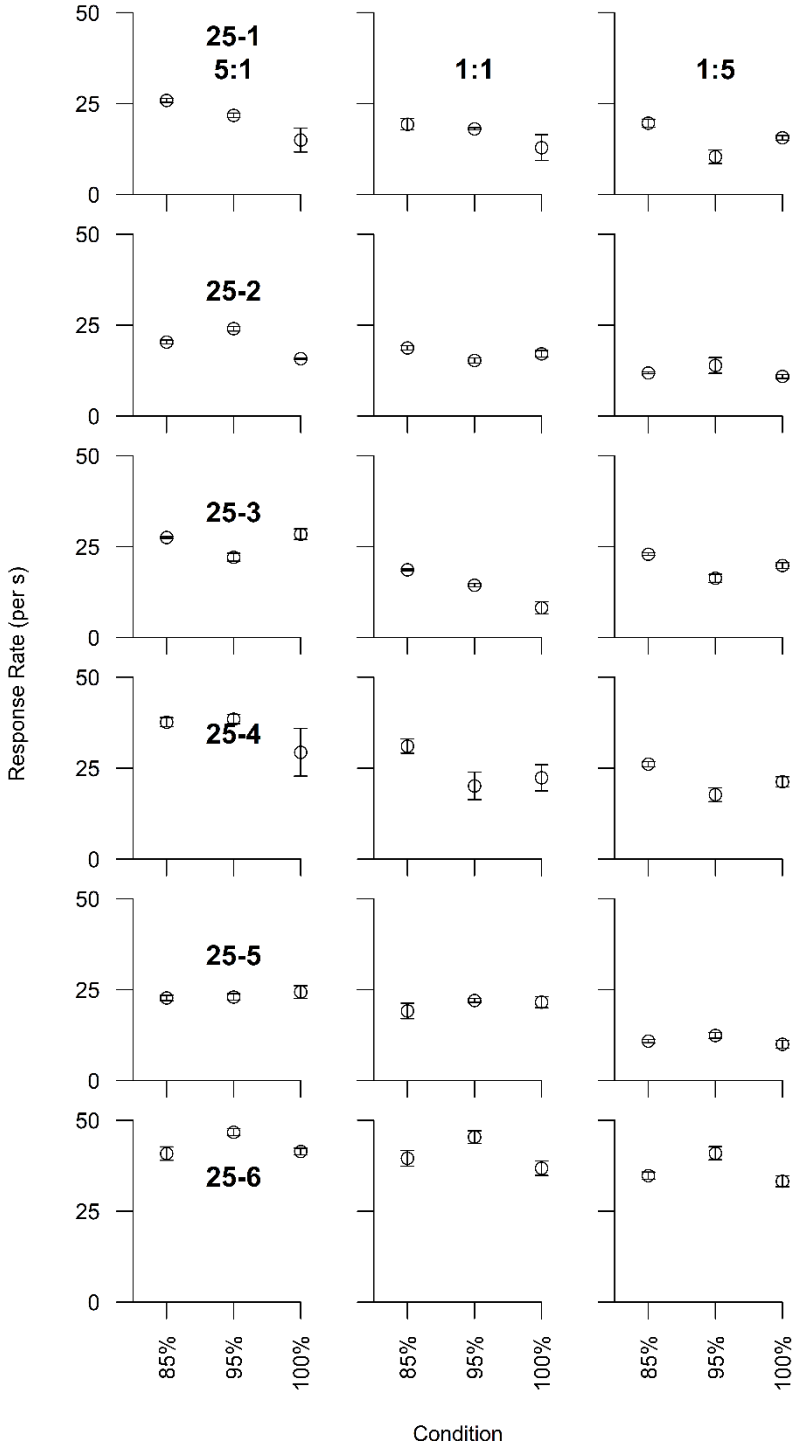

Figure 6.2. Overall response rates (per s) averaged over the last five stable sessions of each condition, for the 85%, 95%, and 100% bodyweight conditions, for each hen. The left panel presents the conditions where a VI 12-s, VI 60-s schedule was in effect; the middle panel presents the conditions where a VI 20-s, VI 20-s schedule was in effect; and the right panel presents the conditions where a VI 60-s, VI 12-s schedule was in effect. The error bars represent ±SEM.

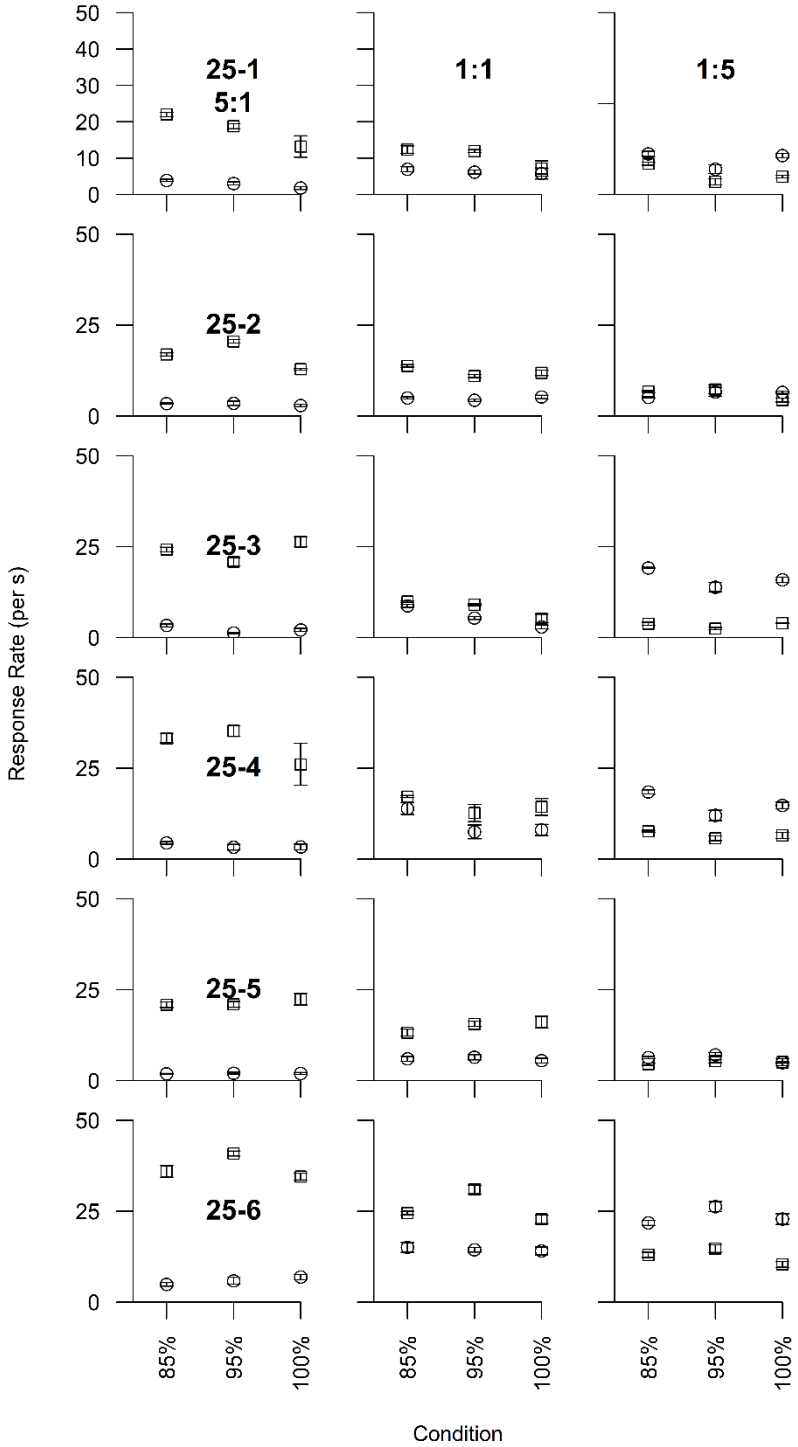

Figure 6.3. Local response rates (per s) for the left (square) and right (circle) stimulus averaged over the last five stable sessions of each condition, for the 85%, 95%, and 100% bodyweight conditions, for each hen. The left panel presents the conditions where a VI 12-s, VI 60-s schedule was in effect; the middle panel presents the conditions where a VI 20-s, VI 20-s schedule was in effect; and the right panel presents the conditions where a VI 60-s VI 12-s schedule was in effect. The error bars represent ±SEM.

Generalised Matching Law

Figure 6.4 presents log response ratios plotted as a function of log reinforcer ratios for each condition. Figure 6.5 presents log time allocation ratios plotted as a function of log reinforcer ratios for each condition. Least squares regression lines are drawn on both figures, and their slopes and intercepts (with their standard errors) are given in Tables 6.2 and 6.3. Figures 6.4 and 6.5 show that all hens tended to show a left bias as both time and response allocations lines cross the y axis above zero.

In most conditions hens undermatched ($a < 1.0$), aside from Hen 25-3 in two conditions with response allocations. For both response and time allocations, the percentage of variance accounted for by the fitted lines was greater than 91.3%.

The estimates of sensitivity (*a*) from Table 6.2 are plotted in Figure 6.6; as shown, there are no systematic trends in *a* across all hens. Estimates of sensitivity were highest in the 85% condition for Hen 25-3; highest in the 95% condition for Hens 25-3, 25-4, and 25-6; and highest in the 100% condition for Hens 25-1 and 25-2. On average, the highest sensitivity value was seen in the 95% condition. The *a* values based on the time data (Table 6.3) are shown on Figure 6.7; as shown, there are no systematic trends in *a* across all hens. The *a* values were highest in the 95% condition for Hens 25-4, 25-5, and 25-6; and highest in the 100% condition for Hens 25-1, 25-2, and 25-3. On average, the highest sensitivity value was seen in the 95% condition.

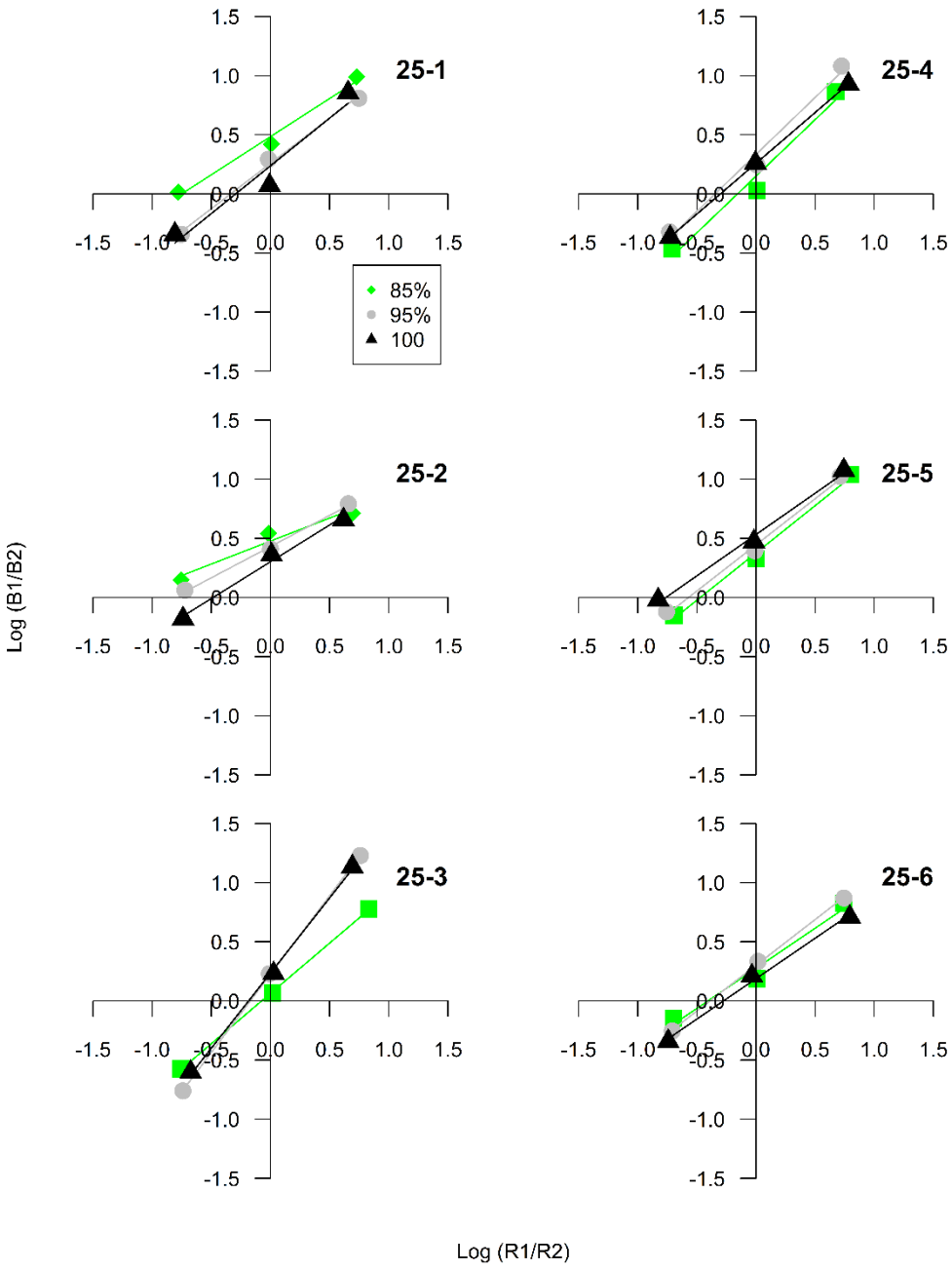

Figure 6.4. Log response ratios plotted as a function of log reinforcer ratios for each condition. Least squares regression lines are drawn, and their slopes and intercepts (with their standard errors) are given in Table 6.2.

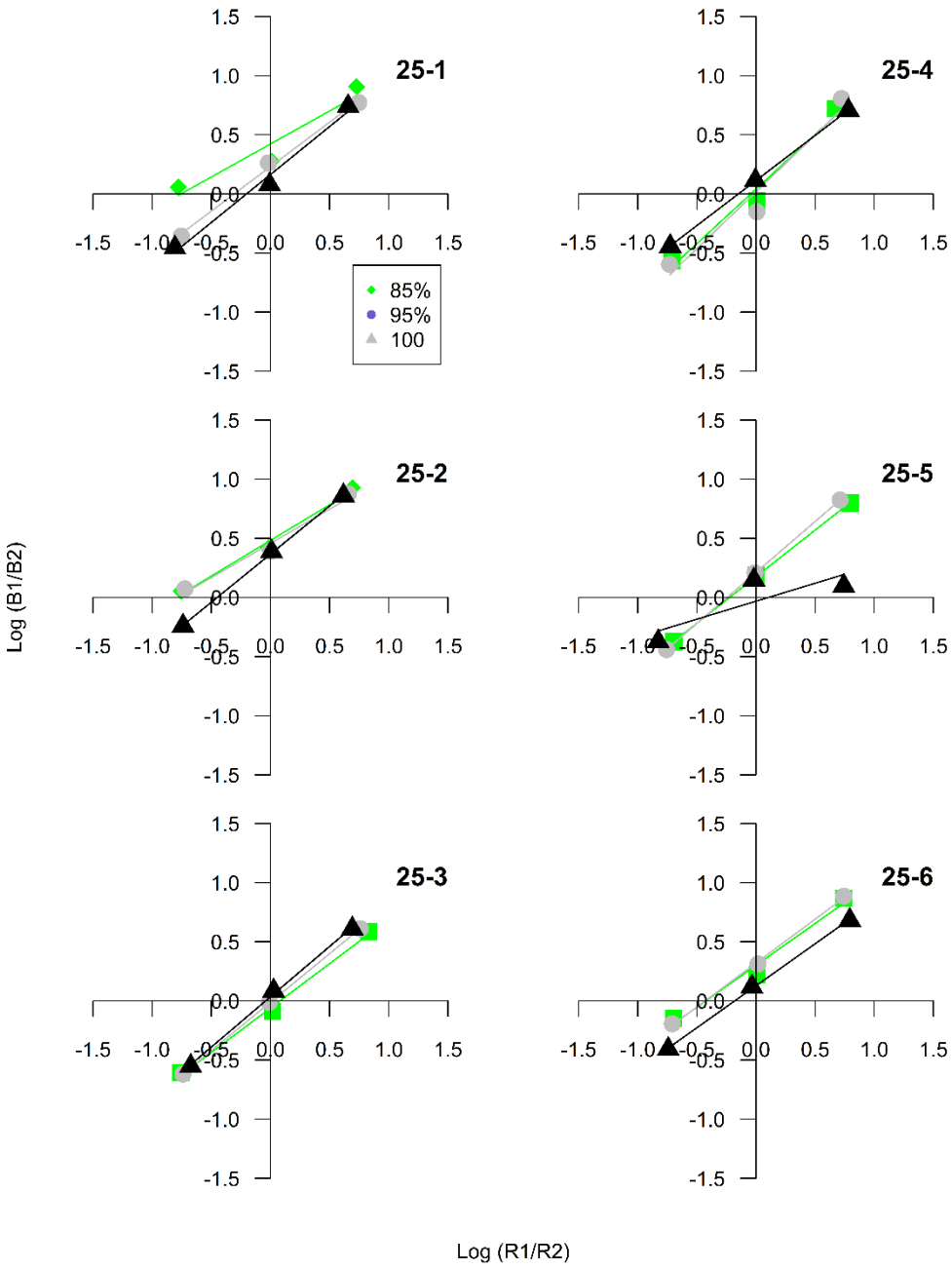

Figure 6.5. Log time allocation ratios plotted as a function of log reinforcer ratios for each condition. Least squares regression lines are drawn, and their slopes and intercepts (with their standard errors) are given in Table 6.3.

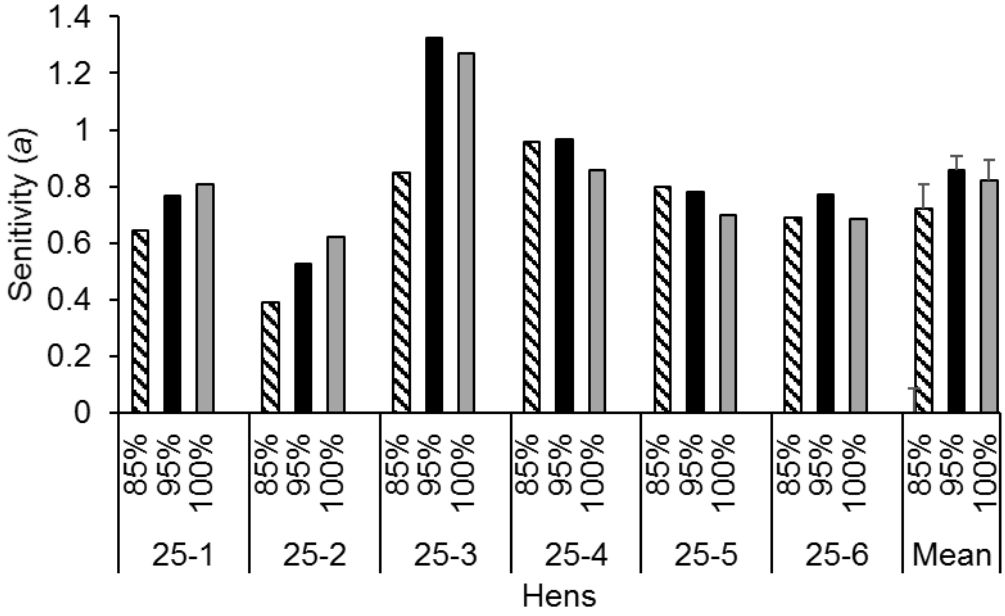

Figure 6.6. Estimates of sensitivity (*a*) derived from the Generalised Matching Law (Equation 1) applied to the response allocations to each stimulus during the last five stable sessions of each condition, for each hen. The error bars represent ±SEM.

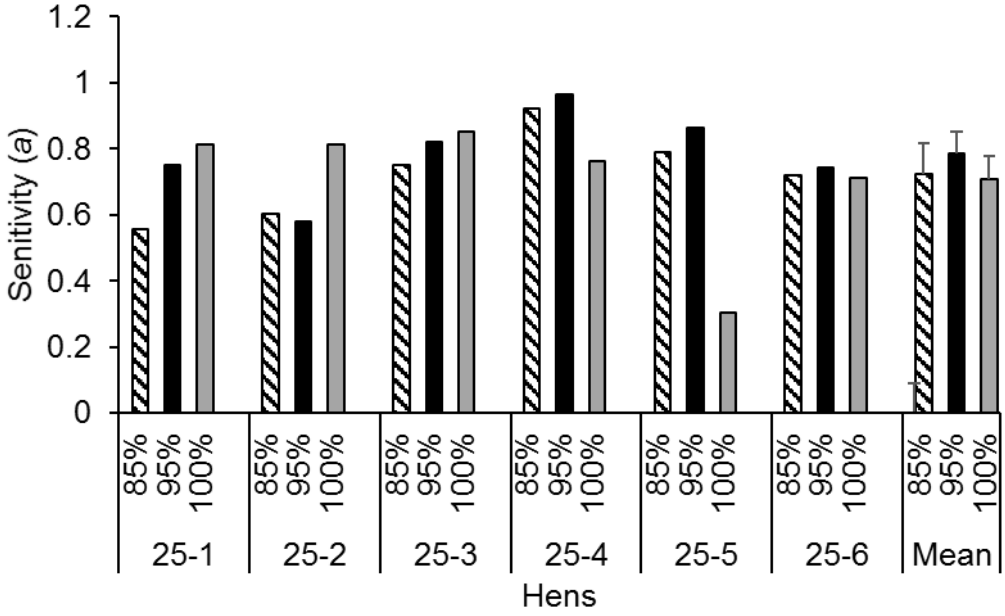

Figure 6.7. Estimates of sensitivity (*a*) derived from the Generalised Matching Law (Equation 1) applied to the time allocations to each stimulus during the last five stable sessions of each condition, for each hen. The error bars represent ±SEM.

Table 6.2.

Estimates of sensitivity (a) and bias log c derived from the Generalised Matching Law (Equation 1) applied to the response allocations to each stimulus during the last five stable sessions of each condition, for each hen. The standard error and the proportion of variance accounted for by the fitted lines are also presented.

Hen	Condition	*a*	Log *c*	se	% VAC
25-1	85%	0.64	0.49	0.09	98.5
	95%	0.77	0.26	0.06	99.5
	100%	0.81	0.24	0.20	94.7
25-2	85%	0.39	0.48	0.09	95.5
	95%	0.53	0.43	0.03	99.7
	100%	0.62	0.30	0.06	98.9
25-3	85%	0.85	0.06	0.02	100.0
	95%	1.33	0.23	0.02	100.0
	100%	1.27	0.24	0.05	99.9
25-4	85%	0.96	0.15	0.16	97.2
	95%	0.96	0.33	0.12	98.6
	100%	0.86	0.26	0.01	100.0
25-5	85%	0.80	0.38	0.06	99.5
	95%	0.78	0.45	0.05	99.5
	100%	0.70	0.53	0.06	99.5
25-6	85%	0.69	0.27	0.11	97.5
	95%	0.77	0.30	0.02	99.9
	100%	0.68	0.19	0.06	99.5
Mean	85%	0.72	0.30	0.09	98.01
	95%	0.86	0.33	0.05	99.55
	100%	0.82	0.29	0.07	98.73

Table 6.3.

Estimates of sensitivity (a) and bias log c derived from the Generalised Matching Law (Equation 1) applied to the time allocations to each stimulus during the last five stable sessions of each condition, for each hen. The standard error and the proportion of variance accounted for by the fitted lines are also presented.

Hen	Condition	*a*	Log *c*	se	% VAC
25-1	85%	0.56	0.42	0.18	91.3
	95%	0.75	0.23	0.05	99.6
	100%	0.81	0.16	0.10	98.7
25-2	85%	0.60	0.48	0.06	98.9
	95%	0.58	0.46	0.08	97.8
	100%	0.81	0.37	0.02	100.0
25-3	85%	0.75	-0.06	0.05	99.6
	95%	0.82	-0.01	0.01	100.0
	100%	0.85	0.04	0.03	99.8
25-4	85%	0.92	0.04	0.13	98.0
	95%	0.96	0.02	0.22	95.4
	100%	0.76	0.11	0.01	100.0
25-5	85%	0.79	0.18	0.01	100.0
	95%	0.86	0.21	0.00	100.0
	100%	0.30	-0.03	0.23	93.5
25-6	85%	0.72	0.30	0.10	98.2
	95%	0.74	0.32	0.03	99.9
	100%	0.71	0.13	0.02	99.9
Mean	85%	0.72	0.23	0.09	97.65
	95%	0.79	0.20	0.07	98.78
	100%	0.71	0.13	0.07	98.64

Figure 6.8 and Table 6.2 presents the estimates of bias (log *c*) derived from Equation 1 applied to the response allocations to each stimulus for the data from the last five stable sessions of each condition, for each hen. Figure 6.8 shows log *c* values were highest in the 85% condition for Hens 25-1 and 25-2, highest in the 95% condition for Hens 25-4 and 25-6, and highest in the 100% condition for Hens 25-3 and 25-5. On average, the highest bias values were seen in the 95% condition. There were no systematic trends in the log *c* over conditions, over all hens.

Data from Table 6.4 are plotted in Figure 6.9 and l*og* (c) for the time allocations is shown; no systematic trends were seen across hens but the data for time allocations were like the data for response allocation bias for each hen (Figure 6.9). Estimates of bias were highest in the 85% condition for Hens 25-1 and 25-2; highest in the 95% condition for Hens 25-4, 25-5, and 25-6; and highest in the 100% condition for Hen 25-3. On average, the highest bias values were seen in the 95% condition.

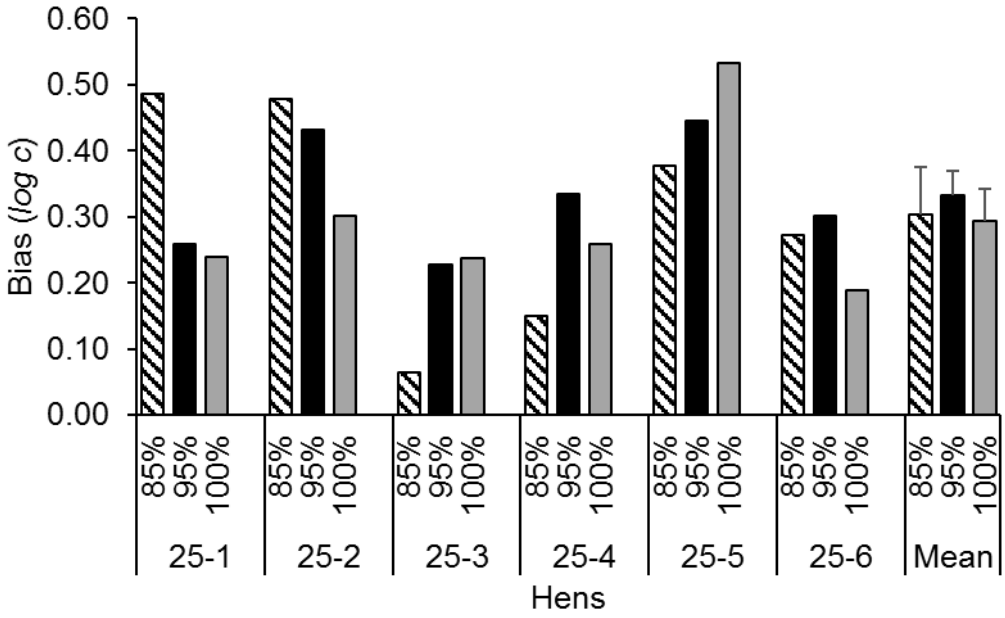

Figure 6.8. Estimates of bias log *c* derived from the Generalised Matching Law (Equation 1) applied to the response allocations to each stimulus during the last five stable sessions of each condition, for each hen (25-1 to 25-6). The error bars represent ±SEM.

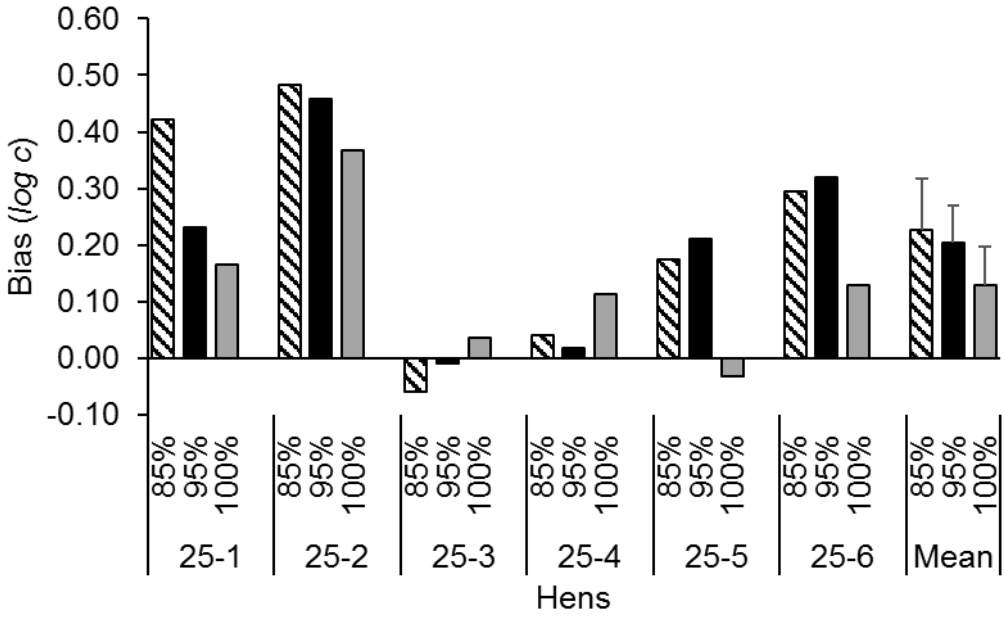

Figure 6.9. Estimates of bias log *c* derived from the Generalised Matching Law (Equation 1) applied to the time allocations to each stimulus during the last five stable sessions of each condition, for each hen (25-1 to 25-6). The error bars represent ±SEM.

Log survivor plots

Figure 6.10 displays a log survivor plot for Hen 25-1 across all conditions. As can be seen when the reinforcer ratio was 5:1 on the VI-12-s, VI-60-s schedules, the shape of the log-survivor plot limbs were similar across all conditions. However, when the rich schedule was in effect on the left the 85% condition limb was slightly steeper than the 95% or 100% condition limbs. When the lean schedule was in effect on the right, the 95% and 100% condition limbs were slightly steeper than the 85% condition limb. When the reinforcer ratios were at ratios of 1:1 and 1:5 on the VI-20-s, VI-20-s and VI-60-s, VI-12-s schedules respectively, the slope and shape of the log-survivor plot limbs were similar across all conditions, on both the left and right sides. Over all conditions and bodyweights, the log-survivor plots did not show the broken-stick appearance reported in previous studies. All plots showed undulations in the shape of the log-survivor distributions.

Figure 6.11 displays a log survivor plot for Hen 25-2 for all conditions. As can be seen on Figure 6.11 across all reinforcer ratios and

sides, the 85% condition limb had the steepest log-survivor limb. Like Hen 25-1 all log-survivor plots showed undulations in the shape of the limbs and none showed the broken-stick appearance.

Figure 6.12 displays a log survivor plot for Hen 25-3 for all conditions. When the 5:1 schedules were in effect the shape of the log-survivor plot limbs were similar across all conditions on the left (rich) side. When the lean schedule was in effect on the right the 85% condition limb was slightly steeper than the 95% or 100% condition limbs. When the reinforcer ratios were equal 1:1 the 85% condition was again slightly steeper than those from the 95% or 100% conditions limbs. When the 1:5 schedules were in effect the 100% condition was slightly steeper than the 85% or 95% condition on both sides. Like Hens 25-1 and 25-2 plots, all log-survivor plots showed undulations in the shape of the limbs and none showed the broken-stick appearance.

Figure 6.13 displays a log-survivor plot for Hen 25-4 for all conditions. As can be seen on Figure 6.13, when the reinforcer ratios were at a ratio of 5:1 on the VI-12-s, VI-60-s schedules the shape of the log-survivor plot limbs were similar across all conditions. However, when the rich schedule was in effect on the left the 85% and 95% conditions' limbs were slightly steeper than the 100% condition limbs. When the lean schedule was in effect on the right all limbs had similar slopes and shapes. When the reinforcer ratios were at ratios of 1:1 and on the VI-20-s, VI-20-s schedule, the shape of the log-survivor plot limbs were similar across all conditions, on both the left and right sides; however, they were slightly steeper for the 85% condition limb. When the reinforcer ratios were at 1:5 on the VI-60-s, VI-12-s schedule the 100% condition limb was slightly steeper than the 85% or 95% condition limbs on the left (lean) side. On the right (rich) side the 85% condition limb was slightly steeper than the 95% or 100% conditions' limbs.

Figure 6.14 displays a log survivor plot for Hen 25-5 for all conditions. As can be seen on Figure 6.14, when the reinforcer ratios were at a ratio of 5:1 on the VI-12-s, VI-60-s schedules the shape of the log-survivor plot limbs were similar across all conditions; however, the slope of the 95% limb was steeper on both the left (lean) and right (rich) side. When the reinforcer ratios were at ratios of 1:1 and on the VI-20-s, VI-20-s

schedule, the shape of the log-survivor plot limbs were similar across all conditions, on both the left and right sides. A similar pattern was observed on the 5:1 VI-60-s, VI 12-s schedules.

Figure 6.15 displays a log survivor plot for Hen 25-6 for all conditions. As can be seen on Figure 6.15, when the reinforcer ratios were at a ratio of 5:1 on the VI-12-s, VI-60-s schedules the shape of the log-survivor plot limbs were similar across all conditions; however, the slope of the 95% limb was less steep on both the left (lean) and right (rich) side than for the 85% and 100% conditions' limbs. When the reinforcer ratios were at ratios of 1:1 and on the VI-20-s, VI-20-s schedule, the shape of the log-survivor plot limbs were similar across all conditions, on both the left and right sides. When the reinforcer ratios were at ratios of 1:5 and on the VI-60-s, VI-12-s schedule, the shape of the log-survivor plot limbs were similar across all conditions; on both the left and right sides the slope of the 95% limb was steeper on both the left (lean) and right (rich) side than for the 85% and 100% conditions' limbs.

In summary, the log-survivor plots of all hens did not show the broken-stick pattern observed in previous studies. All plots showed undulations in the shape of the limbs, which tended to stay the same across different bodyweights, indicating that bodyweight did not alter the shape of the limb. However, changing bodyweight did alter the slope of the limbs for most birds, for more conditions.

Inter-response times

Figure 6.16 displays relative frequencies of different classes of IRTs (in 0.2-s bins) for Hen 25-1 averaged over the last five stable sessions for each condition, for each VI pair. The shape of the distribution changed as bodyweights increased for Hen 25-1, when bodyweight was at 85% there tended to be more IRTs in the 0 – 0.4-s bins, when bodyweight was higher there were more IRTs at values above 0.4-s and the peak between 0 – 0.4s was not evident. Figures 6.17 – 6.21 display the relative frequency distributions of the different classes of IRTs for Hens 25-2, 25-3, and 25-4. As evident on these figures, these hens also demonstrated a similar pattern where, as bodyweights increased, there were more IRTs in the bins above 0.4-s. As shown on Figures 6.20 and 6.21, Hen 25-5 and Hen

25-6 tended to produce similar IRT distributions across different bodyweights. These are similar findings to the overall response rates, as highlighted earlier for Hens 25-1 – 25-4, the overall response rate tended to show a decreasing trend as bodyweight increased. The conditions where the overall response rates were lower and bodyweight was higher also showed more variability in responding; see error bars on Figure 6.2. Hen 25-5 and 25-6 did not show these trends with response rates staying relatively stable across all reinforcer ratios (the only exception was Hen 25-1, on the 1:1 schedules). For Hens 25-2, 25-3, and 25-4 the log-survivor limbs tended to be the steepest when the 85% condition was in effect.

Video analysis

Table 6.4 presents the durations of each part of the peck component based on the Dixon et al. (2008) analysis, for each hen for the 85%, 95%, and 100% conditions, when the VI 20-s, VI 20-s schedules were in effect only. For each of the five stable sessions, 20% of all pecks on both sides were analysed; specifically, pecks occurring during the 10^{th}-20^{th} percentile and the 90^{th}-100^{th} percentile. There was no difference found between pecks from the 10^{th}-20^{th} and 90^{th}-100^{th} percentile, so data were combined and presented here. Pecks made to the left and right sides were not coded separately so are unable to be presented individually. Figure 6.22 presents the mean durations of each component of the peck for the 85%, 95%, and 100% bodyweight conditions when the VI-20-s, VI-20-s schedules were in effect only, across all hens. Error bars represent the standard error of the mean. As shown on Figure 6.14, the peck components were longest in duration over all morphology categories for the 100% condition.

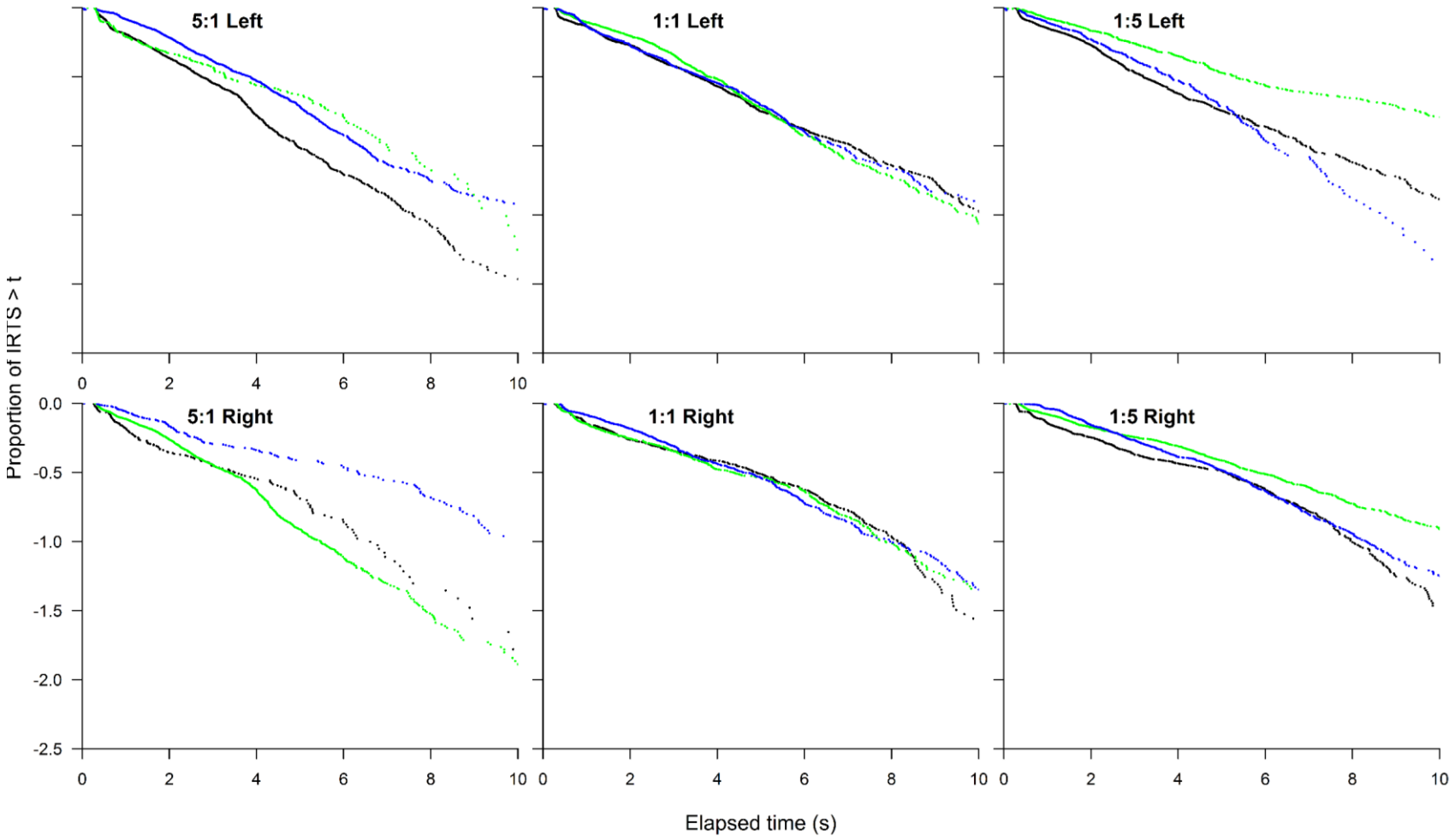

Figure 6.10. Log-survivor functions for Hen 25-1 for all conditions. Log proportions of IRTs greater than some time *(t)* are plotted as a function of elapsed time *(t)*. Black lines represent the 85% condition, green lines the 95% condition and, blue lines the 100% condition.

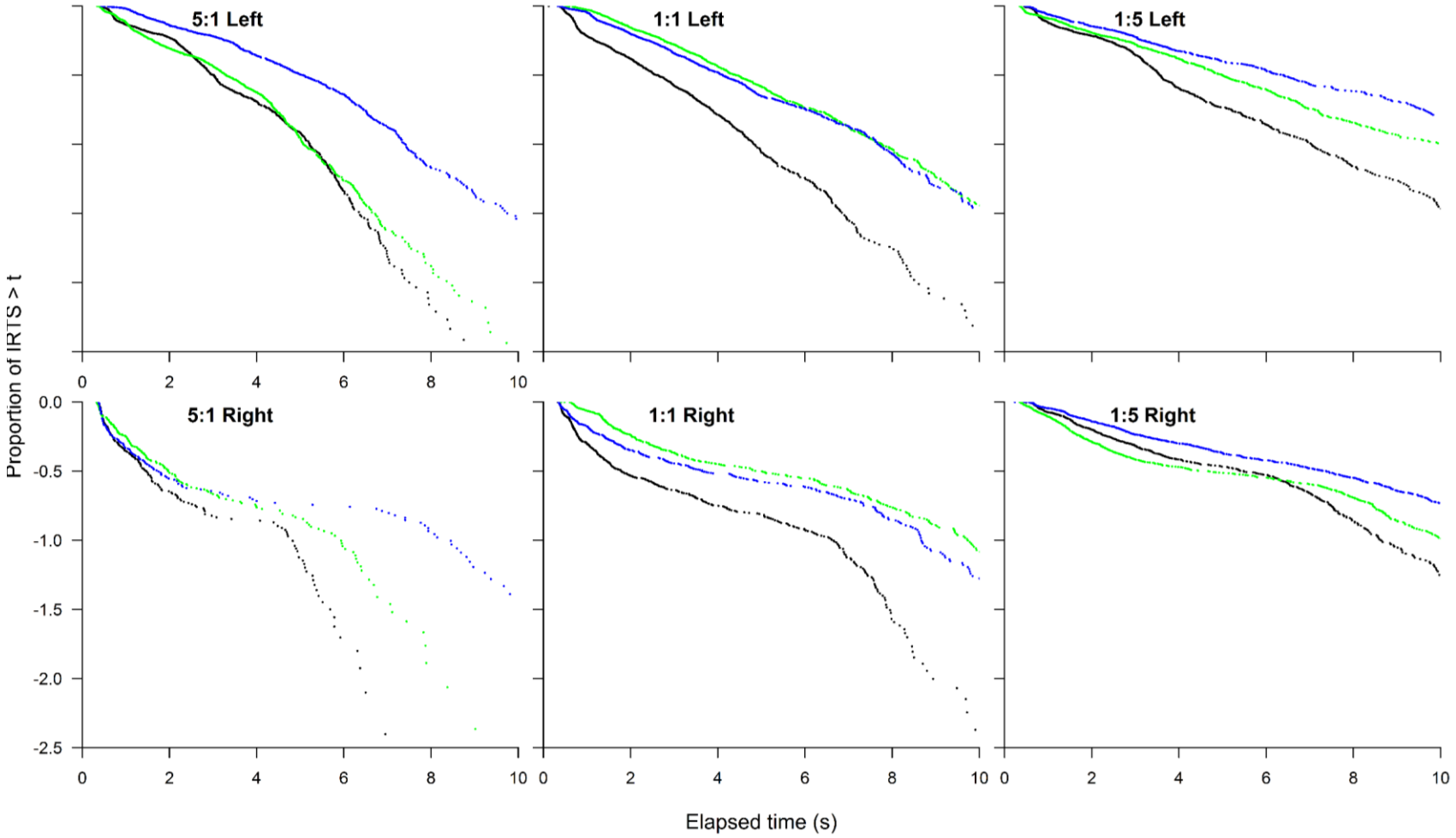

Figure 6.11. Log-survivor functions for Hen 25-2 for all conditions. Log proportions of IRTs greater than some time *(t)* are plotted as a function of elapsed time *(t)*. Black lines represent the 85% condition, green lines the 95% condition and, blue lines the 100% condition.

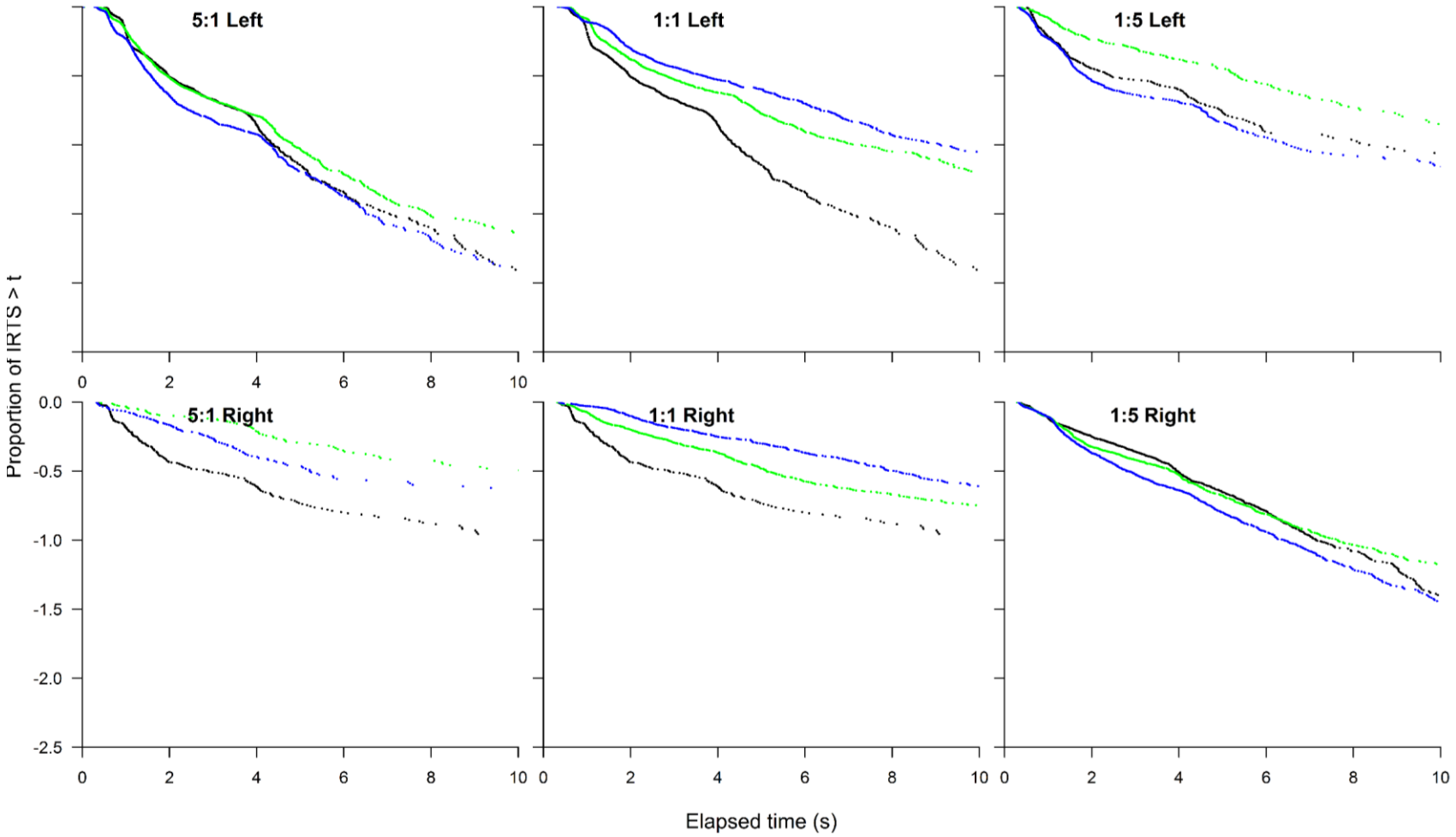

Figure 6.12. Log-survivor functions for Hen 25-3 for all conditions. Log proportions of IRTs greater than some time *(t)* are plotted as a function of elapsed time *(t)*. Black lines represent the 85% condition, green lines the 95% condition and, blue lines the 100% condition.

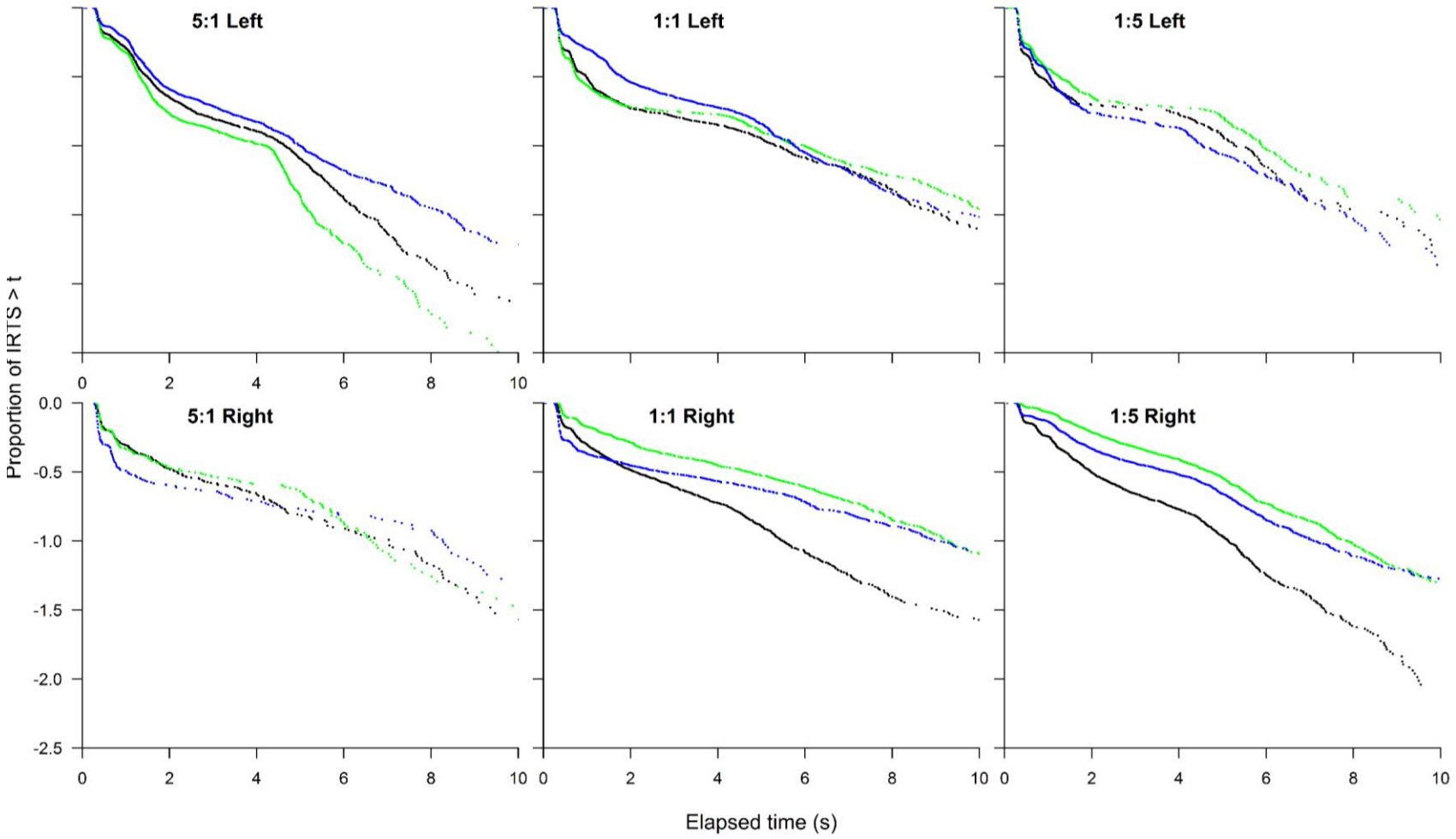

Figure 6.13. Log-survivor functions for Hen 25-4 for all conditions. Log proportions of IRTs greater than some time *(t)* are plotted as a function of elapsed time *(t)*. Black lines represent the 85% condition, green lines the 95% condition and, blue lines the 100% condition.

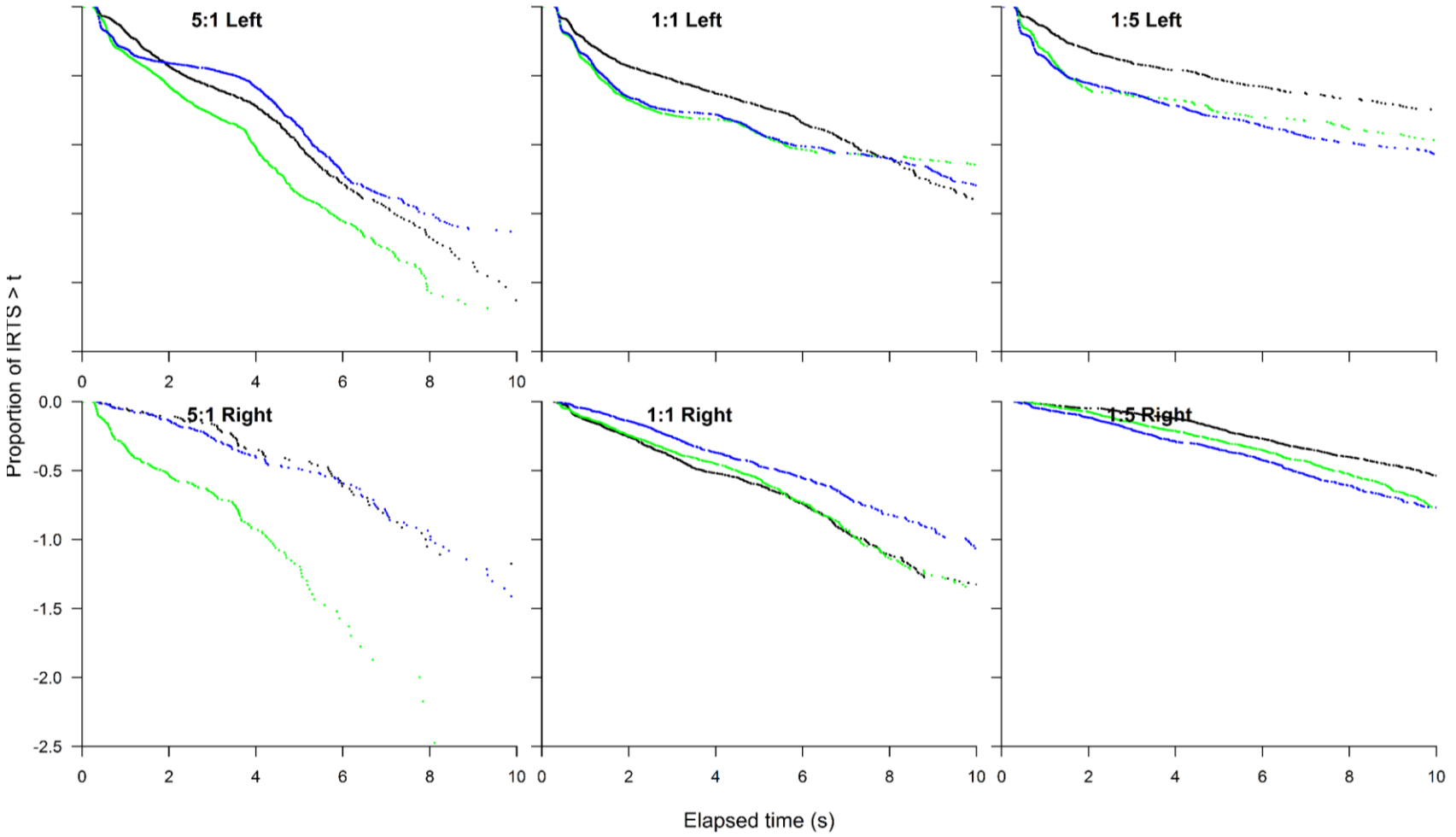

Figure 6.14. Log-survivor functions for Hen 25-5 for all conditions. Log proportions of IRTs greater than some time *(t)* are plotted as a function of elapsed time *(t)*. Black lines represent the 85% condition, green lines the 95% condition, and blue lines the 100% condition.

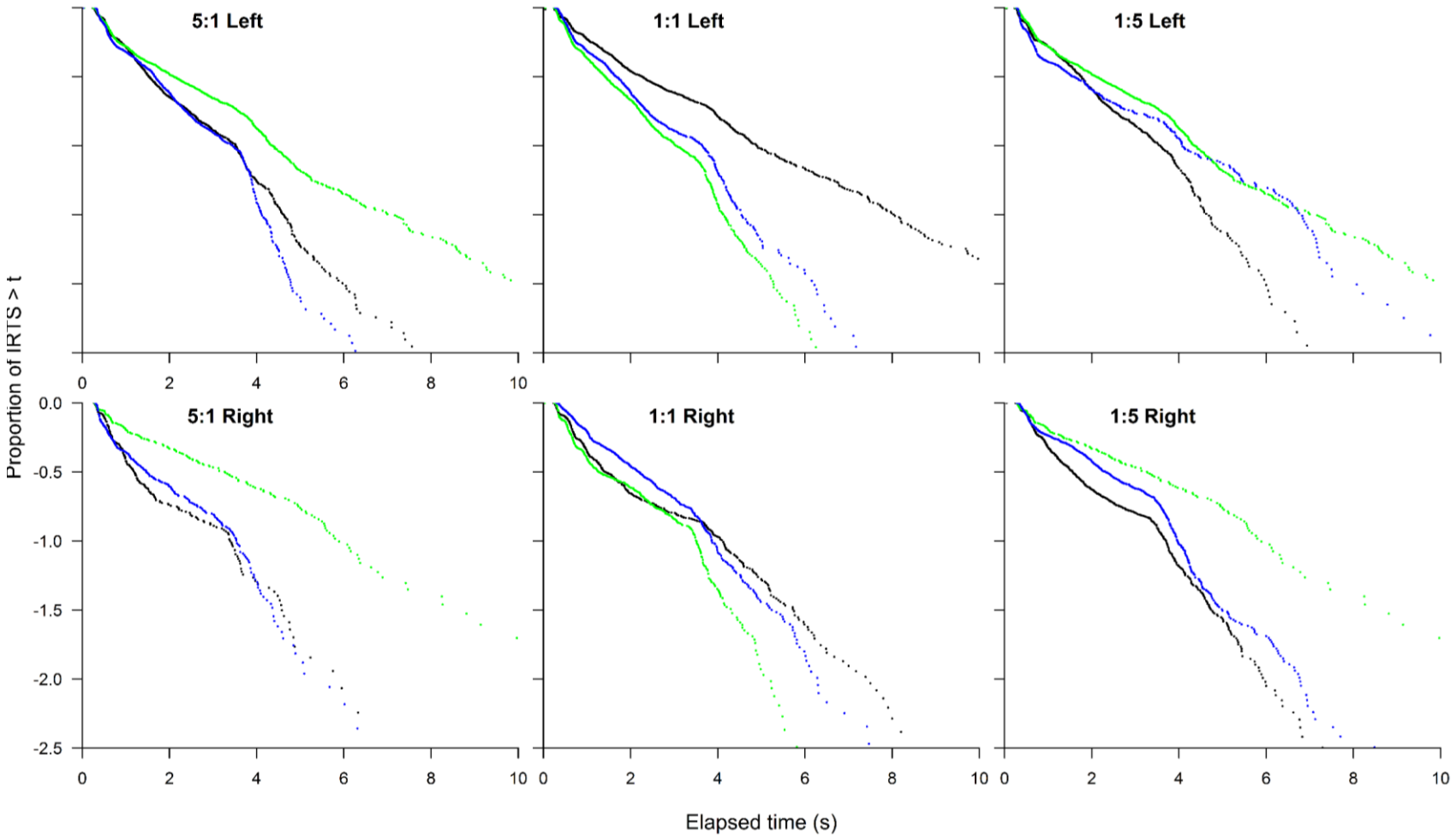

Figure 6.15. Log-survivor functions for Hen 25-6 for all conditions. Log proportions of IRTs greater than some time (t) are plotted as a function of elapsed time (t). Black lines represent the 85% condition, green lines the 95% condition and, blue lines the 100% condition.

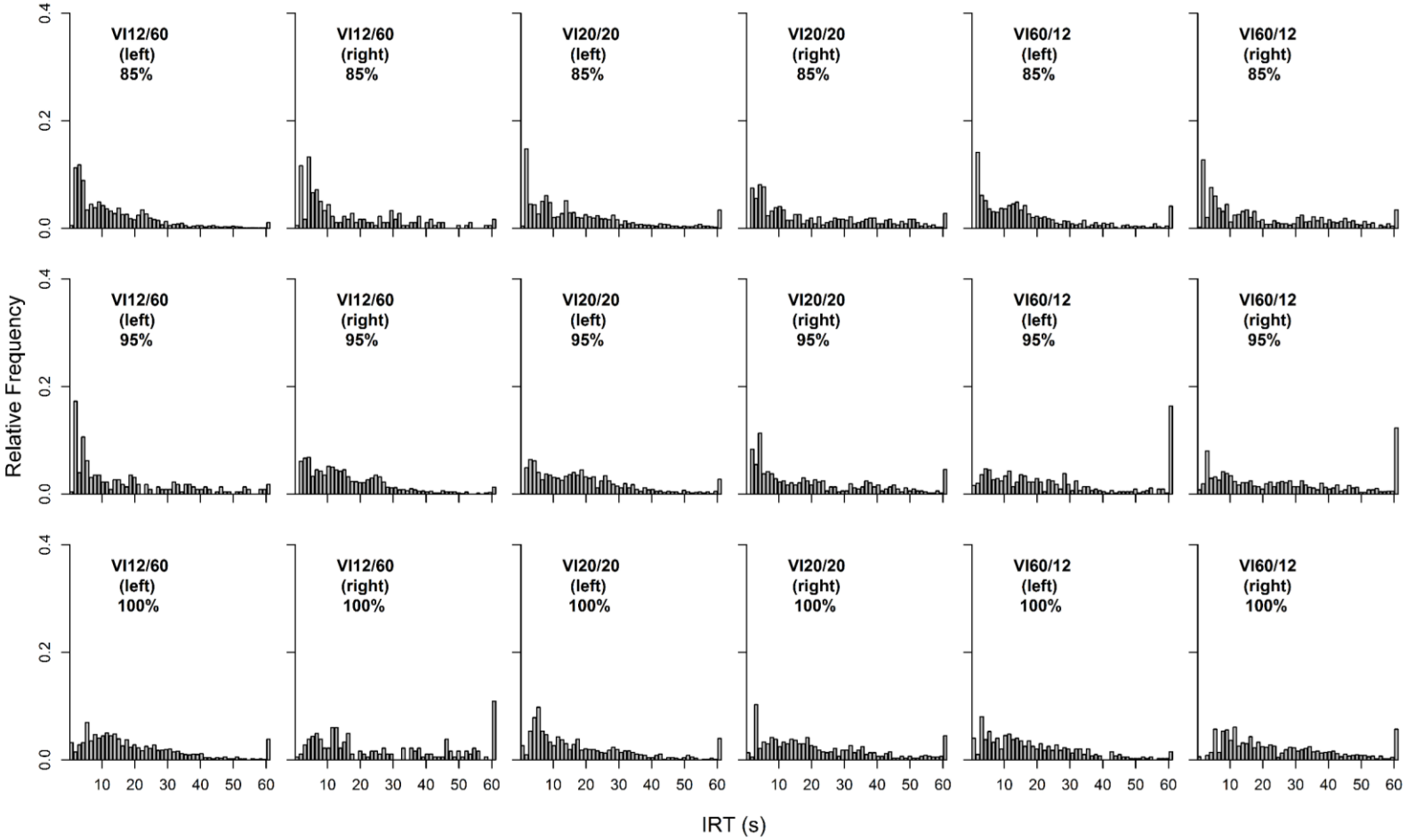

Figure 6.16. Relative frequency plots for Hen 25-1 during the 85%, 95% and 100% conditions. Relative frequency of IRTs is plotted as a function of bin size in 0.2-s bins.

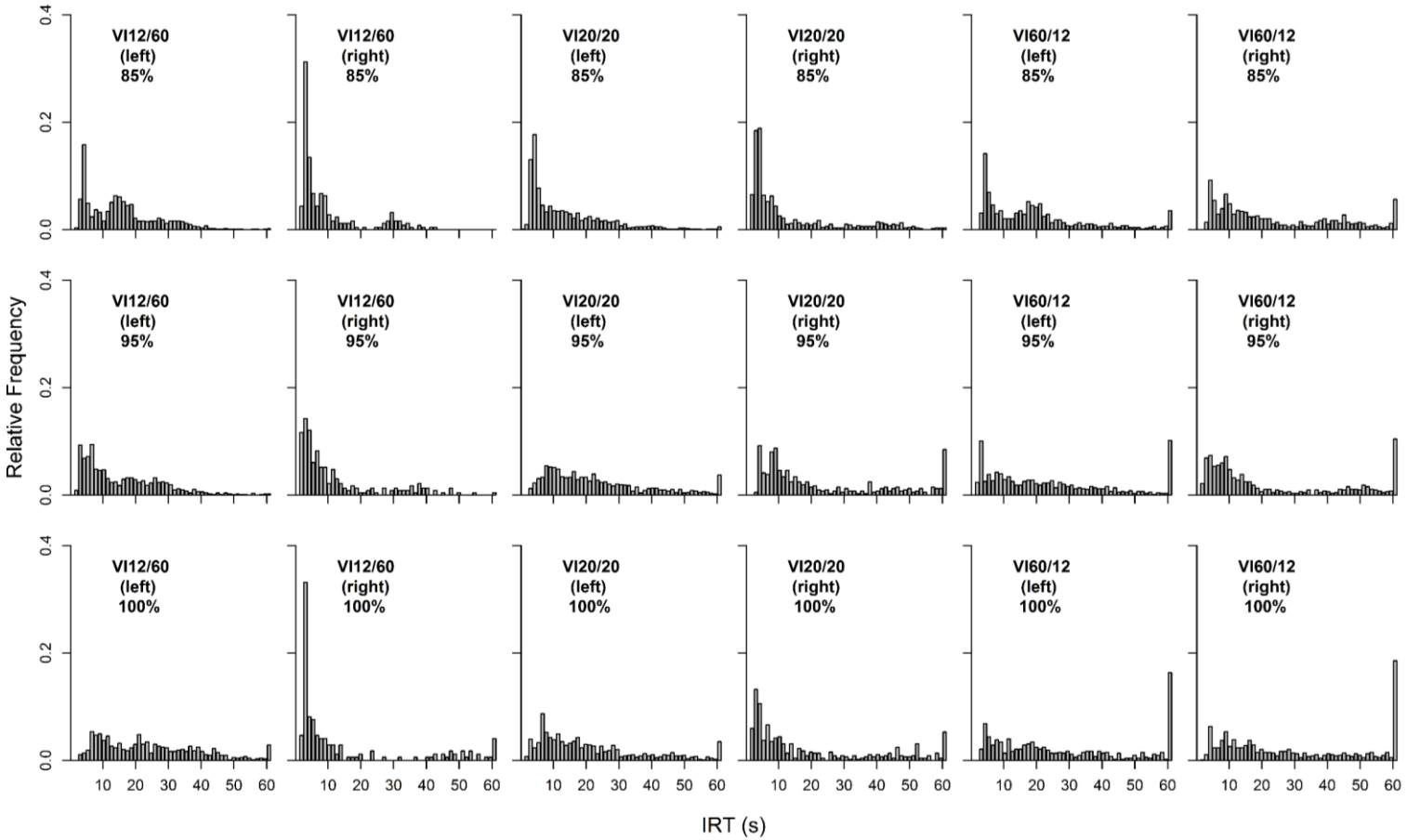

Figure 6.17. Relative frequency plots for Hen 25-2 during the 85%, 95% and 100% conditions. Relative frequency of IRTs is plotted as a function of bin size in 0.2-s.

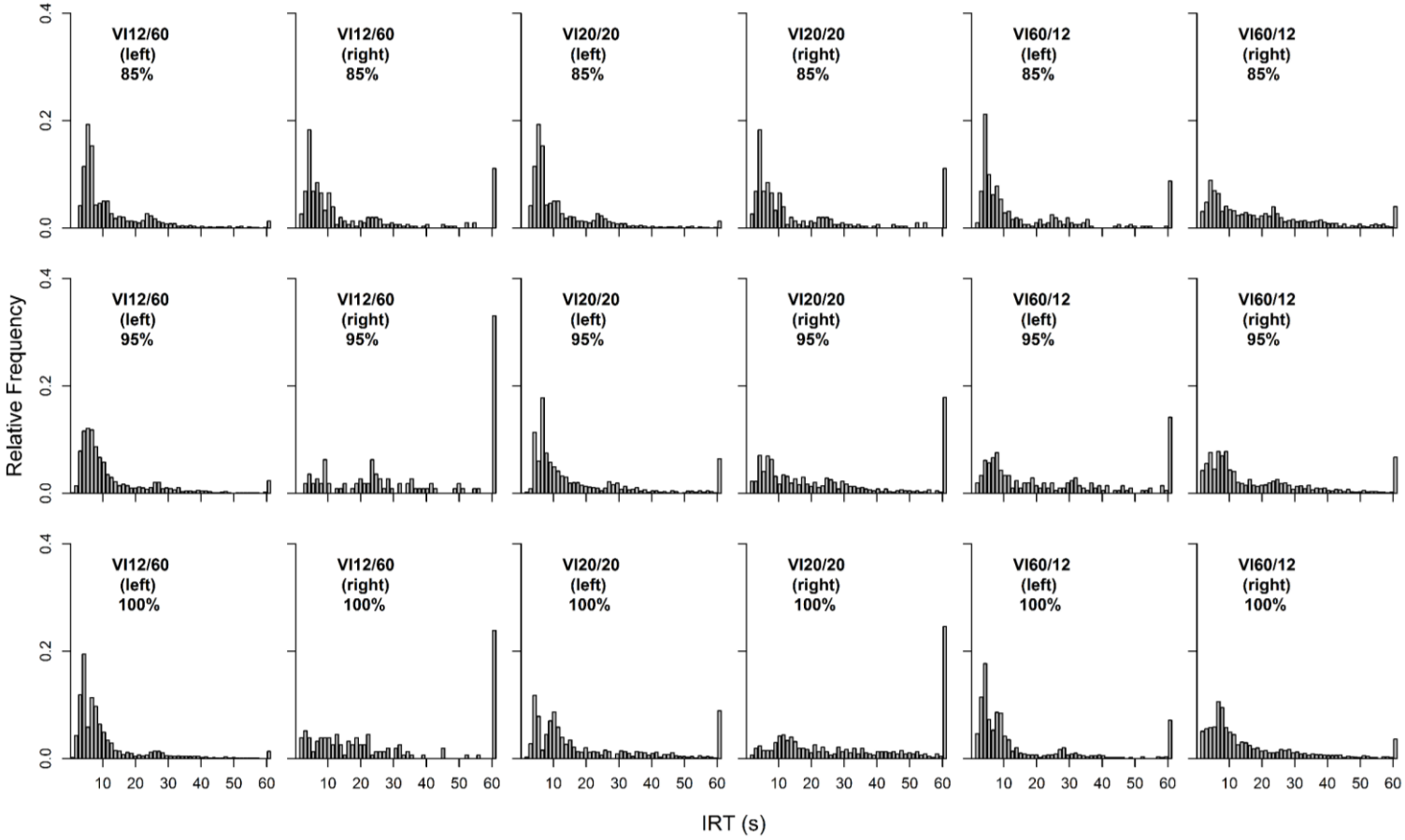

Figure 6.18. Relative frequency plots for Hen 25-3 during the 85%, 95% and 100% conditions. Relative frequency of IRTs is plotted as a function of bin size in 0.2-s.

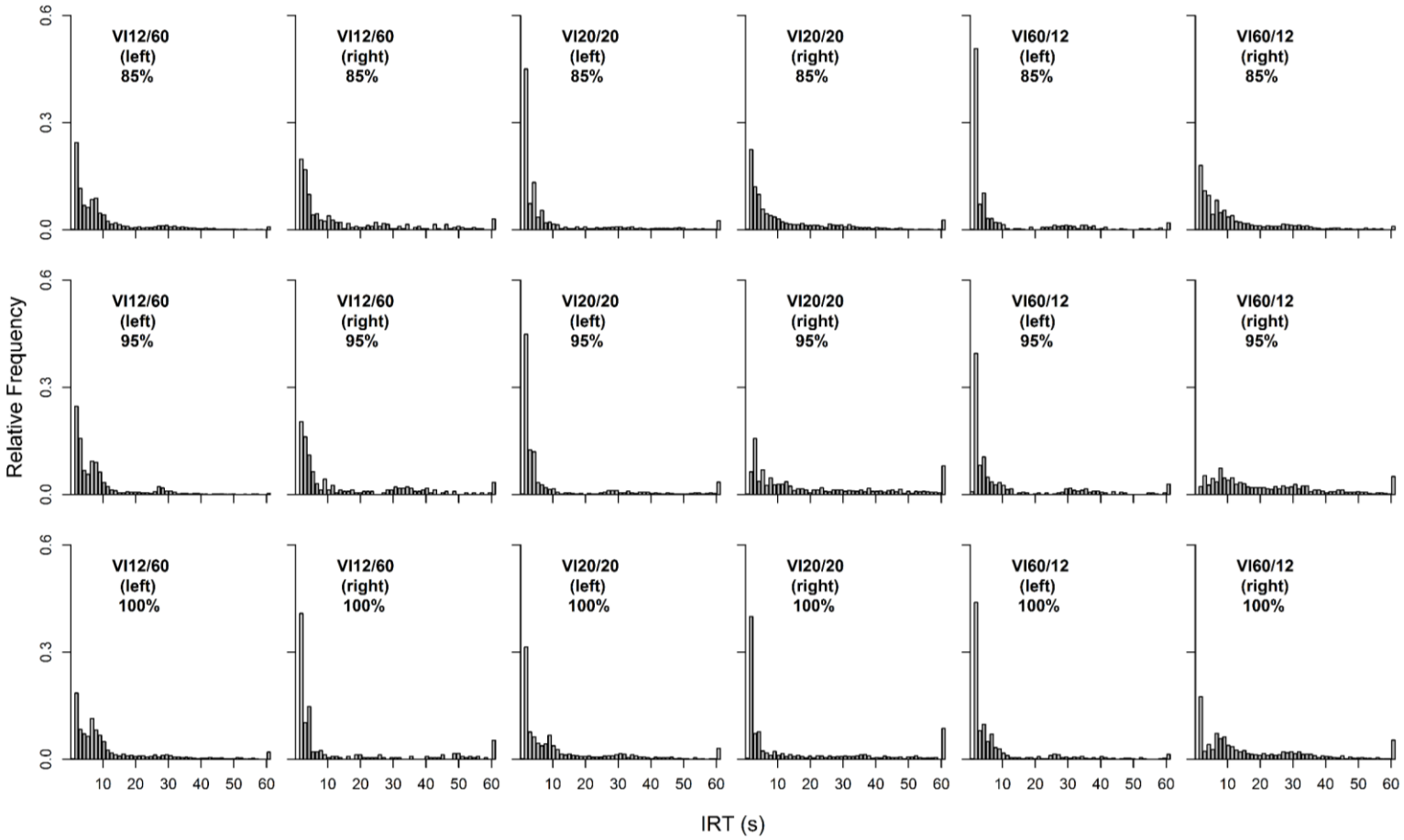

Figure 6.19. Relative frequency plots for Hen 25-4 during the 85%, 95% and 100% conditions. Relative frequency of IRTs is plotted as a function of bin size in 0.2-s.

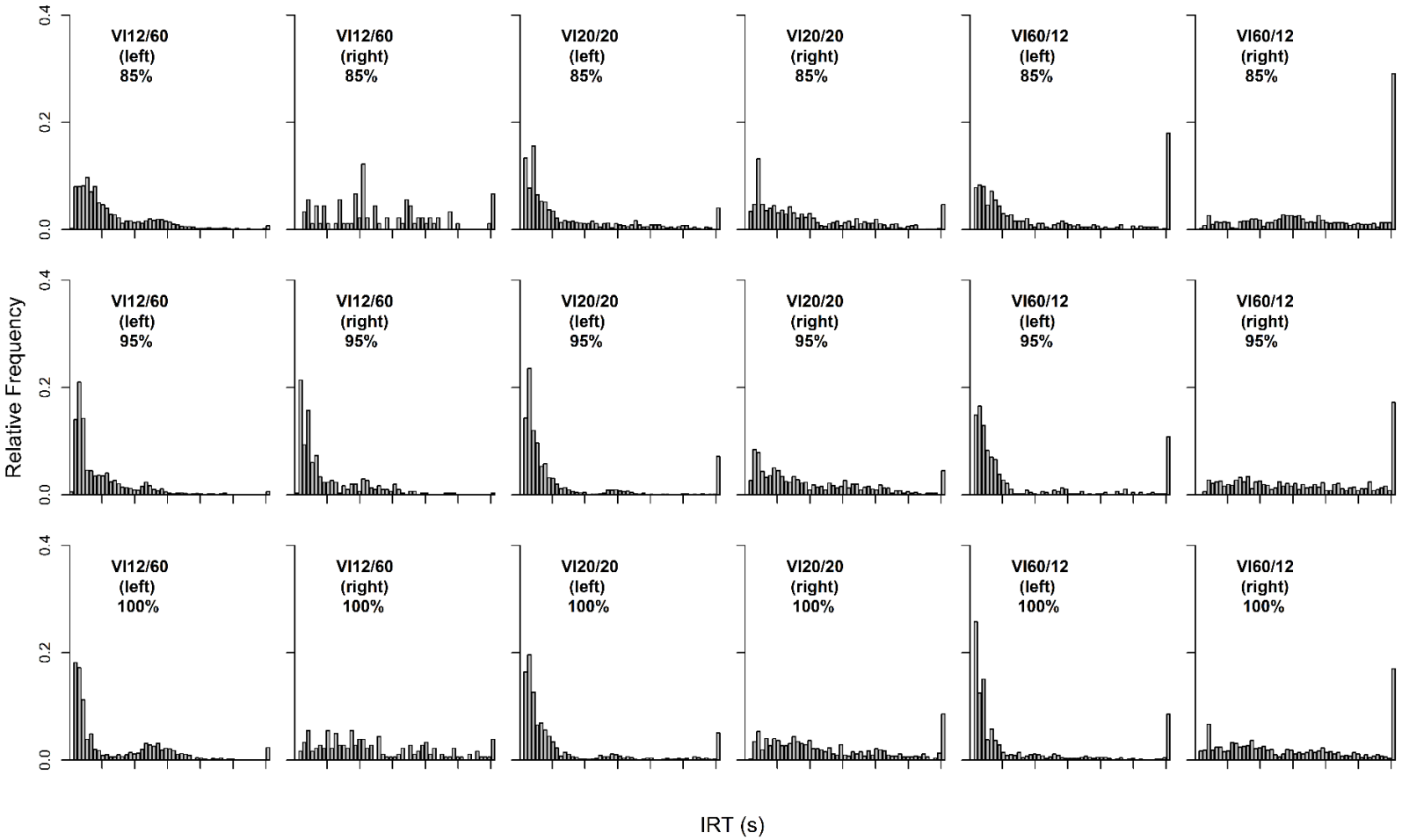

Figure 6.20. Relative frequency plots for Hen 25-5 during the 85%, 95% and 100% conditions. Relative frequency of IRTs is plotted as a function of bin size in 0.2-s bins.

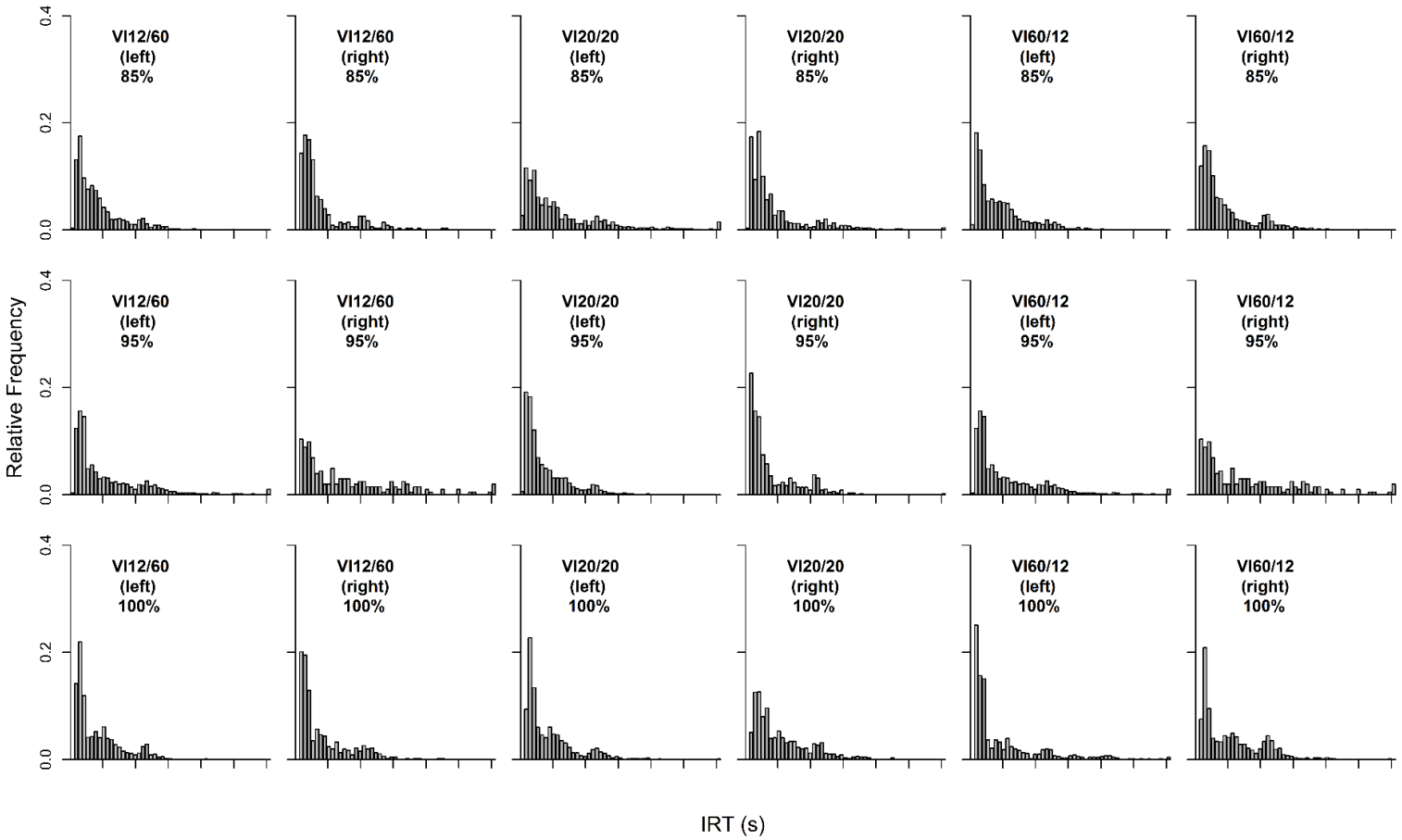

Figure 6.21. Relative frequency plots for Hen 25-6 during the 85%, 95% and 100% conditions. Relative frequency of IRTs is plotted as a function of bin size in 0.2-s.

Table 6.4.

The durations (s) of each component of the peck for the 85%, 95% and 100% bodyweight conditions, when the VI 20-s VI 20-s schedules were in effect, across 20% of all pecks during the last five stable sessions.

Hen	Condition	Beginning fixation to end fixation	Fixation to contact	Contact to no movement	Contact duration
25-1	85%	0.17	0.08	0.16	0.05
	95%	0.18	0.10	0.19	0.05
	100%	0.25	0.08	0.16	0.06
25-2	85%	0.23	0.10	0.17	0.06
	95%	0.19	0.05	0.20	0.04
	100%	0.19	0.08	0.16	0.06
25-3	85%	0.19	0.08	0.16	0.06
	95%	0.18	0.07	0.17	0.04
	100%	0.22	0.07	0.18	0.06
25-4	85%	0.21	0.10	0.20	0.06
	95%	0.26	0.06	0.19	0.08
	100%	0.28	0.08	0.21	0.09
25-5	85%	0.29	0.10	0.20	0.07
	95%	0.18	0.10	0.24	0.06
	100%	0.32	0.09	0.16	0.09
25-6	85%	0.19	0.09	0.18	0.12
	95%	0.28	0.06	0.21	0.08
	100%	0.28	0.07	0.22	0.09

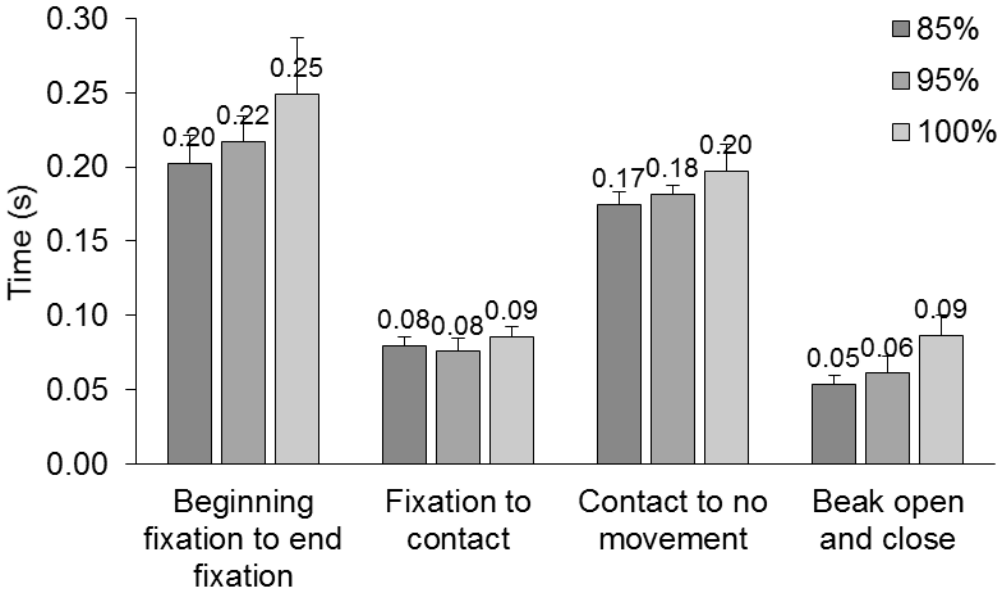

Figure 6.22. The mean durations of each component of the peck for the 85%, 95%, and 100% bodyweight conditions, across all hens. The error bars represent ±SEM.

Discussion

Summary

The aim of Experiment 6.1 was to assess the effect of systematically altering bodyweight while exposing hens to concurrent VI VI schedules. Based on the findings from Experiments 4.1 and 5.1 it was expected that species-specific behaviour (pecking) would be greater at lower bodyweights resulting in higher response rates. This was the case for 4/6 hens in this study who had higher absolute and relative response rates when bodyweight was made lower. For 3/6 of these hens increasing bodyweight increased sensitivity as measured by the parameter *a*; this was more noticeable when the GML was applied to response rather than time allocations. The frequency distributions of the IRTs showed that for the hens that tended to show increasing sensitivity as bodyweights increased, there were more IRTs in bins greater than 0.4 s. This was reflected on the log-survivor plots as the limbs were shallower when bodyweights were higher, indicating that more between-bout responses were occurring. Morphology analysis indicated that the peck components were longest in duration in the beginning fixation to end fixation for the 100% condition; longest in the 95% condition for the contact to no movement component; and similar across all bodyweights for both the fixation to contact and contact duration components.

Discussion

As stated above the results of this experiment showed that increasing bodyweight increased sensitivity as measured by the parameter *a* for 3/6 hens, this was more distinct for these hens when the GML was applied to response data rather than time allocation data. A review of matching research by Wearden and Burgess (1982) reported that undermatching was preeminent in the studies reviewed. Undermatching was also found in this experiment for most hens. However, as in previous studies using multiple schedules sensitivity approached matching as bodyweight increased. For example, both Charman and Davison (1983) and Herrnstein and Loveland (1974) found that sensitivity approached

strict matching (*a* = 1.0) as subjects working on multiple schedules were made less food deprived, indicating that decreasing deprivation increased the ability of some of the hens to match to the reinforcer contingencies. One study using concurrent schedules, Buckley and Rasmussen (2012) found that Zucker rats with an obese phenotype showed higher sensitivity to reinforcer rates than Zucker rats with a lean phenotype when working on concurrent schedules, indicating that a genetic phenotype of bodyweight functioned as an MO, similar to bodyweight that was manipulated in experimental conditions.

As stated above, not all hens in Experiment 6.1 showed increases in sensitivity as bodyweight increased. Wald and Cheney (1975) investigated matching behaviour of four pigeons responding on concurrent VI schedules. The pigeons were held at 73%, 80%, 87%, and 94% of free-feeding bodyweight. In contrast to the majority of hens in this study they found that as weight increased, relative response rate and the relative time spent on the rich schedule remained constant. This was a similar finding to Hen 25-5 and Hen 25-6 who did not display systematic changes in sensitivity as bodyweight was made higher.

The frequency distributions of the IRTs for this experiment showed that for the 4/6 hens that tended to show increasing sensitivity as bodyweights increased, there were more IRTs in bins greater than 0.4 s. As stated in the introduction, Davison (2004) showed that sensitivity values were highest at IRT values greater than 0.4 s, followed by values between 0 – 0.2 s and were the lowest for values around 0.2 – 0.4 s for pigeons working on concurrent VI VI schedules. Davison (2004) found that time allocation to alternatives were mainly determined by IRTs between .08 and 6.4 s and least by IRTs less than 0.8 s. The results of the present study are in line with Davison's findings, as conditions where the four hens that showed higher sensitivity (conditions at a higher bodyweight) showed more IRTs above 0.4 s.

Analysis of the log-survivor plots in this experiment found that they reveal a structure not evident in overall response rates. Specifically, responding was characterised by recurrent classes of IRTs, indicated by

the appearance of clusters of points around a given IRT. This structure is very like previously reported findings (Bennett, Hughes, & Pitts, 2007; Blough, 1963; Davison, 2004; Palya, 1992). These undulations indicate that the rates of extraneous behaviours emitted in between pecks might be quite variable. Extraneous behaviours could include scratching, pecking at bits of equipment, head tilting, etc. None of the log-survivor plots in this study showed the clear broken-stick pattern previously reported with rats (e.g., Shull, 2004). It is possible that, as suggested by Davison (2004), pigeon and hen key pecking may not be composed of clear bouts of engagement and non-engagement with responding. Davison (2004) put forward that the high sensitivity for longer IRTs greater than 0.8 s suggests that "pausing" and emitting extraneous responses may be differentially associated with higher reinforcer-rate alternatives rather than, as might be expected, lower rate alternatives. It is possible that at higher bodyweights hens emit more extraneous responses associated with the higher reinforcer-rate alternative, thereby improving the ability of the hens to respond sensitively to the reinforcer contingencies. If more extraneous behaviours, other than pecking, occur at higher bodyweights then this could be evident on the log-survivor plots. It is important to point out that all log-survivor plots did show undulations and peaks and troughs indicating that extraneous activities may take up reasonably consistent durations.

The log-survivor plots in this study are like the ones found in previous research. Bennett, Hughes, and Pitts (2007) investigated the effects of another MO (methamphetamine) on response rate using a microstructural analysis. They found that administration of methamphetamine decreased overall response rates and tended to shift the log-survivor functions upwards, decreasing their slope (for 3/4 subjects). In contrast, for one pigeon methamphetamine increased overall response rates and shifted the log-survivor functions downward slightly. They suggested that methamphetamine's rate-decreasing effects resulted from a decrease in the reinforcing-effectiveness of food. For Hens 25-1 – 25-4 response rates were slower when the hens were at higher

bodyweights, and for the same hens the log-survivor plots tended to shift upwards at higher bodyweights. This is a similar finding to what was reported by Bennett, Hughes, and Pitts (2007) for 3/4 of their subjects.

In addition, video analysis of the pecks of the hens on the 1:1 schedule showed that peck components tended to slow down when bodyweight increased, particularly in the beginning to end fixation component that occurs just prior to the peck being made. It is possible that a change in different classes of behaviour (extraneous behaviour) emitted between bouts of responding may be responsible for the differential sensitivity demonstrated at different bodyweights. Although there were some consistent patterns seen in the log-survivor plots, these were not always clear. It is possible that bodyweight as an MO does not have a blanket effect on all types of IRTs, suggesting that different classes of IRTs may not be functionally equivalent and MOs may not affect different classes of IRTs equally.

Although there were individual differences shown between the responding of the six hens, overall these results may indicate that increasing bodyweight may differentially effect the topography (and rate) of different classes of behaviours performed between bouts of pecks delivered under VI schedules leading to differences in the distributions of behaviour and therefore effect matching.

There are some limitations, however, to the present study. First, to obtain the most representative matching function, about five different concurrent variable interval variable interval schedules that vary in reinforcer ratios are typically used. Because of the amount of time that was required to obtain stability on each schedule and the difficultly keeping the hens in the appropriate weight range, it was only possible to use three different VI pairs within the time frame of this research.

A second limitation is that to maintain the hens at the different bodyweights it was necessary to feed them varying amounts of pellets outside of experimental sessions. Although hens were fed approximately 20 hours prior to experimental sessions, the open economy may have contributed to some of the individual differences obtained between hens,

particularly if there was any effect of the amount of pellets fed to each hen. Experiment 5.1 found that that 6/10 hens demonstrated an increased preference for the stimulus paired with high deprivation conditions (no pre-feeding) when measured by log ratios of responses, and they also had faster response rates on this stimulus.

The next experiment, Experiment 6.2, investigated what effect pre-feeding hens maintained at the same bodyweight would have on response rates. In summary, this study showed that manipulating bodyweight can affect concurrent schedule performance. This study also found that increasing levels of deprivation can negatively affect the ability of some hens to match behaviour to the reinforcement contingencies by increasing amounts of species-specific behaviour (as seen in Experiments 4.1 and 5.1, when bodyweight was decreased), and possibly also by decreasing extraneous behaviour.

Experiment 6.2: Pre-Feeding as a Motivating Operation for the Structure of Choice on Concurrent Schedules

Introduction

In Experiment 6.1 it was found that increasing bodyweight increased sensitivity as measured by the GML for 3/6 hens, and that these same hens had higher response rates and longer IRT durations when bodyweight was higher. Previous findings in this thesis have indicated that pre-feeding may have differential effects when bodyweights are lower, than when they are higher. For example, in Experiment 5.1, 5/5 of the 95% hens but only 3/5 of the 75% hens had higher rates of responding under no pre-feeding conditions during deprivation/correlation sessions. In addition, hens at 75% bodyweight tended to peck less variably across the screen when pre-fed, but the 95% hens did not exhibit the same change in the level of pecking.

Experiment 6.2 aimed to assess the effect of pre-feeding on concurrent schedule performance. The concurrent VI VI procedure was repeated for the 85% bodyweight condition. In addition, hens were exposed to a second condition where they were maintained at 85% bodyweight but were pre-fed 40 cc of wheat, 40 minutes prior to the experimental session starting.

Studies utilising pre-feeding in general, have produced mixed results; for example, Ferguson and Paule (1995) found no significant effect of pre-feeding intervals ranging from 0.25 to 6 hr before exposing rats to PR schedules. They concluded that this was related to the fact that the rats were maintained below their free-feeding bodyweight which could have been causing an increase in demand for food. However, other studies have found that pre-feeding can function robustly as an MO; e.g., Ladewig et al. (2002) found that rats worked harder to obtain water reinforcers, if water was provided only in the test situation. They concluded that the availability of a commodity used as a reinforcer, outside of the test situation, can significantly affect how fast animals respond for the reinforcer dependant on when access to the commodity is given.

Ladewig et al. (2002) found that demand slopes for a water reinforcer were steepest when water was provided immediately before and after an experimental session, and the slopes were shallowest when additional water was not provided at all (closed economy).

The aim of this experiment was to assess the effect that pre-feeding would have on elements of concurrent VI VI schedule performance of hens, compared to when bodyweight as an MO is manipulated. Based on the finding from Experiment 5.1 that 8/10 subjects had lower rates of responding under pre-feeding conditions during deprivation/correlation sessions, it was hypothesised that when hens were pre-fed they could demonstrate higher sensitivity values, similar to how hens that had higher response rates during Experiment 6.1 had higher sensitivity values. The same data analysis methods from Experiment 6.1 were used; specifically, response rates (overall and relative), IRTs and log-survivor plots to compare the findings between the two experiments.

Method

Subjects

The subjects in this experiment were the same hens from Experiment 6.1 and were maintained as outlined in Experiment 6.1. For pre-feeding conditions only (Conditions 4 – 6) hens were pre-fed 40 cc of wheat 40 minutes prior to experimental sessions. Hens 25-4 and 25-6 died of unrelated causes immediately prior to Condition 4 beginning and thus did not complete the pre-feeding conditions.

Apparatus

The apparatus was the same as outlined in Experiment 6.1.

Procedure

The procedure used was the same as outlined in Experiment 6.1. Table 6.5 presents the order of the experimental conditions, together with the bodyweight percentage, whether the hens were pre-fed or not, and the number of days each condition was in effect for each hen.

Table 6.5.

The order of the experimental conditions, together with the bodyweight percentage, and the number of days each condition was in effect for each hen.

Condition	VI Pair (s)	Pre-feeding	Hen 25-1	Hen 25-2	Hen 25-3	Hen 25-4	Hen 25-5	Hen 25-6
1	20/20	No	72	67	69	69	60	54
2	12/60	No	44	44	44	43	45	40
3	60/12	No	22	18	20	22	19	20
4*	20/20	Yes	44	49	44	-	60	-
5*	12/60	Yes	77	82	58	-	45	-
6*	60/12	Yes	23	15	24	-	19	-

Results

Raw data from all conditions are presented in Appendix F. The data from only the last five stable sessions of each condition were analysed and presented here.

Overall response rates

The overall response rates were calculated by dividing the total session time by the total number of responses. Figure 6.23 presents the overall response rates for the 85% condition and the 85% pre-feeding condition, averaged over the last five stable sessions, for each condition and each bird. The error bars represent the standard errors. The left panel presents the data from the 85% condition and the right panel presents data from the 85% pre-feeding condition. From left to right on each graph is presented the data for the VI 12-s, VI 60-s schedule (1:5 reinforcer ratio); the data for the VI 20-s VI 20-s schedule (1:1 reinforcer ratio); and the data for the VI 60-s, VI 12-s schedule (5:1 reinforcer ratio). All hens showed similar overall response rates across both the 85% and 85% pre-feeding conditions.

Left and right stimulus response rates

Response rates for both the left and right stimuli were calculated separately by dividing the total response counts by the time allocated to that stimulus. Figure 6.24 presents these response rates for each

condition and each bird. The error bars represent the standard error of the mean. The left panel presents the data from the 85% condition and the right panel presents data from the 85% pre-feeding condition. Like the overall response rates, the hens showed very similar patterns in left and right stimulus response rates across both the 85% condition and the pre-feeding condition, when the reinforcer ratios were 1:1 and 1:5 respectively. However, when the 5:1 schedule was in effect, the hens were faster on the rich (left) stimulus than they were on the rich (right) stimulus when the 1:5 schedule was effect. When the hens were pre-fed they showed more separation between the left and right response rates than when they were not pre-fed.

Generalised Matching Law

Figures 6.25 and 6.26 show generalised matching data from all hens. Figure 6.25 presents log response ratios plotted as a function of log reinforcer ratios for each condition. Figure 6.26 presents log time allocation ratios plotted as a function of log reinforcer ratios for each condition. Least squares regression lines are drawn on both figures, and their slopes and intercepts (with their standard errors) are given in Tables 6.6 and 6.7. As can be seen on Figures 6.25 and 6.26, all hens tended to show a left bias in both time and response allocation.

For both response and time allocations, the percentages of variance accounted for by the GML were greater than 96.4%.

Figure 6.25 presents the estimates of sensitivity *a* derived from the GML (Equation 1) applied to the response allocations to each stimulus during the last five stable sessions of each condition for each hen. For allocation of responses, sensitivity values ranged from 0.43 to 1.22 across the 85% conditions and 0.80 to 1.28 across the 85% pre-feeding condition. As shown on Figure 6.25, estimates of sensitivity were highest in the pre-feeding condition for all hens.

Figure 6.27 presents the estimates of sensitivity *a* derived from the GML (Equation 1) applied to the time allocations to each stimulus during the last five stable sessions of each condition for each hen. For allocation of responses, sensitivity values ranged from 0.47 to 0.87 for the 85%

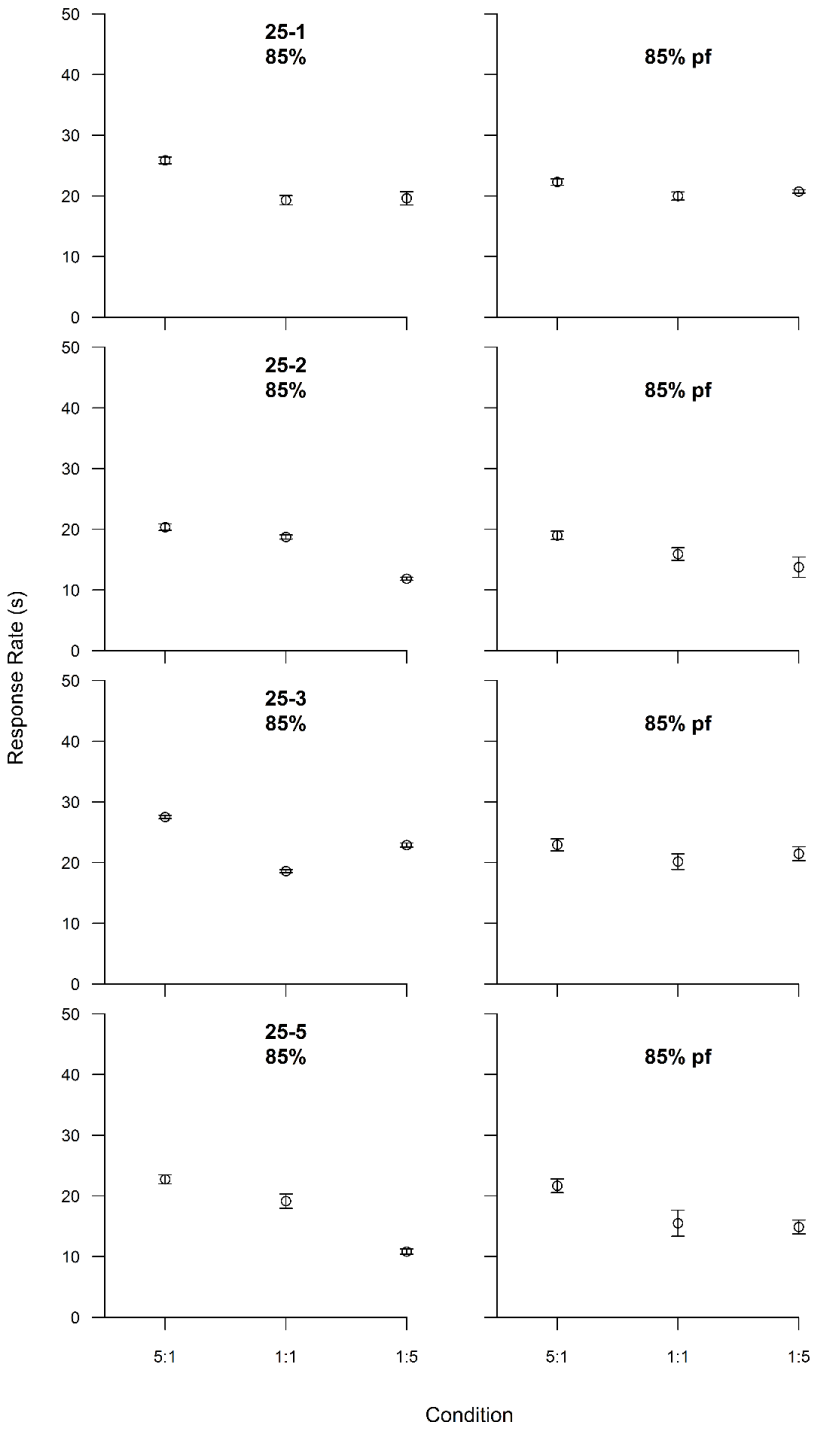

Figure 6.23. Overall response rates (per s) for the left (square) and right (circle) stimulus averaged over the last five stable sessions of each condition, for the 85% bodyweight (left panel) and 85% pre-feeding (right panel) conditions, for each hen and each VI pair. The error bars represent ±SEM.

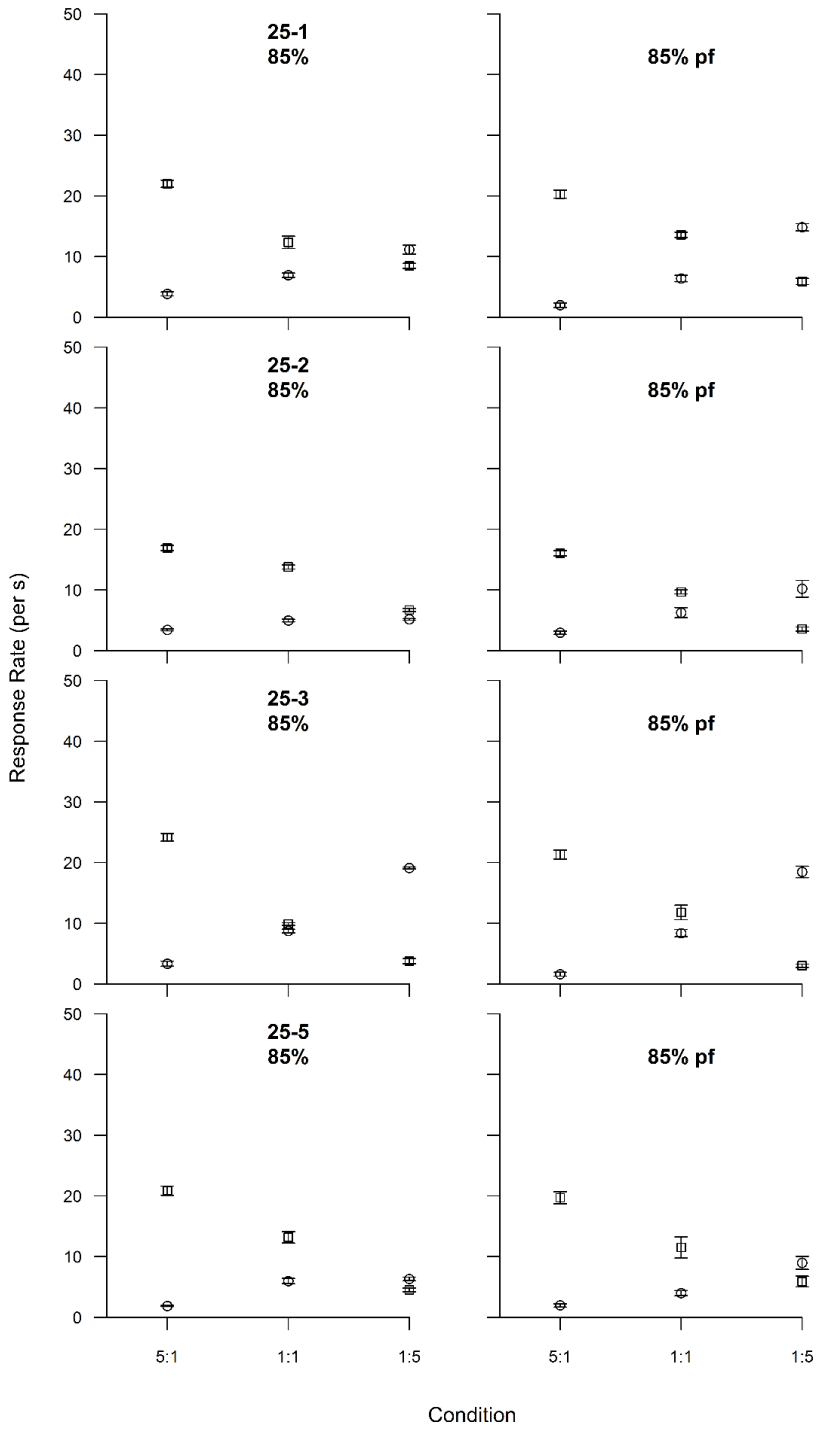

Figure 6.24. Local response rates (per s) for the left (square) and right (circle) stimulus averaged over the last five stable sessions of each condition, for the 85% bodyweight (left panel) and 85% pre-feeding (right panel) conditions, for each hen and each VI pair. The error bars represent ±SEM.

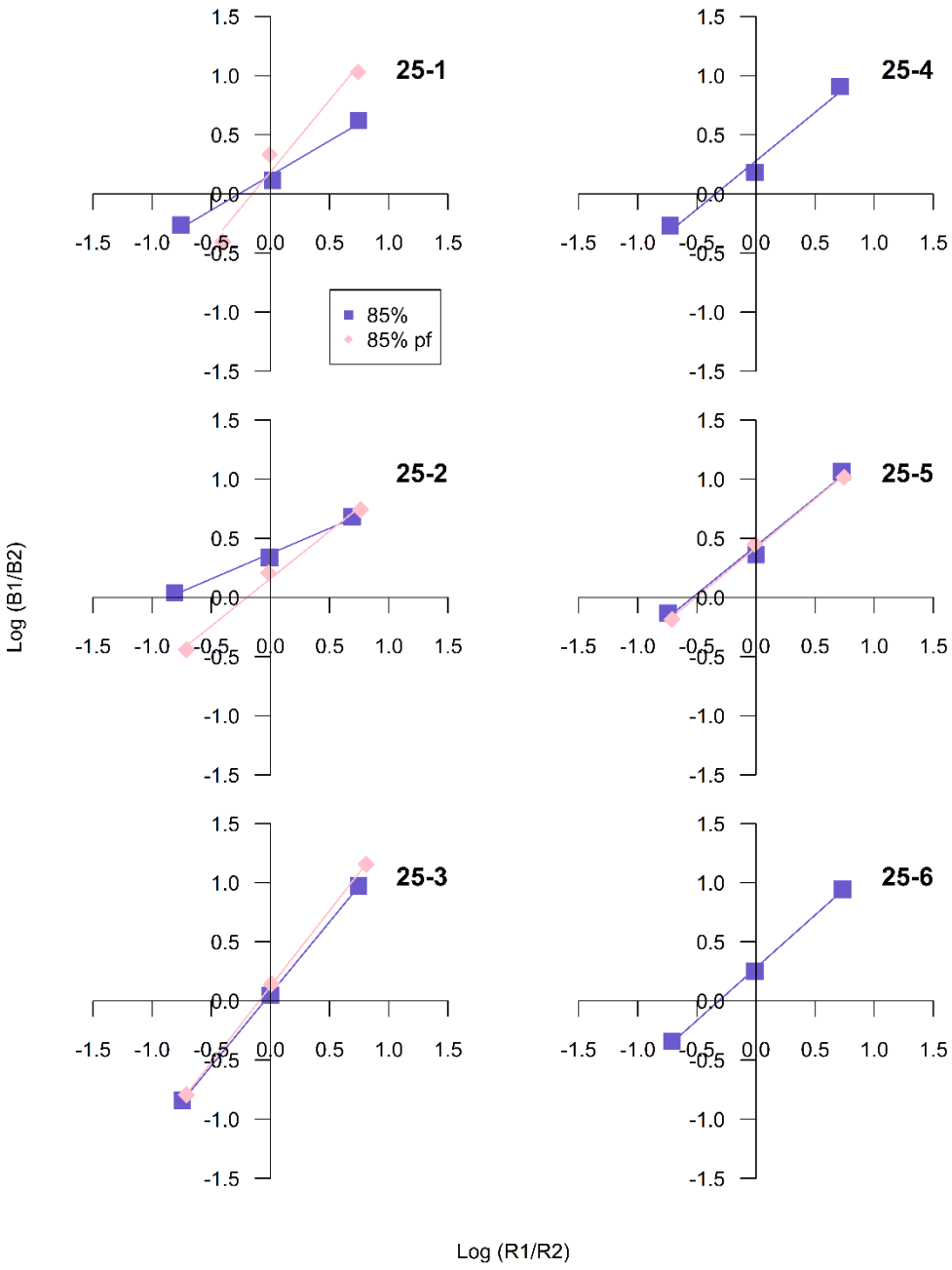

Figure 6.25. Log response ratios plotted as a function of log reinforcer ratios for the 85% and 85% pre-feeding conditions. Least squares regression lines are drawn, and their slopes and intercepts (with their standard errors) are given in Table 6.6.

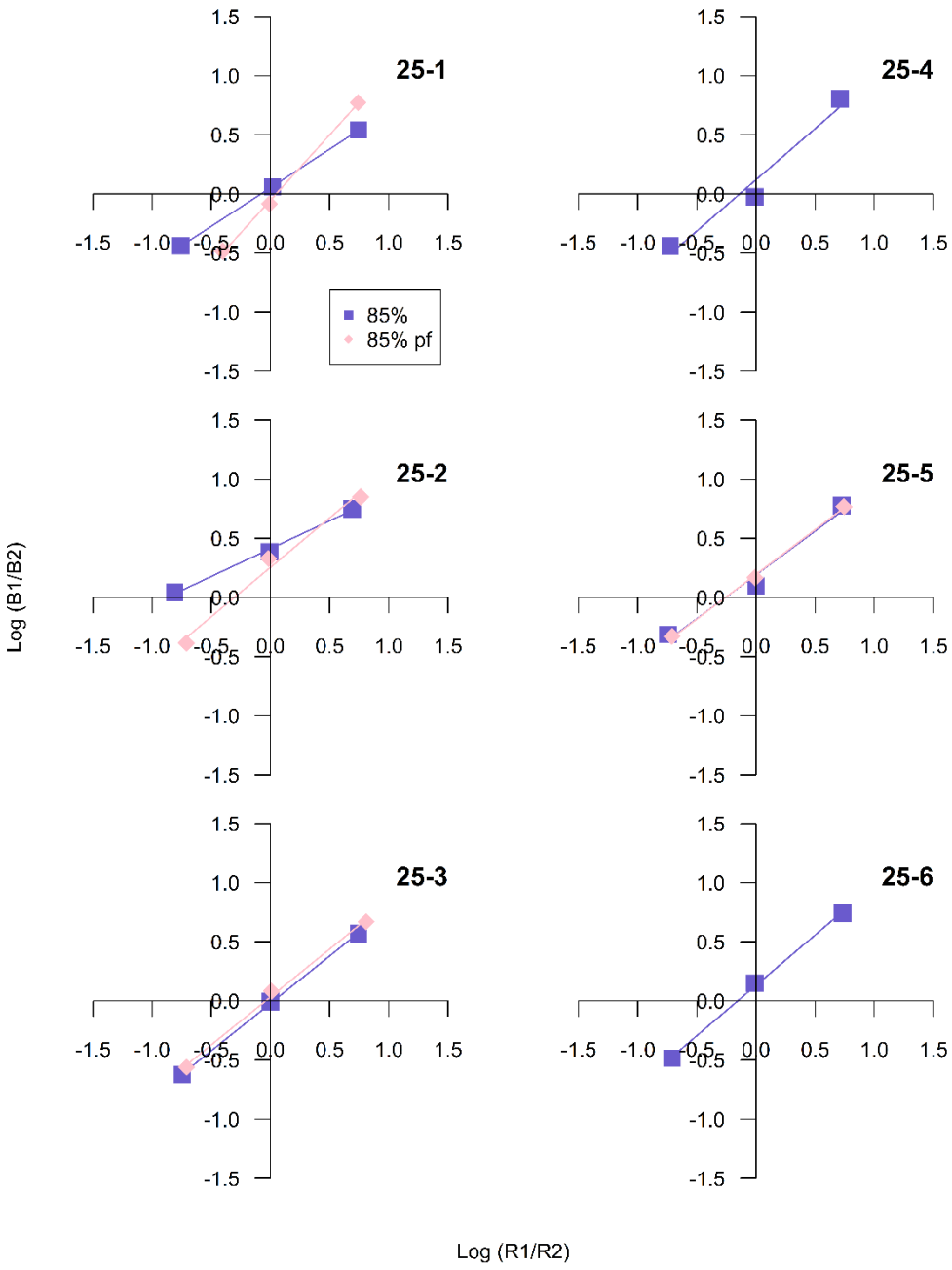

Figure 6.26. Log time ratios plotted as a function of log reinforcer ratios for each condition. Least squares regression lines are drawn, and their slopes and intercepts (with their standard errors) are given in Table 6.7.

Table 6.6.

Estimates of sensitivity (a) and bias log c derived from the Generalised Matching Law (Equation 1) applied to the response allocations to each stimulus during the last five stable sessions of each condition, for each hen. The standard error and the proportion of variance accounted for are also presented.

Hen	Condition	*a*	Log *c*	se	% VAC
25-1	85%	0.59	0.16	0.06	99.0
	85% pf	1.21	0.19	0.19	96.4
25-2	85%	0.43	0.37	0.04	99.3
	85% pf	0.80	0.16	0.07	99.2
25-3	85%	1.22	0.06	0.02	100.0
	85% pf	1.28	0.12	0.01	100.0
25-4	85%	0.82	0.28	0.11	98.2
25-5	85%	0.81	0.44	0.09	98.8
	85% pf	0.83	0.42	0.05	99.7
25-6	85%	0.89	0.28	0.03	99.9
Mean	85%	0.79	0.26	0.06	99.20
	85% pf	1.03	0.22	0.08	98.83

Table 6.7.

Estimates of sensitivity (a) and bias log c derived from the Generalised Matching Law (Equation 1) applied to the time allocations to each stimulus during the last five stable sessions of each condition, for each hen. The standard error and the proportion of variance accounted for are also presented.

Hen	Condition	*a*	Log *c*	se	% VAC
25-1	85%	0.65	0.05	0.01	100.0
	85% pf	1.10	-0.05	0.03	99.9
25-2	85%	0.47	0.41	0.03	99.7
	85% pf	0.84	0.26	0.11	98.5
25-3	85%	0.80	-0.02	0.02	100.0
	85% pf	0.81	0.03	0.05	99.7
25-4	85%	0.87	0.12	0.17	96.5
25-5	85%	0.74	0.19	0.11	97.8
	85% pf	0.76	0.20	0.03	99.9
25-5	85%	0.85	0.13	0.03	99.9
Mean	85%	0.73	0.15	0.06	98.97
	85% pf	0.88	0.11	0.05	99.48

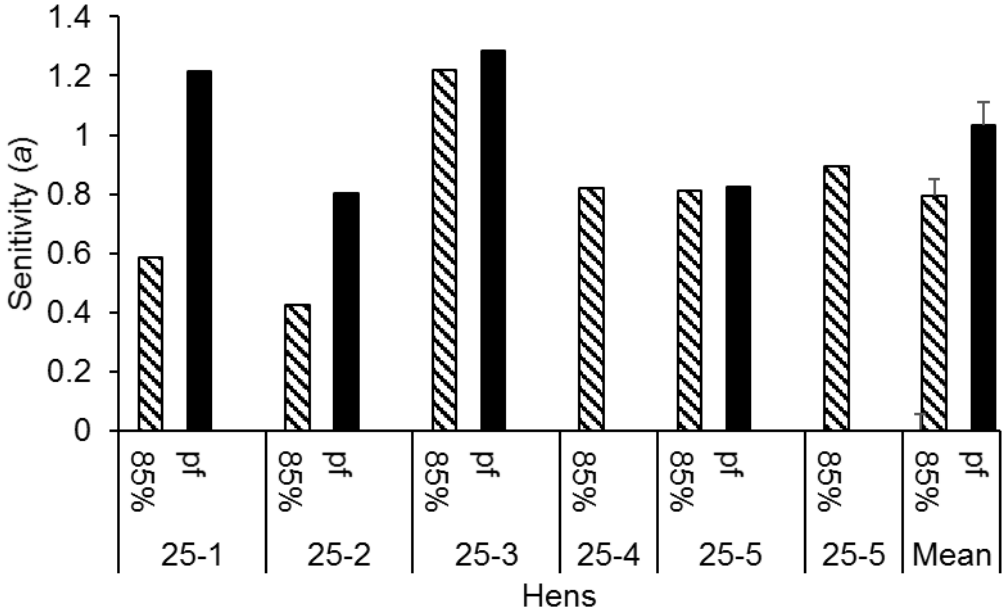

Figure 6.27. Estimates of sensitivity (*a*) derived from the Generalised Matching Law (Equation 1) applied to the response allocations to each stimulus during the last five stable sessions of each condition, for each hen (25-1 – 25-6). The error bars represent ±SEM.

condition and 0.76 to 1.10 for the 85% pre-feeding condition. As shown on Figure 6.28, estimates of sensitivity were highest in the pre-feeding condition for all hens.

Figure 6.29 presents the estimates of bias log *c* derived from the GML (Equation 1) applied to the response allocations to each stimulus during the last five stable sessions of each condition, for each hen. For allocation of responses bias values ranged from 0.06 to 0.44 across the 85% condition and 0.12 to 0.42 across the 85% pre-feeding condition. As shown on Figure 6.29, estimates of bias were highest in the 85% condition for Hens 25-1 and 25-2 and highest in the 85% pre-feeding condition for Hens 25-3 and 25-5. On average, the highest bias value was seen in the 85% condition.

Figure 6.30 presents the estimates of bias, log *c* derived from the GML (Equation 1) applied to the time allocations to each stimulus during the last five stable sessions of each condition, for each hen. For allocation of responses bias values ranged from -0.02 to 0.41 for the 85% condition

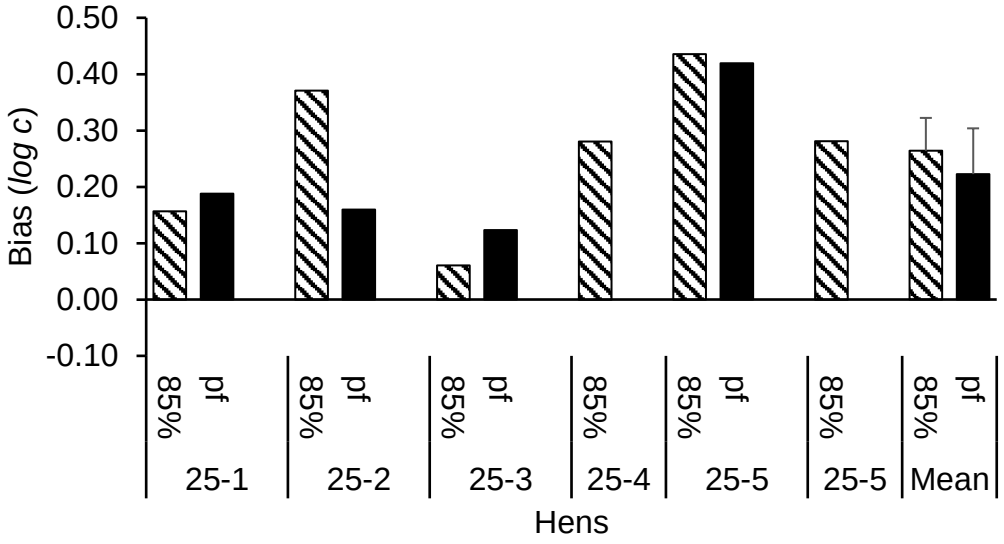

Figure 6.28. Estimates of bias log *c* derived from the Generalised Matching Law (Equation 1) applied to the response allocations to each stimulus during the last five stable sessions of each condition, for each hen (25-1 – 25-6). The error bars represent ±SEM.

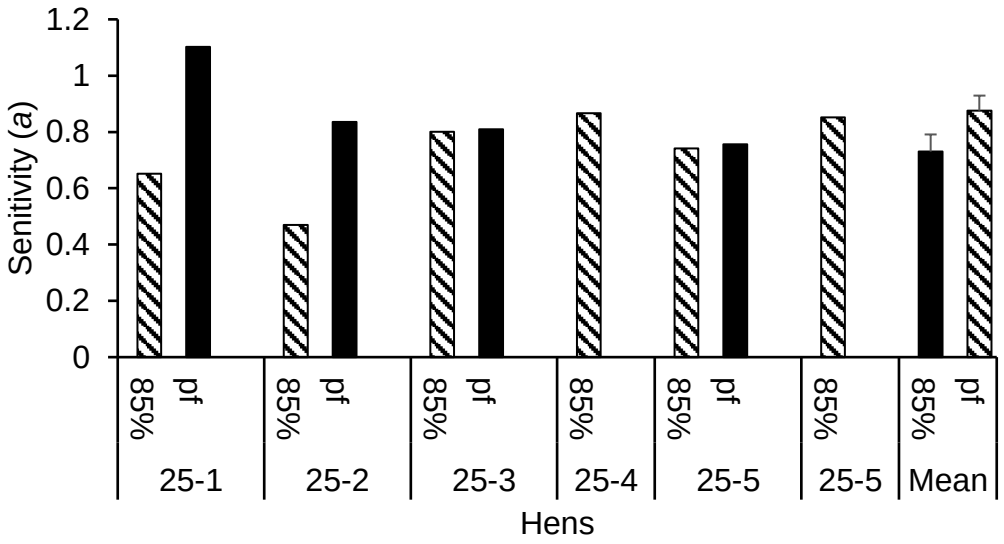

Figure 6.29. Estimates of sensitivity (*a*) derived from the Generalised Matching Law (Equation 1) applied to the time allocations to each stimulus during the last five stable sessions of each condition, for each hen (25-1 – 25-6). The error bars represent ±SEM.

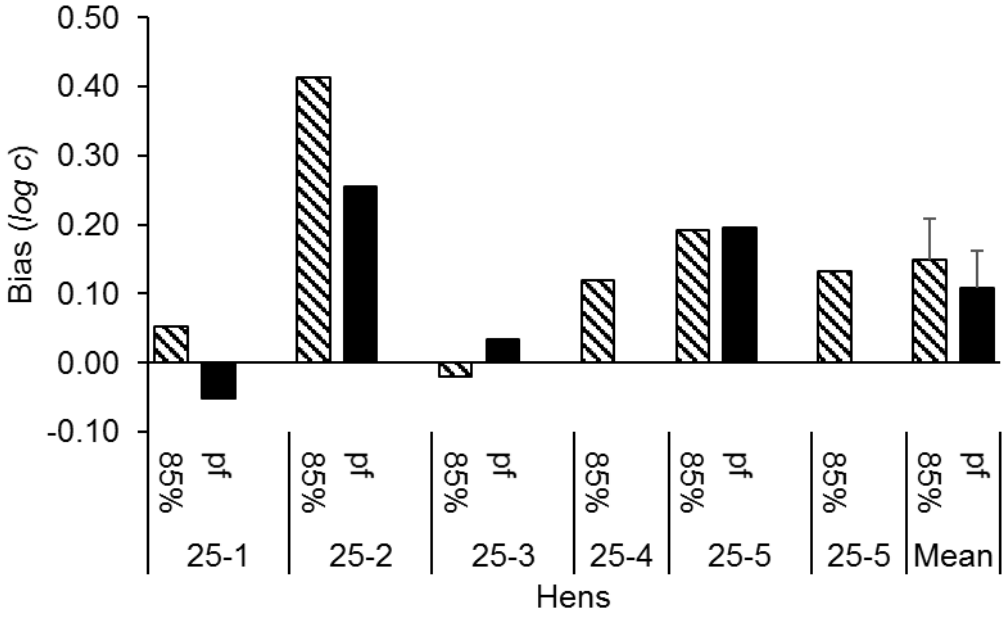

Figure 6.30. Estimates of bias log *c* derived from the Generalised Matching Law (Equation 1) applied to the time allocations to each stimulus during the last five stable sessions of each condition, for each hen (25-1 – 25-6). The error bars represent ±SEM.

and -0.05 to 0.26 for the 85% pre-feeding condition. As shown on Figure 6.30, estimates of bias were highest in the 85% condition for Hens 25-1 and 25-2 and highest in the 85% pre-feeding condition for Hens 25-3 and 25-5. On average, the highest bias value was seen in the 85% condition. In summary, all hens tended to show a left bias in both time and response allocation, and estimates of sensitivity were highest in the pre-feeding condition for all hens for both time and response allocation.

Inter-response times

Figure 6.31 displays relative frequencies of different classes of IRTs (in 0.2-s bins) for Hen 25-1 averaged over the last five stable sessions for each condition, for each VI pair. Figures 6.32 to 6.36 present the IRT distributions for Hens 25-2, 25-3, 25-4, and 25-6. As shown on Figure 6.31, the shape of the IRT distribution differs between the 85% condition and the 85% pre-feeding condition, for Hen 25-1. In the 85% condition, there

tended to be more IRTs in the 0 – 0.4 s bins. In the 85% pre-feeding condition, there were more IRTs at values above 0.4 s. A similar pattern was observed for Hens 25-2 and 25-3. As shown on Figure 4.17, Hen 25-5 tended to show similar IRT distributions when pre-fed and when not pre-fed.

Log survivor plots

Figure 6.37 displays a log survivor plot for Hen 25-1 showing the 85% and 85% pre-feeding conditions. As can be seen on Figure 6.37, for all schedules the shape of the log-survivor plot limbs were similar; however, the log-survivor limbs were shifted upwards for the pre-feeding conditions. The same finding was evident for all hens that completed the pre-feeding condition: the log survivor limbs were shallower, indicating more between-bout responses, when the hens were pre-fed than when they were not.

Discussion

The aim of this experiment was to assess the effect that pre-feeding had on elements of concurrent VI VI schedule performance of hens. The same data analysis methods from Experiment 6.1 were used, specifically, response rates (overall and relative), IRTs, and log-survivor plots to compare the findings between the two experiments.

Overall, the results showed that pre-feeding increased sensitivity as measured by the parameter *a* for all four hens; this was more noticeable when the GML was applied to response data than when it was applied to time data. This indicates that pre-feeding affected the hens' ability to match response and time allocation to the reinforcers delivered.

Although overall response rates during the pre-feeding condition tended to resemble those for the 85% bodyweight condition and remained higher than the previous 95% and 100% bodyweight conditions, the distribution of left and right response rates showed that hens matched

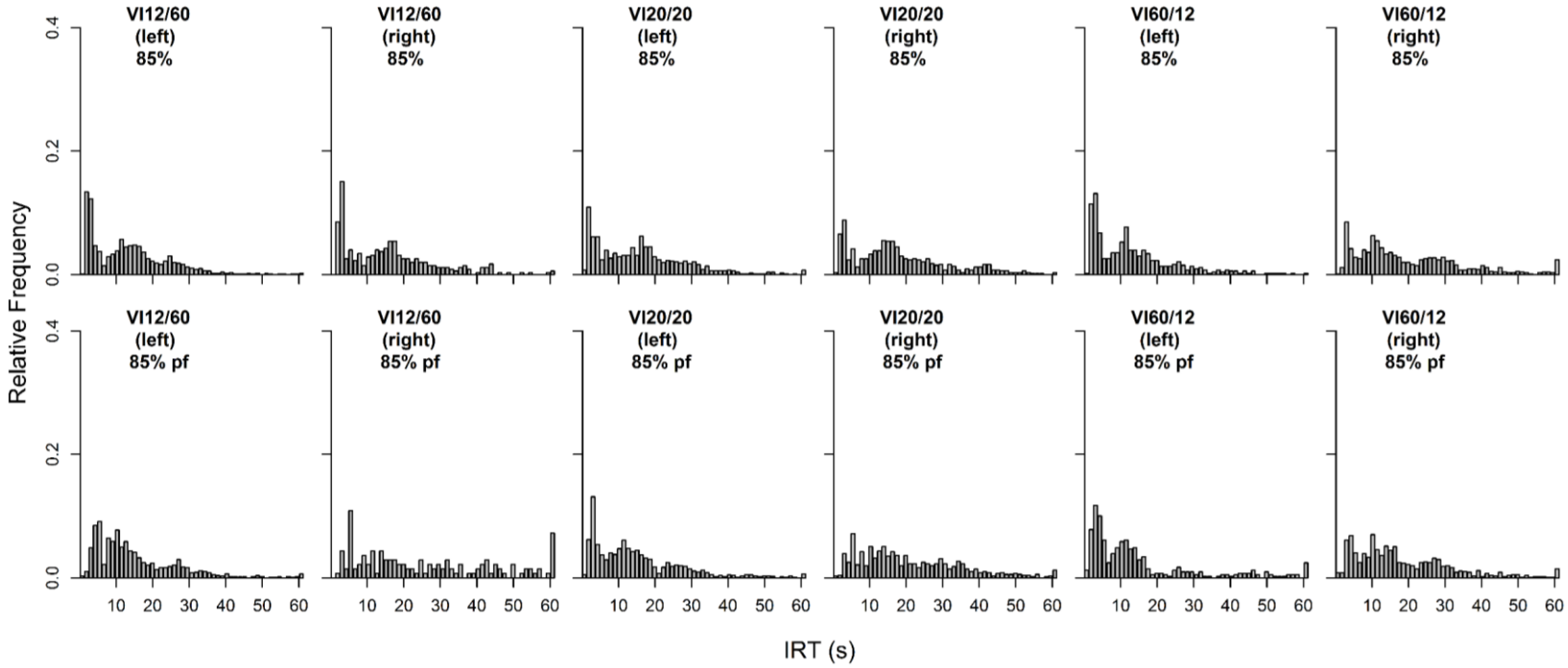

Figure 6.31. Relative frequency plots for Hen 25-1 during the 85% and 85% pre-feeding conditions. Relative frequency of IRTs is plotted as a function of bin size in 0.2 s.

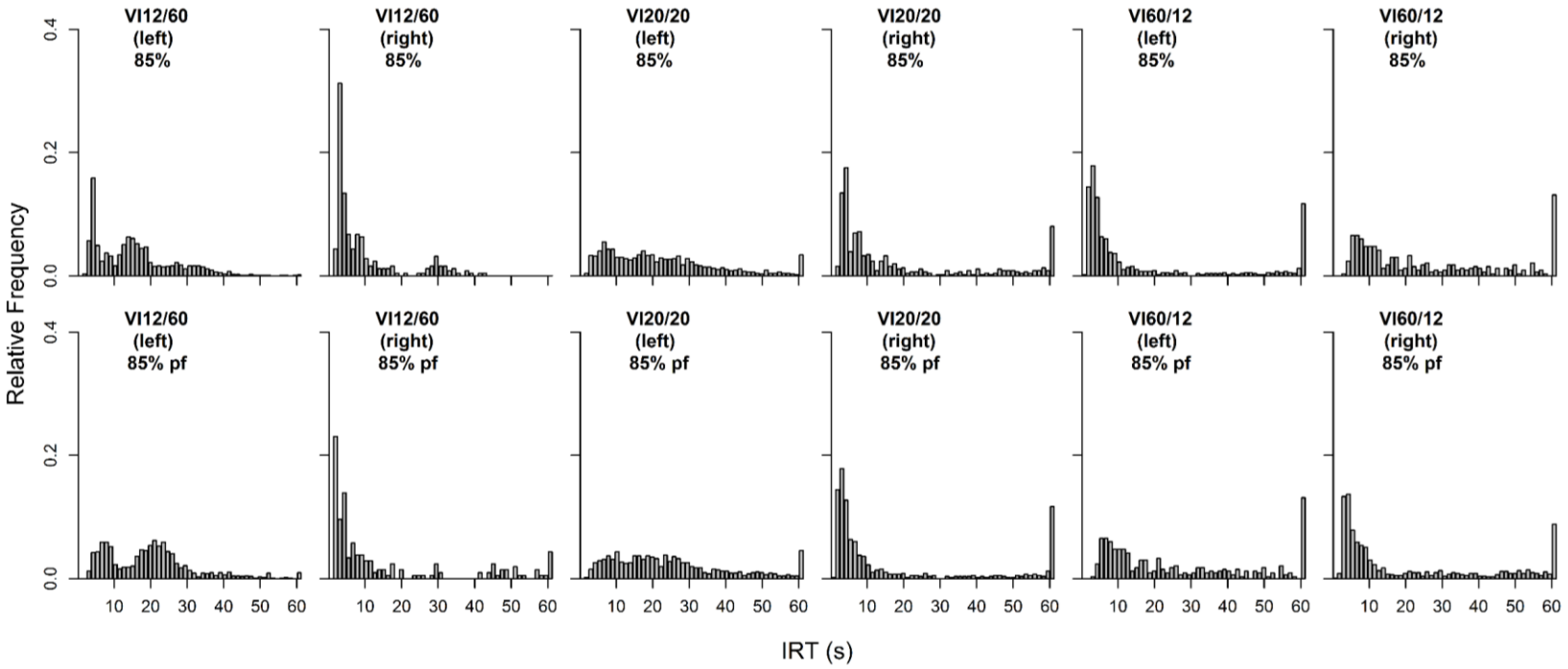

Figure 6.32. Relative frequency plots for Hen 25-2 during the 85% and 85% pre-feeding conditions. Relative frequency of IRTs is plotted as a function of bin size in 0.2 s.

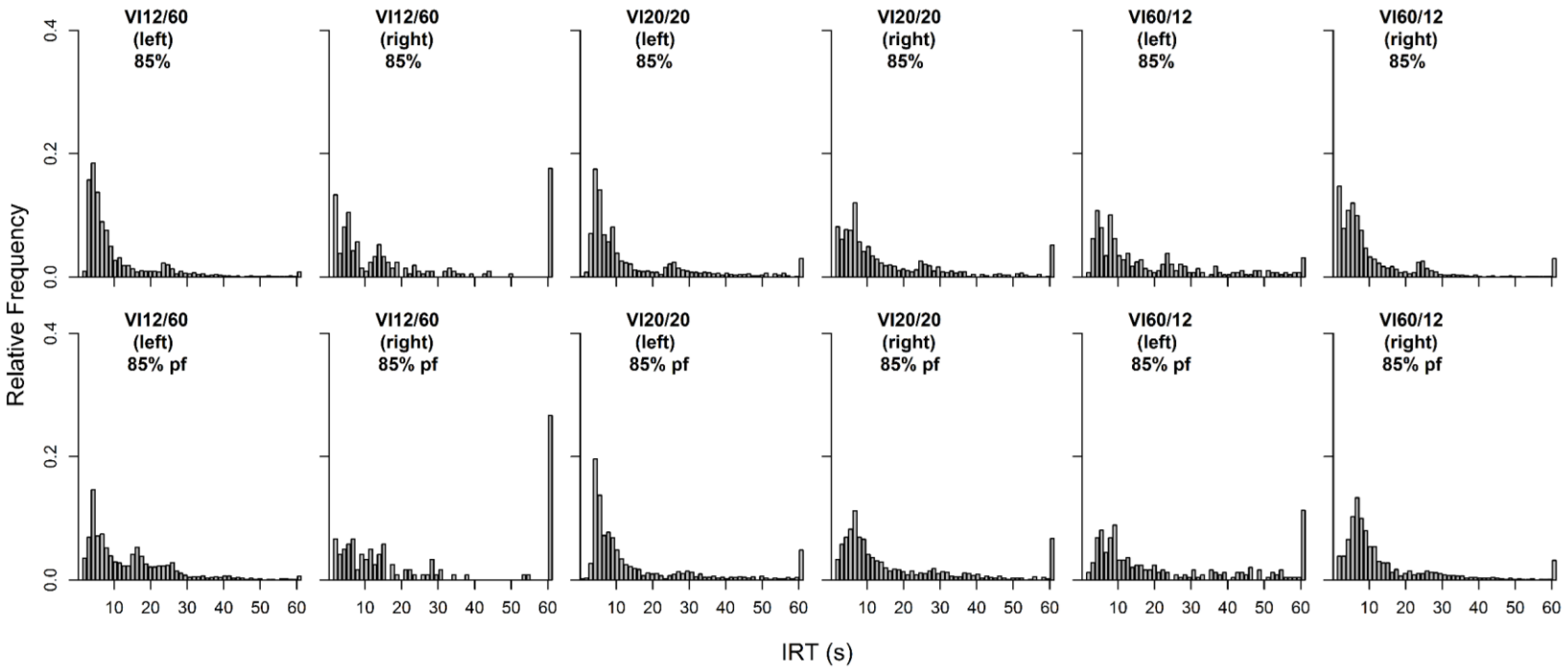

Figure 6.33. Relative frequency plots for Hen 25-3 during the 85% and 85% pre-feeding conditions. Relative frequency of IRTs is plotted as a function of bin size in 0.2 s.

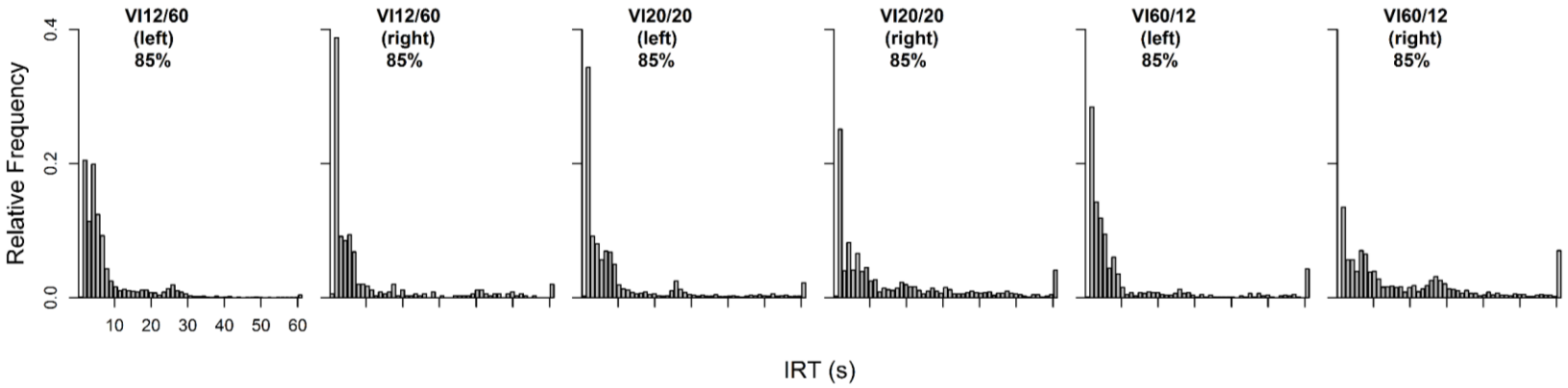

Figure 6.34. Relative frequency plots for Hen 25-4 during the 85% condition. Relative frequency of IRTs is plotted as a function of bin size in 0.2 s.

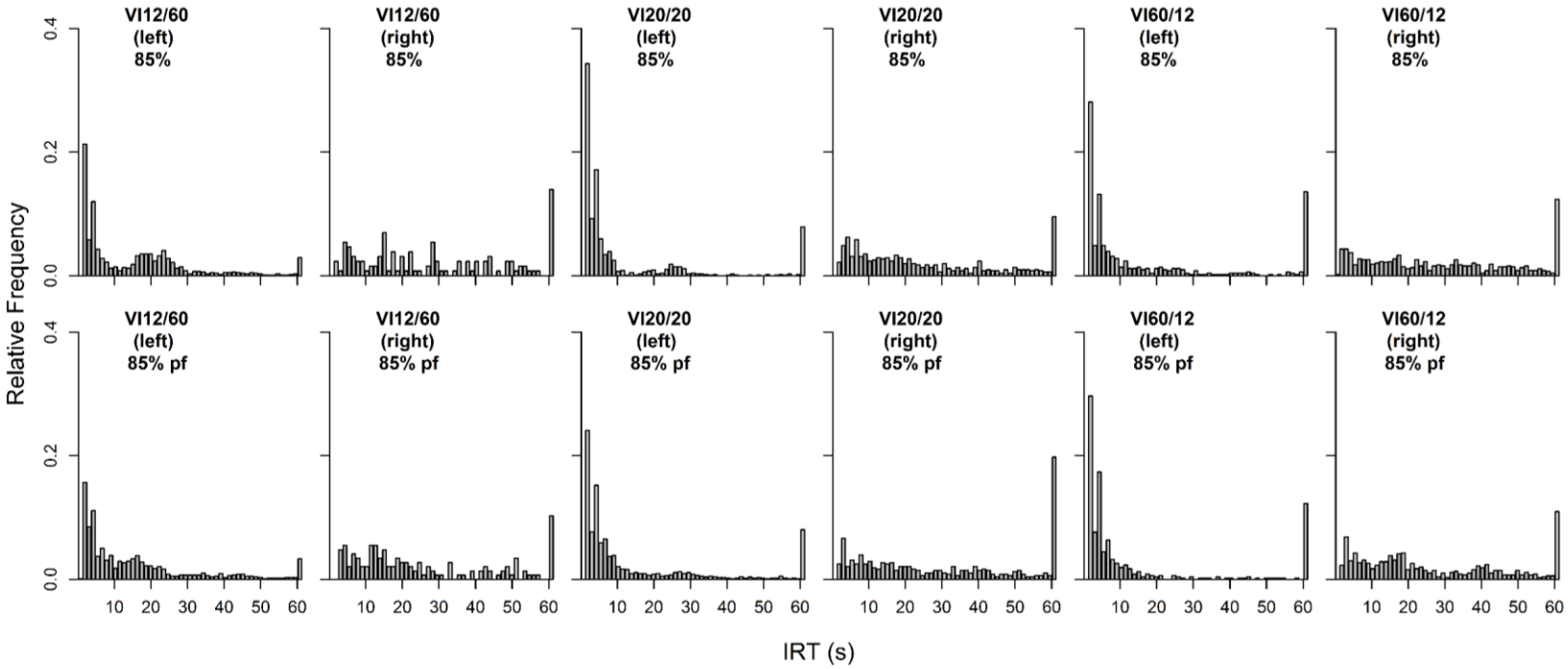

Figure 6.35. Relative frequency plots for Hen 25-5 during the 85% and 85% pre-feeding conditions. Relative frequency of IRTs is plotted as a function of bin size in 0.2 s.

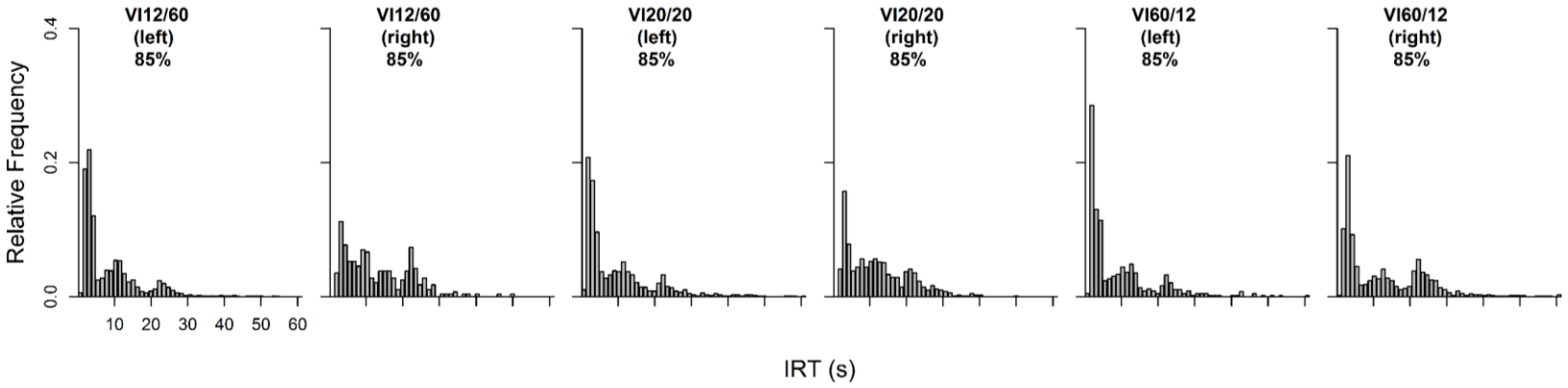

Figure 6.36. Relative frequency plots for Hen 25-6 during the 85% condition. Relative frequency of IRTs is plotted as a function of bin size in 0.2 s.

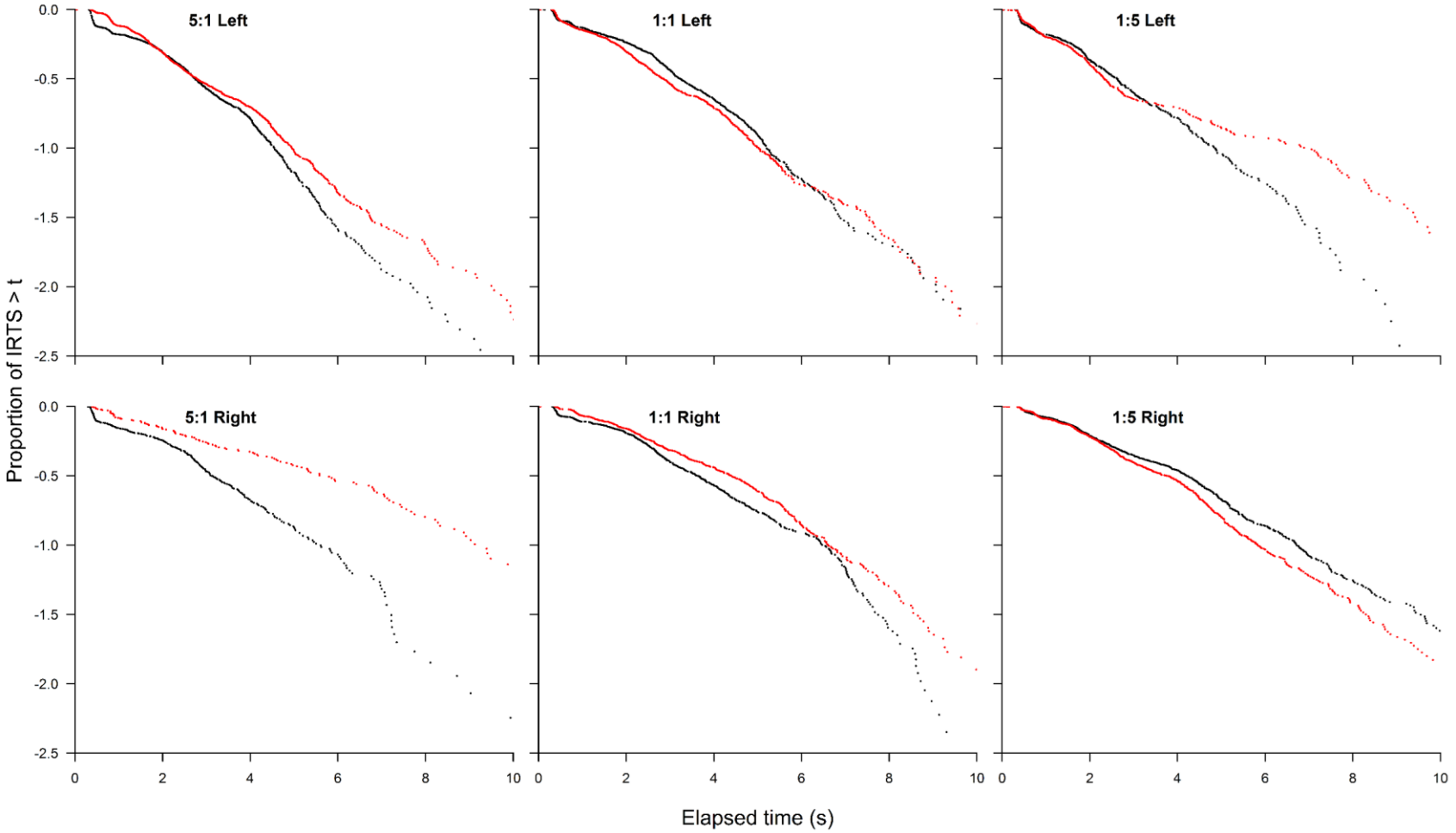

Figure 6.37. Log-survivor functions for Hen 25-1 for all conditions. Log proportions of IRTs greater than some time *(t)* are plotted as a function of elapsed time *(t)*. Black lines represent the 85% condition and red lines represent the pre-feeding condition.

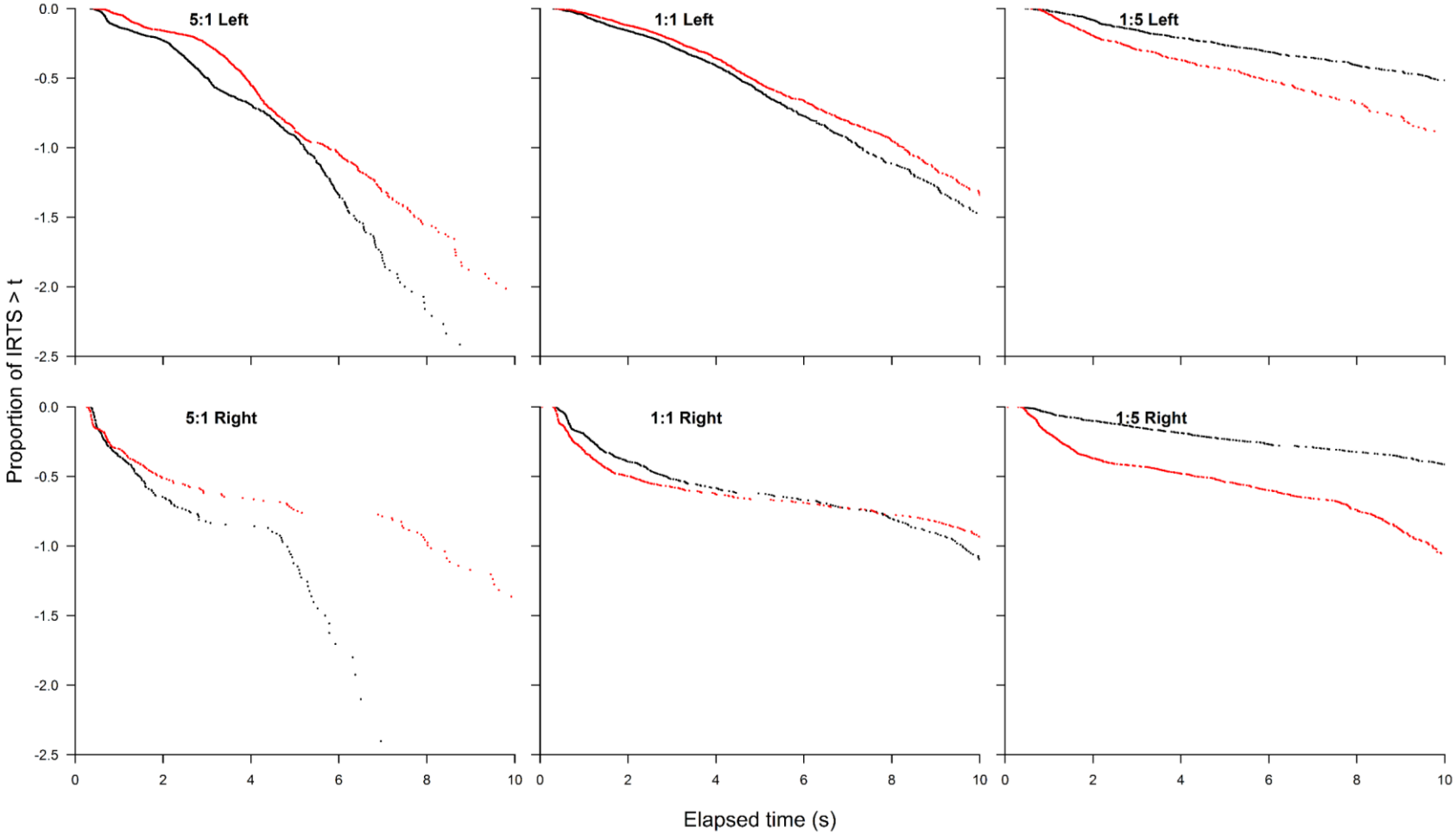

Figure 6.38. Log-survivor functions for Hen 25-2 for all conditions. Log proportions of IRTs greater than some time (t) are plotted as a function of elapsed time (t). Black lines represent the 85% condition and red lines represent the pre-feeding condition.

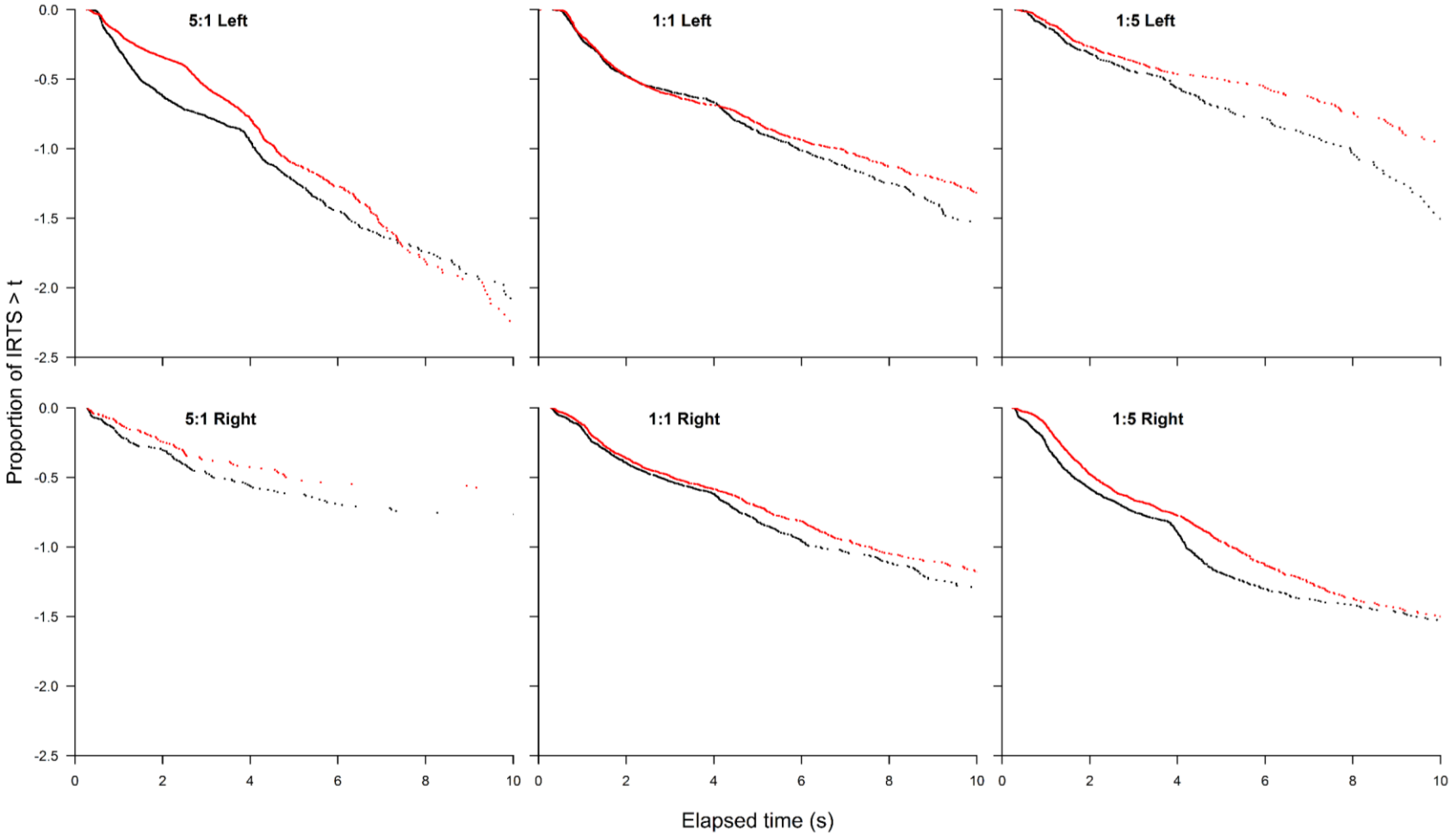

Figure 6.39. Log-survivor functions for Hen 25-3 for all conditions. Log proportions of IRTs greater than some time (t) are plotted as a function of elapsed time (t). Black lines represent the 85% condition and red lines represent the pre-feeding condition.

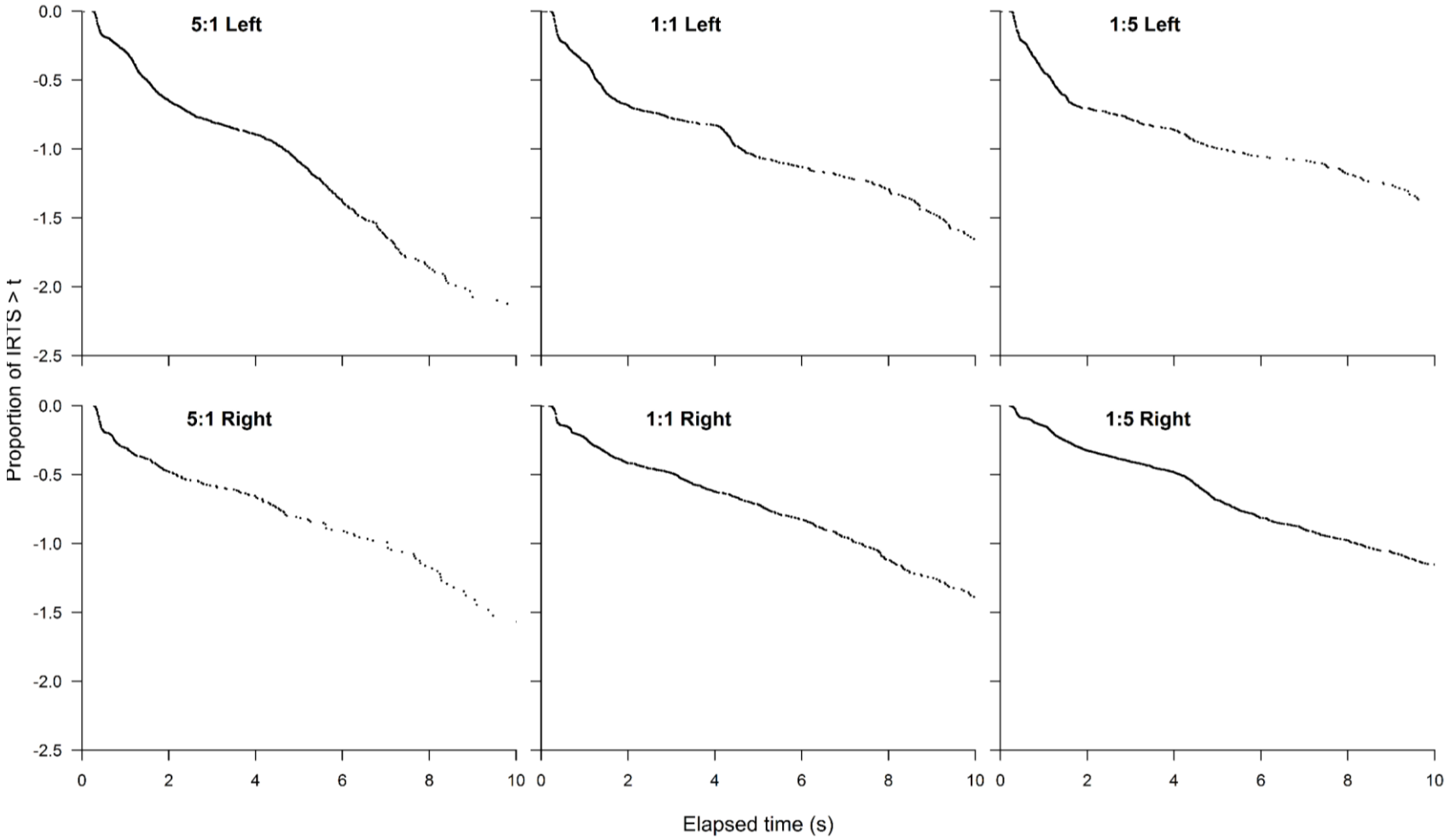

Figure 6.40. Log-survivor functions for Hen 25-4 for the 85% condition. Log proportions of IRTs greater than some time *(t)* are plotted as a function of elapsed time *(t)*.

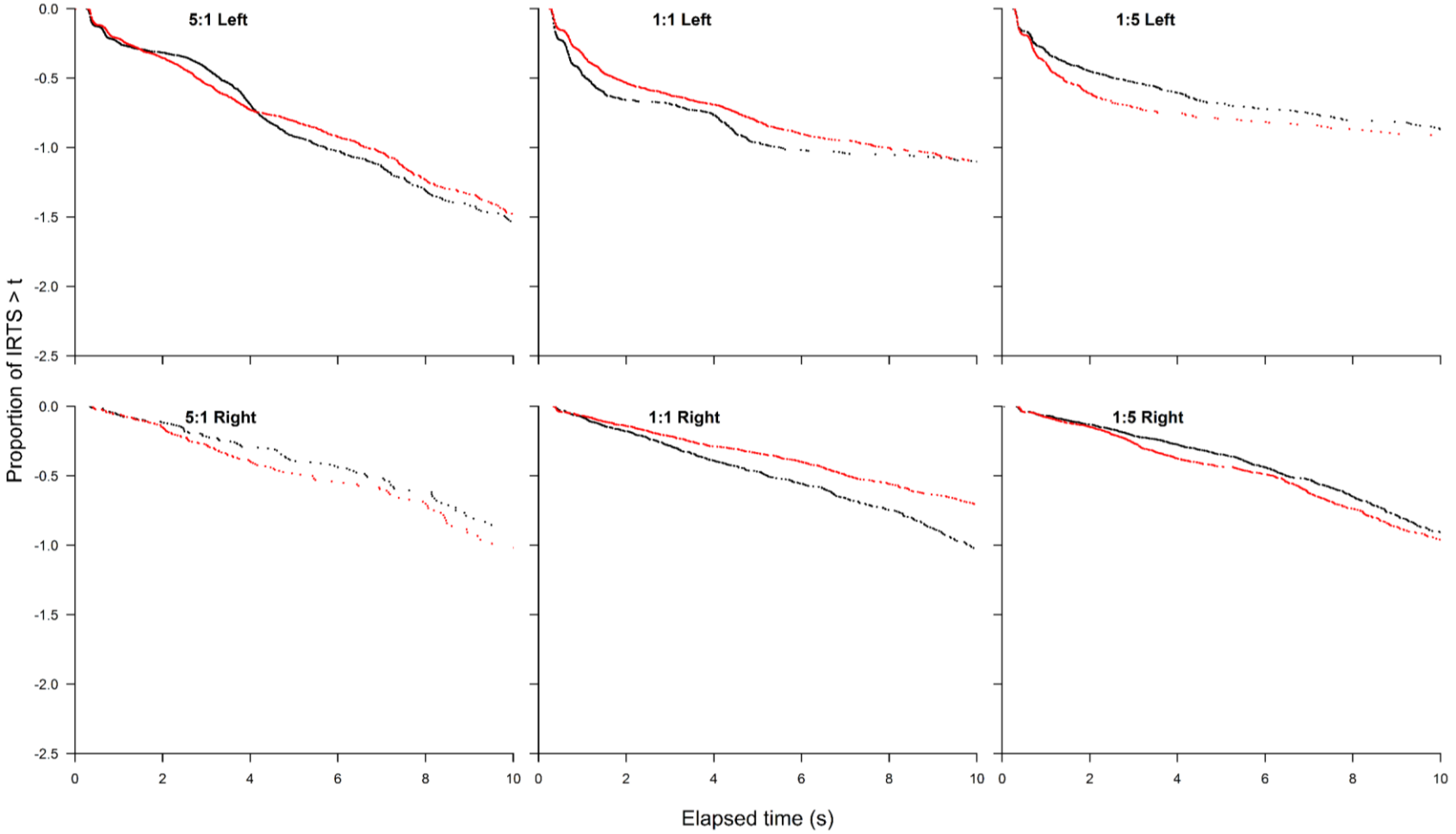

Figure 6.41. Log-survivor functions for Hen 25-5 for all conditions. Log proportions of IRTs greater than some time *(t)* are plotted as a function of elapsed time *(t)*. Black lines represent the 85% condition and red lines represent the pre-feeding condition.

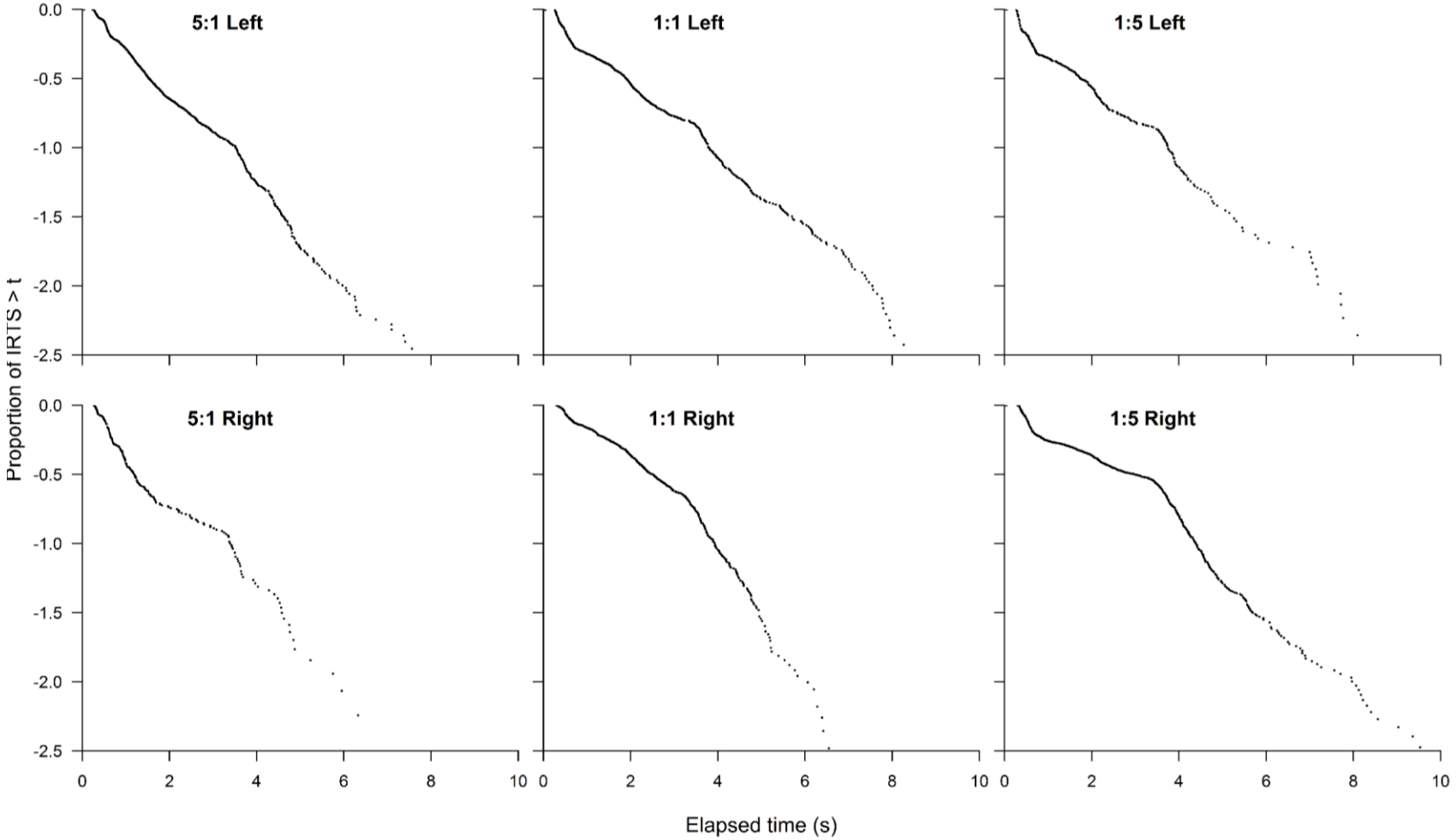

Figure 6.42. Log-survivor functions for Hen 25-6 for the 85% condition. Log proportions of IRTs greater than some time *(t)* are plotted as a function of elapsed time *(t)*.

better to the prevailing reinforcer rates during the pre-feeding condition than they did in the 85% condition.

For all schedules, the shape of the log-survivor plot limbs were similar; however, the log-survivor limbs were shifted upwards for the pre-feeding conditions. The shallower log-survivor limbs, seen when hens were pre-fed compared to when they were not, could indicate more between-bout responses when the hens were pre-fed. It is possible that when hens are pre-fed they emit less extraneous responses associated with the higher reinforcer-rate alternative, thereby improving the ability of the hens to respond sensitively to the reinforcer contingencies. If that is the case, it is possible that a change in different classes of operant behaviour (extraneous behaviours) emitted between bouts of responding may be responsible for the differential sensitivity demonstrated when hens were pre-fed. The frequency distributions of the inter-response times showed that when hens were pre-fed there tended to be more IRTs in bins greater than 0.4 s (as per Experiment 6.1 and Davison, 2004). All hens displayed a bias to the left throughout all conditions of both Experiment 6.1 and 6.2; however, this bias was not as pronounced in the pre-feeding condition.

In summary, this study shows that adding pre-feeding can affect concurrent schedule performance. It is possible that increasing level of deprivation (e.g., maintaining hens at 85% bodyweight) can negatively affect the ability of some hens to match behaviour to the reinforcement contingencies by increasing amounts of species-specific behaviour (as seen in Experiment 4.1, when bodyweight was decreased) and possibly decreasing extraneous behaviour. However, pre-feeding prior to experimental conditions can mitigate this effect and increase the ability of hens to match to the reinforcer contingencies.

Chapter 7 : GENERAL DISCUSSION

Experiment 2.1 used an already published video analysis methodology (Dixon et al., 2008) to assess the morphology of food motivated pecks made to a computer screen by hens; after the hens had been trained to emit the peck using either an autoshaping or handshaping procedure. The intention of this was to then be able to use the video analysis methodology to assess the effect of altering two MOs related to two different reinforcers (e.g., food and water) at one time, in future studies. The study showed that both methods produced similarly formed pecks despite the inherent variability in the handshaping procedure. It was then concluded that it is the nature of the reinforcer that gave rise to the morphology and not that the autoshaping procedure *per se* gave rise to a particular form of elicited responses.

The aim of both Experiment 3.1 and 3.2 was to develop a procedure for restricting access to water in hens, to motivate them sufficiently to respond for water reinforcers. In Experiment 3.1 the effect that gradually decreasing time and amount of water access had on food-restricted hens' water consumption and health was assessed. It was found that hens could be restricted to one hour's access of water (restricted to the maximum amount that hens would consume when access was ad libitum) without adverse effects to health being apparent. However, when the hens were subsequently exposed to FR schedules with a low response requirement in Experiment 3.2, they did not respond consistently. This indicated that the level of restriction was insufficient to motivate responding and this finding, combined with the difficulty of obtaining ethical approval, meant that the proposed experiments utilising water deprivation as an MO had to be abandoned.

Experiment 4.1 used the autoshaping paradigm to assess the acquisition of food motivated pecks to a stimulus, at two different levels of bodyweight (75% and 95%). An infra-red screen was used and this allowed analysis of all pecks separately from learning effects by examining activity levels (location and amount of effective and ineffective pecks). It was found that that higher numbers of effective pecks were made by hens

maintained at 75% free-feeding bodyweight than hens maintained at 95% (different MO conditions). There were also higher numbers of ineffective pecks in the 75% group.

Experiment 5.1 investigated relative preference for stimuli correlated with different MO conditions, high deprivation (no pre-feeding) or low deprivation (pre-feeding), when subjects were maintained at either 75% or 95% of free-feeding bodyweight. The results showed that 6/10 hens demonstrated an increased preference for the stimulus paired with high deprivation conditions (no pre-feeding) when measured by log ratios of responses, and they also had faster response rates on this stimulus. Overall, the 75% bodyweight hens had faster response rates than the 95% hens (as in Experiment 4.1), and 8/10 hens responded faster on the stimulus that was paired with no-prefeeding. Also, in a similar finding to Experiment 4.1, there were higher numbers of ineffective pecks scattered across the screen for the 75% group, than for the 95% group. Pre-feeding prior to an experimental session decreased the scatter of these pecks, for both bodyweights but particularly for the 75% hens.

In Experiments 6.1 and 6.2 concurrent VI VI schedules were used to assess the effect of bodyweight and pre-feeding as MOs on steady state responding. In Experiment 6.1, 10 conditions were run exposing hens to three different VI pairs: VI-12-s, VI-60-s (5:1); VI-20-s, VI-20-s (1:1); and VI-60-s, VI-12-s (1:5). Bodyweight values (85%, 95%, and 100%) were manipulated between hens finishing a series of the three VI pairs. It was found that 4/6 hens had higher absolute and relative response rates when bodyweight was lower. For 3/6 of these hens, increasing bodyweight increased sensitivity as measured by the parameter *a*; this was more distinct when the Generalised Matching Law was applied to response rather than time allocation data. Frequency distributions of IRTs showed that, for the hens that tended to show increasing sensitivity as bodyweights increased, there were more IRTs in bins greater than 0.4 s. This was reflected on the log-survivor plots as the limbs were shallower when bodyweights were higher, indicating that more between-bout responses were occurring, for 3/6 hens. It was also found that pre-feeding at 85% bodyweight increased sensitivity as measured by the parameter *a*

for all hens, compared to no pre-feeding at 85% bodyweight. This was more distinct when the GML was applied to response rather than time allocations.

In Experiment 6.2, six conditions were run exposing hens to the same three different VI pairs from Experiment 6.1: VI-12-s, VI-60-s (5:1); VI-20-s, VI-20-s (1:1); and VI-60-s, VI-12-s (1:5). In all conditions hens were maintained at 85% bodyweight and in three conditions hens were pre-fed 40 cc of wheat, 40 minutes prior to experimental sessions. When hens maintained at 85% were exposed to pre-feeding, although overall response rates tended to resemble those for the 85% bodyweight condition and remain higher than the 95% and 100% bodyweight conditions, the distribution of left and right response rates showed that hens matched better to the prevailing reinforcer rates when they were pre-fed, than when they were not pre-fed. Over both the 85% and pre-feeding conditions the shape of the log-survivor plot limbs were similar; however, the log-survivor limbs were shifted upwards for the pre-feeding conditions. The shallower log-survivor limbs when hens were pre-fed than when they were not, might indicate more between-bout responses when the hens were pre-fed. That is, that change in different classes of extraneous behaviour emitted between bouts of responding may be responsible for the differential sensitivity demonstrated when hens were pre-fed. The frequency distributions of the IRTs showed that when hens were pre-fed there tended to be more IRTs in bins greater than 0.4 s (as per Experiment 6.1 and Davison, 2004).

In summary, this thesis brings together a series of experiments that contribute knowledge on the effects of bodyweight and pre-feeding as MOs. The effects of MOs have been measured during acquisition and steady state responding and effects on preference were examined.

General Discussion

The original aim of this thesis was to manipulate two MOs concurrently (food-deprivation and water-deprivation) and to use autoshaping and concurrent schedules to assess whether the effects of these MOs could be measured by analysing the conditioned responses in

hens using peck morphology. Therefore, it may have been possible to assess whether altering one MO, e.g., food-deprivation, affected responding for another reinforcer, e.g., water. When Experiments 3.1 and 3.2 were not successful at creating a methodology for motivating hens to respond for water reinforcers, the aim of the thesis changed. The revised aim was to assess the effect of bodyweight and pre-feeding as MOs when manipulated individually and concurrently. Therefore, assessing not only the effects of bodyweight and pre-feeding as MOs, but also whether altering them simultaneously would have differential effects on responding.

Major Findings

The main findings of this thesis are: (1) that reducing bodyweights increased amounts of pecking responses (a species-specific behaviour); and (2) that reducing bodyweight results in increases in response rates. As discussed in Experiments 5.1, 6.1, and 6.2, these findings could help explain why changes in preference for stimuli paired with high levels of deprivation are observed during SDVL procedures, and why increased sensitivity to available reinforcement at lower levels of deprivation has been found in studies utilising the GML. As discussed below, these findings contribute to the empirical data informing MOs.

Increased Deprivation Levels Lead to Increased Amounts of Behaviour

In Experiment 4.1 it was found that the hens in the 75% group exhibited higher ineffective pecks and made considerably more pecks to the black screen and near to the stimuli than those maintained at 95%. In Experiment 5.1 it was found that there were also higher numbers of pecks that were more scattered across the screen in the 75% group, than in the 95% group, and that pre-feeding prior to an experimental session decreased the scatter of these pecks. These findings are in line with previous research; for example, Lewis and Dougherty (1992) found that the pigeons who were maintained at lower weights responded more than the schedule required when working on a VRO schedule and therefore omitted more reinforcers. In Experiment 4.1 there were higher ineffective

pecks exhibited by the hens in the 75% group, but they did not acquire the autoshaped response faster than the 95% group. This contrasts with findings reported by Davey and Cleland (1982) and Sparber, Bollweg, and Messing (1991). Those authors found that changing the MO for the reinforcer (by changing either bodyweight or hours of food access) increased the rate at which rats learned to lever press using autoshaping as well as the amount and type of lever directed behaviour of the rats, therefore providing evidence of the value-altering effect. This finding that rats acquired lever-pressing faster when more deprived did not generalise to a new species, hens. The lack of clear difference in acquisition of responding between the two bodyweight groups here does not provide evidence that bodyweight changes the value-altering effect of the MO, with hens.

Altering Deprivation Levels Lead to Changes in Response Rate

In Experiment 6.1 it was found that for 4/6 hens the overall response rates tended to decrease as bodyweight increased from 85% to 100%, and were also more variable at higher bodyweights. Experiment 5.1 produced a similar finding, in that hens maintained at 75% of free-feeding bodyweight had faster response rates during deprivation/correlation sessions than hens maintained at 95% of free-feeding bodyweight. Similarly, McSweeney (1974) found that higher bodyweights produced more variability in IRTs on concurrent VI VI schedules. Previous research has demonstrated higher rates of responding (Ferster & Skinner, 1957; Skinner, 1938) and shorter response latencies (Cotton, 1953; Kimble, 1951) under higher deprivation conditions. The experiments from this thesis contribute to this previous research by finding results like the above-mentioned studies, when using response rate as a dependent variable. In Experiment 6.1, as bodyweight increased four hens showed higher sensitivity values in addition to a decrease in response rate. However, in Experiment 6.2, although all four hens in the experiment showed increases in sensitivity values when they were pre-fed, none showed decreases in response rate. This thesis extends the previous research cited above by using additional dependent measures to carry out a

microstructural analysis of responding to assist in understanding why decreased deprivation levels may lead to increased sensitivity to available reinforcement. It was suggested in Experiment 6.2 that shallower log-survivor limbs when hens were pre-fed than when they were not, could indicate more between-bout responses, when the hens were pre-fed.

Why Decreased Deprivation Levels May Lead to Increased Sensitivity to Available Reinforcement

As stated above, in Experiments 6.1 and 6.2 it was found that decreasing deprivation levels by maintaining hens at higher bodyweights or by pre-feeding prior to experimental sessions increased some hens' ability to match to the reinforcement contingencies, as assessed by the parameter *a* when the GML was applied to the data. The results were more consistent and stronger when pre-feeding was used to decrease deprivation, as opposed to hens being maintained at a higher bodyweight. The results of these experiments are in line with previous findings. For example, as stated in Experiment 6.1, both Charman and Davison (1983) and Herrnstein and Loveland (1974) found that sensitivity approached strict matching (a = 1.0) as subjects were made less food deprived. In addition, Buckley and Rasmussen (2012) found that Zucker rats with an obese phenotype did show higher sensitivity to reinforcer rates than Zucker rats with a lean phenotype. Microanalysis undertaken in this thesis may provide a rationale for how these phenomena occur. Although there were individual differences shown between the data from the six hens in Experiments 6.1 and 6.2, overall the results of these experiments may indicate that increasing deprivation (by decreasing bodyweight or not pre-feeding) may differentially effect the amount, topography, and rate of different classes of behaviours performed between bouts of pecks delivered under variable-interval schedules, therefore affecting the distributions of pecking behaviour and affecting matching. Future experiments could assess whether this hypothesis is correct by videoing and operationally defining all classes of behaviours emitted during stable sessions under VI schedules and assessing changes when MOs are manipulated.

Future experiments could also aim to reduce limitations of Experiments 6.1 and 6.2. The main limitation is that, by necessity, to maintain hens at differing levels of bodyweight they need to receive supplemental feeding outside of experimental sessions. This is a confound in that individual hens may be fed differing amounts to maintain them at the same bodyweight; e.g., two hens may be fed either 150 cc or 100 cc of food per day to maintain them at 100% of free-feeding bodyweight. For this reason, during these experiments hens were fed approximately 23 hr prior to experimental sessions to mitigate this confound as much as possible. However, the different amounts pre-fed to maintain hens at different bodyweights could account for some of the idiosyncrasies between hens. Another limitation is that it is impossible to rapidly change bodyweight between experimental sessions. In addition to this, to control bodyweight as an independent variable, it is necessary to run experimental sessions only when an animal is in a specific bodyweight range. This can cause data collection to take a considerable amount of time, as sessions cannot be run when bodyweight fluctuates outside of the specified range. For both reasons, three VI pairs were utilised in Experiments 6.1 and 6.2, whereas five VI pairs would have yielded more data. Fortunately, the GML, a robust analytical tool in the description of behaviour-environment interactions (Reed & Kaplan, 2011) could be applied to the data from these experiments.

Implications of this Research for the MO Concept

Recent reviews (e.g., Aló & Cançado, 2013; Laraway et al., 2014; Whelan & Barnes-Holmes, 2010) provide updates on the current theoretical status of MOs that are outside of the scope of this thesis. The most recent review, Laraway et al. (2014), states that the MO concept is a high-impact innovation in behaviour analysis that provides a useful theoretical framework for analysis of operant behaviour. However, they also acknowledge that gaps exist in the theoretical structure of the MO and in empirical support for the hypothesised functions that it suggests.

The hypothesised functions of the MO are the value-altering (the capacity of the MO to influence operant consequences to *alter the strength*

of future behaviour) and the behaviour-altering (the capacity to *alter the current strength* of behaviours related to the consequences affect by the MO) effects. Overall the results of this thesis indicate that the behaviour-altering effect may be stronger than the value-altering effect.

Laraway et al. (2014) state that although response rate has served as the traditional dependent variable in behaviour analysis, researchers may measure response strength in different ways (including choice). One of the main findings of this thesis is that when pre-feeding and bodyweight are manipulated differential effects on choice can be seen. For example, Experiments 6.1 and 6.2 showed that decreasing bodyweight can negatively affect the ability of hens to match behaviour to the reinforcement contingencies, but that this effect can be mitigated by pre-feeding prior to experimental sessions, with no effect on response rate. Do these results indicate that manipulating more immediate MOs (e.g., pre-feeding) prior to an experimental session may make hens more sensitive to the current *context* of the experimental chamber? That is to say, that by manipulating the amount of behaviour produced, can the ability to match to the current reinforcement contingencies be changed? It has been proposed that MOs can influence the behaviour-altering effects of discriminative stimuli (SDs) (Laraway et al., 2003; Lotfizadeh et al., 2012; McDevitt & Fantino 1993; Michael 1988, 1993, 2007). For example, Lotfizadeh et al. (2012) reviewed 11 studies concerned with the influence of food or water deprivation on stimulus generalisation. They found that the studies suggested that MOs affect stimulus control by: (1) changing the evocative effect of a just established S^D; (2) changing the range of stimuli that evoke the operant in question; and (3) exerting these effects in a graded fashion. They state that in every study reviewed the fastest or most forceful responding occurred in the presence of the S^D. However, they also say that it is interesting to note that a study by Powell (1971) reported that under some conditions, stimulus control in pigeons responding under multiple schedules with an extinction component decreased as the birds' bodyweights were reduced from 95% to 70% of free-feeding bodyweight. This meant that the relative rate of responding in the presence of the stimulus delta increased as bodyweight decreased.

This is similar to the findings of Experiment 5.1, where the hens maintained at 75% bodyweight and not pre-fed, would peck on the side of the screen that was not active.

Experiment 4.1 used the autoshaping paradigm to assess the acquisition of food motivated pecks to a stimulus, at two different levels of bodyweight (75% and 95%), therefore assessing both the behaviour-altering and value-altering effects. Although the 75% hens exhibited more ineffective pecks than the 95% hens, the difference in acquisition was only marginal, despite the hypothesis that increased levels of behaviour can lead to increased contact with response-reinforcer contingencies, therefore expediting learning via the value-altering effect. Balsam (1985) reported that high activity levels that occur when a pigeon is placed in a context correlated with food (i.e., a chamber in which extensive magazine training has occurred) can inhibit response acquisition in autoshaping procedures. The increased levels of activity (including ineffective pecks) can be explained via the behaviour-altering effect, in that manipulating bodyweight altered the current strength of behaviours related to the history of consequences affected by the MO, to such a degree that these overrode the value-altering effect of the MO.

The increased levels of activity seen in Experiments 4.1 and 5.1 may be able to be explained from a behaviour systems approach. Timberlake (2001) has suggested that motivational operations function to move an animal into a mode relevant to their history and immediate needs; as has Hogan (1988). As noted by Tinbergen (1948), when animals were highly motivated, responses normally emitted in the presence of particular stimuli (releasers) would occur in the presence of stimuli that differed substantially from those releasers, or even in the absence of any relevant antecedents. Therefore, it is possible that when MOs are in strong effect, species-specific behaviour relevant to the reinforcer is activated (behaviour-altering effect) and this retards the ability of the animal to match behaviour to the current reinforcement contingencies (value-altering effect).

As stated above, for practical reasons restriction levels related to food are the most commonly manipulated MOs. Indeed, in this thesis,

Experiments 3.1 and 3.2 failed to obtain sufficient deprivation levels to achieve stable responding for water reinforcers with hens. The scope for future research is large. Future choice research could employ different reinforcers and manipulate different MOs. As has been pointed out in many laboratory (particularly free-operant) situations researchers may have trouble disentangling the value-altering and behaviour-altering effects of a given MO in basic research, because consequences often occur while the MO functions effectively, which confounds the two effects. Pure behaviour-altering effects can be seen most clearly in extinction or before the first occurrence of the relevant consequences. The same issues are true of this series of experiments. Thus, research preparations should control for these contingencies and processes, offering evidence that the value-altering and behaviour-altering effects occur independently of them.

Implications of this Research

As highlighted strongly in the General Introduction to this thesis, the MO as a concept has been used extensively in applied work. This research has applied implications; for example, when trying to work effectively with people with disabilities who exhibit challenging behaviour living in environments with a high level of deprivation, related to a reinforcer, they may display more behaviours related to the behavioural phenotype of their conditions (e.g., ritualistic behaviour in Autism Spectrum Disorder). These high levels of behaviours may inhibit learning (and the ability to match to current reinforcement contingencies), therefore impeding behaviour change.

Conclusions

In conclusion, the main findings of this thesis are: (1) that reducing bodyweights increased the amount of species-specific behaviour; and (2) that reducing bodyweight caused increases in response rate. These findings could explain changes in preference for stimuli paired with high levels of deprivation during SDVL procedures, and increased sensitivity to available reinforcement at lower levels of deprivation (when altered by

increasing bodyweight or adding pre-feeding) found in concurrent schedules when the GML is applied to the data. These findings contribute to the empirical data informing the behavioural treatment of motivation by suggesting that the behaviour-altering effect of the MO is stronger than the value-altering effect. This has applied implications as reinforcement and punishment procedures such as extinction or differential reinforcement of alternative behaviours may no longer be necessary for changing behaviour when the motivation for performing behaviour is gone.

REFERENCES

Aló, R. M., & Cançado, C. R. (2013). Coming to Terms with Motivation in the Behavior-Analytic Literature. *The Psychological Record*, *63*(3), 641-654.

Anderson, K., Velkey, A., & Woolverton, W. (2002). The Generalized Matching Law as a Predictor of Choice between Cocaine and Food in Rhesus Monkeys. *Psychopharmacology, 163*(3-4)*,* 319-326. http://dx.doi.org/10.1007/s00213-002-1012-7

Appleby, M., Mench, J., & Hughes, B. (2004). *Poultry Behaviour and Welfare*. Wallingford, Oxfordshire, UK: CABI Pub.

Aw, J. M., Holbrook, R. I., de Perera, T. B., & Kacelnik, A. (2009). State-Dependent Valuation Learning in Fish: Banded Tetras Prefer Stimuli Associated with Greater Past Deprivation. *Behavioural Processes*, *81*(2), 333-336.

Balsam, P. D. (1985). The functions of context in learning and performance. In P. D. Balsam & A. Tomie (Eds.), *Context and Learning* (pp. 1-21). Hillsdale, NJ: Erlbaum.

Balsam, P. D., & Schwartz, A. L. (1981). Rapid Contextual Conditioning in Autoshaping. *Journal of Experimental Psychology: Animal Behavior Processes*, *7*(4), 382-393.

Baum, W. (1972). Choice in a Continuous Procedure. *Psychonomic Science*, *28*(5), 263-265. http://dx.doi.org/10.3758/bf03328733

Baum, W. (1974). On Two Types of Deviation from the Matching Law: Bias and Undermatching. *Journal of the Experimental Analysis of Behavior*, *22*(1), 231-242. http://dx.doi.org/10.1901/jeab.1974.22-231

Baum, W. (1979). Matching, Undermatching, and Overmatching in Studies of Choice. *Journal of the Experimental Analysis of Behavior*, *32*(2), 269-281. http://dx.doi.org/10.1901/jeab.1979.32-269

Baumeister, A., Hawkins, W. F., & Cromwell, R. L. (1964). Need States and Activity Level. *Psychological Bulletin*, *61*(6), 438-453.

Belke, T. W., & Belliveau, J. (2001). The General Matching Law Describes Choice on Concurrent Variable-Interval Schedules of Wheel-Running Reinforcement. *Journal of the Experimental Analysis of Behavior*, *75*(3), 299-310. http://doi.org/10.1901/jeab.2001.75-299

Belke, T. W., & Pierce, W. D. (2009). Bodyweight Manipulation, Reinforcement Value and Choice between Sucrose and Wheel Running: A Behavioral Economic Analysis. *Behavioral Processes*, *80*(2), 147-156.

Bell, D. (2003). Historical and Current Molting Practices in the U.S. Table Egg Industry. *Poultry Science*, *82*(6), 965-970. http://dx.doi.org/10.1093/ps/82.6.965

Bennett, J. A., Hughes, C. E., & Pitts, R. C. (2007). Effects of Methamphetamine on Response Rate: A Microstructural Analysis. *Behavioural Processes*, *75*(2), 199-205.

Blough, D. S. (1963). Interresponse Time as a Function of Continuous Variables: A New Method and Some Data. *Journal of the Experimental Analysis of Behavior*, *6*(2), 237-246.

Boutros, N., Elliffe, D., & Davison, M. (2011). Examining the Discriminative and Strengthening Effects of Reinforcers in Concurrent Schedules. *Journal of the Experimental Analysis of Behavior*, *96*(2), 227-241. http://dx.doi.org/10.1901/jeab.2011.96-227

Brackney, R., Cheung, T., Neisewander, J., & Sanabria, F. (2011). The Isolation of Motivational, Motoric, and Schedule Effects on Operant Performance: A Modeling Approach. *Journal of the Experimental Analysis of Behavior, 96*(1), 17-38. http://dx.doi.org/10.1901/jeab.2011.96-17

Brackney, R., Cheung, T., Herbst, K., Hill, J., & Sanabria, F. (2012). Extinction Learning Deficit in a Rodent Model of Attention-Deficit Hyperactivity Disorder. *Behavioral and Brain Functions, 8*(59), 1-10. http://dx.doi.org/10.1186/1744-9081-8-59

Bradshaw, C. M., Szabadi, E., Ruddle, HR. V., & Pears, E. (1983). Herrnstein's equation: Effect of Deprivation Level on Performance in Variable-Interval Schedules. *Behaviour Analysis Letters. 3*(5), 267-273.

Broadhurst, P. (1957). Emotionality and the Yerkes-Dodson Law. *Journal of Experimental Psychology*, *54*(5), 345-352. http://dx.doi.org/10.1037/h0049114

Brown, J. (1956). The Effect of Drive on Learning with Secondary Reinforcement. *Journal of Comparative and Physiological Psychology*, *49*(3), 254-260. http://dx.doi.org/10.1037/h0044795

Brown, P. L., & Jenkins, HR. M. (1968). Auto-Shaping of the Pigeon's Key-Peck. *Journal of the Experimental Analysis of Behavior*, *11*(1), 1-8.

Buckley, J., & Rasmussen, E. (2012). Obese and Lean Zucker Rats Demonstrate Differential Sensitivity to Rates of Food Reinforcement in a Choice Procedure. *Physiology & Behavior, 108*, 19-27. http://dx.doi.org/10.1016/j.physbeh.2012.10.001

Cabrera, F., Sanabria, F., Jiménez, Á., & Covarrubias, P. (2013). An Affordance Analysis of Unconditioned Lever Pressing in Rats and

Hamsters. *Behavioural Processes*, *92*, 36-46. Http://Dx.Doi.Org/10.1016/J.Beproc.2012.10.003

Campbell, B. A., & Sheffield, F. D. (1953). Relation of Random Activity to Food Deprivation. *Journal of Comparative and Physiological Psychology*, *46*(5), 320-322.

Carroll, M., & Stotz, D. (1984). Increased Phencyclidine Self-Administration Due to Food Deprivation: Interaction with Concentration and Training Conditions. *Psychopharmacology*, *84*(3), 299-303. Http://Dx.Doi.Org/10.1007/Bf00555202

Charman, L., & Davison, M. (1983). On the Effects of Food Deprivation and Component Reinforcer Rates on Multiple-Schedule Performance. *Journal of the Experimental Analysis of Behavior*, *40*(3), 239-251.

Charlton, S. G. (1984). Hoarding-Induced Lever Pressing in Golden Hamsters (*Mesocricetus Auratus*): Illumination, Time of Day, and Shock as Motivating Operations. *Journal of Comparative Psychology*, *98*(3), 327-332.

Clark, F. (1958). The Effect of Deprivation and Frequency of Reinforcement on Variable-Interval Responding1. *Journal of the Experimental Analysis of Behavior*, *1*(3), 221-228. Http://Dx.Doi.Org/10.1901/Jeab.1958.1-221

Cleland, G. G., & Davey, G. C. (1982). The Effects of Satiation and Reinforcer Devaluation on Signal-Centered Behavior in the Rat. *Learning and Motivation*, *13*(3), 343-360.

Cloar, F., & Melvin, K. (1968). Performance of Two Species of Quail on Basic Reinforcement Schedules. *Journal of the Experimental Analysis of Behavior*, *11*(2), 187-190. Http://Dx.Doi.Org/10.1901/Jeab.1968.11-187

Collett, S. (2012). Nutrition and Wet Litter Problems in Poultry. *Animal Feed Science and Technology*, *173*(1-2), 65-75. Http://Dx.Doi.Org/10.1016/J.Anifeedsci.2011.12.013

Conover, K., Fulton, S., & Shizgal, P. (2001). Operant Tempo Varies with Reinforcement Rate: Implications for Measurement of Reward Efficacy. *Behavioural Processes, 56*(2), 85-101. Http://Dx.Doi.Org/10.1016/S0376-6357(01)00190-5

Cotton, J. W. (1953). Running Time as a Function of Amount of Food Deprivation. *Journal of Experimental Psychology*, *46*(3), 188-198.

Davison, M. (2004). Interresponse Times and the Structure of Choice. *Behavioural Processes*, *66*(3), 173-187. Http://Dx.Doi.Org/10.1016/J.Beproc.2004.03.003

Davison, M., & Hogsden, I. (1984). Concurrent variable-interval schedule performance: Fixed versus mixed reinforcer durations. *Journal of the Experimental Analysis of Behavior*, *41*(2), 169-182. http://dx.doi.org/10.1901/jeab.1984.41-169

Davison, M., & Jenkins, P. (1985). Stimulus Discriminability, Contingency Discriminability, and Schedule Performance. *Animal Learning & Behavior*, *13*(1), 77-84. Http://Dx.Doi.Org/10.3758/Bf03213368

Davison, M., & Jones, B. (1995). A Quantitative Analysis of Extreme Choice. *Journal of the Experimental Analysis of Behavior*, *64*(2), 147-162. Http://Dx.Doi.Org/10.1901/Jeab.1995.64-147

Davison, M., & McCarthy, D. (1988). *The Matching Law: A Research Review*. Hillsdale, NJ: Erlbaum Associates, Inc.

Dickinson, A., Watt, A., & Griffiths, W. J. HR. (1992). Free operant Acquisition with Delayed Reinforcement. *Quarterly Journal of Experimental Psychology, 45*(3), 241–258.

Dixon, L., Duncan, I., & Mason, G. (2008). What's in A Peck? Using Fixed Action Pattern Morphology to Identify the Motivational Basis of Abnormal Feather-Pecking Behaviour. *Animal Behaviour*, *76*(3), 1035-1042. Http://Dx.Doi.Org/10.1016/J.Anbehav.2008.06.001

Dougher, M. J., & Hackbert, L. (2000). Establishing Operations, Cognition, and Emotion. *The Behavior Analyst*, *23*(1), 11-24.

Elliffe, D., & Davison, M. (1996). Closed-Economy Multiple-Schedule Performance: Effects of Deprivation and Session Duration. *Journal of the Experimental Analysis of Behavior*, *65*(1), 111-128. Http://Dx.Doi.Org/10.1901/Jeab.1996.65-111

Elliffe, D., Davison, M., & Landon, J. (2008). Relative Reinforcer Rates and Magnitudes Do Not Control Concurrent Choice Independently. *Journal of the Experimental Analysis of Behavior*, *90*(2), 169-185. Http://Dx.Doi.Org/10.1901/Jeab.2008.90-169

Fagerstrøøm, A., Foxall, G. R., & Arntzen, E. (2010). Implications of Motivating Operations for the Functional Analysis of Consumer Choice. *Journal of Organizational Behavior Management*, *30*(2), 110-126.

Fallon, D., Thompson, D., & Schild, M. (1965). Concurrent Food and Water-Reinforced Responding Under Food, Water, and Food-Plus-Water Deprivation. *Psychological Reports*, *16*(3c), 1305-1311. Http://Dx.Doi.Org/10.2466/Pr0.1965.16.3c.1305

Ferguson, S. A., & Paule, M. G. (1995). Lack of Effect of Prefeeding on Food-Reinforced Temporal Response Differentiation and Progressive Ratio Responding. *Behavioural Processes*, *34*(2), 153-160.

Ferguson, S. A., & Paule, M. G. (1997). Progressive Ratio Performance Varies with Bodyweight in Rats. *Behavioural Processes*, *40*(2), 177-182.

Ferster, C., & Skinner, B. (1957). *Schedules of Reinforcement*. New York: Appleton-Century-Crofts.

Foster, M., Blackman, K., & Temple, W. (1997). Open Versus Closed Economies: Performance of Domestic Hens under Fixed Ratio Schedules. *Journal of the Experimental Analysis of Behavior*, *67*(1), 67-89. Http://Dx.Doi.Org/10.1901/Jeab.1997.67-67

Foster, T., Matthews, L., Temple, W., & Poling, A. (1997). Concurrent Schedule Performance in Domestic Goats: Persistent Undermatching. *Behavioural Processes*, *40*(3), 231-237. Http://Dx.Doi.Org/10.1016/S0376-6357(97)00018-1

Francesch, M., & Brufau, J. (2004). Nutritional Factors Affecting Excreta/Litter Moisture and Quality. *Worlds Poultry Science Journal, 60*(1), 64-75. Http://Dx.Doi.Org/10.1079/Wps20035

Gamzu, E., & Schwam, E. (1974). Autoshaping and Auto maintenance of a Key-Press Response in Squirrel Monkeys. *Journal of the Experimental Analysis of Behavior*, *21*(2), 361-371. Http://Dx.Doi.Org/10.1901/Jeab.1974.21-361

Gibbon, J., Baldock, M. D., Lucurto, C., Gold, L., & Terrace, HR. S. (1977). Trial and Intertrial Durations in Autoshaping. *Journal of Experimental Psychology: Animal Behavior Processes*, *3*(3), 264-284.

Gibbon, J., Locurto, C. M., & Terrace, HR. S. (Eds.). (1981). *Autoshaping and Conditioning Theory*. London: Academic Press.

Gleeson, S. (1991). Response acquisition. In I. Iversen, & K. A. Lattal (Eds.), *Research methods in the behavioral and neural sciences: Experimental analysis of behavior* (pp. 63-86). Amsterdam: Elsevier.

Grant, A., Foster, T., Temple, W., Jackson, S., Kinloch, J., & Poling, A. (2014). Reinforcer Magnitude and Demand under Fixed-Ratio Schedules with Domestic Hens. *Behavioural Processes*, *103*, 199-210. Http://Dx.Doi.Org/10.1016/J.Beproc.2013.12.013

Gunnarsson, S., Matthews, L., Foster, T., & Temple, W. (2000). The Demand for Straw and Feathers as Litter Substrates by Laying Hens. *Applied Animal Behaviour Science*, *65*(4), 321-330. Http://Dx.Doi.Org/10.1016/S0168-1591(99)00065-9

Hall, J. F. (1956). The Relationship between External Stimulation, Food Deprivation, and Activity. *Journal Of Comparative and Physiological Psychology*, *49*(4), 339-341.

Hearst, E., & Jenkins, H.R. M. (1974). *Sign-Tracking: The Stimulus-Reinforcer Relation and Directed Action*. Austin, Texas: Psychonomic Society.

Herrnstein, R. (1961). Relative and Absolute Strength of Response as A Function of Frequency of Reinforcement. *Journal of the Experimental Analysis of Behavior*, *4*(3), 267-272. Http://Dx.Doi.Org/10.1901/Jeab.1961.4-267

Herrnstein, R. J. (1970). On the Law of Effect. *Journal of the Experimental Analysis of Behavior*, *13*(2), 243-266.

Herrnstein, R., & Loveland, D. (1974). Hunger and Contrast in a Multiple Schedule. *Journal of the Experimental Analysis of Behavior*, *21*(3), 511-517. Http://Dx.Doi.Org/10.1901/Jeab.1974.21-511

Ho, M. Y., Wogar, M. A., Bradshaw, C. M., & Szabadi, E. (1997). Choice between Delayed Reinforcers: Interaction between Delay and Deprivation Level. *The Quarterly Journal of Experimental Psychology: Section B*, *50*(3), 193-202.

Hogan, J. A. (1988). Cause and Function in the Development of Behavior Systems. In E.M. Blass (Ed.), *Handbook of Behavioral and Neurobiology: Vol 9. Developmental Psychobiology and Behavioral Ecology* (pp .63-106). New York: Plenum Press.

Holland, J.G., & Skinner, B.F. (1961). *The Analysis of Behaviour.* New York: McGraw-Hill.

Horne, P., & Lowe, C. (1993). Determinants of Human Performance on Concurrent Schedules. *Journal of the Experimental Analysis of Behavior*, *59*(1), 29-60. Http://Dx.Doi.Org/10.1901/Jeab.1993.59-29

Hughes, B. O., & Dun, P. (1983). Production and Behaviour of Laying Domestic Fowls in Outside Pens. *Applied Animal Ethology*, *11*(2), 201.

Hughes, J.E., Amy, HR., Howard, J.L., Nany, K.P., & Pollard G, T. (1994). Health Effects of Water Restriction to Motivate Lever-Pressing in Rats. *Laboratory Animal Science*, *44*(2), 135-40.

Iwata, B., Smith, R., & Michael, J. (2000). Current Research on the Influence of Establishing Operations on Behavior in Applied Settings. *Journal of Applied Behavior Analysis*, *33*(4), 411-418. Http://Dx.Doi.Org/10.1901/Jaba.2000.33-411

Jenkins, HR., & Moore, B. (1973). The Form of the Auto-Shaped Response with Food or Water Reinforcers. *Journal of the Experimental Analysis of Behavior*, *20*(2), 163-181. Http://Dx.Doi.Org/10.1901/Jeab.1973.20-163

Kacelnik, A., & Marsh, B. (2002). Cost Can Increase Preference In Starlings. *Animal Behaviour*, *63*(2), 245-250. Http://Dx.Doi.Org/10.1006/Anbe.2001.1900

Kangas, B., & Branch, M. (2006). Stability of Pigeon Bodyweight under Free-Feeding Conditions. *Journal of the Experimental Analysis of Behavior*, *86*(3), 393-396. Http://Dx.Doi.Org/10.1901/Jeab.2006.40-06

Keller, F.S., & Schoenfeld, W.N. (1950). *Principles of Psychology.* New York: Appleton-Century–Crofts.

Kimble, G. A. (1951). Behavior Strength As A Function Of The Intensity Of The Hunger Drive. *Journal Of Experimental Psychology*, *41*(5), 341-348.

Klatt, K. P., & Morris, E. K. (2001). The Premack Principle, Response Deprivation, and Establishing Operations. *The Behavior Analyst*, *24*(2), 173-180.

Lade wig, J., Sorensen, D. B., Nielsen, P. P., & Matthews, L. R. (2002). The Quantitative Measurement of Motivation: Generation of Demand Functions under Open versus Closed Economies. *Applied Animal Behaviour Science*, *79*(4), 325-331.

LaMon, B., & Zeigler, HR. P. (1988). Control of Pecking Response Form in The Pigeon: Topography of Injective Behaviours and Conditioned Key Pecks with Food and Water Reinforcers. *Animal Learning & Behavior*, *16*(3), 256-267.

Langthorne, P., & McGill, P. (2009). A Tutorial on the Concept of the Motivating Operation and Its Importance to Application. *Behavior Analysis in Practice*, *2*(2), 22.

Laraway, S., Snycerski, S., Michael, J., & Poling, A. (2003). Motivating Operations and Terms to Describe Them: Some Further Refinements. *Journal of Applied Behavior Analysis*, *36*(3), 407-414. Http://Dx.Doi.Org/10.1901/Jaba.2003.36-407

Laraway, S., Snycerski, S., Olson, R., Becker, B., & Poling, A. (2014). The Motivating Operations Concept: Current Status and Critical Response. *The Psychological Record*, *64*(3), 601-623. Http://Dx.Doi.Org/10.1007/S40732-014-0080-5

Lattal, K. A., & Gleeson, S. (1990). Response Acquisition with Delayed Reinforcement. *Journal of Experimental Psychology: Animal Behavior Processes, 16*, 27–39.

Lattal, K. A., & Williams, A. M. (1997). Bodyweight and Response Acquisition with Delayed Reinforcement. *Journal of the Experimental Analysis of Behavior*, *67*(1), 131-143.

Lau, B., & Glimcher, P. (2005). Dynamic Response-By-Response Models of Matching Behavior in Rhesus Monkeys. *Journal of the Experimental Analysis of Behavior*, *84*(3), 555-579. Http://Dx.Doi.Org/10.1901/Jeab.2005.110-04

Lejeune, HR., & Nagy, J. (1986). Operant Conditioning in the Newly Hatched Quail: Fixed Interval Performance. *Behavioural Processes*, *12*(4), 317-325. Http://Dx.Doi.Org/10.1016/0376-6357(86)90002-1

Lewis, P., & Dougherty, D. M. (1992). Pigeon Performance on a Variable-Interval Omission Schedule at Different Levels of Food Deprivation. *Behavioural Processes*, *27*(1), 27-35.

Léon, M., & Hayes, L. (2015). The Effect of the Magnitude of the Food Deprivation Motivating Operation on Free-Operant Preference in Mice. *Behavioural Processes*, *115*, 135-142. Http://Dx.Doi.Org/10.1016/J.Beproc.2015.03.015

Lintern-Moore, S. (1972). The Relationship between Water Intake and the Production of “Wet” Droppings in the Domestic Fowl. *British Poultry Science*, *13*(3), 237-241. Http://Dx.Doi.Org/10.1080/00071667208415943

Lotfizadeh, A. D., Edwards, T. L., Redner, R., & Poling, A. (2012). Motivating Operations Affect Stimulus Control: A Largely Overlooked Phenomenon In Discrimination Learning. *Behavior Analyst*, *35*(1), 89-100.

Lucas, G. A., Timberlake, W., & Gawley, D. J. (1989). Learning and Meal-Associated Drinking: Meal-Related Deficits Produce Adjustments in Postprandial Drinking. *Physiology & Behavior*, *46*(3), 361-367.

Mclean, A., & White, K. (1983). Temporal Constraint on Choice: Sensitivity And Bias in Multiple Schedules. *Journal of the Experimental Analysis of Behavior*, *39*(3), 405-426. Http://Dx.Doi.Org/10.1901/Jeab.1983.39-405

MacDonall, J. (1988). Concurrent Variable-Ratio Schedules: Implications for the Generalized Matching Law. *Journal of the Experimental Analysis of Behavior*, *50*(1), 55-64. Http://Dx.Doi.Org/10.1901/Jeab.1988.50-55

Marsh, B. (2004). Energetic State During Learning Affects Foraging Choices in Starlings. *Behavioral Ecology*, *15*(3), 396-399. Http://Dx.Doi.Org/10.1093/Beheco/Arh034

McAdie, T., Foster, T., & Temple, W. (1996). Concurrent Schedules: Quantifying the Aversiveness of Noise. *Journal of the Experimental Analysis of Behavior*, *65*(1), 37-55. Http://Dx.Doi.Org/10.1901/Jeab.1996.65-37

McDevitt, M. A., & Fantino, E. (1993). Establishing Operations and the Discriminative Stimulus. *The Behavior Analyst*, *16*(2), 225-227.

McPherson, A., & Osborne, J. G. (1988). Control of Behavior by an Establishing Stimulus. *Journal of the Experimental Analysis of Behavior*, *49*(2), 213-227.

McSweeney, F. (1974). Variability of Responding On a Concurrent Schedule as a Function of Bodyweight. *Journal of the Experimental Analysis of Behavior*, *21*(2), 357-359. Http://Dx.Doi.Org/10.1901/Jeab.1974.21-357

McSweeney, F. (1975). Concurrent Schedule Responding as a Function of Bodyweight. *Animal Learning & Behavior*, *3*(3), 264-270. Http://Dx.Doi.Org/10.3758/Bf03213442

McSweeney, F., Weatherly, J., & Roll, J. (1995). Within-Session Changes in Responding During Concurrent Schedules that Employ Two Different Operanda. *Animal Learning & Behavior*, *23*(3), 237-244. Http://Dx.Doi.Org/10.3758/Bf03198920

Michael, J. (1982). Distinguishing Between Discriminative and Motivational Functions of Stimuli. *Journal of the Experimental Analysis of Behavior*, *37*(1), 149-155. Http://Dx.Doi.Org/10.1901/Jeab.1982.37-149

Michael, J. (1988). Establishing Operations and the Mand. *The Analysis of Verbal Behavior*, *6*, 3-9.

Michael, J. (1993). Establishing Operations. *The Behavior Analyst*, *16*(2), 191-206.

Michael, J. (2000). Implications and Refinements of the Establishing Operation Concept. *Journal of Applied Behavior Analysis*, *33*(4), 401-410. Http://Dx.Doi.Org/10.1901/Jaba.2000.33-401

Millenson, J.R. (1967). *Principles of Behavioural Analysis.* New York: The Macmillan Company. Millenson, J.R., & Leslie, J.C. (1979). *Principles of Behavioral Analysis (2nd Ed.)*. New York: The Macmillan Company.

Mishra, A., Koene, P., Schouten, W., Spruijt, B., Van Beek, P., & Metz, J. (2005). Temporal and Sequential Structure of Behavior and Facility Usage of Laying Hens in an Enriched Environment. *Poultry Science*, *84*(7), 979-991. Http://Dx.Doi.Org/10.1093/Ps/84.7.979

Moran, G. (1975). Severe Food Deprivation: Some Thoughts Regarding Its Exclusive Use. *Psychological Bulletin*, *82*(4), 543.

Nicol, C., & Dawkins, M. S. (1990). Homes Fit For Hens. *New Scientist*, *125*(1708), 46-51.

North, S., & Iwata, B. (2005). Motivational Influences on Performance Maintained By Food Reinforcement. *Journal of Applied Behavior Analysis*, *38*(3), 317-333. Http://Dx.Doi.Org/10.1901/Jaba.2005.93-04

National Research Council. (2004). *Nutritional Requirements of Poultry.* (2004). Washington, DC: National Research Council.

Olson, R., Laraway, S., & Austin, J. (2001). Unconditioned and Conditioned Establishing Operations in Organizational Behavior Management. *Journal of Organizational Behavior Management*, *21*(2), 7-35.

O'Reilly, M. F., Edrisinha, C., Sigafoos, J., Lancioni, G., & Andrews, A. (2006). Isolating the Evocative and Ablative Effects of an Establishing Operation on Challenging Behavior. *Behavioral Interventions*, *21*(3), 195-204.

Palya, W.L., 1992. Dynamics in the Fine Structure of Schedule-Controlled Behavior. *Journal of the Experimental Analysis of Behavior, 57*, 267–287.

Ploog, B. (2014). Species-Specific Response-Topography of Chickens' and Pigeons' Water-Induced Autoshaped Responding. *Behavioural Processes*, *106*, 5-11. Http://Dx.Doi.Org/10.1016/J.Beproc.2014.03.007

Ploog, B., & Zeigler, H.R. (1996). Effects of Food-Pellet Size on Rate, Latency, and Topography of Autoshaped Key Pecks and Gapes in Pigeons. *Journal of the Experimental Analysis of Behavior*, *65*(1), 21-35. Http://Dx.Doi.Org/10.1901/Jeab.1996.65-21

Ploog, B., & Zeigler, HR. (1997). Key-Peck Probability and Topography in a Concurrent Variable-Interval Variable-Interval Schedule with Food and Water Reinforcers. *Journal of the Experimental Analysis of Behavior*, *67*(1), 109-129. Http://Dx.Doi.Org/10.1901/Jeab.1997.67-109

Poling, A., Edwards, T.L., Weeden, M., & Foster, T.M. (2011). The Matching Law. *Psychological Record, 61(2)*, 313-322.

Pompilio, L. (2006). State-Dependent Learned Valuation Drives Choice in an Invertebrate. *Science*, *311*(5767), 1613-1615. Http://Dx.Doi.Org/10.1126/Science.1123924

Pompilio, L., & Kacelnik, A. (2005). State-Dependent Learning and Suboptimal Choice: When Starlings Prefer Long Over Short Delays to Food. *Animal Behaviour*, *70*(3), 571-578. Http://Dx.Doi.Org/10.1016/J.Anbehav.2004.12.009

Powell, R. (1971). Evidence of Interaction between Deprivation Effects and Stimulus Control. *Journal of the Experimental Analysis of*

Behavior, *16*(1), 95-104. Http://Dx.Doi.Org/10.1901/Jeab.1971.16-95

Premack, D. (1959). Toward Empirical Behavior Laws: I. Positive Reinforcement. *Psychological Review*, *66*(4), 219.

Premack, D. (1961). Predicting Instrumental Performance from the Independent Rate of the Contingent Response. *Journal of Experimental Psychology*, *61*(2), 163-171. Http://Dx.Doi.Org/10.1037/H0042090

Premack, D. (1962). Reversibility of the Reinforcement Relation. *Science*, *136*(3512), 255-257. Http://Dx.Doi.Org/10.1126/Science.136.3512.255

Premack, D. (1963). Rate Differential Reinforcement in Monkey Manipulation. *Journal of the Experimental Analysis of Behavior*, *6*(1), 81-89. http://dx.doi.org/10.1901/jeab.1963.6-81

Railton, R., Foster, T., & Temple, W. (2014). Object/Picture Recognition in Hens. *Behavioural Processes*, *104*, 53-64. http://dx.doi.org/10.1016/j.beproc.2014.01.013

Rispoli, M., O'Reilly, M., Lang, R., Machalicek, W., Davis, T., Lancioni, G., & Sigafoos, J. (2011). Effects of Motivating Operations on Problem and Academic Behavior in Classrooms. *Journal of Applied Behavior Analysis*, *44*(1), 187-192. http://dx.doi.org/10.1901/jaba.2011.44-187

Reed, D. D., & Kaplan, B. A. (2011). The Matching Law: A Tutorial for Practitioners. *Behavior Analysis in Practice*, *4*(2), 15-24.

Revusky, S. (1963). Effects of Hunger and VI Value on VI Pacing. *Journal of the Experimental Analysis of Behavior*, *6*(2), 163-169. http://dx.doi.org/10.1901/jeab.1963.6-163

Roll, V., Briz, R., & Levrino, G. (2009). Floor Versus Cage Rearing: Effects on Production, Egg Quality and Physical Condition of Laying Hens Housed In Furnished Cages. *Ciência Rural*, *39*(5), 1527-1532. http://dx.doi.org/10.1590/s0103-84782009000500034

Rowland, N. E. (2007). Food or Fluid Restriction in Common Laboratory Animals: Balancing Welfare Considerations with Scientific Inquiry. *Comparative Medicine*, *57*(2), 149-160.

Savory, C. (1978). The Relationship between Food and Water Intake and the Effects of Water Restriction on Laying Brown Leghorn Hens. *British Poultry Science*, *19*(5), 631-641. http://dx.doi.org/10.1080/00071667808416523

Savory, C., Seawright, E., & Watson, A. (1992). Stereotyped Behaviour in Broiler Breeders in Relation to Husbandry and Opioid Receptor

Blockade. *Applied Animal Behaviour Science*, *32*(4), 349-360. http://dx.doi.org/10.1016/s0168-1591(05)80027-9

Savory, C. (1994). Studies on Oral Stereotypies in Restricted-Fed Broiler Breeders. *Applied Animal Behaviour Science*, *40*(1), 93-94. http://dx.doi.org/10.1016/0168-1591(94)90122-8

Savory, J., (2010). Nutrition, Feeding and Drinking Behaviour, and Welfare. In I.J.H. Duncan & P. Hawkins (Eds.), *The Welfare of Domestic Fowl and Other Captive Birds* (pp. 165-188). London: Springer.

Savory, C. J., & Kostal, L. (1996). Temporal Patterning of Oral Stereotypies in Restricted-fed Fowls. Investigations with a Single Daily Meal. *International Journal of Comparative Psychology*, *9*(3), 117-139.

Schwartz, B., & Gamzu, E. (1977). Pavlovian Control of Operant Behavior: an Analysis of Autoshaping and its Implications for Operant Conditioning. In W.K. Honig & J.E.R. Staddon (Eds.), *Handbook of Operant Behavior.* Englewood Cliffs, NJ: Prentice-Hall.

Sheffield, F. D., & Campbell, B. A. (1954). The Role of Experience in the" Spontaneous" Activity of Hungry Rats. *Journal of Comparative and Physiological Psychology*, *47*(2), 97-100.

Shull, R. (2004). Bouts of Responding on Variable-Interval Schedules: Effects of Deprivation Level. *Journal of the Experimental Analysis of Behavior*, *81*(2), 155-167. http://dx.doi.org/10.1901/jeab.2004.81-155

Shull, R. L. (2011). Bouts, Changeovers, and Units of Operant Behavior. *European Journal of Behavior Analysis*, *12*(1), 49-72.

Skinner, B. F. (1938). *The Behavior of Organisms: An Experimental Analysis*. New York: Appleton-Century.

Skinner, B.F. (1953). *Science and Human Behavior*. New York: MacMillan.

Smith, R. (1974). Topography of the Food-Reinforced Key Peck and the Source of 30-Millisecond Interresponse Times. *Journal of the Experimental Analysis of Behavior*, *21*(3), 541-551. http://dx.doi.org/10.1901/jeab.1974.21-541

Smith, T., McLean, A., Shull, R., Hughes, C., & Pitts, R. (2014). Concurrent Performance as Bouts of Behavior. *Journal of the Experimental Analysis of Behavior*, *102*(1), 102-125. http://dx.doi.org/10.1002/jeab.90

Sparber, S. B., Bollweg, G. L., & Messing, R. B. (1991). Food Deprivation Enhances Both Autoshaping and Autoshaping Impairment by a Latent Inhibition Procedure. *Behavioural Processes*, *23*(1), 59-74.

Squires, N., & Fantino, E. (1971). A Model for Choice in Simple Concurrent and Concurrent-Chains Schedules. *Journal of the Experimental Analysis of Behavior*, *15*(1), 27-38. http://dx.doi.org/10.1901/jeab.1971.15-27

Sundberg, M. L. (2004). A Behavioral Analysis of Motivation and Its Relation to Mand Training. In L. W. Williams (Ed.), Developmental Disabilities: Etiology, Assessment, Intervention And Integration (Pp. 199-220). Reno, NV: Context Press.

Sumpter, C., Temple, W., & Foster, T. (1998). Response Form, Force, and Number: Effects on Concurrent-schedule Performance. *Journal of the Experimental Analysis of Behavior*, *70*(1), 45-68. http://dx.doi.org/10.1901/jeab.1998.70-45

Sumpter, C., Foster, T., & Temple, W. (1995). Predicting and Scaling Hens' Preferences for Topographically Different Responses. *Journal of the Experimental Analysis of Behavior*, *63*(2), 151-163. http://dx.doi.org/10.1901/jeab.1995.63-151

Sumpter, C., Foster, M., & Temple, W. (2002). Assessing Animals' Preferences: Concurrent Schedules of Reinforcement. *International Journal of Comparative Psychology*, *15*, 107-126.

Swaddle, J., & Ruff, D. (2004). Starlings Have Difficulty in Detecting Dot Symmetry: Implications for Studying Fluctuating Asymmetry. *Behaviour*, *141*(1), 29-40. http://dx.doi.org/10.1163/156853904772746583

Tanno, T., Kurashima, R., & Watanabe, S. (2011). Motivational Control of Impulsive Behavior Interacts with Choice Opportunities. *Learning and Motivation*, *42*(2), 145-153.

Temple, W., Scown, J., & Foster, T. (1995). Changeover Delay and Concurrent-Schedule Performance in Domestic Hens. *Journal of the Experimental Analysis of Behavior*, *63*(1), 71-95. http://dx.doi.org/10.1901/jeab.1995.63-71

Timberlake, W. (1993). Behavior Systems and Reinforcement: An Integrative Approach. *Journal of the Experimental Analysis of Behavior*, *60*(1), 105-128.

Timberlake, W. (2001). Motivational Modes in Behavior Systems. In R. R. Mowrer and S. B. Klein (Eds.), *Handbook of Contemporary Learning Theories* (pp. 155-209). Hillsdale NJ: Erlbaum Associates.

Timberlake, W., & Allison, J. (1974). Response Deprivation: An Empirical Approach to Instrumental Performance. *Psychological Review*, *81*(2), 146-164. http://dx.doi.org/10.1037/h0036101

Tinbergen, N. (1948). Social Releasers and the Experimental Method Required for Their Study. *Wilson Bulletin, 60*(1), 6–51.

Toth, L.A., & Gardiner, T.W. (2000). Food and Water Restriction Protocols: Physiological and Behavioral Considerations. *Contemporary Topics in Laboratory Animal Science, 39*(6), 9-17.

Uslaner, J. M., & Robinson, T. E. (2006). Subthalamic Nucleus Lesions Increase Impulsive Action and Decrease Impulsive Choice−Mediation by Enhanced Incentive Motivation? *European Journal of Neuroscience*, *24*(8), 2345-2354.

Vasconcelos, M., & Urcuioli, P. (2008). Deprivation Level and Choice in Pigeons: A Test of Within-Trial Contrast. *Learning & Behavior*, *36*(1), 12-18. Http://Dx.Doi.Org/10.3758/Lb.36.1.12

Van Haaren, F. (1992). Response Acquisition with Fixed and Variable Resetting Delays of Reinforcement in Male and Female Wistar Rats. *Physiology and Behavior, 52*(4)*,* 767–772.

Wald, B., & Cheney, C. (1975). Matching Behavior and Deprivation. *Bulletin of the Psychonomic Society*, *6*(1), 4-6. http://dx.doi.org/10.3758/bf03333127

Wearden, J., & Burgess, I. (1982). Matching Since Baum (1979). *Journal of the Experimental Analysis of Behavior*, *38*(3), 339-348. http://dx.doi.org/10.1901/jeab.1982.38-339

Weiss, B., & Gott, C. T. (1972). A Microanalysis of Drug Effects on Fixed-Ratio Performance in Pigeons. *Journal of Pharmacology and Experimental Therapeutics*, *180*(2), 189-202.

Whelan, R., & Barnes-Holmes, D. (2010). Consequence Valuing as Operation and Process: A Parsimonious Analysis of Motivation. *The Psychological Record*, *60*(2), 337-354.

Wilkenfield, J., Nickel, M., Blakely, E., & Poling, A. (1992). Acquisition of Lever-Press Responding in Rats with Delayed Reinforcement: A Comparison of Three Procedures. *Journal of the Experimental Analysis of Behavior, 58*(3), 431–443.

Xin, HR., Gates, R., Puma, M., & Ahn, D. (2002). Drinking Water Temperature Effects on Laying Hens Subjected to Warm Cyclic Environments. *Poultry Science*, *81*(5), 608-617. http://dx.doi.org/10.1093/ps/81.5.608

Yeomans, M. R. (1986, March). Overdrinking in the Domestic-Fowl. *British Poultry Science, 27*, 163.

APPENDICES

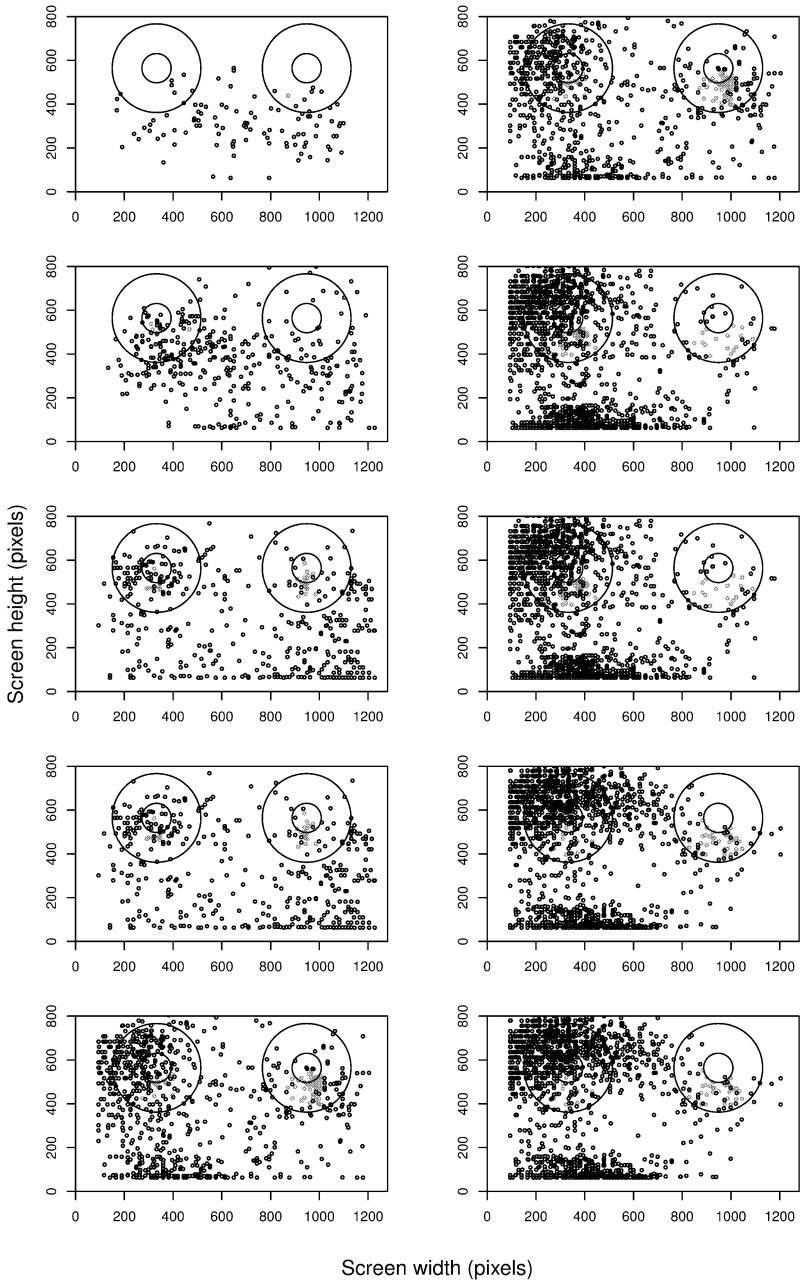

Figure A.1. The location of white circle pecks (grey), near white circle pecks (light grey) and black screen pecks (black), across sessions 1-5 (left panel, from top down) and sessions 6-10 (right panel, from top down) for Hen 1-1, Experiment 4.1.

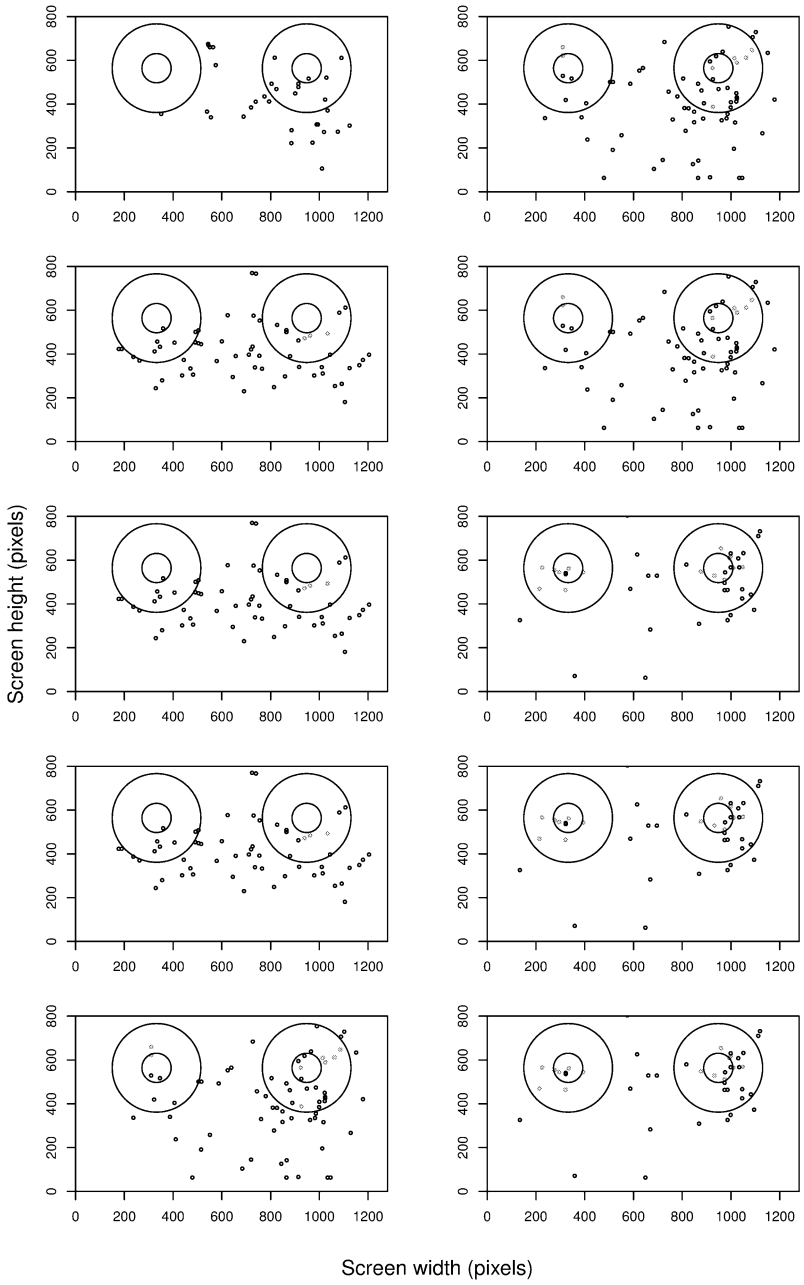

Figure A.2. The location of white circle pecks (grey), near white circle pecks (light grey) and black screen pecks (black), across sessions 1-5 (left panel, from top down) and sessions 6-10 (right panel, from top down) for Hen 1-2, Experiment 4.1.

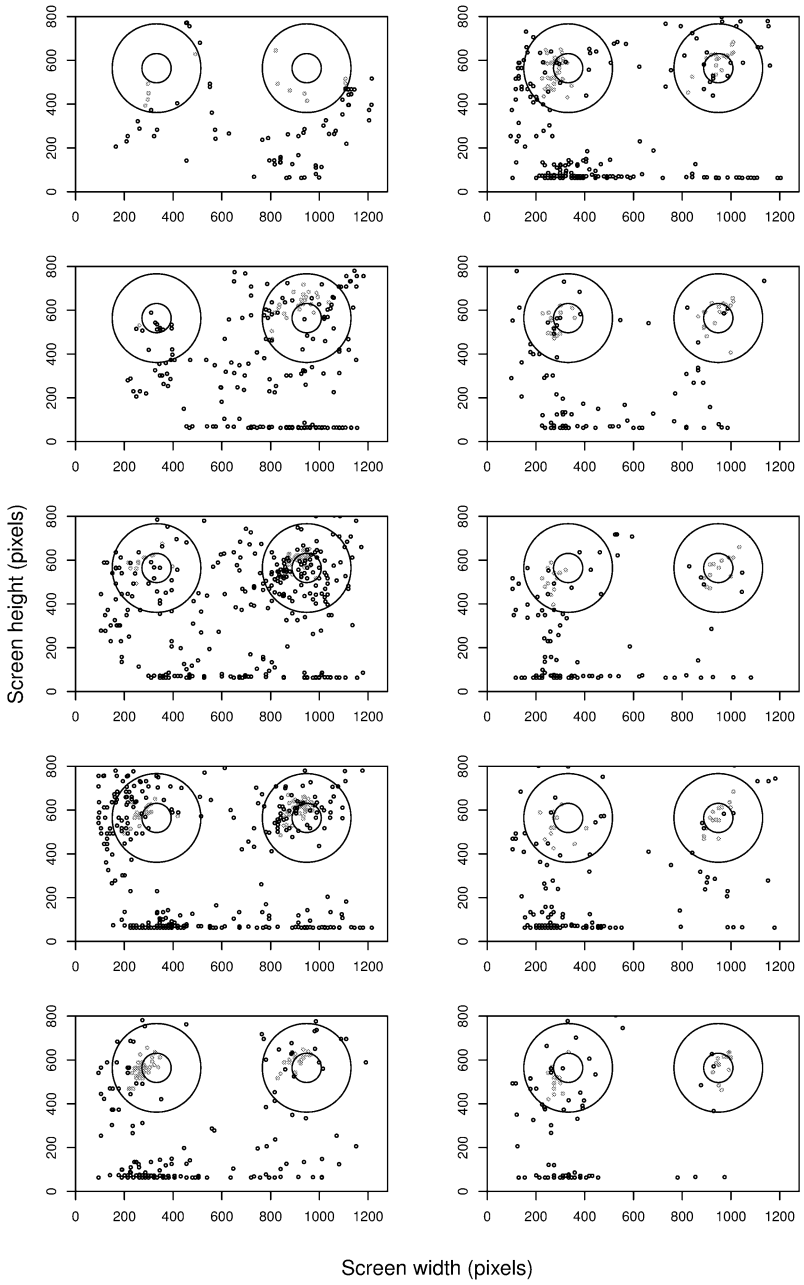

Figure A.3. The location of white circle pecks (grey), near white circle pecks (light grey) and black screen pecks (black), across sessions 1-5 (left panel, from top down) and sessions 6-10 (right panel, from top down) for Hen 1-3, Experiment 4.1.

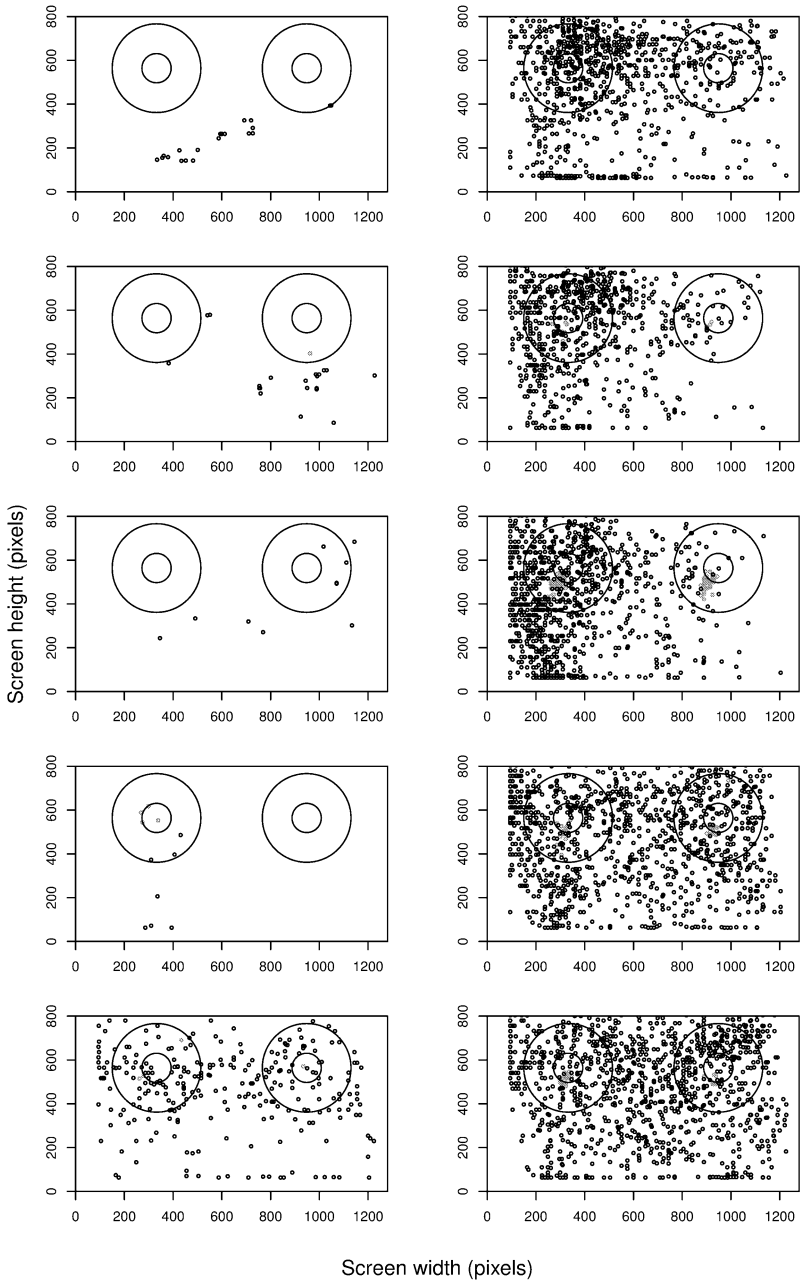

Figure A.4. The location of white circle pecks (grey), near white circle pecks (light grey) and black screen pecks (black), across sessions 1-5 (left panel, from top down) and sessions 6-10 (right panel, from top down) for Hen 1-4, Experiment 4.1.

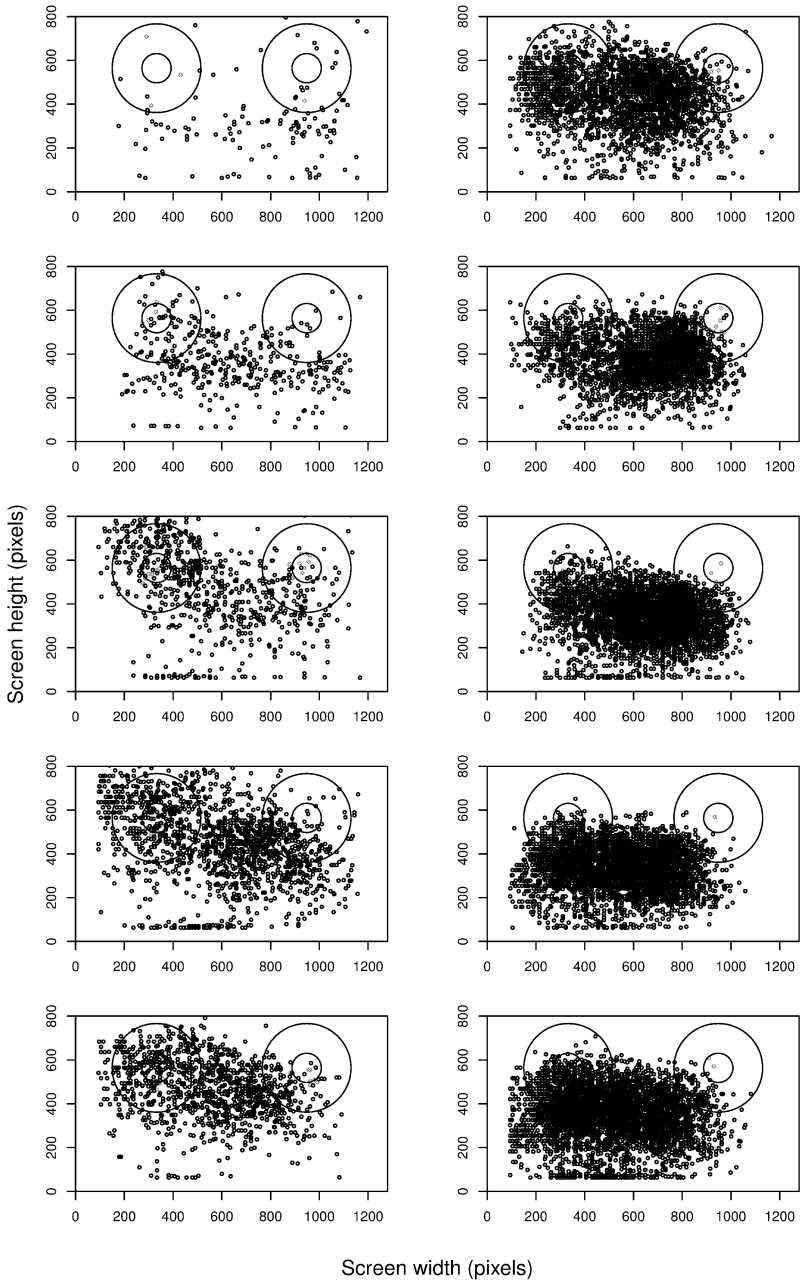

Figure A.5. The location of white circle pecks (grey), near white circle pecks (light grey) and black screen pecks (black), across sessions 1-5 (left panel, from top down) and sessions 6-10 (right panel, from top down) for Hen 1-5, Experiment 4.1.

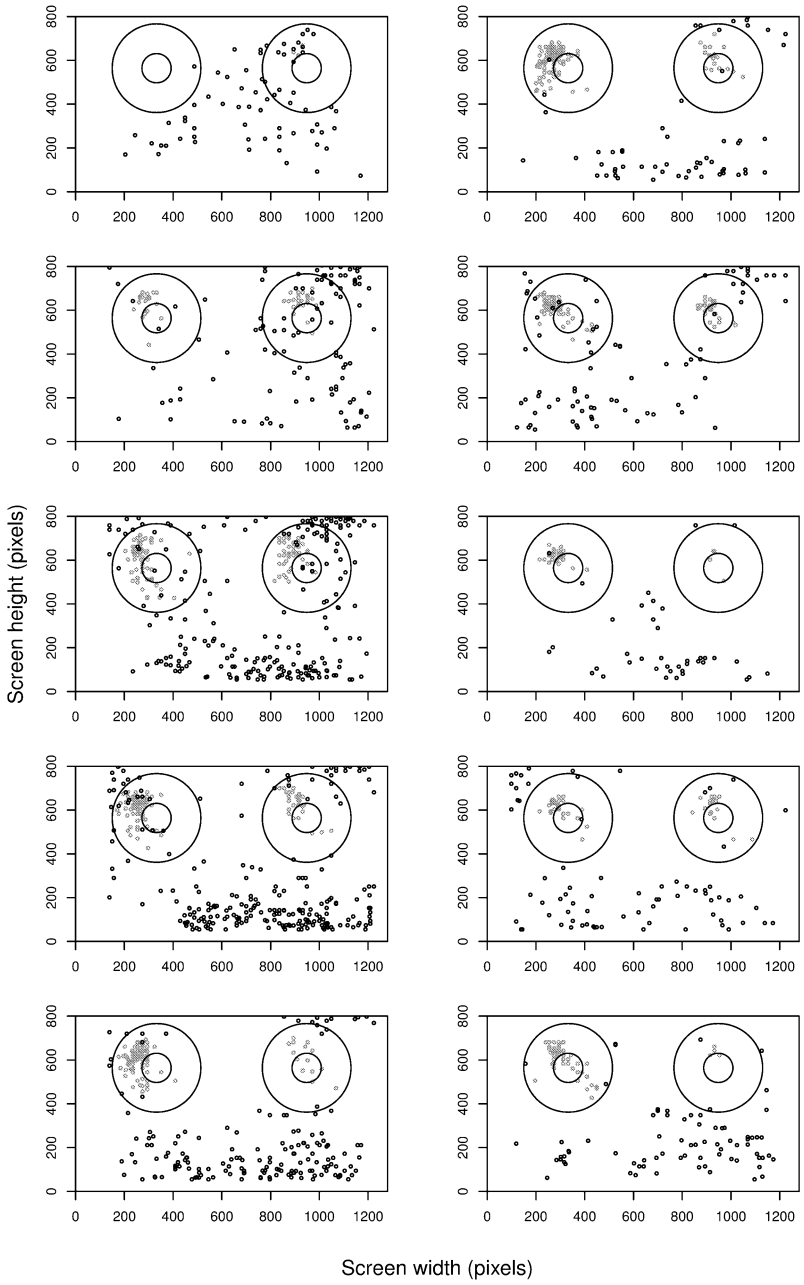

Figure A.6. The location of white circle pecks (grey), near white circle pecks (light grey) and black screen pecks (black), across sessions 1-5 (left panel, from top down) and sessions 6-10 (right panel, from top down) for Hen 1-6, Experiment 4.1.

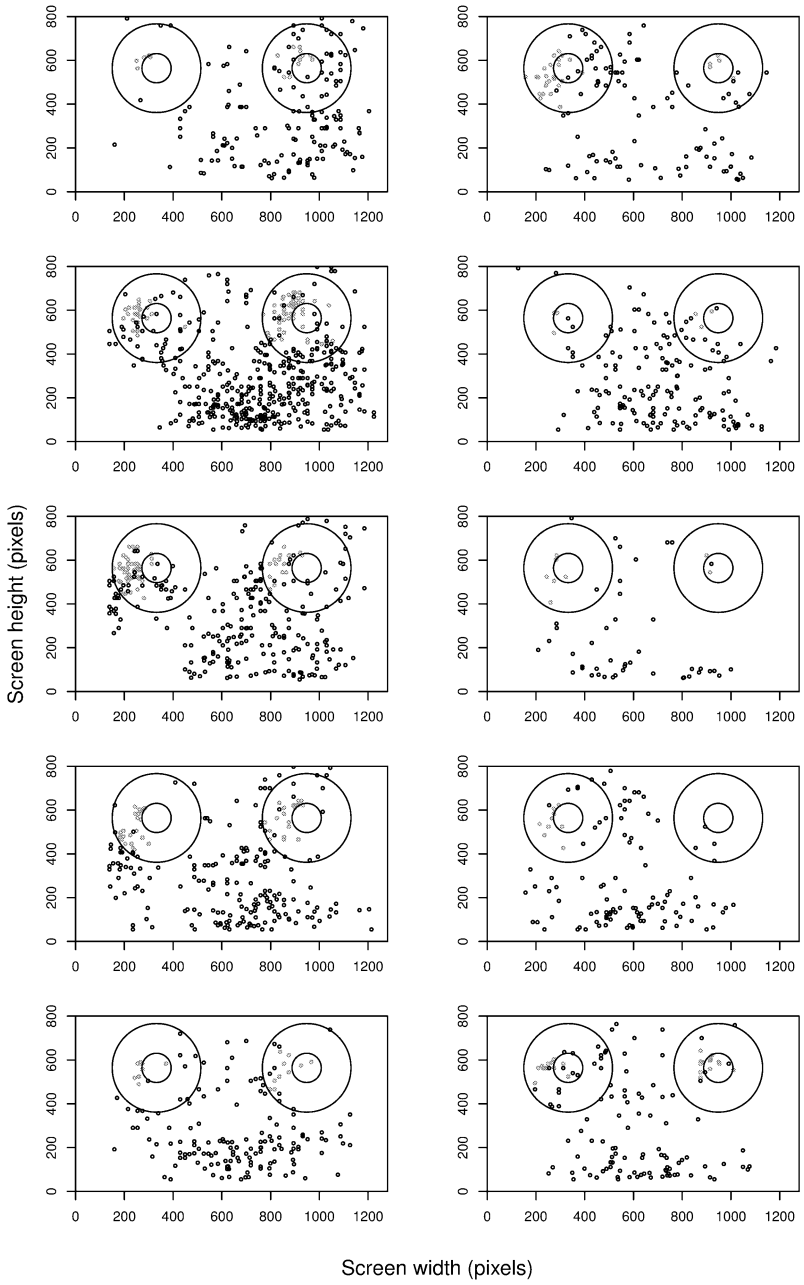

Figure A.7. The location of white circle pecks (grey), near white circle pecks (light grey) and black screen pecks (black), across sessions 1-5 (left panel, from top down) and sessions 6-10 (right panel, from top down) for Hen 1-7, Experiment 4.1.

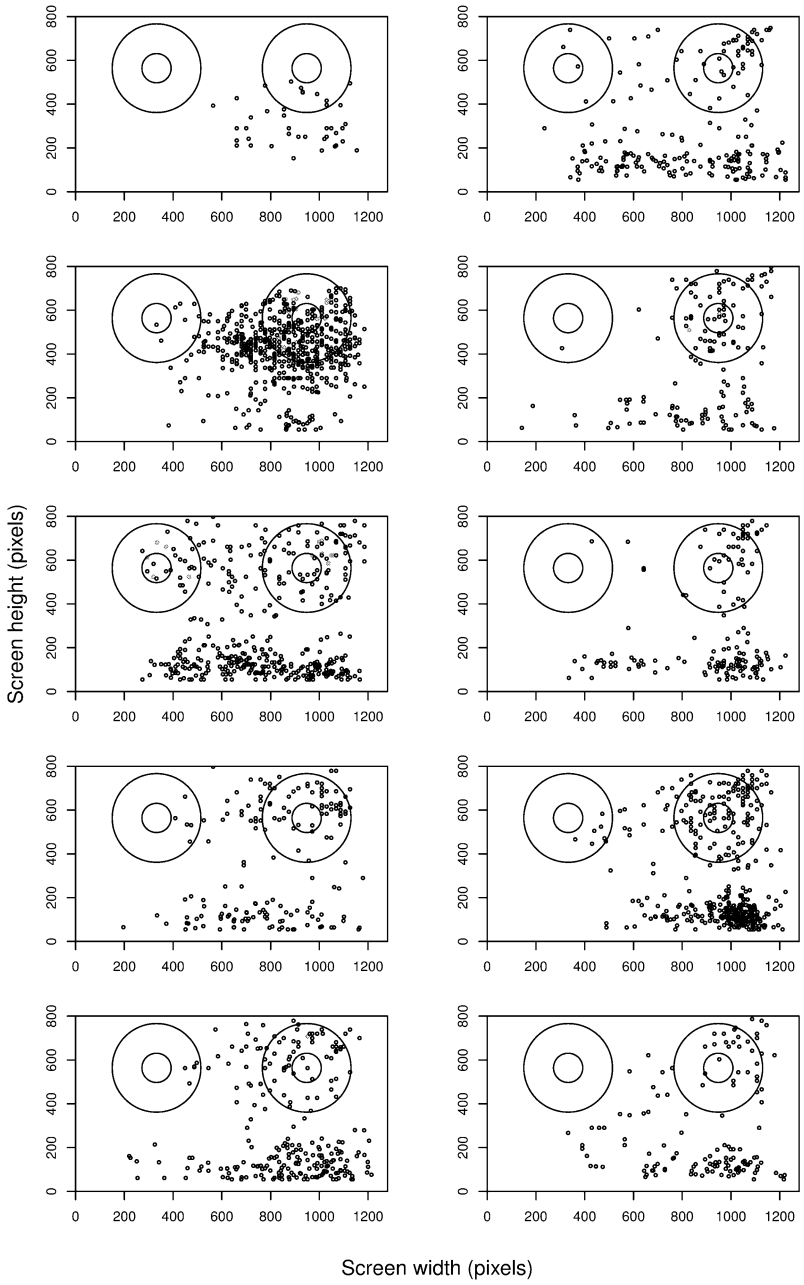

Figure A.8. The location of white circle pecks (grey), near white circle pecks (light grey) and black screen pecks (black), across sessions 1-5 (left panel, from top down) and sessions 6-10 (right panel, from top down) for Hen 1-8, Experiment 4.1.

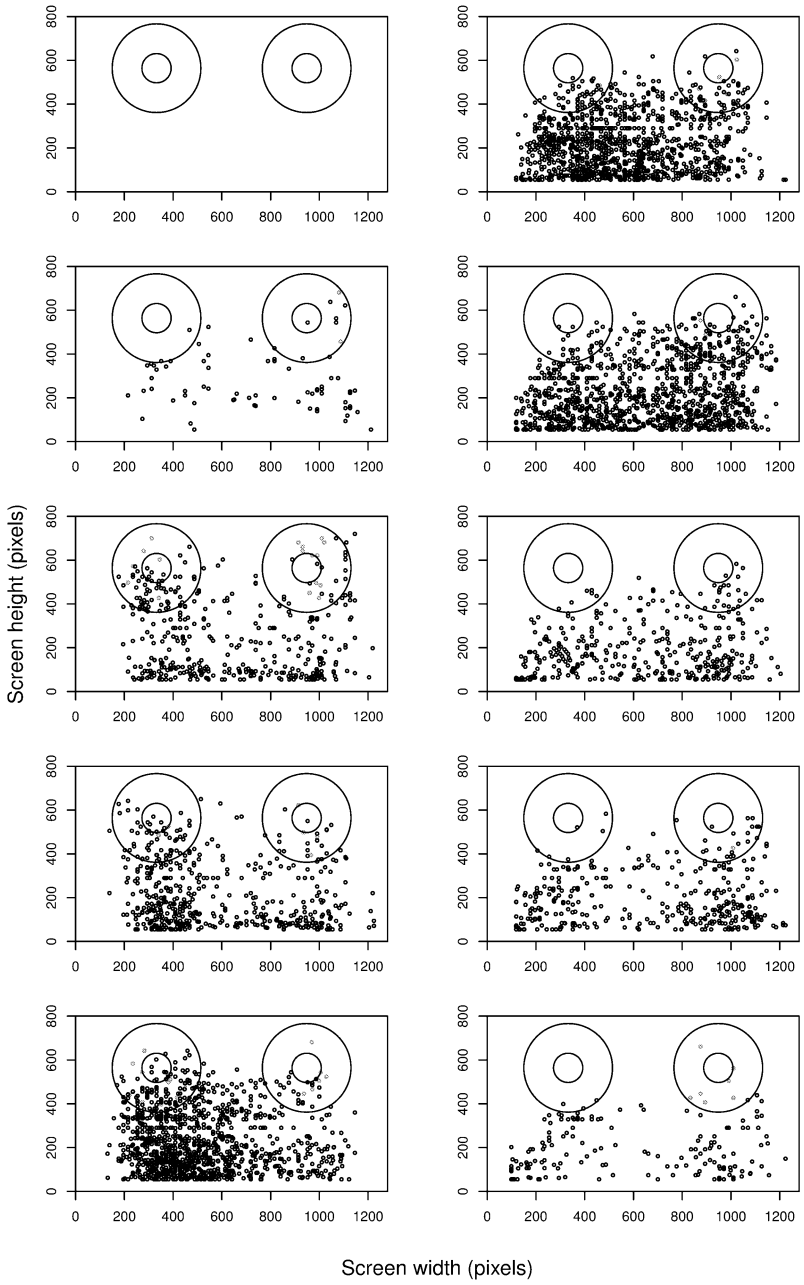

Figure A.9. The location of white circle pecks (grey), near white circle pecks (light grey) and black screen pecks (black), across sessions 1-5 (left panel, from top down) and sessions 6-10 (right panel, from top down) for Hen 1-9, Experiment 4.1.

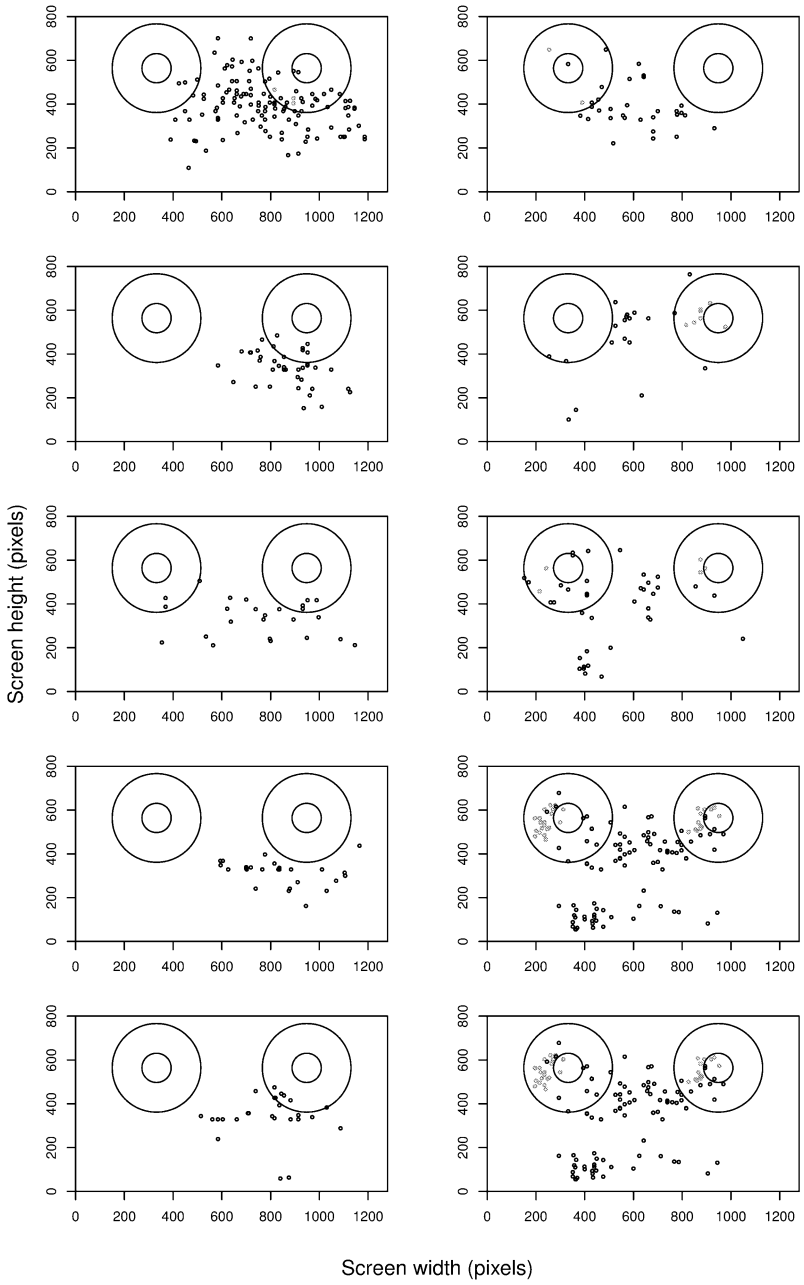

Figure A.10. The location of white circle pecks (grey), near white circle pecks (light grey) and black screen pecks (black), across sessions 1-5 (left panel, from top down) and sessions 6-10 (right panel, from top down) for Hen 1-10, Experiment 4.1.

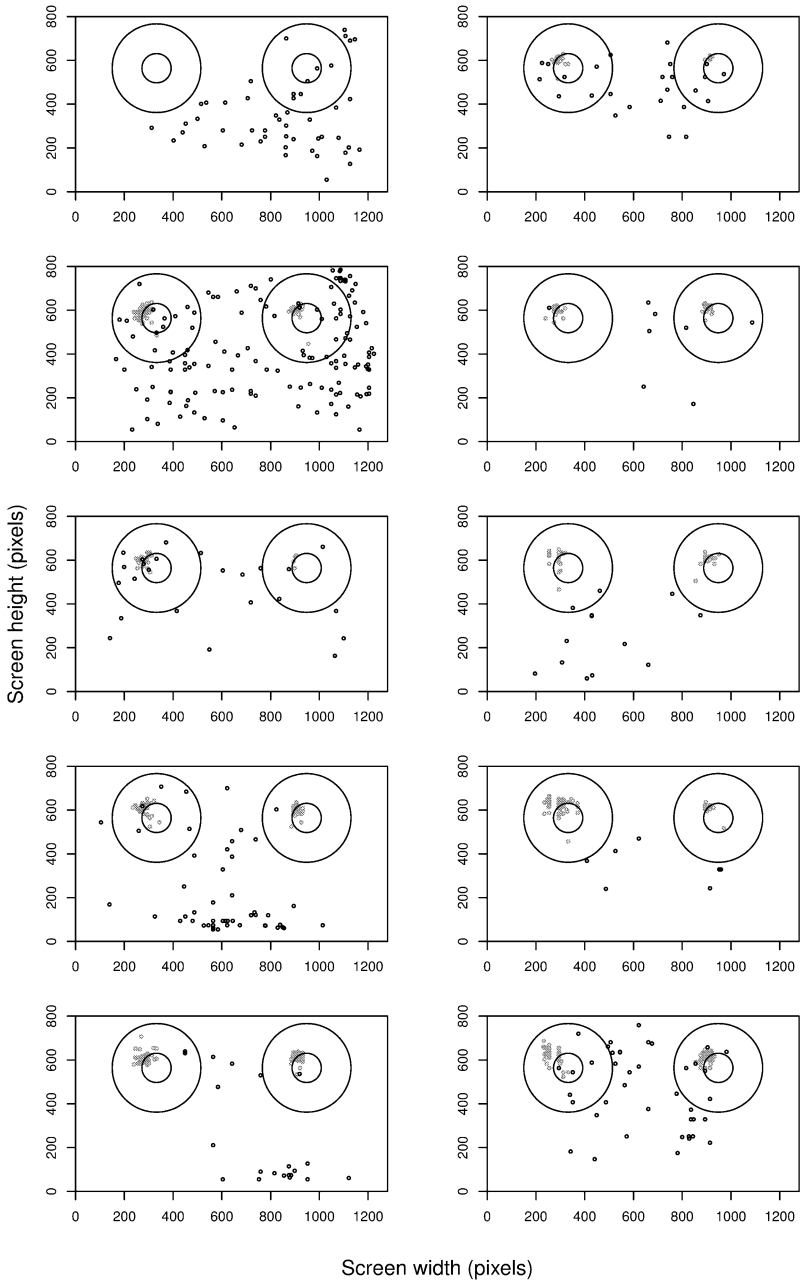

Figure A.11. The location of white circle pecks (grey), near white circle pecks (light grey) and black screen pecks (black), across sessions 1-5 (left panel, from top down) and sessions 6-10 (right panel, from top down) for Hen 1-11, Experiment 4.1.

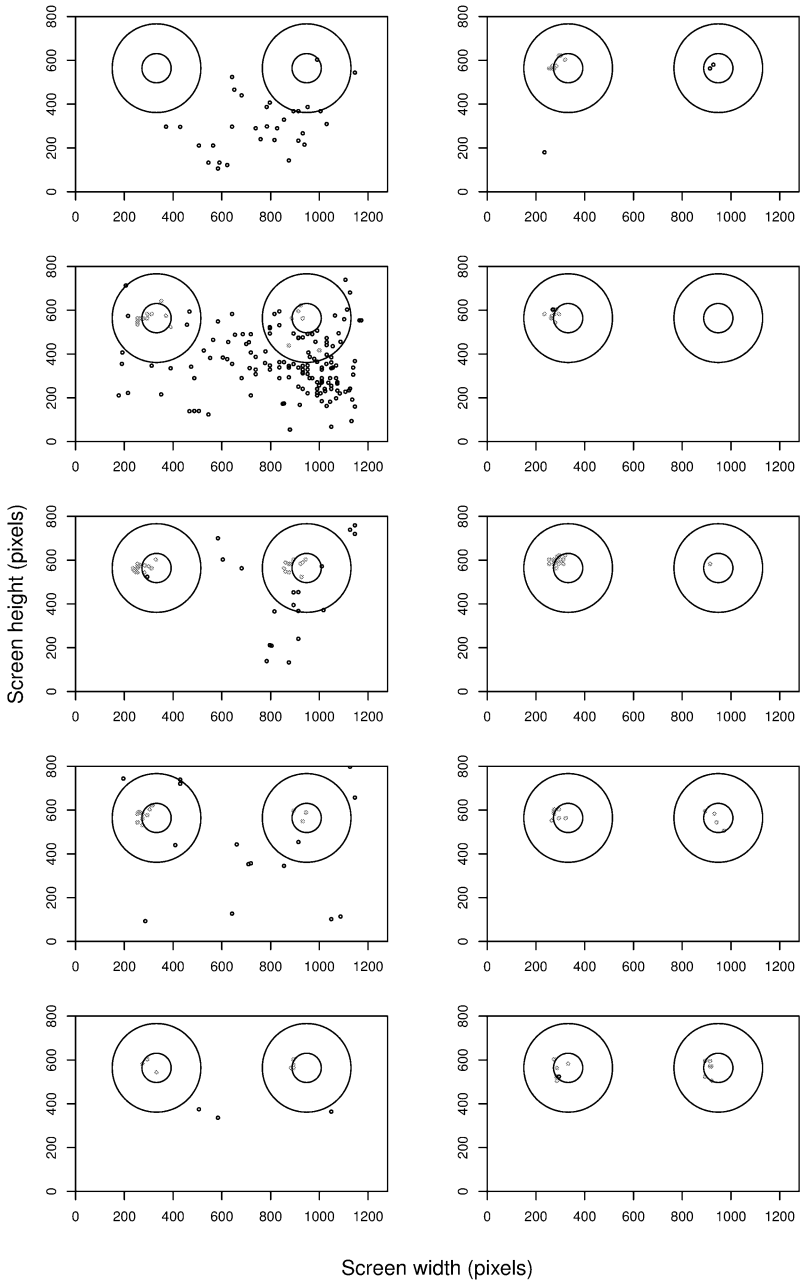

Figure A.12. The location of white circle pecks (grey), near white circle pecks (light grey) and black screen pecks (black), across sessions 1-5 (left panel, from top down) and sessions 6-10 (right panel, from top down) for Hen 1-12, Experiment 4.1.

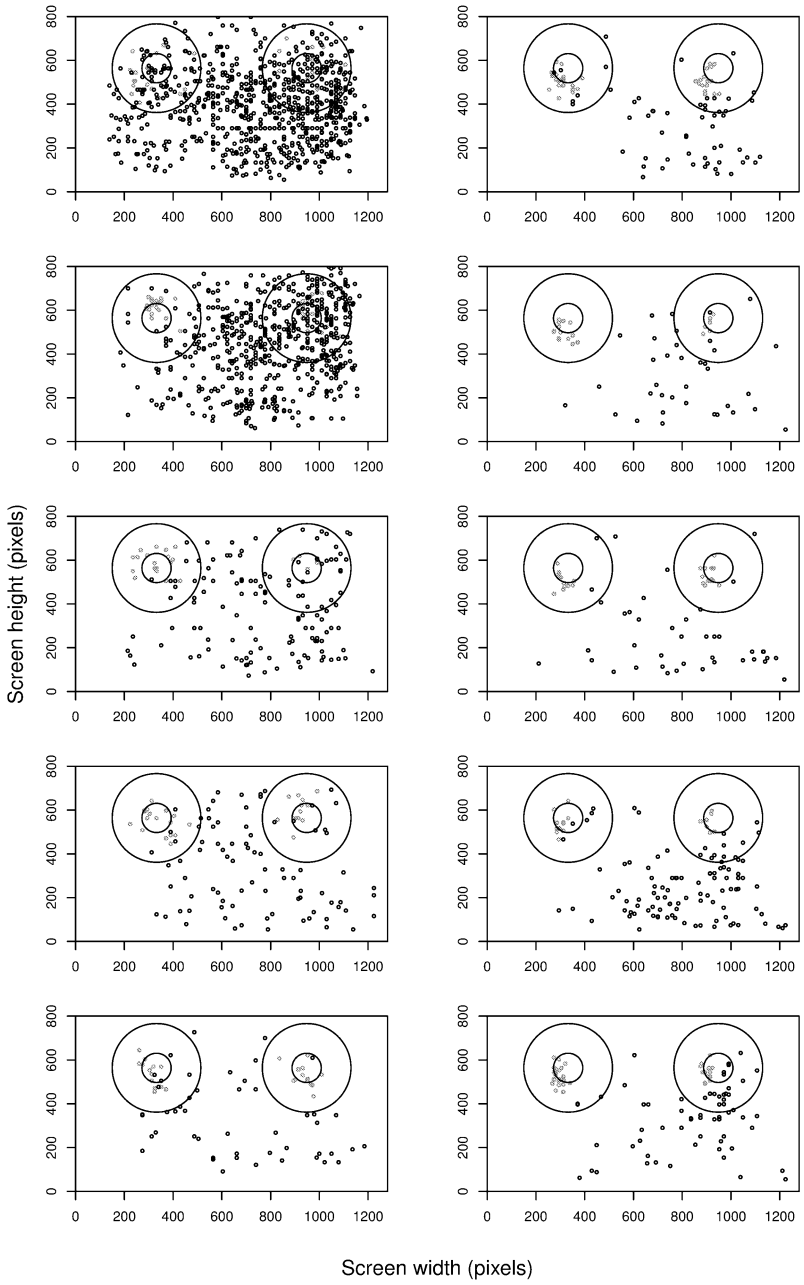

Figure A.13. The location of white circle pecks (grey), near white circle pecks (light grey) and black screen pecks (black), across sessions 1-5 (left panel, from top down) and sessions 6-10 (right panel, from top down) for Hen 1-13, Experiment 4.1.

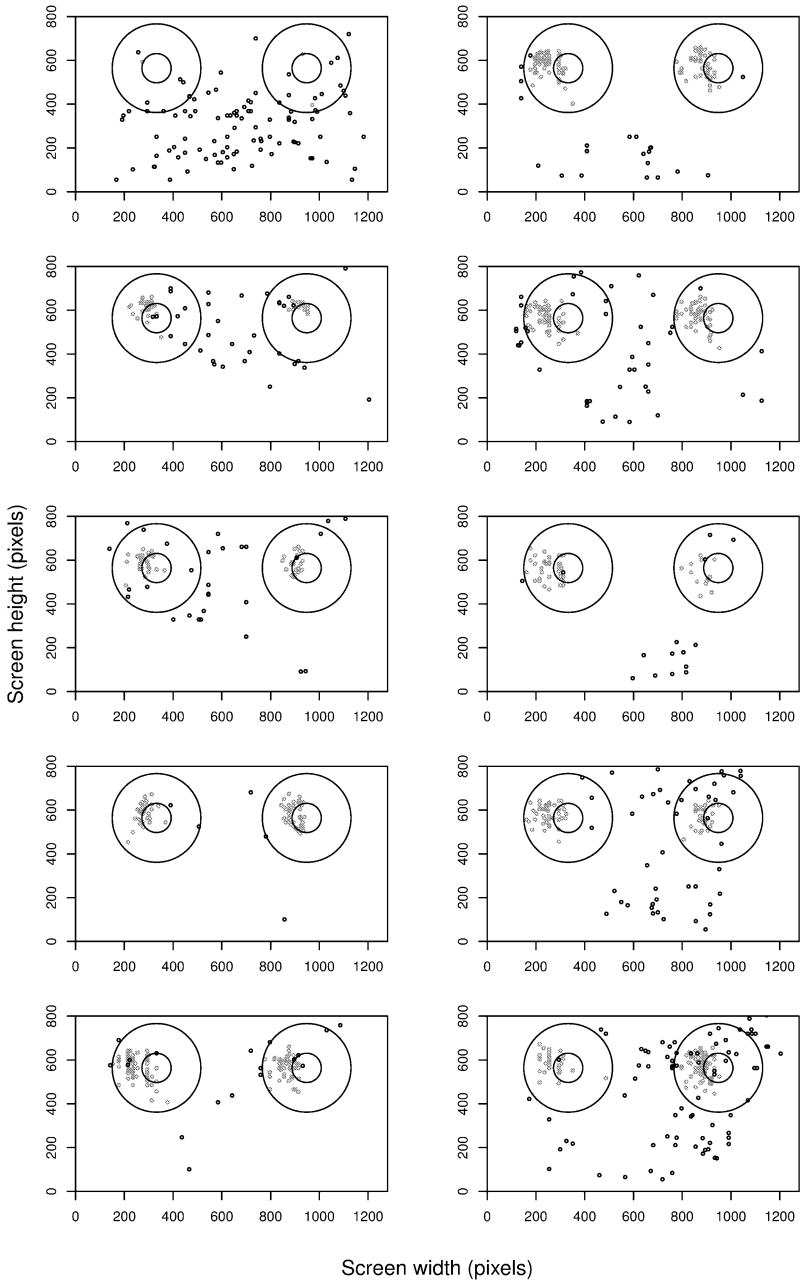

Figure A.14. The location of white circle pecks (grey), near white circle pecks (light grey) and black screen pecks (black), across sessions 1-5 (left panel, from top down) and sessions 6-10 (right panel, from top down) for Hen 1-14, Experiment 4.1.

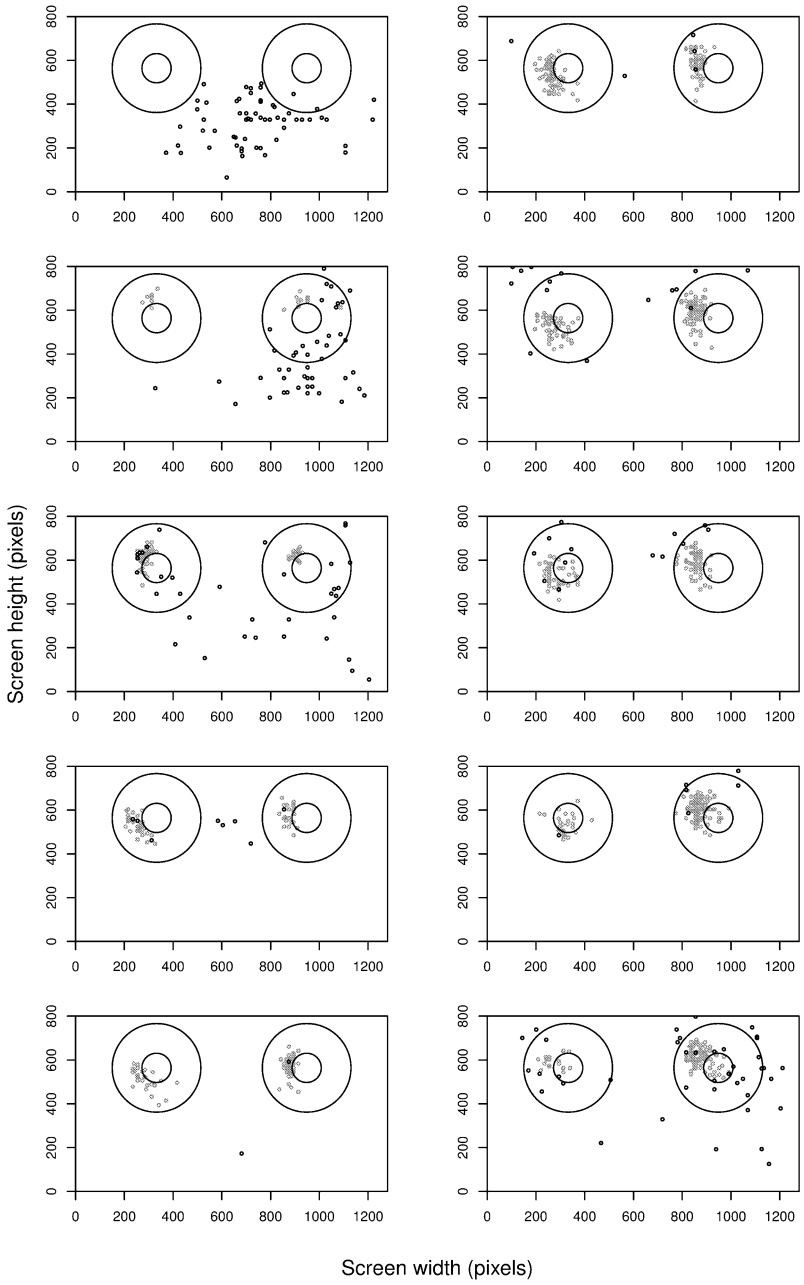

Figure A.15. The location of white circle pecks (grey), near white circle pecks (light grey) and black screen pecks (black), across sessions 1-5 (left panel, from top down) and sessions 6-10 (right panel, from top down) for Hen 1-15, Experiment 4.1.

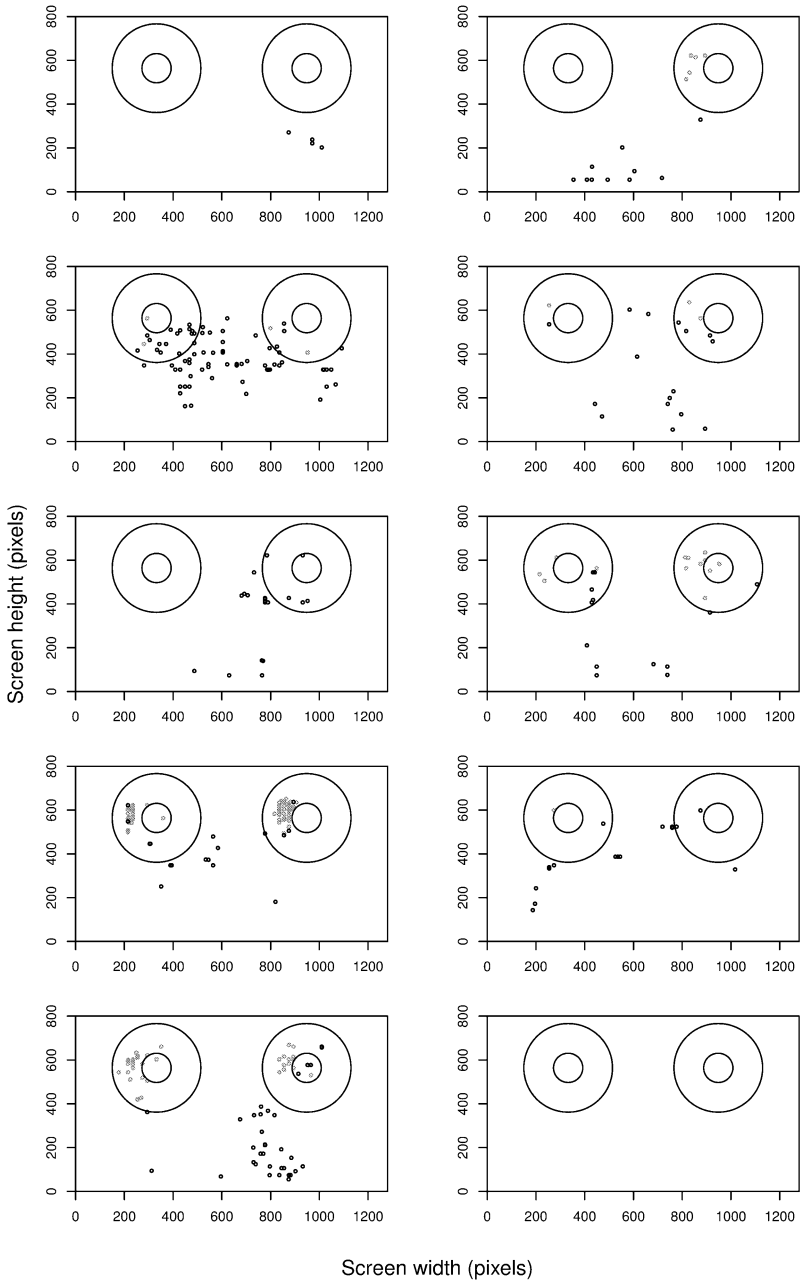

Figure A.16. The location of white circle pecks (grey), near white circle pecks (light grey) and black screen pecks (black), across sessions 1-5 (left panel, from top down) and sessions 6-10 (right panel, from top down) for Hen 2-1, Experiment 4.1.

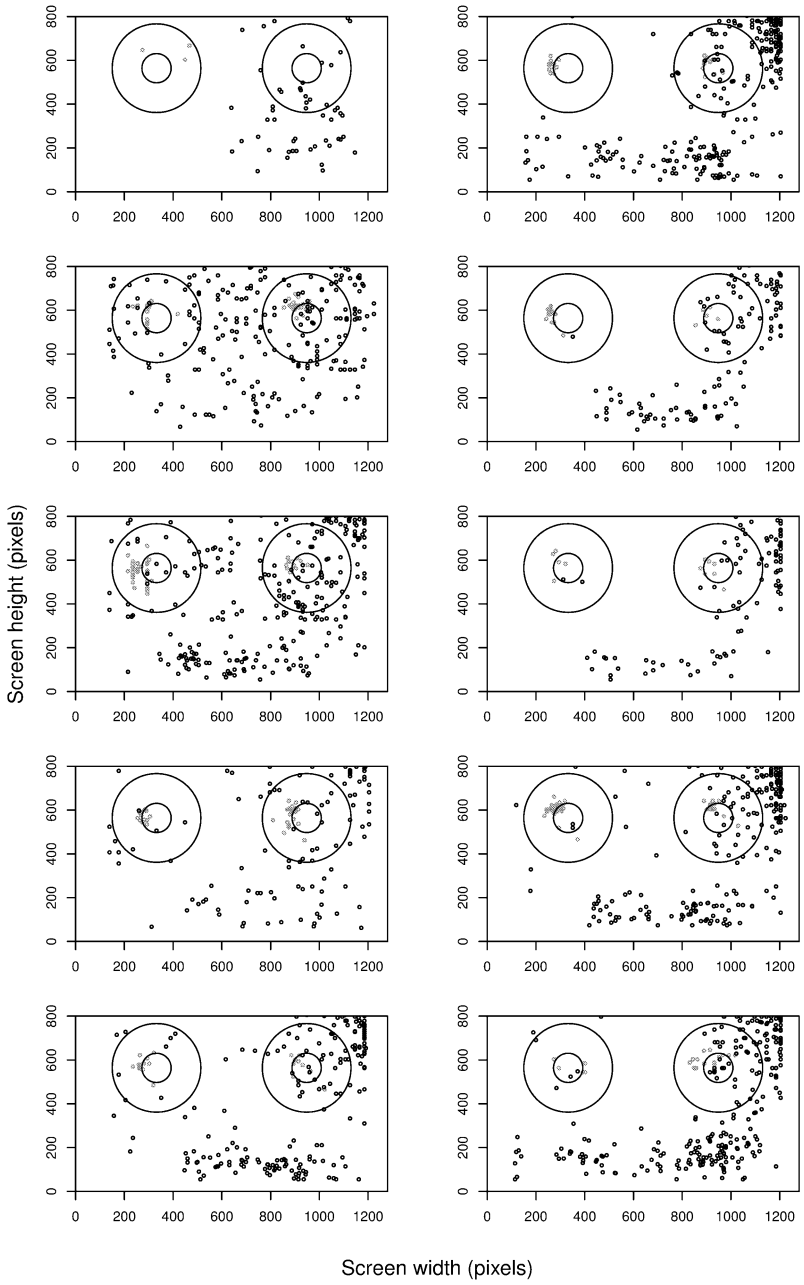

Figure A.17. The location of white circle pecks (grey), near white circle pecks (light grey) and black screen pecks (black), across sessions 1-5 (left panel, from top down) and sessions 6-10 (right panel, from top down) for Hen 2-2, Experiment 4.1.

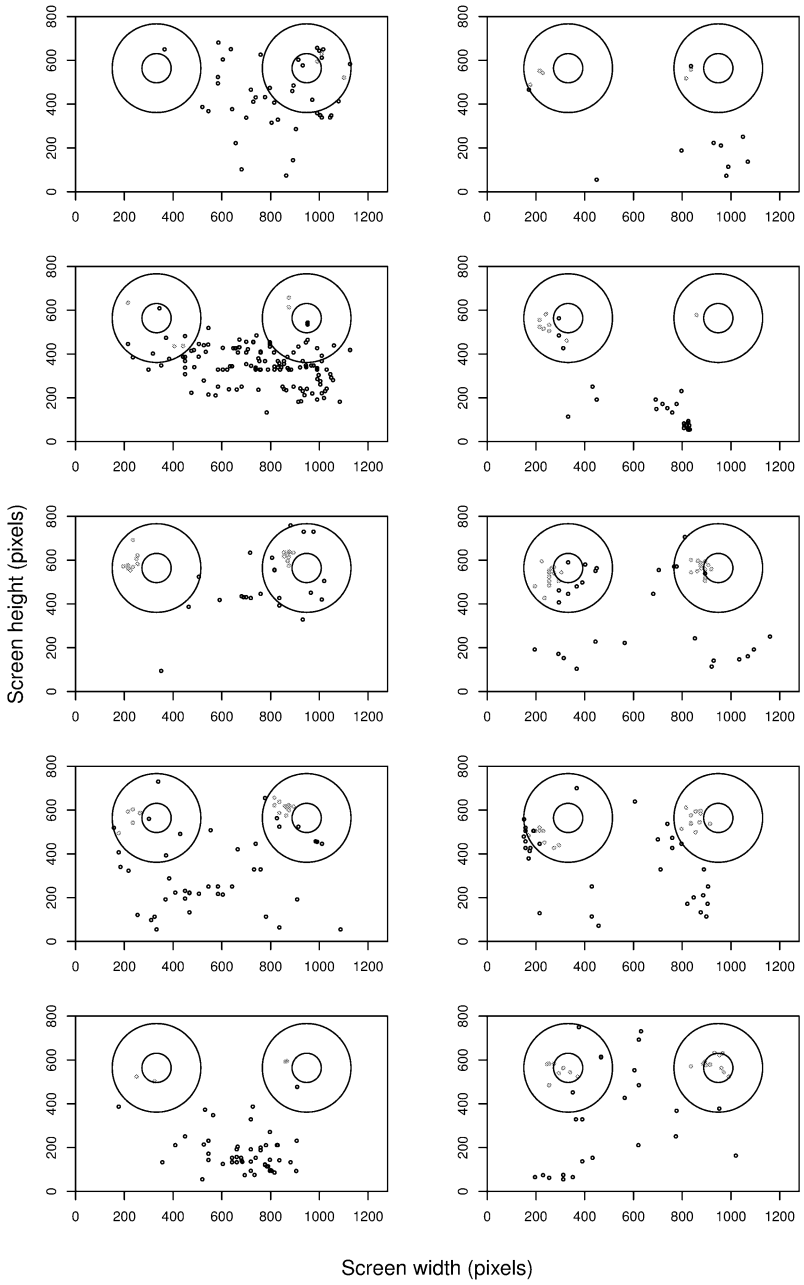

Figure A.18. The location of white circle pecks (grey), near white circle pecks (light grey) and black screen pecks (black), across sessions 1-5 (left panel, from top down) and sessions 6-10 (right panel, from top down) for Hen 2-3, Experiment 4.1.

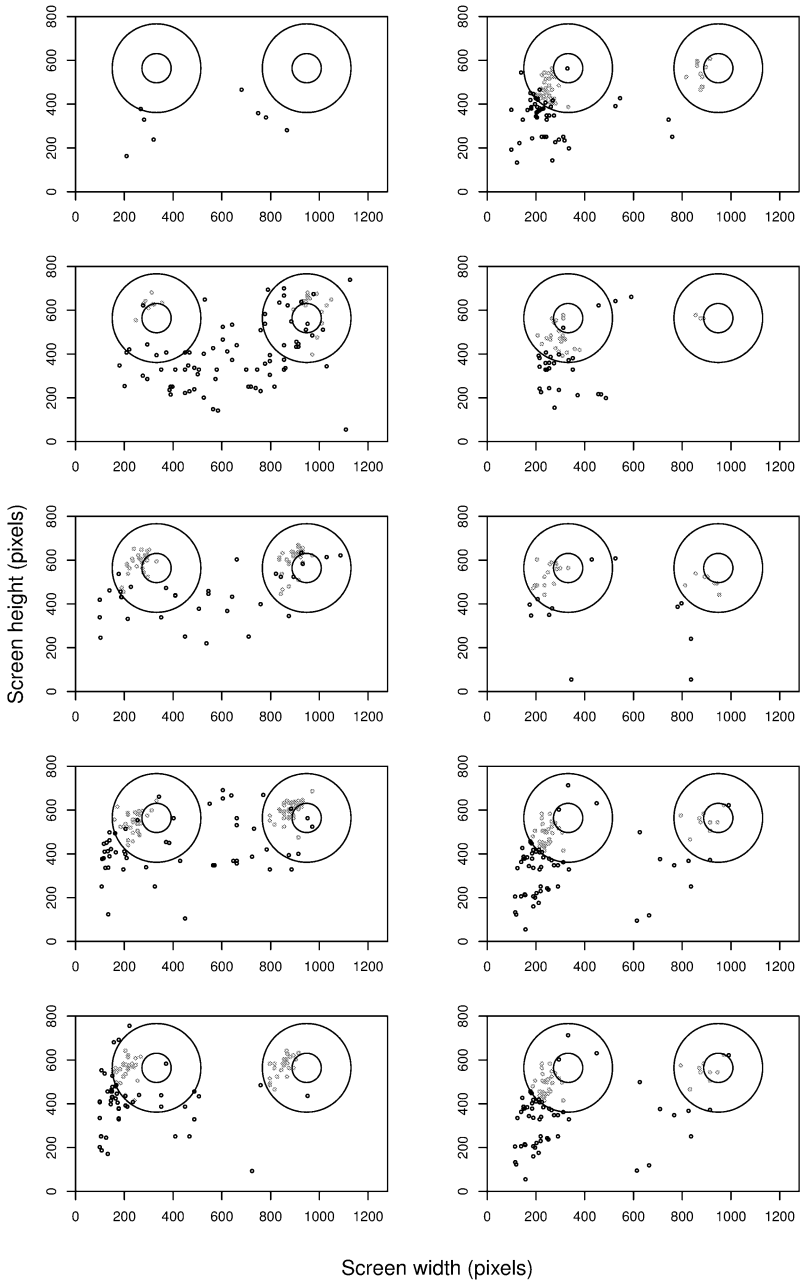

Figure A.18. The location of white circle pecks (grey), near white circle pecks (light grey) and black screen pecks (black), across sessions 1-5 (left panel, from top down) and sessions 6-10 (right panel, from top down) for Hen 2-4, Experiment 4.1.

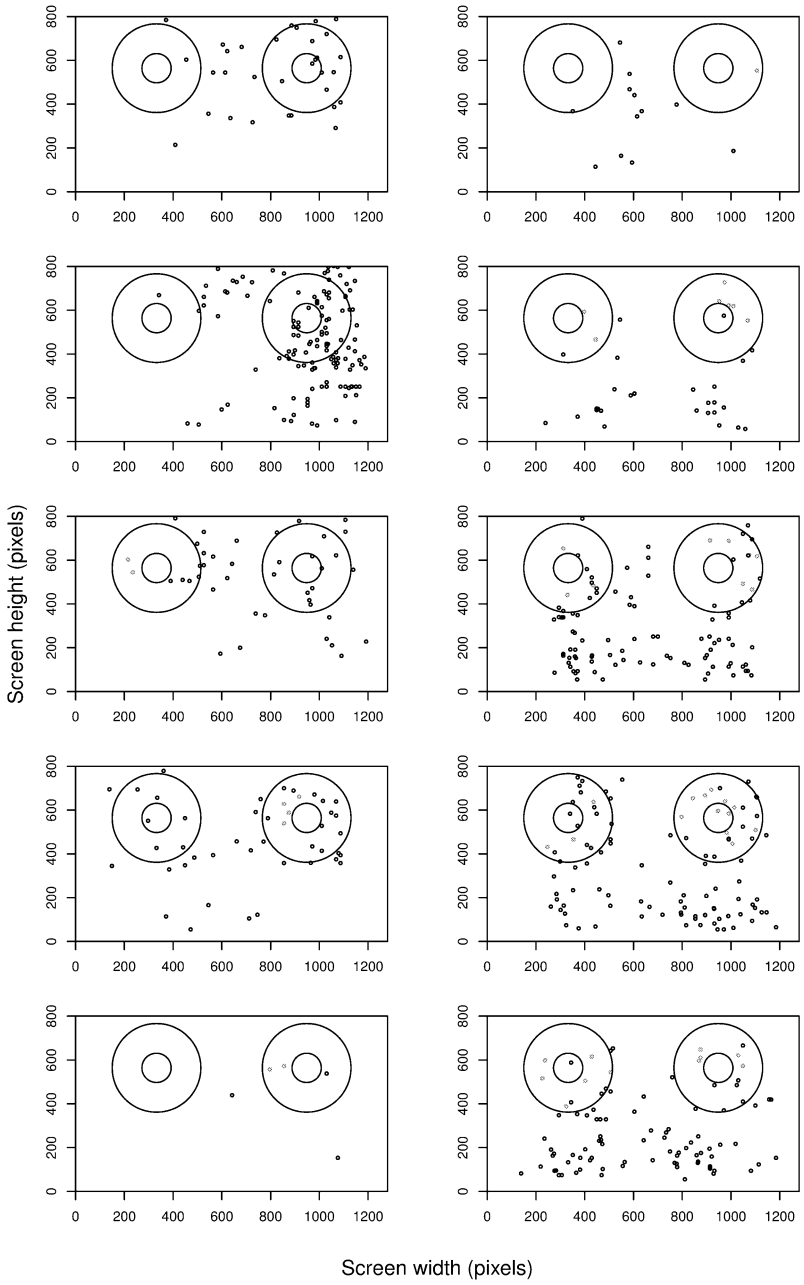

Figure A.20. The location of white circle pecks (grey), near white circle pecks (light grey) and black screen pecks (black), across sessions 1-5 (left panel, from top down) and sessions 6-10 (right panel, from top down) for Hen 2-5, Experiment 4.1.

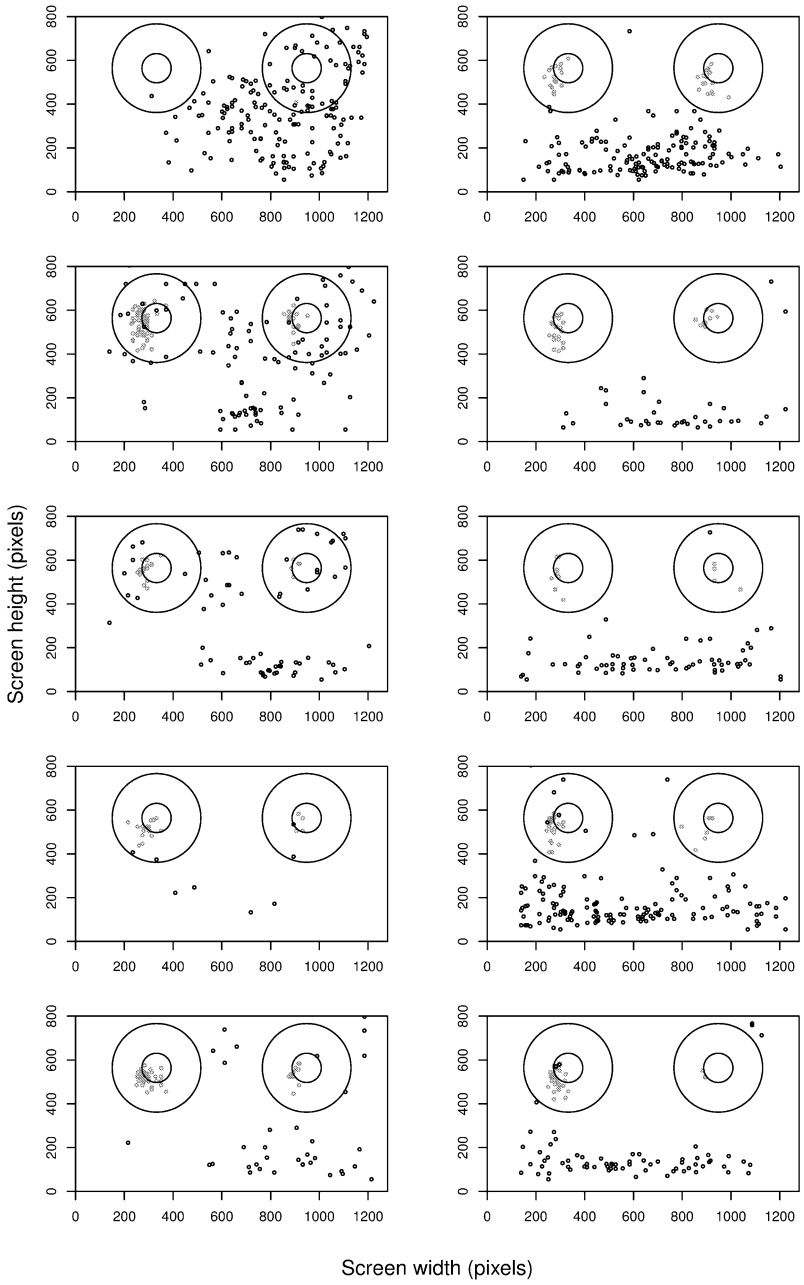

Figure A.21. The location of white circle pecks (grey), near white circle pecks (light grey) and black screen pecks (black), across sessions 1-5 (left panel, from top down) and sessions 6-10 (right panel, from top down) for Hen 2-6, Experiment 4.1.

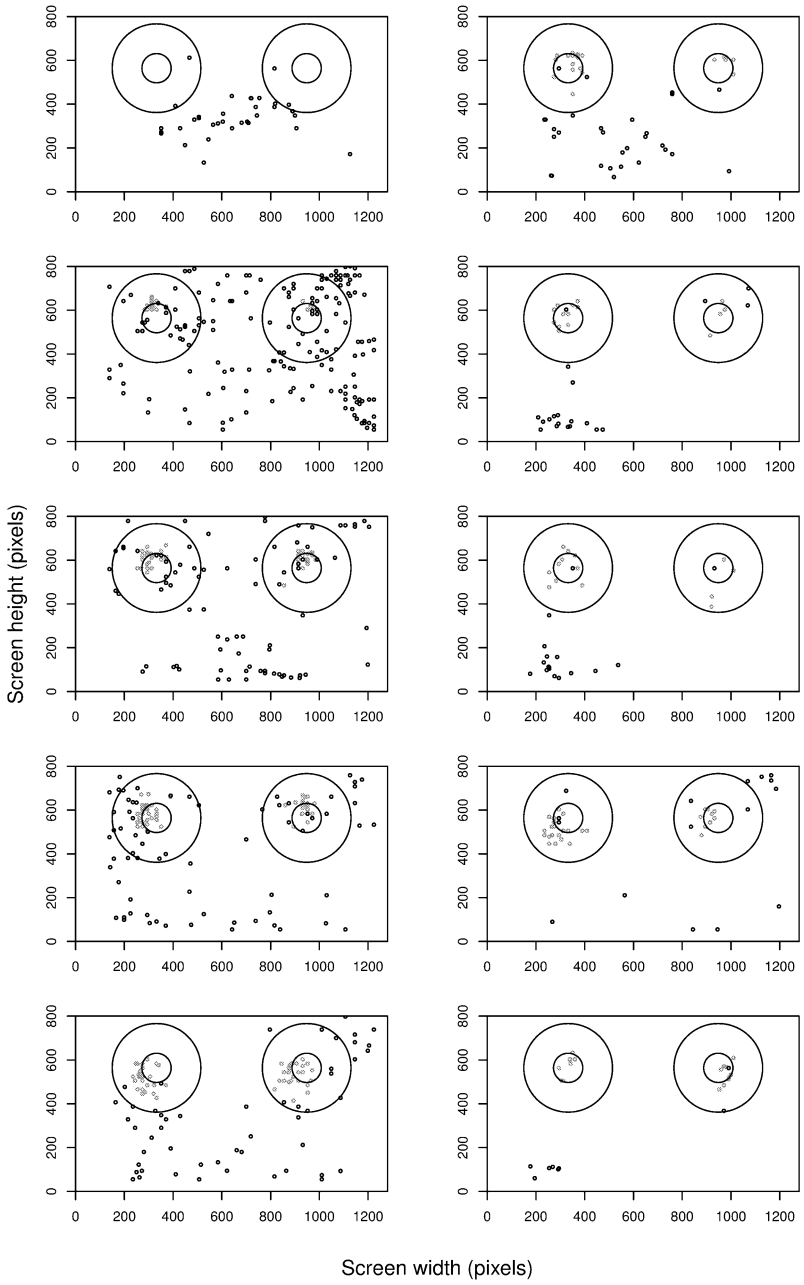

Figure A.22. The location of white circle pecks (grey), near white circle pecks (light grey) and black screen pecks (black), across sessions 1-5 (left panel, from top down) and sessions 6-10 (right panel, from top down) for Hen 2-7, Experiment 4.1.

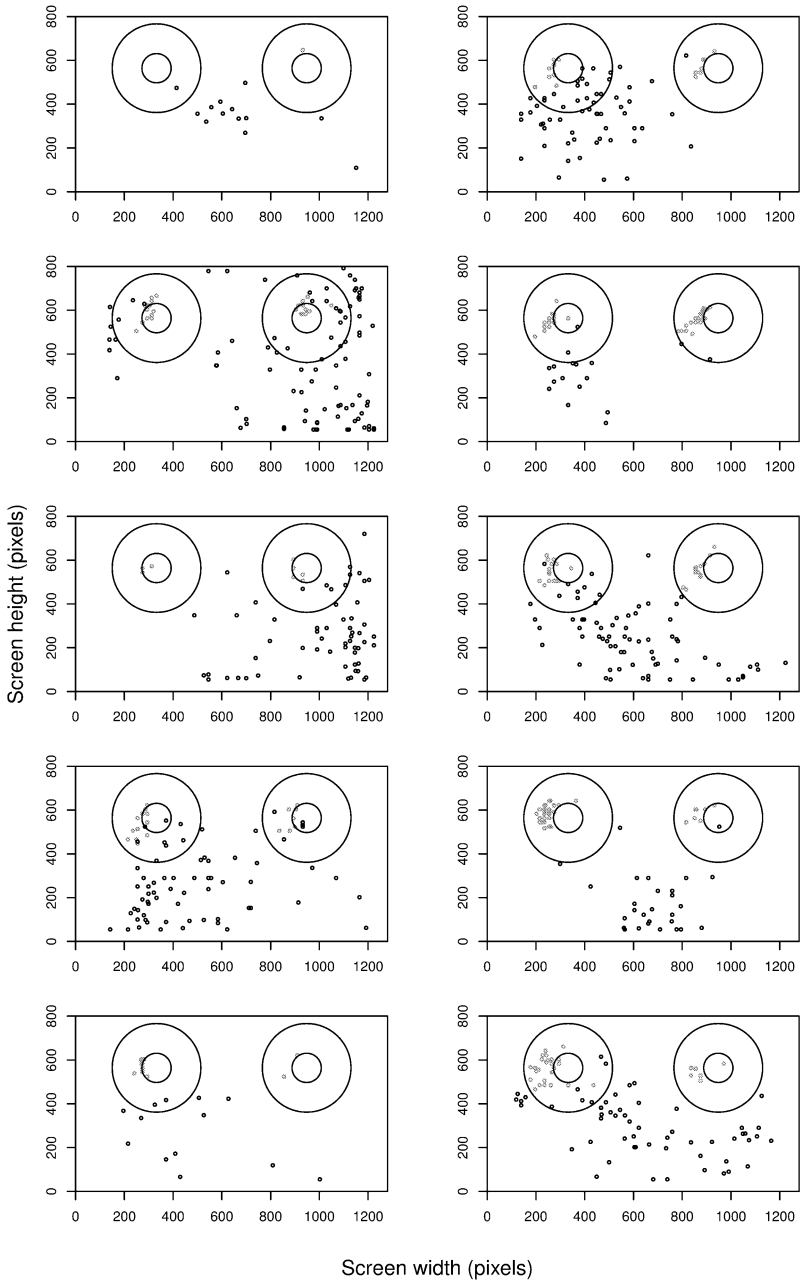

Figure A.23. The location of white circle pecks (grey), near white circle pecks (light grey) and black screen pecks (black), across sessions 1-5 (left panel, from top down) and sessions 6-10 (right panel, from top down) for Hen 2-8, Experiment 4.1.

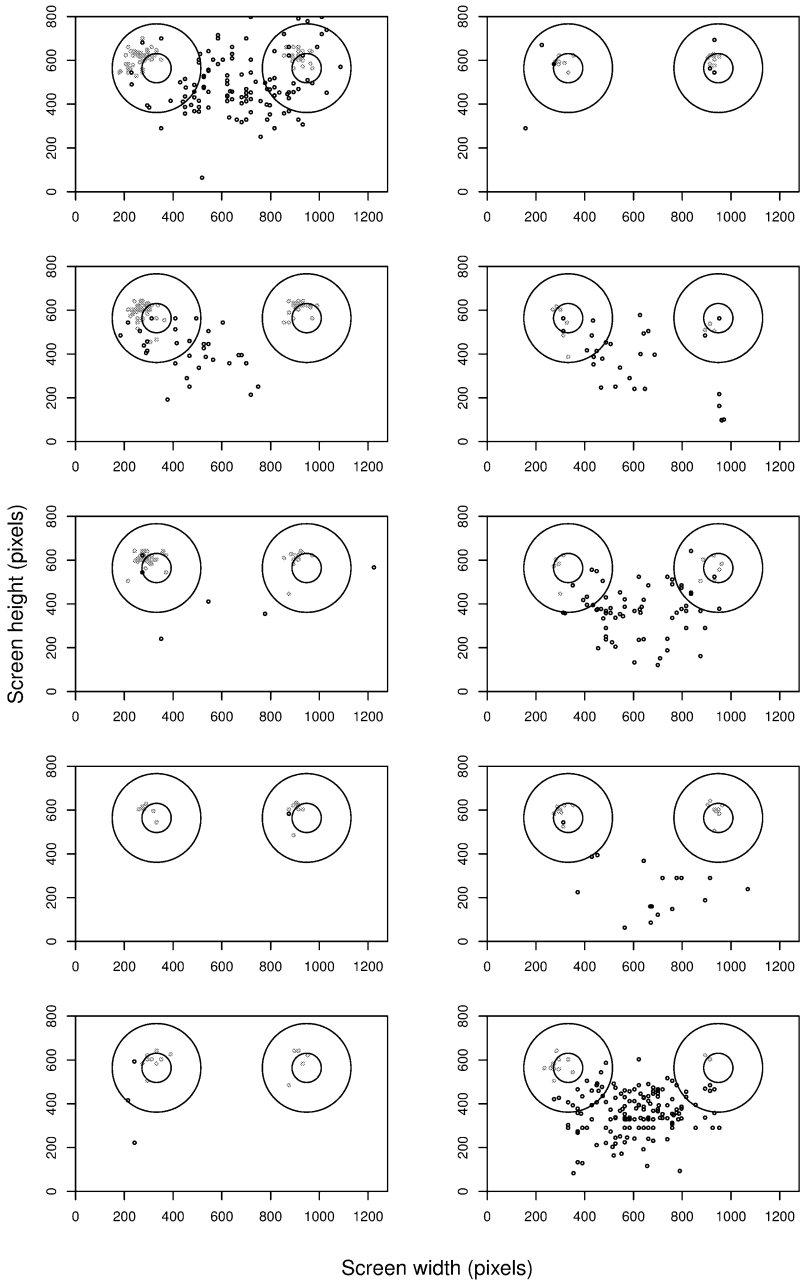

Figure A.24. The location of white circle pecks (grey), near white circle pecks (light grey) and black screen pecks (black), across sessions 1-5 (left panel, from top down) and sessions 6-10 (right panel, from top down) for Hen 2-9, Experiment 4.1.

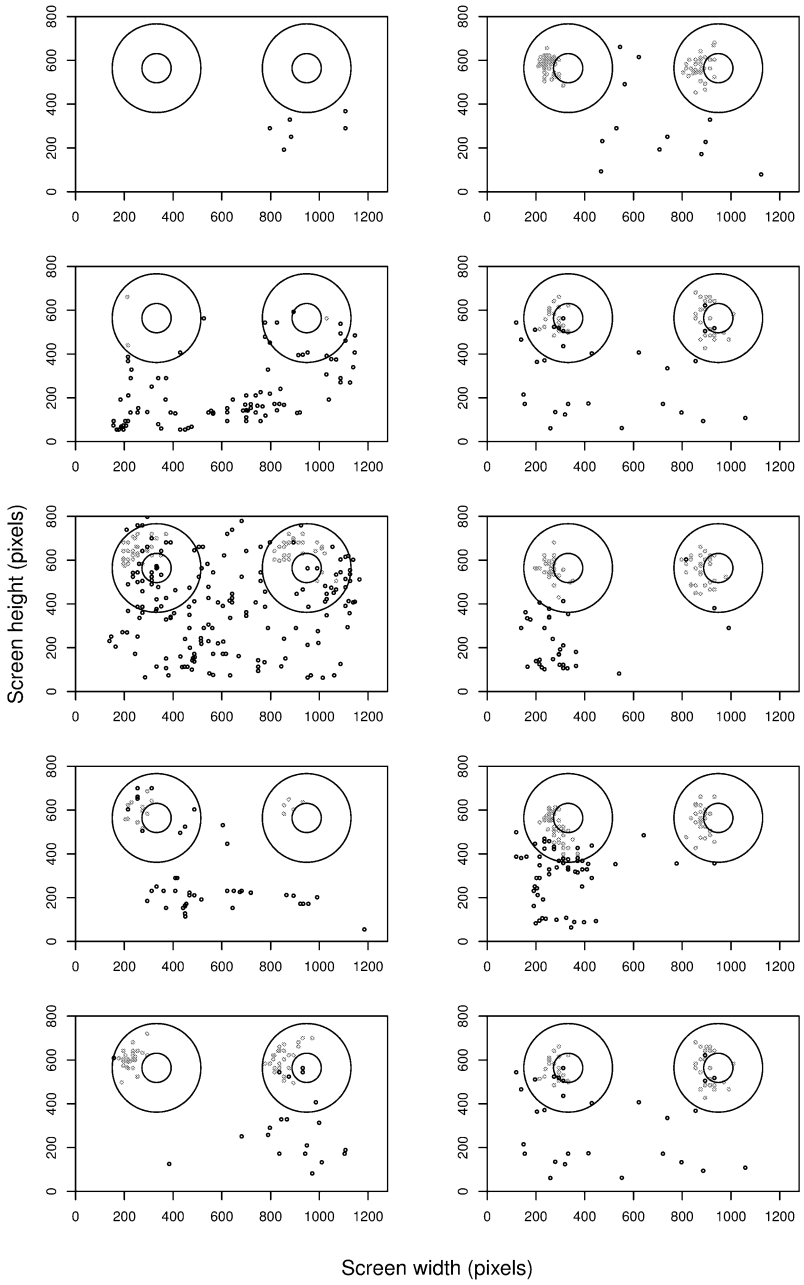

Figure A.25. The location of white circle pecks (grey), near white circle pecks (light grey) and black screen pecks (black), across sessions 1-5 (left panel, from top down) and sessions 6-10 (right panel, from top down) for Hen 2-10, Experiment 4.1.

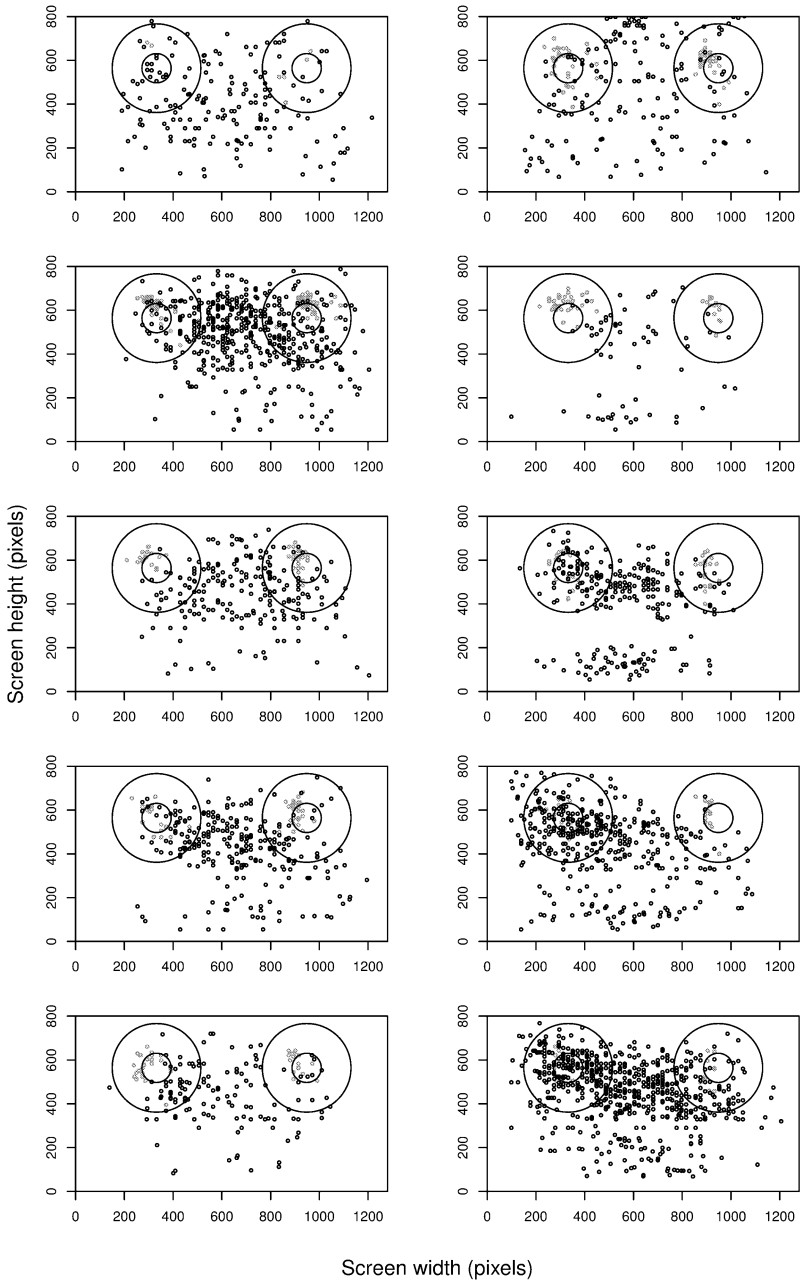

Figure A.26. The location of white circle pecks (grey), near white circle pecks (light grey) and black screen pecks (black), across sessions 1-5 (left panel, from top down) and sessions 6-10 (right panel, from top down) for Hen 2-11, Experiment 4.1.

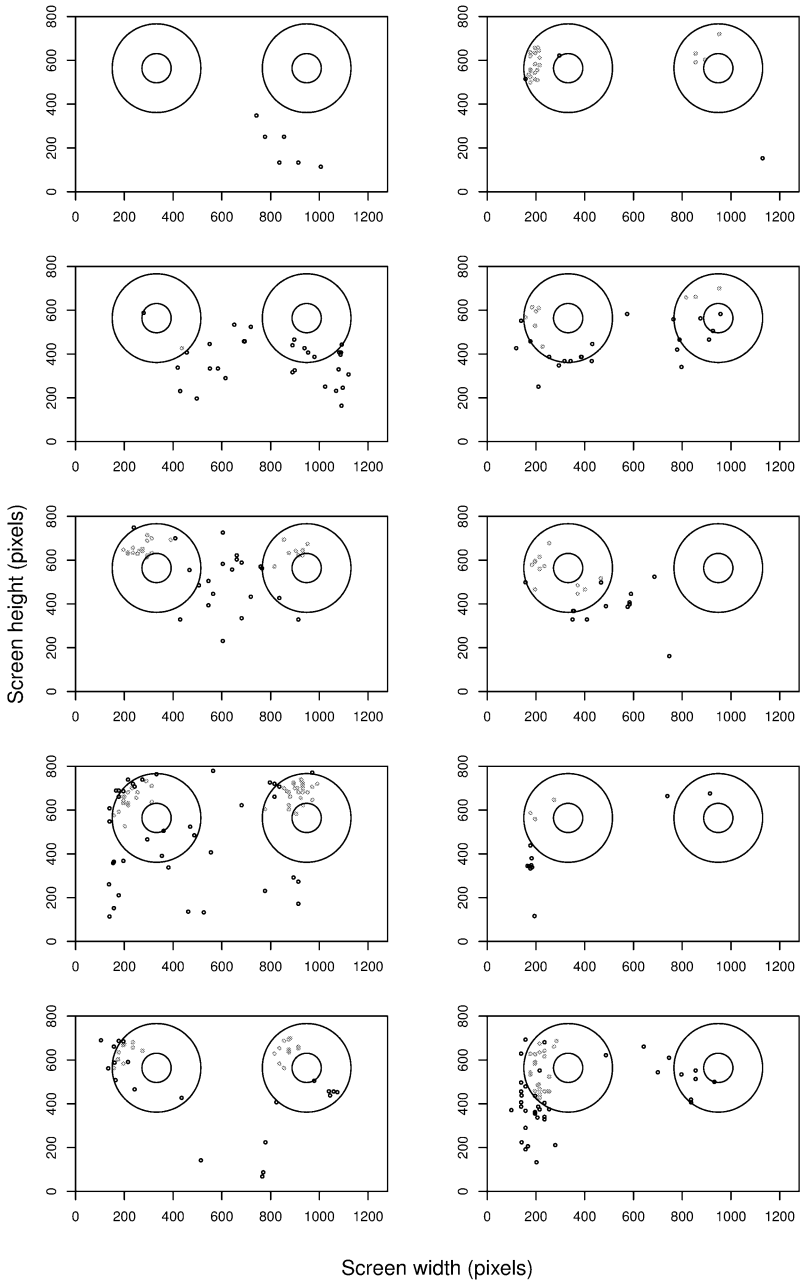

Figure A.27. The location of white circle pecks (grey), near white circle pecks (light grey) and black screen pecks (black), across sessions 1-5 (left panel, from top down) and sessions 6-10 (right panel, from top down) for Hen 2-12, Experiment 4.1.

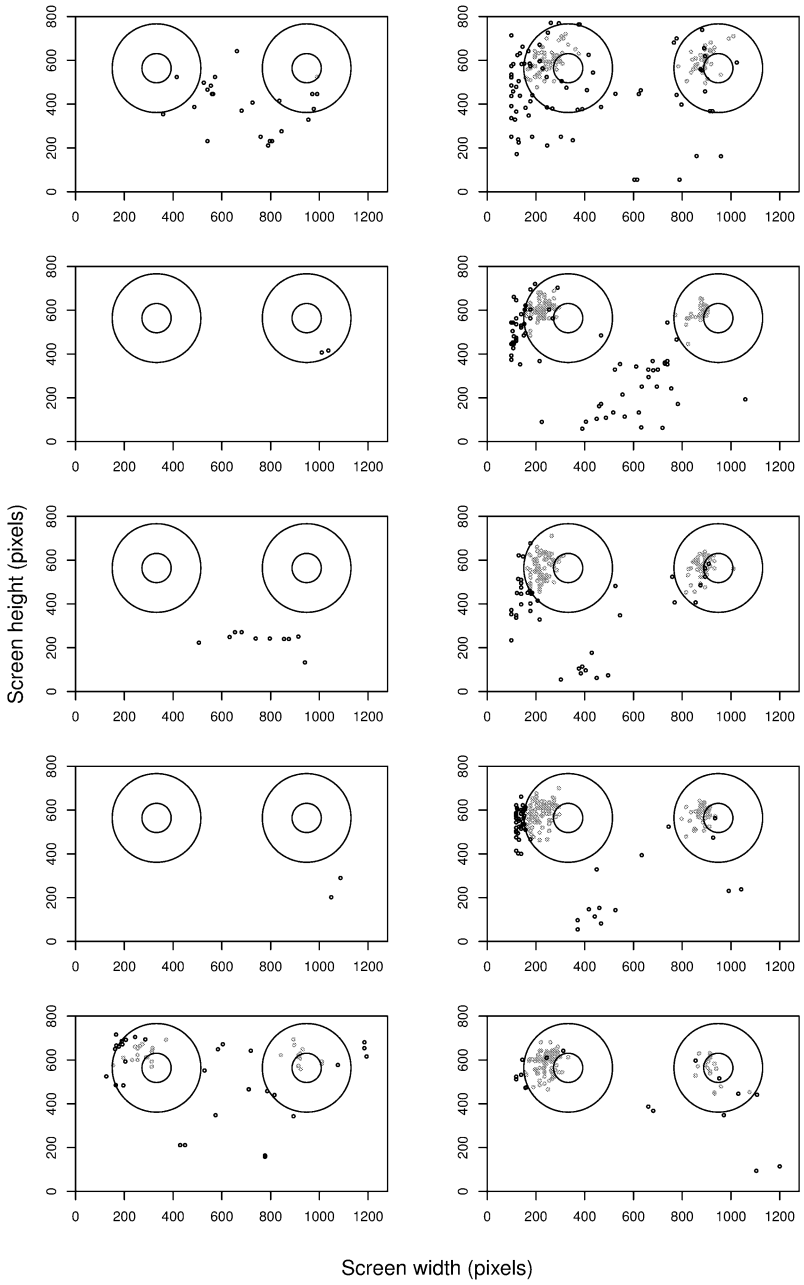

Figure A.28. The location of white circle pecks (grey), near white circle pecks (light grey) and black screen pecks (black), across sessions 1-5 (left panel, from top down) and sessions 6-10 (right panel, from top down) for Hen 2-13, Experiment 4.1.

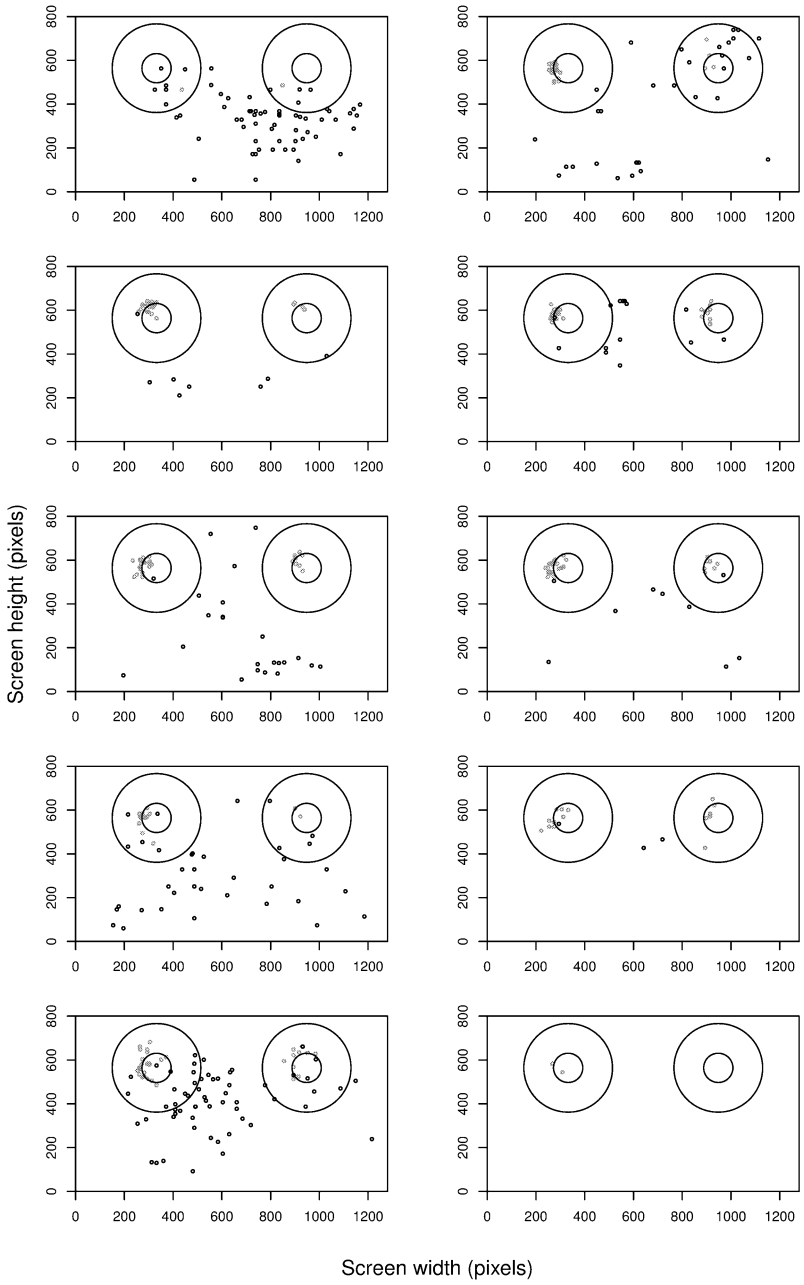

Figure A.29. The location of white circle pecks (grey), near white circle pecks (light grey) and black screen pecks (black), across sessions 1-5 (left panel, from top down) and sessions 6-10 (right panel, from top down) for Hen 2-14, Experiment 4.1.

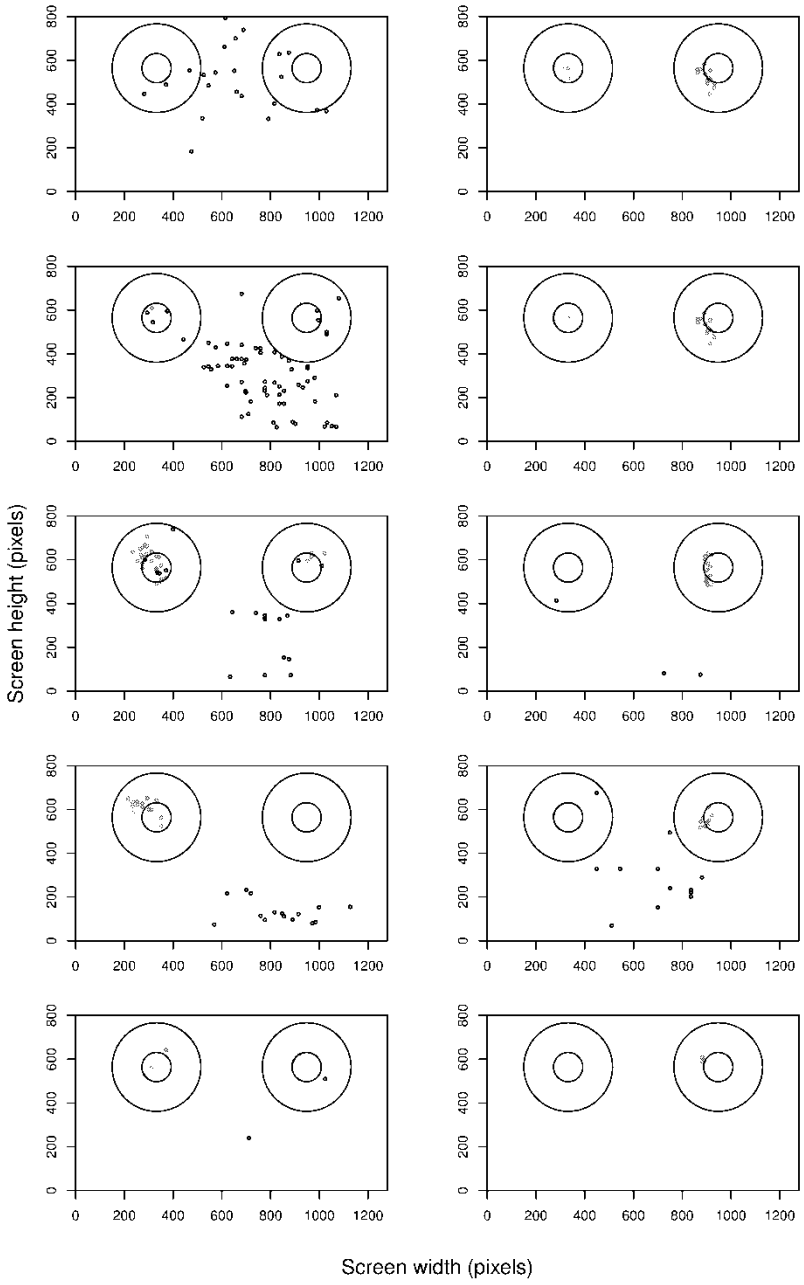

Figure A.30. The location of white circle pecks (grey), near white circle pecks (light grey) and black screen pecks (black), across sessions 1-5 (left panel, from top down) and sessions 6-10 (right panel, from top down) for Hen 2-15, Experiment 4.1.

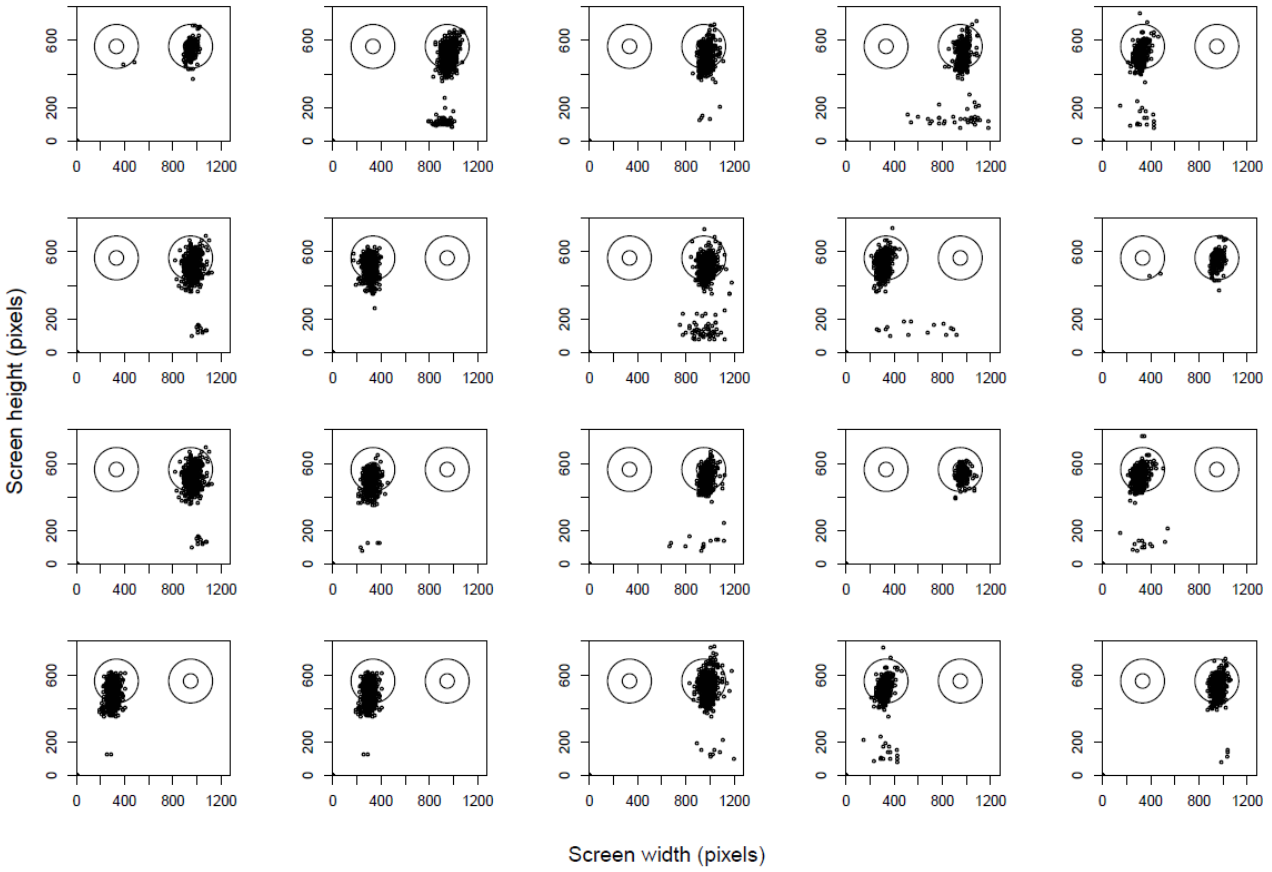

Figure B.1. The location of the pecks during deprivation/correlation sessions for sessions 1-20 (left panel, 1 -4, second from left panel 5 – 8, middle panel 10 – 12, second from right panel 13 – 16 and right panel 17 – 20) and sessions 6-10 for Hen 1-2, Experiment 5.1.

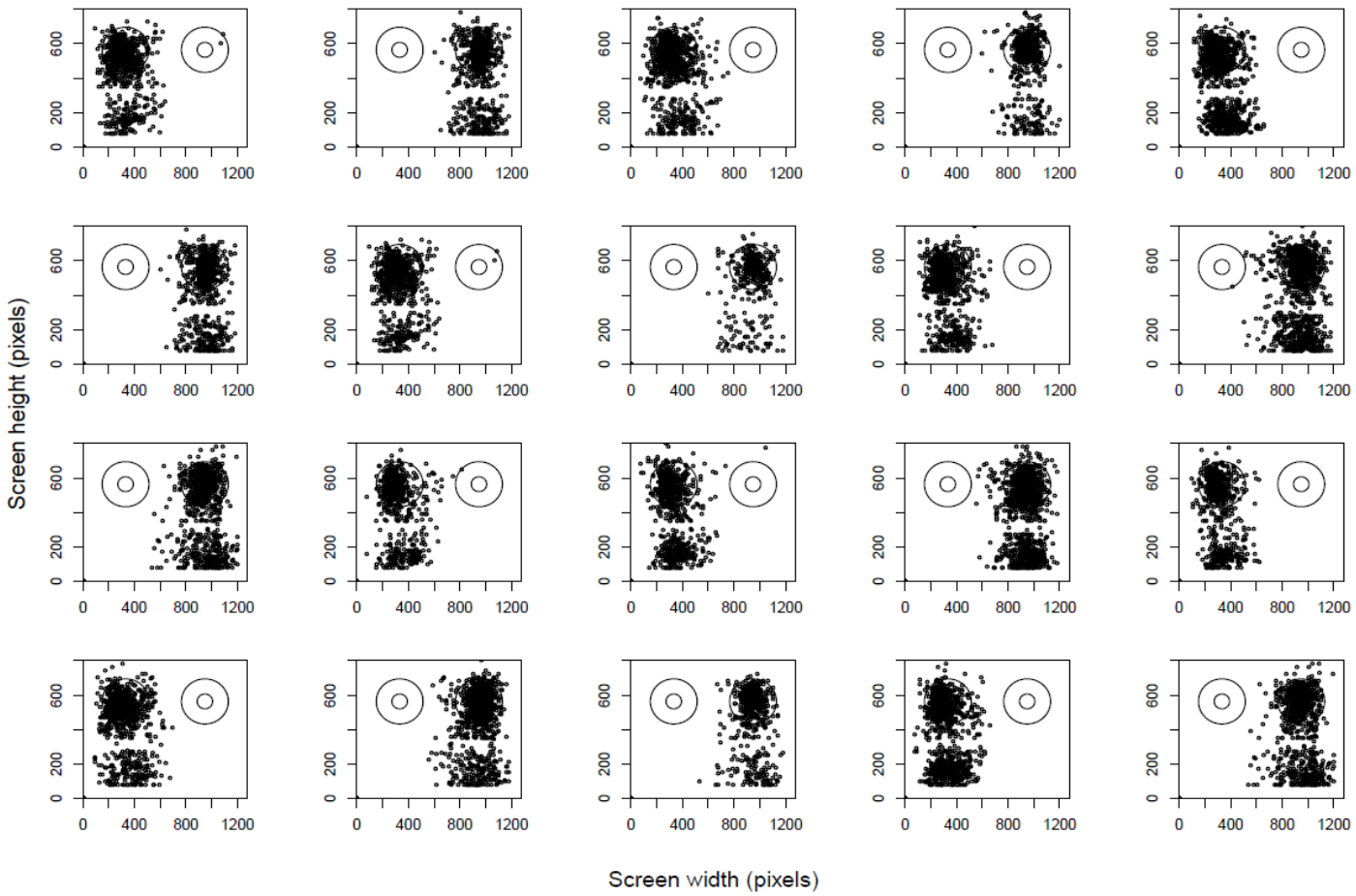

Figure B.2. The location of the pecks during deprivation/correlation sessions for sessions 1-20 (left panel, 1 -4, second from left panel 5 – 8, middle panel 10 – 12, second from right panel 13 – 16 and right panel 17 – 20) and sessions 6-10 for Hen 1-3, Experiment 5.1.

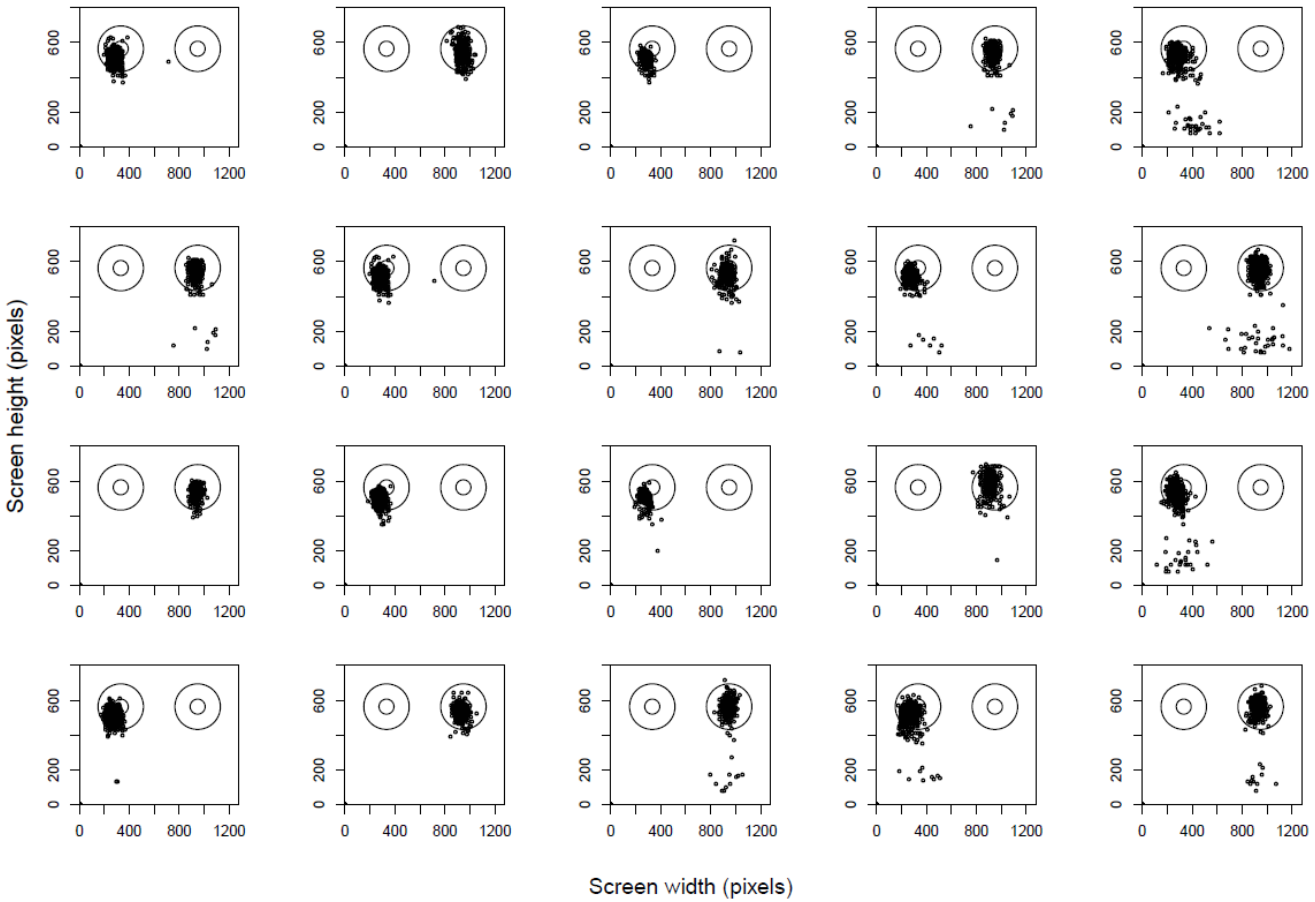

Figure B.3. The location of the pecks during deprivation/correlation sessions for sessions 1-20 (left panel, 1 -4, second from left panel 5 – 8, middle panel 10 – 12, second from right panel 13 – 16 and right panel 17 – 20) and sessions 6-10 for Hen 1-4, Experiment 5.1.

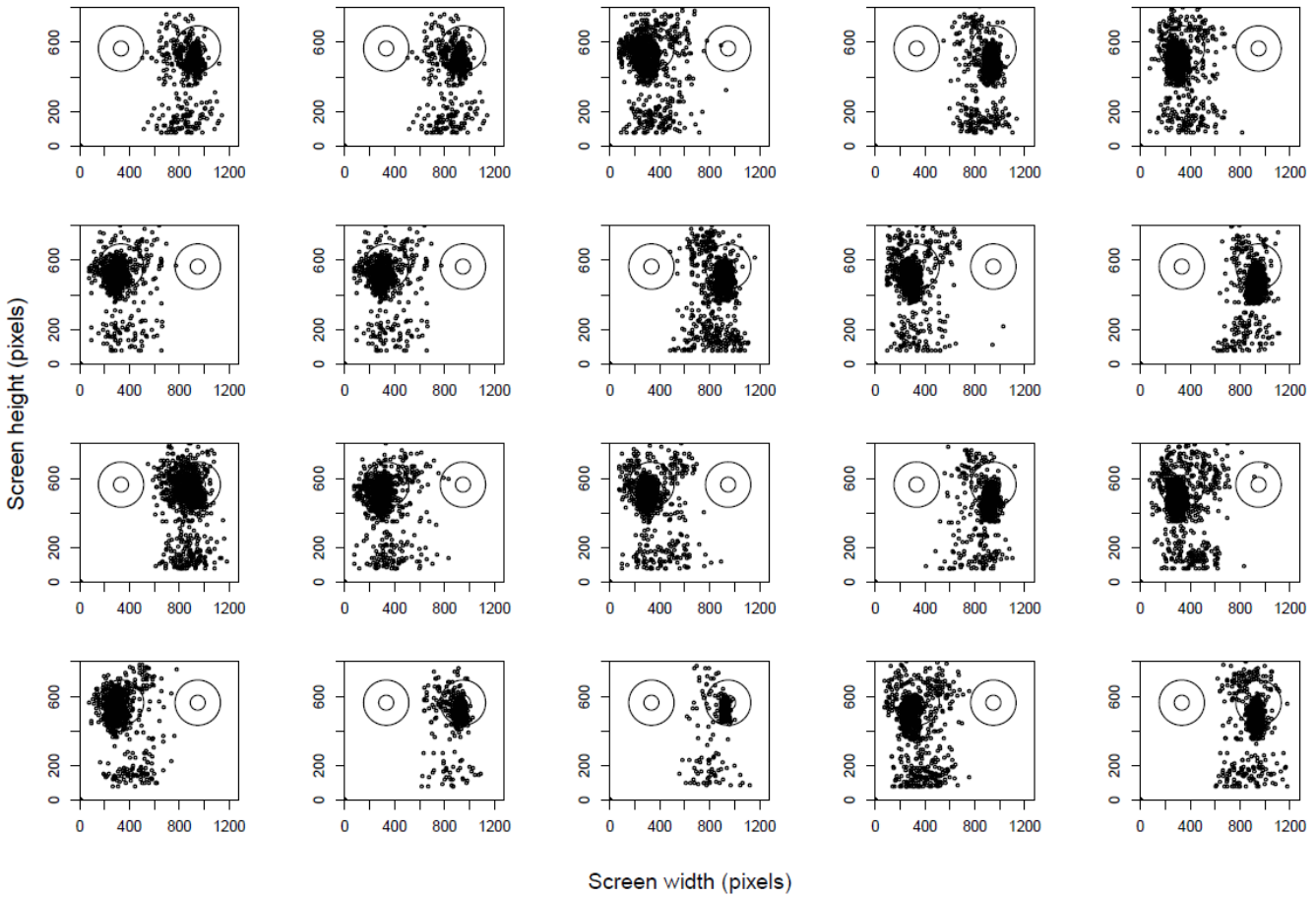

Figure B.4. The location of the pecks during deprivation/correlation sessions for sessions 1-20 (left panel, 1 -4, second from left panel 5 – 8, middle panel 10 – 12, second from right panel 13 – 16 and right panel 17 – 20) and sessions 6-10 for Hen 1-5, Experiment 5.1.

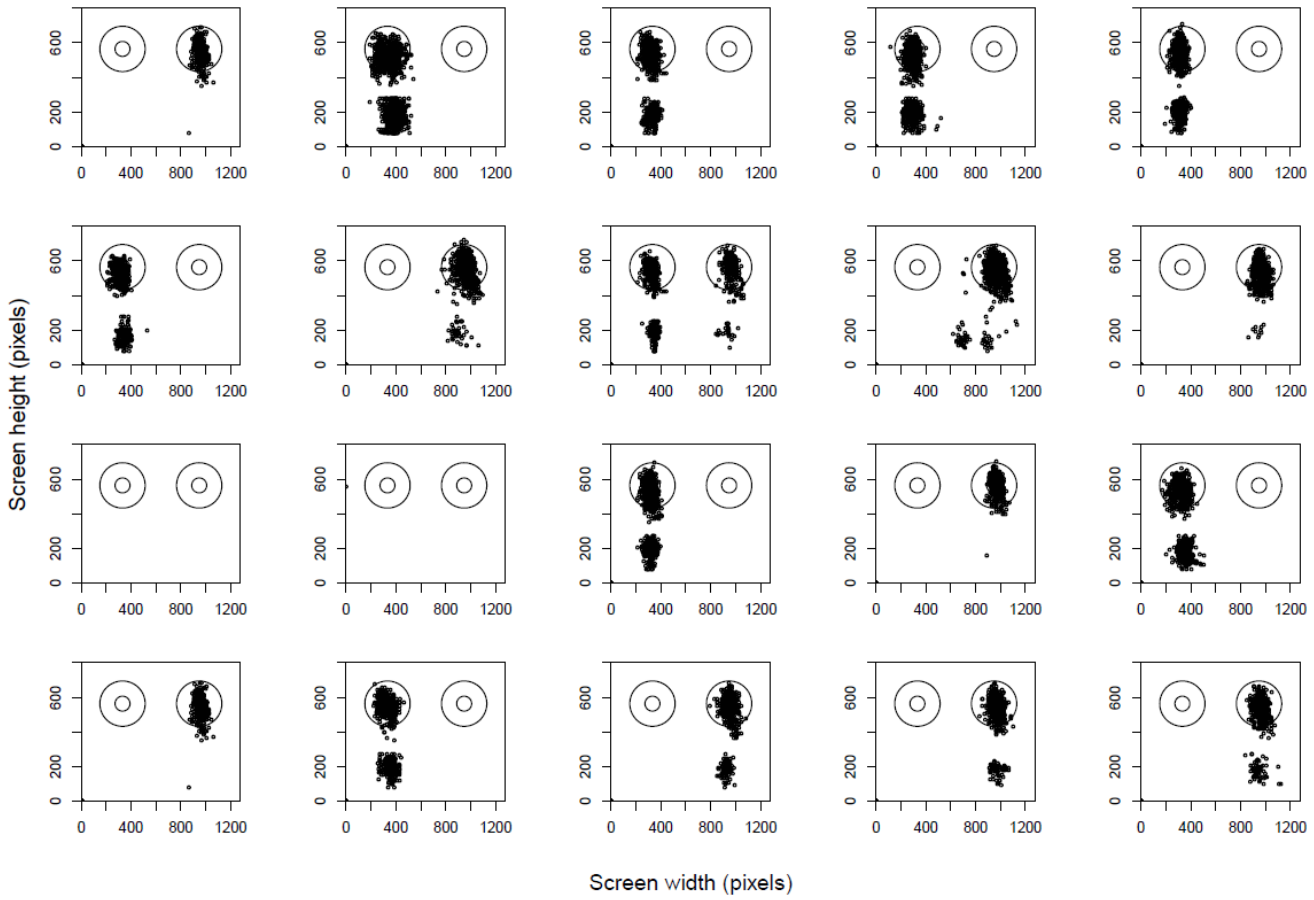

Figure B.5. The location of the pecks during deprivation/correlation sessions for sessions 1-20 (left panel, 1 -4, second from left panel 5 – 8, middle panel 10 – 12, second from right panel 13 – 16 and right panel 17 – 20) and sessions 6-10 for Hen 3-2, Experiment 5.1.

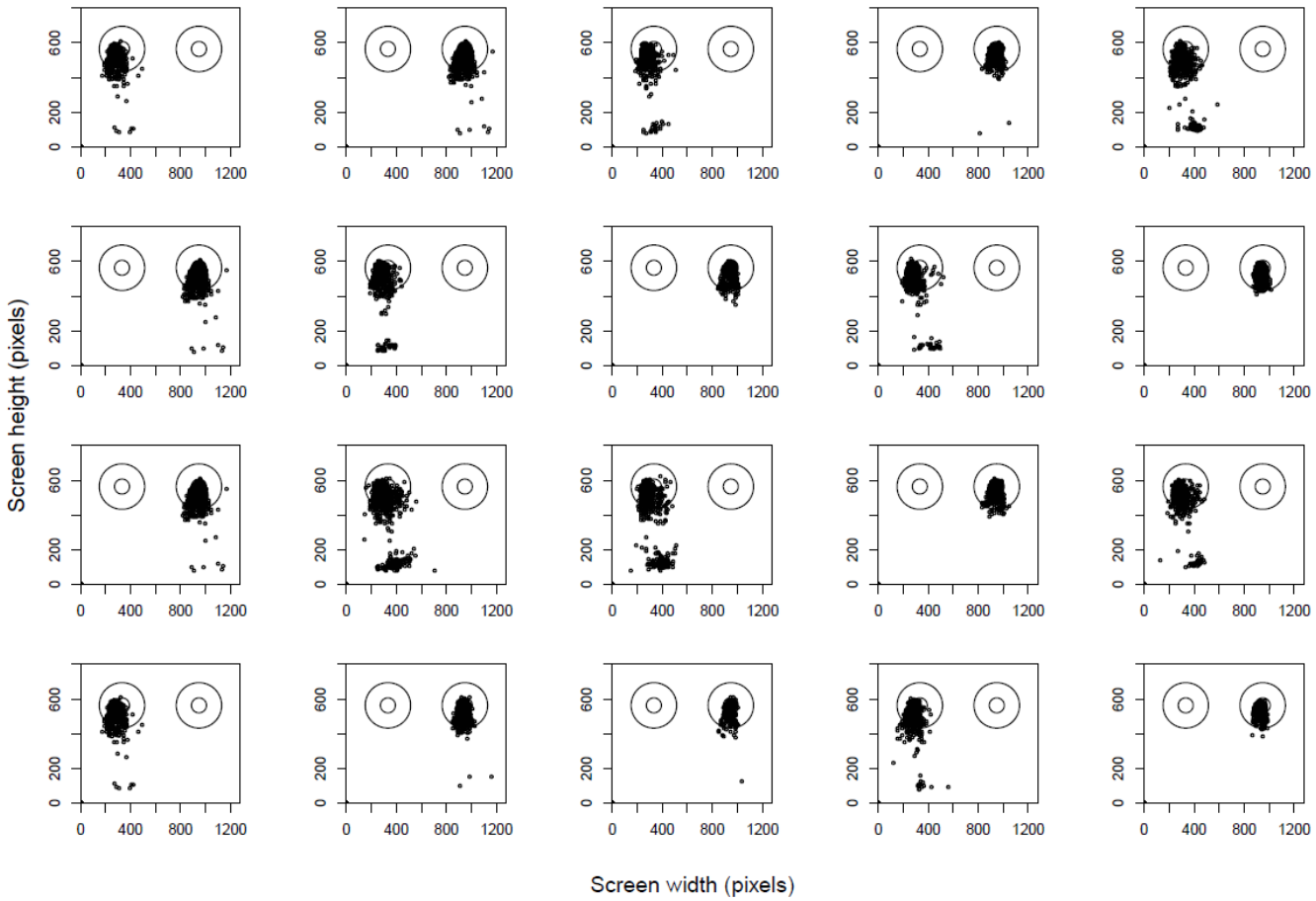

Figure B.6. The location of the pecks during deprivation/correlation sessions for sessions 1-20 (left panel, 1 -4, second from left panel 5 – 8, middle panel 10 – 12, second from right panel 13 – 16 and right panel 17 – 20) and sessions 6-10 for Hen 3-3, Experiment 5.1.

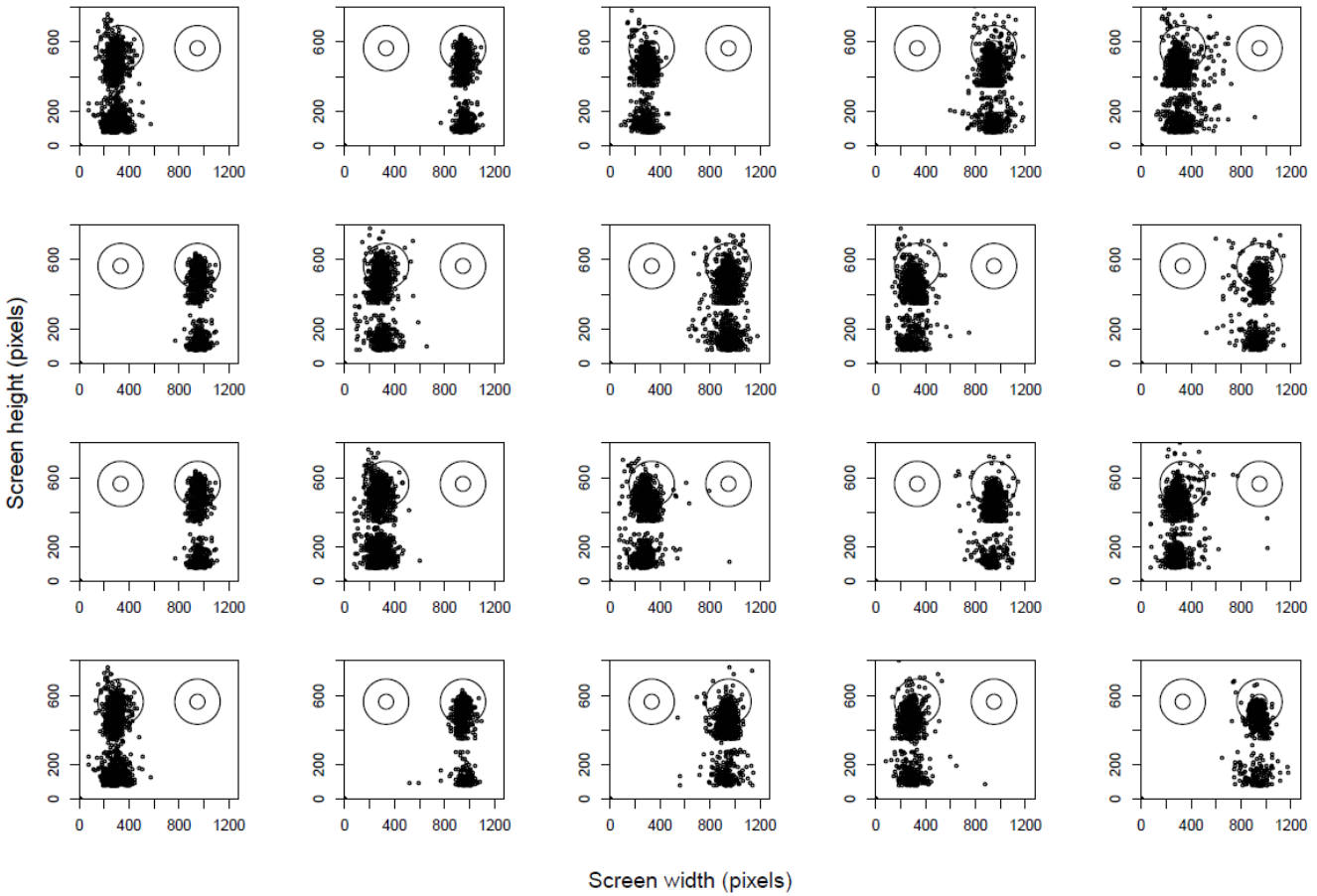

Figure B.7. The location of the pecks during deprivation/correlation sessions for sessions 1-20 (left panel, 1 -4, second from left panel 5 – 8, middle panel 10 – 12, second from right panel 13 – 16 and right panel 17 – 20) and sessions 6-10 for Hen 3-4, Experiment 5.1.

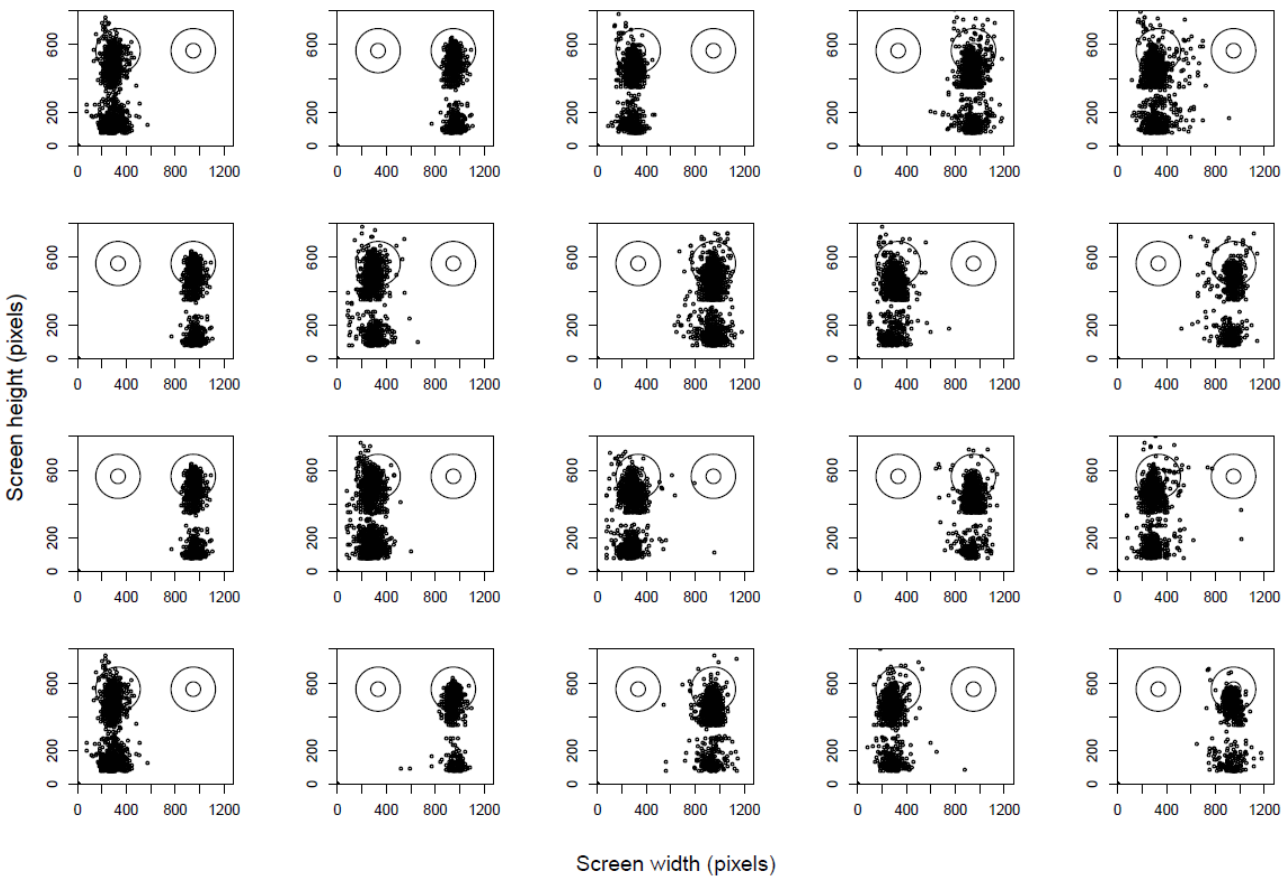

Figure B.8. The location of the pecks during deprivation/correlation sessions for sessions 1-20 (left panel, 1 -4, second from left panel 5 – 8, middle panel 10 – 12, second from right panel 13 – 16 and right panel 17 – 20) and sessions 6-10 for Hen 3-5, Experiment 5.1