INTERNATIONAL JOURNAL OF COMPARATIVE PSYCHOLOGY

2015, 28
Dani Brunner Editor
Research Article
Peer-reviewed

Assessment of Demand for Food using Concurrent PR and FR Schedules in the Brushtail Possum (*Trichosurus vulpecula*)

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The aim of this study was to compare the demand by possums for foods under different arrangements of concurrent progressive-ratio and fixed-ratio schedules of reinforcement. In Experiment 1, every possible food pair made up of berries, chicken, egg, foliage, insects, and mushroom was presented (30 pairs in total). The requirement on the progressive-ratio schedule increased within a session and the fixed-ratio was kept constant at 30. In Experiment 2, a subset of the foods from Experiment 1 were used (chicken, mushroom, egg, and berries) and in separate conditions the fixed-ratio was either 30 or 10 responses. In Experiment 3, the foods were the same as used in Experiment 2 and the progressive-ratio schedule increased every five sessions and the fixed-ratio was kept constant at 30. Exponential models of demand were applied to consumption rates to compare the parameters of initial demand, essential value and P_{max}, and break point and cross point across foods. The models described the data well and consumption rates were similar when the incrementing schedules increased within- and across sessions. Demand was highest for berries, egg, and locust in Experiment 1 and egg and chicken in Experiments 2 and 3. This finding has practical implications for understanding possum food preferences in the wild as a function of other available food sources and for informing pest control strategies of potential lures.

Possums are a pest species in New Zealand requiring intensive pest control as they consume native and exotic forest and plant life, insects, fruit, and birds and their eggs (Nugent, Sweetapple, Coleman, & Suisted, 2000). Single- and paired-preference assessments of foods eaten in the wild by the brushtail possum (*Trichosurus vulpecula*) in New Zealand found that insects, fruit, and egg were generally more highly preferred than mushroom, chicken, and foliage. Preference for individual foods was idiosyncratic across possums (Cameron, Bizo, & Starkey, 2013). One limitation of preference assessments is that choices carry no response cost (DeLeon, Iwata, Goh, & Worsdell, 1997; Fisher et al., 1992). They also do not allow for the assessment of relative demand for different foods. Of specific interest, with regard to the question of food preference in the possum, is how much effort a possum would expend to obtain one food type over another. Therefore, in this study we investigated the strength of preference using a method that required possums to work for different food types.

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To measure the relative demand for a commodity, subjects are required to make multiple responses to obtain it (e.g., Hursh, 1980, 1984). Fixed ratio (FR) schedules have been used to measure the demand for commodities (e.g., Foster, Sumpter, Temple, Flevill, & Poling, 2009; Hursh, Raslear, Shurtleff, Bauman, & Simmons, 1988). When the ratio requirement increases across sessions, these have been referred to as progressive fixed-ratios (PFR) schedules (e.g., Griffiths, Findley, Brady, Dolan-Gutcher, & Robinson, 1975; Jarmolowicz & Lattal, 2010), as distinct from when the ratio requirement increments within sessions as for progressive ratio (PR) schedules (e.g., Killeen, Posadas-Sanchez, Johansen, & Thrailkill, 2009). Under PR schedules the ratio requirement typically increases after each reinforcer delivery, thus only one reinforcer is gained at each ratio (Hodos, 1961). Generally, response rates are higher and more variable as ratio requirement increases under PR schedules compared to FR schedules and demand for food is more inelastic under FR schedules compared to PR schedules (Baron & Derenne, 2000; Foster, Temple, Cameron, & Poling, 1997).

On PR schedules the largest completed ratio before animals cease responding has been referred to as the extinction ratio (Skinner, 1938), or the break point (Hodos, 1961). The greater the extinction ratio or breakpoint the more *valued* the commodity is assumed to be (Hodos & Kalman, 1963; Stafford & Branch, 1998). Break points are higher under FR schedules compared to PR schedules (Foster et al., 1997).

When different commodities are made available on concurrent schedules the choice of one alternative to the exclusion of another can also be considered a measure of preference (Findley, 1958). The use of concurrent schedules requires the subject to *persist* in responding to gain access to one of two commodities under two available schedules of reinforcement (Schwartz & Baer, 1991). When an incrementing schedule is presented concurrently with another schedule that is fixed, responding for one commodity over another can be measured (Hodos & Trumbule, 1967), as well as the degree of substitutability of a commodity for another (Hursh, 1980; 1984). Concurrent PR FR and PFR FR schedules have been used to evaluate the demand for different drugs (e.g., Allen & Leri, 2010), and demand for different foods by hens (*Gallus gallus domesticus*) (Foster et al., 2009), Sprague-Dawley rats (*Rattus norvegicus*) (Madden, Smethells, Ewan, & Hursh, 2007) and pigeons (*Columba livia*) (Bhatt & Wasserman, 1987), and to understand foraging systems with rhesus monkeys (*Macaca mulatta*) (Hineline & Sodetz, 1987), chimpanzees (*Pan troglodytes*) (Hodos & Trumbule, 1967) and pigeons (Neuman, Ahearn, & Hineline, 2000).

Models used in behavioral economics are useful for analyzing choice under schedule arrangements that manipulate price and the commodity. These types of experiments use quantitative accounts of performance to assess how much effort an organism will put into gaining a given commodity or when two commodities are substitutable (Hursh 1980, 1984). Exponential models of demand describe the relationship between the ratio requirement or *price* and consumption of a particular commodity (Hursh & Silberberg, 2008). Consumption of a commodity has been expressed variously as either a total amount (e.g., Foltin, 1991) or as a rate; as in reinforcers per ratio (Foster et al., 1997), reinforcers per day (e.g., Hursh & Natelson, 1981; Lea & Roper, 1977), reinforcers per session (e.g., Gunnarsson, Matthews, Foster, & Temple, 2000; Matthews & Ladewig, 1994), or reinforcers per hour (e.g., Hursh, 1978). Models of demand also provide mathematical accounts of cross point and substitutability using the cross-price demand model (Hursh et al., 2013).

In a concurrent PR FR or PFR FR procedure the equivalence point is where the two ratios are equal; and the cross point is the ratio where responding on both schedules is equal where after responding initially to the richer schedule, responding is of a lower rate than the other schedule (Bhatt & Wasserman, 1987). The distance between the cross point and equivalence point can indicate preference for one commodity over another and whether price has an influence over choice (Sørensen, Ladewig, Matthews, Kj, & Lawson, 2001). If responding under the incrementing schedule was to persist after the point where the two schedules have equal ratio requirements the cross point is *perseverative*. If responding to the constant FR schedule occurs when food under the incrementing schedule requires less effort to obtain the cross point is *conservative* (e.g., Allen & Leri, 2010; Hineline & Sodetz, 1987; Hodos & Trumbule, 1967).

The position of the cross point on concurrent ratio schedules provides clear indication of the substitutability of the commodities associated with them. When commodities are highly substitutable the cross point from the PR to the FR occurs at the point where those schedules are equal. When commodities are not substitutable the cross point will be larger than the equivalence point if demand of the commodity associated with the PR is higher than for the commodity associated with the FR schedule. The cross point will be smaller than the equivalence point if demand of the commodity associated with the PR is lower than for the commodity associated with the FR schedule. For example, Tustin (1994) with humans found that visual and auditory reinforcers were highly substitutable when on offer under PR FR schedules with the cross point equal to the point where the ratio requirements were equal. In comparison, when reinforcers were not substitutable the cross point occurred at a PR value that was larger than the FR requirement. In this case, the reinforcer on the PR was attention and the reinforcer on the FR was access to a visual stimulus.

In Experiment 1, the demand for six foods was tested using concurrent PR FR 30 schedules; in Experiment 2, the PR FR 30 procedure was repeated with four food pairs from Experiment 1 and the FR schedule was decreased to 10 responses in half of the sessions. In Experiment 3, the ratio requirement of the PFR schedule was increased every five sessions, and the FR schedule was 30 responses. It was expected that if a food associated with the incrementing schedule was more highly preferred compared with the food available under the constant FR schedule then more responding would be allocated to the incrementing schedule with break points at larger ratio values and perseverative cross points. If the food available under the constant FR schedule was more preferred break points would be lower for foods under the incrementing schedule and cross points would show conservative errors.

Experiment 1

Method

Subjects. Six brushtail possums (*Trichosurus vulpecula*; two female and four male) served as subjects. All were wild-caught and had been housed in captivity for 4-9 years (*M* = 6.8 years, *SD* = 2.0 years). All had previously participated in other taste preference experiments (Cameron et al., 2013). Possums were maintained at 85% ± 2.5% of their free feeding body weight (see Cameron, Bizo, & Starkey, 2014) and were weighed weekly. Over a two year period when Experiments 1–3 were conducted, average possum body weights deviated from target weights by between -0.18% and 2.62%. The body weight of P2 decreased by 4.75% requiring extra supplementary food during the experimental period.

All possums received supplementary rations of dock leaves (*Rumex obtusifolius*), apple, and food pellets (Camtech Manufacturing Ltd®, New Zealand) approximately two hrs after scheduled experimental sessions were completed. Possums had constant access to water throughout the experiment. The University of Waikato Animal Ethics Committee approved the use of animals for Experiments 1, 2, and 3 (protocol number 881).

Housing. The possums were kept in custom-built individual wire-netting cages (540-mm wide x 1050-mm high x 470-mm deep), with a shelf 700-mm above the floor and a nest box on the top of the cage. They were kept on a 12:12 h reversed dark/light cycle (lights off at 09:15 h) with minimal illumination supplied by red lamps during the dark period. Cleaning and maintenance occurred during the light rotation at about the same time each day.

Apparatus. Each home cage functioned as the experimental chamber. Two laboratory built magazines were attached to the outside of each of the cages. Each magazine unit was a white Perspex box with two openings: the top opening gave the possum 2-s timed access to food, beginning when the possum's head broke an infrared beam at the opening of the magazine, from a tin positioned on an adjustable platform that could ascend and descend via an electronic pulley system. A lever apparatus was positioned above the top opening to the magazine. Immediately above the left and right levers were yellow LED lights that when lit indicated that the schedules of reinforcement were in effect.

The six test foods presented during the experimental sessions were 60-g berries (Pams® Mixed Berries; thawed and drained of juice), 20-g locust (*Locusta migratoria*) cut into 10-mm pieces, 30-g mushroom (cut into 10-mm2 pieces), 30-g foliage (*Pseudopanax arboreus*, lamina and petiole of fivefinger leaves) cut into 10-mm pieces, 100-g whisked egg, and 60-g minced raw chicken breast. These foods were chosen as they were of types typically consumed by possums in the wild (e.g., Nugent et al., 2000). The amount of food in each tin was of a similar volume to cover the same surface area of the tin (Cameron et al., 2013).

Design. Each food item was paired with every other food item making 30 food pairs. For each food pair, the experimental procedure was conducted three times, one session per day over three consecutive days. Possums experienced one food pair per session. Across sessions presentations of food pairs were counterbalanced across the left and right side and the order of presentations was randomized across animals.

The experimental procedure comprised concurrently available PR FR schedules with a different food associated with each schedule. The ratio requirement on the right lever was a PR that increased according to a geometric series; 1, 2, 4, 8, 16, 32, 64, 128, 256, 512, and 1024 in each session. The ratio requirement on the left lever was an FR 30.

Trial Procedure. At the start of a session, the computer program activated one of the stimulus lights at random. The possum received a 2-s access to food. This was repeated with the other stimulus light, therefore the possum consumed both food types to be on offer prior to the session. When the experiment started both stimulus lights were lit and the levers became active. When access to food was scheduled the stimulus lights were turned off and the food was presented. The next trial began when the stimulus lights were re-lit. The ratio schedules were independently arranged.

Sessions ended after 120 minutes and any remaining test foods were removed from the magazines and weighed. A computer system running MEDTM software (Version 4) and interface located in the adjacent room controlled and recorded experimental events.

Results and Discussion

The aim of Experiment 1 was to measure the relative demand for foods using concurrent PR FR schedules. Break point, estimates of initial demand and essential value, and cross point were compared across foods and possums.

Break points under the PR schedule for each food pair for each possum are shown in Table 1. When break points were averaged across food pairs based on the food available on the PR schedule, it revealed that break points were larger when locusts were available and smallest when foliage was available under the PR schedule (see Table 1). The ranked order of the break points for each food, however, did show some variation across possums.

The exponential demand model (Equation 1; Hursh & Silberberg, 2008) was fit to consumption rates using non-linear least squares regression:

$$\ln(Q) = \ln(Q_0) + k(e^{-\alpha Q_0 C} - 1) \tag{1}$$

The parameter α (alpha) represents rate of change in elasticity in consumption (rate) as price increases. This is termed the *essential value* of a commodity with values closest to zero indicating greater demand for a commodity with increases in price. Initial demand, Q_0, is a measure of the estimated consumption (rate) when the price is zero. The parameter *k* is a scaling measure and is the range of the dependent variable. Hursh and Silberberg (2008) state that the *k* value needs to be the same across comparisons and that using an average of all values could be suitable. This is not unreasonable when the estimates of *k* vary over a relatively small range. In Experiment 1, however, the range was large (ln10.08 to ln15.75) and this assumption no longer seems valid. Therefore, in the current experiments *k* was allowed to vary for individual possums. *C* is the cost or response requirement to obtain access to each commodity (Hursh & Silberberg, 2008).

In this analysis, consumption on the progressive and fixed ratio was expressed as consumption rate (e.g., Foster et al., 1997) because the rate of responding on the PR schedule determined the time available to earn food on the FR at each PR value. Thus, consumption rate on the constant FR schedule was calculated over the time it took to earn a reinforcer on the PR schedule. The use of consumption rate also allowed for direct comparison across PR FR and PFR FR conditions when absolute consumption necessarily differed because of greater opportunity to earn reinforcers on the PFR schedule. Across all conditions consumption rate decreased as the ratio requirement on the progressive component increased and for many food pairs continued at a low rate as responding increased under the alternative schedule. Note the model was only fit when more than two degrees of freedom were available for generating parameter estimates. Thus for some food pairs there were missing parameter estimates when animals either responded exclusively on the FR or only responded to the first couple of PR values. Fits of the model accounted for an average of 94.7% of the variance (SD = 5.0%).

Table 1. *Break points, initial demand, essential value (alpha) and P_{max} averaged across all sessions when foods were available under the PR schedule for each possum (Experiment 1)*

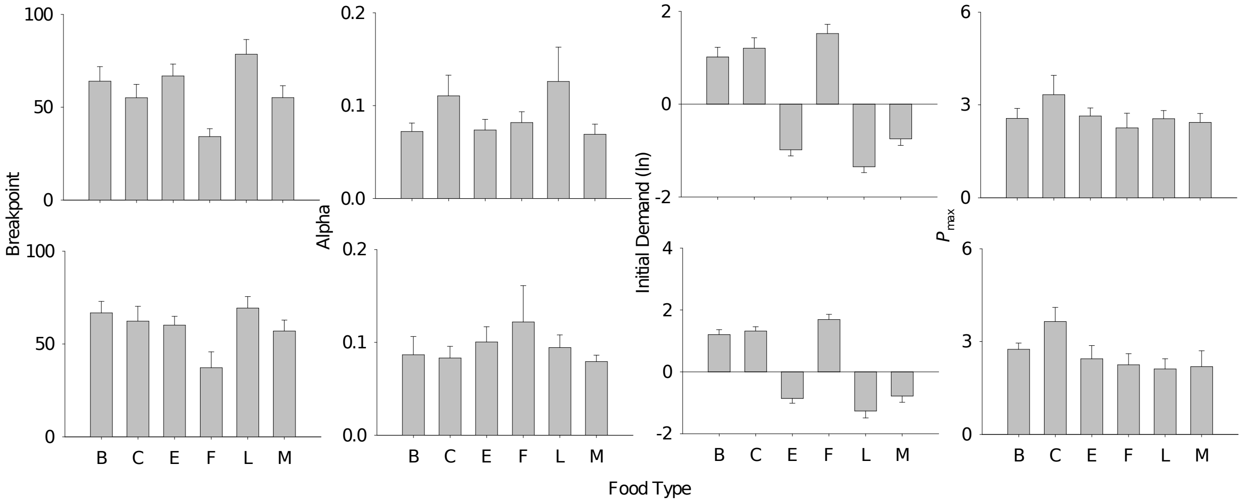
Food	**P1**	**P2**	**P3**	**P4**	**P5**	**P6**	**Average**
B	48.0 (3)	75.6 (1)	55.5 (4)	104.7 (2)	67.6 (1)	29.9 (4)	64.0 (3)
C	18.9 (6)	57.9 (2)	77.3 (3)	78.0 (5)	58.9 (2)	41.1 (2)	55.1 (5)
E	100.3 (2)	37.1 (4)	89.6 (2)	94.9 (3)	46.2 (4)	37.3 (3)	67.6 (2)

F	19.3 (5)	34.0 (5)	50.5 (5)	55.0 (6)	32.4 (6)	19.6 (6)	34.3 (6)
L	134.4 (1)	27.7 (5)	96.1 (1)	168.5 (1)	37.5 (5)	25.6 (5)	78.6 (1)
M	46.4 (4)	57.3 (3)	37.6 (6)	93.3 (4)	54.0 (3)	46.4 (1)	55.2 (4)
B	-1.51 (3)	-0.27 (4)	-0.72 (4)	-2.90 (1)	-1.94 (1)	2.67 (6)	1.01 (4)
C	1.16 (6)	-1.06 (1)	-1.81 (1)	2.47 (6)	-1.23 (5)	0.65 (4)	1.21 (5)
E	-1.74 (2)	-0.10 (5)	-1.47 (3)	-2.38 (2)	-1.85 (2)	-0.32 (3)	-0.98 (2)
F	-0.75 (4)	3.20 (6)	-0.23 (5)	-1.03 (4)	-1.75 (3)	1.84 (5)	1.52 (6)
L	-1.93 (1)	-0.80 (2)	-1.52 (2)	-2.24 (3)	-1.40 (4)	-1.16 (2)	-1.35 (1)
M	-0.58 (5)	-0.35 (3)	-0.18 (6)	-0.78 (5)	-0.27 (6)	-1.23 (1)	-0.75 (3)
B	0.11 (6)	0.06 (1)	0.05 (5)	0.17 (5)	0.10 (5)	0.07 (2)	0.09 (4)
C	0.10 (5)	0.10 (3)	0.05 (6)	0.21 (6)	0.07 (2)	0.16 (5)	0.11 (5)
E	0.06 (3)	0.09 (2)	0.03 (2)	0.12 (4)	0.08 (4)	0.09 (4)	0.07 (2)
F	0.06 (4)	0.12 (4)	0.03 (4)	0.07 (1)	0.12 (6)	0.06 (1)	0.08 (3)
L	0.05 (2)	0.58 (6)	0.03 (3)	0.08 (2)	0.07 (2)	0.27 (6)	0.13 (6)
M	0.04 (1)	0.13 (5)	0.02 (1)	0.08 (3)	0.06 (1)	0.51 (3)	0.07 (1)
B	1.60 (5)	2.49 (4)	1.88 (2)	3.69 (4)	4.23 (1)	0.99 (5)	2.57 (3)
C	0.94 (6)	6.69 (1)	2.92 (5)	4.42 (1)	3.17 (2)	1.05 (4)	3.33 (1)
E	3.40 (3)	2.78 (2)	3.06 (6)	2.53 (5)	2.60 (3)	1.45 (2)	2.64 (2)
F	2.25 (4)	1.16 (5)	2.03 (3)	4.23 (2)	2.11 (6)	1.17 (3)	2.26 (6)
L	4.96 (2)	1.15 (6)	2.55 (4)	4.14 (3)	2.01 (5)	0.71 (6)	2.56 (4)
M	3.55 (1)	2.56 (3)	1.26 (1)	1.98 (6)	2.30 (4)	2.46 (1)	2.44 (5)

Note. B=Berries, C=Chicken, E=Egg, F=Foliage, L=Locust, and M=Mushroom. An average for each food is given in the right most column across possums. The rank order of the break points, initial demand values, essential value and P_{max} for each food are given in parentheses.

The estimates of initial demand were averaged across possums for each food type (Table 1). Paired t-tests were conducted to compare the estimates of initial demand across foods. The tests revealed significantly lower initial demand values for locusts compared with chicken, foliage, and mushrooms (all *p*'s < 0.047, d ≤ 1.53); and for egg compared with mushrooms (*p* = 0.001, d = 0.84). There were no significant differences in estimates of essential values (alpha) across foods indicating that the change in consumption rate as ratio requirement increased was similar across foods (Table 1). Across possums, estimates of essential value were closest to zero for mushrooms and egg.

P_{max} is derived from the equation for elasticity or the *point slope* and is a measure of sensitivity in responding to changes in response requirement (Madden & Hartman, 2006). It can be calculated using Equation 2 using parameters and the constant *k* value



provided by Hursh et al. (2013):

$$P_{\max} = \frac{0.65}{\alpha . Q_0 . k^{1.191}} \, . \tag{2}$$

Figure 1. Estimates of alpha, initial demand (ln), $P_{\max}$ and break point (averaged across all sessions for all possums) plotted as a function of food available under the PR schedule (top panel), and plotted as a function of food available under the FR schedule (bottom panel) across possums. The standard error bars are the standard error of the mean. (B=Berries, C=Chicken, E=Egg, F=Foliage, L=Locust, and M=Mushroom).

The estimates of $P_{\max}$ were similar in value across possums and foods (all *p*'s > 0.05). The $P_{\max}$ values were lower than expected indicating that consumption rate declined steeply at small ratios (Table 1).

To examine the interaction between foods under the PR and FR schedule, the overall averages of break point, and estimates of essential value, initial demand, and $P_{\max}$ for each food under the PR schedule were calculated and are shown in the top row of Figure 1. The same data grouped by food available under the FR schedule are shown in the bottom row. Generally, the dependent variables grouped by the constant FR schedule show the inverse to values grouped under the PR schedule.

The cross-price model of demand (Equation 3) predicts an increase in responding under the FR schedule as ratio requirement increased (Hursh et al., 2013; Hursh & Silberberg, 2008).

$$Q = \ln(Q_{alone}) + I e^{-\beta . C} \tag{3}$$

Q_{alone} is the consumption (rate) under the alternative schedule when the price of the reinforcer is zero, I is the interaction constant, which if negative, indicates that the interaction between the consumption of the two alternative reinforcers is substitutable as price increases, β is the sensitivity of consumption rate on the fixed alternative to changes in response requirement in the other (varying) alternative. C is the cost of the variable alternative. Equation 3 provided a good description of consumption rate under the constant FR schedule (where responding gained more than three reinforcements). The model accounted for an average of 97.6% of the variance (SD = 2.9%). The interaction and sensitivity estimates for responding under the constant FR schedule were negative indicating all foods under the PR and FR schedules were substitutable (Table 2).

The intersection of fitted curves to Equations 2 and 3 is the cross point which gives a measure of substitutability between two commodities. There were more conservative cross points (less than the equivalence point of FR 30) than perseverative cross points (greater than the equivalence point) indicating that possums switched to responding under the constant FR schedule when the ratio requirement under the PR schedule was smaller than that under the constant FR schedule. This might have been due to the large steps between a PR 16, and PR 32 compared to the smaller step sizes between prior ratios. There were perseverative cross points and occurrences of exclusive responding under the PR schedule for chicken, egg and locusts than other foods (Table 2).

Table 2. *Interaction, sensitivity, and cross point values derived from the exponential demand and cross-price demand model averaged across sessions of foods under the PR schedule (Experiment 2).*

Food	P1	P2	P3	P4	P5	P6	Average
B	-	-1.64 (1)	-	-2.39 (2)	-0.86 (1)	-0.55 (2)	1.36 (2)
C	-	-0.62 (2)	-0.48 (3)	-8.88 (1)	-	-2E-05 (3)	-2.49 (1)
E	-	-0.54 (3)	-1.07 (1)	-0.26 (6)	-	-	-0.62 (5)
F	-0.99 (1)	-	-0.17 (4)	-1.08 (4)	-	-1.17 (1)	-0.85 (4)
L	-0.40 (2)	-	-	1.85 (3)	-0.40 (2)	-	-0.88 (3)
M	-0.32 (3)	-	-0.72 (2)	-0.78 (5)	-	-	0.61 (6)
B	-	-0.50 (2)	-	1.50 (2)	-0.03 (1)	-0.23 (2)	0.50 (2)
C	-	-0.30 (1)	-0.16 (2)	4.54 (1)	-	-3.60 (3)	1.02 (1)
E	-	-1.35 (3)	0.30 (1)	-0.22 (5)	-	-	-0.31 (4)
F	-6.09 (3)	-	-0.40 (3)	0.83 (3)	-	-0.002 (1)	-2.54 (5)
L	-1.50 (2)	-	-	0.25 (6)	-4.52 (2)	-	-4.53 (6)
M	-0.13 (1)	-	-12.79 (4)	-0.25 (4)	-	-	0.03 (3)
B	11.38 (5)	56.84*^(2)	19.55 (4)	32.98^(4)	-	2.38*(6)	24.63 (5)
C	-	48.00^ (3)	38.52^(2)	43.59^(2)	2.42* (4)	7.67*(4)	28.04 (4)
E	369.51*^(1)	7.31* (6)	66.92*^(1)	38.69^(3)	18.24* (2)	5.06*(5)	84.29^(1)
F	31.37* (3)	10.51*(5)	28.61 (3)	26.51 (6)	7.11* (3)	30.56*(2)	22.44 (6)
L	76.36*^(2)	14.58 (4)	13.54 (5)	47.95^(1)	37.22*^(1)	13.94 (3)	33.93^(3)
M	28.24* (4)	178.5*^(1)	12.24 (6)	32.87^(5)	-	30.90*(1)	56.55^(2)

Note. B=Berries, C=Chicken, E=Egg, F=Foliage, L=Locust, and M=Mushroom. An average for each food is given in the right most column across possums. The rank order of the interaction and sensitivity values and cross points for each food are given in parentheses. Cross points are given for all sessions with values based on three cross points or fewer marked with an *. Dashes indicate missing data points due to minimal responding to the FR 30 schedule. ^ = perseverative cross points.

Break points, estimates of initial demand and essential value, and cross points provided fairly consistent accounts of food choice within each possum and provided an indication of foods the possums *valued* more than others: Berries, egg, and locusts, and possibly mushrooms were preferred foods whereas chicken and foliage were least preferred; consistent with preferences identified by Cameron et al. (2013).

For two-thirds of food pairs there was either no cross point or there was little responding under the constant FR schedule, therefore these results should be interpreted with some degree of caution. It was surprising that the animals did not respond more to the FR alternative given our piloting of that ratio value to confirm that possums would respond reliably at that FR value. Consequently, in Experiment 2, the ratio requirement under the constant FR schedule was decreased from FR 30 to FR 10 in an attempt to increase responding for food under this schedule.

Experiment 2

In Experiment 2, the concurrent PR FR procedure was repeated with four foods, making up two food pairs; berries and egg, and chicken and mushrooms. These foods were chosen because they produced similar consumption rates across possums in Experiment 1. Each food from each pair was offered on the PR and FR schedule in separate sessions. The constant FR ratio requirement was decreased from 30 responses to 10 responses in an effort to elicit more responding under the FR schedule. It was expected that decreasing the *price* of food under the constant FR schedule from 30 to 10 responses would generate more responding to this schedule, particularly during the FR 10 condition. Lower break points and cross points were expected under the PR schedule when the FR component was 10 responses.

Method

Subjects, Housing, Apparatus. The same possums, P1-P6 and conditions were used in Experiment 2 as in Experiment 1.

Procedure. The procedure was the same as in Experiment 1 except that only four foods were used in this experiment. These were presented in two combinations: berries and egg or chicken and mushroom. Each food was presented on both the left and right side and the order of presentation of the food pairs was randomized across animals.

Design. Experiment 2 was conducted as an ABAB design. Data for the first FR 30 component (A) was provided by Experiment 1. The subsequent FR 10 (B) and FR 30 sessions were conducted in consecutive three session blocks.

Results and Discussion

The demand for different food types based on consumption rates under the PR FR 30 and PR FR 10 schedules was measured to determine if the ratio requirement under the FR schedule affected consumption rates under the PR schedule and increased responding for food under the FR schedule.

The exponential demand model was fit to consumption rates under the PR schedule. The scaling parameter, *k*, ranged from ln9.26 to ln15.75. The model accounted for an average of 92.3% of the variance (SD = 6.3%) for the PR FR 10 schedule and 94.7% of the variance (SD = 5.4%) for the PR FR 30 schedule. The functions in Figure 2 showed some deviation from the data, in particular, underestimating the consumption rates at low ratio requirements. The cross price model was fit to consumption rates under the FR schedules and it accounted for an average 96.4% of the variance (SD = 7.4%) for the PR FR 10 schedule and 97.7% of the variance (SD = 5.8%) for the PR FR 30 schedule. Consumption rates for foods under the PR schedule decreased as price increased (Figures 2 & 3). There was also an increase in responding for foods under the constant FR schedule with only minor differences in consumption rates between the FR 10 and FR 30 conditions.

Paired t-tests were conducted to compare the break point, the estimates of initial demand, essential value or cross point, across foods and conditions. There were few statistically significant differences in break point, the estimates of initial demand, essential value, or cross point between the PR FR 30 and PR FR 10 conditions or food types. Break points were larger during the FR 10 condition compared with the FR 30 condition and were higher for egg compared with berries in the PR FR 30 condition, t (5) = 2.66, p = 0.045, d = 1.09. Conversely, estimates of $P_{\max}$ were significantly higher in the PR FR 10 condition compared with the PR FR 30 condition, t (21) = 2.65, p = 0.015, d = 0.57. This indicated that when a constant FR 10 schedule was the alternative, consumption rates under the PR schedule were higher at larger ratios compared to when the constant FR 30 schedule was the alternative.

The cross-price model (Equation 3) predicted negative interaction estimates (I) indicating all foods were substitutable (Table 4). There were more conservative cross points than perseverative cross points in both the PR FR 10 and PR FR 30 conditions. Paired t-tests comparing the values of interaction and sensitivity across foods and FR conditions revealed no significant differences across foods or FR conditions. On average, mushrooms produced the highest cross points under both FR conditions.

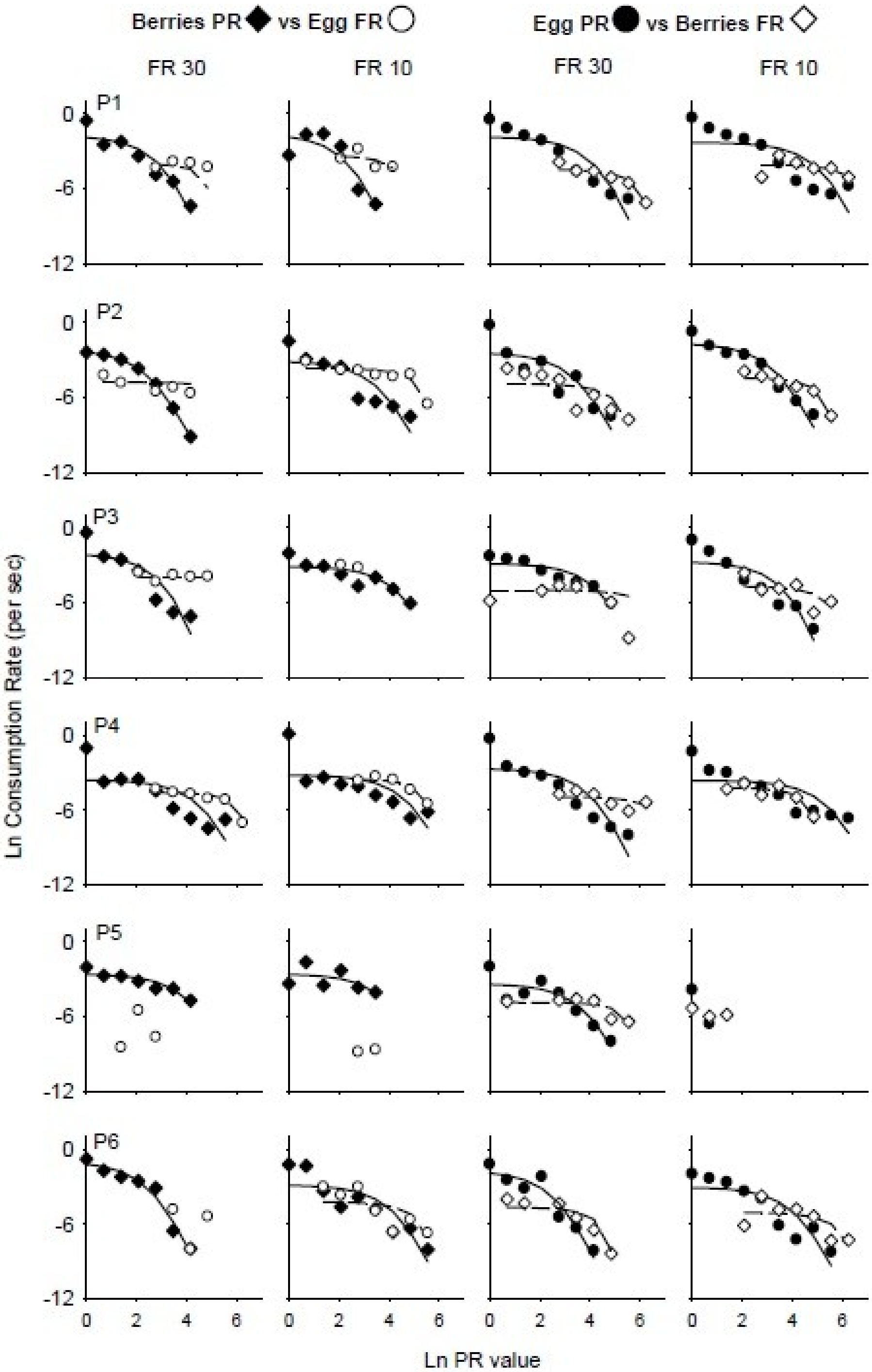
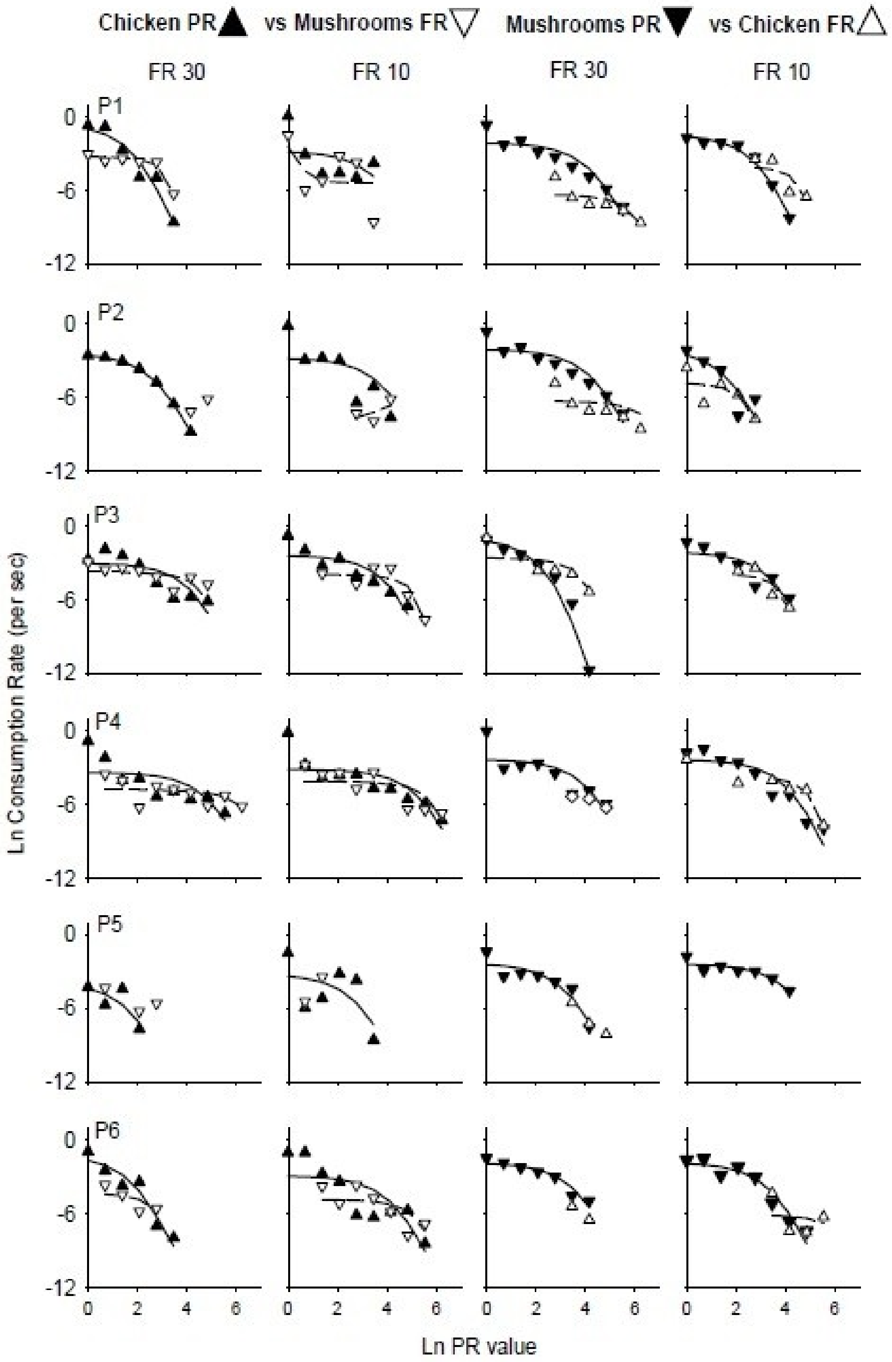


Figure 2. Logarithm of the consumption rate as a function of the logarithm of the PR value for berries and egg under PR (filled symbols) and FR 10 and FR 30 schedules (open symbols).



F**igure 3.** Logarithm of the consumption rate as a function of the logarithm of the PR value for chicken and mushroom under PR (filled symbols) and FR 10 and FR 30 schedules (open symbols).

The attempt made in Experiments 1 and 2 to devise a method for measuring relative demand for concurrently available foods was successful. This was despite the fact it relied on a small number of opportunities for the animals to consume the foods under the PR FR schedules because the PR incremented after each reinforcer was delivered. Responding under the constant FR schedules was low and it may be that there was not enough time for some animals to earn reinforcements under the constant FR schedule while the PR schedule was in effect. Therefore, in the Experiment 3, PFR FR schedules were used where each ratio under the PFR schedule remained in place for five days to allow more opportunity for the possums to earn food under the constant FR schedule.

Table 3. *Break point, initial demand, essential value and P_{max} averaged across sessions of foods available under the PR schedule for each possum (Experiment 2)*

FR	Food Pair	P1	P2	P3	P4	P5	P6	Average
30	B(E)	37.33(3)	33.50 (3)	29.33 (4)	74.67 (3)	25.67 (3)	38.67 (1)	34.17 (4)
	C(M)	29.33 (4)	32.67 (4)	58.67 (2)	137.33 (1)	3.40 (4)	15.67 (4)	39.58 (3)
	E(B)	128.00 (1)	52.00 (2)	61.00 (1)	117.50 (2)	55.33 (1)	33.33 (2)	63.88 (1)
	M(C)	45.33 (2)	109.33 (1)	32.00 (3)	51.00 (4)	27.50 (2)	33.33 (2)	42.64 (2)
10	B(E)	21.33 (3)	48.00 (2)	34.40 (3)	39.33 (4)	17.67 (2)	93.67 (2)	36.34 (4)
	C(M)	12.33 (4)	35.20 (3)	74.67 (1)	245.33 (1)	87.50 (1)	86.00 (3)	77.29 (1)
	E(B)	173.50 (1)	64.67 (1)	56.00 (2)	44.83 (3)	1.33 (4)	100.67 (1)	63.00 (2)
	M(C)	45.33 (2)	6.67 (4)	29.50 (4)	101.50 (2)	14.50 (3)	67.00 (4)	37.79 (3)
30	B(E)	-1.43 (2)	-1.50 (1)	-0.73 (3)	-2.92 (1)	-1.88 (2)	-0.78 (4)	-1.95 (1)
	C(M)	2.85 (4)	0.23 (4)	-1.42 (2)	1.40 (4)	-4.35 (1)	-1.12 (3)	-1.87 (2)
	E(B)	-1.36 (1)	-1.23 (3)	-2.36 (1)	-2.07 (2)	-0.50 (4)	-1.22 (1)	-1.65 (3)
	M(C)	-1.43 (3)	-1.35 (2)	-0.71 (4)	-1.18 (3)	-1.64 (3)	-1.20 (2)	-1.58 (4)
10	B(E)	-0.66 (3)	-1.55 (2)	-3.23 (1)	-2.65 (3)	4.49 (3)	-0.02 (4)	2.72 (2)
	C(M)	4.64 (4)	-1.37 (3)	-2.34 (2)	-2.98 (1)	-1.59 (1)	-1.65 (3)	2.89 (3)
	E(B)	-1.44 (1)	-1.79 (1)	-1.97 (3)	-2.78 (2)	-	-2.59 (1)	-2.00 (1)
	M(C)	-0.99 (2)	2.15 (4)	-0.98 (4)	-1.77 (4)	-1.46 (2)	-1.76 (2)	0.50 (4)
30	B(E)	0.08 (3)	0.27 (4)	0.94 (4)	0.13 (3)	0.10 (2)	0.06 (1)	0.26 (3)
	C(M)	0.10 (4)	-0.08 (2)	0.17 (3)	0.17 (4)	4.03 (4)	0.19 (3)	0.76 (4)
	E(B)	0.03 (1)	0.70 (3)	0.07 (2)	0.07 (2)	0.16 (3)	0.35 (4)	0.14 (2)
	M(C)	0.05 (2)	0.26 (1)	0.04 (1)	0.05 (1)	0.08 (1)	0.09 (2)	0.06 (1)
10	B(E)	0.15 (1)	0.17 (1)	0.09 (3)	0.06 (3)	0.45 (3)	0.10 (2)	0.17 (2)
	C(M)	0.22 (2)	0.22 (2)	0.23 (4)	0.03 (1)	0.14 (2)	0.13 (3)	0.16 (1)
	E(B)	0.29 (3)	0.25 (3)	0.06 (2)	0.10 (4)	-	0.27 (4)	0.29 (3)
	M(C)	0.49 (4)	1.65 (4)	0.05 (1)	0.05 (2)	0.05 (1)	0.08 (1)	0.40 (4)
30	B(E)	1.43 (3)	1.28 (4)	0.63 (4)	3.13 (3)	13.21 (2)	0.90 (3)	3.34 (4)
	C(M)	0.50 (4)	7.30 (1)	1.95 (2)	10.09 (2)	0.40 (4)	0.46 (4)	3.45 (3)
	E(B)	115.70 (1)	5.92 (2)	242.31 (1)	103.06 (1)	2.04 (3)	33.59 (1)	83.67 (1)
	M(C)	3.70 (2)	4.69 (3)	0.82 (3)	2.70 (4)	85.72 (1)	1.57 (2)	16.53 (2)
10	B(E)	0.64 (4)	1.51 (2)	4.99 (2)	6.52 (4)	-	2.66 (4)	2.53 (3)

C(M)	0.68 (3)	0.76 (3)	2.83 (3)	18.47 (2)	0.72 (2)	2.24 (2)	4.28 (2)
E(B)	157.34 (1)	10.26 (1)	287.87 (1)	354.56 (1)	-	254.23 (1)	212.89 (1)
M(C)	0.95 (2)	0.08 (4)	1.32 (4)	3.43 (3)	2.24 (1)	-	1.67 (4)

Table 4. *Interaction, sensitivity and crosspoint values derived from the exponential demand and cross-price demand model averaged across sessions (Experiment 2).*

FR	Food Pair	P1	P2	P3	P4	P5	P6	Average
30	B(E)	-	-	-	-0.45 (3)	-	-2.01 (3)	-0.04 (3)
	C(M)	-0.15 (2)	-	-0.43 (1)	-0.60 (1)	-	-	-0.40 (1)
	E(B)	-0.29 (1)	-0.20 (1)	-	-0.44 (2)	-0.32(1)	-0.21 (1)	-0.29 (2)
	M(C)	-	-	-	-	-	-	-
10	B(E)	-	-0.19 (1)	-	-0.42 (4)	-	-1.21 (1)	-0.61 (2)
	C(M)	-	-	-0.79 (1)	-1.32 (1)	-	-	-0.40 (3)
	E(B)	-0.33 (1)	-0.08 (2)	-0.64 (2)	-0.44 (3)	-	-0.28 (4)	-0.29 (4)
	M(C)	-	-	-	-0.90 (2)	-	-	-0.90 (1)
30	B(E)	-	-	-	-14.18 (3)	-	-	-14.18 (2)
	C(M)	-0.21 (1)	-	-874.21 (1)	-9.25 (2)	-	-	-294.56 (3)
	E(B)	-2.56 (2)	-0.03 (1)	-	-0.40 (2)	-0.04(1)	-0.23 (1)	-8.66 (1)
	M(C)	-	-	-	-	-	-	-
10	B(E)	-	-0.04 (2)	-	-20.24 (3)	-	-	-23.91 (3)
	C(M)	-	-	-11.41 (2)	-4.36 (1)	-	-	-7.89 (1)
	E(B)	-0.33 (1)	-0.02 (1)	-5.26 (1)	-59.51 (4)	-	-12.82(1)	-41.36 (4)
	M(C)	-	-	-	-13.31 (2)	-	-	-13.31 (2)
30	B(E)	22.95*(3)	54.95*^(2)	19.53*(2)	11.56* (3)	-	-	21.80 (3)
	C(M)	15.09*(4)	-	19.77 (1)	66.77*^(1)	-	-	25.41 (2)
	E(B)	51.11^(1)	7.31* (3)	-	28.42* (2)	32.50*(1)	5.06*(1)	20.73 (4)
	M(C)	29.02*(2)	178.50*^ (1)	5.55*(3)	-	-	-	53.27^ (1)
10	B(E)	-	3.35*(1)	-	-	-	40.74*^(1)	14.70 (4)
	C(M)	-	-	29.82* (2)	32.98*^(2)	-	24.29* (3)	21.77 (3)
	E(B)	46.39*^(1)	4.97*(2)	37.88*^(1)	19.53* (3)	-	25.23* (4)	22.34 (2)
	M(C)	33.95*^(2)	-	-	35.95*^(1)	-	28.08* (2)	24.49 (1)

Note. B=Berries, C=Chicken, E=Egg, and M=Mushroom. An average for each food is given in the right most column across possums. The rank order of the break points, initial demand values, essential value and $P_{\max}$ for each food are given in parentheses. Dashes indicate missing data points due to minimal responding to the PR schedule.

Note. B=Berries, C=Chicken, E=Egg, and M=Mushroom. The food under the FR schedule is in parentheses in the food pair column. An average for each food is given in the right most column across possums. The rank order of the interaction and sensitivity values and cross points for each food are given in parentheses. Cross points are given for all sessions with values based on three cross points or fewer marked with an *. Dashes indicate missing data points due to minimal responding to the FR 30 schedule. ^ = perseverative cross points.

Experiment 3

In Experiment 3, each ratio was in place for five days (e.g., Hudson, Foster & Temple, 1999). The four foods used in Experiment 3 were the same as Experiment 2. The aim was to determine whether the conclusions drawn regarding the demand for food using concurrent PR FR schedules would be the same as those using PFR FR schedules.

Method

Animals, Housing and Apparatus. The same possums, housing conditions, and apparatus were the same as used in Experiments 1 and 2.

Procedure. The experimental procedure was the same as in Experiments 1 and 2, however, the ratio requirement on the right lever increased every five days. The ratio requirement on the left lever remained a constant FR 30 as more cross points were generated in the PR FR 30 condition of Experiment 2. If possums did not receive a reinforcer under the PFR schedule for two consecutive days the condition was terminated.

Results and Discussion

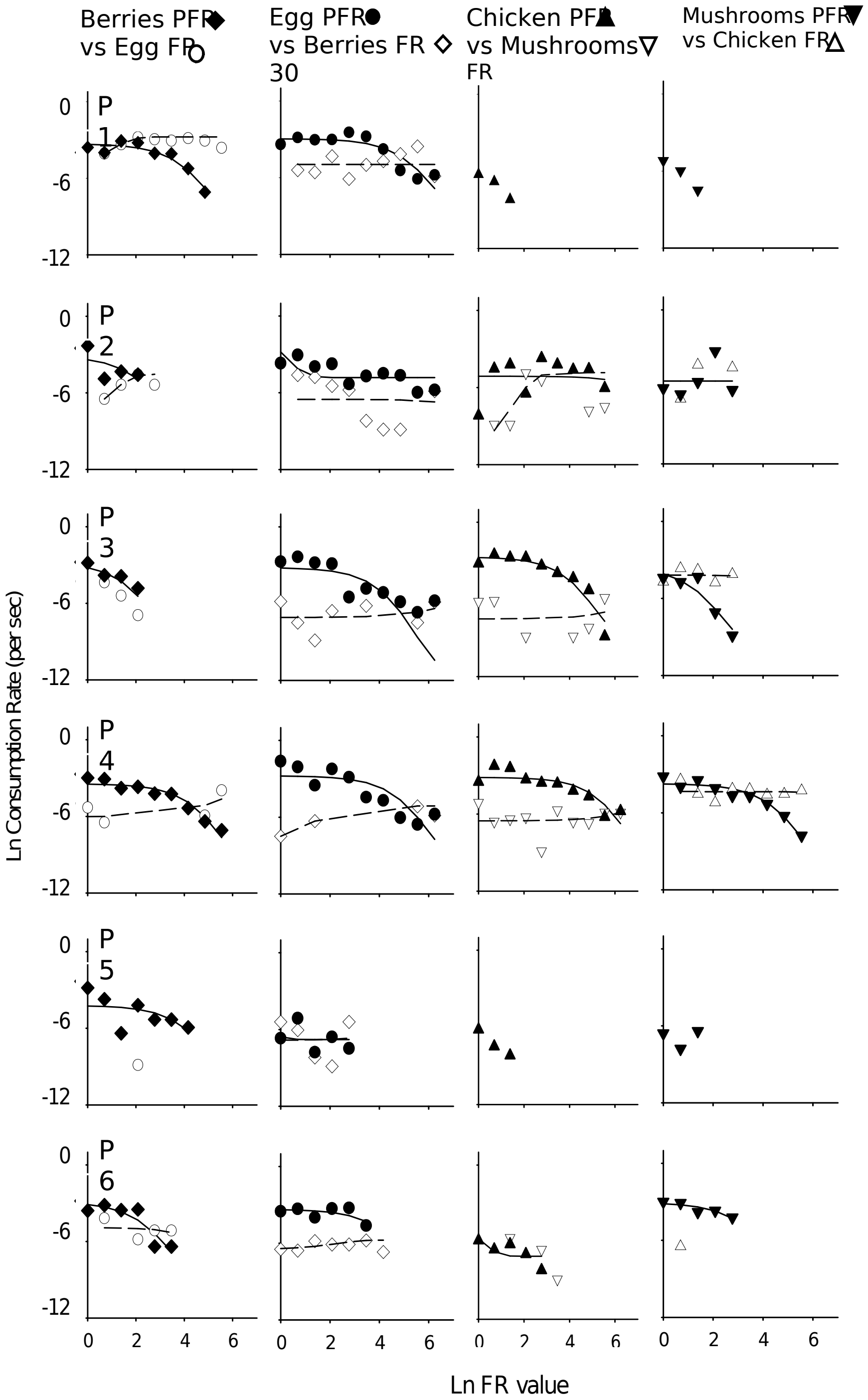
Break points on the PFR schedule for individual conditions and animals are shown in Table 5. The break points under the PFR schedule in the current experiment were compared with break points measured under the PR schedule of the PR FR in Experiment 2. Paired t-tests revealed significantly higher break points in the PFR FR compared with the PR FR irrespective of food type, *t* (23) = 2.75, *p* = 0.011, *d* = 0.56], however, when foods were tested individually the break points for egg were significantly higher in the PFR FR schedules than PR FR schedules, *t* (5) = 2.82, *p* = 0.037, *d* = 1.15.

Table 5. *Break point, initial demand, essential value and P_{max} averaged across sessions of foods available under the PFR FR schedules for each possum (Experiment 3)*

Food Pair	P1	P2	P3	P4	P5	P6	Average
B(E)	256.00 (2)	16.00 (3)	16.00 (3)	256.00 (3)	4.00 (2)	64.00 (1)	106.67 (3)
C(M)	2.00 (3)	256.00 (2)	256.00 (1)	512.00 (1)	4.00 (2)	16.00 (3)	174.33 (2)
E(B)	512.00 (1)	512.00 (1)	256.00 (1)	512.00 (1)	64.00 (1)	32.00 (2)	304.67 (1)
M(C)	2.00 (3)	16.00 (3)	16.00 (3)	256.00 (3)	4.00 (2)	16.00 (3)	51.67 (4)
B(E)	-3.31 (1)	-	-	-3.45 (1)	-4.23 (2)	-2.88 (3)	-3.36 (1)
C(M)	-	-	-2.71 (3)	-3.15 (2)	-	-1.85 (4)	-2.69 (2)
E(B)	-2.95 (2)	0.85 (2)	-3.19 (2)	-2.77 (3)	-0.88 (1)	-3.35 (1)	-0.71 (4)
M(C)	-	0.11 (1)	-3.53 (1)	-	-	-3.06 (2)	-1.19 (3)
B(E)	0.18 (2)	-	-	0.12 (3)	0.43 (1)	0.73 (3)	0.36 (1)
C(M)	-	0.03 (3)	0.09 (1)	0.03 (1)	-	8.54 (4)	2.17 (3)
E(B)	0.04 (1)	0.85 (2)	0.11 (2)	0.04 (2)	7.96 (2)	0.18 (1)	1.46 (2)
M(C)	-	12.88 (1)	3.13 (3)	0.15 (4)	-	0.36 (2)	4.13 (4)
B(E)	4.98 (2)	-	-	7.78 (4)	5.27 (1)	0.91 (3)	4.73 (2)
C(M)	-	192.80 (1)	5.15 (2)	19.84 (1)	-	0.03 (4)	54.45 (1)
E(B)	16.44 (1)	0.03 (2)	7.21 (1)	11.53 (2)	0.01 (2)	6.09 (1)	6.89 (3)
M(C)	-	0.002 (3)	0.34 (3)	7.85 (3)	-	2.25 (2)	2.61 (4)

Note. B=Berries, C=Chicken, E=Egg, and M=Mushroom. An average for each food is given in the right most column across possums. The rank order of the break points, initial demand values, essential value and $P_{\max}$ for each food are given in parentheses. Dashes indicate missing data points due to minimal responding to the PFR 30 schedule.

Consumption rate decreased as the ratio requirement increased for foods available under the PFR schedule. Under the FR 30 schedule consumption rate increased as the ratio requirement on the PFR increased (Figure 4). Equation 2 (Hursh & Silberberg, 2008) was fit to the data using non-linear least squares regression and accounted for an



average of 98.0% of the variance (SD = 2.0). The scaling parameter, *k*, ranged from ln5.38 to ln6.90.

Figure 4. Logarithm of the consumption rate as a function of the logarithm of the FR value for chicken and mushroom under PFR (filled symbols) and FR 30 schedules (open symbols).

Estimates of initial demand for all foods under the PFR FR are shown in Table 5. The estimates of initial demand were significantly lower in Experiment 3 using the PFR FR schedules than in the Experiment 2 using PR FR schedules, *t* (17) = 3.57, *p* = 0.002, *d* = 0.84].

Estimates of essential value (α) were mostly positive and estimates of $P_{\max}$ (calculated using Equation 3) were highest for egg across possums (Table 5). Paired t-tests, however, revealed no significant differences in the estimates of alpha or $P_{\max}$ (all p's > 0.05, $d \leq 0.40$) across foods or between the PFR FR and PR FR schedules (all p's > 0.05, $d \leq 0.09$).

The cross-price demand model (Equation 2) accounted for an average of 97.3% of the variance (SD = 2.0). The estimates of interaction were negative demonstrating that foods under the FR 30 schedule were substitutable for foods under the PFR schedule (Table 6). The model identified more perseverative cross points (greater than the equivalence point) for chicken and egg and conservative cross points for berries and mushrooms, however, exclusive responding under the PFR schedule was evident for the majority of food pairs. Cross points were more variable under PFR FR schedules in Experiment 3 compared with cross points under PR FR 30 schedules in Experiment 2, but were not significantly different (all p's > 0.05, $d \leq 0.01$).

Table 6. *Interaction, sensitivity and cross point values derived from the exponential demand and cross-price demand model averaged across sessions (Experiment 3)*

	Food Pair	**P1**	**P2**	**P3**	**P4**	**P5**	**P6**	**Average**
Interaction values	B(E)	-3.12 (1)	-	-	-	-	-1.59 (1)	-2.35* (2)
	C(M)	-	-7.12 (1)	-1.67 (1)	-1.46 (2)	-	-	-3.42* (1)
	E(B)	-1.45 (2)	-1.94 (2)	-1.28 (2)	-	-1.47 (1)	-0.74 (2)	-1.37 (3)
	M(C)	-	-	-0.55 (3)	-0.95 (2)	-	-	-0.75* (4)
Sensitivity values	B(E)	1187.00 (1)	-	-	-	-	23.31 (2)	605.15* (2)
	C(M)	-	-3830.60 (2)	2.23 (2)	2.62 (2)	-	-	1278.40* (1)
	E(B)	-1.45 (2)	-1.94 (1)	3.68 (1)	-	1.67 (1)	282.04 (1)	57.48 (3)
	M(C)	-	-	-25.56 (3)	-0.80 (2)	-	-	-13.18* (4)
Cross point	B(E)	3.53 (2)	7.12 (1)	-	79.14^(3)	-	16.15 (1)	26.48*(4)
	C(M)	-	-	-	364.84^(1)	-	-	189.83*(1)
	E(B)	196.10^ (1)	-	186.75^(1)	198.07^(2)	5.49 (1)	14.41 (2)	146.60*(2)
	M(C)	-	-	-	27.74 (4)	-	-	27.74*(3)

Note: B=Berries, C=Chicken, E=Egg, and M=Mushroom. The food under the FR schedule is in parentheses in the food pair column. An average for each food is given in the right most column across possums. The rank order of the interaction and sensitivity values and cross points for each food are given in parentheses. Cross points are given for all sessions with values based on three cross points or fewer marked with an *. Dashes indicate missing data points due to minimal responding to the FR 30 schedule. ^ = perseverative cross points.

General Discussion

The purpose of these experiments was to measure the demand for a variety of different food types and establish whether the same conclusions regarding the demand for food was reached under PR FR 30, PR FR 10 and PFR FR schedules.

Breakpoints were generally higher in the PFR FR than in the PR FR condition. This has also been found in previous experiments with hens and pigeons (Foster et al., 1997; Killeen et al., 2009). Across both arrangements, possums responded to higher ratios for egg which suggests that this is a valued commodity, irrespective of whether ratios incremented within or across sessions. Break point appears to be a robust measure of reinforcer efficacy in concurrent arrangements of PR FR and PFR FR schedules, at least for responding under the incrementing schedule. In addition, we would expect that when a preferred food was available under the FR 30 schedule that the break point under the PR schedule would be lower compared with when a preferred food was available. For instance, break points were highest for locusts in Experiment 1, chicken in Experiment 2, and egg in Experiment 3 when those foods were available under the incrementing schedule, suggesting preference for those foods.

The exponential (Equation 1; Hursh & Silberberg, 2008) and cross-price (Equation 3; Hursh et al., 2013) demand models produced good fits to the data and provided estimates of demand for the test foods. The parameter estimates for each possum and food pair were averaged to describe the general trends across foods and indicated similar accounts of preference to those found in single- and paired-preference assessments conducted by Cameron et al. (2013). The individual differences found in food preference with possums is similar to those present in humans (Epstein & Saelens, 2000). These effects also appear to be independent of exposure to foods over time as a variety of foods were offered regularly (Raynor & Epstein, 2001).

The demand analysis in Experiment 1, indicated that preferred foods, such as egg and mushrooms, had higher estimates of essential value (lower alpha) and $P_{\max}$ and lower estimates of initial demand. The lesser preferred foods, such as foliage, had lower estimates of $P_{\max}$ and higher estimates of initial demand values. Some inconsistences were observed between the parameters in their description of demand, such as the low essential value for locust when the break point was highest for that food type. This suggests that although useful, caution needs to be taken when using these parameters in isolation to determine preference.

This feature, where *lesser preferred* foods have high initial demand values has been found in other demand studies (e.g., Foster et al., 2009; Hursh et al., 1988). It has been suggested that subjects respond *faster* when ratio values are low for lesser preferred foods, to gain the same *value* of reinforcement in the session as obtained when preferred foods are available, as responding for these foods continues to higher ratios (Foster et al., 2009).

It was expected that in a comparison of food types, estimates of essential value and $P_{\max}$ would be different for foods as they are likely to differ in value to the subject (Grant et al., 2014). The findings of Experiments 1, 2, and 3 showed that there were only minimal differences in alpha across foods. This is supported by the fact that the estimates of interaction generated by the cross price demand model indicated substitutability between foods.

The Hursh et al. (2013) cross-price demand model (Equation 3) has not been extensively tested to determine the demand for foods under concurrent schedules. In this experiment, the model described the data well and provided estimates of higher order parameters that identified the degree of substitutability between foods under concurrent schedules and cross points. In Experiments 1, 2 and 3, different foods were on offer under the concurrent schedules and cross points tended to be conservative. This means that possums responded for food under the constant FR schedule when the ratio requirement under the incrementing schedule was smaller than that under the FR schedule.

There was, however, some perseverative responding for foods considered preferred: For example, in Experiment 1, perseverative cross points were observed for chicken, egg and locust, and for chicken and egg in Experiment 3. This is not unusual as perseverative cross points have been observed in concurrent PR FR arrangements in foraging studies in pigeons when the same food was offered under both schedules (Wanchisen, Tatham & Hineline 1988). In the current experiment, it suggests that the ratio requirement of the schedules was of less importance to the animal than the food types available.

Exclusive responding to one alternative when another is available can be considered a measure of preference for the first alternative (Findley, 1958; Fisher & Mazur, 1997). Consumption rates from Experiments 1, 2 and 3 demonstrated exclusive responding for foods under the incrementing schedule in more than half of the food pairs. One reason for this might be that the animals actually did not have a strong preference for one food over another, and simply responded for the food that was initially *cheaper* under the incrementing schedule. This does not seem to be universal, however, when considering all the food pairs on offer in Experiment 1. For example, in Experiment 1, there were smaller break points and cross points when foliage was available under the PR schedule suggesting possums did not maintain responding for this food even when available at low ratios under the PR schedule.

Considering the lesser-preferred foods such as foliage, it appears that the initial exposure to low ratios under the incrementing schedule influences subsequent measures such as cross point. In Experiment 2, when berries and chicken were available under the PR schedule, and egg and mushrooms were available under the constant FR schedule, 19 out of 36 food pairs demonstrated perseverative cross points - or occurrences of exclusive responding under the PR schedule. This means that in nearly half the food pairs, responding was allocated to the PR schedule for berries and chicken, and the other half to the constant FR schedule for egg and mushroom. This indicates that the foods were substitutable and the ratio requirement may have dictated responding to the schedules. This degree of similarity was also shown in other experiments when the same foods are on offer on the PR and FR schedules where subjects switched responding at or just below the equivalence point (e.g., Hineline & Sodetz, 1987; Hodos & Trumbule, 1967; Neuman et al., 2000) and when different visual and auditory reinforcers were on offer to human participants (Tustin, 1994).

In comparison, when egg and mushrooms were available under the PR schedule, and berries and chicken available under the constant FR schedule, perseverative cross points or exclusive responding was found in 28 out of a possible 36 food pairs. This means that in three quarters of food pairs possums perseverated on the PR schedule for egg and mushroom. This indicates that, as Tustin (1994) concluded, the choice of where to respond was influenced by the schedule requirement, the preference of the food under the PR and the availability of the alternative.

In conclusion, possums in New Zealand are a pest species that consume a wide variety of native and exotic plants and trees, fruits, flowers, insects, fungi and even birds and their eggs (Nugent et al., 2000). The present study has confirmed the findings of the preference assessments, in particular, the preference for egg and chicken identified in Cameron et al. (2013) was confirmed in Experiments 2 and 3, over that of berries and mushrooms. What was not known was whether possums would *work* to obtain these foods more than other foods as a reflection of previously established preferences. This study validated the suggestion that possums are generally *opportunistic* foragers and would readily substitute food for each other as ratio requirements increased. They would also, however, *work harder* for more highly preferred foods such as locusts, chicken, and egg. This study raises questions regarding the substitutability of foods and the arrangement of contingences to examine demand for foods. These findings have practical implications for understanding how the demand for food, as a function of availability and price, might affect food preferences of the wild possum and in addition, might contribute to pest management by determining highly preferred foods to be used as natural lures and masking agents for pest control strategies.

Acknowledgments

The experiments reported in the paper were presented in partial fulfilment of the requirements for the award of PhD by the first author at the University of Waikato. Portions of these data were also reported at the 38th annual convention of the Association for Behavior Analysis International in Seattle, WA, 2012. The authors would like to thank Jenny Chandler for her technical assistance. This research was conducted following the relevant ethics guidelines and approved by the Animal Ethics Committee at the University of Waikato where this research was conducted.

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Financial conflict of interest: No stated conflicts.
Conflict of interest: No stated conflicts.

Submitted: *November 22nd, 2014*
Revision submitted: March 31st, 2015
Accepted: May 9th, 2015