THE EFFECT OF EFFORT: AN ANALYSIS OF KILLEEN'S (1994) MATHEMATICAL PRINCIPLES OF REINFORCEMENT

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Abstract

Mathematical Principles of Reinforcement (MPR, Killeen, 1994) is a mathematical model comprising three main concepts; an animal's arousal to behaviour based on its motivation for a particular reinforcer, time and energy constraints on responding, and coupling between a response class and reinforcer. This experiment tested the ability of MPR to predict response rates when the minimum force requirement and topography of response was changed. Increasing the minimum force requirement was expected to increase the value of δ, the parameter related to response constraint. Altering the topography of the response was expected to also alter the δ value, as different response forms were expected to take different lengths of time to perform.

There were four conditions; low force key, low force door, high force key and high force door, and 6 hens responded under each of these conditions in an ascending geometric series of Fixed Ratio (FR) values. It was shown that hens responded at a faster rate and to higher FR values when responding on the key than on the door, and for both apparatus, the hens stopped responding at lower FR values when weights were added. Unexpectedly, there were no statistically significant differences in the value of δ across conditions, but the values for *a*, meant to represent the animals' arousal, did change. It was suggested that the changes in *a* reflected changes in the animals' motivation to perform the different responses, probably due to rewarding or aversive properties of the operant response related to the different response forms.

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Introduction

In order to understand behaviour in such a way as to be able to make predictions of future behaviour, it is necessary to know the causes and effects of behaviour. If these are known, it is possible to form a set of rules related to that behaviour, and therefore to predict how that behaviour may appear in the future. There are patterns frequently seen in behaviour, related to the schedule on which a specific behaviour is reinforced (Ferster & Skinner, 1957). An example of the tendency to behave in certain ways under certain schedules is under *Fixed Ratio* (FR) schedules, in which a set number of responses are required to obtain each reinforcer. In FR schedules, the rate of reinforcement is directly proportional to the rate of responding, meaning that the faster the response rate, the greater the reinforcement rate, and inversely proportional to the ratio requirement. That is, the greater the ratio requirement, the lower the rate of reinforcement (Killeen, 1994).

When reinforced according to an FR schedule, animals tend to produce a very high rate of responding, and an appreciable *Post- Reinforcement Pause* (PRP), the length of which increases as the FR requirement increases. Typically, following the pause, the animal returns to a high rate of responding (Ferster & Skinner, 1957). This can mean that at higher FR values, there is a decrease in overall response rate, which may eventually result in the animal ceasing to respond altogether (Pear, 1975). While the increase in PRP means that the animal's response rate decreases, graphing run rates (response rates when the length of the PRP is discarded) shows that the decrease in rate of responding is not entirely due to an increase in the PRP length (Bizo & Killeen, 1997).

Mathematical modelling of behaviour is a way of describing behavioural patterns, such as changes in response rate when the FR value is changed. It is a method of representing a set of variables and their effects in order to describe and account for variations in behaviour (Tsibulsky & Norman, 2007). A mathematical description of a data set would normally be based on a set of assumptions as to what variables affect behaviour, but just because the equation fits the data well, does not mean that the assumptions are correct (Shull, 1991). If the model is based on a sound set of assumptions, it is likely that it will have a relatively stable basic form, although it will always be able to improved (Church, 1997). A model of behaviour which describes patterns of behaviour presents the possibility of simplifying the way that behaviour is understood, by offering a set of common principles that can then be applied and tested in different contexts (Killeen, 1992).

It is possible to form quantitative models predicting behavioural patterns, because of common patterns to responding under different sets of response-reinforcer contingencies. Equations can be developed from reviewing the distributions of many responses, and the mathematical function these resemble (Shull, 1991). In order for an equation to be classified as a *model*, it must be accompanied by a set of principles that have been found to describe an aspect of behaviour (Church, 1997). If the process leading to the behaviour is a simple one, this function will also be simple, but functions can also interact, suggesting several processes giving rise to expressed behaviour might be at work at any given time (Church, 1997). A model can be thought of as a strong metaphor (Killeen, 1992), and in this way can assist understanding not only of the process it was set up to describe, but also offer insight into other aspects of behaviour. One model that aims to predict animals' response rates under different schedules of reinforcement is the *Mathematical Principles of Reinforcement* (MPR, Killeen 1994).

MPR was originally published by Killeen (1994), and is a sophisticated attempt to describe the way that behaviour varies in relation to changes in frequency of reinforcement, aspects of the reinforcer and an animal's motivation for that reinforcer, and response requirements (Tsibulsky & Norman, 2007). It proposes that changes in task requirements, or reinforcement for performing a task, will result in systematic changes in response rate.

MPR consists of three main principles; arousal, constraint and coupling. The first of the three principles is that arousal from feeding cumulates, which is described by the parameter known as *specific activation* (Killeen, 1994). The second principle, *constraint*, refers to limits to responding such as the minimum length of time it takes to form a response, and the energy requirements of responding. The third principle is known as *coupling*, and describes the strength of the association between a reinforcer and a response class. In Equation 1, MPR is expressed as:

$$B = \frac{1-(1-\beta)^n}{\delta} - \frac{n}{\delta a}, \text{ where } a > 0,\ \beta > 0, \text{ and } \delta > 0 \quad \text{(Equation 1)}$$

B refers to the rate at which responses are emitted; β is the proportion of association between the reinforcer and the response immediately preceding it; *n* refers to the FR value; δ is the minimum inter-response time, and *a* is the number of responses that a specific reinforcer will sustain. The ways in which the different parameters behave to fit different patterns in responding are demonstrated in Figure 1.

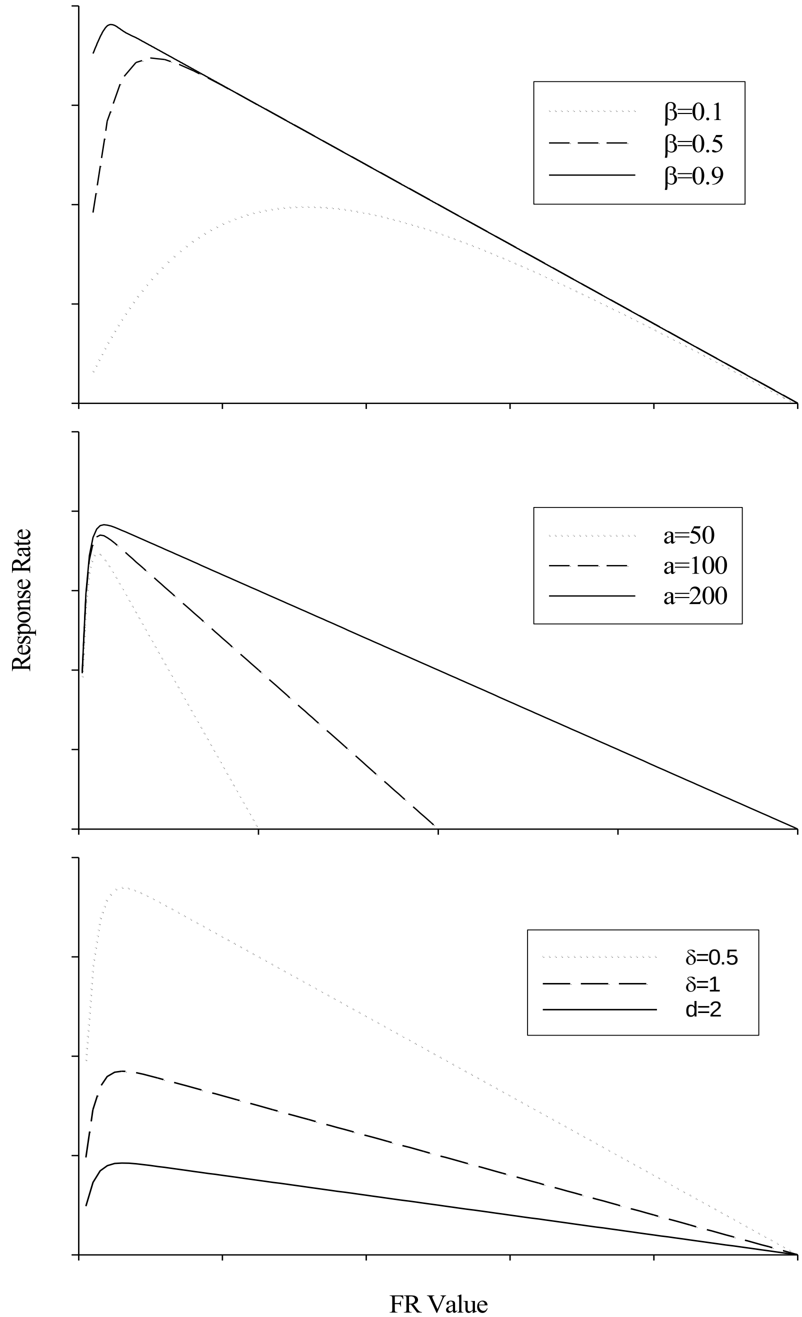

Figure 1. Predicted shape of changes in response rate as the FR increases as parameter estimates change. The top panel shows changes in the value for β, the second panel shows changes in *a* and the third panel shows changes in δ.

Specific activation (a) is proposed in MPR as a measure of motivation, and is the integral of the exponential decay curve of response rates produced when exposed to multiple presentations of incentives (Killeen & Sitomer, 2003). After animals are fed, there is an increase in general activity, and the level of this activity is used as a measure of arousal (Killeen, 1975). It is assumed that the level of arousal is related to the animals' level of deprivation and the power of a particular reinforcer at that point in time (Killeen & Sitomer, 2003). *Specific activation* represents the period of responding that is supported by a single reinforcer. Specific activation has many influencing factors, including whether the animal is operating in an open or closed economy (Zeiler, 1999; Posadas-Sanchez & Killeen, 2005), the animal's level of satiation (Killeen, 1995; Posadas-Sanchez & Killeen, 2005), the size of the reinforcer (Bizo & Killeen, 1997; Rickard, Body, Zhang, Bradshaw & Szabadi, 2009), and the duration for which the reinforcer is available (Bizo & Killeen, 1997), and hence its ability to lead to satiation (Killeen, 1995).

No mention has been made of the role of automatic reinforcement in relation to MPR. Automatic reinforcement is a term used to describe behaviour that is reinforced by something related to performing the action itself (Skinner, 1953). This can include perceptual or sensory stimulation and the body's production of opiates, as well as the removal of something unpleasant, such as an itch (Vollmer, 1994).

While it is generally considered that the type of reinforcer also affects *a* (Bizo & Killeen, 1997), Covarrubias and Aparicio (2008) did not find any significant difference in estimates of *a* for rats when rats' lever pressing was reinforced with either food or saccharin on an ascending series of *Progressive Ratio* (PR) values. The same study found that estimates of *a* were larger when the change in ratio requirement increased in increments of 3 rather than increments of 1 (Covarrubias & Aparicio, 2008). This effect of step size in PR schedules was tested again (Killeen, Posadas-Sanchez, Johansen & Thrailkill, 2009) and a small increase in the value of *a* was found with increase in ratio requirement. It was suggested that this may be due to greater levels of satiation by the end of a session when the increment is smaller, because the animals earned and consumed more food reinforcers during a session (Killeen et al., 2009).

The second principle, c*onstraint,* describes the effect of variables unrelated to arousal or specific activation, that impact on the rate at which responses are emitted (Killeen, 1994). The basis of this principle is that responses may be prompted (that is, the stimulus may be presented) faster than they can be performed (Killeen & Sitomer, 2003). Factors that can influence response constraint include the minimum response duration and the force required to perform a response. The minimum inter-response time, in which one response is immediately followed by another, can be thought of as the minimum response duration an organism is physically able to produce (Killeen & Sitomer, 2003).

The third principle, known as *coupling*, describes the relationship between a reinforcer and a response class, and therefore determines the likelihood of responses from that class being emitted (Killeen & Sitomer, 2003). The strength of the coupling coefficient should not be complete, that is, it should not have a value of 1, as reinforcement does not only act on the response immediately preceding the reinforcer, it also acts on any other responses that preceded reinforcer delivery, that are still present in the organism's memory. When a response is emitted, it has an effect on memory of a certain strength, which decays over time. When another response of the same class is emitted, it adds to strength to the memory trace of the previous response, which continues to decay over time (Killeen, 1994). At lower FR values, the effect of a reinforcer does not contact many responses because responding is interrupted by bouts of feeding. As the FR requirement increases, the effect of each reinforcer contacts more responses, and so response rate is seen to increase. At the same time, however, the arousal level decreases, so the resulting pattern of responding when response rate is plotted as a function of ratio value is described by an inverted U shaped function (Killeen, 1994). Once the number of responses has saturated the memory, responding is governed only by arousal, and is depicted in the downward part of the inverted U (Killeen, 1994). Coupling, represented by the parameter β, is a factor of constraint, represented by δ, and the rate at which response traces decay, represented by lambda (λ).

Several versions of MPR exist, with another instantiation of it including an additional parameter, epsilon (ε). This is the parameter intended to reflect the degree to which the memory of the target response is erased between responses (Killeen & Sitomer, 2003). Values for ε can vary between 0 and 1, with 1 representing complete erasure, and 0 representing total recall. In Equation 2, coupling is expressed as a factor of λ, and includes ε. It can be expressed as:

$$B = \frac{1-(1-(1-\varepsilon e^{-\delta\lambda n})^{n})}{\delta} - \frac{n}{\delta a},$$

where a > 0, λ > 0, δ > 0 and 0 < ε >1 (Equation 2)

The lower response rates seen in interval schedules (when compared with FR schedules) is because the reinforcer is coupled indiscriminately with both target responses and any other responses that occur during the interval (Killeen, 1994).

Reinforcement acts on what the organism does, which is not necessarily the target response defined by the experimenter. This means that any other behaviour the animal performs between reinforcers is also reinforced, so target responses in interval schedules are coupled with a lower proportion of each reinforcer than target responses under ratio schedules.

In addition to the equations for FR schedules shown above, the model has been shown to fit response rate patterns for *Variable Ratio* (VR) schedules (e.g., Bizo, Kettle & Killen, 2001; Bizo, Remington, D'Souza, Heighway & Baston, 2002; Killeen & Sitomer, 2003), and PR schedules (e.g., Covarrubias & Aparicio, 2008; Rickard et al., 2009). The model also provides a good prediction of the obtained response rates amongst a range of species, including; pigeons (e.g., Killeen, 1994; Bizo & Killeen, 1997), humans (e.g., Bizo et al., 2002) and rats (e.g., Bizo, Kettle & Killeen, 2001; Reilly, 2003; Sanabria, Acosta, Killeen, Neisewander, & Bizo, 2008; Rickard et al., 2009).

Bizo and Killeen (1997) tested the model's ability to predict the effect of known preferred foods of pigeons responding on FR and VR schedules. As expected, estimates of a were higher for the most preferred food (popcorn) and lower for the least preferred food (millet). Estimates of a were also higher for longer access to a food reinforcer than for shorter access to the same food reinforcer (Bizo & Killeen, 1997). The different estimates of a for different reinforcers has led to the suggestion that specific activation values may be used as a measure of reinforcer effectiveness, as, when rats were offered sucrose, sucrose and pellet mix or pellets, there were intermediate a values for intermediate reinforcers, such as sucrose/ pellet mixes as opposed to plain sucrose or plain pellets (Reilly, 2003).

The finding that there were higher response rates for longer reinforcer durations, or larger reinforcers, was confirmed with the finding that rats exhibited higher response rates for two pellet reinforcers than for one pellet (Bizo et al., 2001). In the same series of experiments, it was demonstrated that smaller reinforcers resulted in higher response rates at low response requirements, an effect that Bizo et al. (2001) termed the *paradoxical incentive effect*, whereas larger reinforcers were able to support responding at higher ratio requirements, when smaller reinforcers did not (Bizo et al., 2001).

A series of experiments testing MPR in a pharmacological setting found that MPR was able to predict behaviour in this context (Reilly, 2003). Rats were injected with a range of doses of D-amphetamine, and exposed to a range of FR schedules within each session. Each FR value was signalled by a change in colour of a light in the chamber, and it was expected that parameter estimates of specific activation would be higher when rats were dosed with D-amphetamine. Response rates were compared across different dosages, and showed that D-amphetamine increased both δ and λ, but had no significant effect on specific activation, *a* (Reilly, 2003). In this situation, MPR was able to offer insight into what processes the D-amphetamine was affecting. A further experiment, in which rats received dosages of 6-OHDA in order to mimic the effects of Parkinson's Disease, showed that MPR was able to account for variance in response rates before and after the administration of the drug (Avila, Reilly, Sanabria, Posadas-Sanchez, Chavez, Banerjee, Killeen & Castaneda, 2009). This provides support for the use of MPR to model the effects of pharmacological agents on behaviour, and shows how MPR may be able to assist in determining what effect different pharmacological agents have on behavioural processes.

In the only experiment that has investigated response constraint in relation to MPR, Bizo and Killeen (1997) required pigeons to either peck a key or depress a foot treadle. This was to manipulate δ, the response duration. MPR predicts that longer minimum response durations result in lower response rates (Bizo & Killeen, 1997). This prediction was verified by this experiment, as key pecking occurred at a much higher rate than treadle pressing (Bizo & Killeen, 1997). This was attributed to the fact that a key peck took on average 0.32 s, whereas a treadle press took 1.12 s to complete. There was also a longer post-reinforcement pause for treadle pressing.

It is possible to alter these typical patterns of responding in a systematic way by altering response requirements. An experiment investigating changes in rats' responding over a range of FR values and force requirements was conducted by Alling and Poling (1995). Weights were added to response levers to alter the minimum force requirement to form a response. One lever always required 0.25 N, and the force requirement for the other lever changed between 0.25 N, 0.5 N, 1 N and 2 N. It was shown that when the force requirement was increased, the PRP lengthened and response rate decreased, and for some, but not all of the rats, the rate of decrease was proportional to the increase in force requirement. These changes in responding were seen at FR 1, FR 5 and FR 15, and there was no consistent relation between the change in response rate when force was increased and the size of the FR value (Alling & Poling, 1995). This shows that rats are sensitive to changes in force requirement of this magnitude, and that even over a small range of FR values the difference in force requirement has a noticeable effect.

In a study using both rats and pigeons as subjects, McSweeney et al. (1995) reinforced responding initially on a treadle (pigeons) or lever (rats), and they then changed the target operandum to a key (both species). For both species, the minimum force requirement on the key was 0.25 N, and 0.3 N for the treadle or lever. The changeover between operanda occurred at different stages within each session. When comparing response rates on the different operanda, they found that rats were slower at pressing levers than at pressing keys, but pigeons responded at the same rate on either apparatus. The pattern of responding was the same within each session, with responding within a session initially increasing, and then decreasing later in the session. It is not documented whether the pigeons did in fact perform topographically different responses. It may be that they pecked at the treadle, so the response took the same time as pecking the key, or that the difference in force requirement between the two operanda was not significant to the pigeons.

In an experiment similar to the one reported here, and using a door push apparatus similar to the one used in the present experiment, Sumpter, Temple and Foster (1999) exposed hens to varying FR requirements and force requirements on a door push, in order to examine demand for food under different unit price conditions. They showed that response rates decreased as the force requirement for a response increased, and that response rates increased from FR 1 to FR 10, and decreased as the requirement increased beyond FR 10. The PRP also increased as the FR requirement or force requirement increased, and they report that the overall response rates for the door with no added weight and the key were similar (Sumpter et al., 1999). These features are very similar to those found with rats (Alling & Poling, 1995)

Considering factors such as response form, response duration and the animal's level of motivation allows the experimenter to form a better understanding of the relations between variables and the resulting response patterns. It is possible to simplify phenomena in order to study and quantify them, and then test the developed theory in natural settings (Killeen, 1995). This is often necessary as it is difficult to properly control variables in a natural setting; however, in experimental settings it is possible to systematically manipulate individual variables to better understand their influence on behaviour, and facilitate the development of models to predict behavioural patterns.

While many potentially influential variables have been tested in relation to MPR, there has been only one study that has explicitly attempted to manipulate the parameter δ. Bizo and Killeen, (1997) tested the effect of response force on the rate of expression of a target response, and it was found that, as expected, δ was greater for treadle pressing than for pecking. The parameter estimates for *a* were also greater for responding on the treadle, which was an unexpected result, inconsistent with MPR (Bizo & Killeen, 1997).

It is important to confirm that the parameters which the model asserts are related to motivational or structural aspects of the task vary appropriately when motivational or structural aspects of the task are manipulated. It is also important to assess the ability of this model to predict performance when response requirement is manipulated, because it will help disambiguate the relative importance of motivational and structural components of a task which combine to determine the expression of behaviour.

The aim of the present experiment was to test the ability of MPR to predict responding on an ascending series of FR values, when force requirement and response form were altered. In doing this, the experiment provided an opportunity to assess the influence of manipulations that are currently assumed to affect just one parameter. It was expected that by requiring two very different forms of response, either a key peck or a door push, that the responses on the different operanda would be of different durations, which would alter only the parameter estimate of δ. Likewise, when the force required to make an effective response was increased, it was expected that this would increase the estimates of the value of δ. It was expected that at lower δ values, responding would occur at a higher rate than at high δ values, and that in both cases, as the FR requirement was increased, there would be an initial steep increase in response rate, followed by a gradual decline. It was expected that the fastest response rates would be seen with the low force key, and the slowest would be seen for responding on the high force door. It was uncertain as to which would allow faster responding; the high force key, or the low force door. The door was expected to have a longer minimum response duration, but the high force key had a greater minimum force requirement, and the relative effects on δ of force and response duration are not known. It was expected that *a* would be relatively constant across conditions, β may change as the response duration increased, but the main changes in parameter estimates would be seen in δ, resulting in responses rates similar to those shown in Figure 2. This experiment also tested how well the model generalized to another species, domestic hens.

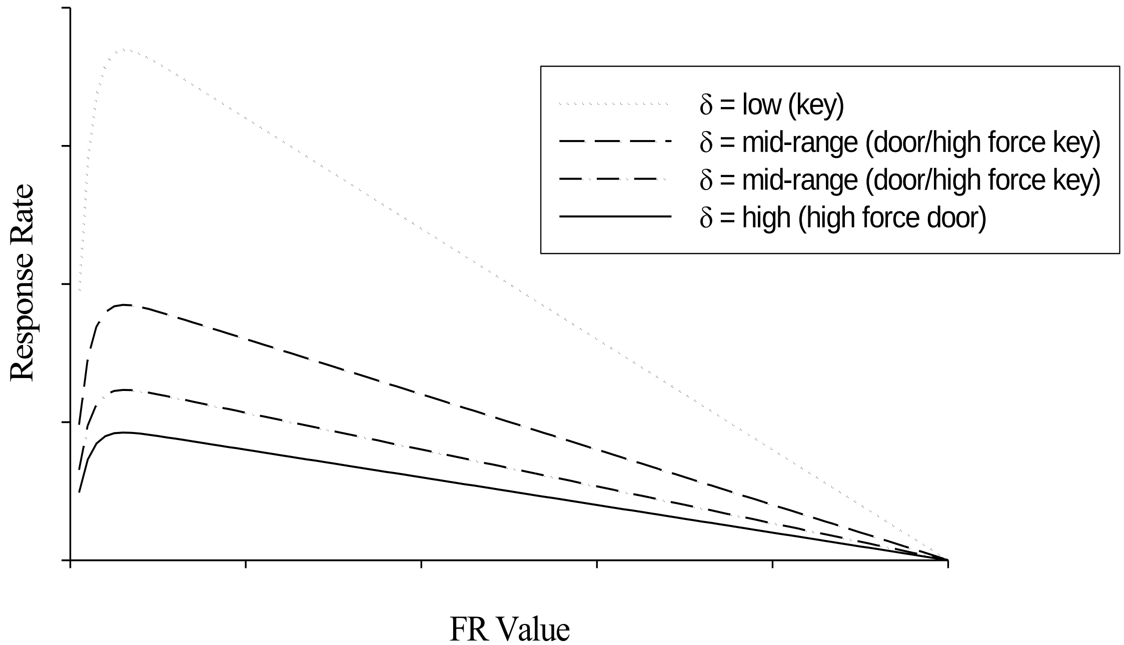

Figure 2. Predicted pattern of responding on the different operanda with different minimum force requirements, assuming *a* and β are constant, and differences in minimum response duration and minimum force requirement are affecting only the parameter δ.

Method

Subjects

Six domestic laying hens (*Gallus gallus domesticus),* were housed individually in wire cages measuring 310-mm wide by 430-mm high by 440-mm deep. They had unlimited access to water in their home cages and received supplemental feed in order to maintain their body weight at 85% ± 5% of their free-feeding weights. Their free-feeding weights were established over 30 days, one month before beginning the first experiment. If their weight was not within this range, they did not experience planned sessions until their weight returned to within the specified range. Hens were also provided with grit and vitamin supplements on a weekly basis. All but one of the hens had previous experience with pecking a response key, but none had previously operated a door push. The experiment was approved by the University of Waikato Animal Ethics Committee, protocol number 784. A copy of the application is available in Appendix A.

Apparatus

The experimental chamber measured 430-mm wide by 520-mm high by 575-mm deep. The interior of this chamber was painted black, and an operant response key, door push and food magazine were mounted on one wall. The response key was approximately 30-mm in diameter and was made of Perspex, and was backlit with a white light. The response key required a minimum force of 0.26 N to operate, and when a 48-g weight was added to it for the high force key condition, it required a minimum force of 1.11 N. The door push consisted of two 220-mm long vertical rods, each with a diameter of 6 mm, and with a 60-mm space between them, suspended from the ceiling of the experimental chamber. The door push required a minimum force of 0.52 N to operate, and in the high force door condition, in which a 200-g weight was added, it required 2.12 N to operate. The door push was situated to the right of the response key, with the food magazine positioned centrally. A white light of the same dimensions as the keylight was positioned behind the door. When the key was pecked or the door push depressed, responses were recorded. A response on either apparatus was defined as the lower microswitch being opened (key or door lifted), followed by the closure of an upper microswitch (key or door up), and the response was defined as finished when the lower microswitch was closed. In all sessions, reinforcement consisted of 1.5-s timed access to wheat from when an infrared beam was broken. If a hen did not attempt to eat from the hopper within 3-s of the hopper being raised, reinforcer delivery was terminated and the next trial begun, with the reinforcer recorded as ‘missed’. This only occurred occasionally.

Once the hen was placed in the experimental chamber, there was a 1-s ‘blackout’, before the key or door light was illuminated. Following each effective response, a 55 dB beep was emitted. If a reinforcer was due, the operandum light was extinguished, the magazine light illuminated and the magazine raised in order to provide access to the reinforcer. Experimental events were programmed and recorded using experimental software programmed in MedPC (Version 4, © Thomas A. Tatham and Med Associates, 1987-2005), running on a PC positioned beside the experimental chamber.

Procedure

A shaping by successive approximations procedure was used to train the hens to operate the door push. This took one to two sessions for hens numbered 91-96, after which they experienced five sessions of continuous reinforcement and two sessions of

FR 2 before the experiment began. Hen 96 was experimentally naïve, and so the shaping procedure described above for the door was repeated with the key.

Experimental sessions were conducted seven days a week and each session lasted for 50 minutes or until the hen had received 50 reinforcers, whichever occurred first. Exposure to the door and key conditions was counterbalanced across hens. Hens 91-93 began with the door as the target operandum, at the lower force requirement. Once they had completed the ratio requirements on this, they proceeded to the key with a lower force requirement. Following this, they returned to the door, but with a higher minimum force requirement, and then finally the key, again with an increased force requirement. Hens 94-96 began with the low force key, then the low force door, followed by the key and then the door, both with increased force requirements. For all conditions, the hens proceeded through a geometric series of FR values. These were FR 2, 4, 8, 16, 32, 64, 128, 256, 512 and 1024. If a hen received no reinforcers at one FR value, that value was repeated the following session. If the hen still did not receive any reinforcers, the series was deemed completed.

Once a series was completed, the hen either started the next series or experienced sessions at FR 20 until she began the next series. The hens experienced each condition for three series before proceeding to the next condition. The conditions and FR values experienced by each hen is presented in Table 1 below. Each hen experienced one session at each FR value. Where there are two numbers (e.g. 64/64), it means that the hen was exposed to FR 64 in two consecutive sessions, because in the first session at that FR value, the hen received no reinforcers. Values that are italicised and in brackets (e.g. *(16)*) denote sessions whose data was excluded, due to factors such as an equipment malfunction or the hen laying an egg during the session. Typically, when hens lay an egg during an experimental session, they either do not respond, or have interrupted or unusual patterns of responding. If the hen did not start responding at the start of a new series, further training was given in a similar format to the initial training, until the hen was consistently responding again.

As the hens were excluded from the experiment when their weight was outside the specified range, the hens progressed between schedule requirements and target operanda at different times. Hen 96 responded at a very low rate on the door, and failed to receive any reinforcers during the high force door condition, even after multiple training sessions, so she was excluded from the high force door condition.

Table 1

Conditions (FR value and operandum) experienced by each hen, in order of exposure.

	91 Door	**92 Door**	**93 Door**	**94 Key**	**95 Key**	**96 Key**
Series 1	2	2	2	2	2	2
	4	4	4	4	4	4
	8	8	8	8	8	8
	16	16	*(16)*	*(16)*	*(16)*	16
	32	32	32	32	32	32
	64	64/64	64	64	64	64
	128		128/128	128	128	128/128
	256/256			256/256	256/256	
Series 2	2	2	2	2	2	2
	4	4	4	4	4	4
	8	8	*(8)*	8	8	8
	16	16	16	16	16	16
	32	32	32	32	32	32
	64	64	64/64	64	64	64
	128	128/128	128/128	128	128	128
	256			256/256	256	256/256
	512/512				512	
					1024/1024	
Series 3	2	2	2	2	2	2
	4	4	4	4	4	4
	8	8	8	8	8	8
	16	16	16	*(16)*	16	*(16)*
	32	32	32	16	32	32
	64	64	64	32	64	64
	128	128/128	128	64	128	128
	256		256/256	128	256	256/256
	512/512			256/256	512	
					1024/1024	

Table 1 cont.

	Key	Key	Key	Door	Door	Door
Series 1	2	2	2	2	2	2
	4	4	4	4	4	4
	8	8	8	8	8	8
	16	16	16	16	16	(16)/16
	32	32	32	32	32	32/32
	64	64	64	64/64	64	
	128	128	128		128	
	256	256/256	256		256/256	
	512		512			
	1024/1024		1024			
Series 2	2	2	2	2	2	2
	4	4	4	4	4	4
	8	8	8	8	8	8
	16	16	16	16	16	16/16
	32	32	32	32	32	
	64	64	64	64	64	
	128	128	128	128/128	128	
	256	256	256		256/256	
	512/512	512/512	512			
			1024/1024			
Series 3	2	2	2	2	2	2
	4	4	4	4	4	4
	8	8	8	*(8)*	8	8
	16	*(16/32)*	4	16	16	16/16
	32	16	16	32	32	
	64	32	32	64/64	64	
	128	64	*(64)*		128	
	256	128	128/128		256/256	
	512	256				
	1024/1024	512/512				

Table 1 cont.

	91 Door Weight	**92 Door Weight**	**93 Door Weight**	**94 Key Weight**	**95 Key Weight**	**96 Key Weight**
Series 1	2	2	2	2	2	2
	4	4	4	4	4	4
	8	8	8	(8)/8	8	(8)/8
	16	16/16	16	16	16	16
	32		32	*(32)*	32	32
	64/64		64	64/64	64	64
			128/128		128	128/128
					256/256	
Series 2	2	2	2	2	2	2
	4	4	4	4	4	4
	8	8	8	*(8)*	8	8
	16	16/16	16	16	16	16
	32		32	32	32	32/32
	64		64	*(64)*	64	
	128		128	64	*(128)*	
	256/256		256/256	128/128	(256)/256	
				256/256		
Series 3	2	2	2	*(2)*	2	2
	4	4	4	*(4)*	*(4)*	4
	8	8	8	*(8)*	8	(8)/8
	16	*(16)*/16	16	*(16)*	16	16
	32		32	*(16)*	*(32)*	32/32
	64		64	16	64	
	128/128		128/128	32	128/128	
				64		
				128/128		

Table 1 cont.

	Key Weight	Key Weight	Key Weight	Door Weight	Door Weight	Door Weight
Series 1	2	2	(2)/2	2/2/2	(2)/2	
	4	4	4	4	4/4	
	(8)/8	8	8	8	8	
	16	16	16	16	16	
	32	32/32	32	32	32	
	64/64		64	64	64/64	
			128	128/128		
			256/256			
Series 2	(2)/2	2	2	2	2	
	4	4	4	4	4	
	8	8/8	8	8/8	8/8	
	16		16	16	16/16	
	32		32/32	32	32	
	64/64			64/64	64/64	
	128/128					
Series 3	2	2/2/2		2		
	4	4/4		4		
	8	8/8		8		
	16			16		
	32/32			32/32		

Results

This experiment exposed six hens to two different operanda, each requiring a topographically different response and a different minimum force to operate (key peck - 0.26 N and door push - 0.52 N). The hens' responding on these operanda was reinforced according to a geometrically ascending series of FR values, from FR 2 to a maximum of FR 1024. They experienced this series three times in succession for each operandum. Response rates across a session for each hen over each of these series are shown for responding on the key (Figure 3) and for responding on the door (Figure 4). Weights were added to both the door and the key, increasing the minimum force requirement for each operandum by a factor of approximately four. The minimum force requirement for the door was then 2.12 N, and the key was then 1.11 N. The response rates obtained on the weighted key are shown in Figure 5 and for the weighted door in Figure 6.

Typically, response rates increased with increase in ratio value up to a point, usually around FR 30, before decreasing at larger ratio values. However, the bitonic pattern of response rates expressed as a function of ratio value was not always obvious, and in some cases, response rates were highest at the smaller ratio values before decreasing in a linear fashion to a minimum at the largest ratio value. Comparing the graphs for responding on the low force key and the low force door, it can be seen that the hens responded at a lower rate when the door was the target operandum. Hens also stopped responding at a lower FR value when responding on the door as opposed to the key. Responding on the high force key occurred at a lower rate for all but one of the hens. The hens again stopped responding at a lower FR value for the high force key compared to the low force key. In the case of the door, the increased force requirement resulted in no difference in response rates, although hens stopped responding at lower

FR values when working on the high force door. Again, the bitonic function was observed for most series for most hens, although in five series (over three hens) for the high force key, and 5 series over four hens for the high force door, a negatively sloped straight line was observed. The smooth curves through the data were fitted using Equation 1, and represent the predictions of MPR. Parameter estimates of *a*, δ and β were obtained from the best fit of Equation 1 to the data for individual animals for each series and each operandum, using non-linear least squares regression.

The variation in the FR values at which hens stopped responding for each apparatus and at each force requirement is captured by the model's estimated values for *a*. These values, as well as the parameter estimates for δ and β; the R^2 values for each series and the standard error values are compared in Table 2, A summary of these values, showing the mean, median, range and standard deviation over all sessions and all hens for each condition can be seen in Table 3. In both tables, it can be seen that estimates for *a* are greatest for the key with a low force requirement, and then decrease as the force requirement increases (from left to right in the table). Likewise, the estimates for δ increase as the force requirement increases, except for the high force door. Estimates for β remain similar.

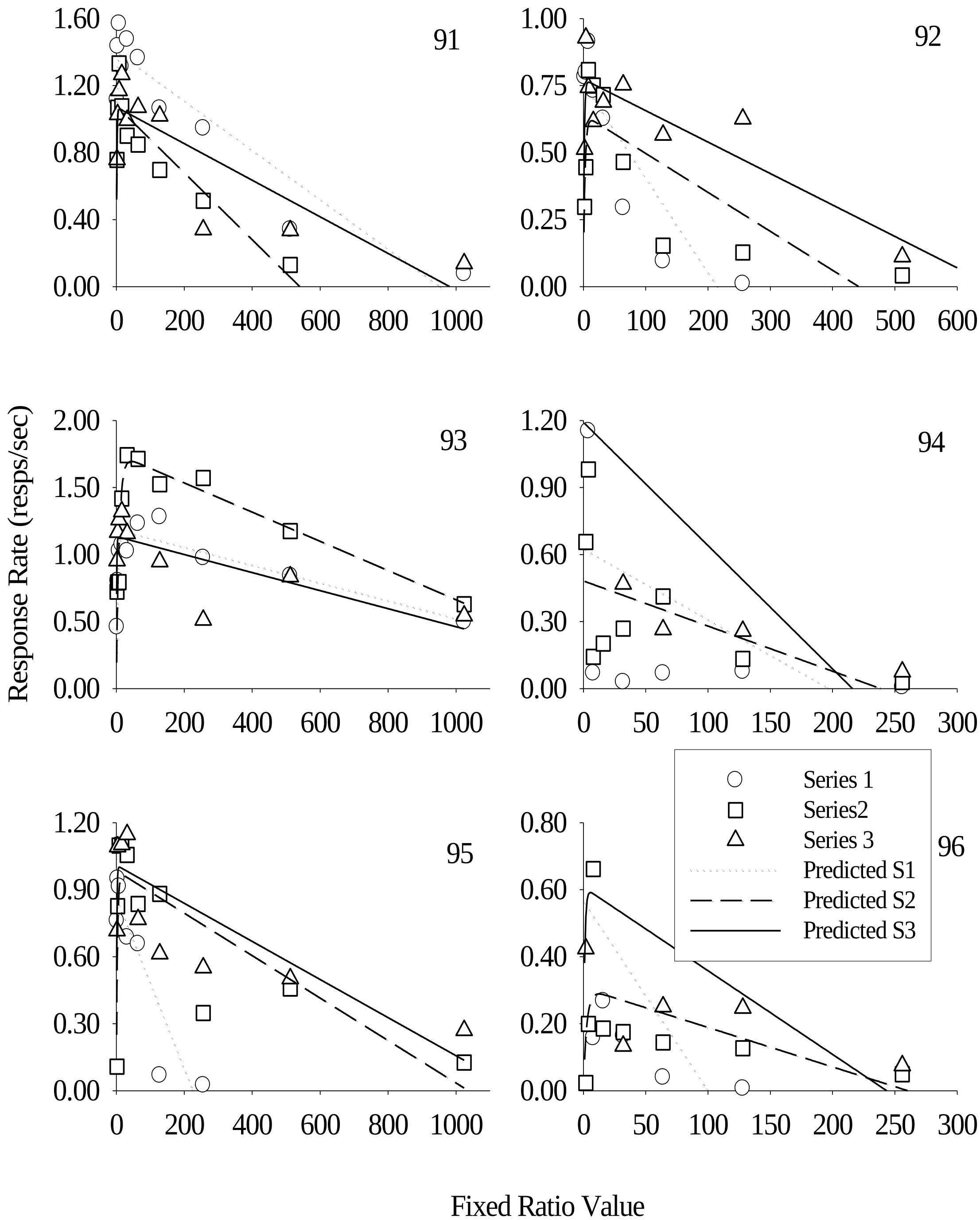

Figure 3. Mean response rates for each session are plotted as a function of FR value for responding on the key. The curves are drawn by Equation 1. The first FR series is denoted by circles and the dotted curve; the second by squares and the dashed curve; the third by triangles and the solid curve. Different scales for both X and Y axes have been used, in order to allow better visual representation of the data.

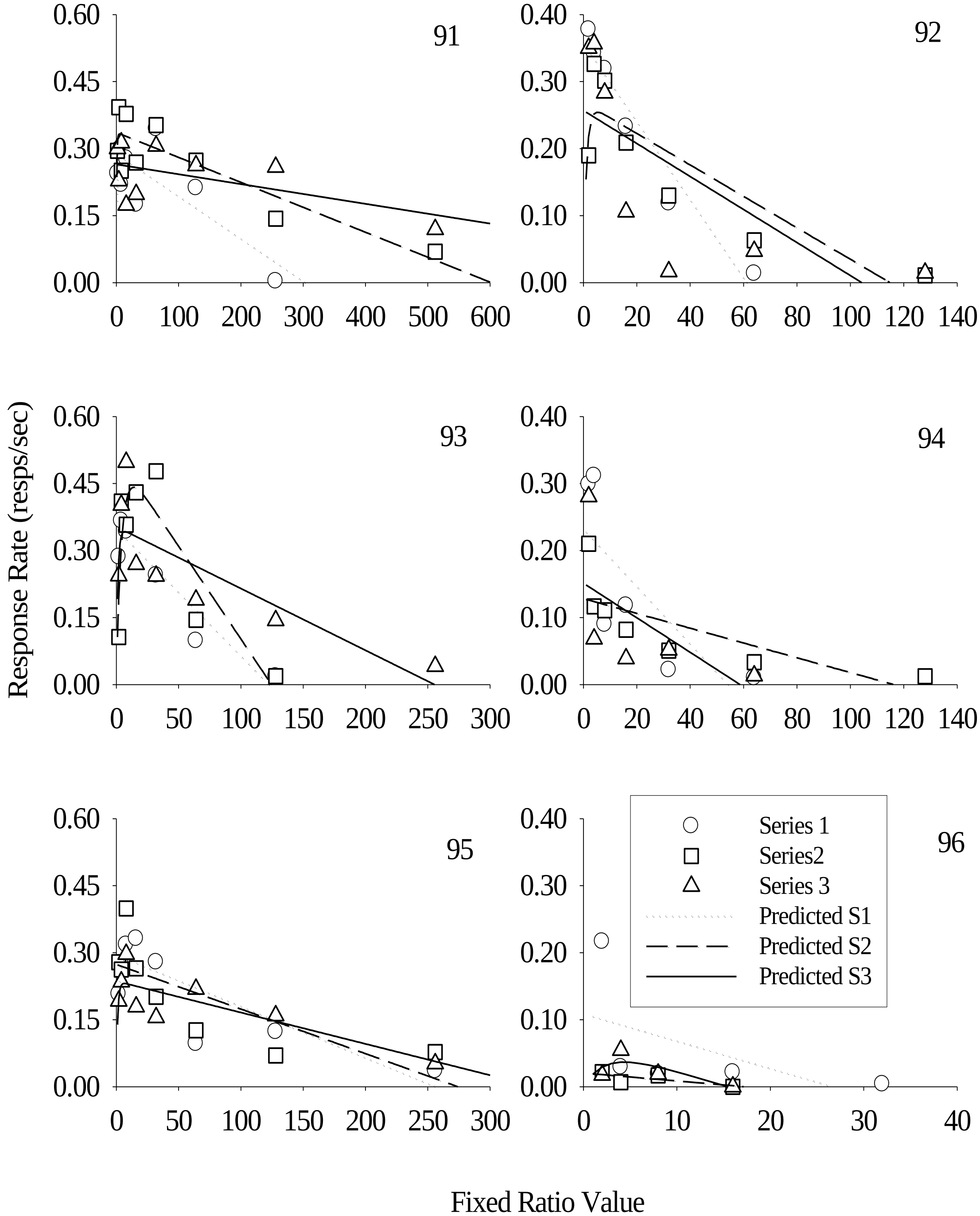

Figure 4. Mean response rates for each session are plotted as a function of FR value for responding on the door. The curves are drawn by Equation 1. The first exposure is denoted by circles and the dotted curve; the second by squares and the dashed curve; the third by triangles and the solid curve. Note that the scales for both X and Y axes are different for each graph.

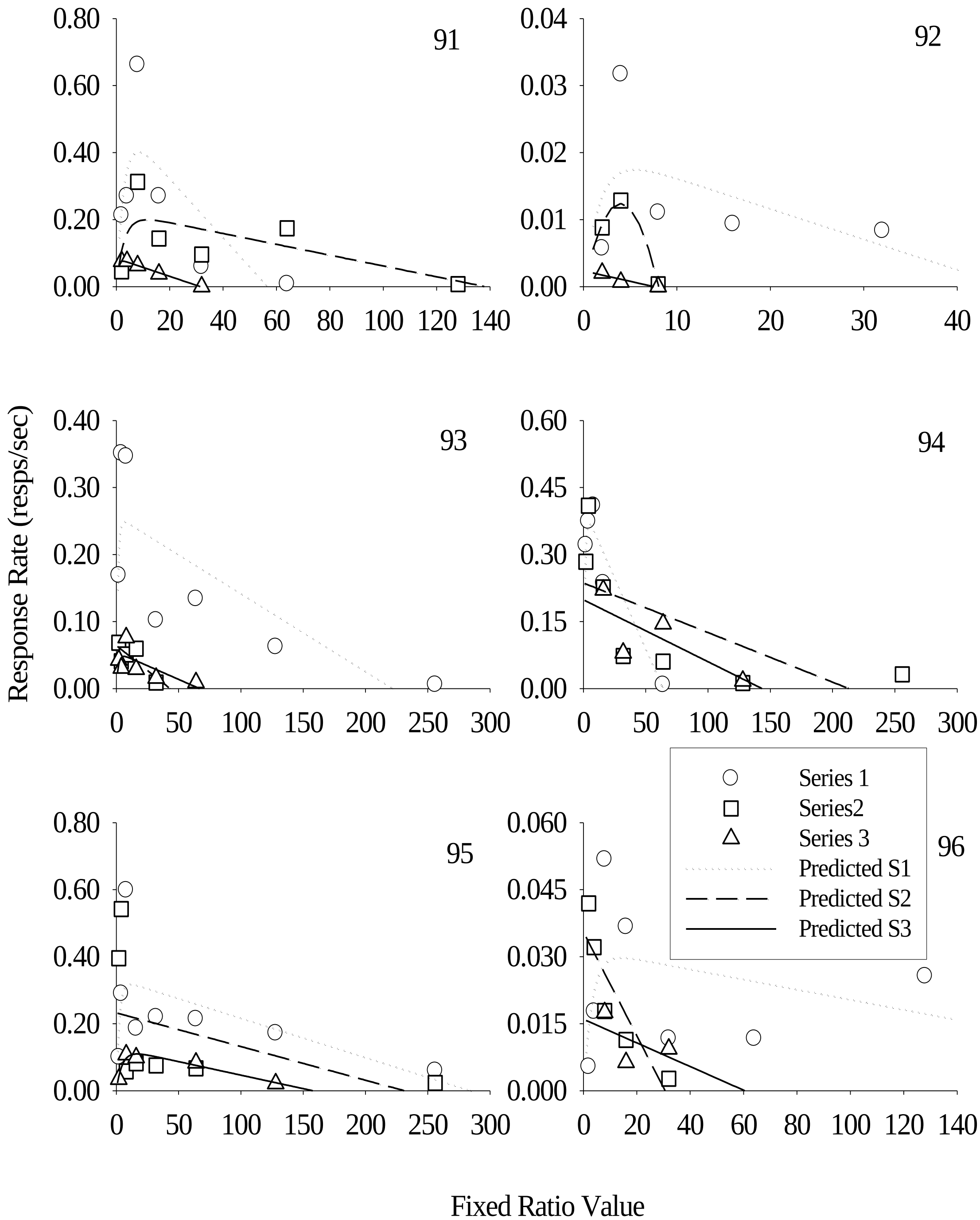

Figure 5. Mean response rates for each session are plotted as a function of FR value for responding on the key with weight added. The curves are drawn by Equation 1. The first exposure is denoted by circles and the dotted curve; the second by squares and the dashed curve; the third by triangles and the solid curve. Note that the scales for both X and Y axes are different for each graph.

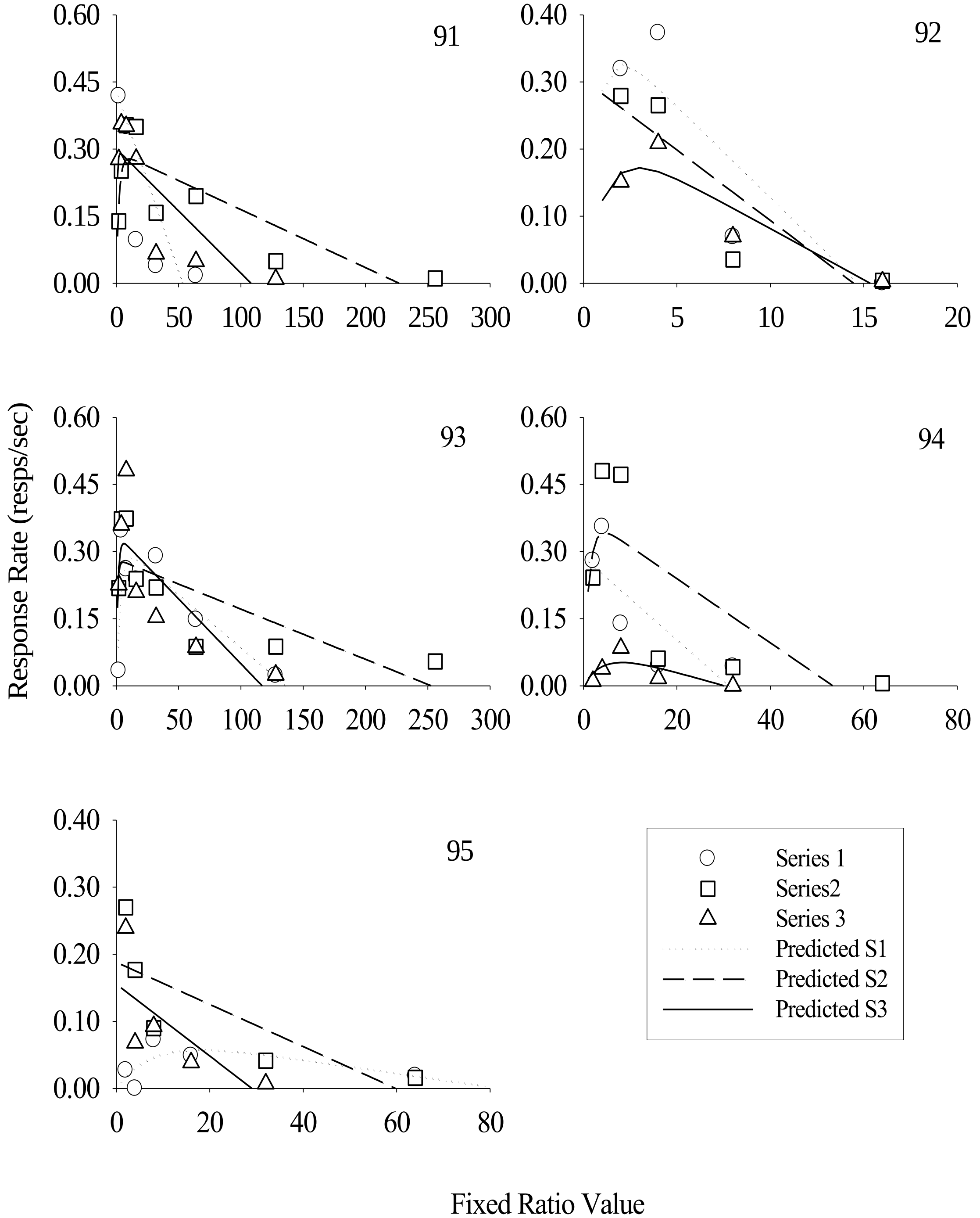

Figure 6. Mean response rates for each session are plotted as a function of FR value for responding on the door with weight added. The curves are drawn by Equation. 1. The first exposure is denoted by circles and the dotted curve; the second by squares and the dashed curve; the third by triangles and the solid curve. Note that the scales for both X and Y axes are different for each graph.

Table 2

The estimated values of a, δ and β, along with the R^2 and standard error values for each fit for each hen for each series of FR values for responding across all conditions, are shown below.

	Hen	**91**			**92**			**93**			**94**			**95**			**96**		
	Series	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**
Key Low (F=0.26N)	**a**	952	540	981	214	442	660	1785	1607	1685	197	238	216	225	1036	1184	100	260	243
	δ	0.71	0.93	0.93	1.32	1.56	1.29	0.84	0.57	0.88	1.60	2.08	0.84	1.16	1.02	0.99	1.77	3.26	1.65
	b	0.58	0.50	0.49	1.00	0.32	0.53	0.23	0.11	0.62	1.00	1.00	1.00	0.70	0.26	0.53	1.00	0.31	0.63
	R^2	0.90	0.92	0.76	0.81	0.67	0.75	0.90	0.86	0.59	0.24	0.31	0.61	0.84	0.72	0.65	0.41	0.30	0.43
	SE of Mean	0.18	0.15	0.22	0.18	0.19	0.13	0.10	0.19	0.22	0.66	0.31	0.46	0.18	0.23	0.23	0.39	0.20	0.32
Door Low (F=0.52N)	**a**	303	602	1198	61	115	104	122	125	255	54	116	59	256	274	337	27	17	15
	δ	3.48	2.97	3.78	2.80	3.71	3.89	2.87	1.93	2.83	4.32	7.81	6.61	3.39	3.65	4.23	9.20	49.58	15.57
	b	0.64	0.70	1.00	1.00	0.58	1.00	0.63	0.21	0.55	1.00	1.00	1.00	0.48	1.00	0.59	1.00	1.00	0.36
	R^2	0.62	0.77	0.32	0.94	0.77	1.00	0.92	0.79	0.67	0.58	0.58	0.37	0.74	0.60	0.69	0.31	0.55	0.64
	SE of Mean	0.08	0.06	0.06	0.04	0.07	0.13	0.05	0.10	0.10	0.11	0.05	0.12	0.07	0.08	0.05	0.10	0.01	0.02

Table 2 *cont.*

	Hen	91			92			93			94			95			96		
	Series	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**
Key High (F=1.11N)	**a**	57	138	31	46	48	8	222	43	67	64	213	143	284	231	158	280	31	60
	δ	2.01	4.49	11.88	48.30	0.31	426.74	3.88	15.56	18.36	2.46	4.23	5.03	2.99	4.30	7.86	31.53	28.09	62.51
	b	0.31	0.28	0.81	0.46	0.02	1.00	0.58	1.00	0.45	0.59	1.00	1.00	0.36	1.00	0.19	0.27	1.00	1.00
	R^2	0.58	0.51	1.00	0.25	0.99	0.86	0.60	0.63	0.49	0.92	0.46	0.62	0.40	0.20	0.94	0.25	0.80	0.31
	SE of Mean	0.19	0.10	0.00	0.01			0.10	0.02	0.02	0.06	0.14	0.09	0.15	0.22	0.01	0.02	0.01	
Door High (F=2.12N)	**a**	53	227	108	15	14	15	136	253	117	31	53	30	82	60	29			
	δ	2.34	3.40	3.33	2.50	3.30	4.28	3.11	3.53	2.95	3.49	2.61	11.31	12.08	5.32	6.43			
	b	1.00	0.36	0.79	0.79	1.00	0.59	0.28	0.64	0.52	1.00	0.57	0.21	0.12	1.00	1.00			
	R^2	0.59	0.72	0.70	0.79	0.79	0.84	0.65	0.60	0.63	0.64	0.55	0.56	0.44	0.63	0.53			
	SE of Mean	0.20	0.08	0.10	0.14	0.12	0.06	0.09	0.09	0.12	0.12	0.19	0.03	0.03	0.09	0.09			

Table 3

Minimum, maximum, mean and median values, with standard deviations of estimates for a, δ and β, along with the R^2 and standard error values over all series and all hens.

		Minimum	**Maximum**	**Mean**	**Median**	**Standard Deviation**
Key Low	**a**	99.84	1785.47	698.10	490.95	567.66
	δ	0.57	3.26	1.30	1.09	0.64
	b	0.11	1.00	0.60	0.56	0.30
	R^2	0.29	0.90	0.67	0.74	0.22
	SE of Mean	0.10	0.66	0.25	0.21	0.14
Door Low	**a**	15.49	1198.32	224.44	119.14	285.07
	δ	1.93	49.58	7.37	3.75	11.02
	b	0.21	1.00	0.76	0.85	0.27
	R^2	0.31	1.00	0.66	0.65	0.20
	SE of Mean	0.01	0.13	0.07	0.07	0.03
Key High	**a**	7.54	284.39	117.98	65.33	92.30
	δ	0.31	426.74	37.81	6.45	98.61
	b	0.02	1.00	0.63	0.58	0.35
	R^2	0.20	1.00	0.60	0.59	0.27
	SE of Mean	0.00	0.22	0.08	0.06	0.07
Door High	**a**	14.45	252.70	81.57	53.32	74.97
	δ	2.34	12.08	4.67	3.40	3.05
	b	0.12	1.00	0.66	0.64	0.31
	R^2	0.44	0.84	0.65	0.63	0.11
	SE of Mean	0.03	0.20	0.10	0.09	0.05

Manipulating the response operanda and minimum force requirement was intended to alter the value of δ, the parameter that refers to constraints on responding. The inverse of the maximum run rate, which is calculated by dividing the number of responses less the number of PRPs, by the total time less the sum length of the PRPs, provides an estimate of the minimum *inter-response time* (IRT). These were calculated for each condition for each hen, and are shown in Table 4. The differences between the minimum IRT and the estimates for δ are assumed to reflect the effect of the varying force requirement. In all conditions for all hens, the estimate of δ is greater than the minimum IRT.

A *Multivariate Analysis of Variance* (MANOVA) was used to compare parameter estimates across conditions, and it revealed that differences in the value for *a* were statistically significant at an alpha of 0.05 for: the key versus door, low force requirement versus high force, and the individual animal. Statistically significant interaction effects were found between: the apparatus and hen, weight condition and hen and the combination of apparatus, weight condition and hen. There was no significant difference in *a* values for the weight added versus no weight added condition. There were no statistically significant differences in δ or β values for any of the independent variables. Table 5 describes these results.

Residual deviations of the best fits of Equation 1 from response rates for each operanda, for each FR value, for each series and each animal were calculated. The residuals are presented in Figure 7 for responding on the low force key, and in Figure 8 for responding on the low force door, in Figure 9 for the high force key, and in Figure 10 for the high force door. It appears that the deviations between the obtained response rates and the model's predictions vary in a systematic manner, with the model tending to underestimate response rates at lower FR values, and to overestimate response rates at higher FR values.

Table 4

Obtained minimum IRTs and mean parameter estimates for δ for each condition for each hen.

	91 min IRT	**Mean δ**	**92 min IRT**	**Mean δ**	**93 min IRT**	**Mean δ**	**94 min IRT**	**Mean δ**	**95 min IRT**	**Mean δ**	**96 min IRT**	**Mean δ**
Key low	0.59	0.89	0.89	1.15	0.40	0.61	0.65	1.34	0.69	1.07	0.80	2.22
Key high	1.15	4.41	24.69	28.13	2.01	10.40	1.96	3.82	1.21	4.23	14.21	38.91
Door low	2.41	3.24	2.22	2.93	1.36	2.12	3.27	7.04	1.87	3.14	21.65	5.86
Door high	1.36	2.60	1.89	2.28	1.51	2.36	1.20	4.81	3.18	8.54		

Table 5

MANOVA results for parameter values as dependent variables, with apparatus, weight condition and hen as independent variables.

	Degrees of Freedom	Sum of Squares	Mean Square	F-Ratio	Probability Level
Parameter a					
Door/key (main effect)	1	259944.80	259944.80	8.78	0.004848*
Low/High Force (main effect)	1	481982.80	481982.80	16.28	0.000209*
Apparatus & Force Condition (interaction)	1	96439.38	96439.38	3.26	0.08
Hen (main effect)	5	1610068.00	322013.60	10.88	0.000001*
Apparatus & Hen (interaction)	5	915686.90	183137.40	6.19	0.000191*
Force Condition & Hen (interaction)	5	1075735.00	215147.00	7.27	0.000046*
Apparatus, Force Condition & Hen (interaction)	5	1154663.00	230932.60	7.80	0.000024*
Parameter δ					
Door/key (main effect)	1	113.91	113.91	0.05	0.83
Low/High Force (main effect)	1	4018.96	4018.96	1.63	0.21
Apparatus & Force Condition (interaction)	1	0.03	0.03	0.00	1.00
Hen (main effect)	5	15111.16	3022.23	1.22	0.31
Apparatus & Hen (interaction)	5	15864.96	3172.99	1.29	0.29
Force Condition & Hen (interaction)	5	14699.06	2939.81	1.19	0.33
Apparatus, Force Condition & Hen (interaction)	5	13967.69	2793.54	1.13	0.36
Parameter β					
Door/key (main effect)	1	0.08	0.08	0.84	0.37
Low/High Force (main effect)	1	0.00	0.00	0.02	0.88
Apparatus & Force Condition (interaction)	1	0.00	0.00	0.00	1.00
Hen (main effect)	5	0.96	0.19	2.01	0.10
Apparatus & Hen (interaction)	5	0.41	0.08	0.85	0.52
Force Condition & Hen (interaction)	5	0.35	0.07	0.73	0.60
Apparatus, Force Condition & Hen (interaction)	5	0.09	0.02	0.20	0.96

* Term significant at alpha = 0.05

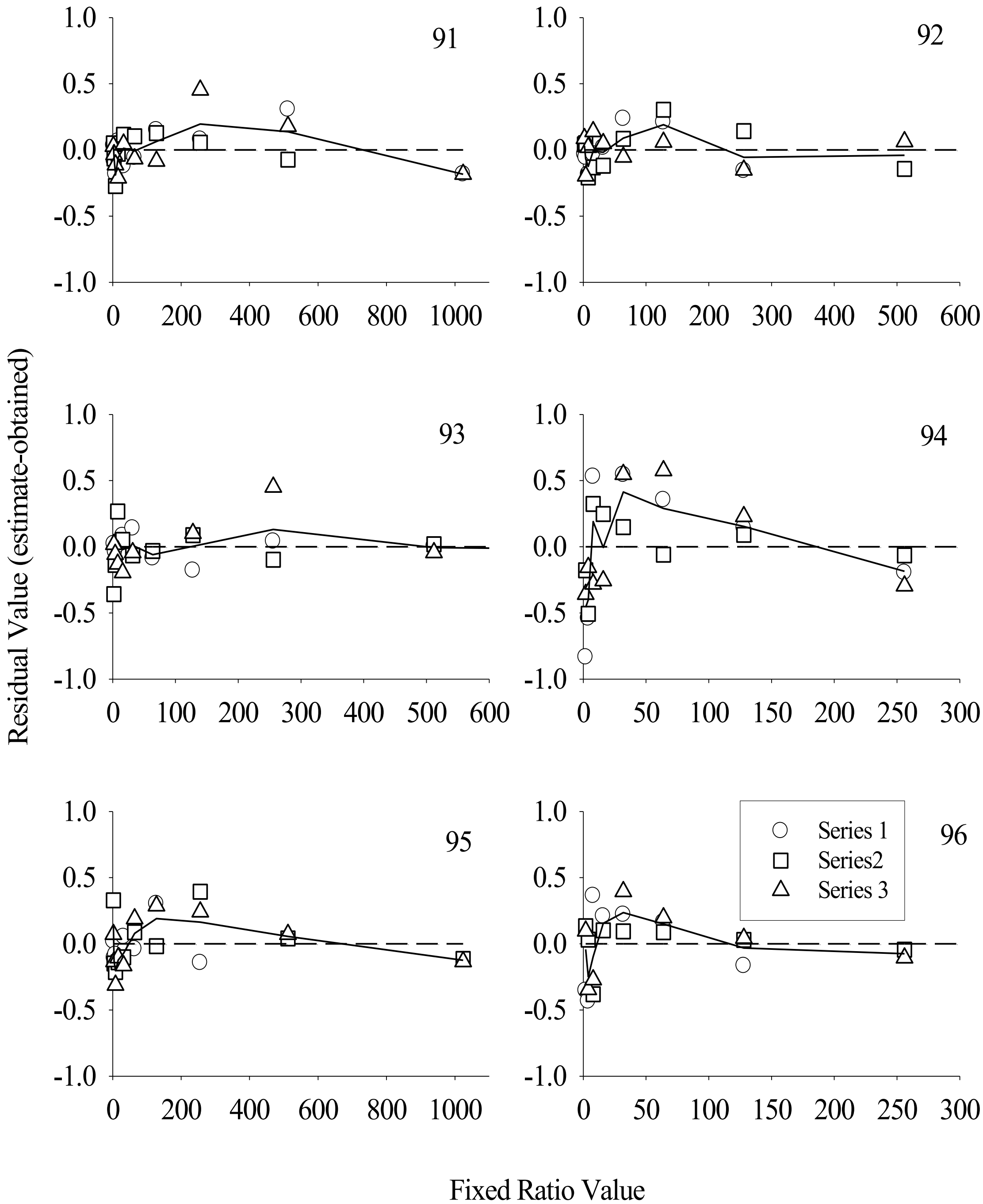

Figure 7. Residual deviations between the obtained response rate, and that predicted by MPR are presented for hens responding on the low force key. The values presented are for the predicted response rate less the obtained response rate, for three series each, for all hens. The solid line represents the mean residual deviation.

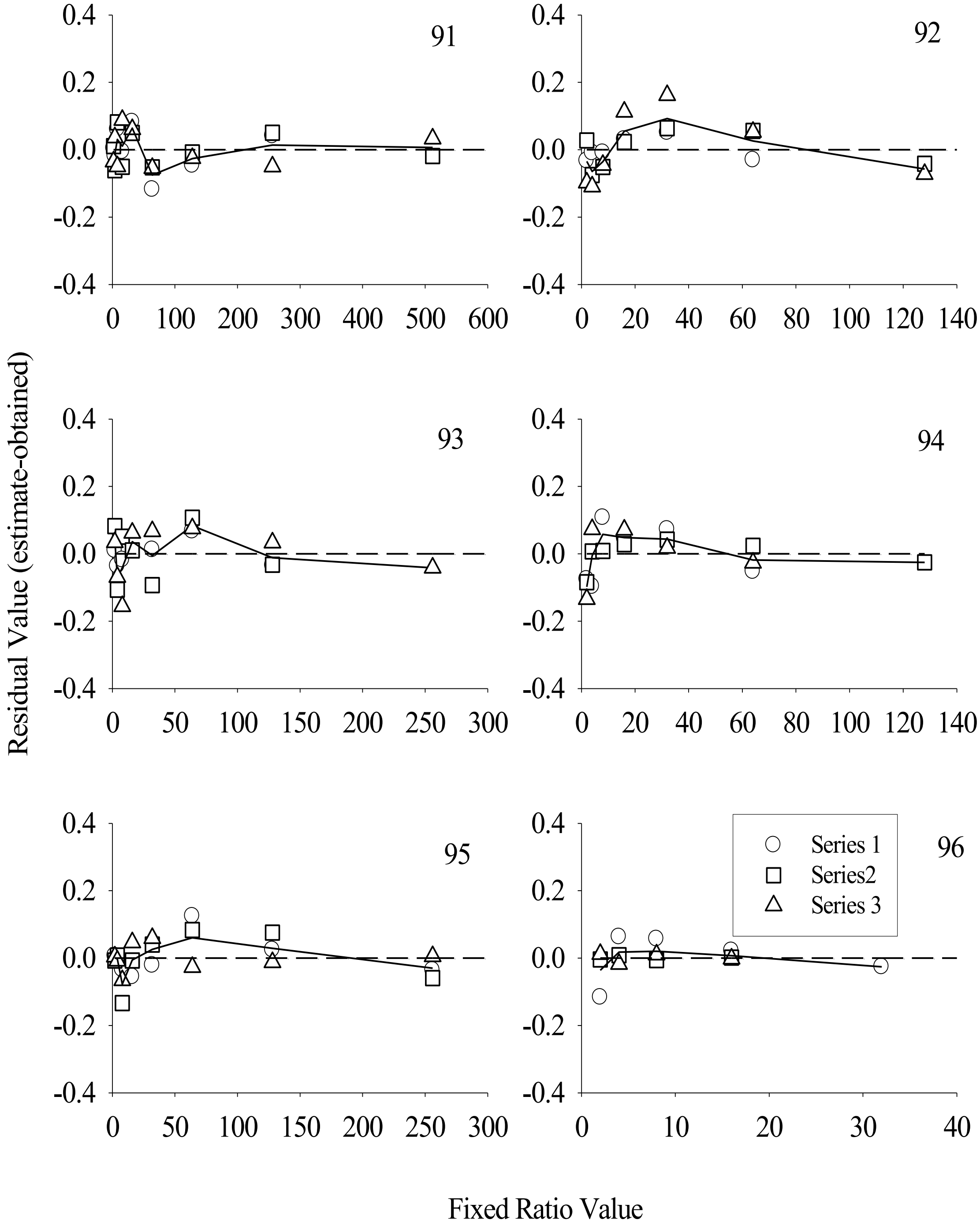

Figure 8. Residual deviations between the obtained response rate, and that predicted by MPR are presented for hens responding on the low force door. The values presented are for the predicted response rate less the obtained response rate, for three series each, for all hens. The solid line represents the mean residual deviation.

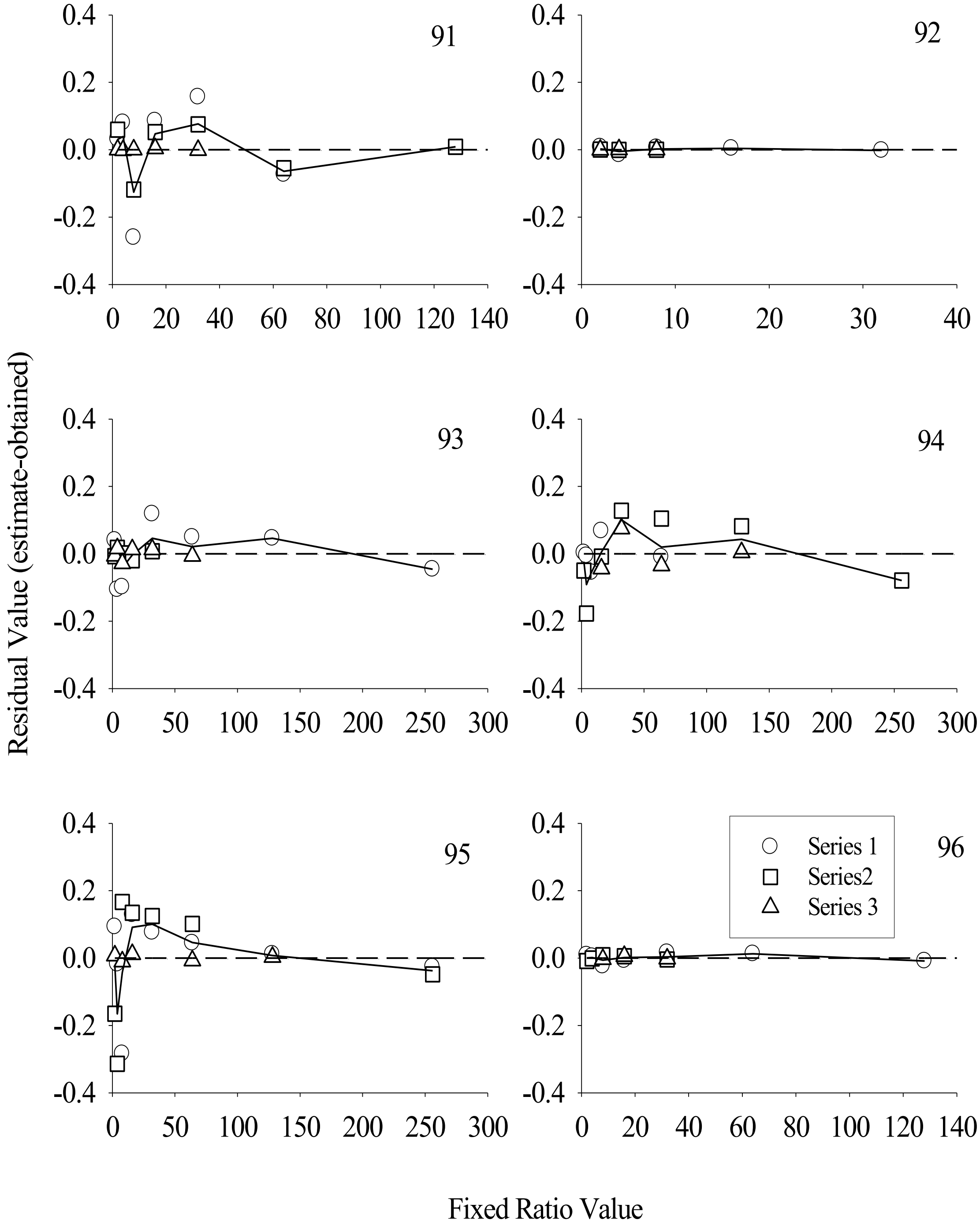

Figure 9. Residual deviations between the obtained response rate, and that predicted by MPR are presented for hens responding on the high force key. The values presented are for the predicted response rate less the obtained response rate, for three series each, for all hens. The solid line represents the mean residual deviation.

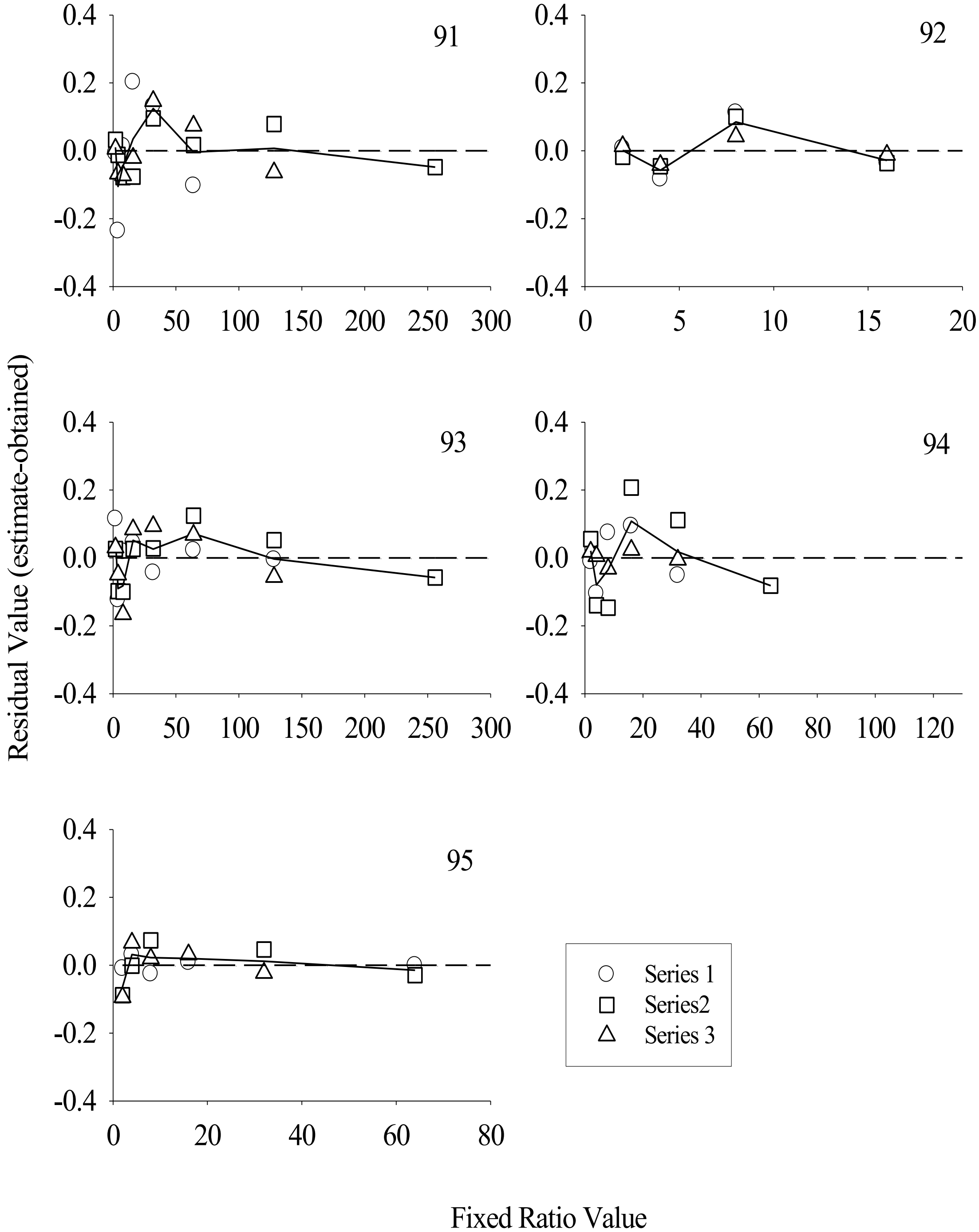

Figure 10. Residual deviations between the obtained response rate, and that predicted by MPR are presented for hens responding on the high force door. The values presented are for the predicted response rate less the obtained response rate, for three series each, for all hens. The solid line represents the mean residual deviation.

Equation 2 contains one more parameter than Equation 1; ε, which represents the erasure of memory of the target response. To determine whether Equation 2 was able to provide a better estimate of the obtained data, it was fitted to the data for the door, at both low and high minimum force requirements. This resulted in an average increase in R^2 value of 0.024, with parameter estimates for *a* and δ, the parameters common to both equations, staying approximately constant. A table showing the obtained parameter estimates, R^2 values and standard error values for Equation 2 can be found in Appendix B, while Table 6 shows the minimum and maximum parameter estimates, along with the mean, median and standard deviations of these. It was determined that, although Equation 2 provided a slightly better fit than Equation 1, the improvement was not enough to justify the extra parameter it requires.

Run rates were calculated for each series for each hen by subtracting the number of PRPs from the number of responses, and dividing this figure by the total time less the sum of the PRPs' length. This captures the rate of responding while the hen is performing the target response, and helps to clarify if changes in response rate are due to changes in PRP length, or if the animal is actually responding at a different rate at different FR values. It removes the possibility that the apparent decrease in response rate is due solely to an increase in PRP length.

Figures 11 and 12 show the run rates and MPR's predictions for the key and door respectively. Each graph ends one FR value earlier than the response rate graphs, as the hens tended to not earn a reinforcer at the final FR value they experienced, meaning that there was no 'run'. The bitonic function is once again present in the majority of cases for both operanda, and run rates are higher for the key than for the door.

Run rates for each operandum at the increased force requirement were also calculated, and are shown in Figures 13 (key) and 14 (door). Run rates for the high force key were lower than for the low force key. Run rates for the high force door did not vary consistently, with two hens exhibiting lower run rates at the higher force requirement, and the others having approximately the same run rates.

The mean PRP for each session on each operanda was calculated, and is shown in Figure 15. As can be seen in this figure, there is generally an increase in the mean PRP for a session as the FR requirement is increased. The increase is smallest for the low force key, and is similar for the other conditions. Note that the X-axis is a log scale and the Y-axis scale varies for each hen.

In summary, when hens responded on the key, responding occurred at a faster rate, and continued to higher FR values, than when hens were responding on the door. The increased force requirement resulted in hens ceasing to respond at lower FR values for both apparatus, and for response rates to be slower for the key, but not the door. In most cases, the obtained response rates were described by a bitonic function of the type predicted by MPR, although in some situations the fitted curve was a straight, negatively inclined line. Graphing the run rates showed that the decrease in response rates at higher FR values was not simply a result of increasing PRPs, although the PRPs did increase as the FR value increased. Statistically significant differences in the estimates for the parameter a were found between the two different operanda, low force versus high force, and between individual hens. Interactions between the apparatus and hen; force condition and hen; and the force condition, apparatus and hen were statistically significant. No significant differences were found in the value for a for the interaction between the apparatus and weight condition, or in any situation for both δ and β values.

Table 6

Minimum, maximum, mean, median and standard deviation values of estimates for a, δ and β, along with the R^2 and standard error values over all series and all hens.

		Minimum	**Maximum**	**Mean**	**Median**	**Standard Deviation**
Door Low	**a**	15.16	1198.32	224.50	119.06	285.75
	λ	0.00	1.61	0.35	0.12	0.45
	δ	2.12	49.58	7.38	3.72	15.32
	ε	0.00	1.00	0.60	0.82	0.42
	R^2	0.31	0.95	0.65	0.66	0.20
	SE of Mean	0.09	373.28	44.83	0.20	150.13
Door High	**a**	14.45	251.05	81.57	53.26	298.16
	λ	0.00	0.80	0.20	0.10	0.45
	δ	2.34	13.97	4.75	3.39	15.54
	ε	0.00	1.00	0.75	1.00	0.38
	R^2	0.53	0.87	0.69	0.70	0.23
	SE of Mean	0.07	0.36	0.20	0.19	142.51

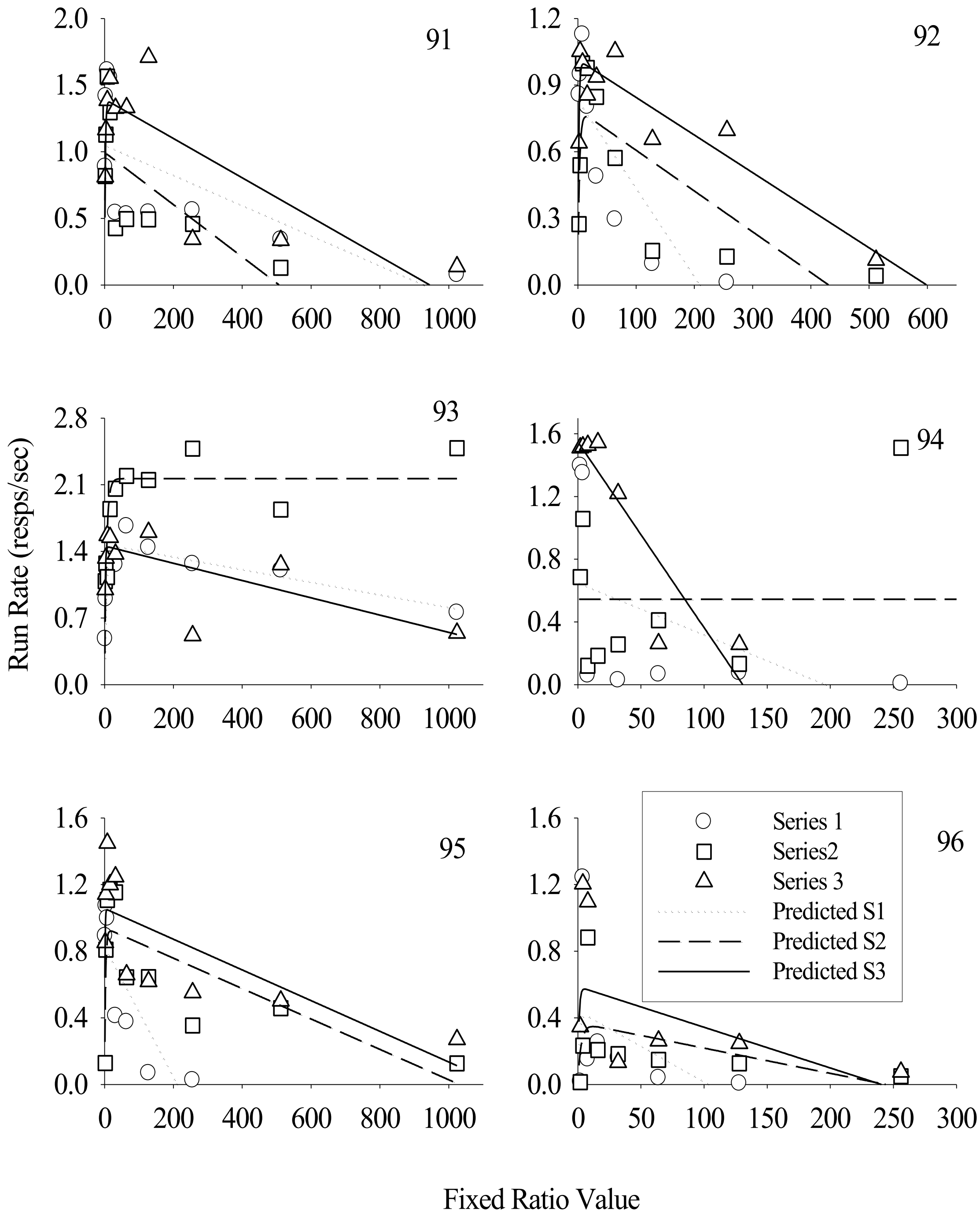

Figure 11. Mean run rates for each session are plotted as a function of FR value for responding on the low force key. The curves are drawn by Equation 1. The first exposure is denoted by circles and the dotted curve; the second by squares and the dashed curve; the third by triangles and the solid curve. Both X and Y axes have different scales for each graph.

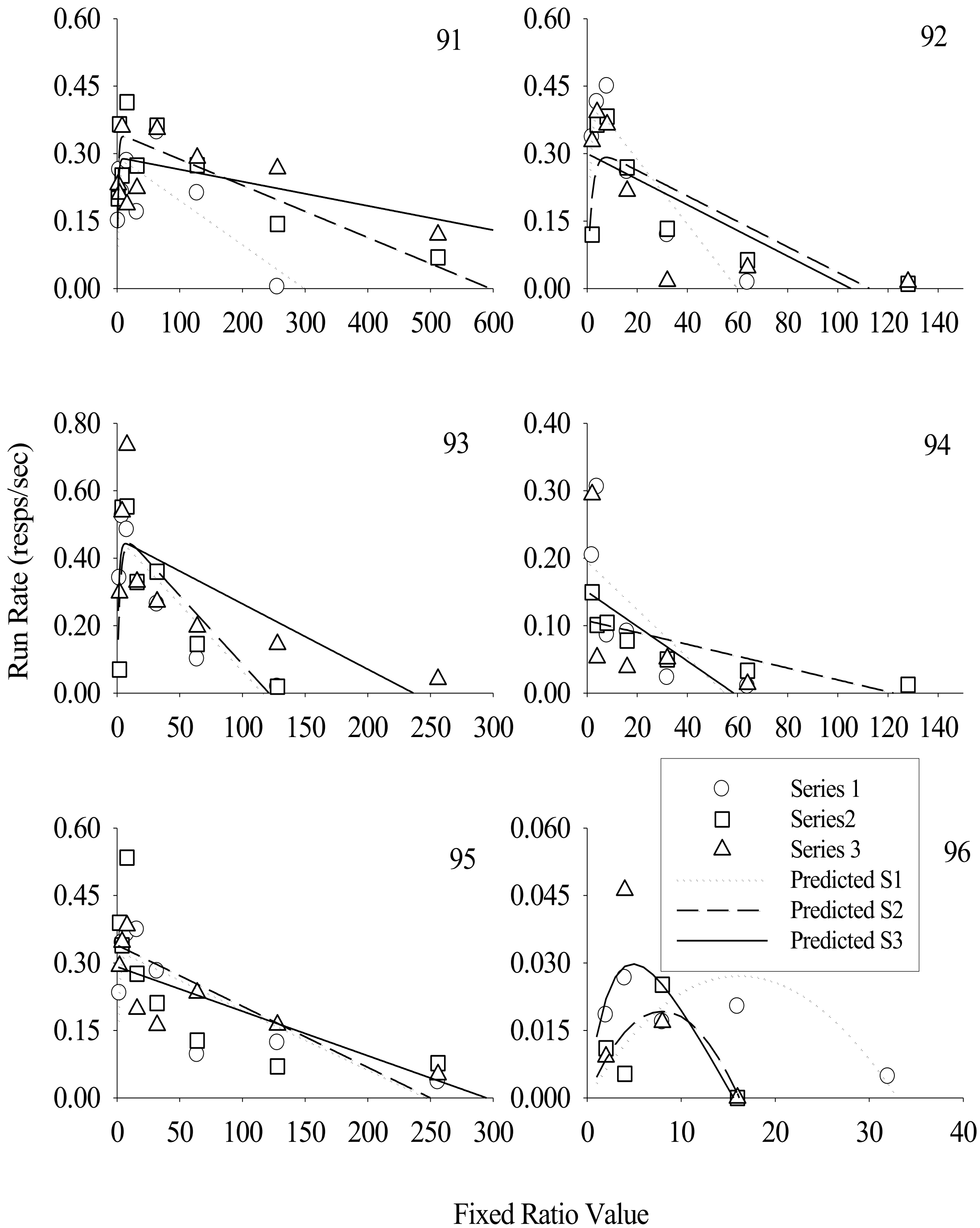

Figure 12. Mean run rates for each session are plotted as a function of FR value for responding on the low force door. The curves are drawn by Equation 1. The first exposure is denoted by circles and the dotted curve; the second by squares and the dashed curve; the third by triangles and the solid curve. Note the different scaling for each graph.

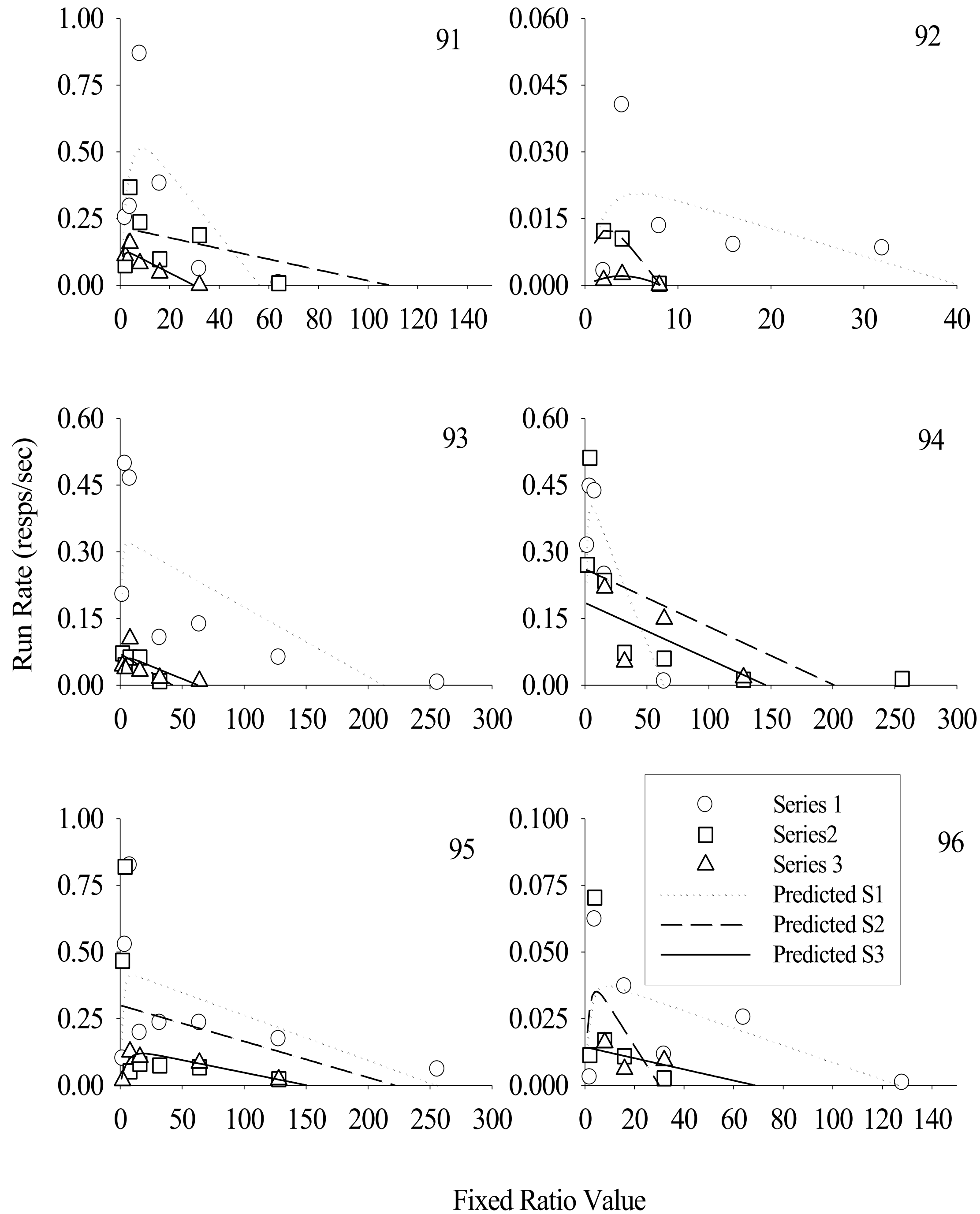

Figure 13. Mean run rates for each session are plotted as a function of FR value for responding on the high force key. The curves are drawn by Equation 1. The first exposure is denoted by circles and the dotted curve; the second by squares and the dashed curve; the third by triangles and the solid curve. Note the different scaling for each graph.

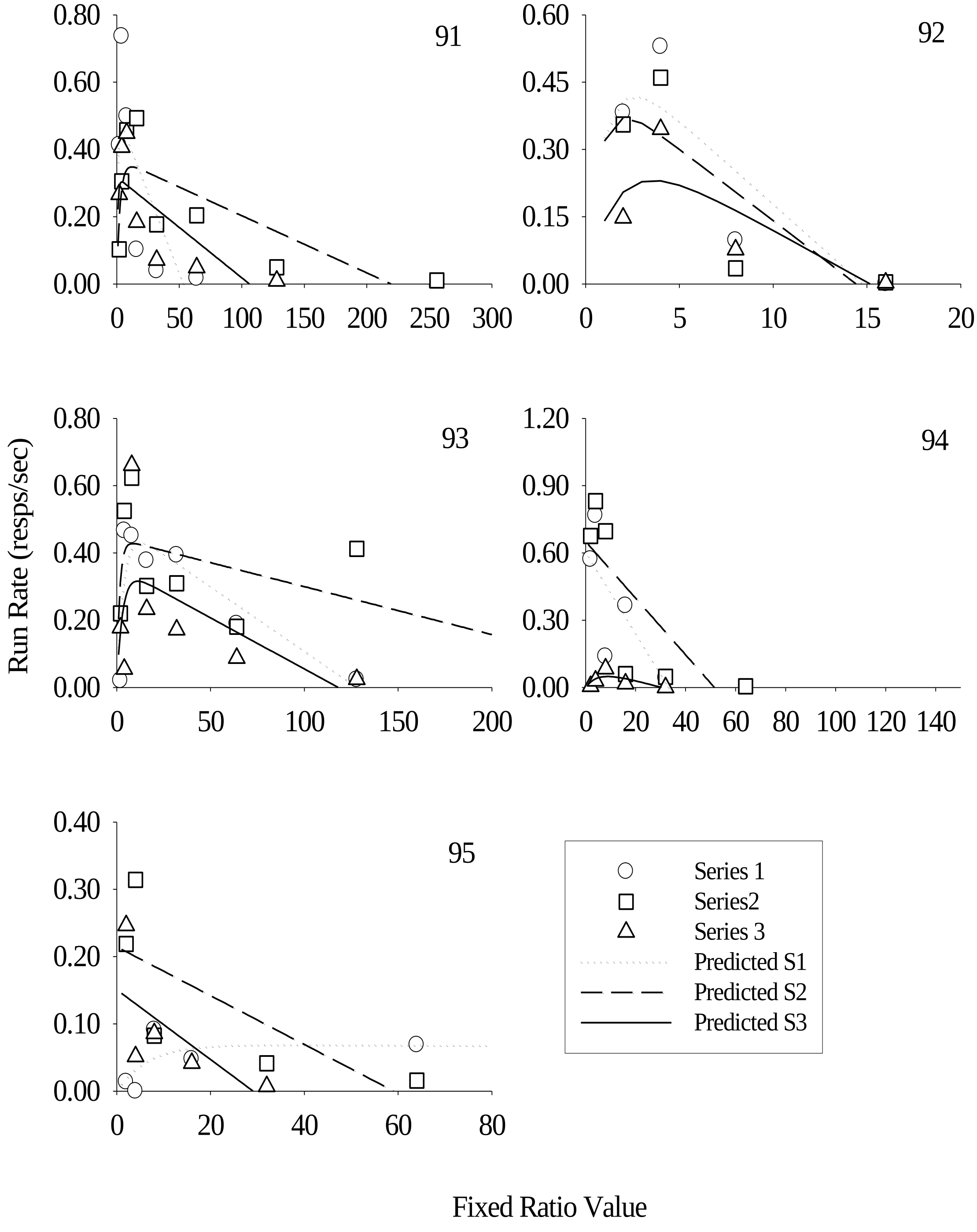

Figure 14. Mean run rates for each session are plotted as a function of FR value for responding on the high force door. The curves are drawn by Equation 1. The first exposure is denoted by circles and the dotted curve; the second by squares and the dashed curve; the third by triangles and the solid curve. Note the different scaling for each graph.

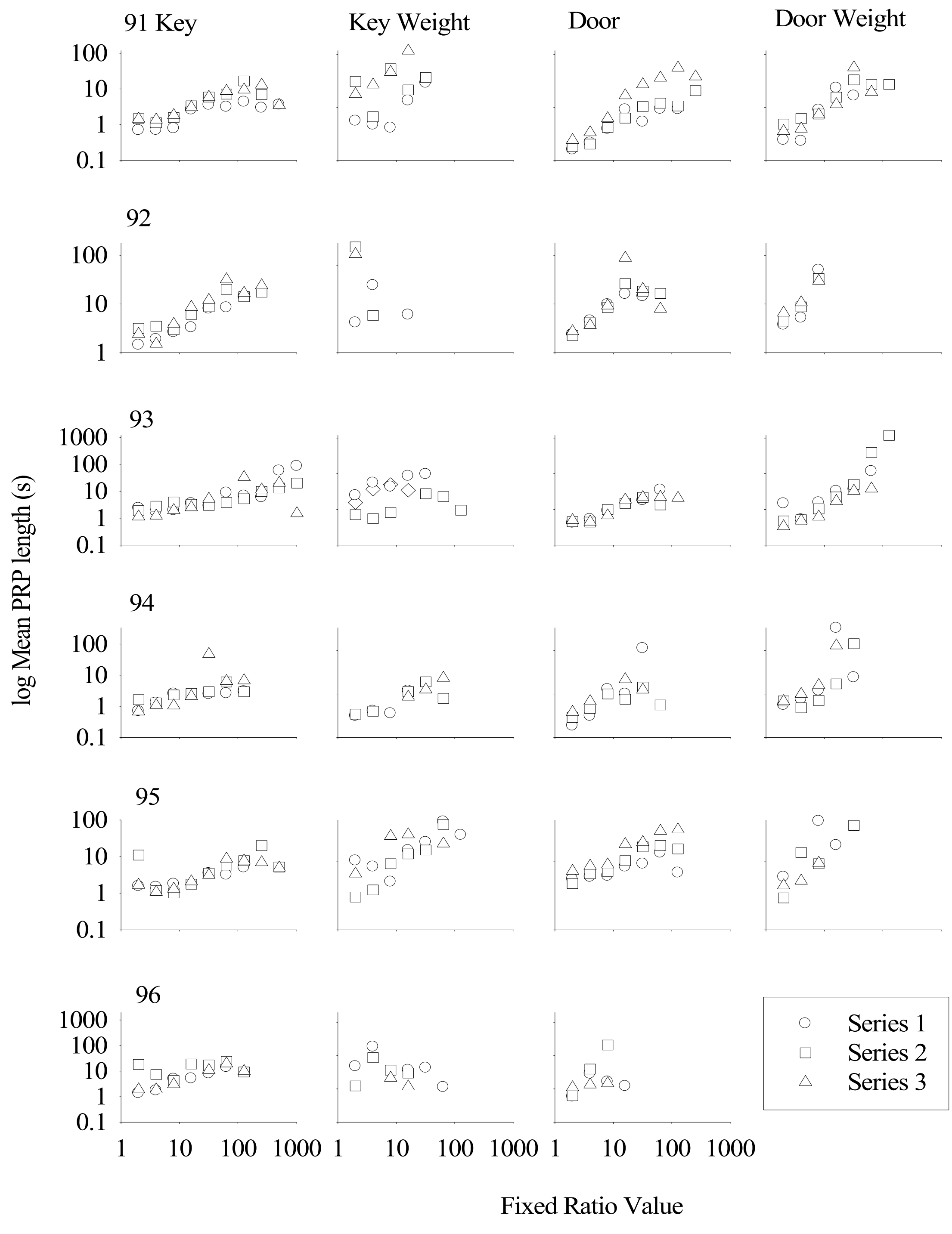

Figure 15. Mean PRP for each session is plotted as a function of FR value for all conditions. The first exposure is denoted by circles, the second by squares and the third by triangles. The scales for Y axis data are different for each hen, in order to better show the data. Note the log axes.

General Discussion

This experiment aimed to test the ability of MPR to predict response patterns when the form of the response and the minimum force requirement were altered. It was shown that response rates were highest for the low force requirement key, followed by the low force requirement door, and that response rates were similar for the key and door when force requirement was increased. The FR value at which hens stopped responding followed the same pattern, with hens working on the low force key responding to the highest FR value (FR 1024), hens working on the low force door stopping by FR 512, and hens on both the key and the door with increased minimum force requirement stopping responding by FR 256. The predictions of MPR provided a fair description of the obtained data, with mean R^2 values ranging from a minimum of 0.25 for the high force key, to 1.00 for the low force door. The overall mean R^2 value was 0.655, with standard deviation of 0.208, and the median was 0.654.

The variance accounted for by MPR in this experiment is similar to that found in an experiment with rats as the subjects, where R^2 values ranged from 0.03 to 0.90 (Covarrubias & Aparicio, 2008). These are worse fits than those reported in other papers investigating MPR, where R^2 values are generally greater. Fitting MPR to response rates generated by humans resulted in mean R^2 values of 0.79, 0.91 and 0.98 (Bizo et al., 2002), fits to data generated by rats ranged from 0.886 (Rickard et al., 2009) to 0.99 (Reilly, 2003) and fits to data generated by pigeons ranged from 0.77 to 0.99 (Bizo & Killeen, 1997). The poorer fits in this experiment are probably in part due to the variability in the data; in this experiment the model is fitted to the data from individual sessions, where other experiments have fitted the model to averaged data, which removes much of the variation between sessions. As no previous experiments have tested MPR with hens, it is not possible to determine whether the poorer fits are also in part due to variations between species.

A study of the residual deviations (Figures 7 through 10) revealed systematic differences between the obtained and predicted response rate values, with MPR underestimating response rates at FR values at both the low and high extremes, and overestimating response rates for mid-range FR values. Although the magnitude of the residuals varied between conditions, they followed the same pattern as FR requirement increased, irrespective of condition. Systematic deviations suggest a weakness in the model, in that it is failing to describe a particular aspect of behaviour (Shull, 1991). Considering the parameter values and the results of the MANOVA may help to see where this weakness may lie.

Equation 1, which was used to fit the model to the obtained data, consists of three parameters; *a,* δ and β. These reflect the number of responses that will be supported by a reinforcer of a particular type and size, under a particular level of deprivation (parameter *a*), the minimum time required to complete a response (parameter δ) and the association between the reinforcer and the response immediately preceding it (parameter β). As the hens in this experiment only participated in experimental sessions when their weight was within 5% of their target weight, and the reinforcer type and duration remained constant, *a* should not vary much between conditions. The change in operandum and the different minimum force requirements was expected to change the estimates for δ, with these expected to increase from key to door, and when weights were added to both. It was also expected that β may increase as the response rates decreased (expected to occur when weights were added to the operanda, and on the door when compared to the key), as the hens were more likely to engage in non-target behaviours. This would mean that the target response was not the only behaviour being reinforced, which would decrease the parameter estimate for β. In all cases, parameter estimates for δ were greater than the minimum IRT. The difference between these values is probably due to the additional effect of the minimum force requirement for each condition. While the minimum IRTs were different for each condition, this did not mirror the order of minimum force requirement (key low, door low, key heavy, door heavy), with the low force requirement door resulting in higher minimum IRTs than the high force requirement door, and the high force key resulting in the largest IRTs. Figure 16 shows that, although in most cases there was a reasonably close correlation between the mean IRT and the parameter estimates for δ, the presence of one extreme outlier reduces the goodness of fit. The curve fit to the data accounts for 0.025 of the variance within the data.

It was found that estimates of both β and δ did not differ significantly across conditions. As the response durations did not change significantly between operanda, or when minimum force was increased, a likely explanation, supported by the statistically significant changes in *a* across conditions, is that *a,* instead of δ, was changing to reflect the differences in response requirements. This may be due to a form of automatic reinforcement in addition to the arranged reinforcers, such as pecking the key providing some form of tactile reinforcement that the door did not, or that pushing the door was in some way aversive. The MANOVA revealed no significant interaction effect between

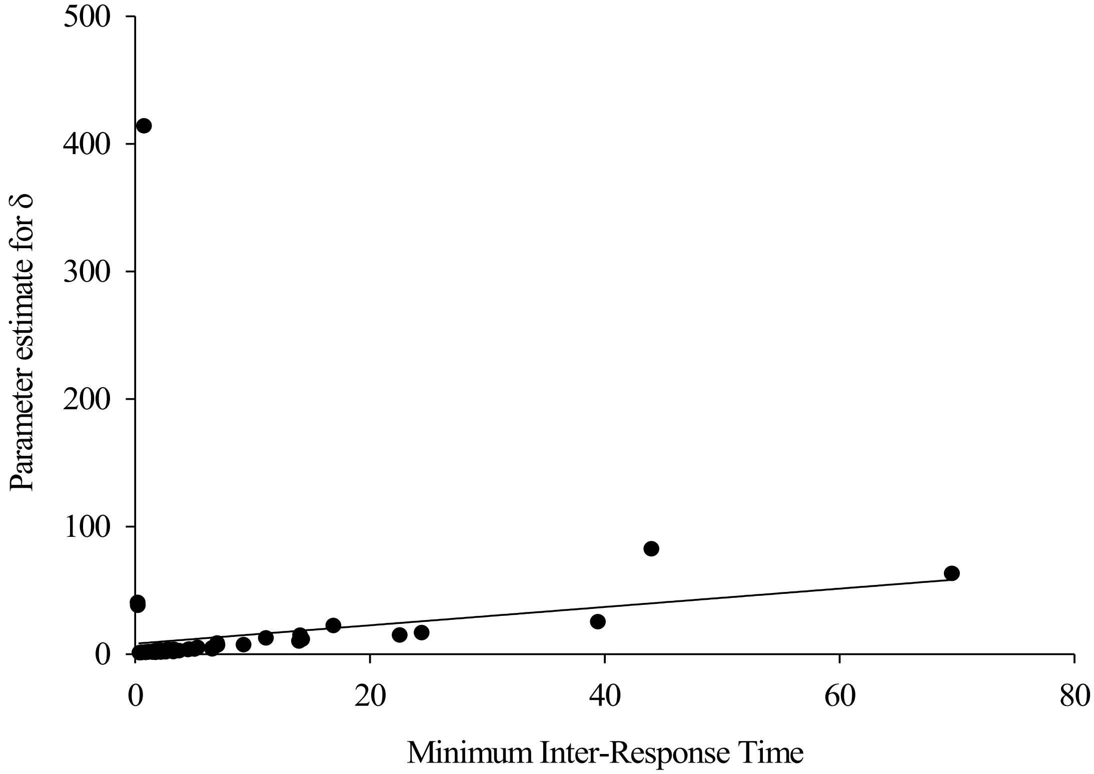

Figure 16. Mean parameter estimates for δ are plotted as a function of the mean IRT for each hen in each condition. The fitted curve is calculated using least-squares linear regression.

the weighted or non-weighted conditions for *a* for responding on both the door and the key. This suggests that it is the operandum, not the changing force requirement that prompted the change in motivational state and again provides support for the theory that the hens received some form of automatic reinforcement or punishment from performing the target responses.

It was expected that adding weights to both the key and the door would increase the δ value; this was not found. Killeen (1994) suggested that there may be an interaction between the minimum response force and minimum response duration, and incorporated both these factors into the parameter δ. The only previous experiment to have investigated response requirement in relation to MPR (Bizo & Killeen, 1997), found that the response duration was a poor indicator of the effort expended in forming a response. It was suggested that effort required to complete a response may need to be represented separately from the time to complete a response (Bizo & Killeen, 1997). This experiment suggests that this is unnecessary, as the differences in δ values did not alter in a significant manner for either the door or the key when weights were added. The only possible explanation for this that would require a separate parameter, would be if, while the minimum force requirement increased, resulting in an increase in δ, the hens were able to complete responses faster, cancelling the effect of the force increase.

The order in which the hens experienced the FR values, and the size of the increments between ratio values, may also have had an effect on the response rates obtained. Reilly (2003) found large differences in responding for rats responding on an ascending series compared to on a descending series. The rats in this experiment experienced multiple FR values in one day, each signalled by a different coloured light. Reilly suggests that the differences found between ascending and descending series of FR values may be because the rats' behaviour was controlled by time in session, rather than the cue lights (Reilly, 2003). The step size between ratio values has also been shown to have an effect, with rats working on a PR schedule completing more ratios when the increment was greater (Covarrubias et al., 2008).

In order to investigate whether step size affected the current experiment, Hen 91 was exposed to two series of ascending FR values, where the FR value increased by 5 each day, until the hen stopped responding. The methodology was otherwise identical to that of the main experiment, and she responded on the high force door. As can be seen in

Figure 17, the hen responded at a similar rate to the previous FR progression, and stopped responding at lower FR values, although because of the decrease in step size, this was in increase in number of sessions completed. The smaller increments in FR brought about a more sudden drop in response rates than seen with the larger increments. The response rate then stabilised as the FR value continued to increase. This provides support for the possibility that the step size between sessions is an important factor in the patterns of responding observed, and this may need to be further investigated in relation to MPR

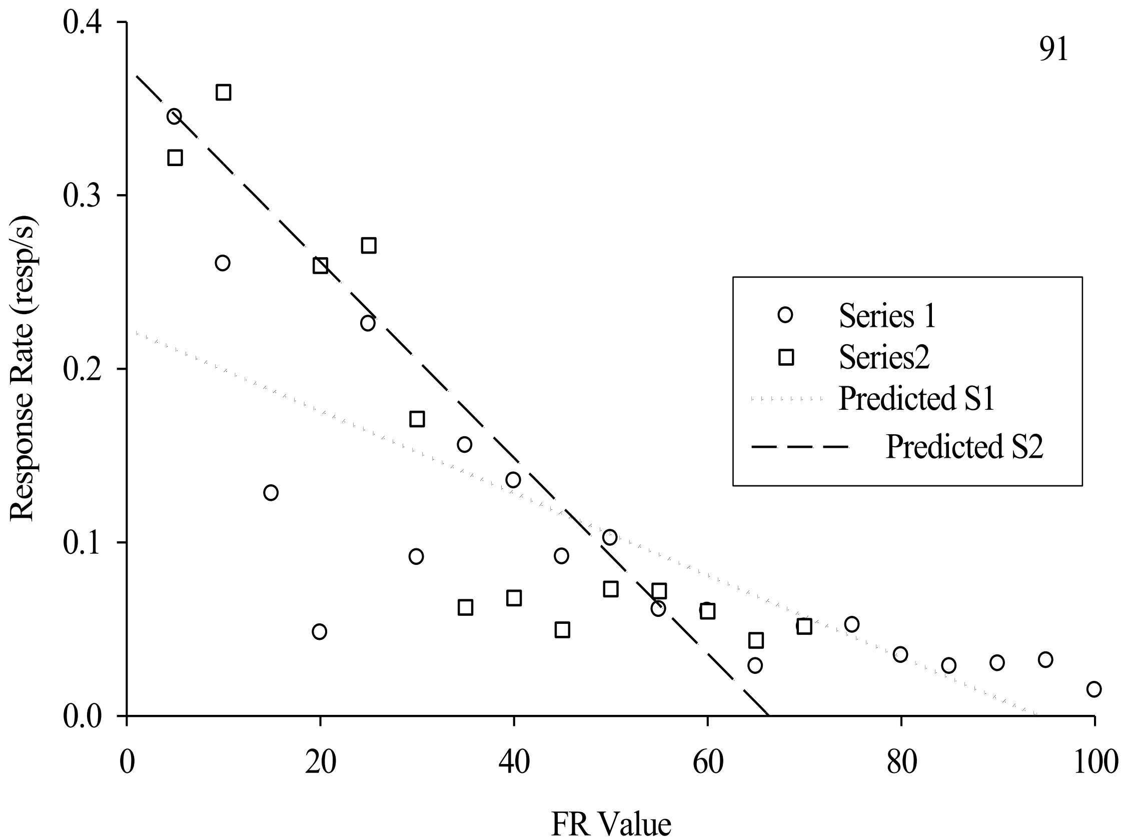

Figure 17. Mean response rates for Hen 91for each session are plotted as a function of FR value for responding on the door with weight added. The curves are drawn by Equation. 2. The first exposure is denoted by circles and the dotted curve; the second by squares and the dashed curve.

Further research in relation to MPR could investigate response related factors affecting *a*. It may be that a further parameter needs to be added to the model to capture the differences observed in the hens' arousal when the operandum was changed. It is interesting to note that δ did not vary significantly with the change in either minimum force requirement or response topography. Further research in this area could alter the minimum response duration and minimum force requirement independent of each other and changes in response form. This could be done by requiring hens to peck and hold the key up for varying lengths of time, and adding weights to the key. More accurate measurement of response durations would also be a useful way of comparing the relative effect of time and force requirement on changes in δ. In conclusion, this experiment shows that further research in this area is required, as there was an unexpected effect of changing the effort required to perform a response, with the parameter meant to represent changes in task requirements not changing significantly, while the parameter representing changes in motivational aspects of the task did.

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Appendix A

Protocol No: 784

THE UNIVERSITY OF WAIKATO

APPLICATION TO THE ANIMAL ETHICS COMMITTEE
FOR APPROVAL OF EXPERIMENTS ON ANIMALS

ANIMAL SPECIES: Hens (Use common name) **NUMBER OF ANIMALS: 6**

STARTING DATE: 22 March 2010 **COMPLETION DATE: 21 March 2011**

1. (a) **Name of applicant:** Rebecca Bjarnesen_

(b) **Position:** Masters student

(c) **Department:** Psychology
/Address for Mailing) 535 Hamurana Rd, RD7 Rotorua 3097

(d) **Contact Phone number & email address:** 0274973407; becs.bjarnesen@gmail.com

(e) **Qualifications and Experience:** BSc

(f) Have you previously carried out related experiments? No

Previous Protocol No(s) [No(s).] [Date]

Applicants should attach a short report on the results of the previous experiment(s)
Please find published abstracts attached.

(g) **Other Personnel involved** (including titles and roles)**:**
Lewis Bizo- primary supervisor; Mary Foster- secondary supervisor; Jenny Chandler- animal technician; Masters and Doctoral students- assistance in running experiments

2. **Title of Project:** The effect of effort: An analysis of the mathematical model of reinforcement

3. **Aim of Project** (written in terms that people with a non-scientific background will understand)**:**

To test the ability of Killeen's (1994) mathematical model of reinforcement to predict hens' performance when responding is reinforced according to ratio schedules of reinforcement and when force requirement to make a response is made harder or easier.

4. **Significance of this Project** (written in terms that people with a non-scientific background will understand)**:**

The significance of this project is that it will test how well a quantitative model of behavior predicts performance when the effort required to make a response is varied. The effect of response effort has not been studied extensively and to date only one study

Updated: December 2008

has explicitly tested the effect on response force on the rate of expression of a target response.

Specifically it is important to confirm that the parameters which the model asserts are related to motivational or structural aspects of the task vary in appropriate ways when motivational or structural aspects of the task are manipulated. In relation to the present experiment, there has only been one experiment to date that has explicitly investigated the effect of response requirement on predictions of the model. It is also important to assess the ability of this model to predict performance when response requirement is manipulated because it will help disambiguate the relative importance of motivational and structural components of a task which combine to determine the expression of behaviour.

5. **Is/Has this work already being/been carried out** (provide details)

(a) In New Zealand? No

(b) Overseas? No

6. **Have alternative methods to achieving the aims that do not involve the use of animals been explored?**
No
Please provide details.

This model describes and predicts the way animals behave when they experience different reinforcement conditions and varying task requirements. This means that the model may only be explored through the use of animals in the experiment.

7. **How will the results of this work be disseminated?**

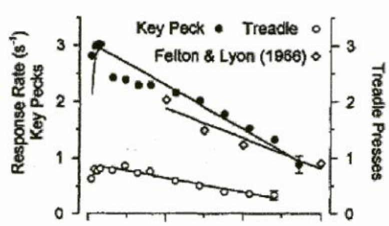
This project will form the basis of my MAppPsyc thesis, and the results of the experiments will possibly be submitted for publication in peer reviewed journals, as well as potentially be presented at either national or international conferences.

8. **Description of Experiments**

All experiments should take into account the statutory responsibility to adhere to the three important principles governing the use of animals in research, testing and teaching:

a) Refinement (refinement of procedures applied to decrease to the minimum practicable extent the negative impacts they have on the animals):
b) Reduction (reduction in the numbers of those sentient animals to the minimum necessary to achieve the scientific objective):
c) Replacement (replacement of animals with non-sentient animals or non-animal alternatives):

(a) Full details of procedures



Two main determinants of the rate at which an individual will work are the pay offs for that work and the amount of effort required to do that work. The rate of work will be higher when a task is easy and the payoff is large. Work and pay off can be studied in the laboratory

Updated: December [illegible]

with animals. Killeen's (1994) Mathematical Principles of Reinforcement is a quantitative model of behaviour that predicts that response rates will vary systematically when response requirement or pay off are manipulated. Figure 1 shows the response rate on either a treadle press or key pecking for pigeons across a range of FR values (Bizo & Killeen 1997). It can clearly be seen that as the ratio requirements increase, initially the response rate also increases, but then as the ratio requirement continues to increase, the response rate decreases. This is one of the predictions of the model. The significance of this project is that it will test the predictions of this model in relation to the effort involved in making a response and the effect of this on response rate.

Prior to the experiment, the hens will be trained to operate the lever press which will form the target response in two of the experimental conditions. They have already been trained to peck a key; the other target response. The reinforcer for the responses will be 2s timed access to wheat.

In order to ensure the hens value the reinforcer, and therefore perform the target behaviour, the hens will be maintained at 85% +/- 3% of their free feeding body weight. Their free feeding body weight will be determined by regular weighings over 2-3 weeks when the hens are allowed free access to food. If they fall below this range they will be temporarily removed from the experiment and provided with supplementary food until their weight returns to the acceptable range. If their weight exceeds the range, they will be removed from the experiment their daily feed regimen reduced until their weight returns to within the desired range. In order to facilitate the management of the hens' weight, they will be housed individually during the experiment. The hens will have free access to water in their home cages, and will be given supplementary feedings of vitamin enriched food, and health grit on a regular basis.

The response key will be a backlit round response key made of Perspex and approximately 3cm in diameter. The lever press consists of two vertical rods suspended from the ceiling of the experimental chamber. When the hen puts her head and neck through these bars, pushing them through an arc of 15 degrees, a response will be recorded. This action requires a minimum force of 2.3N, and weights may be added to increase the force requirement. Sumpter et al. (1999) added up to 750g. Both key pecking and lever pressing will be performed at two force requirements. The specific force requirements will be determined via piloting, but will not exceed force requirements previously reported by Sumpter et al.

Each of these four conditions (key peck low force; key peck high force; lever press low force; lever press high force) will be experienced by each of the hens each time they are exposed to a series of fixed ratio reinforcement schedules. The manner in which these fixed ratios are determined will differ across two different conditions.

The first method will involve exposing the hens to an ascending series of Fixed Ratio schedules that will be determined via piloting, but most likely the Fibonacci series; 1, 2, 3, 5, 8, 13, 21, 34, 55, 89, 144, 233, 377, & 600. All hens will experience the exact same sequenced of fixed ratios and each ratio value will be in effect for several sessions. The second method will involve tailoring the exact FR schedules experienced to each individual hen. This will be achieved by using a similar procedure to that used by Sanabria et al. (2008). There will be five different schedules, numbered N1-N5, with N1 the richest schedule and N5 the poorest. All hens will begin with the same initial FR ratios, which will then be altered according to the following formula to ensure that each hen responds across each of the ratio values. The formula is that used by Sanabria et al. (2008):

$$Nj = [c(j)7/3]$$

where Nj represents the ratio schedule, j represents the ordinal position of the component and c is a value determined by either increasing or decreasing an initial value of 0.4 depending on the nature of N. If N5 is larger than N1, or if N5 is greater than half the maximum response rate throughout the sessions; c will be increased by 0.4. If N5 is less than either of those requirements, c will be decreased by 0.4. Once c is stable (the range over the last five sessions is less than 3.2 and the increases and decreases are approximately equal). Each hen will have its own set of ratio values that will hopefully conform more closely to the bitonic pattern of responding than is typically seen when all animals in an experiment are required to respond n the same sequence of ratio values.

Across conditions behavior will be reinforced with timed access to wheat, and experimental sessions will be in effect for either 60 reinforcers or 50 minutes, whichever occurs first. The hens will be housed individually in cages for the duration of the experiment. After completion of the experiment the animals will be moved from the cages to the group aviaries where they will housed with other hens not currently engaged in experiments.

(b) The statistical design of the experiments

2 (operanda type) x 2(force requirement:high/low) x n (fixed ratio requirement) factorial design, which will be run as a repeated measures design. All hens will experience all conditions. Non-linear least squares regression will be used to fit the quantitative model to the response rate data. Parameter estimates derived from that regression analysis will be treated as higher order dependent variables and will be compared using repeated measures analysis of variance with appropriate post hoc tests.

9. List the relevant SOP's (number and full title) to be used: N/A

10. (a) Where experiments will be conducted: Psychology Animal Behaviour Laboratory, No 3 Dairy

(b) Where the animals will be housed: Individually in cages for the duration of the experiment________________

(c) Person in immediate charge of laboratory and housing: Jenny Chandler_

(d) Veterinary advisor to the laboratory: Gwen Verkirk/Danielle Sijbrant_

11. Is there an operational procedure required for the use of a product (drug/chemical) in these experiments? **No**

If so this will require an Institutional Drug Administration Order, this should be arranged with the Institutional Operating Plan Validator.

See Appendix 1: ***Is an Institutional Drug Administration Order Required?***

Name the product: _

____

12. (a) Anaesthetic:

Local:
___N/A

General:
_____N/A

(b) Method of Restraint:
____________N/A

Updated: December 2008

(c) **Will the animal have to recover from anaesthetic?**
N/A

(d) **How will you deal with post-operative pain and/or discomfort?**
N/A

13. **What is the fate of the animals at termination of experiment?** Retained in experimental colony, rehoused to barnyard flocks or, if ill, humanely euthanized.

14. **Has this application in whole or in part previously been declined approval by another Animal Ethics Committee?** **No**

15. **For experiments to be undertaken at Ruakura or at other facilities under the control of another Animal Ethics Committee, has an application also been made to that Committee:** **No**
If 'YES' state which Committee

16. **Is any of this work being used in a thesis to be submitted for a degree at The University of Waikato?** **Yes**

17. **Are any permits (e.g. DOC) or approvals (e.g. Iwi) required?** **No**

If 'YES':
Have the permits or approvals been obtained?

List details of permits/approvals required ____________________

18. **I have read and understand the conditions outlined in the Code of Ethical Conduct for the Use of Animals for Teaching and Research.** **Yes**
http://www.waikato.ac.nz/research/unilink/uow_only/Approved%20Code%202010%20-%202014.pdf

19. **I have read the Good Practice Guide for the use of Animals in Research, Testing and Teaching**
http://www.biosecurity.govt.nz/files/regs/animal-welfare/pubs/naeac/guide-for-animals-use.pdf Yes

20. **Further conditions:**
In the event of this application being approved, the undersigned agrees to inform the Ethics Committee of any change, subsequently proposed, which may affect animal welfare.

If any death or illness occurs in the animals which may in any way be construed to be part of the experimental condition this must be reported to the Ethics Committee.

Signed by the applicant: [signature] **Date:** 12/3/10

Signed by the Supervisor: [signature] 12/3/10 **Date:**

Updated: December 2008

Approved/~~NOT approved~~

Signed on behalf of the Committee: ....

(Chairperson)

Date: 19/3/10

Appendix B

Parameter estimates Equation 2 for all hens working on the door with and without added weight

	Hen	**91**			**92**			**93**			**94**			**95**			**96**		
	Series	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**
Door (F=0.52N)	**a**	302.7	599.9	1198.3	61.1	114.2	104.3	122.1	128.4	254.4	54.1	116.1	58.7	256.2	274.1	337.6	26.6	17.2	15.2
	λ	0.1	0.2	1.6	0.7	0.1	1.1	0.2	0.0	0.1	0.0	0.0	0.1	0.0	1.1	0.1	0.5	0.5	0.0
	δ	3.5	3.0	3.8	2.8	3.7	3.9	2.9	2.1	2.8	4.3	7.8	6.6	3.4	3.7	4.2	9.2	49.6	15.6
	ε	1.0	1.0	1.0	0.0	1.0	0.1	1.0	1.0	1.0	0.0	0.0	0.0	0.6	0.0	1.0	0.5	0.5	1.0
	R^2	0.6	0.8	0.3	0.9	0.8	0.5	1.0	0.8	0.7	0.6	0.6	0.5	0.7	0.6	0.7	0.3	0.5	0.8
	SE of Mean	0.2	0.2	0.2	0.3	0.1	0.2	0.4	0.2	0.2	0.2	0.1	0.3	1399.4	373.3	405.3	0.2		
Door Weight (F=2.12N)	**a**	53.3	226.7	108.0	14.6	14.4	15.2	136.5	251.0	116.6	31.1	53.0	29.4	85.0	59.7	29.0			
	λ	0.5	0.0	0.2	0.3	0.0	0.1	0.0	0.1	0.1	0.0	0.1	0.0	0.0	0.8	0.7			
	δ	2.3	3.4	3.3	2.5	3.3	4.1	3.2	3.5	2.9	3.5	2.5	11.0	14.0	5.3	6.4			
	ε	0.0	0.9	1.0	1.0	0.0	1.0	1.0	1.0	1.0	0.0	1.0	1.0	1.0	0.3	1.0			
	R^2	0.6	0.7	0.7	0.8	0.8	0.9	0.8	0.6	0.7	0.6	0.6	0.7	0.7	0.7	0.5			
	SE of Mean	0.4	0.1	0.2				0.2	0.1	0.2	0.3	0.3	0.1	0.1	0.2	0.2			