Assessing the food preference of the brushtail possum (*Trichosurus vulpecular*) using fixed-ratio schedules

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Abstract

The quality of different foods has been found in previous studies to effect an animal's performance on fixed-ratio schedules. Foods that are of a higher quality should maintain behaviour to larger fixed-ratio values than foods of a lower quality. The present study examined the performance maintained by increasing fixed-ratio schedules by four different foods (Rolled Oats, Cocoa Puffs™ and flaked barley, All Bran™ and Soy Protein) with six brushtail possum (*Trischosurus vulpecula*). Overall response rates and running response rates both generally showed a bitonic function, and post-reinforcement pauses showed a modest increase with increases in the fixed-ratio. The equations of two quantitative models; Behavioural economics and mathematical principles of reinforcement (MPR) were fitted to the data to see how different food types affected the two models ability to predict behaviour. This was measured through two parameter estimates, alpha (α) and specific activation (α_S). Both demand equations and the MPR equation described the data fairly well. The parameter estimates for specific activation (α_S) showed a significant difference in value across the foods, but there was no significant difference across foods for parameter estimates of alpha (α). There was a weak correlation between parameter estimates of α and α_S ($r = -0.245$, $p = 0.0926$) . The four foods used in this study were also tested in a paired-stimulus preference assessment. The foods that were assessed as being of more value in the behavioural economic equations and the MPR model, for some possums were identified as being more preferred, but this was not consistent for all possums.

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Introduction

A common means of measuring an animal's demand for a commodity is to examine its performance when responding to gain that commodity under increasing fixed-ratio (FR) schedules (Hursh, 1984). Through this method, behaviour can be observed to see what degree it is maintained as ratio values increase. There are several ways of analysing behaviour on these FR schedules, two are based in behaviour economics (Hursh, Raslear, Shurtleff, Bauman, & Simmons, 1988; Hursh & Silberberg, 2008) and one other is known as the mathematical principles of reinforcement (MPR; Killeen, 1994). Although behavioural economics and MPR are formally separate, they can be used to analyse the same data sets and can therefore be compared to see how well each describes and predicts behaviour. One factor which should affect the performance and so change the parameter values for both of the behavioural economic models and MPR is the quality of the food used during experimental sessions. If the quality of the food is varied then food that is more preferred may provide different results from a food that is less preferred, and, of interest here, is how the models deal with the effect of such preference. In order to assess the preference for different food types a preference assessment can be used to establish a preference hierarchy for the foods.

Behavioural Economics

Hursh (1980) proposed a method to analyse behaviour on FR schedules of reinforcement through economically derived concepts. In this instance the subject is substituted as the consumer, the amount of work or effort required becomes the price, and the reinforcer becomes the commodity (Lea, 1978). When manipulating variables such as price (response required) and the commodity (type of reinforcer), changes in behaviour, e.g., number of responses made, can be observed. How performance changes gives a measure of the demand for the commodity. The term demand refers to the relationship between the change in price of a commodity, and the consumption of that commodity (Hursh, 1980). When investigating demand, FR schedules are frequently used because the price of the commodity can be clearly measured as the number of responses required in order to gain access to the commodity (Hursh, 1984).

One way of manipulating demand for a commodity is by altering the economic system in which it is available. The experimental economies might be either closed or open and this has effects on behaviour (Hursh, 1980). In a closed economy, daily consumption of a commodity is only granted based on the organism's fulfilment of the experimental conditions. As the price of the commodity increases, we would expect the rate of response to increase. In this type of economy there is no other supply of the commodity than through fulfilling the schedule requirements. In contrast, an open economy results in the subject having access to the commodity after the experimental session, as well as throughout the session, based on completion of the required tasks. In an open economy a subject's total daily food consumption is partially controlled by the experimenter (Hursh, 1980). An example of this is maintaining a subject's body weight at 80% of its free feeding weight. If food consumption throughout an experimental session does not produce enough to maintain the target weight of 80%, additional food would be provided after the experimental session. Hursh (1980) argued that when exposed to a closed economy, a subject's rate of consumption stayed steady as the response rate increased with the increase of price for the commodity. This is also known as an inelastic demand function. Alternatively, an open economy would produce an elastic demand function if the rate of consumption decreased as the price of a commodity increased (Hursh, 1980).

The slope of the demand curve can be measured to identify the degree of elasticity (Hursh, 1980; 1984). An inelastic demand curve has a slope shallower than negative 1, whereas an elastic demand curve has a slope steeper than negative 1. The elasticity of demand curve does not have to remain fixed with a set price of a commodity. It can shift from inelastic to elastic with an increase in price. The slope of the demand curve can also be measured in order to explain the value of different commodities. A shallow declining demand curve suggests that as the price of a commodity increases, so too does the response rate or effort required to obtain the commodity, suggesting it is regarded as a highly valued commodity. A steeply declining demand curve suggests that as the price of a commodity increases, response rate decreases, as the commodity is not worth the increased effort to obtain access.

The relationship between the schedule and the consumption, gives the demand function. What this function generally shows is that as the price (FR schedule) increases, the consumption of the commodity decreases. Hursh et al. (1988) described the demand functions through the following equation

$$1\text{n}\ (Q) = 1\text{n}\ (L) + b\ (1\text{n}\ (P) - aP \qquad (1)$$

In Equation 1, Q represents consumption, P represents the price, and L, b and a are fitted parameters. Each parameter reflects the following in the demand function: L shows the initial demand or estimates the level of consumption at the minimal unit price such as FR 1, b is the initial slope of the demand function, and a shows the adjustment in the slope as the price increases. Elasticity of the function is measured through the parameters a and b. The term used to describe the price of which maximal output is obtained is P_{max} (Equation 2) which describes the price at which the demand function goes from being inelastic to elastic. Hursh and Winger (1995) gave the following equation for P_{max} which utilises the parameters a and b found in Hursh et al. (1988) (Equation 1).

$$P_{max} = (1 + b) / a \qquad (2)$$

P_{max} is used to reflect the value of a commodity as the higher the P_{max}, the higher the price at which the demand shifts from inelastic to elastic. The more inelastic the demand is, greater expenditure is required as price increases to obtain the stimulus. Therefore, greater the P_{max} shows the organism will work to higher prices to maintain its access to the stimulus.

The function provided in the equation (Equation 1) from Hursh et al. (1998) has been reported to describe the consumption data well. Cronin (2012) applied the function from Equation 1 to the consumption data provided from five possums who were responding under progressive-ratio (PR) and FR schedules of reinforcement. Cronin's (2012) finding suggested that when under a single schedule, the function from Equation 1 showed good variance accounted for. His findings were consistent with what other research has found (e.g., Armistead, 2009; Foster, Blackman, & Temple, 1997). These data, along with those from many other studies, show Equation 1 is suitable for use to describe performance under FR schedules.

Although P_{max} is successful in summarising all the information provided by the demand function, this analysis alone cannot measure the demand, this also requires the values of parameters a and b from Equation 1 that reflect elasticity.

No single parameter reflects the “value” of a reinforcer. As a result, Hursh and Silberberg (2008) proposed a function which might give a single measure of “value” from the demand function. This measure is determined through using the single parameter, Alpha (α), in the following Equation.

$$1n\ Q = 1n\ Q_0 + k\ (\ e^{-\alpha p} - 1\ ) \qquad (3)$$

P and Q are represented the same as in Equation 1, whereas Q_0 is similar to the L parameter in Equation 1 as it estimates the highest level of consumption at minimal price. The value k specifies the range of consumption over price, and the rate constant, α, determines the change in consumption with an increase in price. Hursh and Silberberg (2008) refer to α as a measure of the ‘essential value’ of a commodity, as the value of α reflects the rate of change in elasticity. If the range of data, k, is set to the same value across comparisons then α can be used to compare the changes in elasticity from different demand functions. Another characteristic of α in this equation is that the scalar properties of a commodity or reinforcer such as quantity or magnitude should have no effect on this parameter. The greater the value of α, the more elastic the function becomes, resulting in a steeper demand curve and a smaller essential value of that reinforcer. Equation 3, then, determines the essential value of a reinforcer using one single parameter, α, to measure the elasticity of demand. Hursh and Silberberg (2008) have concluded that this is superior to the analysis of Hursh et al. (1988) to determine elasticity.

It is important to acknowledge however, that there is another value which arguably could too reflect the aspect of the “value” of a commodity. The value of P_{max} measures the shift in demand from -1.0 to 1.0, and so provides the value at which maximal responding occurs on a demand curve. However, P_{max} will change with the scalar value of a commodity. Therefore, of interest is comparing the values of α and P_{max} over a range of commodities of different values to see how both change.

Hursh, Madden, Spiga, DeLeon, and Francisco (2013) have described how α and P_{max} can be used to compare the value of different reinforcers. By summarising the results provided by Hursh and Winger’s (1995) study with monkeys and self-administered drug reinforcement, Hursh et al. (2013) applied the function from Equation 3 to the data of two different drug reinforcers (alfentanil and methohexital), with three different orders of magnitude. Because α is not affected by scalar properties such as magnitude, the α value given at each dose of the drug remained constant, and therefore a direct comparison between the essential value (α) of the two drugs could be made. Their results showed that despite providing a much higher dosage then that of alfentanil, methohexital showed much lower values of essential value (α), and this was also reflected in smaller P_{max} values as compared to alfentanil. Therefore Hursh et al. (2013) demonstrated the close relationship between α and P_{max}.

As previously mentioned, Hursh and Silberberg (2008) refer to parameter α as a measure of the essential value of a commodity. One study which has looked to capture α in this capacity is research by Foster, Sumpter, Temple, Flevill, and Poling, (2009), where the value of α was compared across three different food types (wheat, puffed wheat and honey puffed wheat with hens). They found, when applying Hursh and Silberbergs (2008) equation (Equation 3), that the less preferred food (puffed wheat, determined previously through a preference assessment) showed smaller values of α (greater essential value) and higher values of P_{max} compared to that of wheat and honey puffed wheat which seemed contrary to what might be expected for a preferred food.

Other research has looked at the effect varying reinforcer magnitudes has on the demand of different commodities (Grant et al., 2014). Similar to the procedures established by Foster et al. (2009), preference measures were determined for different durations of reinforcer access. Preference was greater the longer the duration of access to food. The demand for each duration was then examined using FR schedules. Hursh and Silberberg's (2008) equation was applied to demand data, which showed the value of α decreased as the duration to food increased. This suggests that a scalar property such as magnitude was having an effect on the essential value, but, that similar to Foster et al. (2009) the greater the preference for a food the less the essential value. Of interest to this study is therefore gathering more data on how α changes with different qualities of food and whether the value of α changes across different food types.

MPR

An alternative method that is used to analyse behaviour on FR schedules is Killeen's (1994) MPR, which is a quantitative account of behaviour on schedules of reinforcement and it assumes that three key constructs control behaviour: arousal, constraints on behaviour and coupling of behaviours to consequences. The first construct, arousal, refers to the behaviours that are emitted in the presence of a reinforcer. The second construct, constraints, refers to the specific limits that are placed on responding such as the time it takes to respond, and the third construct, coupling, refers to the association between a reinforcer and response class. All three constructs represent three parameters that play a fundamental role in the MPR theory.

The state of excitement, known as *arousal*, is gathered and combined through increases in the frequency of reinforcement. The state of arousal is brought on through periodic feeding (Killeen, 1975). The parameter that is used to define this sense of arousal is *specific activation* (α) (Killeen, 1994). As the symbol (α) has already been used in the Hursh et al. (1988) nonlinear demand equation, specific activation known as (α) will be represented as (α_s) in this report (Stuart, 2013). Specific activation measures motivational levels when a reinforcer is introduced. Motivation is measured through the rate of response as this is assumed to be proportional to the level of arousal (e.g., Killeen, 1975). When exposed to repeated incentives, parameter therefore "becomes the integral of the exponential decay curve of responses per reinforcer" (Killeen & Sitomer, 2003, p. 53). This in turn measures the value of an reinforcer through measuring the number of seconds of responding that is evoked when introduced to the incentive.

The second construct, *constraint*, refers to the factors that explain why response rates may fall shorter than the theoretical asymptote (Killeen & Sitomer, 2003). Although one particular response pattern is required to receive a reinforcer, this does not eliminate competition from other available response classes. Another factor is the time it takes to make a response. Killeen and Sitomer (2003) suggest that the responses may be elicited at a faster rate to which they can be emitted, therefore potentially causing response rates to fall shorter than the theoretical curve. Both of these factors can influence the time it takes to emit a response. The minimum inter-response time (IRT) that is possible for an organism to produce is captured in the model as delta (δ) (Killeen & Sitomer, 2003).

The third construct, *coupling*, refers to the association that is formed between a reinforcer and a response class. It assumes that all responses leading up to the target response are reinforced to some extent by the reinforcer that follows the last response of the schedule requirement. This type of response pattern can be demonstrated through a FR schedule of reinforcement. In order to receive reinforcement, a target response must be emitted. As the FR requirement increases, more responses are required for the delivery of a reinforcer, therefore resulting in an increase in response rate because the target response occupies the animal’s memory for what caused the reinforcer delivery. When the FR requirement is small, other activity such as eating, cleaning and exploring the chamber weaken the association between the target response and reinforcer, and thus results in lower response rates at smaller FR values. Therefore, as FR schedule requirements increase, MPR predicts that responding will be described by an inverted U (Killeen, 1994). The downward part of the inverted U represents responding that is only governed by arousal, this happens when the accumulated responses in the memory have saturated (Killeen, 1994). In MPR, the parameter β represents coupling, and lambda (λ) represents the rate at which response traces fade. When schedules of reinforcement are used, the coupling coefficient (*c.*) describes the amount of association between reinforcement and the response operant class. If the same target response is required in a FR schedule, each response that receives a reinforcer strengthens the next response. As FR requirements increase, the response class is too strengthened. The following equation refers to the coupling coefficient.

$$b = \mathrm{c.}/\delta - \mathrm{n}/\delta a \text{ where } \alpha > 0,\ \beta > 0, \text{ and } \delta > 0 \qquad (4)$$

In this equation c. is the coupling coefficient for the ratio schedule in force, *b* refers to response rate, n represents the FR value, the parameter that represents the IRT is δ, and the number of target responses that can be maintained by a reinforcer is represented through the parameter α_s (Killeen & Sitomer, 2003).

Another useful equation within MPR includes the additional parameter epsilon (ε), which has been added to the equation to assess to what degree target responding is erased between responding (Killeen & Sitomer, 2003). This equation is as follows:

$$C_{FRn} = 1 - \varepsilon\, e^{-\lambda\delta \mathrm{N}} \qquad (5)$$

The values of ε range between 0 and 1, with absolute recall represented by 0, and complete erasure represented by 1. This effect was researched by Killeen and Smith (1984) who found that consumption and post-reinforcement pauses affected the memory of pigeons when trying to recall pervious target responses.

Therefore, in Equation 5, parameter ε refers to the incomplete erasure of short term memory to the target response.

MPR has been used to describe performance on schedules of reinforcement. Bizo and Killeen (1997) assessed pigeons on FR and variable (VR) schedules using different types of food. There results showed that when the quality and quantity of a reinforcer is increased, there is an increase in the overall rate in responding and an increase in the break points. The MPR model was able to capture this well with the parameter α_s. It was reported that a larger and more preferred food (popcorn) yielded higher estimates of α_s, as compared to smaller and less preferred food (millet). Furthermore, Bizo and Killeen's (1997) findings suggest that reinforcer effectiveness may be measured through specific activation values, however, reinforcer effectiveness is sensitive to the quality of the reinforcer and the level of manipulation.

Previous research has also investigated the ability of MPR to predict response rates when the force required and topography of the response changes (Bjarnesen, 2011). Six hens responded under four conditions (low force key, low force door, high force key, high force door) in a geometrically ascending series of FR values. Results found that the hens responded to a faster rate and worked at larger FR values when responding on the key, rather than the door. Although MPR predictions failed to capture the change in response requirement through the parameter δ, the model did capture differences in α_s, suggesting changes in motivation to perform the responses required for each of the conditions.

MPR has also been used to predict and describe behaviour with behavioural pharmacology. Reilly (2003) investigated the effects different levels of D-amphetamine had on the operant behaviour of rats across a five-component multiple FR schedule. When the MPR estimates were applied to the data, it was reported that higher doses of D-amphetamine decreased the value of food and this was captured through the lower estimates of α_s.

The predictions of MPR have been applied in a variety of different areas with different species, however, of interest to this study is to collect further data to see how α_s changes with different qualities of food, and whether α_s changes across different food types with possums.

Comparing Behavioural Economics Models and MPR

Research by Stuart (2013) compared the behavioural economic models and the MPR model when applying them to response under FR schedules by using hens when delay to the reinforcer was varied. Both models should be able to account for the value of a reinforcer and increasing the delay to the reinforcer is known to make reinforcers less effective and therefore of lesser value. The values from the parameter alpha (α) (Hursh & Silberberg, 2008), and specific activation (α_s) (MPR), can be compared to see if there is a relationship. Stuart's (2013) findings suggested that for two of the conditions (16-s ITI and 16-s delay) there was a moderately strong positive relationship between the parameter values alpha (α) and specific activation (α_s), and therefore showed that there was minimal differences between the two parameters for the longer delays before receiving a reinforcer. However, when looking at the correlations between the 4-s conditions (4-s ITI and 4-s delay) there was more variability between parameter values, suggesting that ITI and delay may have had a larger impact at shorter durations.

Although Stuart's (2013) findings have suggested that there was similarities in how the parameter values (α) and (α_s) describe the data at longer durations (16-s ITI and 16-s delay), there was still inconsistencies for the shorter durations (4-s ITI and 4-s delay). Therefore, it is of interest to see how the two parameter values (α and α_s) can interpret different foods of varying quality and to see how these results compare to a preference assessment. It is also of interest to see whether the same foods that are identified as showing smaller values for (α) and larger values for (α_s), also show higher preference rankings when identified through a preference assessment.

Preference

Of interest here is how the analysis proposed in the behavioural economics and that of the MPR models, are affected by different quality foods. Another measure that compares food of a different quality can be found by a preference assessment. This would allow the question of how preference for different food affects the predictions of both types of models. There are many different ways of administering a preference assessment which include indirect measures, and direct measures such as engagement based and approach based measures of assessment.

Indirect Measures

Assessments of preference can provide the opportunity for communication through means other than verbal commands, making it appropriate for both human and animal populations where language is non-existent or is limited. If communication becomes a barrier, there are indirect ways of preforming preference assessments that do not directly involve the subject. Indirect measures can be demonstrated largely with human populations as preference assessments that are based on the opinions of family or caregivers of the client (Hagopian et al., 2004). An indirect assessment can be carried out through surveys, interviews or checklists (Hagopian et al., 2004; Matson et al., 1999). Although not as common, indirect measures have also been used with animal populations. Research by Chen, Hung and Peng (2012) investigated pet owner's preferences of pet services, and similar research investigated the preference of pet owners of overweight dogs when buying commercial dog food (Suarez et al., 2012). The human literature surrounding indirect measures of preference assessment have found many limitations with this form of preference assessment. Therefore, it has been argued that caregiver or staff opinions should not be used exclusively when assessing preference for another and other measures of preference assessment such as approach based measures should be used in conjunction with indirect measures of preference (Green et al., 1988; Reid, DiCarlo, Schepis, Hawkins, & Stricklin, 2003).

Engagement Based Measures

Preference can also be assessed through engagement based measures of assessment where the emphasis is on the amount of time an organism spends with a stimulus. Through this type of assessment you would expect an organism to spend more time or attention towards a preferred stimulus than they would towards a less preferred stimulus (DeLeon, Iwata, Conners, & Wallace, 1999; Roane, Vollmer, Ringdahl, & Marcus, 1998). Free access experiments have also been widely used with animal populations. Research by Jensen, Studnitz, Halekoh, Pedersen, and Jørgensen (2008) used free access procedures in order to investigate pig's preference for rooting materials. Similar research has been produced by Blom, Baumans, Van Vorstenbosch, Van Zutphen, and Beynen (1993) and Blom,Van Tintelen, Baumans, Van Den Broek, and Beynen (1995) where free access procedures where used to determine rats preferences for flooring materials and cage heights. A limitation that has been identified when implementing free access procedures is that when multiple stimuli are made available, it does not adequately measure the different levels of preference towards all available stimuli (Sumpter, Foster, & Temple, 2002). In particular, if the available stimuli require different responses, using a free access procedure may be inadequate. Therefore, Sumpter et al. (2002) have highlighted that when an organism does not choose a particular stimulus, it does not necessarily mean that it is less preferred.

Approach Based Measures

Identifying human and animal preference for food, toys and activities has been done through direct observation in what have been called approach based measures of preference (e.g., Hagopian et al., 2004). When observing this type of preference assessment used with humans, communicating what is preferred does not necessarily take place through verbal commands. Using body language such as hand signals can help relay preference for commodities. Observing and understanding the preference of an animal is not as simple. To determine what an animal prefers requires more thought around observing the behaviour of the animal. The alternative method of measuring how hard an animal will work for something has become the most common means of assessing an animal's preference (Broom, 1991; Dawkins, 2006; Patterson-Kane, Pittman, & Pajor, 2008). This is implemented through reinforcing behaviour on schedules of reinforcement for an object using FR schedules, PR schedules, or concurrent ratio schedules (Glover, Roane, Kadey, & Grow, 2008). Stimuli can be presented as either an single stimulus (SS) in which the approach or non-approach towards a stimuli is measured (DeLeon & Iwata, 1996; Pace, Ivancic, Edwards, Iwata, & Page, 1985), a paired-stimulus (PS) which assess the simultaneous presentation of two stimuli, with access given to the stimuli that is approached first (e.g., Fisher et al., 1992), a multiple stimulus with replacement (MSW) which consists of multiple stimuli being presented at the same time and the first stimulus to be chosen is considered to be preferred (Windsor, Piché, & Locke, 1994), or lastly through multiple stimulus without replacement (MSWO) (DeLeon & Iwata, 1996). A MSWO procedure consists of multiple stimuli being presented simultaneously, however, once a stimulus is chosen, it is removed from the array of stimuli for the next presentation. Therefore producing a hierarchy of preference amongst the available remaining stimuli.

Given all the preference measures that have been mentioned above, when working with animals, a common means of testing preference is done through a

PS assessment (Cameron, Bizo & Starkey, 2013; Cronin, 2012; Fernandez, Dorey, & Rosales-Ruiz, 2004; Hudson, Foster & Temple, 1999; Martin, 2002). Through this method two foods are simultaneously presented for a given time frame, and the food that is selected first is recorded (Fisher et al., 1992; Pace et al., 1985). A PS assessment can be used to provide the relative preference for one food over another as the foods can be ranked in a hierarchical order of preference (e.g., DeLeon & Iwata, 1996; Pace et al., 1985). This method has been reported to identify preference more accurately than a single stimulus method (e.g., Fisher et al., 1992) and is quicker to administer than the MSW or MSWO methods (e.g., DeLeon & Iwata, 1996), therefore a PS method of preference assessment was used in the following study.

This Study

The aim of this study was twofold. Firstly, this study sought to assess what degree different foods (Rolled Oats, Cocoa Puffs™ and flaked barley, All Bran™ and Soy Protein) affected responding of possums on ratio schedules and to compare the predictions of two quantitative models. Behavioural economics and the MPR model informally come together as they utilise the same data sets, and they are both describing performance on ratio schedules. In which case are there similarities in what they are saying, e.g., parameter α and α_s, as one would assume for foods where the demand is less elastic (e.g., lower estimates of α and higher estimates of α_s) arguably it is a better quality food. It is hypothesised that different foods will result in different parameter values, and that if the foods are of a different quality, this should be demonstrated through different values of P_{max}. Secondly, to implement a PS preference test with the same foods to ascertain the relationship between preference and demand.

Method

Subjects

Six common brushtail possums (*Trichosurus vulpecular*) served as subjects, with five of them being female (Booboo, Caper, Screech, Monkey, Charlotte) and 1 male (Peppi). At the start of the experiment the possums were at the approximate ages; Booboo was 6 years, Caper 8 years, Peppi 7 years, Screech 9 years, Monkey 3 years and Charlotte 10 years.

All of the possums had participated in at least one previous experiment, and all, except for Booboo, had been trained to press a lever for food. Previous experiments included time perception (Caper, Peppi and Screech), food/taste preference (Peppi, Screech and Boo Boo), weight management (Charlotte), fixed interval timing (Caper, Peppi, Screech, Monkey and Charlotte), determining an audiogram (Caper and Peppi), and possum memory (Screech and Charlotte).

All possums were housed individually in cages that also functioned as their experimental chambers. The rooms in which the possums were housed were maintained on a reverse day/night light cycle. The lights turned on from 9:00pm and turned off at 9:00am. During the light cycle the room was illuminated by two 100 watt white light bulbs and during the night cycle the room was illuminated by three 60 watt red lamps.

The possums' diet consisted of the food they received during the experiment, plus a supplementary ration of green dock leaves, apple or carrot and pellets (Dunstan Manufacturing Ltd) that were fed to them after experimental sessions had finished for that day. The possums were weighed weekly to ensure that their body weight was within a healthy weight range, and their supplementary feed was adjusted accordingly to help maintain their target weight.

One of the possums 'Screech' didn't maintain her target weight on that diet and consequently was fed additional food to try and increase her weight. The additional food included avocado, banana, and a variety of plants that were easily sourced from the surrounding farm. These included maple leaf, white and red clover flowers, dandelions and sow thistle.

Apparatus

There were two types of food preference apparatus used in the experiments, one for the FR food preference experiment and another for the PS assessment. The FR apparatus consisted of a laboratory built food dispenser that delivered a single food type. The food dispenser was attached to the outside of the cages allowing for restricted access to the food on a timed basis. The lever was a micro switch, Honeywell BZ-2rW863/A2 with a 15-mm wide ‘activator’ made of steel and was located at the top of the response panel. Immediately above the lever was a yellow LED light that indicated whether the experiment was in effect.

The apparatus used for the PS experiment was primarily made of plywood and attached to the bottom of the possum’s home cage. At the bottom of the apparatus there was an opening that created access to a steel grate that contained four 75-mm by 75-mm square openings. These openings allowed for food to be manually presented through 55-mm high aluminium tins with a diameter of 75-mm. The purpose of the grate was to prevent the possums from choosing two foods simultaneously. Food was inaccessible between preference trials and as this was a PS assessment, only two types of food were ever available at one time, and therefore only two of the square openings were used. A Perspex panel was placed above the grate and between the experimenter and the possum, in order for the experimenter to identify the food choice made by the possum.

Each home cage was approximately 850-mm high, 510-mm wide and 500-mm deep. A nesting box was accessible through a hole at the top of the cage, and each cage had a shelf that sat approximately 550-mm from the bottom of the cage and went across the width of the cage.

The foods used in both experiments included Rolled Oats, Cocoa Puffs™ /flaked barley mixture (a ratio of one part Cocoa Puffs™ to 15 parts hulled flaked barley, as measured by volume), All Bran™ (Bran) and Soy Protein (a form of textured vegetable protein). For the FR experiment only one food type was made available at any time, however, the PS assessment had two concurrent foods available at one time.

Two different computer software systems were used for each experiment. The FR experiment used a computer system operating MED IV™ software and interface that was located in the adjacent room to the experimental chambers. The software recorded all data and controlled experimental events. The PS assessment used a computer programme written in Object Pascal which was used to assist in the timing intervals for the assessment. This was solely for the benefit of the experimenter as the programme displayed two buttons on the computer screen which corresponded to the position of the foods presented to the possum on either the left or right side. When a food choice had been made, the corresponding button could be clicked with the mouse, and the programme would then go on to time the access to reinforcement, and the inter-trial interval (ITI). Once the programme had timed the ITI, both buttons were accessible on the computer screen and the next trial could begin.

Procedure

Fixed-Ratio Assessment

Lever-press training: Booboo was the only possum that required training to press a lever. Booboo was trained across a period of a week to press the lever without any prompting from the experimenter. After the possum pressed the lever reliably on three consecutive days she was exposed to the training condition on the set FR.

Initial exposure to foods: Prior to the first experimental session for each food type the test foods were placed in the food hopper for a minimum of four days and were kept on a FR 20. This allowed for the possums to have prior exposure to each food condition.

Experimental conditions: All experimental conditions began between 9:00am and 11.30am. Each session took approximately 40 minutes to run. Before each session started, the MED™ software was tested in conjunction with the equipment to ensure that all aspects of the food dispensers and equipment were working. The levers were inserted into the holes, allowing access for the possums, and were also manually pressed by the experimental runner to check everything was working accordingly. All possums were inspected to ensure that they were down from their nesting boxes above their cage. When the yellow LED light above the lever turned on it signalled the beginning of the session.

The schedules used for all six possums were the same, and were controlled by MED™ computer programme. The first session on a new food type always started on a FR 1 and the increases in the FR requirement followed a geometric progression, doubling each session. This progression continued up until each possum received no reinforcement on an FR for two days, after which the FR was changed to FR 20 until the next condition started. At the end of each session, the data was recorded on a computer and manually written in a data book. The data collected included the FR value, total responses made, total reinforcers gained, total eat time, total post reinforcement pause, total key time, and total run time. The order of conditions for all six possums were Rolled Oats, Cocoa Puffs™ and flaked barley, All Bran™ and Soy Protein.

Two of the possums, Peppi and Screech, suffered from re-occurring medical conditions such as gas in the intestines and loss of appetite, which required veterinarian intervention. In order to allow for the possum's health to recover, or to reinstate responding, on multiple occasions both possums were given breaks in between experiment sessions where they would not run at all, or the occasional session at FR 1 in order to encourage responding on lever pressing.

Paired-Stimulus Assessment

The four food types were presented across all possible pairings for a total of 12 different food pair trials. This procedure was then repeated a total of five times resulting in a subsequent 60 trial session. The food tins were each filled with a different food type and were filled to half volume. The mass of each food type was weighed before the experimental session began, and again afterwards to determine overall consumption.

The PS assessment was administered to one possum at a time. The possum was presented with two tins that were placed in the middle of the apparatus (middle left and middle right). The possum had 30-s to choose a food, and the food selected was then recorded. This was followed by allowing 5-s access to consume the food, or until the possum raised its head past the grate. After a 30-s ITI, a new pair from the four food choices was presented. If no choice was made in 30-s, the trial ended and was recorded as ‘no choice’. After another 30-s ITI a new trial began, however, if two consecutive trials resulted in ‘no choice’, the experimental session was terminated. If the possum continued to make a choice throughout each presented trial, the session would then continue until all possible food combinations had been presented up to 60 trials. If at any time throughout the session the possum moved from the bottom of their cage to their nest box, the experiment was paused until the possum was back down on the bottom of their cage and facing the PS apparatus.

Results

This experiment had six possums performing on FR schedules across four different conditions where the food delivered as a reinforcer was either; Rolled Oats, Cocoa Puffs™ and flaked barley, All Bran™ or Soy Protein. The possums responding was reinforced as per the fulfilment of a geometrically ascending series of FR values, from FR 1 to FR 2048. Each condition was repeated at least twice across two separate runs. The data from four series (overall response rate, running response rate, post reinforcement pause and consumption) were compared across food types as two separate runs, and then again presented as the average of both runs for each food type for each possum.

Overall Response Rate

Mean overall response rates were calculated by dividing the total number of responses at each FR value by the key time and these were presented for each possum, for both series of runs across each food. Across all six possums, responding generally increased up to a maximum of about FR 32 or FR 64 and then decreased at larger FR values (See Figures 1- 4). Although some possums showed variability across the two runs performed for each food, the majority of the possums showed consistency in the overall response rate across both series of runs. Given the similarity of the two runs for the overall response rate, the data were averaged for each food and these are presented in Figure 5. Generally, across five of the possums overall responding was lower for the Cocoa Puffs™ and flaked barley condition, however, for Screech the overall response rate was lower for the All Bran™ condition. For the possum Booboo, the total response rate peaked at higher FR values in the Soy Protein condition, whereas possums Caper and Screech showed similar behaviour for the Cocoa Puffs™ and flaked barley condition. This was again similar for the possum Peppi who showed peak responding at higher FR values for the Rolled Oats condition. For possums Monkey and Charlotte peak responding showed at lower FR values for the All bran™ and Soy Protein conditions.

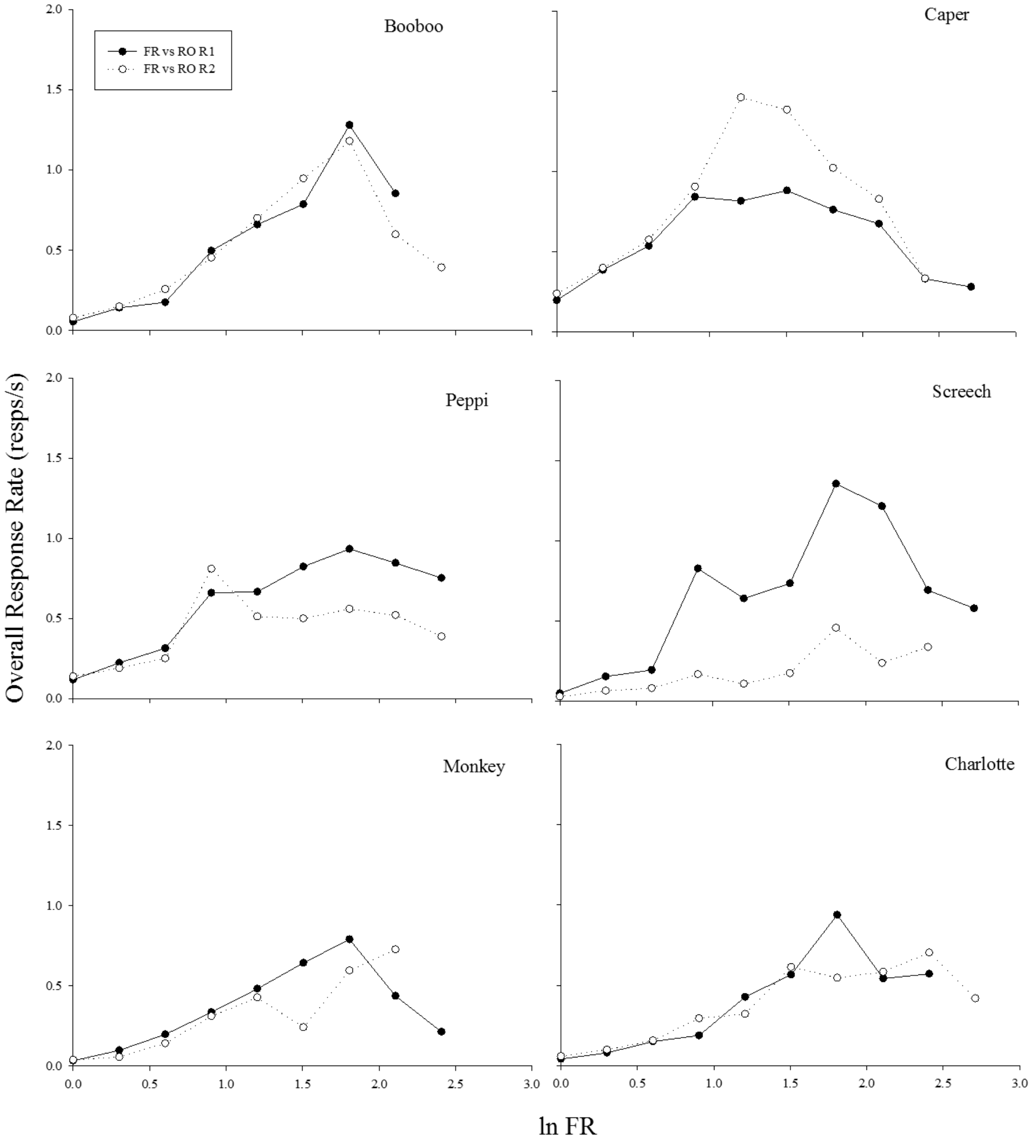

Figure 1. The overall response rates (resps/s), plotted as a function of ln FR values for both series of runs for the Rolled Oats condition for individual possums.

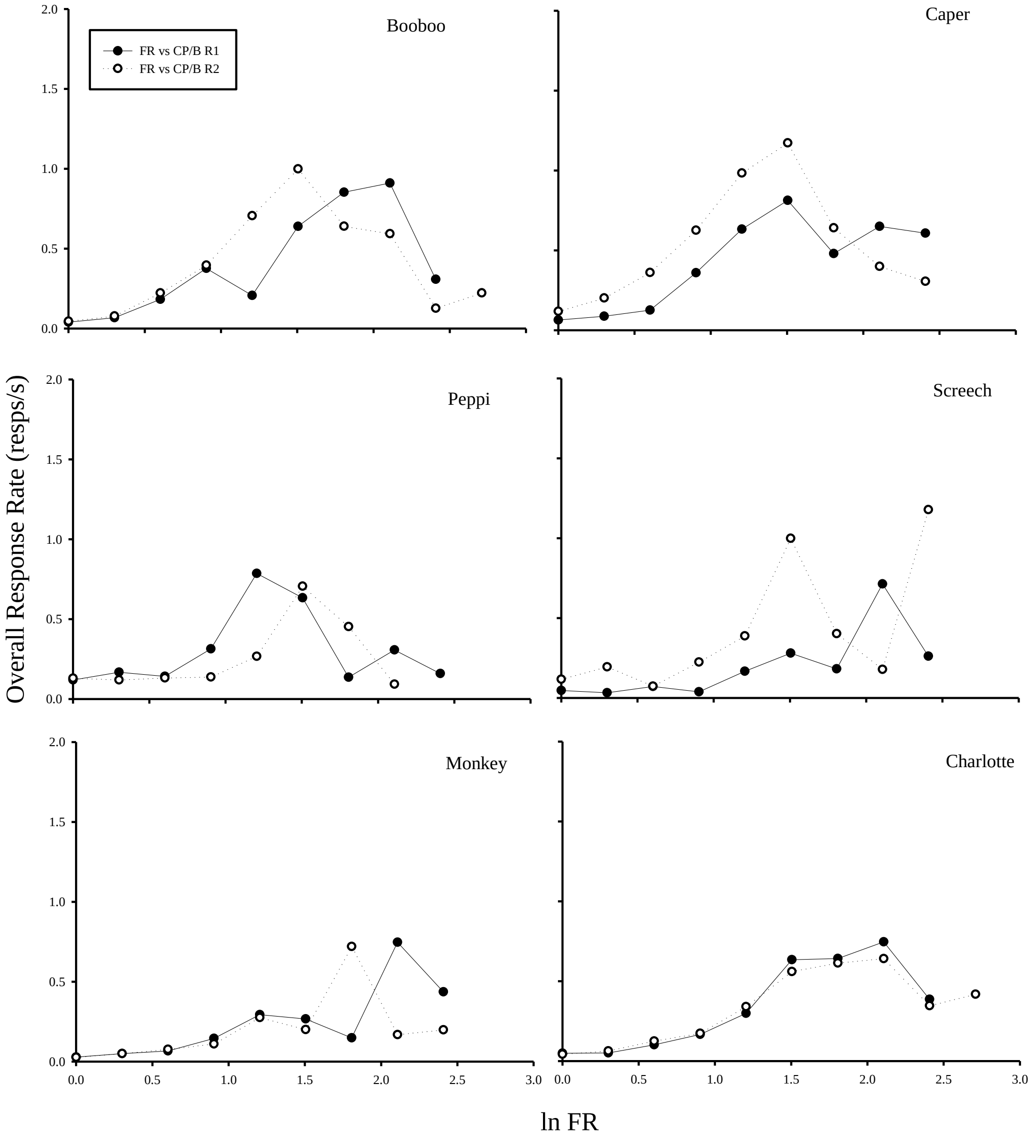

Figure 2. The overall response rates (resps/s) plotted as a function of ln FR values for both series of runs for the Cocoa Puffs™ and flaked barley condition for individual possums.

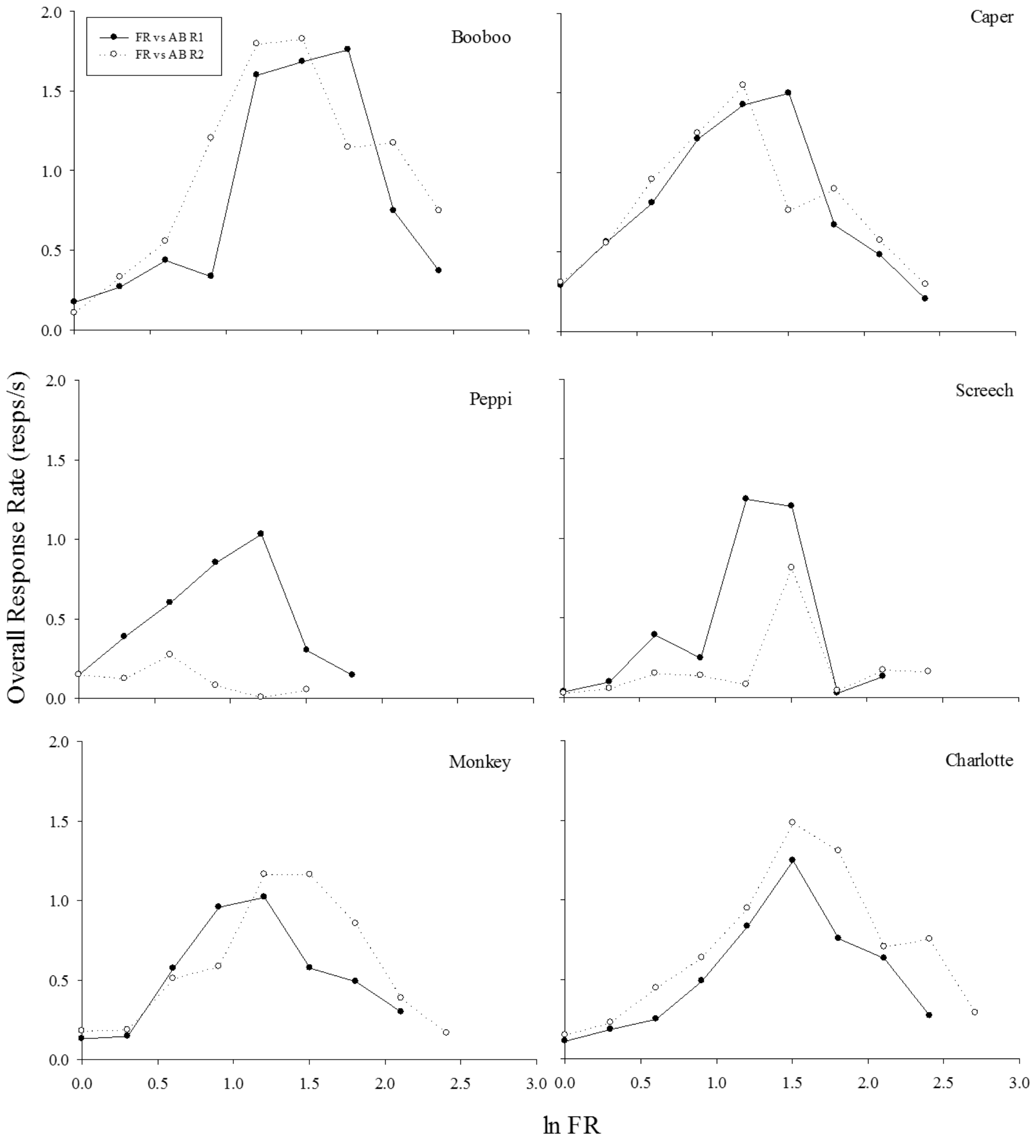

Figure 3. The overall response rates (resps/s) plotted as a function of ln FR values for both series of runs for the All Bran™ condition for individual possums.

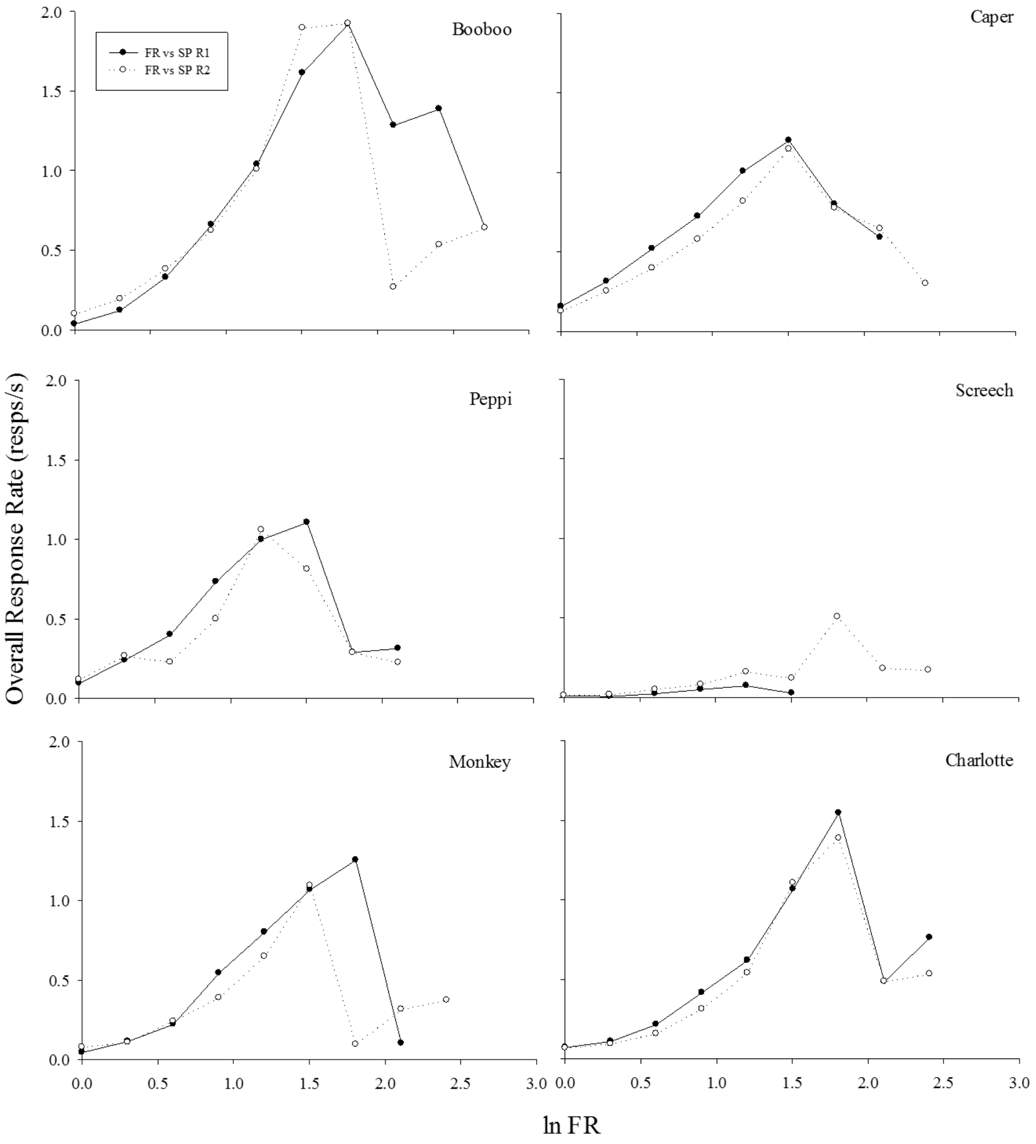

Figure 4. The overall response rates (resps/s) plotted as a function of ln FR values for both series of runs for the Soy Protein condition for individual possums.

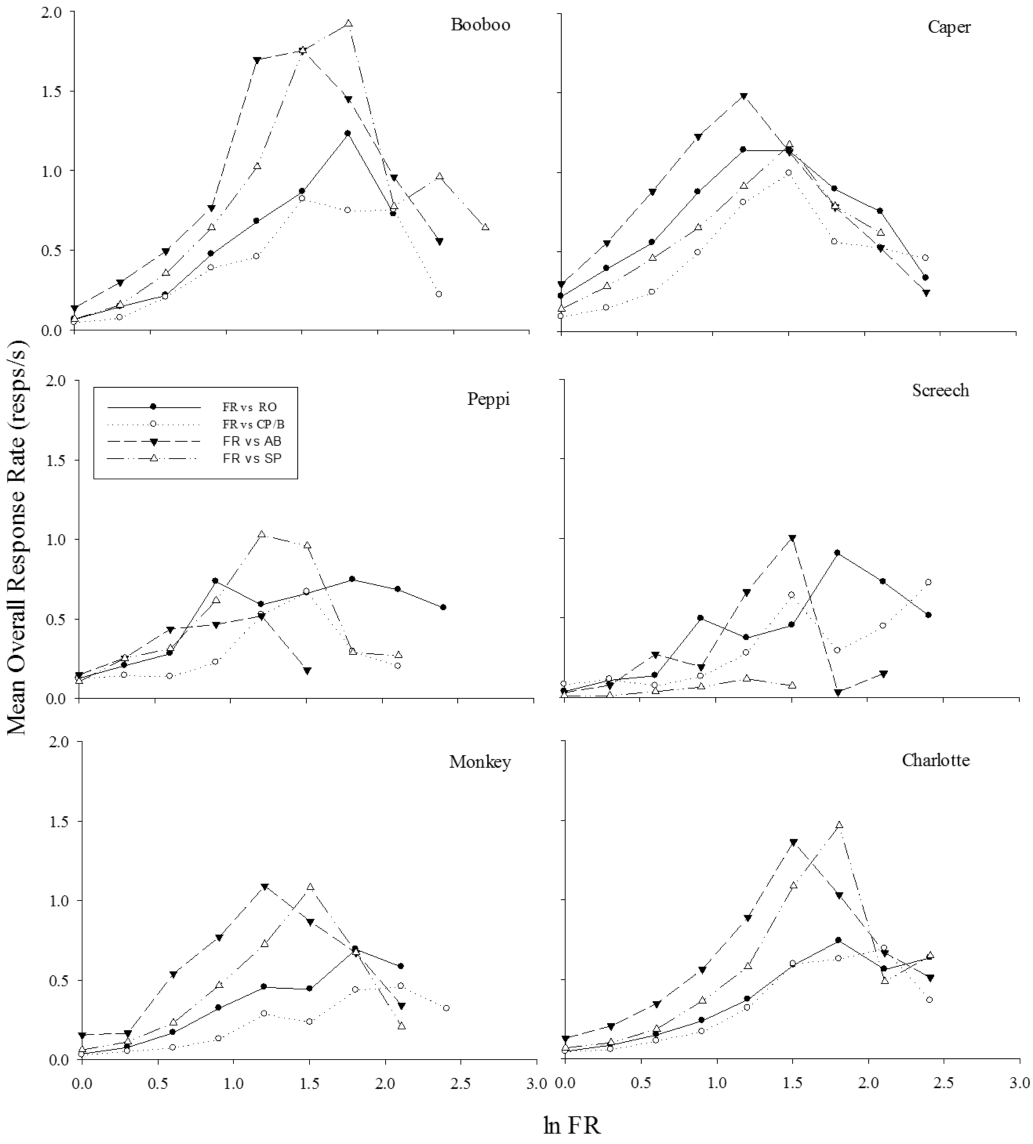

Figure 5. The mean overall response rates (resps/s) plotted as a function of ln FR for each condition for each individual possum. The data are means of the two series of runs for the Rolled Oats, Cocoa Puffs™ and flaked barley, All Bran™ and Soy Protein conditions.

Running Response Rate

Running response rates were calculated at each FR value by dividing the total number of responses by the run time (total time available to respond minus post-reinforcement pause) and were presented for each possum, for both series of runs across each food. The running response rates are determined for all FR values other than FR 1 (see Figures 6 – 9). Generally, across all six possums the running response rates increased across small to mid FR values to a maximum and then decreased at higher FR values. Similar to the data presented for overall response rate, the data for running response rate showed consistent performance by majority of the six possums across the two runs. As a result, the data was averaged and are presented in Figure 10 to show comparisons across the four foods. For five of the possums there were slight increases in response rates at higher FR values for the Soy Protein condition, and responding was generally lower for the Rolled Oats and Cocoa Puffs™ and flaked barley conditions, however, for the possum Screech, responding increased over larger FR values for the Rolled Oats condition.

Post-Reinforcement Pause

The post reinforcement pause durations (PRP) for each possum for both series of runs across all four foods are presented in Figures in 11 to 14. For some of the possums (Booboo, Peppi, Screech and Charlotte) several data points lay beyond the graph axes. This is demonstrated when PRP occur at larger FR values where few reinforcers were obtained. This can be due to several reasons such as a possum pausing for a long duration after a reinforcer has been received or, because a possum has stopped responding mid-way through a session after receiving a reinforcer. The relevant values are displayed numerically next to the relevant graphs. When analysing the data points for both series of runs, generally, as the FR requirement increased, the PRPs showed a modest increase, regardless of the food type. Majority of the possums showed consistency in the PRP durations for both run 1 and run 2, and therefore the data was averaged to show comparisons across all four foods (see Figure 15). For possums Booboo, Caper, Peppi, Screech and Charlotte, the All Bran™ and Soy Protein conditions produced higher PRP durations than Rolled Oats and Cocoa Puffs™ and flaked barley. For the possum Monkey, high PRP durations occurred for the Cocoa Puffs™ and flaked barley condition.

Consumption

Consumption is the number of reinforcers obtained at each FR value in each session of 40 minutes key time for each possum. This was calculated for each individual possum for both series of runs across each food. The natural logarithms of the number of reinforcers are plotted against the natural logarithms of the FR value (see Figures 16 – 19). Generally, across all foods, the rate of consumption increased over the smaller FR values, and decreased as the FR requirement continued to increase. For certain possums there are data points which began to decrease, but then show an increase at the next FR value. This is consistent for Screech across almost all conditions, and also occurs for Booboo, Peppi and Monkey. Both series of runs show similarities for majority of the six possums and therefore the data for consumption has been averaged to show comparisons across all four foods (see Figure 20). What is generally shown is that higher rates of initial consumption occurred for the All Bran™ condition, and lower rates of consumption occurred for the Cocoa Puffs™ and flaked barley condition for all possums.

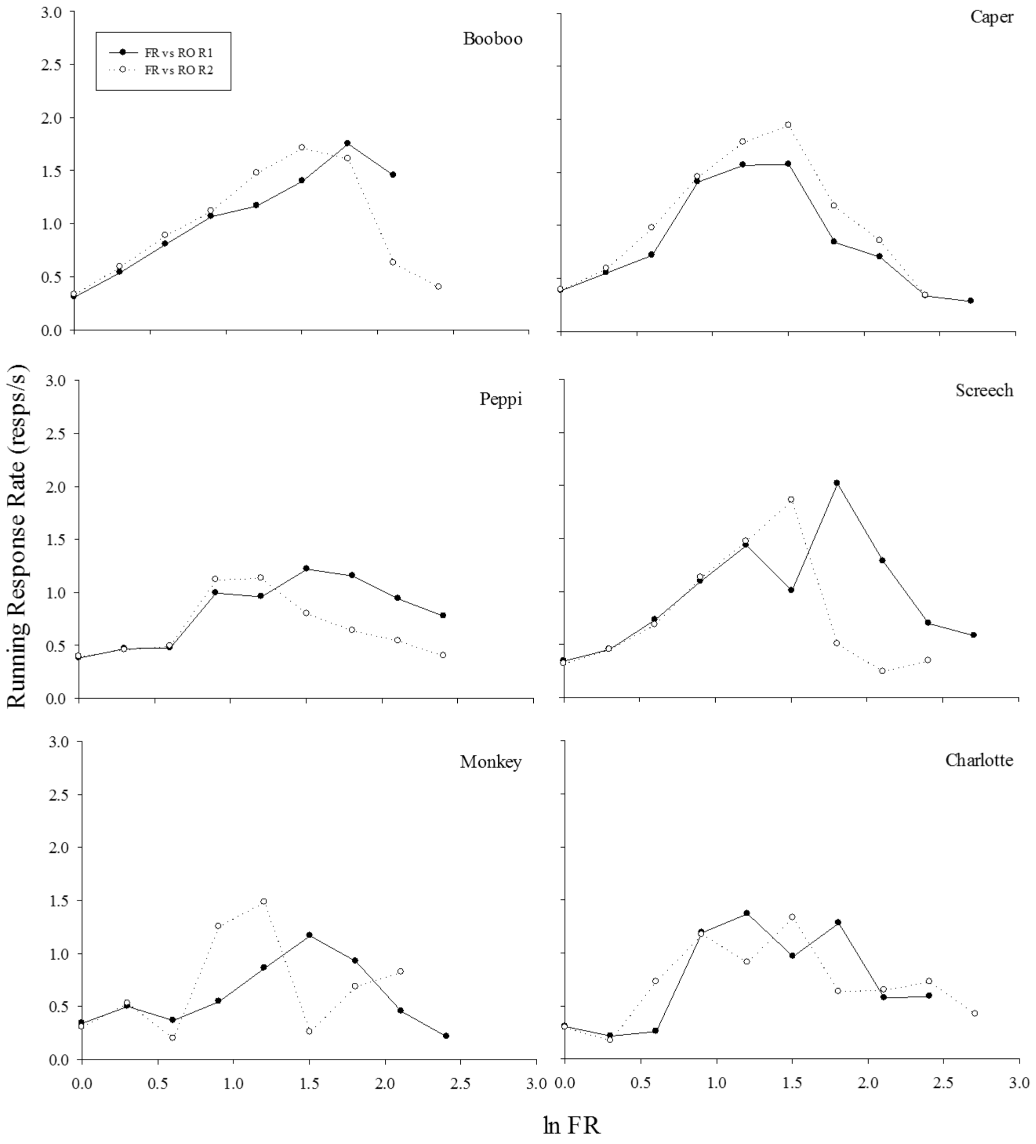

Figure 6. The running response rates (resps/s) plotted as a function of ln FR values for both series of runs for the Rolled Oats condition for each individual possum.

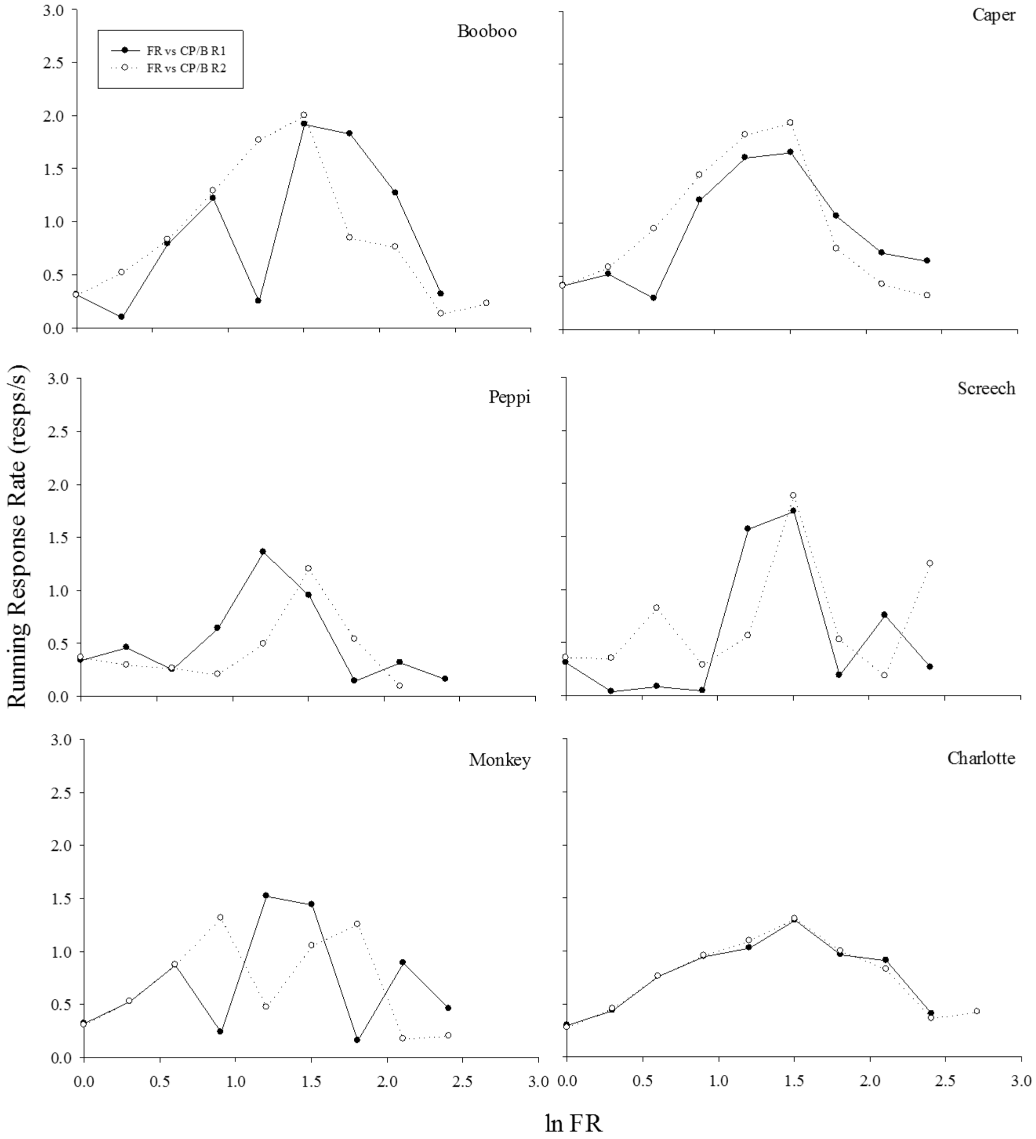

Figure 7. The running response rates (resps/s) plotted as a function of ln FR values for both series of runs for the Cocoa Puffs™ and flaked barley condition for each individual possum.

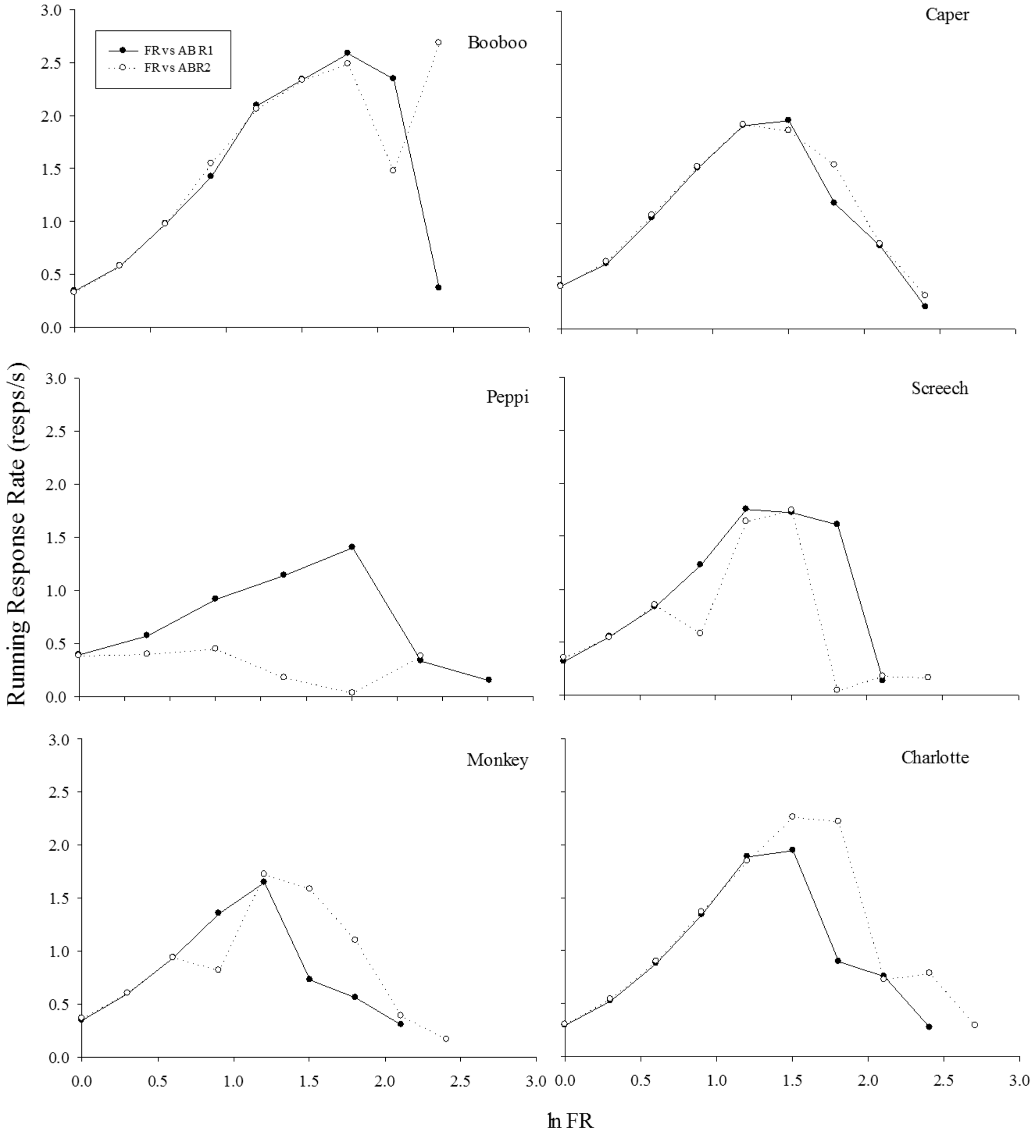

Figure 8. The running response rates (resps/s) plotted as a function of ln FR values for both series of runs for the All Bran™ condition for each individual possum.

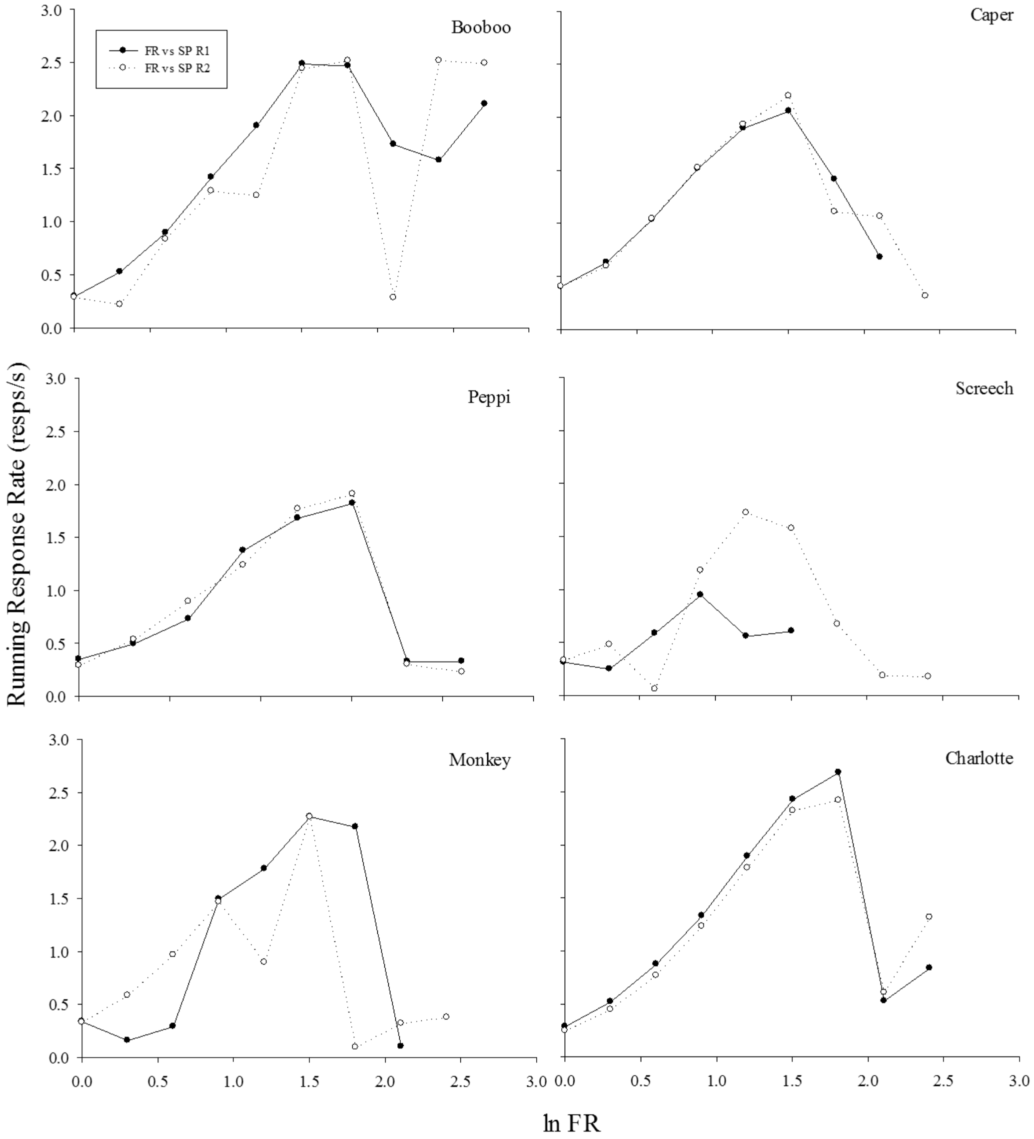

Figure 9. The running response rates (resps/s) plotted as a function of ln FR values for both series of runs for the Soy Protein condition for each individual possum.

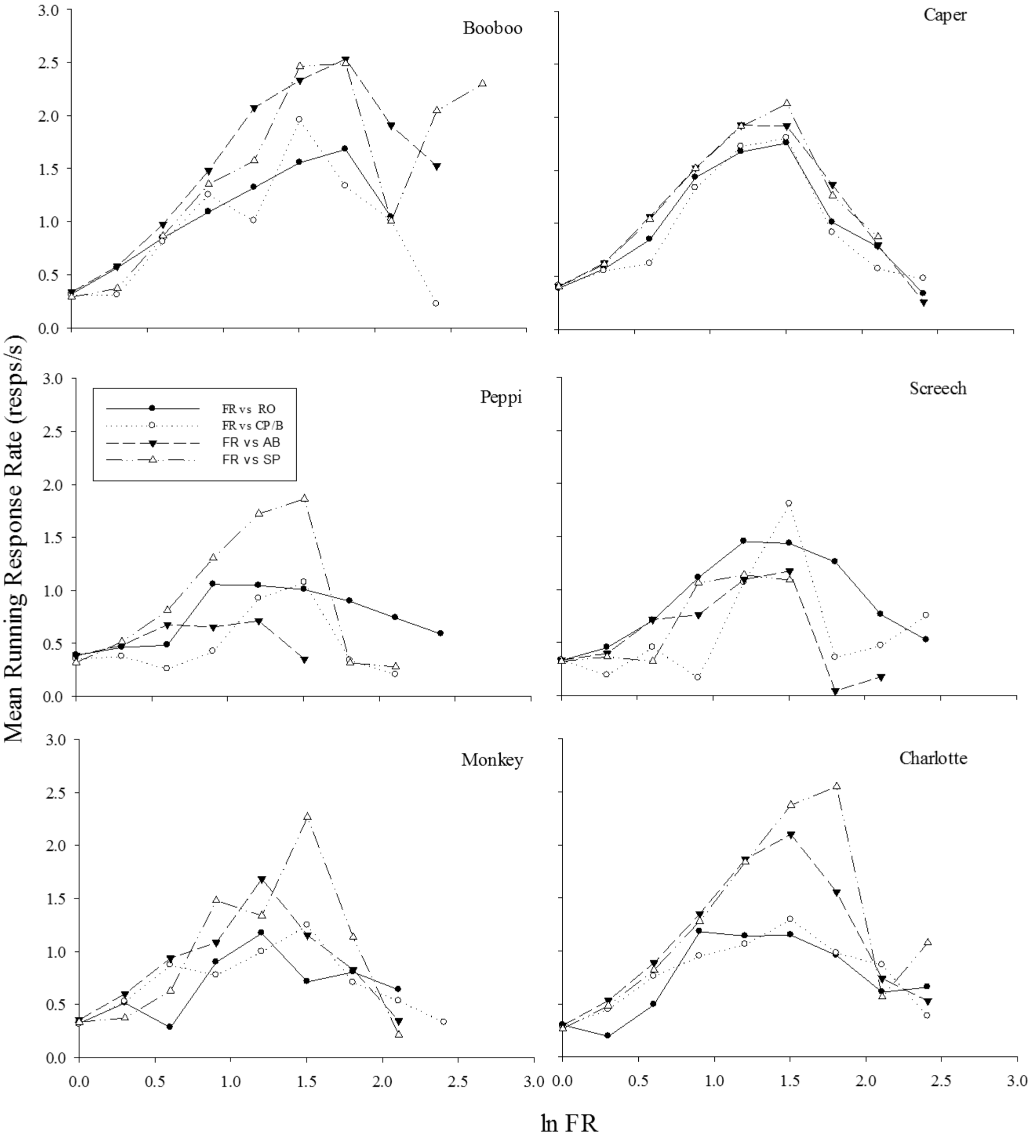

Figure 10. The mean running response rate (resps/s) of both series of runs plotted as a function of ln FR values for each individual possum across the foods Rolled Oats, Cocoa Puffs™ and flaked barley, All Bran™ and Soy Protein.

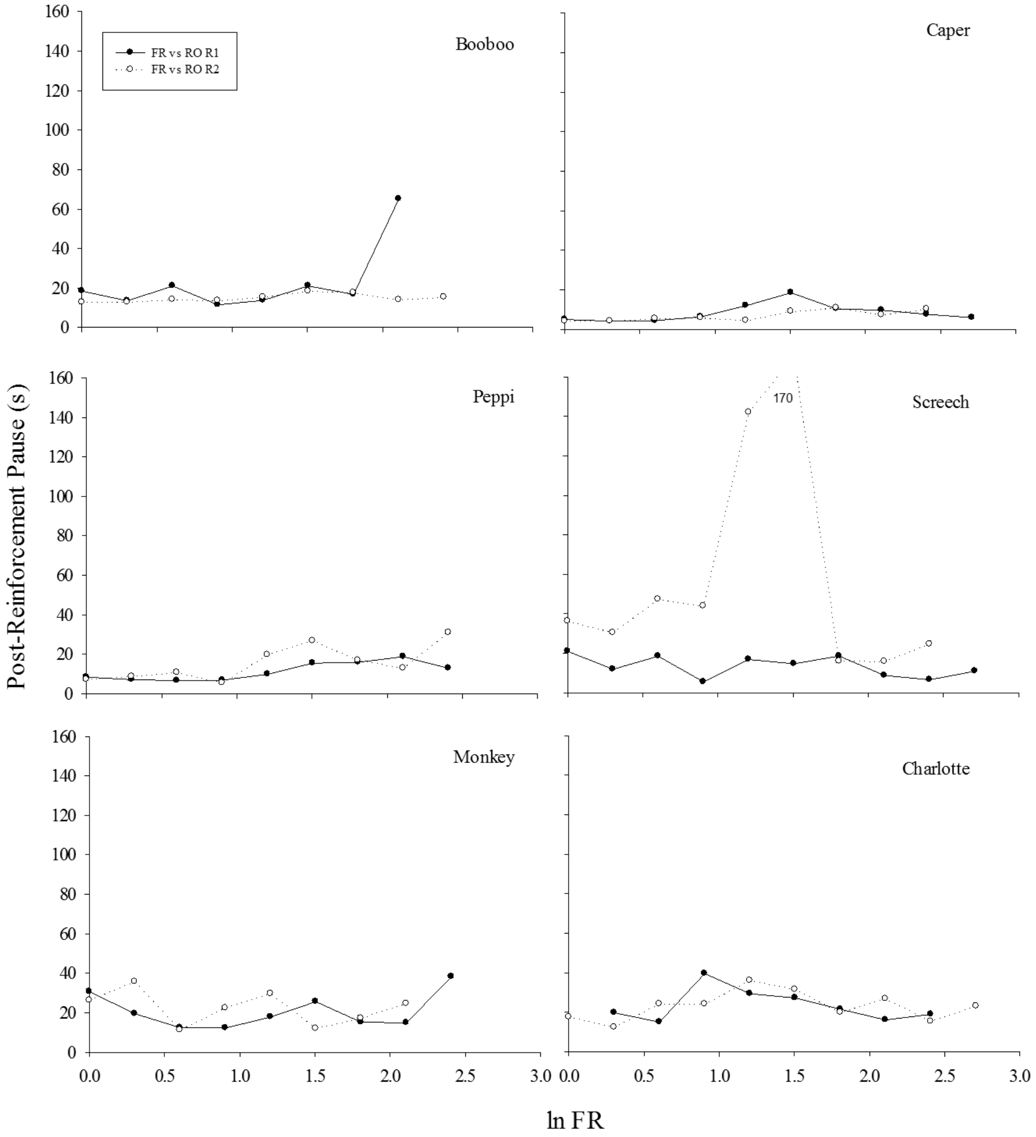

Figure 11. The post-reinforcement pause durations plotted as a function of ln FR values for both series of runs for the Rolled Oats condition for each individual possum. Data points that go beyond the axes are displayed numerically (FR, pause duration) alongside the relevant graphs.

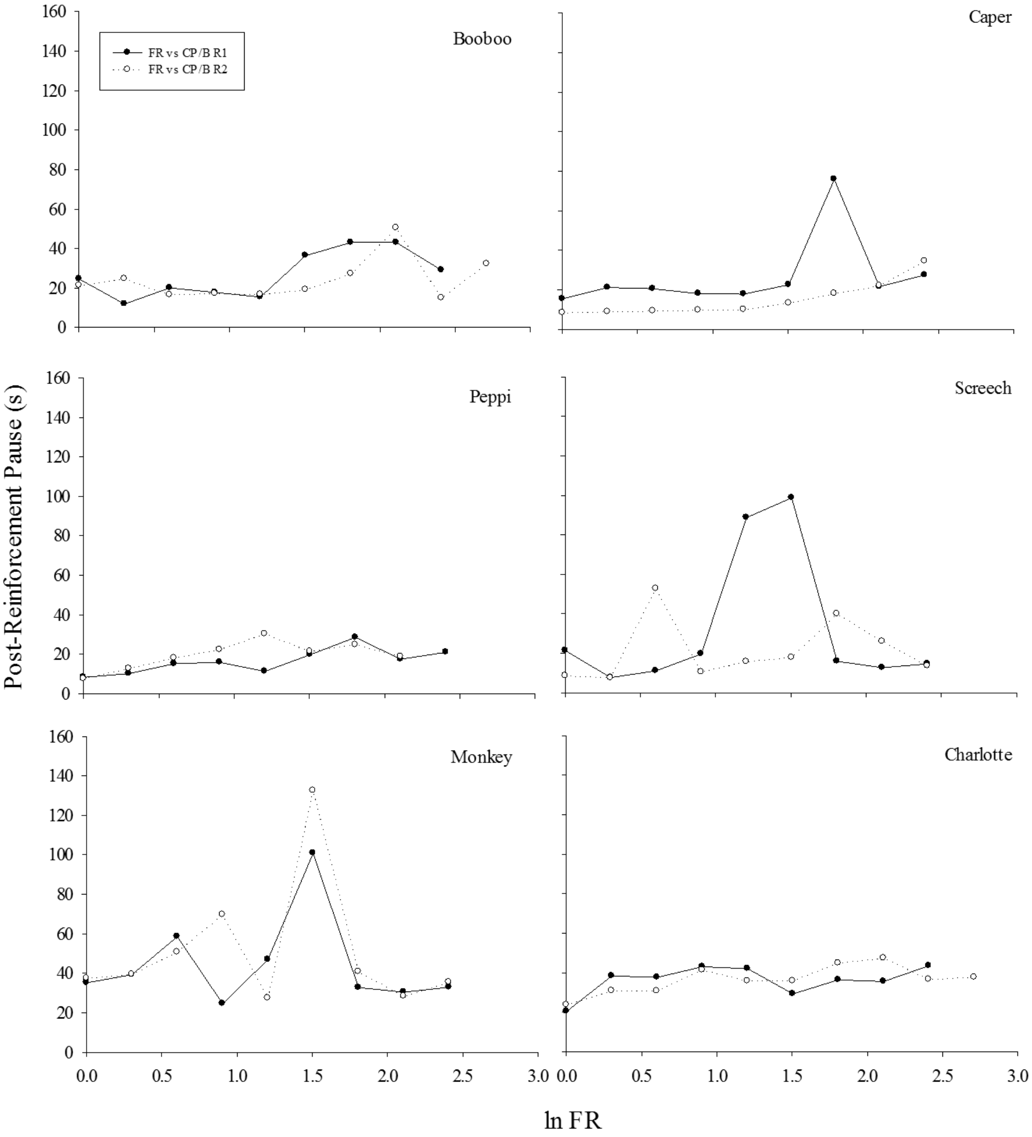

Figure 12. The post-reinforcement pause durations plotted as a function of ln FR values for both series of runs for the Cocoa Puffs™ and flaked barley condition for each individual possum. Data points that go beyond the axes are displayed numerically (FR, pause duration) alongside the relevant graphs.

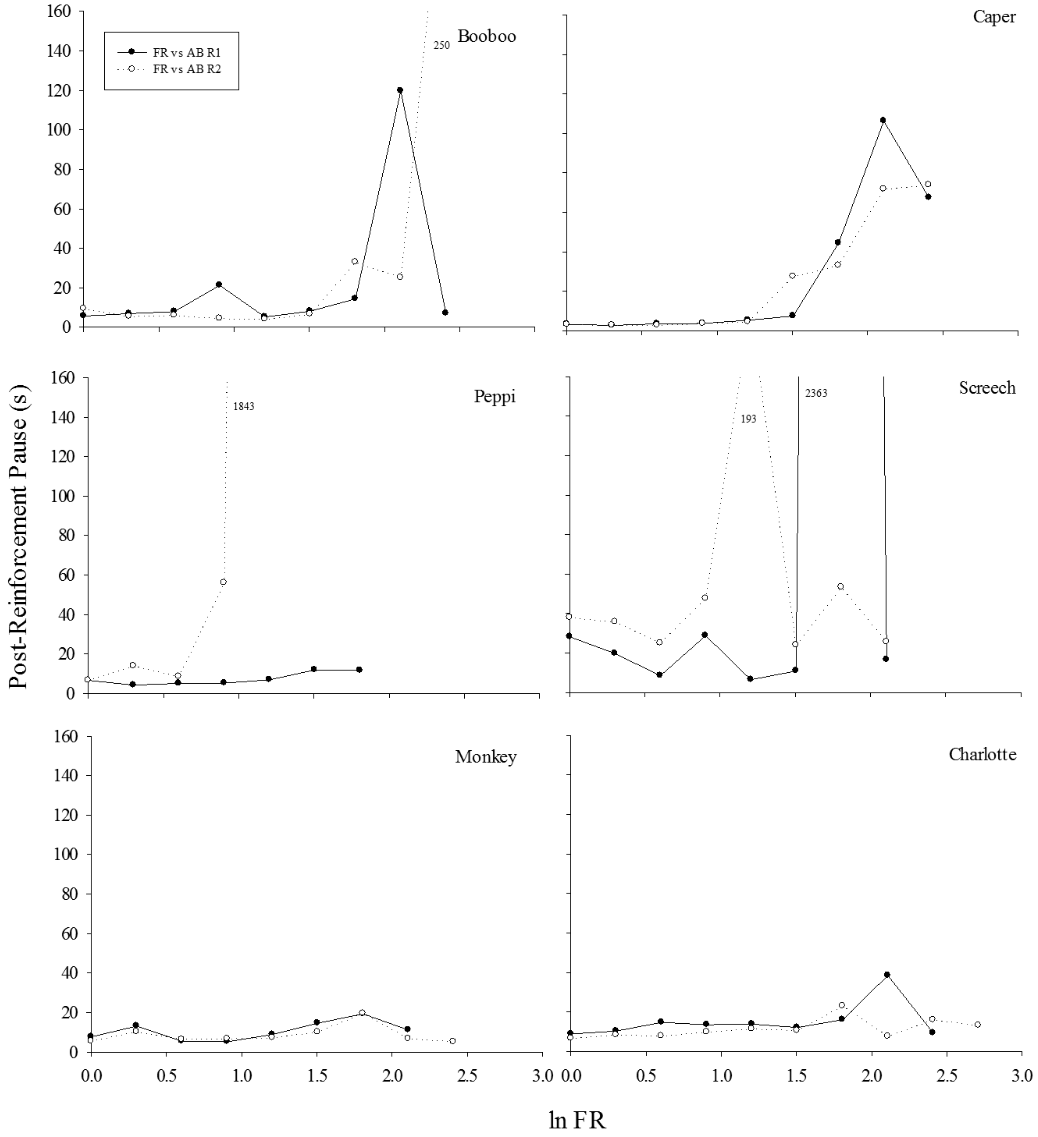

Figure 13. The post-reinforcement pause durations plotted as a function of ln FR values for both series of runs for the All Bran™ condition for each individual possum. Data points that go beyond the axes are displayed numerically (FR, pause duration) alongside the relevant graphs.

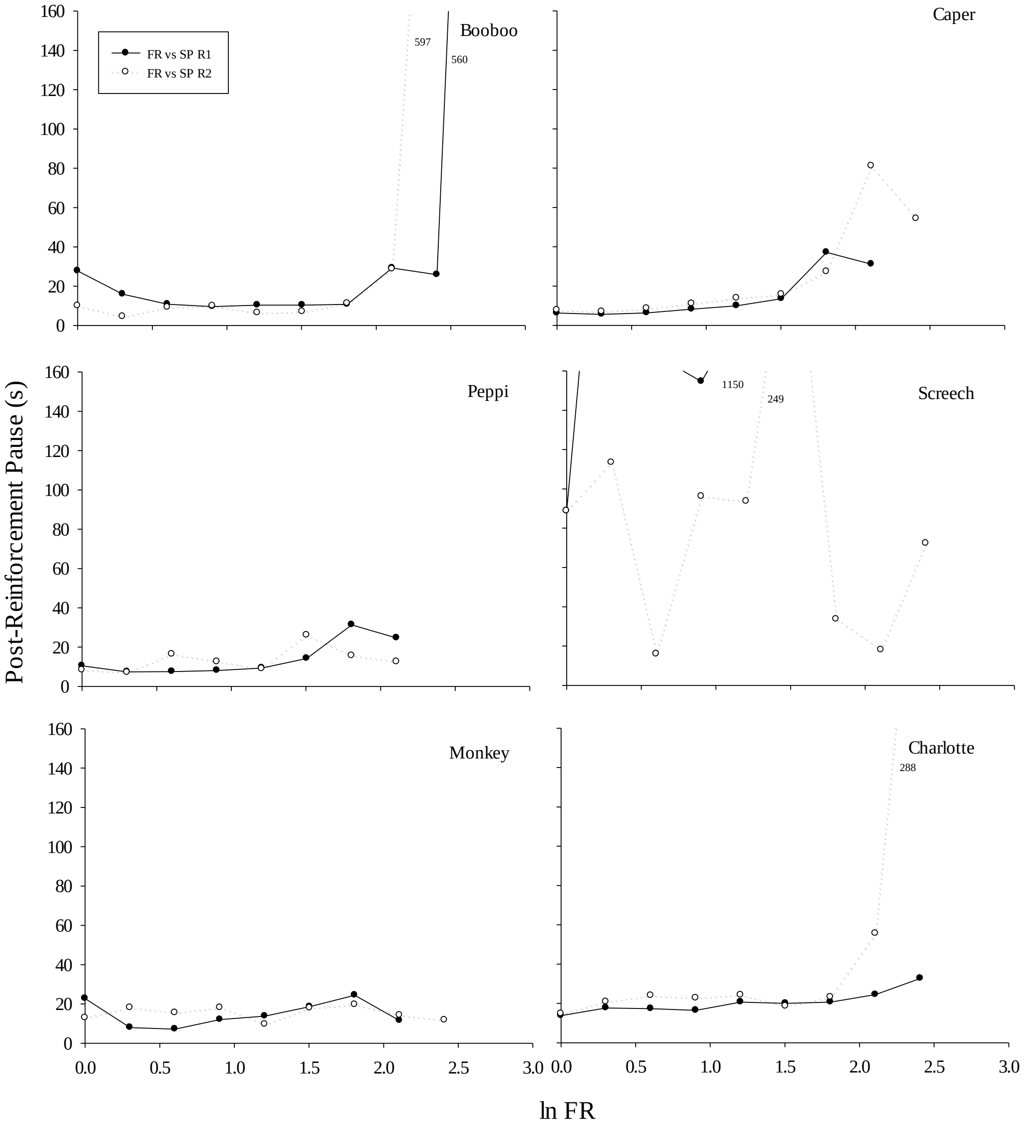

Figure 14. The post-reinforcement pause durations plotted as a function of ln FR values for both series of runs for the Soy Protein condition for each individual possum. Data points that go beyond the axes are displayed numerically (FR, pause duration) alongside the relevant graphs.

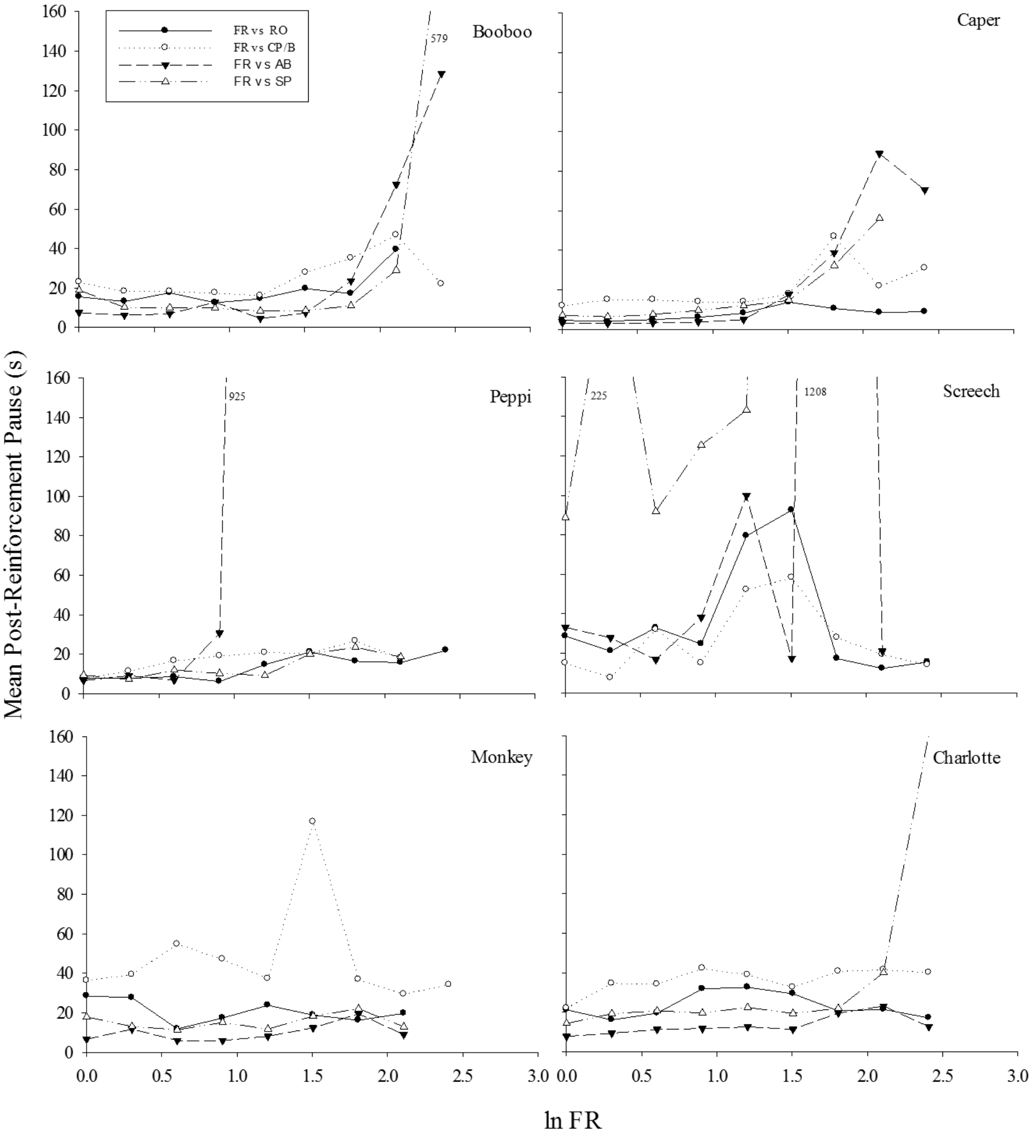

Figure 15. The mean post-reinforcement pause durations, plotted as a function of ln FR values for each condition for each individual possum. The data are means of the two series of runs for the Rolled Oats, Cocoa Puffs™ and flaked barley, All Bran™ and Soy Protein conditions. Data points that go beyond the axis are displayed numerically (FR, pause duration) beside the relevant graphs.

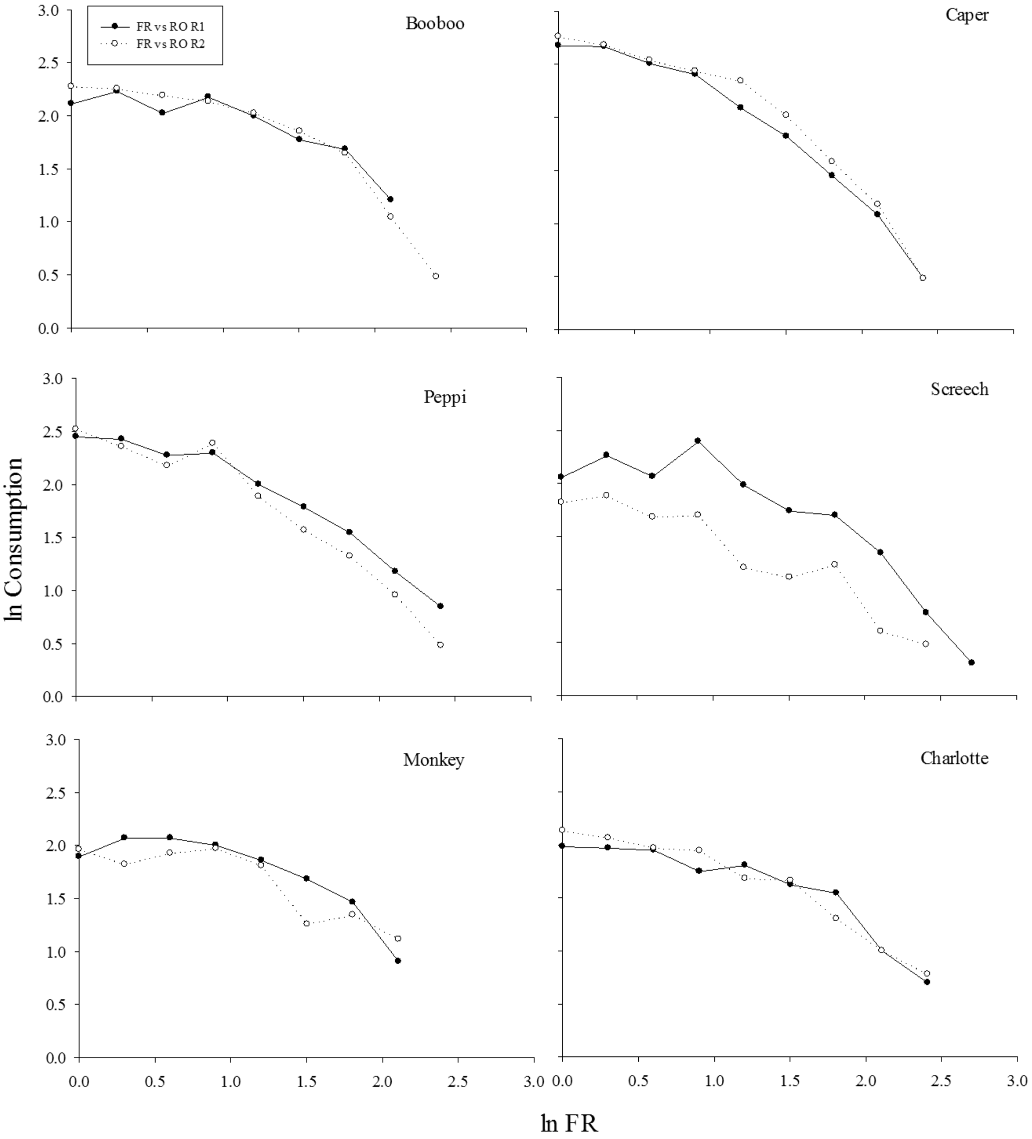

Figure 16. The ln consumption data for Rolled Oats plotted as a function of ln FR value for both series of runs for individual possums.

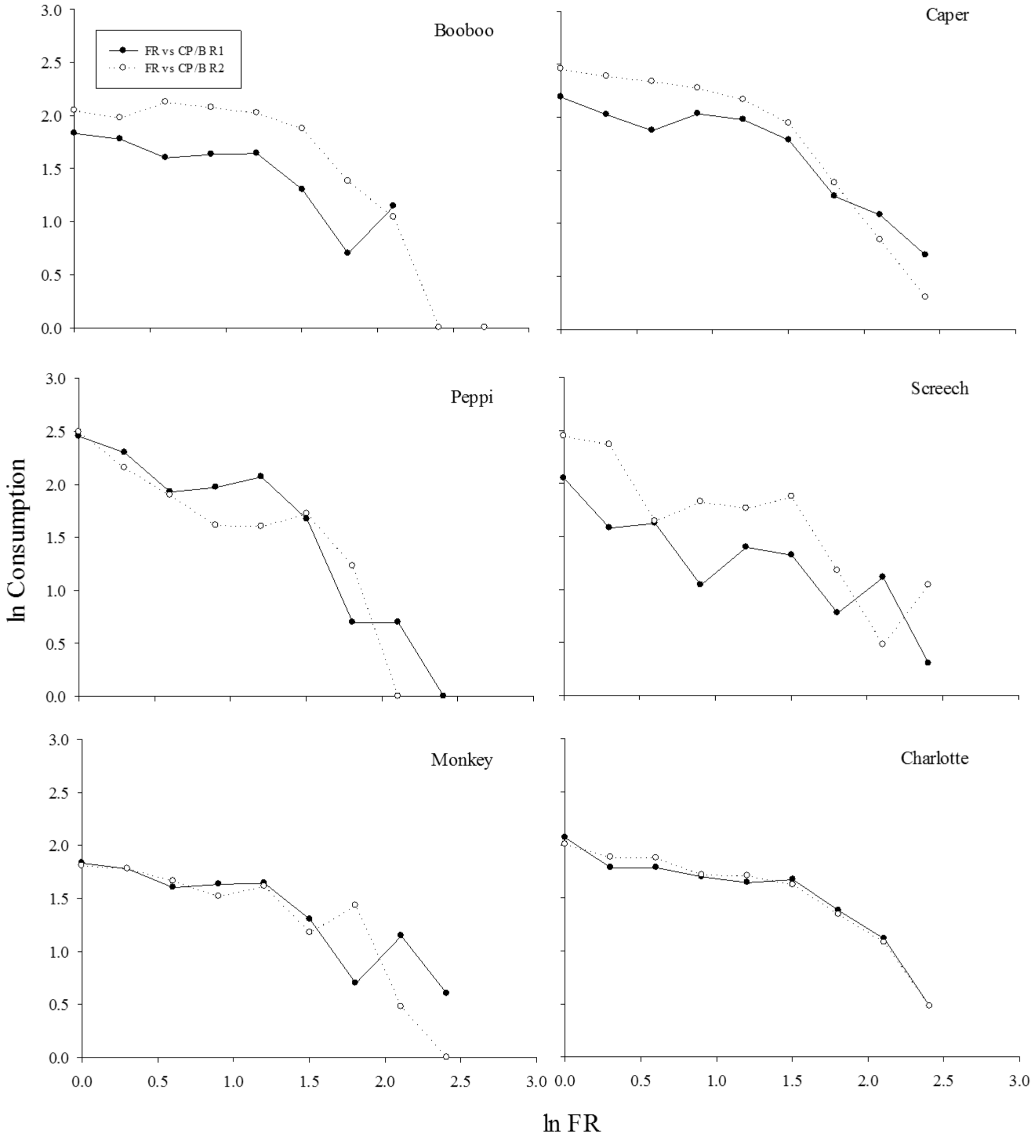

Figure 17. The ln consumption data for the Cocoa Puffs™ and flaked barley condition plotted as a function of ln FR value for both series of runs for individual possums.

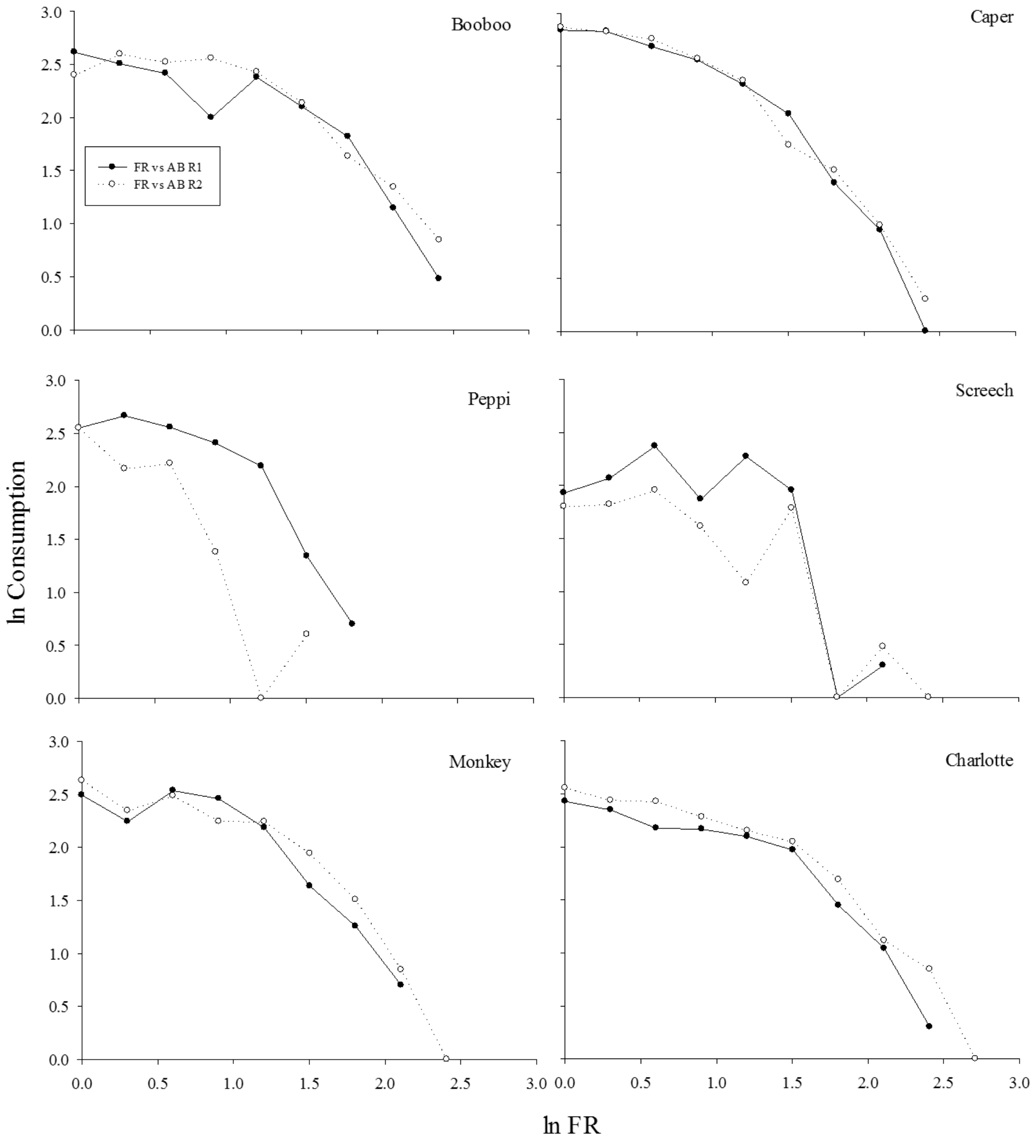

Figure 18. The ln consumption data for the All Bran™ condition plotted as a function of ln FR value for both series of runs for individual possums.

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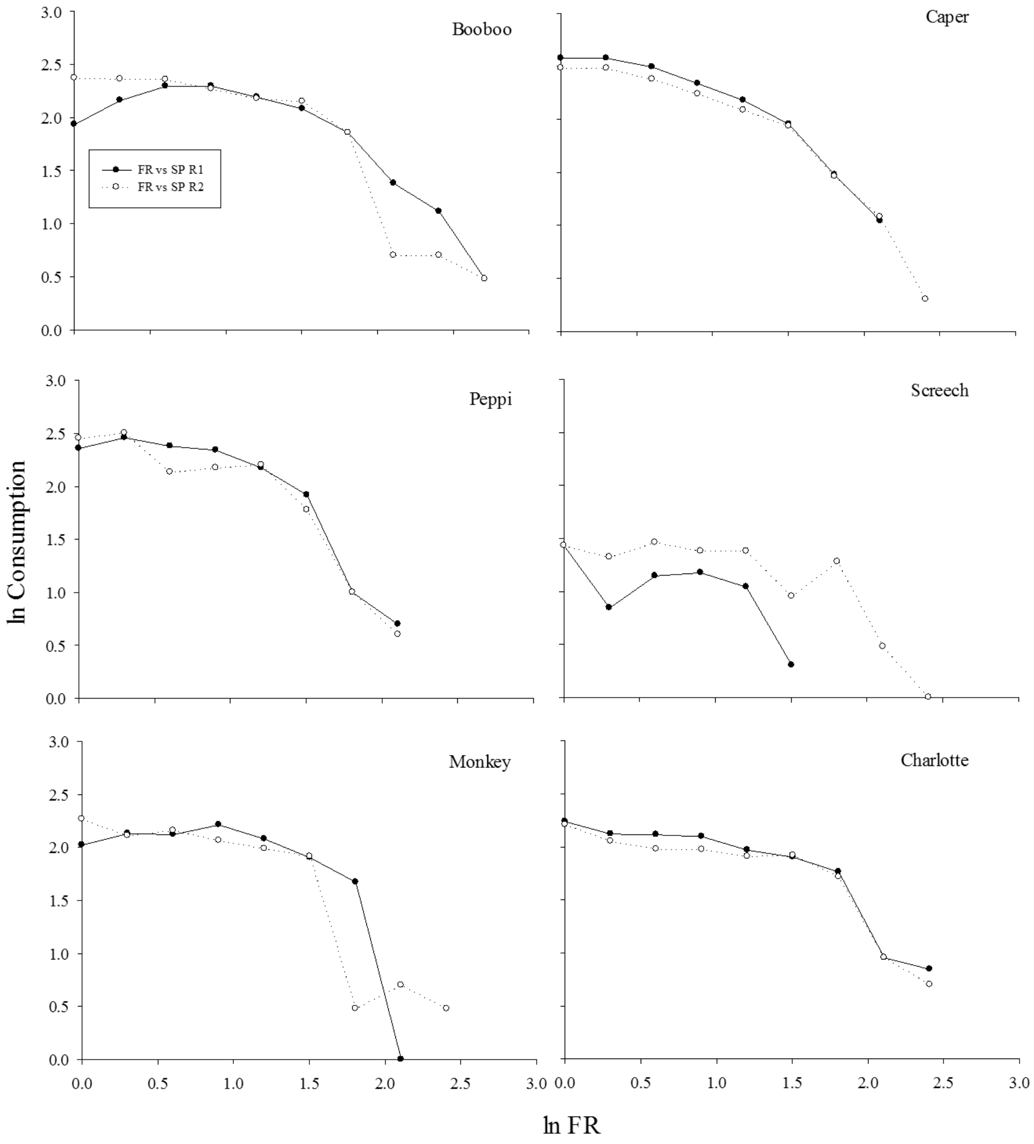

Figure 19. The ln consumption data for the Soy Protein condition plotted as a function of ln FR value for both series of runs for individual possums.

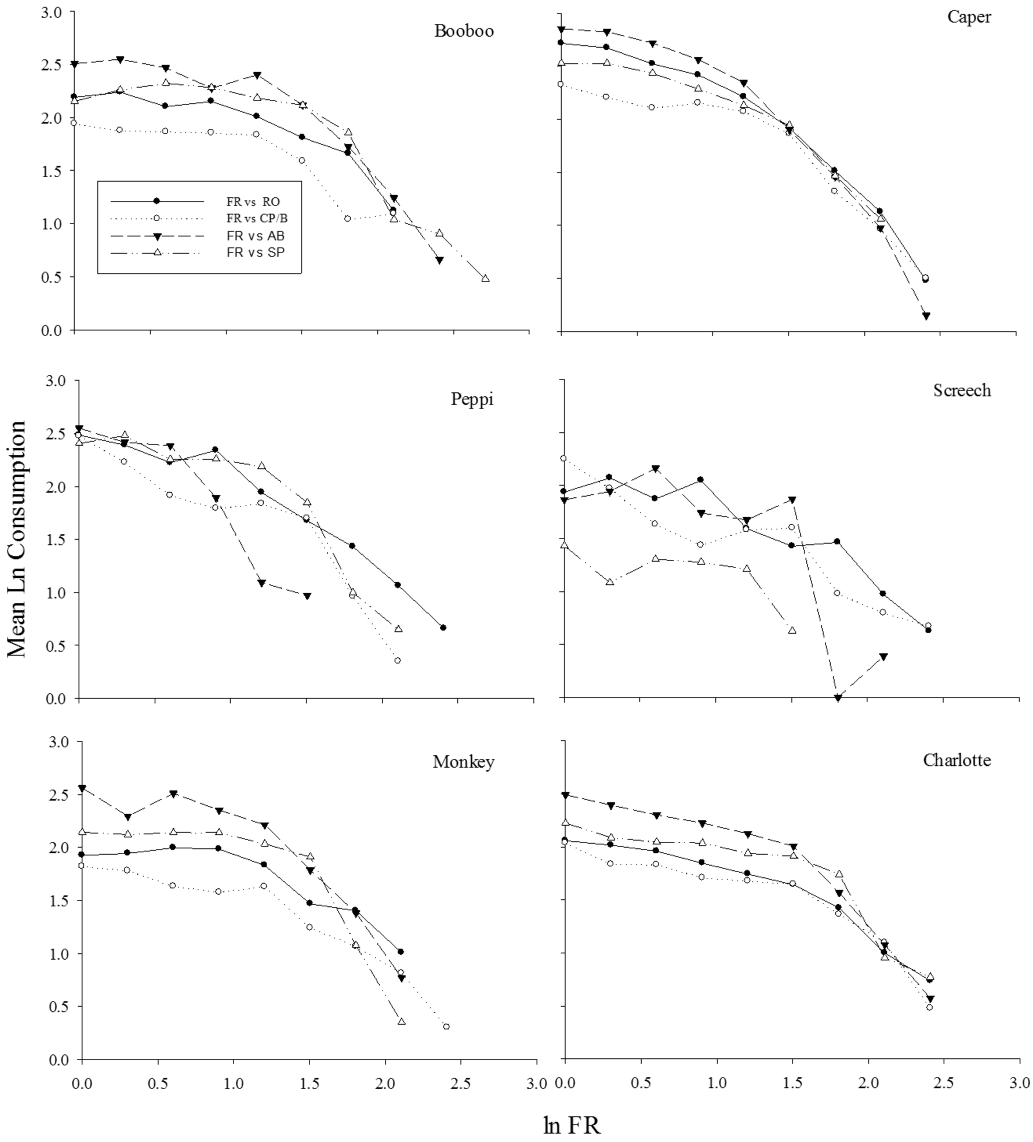

Figure 20. The ln consumption data plotted as a function of the ln FR value for each individual possum. The data are means of the two series of runs for Rolled Oats, Cocoa Puffs™ and flaked barley, All Bran™ and Soy Protein.

MPR

Response rates were calculated by dividing the total number of responses by the total time available for making responses and averaging across individual possums separately for each condition. Response rates (per s) were plotted against FR values for both series of runs across all four foods for all six possums (Figures 21 – 24). Across conditions Rolled Oats and All Bran™, half of the possums responded to longer ratio values on the first run, and the other half on the second run, whereas for conditions Cocoa Puffs™ and flaked barley and Soy Protein, the second run generally extended out to larger FR values compared to the first run. Typically, response rates increased across smaller FR values and began to decrease as the FR requirement increased, regardless of the food type.

The best fits of the MPR model to the response rate data from Equation 4 are drawn by the smooth lines in the figures (see Figures 21 – 24), and the parameter estimates are given in Table 1 and Table 2 as well as the values for R^2, *DF* and *SE of Y*. The averaged parameters (α_s, λ, δ, ε) for each food type are also shown in Figure 25. Generally, the model gives a good account of the data, with R^2 values ranging from 0.263 – 0.987. The values for parameter α_s are systematically larger for the Rolled Oats and Cocoa Puffs™ and flaked barley condition than they are for the All Bran™ and Soy Protein condition. When comparing the average parameter values for λ, All Bran™ showed systematically larger values, and Cocoa Puffs™ and flaked barley showed much smaller values than all other foods. The average values for parameter δ are largest for Cocoa Puffs™ and flaked barley, but similar values are shown for the other three foods. There were no systematic differences in the averages across the four foods for the parameter ε.

Table 1.

Parameter estimates from Killeen and Sitomer's (2003) MPR equation (Equation 4) are shown. Estimates of $a_{s,}$ λ, δ *and* ε *for both series of runs for conditions Rolled Oats and Cocoa Puffs™ and flaked barley for individual possums are shown. Also shown are the values for* $R^{2,}$ *DF and SE of Y*

Condition	**Possum**	α_s	λ	δ	ε	**R2**	**DF**	**SE of Y**
Rolled Oats Run 1	Booboo	211.2	0.057	0.383	0.98	0.954	4	0.120
	Caper	1007.0	0.304	1.274	1.00	0.860	7	0.129
	Peppi	683.4	0.080	0.967	0.91	0.930	6	0.077
	Screech	1122.2	0.069	0.833	0.96	0.812	7	0.227
	Monkey	516.6	0.059	1.400	1.00	0.899	6	0.081
	Charlotte	662.9	0.038	1.135	1.00	0.896	6	0.111
	Average	700.6	0.101	0.999	0.98	0.892	-	-
	SD	330.7	0.100	0.364	0.04	0.051	-	-
Rolled Oats Run 2	Booboo	499.0	0.081	0.927	1.00	0.906	6	0.133
	Caper	506.0	0.237	0.776	1.00	0.861	6	0.160
	Peppi	636.8	0.157	1.614	1.00	0.809	6	0.139
	Screech	696.5	0.011	2.254	0.92	0.721	6	0.084
	Monkey	700.4	0.053	0.034	1.00	0.841	5	0.124
	Charlotte	1429.5	0.034	1.438	0.94	0.919	7	0.077
	Average	744.7	0.098	1.086	0.98	0.843	-	-
	SD	347.0	0.086	0.768	0.04	0.072	-	-
Cocoa Puffs™ & flaked barley Run 1	Booboo	485.4	0.034	0.916	0.97	0.852	6	0.115
	Caper	620.8	0.068	1.270	1.00	0.846	6	0.115
	Peppi	489.1	0.092	1.984	1.00	0.468	6	0.203
	Screech	528.5	0.011	1.239	0.98	0.694	6	0.130
	Monkey	629.9	0.010	0.982	0.95	0.664	6	0.145
	Charlotte	577.4	0.031	1.150	1.00	0.935	6	0.059
	Average	555.2	0.041	1.257	0.98	0.743	-	-
	SD	63.80	0.033	0.383	0.02	0.169	-	-
Cocoa Puffs™ & flaked barley Run 2	Booboo	1204.5	0.09	1.494	1.00	0.668	7	0.223
	Caper	518.6	0.148	1.112	1.00	0.762	6	0.204
	Peppi	241.3	0.039	1.620	0.95	0.648	5	0.163
	Screech	772.4	0.052	1.373	0.99	0.320	6	0.269
	Monkey	519.1	0.023	2.073	1.00	0.526	6	0.165
	Charlotte	1571.9	0.035	1.631	1.00	0.889	7	0.090
	Average	804.6	0.065	1.550	0.99	0.636	-	-
	SD	496.1	0.047	0.320	0.02	0.196	-	-

Table 2.

Parameter estimates from Killeen and Sitomer's (2003) MPR equation (Equation 4) are shown. Estimates of $a_{s,}$ λ, δ and ε for both series of runs for conditions All Bran™ and Soy Protein for individual possums are shown. Also shown are the values for $R^{2,}$ DF and SE of Y

Condition	**Possum**	**α_s**	**λ**	**δ**	**ε**	**R2**	**DF**	**SE of Y**
All Bran™ Run 1	Booboo	462.2	0.148	0.601	1.00	0.759	6	0.358
	Caper	469.6	0.396	0.855	1.00	0.684	6	0.298
	Peppi	112.2	0.294	1.207	1.00	0.657	4	0.283
	Screech	215.0	0.125	1.109	1.00	0.468	5	0.456
	Monkey	239.6	0.230	1.156	1.00	0.783	5	0.209
	Charlotte	534.1	0.108	1.023	1.00	0.829	6	0.166
	Average	338.8	0.217	0.992	1.00	0.697	-	-
	SD	171.4	0.112	0.228	0.00	0.129	-	-
All Bran™ Run 2	Booboo	499.2	0.250	0.586	1.00	0.904	6	0.239
	Caper	466.5	0.464	0.894	1.00	0.742	6	0.261
	Peppi	274.6	0.000	0.791	0.87	0.347	2	0.119
	Screech	486.2	0.034	2.855	1.00	0.263	6	0.247
	Monkey	843.5	0.180	1.211	1.00	0.589	7	0.316
	Charlotte	613.3	0.130	0.752	1.00	0.873	6	0.194
	Average	530.6	0.176	1.181	0.98	0.620	-	-
	SD	188.3	0.168	0.845	0.05	0.269	-	-
Soy Protein Run 1	Booboo	767.2	0.108	0.519	1.00	0.952	6	0.169
	Caper	222.6	0.154	0.769	0.97	0.959	4	0.092
	Peppi	152.7	0.164	0.869	1.00	0.778	4	0.234
	Screech	101.6	0.043	0.284	1.00	0.953	2	0.009
	Monkey	138.5	0.090	0.262	1.00	0.987	4	0.071
	Charlotte	462.2	0.072	0.730	1.00	0.749	5	0.305
	Average	307.5	0.105	0.572	0.99	0.896	-	-
	SD	259.8	0.047	0.258	0.01	0.104	-	-
Soy Protein Run 2	Booboo	660.9	0.135	0.680	1.00	0.544	6	0.511
	Caper	338.3	0.117	0.905	0.97	0.936	5	0.104
	Peppi	145.6	0.132	0.993	1.00	0.732	4	0.228
	Screech	533.4	0.014	2.639	1.00	0.635	6	0.107
	Monkey	406.0	0.093	1.498	1.00	0.408	5	0.318
	Charlotte	362.8	0.066	0.718	1.00	0.800	5	0.258
	Average	407.8	0.093	1.239	1.00	0.676	-	-
	SD	176.3	0.047	0.746	0.01	0.188	-	-

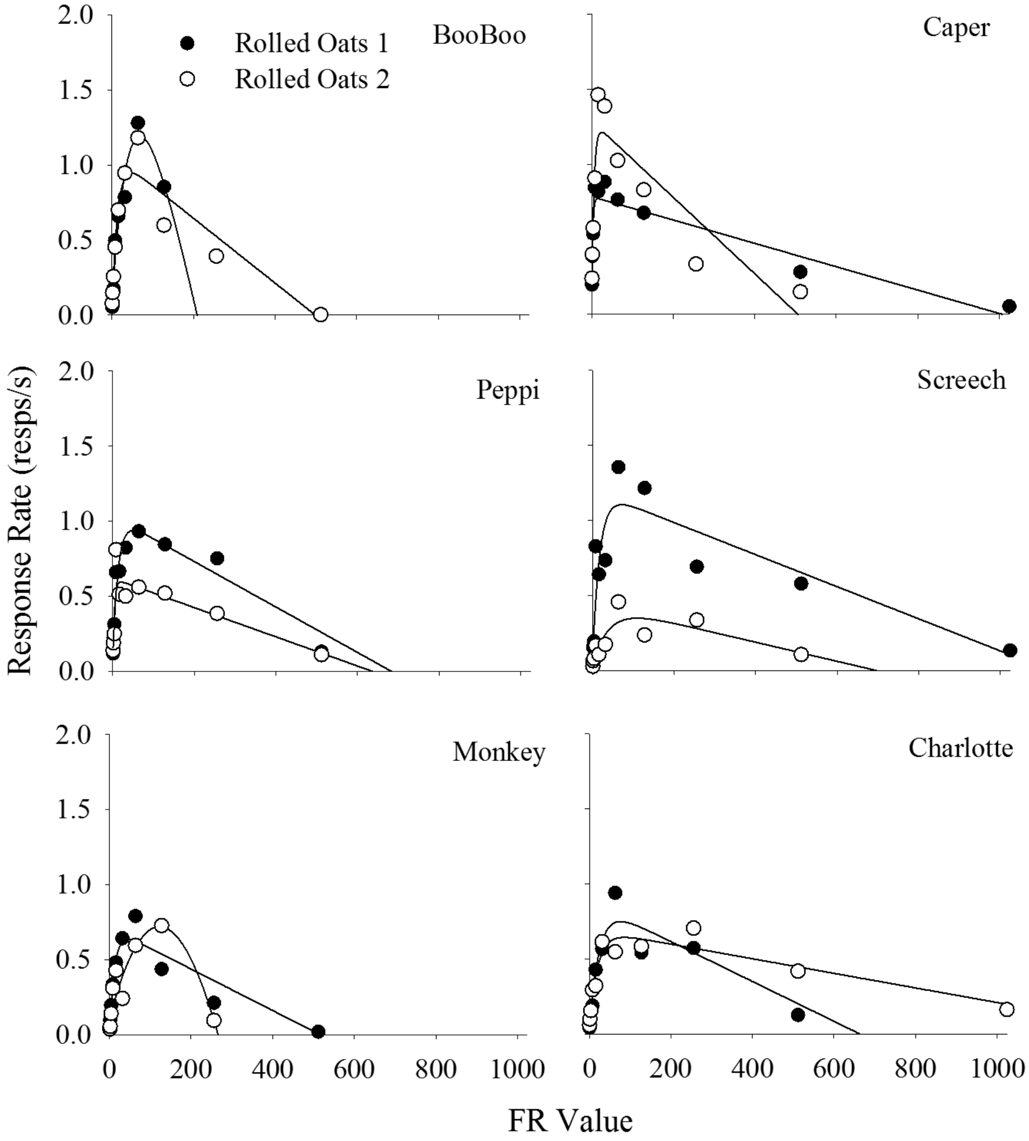

Figure 21. Response rates for runs 1 and 2 under the rolled oats condition are plotted as a function of the FR value. The curved lines were fit by Equation 4.

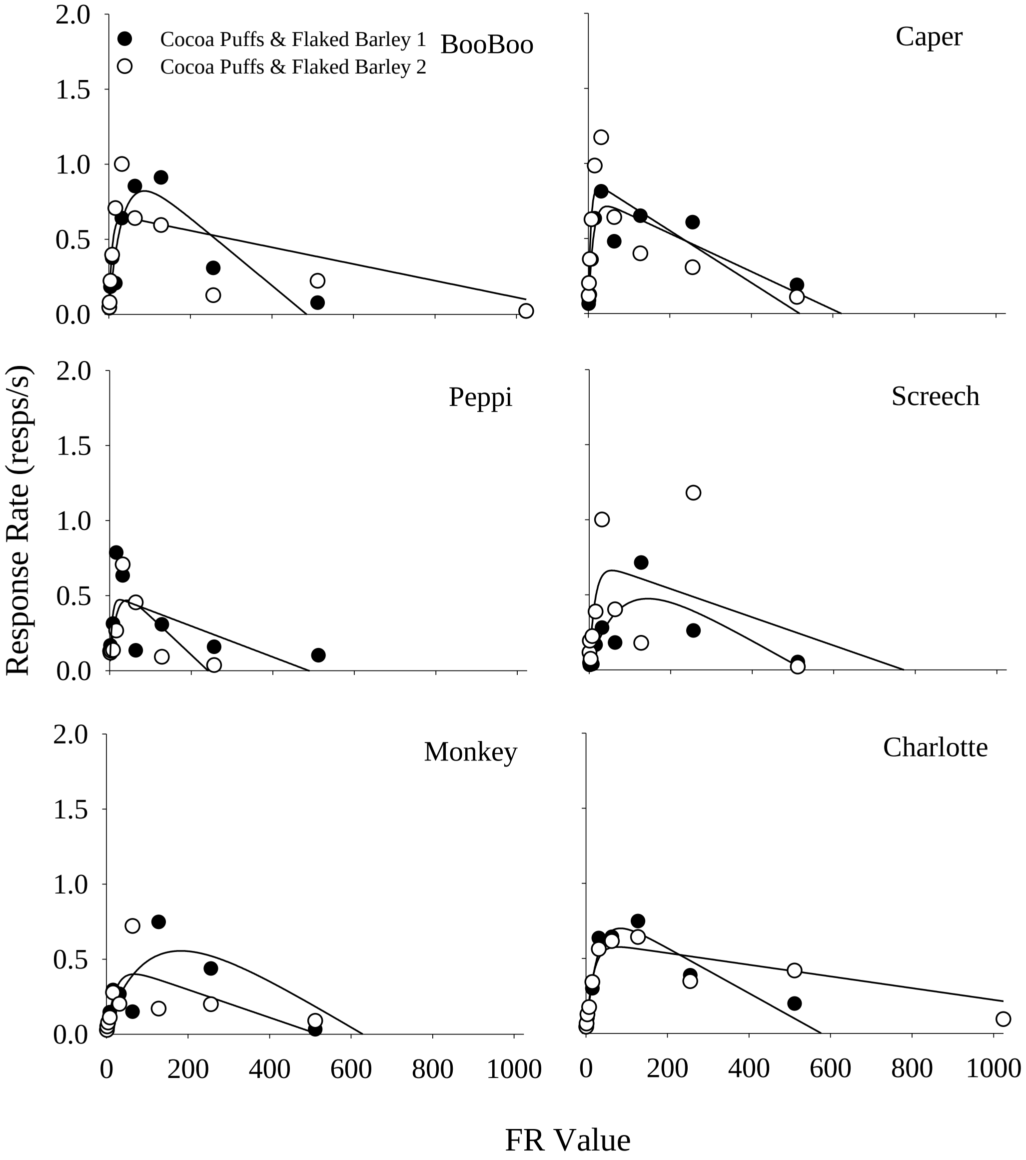

Figure 22. Response rates for runs 1 and 2 under the Cocoa Puffs™ and flaked barley condition are plotted as a function of the FR value. The curved lines were fit by Equation 4.

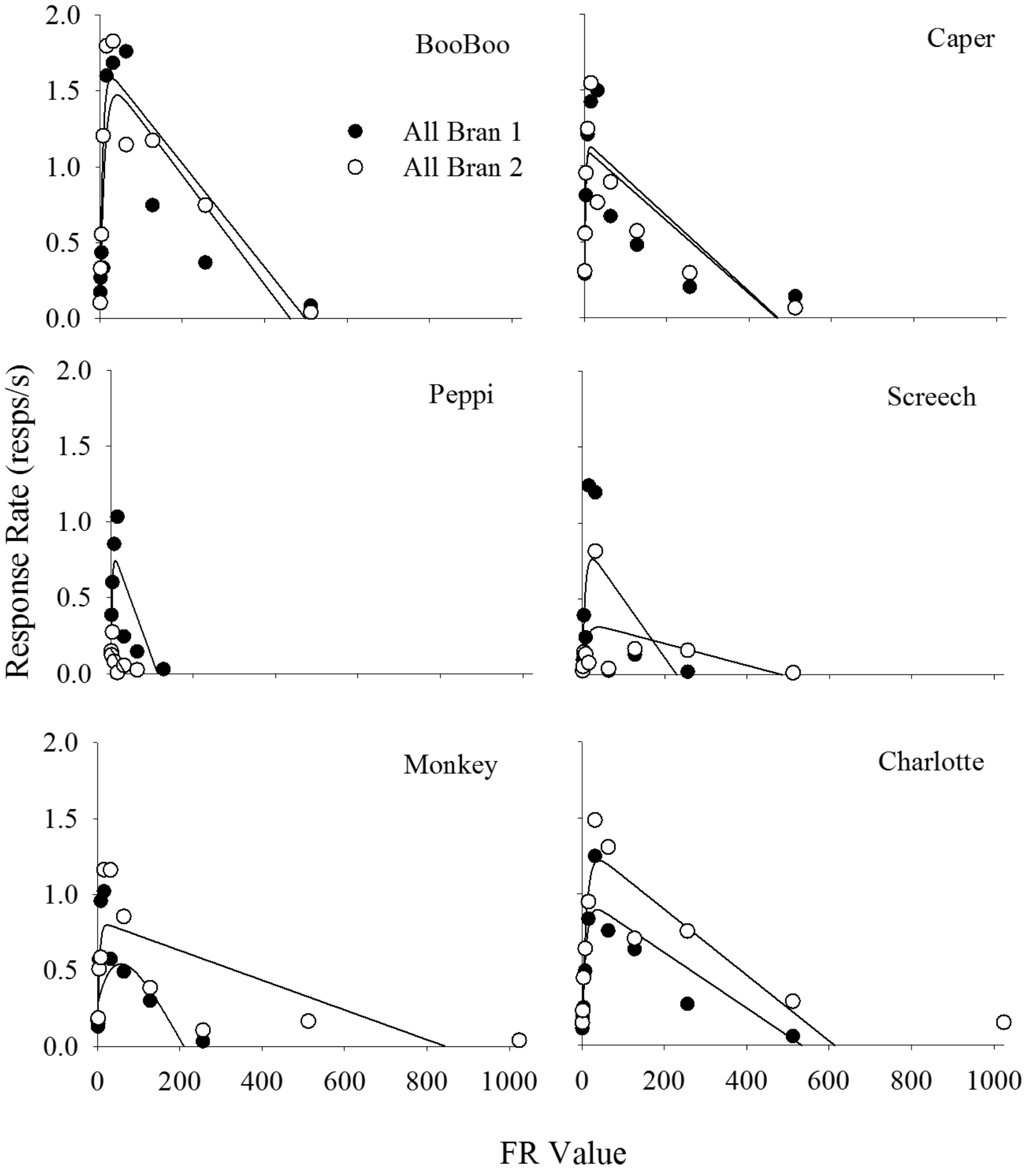

Figure 23. Response rates for runs 1 and 2 under the All Bran™ condition are plotted as a function of the FR value. The curved lines were fit by Equation 4.

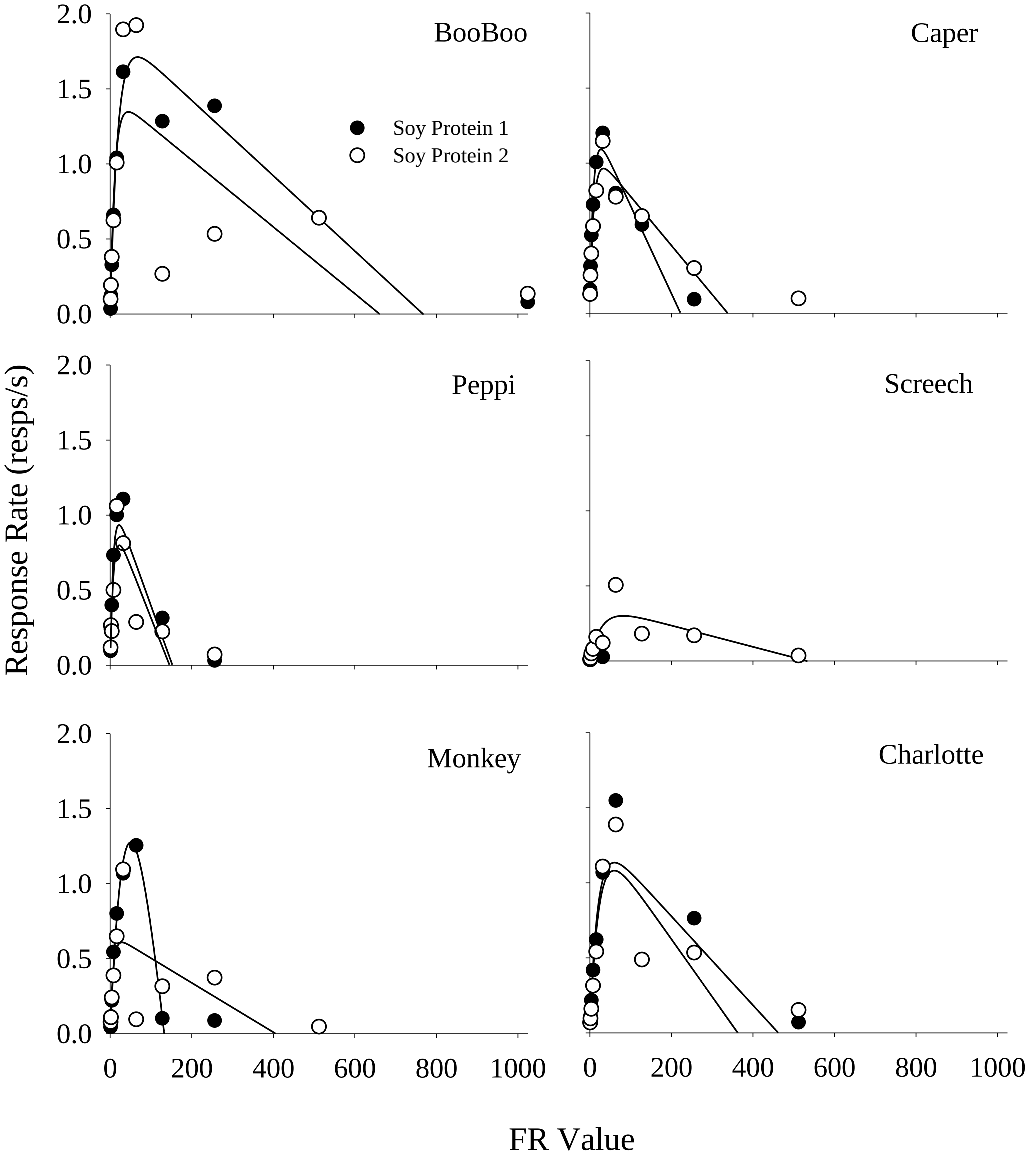

Figure 24. Response rates for runs 1 and 2 under the Soy Protein condition are plotted as a function of the FR value. The curved lines were fit by Equation 4.

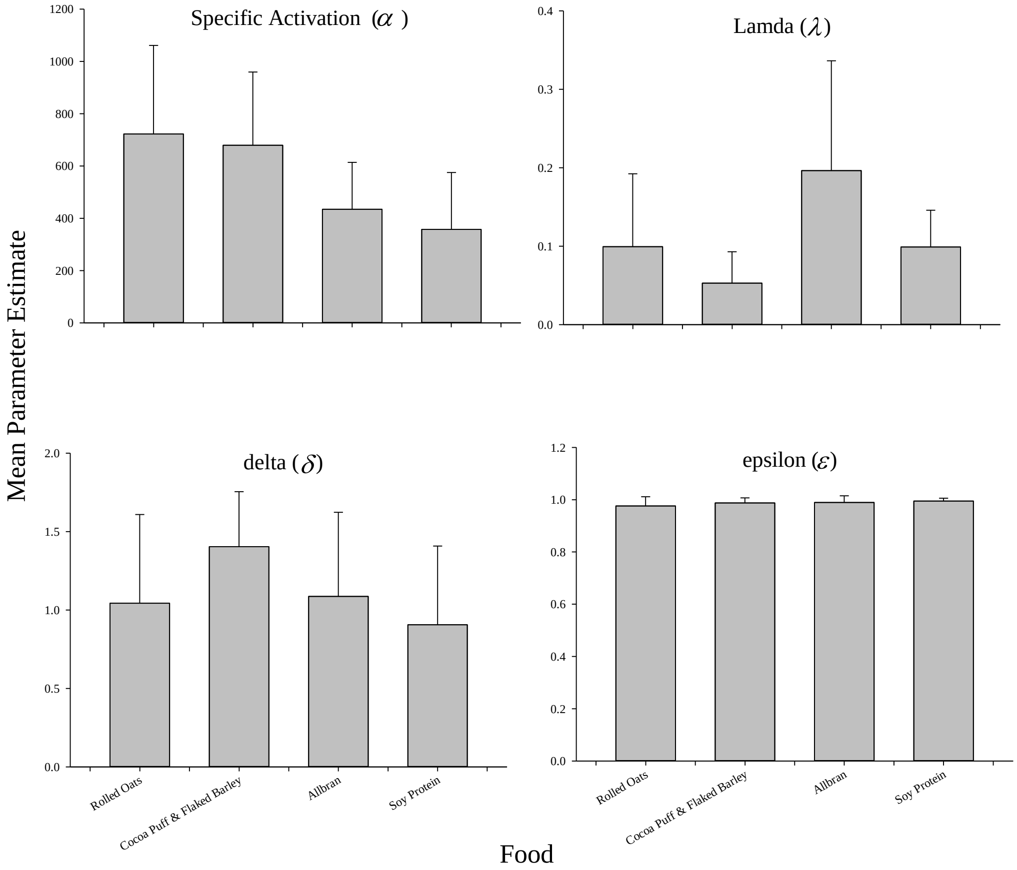

Figure 25. The average values for MPR parameter estimates α_s, λ, δ, and ε for each food type.

Hursh et al. (1988) Nonlinear Demand Function

Presented in Table 3 are the parameter estimates derived from fitting the Hursh et al. (1988) equation (Equation 1) to the relation between the number of reinforcers earned (consumption) and response requirements (price), averaged over both series for each of the foods. Also presented in Table 3 are the P_{max} values as calculated in Equation 2. For five of the possums, across all conditions Equation 1 fitted the data well, accounting for over 82% of the variance. The function accounted for over 82% of the variance for all possums for Rolled Oats. For the other foods Screeches data were variable, and for this possum the variance accounted for ranged from 60.9 – 82.6% across all foods.

For all five of the possums (except Screech), the largest initial demand (ln L values) occurred in the All Bran™ condition, and the smallest initial demand occurred in the Cocoa Puffs™ and flaked barley condition. For three of the possums, the steepest initial slope (b) were in the All Bran™ condition, and for the others the steepest initial slope were found across Soy Protein (Booboo), Rolled Oats (Peppi) and Cocoa Puffs™ and flaked barley (Screech). For three of the possums the smallest a values were found for the Cocoa Puffs™ and flaked barley condition, as were the largest P_{max} values for the same possums (Caper, Screech and Monkey). For possums Peppi and Charlotte, the smallest a values and the largest P_{max} values occurred in the Rolled Oats condition, and Booboo showed similar patterns but for the Soy Protein condition.

Hursh and Silberberg's (2008) Exponential Equation (k set as largest consumption data)

Presented in Table 4 are the parameter estimates of the exponential function (Equation 3) when fitted to the consumption (number of reinforcers) and price (FR value), averaged over both series for each possum and each food. The value of k for each possum was determined by the maximum range of consumption across all the foods for that possum, and the values for α (essential value) were divided by 1000 to make comparisons easier. The values of initial consumption (ln Q_0), variance accounted for (% VAC) and P_{max} are all displayed. For five of the possums, the function from Equation 3 fitted the data well as it accounted for over 85% of the variance, and in most cases the %VAC value was above 90%. For the possum Screech, the variance accounted for ranged from 71% - 93%.

For all possums, initial consumption was the largest for the All Bran™ condition, and for four of the possums, Cocoa Puffs™ and flaked barley showed the smallest ln Q_0 values. For three of the possums, the Cocoa Puffs™ and flaked barley condition showed the largest P_{max} values, and for all possums, the All Bran™ condition had the smallest P_{max} values. The values for α across all possums were higher for Cocoa Puffs™ and flaked barley than they were for Rolled Oats, for four of the possums α was overall lowest for All Bran™, and for four of the possums the α values were the second smallest for Soy Protein.

Comparison of Hursh et al. (1988) parameter a from Equation 1, Hursh and Silberberg's parameter alpha (a) from Equation 3, and Killeen and Sitomer's (2003) parameter specific activation(a_s) from Equation 4.

Presented in Figure 26 is the comparison of parameters *a* and α given by each of the two behavioural economic models, and α_s from the MPR model. The figure shows that there is a weak correlation between the parameter estimates and a flat relation is shown between α and α_s.

Paired-Stimulus Assessment

Presented in Figure 27 is the percentage of times each of four foods (Rolled Oats, Cocoa Puffs™ and flaked barley, All Bran™ and Soy Protein) were chosen out of a total of up to 60 trials across all six possums. For possums Booboo, Peppi and Monkey, Rolled Oats was selected the most times across the four foods; however possums Caper, Screech and Charlotte showed overall preference for All Bran™, Soy Protein, and Cocoa Puffs™ and flaked barley.

Table 3.

Hursh et al. (1988) nonlinear equation (Equation 1) showing the parameters a, b and ln L, fitted to the natural logarithm of the mean consumption data from all four foods. Also shown are the values for % VAC and P_{max}.

Condition	**Possum**	**ln *L***	***b***	***a***	**% VAC**	P_{max}
Rolled Oats	Booboo	5.14	-0.088	0.016	86.3	56
	Caper	6.48	-0.492	0.011	88.2	47
	Peppi	5.84	-0.468	0.005	84.3	113
	Screech	4.83	-0.199	0.009	82.6	89
	Monkey	4.63	-0.095	0.015	82.8	61
	Charlotte	4.86	-0.278	0.007	87.3	105
Cocoa Puffs™ and flaked barley	Booboo	4.71	-0.030	0.016	87.7	60
	Caper	5.54	-0.336	0.010	85.6	64
	Peppi	5.43	-0.367	0.020	83.9	32
	Screech	5.11	-0.564	0.001	79.4	541
	Monkey	4.22	-0.235	0.008	87.0	99
	Charlotte	4.51	-0.171	0.010	87.8	87
All Bran™	Booboo	6.03	-0.241	0.013	87.0	59
	Caper	6.92	-0.565	0.014	87.8	32
	Peppi	5.97	-0.037	0.101	82.9	9
	Screech	4.78	-0.115	0.032	60.9	28
	Monkey	6.09	-0.462	0.010	84.0	53
	Charlotte	5.84	-0.332	0.010	87.2	64
Soy Protein	Booboo	5.54	-0.258	0.006	83.4	121
	Caper	6.00	-0.300	0.017	86.5	41
	Peppi	5.79	-0.240	0.027	82.8	28
	Screech	3.05	0.188	0.059	65.3	20
	Monkey	4.93	0.136	0.035	87.3	32
	Charlotte	5.09	-0.178	0.010	82.6	82

Table 4.

Hursh and Silberberg's (2003) exponential equation (Equation 3) with the parameters ln Q, and α, and the values of k derived from the function of Equation 3 with k set as the maximum range of consumption data for each possums across conditions. Also included are the % VAC and the P_{max} values (in units of price (FR value)).

Condition	**Possum**	**ln Q_0**	***k***	**α / 1000**	**%VAC**	**P_{max}**
Rolled Oats	Booboo	2.20	2.00	0.027	0.98	49.60
	Caper	2.61	2.00	0.016	0.98	29.28
	Peppi	2.25	2.00	0.019	0.85	58.39
	Screech	2.01	2.00	0.039	0.93	63.28
	Monkey	1.98	2.00	0.046	0.96	53.08
	Charlotte	1.96	2.00	0.036	0.95	68.41
Cocoa Puffs™ and flaked barley	Booboo	2.07	2.50	0.038	0.97	47.27
	Caper	2.25	2.81	0.025	0.97	42.35
	Peppi	2.22	2.70	0.050	0.93	23.34
	Screech	1.88	2.23	0.050	0.71	66.12
	Monkey	1.70	2.34	0.067	0.95	69.98
	Charlotte	1.87	2.43	0.045	0.97	67.44
All Bran™	Booboo	2.54	2.50	0.016	0.99	38.73
	Caper	2.82	2.81	0.015	0.99	18.94
	Peppi	2.64	2.70	0.055	0.99	8.16
	Screech	2.16	2.23	0.108	0.77	15.97
	Monkey	2.51	2.34	0.029	0.96	25.16
	Charlotte	2.40	2.43	0.023	0.99	39.12
Soy Protein	Booboo	2.30	2.50	0.016	0.96	67.68
	Caper	2.49	2.81	0.020	0.98	30.13
	Peppi	2.48	2.70	0.033	0.97	19.81
	Screech	1.39	2.23	0.365	0.73	28.05
	Monkey	2.25	2.34	0.047	0.94	27.85
	Charlotte	2.14	2.43	0.027	0.94	60.01

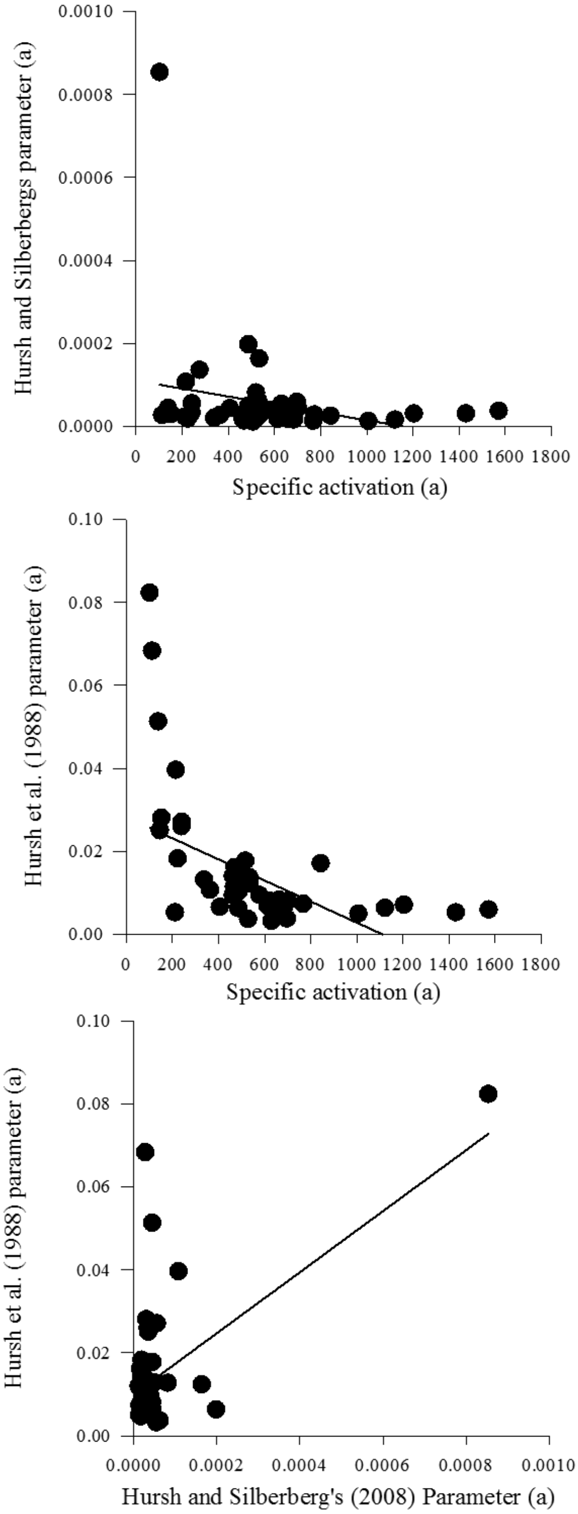

Figure 26. The parameter estimates *a*, (α) given in each of the behaviour economic equations (Equation 1 and Equation 2) and parameter α_s given in the MPR equation (Equation 4) compared against one another.

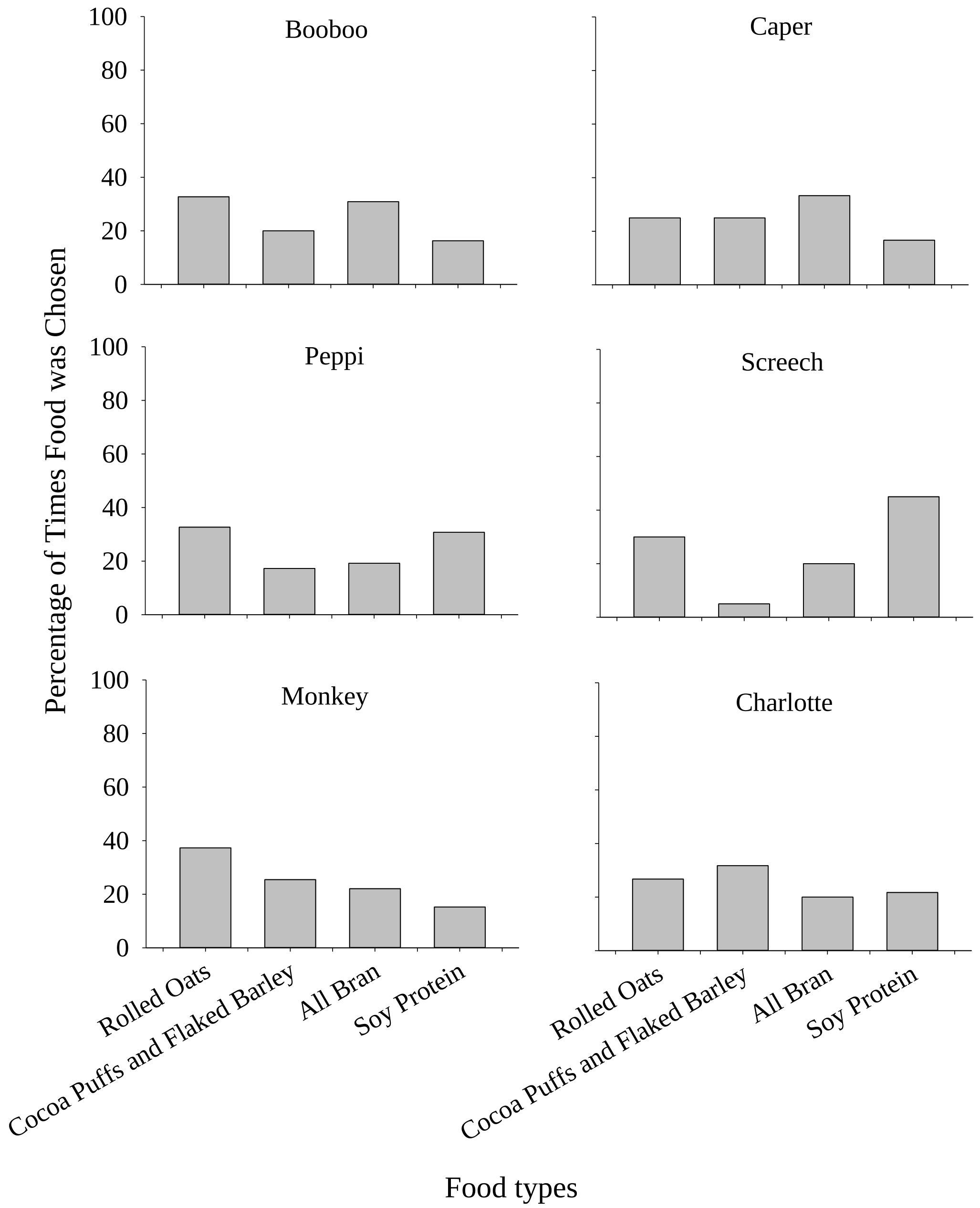

Figure 27. Percentage of times each food was selected by a possum, relative to the number of times they were presented under a paired-stimulus (PS) assessment.

Discussion

Performance on FR Schedules

This experiment examined the effects of different food types (Rolled Oats, Cocoa Puffs™ and barley, All Bran™ and Soy Protein) on the overall response rate, running response rate and post-reinforcement pause of possum under increasing FR schedules. Previous research (e.g., Armistead, 2009; Cronin, 2012; Foster et al., 1997; Foster et al., 2009; Grant et al., 2014; Hudson et al., 1999; Stuart, 2013) has described animal behaviour on increasing FR schedules. Past results have generally shown that as FR requirements increase, overall response rates were bitonic, running response rates tended to decrease, and PRPs increased. These patterns are consistent with the general changes in behaviour shown in the present study.

One aim of the present study was to see to what degree the different feeds maintained behaviour as the FR schedules were increased. Consistent with similar findings reported by Cronin (2012) for possums, all foods used in the experiment maintained responding as the FR requirements increased but to different degrees.

First, in general, overall response rates either increased over small FR values and then remained constant as the FR increased further, or gave a bitonic function as they decreased over the larger FR values. These findings are similar to those already reported with other animals (Armistead, 2009; Hursh, 1980; Hursh, 1984; Stuart, 2013).

Previous research has described how different food types can affect performance on FR schedules (e.g., Armistead, 2009; Cronin, 2012; Grant et al. 2014; Foster et al. 2009) and the present results can be compared with those earlier findings. The overall response rates for all possums were greater, regardless of the FR, for All Bran™, Soy Protein, and Rolled Oats conditions (see Figure 5). There were variations in the way the overall response rate changed across some possums, with responding remaining at low levels across small FRs for Cocoa Puffs™ and barley and All Bran™ (Peppi, Monkey and Screech), but this is consistent with Cronin's (2012) findings, where there were differences in the way overall response rate changed across the foods for some possums.

One question was the relation between preferences for the foods and overall response rate. Half of the possums showed the highest overall response rate for foods that were considered more preferred (ranked either first or second in the preference test). This is consistent with previous findings (e.g., Armistead, 2009; Cronin, 2012) which suggested more preferred foods maintain higher overall responding at larger FR values than less preferred foods

The running response rates for each food for all possums decreased as FR requirements increased (see Figure 10), and this was consistent with previous findings with other animals (Armistead, 2009; Foster et al., 1997). Four of the possums (excluding Booboo and Screech) showed higher running response rates at small to mid ratio values for the Soy Protein condition, and four of the possums (Booboo, Caper, Monkey and Charlotte) showed lower running response rates for the Rolled Oats and Cocoa Puffs™ and flaked barley condition, regardless of the FR value. Armistead (2009) reported that different foods produced different running response rates with her horses, consistent with the present findings.

Half of the possums showed that the foods which maintained higher running response rates at small to mid FR values were foods that were identified as being more preferred. This aligns with what Armistead (2009) found, that foods that were more preferred maintained the highest running response rates at smaller FR values.

A consistent pattern found in the response rates (both overall response and running response) in the present study, and that supports pervious findings (e.g., Armistead, 2009; Cronin, 2012), was that half of the possums showed greater responding (overall response and running response) across FR values for foods that were identified as being more preferred (ranked either first or second in the preference assessment). However, for the remaining possums, the foods that showed greater levels of responding over small to mid FR values were identified as being less preferred. Foster et al. (2009) reported that at smaller ratios, less preferred foods showed higher overall response rates with their hens. In both instances (overall response and running response) half of the possums showed results consistent with Foster et al. (2009) as the foods which maintained greater initial levels of responding were identified as being less preferred.

The PRPs, for each food across possums, generally increased as the FR requirements increased, and this coincides with what has been reported in previous studies (e.g., Armistead, 2009; Cronin, 2012; Grant et al., 2014; Foster et al., 1997; Hudson et al., 1999; Stuart, 2013).

All Bran™ and Soy Protein yielded the longest PRP values regardless of the FR size in all cases except one, Monkey, who instead showed longer pauses for Cocoa Puffs™ and barley. Some of the possums (Peppi, Screech and Monkey) PRPs for certain foods (All Bran™, Soy Protein, and Cocoa Puffs™ and flaked barley) showed longer PRPs across small to mid FR values, than over larger FR values. Previous research with hens (e.g., Foster et al., 2009) suggested that different PRPs across food types could be due to either responding having stopped earlier in a session, or because certain foods resulted in longer pause durations. Foster et al. (2009) also suggested that more preferred foods may result in longer PRPs over smaller FR values, and this could explain the PRP behaviour for four of the possums (Caper, Screech, Monkey and Charlotte), as the foods that elicited higher PRPs across small FR values were identified as being more preferred. Alternatively, Armistead (2009) found that stimuli that produced higher response rates, generally produced lower PRPs. This is consistent with response rate and PRP data from the present study, but only across the smaller FR values. In all cases, the foods that produced higher rates of response (overall response and running response) showed smaller PRPs across small to mid FR values.

MPR

The data obtained from the FR schedule assessment was also used to test predictions of MPR (Equation 4) to predict response patterns. Generally, across all possums, responding increased over small FR values, and then decreased as the FR requirement incremented. The predictions of MPR described the bitonic response rate functions well and the pattern of responding was consistent with the pattern of responding reported by others with hens (e.g., Bjarnesen, 2011; Stuart, 2013), rats (Bizo, Kettle, & Killeen, 2001; Reilly, 2003), and pigeons (Bizo & Killeen, 1997).

The parameter estimates (α_s, λ, δ, and ε) from Equation 4 were derived from fits of the model to the data. Each parameter estimate reflects a different aspect of responding such as the rate of response elicited by a stimulus (α_s), the rate of decay of response traces (λ), the minimum time required to emit a response (δ), and the degree to which target responses are erased from memory (ε) (Killeen

& Sitomer, 2003). It was expected that different food types may be seen to differ in quality, which would result in variance across response rates, and that this change could be captured by the parameter α_s. This was found in the present study as the mean estimates given by the parameter α_s across the possums showed that specific activation (α_s) was highest for Rolled Oats, and lowest for Soy Protein. These findings were consistent with further analysis that showed α_s was significantly different across food types. These results are consistent with the general preferences of the possums as all six possums ranked Rolled Oats either first or second in the preference assessment, and four of the possums ranked Soy Protein as less preferred (ranked either third or fourth).

A question in the present study was how did the foods identified as being more preferred in the preference assessment compare to the foods that yielded the largest and smallest α_s values for each individual possum. Booboo showed that the largest α_s values were for Cocoa Puffs™ and flaked barley (ranked third) and the smallest were for Rolled Oats (ranked first). Caper showed largest α_s values for Rolled Oats (ranked second) and smallest were for Soy Protein (ranked fourth). Peppi showed largest α_s values for Rolled Oats (ranked first) and the smallest were for Soy Protein (ranked second). Screech showed largest α_s values for Rolled Oats (ranked second) and the smallest were for Soy Protein (ranked first). Monkey showed largest α_s values for Rolled Oats (ranked first) and smallest were for Soy Protein (ranked fourth), and Charlotte showed the largest α_s values for Cocoa Puffs™ and flaked barley (ranked first) and smallest were for Soy Protein (ranked third).

In only one instance (Booboo) was the food that yielded the highest α_s value not recognised as one of the two preferred foods, and three of the possums (Booboo, Peppi and Screech) showed lower values of α_s for foods that were identified as being more preferred in the PS assessment (ranked either first or second). These results generally show that MPR was able to make good predictions on performance across different foods.

As there was a large number of variance in responding for the foods across both series of runs, this may have had an impact on the other parameter estimates (λ, δ, and ε). The mean estimates for λ were largest for All Bran™ and smallest for Cocoa Puffs™ and flaked barley. When looking at the parameter estimates for

δ Cocoa Puffs™ and flaked barley were the highest and Soy Protein the smallest, and estimates for ε remained consistent across the foods.

The MPR equation (Equation 4) for most possums has accounted for the variance in the data well, and generally gives an accurate account of the mean data. Mean R^2 values range from 0.620 – 0.896. These values are slightly lower than what has been reported previously with rats (0.79 - 0.98, Reilly, 2003), but are comparable and a little better than other the fits produced by fits to data from hens which ranged from 0.25 – 1 (Bjarnesen, 2011; Stuart, 2013). As mentioned earlier, there was great variability in response rates across animals, for foods and each series of runs. The reported averages were of the R^2 values, per food, per run, however, if individual fits were to be reported for each possum and each run across all foods the range would be from 0.260 – 0.896.

The reason for such variance in responding across certain possums is not clear. The MPR model struggled with such variance in response rates, particularly when accounting for responses at larger FR values that did not show smooth bitonic functions. This type of responding was consistent across all possums, and therefore, could have affected the models ability to predict behaviour. Future research could look to have multiple days at each FR value in order to give the subject more experience at each schedule, which could in turn provide a better estimate of the performance at each ratio value. Or perhaps increasing the FR schedule at smaller values could result in more accurately described behaviour. Furthermore, Bizo and Killeen (1997) reported that FR schedules produced higher response rates at smaller ratios than variable-ratio schedules (VR), and that the slope of the inverted U is more gradual for VR schedules than for FR schedules. Future research could also study the affect different foods had on performance on VR schedules and compare the findings to performance on FR schedules.

One possible factor that could have had an impact on the response rates may have been due to the health of the possums, in particular Peppi and Screech, who both showed low R^2 values across certain foods and both possums had experienced illness throughout experimenting. Possum illness was handled with the upmost care and possums were removed from experiments until they were showing signs of better health, but there is still the chance that there health may have affected particular runs for particular foods.

Behavioural Economics

The consumption data shown in Figure 20, gives demand functions that are consistent with pervious research (e.g., Cronin, 2012; Foster et al., 2009; Hursh, 1980; Hursh, 1984; Stuart, 2013). Generally, across smaller FR values there are small increases in consumption, but as FR requirements increased consumption decreased. For five of the possums (Booboo, Caper, Peppi, Monkey and Charlotte) across small FR values, All Bran™ showed the greatest initial levels of consumption, and for Screech this occurred for the Cocoa Puffs™ and barley condition. Previous research (e.g., Bruce, 2007; Flevill, 2002; Grant, 2005) suggests that foods that are less preferred produce higher consumption at small FR values. This is consistent with the findings in the present study, as for four of the possums (Peppi, Screech, Monkey and Charlotte) the foods that showed largest initial consumption were identified as less preferred (ranked lowest or second lowest). Conversely, Armistead (2009) found for her horses the food that was more preferred gave greater initial levels of consumption, and this is what was shown for possums Booboo and Caper, where All Bran™ was identified as being more preferred (ranked highest or second highest).

Hursh et al. (1998) Nonlinear Equation

An aim of the present study was to apply Hursh et al. (1998) nonlinear equation (Equation 1) to the consumption data. Equation 1 described the trend in the observed demand well, with all of the possums except one showing %VAC values above 82%. The only possum to show values below this was Screech. The values of the other possums are similar to those reported in previous research (e.g., Cronin, 2012; Foster et al., 1997; Hursh et al. 1988; Stuart, 2013), and so the %VAC values below 82% may be due to the idiosyncratic behaviour of the one particular possum.

The functions generally showed mixed elasticity. All the values for parameter b (except two instances) showed initial inelastic demand at the smaller FR values, and in comparison, all the values for parameter a were smaller positive numbers, suggesting that as the FR requirement increased, the demand function changed from inelastic to elastic. The P_{max} values were calculated using Equation 2, and showed the ratio value where the demand function became steeper than -1, shifting from inelastic to elastic. For possums Caper, Screech and Monkey, the largest P_{max} values were shown in the Cocoa Puffs™ and flaked barley condition, whereas Peppi and Charlotte showed largest P_{max} values in the Rolled Oats condition, and for Booboo these were found in the Soy Protein condition

When comparing the results of the preference assessment with the foods that elicited the largest and smallest P_{max} values there were mixed results. Booboo showed largest P_{max} values for Soy Protein (ranked fourth) and the lowest for Rolled Oats (ranked first). Caper showed the largest values for Cocoa Puffs™ and flaked barley (ranked second) and the lowest for All Bran™ (ranked first). Peppi showed the largest values for Rolled Oats (ranked first) and lowest for All Bran (ranked third). Screech showed largest values for Cocoa Puffs™ and flaked barley (ranked fourth) and the smallest for Soy Protein (ranked first). Monkey showed the largest values for Cocoa Puffs™ and flaked barley (ranked second) and lowest for Soy Protein (ranked fourth), and Charlotte showed the largest values for Rolled Oats (ranked second) and lowest for All Bran™ (ranked fourth).

For possums Screech and Booboo, the two foods where maximal responding was the highest (Cocoa Puffs™ and flaked barley and Soy Protein), were identified as being the least preferred food, and only Peppi showed maximal responding for the food that was recognised as being the most preferred (Rolled Oats). This is contrary to what has been found in previous research (e.g., Flevill, 2002; Grant, 2005) where larger P_{max} values were generally produced for more preferred foods.

For two of the possums, Screech and Monkey, the Soy Protein condition produced positive *b* estimates (0.188 and 0.136), suggesting that this particular food type, demand remained elastic through the function. This is also reflected in their P_{max} values which show the lowest P_{max} values (20 and 32) across the four foods for these two possums. These results are surprising as previous research has found in an open economy the demand for reinforcement would show mixed elasticity (e.g., Armistead, 2009; Stuart, 2013), however, these results are more consistent with what Hursh (1980; 1984) has described for a closed economy. Similar findings were found by Cronin (2012) with a possum, for the food type San Bran™ (All Bran™ equivalent). Cronin (2012) suggests that this could have been due to the limited number of actual data points he found, and this could have led to inaccurately described demand functions.

In the present study there are no other consistent patterns for the two parameters measuring elasticity (*a* and *b*) across foods, however comparisons can be made between ln L and P_{max}. For example, possums Peppi and Screech showed that the food that produced the largest ln L value, also showed the largest P_{max} value, however, possums Caper and Monkey showed that the food that produced the largest values of initial consumption (ln L), produced the lowest P_{max} values. This result is similar to findings by Cronin (2012) and Stuart (2013) who also found that when the ln L values were higher, P_{max} values were lower.

Hursh and Silberberg's (2003) Exponential Equation

As mentioned earlier, Hursh and Silberberg argue that the exponential equation (Equation 3) is superior to that of the Hursh et al. (1988) nonlinear equation, in that it provides a single parameter, a, to determine the essential value of a commodity. In order to compare the value of different foods, k must remain constant across the foods for each possum. In the present study, k for each possum was determined by the maximum range of consumption across all the foods for that possum. This allows comparison of α across foods for each possum. Hursh and Silberberg (2008) argued that α should not be affected by scalar properties of the reinforcer such as quantity or magnitude. One aim of the present study was to see how α varied with different foods types. If the foods were simply different substitutes for each other, then α should not change, but if the foods were not just substitutes but differed along other dimensions, then a change in α across food types might be expected. Results showed that there were some consistent changes in α for different foods across possums. For all possums, α values for Cocoa Puffs™ and flaked barley were higher than α values for Rolled Oats. Four possums showed that All Bran™ gave overall lower values of α and four possums also showed Soy Protein to be the second most valued food. This suggests that α was changing with these foods. However, despite these consistencies an ANOVA applied to the α values across foods showed no significant differences resulting from the foods [F (3) = 0.942, p = 0.4290]. This suggests that the α was not changed by the food type.

Previous research (e.g., Cassidy & Dallery, 2012 (in their open economy); Foster et al., 2009; Grant et al., 2014) has reported a change in the value of α across different foods with different animals. Cassidy and Dallery (2012) found with rats, α changed with changes in the magnitude of the reinforcer (one pellet or two pellets), and the larger the reinforcer the lower the essential value. Grant et al. (2014) reported similar findings with hens for different durations of reinforcer access and Foster et al. (2009) compared the values of α across wheat, puffed wheat, and honey puffed wheat with hens and found that the more preferred food had the lowest essential value. These finding are consistent with the present study, in that the foods that were found to be less preferred in the preference assessment (All Bran™ and Soy Protein, ranked either third or fourth), gave the smallest α values, and were therefore determined as the most valued foods using Equation 3. Therefore, the findings from the present study, along with those mentioned above, suggest that α could be affected by scalar properties. On the other hand, the lack of significant differences in the present α values across foods could be taken to mean that it did not change with food type. Which interpretation best remains for further research.

When comparing the results of the preference assessment with the foods that showed the largest and smallest values of α there were mixed results. Booboo showed the largest α values for Cocoa Puffs™ and flaked barley (ranked third) and the smallest equal values for All Bran™ (ranked second) and Soy Protein (fourth). Caper showed the largest values for Cocoa Puffs™ and flaked barley (ranked second) and smallest for All Bran™ (ranked first). Peppi showed the largest values for All Bran™ (ranked third) and the smallest for Rolled Oats (ranked first). Screech showed the largest values for Soy Protein (ranked first) and the smallest for Rolled Oats (ranked second). Monkey showed the largest values for Cocoa Puffs™ and flaked barley (ranked second) and the smallest for All Bran™ (ranked third), and Charlotte showed the largest values for Cocoa Puffs™ and flaked barley (ranked first) and the smallest for All Bran™ (ranked fourth).

If the values of α were to correlate with the results of the preference assessment, the foods that had the smallest values of α should show the most preferred foods (ranked either first or second), and the foods that had the largest values of α should show the less preferred foods (ranked either third or fourth). For three possums (Caper, Peppi and Screech) the foods that showed greater essential value (smaller estimates of α), were also found to be more preferred. But, in only two instances (Booboo and Peppi) were the foods that showed the smallest essential value (higher estimates of α), also found to be less preferred.

The results for all other possums did not show a relation between the values of α and the foods that were found to be more or less preferred.

The function from Equation 3 (Hursh and Silberberg, 2008) describes the data well, and for five of the possums, accounted for over 85% of the variance. Screech showed the lowest value for %VAC which was 71%, however, this is considerably higher than the lowest estimated fit provided by the Hursh et al. (1998) equation (Equation 1) suggesting that Equation 3 fitted to the data better. This is consistent with previous findings by Armistead (2009) who also compared both demand equations. When comparing the P_{max} values obtained through Equation 3, with those produced in Equation 2, there are consistent similarities. For three of the possums, P_{max} was largest in the Cocoa Puffs™ and flaked barley condition, for two of the possums this was found in the Rolled Oats condition, and for Booboo this was found in the Soy Protein condition. The only consistent finding across all six possums was that the largest ln Q_0 values and the smallest P_{max} values occurred for the All Bran™ condition and for four of the possums this same condition also produced the smallest a values (values for Caper were constant and values for Booboo were the same for All Bran™ and Soy Protein). Previous research (e.g., Cronin, 2012; Stuart, 2013) has found similar results when applying the Hursh et al., (1998) equation (Equation 1) as they found that when Ln Q_0 was largest, P_{max} was smallest.

It was also found in the present experiment that for four the possums, Cocoa Puffs™ and flaked barley had smaller initial consumption for the demand function (i.e., smaller ln Q_0 values) than the other foods. For all four possums, Cocoa Puffs™ and flaked barley was ranked either first or second in the preference assessment, therefore suggesting that the more valued the reinforcer, the less demand across small FR values. These findings are in accordance with what Foster al., (2009) found when comparing different foods, and Stuart's (2013) findings when comparing ITI and delay.

A limitation of this study which could have affected the value of α was the similarity of foods used. If this study was to be replicated, it could be of interest to try different foods that aren't substitutable e.g., Cameron (2013) provides comparisons of foods that are consumed frequently by possum in the wild, ranging from chicken and locusts to eggs and berries. Future research could look at implementing these foods into a similar study to see what affect foods that are non-substitutable have on the estimates of α.

Another suggestion for future research could be to assess the effect different amounts of food have on the estimates of α, as done previously with rats (Cassidy & Dallery, 2012) and with hens (Grant et al., 2014). It could be of interest to see whether possum behaviour is similar to what has been seen in other species when the magnitude of a reinforcer is manipulated.

Comparing MPR and Behavioural Economics

The last aim of the present study was to compare two demand equations and MPR using the same set of data. The two different demand equations were fitted to the consumption data; Hursh et al. (1988) nonlinear equation (Equation 1, Table 3) and Hursh and Silberberg's (2009) exponential equation (Equation 3, Table 4). Both equations described the data well for all but one case, with the variance accounted for being higher than 82% for Hursh et al. (1998) and 85% for Hursh and Silberberg (2008), respectively. The MPR predictions also described the data adequately, reporting R^2 values ranging from 0.263 – 0.987, however, for majority of the possums for each food type and each run, variance accounted for remained above 0.600.

While these two models do not come together formally, they both analyse the same data set and therefore comparisons can be made. Both models claim to include parameters that can reflect the value of a reinforcer. In MPR, specific activation (α_s) reflects the value of a reinforcer as the number of responses a single reinforcer obtains, or the level of motivation that is elicited by a reinforcer. In Hursh and Silberberg's (2008) equation (Equation 3) the parameter alpha (α) reflects the essential value. As both parameters (α_s and α) are said to measure the value of a reinforcer, it could be assumed that there would be a relation between the values of each parameter. What was found in the present study is that the less preferred foods had lower values of α (higher essential value), which should have shown a negative relation between α and α_s. If α values were lower for more preferred foods (as might be predicted), then this would have shown a positive relation between α and α_s. However, what was found in Figure 26 is that the relation between α and α_s remained flat, and there was no significant correlation between α and α_s ($p = 0.0926$). Further analysis has previously shown that different foods had a significant effect on parameter α_s [$F(3) = 4.808$, $p = 0.006$], supporting the previous findings that suggested specific activation changed across food types, but the same analysis for Hursh and Silberberg's (2008) parameter α showed there was no significant differences across foods [F(3) = 0.942, p = 0.4290]. These analyses, then, support the finding of no relation between α and α_s as shown in Figure 26.

These findings are different from those of Stuart (2013) when analysing the parameter values α and α_s across different delays (4-s and 16-s), as she found a moderately strong correlation between the parameter values in the 16-s ITI (p = 0.29) and delay (p = 0.44) conditions, suggesting minimal differences in the parameter values for those conditions. Results for the 4-s ITI and delay conditions in that study did not show the same relationship between parameters as the correlations were weak (4-s ITI) and moderately strong but negative (4-s delay). Stuart (2013) suggests that the differences between the two conditions (16-s and 4-s) could be because ITI or delay has more of an impact at shorter durations, therefore creating more variability in parameter values. Her data may reflect the fact that there were differences in alpha across these conditions and that α is affected by scalar properties.

In sum, the present study found that different food types did affect possum performance on FR schedules. This was shown through different degrees of responding for each individual possum in the overall response rate, running response rate, and for post-reinforcement pause. The data was described well by both behavioural economics equations, and by the MPR equation, but there were inconsistencies between the parameter estimates, alpha (a) and specific activation (α_s) which was shown through a weak correlation (p = 0.0926). Specific activation (α_s) showed a significant difference in value across the foods, and these results were consistent with what was found for the foods in the preference assessment. There was no significant difference across foods for alpha (α) and the results from this analysis were consistent with some of the possum preferences for the foods but not for all animals.

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