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**Food preferences and demand in the
brush-tail possum (*Trichosurus vulpecula*)**

A thesis
submitted in fulfilment
of the requirements for the degree
of
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at
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THE UNIVERSITY OF
WAIKATO
Te Whare Wānanga o Waikato

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Abstract

The common brushtail possum (*Trichosurus vulpecula*) has been reported to eat vegetation, fruit, invertebrates, and occasionally fungi, eggs and meat in the wild. The relative preference between food types found in the wild, however, has not been investigated in a controlled laboratory study. In this series of experiments, single and paired preference assessments and demand procedures were conducted systematically under laboratory conditions to investigate the preference and demand for food types reportedly consumed by possums.

In Experiment 1, 20 possums were used in a single stimulus assessment where the consumption of individually presented food items was measured. The foods presented were berries, raw chicken, egg, fivefinger leaves, locusts and mushrooms. More than 75% of possums consumed berries, locusts and mushrooms but fewer than 50% of possums consumed fivefinger, raw chicken and eggs. In Experiment 2, 12 possums were used in a paired stimulus assessment to establish *relative preference* for the same foods. The results showed that no single food was preferred by all possums. Overall locusts were the most preferred food, followed in order of preference by berries, egg, mushrooms, chicken and foliage. The single stimulus preference assessment confirmed the palatability of foods. The paired stimulus assessment provided a rank order of food preferences.

In Experiments 3 and 4, the demand for these foods were measured under concurrent progressive-ratio (PR) and fixed-ratio (FR) schedules of reinforcement. In Experiment 3, the same six food types were used and every possible food pair (30 pairs in total) was presented to six possums in concurrent PR and FR 30 schedules. Exponential models of demand were applied to consumption rates and P_{\max} , break point and cross point values were generated.

The rank orders for each parameter were compared. Overall, more responding was allocated to the PR schedule when a preferred food was available compared to the constant FR schedule. Cross points were larger for chicken, egg and locust, however, stable responding under the constant fixed-ratio schedule was not observed.

The aim of Experiment 4 was to investigate possible reasons for the lack of stable responding. The experimental procedure of Experiment 3 was replicated with four food pairs and the constant FR schedule was alternated between 30 and 10 responses across sessions. Responding under the constant FR schedule was similar to that in Experiment 3 but the demand for foods under the PR schedule was similar.

In Experiment 5, the same methodology in Experiments 3 and 4 was used except that each ratio requirement of the PR schedule was increased every five days, termed a PFR schedule. The same food pairs were used (berries and egg, and chicken and mushrooms). The same descriptions of demand were found in Experiment 5 as in Experiment 4, with higher demand for egg and chicken compared to berries and mushroom. A comparison of the linear (Hursh, Raslear, Shurtleff, Bauman, & Simmons, 1988) and exponential demand (Hursh & Silberberg, 2008) models showed that the exponential model provided better fits to the data. In addition, the cross price model (Hursh, Madden, Spiga, DeLeon, & Francisco, 2013) plotted with the exponential model of demand accounted for better cross points than the linear model.

In Experiment 6, the aim was to confirm the similarity in performance under concurrent schedules where the incrementing schedules increased within or across sessions. Twelve possums were exposed to schedules that increased within

a session using the same procedure as Experiments 3 and 4; and schedules that increased across sessions in a semi-replication of Experiment 5 where each ratio requirement was in place for one day. The progression of the incrementing schedule was also varied between a geometric sequence (basis 2), and an arithmetic sequence (step 5) to ascertain if progression type affected the demand for foods. The food pairs of berries and egg, and two new foods of a barley and coco-pop® mix and rolled oats were tested. The same response rate patterns were observed under the geometric and arithmetic progressions. The parameters of the exponential and cross price demand models predicted estimates that differed in their description of demand across PR and PFR schedules, progression and food type. The break points and cross points were larger under PFR FR schedules and geometric progressions.

In conclusion, the preference assessments (Experiments 1 and 2) identified that locust was the most preferred food across possums but individual food choices were idiosyncratic. The demand procedures (Experiments 3 – 6) identified that possums are opportunistic in their food choice as they will respond for all foods at low ratio requirements and will respond at higher ratio requirements for more preferred foods even when another food is available for a lower cost. This series of experiments also highlighted that systematic studies are required to investigate what possums *will* eat and what they *prefer* to eat.

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List of Publications

- Cameron, K. E., Bizo, L. A., & Starkey, N. J. (2013). Food preferences of the Brushtail Possum (*Trichosurus vulpecula*). *International Journal of Comparative Psychology*, 26, 324-336.
- Cameron, K. E., Bizo, L. A., & Starkey, N. J. (2014). Body weight stability of the Brushtail Possum (*Trichosurus vulpecula*). *Laboratory Animals*, 26, 324-336.
- Cameron, K. E., Bizo, L. A., & Starkey, N. J. (Submitted to IJCP). Assessment of Demand for Food under concurrent schedules in the Brushtail Possum (*Trichosurus vulpecula*).
- Cameron, K. E., Bizo, L. A., & Starkey, N. J. (In preparation). Demand for food under concurrent fixed-ratio schedules in the Brushtail Possum (*Trichosurus vulpecula*).

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Chapter 1 - The Possum

The common brushtail possum (*Trichosurus vulpecula*), a native Australian marsupial, was successfully introduced to New Zealand in 1858 to establish a fur trade in what was thought was a failing ecosystem (Cowan, 1990; Pracy, 1974). The population became well established in New Zealand with little competition for food by other browsers, plenty of habitable areas for nest sites and a lack of predation, except by humans (Gilmore, 1977).

There have been many possum population increases seen in different terrains of New Zealand, which illustrates the suitability of the species to the New Zealand environment (Rouco, Norbury, Smith, Byrom, & Pech, 2012). One such population growth was seen in the Catlins area of the South Island where after 42 possums were originally released in 1894, 60,000 possum pelts were taken from the area 18 years later (Wodzicki, 1948). The possum is viewed as a pest species due to their negative impact on the native flora and fauna of their habitat and the economic effect on agriculture (Brockerhoff et al., 2010; Warburton, Cowan, & Shepard, 2009). Therefore, intensive and diverse pest control is carried out to manage the possum population (Cowan, 1990; McGlone et al., 2014).

In contrast to New Zealand, possums in Australia are in competition with many other arboreal species for food and nesting sites; are predated upon by small carnivores such as the dingo and snake and are threatened by loss of habitat (Gilmore, 1977). For these reasons, possums are considered endangered and are a protected species in some areas of Australia (How & Kerle, 1995).

Basic Physiology

The brushtail possum, *Trichosurus vulpecula*, is of the order *Diprotodonia*, and family *Phalangeridae*. The brushtail possum is an arboreal marsupial similar in physical appearance to a large cat with pointed ears, a small nose with prominent teeth, and large eyes and whiskers (Figure 1.0). Their fur is dense and appears woolly in shades of grey, black or reddish-brown. The tail is prehensile and is mostly bushy with a scaly underside. They also have claws on their front feet but not the hind feet, which they cannot retract, and opposable toes on their hind feet to aid in climbing (Tyndale-Biscoe, 1973).



Figure 1.0. The brushtail possum, *Trichosurus vulpecula*. Photograph supplied and reproduced with permission from David Cook, davidcook.com.au.

Possums are solitary animals with a single social bond between the mother and joey. Adult possums only pair up during mating season (Kean, 1967). Any interactions between possums of either gender are hostile, except during periods

of oestrus. Male possums seek copulation by making a 'lost juvenile call' as a way to reduce the avoidance behaviour of the female (Tyndale-Biscoe, 1973).

Possums use vocal and olfactory indicators to mark their territory and location of their den, and respond to intruders with screeching noises (Green, 1984). The possum has sebaceous glands on the chest and chin and pericloacal glands in their urine which project a holocrine secretion to mark territory. The possum also secretes an apocrine chemical when showing 'fear' (Tyndale-Biscoe, 1973).

In New Zealand, the breeding season is between March and April, and September to October (Gilmore, 1969). Female brushtail possums have gestation periods of 17.5 days (Lyne & Verhagen, 1957). They are able to breed in their second year and raise up to two young per year in habitats with few possums and plenty of food (Kean, 1959). Possums give birth to very small young that crawl into the pouch under the mother's stomach to suckle and grow. After approximately five months the joey begins to venture out as a 'back rider'. The length of time the joey stays with the mother depends on the availability of resources, but it is typically around two months (Tyndale-Biscoe, 1973).

Territory and Home Range

There are several different reports as to the territorial behaviour of the possum in Australia. The observations by Dunnet (1964) and reanalysis by Green (1984) showed that both male and female possums were territorial in defending their home ranges. Female possums were more likely to have overlapping home ranges, although this is considered atypical (Dunnet, 1964). Male possums will defend their home range against immature males less than one year old, and other

animals (Dunnet, 1964). In addition, male possums tend to have larger home ranges and travel greater distances than females (Green, 1984; Ward, 1984). Winter (1976) theorised that females only need a den and sufficient food resources, thus, require a small home range, whereas male possums have large home ranges as they require a den, food resources and 'access' to a female possum. Overlapping territories of males and females would then be expected during periods of oestrus. Winter (1976) also described the interaction of possums of the same sex as 'mutual avoidance' (Green, 1984, p. 492) with defensive behaviours limited to the den site.

In New Zealand, home ranges tend to be smaller than in Australia as possums live near concentrated food sources (Green, 1984). When food is more sparsely distributed, possums have larger foraging and home ranges, and are less territorial (Green & Coleman, unpublished as cited in Green, 1984). For example, in a pine forest Clout (1977) reported low densities of between 2-3 possums per hectare, and thus had large home ranges whereas in habitats of forest and pasture, population densities tend to be higher (e.g., 25 possums per hectare) with home ranges between 18 - 24 per hectare (Green & Coleman, unpublished as cited in Green, 1984). In addition, in high density areas male possums are more territorial. Dominance hierarchies have been found when population densities reach between 8 - 10 possums per hectare, but only during feeding as possums travel into the home ranges of other possums to find food (Ward, 1984). Table 1.0 shows population densities reported in recent studies discussed by Rouco et al. (2012) for various forest types.

Table 1.0. Mean home range sizes and population densities of brushtail possums in various habitat types in New Zealand studies conducted since 2000. From Rouco, C., Norbury, G. L., Smith, J., Byrom, A. E., & Pech, R. P. (2012). Population density estimates of brushtail possums (*Trichosurus vulpecula*) in dry grassland in New Zealand. *New Zealand Journal of Ecology*, 37, 12–17.

Habitat	Site	Mean home range area (ha) ¹	Method ²	Density (possum ha ⁻¹) ³	Method ⁴	Reference
Podocarp-broadleaved	Auckland region	-	-	3.3-4.1	LT	Ji et al. (2005)
Podocarp-broadleaved	Waikato region	0.5 ^{KHR}	G	14	RT	Blackie et al. (2011)
Podocarp-broadleaved	Orongorongo Valley	-	-	9-12	LT	Arthur et al. (2004)
Podocarp-broadleaved	Orongorongo Valley	0.7 ^{KHR}	R	-	-	Ramsey & Cowan (2003)
Podocarp-broadleaved	Dunedin Region	-	-	16	LT	Efford et al. (2000)
<i>Nothofagus</i> spp.	Kaimanawa Range	3.1 ^{KHR}	G	5.6	RT	Pech et al. (2010)
<i>Nothofagus</i> spp.	Craigieburn Range	-	-	2	RT	Sweetapple (2008)
Mixed podocarp	Maungatautari	-	-	5.2 ^{TCI}	RT	Forsyth et al. (2005)
Mixed broadleaved	Wanganui area	-	-	10.8	LT	Nugent et al. (2010)
<i>Pinus radiata</i>	Waitarere	4.4 σ	LT	1.7-2.5	LT	Efford et al. (2005)
Farmland	Miranda	-	-	4.4 ^{TCI}	RT	Forsyth et al. (2005)
Mixed farmland and beech forest	Mount Somers	6.0 ^{KHR}	R	-	-	Ball et al. (2005)
Grassland/shrubland	Molesworth Station	5.1 ^{MCP}	R	1.7 ^{TCI}	RT	Glen et al. (2012)
Grassland/shrubland	Molesworth Station	23.1 ^{KHR}	G	-	-	Nugent et al. Unpubl. Data
Grassland/shrubland	Central Otago	36.2-54.1	LT	.4-.7	LT	Rouco et al. (2012)

Information prior to 2000 is summarized in Montague (2000).

¹95% kernel home range (KHR) except for Ramsey & Cowan (2003), which uses 80% KHR, minimum convex polygon MCP, sigma home range σ

²Home ranges estimated by: GPS collar G (which represents night-time movements), radio-tracking R (usually day-time movements, except for Ball et al. (2005), which represents night time movements).

³TCI-estimated density based on formula (Residual Trap-Catch Index – 0.55)/4.86 (Ramsey et al. (2005)).

⁴Density estimates based on: removal trapping RT, live trapping LT

In Australia, possums inhabit a wide variety of forest types with varying population densities, however, the brushtail possum population in Australia is naturally reduced due to predation, loss of habitat and food availability with the species protected in the mainland states (How & Kerle, 1995). Population densities in Australia are lower than in New Zealand and range between 0.01 per hectare and 2.84 per hectare (see How & Hillcox, 2000; Kerle, 1984; LeMar & McArthur, 2005).

Body Weight

The body weight of possums in the wild appears to be influenced by location and food availability, season, climate and population density (Green & Coleman, 1984; Owen & Norton, 1995). Kerle, McKay, and Sharman (1991) surveyed 18 possum populations throughout Australia. They concluded that body weight generally increased with latitude and that the largest animals lived in Tasmania. Overall, weights ranged from 1.40 kilograms to 3.50 kilograms for males and between 1.3 kilograms to 3.2 kilograms for females. A similar result was found by Fitzgerald (1984) who investigated the effects of folivore browsing in three Tasmanian forests. She found that the average male possum weighed between 3.37 kilograms and 3.76 kilograms and the average female possum weighed between 2.99 kilograms and 3.57 kilograms with the heaviest and healthiest animals living in regenerated forests.

In New Zealand, possum densities and general body weights are typically greater than populations within Australia (Tyndale-Biscoe, 1981). This is due to a more varied diet and the lack of competition or predation in New Zealand (Kerle, 1984; Tyndale-Biscoe, 1973). Over a period of 10 years, Bell (1981) studied

possum body weights from two trapped areas within the Orongorongo Valley, New Zealand and found that the availability of foods and population density of animals impacted seasonal variation in body weight. The body weight of female possums ($M = 2.20 - 2.31$ kilograms) during the breeding season was positively correlated with breeding success. This would impact the population density of the following year; which, if low resulted in heavier animals in subsequent years (Green & Coleman, 1984).

There are very few studies examining weight change in the captive possum where factors such as food availability, population density, and climate are controlled. Baker, Gemmell, and Gemmell (1998) caught and rehoused the wild possums in laboratory habitats where measures such as body weight were regularly taken to assess acclimatization to captivity. Possums were kept in colonies and free-fed vegetables, fruit and dog biscuits. All possums initially lost weight after capture before their weights began to increase, and then stabilize. One group of male possums had an average capture weight of 1.78 kilograms and showed an average stabilized weight of 2.03 kilograms after 20 weeks. The remaining possums had an average capture weight of 1.20 kilograms and showed an average stabilized weight of 1.74 kilograms after 20 weeks. The female possums had an average capture weight of 1.27 kilograms and showed an average weight of 1.84 kilograms after 20 weeks.

In a similar study, Day and O'Connor (2000) showed that body weights of newly captive possums ($M = 2.80$ kilograms), housed separately, did not change within the first 14 days of confinement. Body weights increased significantly after 28 days with an average increase of 0.20 kilograms, and after 42 days with an average increase of 0.30 kilograms. The population density of the shared colony

in the Baker et al. (1998) experiment may have contributed to the lower body weights of the possums ($M = 1.74 - 2.03$ kilograms), comparable to the low body weights of wild populations of mixed population densities (Green & Coleman, 1984). Housing possums individually gives added control over body weight in captive populations, especially in experimental conditions that require possums to be motivated to respond for food.

The control of body weight is an important variable in experimental studies when animals are expected to make responses for food rewards, however, there is no guideline for assessing an optimal, or stable body weight in the possum. In an effort to explore body weight trends in the captive possum two preliminary studies were conducted at the beginning of this research. The first study measured the trends in body weight of three possums on a free-feeding regime over 12 months. It was found that all possums continued to gain weight over the 12 month period but showed short bouts of body weight stability (Appendix A).

A second study investigated multiple methods for assessing the stability for possum body weight in the laboratory. The criteria for stability considered the most appropriate included calculating the percentage change in body weight between weigh sessions and visual inspection of graphed body weights where no more than two consecutive increases, or decreases in body weight were permitted. The criteria was suggested as a viable method for use with non-traditional laboratory animals, such as the possum, and also traditional laboratory animals where a general 'standard' for determining body weight stability might be validated. This experiment was recently published as a 'Short Report' in the journal *Laboratory Animals* and is included in Appendix B.

Pest Control

The management of the possum population in New Zealand typically uses lethal methods; including poison baits, (e.g., Eason, Ross, Blackie, & Fairweather, 2013; Nugent & Morriss, 2013; Ogilvie, Thomas, Morriss, Morgan, & Eason, 2000), and trapping and shooting (e.g., Duckworth, Brown, & Arrow, 2013; Linklater et al., 2013; Warburton & Gormley, 2013). Most recently, methods of delivering poison to pest species (e.g., King, McDonald, Martin, Tempero, & Holmes, 2007) and the reduction of possum fertility have been addressed, however, the latter is only in the research phase (e.g., Cui et al., 2010; Tompkins, Gemmell, & Dowling, 2013; Walcher et al., 2008).

Lethal doses of poisons are the most commonly used method to reduce the possum population in isolated and unrestricted conservation. The most commonly used poisons are sodium monofluoroacetate (1080) or cyanide. Chemicals such as phosphorus and brodifacoum are occasionally used (Eason, Frampton, Henderon, Thomas, & Morgan, 1993; Henderson, Frampton, Morgan, Hickling, & Box, 1999; Ogilvie, Thomas, Fitzgerald, & Morgan, 1996; Ogilvie et al., 2000). Scent-based lures such as cinnamon are used to mask the flavour and odour of 1080 or cyanide poisons (Sherley, 1992). According to Morgan, Innes, Frampton, and Woolhouse (1995) the most effective testing scents for masking 1080 were cinnamon, aniseed, plum, cherry and orange. These scents, however, were not able to sufficiently mask the hydrocyanic acid gas produced by cyanide.

The efficiency of poison, in that, ingestion results in death, is dependent on the palatability and toxicity of the bait (Henderson et al., 1999). If a non-lethal amount of bait is consumed the poison is slow to kill and results in physical and behavioural indicators of distress in animals, and in humans (Sherley, 2004;

2007). If the possum survives, the partial-consumption of bait can result in possums showing taste aversion to baits or specific odours, that inhibits eradication through bait systems (Henderson et al., 1999; Moss, O'Connor, & Hickling, 1998).

To combat the development of bait shyness, a treatment area is exposed to non-lethal dosed bait prior to a lethal bait drop. Pre-feeding increased the consumption of scented toxic bait in pre-fed captive possums compared to non-pre-fed animals (Moss et al., 1998). It has not been determined, however, to what extent appearance, lure odour or bait types are responsible for bait shyness (Moss et al., 1998; Ogilvie et al., 1996, 2000). Morgan, Morriss, and Hickling, (1996) identified the base bait (e.g., cereal or flour) as the main aversive component with the appearance of the bait functioning as a secondary cue and suggested that changing both base (cereal to carrot) and scent (cinnamon to orange) might increase consumption of baits.

Another advantage to pre-feeding is known as 'stimulus specificity' in the associative conditioning literature. An organism will only avoid a particular scent or bait flavour that has caused taste aversion, which is unlikely to decrease consumption of other flavours. This means that using a different flavour to mask a poison will likely result in consumption of lethal doses of the bait (Morgan et al., 1995; Moss et al., 1998). In addition, research is currently investigating the use of pheromones as lures in previously baited areas to increase the likelihood that possums will approach and interact with bait stations (e.g., Duckworth, Brown, & Arrow, 2013; Linklater et al., 2013).

Feeding Behaviour

There is extensive research of *what* the brushtail possum will eat in both the New Zealand and Australian environments. Many studies depend on the estimation of food availability in the wild (e.g., Sweetapple, Nugent, Whitford, & Knightbridge, 2002), with subsequent observations of how the sample area has changed over time. Other methods of assessing what possums eat include analysing faecal pellets (e.g., Coleman, Gillman, & Green, 1980) or stomach contents (e.g., Gilmore, 1965). A literature review of this research is included in Appendix C and the different methods for measuring what possums eat in the wild are discussed in the following description.

Wild possums are predominantly folivores in Australia and New Zealand as they have been reported to consume over 150 species of native and exotic trees (e.g., DeGabriel, Foley, & Wallis, 2002; Henderon, O'Connor, & Morgan, 1999; Nugent, Sweetapple, Coleman, & Suisted, 2000). Field studies conducted in various forestry areas in New Zealand (e.g., the Orongorongo Valley in Wellington, Mt Bryan O'Lynn in Westland and Banks Peninsula), have found possums consume the leaves, flowers and fruit of numerous species (Bell, 1981; Coleman, Green, & Polson, 1985; Gilmore, 1965). The species most often reported as consumed are Fivefinger (*Pseudopanax arboreus*), including the petiole (e.g., Nugent, Fraser, & Sweetapple, 1997; Sherley, 1992) and lamina (e.g., Kean & Pracy, 1953; Leathwick, Hay, & Fitzgerald, 1983), Kamahi (*Macropiper excelsum*; e.g., Cochrane, Norton, Miller, & Allen, 2003; Coleman et al., 1980), Kaikomako Bellbird tree (*Weinmannia racemosa*; e.g., Owen & Norton, 1995; Sweetapple, Fraser, & Knightbridge, 2004), Tawa (*Beilschmiedia tawa*; e.g., Fitzgerald, 1976; Sweetapple et al., 2004), Blackberry shrub (*Rubus*

species; e.g., Harvie, 1973; Jacometti, Frampton, & Hickling, 2007; Leathwick et al., 1983), Mahoe (*Melicytus ramiflorus*; e.g., Fitzgerald & Waddington, 1979; Fitzgerald, 1976), *Coprosma* species (e.g., Gilmore, 1965, 1967; Harvie, 1973), Rata (*Metrosideros robusta*; e.g., Cochrane et al., 2003; Coleman et al., 1980), Fuchsia, (*Fuchsia excorticata*; e.g., Clout, 1977; Fitzgerald & Wardle, 1979), and numerous *Fern* species (e.g., Gilmore, 1965; Mason, 1958).

In their native Australia, possums are also reported to consume a wide variety of foods, with the bulk of their diet being made up of different species of foliage, such as variants of the *Eucalyptus* species (Marsh, Foley, Cowling, & Wallis, 2003). Possums have adapted to a variety of environments by maximising their nutrient intake by eating many varieties of foliage to reduce the effects of toxins found in *Eucalyptus* species (see Marsh, Wallis, & Foley, 2005; Marsh, Wallis, McLean, Sorensen, & Foley, 2006; Pass & Foley, 2000; Wiggins, McArthur, & Davies, 2006).

Possums' preference for different food types can be determined by estimating a preference index (PI) for each food type. The PI describes the relationship between food consumed and its availability in the environment. Scores range from +1 (more food is consumed from the environment than remains) to -1 (food is not consumed and remains in the environment); a score of zero indicates that the proportions of foods consumed equals the proportions still available (Nugent, 1990). Using this measure for estimating a PI, Sweetapple et al. (2002) found that in 10, 20 and 30 year old beech forests in South Westland, New Zealand, the most consumed foliage types were Mistletoe (*Peraxilla colensoi* or *Tupeia antartica*), Pohuehue (*Muehlenbeckia australis*), and Kowaowao (Hound's tongue; *Phymatosorus pustulatus*) with high PI values (>

0.90). The PI of any specific foliage very much depends upon season, location and the age of the forest. For example, in the Haast Valley (New Zealand), Owen and Norton (1995) reported that Mistletoe had a PI value of 0.69 in spring and a value between -1 to 0.01 during the rest of the year. Pohuehue had PI values between 0.86 - 0.95 in summer, autumn and spring and a PI of -0.64 in winter. The PI of the type described above provides an estimate of preference for foods in relation to a particular location, season and forest regeneration status. Field studies of this type, however, are limited in a couple of important ways: they do not control food availability which limits wider conclusions regarding possums' food preferences and may be confounded by the relative availability of different foods.

Additionally, field studies of this type cannot provide information regarding the food preferences of individual possums, nor the stability of those preferences over time. This is because they look at whole populations only, or involve the analysis of stomach contents of deceased animals (e.g., Gilmore, 1965; Harvie, 1973), or faecal pellets of unknown animals (e.g., Coleman et al., 1980; Cowan & Moeed, 1987).

A number of studies have confirmed that possums also consume fungi (Cochrane, et al., 2003; Sweetapple et al., 2004), invertebrates (Cowan & Moeed, 1987; Owen & Norton, 1995), birds (Morgan, 1981) and eggs (e.g., Brown, Innes, & Shorten, 1993) in varying amounts. Cochrane et al. (2003) found remnants of fungi in 27 - 71% of possum stomachs with an average percentage (dry weight) of 3.3% of stomach contents demonstrating prevalence for fungi in the possums' diet. In contrast, Sweetapple et al., (2004) identified less fungi (1.6% dry weight) in possums' stomachs obtained from a 30 year old forest and even less in 10 and 20 year old forests (< 0.1%). While mushrooms only constituted a relatively small

proportion of the stomach contents, the authors of both these studies concluded that fungi were 'moderately preferred' (Sweetapple et al., 2004, p. 25) or a 'principal food type' (Cochrane et al., 2003, p. 62). A drawback of both of these studies is the lack of information regarding the availability of fungi. A study of possums in the Hihitahi Forest Sanctuary analyzed stomach contents and also calculated a PI for fungi (Rogers, 1997). Fungus species made up 1.25% of stomach contents by dry weight and the reported PI of 0.99 indicated that when it was available, it was consumed. There are two issues that limit conclusions about the preference of fungi: Firstly, the availability of fungi was not controlled, since it tends to vary widely in its availability and it may simply be the case that novel foods or foods that are only intermittently available, are consumed more when they are available (e.g., Nugent et al., 2000). Secondly, it is not clear what effect the relative availability of other foods might have on consumption of fungi.

Early studies reported that insects were consumed rarely by possums (Clout, 1977; Gilmore, 1967; Mason, 1958; Purchas, 1975; Warburton, 1978), however, this may have been due to methodological issues of analysis rather than low rates of consumption (Cowan & Moeed, 1987). In particular, the contents of stomach or faecal pellets may have been lost during preparation of samples for analysis (e.g., Gilmore, 1967) or calculated from combined stomach contents (e.g., Clout, 1977; Purchas, 1975; Warburton, 1978), thus resulting in an underestimate of consumption of invertebrates in comparison to other foods (Cowan & Moeed, 1987). In more recent studies, a variety of invertebrate species have been found in high quantities in a large proportion of possum faecal samples and stomach contents (Cochrane et al., 2003; Cowan & Moeed, 1987). Stick insect (*Phasmatodea* spp.), cicada (*Hemiptera* spp.), weta (*Orthoptera* spp.),

beetle (*Coleoptera* spp.), fly larvae (*Diptera* spp.) and mite (*Acari* spp.) remnants made up 81.8% of the invertebrates found in possum faecal pellets. Some faecal pellets in that analysis (9.1% - 25.6%) contained just one species of invertebrate but frequently up to four different species were present (Cowan & Moeed, 1987). Analysis of stomach contents found invertebrate species in up to 50% of the samples, including *Coleopteran* (beetle) larvae (8- 50%), *Acari* spp. (10%), Arachnid (8%), and *Orthoptera* spp. (14 -21%; Cochrane et al., 2003). Owen and Norton (1995) concluded that insect larvae (mainly *Diptera* spp.) was the third most important food type for possums with the largest quantity (28.1% average dry weight) found in samples of possum stomach contents in August.

Observational studies of free fed captive possums found that some will eat birds and eggs (Brown et al., 1993; Brown, Moller, & Innes, 1996; Morgan, 1981). Analyses of the contents of over 2000 wild possums' stomachs, however, did not identify meat or egg remnants definitively (e.g., Clout, 1977; Cochrane et al., 2003; Gilmore, 1965, 1967; Harvie, 1973; Mason, 1958; Purchas, 1975; Warburton, 1978); thus, the frequency of which these foods are consumed in the wild is unclear.

Together these studies provide information regarding foods reported to be eaten by possums in the wild, however, some findings are inconsistent, particularly with regard to possums' consumption of meat and eggs. The majority of studies assessing possums' food choices are field studies which are limited because they do not control food availability which may affect assessments of preference. Additionally, these studies do not assess the food preferences of individual possums or the stability of those preferences within the same individual possums.

It is important to study the food choices of possums; the majority of studies investigating what possums eat have identified that food availability is a mitigating factor in possum population density, breeding and their food selection. In field studies investigating food preference, there has been little control in terms of food availability, therefore, foods identified as preferred may have been consumed because they were palatable, or simply because they were convenient. To accurately determine the food preferences of the possum, studies need to be carried out in more controlled experiments.

Chapter 2 - Preference Assessments

In Experiments 1 and 2, single and paired preference assessments were conducted under laboratory conditions to assess the food preferences of captive possums using food types reported to be consumed in the wild.

The identification of reinforcers through the use of preference assessments has been widely studied in humans. In particular, these assessments are used to identify food and leisure items to be used in teaching individuals with intellectual disability. They include: free operant, (e.g., Ortiz & Carr, 2000; Roane, Vollmer, Ringdahl, & Marcus, 1998), single (e.g., Pace, Ivancic, Edwards, Iwata, & Page, 1985), paired (Fisher et al., 1992; Piazza, Fisher, Hagoplan, Bowman, & Toole, 1996) and multiple presentations of stimuli (DeLeon & Iwata, 1996). Modified versions of these methods can also be used in preference testing in animals: for example, in rats (e.g., Weiner & Stellar, 1950, 1951), pigs (e.g., Smith, Wathes, & Baldwin, 1996) and exotic animals such as the giant panda and elephant (e.g., Gaalema, Perdue, & Kelling, 2011) and the brushtail possum (e.g., Hudson, Foster, & Temple, 1999).

Preference assessment methods in general consist of the presentation of stimuli with the behaviour by the participant, in terms of approach, recorded. Methods such as single, paired or multiple presentations of stimuli are of low response effort by the subject because they require the subject to make only one response or selection, before they receive that stimulus as a reward, to either play with or eat (DeLeon, Iwata, Goh, & Worsdell, 1997; Fisher et al., 1992).

Free operant preference assessment

The free operant preference assessment involves the observation of behaviour when a subject has unrestricted access to a wide variety of activities or items. The activity where the subject spends most of their time can be assessed to be reinforcing, and can be used to reward desired behaviour. The selection of stimuli can be ‘contrived’, in that the experimenter ‘salts’ the environment with particular stimuli and measures preference for items the experimenter has concluded *might* be reinforcing. The other method is ‘naturalistic’ where behaviour is recorded within the subject’s everyday environment (Cooper, Heron & Heward, 2007).

Free operant preference assessments tend to avoid undesirable behaviour because the participant is not under pressure to respond in a particular way. The assessments are also quick to accomplish (Roane et al., 1998), however, they tend to identify a limited number of preferred items. Some items, considered preferred, may not be approached as interaction only occurs with other preferred items on offer, excluding those that are preferred but not at that moment (Ortiz & Carr, 2000).

Single stimulus preference assessment

The single stimulus preference assessment is a basic method used to determine preference. It involves presenting one item at a time and recording responses (e.g., Weiner & Stellar, 1951). This method can be also be used to assess food preference by measuring the frequency of specific food consumption and the amount of food consumed, however, it may overestimate preference (Fisher et al., 1992). In addition, it does not identify the degree of preference

between highly preferred reinforcers (Higbee, Carr, & Harrison, 1999). This method is useful for determining the *relative acceptability* of food because a choice is made between whether to consume and not consume a particular food (Young & Greene, 1953a), as in the context of pest control. It may also be helpful in identifying foods that are effective lures or masking odours for use in pest management as one flavoured bait is typically used at a time (e.g., Morgan, 1990; Ogilvie et al., 1996).

Paired stimulus preference assessment

The *relative preference* between items can be determined using the *paired stimulus* assessment method (e.g., DeLeon & Iwata, 1996; Fisher et al., 1992; Young & Greene, 1953a, 1953b). Subjects are presented with two items simultaneously and a recording is made of which food is consumed first within a given time frame (Gaalema et al., 2011). This method is considered a more consistent, efficient and reliable procedure than the single stimulus assessment as it identifies preference where one stimulus is chosen over another (Young & Greene, 1953a). In addition, the assessment provides a ranking of preferred items (DeLeon & Iwata, 1996; Pace et al., 1985), when items are presented in a counter balanced manner with each food presented with every other food.

Multiple stimulus preference assessment

As preference assessments have a tendency to be time consuming the *multiple stimulus* presentation method has been used to improve the efficiency of the paired stimulus method by presenting a greater array of stimuli to the subject simultaneously (Windsor, Piche, & Locke, 1994). This is similar to the free

operant method although fewer stimuli (e.g., approximately seven) are used. The multiple stimulus with replacement (MSW) assessment involves presenting the stimuli to the subject and after selection has been made that stimulus is returned to the array, where it is again presented to the subject (DeLeon & Iwata, 1996). In contrast, in the multiple stimulus without replacement (MSWO) assessment, the selected stimuli are not returned to the array. For example, after the first presentation of the array, one item is chosen, it is then given to the subject for a period of time or to be consumed. This item is not replaced in the array; however, the remaining items are rearranged for the next trial. The items are replaced during subsequent trials. The *brief multiple stimulus* assessment, a variation of Fisher et al.'s (1992) paired stimulus method further reduces session time because after a stimulus is selected from an array it is not replaced when the session is repeated (DeLeon & Iwata, 1996). Results obtained from the multiple stimulus preference assessment and the paired stimulus method are comparable (DeLeon & Iwata, 1996), however, the paired stimulus preference assessment is more time consuming.

Preference assessments in animals

Preference assessments in animals have been used to assess the preference of different food types (e.g., Foster, Sumpter, Temple, Flevill, & Poling, 2009), for particular environments (e.g., Hardy, Windle, Baker, & Ridley, 2004; Smith et al., 1996) and for enrichment items (e.g., Swaisgood, White, Zhou, Zhang, & Lindburg, 2005). Typically, the methods of assessment are modified from those used in humans, for example, Gaalema et al. (2011) used paired stimulus assessments to assess the food preferences of elephants. The elephants extended

their trunks into long pipes containing food in order to smell each sample. After the elephants had smelled both foods, they were allowed to approach one of the foods to eat.

Preference assessments in possums

Taste preference experiments conducted with possums in the laboratory have set out to identify preferred foods to be used as reinforcers (e.g, Martin, 2002), determine preferred flavours to mask bait (e.g., Morgan, 2006) and elucidate natural food preferences for foods found in Australia (Wiggins, McArthur, McLean & Boyle, 2003; Wiggins et al., 2006).

Identifying reinforcers. Single and paired stimulus preference assessments have been used to determine a potential reinforcer for use in operant experiments. Martin (2002) measured the consumption of a crushed barley mix, rolled oats, barley flakes, sunflower seeds, San Bran, dried peas, pasta letters, Coco-pops®, pumpkin seeds, banana chips, mango pieces, Banana Ricies™, vegetable protein, buck wheat and maple peas using a single stimulus preference assessment. She found that possums would consume all foods except for vegetable protein, buck wheat and maple peas. Using a paired stimulus preference assessment she found possums preferred different foods; but overall mango, pasta letters, rolled oats, banana chips and coco-pops were preferred. As some of the preferred foods were impractical for further research as they would stick or not flow in the food hoppers, dry foods of rolled oats, san bran and a flaked barley and sunflower seed mix were chosen for further experimentation.

Using a paired stimulus assessment, Hudson et al. (1999) presented possums with all possible pairs of nine different food types: carob, dock leaves

(*Rumex obtusifolius*), sultanas, condensed milk, lemon rind, apple, dried pineapple pieces, aniseed sweets and *Pebbles*TM (sugar coated chocolate). Generally possums chose carob chips most often, then dock leaves and apple. They chose lemon rind the least often. The possums were idiosyncratic in their food choices with some possums identifying particular foods as highly preferred and for others the least preferred.

Flavours and odours to mask bait. Using a multiple stimulus preference assessment without replacement (MSWO), Morgan (1990) investigated the preference and aversion to flavours used to mask 1080 bait. The palatability of 39 flavours used to mask bait odour was tested in nightly trials. Each trial consisted of three flavoured flaked barley samples offered in addition to a control test of non-flavoured flaked barley to one possum (for each of 13 nights). Out of the 39 flavours, the orange flavoured flaked barley was the only one to significantly increase consumption in comparison to the non-flavoured flaked barley. In subsequent tests, using orange and cinnamon flavours to mask the 1080 odour both flavours masked the scent of toxic and non-toxic bait. This was because possums tasted the bait prior to rejection, instead of only smelling the bait. A few possums, however, rejected bait laced with cinnamon, with the authors concluding that orange flavoured bait increased the likelihood of possums consuming baits and receiving a fatal dose of poison.

A range of lures commonly used by possum hunters was tested by Morgan et al. (1995) using a MSWO preference assessment including flavours such as orange, ginger, aniseed, cherry, peanut butter, and amyl acetate (apple odour); secretions such as possum urine, samples from the paraoccal glands of male and female possums and *Dactylanthus* nectar (a plant eaten by possums) and water.

Three pellets tainted by a synthetic flavour, secretion and water were hidden within the possums' aviary each night. The most highly ranked lures were cinnamon, aniseed, cherry, orange and plum, however, possums located possum urine the fastest. In a subsequent field test, using the top five flavours as lures to toxic bait, only cinnamon improved the effectiveness of using cyanide baits to kill possums compared to the other lures.

The preference for odours used as lures was evaluated using paired stimulus assessments in singly housed possums (Todd, Connor, & Waas, 1998). Five essential oils, orange, cinnamon, peanut, cloves and almond were each mixed with water as a base. These were presented in pairs (with water as an added control) and attached in small jars to the side of each cage. There was little difference in the number of responses made or time spent sniffing each odour, or the water control. The authors concluded that the lack of preference might have been due to the possums' inability to discriminate the odours, they were equally preferred or there was a lack of 'motivation' to sniff the odours. Other researchers have observed odour preferences in the laboratory, but these did not function as lures in to bait in the wild (Morgan et al., 1995).

In a modified replication of Todd et al. (1998), a paired stimulus preference assessment using the same odours as the previous experiment was conducted in an outdoor aviary environment (Todd, Waas & O'Conner, 2000). There were no significant differences between responses to the odours and water control and no change in individual possum preferences over 40 days. A third experiment was conducted using the same methodology but different odours: *Dactylanthus* nectar, orange and peppermint. The researchers again found no

significant difference between responses to the odours, although observed that on many occasions the possums did not approach the odours presented.

Natural food preferences. The single stimulus preference assessment has been used to investigate the preference of foods containing toxic plant metabolites (PSM) such as *Eucalyptus* species in Australian possums (Wiggins et al., 2003, 2006). Wiggins et al. (2003) offered possums their typical basal diet tainted with varying concentrations of cineole, a PSM found in Eucalyptus oil. Nocturnal feeding behaviour of the possums was measured over seven nights for each concentration of cineole. Generally, there were a higher number of feeding bouts when the food on offer had a high concentration of cineole, however, possums consumed the least amount of this diet compared to the other foods on offer.

In a second experiment Wiggins et al. (2003) offered possums a choice between two diets tainted with two PSMs, cineole and gallic acid using a paired stimulus preference assessment. They found that possums offered the choice of two diets consumed more food with fewer feeding bouts than when offered only one type of food. Wiggins et al. (2006) built upon this research and offered possums two different species of *Eucalyptus* containing different PSMs and found that possums consumed more foliage and switched more often between the two choices when both species were offered for 8 hours, than when they were offered for shorter periods of time or when presented singly. The latter two studies did not, however, assess relative preference for the different food types. This means that being able to choose between two species of *Eucalyptus* led to more consumption of both foods and allowed for more overall consumption of food while decreasing the toxic effects of the PSMs that occurs when only one species is available.

In summary, preference assessments have identified food and odours in possums for application to operant research in the laboratory, for use in pest control in New Zealand and the understanding of food choice in possums in Australia. In Experiments 1 and 2, single and paired stimulus preference assessments were used to measure possums' food preferences for food types found in the wild of New Zealand.

Chapter 3 - Behavioural Economics

A variety of methods have been developed to assess the demand for different commodities. One such method is requiring subjects to ‘pay a price’ by making multiple responses, such as lever pressing, to obtain a desired commodity. These responses are used as a measure of the effort a subject will expend to obtain that commodity (e.g., Hursh, 1980; 1984). It has been argued that the more ‘motivated’ the subject is to obtain a particular commodity, indicated by increased responses, the more it is valued (e.g., Dawkins, 1983; 2004; Sørensen, Ladewig, Matthews, Kj, & Lawson, 2001)

Quantitative accounts of performance have been provided by Hursh (1980, 1984), Hursh, Raslear, Shurtleff, Bauman, and Simmons (1988) and Hursh and Silberberg (2008) in the field of behavioural economics. The demand curve describes the “relationship between total consumption of a commodity and its price, expressed as effort per unit of reinforcement” (Hursh & Winger, 1995, p. 374). ‘Elasticity’ of the demand curve is the change in consumption as price increases (Hursh, 1984). Typical dependent variables measured in these experiments include measures of consumption, in the number of reinforcers consumed, P_{\max} , (Hursh & Winger, 1995; Hursh, 1980, 1984), cross point and substitutability (Hursh, 1980; Sørensen et al., 2001), and break point (Hodos, 1961; Hodos & Kalman, 1963).

Hursh et al. (1988) used Equation 1 to describe the interaction between consumption in log units ($\ln Q$) and ratio requirement or price ($\ln P$), to predict two parameters, a and b , that describe the ‘value’ of the reinforcer:

$$\ln(Q) = \ln(L) + b[\ln(P)] - a(P) \quad (1)$$

The three parameters in Equation 1 are L , the initial consumption at the minimum ratio requirement (y-intercept); b , the slope of the curve at the initial ratio requirement, and a , the rate of change in elasticity as ratio requirement increases. For preferred stimuli, the slope (b) is close to zero and negative (as the slope declines) with the change in ‘value’ of a stimulus reflected in the a parameter. If a was close to zero, then there would be minimal changes in elasticity as ratio requirement increased (Hursh & Winger, 1995). The normalized version of Equation 1 requires that consumption at ‘price’ of ratio requirement be proportional to consumption at the smallest ratio requirement. This allows the direct comparison of demand for such commodities as different concentrations of the same drug (Hursh & Winger, 1995).

In more recent studies, Hursh and Silberberg, (2008) provide an equation that uses *one* parameter to measure the ‘essential value’, α , of a reinforcer. The value of α represents the rate of change in elasticity of the demand curve as price increases (Figure 3.0; Hursh, Madden, Spiga, DeLeon & Francisco, 2013). When essential value is close to zero there is little change in elasticity as price increases. Larger values of essential value indicate greater elasticity of demand, in that, consumption will decrease as ratio requirement increases. According to Hursh et al. (2013) essential value should vary for reinforcers that differ in ‘value’ to the subject, such as food, but not those that vary in magnitude such as access time to the reinforcer (e.g., Grant, Foster, Temple, Jackson, Kinloch & Poling, 2014).

The measure of estimated consumption at a price of zero, Q_0 , is the initial demand for a commodity (Hursh & Silberberg, 2008). Recent studies in hens have found that more highly valued commodities, such as foods (e.g., Foster et al.,

2009), longer access times to foods (e.g., Grant et al., 2014) and different concentrations of the same drug (Hursh et al., 1988) show lower initial demand.

Equation 2 is similar to Equation 1 as the parameter b is replaced in Equation 2 by the scaling parameter k which represents the range of the dependent variable in logarithmic units. When k is constrained, elasticity is reflected in the essential value parameter (α). Equation 2 also provides normalized values of price, termed the ‘cost’ or ratio requirement per reinforcer multiplied by the initial demand ($Q_0.C$).

$$\ln(Q) = \ln(Q_0) + k(e^{-\alpha Q_0 C} - 1) \quad (2)$$

Demand for a commodity is deemed ‘inelastic’ when the derived curve has a negative slope of greater than -1 at a given ratio requirement; consumption of the commodity decreases minimally as price increases, in that, consumption of the commodity is ‘defended’ or maintained as ratio requirement increases (Hursh, 1984). It also implies that the commodity is of value to the subject (Dawkins, 1988). The derived curve has a flatter slope with minimal change in consumption as ratio requirement increases (Kagel, Battalio, Green, & Rachlin, 1980). Elastic demand is when the curve has a slope of less than -1 as the consumption of a commodity decreases substantially as price increases (Hursh, 1980), and is seen when the commodity is a ‘luxury’ rather than a ‘need’ (Hursh, 1984).

To illustrate demand elasticity; Dawkins, (1983) demonstrated that when hens were given restricted time periods for feeding and to perform litter behaviours (such as dust bathing) the consumption of food during those periods increased. This indicated that feeding was a ‘need’. Conversely, the hens did not

increase their time on the litter during the restricted period indicating it was not as ‘valued’ as feeding.

In most instances, demand elasticity has been found to be mixed, where demand is initially inelastic but as ratio requirement increases, becomes elastic. Hursh (1984) details the consumption of water and food by two monkeys under fixed-ratio (FR) schedules that increased in price each day. At low FR values consumption for food and water was inelastic, as the increasing ratio requirement did not impact demand for food or water; however, elastic demand was evident as the ratio requirement increased beyond 200 responses.

The ratio requirement at which responding moves from ‘inelastic’ to ‘elastic’, or passes from a slope of greater than -1 to a slope less than -1 is termed ‘ P_{\max} ’. It is also the point of maximal responding calculable when demand elasticity is mixed (Hursh & Winger, 1995; Hursh & Silberberg, 2008). P_{\max} is derived from the equation for elasticity and can be calculated using Equation 3 (Hursh & Winger, 1995) and Equation 4 (Hursh et al., 2013).

$$P_{\max} = \frac{1+b}{\alpha} \quad (3)$$

$$P_{\max} = \frac{0.65}{\alpha \cdot Q_0 \cdot k^{1.191}} \quad (4)$$

P_{\max} is correlated with the break point (the final completed ratio requirement) and is a measure of sensitivity to changes in ratio requirement (Madden & Hartman, 2006). Small P_{\max} values indicate sensitivity to changes in ratio requirement as consumption decreases as ratio requirement increases. For example, Cronin (2012, unpublished) found that P_{\max} and break point values were

higher when possums responded for rolled oats under a progressive-ratio (PR) schedule when foods such as soy protein or bran were available under a FR 20 or FR 50 schedule.

A theoretical demand curve is shown in Figure 3.0. The curve shows the initial demand value (the y-intercept), P_{\max} (measured on the x-axis) where the slope is -1, and essential value, α (k is constrained). Large essential values indicate that elasticity changes considerably as ratio requirement increases, whereas values close to zero indicate little change in elasticity as ratio requirement increases.

It is possible to compare the demand for reinforcers available concurrently with schedules of the same or differential rates of reinforcement (Hursh, 1984). The “cross-price relations” (Hursh, 1984, p. 443) would provide information about the relationship between the two commodities such as if they were substitutes and could function in place of one another; or complements where as demand increases or decreases for one commodity the other commodity shows a similar level of demand (Hursh 1980, 1984).

A recent mathematical model by Hursh et al. (2013) describes the ‘cross-price change’ in demand because the demand of one alternative is measured by the (normalized) price of other alternative:

$$Q = \log(Q_{\text{alone}}) + I e^{-\beta.C} \quad (5)$$

Q_{alone} is consumption when the price of the reinforcer is zero, I is the interaction constant which if negative indicates that the two alternative reinforcers are substitutable as ratio requirement increases, β is the sensitivity value of

consumption on the fixed alternative to changes in the other (varying) alternative.

C is the cost of the alternative.

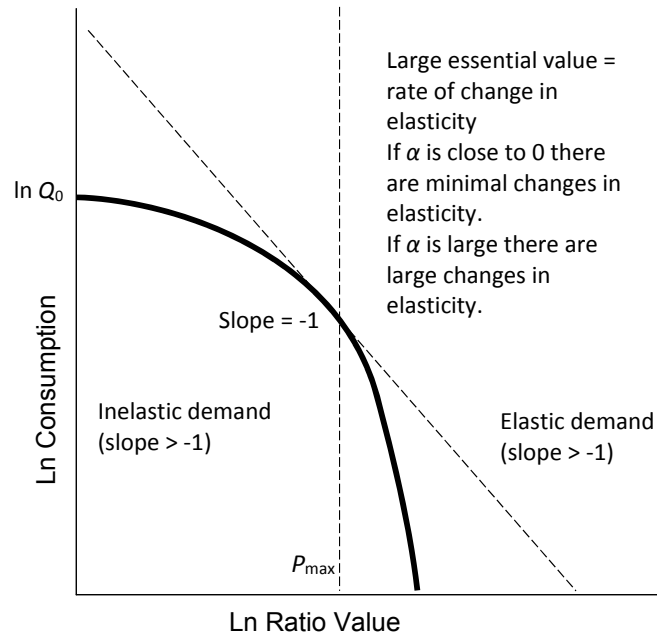


Figure 3.0. A theoretical demand curve showing the higher order dependent variables derived from Equation 2 (Hursh & Silberberg, 2008). Initial demand, Q_0 is the y-intercept, P_{\max} is the ratio requirement on the x-axis when the slope of the curve is -1, and essential value, α is the rate of change in elasticity; large values indicate large differences in elasticity as ratio requirement increases.

The cross-price exponential demand model provides a derived curve of responding for the ‘alternative’ commodity to be compared with the curve derived from the exponential model (Hursh & Silberberg, 2008). The point where curves describing responding under two schedules intersect is the ‘cross point’ (Figure 3.1). This is where responding, and thus consumption is identical for the two commodities (Holm, Jensen, Pedersen, & Ladewig, 2008; Hursh et al., 1988). The interaction between the two curves gives a measure of substitutability or complementarity of the two items. The absence of a cross point might also

indicate that the foods are independent of one another (Green & Freed, 1993; Hursh, 1980, 1984; Petry, 2001).

Consider the examples of commodities: A and B in Figure 3.1.

Commodity A increases in ratio requirement within the session and Commodity B stays at a constant requirement. If the consumption of Commodity A decreases as the price for A increases, the consumption of Commodity B should increase. This suggests that the two commodities are of equal value to the subject and will substitute or replace each other as one becomes 'cheaper' than the other (Figure 3.1.a ; Hursh et al. 2013). In contrast, in (b) if consumption of both Commodity A and Commodity B was to decrease then the two commodities could be described as 'complementing' each other, and we would not expect to observe a cross point.

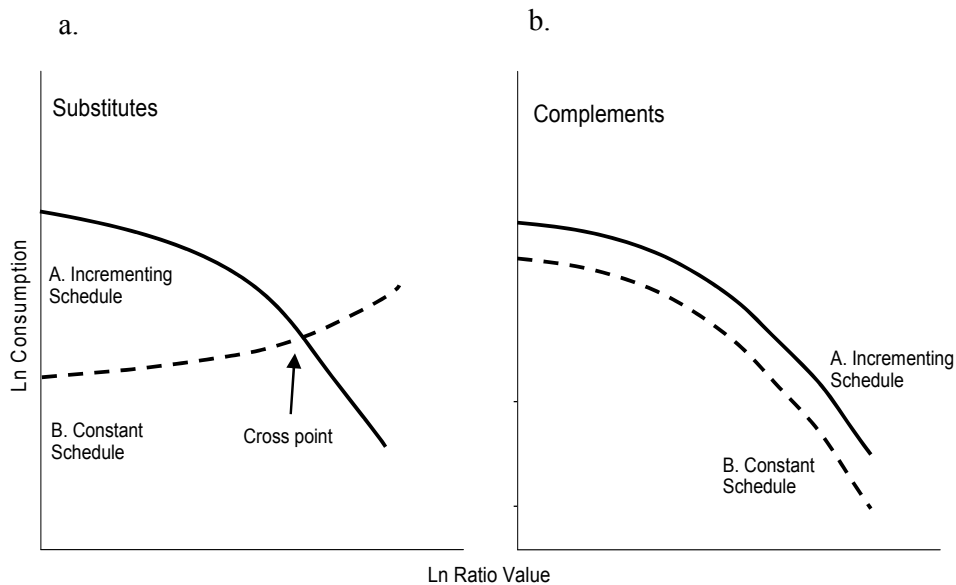


Figure 3.1. Theoretical curves showing commodities A and B as substitutes (a) and complements (b).

An experimental example that illustrates substitutability under concurrent schedules is provided by Lappalainen and Epstein (1990). The demand for highly-

or moderately preferred sandwiches was measured in university students (Figure 3.2). The students had to play a computer game and earn points which corresponded to earning a highly preferred or moderately preferred sandwich. In each condition, the number of responses required to earn a point progressively increased for the highly preferred sandwich (top line of x-axis labels) but was kept constant for the other sandwich (bottom line of x-axis labels). Responding for the highly preferred sandwich was high when the ratio requirement was low and decreased as the requirement increased. Conversely, responding for the moderately preferred sandwich increased as the ratio requirement was comparatively lower compared to the highly preferred sandwich. The cross point describes the ratio requirement where responding for the highly preferred sandwich was too costly, therefore, responding increased for the moderately preferred sandwich, which was available for fewer responses.

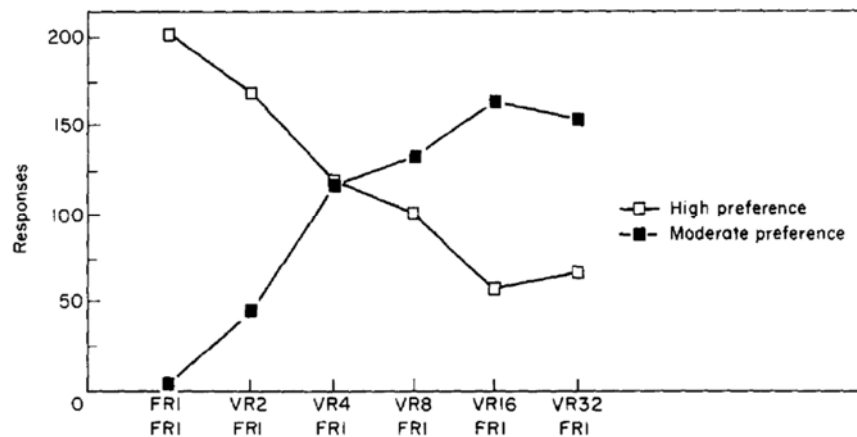


Figure 3.2. The number of responses to each concurrent pair for high and moderate sandwiches. The top line of the x-axis label is the ratio requirement to earn the highly preferred sandwich and the bottom line of the x-axis label is the ratio requirement to earn the moderately preferred sandwich. From Lappalainen, R., & Epstein, L. H. (1990). A behavioural economics analysis of food choice in humans. *Appetite*, 14, 81–93. Used with permission from Elsevier.

In a concurrent schedule procedure shifts in responding from the one schedule to the other would “occur at a point where the incentive value of a constant schedule is first greater than that of the forthcoming component of the incrementing schedule” (Bhatt & Wasserman, 1987, p. 49). If responding under an incrementing schedule was to persist after the point where two schedules have equal ratio requirements the subject is making a ‘perseverative’ error (e.g., Allen & Leri, 2010; Wanchisen, Tatham, & Himeline, 1988); or if responding to the constant schedule when food under the incrementing schedule requires fewer responses to obtain, the subject is making a ‘conservative’ error (e.g., Allen & Leri, 2010; Himeline & Sodetz, 1987; Hodos & Trumbule, 1967).

The break point is the last completed ratio requirement under FR or PR schedules of reinforcement and has previously been called the breakpoint (Hodos, 1961), or extinction ratio (Bizo & Killeen, 1997). The break point is a measure of relative reward strength for different commodities (Hodos, 1961) or the reinforcing efficacy of a commodity (Rodefer & Carroll, 1996). Generally, the higher the break point, the greater the ‘value of the reinforcer to the subject (Hodos & Kalman, 1963; Stafford & Branch, 1998).

Break point was first used by Hodos (1961) as an index of the relative reward strength for different concentrations of sweetened condensed milk in rats at different deprivation levels. He found that subjects would respond to higher ratio requirements for preferred foods. In addition, higher break points were observed in subjects that were food deprived or if the concentration of sweetened condensed milk was increased. In subsequent experiments, break points have been shown to vary as a function of the quality of the commodity (Hodos & Kalman, 1963; Hodos, 1961), magnitude of the commodity (Rickard, Body, Zhang,

Bradshaw, & Szabadi, 2009; Skjoldager, Pierre, & Mittleman, 1993) and schedule requirement (Killeen, Posadas-Sanchez, Johansen, & Thrailkill, 2009).

The use of demand models to assess the effort an organism will put into obtaining different foods can indicate the 'value' of different commodities to the subject. The logic being that animals will work harder to gain an item of higher value, over one of lesser value. This effect is measured by dependent variables such as essential value, initial demand, P_{max} , cross point, and break point. When these values are compared they indicate the relative demand for different commodities.

Open and closed economies

Responding to gain access to commodities can occur in contexts of either 'open' or 'closed' economies (Hursh, 1980, 1984; Rachlin, Battalio, Kagel, & Green, 1981). In an open economy, short sessions are conducted within a laboratory environment and extra food is supplied to maintain a stable body weight after the experimental session. In contrast, in a closed economy the intake of food is a function of behaviour which is typical of foraging consumption of animals in the wild (Hursh, 1980, 1984). The type of economy of which an operant experiment is conducted can affect the results, in that, the economy predicts the rate of reinforcement more so than schedule type, session length or the state of deprivation (Hursh, 1980).

Experiments arranged in open and closed economies, can result in different patterns of behaviour. Collier, Hirsch, and Hamlin (1972) observed rats in a 24 hour closed economy with reinforcement contingent on bar presses on an FR schedule that increased every 10 days. The cumulative results showed the rats

continued to respond as the rate of reinforcement became progressively leaner. The asymptote for the number of responses at the largest ratio requirement, FR 240, was approximately 70,000 where one rat spent 14 hours per day bar pressing and on average was making 110 responses per minute. These data shows that in a closed economy, rate of responding positively adjusts with the increase in 'cost', as to uphold daily food intake dependent on responding.

In contrast, Felton and Lyon (1966) found response rates initially increased under incrementing FR schedules. Ratio strain was observed (a decline in responding) when the ratio requirement was increased to 150 responses in an open economy. Similarly, Catania and Reynolds (1968) increased the intervals in a variable interval (VI) schedule from 15-s to 480-s with pigeons. They found an initial increase in responding as the intervals increased which then reached an asymptote when the VI was greater than approximately 50 seconds.

Under concurrent schedules, Hursh (1978) compared responding of two Rhesus monkeys in closed and open economies. Food was available under a VI 60 s and under a varied VI schedule that ranged between 30-s to 480-s. Water was available under a VI 60 s schedule. In the closed economy, responses to the VI 60 s schedule for food decreased minimally, remained constant for water and increased for the varied schedule for food. In contrast, in the open economy, responses to the VI 60 s schedule for food decreased as the rate of reinforcement decreased whereas responding to the varied schedule initially increased before decreasing at a low rate, whereas responding for water increased.

Responding to obtain qualitatively different commodities such as electrical brain stimulation (EBS) and food in a concurrent arrangement leads to different response patterns in rats in closed economies (Hursh & Natelson, 1981). Rats

responded to higher rates for food to maintain a constant reinforcement rate over the 24 hour period showing inelastic demand. In contrast, responding decreased for EBS showing elastic demand.

Response rates during long and short sessions in closed and open economies in hens were compared by Foster, Blackman, and Temple (1997). Response rates were higher during the long sessions in closed economies and responding persisted to higher ratio requirements compared to shorter sessions in open economies. In addition, the demand for food was more inelastic during the longer sessions and in closed economies, and was elastic at low ratio requirements in the open economies.

In summary, higher response rates are observed, and in concurrent arrangements more responding is allocated to alternatives of differing ratio requirements to maximise reinforcement rates under each schedule in closed economies. In an open economy, there tends to be lower response rates and elastic demand for food and in concurrent arrangements there is increased responding allocated to one of the schedules over the alternatives.

Chapter 4 - Measuring Preference and Demand

The behavioural economic paradigm has been used to study demand for different commodities such as food (e.g., Foster et al., 2009), water (e.g., Sørensen et al., 2001), drugs (e.g., Christensen, Silberberg, Hursh, Roma, & Riley, 2008) or substrate (e.g., Holm et al., 2008) in animals under different schedule arrangements such as FR schedules (e.g., Hudson et al., 1999), or PR schedules (e.g., Foster, Temple, Cameron, & Poling, 1997), and concurrent arrangements of ratio schedules (e.g., Holm, Ritz & Ladewig, 2007). Variables also manipulated in demand experiments include reinforcer magnitude (e.g., Grant et al., 2014), and step-size between ratio requirement increments (e.g., Killeen et al., 2009).

Ratio schedules

Ratio schedules require that a predetermined number of responses are made to obtain a reinforcer (Skinner, 1938). The ratio requirement typically increases *across* sessions in FR schedules (see Stafford, LeSage, & Glowa, 1998), or *within* a session in PR schedules (Hodos, 1961).

Foster et al. (2009) examined the effect of different types of wheat (puffed, honey-puffed and whole wheat) on response rates using FR schedules. An initial preference assessment using concurrent random interval (RI) schedules, identified wheat as the most preferred food, followed by honey puffed wheat, and then puffed wheat. Following the preference assessment, the hens were required to peck a lit key for either plain, puffed and honey puffed wheat under single FR schedules. Foster et al. (2009) used Hursh et al.'s (1988) model and found it fit their data well ($M_{VAC} > 80\%$). Wheat produced the highest P_{max} values but lowest

initial demand values and puffed wheat produced the highest initial demand values indicating there were higher response rates at low ratio requirements for this food. The authors stated that the hen was “defending its consumption, that is, producing greater access to the less preferred food in order to gain the same overall value per session that it does with the most preferred food” (Foster et al., 2009, p.320), by responding more for that food at higher ratio requirements.

The effect of differing magnitudes of a food reward on demand can be tested by changing the number of seconds access to wheat given to the subject (Grant et al., 2014). Hens were given 2-s, 8-s or 12-s access to wheat under FR schedules that doubled in ratio requirement each day. Response rates increased as the ratio requirement increased and were lower with shorter access times. The linear and exponential demand models (Equations 1 & 2) fit the data well, however, gave unexpected parameter estimates. As the magnitude of the same reinforcer, wheat, was varied it was expected that initial demand would vary and the rate of change value (α) would not vary. These results, however, showed that initial demand did not change with longer access times and alpha varied across access times and declined as access time increased. This means that the “value” of the food increased as access times increased. P_{\max} was highest for the 12-s access time as expected.

In an experiment using possums, Hudson et al. (1999) assessed the level to which possums’ would continue to respond for a preferred food under FR schedules. Carob chips were identified in a paired stimulus preference assessment as the most preferred food. Possums were required to press a lever to obtain 3-s access to the carob chips. The ratio requirement was increased by a factor of 1.5

responses every 5 days beginning with a FR 5. For the majority of possums, carob chips maintained behaviour to break points of up to 450 responses.

Progressive ratio schedules have been used to measure the strength, potency or effectiveness of reinforcers (Poling, 2010), under different motivational conditions such as deprivation (Hodos, 1961). They also speed up the process of testing with exposure to just one ratio requirement per trial (Roane, Lerman, & Vorndran, 2001). This type of schedule is frequently used to test the effect of drugs on ratio performance (e.g., Aberman, Ward, & Salamone, 1998; Allen & Leri, 2010; Hamill, Trevitt, Nowend, Carlson, & Salamone, 1999), and measure to what ratio requirement (break point) an animal will respond to as an indicator of 'motivation' (e.g., Finger, Dinan, & Cryan, 2010; Ho, Body, Kheramin, Bradshaw, & Szabadi, 2003).

Responding under FR and PR schedules has been described by very similar functions (Baron & Derenne, 2000; Killeen et al., 2009). Response rates typically increase as the ratio requirement increases to a point, then response rates decrease. When the ratio requirement is sufficiently large, responding ceases all together (Bizo, Kettle, & Killeen, 2001; Bizo & Killeen, 1997). The main difference is that the reinforcer ratio under a FR schedule remains constant during a session, increasing across sessions, whereas under a PR schedule it becomes progressively leaner as the ratio requirement increases. Because of these continuing increases in requirement, responding under PR schedules is influenced by the requirement of the prior and present ratio requirement, as large increments impact responding more so than small increments (Killeen et al., 2009; Sørensen et al., 2001).

Despite these differences, Baron and Derenne (2000) suggested that PR schedules were an “efficient way of studying issues that are ordinarily studied with FR schedules, particularly when concern is with relations between experimental variables and ratio size” (p.301). Research with hens (Foster et al., 1997b) and rats (Baron & Derenne, 2000) comparing performance under FR and PR schedules have pinpointed few differences.

In a comparison of FR and PR schedules in hens, response rates were higher under the PR schedule but were more varied compared to response rates under the FR schedule (Foster et al., 1997b). This indicated that the high rate of responding observed under the PR schedule was more disrupted by ratio requirement increases, than the lower rate responding under the FR schedule (also see Baron & Derenne, 2000). Break points were higher under the FR schedule. In addition, Foster et al. (1997b) found that Equation 1 (Hursh et al., 1988) generally fit the data well ($M_{VAC} > 85\%$) in their comparison of FR and PR schedules. Essential value was slightly higher under the FR schedule than PR schedule suggesting the slopes were flatter, or more ‘inelastic’, when the ratio requirement increased each day.

There is no general guideline or “characterization of behaviour” for the use of PR schedules (Killeen et al., 2009, pg 35). Also lacking, are concrete reasons for the use of particular progressions such as arithmetic, geometric, polynomial or harmonic progressions (Stafford et al., 1998). There is one exception, however, that geometric progressions may hasten the collection of data, although, any progression might be tailored to achieve that end.

A comparison of responding between geometric and arithmetic progressions by Killeen et al. (2009) showed that break points were larger under

geometric progressions compared to arithmetic progressions in pigeons. Under arithmetic progressions, response rates increased during the first few ratio requirements prior to peaking. Response rate then declined linearly as ratio requirement increased. Under geometric progressions, there were sharper increases in response rate than the arithmetic progressions, followed by steeper declines which then levelled out. Responding continued to high ratio requirements but at a low rate.

The considerable differences in responding and break point between geometric and arithmetic progressions has been ascribed to the large step-sizes of the geometric progression compared to the uniform step-sizes in an arithmetic progression (Killeen et al., 2009); and can be explained by the influence of the prior and current ratio requirement on the next ratio requirement. The large jump in ratio requirement in the geometric progression affects the adaptation to the next, much larger ratio requirement resulting in more variable behaviour. To illustrate this, Killeen et al. (2009), in what could be described as a *repetitive* PR schedule, increased the ratio requirement after the sixth reinforcer was earned at each ratio requirement. It was found that responding for low ratios was consistent after obtaining six reinforcers at low ratios, but response rates varied considerably at the higher ratio requirements. This demonstrated that the adaptation, characterized by consistent responding, to large ratio requirements takes longer than to short ratio requirements.

Research has focused on the effect of step-size on responding, particularly in arithmetic progressions. A general finding within arithmetic progressions is the similarity in responding over a range of step sizes (Killeen et al., 2009; Stafford & Branch, 1998). When step-sizes increased each day by values of 1, 2 or 5

responses, response rates declined slightly but break points were similar (Killeen et al., 2009; Stafford & Branch, 1998). In contrast, Covarrubias and Aparicio (2008) found that break point increased with step sizes of 1 and 3 responses. It also increased with food quality as rats responded to higher ratio requirements when saccharin was offered as compared to food pellets (Hodos & Kalman, 1963).

Progressive ratio schedules are useful for obtaining data quickly, as it would otherwise take much longer using FR schedules that increase in ratio requirement each day. Baron and Dereene (2000) suggested that PR and FR schedules measure the same patterns of behaviour, however, there are conflicting reports in the literature regarding response rates, measures of demand and break points between PR and FR schedules that increment according to different progressions (e.g., Foster et al., 1997b; Killeen et al., 2009).

Concurrent Ratio Schedules

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). Two concurrently available FR schedules have been arranged where one, or both schedules vary in ratio requirement across trials *within* a session, termed PR FR schedules (e.g., Findley, 1958; Rodefer & Carroll, 1996), across phases (e.g., DeLeon, Iwata, & Roscoe, 1997), or across days (e.g., Martin, 2002). In this thesis, FR schedules that increase in ratio requirement across days are

referred to as PFR schedules to distinguish them from PR schedules (Jarmolowicz & Lattal, 2010).

Concurrent schedules are similar to paired and multiple preference assessments as they provide more 'sensitive' information about the relative preferences of two alternatives. The two schedules 'compete' with each other and responding is allocated to the more valued reinforcer (Fisher & Mazur, 1997). This is important as on single schedules responding for all preferred items can result in similar orders of preference but when offered simultaneously a clear preference for one item over the other is found.

Possums responded under concurrent VI VI schedules for different food types such as coconut, coco-pops® and flaked barley with varying amounts of salt added (Bron, Sumpter, Foster, & Temple, 2003). The same number of responses, and time spent responding was given to coco-pops® and flaked barley, or the 0% salted barley and 2% salted flaked barley when offered together, however, more responding was allocated to flaked barley over coconut, and all food types when the alternative was 4% or 6% salted flaked barley.

The demand for cigarettes and money in humans was measured using concurrent FR schedules where one schedule increased in ratio requirement each day and the other remained constant (PFR FR; Bickel & Madden, 1999). When the ratio requirement was small participants responded more for money and then switched to responding for cigarettes at larger ratio requirements. This was termed a 'preference reversal' (another name for cross point). The authors found that their measures of reinforcer efficacy, consumption, response rate and break point, did not provide consistent accounts of cigarettes and money in terms of their 'reinforcing effects'. Break point, however, correlated with P_{\max} and consumption

for commodities under the concurrent schedules was similar to the under single schedules.

The distance between the cross point and the equivalence point (the ratio requirement where two schedules are equal) was used by Sørensen et al. (2001) to measure the demand for distilled, acidified and saccharine water using concurrent PFR FR schedules. The ratio requirement under the PFR schedule increased every five days (e.g., FR 10 to FR 100). The other schedule remained constant at 55 responses. The ratio requirements under the two levers were always equivalent at FR 55. Overall, the average cross points were perseverative, as they were larger than the equivalence point. This means that the rats responded more for water under the PFR schedule when fewer responses were required to obtain water under the constant FR schedule. This experiment was conducted in a closed economy where rats were water deprived for 22 hours prior to each session.

In a similar experiment, the ratio requirement under the PFR schedule increased each session by 10 responses and always offered distilled water (Holm et al., 2007). The other schedule remained constant for each block of sessions (e.g., FR 30), or was of the same ratio requirement as the PFR schedule and offered either distilled or quinine water. The ratio requirements under the two levers were always equivalent at a ratio requirement of FR 30. Cross points were slightly perseverative meaning that the rats worked harder to obtain the distilled water than the quinine or distilled water even when it required fewer responses to obtain. The limitation of this study was that the side the distilled water was offered was not varied which led to near exclusive responding for this commodity.

The cross point has been used to assess the 'relative attractiveness' of different substrates in pigs (Holm et al., 2008; Pedersen, Holm, Jensen, &

Jørgensen, 2005). Under concurrent FR schedules of differing ratio requirements (e.g., FR8 FR 40) pigs responded for four rooting materials: long straw was always available under one schedule and either chopped straw, fir branches, peat and long straw was available under the other schedule (Pedersen et al., 2005). Cross points were used to measure the pigs' preferences between the reference material and other substrate in relation to a previously identified equivalence point of FR 24 (when long straw was available under both schedules). Cross points between alternating substrates were generally conservative (responding at ratio requirements smaller than FR 24) for fir, peat and chopped straw when the other commodity was 'cheaper', but were perseverative for long straw. This means that the pigs would *work harder* to obtain straw even if another rooting material was available for *less work*.

In a similar experiment, pigs responded to gain access to a mixture of foods and substrates: peat, sand, carrots or sand with carrots under concurrent PFR FR schedules (Holm et al., 2008). Cross points for sand with carrots or carrots only versus peat, produced conservative cross points. Conversely, perseverative cross points were found for sand with carrots and carrots only when they were available under the PFR schedule when sand was the alternative option. This suggests that more responding was allocated to the schedule with carrots with sand, or carrots only even when the alternative, in this case, sand or peat, required less work to obtain.

When paired with a constant FR schedule, concurrently arranged PR FR schedules have been used to measure the demand for one commodity over another as a function of ratio requirement and the degree of substitutability between commodities (Hursh, 1980; 1984). This type of arrangement has been used to

evaluate the demand for different drugs (e.g., Hursh et al., 1988) and different foods for possums (e.g., Cronin, 2012) and rats (e.g., Bhatt & Wasserman, 1987).

In Findley's (1958) switching experiment, responding under concurrent PR schedules to obtain the same type of reinforcer was measured. One schedule increased by 100 responses (red key) and the other by 500 responses, with an initial ratio requirement of 100 responses (green key). The signalling stimuli were then reversed in a second condition. The results showed responding was allocated to the key with the lesser ratio requirement, and greater reinforcement rate which was the red key in the first condition and green in the second condition.

Concurrent PR FR schedules were used to investigate the effects of cocaine on responding in rats (Allen & Leri, 2010). After training, rats were exposed to a geometric PR schedule and constant FR 25 schedule in which responding earned sucrose pellets. Following baseline, four rats were given one of four different concentrations of cocaine before repeating the PR FR procedure. Generally, rats tended to make the switch from the PR schedule to the constant FR schedule soon after the equivalence point matching their behaviour to the schedule with the highest reinforcement rate, however, rats exposed to the highest dose of cocaine switched from the PR schedule to the FR schedule before the equivalence point and made fewer perseverative errors and more conservative errors.

The use of PR schedules is analogous to animals foraging in the wild (Wanchisen et al., 1988). Himeline and Sodetz (1987) considered the PR schedule to be a progressively depleting patch and the FR schedule to be the 'cost of travel' to a full, renewing patch. In two similar procedures, chimpanzees responded under concurrent PR FR schedules where the PR component increased by 20 responses

after each reinforcer and the FR component remained constant during a session and varied across conditions between 40 and 1000 responses (Hodos & Trumbule, 1967). The chimpanzees maximised reinforcement and conserved the number of responses made by responding up to the equivalence point then switching to the constant FR schedule (Hineline & Sodetz, 1987; Hodos & Trumbule, 1967).

A similar trend was found in pigeons, whereby the birds switched from responding under the PR schedule to the constant FR schedule when the ratio requirement of the PR schedule (with increments of 20 responses) equalled or was slightly higher than the requirement under the constant FR schedule (Wanchisen et al., 1988). In contrast, when comparing similarly incrementing geometric and arithmetic progressions of small values (e.g., increments of 3 responses or multiples of 1.10 or 1.15), and constant FR values of 15, 30 or 60 responses, Neuman, Ahearn, and Hineline (2000) found that the switch points were fewer than the equivalent ratio requirements under both progressions.

In the foraging experiments discussed previously the food available under the concurrent PR FR schedules was the same. Cronin (2012) tested whether possums would allocate their behaviour according to the schedule requirement, where the PR schedule would increment by 10 responses, and the constant FR schedule was either 20 or 50 responses during each session; or by food type where flaked barley and coco-pops® was available under the PR schedule and another food such as rolled oats was available under the constant FR schedule. Foods considered preferred under the PR schedule increased break point and response rates and the Hursh et al. (1988) linear demand model (Equation 1) predicted lower rate of change in elasticity values than lesser preferred foods. Break point, initial demand and P_{\max} values were higher when the constant FR 50 schedule was

in effect but consumption (rate) did not differ between FR conditions. Although no cross price analysis was completed it is clear that responding was allocated to the PR schedule *more* when the alternative FR schedule was greater as this maximised the rate of food deliveries under the PR schedule, compared to when the alternative was the FR 20 schedule.

In summary, concurrent PR FR and PFR FR schedules provide information about the demand for commodities in relation to ratio requirement. Under PR FR schedules for the same foods, organisms tend to maximise their reinforcement rate by swapping between schedules at the equivalence point. In contrast, under PFR FR schedules, cross points tend to be perseverative or the same as the equivalence point (Hineline & Sodetz, 1987; Hodos & Trumbule, 1967; Wanchisen et al., 1988). For possums exposed to PR FR schedules with different foods, response rates and measures of demand indicated higher consumption of preferred foods under the PR schedule compared to a constant FR schedule (Cronin, 2012).

Current Study

Behavioural economic techniques have been used to study the demand for different commodities (e.g., Foster et al., 2009; Sørensen et al., 2001) across a range of schedule requirements (e.g., Foster et al., 1997b; Pedersen et al., 2005), arrangements (e.g., Allen & Leri, 2001; Findley, 1958) and ratio progressions (e.g., Killeen et al., 2009). Parameters derived from fits of behavioural economic demand models to consumption (Hursh et al., 1988; Hursh & Silberberg, 2008) yield higher-order dependent variables for assessing demand for different commodities, such as initial demand, essential value and P_{\max} (e.g., Hursh et al., 1988; Hursh & Silberberg, 2008). There are other measures of break point and cross point, which can be derived directly from performance on the concurrent schedules and describe the strength and the substitutability of reinforcers respectively (e.g., Hodos, 1961; Hodos & Trumbule, 1967).

It is due to the applicability of the demand model that the feeding behaviours of the brushtail possum can be studied systematically as the 'price' of foods are varied. Possums consume a wide variety of foods (e.g., Nugent et al., 2000) with relatively small home ranges (Green, 1984). My research examines what possums *prefer* to eat. Furthermore, if a particular food requires more effort to obtain will the possum expend that energy to procure it?

Firstly, it was deemed important to be able to control for body weight prior to any experimentation regarding taste preference. Two pilot studies were carried out that examined how possum body weights changed over a 12 month period on free feeding regime (Appendix A). Then a criteria for assessing when body weights were stable was developed (Appendix B).

Experiments 1 and 2 investigated the use of single and paired preference assessments in determining orders of preference in foods that were reportedly consumed by possums available in the wild.

As preference assessments require little by way of response cost to obtain food the next series of experiments were carried out to test the demand for the different foods, that is, how much *effort* a possum expended to obtain a preferred food, over a lesser preferred food. Concurrently arranged PR and constant FR schedules were used to allow a choice between foods and to test the relationship between food preference and ratio requirement. In Experiment 3, the demand for six foods were tested using concurrent PR FR 30 schedules. The exponential (Equation 2; Hursh & Silberberg, 2008) and cross-price models of demand (Equations 5; Hursh et al., 2013) were used to analyse consumption rates under the PR and FR schedules. In Experiment 4, the experimental procedure in Experiment 3 was repeated for four food pairs; however, the constant FR schedule was alternated between a FR 30 and FR 10 in an ABAB design.

In Experiment 5, the ratio requirement under an PFR schedule, (previously the PR schedule), was increased every five sessions in an effort to procure stable data for comparing consumption rates to the PR FR consumption rates in Experiment 4. In addition, consumption rates were fit to the linear (Equation 1; Hursh et al., 1988) and exponential demand models (Equation 2).

In Experiment 6, concurrent PR FR and PFR FR schedules were used and food type and schedule progression varied. The ratio progressions presented were a geometric progression of 2 and an arithmetic progression of 5. The progressive ratio schedule was increased within (PR FR) or across sessions (PFR FR) and the alternative schedule was a constant FR 30. The primary dependent variables

derived from the exponential and cross price models of demand (Equations 2 & 5), break points and cross points were used to identify whether procedural differences affect the demand for foods by the brushtail possum.

Chapter 5 – Single and Paired Preference Assessments¹

Experiment 1

The purpose of Experiments 1 and 2 was to assess possums' preferences for food types that are reported to be consumed in the wild. This study uses well established methods of single and paired stimulus preference assessment in a laboratory environment. These methods control overall food availability which is a previously reported limitation of field studies. The aim of Experiment 1 was to assess the palatability of the test foods in the possums and to determine which foods were more preferred than others. It was expected that as a group, the possums will consume most, if not all food types, but not *all* possums will eat *all* foods.

Method

Subjects

Twenty brushtail possums (9 females and 11 males) weighing between 2732 g and 4292 g ($\bar{X} = 3485$ g, $\sigma = 459$ g) were used in the experiment. All possums were 'wild caught' and had been housed in captivity for 1 - 12 years ($\bar{X} = 4.5$ years, $\sigma = 3.5$ years). At the start of the experiment eight of the possums were experimentally naïve and the remainder had participated in other behavioural experiments.

Experiments 1 and 2 have been published in the International Journal of Comparative Psychology:

Cameron, K. E., Bizo, L. A., & Starkey, N. J. (2013). Food preferences of the Brushtail Possum (*Trichosurus vulpecula*). *International Journal of Comparative Psychology*, 26, 324-336.

Possums were weighed every second non-experiment day (every eighth day). Supplementary feed of dock leaves, sliced apple, and food pellets (Camtech Manufacturing Ltd, New Zealand) were provided at 14:00 h each day after experimental sessions were completed. Possums had constant access to water.

Housing

Fourteen possums were kept in laboratory built individual wire-netting cages (540-mm wide x 850-mm high x 470-mm deep) with a shelf halfway up the cage and a nest box (450-mm wide x 300-mm high sloping from 360-mm to 195-mm) on top of the cage (Figure 5.0). The remaining six possums were housed in slightly larger cages (540-mm wide x 1050-mm high and 470-mm deep) with a wire shelf 700-mm above the floor of the cage.



Figure 5.0. The photo on the left shows two possum home cages. Nest boxes are on top of the cages. The photo on the right shows the food trays used for delivering food in Experiment 1.

The possums were housed in a laboratories with a 12:12 h reversed dark/light cycle in effect (lights off at 08:45 h) with minimal illumination supplied by red lamps during the dark period. Cleaning and maintenance occurred during the light rotation at the same time each day.

Apparatus

The home cage functioned as the experimental chamber with test foods presented in the same way as the pellet portion of their standard diet. The front of each cage was designed to allow a small tray (70-mm wide x 130-mm long x 30-mm deep) to be slotted into the cage (Figure 5.0).

Test food choice. Test foods were chosen to represent the main food categories (foliage, fruit, fungi, invertebrates, meat and eggs) that possums eat in the wild. The specific foods were chosen based on availability, practicality and cost. Fivefinger (*Pseudopanax arboreus*) was selected as the foliage food type because it is eaten by possums in New Zealand (Fitzgerald, 1978; Kean & Pracy, 1953) and there was a guaranteed fresh supply of the plant available from the university campus. The fruit was a mixture of raspberries, blueberries and blackberries (Pams® Mixed Berries), which could be purchased year round from a local supermarket as were the field mushrooms and minced raw chicken. Locusts (frozen) (*Locusta migratoria*) were purchased in bulk from a breeder, and quail eggs were sourced from a local poultry farm. Table 5.0 gives an indicative guide to the nutritional content of the test foods.

The six test foods presented during the experimental sessions were; 20-g fresh fivefinger leaves (*Pseudopanax arboreus*), 20-g berries (defrosted and drained of juice), 20-g mushrooms, 3 locusts (defrosted), 20-g minced raw chicken, and 1 quail egg (approximately 15 g).

Table 5.0. Approximate nutritional compositions of 1 gram of test foods, energy (kJ/g), protein (mg/g) and fat (mg/g). Berries (retrieved from Pams®), locusts (Oonincx & van der Poel, 2011), mushrooms, eggs and chicken (USDA food database, 2010), and fivefinger (Fitzgerald, 1978).

	Energy (kJ/g)	Protein (mg/g)	Fat (mg/g)
Berries	2	10	< 1.0
Chicken	5	23	3
Egg (hen)	3.4	8	6
Fivefinger	22.5	-	-
Locusts	21.3	65	19
Mushrooms	0.9	2	< 1.0

Design

Each possum received the same test food every day for three consecutive days at 10:00 h. All six test foods were given to each possum during the experimental period (18 presentations of food in total). The food was distributed between possums in a randomised order that was counterbalanced to avoid adjacent possums receiving the same test food concurrently. The fourth day was a rest day where possums received 100% of their supplementary diet. The quantities of foods were not equated on weight; rather the amounts were determined such that each occupied approximately the same surface area on the bottom of the food dish. To guard against satiation the maximum amount of test food offered to each possum did not exceed 11% of their daily food intake (by weight). Additionally, the amount of supplementary feed provided for each possum was adjusted depending on how much of the test food they consumed.

Procedure

A trial began during the second hour of the dark cycle. The sample of food was delivered in the food tray. The food tray was removed after 2 hours and any remaining food - in the tray and in and under the cage - was weighed and

recorded. Instances where a food was disturbed, for example, if a quail egg was broken but not consumed, was noted but not recorded as being 'consumed'. A food type was considered 'consumed' if less than 12.5% (by weight) remained at the end of the session, except for locusts which were considered 'consumed' if one or part of one locust was left over. Unbroken eggs in the cage after day 1 were broken for the possum on days 2 and 3. Food trays were cleaned at the end of each experimental session.

Data Analysis

The food consumed by each possum was recorded after each presentation and the percentage of possums that consumed each food on each day was calculated. To allow comparison of food consumption across Experiments 1 and 2 the total number of trials each food was consumed by each possum was summed across days, and then reported as a percentage of total trials.

Results

The results from Experiment 1 showed that all food types were consumed by some possums across the three days. Figure 5.1 shows that berries were consumed on the greatest number of trials, followed by locusts, mushrooms, fivefinger, egg, and chicken. A repeated measures ANOVA revealed a significant difference in the mean percentage of trials when each food was chosen [$F(5, 95) = 15.69, p < 0.001, \eta_p^2 = 0.45$]. Pairwise comparisons confirmed that berries, locusts and mushrooms were consumed in a significantly higher percentage of trials than fivefinger, egg and chicken (all p 's < 0.006). Nineteen possums consumed berries, 18 possums consumed locusts, 20 possums consumed mushrooms, 14 possums consumed fivefinger, 11 possums consumed egg and 8

possums consumed chicken. It should be noted, however, while more animals might have tried a food such as mushrooms at least once, if it was only consumed on one of the three days there would be a lower percentage of trials overall when mushrooms were consumed.

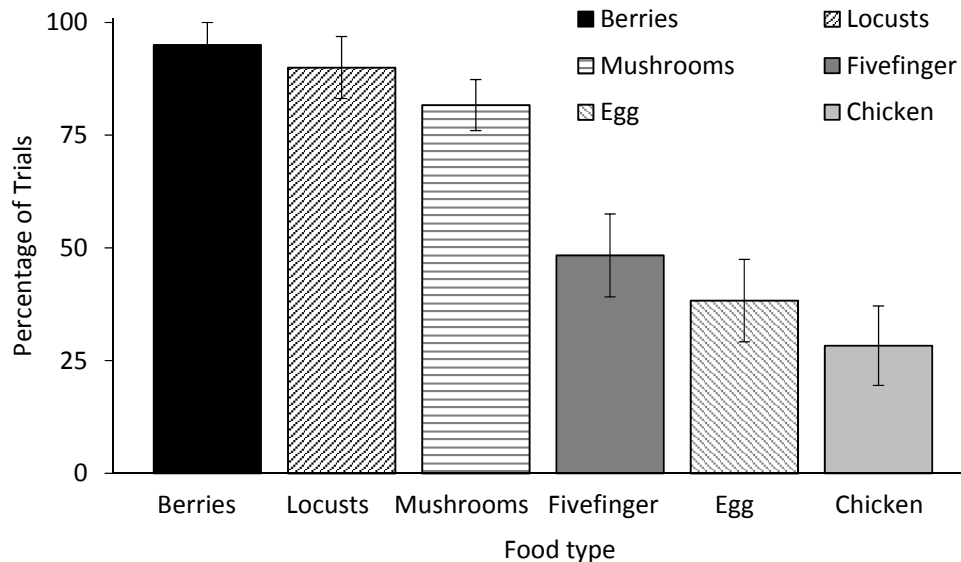


Figure 5.1. The percentage of trials when each food was consumed in Experiment 2. Error bars are the standard error of the mean.

Discussion

These findings reveal that all foods were consumed to some extent, supporting the findings of earlier field studies (e.g., Cowan, 1990; Nugent et al., 2000). These data show that possums consume a wide variety of foods and that the single stimulus preference assessment can identify palatable foods. A preference assessment, however, where there is a choice between foods is required to provide a measure of most and least preferred foods. This measure is frequently lost in single stimulus preference assessments which tend to overestimate preference (Fisher et al., 1992). Sumpter, Foster, and Temple (2002) in reviewing

different methods for assessing preference concluded that free choice or single stimulus methods provide limited information about preference (in *only* what animals will consume), and methods offering a discrete choice between two or more options can be used to indicate the *degree* of preference. In applied behaviour analysis setting with humans it was found that offering more than one commodity at a time produced more accurate results regarding preference (e.g., DeLeon & Iwata, 1996; Young & Greene, 1953a, 1953b). Therefore, in Experiment 2, paired stimulus preference assessments were conducted to determine the *relative preference* of the foods.

Experiment 2

The aim of Experiment 2 was to determine the relative preference of the test foods used in Experiment 1 using a paired stimulus assessment. It was expected that foods that were consumed the most, or by the greatest number of possums in Experiment 1, would also be the most preferred foods when presented concurrently with foods that were consumed less frequently in Experiment 2.

Method

Subjects

Twelve possums, P1 – P12, (4 female and 8 male) weighing between 2732 g and 4204 g ($\bar{X} = 3369$ g, $\sigma = 391$ g) were used in this experiment. Possums had been housed in captivity for 1-10 years ($\bar{X} = 3$ years, $\sigma = 2.8$ years). The possums were selected at random from those used in the single stimulus assessment. Feeding and cleaning procedures were the same as Experiment 2. P12 did not eat any of the foods presented in the experiment and their data were not included in the analysis.

Housing

Six possums, P1 – P6, were housed in the larger cages (540-mm wide x 1050-mm high x 470-mm deep) and six possums (P7 – P12) were housed in the smaller cages (540-mm wide x 850-mm high x 470-mm deep).

Apparatus

Each home cage functioned as the experimental chamber. A custom built assessment device was attached to the door frame, replacing the door during each session. The device allowed the experimenter to view the possum during the

experiment but prevented the possum from escaping. Figure 5.2 shows a diagram of the apparatus.

The foods used in this experiment were the same as for Experiment 1 except quail eggs were replaced with hen eggs and smaller amounts were presented in each trial. This allowed multiple presentations of each food pair within an experimental session, whilst limiting the total amount of food a possum could eat in an experimental session to no more than 11% of the possum's daily food intake (as in Experiment 1). The test foods presented during each experimental session were 2-g berries (defrosted and drained of juice), 1 locust, 2-g mushrooms (cut into 10-mm pieces), 0.5-g fivefinger leaves cut into 10-mm pieces, 2-g whisked egg and 2-g minced raw chicken breast. The foods were presented in round tins (50-mm high and 70-mm in diameter) attached by magnets to the base apparatus. Each food covered approximately the same surface area of the bottom of the tin (with the exception of egg).

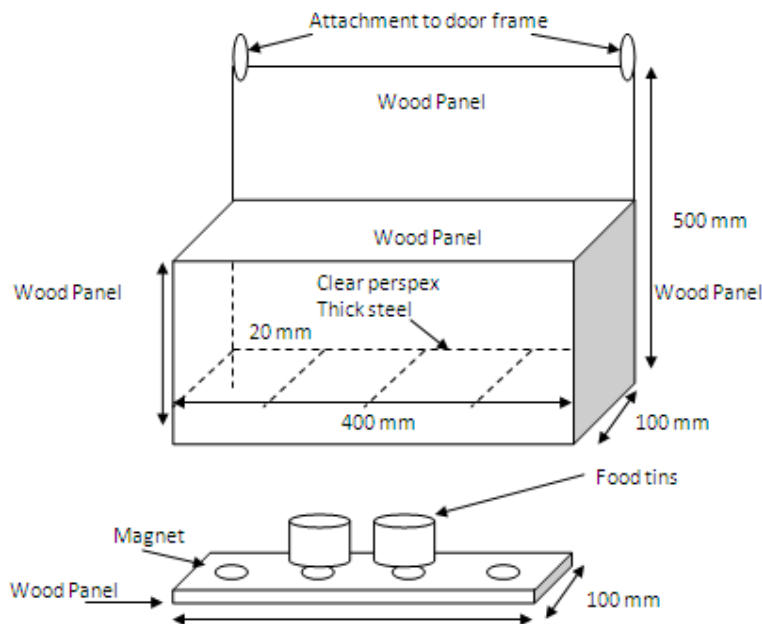


Figure 5.2. A diagram of the paired stimulus apparatus in Experiment 2.

Procedure

To familiarise the possums with the test foods, a teaspoon (approximately 5-ml or 0.2-g) of all foods (or 1 locust) was presented individually in a separate tin in a random order to each possum before the experimental trials began for that day. When the possum had either sampled the food in each tin or if the possum's nose had been in and out of the tin without consumption the tin was removed.

An experimental trial consisted of presentation of the food tins in the centre of the tray when the possum was facing the apparatus. A choice was recorded if the possum consumed the food in the tin, that is, the possum either removed a 'mouthful' of the food (e.g., a berry, piece of mushroom or fivefinger or 1 locust) or lapped at the food (e.g., egg or raw chicken). After a 'choice' was made, the tins were removed. If no food was consumed after 30 s, the food pair was removed and the next food pair was presented. If no choices were made on 10 consecutive food pair presentations the session was terminated.

The possums experienced the experimental procedure in three sessions run on consecutive days (Series 1). Within each experimental session, each food item was paired with every other food item resulting in 15 different food pair combinations. Food pairs were presented twice per session, with each of the foods presented on the left, and the right (30 food pair trials in total). The procedure was repeated on days 2 and 3 with the order of food pairs varied each day. The three day procedure was repeated two weeks after the first series (Series 2).

Data Analysis

For each food pair the number of times a food was chosen was summed across trials. The percentage of total trials when each food was consumed was then calculated for each possum, for each series (the total number of trials being

the number of times that food was presented). The percentage of total trials when a food was chosen was used to assess possums' relative preference for each food type.

Results

A Wilcoxon signed ranks test revealed that the median percentages of choices between the first and second series were not significantly different for any food type [$z = -0.64, p = 0.523$]. Consequently, the percentage of trials when each test food was chosen from each food pair was combined across the two series for each possum. The average percentage of trials when each food was consumed from each pair is shown in Table 5.1. Locusts, berries and mushrooms were chosen most frequently when paired with fivefinger. Berries were chosen in approximately 50% of trials irrespective of the alternative food. Fivefinger was chosen in fewer than 20% of trials and the percentage of trials when no food was selected from a food pair ranged from 6 - 48% of trials and most often when fivefinger was presented.

Table 5.1. Average percentage of trials when each food was consumed within each food pair across possums. The percentage of trials when no food was chosen for that food pair is shown in brackets.

		Berries	Locusts	Mushrooms	Egg	Fivefinger	Chicken
Food chosen	Berries	-	55	49	55	62	58
	Locusts	39 (6)	-	64	62	79	61
	Mushrooms	41 (10)	24 (12)	-	29	55	53
	Egg	31 (14)	28 (10)	57 (14)	-	56	20
	Fivefinger	10 (28)	6 (15)	5 (40)	9 (35)	-	19
	Chicken	17 (25)	29 (10)	32 (15)	45 (35)	35 (48)	-

There was variability between possums with no single food type being highly preferred by *all* possums. Table 5.2 presents a ranked order of preference

for each food type for each possum. The most highly preferred foods were locusts ($n = 4$), berries ($n = 4$) and raw chicken ($n = 3$). For nine possums, the least preferred (or unselected food) was fivefinger. When data were averaged across possums, locusts were the most preferred food, followed by berries, egg, mushrooms, chicken and fivefinger (Figure 5.3). The ranked preferences shown by individual possums were not consistent with the overall (group) food preferences.

Table 5.2. Possums' relative preference for each food type. Data are presented for individual possums and for the group overall.

Possum	Most Preferred					Least Preferred 6 th	Non Selected
	1 st	2 nd	3 rd	4 th	5 th		
P1	Locusts (95)	Egg (72)	Mushrooms (58)	Berries (7)			Fivefinger Chicken (0)
P2	Berries (52)	Locusts (48)	Mushrooms (41)	Egg (5)	Fivefinger (2)		Chicken (0)
P3	Chicken (68)	Mushrooms (65)	Egg (63)	Berries (55)	Locusts (48)		Fivefinger (0)
P4	Berries (85)	Locusts (77)	Mushrooms (58)	Egg (58)	Fivefinger (2)		Chicken (0)
P5	Locusts (88)	Mushrooms (87)	Berries (40)	Fivefinger (12)			Egg Chicken (0)
P6	Berries (77)	Locusts (68)	Mushrooms (54)	Fivefinger (23)	Egg (22)		Chicken (0)
P7	Chicken (92)	Egg (72)	Berries (58)	Locusts (57)	Mushrooms (8)	Fivefinger (2)	
P8	Chicken (67)	Egg (63)	Berries (62)	Locusts (57)	Mushrooms (17)	Fivefinger (2)	
P9	Berries (85)	Chicken (77)	Egg (72)	Locusts (47)			Mushrooms Fivefinger (0)
P10	Locusts (72)	Fivefinger (62)	Berries Mushrooms (55)		Egg (52)	Chicken (5)	
P11	Locusts (50)	Berries (7)					Chicken Egg Mushrooms Fivefinger (0)
Overall	Locusts (64)	Berries (53)	Egg (43)	Mushrooms (40)	Chicken (28)	Fivefinger (9)	

Note: Relative preference was calculated by dividing the number of trials when a food was chosen by the total number of trials when that food was presented

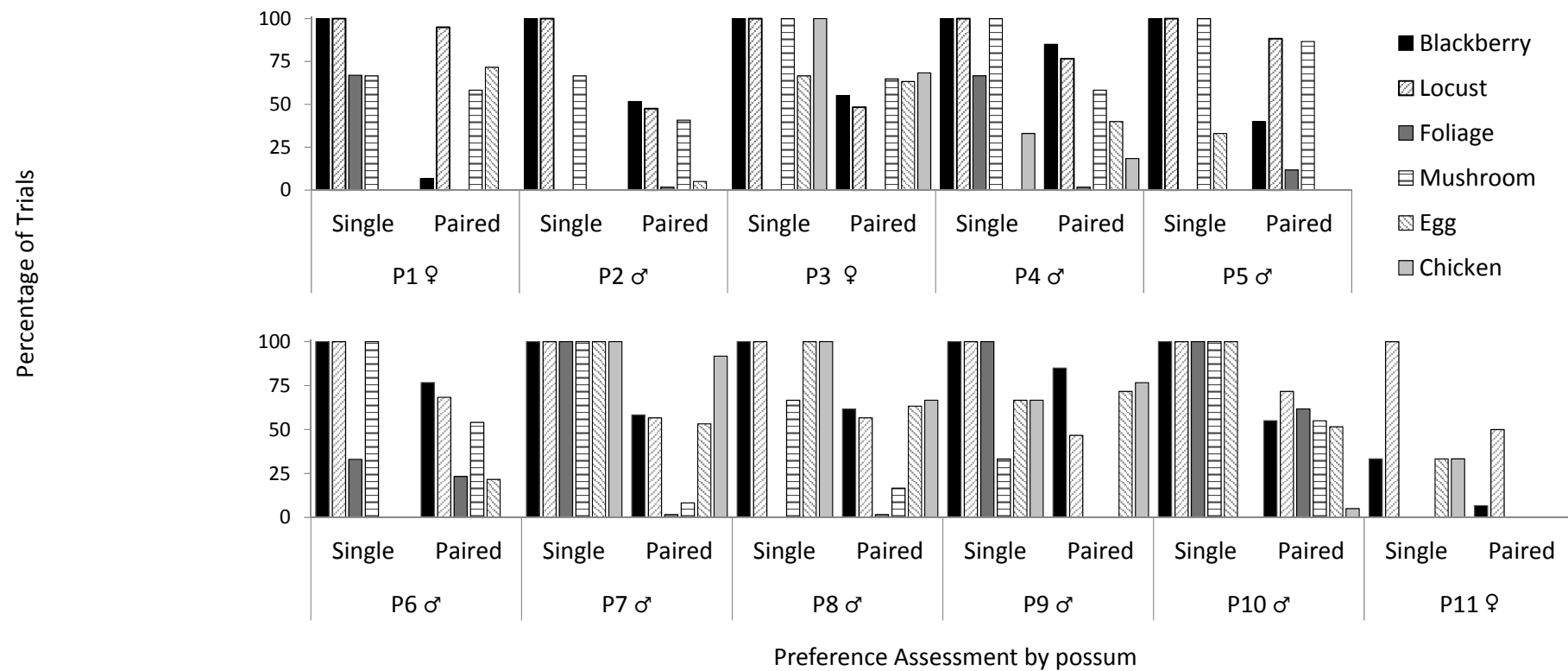


Figure 5.3. Mean percentage of trials when each food was selected by each possum that had participated in both the single stimulus assessment (Experiment 1) and the paired stimulus assessment (Experiment 2) for P1 - 11.

For the paired stimulus data, a repeated measures ANOVA revealed a significant difference between the mean percentage of trials when each food was chosen [$F(5, 50) = 6.17, p = 0.003, \eta_p^2 = 0.38$]. Pairwise comparisons confirmed that berries were consumed in a significantly higher percentage of trials than fivefinger ($p = 0.001$), and chicken ($p = 0.023$). Locusts were consumed significantly more than all other foods except berries (all p 's < 0.037), mushrooms were consumed in significantly more trials than locusts ($p = 0.005$) and fivefinger was consumed in fewer trials than all foods except chicken (all p 's < 0.015).

The percentage of trials when each food was consumed for each possum was compared between the single and paired stimulus assessments in Figure 5.4. For example, P7 consumed all food in Experiment 1, but in Experiment 2 chicken was chosen most often, berries, egg and locusts half the time and little fivefinger and mushrooms. P8 consumed berry, locusts, mushrooms and chicken during the single stimulus, but during the paired stimulus consumed egg, a previously ignored food type. For possums, P2, P4, P5, P8, and P10 foods not sampled in Experiment 1 were eaten in Experiment 2, albeit in a low percentage of trials.

To determine if one food was consumed more often than another paired sample t-tests were conducted. The tests revealed that berries [$t(10) = 6.05, p = 0.001, d = 1.73$], locusts [$t(10) = 6.96, p = 0.001, d = 2.97$], fivefinger [$t(10) = 2.58, p = 0.028, d = 0.96$] and mushrooms [$t(10) = 4.73, p = 0.001, d = 1.12$] were consumed on a significantly higher percentage of trials in Experiment 1, the single stimulus assessment compared to Experiment 2.

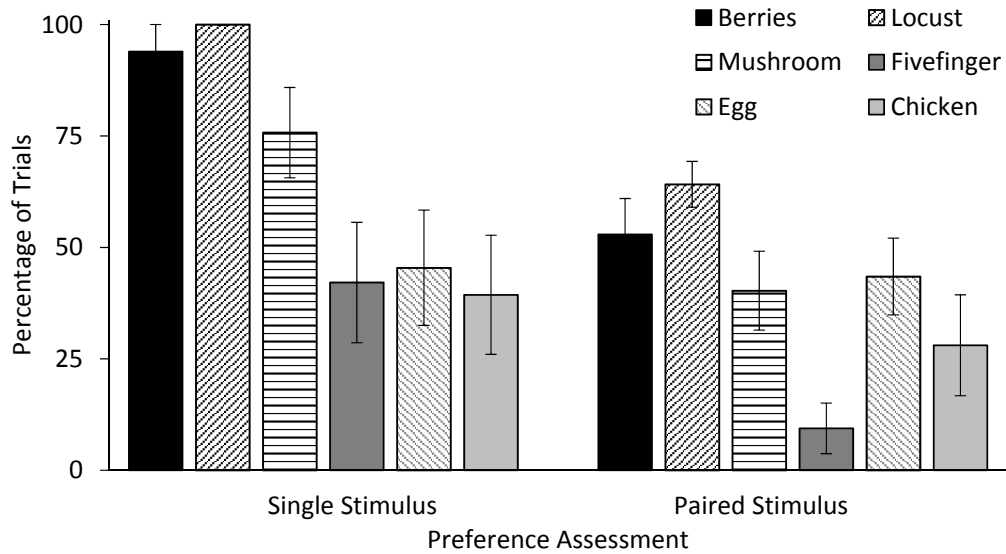


Figure 5.4. Mean percentage of trials when each food was selected by possums that had participated in both the single stimulus assessment (Experiment 1) and the paired stimulus assessment (Experiment 2) for P1 – 11. Error bars are the standard error of the mean.

Discussion

The purpose of the present experiments was to identify what possums would consume using the single stimulus method (Experiment 1), and to ascertain relative preferences for those same foods when offered as a choice between two food types (Experiment 2). The results of Experiment 1 showed that all the test foods were consumed by at least one possum; berries were the most consumed food, followed by locusts, mushrooms, fivefinger, egg, and chicken. In Experiment 2, when alternative foods were available, no single food was preferred by all possums; locusts were the most preferred food, followed in order of preference by berries, egg, mushrooms, chicken and fivefinger.

These findings are similar to those of previous field and experimental studies. All possums ate berries in both Experiments 1 and 2, which was

consistent with accounts of previous studies of possums in the wild (e.g., Harvie, 1973; Gilmore, 1965, 1967). Berries or fruit in general, are a preferred food in a possum's diet and are likely to be consumed when available.

It was surprising to us that some possums did not consume fivefinger in the single and paired assessments as foliage makes up between 50 - 95% of a possum's diet and fivefinger in particular is reported to be consumed by wild possums in New Zealand (e.g., Fitzgerald, 1978; Kean & Pracy, 1953). The high proportion of foliage in the diet of wild possums may be a result of availability relative to other food types rather than it being highly preferred (Nugent et al., 2000). Fivefinger was collected fresh each morning and was prepared for the experiment by cutting the leaves into small pieces. It is possible that in attempting to control for consistent presentation that we made the fivefinger more difficult for the possums to eat and less recognizable as a leaf. This might explain the minimal selection of fivefinger by most possums; however, one possum (P10) consistently consumed it in Experiments 1 and 2 suggesting that it was palatable.

With regard to consumption of invertebrates, locusts were ranked as the most preferred food in both the single and paired assessments. These findings add further support to the suggestion of Cowan and Moeed (1987) and Cochrane et al. (2003) that invertebrates may be a source of food for possums. Mushrooms were also consumed by most of the possums and were ranked as the 3rd most preferred food in the single stimulus assessment and the 4th most preferred food in the paired stimulus assessment.

Foods consumed in the single stimulus assessment were consumed in the paired stimulus assessment in a similar order of preference. In both assessments locusts were the most preferred followed by berries. In the single stimulus

assessment mushrooms were preferred over egg, but this order was reversed in the paired stimulus assessment, as was the case with fivefinger and chicken.

Fewer than half the possums (45%) consumed chicken in the single stimulus preference assessment, making it the 6th ranked food overall, except for three possums where chicken was the most highly preferred food. The percentage of possums consuming meat in our study was considerably higher than the 18% of possums reported to eat dead chicks in earlier studies (Brown et al., 1996), however, this may be due to how the food was presented; the smell and appearance of minced chicken is quite different to dead chicks used in that study.

Over half of the possums (55%) consumed egg in the single stimulus experiment, 82% consumed egg in the paired stimulus experiment and overall it was ranked as the 3rd most preferred food. The proportion of possums eating egg in the first experiment was lower than the 85% of possums reported by Brown et al. (1996), although this may be because Brown et al. (1996) classified damaged eggs as eaten.

Preference assessments are typically used to establish a reinforcer, usually a food, to reward the occurrence of a particular behaviour for that subject (Pace et al., 1985). It is crucial for operant work that an effective reinforcer is found to maintain behaviour, such as response rates (e.g., Mintz, Wallace, Najdowski, Atcheson, & Bosch, 2007). It should be noted, that food preferences varied across animals and it would be misleading to assume that the averaged preferences hold for all animals. For example, for three possums minced chicken was a highly preferred food but for the remaining possums chicken was either one of the least preferred or non-selected foods. Similarly, Laska (2001) also found that the

grouped ranking of food preferences did not represent individual food preferences of pigtail macaques.

The strength of this study is that it provides a systematic assessment of possums' food preference whilst controlling food availability. This addresses one of the major limitations of field studies which may underestimate possums' preference for certain food due to their local and/or seasonal availability. In addition, the current study provides a ranked order of preference for foods possums have been reported to eat in the wild. To date preference indices, used to calculate consumption of foods in the wild by possums (Nugent, 1990), have only been calculated consistently for foliage and not for other foods (invertebrates, meat and eggs).

In Experiments 1 and 2 it was not possible to control all the dimensions on which the different food presentations could vary. It was not possible to deliver the same weight of each food type because they differed markedly in their density and consistency; however, the same surface area of the tin was covered by each food. Given that the supplementary diet was the same across possums it seems unlikely that nutritional composition alone can account for the individual differences in taste preferences for the test foods, but it may have contributed to overall trends as possums generally preferred sweeter foods such as berries, and foods with more protein such as locust, over others.

It is unlikely also that a single nutritional element determines preference. Table 5.0 shows the approximate energy, protein and fat content of each of the foods. Fivefinger and locusts contain the most energy with mushrooms the least; and locusts and chicken have the most protein. In addition, the selection of locusts and mushrooms may be due to the complex carbohydrates found in chitin which

makes up the exoskeleton of locusts and cell walls of mushrooms. The nutritional content of the foods may help explain the preference for locusts, however, it does not account for the overall lack of preference for chicken (high in protein) and fivefinger (high in energy). It is highly likely that multiple factors contribute to selection of foods such as other mineral content and size (Cowan, 1992), smell (Morgan, 1981), and texture and consistency.

The findings are unlikely to have been influenced by possums becoming satiated as all possums subsequently consumed their normal daily supplementary feed that was presented after experimental sessions, and the total amount of food presented during an experimental session never exceeded 11% of the possums total daily food intake by weight. Testing a wider variety of foods, specifically foliage, would have allowed for greater generalization of the findings, however, there were limitations in terms of the foods that were available in sufficient quantities throughout the experiment.

In summary, the study findings show that; 1) possums will choose to eat foods other than foliage when available, 2) possums will eat meat and eggs, and 3) invertebrates and berries are a highly preferred food of possums. Both preference assessments, however, identified foods that were equally as palatable or preferred by each possum. In the next series of experiments preference for each food type will be measured by requiring the possums to *work* to obtain the food in the form of lever pressing. It is expected that possums will expend more effort to obtain preferred foods.

Chapter 6 – Concurrent PR FR Schedules

Experiment 3

The results from Experiments 1 and 2 suggest that possums' preferences are idiosyncratic and that possums tend to prefer locusts, berries and egg, with some preferring chicken and mushrooms. It was clear that foliage was not a preferred food. The single and paired stimulus assessments, however, do not allow calculation of the relative demand for foods. Techniques used in behavioural economics might provide insight into the demand for different foods because when animals are required to work to obtain food the amount of work expended gives an estimate of the 'value' of the food to the animal.

In the next series of experiments the demand for the different foods was assessed using a concurrent PR FR schedule procedure. The PR schedule doubled in ratio requirement using a geometric progression (basis 2) and the FR 30 schedule remained constant during each session. This progression was chosen because it had been used in previous experiments that investigated the demand for different foods such as Foster et al., (2009).

The demand for food was measured by consumption rate, which was analysed using the exponential and cross price models of demand (see the Behaviour Economic chapter p. 26; Hursh & Silberberg, 2008; Hursh et al., 2013), where the parameters of initial demand, essential value and P_{\max} were compared across foods. Also analysed were response rates, post reinforcement pauses, break points and cross points.

It is predicted that measures such as initial demand, essential value, P_{\max} , break point and cross point values will indicate higher demand for food previously

identified as preferred in Experiments 1 and 2 under the PR schedule. When preferred foods are available under the constant FR 30 schedule measures of initial demand and essential value are expected to increase, and P_{\max} , break point and cross point are expected to decrease for foods under the PR schedule.

Method

Subjects

Six brushtail possums (*Trichosurus vulpecula*), P1 - 6 (2 female and 4 male) were used in the experiment. All possums were 'wild caught' and had been housed in captivity for 4 - 9 years ($\bar{X} = 6.8$ years, $\sigma = 2.0$ years) at the start of the experiment. All possums had participated in taste preference experiments (Experiments 1 and 2) and had previously been exposed to a range of FR schedules as part of a pilot study.

Possoms were maintained at $85\% \pm 2.5\%$ of their free feeding body weight, between 3020 g and 3880 g ($M = 3439$ g, $\sigma = 268$ g). They were weighed weekly and received supplementary rations of dock leaves (*Rumex obtusifolius*), apple, and food pellets (Camtech Manufacturing Ltd^(R), New Zealand) after the experimental sessions were completed. Possoms had constant access to water.

Housing

The possums were housed in the same cages as in previous experiments. The cages were 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.

Apparatus

Each home cage functioned as the experimental chamber. Two laboratory built magazines were attached to the outside of each of the cages (Figure 6.0). The

magazine unit was a white Perspex box with two openings: the top opening gave the possum 2-s timed access to food from a tin (50-mm high and 70-mm in diameter) 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. Yellow LED lights were positioned 10-mm above the left and right levers that when lit indicated that the schedules of reinforcement were in effect.

The six test foods presented during the experimental sessions were the same as Experiments 1 and 2. The amounts of each food type differed because of the nature of the foods; however, the amounts filled approximately the same volume of the tin: 60-g berries Pams[®] (thawed and drained of juice), 20-g locust cut into 10 mm pieces, 30-g mushrooms cut into 10-mm pieces, 30-g foliage (fivefinger leaves (lamina and petiole) cut into 10-mm pieces), 100-g whisked egg and 60-g minced raw chicken breast.

Design

For each condition the experimental procedure was conducted three times, one session per day over three consecutive days. Each food item was paired with every other food item and presented on both the left and right side so that each possum was presented with 30 food pairs over 90 days. The order of presentation of the food pairs was randomised.

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

ratio requirement was used as possums responded at a steady rate at this value during a pilot study where the possums responded to a range of FR schedules (FR 1 to FR 512), reinforced with 2.5-s access to a flaked barley and coco-pop® mix.

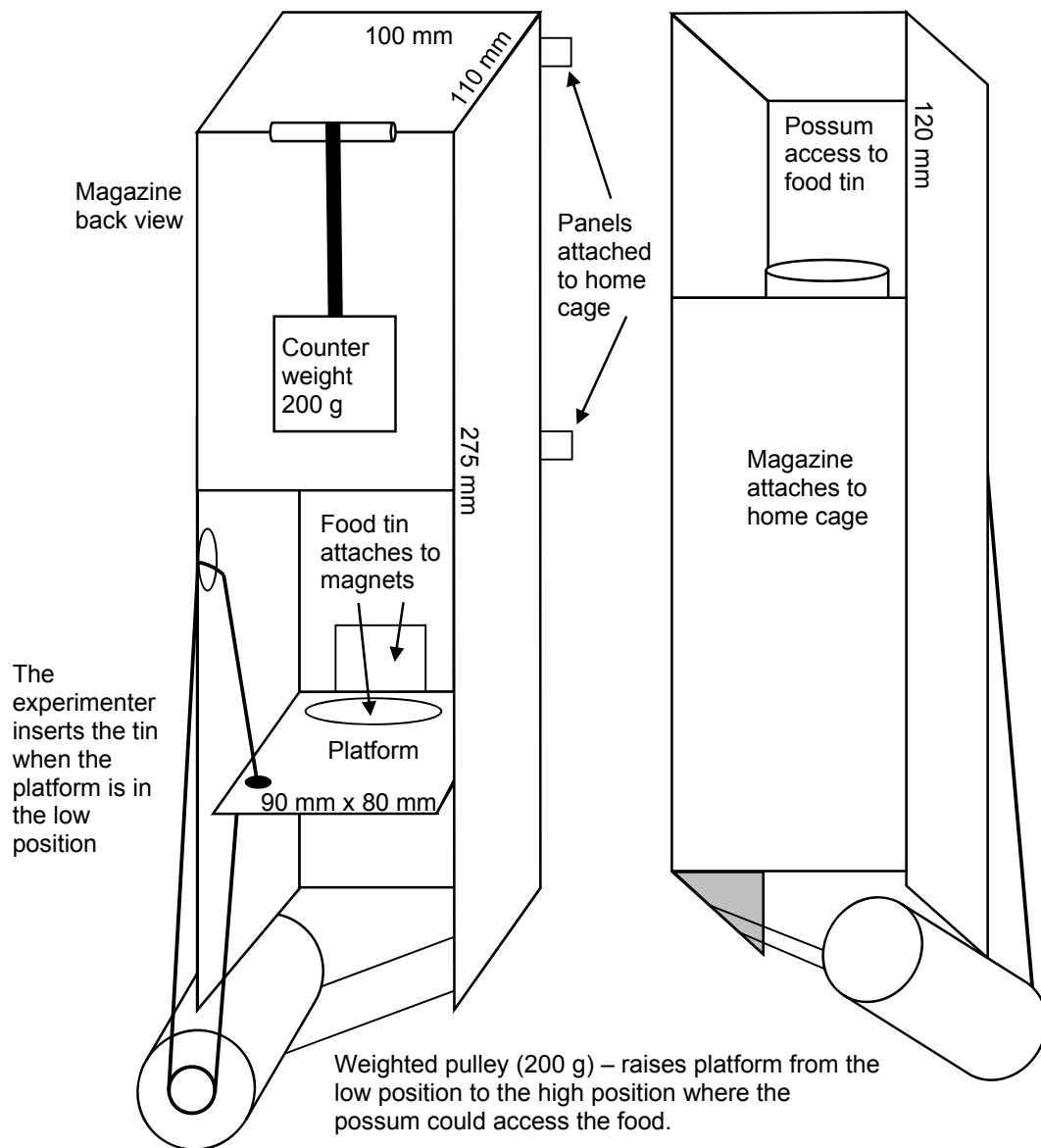


Figure 6.0. The diagram on the left shows the back view of the custom built magazine. The food tin attached to magnets on the platform, which would rise up to be accessed by the possum. The diagram on the right is the front view (possum's view) of the magazine where the possum could access the food tin.

Trial Procedure

At the start of an experimental session the possums received one response-independent presentation of each food. The stimulus lights were then lit and the levers became active. The PR and constant FR schedules were independent and responses continued to accumulate when access to the food was gained on the alternative lever. When access to food was scheduled the stimulus lights were turned off and the food container was presented. After reinforcement was delivered the stimulus lights were re-lit.

All sessions ended after 120 minutes and any remaining test foods were removed from the magazines and weighed. A computer system running MED™ software and interface located in the adjacent room controlled and recorded experimental events.

Results

Breakpoints and estimates of initial demand, essential value and P_{\max} , derived from the exponential and cross-price models of demand (Hursh & Silberberg, 2008; Hursh et al., 2013) and cross points were used to obtain a measure of the demand for foods.

Average break points under the PR schedule for each food pair for each possum are shown in Table 6.0. Break points were higher when berries, chicken, egg and locusts were available under the PR schedule and when foliage or locusts were available under the constant FR schedule. Low break points were observed when foliage was available under the PR schedule and mushrooms under the constant FR schedule. A paired samples t-test revealed significantly lower break points for foliage compared with other foods (all p 's < .05), except locusts.

Table 6.0. Break points were averaged across sessions for each possum and then averaged for each food pair. Food available under the PR schedule and the food available on the constant FR schedule is shown in parentheses in the food pair column. The final five rows are the average for each food type available on the PR for P1 - 6. The rank order is given in parentheses.

Food Pair	P1	P2	P3	P4	P5	P6	Average
B(C)	20.00	213.33	106.67	106.67	256.00	64.00	127.78
B(E)	37.33	3.00	16.00	106.67	8.00	42.67	35.61
B(F)	128.00	106.67	74.67	32.33	48.00	8.00	66.28
B(L)	26.67	7.00	40.00	171.33	24.00	13.33	47.06
B(M)	28.00	48.00	40.00	106.67	2.00	21.33	41.00
C(B)	24.33	13.33	42.67	74.67	12.00	32.00	33.17
C(E)	8.67	74.67	53.33	14.00	13.33	24.00	31.33
C(F)	26.67	170.67	34.67	256.00	213.33	37.33	123.11
C(L)	8.00	18.67	170.67	26.67	53.33	85.33	60.44
C(M)	26.67	12.00	85.33	18.67	2.67	26.67	28.67
E(B)	85.33	18.67	64.00	106.67	106.67	32.00	68.89
E(C)	96.00	21.33	149.33	66.67	32.00	42.67	68.00
E(F)	170.67	13.33	106.67	85.33	85.33	32.00	82.22
E(L)	64.00	4.33	96.00	45.33	5.33	26.67	40.28
E(M)	85.33	128.00	32.00	170.67	1.67	53.33	78.50
F(B)	37.33	37.33	21.33	37.33	21.33	13.33	28.00
F(C)	24.00	13.33	85.33	85.67	85.33	64.00	59.61
F(E)	14.67	37.33	16.00	22.00	32.00	8.00	21.67
F(L)	18.67	80.00	128.00	128.00	21.33	10.67	64.44
F(M)	2.00	2.00	2.00	2.00	2.00	2.00	2.00
L(B)	96.00	27.33	64.00	138.67	53.33	21.33	66.78
L(C)	106.67	42.67	53.67	213.33	32.00	13.33	76.94
L(E)	85.33	21.33	106.67	170.67	53.33	26.67	77.33
L(F)	256.00	10.00	128.00	256.00	6.00	32.00	114.67
L(M)	128.00	37.33	128.00	64.00	42.67	34.67	72.44
M(B)	37.33	16.00	12.00	256.00	106.67	85.33	85.56
M(C)	53.33	213.33	37.33	32.67	43.00	42.67	70.39
M(E)	2.67	42.67	26.67	7.33	106.67	42.67	38.11
M(F)	85.33	9.33	64.00	85.33	11.67	53.33	51.50
M(L)	53.33	5.33	48.00	85.33	2.00	8.00	33.67
Average							
Berries	48.00 (3)	75.60 (1)	55.47 (4)	104.73 (2)	67.66 (1)	29.87 (4)	64.54 (3)
Chicken	18.87 (6)	57.87 (2)	77.33 (3)	78.00 (5)	58.93 (2)	41.07 (2)	55.34 (5)
Egg	100.27 (2)	37.13 (4)	89.60 (2)	94.93 (3)	46.20 (4)	37.33 (3)	67.58 (2)
Foliage	19.33 (5)	34.00 (5)	50.53 (5)	55.00 (6)	32.40 (6)	19.60 (6)	35.14 (6)
Locusts	134.40 (1)	27.73 (5)	96.07 (1)	169.53 (1)	37.47 (5)	25.60 (5)	81.63 (1)
Mushrooms	46.40 (4)	57.33 (3)	37.60 (6)	93.33 (4)	54.00 (3)	46.40 (1)	55.84 (4)

Note: B=Berries, C=Chicken, E=Egg, F=Foliage, L=Locusts, and M=Mushrooms.

Break points were not the same for each food on each day for each possum (see Tables E1 - 6 in Appendix E). For example, P3 shows break points of 32, 64 and 8 over the three days for chicken under the PR schedule and foliage under the constant FR schedule. For all other food pairs, break points differed by up to two geometric increments over the three days.

Despite the general lack of statistically significant differences between foods (possibly due to the averaging of values), when break points were ordered from highest to lowest, they showed idiosyncratic choice by the possums (Table 6.0). Berries and locusts were ranked first by five possums and chicken was ranked fifth on average despite being ranked second by half the possums. A series of Wilcoxon signed- rank tests showed the mean ranks of foliage were significantly lower than the mean ranks of berries, chicken, egg and locusts (all p 's < .041).

Response rates were variable under the PR schedule and generally peaked when the ratio requirement was low then decreased as the ratio requirement increased (Figure 6.1). Response rates under the constant FR schedule were low and would occasionally be higher than rates under the PR schedule. Response rate figures for individual possums are included in Appendix D (Figures D1 - 3).

Post reinforcement pauses (PRPs) were measured from when the stimulus lights were lit after each reinforcer was obtained from the PR and constant FR schedule until the first response made under each respective schedule. PRPs increased in length under the PR schedule as ratio requirement increased. Under the constant FR schedule, PRPs were less varied compared to those under the PR schedule (see Figures D4 - 7 in Appendix D).

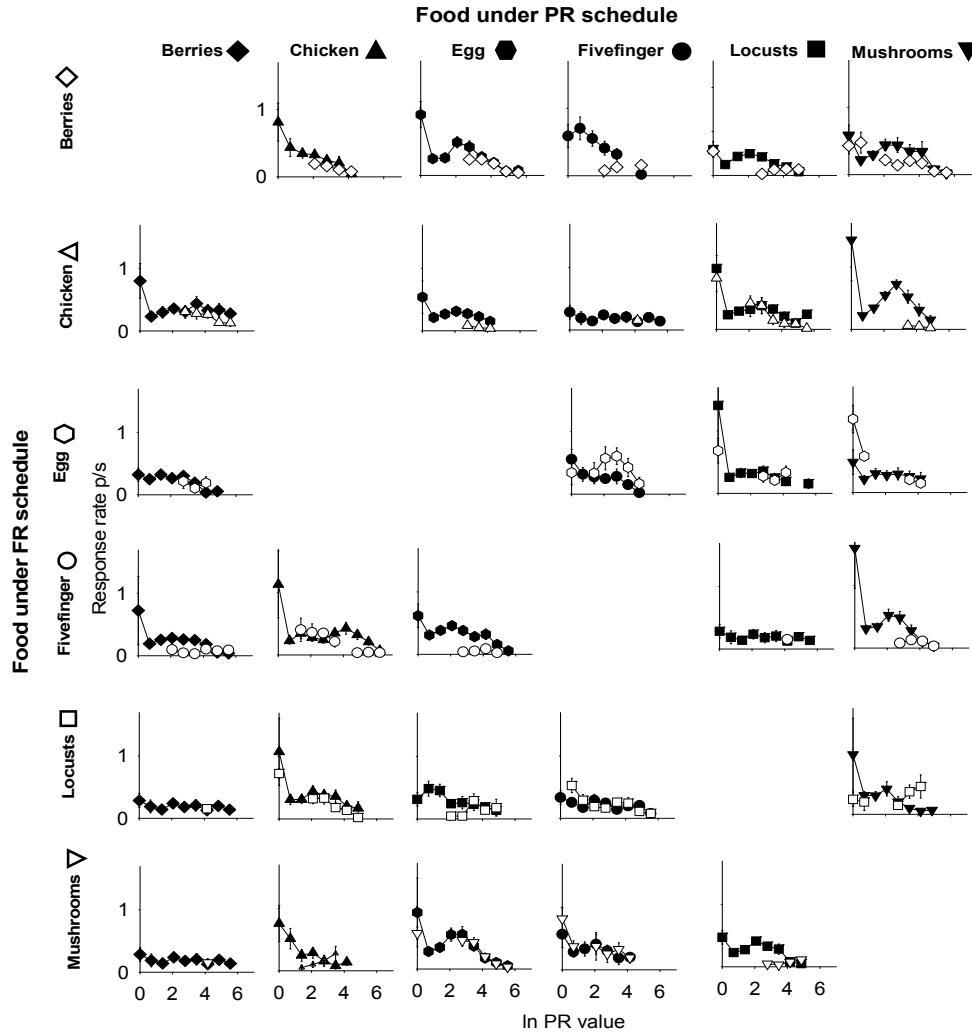


Figure 6.1. Response rates (p/s) averaged across sessions and possums for each food pair. The food under the PR schedule is along the top and the food under the constant FR schedule is on the left side of the graphs. Response rates are presented when response rates of three or more possums contributed to each data point.

Consumption is the dependent variable used when studying the demand for commodities when the same ratio requirement is in place for each session. This measure is a rate as it is the number of reinforcers earned during the session of a particular length. The time base, however, is constant, and thus rarely mentioned in the calculation. In PR schedules, the ratio requirement increases each trial, therefore the time base is not constant. In this experiment, the time base

for consumption rate was the time taken to obtain one reinforcer on the PR schedule. Reinforcers gained on the constant FR schedule were also calculated using this time base for each PR ratio requirement.

Consumption rate decreased as the ratio requirement increased under the PR schedule (Figures 6.2 – 6.4). The exponential model of demand (Equation 2) was fit when two or more degrees of freedom were available for generating parameter estimates. The range of the estimates of k was large and the assumption for keeping k constant did not appear to be valid, therefore, k values were determined for each animal across food pairs. The scaling parameter, k , was set to equal the range of the consumption rates across food pairs for each possum (ln 10.08 - ln 15.75). The model accounted for an average of 94.7% of the variance ($\sigma = 5.0\%$). Parameter tables for individual possums are included in Appendix E (Tables E1 - 6).

The estimates of initial demand averaged across possums for each food type were greater than -1 in 19 out of 36 food pairs which is consistent with inelastic demand for foods under the PR schedule, the remainder were less than -1 which is consistent with elastic demand (Table 6.1). A series of paired t tests revealed significantly lower initial demand values for locusts compared to chicken, foliage and mushrooms (all p 's < .044); and for egg compared to mushrooms ($p = .001$). No correction was applied to the p-values as given the large number of comparisons, any interesting effects would have been very difficult to detect.

When initial demand values of foods were ranked in order from lowest to highest for each possum, individual differences were observed. Berries, egg and locusts ranked highly for most possums. Foliage was ranked fifth and chicken

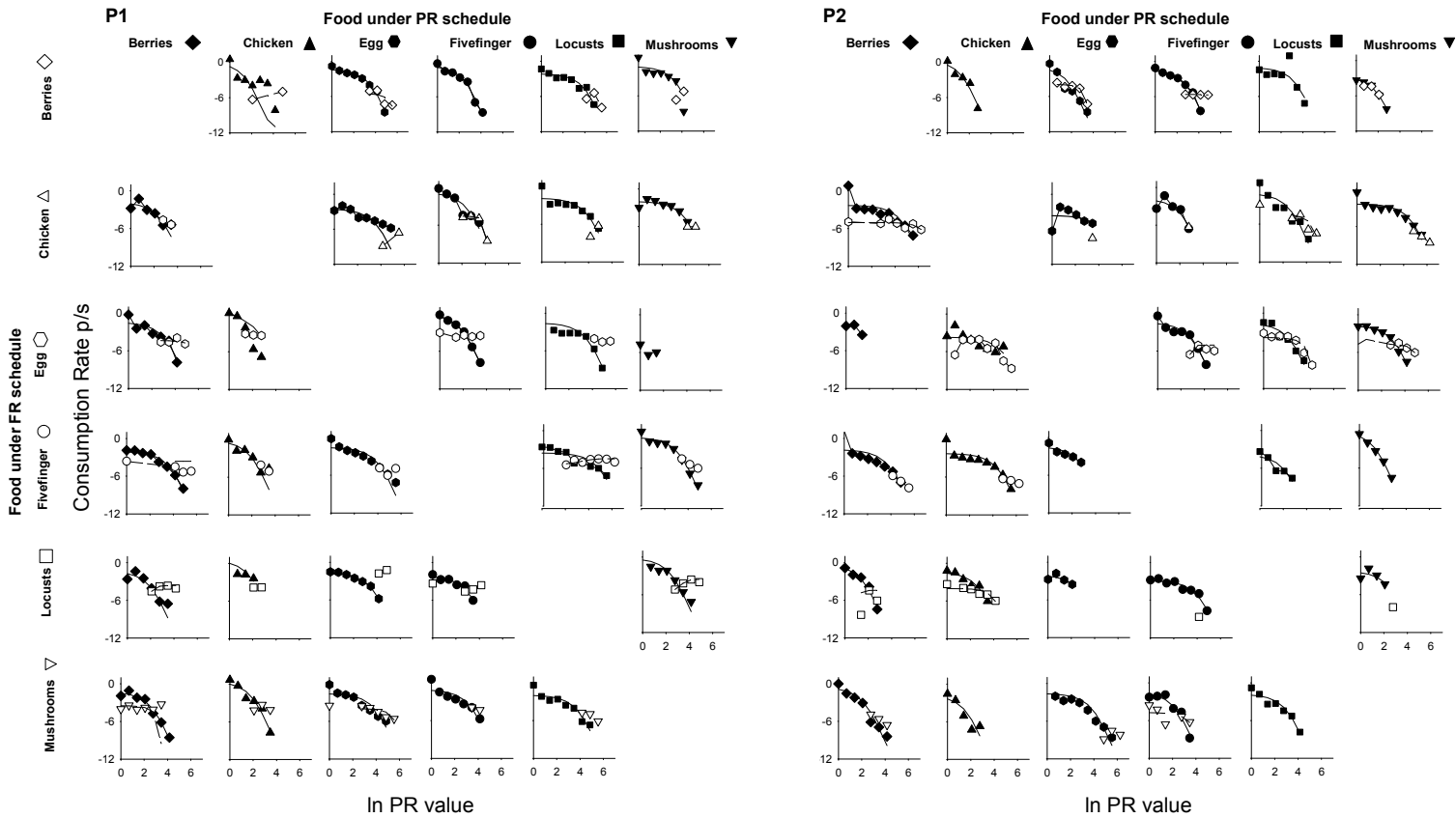


Figure 6.2. Ln Consumption rates (p/s) averaged across sessions for each food pair for P1 and P2. The food under the PR schedule is along the top and the food under the constant FR schedule is on the left side of the graphs. To illustrate the pattern of consumption all data was included in the fits.

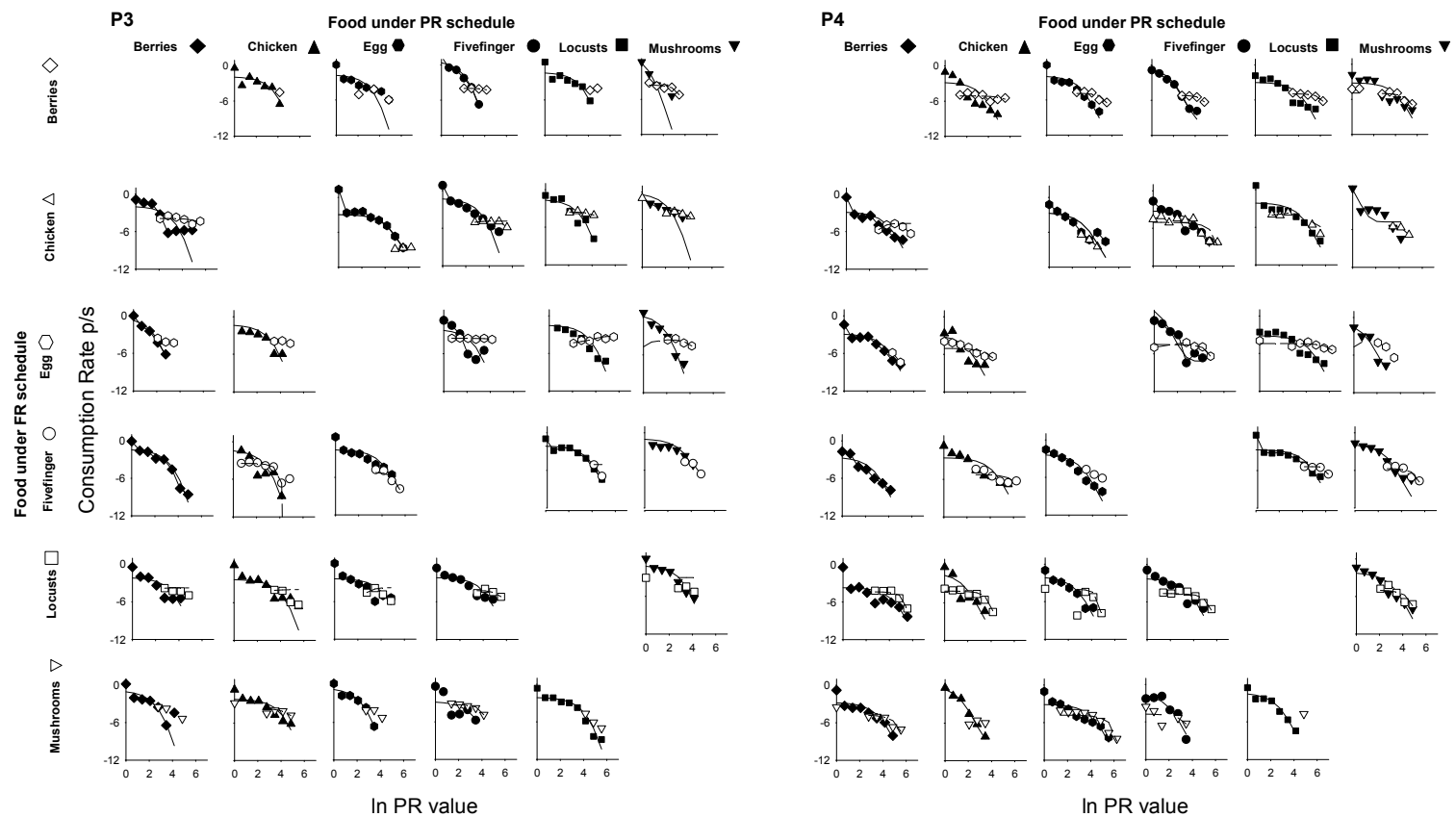


Figure 6.3. Ln Consumption rates (p/s) averaged across sessions for each food pair for P3 and P4. The food under the PR schedule is along the top and the food under the constant FR schedule is on the left side of the graphs. To illustrate the pattern of consumption all data was included in the fits.

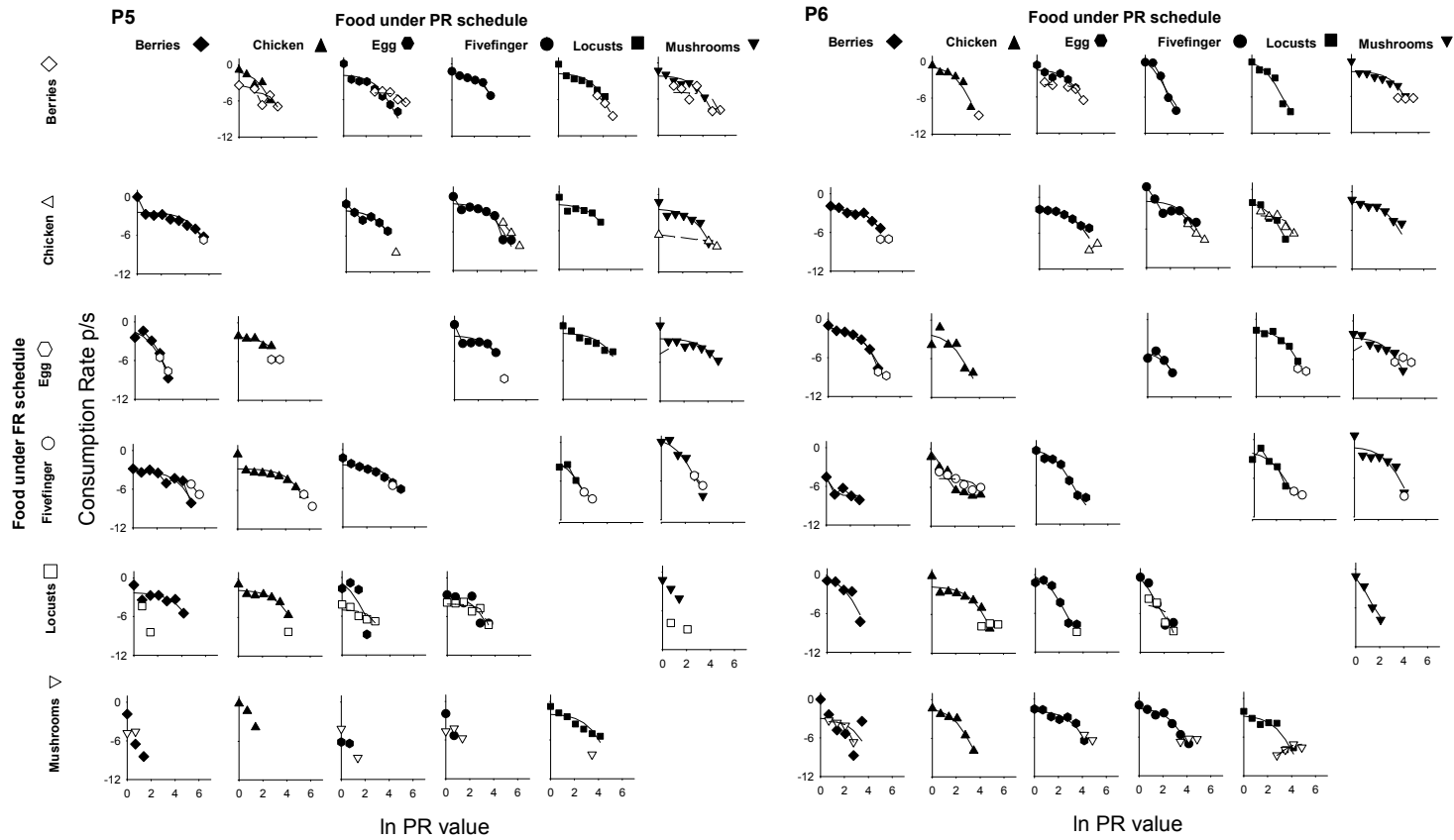


Figure 6.4. Ln Consumption rates (p/s) averaged across sessions for each food pair for P5 and P6. The food under the PR schedule is along the top and the food under the constant FR schedule is on the left side of the graphs. To illustrate the pattern of consumption all data was included in the fits.

ranked sixth on average with every food type, except egg and locusts, ranked the lowest by at least one possum. Wilcoxon ranked-signs tests showed the mean ranks of locusts were significantly higher than the mean ranks of the other foods (all p 's < .045) indicating that locusts were more valued than the other foods.

Table 6.1. Estimates of initial demand, essential value and P_{\max} derived from the exponential demand (Equation 2) and cross-price demand (Equation 5) model averaged across sessions. A rank order is given in parentheses for P1 - 6.

	Food	P1	P2	P3	P4	P5	P6	Average
Initial demand	B	-1.64 (3)	-0.48 (3)	-0.74 (4)	-2.89 (1)	-0.14 (3)	2.57 (6)	1.03 (4)
	C	3.12 (6)	-1.64 (4)	-1.71 (1)	2.54 (6)	0.82 (6)	0.71 (4)	1.22 (5)
	E	-1.74 (2)	-0.19 (2)	-1.43 (3)	-1.82 (3)	0.63 (5)	-0.32 (2)	-0.97 (2)
	F	-0.86 (4)	-2.94 (6)	-0.23 (5)	-1.26 (4)	-1.53 (2)	2.21 (5)	1.54 (6)
	L	-1.88 (1)	-0.67 (1)	-1.54 (2)	-2.21 (2)	-1.62 (1)	-1.11 (1)	-1.36 (1)
	M	-0.66 (5)	2.18 (5)	0.34 (6)	0.52 (5)	-0.13 (4)	0.58 (3)	-0.74 (3)
Essential value	B	0.11 (6)	0.06 (1)	0.05 (5)	0.17 (5)	0.10 (5)	0.07 (2)	0.06 (2)
	C	0.10 (5)	0.10 (3)	0.05 (6)	0.21 (6)	0.07 (3)	0.16 (5)	0.06 (1)
	E	0.06 (3)	0.09 (2)	0.03 (2)	0.12 (4)	0.08 (4)	0.09 (4)	0.07 (3)
	F	0.06 (4)	0.12 (4)	0.03 (4)	0.07 (1)	0.12 (2)	0.06 (1)	0.08 (5)
	L	0.05 (2)	0.58 (6)	0.03 (3)	0.08 (2)	0.07 (1)	0.27 (6)	0.07 (4)
	M	0.04 (1)	0.13 (5)	0.02 (1)	0.08 (3)	0.07 (1)	0.51 (3)	0.09 (6)
P_{\max}	B	1.60 (5)	2.49 (4)	1.88 (2)	3.68 (4)	6.04 (1)	0.99 (5)	2.47 (5)
	C	0.93 (6)	6.69 (1)	2.92 (5)	4.42 (1)	2.97 (2)	1.05 (4)	3.35 (1)
	E	3.40 (3)	2.78 (2)	3.06 (6)	2.53 (5)	2.91 (3)	1.45 (2)	2.66 (3)
	F	2.25 (4)	1.16 (5)	2.03 (3)	4.23 (2)	1.82 (6)	1.17 (3)	2.34 (6)
	L	4.96 (2)	1.15 (6)	2.55 (4)	4.14 (3)	2.01 (5)	0.71 (6)	2.67 (2)
	M	3.55 (1)	2.56 (3)	1.26 (1)	1.98 (6)	2.30 (4)	2.46 (1)	2.48 (4)

Note: B=Berries, C=Chicken, E=Egg, F=Foliage, L=Locusts, and M=Mushrooms.

The estimates of essential values (alpha) were similar across foods. This was confirmed by the non-significant results of a paired samples t-test and Wilcoxon ranked-signs tests. This suggests that the change in consumption rate or elasticity, as ratio requirement increased was similar across foods (Table 6.1). Mushrooms were the highest ranked food for three possums and foliage was the highest ranked food for two others, however, on average these foods were ranked in 6th and 5th position, respectively.

The estimates of P_{\max} were similar in absolute value and rank order across possums (all p 's $> .05$). The highest P_{\max} values were found for chicken, mushrooms and berries, however, based on the averaged values, chicken and locusts were ranked the highest (Table 6.1). To examine the relationship between P_{\max} , initial demand, alpha, and break point values Pearson correlations were conducted and revealed that P_{\max} and break point ($r = .456, p < .001$), and P_{\max} and alpha ($r = .274, p < .001$) were positively correlated. Whereas, break point and alpha were negatively correlated ($r = -.108, p = .027$). As alpha increased break points decreased, and P_{\max} increased. As P_{\max} increased break points and alpha increased.

The cross-price demand model (Equation 5) 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 ($\sigma = 2.9\%$). Parameter tables for individual possums are included in Appendix E (Tables E1 - 6).

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 6.2). Interaction and sensitivity values, however, were not significantly different from each other. Despite this, foods with more negative interaction estimates and higher sensitivity estimates were berries, chicken and egg indicating they were the most substitutable under the constant FR schedule with foods available under the PR schedule.

The intersection of fitted curves to Equations 2 and 5 is the cross point which gives a measure of substitutability between two commodities (Table 6.2). The values and rank ordered cross points were not significantly different across

foods. There were more perseverative cross points and occurrences of exclusive responding under the PR schedule for chicken, egg and locusts than other foods indicating they possums would perform more responses for these foods than for foods under the constant FR schedule (which required fewer responses to obtain). There were, however, more conservative cross points overall. This indicates that possums switched to responding under the constant FR schedule when the ratio requirement under the PR schedule was smaller than the equivalence point.

Table 6.2. Estimates of interaction, sensitivity, and cross point values of foods available under the PR schedule derived from the exponential demand (Equation 2) and cross-price demand (Equation 5) model averaged across sessions of foods for P1 - 6. The rank order is given in parentheses. Cross points are given for all sessions.

	Food	P1	P2	P3	P4	P5	P6	Average
Interaction	B	-	-1.64 (1)	-	-2.39 (2)	-0.86 (1)	-0.55 (2)	1.36 (6)
	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 (4)
	F	-0.99 (1)	-	-0.17 (4)	-01.08 (4)	-	-1.17 (1)	-0.85 (3)
	L	-0.40 (2)	-	-	1.85 (3)	-0.40 (2)	-	-0.88 (2)
	M	-0.32 (3)	-	-0.72 (2)	-0.78 (5)	-	-	0.61 (5)
Sensitivity	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)	-	-.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)
Cross point	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=Locusts, and M=Mushrooms.

* = values based on three data points or fewer.

- = responding was exclusively allocated to the PR schedule

To examine the interaction between foods under the PR and FR schedule, the overall averages of break point, essential value, initial demand, and P_{\max} for

each food under the PR schedule is shown in the top row of Figure 6.5. The same data grouped by food available under the FR schedule is 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. Figure 6.5 shows break points were higher for berries, egg, locusts and mushrooms and lower for chicken and foliage under the PR schedule than under the constant FR schedule. Initial demand was low for chicken, egg, locusts and mushrooms under the PR schedule and increased when these foods were available under the constant FR schedule. Initial demand was higher for berries and foliage under the PR schedule than when these foods were available under the constant FR schedule. Alpha was low (high essential value) for egg and high for locusts and chicken under the PR schedule. Under the constant FR schedule, alpha was high (low essential value) for egg and lower for chicken and locusts. P_{\max} was higher for berries, egg and foliage under the PR schedule compared to when these foods were available under the constant FR schedule. Conversely, P_{\max} increased for foods under the PR schedule when chicken and foliage were available under the constant FR schedule.

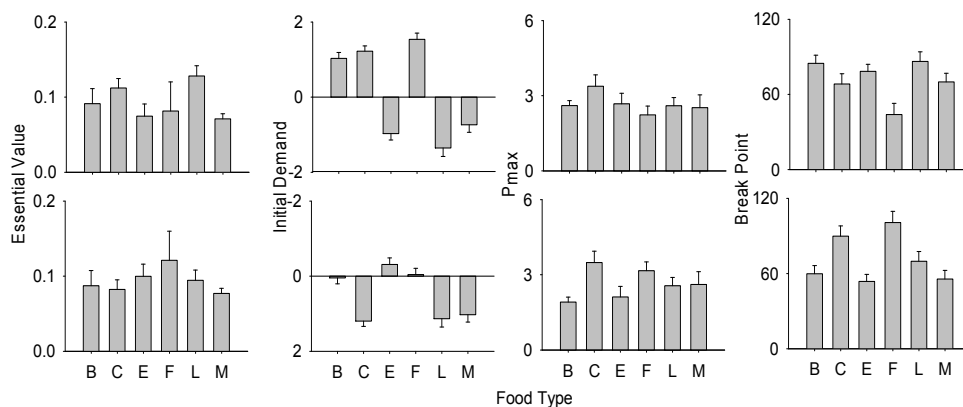


Figure 6.5. Dependent variables, essential value (alpha), initial demand, P_{\max} and break point values averaged across foods under the PR schedule (top panel), and constant FR schedule (bottom panel) across possums with standard error bars.

Discussion

The aim of Experiment 3 was to measure the *relative demand* for foods using concurrent PR FR schedules. Break points under the PR schedule and estimates derived from the exponential and cross price models of demand (initial demand, essential value and P_{\max}), and cross points were compared and rank ordered to provide a measure of relative demand for different foods. These were also compared with the food preferences identified in Experiments 1 and 2.

Break points were lower for foliage than other foods, except locusts. Break point has been used to measure the reinforcement strength of commodities that differ in quantity (e.g., Hodos & Kalman, 1963), concentration (e.g., Hodos, 1961) or quality, such as drugs (e.g., Rodefer & Carroll, 1996) or food type (e.g., Foster et al., 1997b). The number of responses made in the final ratio, however, when aggregated across sessions decreased with higher quantities and concentrations of the commodity (Hodos, 1961; Hodos & Kalman, 1963). This was attributed to satiation due to the use of small increments of the PR schedule. In Experiment 3, a geometric progression was used to increment ratios under the PR schedule, therefore, it was unlikely that satiation occurred for any food types.

Break points decreased for food under the PR schedule when preferred commodities were available under the constant FR schedule (Figure 6.5). This suggests that the break point may be an indirect measure of preference for foods under the constant FR schedule. One needs to be cautious, however, about interpreting the break point on its own as a measure of preference as other measures, such as cross point, can vary independently of it.

The exponential model of demand predicted the decline in responding as ratio requirement increased under the PR schedule (Hursh & Silberberg, 2008).

The initial demand values were greater than -1 in more than half of the food pairs, which is consistent with inelastic demand. This means that consumption rate did not decrease at very low ratio requirements. The P_{\max} values, however, were lower than expected indicating that consumption rate was not maintained as the ratio requirement increased as consumption rate became elastic at small ratio requirements of approximately PR 2.

The estimates of initial demand were lower for berries, eggs and locusts, and higher for chicken, foliage and mushrooms. This feature, where 'lesser preferred' foods have high initial demand values has also been found in other demand studies (e.g., Foster et al., 2009; Hursh et al., 1988). It has been suggested that lesser preferred foods have higher consumption rates at low ratio requirements because the subject responds faster to gain the same 'value' of reinforcement in the session as obtained when preferred foods are available (Foster et al., 2009). This is because more responding is allocated to obtain preferred foods during the session.

It was expected with the comparison of different food types that the estimates of essential value and P_{\max} would be different across foods if they differed in value to the subject (Grant et al., 2014), however, there were only minimal differences across foods. In addition, estimates of the interaction between foods indicated substitutability between foods. Although functionally equivalent according to the estimates of essential value and interaction, there was consistency in the rank orders of foods based on the estimates of break point, initial demand, essential value, and P_{\max} . These indicated that preferred foods, such as berries, egg, locusts and occasionally mushrooms, had higher break points, estimates of essential value (lower alpha) and P_{\max} and lower estimates of initial demand. The

lesser preferred foods, such as chicken and foliage, had lower break points, estimates of essential value (higher alpha) and P_{\max} and higher estimates of initial demand.

The cross-price model of demand predicts an increase in responding under the FR schedule as ratio requirement increased (Hursh et al., 2013; Hursh & Silberberg, 2008). Cross points provide a measure of substitutability between two commodities under schedules of differing ratio requirements based on the interaction of the exponential and cross-price demand curves. In Experiment 3, cross points were perseverative for chicken, egg and locusts indicating that responding persisted to higher ratio requirements under the PR schedule before switching to the constant FR schedule. This is not unusual as perseverative errors were also found in concurrent PR FR arrangements where the same food was offered under both schedules in foraging studies in monkeys (Hodos & Trumbule, 1967), chimpanzees (Hineline & Sodetz, 1987), and pigeons (Wanchisen et al., 1988).

When different foods were on offer under concurrent schedules, cross points tended to be conservative. This means that possums responded for food under the constant FR schedule when the ratio requirement was smaller than that under the PR schedule indicating that the ratio requirement was of less importance in the allocation of responding than the type of food available. This is further evidenced by the interaction parameter of the cross-price model indicating that all foods were substitutable. Lesser preferred foods (e.g., chicken) were slightly more substitutable under the PR schedule than preferred foods meaning that possums would switch to the constant FR schedule more readily for a more preferred food.

One issue that needs to be addressed is the scaling parameter, k , of the

exponential demand model (Hursh & Silberberg, 2008). 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 relatively small ranges. When the range is large, as in Experiment 3 (ln 10.08 to 15.75), this assumption no longer seems to be a valid, and using an average is not a fair representation of the data. Consequently, in Experiments 3 – 6, k was allowed to vary across animals but was kept constant within each animal in each experiment.

Idiosyncratic food choice was evident in analyses of break point, initial demand, essential value, P_{\max} and even cross point. Each variable provided fairly consistent rank orders for food 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 which is consistent with preferences identified in Experiments 1 and 2; although two possums showed some preference for chicken.

For two-thirds of food pairs there was either no cross point or there was very little responding under the constant FR schedule, therefore these results should be interpreted with caution. It was surprising that the animals did not respond more to the FR alternative given our piloting of that ratio requirement. Consequently, in Experiment 4, elements of the current experiment were rerun and the ratio requirement under the constant FR schedule was decreased to FR 10 to increase responding for food under this schedule.

Experiment 4

In Experiment 4, the concurrent PR FR procedure was repeated with four of the food pairs used in Experiment 3; berries and egg, and chicken and mushrooms, and the constant FR ratio requirement was decreased from 30 responses to 10 responses in an effort to produce more responding under the FR schedule. The two food combinations in Experiment 4 were chosen because they produced similar consumption rates across possums in Experiment 3. The presentation of foods was counter balanced across the PR and FR schedules.

It was surprising that in Experiment 3 the possums did not respond for food under the constant FR schedule on more occasions. In Experiment 4, it is expected that decreasing the ‘price’ of food under the constant FR schedule from 30 to 10 responses will generate more responding to this alternative and will also indicate if the low responding to the constant FR schedule in the PR FR 30 in Experiment 3 is due to ratio strain.

Method

Subjects

The same possums, P1 - 6, were used in this experiment.

Housing

Possums were housed in the same cages as in previous experiments.

Apparatus

The feeding and weighing regimes were the same as previous experiments.

The same magazines used in Experiment 3 were used in Experiment 4.

Four foods were used in Experiment 4 presented in two food-pair combinations: berries and egg; and chicken and mushrooms. The foods were

counter balanced across PR and FR schedules making four food pairs. The order of presentation of the food pairs was randomised.

Procedure

Experiment 4 was conducted as an ABAB design. Data for the first FR 30 component (A) was provided by Experiment 3. The subsequent FR 10 (B) components and second FR 30 component (A) were conducted in three blocks of three sessions each.

Results

Break points were averaged across sessions for each food available under the PR schedule and are shown in Table 6.3. Break points varied across possums and FR conditions. Break points for berries and chicken were higher in the PR FR 10 condition than PR FR 30 condition, however, break points for egg and mushrooms were either the same or higher in the PR FR 30 condition than PR FR 10 condition. Paired t-tests revealed significantly higher break points for egg compared to berries in the PR FR 30 condition [$t(5) = 2.66, p = .045, d = 1.09$]. Breakpoints were not significantly different between the other food pairs [$t(5) < 1.90, p > .05$].

Response rates under the PR schedule were high before declining as response requirement increased (Figure 6.6). Rates were less varied for berries and egg compared to chicken and mushroom, however, there were secondary peaks in response rate observed only for chicken and mushrooms. Responding was observed under the constant FR schedules for all foods and more responding under the FR schedule for berries occurred when the ratio requirement was low for egg under the PR schedule. Response rates for individual animals are included in Appendix D (Figures D8 - 9).

Table 6.3. Break point and initial demand, essential value and P_{\max} values derived from the exponential demand model (Equation 2) averaged across sessions of foods available under the PR schedule for P1 – P6. An average for each food across possums is included. A rank order is given in parentheses for each possum.

	FR	Pair	P1	P2	P3	P4	P5	P6	Average
Break point	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)
Initial Demand	30	B(E)	-1.56 (2)	-2.32 (1)	-1.56 (3)	-2.93 (1)	-2.50 (2)	-0.84 (4)	-1.95 (1)
		C(M)	-0.19 (4)	-1.99 (2)	-2.23 (2)	-1.24 (4)	-4.35 (1)	-1.22 (3)	-1.87 (2)
		E(B)	-1.44 (3)	-1.23 (4)	-2.44 (1)	-2.25 (2)	-0.60 (4)	-1.50 (1)	-1.65 (3)
		M(C)	-1.78 (1)	-1.72 (3)	-0.89 (4)	-1.53 (3)	-2.06 (3)	-1.39 (2)	-1.58 (4)
	10	B(E)	-1.36 (3)	-2.10 (1)	-3.27 (1)	-2.80 (3)	-0.31 (3)	-1.58 (4)	-1.90 (2)
		C(M)	0.55 (4)	-0.58 (3)	-2.39 (2)	-3.27 (1)	-1.59 (1)	-1.88 (3)	-1.52 (3)
		E(B)	-1.72 (2)	-2.07 (2)	-2.04 (3)	-2.95 (2)	-	-2.69 (1)	-2.29 (1)
		M(C)	-1.81 (1)	0.27 (4)	-1.23 (4)	-1.98 (4)	-1.49 (2)	-1.95 (2)	-1.36 (4)
Essential value	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)
P_{\max}	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)	157.54 (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)	2.01 (3)	1.67 (4)

Note: B=Berries, C=Chicken, E=Egg, F=Foliage, L=Locusts, and M=Mushrooms.

The exponential demand model was fit to consumption rates under the PR schedule when two or more degrees of freedom were available to estimate parameters. The scaling parameter, k , was set to equal the range of the consumption rates across conditions ($\ln 9.26 - \ln 15.75$). The model accounted for an average of 93.6% of the variance ($\sigma = 3.2\%$). The cross price model was fit to consumption rates under the FR schedules and it accounted for an average of

97.1% of the variance ($\sigma = 4.0\%$). Consumption rates for foods under the PR schedule decreased as price increased. 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 (Figures 6.7 – 6.8).

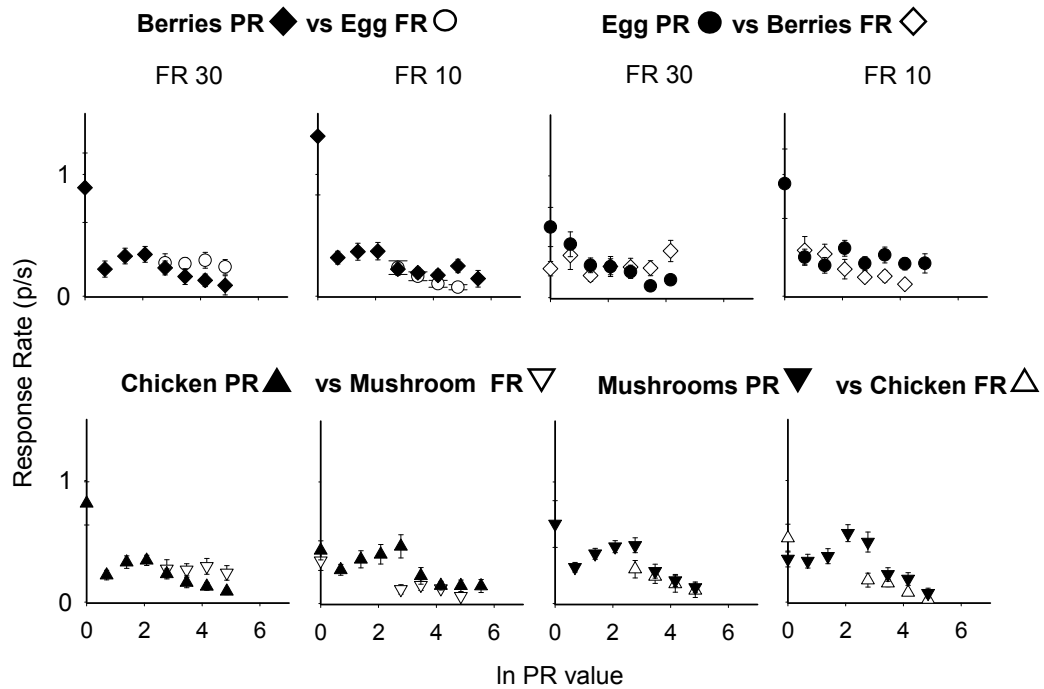


Figure 6.6. Response rates (p/s) averaged across sessions and possums as a function of ln PR value for berries and egg, and chicken and mushroom pairs under PR (filled symbols) and FR 10 and FR 30 schedules (open symbols). Response rates are presented when three or more possums contributed to the data point.

The average estimates of initial demand were lower across possums for berries, chicken and mushroom under the PR schedule during the PR FR 30 condition compared with the PR FR 10 condition (Table 6.3). Initial demand was highest for mushrooms and lowest for egg under the PR schedule during the PR FR 30 condition and highest for chicken and lowest for egg during PR FR 10 condition. There were no significant differences between the foods across the FR conditions (all p 's > .05).

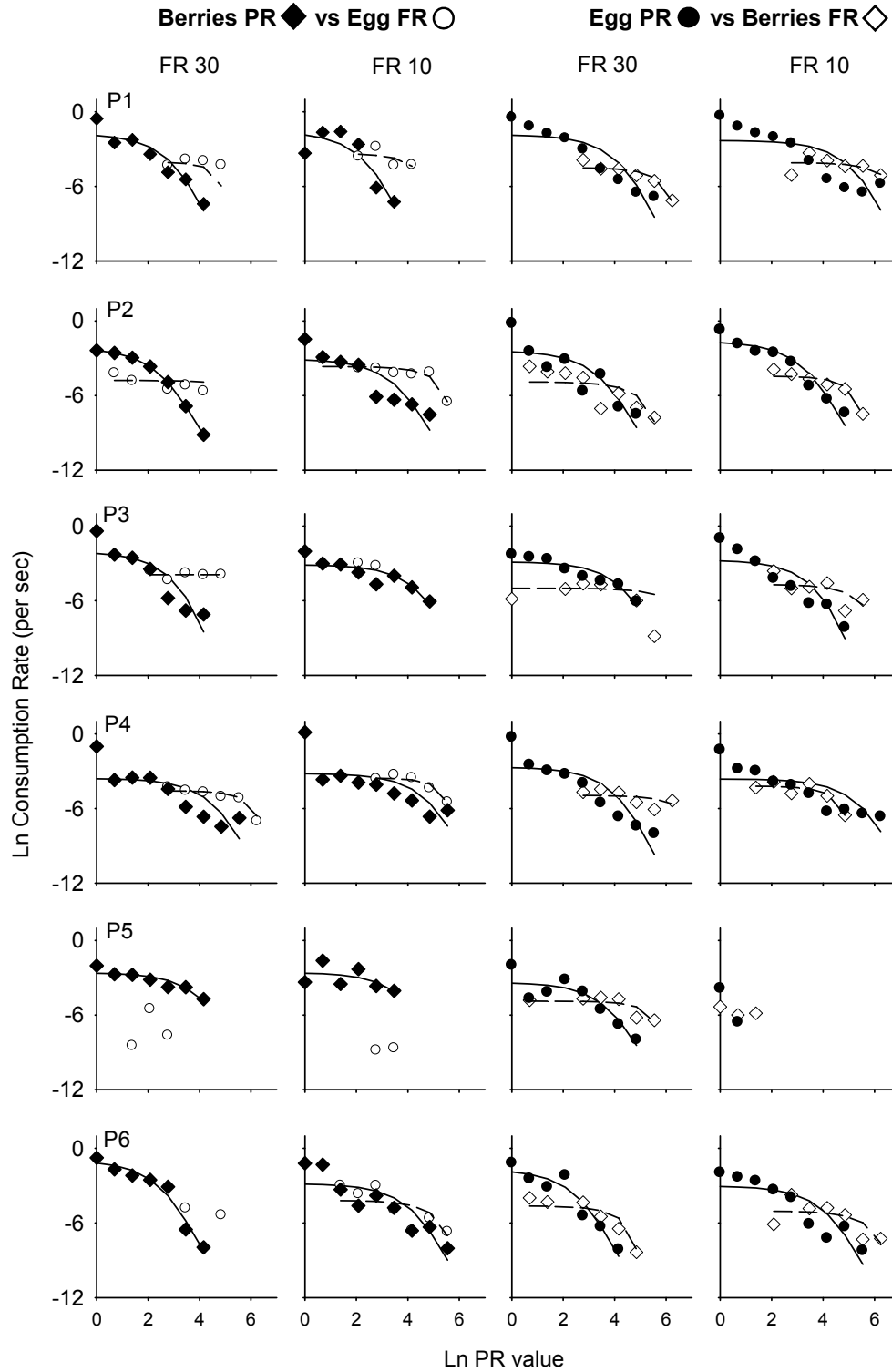


Figure 6.7. Ln consumption rate as a function of ln PR value for berries and egg under PR (filled symbols) and FR 10 and FR 30 schedules (open symbols). Smooth curves are drawn by Equations 2 (solid) and 5 (dashed) when the $df \geq 1$.

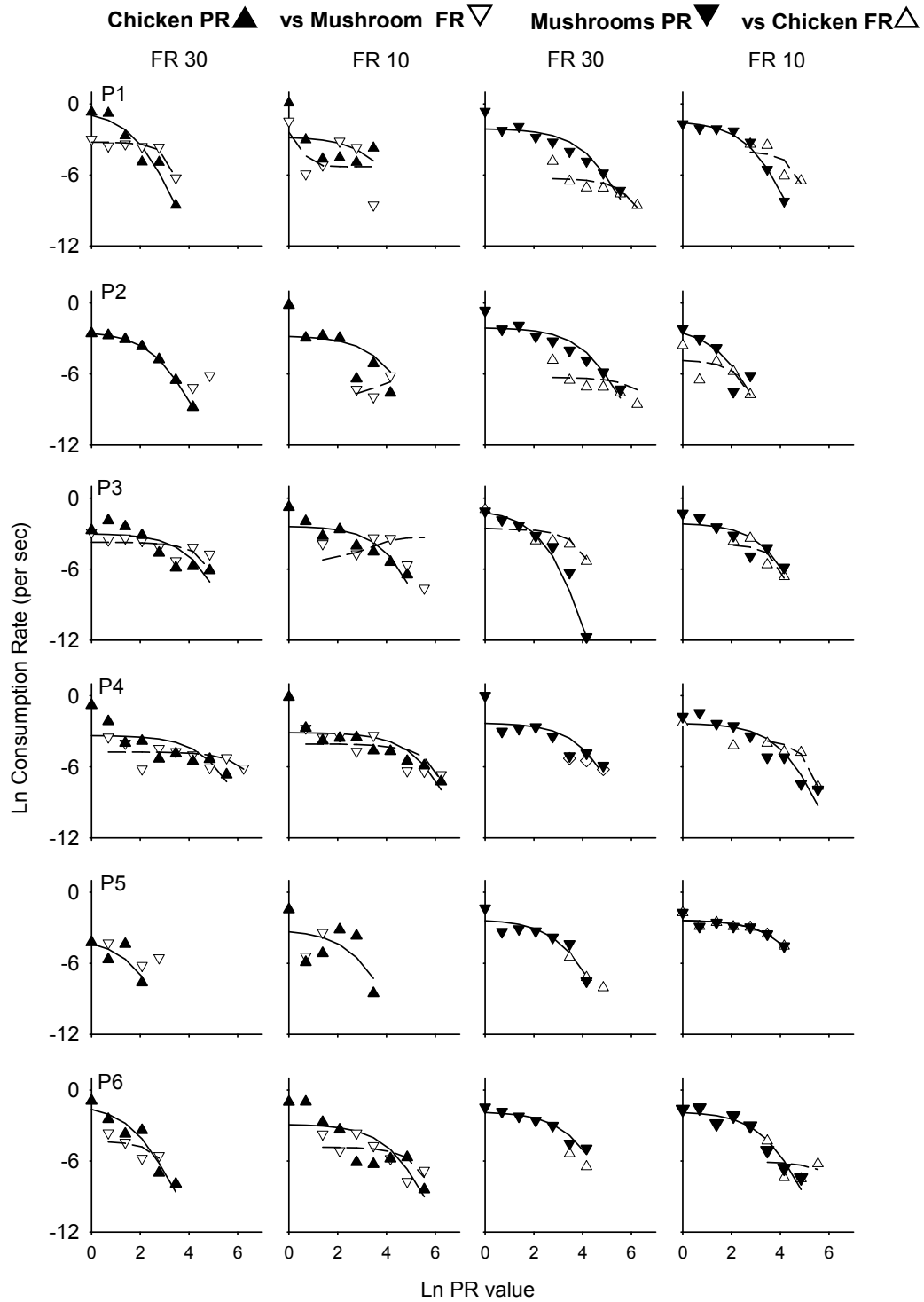


Figure 6.8. Ln consumption rate as a function of ln PR value for chicken and mushrooms under PR (filled symbols) and FR 10 and FR 30 schedules (open symbols). Smooth curves are drawn by Equations 2 (solid) and 5 (dashed) when the $df \geq 1$.

The estimates of essential value were different for the food pairs in the PR FR 30 and PR FR 10 condition. In the PR FR 30 condition, essential value was highest for mushrooms and lowest for chicken and in the PR FR 10 condition, essential value was highest for chicken and lowest for mushroom (Table 6.3). Similarly, essential value was higher for egg than berries in PR FR 30 and in the PR FR 10 condition essential value was higher for berries than egg. There were no significant differences between foods across conditions (all p 's > .05).

The estimates of P_{\max} were higher for egg than all other foods and were higher for berries and mushrooms under the PR schedule in the PR FR 30 condition compared to the PR FR 10 condition. P_{\max} was higher for chicken and egg in the PR FR 10 condition than in the PR FR 30 condition (Table 6.3). There were significantly higher estimates of P_{\max} in the PR FR 10 than PR FR 30 condition [$t(21) = 2.65, p = .015, d = 0.57$]; and between egg and all other foods in the PR FR 10 condition (all p 's < .024). In addition, egg was ranked the highest by P_{\max} value.

The cross-price model (Equation 5) predicted negative interaction estimates (I) indicating all foods were substitutable. In some cases the foods under the PR schedule considered the most substitutable with foods under the FR 30 schedule were the least substitutable under the FR 10 schedule across possums (Table 6.4). No statistics could be computed as not all possums responded for mushrooms in the PR FR 30 condition or responded to fewer than three PR ratio requirements. A rank order of the estimates of the interaction parameter, however, showed that chicken and mushrooms were the most substitutable in both FR conditions when chicken was available under the PR schedule in the PR FR 30 condition and mushrooms in the PR FR 10 condition.

There were more conservative cross points than perseverative cross points in the PR FR 10 and PR FR 30 conditions (Table 6.4), similar to the results in Experiment 3. The range of cross points was smaller in the PR FR 10 condition compared to the PR FR 30 condition, however, the values were not significantly different across foods or FR conditions. On average, mushrooms produced the highest cross points under both FR conditions. There were significantly higher cross points for mushrooms than for chicken in the PR FR 10 condition [$t(2) = 10.54, p = .009, d = 6.08$].

Table 6.4. Estimates of interaction, sensitivity and cross point values derived from the exponential demand (Equation 2) and cross-price demand (Equation 5) model averaged across sessions. A rank order is given in parentheses for P1 - 6.

	FR	Pair	P1	P2	P3	P4	P5	P6	Average
Interaction	30	B(E)	-	-	-	-0.04 (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 (3)
		C(M)	-	-	-0.79 (1)	-1.32 (1)	-	-	-1.06 (1)
		E(B)	-0.33 (1)	-0.08 (2)	-0.64 (2)	-0.44 (3)	-	-0.28 (4)	-0.35 (4)
		M(C)	-	-	-	-0.90 (2)	-	-	-0.90 (2)
Sensitivity	30	B(E)	-	-	-	-14.18 (3)	-	-	-14.18 (2)
		C(M)	-0.21 (1)	-	-874.2 (2)	-9.25 (2)	-	-	-294.56 (3)
		E(B)	-2.56 (2)	-0.03 (1)	-	-0.40 (1)	-0.04 (1)	-0.23 (1)	-8.66 (1)
		M(C)	-	-	-3.43 (1)	-	-	-	-
	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)
Cross point	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)	32.5*(1)	5.06*(1)	20.73 (4)
		M(C)	29.02*(2)	178.5*(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, F=Foliage, L=Locusts, and M=Mushrooms.

* = values based on three data points or fewer.

- = responding was exclusively allocated to the PR schedule

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 response requirement under the FR schedule affected consumption rates under the PR schedule. It was anticipated that decreasing the 'price' of food under the constant FR from 30 to 10 responses would generate more responding to this alternative as in Experiment 3 the possums did not respond to the alternative schedule on a number of occasions. Decreasing the FR requirement in Experiment 4 was also an attempt to determine if the low responding was due to ratio strain. It was surprising that the change from PR FR 30 to PR FR 10 did not increase responding under the constant FR schedule as the number of food pairs where cross points could be calculated was higher in Experiment 3 (29 cross points) compared to Experiment 4 (17 cross points). In addition, one cannot claim that the low responding under the FR schedules was due to ratio strain as possums would reliably respond up to 256 times under the PR schedule.

Generally, there were no marked differences in break point, initial demand, essential value, or cross point across PR FR conditions or food types, except for the occasional differences. For example, break points were higher for egg compared to berries in the PR FR 30 condition, P_{\max} was higher for egg compared to all other foods in the PR FR 10 condition, and cross points were higher for mushrooms compared to chicken in the PR FR 10 condition. P_{\max} values and cross points were higher in the PR FR 10 condition compared to the PR FR 30 condition.

Initial demand was less than -1 which was consistent for the majority of food pairs in the PR FR 10 and PR FR 30 conditions (see Table 6.3). This means

that at low ratio requirements consumption rates were low. In contrast, in Experiment 3, using PR FR 30 schedules the initial demand values were greater than -1, which is consistent with inelastic demand across foods. In both experiments, estimates of initial demand were lower for preferred foods, as found by Foster et al. (2009) and Hursh et al. (1988).

There were no significant differences in essential value across FR conditions or food types in Experiment 4. This was also evident in Experiment 3, and indicates that the same decline in consumption rate occurred across foods regardless of ratio requirement under the constant FR schedule. Essential values for qualitatively different commodities such as different foods should vary (Foster et al., 2009), in contrast to qualitatively similar but quantitatively different commodities such as access time to the same foods (Grant et al., 2014).

The elastic initial demand values, and high elasticity of demand impacted values of P_{\max} , as the estimates of this parameter were low for all foods, except egg in Experiment 4. Although, in comparison with other derived parameters P_{\max} was significantly higher under the PR schedule in the FR PR 10 condition, than PR FR 30 condition. This indicates that when the ratio requirement under the alternative schedule was lower the consumption rates under the PR schedule remained high to larger ratio requirements compared to when the alternative ratio requirement was also larger.

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 3 and 4 demonstrated exclusive responding for foods under the PR schedule in more than half of the food pairs. One reason for this might be that the animals actually do not have a

strong preference for one food over another, and are simply responding for the food that was initially ‘cheaper’ under the PR schedule. This argument, however, does not seem to be universal when one considers all the food pairs on offer in Experiment 3. In Experiments 1 and 2 it was confirmed that foliage was the least preferred food for many possums. This was confirmed again in Experiment 3 where foliage under the PR schedule led to smaller break points and cross points but is inconsistent with the argument that foods are preferred because they are available under the PR schedule.

Conversely, if the foods were substitutable, which the foods in Experiments 3 and 4 appeared to be, then whichever food was available under the PR schedule ends up being allocated more responding because it was initially the “cheaper” alternative. This was not completely the case either: initial exposure to a food at a low PR value did influence subsequent measures such as cross point but it did not seem as if that completely overwhelmed relative demand for more highly preferred foods. This is evidenced by an analysis of the number of occurrences of perseverative cross point or, if no cross point was found, then where exclusive responding occurred under the PR schedule for common food pairs. When berries and chicken were available under the PR schedule, and egg and mushrooms under the constant FR schedule, there was a preference for food under the PR schedule in 19 out of 36 food pairs. 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. In comparison, when egg and mushrooms were available under the PR schedule, and berries and chicken available under the constant FR schedule, responding was allocated to food under the PR schedule in 28 out of a possible 36 food pairs. This

means that in three quarters of food pairs responding was allocated to the PR schedule for egg and mushroom indicating that the allocation of responding was influenced by the preference of the foods as well as schedule requirement.

In order to compare consumption at different ratio requirements of the PR schedule with the concurrently available FR schedule it was necessary to use consumption rate as the primary dependent measure. This is because the rate of reinforcement and the rate of responding on ratio schedules are perfectly correlated (Bizo & Killeen, 1997). Consumption rates were calculated separately for the PR and FR component by dividing the number of reinforcers earned by the time taken to complete the PR ratio requirement. Thus, it was the PR requirement that determined the denominator for the calculation of PR and FR consumption rates. In other studies where concurrent PFR FR schedules are used, where the PFR schedule increases across sessions, session duration is kept constant and there is no need to calculate a rate of consumption because the time over which animals earn food at different PR values does not change. Researchers typically compare the total number for reinforcers earned on the two FR schedules (e.g. Bickel & Madden, 1999; Sørensen et al., 2001). These can be thought of, however, as a consumption rate - number consumed per session - but they are rarely reported as such (e.g., Foster et al., 1997a).

The attempt made in Experiments 3 and 4 to devise a method for measuring relative demand for concurrently available foods was a qualified success. 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 minimal 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 next experiment PFR FR schedules were used where each ratio requirement under the PFR schedule remained in place for five days as a way of allowing more opportunities for the possums to earn food under the constant FR schedule.

Chapter 7 – Concurrent PFR FR schedules

Experiment 5

In previous experiments a concurrent PR FR schedule arrangement was used to measure the demand for qualitatively different foods using a geometrically incrementing PR schedule *within* a session. It was found that on many occasions there was minimal responding under the constant FR component of the PR FR schedule when the FR requirement was 30 or 10 responses. In addition, when the PR schedule increased *within* a session, more responding was allocated to the schedule that corresponded to the preferred foods in comparison with lesser preferred foods.

In Experiment 5, the aim was to allow more opportunities to gain food under the constant FR schedule by increasing the incrementing schedule ratio requirements across days, rather than within a session, using concurrent PFR FR schedules. Each ratio requirement was in place for five days (e.g. Hudson et al., 1999). The four foods used in Experiment 5 were the same as Experiment 4: berries and egg, and chicken and mushrooms. It was of interest whether the conclusions drawn regarding the demand for food using concurrent PR FR schedules would be the same as those using PFR FR schedules.

The behavioural economic models of demand (see Equations 1 and 2, Chapter 3, p. 27 - 28) described by Hursh et al. (1988) and Hursh and Silberberg (2008) were fit to consumption rates to assess the reliability of the models to predict the demand for foods under the PFR schedule in the possums. Similarly, a non-linear least squares regression and the cross-price model of demand (see Equation 5, Chapter 3, p. 30) were fit to consumption rates under the constant FR

schedules and used to generate cross points. A comparison of the reliability of Equation 3 (Hursh & Winger, 1995) and Equation 4 (Hursh et al., 2013) for calculating P_{\max} were also compared (see Chapter 3, p. 39).

Comparisons of the demand models conducted by Foster et al., (2009) and Grant et al., (2014) found the linear model, Equation 1 (Hursh et al., 1988) accounted for data better than the exponential model, Equation 2 (Hursh & Silberberg, 2008). It was expected that the models would describe the data equally well, however, the models produced opposing accounts of demand for foods based on the measures of initial demand, essential value and P_{\max} (Foster et al., 2009). The cross price demand model, a recent addition to the mathematical models used to describe demand, provides reliable measures of substitutability and cross point.

The idiosyncratic nature of food choice in possums has been identified in Experiments 1 - 4. In Experiment 5, the demand for foods was compared with the data from Experiment 4. It was expected that the estimates of initial demand, essential value, P_{\max} , break point and cross point would provide similar descriptions of demand for the same foods across possums.

Method

Subjects

The same possums, P1 - 6, used in Experiment 5 as Experiments 3 and 4.

Housing

Possums were housed in the same cages as in previous experiments.

Apparatus

The feeding and weighing regimes were the same as previous experiments.

The same magazines used in Experiment 3 were used in Experiment 4.

The foods in Experiment 4 were used in Experiment 5 and were presented in the same pairs (berries and egg, and chicken and mushrooms). The same volume of each food used in Experiment 3 and 4 was used and each food from each pair was presented under the PFR and FR 30 schedule in four conditions.

Procedure

The experimental procedure was the same as other experiments, where the ratio requirement on the right lever increased according to a geometric series; 1, 2, 4, 8, 16, 32, 64, 128, 256, 512, and 1024 every five days. The ratio requirement on the left lever was a constant FR 30 for each session. If possums did not receive a reinforcer under the PFR schedule for two consecutive days the condition was terminated.

Results

Response rates were calculated by dividing the total number of responses made under each schedule by the session length minus the total reinforcer access duration (Figure 7.0). Response rates increased as the ratio requirement progressed. There were also increased response rates at higher ratio requirements under PFR schedule for chicken in comparison with the other foods and schedules. The response rates for berries, egg and mushrooms under the PFR schedule peaked between FR 8 (berries and mushrooms) and FR 32 (egg). Responding under the FR 30 schedule was low for all foods.

In comparison, response rates under the PR FR from Experiment 4 (lower panel of Figure 7.0) were higher and more variable for berries, egg and mushrooms compared to the PFR schedule. Response rates under the FR 30 schedule of the PR FR were higher than the FR 30 of the PFR FR schedule.

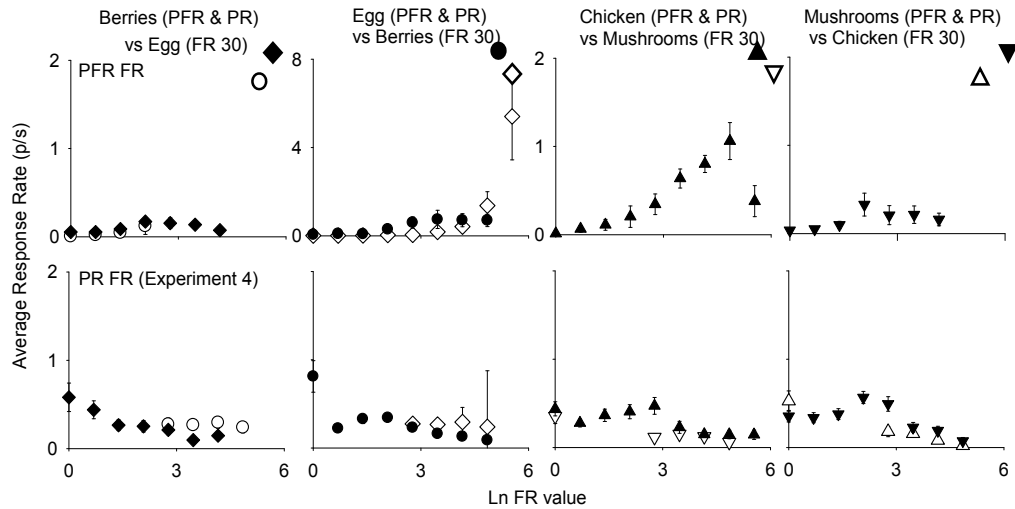


Figure 7.0. Response rate (p/s) plotted as a function of ln FR value for all foods under the PFR FR and PR FR schedules (Experiment 4). Filled symbols correspond to foods under the PR and PFR schedules, and the unfilled symbols correspond to foods under the constant FR schedule. Note the different y-axis values. Response rates are presented when 50% or more of possums contributed to each data point.

Break points were variable across foods and possums under the PFR schedule (Table 7.0). Paired t-tests revealed significantly higher break points for chicken compared to berries [$t(5) = 3.05, p = .028, d = 1.25$]; and egg compared to mushrooms [$t(5) = 3.09, p = .027, d = 1.38$].

The break points under the PFR schedule of the PFR FR were compared with break points measured under the PR schedule of the PR FR in Experiment 4. Paired t-tests revealed significantly higher break points in the PFR FR compared to the PR FR irrespective of food type [$t(23) = 2.75, p = .011, d = 0.56$]. Only break points for egg were significantly higher in the PFR FR schedules than PR FR schedules [$t(5) = 2.82, p = .037, d = 1.15$].

Table 7.0. Average break point values across food pairs available under the PFR FR schedules for P1 - 6. Values from the PR FR schedules in Experiment 4 were included for comparison.

Pair	Schedule	P1	P2	P3	P4	P5	P6	Average
B(E)	PFR FR	256	16	16	256	4	62	107
	PR FR	48	76	55	105	67	30	65
C(M)	PFR FR	2	256	256	512	4	16	174
	PR FR	19	58	77	78	59	41	55
E(B)	PFR FR	512	512	256	512	64	32	305
	PR FR	100	37	90	95	46	37	68
M(C)	PFR FR	2	16	16	256	4	16	52
	PR FR	46	57	38	93	54	46	56

Note: B=Berries, C=Chicken, E=Egg, and M=Mushrooms.

Consumption rate was calculated by dividing the total number of reinforcers earned separately on the PFR and constant FR schedules by the session length minus the total reinforcer access durations for each schedule across days. Consumption rate decreased as ratio requirement increased for food available under the PFR schedule. Under the FR 30 schedule consumption rate increased as ratio requirement increased (Figures 7.1 and 7.2). Equations 1 (columns 1 & 3; Hursh et al., 1988) and 2 (columns 2 & 4; Hursh & Silberberg, 2008) were fit to the consumption rates averaged across days. Equation 1 (Hursh et al. 1988) accounted for an average of 72.3% of the variance ($\sigma = 0.21$) and Equation 2 (Hursh & Silberberg, 2008) accounted for an average of 98.0% of the variance ($\sigma = 0.02$). Parameter tables for individual possums are included in Appendix E, Tables E13 - 14.

The scaling parameter, k , was set to equal the range of the consumption rates across food pairs for each possum and ranged from ln 5.38 to ln 6.90. The model was only fit when more than two degrees of freedom were available for generating parameter estimates.

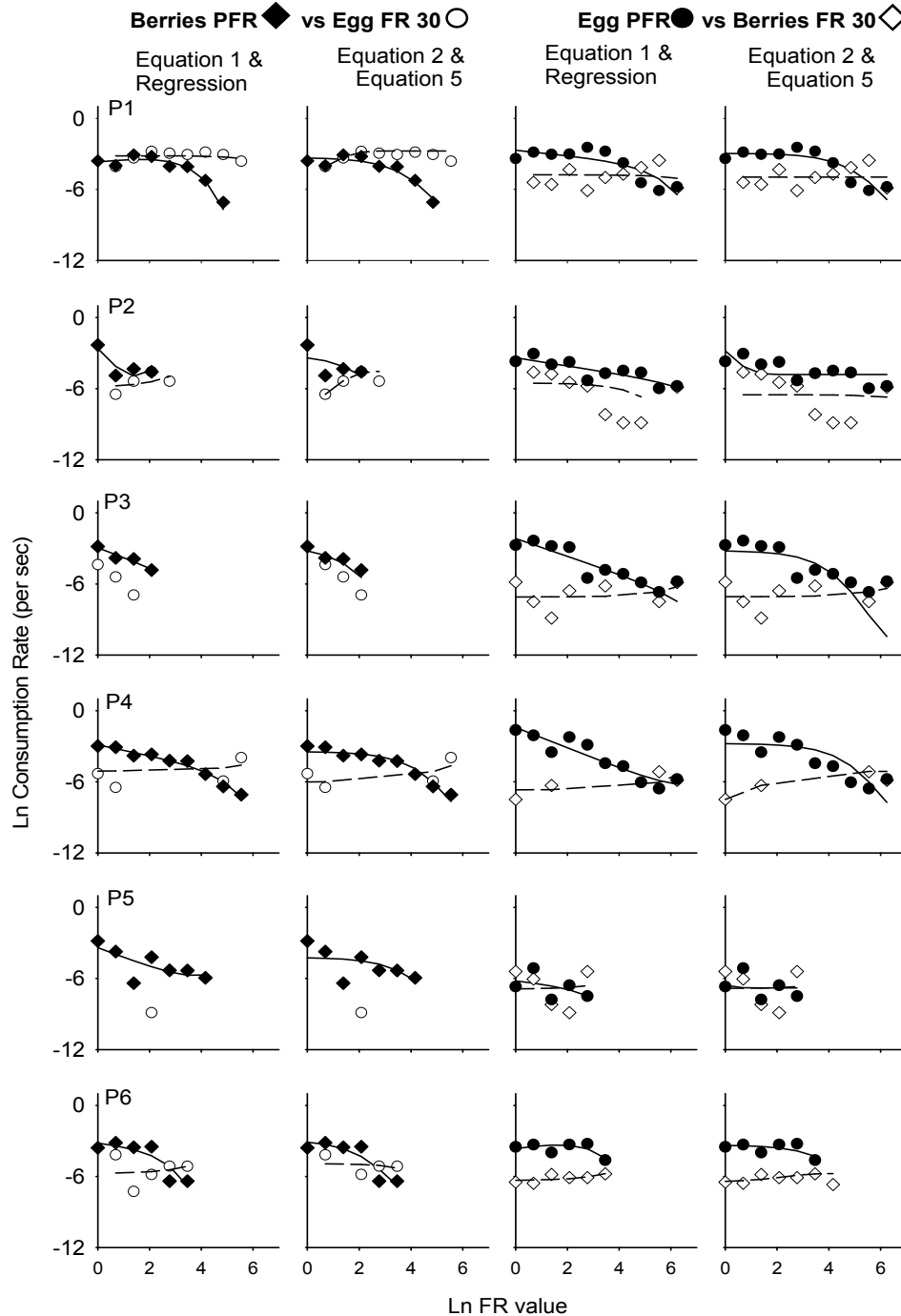


Figure 7.1. Ln consumption rate (p/s) plotted as a function of Ln FR value for berries and egg. Predicted consumption rates were generated using Equation 1 (Hursh et al. 1988) and non-linear least squares regression in columns 1 and 3; and using Equation 2 (Hursh & Silberberg, 2008) and Equation 5 (Hursh et al., 2013) in columns 2 and 4 for P1 - 6. Filled symbols correspond to foods under FR or PR schedules, and the unfilled symbols correspond to foods under the FR 30 schedules.

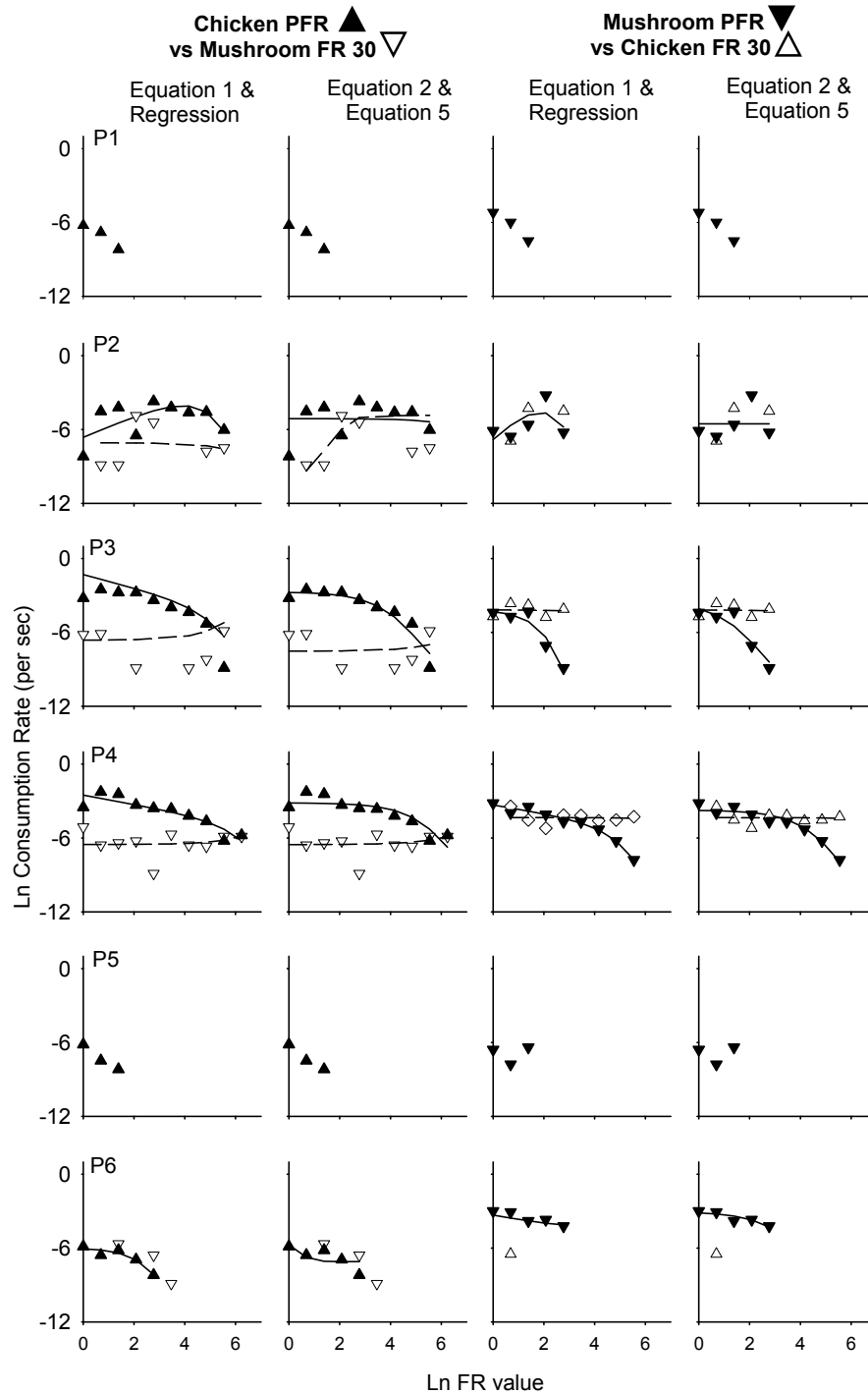


Figure 7.2. Ln consumption rate (p/s) plotted as a function of Ln FR value for chicken and mushrooms. Predicted consumption rates were generated in columns 1 and 3 using Equation 1 (Hursh et al. 1988) and non-linear least squares regression; and in columns 2 and 4 using Equation 2 (Hursh & Silberberg, 2008) and Equation 5 (Hursh et al., 2013) for P1 - 6. Filled symbols correspond to foods under PFR or PR schedules, and the unfilled symbols correspond to foods under the FR 30 schedules.

The fits derived by Equations 1 and 2 showed similar curves, however, as expected, the curves from Equation 2 generally provided sigmoidal functions in comparison to the linear functions produced by Equation 1. Comparisons are shown of the curves under the PR FR schedules (columns 1 & 3) and the PFR FR schedules (columns 2 & 4) in Figures 7.3 – 7.4. The curves under the PFR FR schedules are generally flatter than those in the PR FR schedules.

The estimates of initial demand for all foods under the PFR FR are shown in Table 7.1. All values are less than -1 which is consistent with elastic demand (Eq 1. $M_{logL} = -2.80$, $\sigma = -2.56$; Eq 2. $M_{Qo} = -1.37$, $\sigma = -.54$). There were no significant differences in initial demand values derived from Equation 1 or 2 (all p 's $>.05$). In comparison to Experiment 3, estimates of initial demand were more variable and significantly higher in Experiment 2 under PR FR schedules than in the Experiment 3 under PFR FR schedules [$t(17) = 3.57$, $p = .002$, $d = 0.84$].

Table 7.1. Estimates of initial demand values (ln) across food pairs available under the PFR FR for P1 - 6 derived using Equation 1 and Equation 2. Estimates of initial demand from Experiment 4 (PR FR) are included for comparison.

Food Pair	Schedule	P1	P2	P3	P4	P5	P6	Average
B(E)	Eq. 1.	-3.64	-	-	-2.89	-3.42	-3.10	-3.22
	Eq. 2.	-3.31	-	-	-3.45	-4.23	-2.88	-3.36
	PR FR	-1.43	-1.5	-0.73	-2.92	-1.88	-0.78	1.13
C(M)	Eq. 1.	-	-6.62	-1.30	-2.52	-	-5.91	-2.41
	Eq. 2.	-	-	-2.71	-3.15	-	-1.85	-2.69
	PR FR	2.85	0.23	-1.42	1.40	-4.35	-1.12	1.35
E(B)	Eq. 1.	-2.69	-0.36	-2.17	-1.42	-6.16	-3.58	-2.51
	Eq. 2.	-2.95	0.85	-3.19	-2.77	-0.88	-3.35	-0.71
	PR FR	-1.36	-1.23	-2.36	-2.07	0.50	-1.22	-0.66
M(C)	Eq. 1.	-	-6.50	-3.96	-3.74	-	-3.34	-3.77
	Eq. 2.	-	0.11	-3.53	-	-	-3.06	-1.19
	PR FR	-1.43	-1.35	-0.71	-1.18	-1.64	-1.20	-1.21

Note: B=Berries, C=Chicken, E=Egg, and M=Mushrooms.

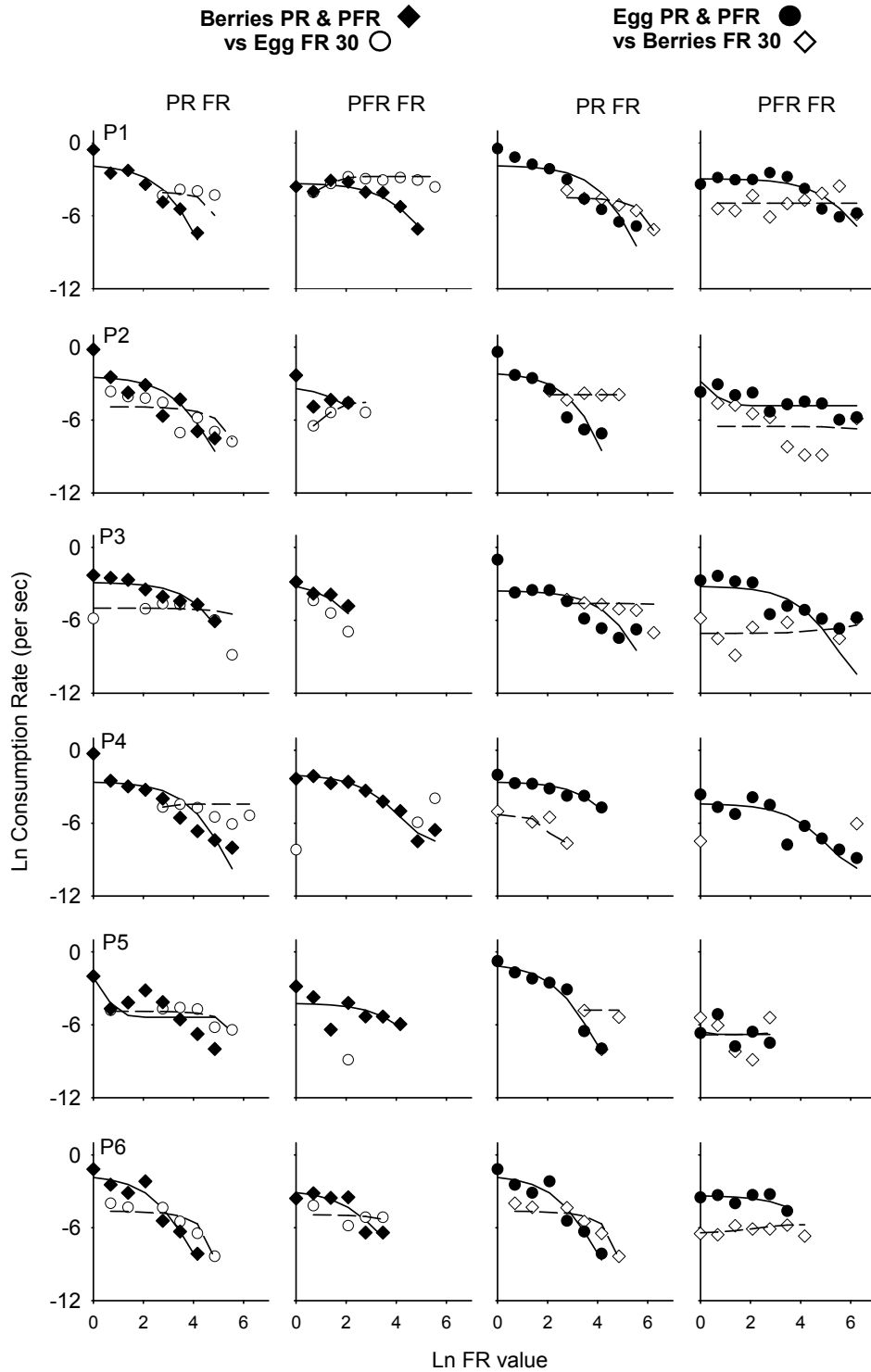


Figure 7.3. Ln consumption rate (p/s) plotted as a function of Ln FR value for berries and egg under the PR FR schedules (Experiment 4) and PFR FR schedules (Equation 2; Hursh & Silberberg, 2008) for P1 - 6. Filled symbols correspond to foods under PFR or PR schedules, and the unfilled symbols correspond to foods under the FR 30 schedules.

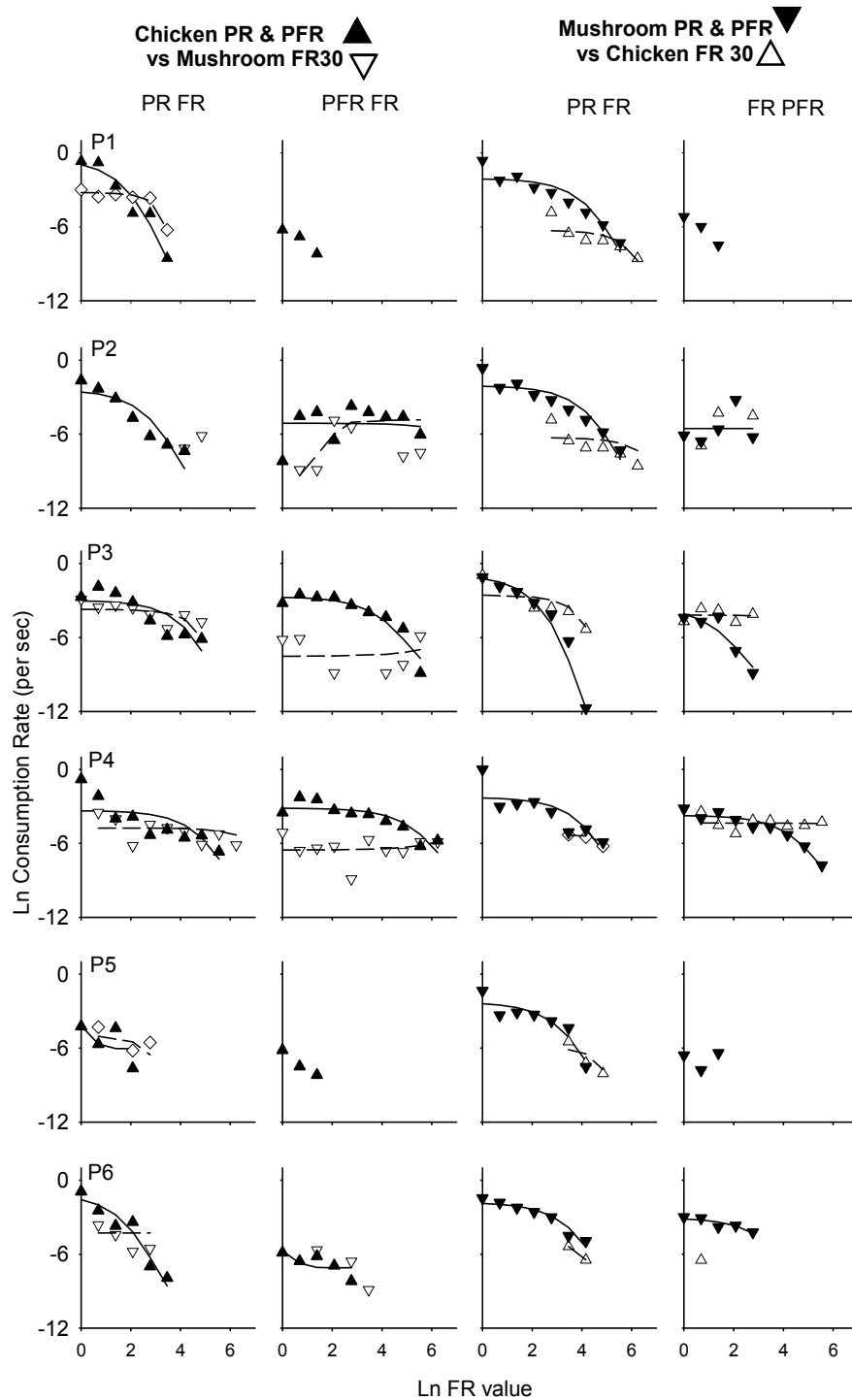


Figure 7.4. Ln consumption rate (p/s) plotted as a function of Ln FR value for chicken and mushrooms under the PR FR schedules (Experiment 4) and PFR FR schedules (Equation 2; Hursh & Silberberg, 2008) for P1 - 6. Filled symbols correspond to foods under PFR or PR schedules, and the unfilled symbols correspond to foods under the FR 30 schedules.

The rates of change in slope (α) estimated by Equation 1 and the essential value parameter, also α , from Equation 2 were mostly positive with lower alpha values estimated by Equation 1 ($M_a = 0.06$, $\sigma = 0.11$; Table 7.2), and Equation 2 ($M_a = 1.97$, $\sigma = 3.78$), however, these were not significantly different (all p 's $> .05$). Three extreme values are worth noting for individual possums; for P2 $\alpha = 12.88$, P5 $\alpha = 7.96$ and P6 $\alpha = 8.54$ due to only three ratio requirements of the PR schedule being completed during the session (See tables E13 - 14 in Appendix E).

The parameters estimated by Equation 1 include the initial slope (b) and the change in slope or rate (α) as a function of price. Both are required to estimate the elasticity in demand using Equation 1 (included in Appendix E, Table E13). The averaged initial slopes (b) were generally negative and close to zero; with all values (except one) within 1 unit from zero with no significant effects of food type on initial slope (all p 's $> .05$).

Table 7.2. Estimates of essential value across food pairs available under the PFR FR for P1 - 6 derived using Equation 1 and Equation 2. Estimates of essential value from Experiment 4 (PR FR) were included for comparison.

Food Pair	Schedule	P1	P2	P3	P4	P5	P6	Average
B(E)	Eq. 1.	0.04	-	-	0.01	-0.02	0.09	0.03
	Eq. 2.	0.18	-	-	0.12	0.43	0.73	0.36
	PR FR	0.08	0.27	0.94	0.13	0.1	0.06	0.26
C(M)	Eq. 1.	-	0.02	0.01	0.003	-		0.05
	Eq. 2.	-	0.03	0.09	0.03	-	8.54	2.17
	PR FR	0.10	-0.08	0.17	0.17	4.03	0.19	0.76
E(B)	Eq. 1.	0.005	0.001	0.001	-0.001	0.04	0.06	0.02
	Eq. 2.	0.04	0.45	0.11	0.04	7.96	0.18	1.46
	PR FR	0.03	0.7	0.07	0.07	0.16	0.35	0.14
M(C)	Eq. 1.	-	0.33	0.35	0.01	-	-0.02	0.17
	Eq. 2.	-	12.88	3.13	0.15	-	0.36	4.13
	PR FR	0.05	0.26	0.04	0.05	0.08	0.09	0.06

Note: B=Berries, C=Chicken, E=Egg, and M=Mushrooms.

The estimates of P_{\max} are given in units of ratio requirement or cost; C in Equations 3 and 4 (Table 7.3). Estimates of P_{\max} were highest for chicken calculated by Equation 3 and egg calculated by Equation 4 across possums. The estimates using Equation 3 ($M_{P_{\max}} = 132.02$, $\sigma = 243.84$) were higher than those using Equation 4 ($M_{P_{\max}} = 16.03$, $\sigma = 44.48$), however, P_{\max} was not significantly different across equations, foods, or schedules (all p 's > .05).

Table 7.3. Estimates of P_{\max} across food pairs available under the PFR FR for P1 - 6 derived using Equation 3 and Equation 4. Estimates of P_{\max} from Experiment 4 (PR FR) were included for comparison.

Food Pair	Schedule	P1	P2	P3	P4	P5	P6	Average
B(E)	Eq. 3.	30.51	-	-	73.78	-	8.52	37.60
	Eq. 4.	4.98	-	-	7.78	5.27	0.91	4.73
	PR FR	1.43	1.28	0.63	3.13	13.21	0.90	3.34
C(M)	Eq. 3.	-	110.04	58.33	233.93	-	6.97	102.32
	Eq. 4.	-	192.78	5.15	19.84	-	0.03	54.45
	PR FR	0.50	7.30	1.95	10.09	0.40	0.46	3.45
E(B)	Eq. 3.	169.76	971.20	199.83	-	18.38	20.75	275.98
	Eq. 4.	16.44	0.03	7.21	11.53	0.01	6.09	6.89
	PR FR	115.70	5.92	242.31	103.06	2.04	33.59	83.67
M(C)	Eq. 3.	-	9.58	3.39	65.37	-	-	26.11
	Eq. 4.	-	0.00	0.34	7.85	-	2.25	2.61
	PR FR	3.70	4.69	0.82	2.70	85.72	1.57	16.53

Note: B=Berries, C=Chicken, E=Egg, and M=Mushrooms.

To examine the interaction between the PFR and FR 30 schedules, a non-linear least squares regression was fit to consumption rates under the FR 30 schedule. This was done because the Hursh et al. (1988) equation had no model that accounted for performance under the constant FR schedule in comparison to performance under the PR schedule. Consequently, the non-linear least squares regression was fit to the data points because it provided a conservative method for calculating a cross point where consumption rates under the constant FR schedule

and consumption rates of the PFR schedule intersected. The consumption rates under the FR 30 schedule were also fit to the cross price exponential demand model (Equation 5) and then plotted on the same graph as consumption rates of the PFR schedule fit to Equation 2. Overall, the least squares regression accounted for an average of 16.3% of the variance ($\sigma = 2.7\%$) and Equation 2 accounted for an average of 97.3% of the variance ($\sigma = 2.0\%$).

Considering the better fits of Equation 2 and Equation 5 to the consumption rates under the PFR schedule and FR 30 schedule the estimates of interaction and sensitivity were also examined. The estimates of interaction were negative demonstrating that foods under the FR 30 schedule were substitutable for foods under the PFR schedule (Table 7.4). The most substitutable food on average was mushrooms when chicken was available under the PFR schedule ($M_I = -3.42$, $\sigma = 3.21$). The sensitivity values ranged from -25.56 to 1187.0 across foods and possums. Generally, the consumption rate for mushrooms under the FR 30 schedule was the most sensitive to changes in responding for chicken under the PFR schedule ($M_\beta = 1278.4$, $\sigma = 2210.0$). No other statistics could be calculated due to some possums not responding for chicken or mushrooms.

Cross points were identified by the point of intersection of the PFR schedule and FR 30 curves. All cross points are given in Table 7.4. There were no significant differences between the cross points generated by Equation 1 and the non-linear least squares regression or Equations 2 and 5 (all p 's $> .05$). The former, however, were more variable and tended to produce more intersecting curves than Equations 2 and 5. The models identified more perseverative cross points for chicken and egg and conservative cross points for berries and mushrooms, however, exclusive responding under the PR schedule was evident

for the majority of food pairs. In a comparison to the PR FR condition in Experiment 4, the cross points were more variable under the PFR FR condition, but did not differ significantly (all p 's > .05).

Table 7.4. Estimates of interaction and sensitivity and cross point values derived from Equation 2 and 5 across food pairs available under the PFR FR schedules for P1 - 6 derived using Equation 1 and Equation 2. Estimates from Experiment 4 (PR FR) were included for comparison.

	Sch.	Pair	P1	P2	P3	P4	P5	P6	Average
Interaction values	PFR FR	B(E)	-3.12	-	-	-	-	-1.59	-2.35*
		C(M)	-	-7.12	-1.67	-1.46	-	-	-3.42*
		E(B)	-1.45	-1.94	-1.28	-	-1.47	-0.74	-1.37
		M(C)	-	-	-0.55	-0.95	-	-	-0.75*
	PR FR Exp. 4	B(E)	-	-	-	-0.004	-	-	-0.04
		C(M)	-0.15	-	-0.43	-0.6	-	-	-0.4
		E(B)	-0.29	-0.2	-	-0.44	-0.32	-0.21	-0.29
		M(C)	-	-	-	-	-	-	-
Sensitivity values	PFR FR	B(E)	1187.0	-7.12	-	-	-	23.31	605.15*
		C(M)	-	3830.2	2.23	2.62	-	-	1278.4*
		E(B)	-1.45	-1.94	3.68	-	1.67	282.04	57.48
		M(C)	-	-	-25.56	-0.80	-	-	-13.18*
	PR FR Exp. 4	B(E)	-	-	-	-14.18	-	-	-14.18
		C(M)	-0.21	-	-874.21	-9.25	-	-	-294.6
		E(B)	-2.56	-0.03	-	-0.4	-0.04	-0.23	-8.66
		M(C)	-	-	-3.43	-	-	-	-
Cross point values	PFR FR Equation 1 & N-L LS Regression	B(E)	-	-	-	-	-	17.80	17.80*
		C(M)	-	-	178.05	416.57	-	-	297.31*
		E(B)	208.48	-	261.09	287.10	5.52	14.41	190.55*
		M(C)	-	-	-	-	-	-	14.41*
	PFR FR Equation 2 & Equation 5	B(E)	3.53	7.12	-	79.14	-	16.15	26.48*
		C(M)	-	-	-	364.84	-	-	189.83*
		E(B)	196.10	-	186.75	198.07	5.49	14.41	146.60*
		M(C)	-	-	-	27.74	-	-	27.74*
PR FR Exp. 4	B(E)	22.95*	54.95*	19.53*	11.56*	-	-	21.8	
	C(M)	15.09*	-	19.77	66.77*	-	-	25.41	
	E(B)	51.11	7.31*	-	28.42*	32.5*	5.06*	20.73	
	M(C)	29.02*	178.5*	5.55*	-	-	-	53.27	

Note: B=Berries, C=Chicken, E=Egg, F=Foliage, L=Locusts, and M=Mushrooms.

* = values based on three data points or fewer.

- = responding was exclusively allocated to the PR schedule

Discussion

The purpose of this experiment was to allow more opportunity for the possums to gain reinforcement under the constant FR schedule and to establish whether the same conclusions regarding the demand for food was reached under PR FR and PFR FR schedules. The linear (Equation 1, Hursh et al., 1988) and exponential models of demand (Equation 2, Hursh & Silberberg, 2008; Equation 5, Hursh et al., 2013) were also compared.

The models generally produced similar fits to the data, however, the cross-price demand model (Equation 5) was a much better fit to consumption rates under the constant FR schedule than a simple non-linear least squares regression. These provided a similar indication of demand for the tests foods where the estimates of initial demand were lower and estimates of essential value were higher for berries and mushrooms, whereas the estimates of P_{\max} were higher for chicken and egg. Cross points were highest for chicken under the PFR FR schedules and mushrooms under the PR FR schedules.

The response rates under the PR FR were higher than those under the PFR FR, which was also found by Foster et al. (1997b). Equation 1 fit the consumption rates under the PFR schedule well as the average VAC was 72.3%, however, Equation 2 fit better with an average VAC of 98.0%. Additionally, Equation 2 predicted a sigmoidal curve whereas Equation 1 predicted linear curves as ratio requirement increased. This was reflected by lower rate of change values predicted by Equation 1 compared to Equation 2.

The parameters for each possum and food pair were averaged to describe the general trends across foods. The estimates of initial demand values were consistent with inelastic demand in 4 out of 34 cases, as they were greater than -1,

however, Equation 1 provided higher values for berries and chicken, than Equation 2; and lower values, for egg and mushrooms, than Equation 2. Estimates of initial demand in the PR FR in Experiment 4 were greater than -1 in 7 out of 18 cases. This means that possums were responding more when the PR schedule was at low values in comparison to the PFR FR where responding, and therefore, consumption rate was lower. These results are consistent with those from Foster et al. (2009) and Grant et al. (2014) that consumption rates are higher at low ratio requirements and when ratio requirements increase within a session compared to across sessions.

The estimates of P_{\max} predicted by Equation 3 were considerably higher than those predicted by Equation 4. This is because the parameters used to calculate P_{\max} based on Equation 3 (Hursh & Winger, 1995) include the initial slope (b) and rate of change value (a), but do not take into account the initial demand value ($\ln L$). This means that P_{\max} calculated by Equation 3 is the point on the x-axis, when the slope changes from greater than -1 to less than -1, without regard for the initial demand, measured on the y-axis. Equation 4 uses constants provided by Hursh et al. (2013) and derived parameters of initial demand, essential value (α) and the scaling parameter (k) to calculate P_{\max} . This means, that unlike Equation 3, initial demand is taken into account. If initial demand is less than -1, which is consistent with elastic demand, the resulting P_{\max} value is also low, and unreliable as a measure of the demand for foods.

Breakpoints were generally higher in the PFR FR than in the PR FR condition, except for mushrooms. This has also been found in previous experiments with hens and pigeons (Foster et al., 1997b; Killeen et al., 2009). Across both arrangements possums responded to higher ratio requirements for egg

which suggests that this is a valued commodity, irrespective of *when*, within or across sessions the ratio requirements incremented. In this way break point appears to be a robust measure reinforcer efficacy in concurrent arrangements of PR FR and PFR FR schedules, at least for responding under the incrementing schedule. In addition, I would expect that when a preferred food was available under the FR 30 schedule that break point would be lower compared to when a preferred food was available. For instance, the break points were highest for egg and chicken under the PFR FR schedule, suggesting preference for these foods. This infers that responding was being allocated to the FR 30 schedule, for egg and chicken, respectively.

The Hursh et al. (2013) cross-price demand model (Equation 5) has not been extensively tested. There are no published articles that use this model 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 how consumption rate under the constant schedule was affected by consumption rate under the incrementing schedule. Overall, all interaction values were negative indicating all foods were substitutable.

More cross points were generated by curves using Equation 2 and Equation 5. This is due to the cross price model (Equation 5) using the normalized price of the predicted PR schedule curve in the calculation of the slope. The normalized functions were not provided as an analysis of demand for the different foods being studied; furthermore to equate the foods using a normalization procedure would impede any investigation into why one food might be preferred over another. The cross point analysis provided a very similar result to that of the

break point analysis; that there is greater demand for egg and chicken over berries and mushrooms because possums will persevere in responding and switch to the alternative schedule at higher ratio requirements, that is, they will do *more* work for egg and chicken rather than obtain berries or mushrooms for *less* work.

In conclusion, the Hursh et al. (1988) and Hursh and Silberberg (2008) models provided similar accounts of the demand for foods in the possum. The cross price demand model (Hursh et al., 2013) fit the PFR FR data well and provided a reliable measure of the cross point. In addition, the comparison of PR FR and PFR FR conditions provided similar accounts of demand for egg and chicken in possums.

In the next experiment, the aim was to confirm the similarity in performance between PR FR and PFR FR schedules by replicating the procedure of Experiments 3 and 4, and a semi-replicating Experiment 5, in that, each ratio requirement was in place for one day. The foods tested were berries and egg, and two new foods: a flaked barley and coco-pop® mix and rolled oats. In addition, the type of series progression, geometric with a basis 2 and arithmetic with a step of 5, was varied under the PR and PFR schedules to ascertain if progression type affected the demand for foods.

Chapter 8 – Concurrent Schedules and Progressions

Experiment 6

The previous experiments investigated the demand and preference for foods under geometric progressions that increased *within* and *across* sessions. In Experiment 6, the aim was to confirm the similarity in performance under concurrent schedules where the incrementing schedules increased within or across sessions. The ratio progression of the incrementing schedule was also varied between a geometric sequence (basis 2), and an arithmetic sequence (step 5) to see if procedural differences in the way the ratio requirements incremented affected the demand for foods. In this experiment two new foods were introduced as they were known reinforcers for possums in operant experiments (e.g., Hudson et al., 1999), and therefore may produce more responding than previously observed using foods obtained in the wild. The primary dependent variables derived from the exponential and cross price models of demand (Grant et al., 2014; Hursh & Silberberg, 2008) were used to identify whether methodological differences of how the schedules were presented affected the demand for foods.

It was predicted that the estimates of essential value and initial demand will be lower, and P_{\max} , break point and cross point would be higher for foods previously identified as preferred, such as egg. Across progressions break point would also be higher under the geometric progression as step-sizes are larger than under the arithmetic progression. The response and consumption rates would be similar under the different schedule arrangements but higher estimates of initial demand and rate of change under the PR FR schedule arrangement were expected.

Method

Subjects

Twelve brushtail possums, P1 - 12 (4 female and 8 male) were used. All possums were 'wild caught' and had been housed in captivity for 4 - 9 years ($\bar{X} = 6.8$ years, $\sigma = 2.0$ years). At the start of the experiment P1 - 6 had participated Experiments 1 - 5 and P6 - P10 in Experiments 1 and 2. P11 and P12 had participated in Experiment 1.

During the experiment, possum body weights fluctuated based on food obtained in the experiment ($\bar{X} = 3737$ g, $\sigma = 490$ g). The average body weight percentage change across possums was 9.5% during the two phases of the experiment. Weigh sessions occurred weekly. The supplementary feeding regime was the same as Experiments 3 - 5.

Housing

Possums were divided into two groups, P1 - 6 and P7 - 12, and were housed in two laboratory rooms.

Apparatus

The apparatus was the same as in Experiments 3 - 5, except that the magazine used to deliver 'wet' food was different from those used to deliver 'dry' foods. The magazine used in Experiments 3 - 5 was used to deliver the 'wet' foods. The 'dry' foods were delivered in food hoppers where the food container moved on a fulcrum which became accessible when the hopper moved forward using a spring system to the opening in the possum's cage (Figure 8.0). When activated the food magazine and hopper provided 2-s access to food.

The four test foods were used in this experiment because possums' responded reliably under FR schedules for them. Food pairs were made up of egg

and berries, and rolled oats and a 15:1 ratio mix of flaked barley and coco-pops® (Cronin, 2012; Martin, 2002).

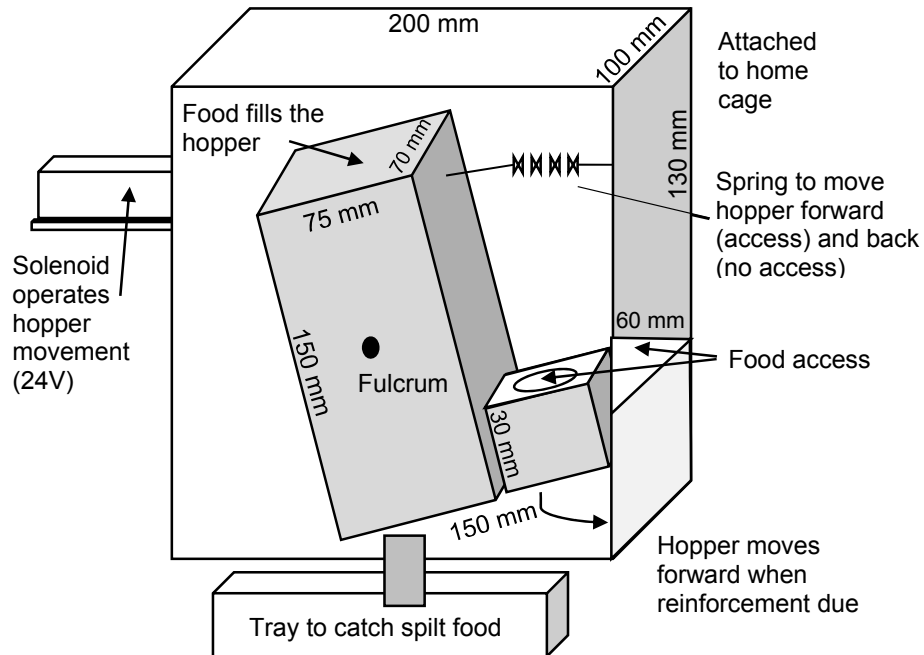


Figure 8.0. Cross section of the food hopper for the delivery of dry foods. The hopper moved forward to allow the possum access to the food.

Procedure

The experiment consisted of two main conditions: one was the concurrent PR FR schedule and the other was a concurrent PFR FR schedule. The constant FR schedule was always a FR 30 and corresponded to the left lever. The incrementing ratio requirement was always on the right lever which incremented according to a geometric series; 1, 2, 4, 8 and so forth; or an arithmetic series; 1, 6, 11, 16 and so forth. The two foods in each group were presented under both schedules during the geometric and arithmetic sessions and the order of presentation was counter balanced across possums. Conditions are shown in Table 8.0.

Table 8.0. Description of conditions detailing schedule, progression and food type. The order was randomized across possums. P1 - 6 completed the wet conditions first and P7 - 12 completed the dry conditions first.

Schedule type	Progression	PR food (FR food)
PFR FR	Arithmetic	Berries (Egg)
		Egg (Berries)
		Flaked Barley mix (Rolled Oats)
		Rolled Oats (Flaked Barley mix)
	Geometric	Berries (Egg)*
		Egg (Berries)*
		Flaked Barley mix (Rolled Oats)
		Rolled Oats (Flaked Barley mix)
PR FR	Arithmetic	Berries (Egg)
		Egg (Berries)
		Flaked Barley mix (Rolled Oats)
		Rolled Oats (Flaked Barley mix)
	Geometric	Berries (Egg)
		Egg (Berries)
		Flaked Barley mix (Rolled Oats)
		Rolled Oats (Flaked Barley mix)

* denotes conditions completed in Experiment 5 for P1 - 6 where data from the first day of the five days was used.

For the PR FR schedule, the ratio requirement was increased under the PR schedule within a session as in Experiments 3 - 5. The experimental procedure was conducted three times, one session per day over three consecutive days. For the PFR FR schedules, the ratio requirement under the PFR schedule was increased each session. If no food was obtained under this schedule during a session, it was repeated in the next session and the condition ended if no food was obtained on the second attempt.

The PR FR and PFR FR schedules with the wet foods were completed first by P1 - 6 and the dry food conditions first for P7 - 12. For P1 - 6 data from Experiment 5 was used for the geometric PFR FR schedule for the wet foods.

After the six conditions were complete P1 - 6, and eight conditions for P7 - 12 the possums were moved. P1 - 6 were moved to the P7 - 12 cages and P7 - 12 were moved to the P1 - 6 cages. The possums were given one week to habituate to the new cages and neighbour possums before P1 - 6 began the dry food conditions and P7 - 12 began the wet food conditions.

Trial Procedure

The procedure was the same as Experiments 3 - 5.

Results

Average response rates across the range of ratio requirements differed across schedule and progression (Figure 8.1). Under the PR FR schedules, response rates were high at the lowest ratio requirement and then decreased with increases in the ratio requirement. Under the PFR FR schedules, response rates were initially low before increasing to a peak, then declining. Under the constant FR schedules of both the PR FR and PFR FR schedules there were increases in response rate as the ratio requirement increased.

Averaged response rates are shown in Figure 8.1. Response rates peaked at low ratio requirements under the geometric PR FR schedules ($PR_M = 1$) and arithmetic PR FR schedules ($PR_M = 11$). Comparatively, response rates peaked at higher ratio requirements under the geometric PFR FR schedules ($PFR_M = 44$, between PR 32 and PR 64) and arithmetic PFR FR schedules ($PFR_M = 36$). Overall, response rates were similar for the foods across schedule and progression type. Response rates for individual possums are included in Appendix D (Figures D10 – 14).

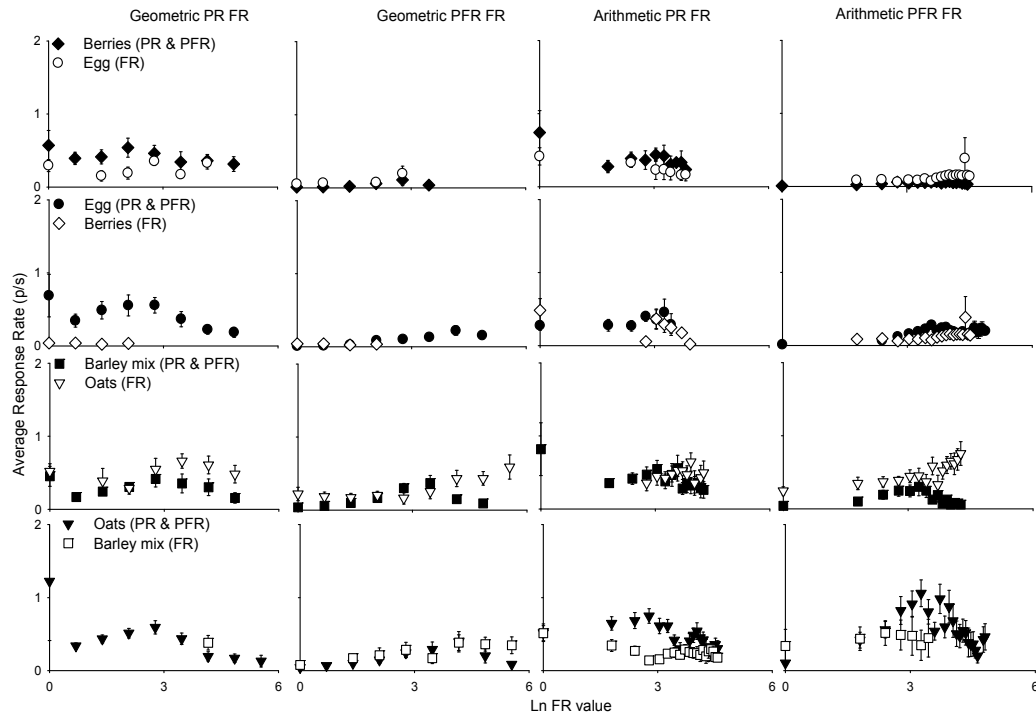


Figure 8.1. Average response rate (p/s) as a function of ln FR value for all foods under the geometric and arithmetic progressions of the PR FR and PFR FR schedules. Filled symbols correspond to foods under the PR or PFR schedule, and the unfilled symbols correspond to foods under the FR schedule. Response rates are presented more than five possums contributed to each data point.

Average break point values were higher under the PFR FR schedules ($M_{BP} = 115.99$, $\sigma = 109.11$), than PR FR schedules ($M_{BP} = 71.75$, $\sigma = 67.73$), however, paired samples t-tests did not reveal a significant difference between break points across schedules. Break points were significantly higher under the geometric progression across foods (Table 8.1.). The highest break points were found for egg, followed by berries, rolled oats and flaked barley and were significantly higher for rolled oats compared to flaked barley and berries (all p 's < .013).

Table 8.1. Estimates of essential value, α ; initial demand, $\ln Q_0$ VAC, SE, df, P_{\max} derived from Equation 2 (Hursh & Silberberg, 2008), and interaction, I ; sensitivity, β ; and cross points derived from Equation 5 (Hursh et al., 2013) averaged across P1 - 12 for each schedule condition, PR FR and PFR FR schedules, progression and food pair.

Schedule	Progression	Food Pair	α	$\ln Q_0$	VAC	SE	df	P_{\max}	BP	I	β	VAC	SE	df	Xpt
PFR FR	Arithmetic	Berries (Egg)	0.292	-2.409	0.970	1.244	9	3.9	96.9	-1.106	5.164	0.988	0.764	14	73.7
		Egg (Berries)	0.261	-2.393	0.976	0.982	5	4.1	93.9	-2.631	83.562	0.989	0.983	7	68.7
		Flaked Barley mix (Rolled Oats)	0.034	-1.805	0.959	0.682	17	4.0	76.4	-1.362	5.150	0.969	0.600	15	197.1
		Rolled Oats (Flaked Barley mix)	0.030	-1.647	0.959	0.934	16	3.7	91.4	-2.020	4.298	0.971	0.785	14	60.6
	Geometric	Berries (Egg)	0.142	-1.709	0.974	0.562	4	2.3	56.5	-1.994	4.092	0.983	0.711	3	40.0
		Egg (Berries)	0.080	-2.316	0.951	0.876	5	7.8	190.7	-1.754	17.373	0.988	0.888	4	170.4
		Flaked Barley mix (Rolled Oats)	0.051	-2.115	0.952	0.949	4	4.9	119.0	-6.215	89.479	0.972	0.719	5	57.3
		Rolled Oats (Flaked Barley mix)	0.022	-1.764	0.991	0.551	5	5.2	138.7	-2.483	11.189	0.970	0.993	5	87.6
PR FR	Arithmetic	Berries (Egg)	5.661	-1.858	0.909	1.782	7	2.5	38.9	-56.91	125.87	0.949	1.572	3	28.3
		Egg (Berries)	1.750	-2.280	0.914	1.578	12	1.8	51.6	-0.724	-179.50	0.982	0.908	5	13.3
		Flaked Barley mix (Rolled Oats)	3.492	0.582	0.865	1.945	11	13.8	60.4	-826.59	211.29	0.963	0.840	6	34.9
		Rolled Oats (Flaked Barley mix)	4.224	-2.778	0.896	1.859	13	6.3	79.3	-2.335	-251.53	0.989	0.734	9	32.5
	Geometric	Berries (Egg)	2.483	-2.414	0.864	2.006	4	5.6	88.4	-1.069	-8.590	0.983	1.271	2	99.0
		Egg (Berries)	4.289	-2.188	0.878	2.070	4	3.6	90.9	-0.370	-38.345	0.996	0.608	2	37.2
		Flaked Barley mix (Rolled Oats)	1.108	-0.144	0.869	1.849	5	3.5	81.6	-0.397	-115.73	0.993	0.390	4	54.8
		Rolled Oats (Flaked Barley mix)	1.500	-1.903	0.851	2.092	4	4.5	101.3	-0.691	8.011	0.994	0.557	2	36.1

To measure consumption rate under the PR FR schedules, the number of reinforcers earned under each schedule was divided by ratio duration of the PR schedule. To measure consumption rate under the PFR FR schedule, the number of reinforcers earned under each schedule was divided by the session length minus the reinforcer access times. Consumption rates were used to analyse performance using the exponential demand model (Equation 2; Hursh & Silberberg, 2008). This was fit to consumption rates under the PR and PFR schedule and the cross-price exponential model was fit to consumption rates under the constant FR schedules (Equation 5; Hursh et al., 2013), using non-linear least squares regression. Parameter estimates for individual possums are included in Appendix E, Tables E15 - 22.

The exponential demand model (Equation 2; Hursh & Silberberg, 2008) accounted for the data well, with the an average VAC of 88.1% ($\sigma = 8.2\%$) for the PR FR schedule and 98.3% ($\sigma = 1.6\%$) for the PFR FR schedule. The model was fit to data when two or more degrees of freedom were available for generating demand curves. Averaged parameter estimates are given in Table 8.1. The scaling parameter, k , was the range of the consumption rates across food pairs, progressions and schedules for each possum. These values ranged from ln 7.81 to ln 11.78 for the PR FR schedule and ln 5.34 to ln 8.14 for the PFR FR schedule.

Consumption rates under the PR and PFR schedules decreased as the ratio requirement increased shown in Figures 8.2 - 8.5. Consumption rates under the constant FR schedules increased as ratio requirement under the incrementing schedules was increased. Reinforcers were earned when the PFR ratio requirements were low under the constant FR schedule under the PFR FR

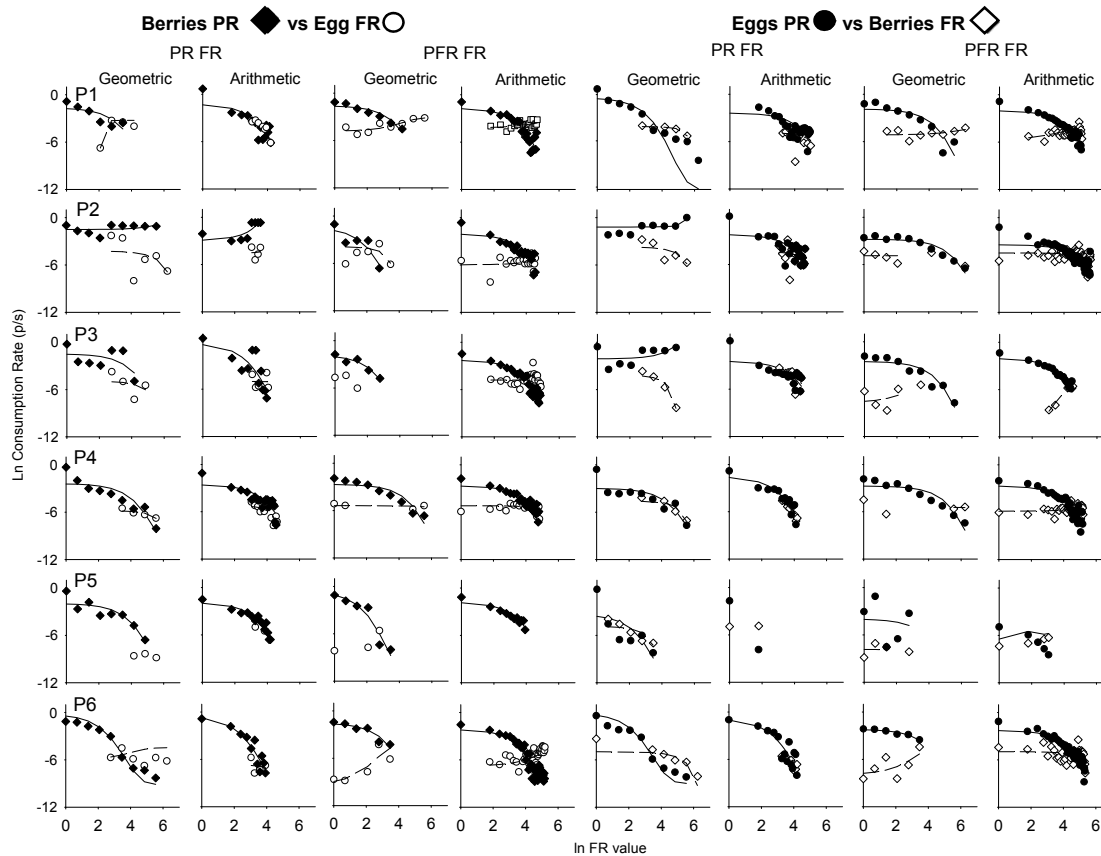


Figure 8.2. Ln consumption rate (p/s) as a function of ln FR value for berries and egg under the geometric and arithmetic progressions of the PR FR and PFR FR schedules for P1 - 6. Smooth curves were drawn by Equation 2 (solid) and Equation 5 (dashed). Filled symbols correspond to foods under the PR or PFR schedules, and the unfilled symbols correspond to foods under the constant FR schedule (NR = no responses made).

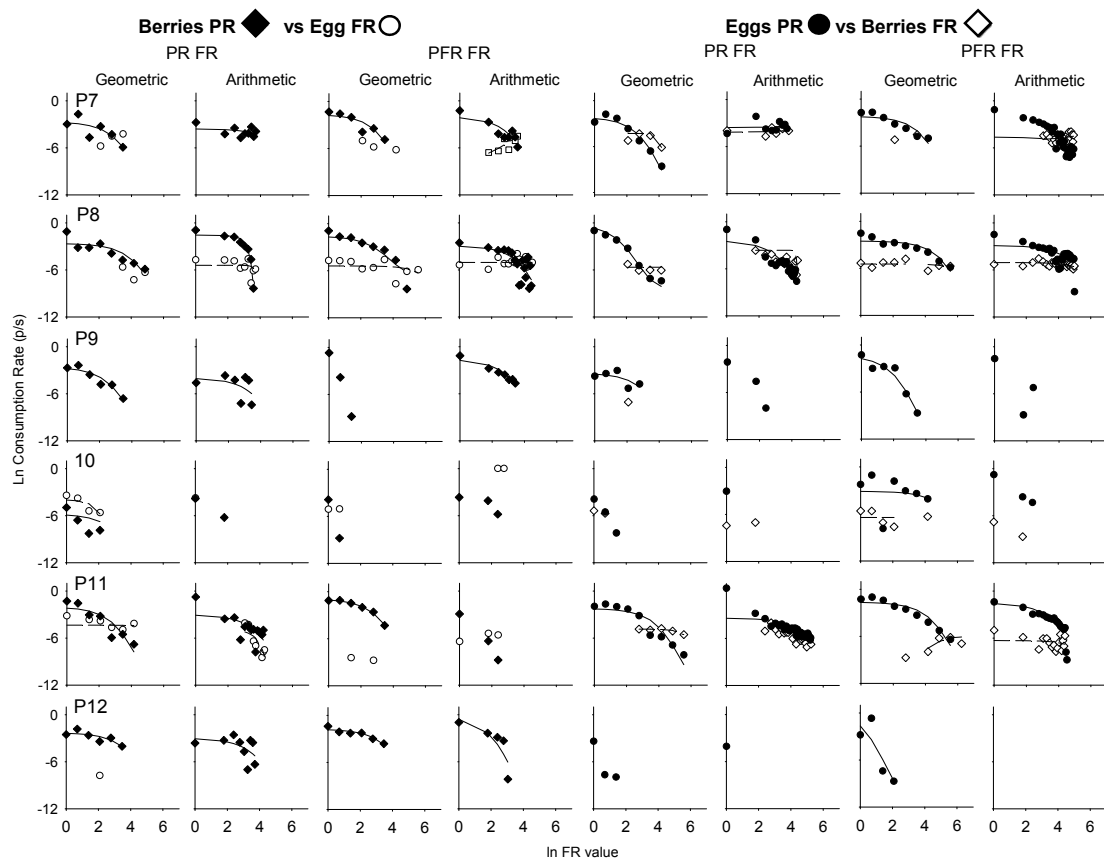


Figure 8.3. Ln consumption rate (p/s) as a function of Ln FR value for berries and egg under the geometric and arithmetic progressions of the PR FR and PFR FR schedules for P7 - 12. Smooth curves were drawn by Equation 2 (solid) and Equation 5 (dashed). Filled symbols correspond to foods under the PR or PFR schedules, and the unfilled symbols correspond to foods under the constant FR schedule (NR = no responses made).

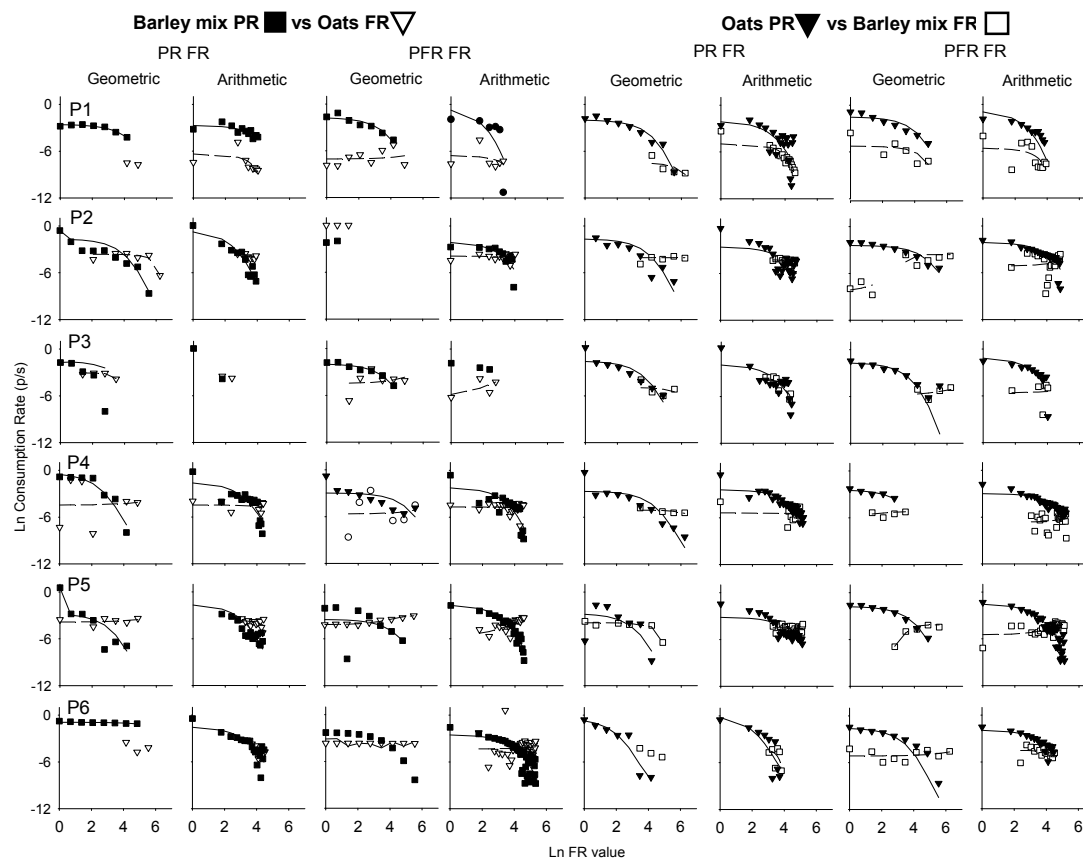


Figure 8.4. Ln consumption rate (p/s) as a function of Ln FR value for chicken and mushrooms under the geometric and arithmetic progressions of the PR FR and PFR FR schedules for P1 - 6. Smooth curves were drawn by Equation 2 (solid) and Equation 5 (dashed). Filled symbols correspond to foods under the PR or PFR schedules, and the unfilled symbols correspond to foods under the constant FR schedule (NR = no responses made).

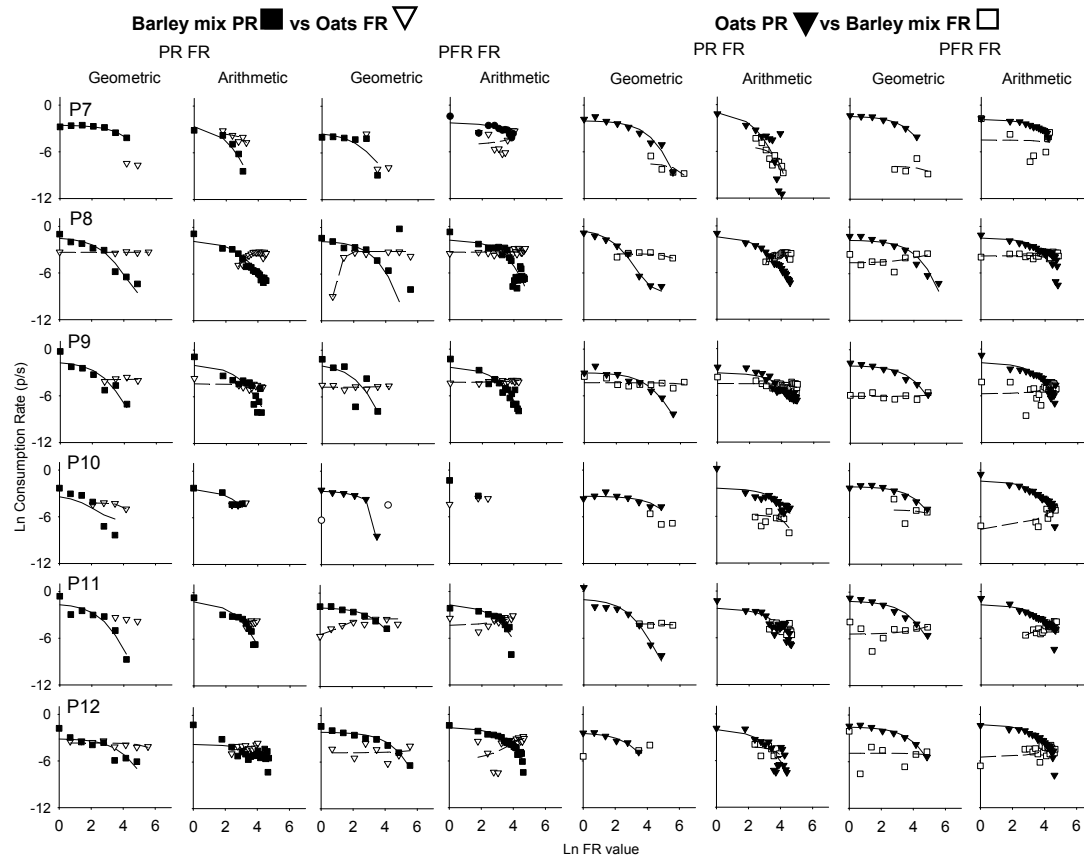


Figure 8.5. Ln consumption rate (p/s) as a function of Ln FR value for chicken and mushrooms under the geometric and arithmetic progressions of the PR FR and PFR FR schedules for P7 - 12. Smooth curves were drawn by Equation 2 (solid) and Equation 5 (dashed). Filled symbols correspond to foods under the PR or PFR schedules, and the unfilled symbols correspond to foods under the constant FR schedule (NR = no responses made).

schedules, but were not earned until the PR ratio requirement was larger under the PR FR schedule. Across progressions, the shape of the functions was similar with more ratio requirements completed (and more reinforcers were obtained) under the arithmetic progression compared to the geometric progression. Generally, the pattern of consumption rates was similar across schedule type, progression and food type.

Averaged estimates of initial demand were greater than -1 for consumption rates under the PR FR schedule ($M_{lnQ_0} = -0.83$, $\sigma = 1.25$), which is consistent with inelastic demand. In contrast, initial demand was less than -1 in the PFR FR schedule ($M_{lnQ_0} = -1.30$, $\sigma = 0.02$), which is consistent with elastic demand. Across progressions, the averaged estimates of initial demand were greater than -1 under the arithmetic progression ($M_{lnQ_0} = -0.80$, $\sigma = 1.28$), and less than -1 under the geometric progression ($M_{lnQ_0} = -1.12$, $\sigma = 0.84$) and the lowest estimates were for egg compared to other foods (Table 8.1). The average of the estimates of initial demand under the PR FR schedules and arithmetic progression were consistent with inelastic demand, and the estimates under the PFR FR schedules and geometric progression consistent with elastic demand, but there were no significant differences across schedule or progression type. There was, however, a significantly lower initial demand value for egg compared to berries [$t(48) = 2.10$, $p = .041$, $d = 0.30$].

The estimates of essential value, summarised in Table 8.1., were closer to zero for foods under the PFR FR schedules ($M_{\alpha} = 0.65$, $\sigma = 0.84$), and were significantly higher and more variable under the PR FR schedules ($M_{\alpha} = 3.18$, $\sigma = 6.87$); with significant differences in essential value between the PR FR and PFR FR schedules [$t(82) = 2.91$, $p = .005$, $d = 0.32$]. The estimates of essential value

were closest to zero under the arithmetic PFR FR schedules ($M_\alpha = 0.62, \sigma = 0.69$), and geometric PFR FR schedules ($M_\alpha = 0.68, \sigma = 0.98$) compared to the geometric PR FR schedules ($M_\alpha = 2.24, \sigma = 4.22$), and arithmetic PR FR schedules ($M_\alpha = 4.05, \sigma = 8.57$). There were significant differences in essential values in the geometric PFR FR schedules compared to the geometric PR FR schedules [$t(47) = 2.42, p = .019, d = 0.35$], and arithmetic PFR FR schedules compared to the arithmetic PR FR schedules [$t(47) = 3.37, p = .002, d = 0.49$].

Estimates of essential value also differed between foods across schedules and progressions. Under the arithmetic PFR FR schedules, there were significantly lower estimates of essential value for rolled oats compared to flaked barley ($p = .015$) or egg ($p = .017$) and significantly higher estimates of essential value for berries under the arithmetic progression compared to egg under the arithmetic progression ($p = .009$) or geometric progression ($p = .008$). Under the PR FR schedules, there were significantly lower estimates of essential value for rolled oats compared to egg ($p = .013$), and egg compared to berries ($p = .005$) under the geometric progression. There were significantly higher estimates of essential value for berries under the arithmetic progression compared to berries, egg, or flaked barley under the geometric progression (all p 's $< .019$). The estimates of essential value were lower for rolled oats under the geometric progression and egg under the arithmetic progression ($p = .007$).

Averaged estimates of P_{\max} were higher under the PFR FR schedules ($M_{P_{\max}} = 66.72, \sigma = 83.95$) than in the PR FR schedules ($M_{P_{\max}} = 5.59, \sigma = 19.65$; Table 8.1). They were also higher under the geometric progression ($M_{P_{\max}} = 26.17, \sigma = 65.16$) compared to the arithmetic progression ($M_{P_{\max}} = 17.96, \sigma = 39.61$). The largest averaged estimate of P_{\max} was for egg under the geometric

PFR FR schedules ($M_{Pmax} = 7.77, \sigma = 5.41$) and for flaked barley under the arithmetic PR FR schedules ($M_{Pmax} = 13.83, \sigma = 45.23$). All other estimates were between FR 1.8 and FR 6.6. These, however, were not statistically significant different across schedule, progression or food type [$t (\leq 29) < 3.38, p > .05$].

The cross price exponential model (Equation 5, Hursh et al., 2013) accounted for an average of 97.8% of the variance ($\sigma = 5.1\%$) for the PR FR schedules and 95.7% of the variance ($\sigma = 14.2\%$) for the PFR FR schedules. The parameter estimates derived from fits to the cross price model yielded negative values for the interaction (I) parameter indicating that foods were substitutable.

The PR FR schedules produced slightly more substitutable relationships between foods ($M_I = -256.63, M_\beta = -44.58$) than the PFR FR schedules ($M_I = -2.97, M_\beta = 89.60$). The arithmetic progression produced more highly substitutable relationships between foods, although less sensitivity to changes in ratio requirement under the incrementing schedule ($M_I = -224.60, M_\beta = -29.65$) than the geometric progression ($M_I = 91.46, M_\beta = 312.66$). Of the four foods, flaked barley (PFR schedule) and rolled oats (constant FR schedule) were the most substitutable.

Cross points were greater under the PFR FR schedules ($M_{Xpt} = 64.31, \sigma = 64.13$), compared to the PR FR schedules ($M_{Xpt} = 12.73, \sigma = 17.99$), however, they did not differ significantly across schedule type. Cross points were significantly higher under the geometric progression ($M_{Xpt} = 44.70, \sigma = 53.21$) compared to the arithmetic progression ($M_{Xpt} = 34.12, \sigma = 53.30; t(36) = 17.46, p < .001, d = 2.87$).

The average cross points showed perseverative error as they were greater than the FR 30 equivalence point; egg had the highest cross point on average

($M_{X_{pt}} = 54.33$, $\sigma = 62.07$). There were significantly higher cross points for flaked barley under the arithmetic PR FR schedules, compared to egg and berries under the geometric PR FR schedules ($p = .013$), and egg under the arithmetic PR FR schedules ($p = .010$). Cross points were significantly higher for rolled oats under the arithmetic PR FR schedules compared to flaked barley under the geometric PR FR schedules ($p = .004$), but were lower than rolled oats under the geometric PFR FR schedules ($p = .022$), and egg under the arithmetic PFR FR schedules ($p = .008$). Cross points for rolled oats under the geometric PR FR schedules were also higher than for flaked barley under the geometric PFR FR schedules ($p = .046$). There were significantly higher cross points for berries under the arithmetic PR FR schedules compared to berries under the geometric PR FR schedules ($p = .046$). Cross points were higher for egg under the arithmetic PFR FR schedules compared to berries under the arithmetic PR FR schedules ($p = .015$) and geometric PFR FR schedules ($p = .007$).

Discussion

This experiment examined the differences between performance under concurrent PR FR and PFR FR schedules and geometric and arithmetic progressions for different foods. The estimates of parameters derived from the exponential (Equation 2; Hursh & Silberberg, 2008) and cross-price (Equation 5; Hursh et al., 2013) demand models, break point and cross points differed in their description of demand across PR and PFR schedules, progression and food type.

Response rates were similar under the geometric and arithmetic PR FR schedules. These best-resembled the pattern of response rates under a geometric progression described as a sharp increase in response rate followed by a steep

decline before levelling out (Killeen et al., 2009). It was expected that the response rates under the arithmetic PR FR schedules would increase gradually to a peak over the first few ratio requirements, then decline linearly as ratio requirement increased (Killeen et al., 2009). Instead, the response rates under both the geometric and arithmetic PFR FR schedules resembled the pattern expected of response rates under the arithmetic progression. This was a surprising result as previous research has shown different patterns of response rates under the geometric and arithmetic progression and a similar pattern under each progression under PR FR and PFR FR schedules (Baron & Derenne, 2000; Foster et al., 1997b). One can only speculate as to the reason for this, except to say that the schedule type had more of an effect on performance than the progression type.

Break points were higher under the PFR FR schedules than the PR FR schedules. This might have been due, at least under the arithmetic progression, to the small increases in ratio requirement from session to session which may have maintained responding at high ratio requirements (Killeen et al., 2009). In comparison the large jumps in ratio requirement, particularly at large ratio requirements of the PR FR schedule, within a session, may have resulted in ratio strain, where responding decreased and eventually stopped.

Egg had the highest break point, followed in descending order by berries, rolled oats and flaked barley. Break points were highest under the geometric progression as more responses were required to obtain access to food compared to the arithmetic progression. For example: to obtain eight reinforcers under the geometric PR FR schedule, 255 responses had to be made to reach a FR 128. In contrast, under the arithmetic progression just over half the number of responses were required to obtain the same number of reinforcers. Other researchers also

found that break points were higher when progressions had larger step sizes (Covarrubias & Aparicio, 2008; Killeen et al., 2009).

The trend in consumption rates under the PR and PFR schedules were as expected with Figures 8.2 - 8.5 depicting decreased consumption rates as ratio requirement increased under the incrementing schedules across all manipulations. It appeared that PR and PFR schedules produced similar patterns of consumption rate across schedules as proposed by other researchers (e.g., Baron & Derenne, 2000; Foster et al., 1997b, Stafford & Branch, 1998). Consumption rates under the constant FR schedules increased as the ratio requirement of the PR or PFR schedules increased.

The estimates of essential value were significantly different across schedules, progressions and foods. In particular, differences were found under the arithmetic PFR FR schedules and the geometric PR FR schedules. This is consistent with theoretical predictions made by the exponential model that essential value *should* vary for foods that differ in value (e.g., Foster et al., 2009; Hursh et al., 1988). Foster et al. (2009) analysed consumption using the exponential demand model (Equation 2; Hursh & Silberberg, 2008) and found that estimates of essential value were significantly different for different types of wheat in hens, although these differences were dependent on a large value of the scaling parameter, k . In Experiments 4 and 5, there were no differences in essential value across foods using geometric progressions and PR FR and PFR FR schedules using a similarly large sized k value to Foster et al. (2009). One might speculate that similar consumption rates were observed across foods when the same experimental conditions of schedule type and progression were in place for long periods of time, as was the case in Experiments 3 - 5 (see Appendix F).

When experimental conditions of progression and schedule type were varied relatively often, as in Experiments 6, consumption rate, and thereby elasticity of demand, appeared to vary across foods.

The interaction parameter of the cross-price demand model (Hursh et al., 2013) provided a measure of substitutability between two foods. The arithmetic progression produced more substitutable relationships between foods but the cross points were consistently lower under the arithmetic PR FR schedules compared to the geometric PR FR schedules and cross points from the geometric and arithmetic PFR FR schedules. The reason for this is unclear. It is unlikely to be related to the number of reinforcers earned because this was controlled in the selection of the arithmetic increment. Under the geometric progression five reinforcers were earned before the equivalence point and under the arithmetic progression six reinforcers were earned before the equivalence point. A more plausible explanation might simply be that cross points under the arithmetic PR FR schedules were lower than those under the geometric PR FR schedules because the first ratio requirement after the equivalence point under the geometric progression was large (FR 64). The possums continued to respond, as a product of prior reinforcement, on this schedule to higher ratio requirements before switching to the other schedule.

Cross points were perseverative under the PFR FR schedules, similar to the findings of previous research (e.g., Holm et al., 2007; Sørensen et al., 2001). This indicates that the possums were not ‘maximising their reinforcement rate’ under either the incrementing or constant schedules. In contrast, under the PR FR schedule, the average cross point was only slightly higher than the equivalence point, similar to the findings of Wanchisen et al. (1988) in pigeons. In Experiment

6, the possums were maximising their reinforcement rates more effectively, although fewer cross points were generated, especially when berries were available on the PR schedule of the PR FR schedule.

In conclusion, response rates of the PR FR schedules resembled the pattern of responding typically seen in geometric progressions and the PFR FR schedules resembled the pattern seen in arithmetic progressions. The parameters of the exponential and cross price demand models predicted estimates that differed in their description of demand across PR and PFR schedules, progression and food type. The break points and cross points were larger under PFR FR schedules and for geometric progressions compared to PR FR and arithmetic progressions.

When considering the use of PR FR or PFR FR schedules for assessing demand one expects to reach the same conclusions across different tasks. The results of this experiment, however, produced estimates that differed in the description of demand for the same foods. This might be a product of the foods as they were substitutable and were chosen because possums responded reliably for berries and egg in Experiments 3 - 5, and in previous experiments for flaked barley and coco-pops® and rolled oats (e.g., Cronin, 2012; Martin, 2002). In retrospect, it may have been useful to have used a food, such as foliage, which was identified in Experiments 1 - 3 to be a lesser preferred food, to obtain a better account of the differences in the demand for foods across PR FR and PFR FR schedules and progressions.

Chapter 9 - General Discussion

The purpose of this research was to investigate what foods possums prefer to eat and determine if those preferences would remain consistent across six methods of testing preference and demand for foods. These included single and paired preference assessments (Chapter 5) and a series of concurrent schedules of progressive- and fixed-ratio schedules where the incrementing schedule increased within a session using PR FR schedules (Chapter 6), and every five days, using PFR FR schedules (Chapter 7). In Chapter 8, the demand for foods was assessed using different progression types under the incrementing schedule using concurrent PR FR and PFR FR schedules.

Higher order parameters derived from the exponential and cross-price models of demand, break points and cross points were used to assess the demand for the different foods. It was identified that the cross point, a measure that reflects food preference and schedule requirement was the most useful for assessing the demand for commodities available under concurrent schedules. In addition, using the cross point, the most consistent order of preference within each experiment was identified (Table 9.0).

Table 9.0. Overall order of preference determined by single (Experiment 1) and paired (Experiment 2) preference assessments, and cross points for Experiments 3 – 6.

Rank	Exp 1	Exp 2	Exp 3	Exp 4		Exp 5	Exp 6			
	Single Stimulus	Paired Stimulus	PR FR 30	PR FR 30	PR FR 10	PFR FR (5 days)	PR FR (arith)	PR FR (geo)	PFR FR (arith)	PFR FR (geo)
1	Locusts	Locusts	Egg	Mushrooms	Mushrooms	Egg	Barley	Berries	Barley	Barley
2	Berries	Berries	Mushrooms	Chicken	Egg	Chicken	Oats	Barley	Berries	Berries
3	Mushrooms	Egg	Locust	Berries	Chicken	Mushrooms	Berries	Egg	Egg	Egg
4	Egg	Mushrooms	Chicken	Egg	Berries	Berries	Egg	Oats	Oats	Oats
5	Foliage	Chicken	Berries	-	-	-	-	-	-	-
6	Chicken	Foliage	Foliage	-	-	-	-	-	-	-

When possums were offered six food types that they had been reported to consume in the wild, and at a low response cost, possums preferred locusts in Experiments 1 and 2 over berries, chicken, egg, foliage and mushrooms (Table 9.0). In Experiments 3 - 6, possums had to expend effort in order to earn food that was offered under concurrent schedules of differing ratio requirements. Using the cross point as the dependent measure, egg was preferred in Experiment 3 over berries, chicken, foliage, locust and mushrooms. In Experiment 4, berries, chicken, egg and mushrooms were offered. Mushrooms were preferred in Experiment 4 and egg in Experiment 5. In the final experiment, two wet foods (berries and egg) and two dry foods (flaked barley and coco-pop mix and rolled oats) were offered. Possums preferred the flaked barley mix over other foods using the cross point as the dependent measure.

In Experiments 3 - 6, concurrent PR FR and PFR FR schedules were used to assess the demand for different foods. In Experiment 6, the demand for food under geometric and arithmetic progressions was also assessed. The PR FR schedule arrangement under a geometric progression was the most efficient method for determining demand as results were obtained in short periods of time. The conclusions regarding the demand for foods were also consistent with those obtained in the PFR FR conditions (Experiment 5 & 6). The more traditional methods of increasing ratio requirement across sessions (Experiments 5 & 6), necessitate more time and effort on the part of the researcher (Hursh, 1984). Therefore, one might intuit that if all 30 food pairs compared in Experiment 2 and 3 were used throughout the subsequent experiments the same result would have been obtained – that the demand for locust would be high. It is also worth considering that if the aim was only to obtain information regarding preference

the paired stimulus preference assessment would have sufficed and provided enough precision in terms of what possums prefer to eat.

The preference for foods is relatively simple to interpret in Experiment 1 and 2 as there was one dependent variable, the number of trials where each food was consumed. This provided a clear rank of food preference. In the concurrent schedule experiments the exponential and cross price models of demand were used to analyse the data (Hursh & Silberberg, 2008; Hursh et al., 2013). The models fit the data well, and provided parameter estimates of initial demand, essential value and P_{\max} . It was difficult to infer preference from these parameters however, because they did not behave as expected, as also found by other researchers (e.g., Bickel & Madden, 1999): if one assumed a food was preferred then estimates of the parameters of initial demand, essential value and P_{\max} would be high. When I examined these parameter estimates across the different foods there was no clear pattern and no single food that produced consistently high or low values across measures. To illustrate this, Table 9.1 shows the ranked order of preference found in the paired assessment in Experiment 2 for each food and the subsequent values of initial demand, essential value and P_{\max} found for the foods in the concurrent PR FR schedules used in Experiment 3.

Table 9.1. Order of preference found in Experiment 2 and values for initial demand, essential value and P_{\max} from Experiment 3 averaged across P1 - 6.

Food	Exp 2	Exp 3		
	Rank	Q_0	α	P_{\max}
Berries	3	1.03	0.06	2.47
Chicken	5	1.22	0.06	3.35
Egg	4	-0.97	0.07	2.66
Foliage	6	1.54	0.08	2.34
Locusts	1	-1.36	0.07	2.67
Mushrooms	2	-0.74	0.09	2.48

In addition to the measures of demand, the break point and cross point should also be larger when a food is more preferred. In contrast to the parameters generated by the demand models the cross point and break point were the most reliable measures across foods. When preferred foods were available under the PR or PFR schedule higher cross points and break points were observed and were lower when a preferred food was available under the constant FR schedule. In Experiment 3, initial demand was greater than -1 when all foods were available under the PR schedule. This is consistent with inelastic demand. This means that consumption rate was high when the ratio requirement under the PR schedule was low. In Experiments 4 - 6, initial demand was generally less than -1 across foods, which is consistent with elastic demand and indicates that consumption rates were low when ratio requirements were also low. In addition, these results were consistent with previous research by Foster et al. (2009), Grant et al. (2014) and Hursh et al. (1988) that foods considered more highly preferred had lower initial demand values compared to other foods.

It was expected that essential value, the rate of change in elasticity as ratio requirement increased, would differ for qualitative commodities such as food type, and would be similar for quantitatively different commodities such as access times to the same foods (Grant et al., 2014). There was, however, no significant difference in essential value for food comparisons in Experiments 3 – 5. This suggests that the foods, although vastly different in terms of texture, nutritional content and taste – from a human perspective – produced similar decreases in consumption rate as ratio requirement increased and were of similar ‘importance’ to the possums. It was only when schedule and progression type was varied in

Experiment 6 that estimates of essential value differed across foods indicating that these variables influenced the possums' consumption rates of the different foods.

Other researchers have attempted to equate qualitative differences between commodities such as drugs (e.g., Christiansen et al., 2008; Hursh et al., 2013) and food (e.g., Foster et al., 2009) using normalization procedures. One drawback of this is the reduction of the effects on performance due to the inherent differences between commodities that ultimately identifies preferences for different food types. Foster et al. (2009) stated that the utility of standardizing demand curves for different commodities, such as food, is yet to be determined. This author adds to that sentiment by asking whether it is actually important to equate food type and that there is no sensible way of equating 'qualities' of commodities that differ on dimensions that are based on physical dimensions, such as size (e.g., Bizo, Kettle & Killeen, 2001), drug (e.g., Allen & Leri, 2010) or additive concentration (e.g. Hodos, 1961; Young & Green, 1953).

The estimates of P_{\max} in Experiment 3 were similar and low showing that consumption rate was inelastic, at very low values. This suggests that response requirements of two and four responses to obtain the food impacted consumption rate. In Experiments 4 - 6 there was near exclusive elastic initial demand. This renders the use of P_{\max} unhelpful as there is no point of maximal responding of which to reliably base a measure of demand.

One issue that requires clarification in the use of the exponential demand model (Hursh & Silberberg, 2008) is the use of the scaling parameter, k , as an estimate of the range of the dependent variable (consumption rate). Hursh and Silberberg (2008) state that the largest range across data sets or the average of the range across data sets and individual animals would be an appropriate estimate of

k , however, this is only appropriate when the estimates of k for individual animals vary over relatively small ranges. This was not the case in Experiments 3 - 6: In Experiment 3 the range was ln 10.08 to ln 15.75; in Experiment 4 the range was ln 9.26 to ln 15.75, in Experiment 5 the range was ln 5.38 to ln 6.90, and in Experiment 6 the range was ln 7.81 to ln 11.78 for the PR FR schedules and ln 5.35 to ln 8.14 for the PFR FR schedules. Using the average k value is unsuitable when estimates vary widely. Foster et al. (2009) also found large ranges in the estimates of k and used two values, $k = 3.5$ and $k = 8$ and observed that estimates of essential value were lower and varied more across foods when a larger k value is used. Consequently, in Experiments 3 - 6, the estimate of k was allowed to vary across animals but was kept constant within each animal in each experiment.

The cross-price demand model (Hursh et al., 2013) indicated that all foods under the PR and FR schedules were substitutable. It was evident that the foods on offer in each of the experiments were substitutes considering the similarity of the essential values. Some foods were more 'valued' by the possums shown by the interaction of responding for food under the PR schedule compared to than under the constant FR schedule. For example, in Experiment 6 egg was more 'valued' than berries. When berries were available under the PR schedule of the PR FR condition at low values possums responded for egg under the FR 30 schedule, even though egg required more effort to obtain. In contrast, when egg was available under the PR schedule and berries under the FR schedule, possums responded for egg under the PR schedule and only responded for berries later in the session when it the ratio requirement for egg was much higher.

The intersection of curves derived using the exponential and cross-price demand models (Hursh & Silberberg, 2008; Hursh et al., 2013) provided cross

points as a measure of the substitutability between two commodities under two schedules as a function of demand *and* ratio requirement. Generally, cross points were perseverative for preferred foods under the incrementing schedules, and were conservative for preferred foods under the constant FR schedules. In particular, the usefulness of the cross-price demand model in determining demand and a reliable curve to calculate the cross point has been confirmed and is a positive addition to the behaviour economics for analysing performance under concurrent schedules.

Previous researchers identified perseverative cross points for preferred commodities under the PFR schedule of PFR FR schedules in rats (Holm et al., 2007; Sørensen et al., 2001) and pigs (Holm et al., 2008; Pedersen et al., 2005) when two different foods or substrates were available. Conversely, conservative cross points were observed under the PR schedule of PR FR schedules when the same foods was available for monkeys (Hineline & Sodetz, 1987; Hodos & Trumbule, 1967). This shows that schedule requirements tend to impact more on the allocation of behaviour when the same foods are available under both schedules. In contrast, in Experiments 3 - 6, different foods were available under the concurrent schedules and it was observed that more responding was allocated to the preferred food irrespective of ratio requirement, suggesting that when qualitatively different commodities are available the preference for the item is more important than the cost to obtain it.

The break point measures the ‘strength’ of a reinforcer, where higher break points indicate greater value of the commodity to the subject (Hodos & Kalman, 1963; Stafford & Branch, 1998). Across experiments, break points were highest under the PR schedule for locust in Experiment 3 and egg in Experiments

4, 5 and 6. The break point measured the persistence in responding for food under the PR or PFR schedule, but only indirectly accounted for responding under the alternative schedule. In Experiment 3, when preferred foods, such as locust were available under the FR schedule, break points were smaller for foods under the PR schedule.

The break point is only measured by the final point in the session and ignores responding that occurs under the PR or PFR schedule before the final ratio requirement, and responding that occurs before and after the final ratio requirement under the PR or PFR schedule. It has also been argued that break point becomes 'cruder' as step-size increases and because of this commodities that reach the same break point may not be equal in terms of reinforcing value (Christensen et al., 2008; Hodos & Kalman, 1963). In the Experiment 6, break points were more variable under the geometric progression with a larger range (FR 1 to FR 512) compared to the arithmetic progression (FR 1 to FR 276). This suggests that when step-sizes are large, at the higher ratio requirements of the geometric progression, break points differ more than when ratio requirements increase by a constant amount.

For these reasons, the cross point was deemed a *better* measure for evaluating the demand for two commodities, and indicates a preference for one commodity over another as it accounts for responding under both available schedules for different commodities. In addition, it is not limited to just the final stretch of responding under one schedule. Cross points, however, were not always generated in these experiments due to minimal responding under the constant FR schedule when responding was being allocated to the PR schedule. This means

that, at least on some occasions, exclusive responding to the FR schedule occurred after responding had concluded on the PR schedule.

One explanation for the minimal responding under the constant FR schedule was that the possums were biased to the right lever, which always corresponded to the PR schedule. Holm et al. (2007) observed exclusive responding for the preferred commodity when it was always offered on an incrementing schedule on the same lever in comparison with an alternating commodity on the other lever. This extreme exclusivity to one schedule was not observed in the current study. In Experiments 3 - 6, the presentation of foods was counterbalanced across the incrementing and constant schedules and when preferred foods were available on the PR or PFR schedules it did not interfere with responding to the constant FR schedule to the degree that Holm et al. reported. The possums continued to respond to the constant FR schedule.

It is likely that a small amount of bias to the incrementing schedules occurred due to initially low ratio requirements, however, it does not provide a satisfactory reason for the minimal responding observed under the constant FR schedule or how food preference might have affected responding. The analysis of cross point data in Experiments 3 and 4 showed that the number of perseverative cross points for food under the PR schedule (or exclusive responding under the PR schedule if no cross point was obtained) was equivalent to the number of conservative cross points for food under the constant FR schedule. This indicates substitutability between foods as responding was allocated fairly evenly to both the PR and FR schedules. When preferred foods were available under the PR schedule, however, there were more perseverative cross points indicating that the *preference* of these foods overwhelmed the increased amount of effort required to

obtain the foods when other foods were available for less work. It is likely that the initial low ratio requirements of the PR schedule 'encouraged' responding under this schedule, but the preference for the foods maintained responding under the PR schedule or pre-empted a switch to the constant FR schedule.

In addition, the design used in the current experiments was consistent with previous behavioural economic studies (e.g., Hursh 1978; Hursh & Natelson, 1981), where it does not appear that counterbalancing occurred across manipulanda when multiple or concurrent schedules were in place. In other experiments, however, counterbalancing occurred across animals (e.g. Allen & Leri, 2010; Bhat & Wasserman, 1987). This would be an appropriate way to address this concern in future replications of these experiments.

One issue to consider is that of the open economy in which the experiments were conducted. This means that supplementary feeding was given after each experimental session to maintain the possums at 85% of their free feeding body weight. In a closed economy, it would be expected that *more* responding would have occurred as the entirety of the possums diet would have had to be gained during long experimental sessions (Foster et al., 1997a; Hursh, 1980; 1984). Conducting the current set of experiments in a closed economy would not be practical as the food types used would need to keep well over time as foods such as egg or chicken would spoil quickly. There are also concerns regarding the welfare of captive possums receiving foods high in protein and sugar without sufficient roughage and fibre for digestion in maintaining general health.

As these experiments used consumption as a dependent measure, satiety to the foods became an issue due to the prolonged exposure to the same foods in

Experiments 4 - 6. This might have contributed to the low estimates of initial demand and similar alpha values in Experiments 4 - 6. In Experiment 4, the same two foods were presented for approximately 12 consecutive days, and in Experiments 5 and 6 for months at a time. In contrast, possums in Experiments 1 and 3 were exposed to a different pair of foods every three days, and in Experiment 2 all foods within a session. Human and animal research has found that offering a variety of foods increased consumption within and across meals (Raynor & Epstein, 2001). It is also not surprising that when the variety of foods consumed is decreased, such as when eating the same foods each day, consumption for that food will decrease in animals and humans (Raynor, 2012). In fact, it is even considered a good way to lose weight. In light of this finding, the design Experiments 4 - 6 could have been modified so that each day a different pair of foods was offered to the possums.

It has been theorised that possums consume a wide variety of foods to maximise their nutritional intake (Kerle, 1984). One might speculate that possums preferred egg and chicken because of their comparatively higher levels of protein, energy (chicken) or fat (egg) content compared to berries and mushrooms. The preference of berries, chicken and locust in Experiments 1 and 2 could be due to the possums preferring to consume foods high in protein. In Experiment 3, however, berries were only preferred when the effort required to obtain them was low and not all possums responded at high rates for chicken.

In conclusion, possums in the laboratory consumed a variety of foods and showed idiosyncratic preferences across the six food types offered in Experiments 1 - 3. This is similar to reports of possums in the wild that browse on a large number of plant and tree species, insects, and birds and their eggs (Nugent et al.,

2000). Using concurrent schedules, in Experiments 3 - 6, the measures of demand confirmed that possums were opportunistic in their feeding behaviours (Cowan & Moeed, 1987; Kerle, 1984), as they responded for all foods at low ratio requirements. The break points and cross points indicated that possums would persist in responding to high ratio requirements for their preferred foods and that if a food was readily available and required little effort to obtain possums are likely to consume it. They will, however, put *more* effort into obtaining their most preferred foods, even if another food is available for *less* effort.

This series of experiments has highlighted the need to validate preference assessments in non-traditional species especially if the results are to be used in practical applications, such as pest management. There is a functional similarity between the use of preference assessments in applied studies with humans and animals, in the need to identify effective reinforcers for teaching and for use in operant experiments. The number of times one commodity is chosen over another is a simple method for identifying a favoured commodity over others (Young & Greene, 1953a). One advantage of using animals to validate preference testing methods is that one has the opportunity to control for more variables in the laboratory, such as deprivation level, and test procedures and equipment for using with non-traditional animals. For example, for the possum, specialised apparatuses are required that are robust, prevent escaping and protect the experimenter from sharp claws.

Furthermore, procedures that are used to test the effectiveness of these commodities as reinforcers can be achieved using demand procedures. However, parameters derived from models designed to describe the demand for commodities, such as initial demand, essential value and P_{\max} should be used with

caution if one was to try to use these parameters as a proxy for a measure of preference.

Another consideration of this research is that of the improvement in the welfare and wellbeing of laboratory animals by ensuring animals' "get what they want" (Dawkins, 2004, p.3). Knowing what animals prefer and providing those commodities or environments to them can improve physiological and psychological welfare in captive environments such as zoos, farms and laboratories. The current series of experiments identified that possums consume a variety of foods, and will *work* hard to obtain them. This suggests that possums in captivity might have improved welfare if they were offered a variety of foods during non-experimental periods. In addition, it was surprising and fortuitous that no adverse or long-term health problems were observed in P1 - 6 in the four years it took to complete the experiments indicating that varied diets improved, or at least maintained the health of the possums.

These findings have implications for pest management of possums in New Zealand. The management of pests remains a high profile issue with a recent publication by McGlone et al. (2014) for the Royal Society of New Zealand, which stated that the biggest threat to native plants, birds and bats are possums and other vertebrate pests (Brockerhoff et al., 2010). Improved knowledge of possum food preferences may inform the refinement of existing lures and bait delivery systems such as the use of synthetic insect flavour or scent as a lure. Some of the wet foods such as berries, chicken and egg might present a challenge, although recent technology developed to control mustelids might offer a solution. King et al. (2007) made use of aerosol cans containing an egg and oil mix or homogenated sheep brain, with some success.

In New Zealand, there are a number of pest species that adversely affect native flora and fauna. To efficiently control the pest population, systematic studies are needed to determine what they eat, and what they *prefer* to eat. This series of experiments has shown that possums' food preferences are idiosyncratic. Therefore, the use of a variety of flavours and bait types that appeal to a greater number of possums will enhance existing pest control methods. It might also be time to try a combination of the possums' most preferred foods of locust, egg, or barley and coco-pops® in these possum control efforts.

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Appendix A.

Abstract

Animals in captivity can develop physiological characteristics such as obesity that negatively affect their welfare. In the captive brushtail possum (*Trichosurus vulpecula*) it is unknown what effect long term captive and free-feeding has on body weight. Over a 12 month period, three possums were fed according to a free-feeding regime and their food intake and weight was measured every four days. The possums all gained weight but showed bouts of stable body weights. It was concluded that long term free-feeding did not maintain the health and welfare of the possums, therefore, a controlled feeding regime is required for possums.

Introduction

Captive animals in farms, zoos and laboratories with relatively small enclosures and barren environments can develop physiological characteristics such as obesity that negatively affect their welfare. This has been observed in laboratory animals such as mice and rats (e.g., Sclafani & Springer, 1976) and zoo animals such as primates (e.g, Brent, Lee, & Eichberg, 1989; Brent, 1995). In particular, animals, such as primates, are heavier in captivity than in the wild (Leigh, 1994), due to the plentiful and nutritious food sources in captivity (Swaisgood, White, Zhou, Zhang, & Lindburg, 2005). In comparison, in the wild food is often sparse, requires more effort to obtain and could be less nutritional (Brent, 1995).

The brushtail possum (*Trichosurus vulpecula*) is a pest species in New Zealand and due to their prolific nature pest management is required to curb the population (Brockerhoff et al., 2010), negatively affecting agricultural and ecological industries (Cowan, 1990). It is for these reasons that researchers keep

captive colonies of possums to test methods and tools to eradicate the pest and as a laboratory animal receives the same welfare considerations and standards as the typical traditional lab rat or mouse (Ator, 2004). In addition, they are also susceptible to becoming overweight.

The University of Waikato's *Learning, Behaviour and Welfare Research Unit* has maintained a colony of possums for 20 years. For most of this time adult possums were employed as subjects of operant experiments and were kept on food restricted diets. It is not known how long term captivity and *ad libitum* food regimes affect possum body weights and whether, seasonal variation in body weight observed in the wild occurs in the laboratory.

A longitudinal field study measuring population health and growth in two locations within the Orongorongo Valley, near Wellington found seasonal variation in possum body weights (Bell, 1981). Female body weights changed substantially by season with peak body weights occurring in autumn (Location A) and winter (Location B), with the lowest body weights in winter (with no young) and summer for possums rearing young (Location A), and spring (Location B). Bell (1981) suggests that this difference may be attributed to the considerable demographic differences between the two areas, such as food availability.

There are no shortages of food in the laboratory to influence trends of body weight in the captive animal that have been observed in the wild, therefore, it is unlikely that body weight trends would be related to seasonal variation. To examine this the food intake and body weights of three captive free-fed brushtail possums were monitored to measure the trends in body weight over a 12 month period on a free-feeding regime. It was expected that the possums would initially gain weight but showed bouts of stable body weight.

Method

Three brushtail possums (two female, P21 and P22, and one male P23) aged between 2-9 years were wild caught and had been housed in captivity for 2-8 years. Possums were kept in custom built individual wire-netting cages with a nest box on top under a 12:12 h reversed dark/light cycle beginning at 9am. Cleaning and maintenance occurred during the light rotation. The possums had constant access to water. Possums received a minimum of 200 g of food (dock (*Rumex obtusifolius*), apple, and pellets (Camtech Manufacturing Ltd) at 1030 h each day. At 0800 h each morning, leftover food was weighed. The amount of a food offered was increased if less than 50 g was left by the possums and decreased if more than 100 g was left.

Possums were weighed every four days. The procedure involved possums moving from their home cage into a metal box for a food reward. They were then transferred a short distance to a scale, rewarded with sultanas, then returned to their cage for their daily food ration.

Results

All three possums gained weight during the 12 month period (Figure A1). Food intake fluctuated daily with average daily difference in food eaten varying across possums: P21 ($M = 57.5$ g, $\sigma = 52.2$ g); P22 ($M = 73.3$ g, $\sigma = 63.0$ g); and P23 ($M = 105.4$ g, $\sigma = 91.7$ g). P23 had the highest and most varied daily food intake and the greatest fluctuation in body weight.

A mathematical model used to estimate the point of stability in response rate curves was applied to the body-weight data to identify when the weights were mathematically stable (Figure A1; Killeen, 1978). Equation 1 has two parameters

(J = number of days and C = a time constant), R is the predicted body weight and dependent variable, and A is the asymptote or point of stability. Equation 2 has added parameter where the starting point of the dependent variable does not have to be zero. Equation 3 has been used to estimate termination points for when stability of response rates in pigeons (Killeen, 1978):

$$R = A(1 - e^{-\frac{J}{C}}), \quad (1)$$

$$R = A(1 - e^{-\frac{J}{C}}) + x, \quad (2)$$

$$R = \frac{A \cdot J}{C + J}. \quad (3)$$

Non-linear least squares regression was used to determine the best fits of the equation to the data and is presented in Figure A1. Equation 2 approximates the body weights of P21 and P22 well (the average variance accounted for was 92.1%). The derived asymptotes predicted that 99% of body weights would reach a stable value after an average of 299 weigh sessions. Equation 3 approximated the body weight of P23 moderately well (the variance accounted for was 74.5%), however, this indicated that stability was reached in 0.5 weigh sessions, which is not accurate looking at Figure A1. Equations 1 and 2 were poor fits to body weights for P23 ($M = 23.3\%$, $\sigma = 26.2$).

The percentage change in body weight since the previous weight was calculated to identify bouts of stability that did not exceed 2.5% above or below previous weights (see Figure A2). Across days the majority of body weights of P21 and P22 were within 2.5% above or below the previous weights and in

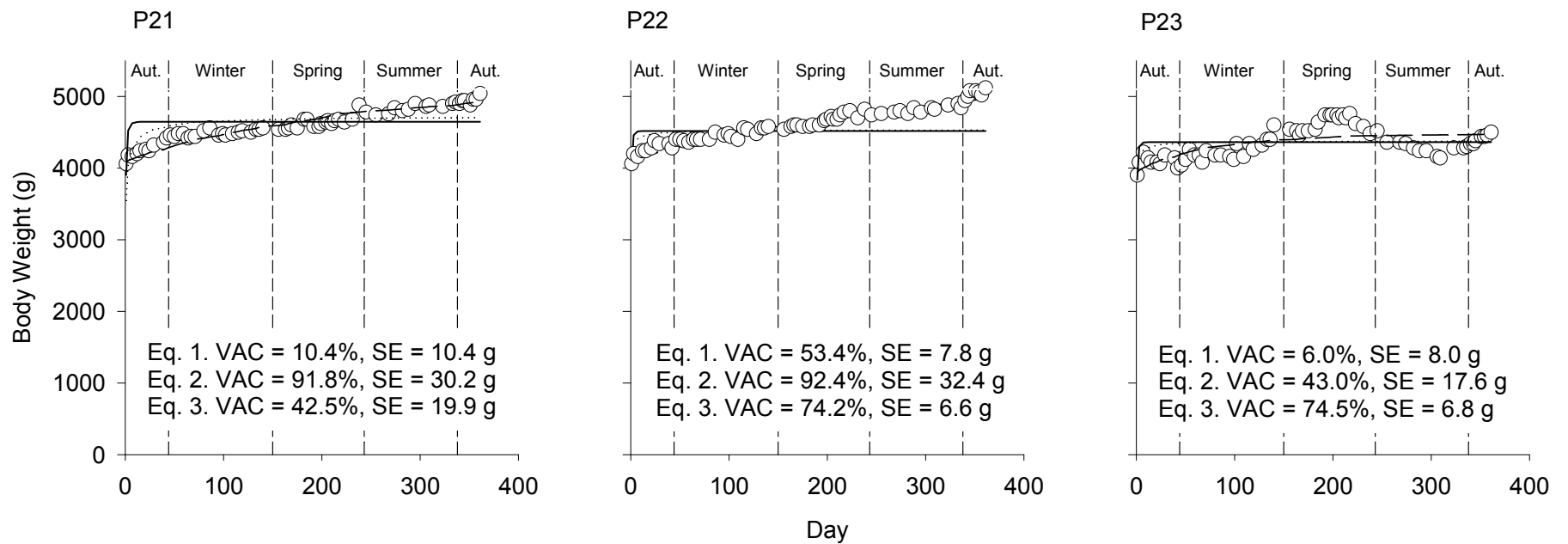


Figure A1. Body weight (g) of P21, P22, P23 across days and season (Aut. = Autumn). (VAC = variance accounted for; SE = standard error).

addition there were few instances when there were more than three consecutive body weight increases or decreases. This indicates that there were bouts of stability during the 12 month period. For P23 there were fewer bouts of stability, the longest time period being between 150 and 200 days.

Discussion

The measurement of possum body weights over 12 months on a free-feeding regime suggests that possums will continue to gain weight. The two female possums were heavier than the male possum which is similar to reports of female chimpanzees in zoos (Brent, 1995). There was also no indication that the possum body weights in captivity were related to season as observed by wild possums in the Bell (1981) study.

This study gives an indication that long term captivity under free-feeding leads to weight gain and possibly 'obesity' in laboratory possums. This means that to maintain healthy animals in the laboratory, researchers will need to be aware of the propensity of possums to gain weight on free-feeding regimes. In conclusion, long term free-feeding may put possums' health at risk as they are likely to continue to gain weight. In addition, a body score index based on visual inspection may need to be implemented to evaluate possum health as well as regular weigh sessions to observe changes in body weight.

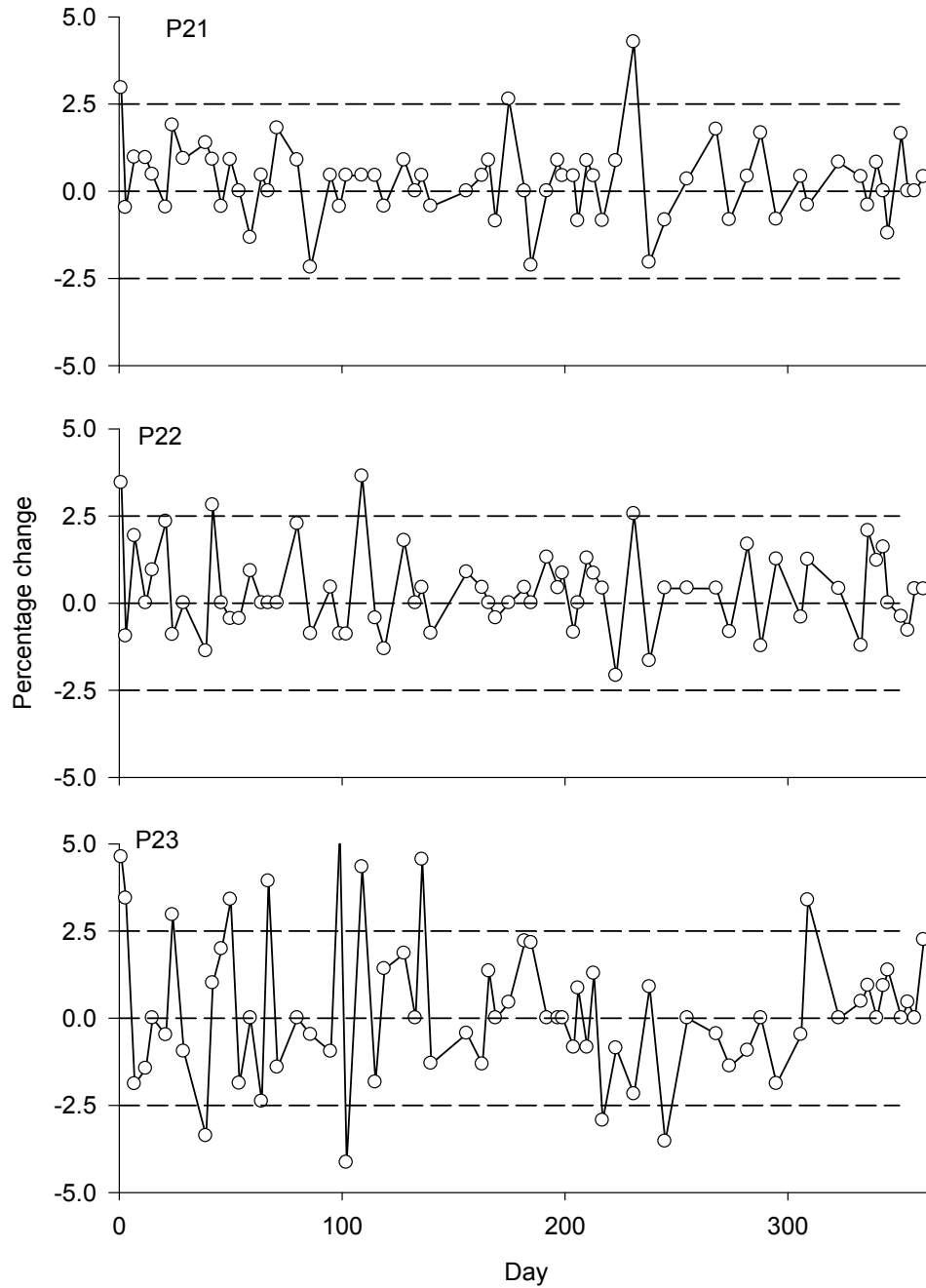


Figure A2. Percentage change in body weight between weigh days. The dashed lines represent $\pm 2.5\%$ change from the previous weight.

Acknowledgements

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Appendix B².

Abstract

When conducting controlled laboratory studies with non-traditional laboratory animals it is important that methods for determining body weight stability are reliable. This helps ensure the health and welfare of animals when they are maintained during periods of free feeding or food restriction. This study compared different methods for determining body weight stability of six common brushtail possums (*Trichosurus vulpecula*) maintained on a free-feeding diet under laboratory conditions. A criterion of five consecutive weighs with less than $\pm 2.5\%$ change across days and no more than two consecutive days of weight loss or weight gain was judged to be the most suitable criteria for determining stability. It is important to study non-traditional animals, especially endangered or pest species under controlled laboratory conditions and have robust methods for establishing body weight stability.

Body Weight Stability in the Brushtail Possum (*Trichosurus vulpecula*)

One of the most important considerations when keeping laboratory animals is the control of physiological variables, such as body weight (Ator, 2004). There is no agreed method, however, on how to control body weight in non-traditional laboratory animals that does not compromise health, welfare (Animal Welfare Act, 2013) or the natural feeding behaviour of the animals (Poling, Nickel, & Alling, 1990). No universally accepted standard exists on *how* to assess *when*

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body weights are stable during periods of free feeding or food restriction. This is particularly important for non-traditional laboratory animals with large individual differences, in contrast to those bred specifically for laboratory use (Turturro et al., 1999).

In many experimental protocols restricting food intake or availability to some percentage of an animal's free-feeding body weight and/or usual food consumption is used to establish a state of hunger to maintain motivation for responding during experiments (Animal Welfare Act, 2013; Ator, 1991; Kangas & Branch, 2006; Sargisson, McLean, Brown, & White, 2007; Toth & Gardiner, 2000). The free-feeding weight established prior to food restriction is typically the average of some number of days (Kangas & Branch, 2006), and ideally weights will have been judged as stable over that time. A variety of methods have been used to determine 'stability'. The most basic method is a visual inspection of graphed weight data (Ator, 1991). Statistical methods involving averaging across animals (Case, Nichols, & Fantino, 1995; Kangas & Branch, 2006), and percentage change across weights or specified periods of time for individual animals (Zeigler, Green, & Siegel, 1972), have been used.

The brushtail possum, *Trichosurus vulpecula*, is an arboreal omnivore from Australia introduced to New Zealand in the 1900's (Cowan, 1990). In New Zealand they consume native and exotic flora and fauna, predate and compete with native animals, and have a negative impact on agriculture (Cowan, 1990; Nugent, Sweetapple, Coleman, & Suisted, 2000). For these reasons, it is important to maintain captive populations of possums so that research can be undertaken to better understand this animal. There is no existing standard, however, for determining a stable or optimum body weight in the possum in captivity.

Possums are an example of a species where individuals fluctuate in body weight. Wild caught possums in Australia range from 1350 - 3500 g for males and 1300 - 3150 g for females (Kerle, McKay, & Sharman, 1991). They are generally heavier in New Zealand, (e.g. males 1400 - 3900 g, females 1400 - 3300 g) (Bell, 1981; Harvie, 1973; Tyndale-Biscoe, 1973). Possums in the wild are of limited use in estimating optimum body weight because their weight is influenced by health, location, food availability, climate and population density (Green & Coleman, 1984; Owen & Norton, 1995)

Studies of newly captured possums claimed possums' body weights took over 20 weeks to appear stable in shared enclosures (Baker, Gemmell, & Gemmell, 1998) and approximately six weeks when housed individually (Day & O'Connor, 2000). Neither study explained how body weight stability was determined except for visual inspection of graphed body weights.

In the current study we compared three different ways (visual inspection of graphs, a mathematical model and percentage change in body weight) of establishing the stability of free feeding body weight in possums. The aim was to determine which method was most reliable and feasible for use in the laboratory. Six brushtail possums (two female and four male) aged between 2-6 years were wild caught and had been housed in captivity for 3-8 years. Possums were kept in custom built individual wire-netting cages with a nest box on top under a 12:12 h reversed dark/light cycle. Cleaning and maintenance occurred during the light rotation. The possums had constant access to water. Possums received a minimum of 200 g of food (dock (*Rumex obtusifolius*), apple, and pellets (Camtech Manufacturing Ltd) at 1030 h each day. At 0800 h each morning, leftover food

was weighed. The amount of a food offered was increased if less than 50 g was left by the possums and decreased if more than 100 g was left.

To facilitate weighing the possums were trained to move from their home cage into a metal box for a food reward. The box was weighed and the possums returned to their home cage. Possums were weighed every four days to minimise stress.

Visual inspection of body-weight data revealed all six possums gained weight during free feeding with very short bouts of apparent ‘stability’ (Figure B1). A second method using visual inspection involved averaging body weights over three weigh days (Case et al., 1995), but again this did not show stability as weights continued to increase over time (Figure A1).

A mathematical model previously used to assess stability in response rate curves was applied to the body-weight data in an attempt to identify the asymptote or point of stability (Killeen, 1978). The equation has two parameters (J = number of days and C = a time constant), R is the predicted body weight and dependent variable, A is the asymptote:

$$R = \frac{A \cdot J}{C + J} . \quad (1)$$

Non-linear least squares regression was used to determine the best fits of the equation to the data and are presented as the solid lines in Figure B1; they approximate the body weights well (the average variance accounted for was 99.8%). The model predicted that 99% of body weight stability will be reached after 12 days. Visual inspection of the data suggests, however, that there were still upward trends in weight after asymptote was reached.

Others have used the percentage change in weight using no more than 3% difference in individual body weights as a stability criteria (Zeigler et al., 1972). We applied a criterion to our data that body weight could not vary more than $\pm 2.5\%$ from the previous weight. Five percent total variability was chosen as it is a commonly used range in studies requiring animals to be food deprived. Inspection of the data indicated that it was necessary to add another component to this criterion to avoid increasing or decreasing trends in body weight (Figure B1). Thus, for stability to be established there had to be fewer than three consecutive increases or decreases in body weight identified by a visual inspection of Figure B2. The dark bands show periods of stability within $\pm 2.5\%$ of the previous weight and fewer than three consecutive weight gains or losses. Using this percentage change criteria, the body weights of P1, P2, and P6 were stable after 10-12 weigh sessions and P3 showed a longer period of stability in body weight by the end of the free feeding period (60 days). P4 and P5 showed short periods of stability during the 60 days.

Body weights of four possums during the 60 day period showed periods of stability according to the mathematical and visual criteria, however, the criterion of $\pm 2.5\%$ may have been too conservative for two possums as there were fewer than five consecutive stable weighs within the free feeding period. Another consideration is the minimum number of days that meet the criterion for body weight to be considered stable. Some possums showed longer periods of stability than others therefore a minimum period might be required to ensure there are no increasing or decreasing trends in body weight. If the tolerance was widened to $\pm 3\%$ then bouts of stability would have been longer for all animals.

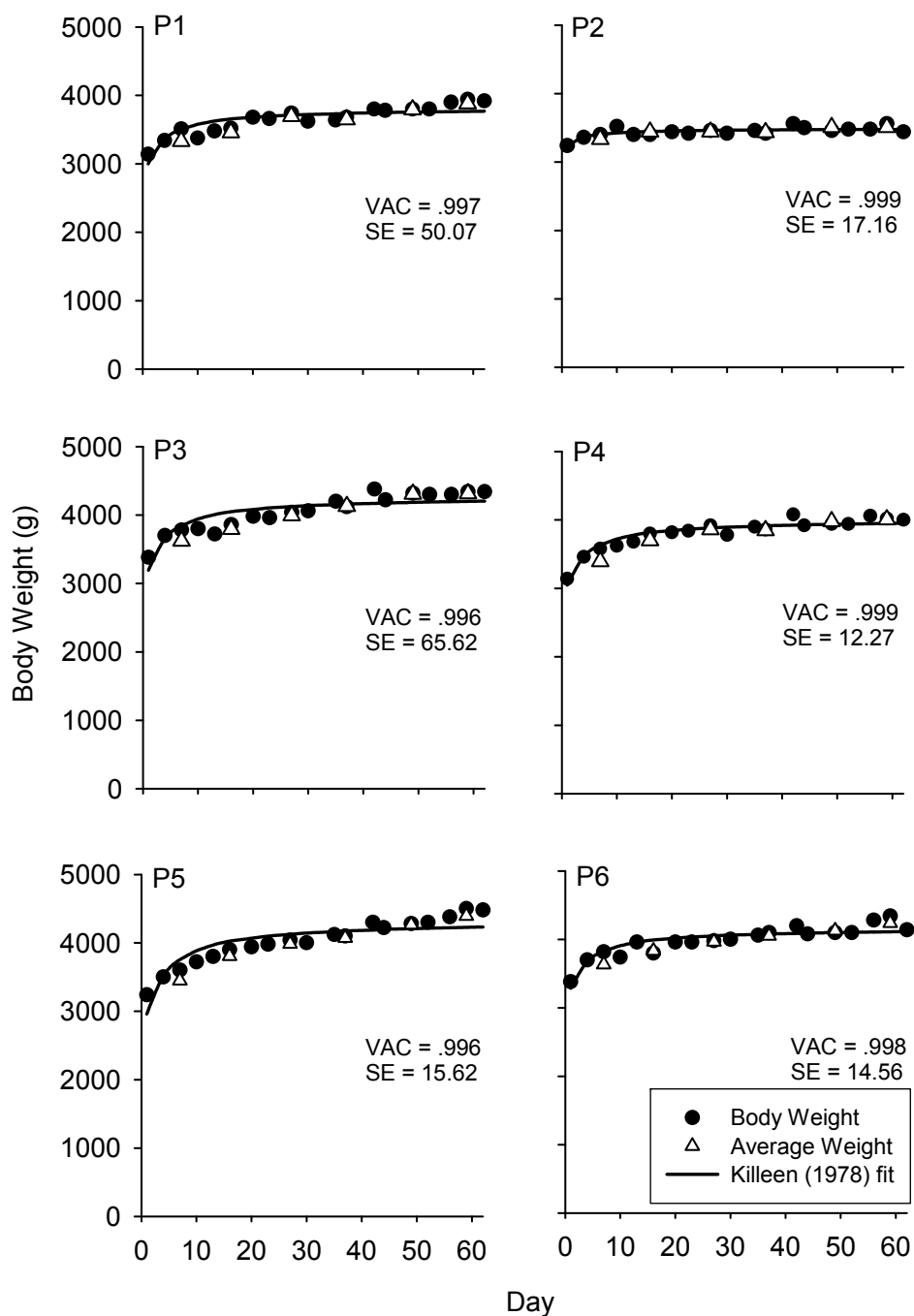


Figure B1. Body weight (grams) for the 60 day free feeding regime for all possums across days. Open triangles are the weights averaged over three weigh days. (VAC = variance accounted for; SE = standard error)

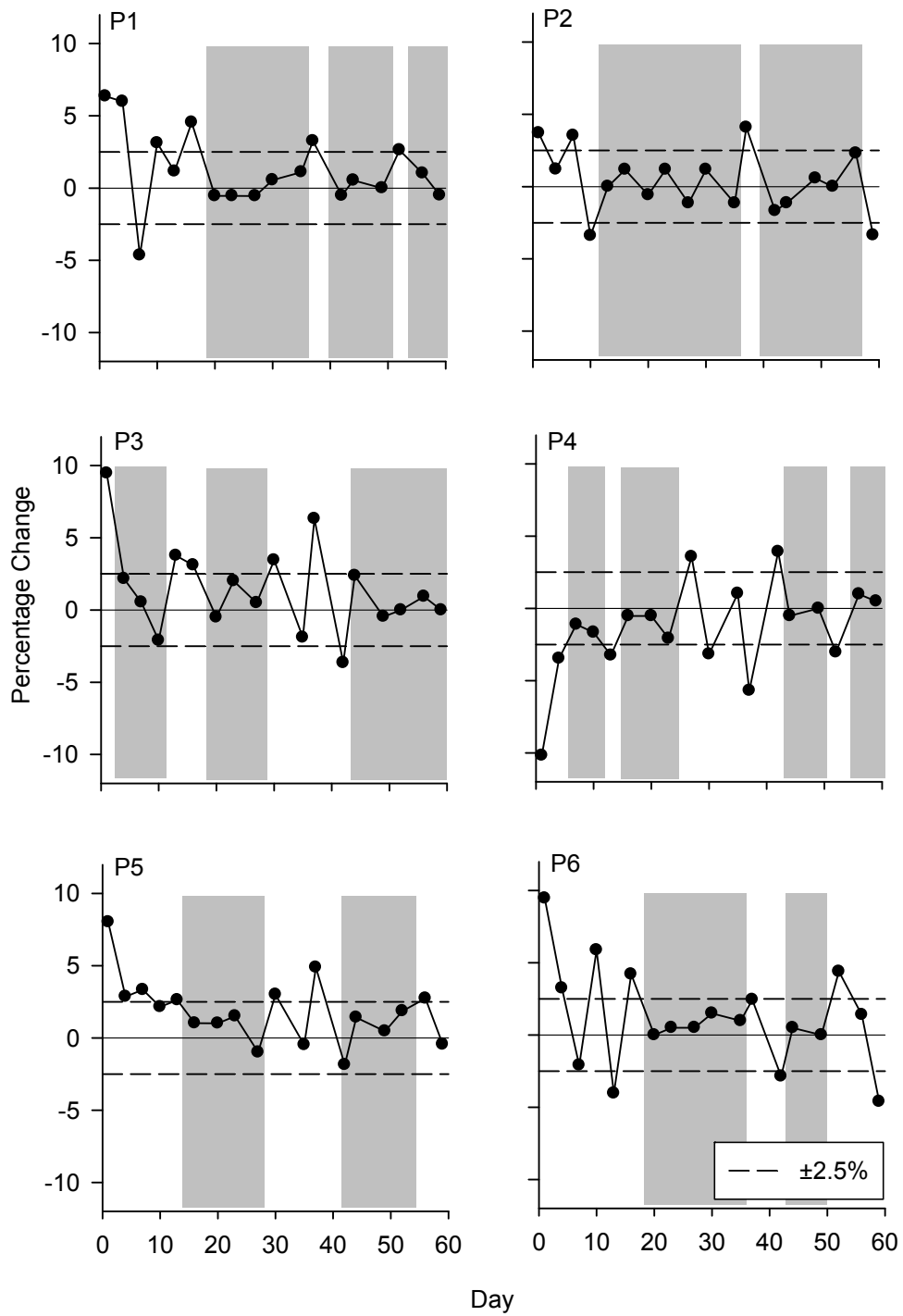


Figure B2. The percentage change between days of body weights of six possums. The shaded bands show periods of stability according to the percentage change criterion.

When non-traditional animals are used in laboratory studies, weight ranges, food intake and body condition score are considered when determining a stability criteria (Fitzgerald et al., 1981; Warburton & Orchard, 1996). In addition, body weights of these animal's should only be measured against the same individuals data rather than a 'standard'. Visual inspection of the data can reveal trends over long periods of time even when those increases are relatively small (e.g. see Figure 1), and that consecutive gains and losses around the zero point indicate near stable body weight (Zeigler et al., 1972). Reliance cannot be placed solely on the percentage change in body weight to assess stability, as minimal percentage change between weigh sessions may hide continually increasing body weights. The mathematical model underestimated the number of weigh sessions required to reach stability as determined by either visual inspection or percentage variation stability. For possums settled in a laboratory environment when provided ad-libitum access to food it will require between 20 and 60 days to reach a stable weight as determined by both visual and percentage variation stability criteria.

We recommend using more than one method to determine the stability of an animal's body weight. A combination of visual inspection and percentage change analysis provided a practical and robust method for determining stable body which could be used in a wide range of non-traditional laboratory animals. Further research comparing and verifying these methods with traditional laboratory species, such as rats or mice would validate a general 'standard practice' for assessing stable body weights in captive and laboratory animals. It would also provide an opportunity for determining how best to establish body weight criteria across the range of species used in animal research.

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Appendix C.

Summary tables of species consumed by possums.

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Table C1. Summary table of native trees species (foliage, fruit and flowers) identified as consumed by possums.

	Common name	Reports of foliage, fruit & flowers	Research
Native Trees	Mahoe	11	Coleman et al. (1980) [^] ; Coleman et al. (1985) [^] ; Fitzgerald (1976) [^] ; Fitzgerald & Waddington (1979) [^] ; Fitzgerald & Wardle (1979) [^] ; Gilmore (1967) [^] ; Harvie (1973) [*] ; Leathwick et al. (1983) [^] ; Nugent et al. (1997) [*] ; Sweetapple et al. (2004) ["]
	Fivefinger	10	Clout (1977) [*] ; Cochrane et al. (2003) [*] ; Fitzgerald (1976) [^] ; Fitzgerald & Waddington (1979) [^] ; Jacometti et al. (2007) ["] ; Leathwick et al. (1983) [^] ; Nugent et al. (1997) [*] ; Sweetapple et al. (2004) ["] ; Warburton (1978) [*]
	Fuchsia	10	Clout (1977) [*] ; Cochrane et al. (2003) [*] ; Fitzgerald (1976) [^] ; Fitzgerald & Wardle (1979) [^] ; Gilmore (1967) [^] ; Leathwick et al. (1983) [^] ; Mason (1958) [*] ; Rogers (1997) [^] ; Sweetapple et al. (2004) ["]
	Hinau	7	Coleman et al. (1985) [^] ; Fitzgerald & Wardle (1979) [^] ; Harvie (1973) [*] ; Leathwick et al. (1983) [^] ; Nugent et al. (1997) [*] ; Sweetapple et al. (2004) ["]
	Kamaha	7	Cochrane et al. (2003) [*] ; Coleman et al. (1985) [^] ; Fitzgerald & Waddington (1979) [^] ; Leathwick et al. (1983) [^] ; Mason (1958) [*]
	Rata	7	Cochrane et al. (2003) [*] ; Coleman et al. (1980) [^] ; Fitzgerald (1976) [^] ; Fitzgerald & Waddington (1979) [^] ; Fitzgerald & Wardle (1979) [^] ; Leathwick et al. (1983) [^] ; Mason (1958) [*]
	Totara	7	Cochrane et al. (2003) [*] ; Coleman et al. (1985) [^] ; Gilmore (1965) [*] ; Harvie (1973) [*] ; Rogers (1997) [^] ; Nugent et al. (1997) [*]
	Matai	6	Fitzgerald (1976) [^] ; Gilmore (1965) [*] ; Leathwick et al. (1983) [^] ; Rogers (1997) [^] ; Nugent et al. (1997) [*]
	Seven Finger	6	Cochrane et al. (2003) [*] ; Coleman et al. (1980) [^] ; Fitzgerald & Wardle (1979) [^] ; Gilmore (1967) [^] ; Leathwick et al. (1983) [^] ; Mason (1958) [*]
	Kapuka	5	Coleman et al. (1985) [^] ; Gilmore (1965 [*] , 1967 [^]); Jacometti et al. (2007) ["] ; Rogers (1997) [^]
	Beech	4	Cochrane et al. (2003) [*] ; Warburton (1978) [*]
	Honeysuckle	4	Fitzgerald (1976) [^] ; Harvie (1973) [*] ; Leathwick et al. (1983) [^] ; Mason (1958) [*]
	Wineberry	4	Nugent et al. (1997) [*] ; Rogers (1997) [^] ; Sweetapple et al. (2004) ["]
	Kawakawa	3	Gilmore (1965 [*] , 1967 [^]); Leathwick et al. (1983) [^]
	Lancewood	3	Coleman et al. (1985) [^] ; Mason (1958) [*] ; Warburton (1978) [*]
	Puketea	3	Fitzgerald (1976) [^] ; Leathwick et al. (1983) [^] ; Mason (1958) [*]
	Bushman's Friend	3	Gilmore (1965) [*] ; Jacometti et al. (2007) ["] ; Leathwick et al. (1983) [^]
	Tawa	3	Fitzgerald (1976) [^] ; Gilmore (1965) [*] ; Mason (1958) [*]
	Titoki	3	Fitzgerald (1976) [^]
	Marbleleaf	3	Coleman et al. (1985) [^] ; Nugent et al. (1997) [*] ; Rogers (1997) [^]
	Cedar (NZ)	2	Coleman et al. (1985) [^] ; Rogers (1997) [^]
	Miro	2	Nugent et al. (1997) [*]
	Kowhai	2	Jacometti et al. (2007) ["] ; Warburton (1978) [*]
	Lemonwood	2	Jacometti et al. (2007) ["] ; Rogers (1997) [^]
	Manuka	2	Gilmore (1965) [*] ; Warburton (1978) [*]
	Matipo	2	Mason (1958) [*] ; Warburton (1978) [*]
	Black maire	1	Leathwick et al. (1983) [^]
	Konini	1	Gilmore (1965) [*]
Lacebark	1	Mason (1958) [*]	
Rimu	1	Coleman et al. (1985) [^]	
Pepperwood	1	Rogers (1997) [^]	
Rohutu	1	Cochrane et al. (2003) [*]	
Jasmine	1	Rogers (1997) [^]	

Methods of analysis are given next to the citation (analysis of faecal matter = [^], stomach contents = ^{*}, forest composition = ["], and controlled laboratory studies = ^L).

Table C2. Summary table of native fern, grass and plant species (foliage, fruit and flowers) and exotic tree species (foliage, fruit and flowers) identified as consumed by possums.

	Common name	Reports of foliage, fruit & flowers	Research
Native Ferns	Fern spp.	12	Clout (1977)*; Cochrane et al. (2003)*; Fitzgerald & Wardle (1979)^; Gilmore (1965*, 1967^); Harvie (1973)*; Leathwick et al. (1983)^; Mason (1958)*; Nugent et al. (1997)^; Purchas (1975)*.
	<i>Blechnum</i> spp.	6	Cochrane et al. (2003)*; Nugent et al. (1997)^; Sweetapple et al. (2004)".
	Prickly shield Fern	3	Cochrane et al. (2003)*; Nugent et al. (1997)^; Sweetapple et al. (2004)".
	Common Crape Fern	2	Nugent et al. (1997)^.
	Tree Fern	2	Coleman et al. (1985)^; Jacometti et al. (2007)".
	Bat's Wing Fern	2	Coleman et al. (1985)^; Nugent et al. (1997)^.
	Hound's Tongue	2	Nugent et al. (1997)^; Sweetapple et al. (2004)".
	Mother Spleenwort	2	Coleman et al. (1985)^; Nugent et al. (1997)^.
	Smooth Shield Fern	1	Cochrane et al. (2003)*;
	Soft Tree Fern	1	Coleman et al. (1985)^.
Native Grasses	Grasses spp.	5	Cochrane et al. (2003)*; Coleman et al. (1985)^; Jacometti et al. (2007)"; Nugent et al. (1997)^; Warburton (1978)*.
	Hangehange	4	Fitzgerald (1976)^; Fitzgerald & Waddington (1979)^; Gilmore (1965)*; Leathwick et al. (1983)^.
	Ryegrass	1	Gilmore (1965)*.
	Meadow grass	1	Gilmore (1965)*.
	Pampas grass	1	Jacometti et al. (2007)".
Native Plants	Pohuehue	6	Cochrane et al. (2003)*; Gilmore (1965)*; Leathwick et al. (1983)^; Nugent et al. (1997)^; Rogers (1997)^; Sweetapple et al. (2004)".
	Supplejack	4	Fitzgerald (1976)^; Fitzgerald & Wardle (1979)^; Leathwick et al. (1983)^; Mason (1958)*.
	Bush lawyer	3	Gilmore (1965)*; Jacometti et al. (2007)"; Mason (1958)*.
	Houhere	5	Coleman et al. (1980)^; Gilmore (1965*, 1967^); Leathwick et al. (1983)^; Sweetapple et al. (2004)".
	Kumarahou	2	Jacometti et al. (2007)"; Warburton (1978)*.
	Koromiko	3	Coleman et al. (1985)^; Jacometti et al. (2007)"; Warburton (1978)*.
	Tutu	3	Clout (1977)*; Jacometti et al. (2007)".
	Flax	2	Jacometti et al. (2007)".
	Toetoe	2	Jacometti et al. (2007)"; Warburton (1978)*.
	Soft Mingimingi	1	Rogers (1997)^.
Poataniwha	1	Nugent et al. (1997)^.	
Exotic Trees	Pine	4	Clout (1977)*; Gilmore (1965)*; Harvie (1973)*; Mason (1958)*.
	Poplar	1	Harvie (1973)*.
	Bluegum	3	Harvie (1973)*; Jacometti et al. (2007)"; Purchas (1975)*.
	Broom	2	Clout (1977)*; Purchas (1975)*.
	Lotus	1	Jacometti et al. (2007)".
	Macrocarpa	1	Gilmore (1965)*.
	Mexican Cypress	1	Jacometti et al. (2007)".
	Mistletoe	2	Gilmore (1965)*; Sweetapple et al. (2004)".
Eucalyptus	1	Gilmore (1965)*.	

Methods of analysis are given next to the citation (analysis of faecal matter = ^, stomach contents = *, forest composition = “, and controlled laboratory studies = L).

Table C3. Summary table of native and exotic plant species (foliage, fruit and flowers) identified as consumed by possums.

	Common name	Reports of foliage, fruit & flowers	Research
Native and Exotic Plants	Coprosma	18	Clout (1977)*; Cochrane et al. (2003)*; Coleman et al. (1985)^; Gilmore (1965*, 1967^); Harvie (1973)*; Mason (1958)*; Nugent et al. (1997)^; Rogers (1997)^; Sweetapple et al. (2004)".
	Blackberry	15	Clout (1977)*; Cochrane et al. (2003)*; Coleman et al. (1980^, 1985^); Gilmore (1965)*; Harvie (1973)*; Jacometti et al. (2007)" ; Leathwick et al. (1983)^; Nugent et al. (1997)^; Rogers (1997)^; Sweetapple et al. (2004)".
	Buttercup	7	Coleman et al. (1985)^; Fitzgerald & Wardle (1979)^; Gilmore (1967)^; Leathwick et al. (1983)^; Mason (1958)*; Nugent et al. (1997)^; Warburton (1978)*.
	Myrtle	6	Gilmore (1965*, 1967^); Mason (1958)*; Nugent et al. (1997)^; Rogers (1997)^; Warburton (1978)*.
	Clover	4	Cochrane et al. (2003)*; Coleman et al. (1985)^; Harvie (1973)*; Jacometti et al. (2007)".
	Dandelion	4	Cochrane et al. (2003)*; Gilmore (1965)*; Purchas (1975)*; Warburton (1978)*.
	Gorse	3	Cochrane et al. (2003)*; Harvie (1973)*; Jacometti et al. (2007)".
	Thistle	3	Cochrane et al. (2003)*; Jacometti et al. (2007)*; Warburton (1978)*.
	Wood	3	Cochrane et al. (2003)*; Rogers (1997)^.
	Pigeonwood	3	Fitzgerald (1976)^; Mason (1958)*; Nugent et al. (1997)^.
	Sweet Vernal	3	Gilmore (1967)^; Mason (1958)*; Warburton (1978)*.
	Tea Tree	3	Gilmore (1967)^; Leathwick et al. (1983)^; Mason (1958)*.
	Unidentified species	3	Clout (1977)^; Cochrane et al. (2003)*; Gilmore (1965)*.
	Bittercress	2	Cochrane et al. (2003)*; Purchas (1975)*.
	Boxthorn	2	Harvie (1973)*; Purchas (1975)*.
	Coral Bead Plant	2	Cochrane et al. (2003)*.
	Kumarahou	2	Jacometti et al. (2007)'; Warburton (1978)*.
	Mountain Neinei	2	Coleman et al. (1985)^; Warburton (1978)*.
	Palm	2	Fitzgerald & Wardle (1979)^; Leathwick et al. (1983)^.
	Sorrell	2	Gilmore (1967)"; Mason (1958)*.
	Willow	2	Gilmore (1965)*; Harvie (1973)*.
	Nettle	1	Cochrane et al. (2003)*.
	Wattle	1	Jacometti et al. (2007)".
	Scrub	1	Clout (1977)*.
	Urban Garden	1	Clout (1977)*.
	Pasture	1	Clout (1977)*.
	Catsear	1	Warburton (1978)*.
	Clubmoss spp.	1	Cochrane et al. (2003)*.
	Common rush	1	Jacometti et al. (2007)".
	Cudweed	1	Warburton (1978)*.
	Dichondra	1	Warburton (1978)*.
	Fireweed	1	Jacometti et al. (2007)'.
	Hawksweed	1	Cochrane et al. (2003)*.
	Orchard	1	Clout (1977)*.
Pokaka	1	Gilmore (1965)*.	
Poroporo	1	Mason (1958)*.	
Quintinia	1	Coleman et al. (1985)^.	
Slender Birdsfoot Treefoil	1	Jacometti et al. (2007)".	
Wood groundsel	1	Warburton (1978)*.	
Wooly mullein	1	Warburton (1978)*.	
Yarrow	1	Gilmore (1965)*.	

Methods of analysis are given next to the citation (analysis of faecal matter = ^, stomach contents = *, forest composition = “, and controlled laboratory studies = L).

Table C4. Summary table of native fern, grass and plant species (foliage, fruit and flowers) and exotic tree species (foliage, fruit and flowers) identified as consumed by possums.

	Common name	Reports of foliage, fruit & flowers	Research
Moss	Moss	4	Cochrane et al. (2003)*; Nugent et al. (1997) [^] ; Rogers (1997) [^] ; Warburton (1978)*.
Fungi	Fungi	3	Cochrane et al. (2003)*; Nugent et al. (1997) [^] ; Sweetapple et al. (2004) [^] .
Lichen	Lichen	2	Harvie (1973)*; Nugent et al. (1997) [^] .
Herbs	Herb (Dicotyledonoyus)	3	Nugent et al. (1997) [^] ; Rogers (1997) [^] ; Sweetapple et al. (2004) [^] .
Other	Bark	4	Cochrane et al. (2003)*; Clout (1977)*; Harvie (1973)*; Rogers (1997) [^] .
	Pollen cones	2	Clout (1977)*.
	Bracken	1	Jacometti et al. (2007) [^] .
	Soil	1	Harvie (1973)*.
Invertebrates	Larvae	4	Cowan & Moeed (1987)*; Clout (1977)*; Nugent et al. (1997) [^] ; Warburton (1978)*.
	Cicada	2	Cowan & Moeed (1987)*; Harvie (1973)*.
	Non-specified	2	Nugent et al. (1997) [^] ; Rogers (1997) [^] .
	Mite	2	Cochrane et al. (2003)*; Cowan & Moeed (1987)*.
	Stick Insect	1	Cowan & Moeed (1987)*.
	Weta	1	Cowan & Moeed (1987)*.
	Beetle	1	Cowan & Moeed (1987)*.
Birds ^{Note}	Sparrow	2	Brown et al. (1993) [^] ; Morgan (1981) [^] .
	Birds	2	Brown et al. (1993) [^] ; 1996) [^] .
Eggs ^{Note}	Hen eggs	2	Brown et al. (1993) [^] ; 1996) [^] .

Note: For birds and eggs food availability was controlled.

Methods of analysis are given next to the citation (analysis of faecal matter = [^], stomach contents = *, forest composition = “, and controlled laboratory studies = ^L).

Appendix D.

Supplementary Figures

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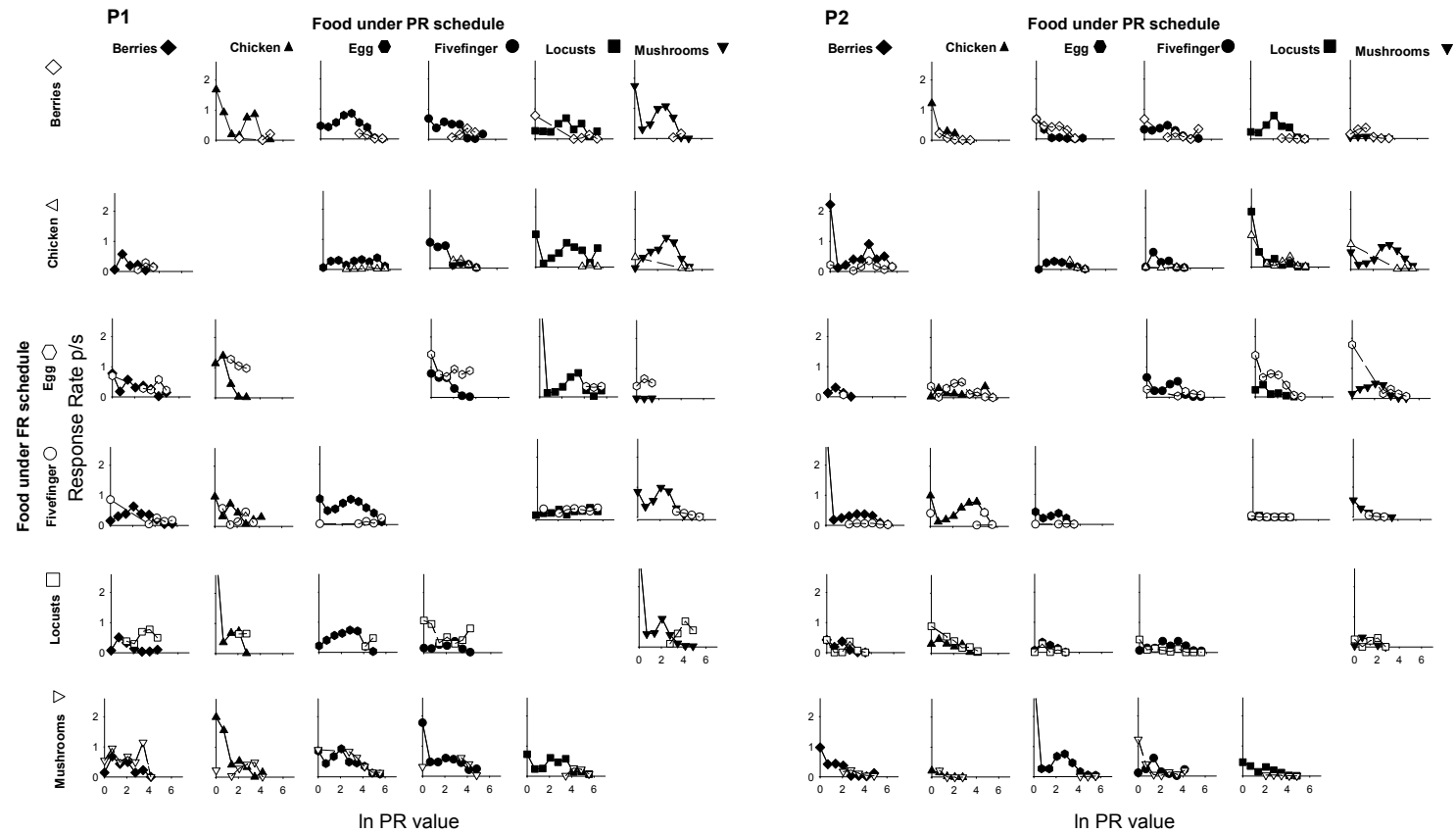


Figure D1. Response rate (per sec) of each food on the PR FR schedule for P1 and P2 averaged across days in Experiment 3. Filled symbols represent foods on the PR schedule, and unfilled symbols represent foods on the FR schedule.

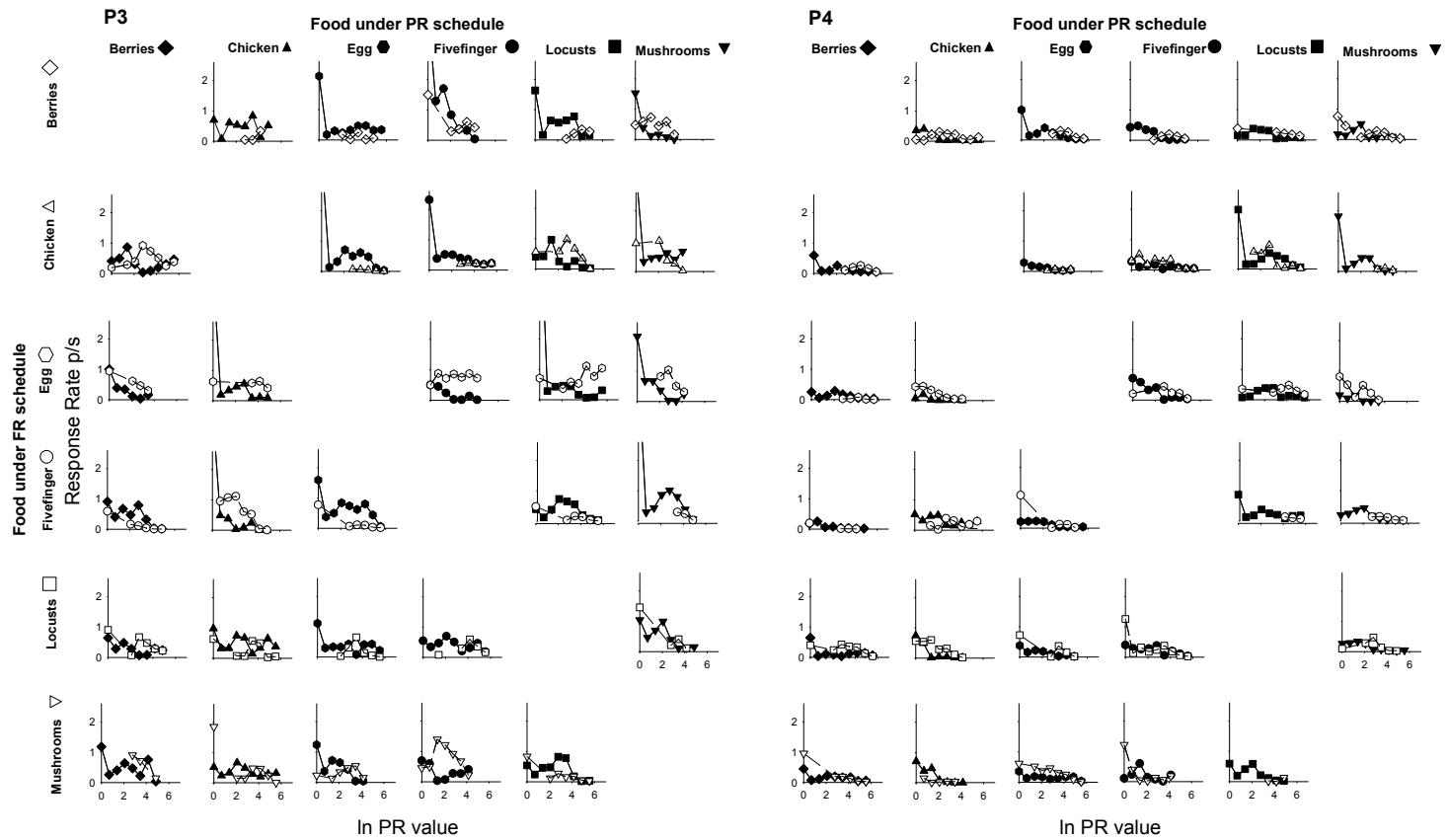


Figure D2. Response rate (per sec) of each food on the PR FR schedule for P3 and P4 averaged across days in Experiment 3. Filled symbols represent foods on the PR schedule, and unfilled symbols represent foods on the constant FR schedule.

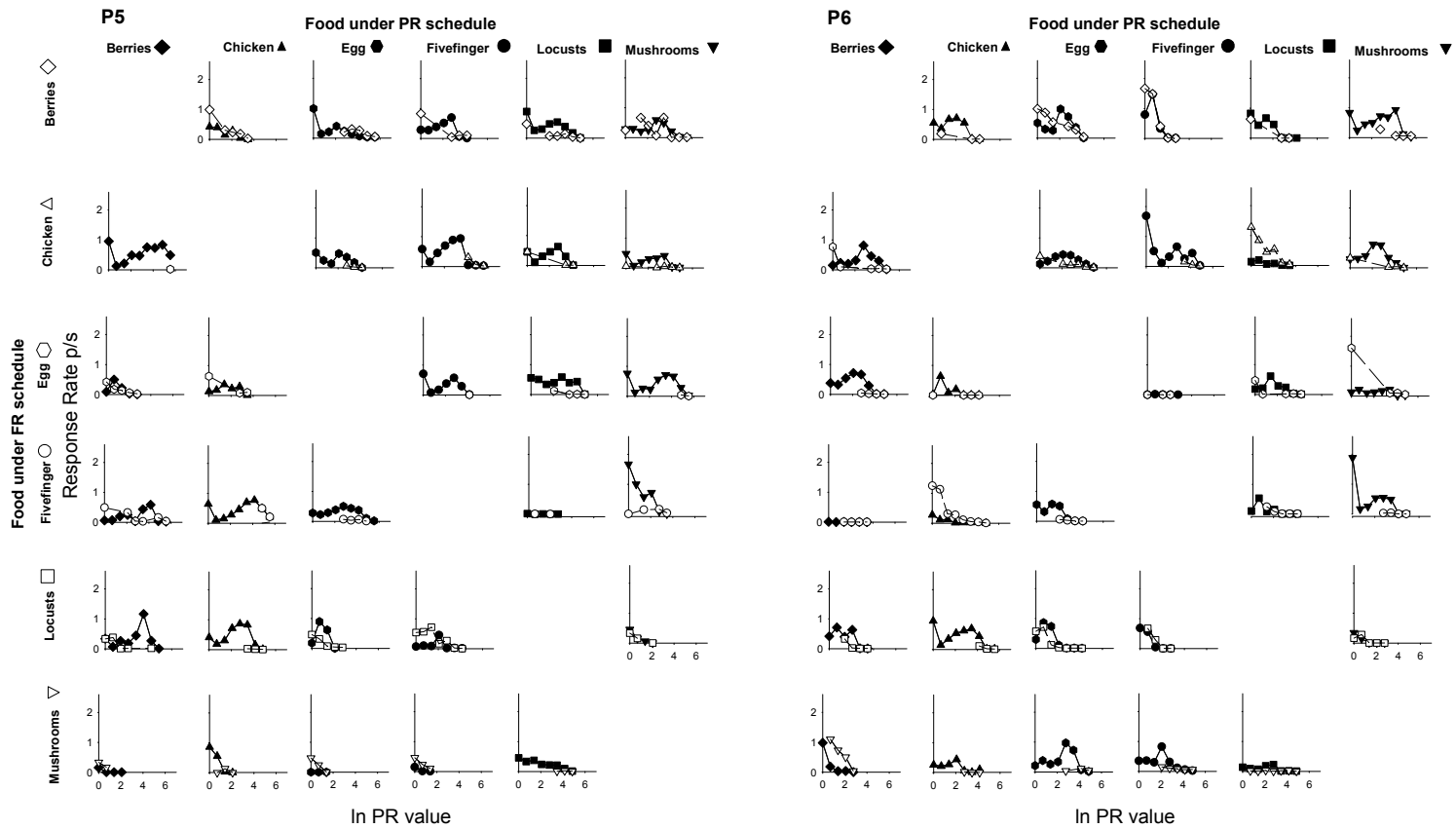


Figure D3. Response rate (per sec) of each food on the PR FR schedule for P5 and P6 averaged across days in Experiment 3. Filled symbols represent foods on the PR schedule, and unfilled symbols represent foods on the constant FR schedule.

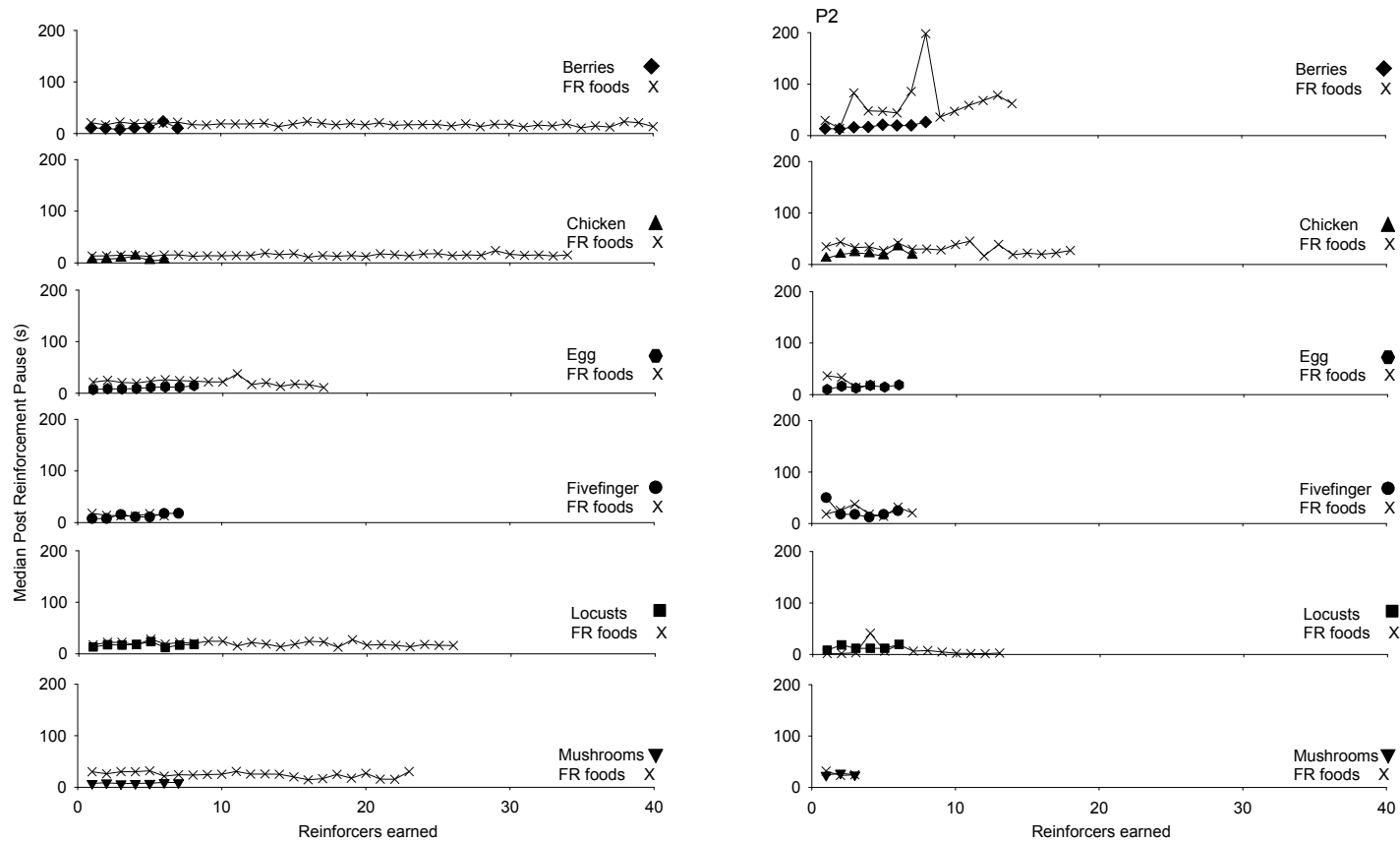


Figure D4. Median Post Reinforcement Pause (per sec) of each food on the PR FR schedule for P1 and P2 across days in Experiment 3. Filled symbols represent foods on the PR schedule, and the cross represents the median of all foods on the constant FR schedule.

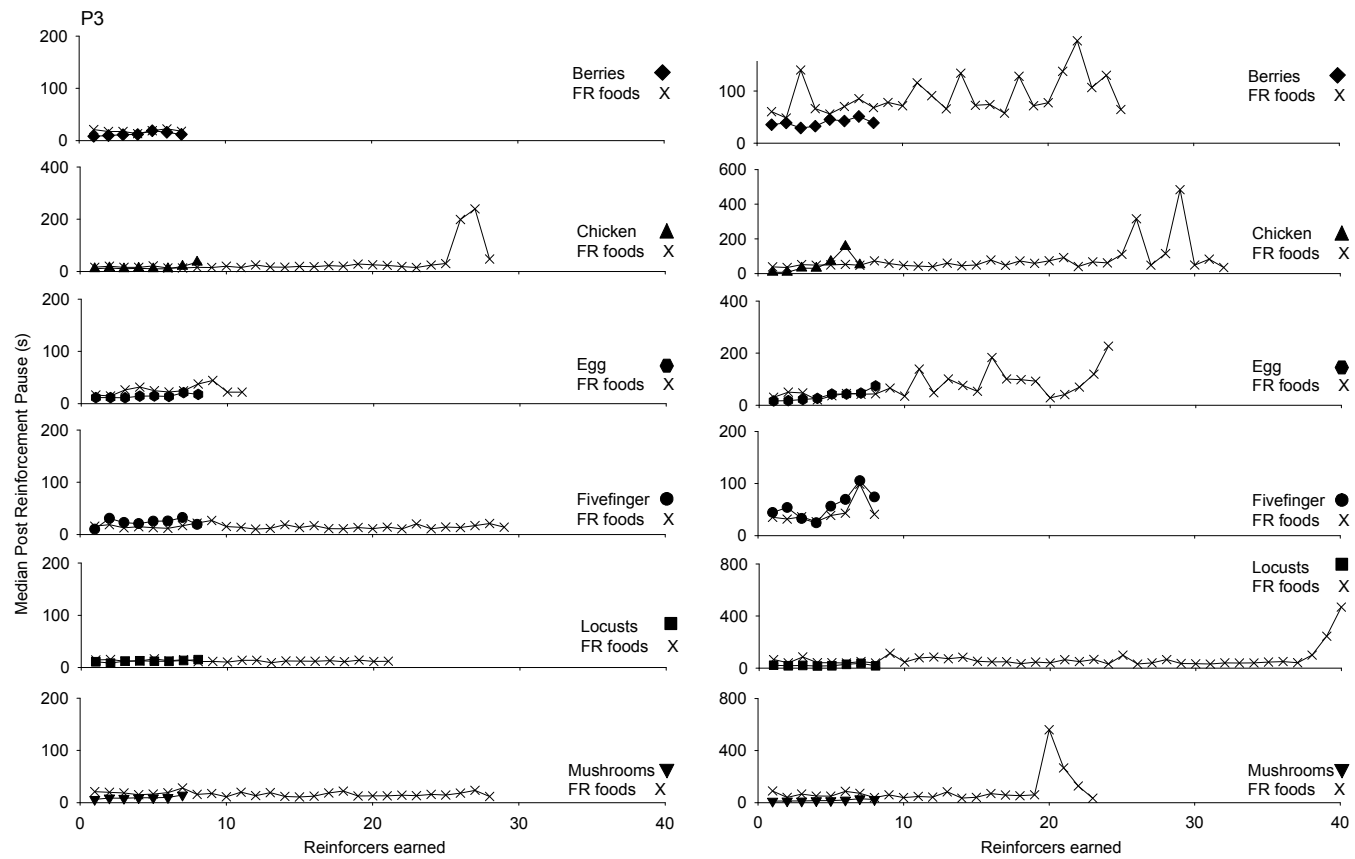


Figure D5. Median Post Reinforcement Pause (per sec) of each food on the PR FR schedule for P3 and P4 across days in Experiment 3. Filled symbols represent foods on the PR schedule, and the cross represents the median of all foods on the constant FR schedule.

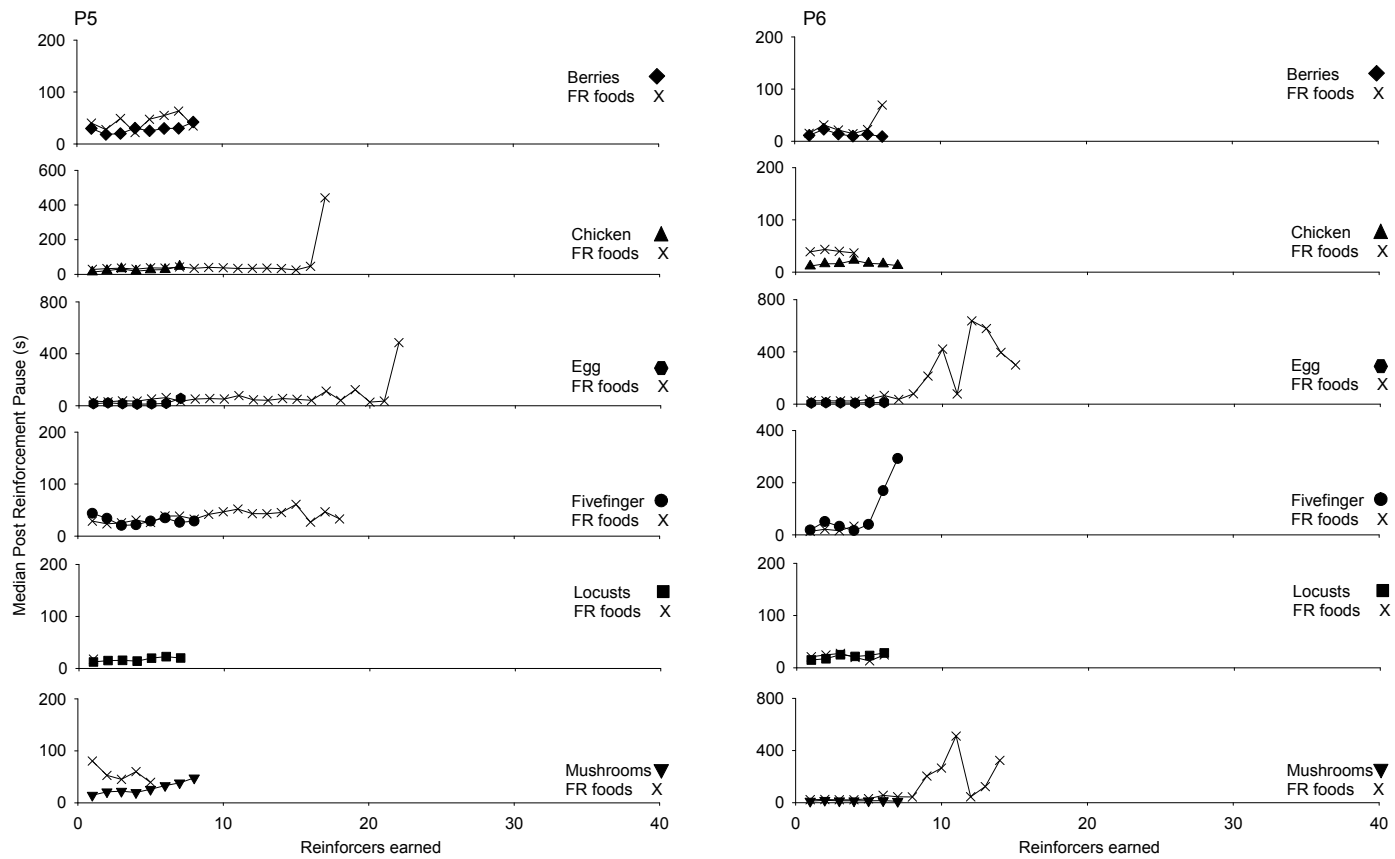


Figure D6. Median Post Reinforcement Pause (per sec) of each food on the PR FR schedule for P5 and P6 across days in Experiment 3. Filled symbols represent foods on the PR schedule, and the cross represents the median of all foods on the constant FR schedule.

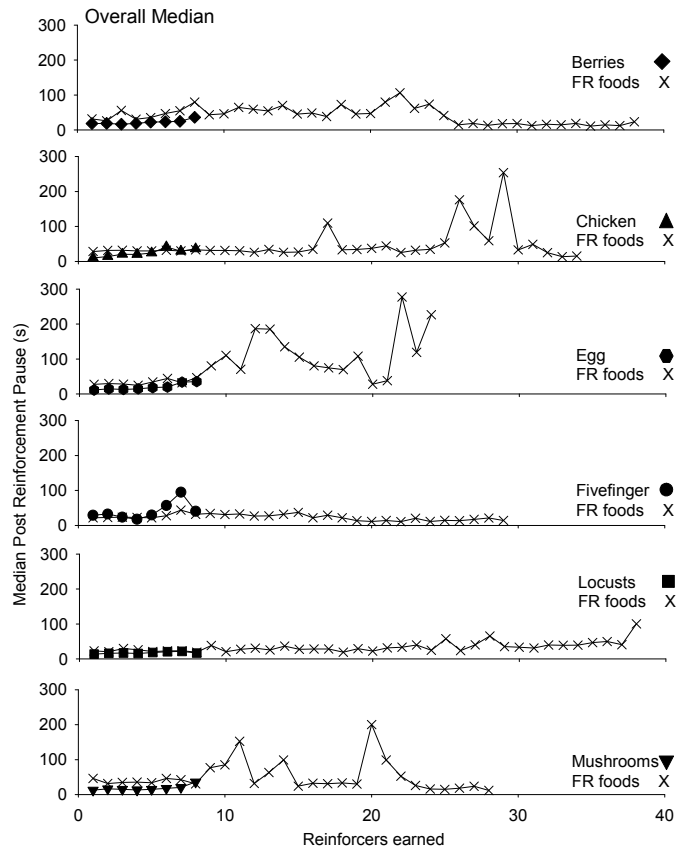


Figure D7. Overall Median Post Reinforcement Pause (per sec) of each food on the PR FR schedule for all possums across days in Experiment 3. Filled symbols represent foods on the PR schedule, and the cross represents the median of all foods on the constant FR schedule

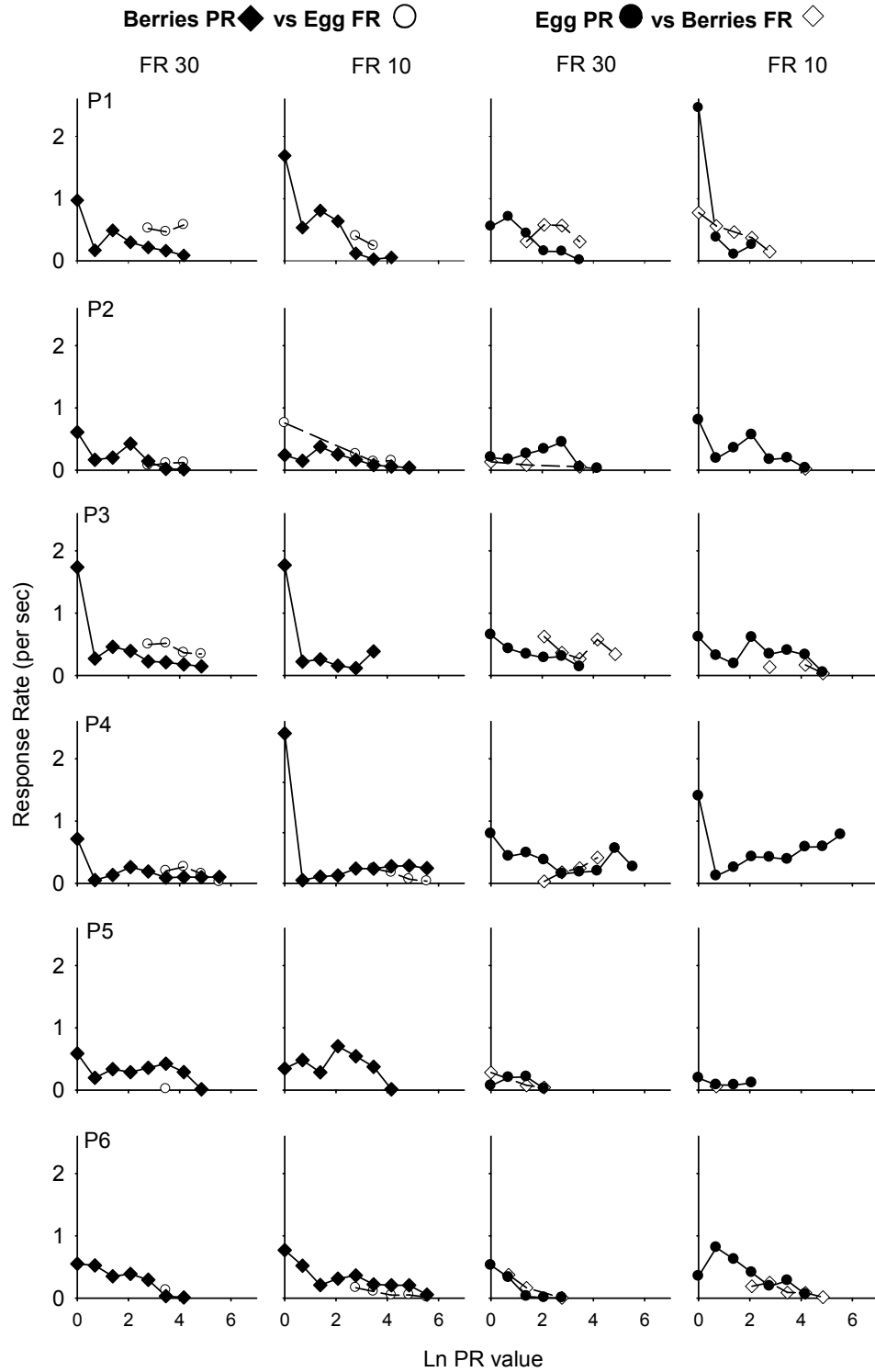


Figure D8. Response rate (per sec) of each food on the PR and PFR schedules and constant FR schedule for P1 - 6 averaged across days for berries and egg in the FR 30 and FR 10 condition in Experiment 4. Filled symbols represent foods on the PR schedule, and unfilled symbols represent foods on the constant FR schedule.

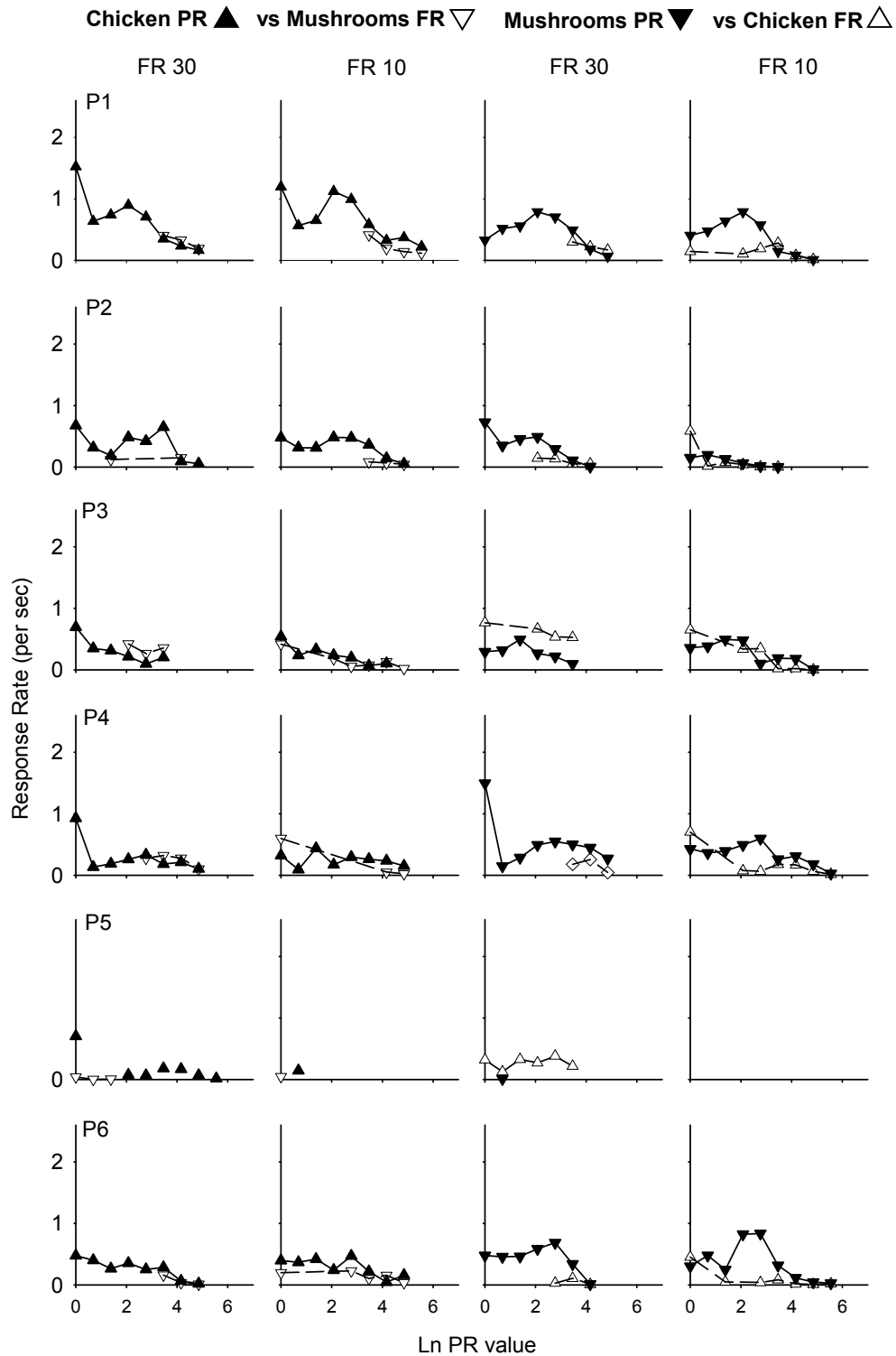


Figure D9. Response rate (per sec) of each food on the PR and PFR schedules and constant FR schedule for P1 - 6 averaged across days for chicken and mushroom in the FR 30 and FR 10 condition in Experiment 4. Filled symbols represent foods on the PR schedule, and unfilled symbols represent foods on the constant FR schedule.

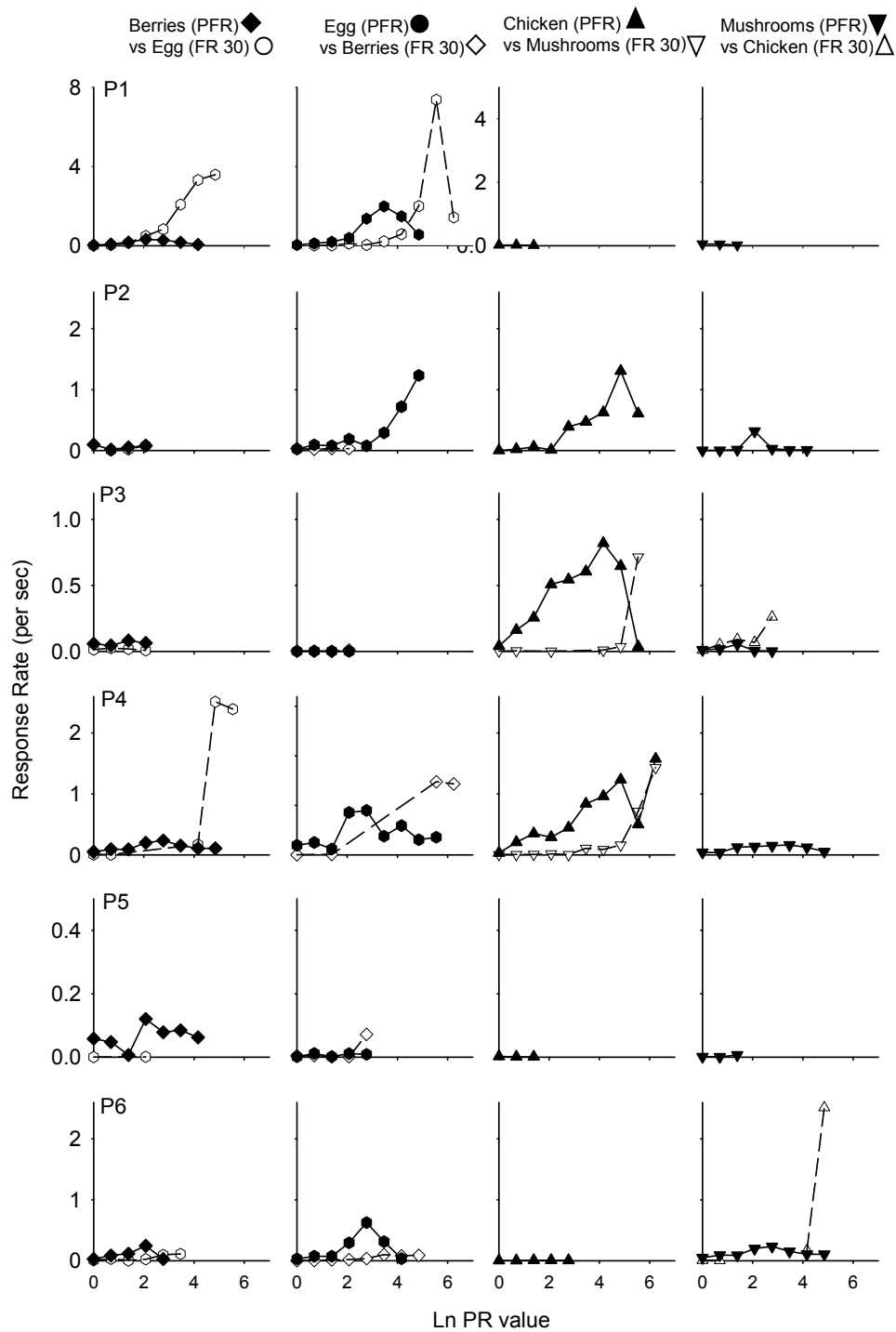


Figure D10. Response rate (per sec) of each food on the PR and PFR schedules and constant FR schedule for P1 - 6 averaged across days for all foods for Experiment 5. Filled symbols represent foods on the PR schedule, and unfilled symbols represent foods on the constant FR schedule.

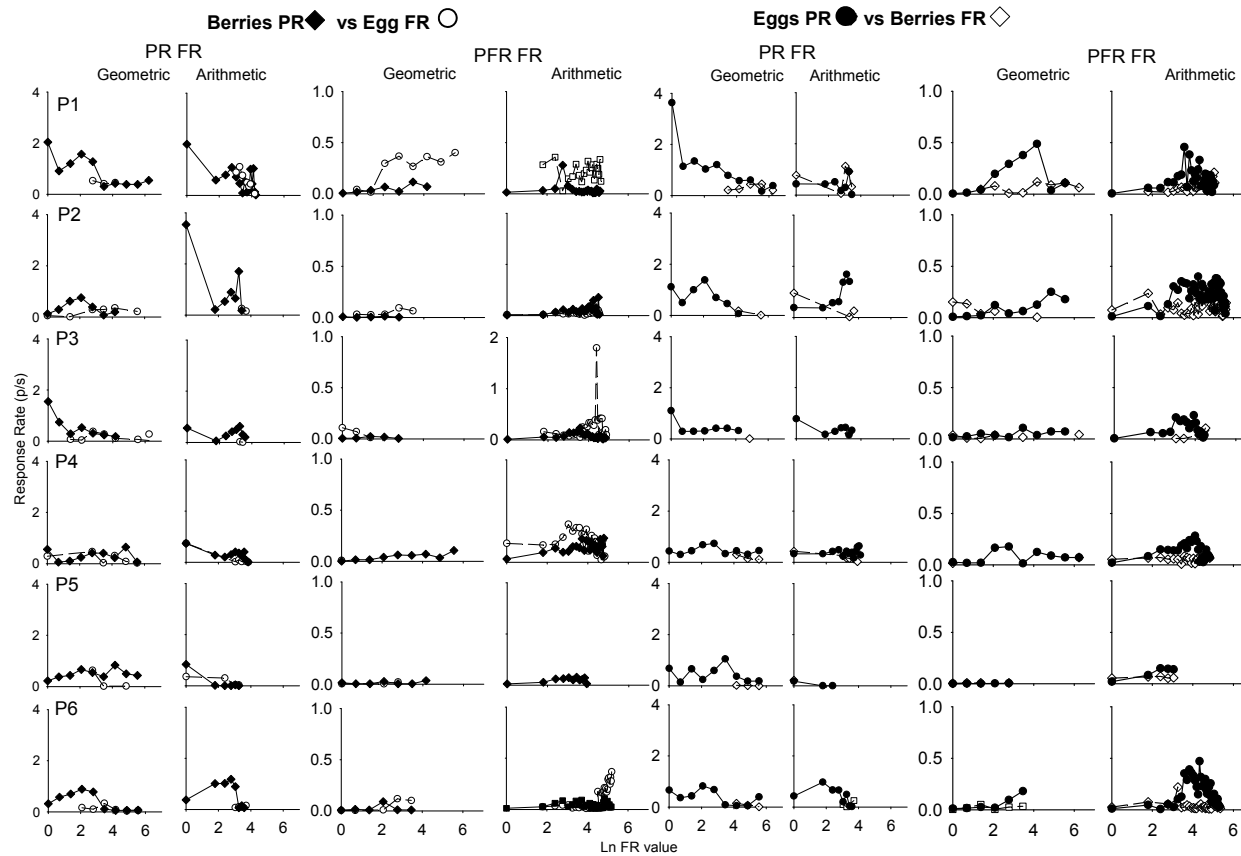


Figure D11. Response rate (per sec) of each food on the PR FR schedule for P1-6 averaged across days for berries and egg for Experiment 6. Filled symbols represent foods on the PR schedule, and unfilled symbols represent foods on the constant FR schedule.

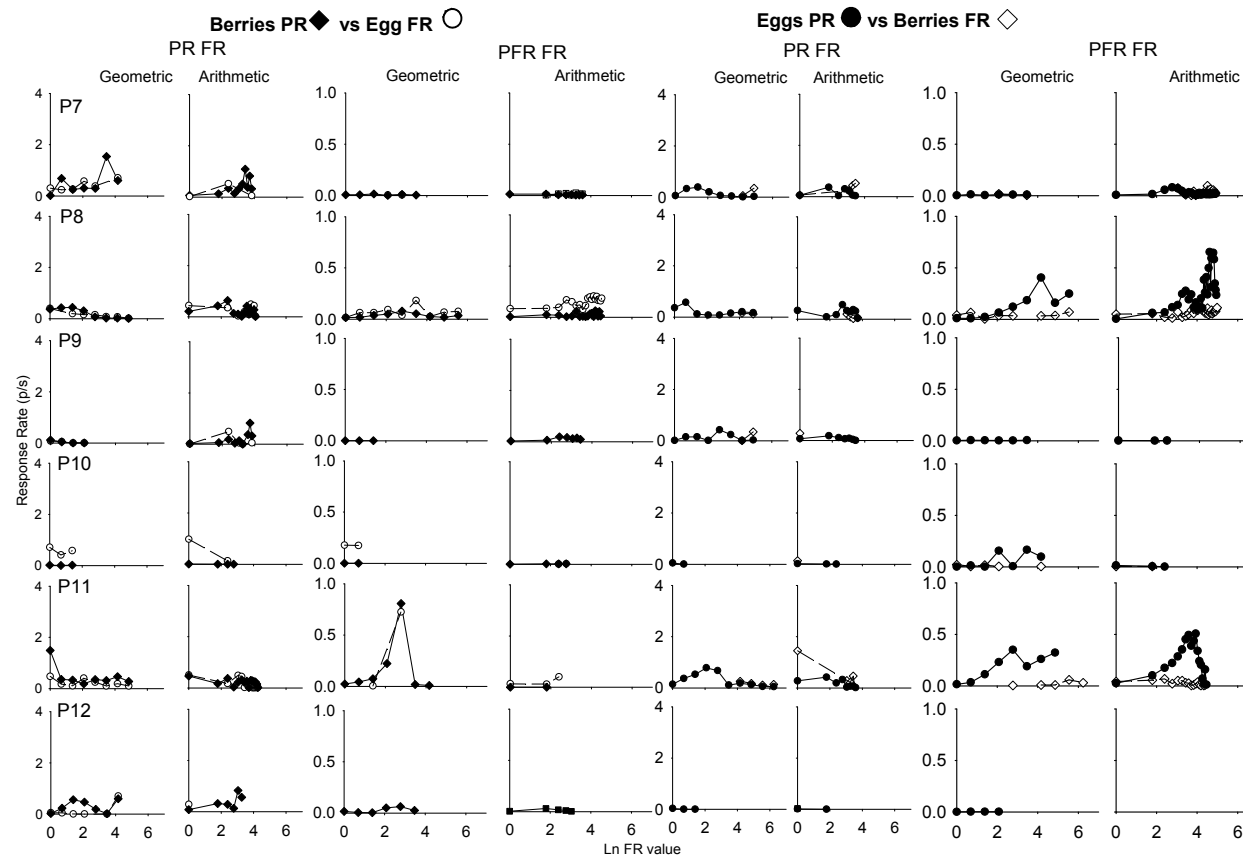


Figure D12. Response rate (per sec) of each food on the PR and PFR schedules and constant FR schedule for P7-12 averaged across days for berries and egg for Experiment 6. Filled symbols represent foods on the PR schedule, and unfilled symbols represent foods on the constant FR schedule.

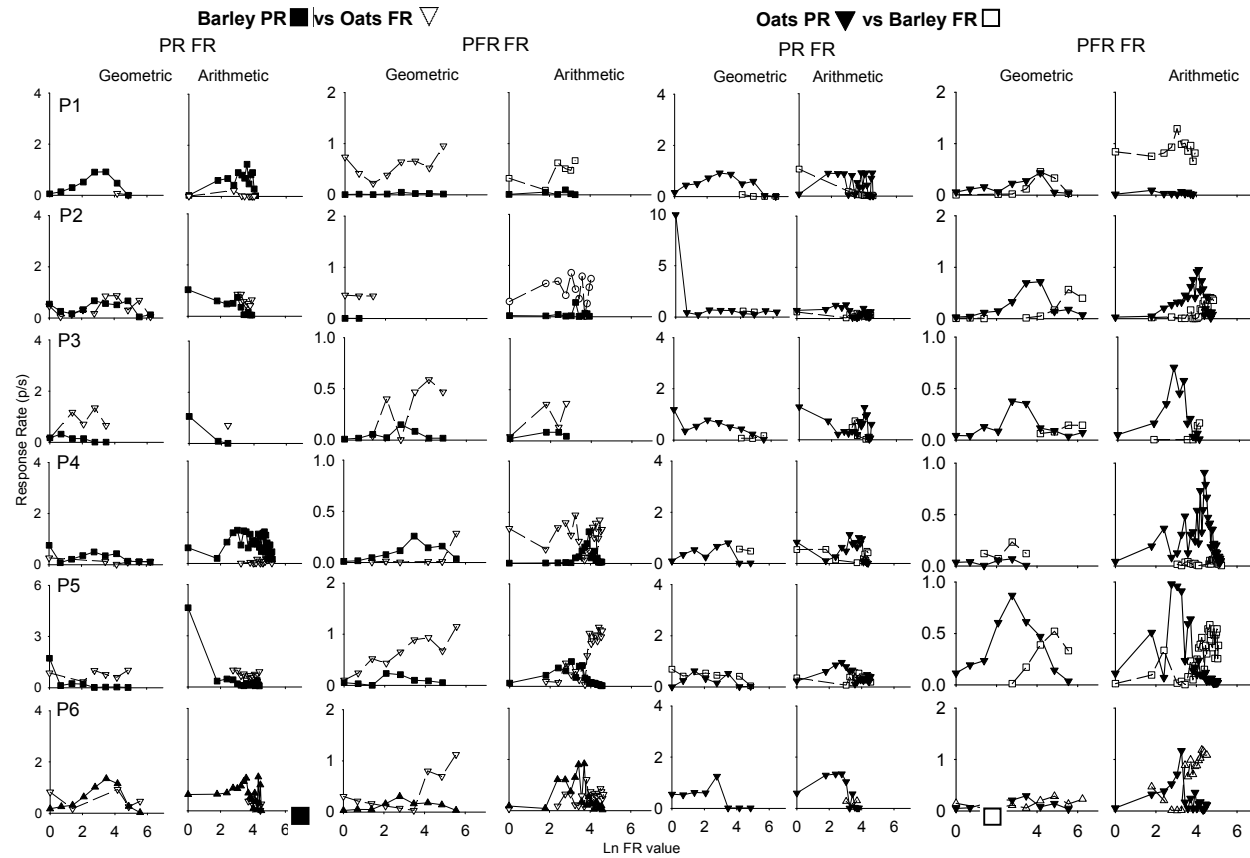


Figure D13. Response rate (per sec) of each food on the PR and PFR schedules and constant FR schedule for P1-6 averaged across days for barley and oats for Experiment 6. Filled symbols represent foods on the PR schedule, and unfilled symbols represent foods on the constant FR schedule.

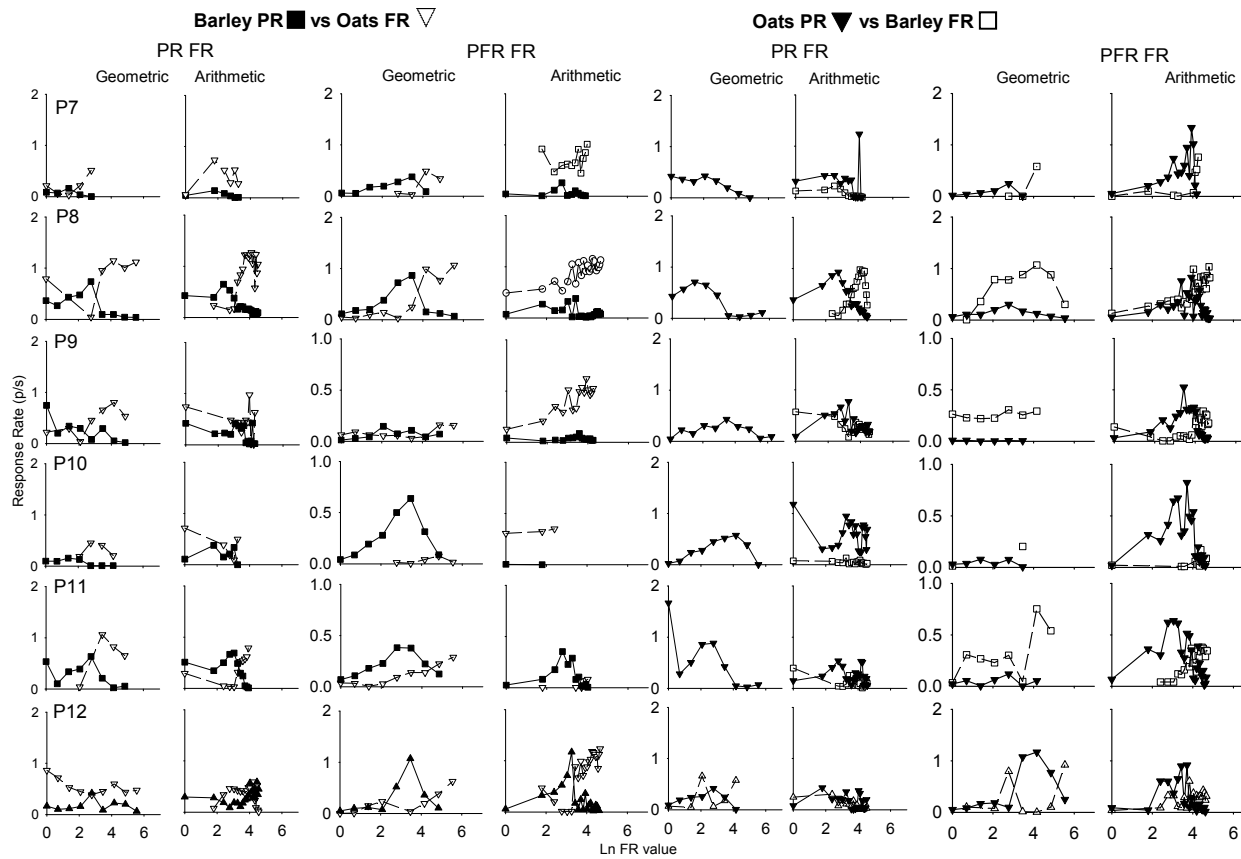


Figure D14. Response rate (per sec) of each food on the PR and PFR schedules and constant FR schedule for P7-12 averaged across days for barley and oats for Experiment 6. Filled symbols represent foods on the PR schedule, and unfilled symbols represent foods on the constant FR schedule.

Appendix E.

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Table E1. Parameter estimates for initial demand, Q_0 ; essential value, α ; P_{max} , interaction, I , and sensitivity, β ; break point and cross point data for P1 in Experiment 3.

PR(FR)	a	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{max}	BP	I	β	Q_{alone}	VAC	SE	df	Xpt
B(C)	0.190	0.072	-2.638	11.143	0.880	2.434	1	1.31	8	-	-	-	-	-	-	-
B(C)	0.112	0.126	-2.074	11.143	0.953	1.194	3	1.26	32	-	-	-	-	-	-	-
B(C)	-	-	-	11.143	-	-	-	-	-	-	-	-	-	-	-	-
B(E)	0.060	0.073	-2.616	11.143	0.989	0.483	3	4.04	32	-	-	-	-	-	-	-
B(E)	0.067	0.324	-1.128	11.143	0.987	0.523	2	0.81	16	-	-	-	-	-	-	-
B(E)	0.053	0.287	-1.248	11.143	0.951	1.348	4	1.17	64	-74.14	0.417	0.022	0.983	-	0	31.39
B(F)	0.081	0.042	-3.165	11.143	0.974	0.922	5	5.17	128	-	-	-	-	-	-	-
B(F)	0.065	0.107	-2.230	11.143	0.982	0.796	5	2.53	128	-1.008	-1.357	0.027	0.953	2.155	1	-
B(F)	0.047	0.183	-1.698	11.143	0.991	0.560	5	2.08	128	-0.930	-0.027	0.012	0.974	-	0	-
B(L)	0.104	0.382	-0.963	11.143	0.948	1.410	2	0.44	16	-9.306	0.708	0.032	1.000	-	0	8.00
B(L)	0.175	0.123	-2.098	11.143	0.951	1.460	3	0.83	32	-0.484	-0.126	0.032	0.989	0.894	1	8.48
B(L)	0.290	0.048	-3.044	11.143	0.975	1.055	3	1.28	32	-42.70	4.759	0.030	0.999	-	0	3.75
B(M)	0.031	0.720	-0.329	11.143	0.992	0.531	4	0.79	64	-	-	-	-	-	-	-
B(M)	0.003	0.031	-3.463	11.143	0.906	-	0	194.85	4	-0.335	-3.859	0.033	0.996	0.498	1	-
B(M)	0.191	0.186	-1.681	11.143	0.957	1.379	2	0.50	16	-5.297	3.490	0.032	1.000	-	0	5.29
C(B)	0.411	77.282	4.347	11.143	0.916	4.134	1	0.00	8	-	-	-	-	-	-	-
C(B)	0.080	0.114	-2.173	11.143	0.964	1.053	4	1.96	64	-	-	-	-	-	-	-
C(B)	-	-	-	-	-	-	0	-	1	-	-	-	-	-	-	-
C(E)	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-
C(E)	0.130	0.379	-0.971	11.143	0.921	0.147	2	0.36	16	-	-	-	-	-	-	-
C(E)	0.002	211.92	5.356	11.143	0.997	0.931	1	0.04	8	-8.492	0.075	0.044	0.998	-	0	-
C(F)	0.089	0.731	-0.313	11.143	0.948	1.664	2	0.27	16	-	-	-	-	-	-	-
C(F)	0.042	0.503	-0.688	11.143	0.947	1.135	3	0.85	32	-	-	-	-	-	-	-
C(F)	0.036	0.452	-0.795	11.143	0.912	1.220	3	1.09	32	-	-	-	-	-	-	-
C(L)	0.075	0.758	-0.277	11.143	0.946	1.350	1	0.31	8	-	-	-	-	-	-	-
C(L)	0.021	2.444	0.894	11.143	0.860	3.011	1	0.35	8	-	-	-	-	-	-	-
C(L)	0.040	0.396	-0.927	11.143	0.929	1.047	1	1.11	8	-	-	-	-	-	-	-
C(M)	0.131	0.288	-1.245	11.143	0.986	0.853	3	0.47	32	-0.069	-40.93	0.040	0.989	-	0	-
C(M)	0.140	0.153	-1.874	11.143	0.581	2.409	2	0.83	16	-	-	-	-	-	-	-
C(M)	0.140	0.167	-1.791	11.143	0.793	2.967	3	0.76	32	-	-	-	-	-	-	-
E(B)	0.050	0.122	-2.108	11.143	0.975	0.731	4	2.90	64	-0.010	-0.374	0.010	0.998	-	0	40.98
E(B)	0.031	0.241	-1.421	11.143	0.979	0.627	4	2.34	64	-	-	-	-	-	-	-

PR(FR)	a	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{max}	BP	l	θ	Q_{alone}	VAC	SE	df	Xpt
E(B)	0.025	0.313	-1.160	11.143	0.985	0.624	5	2.25	128	-	-	-	-	-	-	-
E(C)	0.319	0.065	-2.731	11.143	0.971	1.239	3	0.85	32	-	-	-	-	-	-	-
E(C)	0.046	0.065	-2.730	11.143	0.976	0.767	5	5.90	128	-	-	-	-	-	-	-
E(C)	0.042	0.114	-2.172	11.143	0.815	2.566	5	3.67	128	-	-	-	-	-	-	-
E(F)	0.026	0.310	-1.171	11.143	0.959	1.146	5	2.17	128	-0.312	-2.330	0.008	0.996	-	0	-
E(F)	0.028	0.085	-2.464	11.143	0.987	0.637	5	7.53	256	-	-	-	-	-	-	-
E(F)	0.029	0.099	-2.315	11.143	0.945	1.065	5	6.11	128	-	-	-	-	-	-	-
E(L)	0.032	0.241	-1.421	11.143	0.995	0.282	4	2.26	64	-	-	-	-	-	-	-
E(L)	0.047	0.135	-1.999	11.143	0.978	0.680	4	2.81	64	-	-	-	-	-	-	-
E(L)	0.040	0.194	-1.642	11.143	0.998	0.168	4	2.31	64	-	-	-	-	-	-	-
E(M)	0.058	0.057	-2.866	11.143	0.938	1.338	5	5.38	128	-0.324	-0.130	0.031	0.997	0.309	3	698.05
E(M)	0.018	0.448	-0.804	11.143	0.929	1.097	4	2.23	64	-	-	-	-	-	-	-
E(M)	0.056	0.138	-1.980	11.143	0.970	0.856	4	2.30	64	-	-	-	-	-	-	-
F(B)	0.042	0.495	-0.703	11.143	0.962	1.188	4	0.85	64	-	-	-	-	-	-	-
F(B)	0.053	0.125	-2.079	11.143	0.964	0.818	2	2.65	16	-	-	-	-	-	-	-
F(B)	0.156	0.152	-1.882	11.143	0.925	1.886	3	0.75	32	-1.964	0.000	0.014	0.980	-	0	17.95
F(C)	0.043	0.492	-0.709	11.143	0.904	1.649	3	0.83	32	-0.001	-0.257	0.008	1.000	-	0	21.57
F(C)	0.143	0.174	-1.747	11.143	0.923	1.897	3	0.71	32	-	-	-	-	-	-	-
F(C)	0.048	1.517	0.417	11.143	0.989	0.604	1	0.25	8	-	-	-	-	-	-	-
F(E)	0.032	1.245	0.219	11.143	0.977	0.946	3	0.44	32	-	-	-	-	-	-	-
F(E)	0.005	0.308	-1.177	11.143	0.827	2.807	1	11.54	8	-	-	-	-	-	-	-
F(E)	0.507	0.437	-0.827	11.143	0.696	-	0	0.08	4	30.229	153.57	0.049	0.980	-	0	-
F(L)	0.052	0.319	-1.143	11.143	0.991	0.439	3	1.06	32	-	-	-	-	-	-	-
F(L)	0.813	0.036	-3.331	11.143	0.981	1.261	1	0.61	8	-0.368	-2.307	0.030	0.991	-	0	54.60
F(L)	0.047	0.029	-3.542	11.143	0.853	3.096	2	13.05	16	-0.396	-1.499	0.037	0.993	0.560	2	-
F(M)	0.018	0.560	-0.581	11.143	0.941	1.070	4	1.74	2	-	-	-	-	-	-	-
F(M)	0.038	0.304	-1.190	11.143	0.920	1.528	4	1.54	2	-	-	-	-	-	-	-
F(M)	0.071	0.175	-1.742	11.143	0.974	0.710	2	1.42	2	-	-	-	-	-	-	-
L(B)	0.062	0.056	-2.877	11.143	0.994	0.422	5	5.07	128	-	-	-	-	-	-	-
L(B)	0.049	0.116	-2.156	11.143	0.975	0.873	5	3.11	128	-	-	-	-	-	-	-
L(B)	0.059	0.454	-0.789	11.143	0.914	1.762	3	0.66	32	-	-	-	-	-	-	-
L(C)	0.046	0.304	-1.191	11.143	0.933	1.513	4	1.27	64	-	-	-	-	-	-	-
L(C)	0.026	0.145	-1.930	11.143	0.941	1.127	5	4.63	128	-	-	-	-	-	-	-
L(C)	0.049	0.109	-2.213	11.143	0.969	0.943	5	3.31	128	-	-	-	-	-	-	-
L(E)	0.053	0.140	-1.968	11.143	0.905	1.619	4	2.39	64	-	-	-	-	-	-	-

PR(FR)	a	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{max}	BP	l	β	Q_{alone}	VAC	SE	df	Xpt
L(E)	0.027	0.349	-1.053	11.143	0.932	1.821	5	1.88	128	-0.668	0.012	0.012	0.997	-	0	-
L(E)	0.065	0.028	-3.564	11.143	0.959	1.085	4	9.61	64	-	-	-	-	-	-	-
L(F)	0.095	0.015	-4.175	11.143	0.977	0.036	6	12.16	256	-0.392	-13.82	0.013	0.991	0.664	3	36.58
L(F)	0.059	0.035	-3.360	11.143	0.958	1.199	6	8.70	256	-1.584	1.639	0.011	0.943	1.632	3	130.10
L(F)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
L(M)	0.079	0.043	-3.154	11.143	0.966	1.047	5	5.24	128	-0.382	-3.617	0.011	0.996	-	0	-
L(M)	0.033	0.214	-1.542	11.143	0.966	1.001	5	2.52	128	-0.171	-5.180	0.014	0.998	-	0	-
L(M)	0.037	0.136	-1.992	11.143	0.948	1.179	5	3.47	128	-0.038	-0.126	0.007	1.000	-	0	62.39
M(B)	0.023	0.428	-0.848	11.143	0.896	1.211	3	1.82	32	-	-	-	-	-	-	-
M(B)	0.002	1.287	0.253	11.143	0.885	1.277	2	6.68	16	-	-	-	-	-	-	-
M(B)	0.001	2.060	0.723	11.143	0.923	0.701	4	5.99	64	-	-	-	-	-	-	-
M(C)	0.031	0.171	-1.768	11.143	0.996	0.267	4	3.40	64	-	-	-	-	-	-	-
M(C)	0.045	0.122	-2.101	11.143	0.921	1.311	4	3.25	64	-	-	-	-	-	-	-
M(C)	0.031	0.046	-3.078	11.143	0.909	1.483	3	12.38	32	-	-	-	-	-	-	-
M(E)	-	-	-	-	-	-	0	-	2	-	-	-	-	-	-	-
M(E)	-	-	-	-	-	-	0	-	2	-	-	-	-	-	-	-
M(E)	0.003	0.003	-5.755	11.143	0.998	-	0	1939.3	4	-0.107	-119.8	0.026	0.998	-	0	-
M(F)	0.055	0.116	-2.157	11.143	0.963	1.117	5	2.77	128	-	-	-	-	-	-	-
M(F)	0.072	0.148	-1.908	11.143	0.977	0.844	4	1.66	64	-0.385	-0.107	0.011	0.994	-	0	32.16
M(F)	0.026	1.128	0.121	11.143	0.952	1.473	4	0.60	64	-	-	-	-	-	-	-
M(L)	0.145	0.103	-2.274	11.143	0.936	1.522	3	1.19	32	-94.43	0.509	0.031	1.000	-	0	17.76
M(L)	0.020	0.967	-0.034	11.143	0.946	1.576	4	0.91	64	-0.371	-0.009	0.032	0.987	-	0	-
M(L)	0.073	0.126	-2.068	11.143	0.955	1.162	4	1.93	64	-83.37	0.941	0.029	1.000	-	0	34.81

Note: B = Berries, C = Chicken, E = Egg, F = Foliage, L = Locusts & M = Mushrooms.

Table E2. Parameter estimates for initial demand, Q_0 , essential value, α ; P_{\max} , interaction, I , and sensitivity, β ; break point and cross point data for P2 in Experiment 3.

PR(FR)	α	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{\max}	BP	I	β	Q_{alone}	VAC	SE	df	Xpt
B(C)	0.234	0.018	-4.006	11.116	0.974	1.148	5	4.16	128	-0.621	-0.301	0.011	0.993	0.659	3	25.23
B(C)	0.026	0.092	-2.390	11.116	0.892	2.021	5	7.40	256	-2.748	-0.005	0.092	0.999	0.265	1	126.66
B(C)	0.021	0.149	-1.905	11.116	0.922	1.680	5	5.73	256	-	-	-	-	-	-	-
B(E)	0.104	0.363	-1.014	11.116	0.959	-	0	0.47	4	-	-	-	-	-	-	-
B(E)	-	-	-	-	-	-	0	-	1	-	-	-	-	-	-	-
B(E)	0.107	6.355	1.849	11.116	0.981	-	0	0.03	4	-	-	-	-	-	-	-
B(F)	0.065	0.061	-2.800	11.116	0.986	0.649	5	4.53	128	-	-	-	-	-	-	-
B(F)	0.053	0.080	-2.529	11.116	0.981	0.724	5	4.17	128	-	-	-	-	-	-	-
B(F)	0.028	0.443	-0.814	11.116	0.906	1.994	4	1.42	64	-	-	-	-	-	-	-
B(L)	0.036	2.016	0.701	11.116	0.991	0.609	2	0.24	16	-	-	-	-	-	-	-
B(L)	0.093	8.362	2.124	11.116	0.982	-	0	0.02	4	-	-	-	-	-	-	-
B(L)	-	-	-	-	-	-	0	-	1	-	-	-	-	-	-	-
B(M)	0.047	1.196	0.179	11.116	0.991	0.681	3	0.31	32	-3.751	0.038	0.004	0.940	-	0	18.64
B(M)	0.063	0.330	-1.110	11.116	0.963	1.285	4	0.85	64	-3.029	-0.023	0.330	1.000	-	0	-
B(M)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
C(B)	0.013	43.662	3.776	11.116	0.948	2.850	1	0.03	8	-	-	-	-	-	-	-
C(B)	0.074	0.759	-0.276	11.116	0.929	1.791	2	0.32	16	-	-	-	-	-	-	-
C(B)	0.071	0.980	-0.020	11.116	0.981	0.982	2	0.25	16	-	-	-	-	-	-	-
C(E)	0.151	0.198	-1.619	11.116	0.979	0.072	3	0.59	32	-2.826	-0.010	0.198	0.978	-	0	20.09
C(E)	0.410	0.017	-4.088	11.116	0.903	0.031	4	2.59	64	-0.481	-0.966	0.026	0.992	0.288	4	54.60
C(E)	0.098	0.007	-4.909	11.116	0.936	0.011	5	24.56	128	-0.923	-0.825	0.014	0.984	1.632	1	148.41
C(F)	0.030	0.103	-2.270	11.116	0.936	1.565	5	5.79	256	-	-	-	-	-	-	-
C(F)	0.031	0.085	-2.469	11.116	0.937	1.161	5	6.86	128	-	-	-	-	-	-	-
C(F)	0.033	0.102	-2.282	11.116	0.965	0.880	5	5.28	128	-	-	-	-	-	-	-
C(L)	0.111	0.754	-0.282	11.116	0.953	1.612	1	0.21	8	-0.045	-0.191	0.022	0.950	-	0	4.61
C(L)	0.161	0.075	-2.596	11.116	0.966	1.040	2	1.48	16	-1.165	-0.317	0.075	0.993	0.716	1	12.30
C(L)	0.042	0.460	-0.776	11.116	0.983	0.608	3	0.93	32	-	-	-	-	-	-	-
C(M)	0.044	3.496	1.252	11.116	0.996	-	0	0.11	4	-	-	-	-	-	-	-
C(M)	0.140	0.005	-5.348	11.116	0.941	2.633	2	26.73	16	-	-	-	-	-	-	-
C(M)	0.000	26.283	3.269	11.116	0.988	1.159	2	6.76	16	-	-	-	-	-	-	-
E(B)	0.017	7.507	2.016	11.116	0.974	1.234	3	0.14	32	-0.024	-0.020	0.018	0.999	0.295	1	6.11
E(B)	0.415	0.083	-2.489	11.116	0.988	0.834	2	0.52	16	-2.797	-0.027	0.083	0.917	2.344	2	8.50

PR(FR)	a	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{\max}	BP	l	β	Q_{alone}	VAC	SE	df	Xpt
E(B)	0.061	5.687	1.738	11.116	0.995	0.853	1	0.05	8	-	-	-	-	-	-	-
E(C)	0.458	0.070	-2.660	11.116	0.915	2.335	2	0.55	16	-	-	-	-	-	-	-
E(C)	-0.334	0.013	-4.365	11.116	0.849	2.748	2	-	16	-	-	-	-	-	-	-
E(C)	0.075	0.017	-4.086	11.116	0.856	2.478	3	14.17	32	-	-	-	-	-	-	-
E(F)	0.000	0.035	-3.362	11.116	0.884	1.958	2	-	16	-	-	-	-	-	-	-
E(F)	0.042	0.624	-0.472	11.116	0.954	0.937	2	0.68	16	-	-	-	-	-	-	-
E(F)	-10.72	0.001	-7.004	11.116	0.984	1.671	1	-	8	-	-	-	-	-	-	-
E(L)	0.091	0.288	-1.246	11.116	0.974	0.809	1	0.68	8	-	-	-	-	-	-	-
E(L)	0.170	1.781	0.577	11.116	0.954	-	0	0.06	4	-	-	-	-	-	-	-
E(L)	-	-	-	-	-	-	0	-	1	-	-	-	-	-	-	-
E(M)	0.054	0.170	-1.771	11.116	0.983	0.660	4	1.94	64	-	-	-	-	-	-	-
E(M)	0.044	0.081	-2.514	11.116	0.993	0.534	5	4.95	256	-	-	-	-	-	-	-
E(M)	0.026	0.505	-0.684	11.116	0.903	2.044	4	1.34	64	-	-	-	-	-	-	-
F(B)	0.060	0.487	-0.720	11.116	0.968	1.041	3	0.61	32	-	-	-	-	-	-	-
F(B)	0.090	0.125	-2.078	11.116	0.990	0.584	4	1.57	64	-	-	-	-	-	-	-
F(B)	0.097	0.205	-1.585	11.116	0.967	0.911	2	0.89	16	-	-	-	-	-	-	-
F(C)	0.489	0.140	-1.963	11.116	0.909	2.982	1	0.26	8	-	-	-	-	-	-	-
F(C)	0.089	0.364	-1.010	11.116	0.947	1.275	2	0.55	16	-	-	-	-	-	-	-
F(C)	0.118	243.741	5.496	11.116	0.876	3.361	2	0.00	16	-	-	-	-	-	-	-
F(E)	0.424	0.046	-3.090	11.116	0.933	2.000	3	0.92	32	-3.494	0.036	0.046	1.000	-	0	18.38
F(E)	0.053	0.248	-1.395	11.116	0.978	0.836	4	1.34	64	-0.071	-0.084	0.007	1.000	-	0	-
F(E)	0.112	0.189	-1.665	11.116	0.852	2.289	2	0.84	16	-	-	-	-	-	-	-
F(L)	0.230	0.040	-3.228	11.116	0.934	1.625	3	1.95	32	-	-	-	-	-	-	-
F(L)	0.062	0.074	-2.610	11.116	0.994	0.328	5	3.92	128	-	-	-	-	-	-	-
F(L)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
F(M)	1.490	0.039	-3.255	11.116	0.988	1.219	1	0.31	2	-1.254	-2.411	0.039	0.976	1.911	1	2.63
F(M)	0.070	0.481	-0.732	11.116	0.981	0.877	3	0.53	2	-	-	-	-	-	-	-
F(M)	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-
L(B)	0.053	0.202	-1.600	11.116	0.985	0.643	4	1.66	64	-	-	-	-	-	-	-
L(B)	-0.229	0.078	-2.547	11.116	0.947	0.980	2	-	16	-	-	-	-	-	-	-
L(B)	-	-	-	-	-	-	0	-	2	-	-	-	-	-	-	-
L(C)	0.019	4.783	1.565	11.116	0.963	1.527	3	0.20	32	-3.751	0.038	0.003	0.995	-	0	12.49
L(C)	0.080	0.188	-1.670	11.116	0.967	1.135	4	1.18	64	-0.729	-0.063	0.012	0.981	1.699	1	26.48
L(C)	0.165	0.062	-2.776	11.116	0.980	0.817	3	1.73	32	-3.029	-0.023	0.062	0.846	3.777	1	33.00
L(E)	0.304	0.038	-3.261	11.116	0.997	0.349	2	1.52	16	-0.176	-2.311	0.038	0.996	0.376	3	1.49

PR(FR)	a	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{\max}	BP	l	β	Q_{alone}	VAC	SE	df	Xpt
L(E)	0.313	0.072	-2.636	11.116	0.958	1.520	3	0.79	32	-0.909	-0.392	0.049	0.981	1.031	3	5.99
L(E)	0.077	0.694	-0.365	11.116	0.985	0.780	2	0.33	16	-0.521	-0.082	0.032	0.991	0.974	1	8.01
L(F)	2.522	0.008	-4.837	11.116	0.969	1.744	2	0.89	16	-	-	-	-	-	-	-
L(F)	1.300	0.090	-2.404	11.116	0.953	-	0	0.15	4	-	-	-	-	-	-	-
L(F)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
L(M)	0.103	0.211	-1.557	11.116	0.932	1.633	3	0.82	32	-	-	-	-	-	-	-
L(M)	0.132	0.182	-1.706	11.116	0.951	1.248	2	0.74	16	-	-	-	-	-	-	-
L(M)	0.149	0.052	-2.961	11.116	0.987	0.691	4	2.30	64	-	-	-	-	-	-	-
M(B)	0.640	0.068	-2.683	11.116	0.994	0.662	2	0.41	16	-	-	-	-	-	-	-
M(B)	0.331	1.256	0.228	11.116	0.717	4.668	2	0.04	16	-	-	-	-	-	-	-
M(B)	0.119	0.021	-3.845	11.116	0.887	2.855	2	6.97	16	-	-	-	-	-	-	-
M(C)	0.034	0.092	-2.391	11.116	0.976	0.922	5	5.76	256	-0.199	-4.788	0.001	0.999	-	0	178.50
M(C)	0.026	0.092	-2.387	11.116	0.948	1.286	5	7.37	256	-	-	-	-	-	-	-
M(C)	0.035	0.087	-2.445	11.116	0.969	0.825	5	5.88	128	-	-	-	-	-	-	-
M(E)	0.091	0.095	-2.355	11.116	0.977	0.847	4	2.06	64	-0.046	-0.284	0.011	0.998	-	0	-
M(E)	0.075	0.300	-1.205	11.116	0.997	0.284	3	0.79	32	-2.797	-0.027	0.300	0.994	-	0	-
M(E)	0.075	0.300	-1.205	11.116	0.997	0.284	3	0.79	32	-0.045	-0.191	0.014	0.997	-	0	-
M(F)	0.352	0.402	-0.910	11.116	0.872	-	0	0.13	4	-	-	-	-	-	-	-
M(F)	0.039	2.039	0.712	11.116	0.984	0.876	2	0.22	16	-	-	-	-	-	-	-
M(F)	1.484	0.065	-2.726	11.116	0.990	1.224	1	0.18	8	-	-	-	-	-	-	-
M(L)	0.133	0.195	-1.635	11.116	0.852	2.412	1	0.68	8	-	-	-	-	-	-	-
M(L)	1.274	120.127	4.789	11.116	0.949	-	0	0.00	4	-	-	-	-	-	-	-
M(L)	0.094	8.101	2.092	11.116	0.977	-	0	0.02	4	-	-	-	-	-	-	-

Note: B = Berries, C = Chicken, E = Egg, F = F = Foliage, L = Locusts & M = Mushrooms.

Table E3. Parameter estimates for initial demand, Q_0 ; essential value, α ; P_{\max} , interaction, I , and sensitivity, β ; break point and cross point data for P3 in Experiment 3.

PR(FR)	α	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{\max}	BP	I	β	Q_{alone}	VAC	SE	df	Xpt
B(C)	0.049	0.039	-3.243	15.747	0.895	1.212	5	6.50	128	-0.279	-0.427	0.040	0.998	0.283	2	9.93
B(C)	0.053	0.116	-2.151	15.747	0.906	1.765	4	2.04	64	-0.224	-0.120	0.032	0.998	0.396	1	16.80
B(C)	0.040	0.072	-2.625	15.747	0.834	2.471	5	4.29	128	-0.546	-0.033	0.033	0.993	0.472	3	31.12
B(E)	0.077	0.453	-0.791	15.747	0.988	0.763	2	0.36	16	-	-	-	-	-	-	-
B(E)	0.150	0.136	-1.992	15.747	0.915	1.986	2	0.61	16	-0.490	-21.39	0.039	0.984	-	0	-
B(E)	0.022	1.893	0.638	15.747	0.975	1.021	2	0.31	16	-	-	-	-	-	-	-
B(F)	0.024	0.234	-1.455	15.747	0.985	0.723	5	2.25	128	-	-	-	-	-	-	-
B(F)	0.028	0.644	-0.440	15.747	0.974	0.905	3	0.69	32	-	-	-	-	-	-	-
B(F)	0.024	0.366	-1.005	15.747	0.967	1.003	4	1.42	64	-	-	-	-	-	-	-
B(L)	0.052	0.092	-2.388	15.747	0.923	1.511	4	2.63	64	-0.132	-0.189	0.024	0.999	0.230	1	20.34
B(L)	0.037	0.648	-0.433	15.747	0.983	0.663	2	0.53	16	-	-	-	-	-	-	-
B(L)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
B(M)	0.026	1.366	0.312	15.747	0.954	1.317	2	0.36	16	-	-	-	-	-	-	-
B(M)	0.032	0.130	-2.041	15.747	0.904	1.488	4	2.99	64	-	-	-	-	-	-	-
B(M)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
C(B)	0.026	0.148	-1.913	15.747	0.863	1.561	3	3.29	32	-	-	-	-	-	-	-
C(B)	0.034	0.154	-1.869	15.747	0.959	1.000	4	2.41	64	-	-	-	-	-	-	-
C(B)	0.037	0.146	-1.926	15.747	0.547	1.552	3	2.31	32	-	-	-	-	-	-	-
C(E)	0.030	0.426	-0.853	15.747	0.923	0.468	3	0.97	32	-	-	-	-	-	-	20.09
C(E)	0.048	0.095	-2.356	15.747	0.953	0.076	4	2.77	64	-0.117	-0.025	0.020	0.999	-	0	54.60
C(E)	0.022	0.425	-0.856	15.747	0.911	1.471	4	1.34	64	-0.031	-0.057	0.027	1.000	-	0	54.60
C(F)	0.084	0.118	-2.139	15.747	0.844	3.332	3	1.26	32	-0.169	-0.402	0.044	0.998	0.280	3	8.30
C(F)	0.058	0.161	-1.827	15.747	0.902	2.079	4	1.35	64	-0.900	-0.063	0.044	0.963	0.237	3	17.25
C(F)	0.092	0.405	-0.903	15.747	0.836	2.974	1	0.34	8	-	-	-	-	-	-	-
C(L)	0.028	0.102	-2.280	15.747	0.944	1.212	5	4.44	128	-0.343	-0.082	0.016	0.991	1.023	1	32.14
C(L)	0.017	0.086	-2.458	15.747	0.920	1.613	5	8.38	256	-0.117	-0.128	0.019	0.998	-	0	101.71
C(L)	0.017	0.149	-1.905	15.747	0.862	1.810	5	4.98	128	-	-	-	-	-	-	-
C(M)	0.038	0.062	-2.788	15.747	0.964	0.996	5	5.41	128	-0.720	-12.79	0.062	0.985	0.782	2	23.32
C(M)	0.050	0.082	-2.497	15.747	0.986	0.597	4	3.03	64	-9.564	1.058	0.016	0.994	-	0	34.66
C(M)	0.140	0.152	-1.886	15.747	0.934	1.222	4	0.59	64	-	-	-	-	-	-	-
E(B)	0.088	0.050	-2.995	15.747	0.966	1.011	3	2.85	32	-	-	-	-	-	-	-
E(B)	0.019	0.131	-2.032	15.747	0.946	1.101	5	4.92	128	-	-	-	-	-	-	-

PR(FR)	a	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{max}	BP	l	θ	Q_{alone}	VAC	SE	df	Xpt
E(B)	0.035	0.256	-1.362	15.747	0.886	1.707	3	1.38	32	-	-	-	-	-	-	-
E(C)	0.016	0.168	-1.787	15.747	0.942	1.443	6	4.77	256	-	-	-	-	-	-	-
E(C)	0.026	0.200	-1.610	15.747	0.894	1.719	4	2.37	64	-	-	-	-	-	-	-
E(C)	0.017	0.198	-1.620	15.747	0.906	1.682	5	3.76	128	-	-	-	-	-	-	-
E(F)	0.021	0.240	-1.428	15.747	0.954	1.242	5	2.53	128	-0.878	-2.342	0.008	0.962	2.469	1	69.77
E(F)	0.015	0.287	-1.250	15.747	0.914	1.214	4	2.92	64	-	-	-	-	-	-	-
E(F)	0.011	0.191	-1.658	15.747	0.947	0.919	5	5.78	128	-	-	-	-	-	-	-
E(L)	0.026	0.105	-2.254	15.747	0.863	2.034	5	4.62	128	-0.247	-0.204	0.023	0.993	-	0	64.07
E(L)	0.042	0.089	-2.416	15.747	0.938	1.236	4	3.35	64	-	-	-	-	-	-	-
E(L)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
E(M)	0.042	0.238	-1.436	15.747	0.954	1.045	3	1.27	32	-	-	-	-	-	-	-
E(M)	0.025	0.719	-0.330	15.747	0.983	0.717	3	0.69	32	-0.068	-0.048	0.019	0.999	-	0	-
E(M)	0.037	0.485	-0.724	15.747	0.933	1.626	3	0.69	32	-2.403	0.557	0.022	0.901	-	0	-
F(B)	0.009	2.012	0.699	15.747	0.982	0.624	3	0.67	32	-	-	-	-	-	-	-
F(B)	0.019	2.247	0.810	15.747	0.978	0.926	2	0.30	16	-	-	-	-	-	-	-
F(B)	0.010	4.506	1.505	15.747	0.899	1.809	2	0.28	16	-	-	-	-	-	-	-
F(C)	0.045	0.055	-2.900	15.747	0.951	1.235	5	5.03	128	-0.177	-0.132	0.009	0.999	0.269	2	54.72
F(C)	0.020	0.360	-1.021	15.747	0.922	1.461	4	1.76	64	-	-	-	-	-	-	-
F(C)	0.016	0.432	-0.839	15.747	0.920	1.435	4	1.76	64	-	-	-	-	-	-	-
F(E)	0.153	0.486	-0.721	15.747	0.939	2.555	1	0.17	8	-0.101	-0.209	0.034	0.999	0.259	1	2.50
F(E)	0.025	0.640	-0.446	15.747	0.789	3.016	3	0.79	32	-0.041	-0.040	0.030	1.000	0.097	1	16.11
F(E)	-0.040	0.204	-1.587	15.747	0.640	5.640	1	-	8	-0.062	-0.470	0.034	1.000	0.109	1	-
F(L)	0.027	0.098	-2.319	15.747	0.926	0.637	5	4.80	128	-0.122	-0.122	0.028	0.998	0.451	1	35.56
F(L)	0.022	0.134	-2.009	15.747	0.922	1.413	5	4.30	128	-38.14	0.831	0.020	0.996	0.536	1	51.27
F(L)	0.024	0.089	-2.422	15.747	0.954	1.023	5	5.78	128	-0.289	-0.093	0.013	0.997	0.564	1	76.78
F(M)	0.070	0.453	-0.792	15.747	0.913	2.029	2	0.40	2	-0.008	-0.512	0.043	1.000	-	0	4.97
F(M)	0.077	0.169	-1.777	15.747	0.902	1.977	3	0.96	2	-0.212	-0.297	0.051	0.998	0.289	1	7.56
F(M)	0.097	0.063	-2.761	15.747	0.855	2.284	3	2.05	2	-0.121	-0.681	0.050	0.999	0.230	1	8.00
L(B)	0.019	0.331	-1.104	15.747	0.917	1.417	4	2.00	64	-	-	-	-	-	-	-
L(B)	0.029	0.187	-1.675	15.747	0.966	0.881	4	2.34	64	-	-	-	-	-	-	-
L(B)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
L(C)	0.037	0.221	-1.508	15.747	0.913	1.377	3	1.51	64	-	-	-	-	-	-	8.30
L(C)	0.077	0.092	-2.382	15.747	0.927	1.735	4	1.75	64	-0.012	-0.934	0.033	1.000	-	0	9.37
L(C)	0.047	0.264	-1.330	15.747	0.942	1.299	3	1.01	32	-9.609	1.327	0.036	0.994	-	0	11.85
L(E)	0.049	0.065	-2.727	15.747	0.935	1.518	5	3.92	128	-1.069	0.302	0.036	0.999	0.007	3	24.62

PR(FR)	a	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{\max}	BP	l	θ	Q_{alone}	VAC	SE	df	Xpt
L(E)	0.018	0.309	-1.174	15.747	0.916	2.048	5	2.25	128	-54.68	0.378	0.046	0.996	-	0	-
L(E)	0.016	0.694	-0.365	15.747	0.939	1.709	4	1.15	64	-0.182	-0.019	0.042	0.993	-	0	-
L(F)	0.028	0.129	-2.051	15.747	0.957	1.119	5	3.53	128	-	-	-	-	-	-	-
L(F)	0.031	0.093	-2.370	15.747	0.979	0.745	5	4.33	128	-	-	-	-	-	-	-
L(F)	0.045	0.103	-2.271	15.747	0.986	0.716	5	2.70	128	-	-	-	-	-	-	-
L(M)	0.028	0.098	-2.322	15.747	0.971	1.056	6	4.62	256	-	-	-	-	-	-	-
L(M)	0.022	0.264	-1.333	15.747	0.961	0.918	4	2.13	64	-	-	-	-	-	-	-
L(M)	0.029	0.155	-1.863	15.747	0.994	0.347	4	2.83	64	-	-	-	-	-	-	-
M(B)	-0.012	2.192	0.785	15.747	0.873	2.410	2	-	16	-1.201	-0.098	0.040	0.984	0.978	1	11.64
M(B)	0.015	9.818	2.284	15.747	0.983	-	0	0.08	4	-	-	-	-	-	-	-
M(B)	-0.018	0.422	-0.863	15.747	0.835	2.520	2	-	16	-0.315	-0.212	0.043	0.999	0.380	1	-
M(C)	0.044	0.382	-0.961	15.747	0.948	1.361	3	0.74	32	-1.417	-3.435	0.754	0.896	1.873	1	3.33
M(C)	0.144	0.126	-2.069	15.747	0.928	1.761	2	0.69	16	-0.080	-0.516	0.039	1.000	0.064	1	4.60
M(C)	0.016	1.108	0.103	15.747	0.898	2.814	4	0.71	64	-	-	-	-	-	-	-
M(E)	0.045	0.444	-0.812	15.747	0.950	1.461	3	0.63	32	-1.875	1.066	0.037	0.974	1.184	1	10.80
M(E)	0.016	1.794	0.584	15.747	0.941	1.695	3	0.43	32	-0.221	-0.015	0.035	0.996	-	0	-
M(E)	0.019	2.381	0.868	15.747	0.994	0.514	2	0.27	16	0.455	13.305	0.035	0.814	-	0	-
M(F)	0.015	0.362	-1.017	15.747	0.915	1.346	4	2.27	64	-	-	-	-	-	-	-
M(F)	0.014	0.410	-0.891	15.747	0.887	1.979	4	2.13	64	-	-	-	-	-	-	-
M(F)	0.016	0.279	-1.278	15.747	0.955	0.864	4	2.75	64	-	-	-	-	-	-	-
M(L)	0.041	0.122	-2.102	15.747	0.953	1.100	4	2.51	64	-0.961	-0.095	0.050	0.978	1.306	1	30.82
M(L)	0.029	0.655	-0.423	15.747	0.987	0.488	2	0.66	16	-	-	-	-	-	-	-
M(L)	0.018	0.550	-0.598	15.747	0.960	1.111	4	1.26	64	-	-	-	-	-	-	-

Note: B = Berries, C = Chicken, E = Egg, F = Foliage, L = Locusts & M = Mushrooms.

Table E4. Parameter estimates for initial demand, Q_0 , essential value, α ; P_{\max} , interaction, I , and sensitivity, β ; break point and cross point data for P4 in Experiment 3.

PR(FR)	α	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{\max}	BP	I	β	Q_{alone}	VAC	SE	df	Xpt
B(C)	0.267	0.012	-4.418	10.500	0.976	1.096	5.0	5.87	128	-30.99	17.613	0.010	0.967	1.575	2	21.78
B(C)	0.109	0.057	-2.863	10.500	0.913	1.872	5.00	3.04	128	-2.517	0.969	0.009	0.987	0.971	2	36.88
B(C)	0.134	0.076	-2.571	10.500	0.995	0.412	4.00	1.85	64	-2.145	-0.027	0.010	0.845	-	0	51.91
B(E)	0.187	0.062	-2.775	10.500	0.986	0.763	4.00	1.62	64	-	-	-	-	-	-	-
B(E)	0.137	0.048	-3.037	10.500	0.979	0.637	5.0	2.87	128	-	-	-	-	-	-	-
B(E)	0.136	0.120	-2.123	10.500	0.929	2.202	5.00	1.16	128	-	-	-	-	-	-	-
B(F)	-	-	-	-	-	-	0.00	-	1	-	-	-	-	-	-	-
B(F)	0.271	0.042	-3.163	10.500	0.959	1.440	4.0	1.64	64	-	-	-	-	-	-	-
B(F)	0.224	0.121	-2.114	10.500	0.988	0.746	3.00	0.70	32	-	-	-	-	-	-	-
B(L)	0.105	0.027	-3.601	10.500	0.920	2.112	5.00	6.60	256	-0.192	-0.390	0.016	0.997	0.472	2	27.02
B(L)	-	-	-	-	-	-	1.0	-	2	-	-	-	-	-	-	-
B(L)	0.207	0.009	-4.705	10.500	0.988	0.863	5.00	10.09	256	-	-	-	-	-	-	-
B(M)	0.165	0.025	-3.686	10.500	0.988	0.670	5.00	4.57	128	-1.190	-0.181	0.031	0.987	0.878	3	27.14
B(M)	0.150	0.042	-3.176	10.500	0.992	0.597	5.0	3.01	128	-0.177	-0.483	0.008	0.999	-	0	33.13
B(M)	0.080	0.083	-2.490	10.500	0.912	1.634	4.00	2.83	64	-	-	-	-	-	-	-
C(B)	1.402	0.005	-5.371	10.500	0.977	1.305	3.0	2.89	32	-3.541	-0.005	0.007	0.984	1.114	2	4.85
C(B)	0.138	0.063	-2.764	10.500	0.924	1.832	5.00	2.18	128	-0.605	-0.057	0.015	0.991	0.672	3	24.45
C(B)	0.016	9.941	2.297	10.500	0.980	1.018	4.00	0.12	64	-0.016	-0.007	0.010	0.999	0.283	1	-
C(E)	0.896	0.366	-1.004	10.500	1.000	0.011	0.0	0.06	2	-2.000	0.029	0.020	0.829	-	0	1.89
C(E)	0.318	0.126	-2.075	10.500	0.939	0.067	3.00	0.47	32	-0.430	-0.189	0.010	0.993	0.718	2	8.46
C(E)	0.045	16.763	2.819	10.500	0.996	0.736	1.00	0.03	8	-6.812	0.160	0.016	0.900	3.453	1	-
C(F)	0.035	0.095	-2.359	10.500	0.917	1.772	5.0	5.72	256	-1.718	2.694	0.010	0.956	1.655	3	70.71
C(F)	0.038	0.102	-2.279	10.500	0.911	1.921	5.00	4.85	256	-0.993	-0.019	0.016	0.975	1.447	2	81.09
C(F)	0.085	0.017	-4.074	10.500	0.984	0.840	5.00	13.05	256	-9.375	1.318	0.002	1.000	-	0	184.44
C(L)	0.425	0.040	-3.212	10.500	0.961	1.446	3.00	1.10	32	-0.313	-0.947	0.025	0.998	0.286	3	4.69
C(L)	0.031	102.099	4.626	10.500	0.994	0.696	2.00	0.01	16	-0.687	-0.001	0.024	0.982	1.178	2	11.75
C(L)	0.008	49.078	3.893	10.500	0.969	1.375	3.0	0.05	32	-9.236	0.029	0.023	0.857	3.307	2	-
C(M)	0.027	2.295	0.831	10.500	0.988	0.598	2.00	0.30	16	-	-	-	-	-	-	-
C(M)	0.000	8.202	2.104	10.500	0.987	0.883	3.0	23.00	32	-	-	-	-	-	-	-
C(M)	0.865	0.148	-1.910	10.500	0.996	0.787	1.00	0.15	8	-	-	-	-	-	-	-
E(B)	0.058	0.188	-1.673	10.500	0.958	1.292	5.00	1.74	128	-2.118	0.705	0.012	0.926	2.398	2	28.42
E(B)	0.115	0.049	-3.026	10.500	0.980	0.796	5.00	3.39	128	-0.070	-0.200	0.006	1.000	-	0	-

PR(FR)	a	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{\max}	BP	l	β	Q_{alone}	VAC	SE	df	Xpt
E(B)	0.065	0.239	-1.432	10.500	0.937	1.507	4.0	1.22	64	-2.698	0.478	0.009	0.960	-	0	-
E(C)	0.219	0.032	-3.441	10.500	0.883	2.312	4.00	2.69	64	-	-	-	-	-	-	-
E(C)	0.107	1.178	0.164	10.500	0.993	0.702	1.0	0.15	8	-	-	-	-	-	-	-
E(C)	0.162	0.054	-2.921	10.500	0.947	1.633	5.00	2.16	128	-	-	-	-	-	-	-
E(F)	0.150	0.046	-3.082	10.500	0.959	1.379	5.00	2.74	128	-	-	-	-	-	-	-
E(F)	0.195	0.057	-2.860	10.500	0.991	0.608	4.0	1.69	64	-0.210	-26.534	0.009	0.998	-	0	-
E(F)	0.107	0.156	-1.859	10.500	0.978	0.943	4.00	1.13	64	-	-	-	-	-	-	-
E(L)	0.125	0.134	-2.011	10.500	0.962	1.284	4.00	1.12	64	-0.092	-0.221	0.014	0.999	-	0	-
E(L)	0.102	0.126	-2.074	10.500	0.943	1.467	4.0	1.47	64	-0.203	-0.167	0.011	0.998	-	0	-
E(L)	-0.059	0.028	-3.569	10.500	0.990	0.729	1.00	-	8	-	-	-	-	-	-	-
E(M)	0.077	0.062	-2.778	10.500	0.942	1.397	5.00	3.94	128	-0.678	1.449	0.018	1.000	2.535	3	28.85
E(M)	0.091	0.053	-2.943	10.500	0.959	1.200	5.00	3.92	128	-0.377	-0.138	0.009	0.997	0.491	2	48.53
E(M)	0.102	0.027	-3.626	10.500	0.950	1.610	5.0	6.94	256	-0.872	-0.130	0.019	0.970	1.270	5	48.93
F(B)	0.061	0.381	-0.964	10.500	0.979	0.910	4.00	0.81	64	-0.043	0.000	0.008	1.000	-	0	-
F(B)	0.074	0.599	-0.513	10.500	0.979	0.956	3.0	0.43	32	-0.437	0.000	0.007	0.993	-	0	-
F(B)	0.139	0.629	-0.464	10.500	0.970	1.419	2.00	0.22	16	-	-	-	-	-	-	-
F(C)	0.113	0.077	-2.562	10.500	0.922	1.917	5.0	2.16	128	-0.092	-0.392	0.016	1.000	-	0	20.08
F(C)	-	-	-	-	-	-	0.00	-	1	-	-	-	-	-	-	-
F(C)	0.035	0.019	-3.972	10.500	0.895	2.482	5.00	28.82	128	-1.214	-0.282	0.019	0.975	1.206	5	-
F(E)	0.029	0.639	-0.447	10.500	0.854	2.418	4.00	1.01	64	-0.232	-0.028	0.015	0.999	0.373	1	34.69
F(E)	-	-	-	-	-	-	0.0	-	1	-	-	-	-	-	-	-
F(E)	-	-	-	-	-	-	0.00	-	1	-	-	-	-	-	-	-
F(L)	0.133	0.035	-3.348	10.500	0.943	1.524	5.00	4.05	128	-0.559	-0.191	0.015	0.991	0.744	3	33.59
F(L)	0.042	0.178	-1.727	10.500	0.933	1.443	5.0	2.51	128	-0.289	-0.056	0.015	0.998	0.516	1	41.53
F(L)	0.117	0.036	-3.314	10.500	0.952	1.348	5.00	4.42	128	-0.632	-0.153	0.011	0.984	1.006	3	-
F(M)	1.577	0.040	-3.224	10.500	0.988	1.208	1.0	0.30	2	-1.017	-2.582	0.029	0.975	1.937	1	2.64
F(M)	0.076	0.484	-0.725	10.500	0.980	0.917	3.00	0.51	2	-	-	-	-	-	-	-
F(M)	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-
L(B)	0.081	0.037	-3.303	10.500	0.934	1.786	5.00	6.36	256	-4.769	4.258	0.011	0.974	0.061	2	40.77
L(B)	0.125	0.201	-1.607	10.500	0.968	1.110	3.00	0.75	32	-	-	-	-	-	-	-
L(B)	0.095	0.077	-2.566	10.500	0.981	0.858	5.0	2.59	128	-	-	-	-	-	-	-
L(C)	0.075	0.045	-3.100	10.500	0.969	1.193	5.00	5.59	256	-0.790	-0.126	0.027	0.972	0.000	2	55.70
L(C)	0.028	0.156	-1.857	10.500	0.926	1.822	5.0	4.38	256	-	-	-	-	-	-	-
L(C)	0.050	0.128	-2.054	10.500	0.982	0.738	5.00	2.95	128	-	-	-	-	-	-	-
L(E)	0.176	0.030	-3.504	10.500	0.971	1.146	5.00	3.57	128	-0.193	-0.430	0.020	0.996	0.453	2	11.54

PR(FR)	a	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{\max}	BP	l	β	Q_{alone}	VAC	SE	df	Xpt
L(E)	0.093	0.052	-2.949	10.500	0.957	1.233	5.00	3.87	128	-0.210	-0.180	0.013	0.997	0.475	2	34.53
L(E)	0.062	0.048	-3.043	10.500	0.972	1.092	5.0	6.34	256	-0.224	-0.076	0.019	0.998	0.329	2	38.06
L(F)	0.041	0.078	-2.549	10.500	0.937	1.447	6.0	5.87	256	-0.187	-5.107	0.005	0.999	0.274	1	107.08
L(F)	0.044	0.050	-2.987	10.500	0.969	0.954	6.00	8.45	256	-0.011	-18.545	0.006	1.000	-	0	-
L(F)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
L(M)	0.063	0.285	-1.254	10.500	0.967	1.106	4.00	1.04	64	-	-	-	-	-	-	-
L(M)	0.071	0.263	-1.337	10.500	0.979	0.888	4.0	1.01	64	-	-	-	-	-	-	-
L(M)	0.102	0.083	-2.484	10.500	0.986	0.660	4.00	2.21	64	-	-	-	-	-	-	-
M(B)	-0.018	0.422	-0.863	10.500	0.896	1.728	5.0	-	256	-4.137	5.859	0.016	0.903	2.733	2	17.05
M(B)	0.089	0.042	-3.167	10.500	0.944	1.715	5.00	5.02	256	-0.358	-0.182	0.009	0.991	0.870	2	57.69
M(B)	-0.012	0.129	-2.050	10.500	0.914	1.799	5.00	-	256	-1.201	-0.098	0.015	0.933	1.903	3	-
M(C)	0.045	15.485	2.740	10.500	0.944	-	0.00	0.03	2	-	-	-	-	-	-	-
M(C)	0.092	0.119	-2.126	10.500	0.991	0.533	4.0	1.73	64	-	-	-	-	-	-	-
M(C)	0.043	0.731	-0.313	10.500	0.916	1.866	3.00	0.60	32	-	-	-	-	-	-	-
M(E)	0.079	1.404	0.340	10.500	0.974	1.274	2.00	0.17	16	-0.118	-0.067	0.018	0.999	-	0	-
M(E)	0.115	5.306	1.669	10.500	0.953	-	0.0	0.03	4	-	-	-	-	-	-	-
M(E)	0.770	0.900	-0.106	10.500	0.997	-	0.00	0.03	2	50.506	119.049	0.028	0.811	-	0	-
M(F)	0.096	0.118	-2.139	10.500	0.983	0.750	4.00	1.67	64	-0.745	1.010	0.007	0.965	2.086	1	26.60
M(F)	0.062	0.300	-1.204	10.500	0.991	0.548	4.0	1.02	64	-0.188	-0.053	0.004	0.999	-	0	31.63
M(F)	0.192	0.029	-3.551	10.500	0.945	1.623	5.00	3.43	128	-0.519	-0.190	0.003	0.996	0.480	2	58.42
M(L)	0.199	0.097	-2.332	10.500	0.957	1.521	4.0	0.98	64	-1.327	-0.078	0.017	0.964	1.893	2	19.11
M(L)	0.107	0.165	-1.802	10.500	0.950	1.267	4.00	1.07	64	-0.574	-0.037	0.015	0.992	1.056	1	19.58
M(L)	0.076	0.102	-2.287	10.500	0.976	0.945	5.00	2.43	128	-	-	-	-	-	-	-

Note: B = Berries, C = Chicken, E = Egg, F = Foliage, L = Locusts & M = Mushrooms.

Table E5. Parameter estimates for initial demand, Q_0 , essential value, α ; P_{\max} , interaction, I , and sensitivity, β ; break point and cross point data for P5 in Experiment 3.

PR(FR)	α	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{\max}	BP	I	β	Q_{alone}	VAC	SE	df	Xpt
B(C)	0.030	0.078	-2.546	10.079	0.947	1.271	5	8.42	256	-	-	-	-	-	-	-
B(C)	0.030	0.069	-2.670	10.079	0.925	1.550	5	9.54	256	-	-	-	-	-	-	-
B(C)	0.022	0.094	-2.364	10.079	0.957	1.051	5	9.40	256	-	-	-	-	-	-	-
B(E)	0.084	0.290	-1.237	10.079	0.962	-	0	0.80	4	-	-	-	-	-	-	-
B(E)	0.213	0.327	-1.118	10.079	0.984	0.980	2	0.28	16	-	-	-	-	-	-	-
B(E)	0.706	0.050	-3.003	10.079	0.814	-	0	0.56	4	-	-	-	-	-	-	-
B(F)	0.166	0.068	-2.686	10.079	0.998	0.315	1	1.73	8	-	-	-	-	-	-	-
B(F)	0.246	0.052	-2.959	10.079	0.994	0.521	1	1.53	8	-	-	-	-	-	-	-
B(F)	0.104	0.044	-3.124	10.079	0.978	0.878	5	4.28	128	-	-	-	-	-	-	-
B(L)	0.170	5.631	1.728	10.079	0.989	-	0	0.02	4	-	-	-	-	-	-	-
B(L)	0.138	0.601	-0.509	10.079	0.800	-	0	0.24	4	-	-	-	-	-	-	-
B(L)	0.050	0.122	-2.105	10.079	0.987	0.497	4	3.25	64	-	-	-	-	-	-	-
B(M)	-	-	-	-	-	-	0	-	1	-	-	-	-	-	-	-
B(M)	-	-	-	-	-	-	0	-	1	-	-	-	-	-	-	-
B(M)	0.141	3.879	1.356	10.079	0.949	-	0	0.04	4	-	-	-	-	-	-	-
C(B)	0.370	0.338	-1.086	10.079	0.877	-	0	0.16	4	-0.093	-1.325	0.034	1.000	-	0	2.42
C(B)	0.095	0.325	-1.124	10.079	0.937	1.327	2	0.63	16	-	-	-	-	-	-	-
C(B)	0.070	1.240	0.215	10.079	0.990	0.692	2	0.23	16	-	-	-	-	-	-	-
C(E)	0.115	0.208	-1.570	10.079	0.973	0.082	2	0.82	16	-	-	-	-	-	-	-
C(E)	0.110	0.072	-2.638	10.079	0.945	0.073	1	2.50	8	-	-	-	-	-	-	-
C(E)	0.104	0.102	-2.279	10.079	0.977	0.071	2	1.83	16	-	-	-	-	-	-	-
C(F)	0.043	0.039	-3.246	10.079	0.994	0.428	5	11.60	256	-	-	-	-	-	-	-
C(F)	0.040	0.112	-2.188	10.079	0.930	1.344	5	4.38	128	-	-	-	-	-	-	-
C(F)	0.034	0.068	-2.692	10.079	0.969	0.986	5	8.48	256	-	-	-	-	-	-	-
C(L)	0.040	0.158	-1.848	10.079	0.989	0.404	3	3.11	32	-	-	-	-	-	-	-
C(L)	0.039	0.181	-1.708	10.079	0.969	0.760	4	2.74	64	-	-	-	-	-	-	-
C(L)	0.051	0.154	-1.872	10.079	0.977	0.701	4	2.51	64	-	-	-	-	-	-	-
C(M)	0.010	26.568	3.280	10.079	0.979	-	0	0.07	4	-	-	-	-	-	-	-
C(M)	-	-	-	-	-	-	0	-	2	-	-	-	-	-	-	-
C(M)	-	-	-	-	-	-	0	-	2	-	-	-	-	-	-	-
E(B)	0.059	0.205	-1.585	10.079	0.960	1.261	5	1.62	128	-0.323	-0.042	0.012	0.993	0.722	2	32.50
E(B)	0.120	0.049	-3.015	10.079	0.981	0.794	5	3.32	128	-0.070	-0.198	0.006	1.000	-	0	-

PR(FR)	a	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{\max}	BP	l	θ	Q_{alone}	VAC	SE	df	Xpt
E(B)	0.067	0.251	-1.382	10.079	0.938	1.491	4	1.17	64	-1.909	0.419	0.009	0.960	-	0	-
E(C)	0.065	0.160	-1.830	10.079	0.929	1.221	3	1.87	32	-	-	-	-	-	-	-
E(C)	0.126	0.200	-1.607	10.079	0.968	1.086	3	0.77	32	-	-	-	-	-	-	-
E(C)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
E(F)	0.080	0.029	-3.531	10.079	0.985	0.679	5	8.38	128	-	-	-	-	-	-	-
E(F)	0.051	0.151	-1.891	10.079	0.986	0.547	4	2.52	64	-	-	-	-	-	-	-
E(F)	0.043	0.186	-1.682	10.079	0.978	0.653	4	2.45	64	-	-	-	-	-	-	-
E(L)	-0.055	0.003	-5.929	10.079	0.949	-	0	-	4	-0.068	-309.16	0.016	1.000	-	0	3.92
E(L)	0.056	2.654	0.976	10.079	0.799	4.272	1	0.13	8	-	-	-	-	-	-	-
E(L)	0.069	0.808	-0.213	10.079	0.971	-	0	0.35	4	-	-	-	-	-	-	-
E(M)	-	-	-	-	-	-	0	-	2	-	-	-	-	-	-	-
E(M)	-	-	-	-	-	-	0	-	1	-	-	-	-	-	-	-
E(M)	0.095	17.754	2.877	10.079	1.000	-	0	0.01	2	-0.053	-0.064	0.024	1.000	-	0	-
F(B)	0.071	0.203	-1.596	10.079	0.968	0.826	3	1.36	32	-	-	-	-	-	-	-
F(B)	0.053	0.118	-2.137	10.079	0.991	0.391	2	3.11	16	-	-	-	-	-	-	-
F(B)	0.050	0.218	-1.524	10.079	0.999	0.128	2	1.79	16	-	-	-	-	-	-	-
F(C)	0.074	0.098	-2.319	10.079	0.971	0.856	4	2.69	64	-	-	-	-	-	-	-
F(C)	0.043	0.269	-1.312	10.079	0.934	1.297	4	1.68	64	-	-	-	-	-	-	-
F(C)	0.042	0.234	-1.452	10.079	0.958	1.170	5	1.99	128	-0.188	-0.048	0.008	0.998	-	0	-
F(E)	0.057	0.199	-1.612	10.079	0.885	1.614	3	1.72	32	-	-	-	-	-	-	-
F(E)	0.098	0.083	-2.484	10.079	0.946	1.167	3	2.41	32	-	-	-	-	-	-	-
F(E)	-0.090	0.540	-0.615	10.079	0.925	5.832	3	-	32	-	-	-	-	-	-	-
F(L)	0.458	0.044	-3.117	10.079	0.847	2.972	2	0.97	16	-0.229	-1.985	0.022	0.999	-	0	7.11
F(L)	0.464	0.043	-3.138	10.079	0.934	1.931	3	0.97	32	-0.177	-2.112	0.025	0.989	1.051	1	-
F(M)	-	-	-	-	-	-	0	-	2	-	-	-	-	-	-	-
F(M)	-	-	-	-	-	-	0	-	2	-	-	-	-	-	-	-
F(M)	-	-	-	-	-	-	0	-	2	-	-	-	-	-	-	-
L(B)	0.035	0.555	-0.589	10.079	1.000	1.160	3	1.00	32	-	-	-	-	-	-	-
L(B)	0.036	0.235	-1.446	10.079	0.919	1.320	4	2.31	64	-	-	-	-	-	-	-
L(B)	0.067	0.115	-2.167	10.079	0.997	0.274	4	2.55	64	-	-	-	-	-	-	-
L(C)	0.072	0.159	-1.838	10.079	0.989	0.469	3	1.72	32	-	-	-	-	-	-	-
L(C)	0.084	0.118	-2.135	10.079	0.880	1.776	3	1.96	32	-	-	-	-	-	-	-
L(C)	0.065	0.111	-2.196	10.079	0.981	0.609	3	2.73	32	-	-	-	-	-	-	-
L(E)	0.060	0.435	-0.832	10.079	0.980	0.748	3	0.75	32	-	-	-	-	-	-	-
L(E)	0.034	0.139	-1.975	10.079	0.926	1.142	4	4.11	64	-	-	-	-	-	-	-

PR(FR)	a	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{\max}	BP	l	θ	Q_{alone}	VAC	SE	df	Xpt
L(E)	0.046	0.175	-1.745	10.079	0.983	0.580	4	2.46	64	-	-	-	-	-	-	-
L(F)	0.586	0.183	-1.697	10.079	0.988	1.121	1	0.18	8	-	-	-	-	-	-	-
L(F)	0.005	0.010	-4.654	10.079	0.870	-	0	447.96	4	-	-	-	-	-	-	-
L(F)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
L(M)	0.063	0.099	-2.313	10.079	0.965	0.901	4	3.14	64	-	-	-	-	-	-	-
L(M)	0.215	0.117	-2.144	10.079	0.984	0.836	3	0.78	32	-	-	-	-	-	-	-
L(M)	0.048	0.712	-0.339	10.079	0.983	0.714	3	0.58	32	-	-	-	-	-	-	-
M(B)	0.074	0.172	-1.760	10.079	0.837	2.776	5	1.54	128	-1.388	-0.025	0.023	0.965	1.803	2	37.22
M(B)	0.052	0.131	-2.031	10.079	0.991	0.510	5	2.89	128	-	-	-	-	-	-	-
M(B)	0.073	0.166	-1.797	10.079	0.949	-	4	1.61	64	-	-	-	-	-	-	-
M(C)	0.097	0.107	-2.231	10.079	0.964	1.078	4	1.88	64	-	-	-	-	-	-	-
M(C)	0.102	0.123	-2.093	10.079	0.959	1.200	4	1.56	64	-	-	-	-	-	-	-
M(C)	-	-	-	-	-	-	0	-	1	-	-	-	-	-	-	-
M(E)	0.057	0.080	-2.524	10.079	0.963	0.895	4	4.31	64	-	-	-	-	-	-	-
M(E)	0.035	0.128	-2.053	10.079	0.945	1.133	5	4.32	128	-	-	-	-	-	-	-
M(E)	0.039	0.073	-2.615	10.079	0.917	1.421	5	6.81	128	-	-	-	-	-	-	-
M(F)	-	-	-	-	-	-	0	-	1	-	-	-	-	-	-	-
M(F)	0.024	2.702	0.994	10.079	0.984	0.845	3	0.31	32	-	-	-	-	-	-	-
M(F)	-	-	-	-	-	-	0	-	2	-	-	-	-	-	-	-
M(L)	-	-	-	-	-	-	0	-	1	-	-	-	-	-	-	-
M(L)	0.044	5.203	1.649	10.079	0.985	-	0	0.09	4	-	-	-	-	-	-	-
M(L)	-	-	-	-	-	-	0	-	1	-	-	-	-	-	-	-
F(L)	0.135	0.032	-3.446	10.079	0.825	3.907	2	4.57	16	-0.399	-4.515	0.022	0.996	0.498	2	-

Note: B = Berries, C = Chicken, E = Egg, F = Foliage, L = Locusts & M = Mushrooms.

Table E6. Parameter estimates for initial demand, Q_0 ; essential value, α ; P_{\max} , interaction, I , and sensitivity, β ; break point and cross point data for P6 in Experiment 3.

PR(FR)	α	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{\max}	BP	I	β	Q_{alone}	VAC	SE	df	Xpt
B(C)	0.052	0.072	-2.629	10.463	0.979	0.662	4	5.06	64	-	-	-	-	-	-	-
B(C)	0.087	0.137	-1.985	10.463	0.969	1.014	4	1.59	64	-	-	-	-	-	-	-
B(C)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
B(E)	0.064	0.422	-0.862	10.463	0.970	0.977	3	0.70	32	-	-	-	-	-	-	-
B(E)	0.036	0.372	-0.988	10.463	0.977	0.757	4	1.41	64	-	-	-	-	-	-	-
B(E)	0.074	0.243	-1.414	10.463	0.981	0.699	3	1.06	32	-	-	-	-	-	-	-
B(F)	0.047	25.584	3.242	10.463	0.978	1.537	2	0.02	16	-	-	-	-	-	-	-
B(F)	9.167	0.007	-4.954	10.463	0.990	-	0	0.29	4	-	-	-	-	-	-	-
B(F)	0.190	12.125	2.495	10.463	0.999	-	0	0.01	4	-	-	-	-	-	-	-
B(L)	0.024	6.206	1.825	10.463	0.968	1.304	1	0.13	8	-	-	-	-	-	-	-
B(L)	0.160	0.231	-1.466	10.463	0.893	2.140	2	0.51	16	-	-	-	-	-	-	-
B(L)	0.154	0.237	-1.438	10.463	0.907	1.969	2	0.51	16	-	-	-	-	-	-	-
B(M)	0.004	117.263	4.764	10.463	0.893	2.228	3	0.04	32	-0.051	0.709	0.034	0.882	-	0	-
B(M)	0.031	14.607	2.682	10.463	0.979	1.397	2	0.04	16	-0.745	-0.007	0.039	0.988	1.158	1	2.38
B(M)	0.040	5.198	1.648	10.463	0.986	1.015	2	0.09	16	-5.625	0.240	0.036	0.808	-	0	-
C(B)	0.042	0.684	-0.380	10.463	0.962	1.046	3	0.65	32	-	-	-	-	-	-	-
C(B)	0.057	0.466	-0.764	10.463	0.971	0.925	3	0.71	32	-	-	-	-	-	-	-
C(B)	0.066	0.378	-0.974	10.463	0.974	0.886	3	0.76	32	-	-	-	-	-	-	-
C(E)	0.567	0.048	-3.034	10.463	0.876	0.057	2	0.69	16	-	-	-	-	-	-	-
C(E)	0.221	0.153	-1.879	10.463	0.962	0.080	3	0.56	32	-	-	-	-	-	-	-
C(E)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
C(F)	0.030	25.257	3.229	10.463	0.999	0.320	2	0.03	16	-1.170	-0.002	0.028	0.983	1.241	2	1.96
C(F)	0.190	0.248	-1.394	10.463	0.957	1.626	3	0.40	32	-	-	0.000	-3.605	0.971	0	5.13
C(F)	0.311	0.035	-3.361	10.463	0.926	1.973	4	1.75	64	-0.600	-0.526	0.015	0.994	0.839	1	15.90
C(L)	0.047	0.109	-2.215	10.463	0.969	0.780	4	3.66	64	-	-	-	-	-	-	-
C(L)	0.034	0.199	-1.616	10.463	0.943	1.278	5	2.77	128	-	-	-	-	-	-	-
C(L)	0.053	0.232	-1.461	10.463	0.943	1.307	4	1.52	64	-	-	-	-	-	-	-
C(M)	0.145	0.262	-1.341	10.463	0.964	1.347	3	0.50	32	-	-	-	-	-	-	-
C(M)	0.140	0.194	-1.640	10.463	0.967	1.192	3	0.70	32	-	-	-	-	-	-	-
C(M)	0.140	0.276	-1.286	10.463	0.966	1.128	2	0.49	16	-	-	-	-	-	-	-
E(B)	0.385	0.032	-3.441	10.463	0.957	1.447	3	1.53	32	-0.553	-0.225	0.029	0.945	1.827	2	5.06

PR(FR)	a	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{\max}	BP	l	β	Q_{alone}	VAC	SE	df	Xpt
E(B)	0.030	0.238	-1.437	10.463	0.955	0.751	3	2.61	32	-	-	-	-	-	-	-
E(B)	0.037	0.609	-0.497	10.463	0.968	0.841	3	0.84	32	-	-	-	-	-	-	-
E(C)	0.077	0.155	-1.861	10.463	0.997	0.267	3	1.57	32	-	-	-	-	-	-	-
E(C)	0.056	0.108	-2.230	10.463	0.987	0.518	4	3.14	64	-	-	-	-	-	-	-
E(C)	0.087	0.100	-2.307	10.463	0.995	0.338	3	2.18	32	-	-	-	-	-	-	-
E(F)	0.237	0.064	-2.754	10.463	0.958	1.479	4	1.25	64	-	-	-	-	-	-	-
E(F)	0.068	0.800	-0.223	10.463	0.929	1.646	2	0.35	16	-	-	-	-	-	-	-
E(F)	0.039	0.857	-0.155	10.463	0.993	0.365	2	0.56	16	-	-	-	-	-	-	-
E(L)	0.033	2.291	0.829	10.463	0.988	0.740	3	0.25	32	-	-	-	-	-	-	-
E(L)	0.073	0.882	-0.126	10.463	0.959	1.346	2	0.29	16	-	-	-	-	-	-	-
E(L)	0.037	4.312	1.461	10.463	0.955	1.688	3	0.12	32	-	-	-	-	-	-	-
E(M)	0.044	0.148	-1.912	10.463	0.954	0.971	4	2.87	64	-	-	-	-	-	-	-
E(M)	0.054	0.133	-2.019	10.463	0.982	0.562	3	2.62	32	-	-	-	-	-	-	-
E(M)	0.088	0.133	-2.018	10.463	0.958	1.189	4	1.62	64	-	-	-	-	-	-	-
F(B)	0.021	1.717	0.540	10.463	0.676	4.639	2	0.52	16	-	-	-	-	-	-	-
F(B)	0.018	27.673	3.320	10.463	0.951	1.942	2	0.04	16	-	-	-	-	-	-	-
F(B)	0.064	2.473	0.905	10.463	0.890	3.219	1	0.12	8	-	-	-	-	-	-	-
F(C)	0.054	0.211	-1.555	10.463	0.898	1.763	4	1.65	64	-	-	-	-	-	-	-
F(C)	0.094	0.097	-2.335	10.463	0.963	1.065	4	2.09	64	-	-	-	-	-	-	-
F(C)	0.038	0.127	-2.067	10.463	0.816	2.211	4	3.94	64	-	-	-	-	-	-	-
F(E)	0.118	28.206	3.340	10.463	0.985	1.756	1	0.01	8	-	-	-	-	-	-	-
F(E)	0.049	48.116	3.874	10.463	0.940	3.201	1	0.01	8	-	-	-	-	-	-	-
F(E)	0.996	0.698	-0.359	10.463	0.774	6.069	1	0.03	8	-	-	-	-	-	-	-
F(L)	0.021	11.005	2.398	10.463	0.980	1.275	1	0.08	8	-0.998	-0.009	0.027	0.969	-	0	6.68
F(L)	0.037	10.129	2.315	10.463	0.959	1.953	2	0.05	16	-	-	-	-	-	-	-
F(L)	0.056	5.560	1.716	10.463	0.995	0.741	1	0.06	8	-	-	-	-	-	-	-
F(M)	0.071	0.189	-1.668	10.463	0.964	1.072	4	1.41	2	-	-	-	-	-	-	-
F(M)	0.067	0.232	-1.462	10.463	0.929	1.583	4	1.21	2	-21.93	0.442	0.002	0.999	-	0	42.51
F(M)	0.246	0.028	-3.575	10.463	0.939	1.653	4	2.74	2	-1.400	0.638	0.003	1.000	-	0	42.51
L(B)	0.080	0.673	-0.396	10.463	0.947	1.436	2	0.35	16	-	-	-	-	-	-	-
L(B)	0.057	0.859	-0.152	10.463	0.982	0.889	3	0.39	32	-	-	-	-	-	-	-
L(B)	0.054	1.520	0.419	10.463	0.951	1.587	2	0.23	16	-	-	-	-	-	-	-
L(C)	0.159	0.409	-0.894	10.463	0.968	1.235	1	0.29	8	-0.051	-0.527	0.014	1.000	-	0	6.38
L(C)	0.534	0.103	-2.276	10.463	0.991	0.824	2	0.34	16	0.000	-3.605	0.033	0.907	2.513	2	2.06
L(C)	0.526	0.060	-2.805	10.463	0.982	1.026	2	0.59	16	-0.426	-0.575	0.023	0.960	2.117	1	4.66

PR(FR)	a	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{\max}	BP	l	β	Q_{alone}	VAC	SE	df	Xpt
L(E)	0.077	0.548	-0.602	10.463	0.968	1.202	3	0.44	32	-	-	-	-	-	-	-
L(E)	-0.444	0.015	-4.172	10.463	0.892	2.074	2	-	16	-	-	-	-	-	-	-
L(E)	0.260	0.049	-3.013	10.463	0.917	1.891	3	1.48	32	-	-	-	-	-	-	-
L(F)	0.168	0.250	-1.386	10.463	0.979	1.068	3	0.45	32	-	-	-	-	-	-	-
L(F)	0.147	0.212	-1.553	10.463	0.966	1.237	3	0.61	32	-	-	-	-	-	-	-
L(F)	1.394	0.015	-4.186	10.463	0.972	1.507	3	0.89	32	-	-	-	-	-	-	-
L(M)	0.269	0.050	-3.005	10.463	0.968	1.275	4	1.41	64	-1.507	15.017	0.001	0.992	-	0	42.66
L(M)	0.132	0.162	-1.822	10.463	0.950	1.360	3	0.89	32	-	-	-	-	-	-	-
L(M)	2.620	0.035	-3.366	10.463	0.990	1.260	1	0.21	8	-	-	-	-	-	-	-
M(B)	0.026	0.147	-1.915	10.463	0.935	1.158	5	4.85	128	-	-	-	-	-	-	-
M(B)	0.002	1.287	0.253	10.463	0.938	1.438	4	6.68	64	-	-	-	-	-	-	-
M(B)	0.060	0.312	-1.166	10.463	0.746	2.012	4	1.00	64	-	-	-	-	-	-	-
M(C)	0.059	0.488	-0.717	10.463	0.940	1.410	3	0.66	32	-	-	-	-	-	-	-
M(C)	0.061	0.150	-1.898	10.463	0.997	0.226	3	2.05	32	-	-	-	-	-	-	-
M(C)	0.034	0.185	-1.685	10.463	0.990	0.414	4	2.96	64	-	-	-	-	-	-	-
M(E)	0.205	0.054	-2.927	10.463	0.968	1.182	4	1.72	64	-0.428	-0.106	0.004	0.995	-	0	30.90
M(E)	0.174	0.037	-3.291	10.463	0.969	1.026	3	2.92	32	-	-	-	-	-	-	-
M(E)	0.106	0.088	-2.434	10.463	0.939	1.284	3	2.03	32	-	-	-	-	-	-	-
M(F)	0.038	0.426	-0.852	10.463	0.924	1.698	4	1.17	64	-	-	-	-	-	-	-
M(F)	0.051	0.200	-1.607	10.463	0.977	0.634	3	1.85	32	-	-	-	-	-	-	-
M(F)	0.092	0.129	-2.050	10.463	0.969	1.034	4	1.60	64	-	-	-	-	-	-	-
M(L)	6.664	0.006	-5.143	10.463	0.982	1.788	1	0.49	8	-	-	-	-	-	-	-
M(L)	0.038	7.014	1.948	10.463	0.981	1.433	1	0.07	8	-	-	-	-	-	-	-
M(L)	0.055	16.207	2.785	10.463	0.995	0.927	1	0.02	8	-	-	-	-	-	-	-

Note: B = Berries, C = Chicken, E = Egg, F = Foliage, L = Locusts & M = Mushrooms.

Table E7. Parameter estimates for initial demand, Q_0 ; essential value, α ; P_{\max} , interaction, I , and sensitivity, β ; break point and cross point data for P1 in Experiment 4 for the PR FR 30 and PR FR 10 conditions.

Condition	PR(FR)	α	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{\max}	BP	I	β	Q_{alone}	VAC	SE	df	Xpt
FR10	B(E)	0.126	0.255	-1.368	11.111	0.934	1.551	2	0.55	16	-	-	-	-	-	-	-
FR10	B(E)	0.026	2.167	0.773	11.111	0.894	1.939	3	0.31	16	-	-	-	-	-	-	-
FR10	B(E)	0.108	0.278	-1.28	11.111	0.953	1.472	3	0.59	32	-0.472	-14.738	0.061	0.971	-	0	-
FR10	B(E)	0.090	0.201	-1.604	11.111	0.931	1.488	3	0.99	32	-	-	-	-	-	-	-
FR10	B(E)	0.223	0.142	-1.953	11.111	0.964	1.273	2	0.56	16	-0.591	-14.738	0.061	0.949	-	0	-
FR10	B(E)	0.303	0.070	-2.660	11.111	0.688	4.577	2	0.84	16	-	-	-	-	-	-	-
FR30	B(E)	0.060	0.073	-2.616	11.111	0.989	0.483	3	4.04	32	-	-	-	-	-	-	-
FR30	B(E)	0.113	0.266	-1.324	11.111	0.933	1.229	3	0.59	16	-	-	-	-	-	-	-
FR30	B(E)	0.067	0.324	-1.128	11.111	0.987	0.523	2	0.81	16	-	-	-	-	-	-	-
FR30	B(E)	0.153	0.139	-1.972	11.111	0.980	0.882	3	0.84	32	-0.087	-17.932	0.035	0.971	-	0	-
FR30	B(E)	0.053	0.287	-1.248	11.111	0.951	1.348	4	1.17	64	-74.14	0.417	0.022	0.983	-	0	31.39
FR30	B(E)	0.045	0.350	-1.051	11.111	0.931	1.583	4	1.13	64	-0.002	-17.932	0.033	0.663	4.452	1	14.50
FR10	C(M)	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-
FR10	C(M)	0.017	64.110	4.161	11.111	0.954	1.828	2	0.02	8	-0.104	-1.525	0.054	0.999	-	0	-
FR10	C(M)	0.668	0.054	-2.914	11.111	0.942	1.544	2	0.49	8	-0.150	-306.19	0.094	0.998	0.277	1	-
FR10	C(M)	0.377	0.037	-3.30	11.111	0.987	0.645	3	1.28	16	0.290	3.000	0.092	0.823	-	0	-
FR10	C(M)	0.001	452.561	6.115	11.111	0.984	0.707	2	0.03	8	-0.037	-0.040	0.064	1.000	-	0	-
FR10	C(M)	0.042	0.267	-1.319	11.111	0.864	1.494	4	1.58	32	-	-	-	-	-	-	-
FR30	C(M)	0.131	0.288	-1.245	11.111	0.986	0.853	3	0.47	32	-0.069	-40.933	0.040	0.989	-	0	-
FR30	C(M)	0.028	2.367	0.862	11.111	0.966	1.138	4	0.27	32	-0.043	-5.758	0.032	1.000	-	0	-
FR30	C(M)	0.140	0.153	-1.874	11.111	0.581	2.409	2	0.83	16	-	-	-	-	-	-	-
FR30	C(M)	0.150	0.187	-1.678	11.111	0.974	0.952	4	0.64	32	-0.001	-138.60	0.032	1.000	-	0	29.09
FR30	C(M)	0.140	0.167	-1.791	11.111	0.793	2.967	3	0.76	32	-	-	-	-	-	-	-
FR30	C(M)	0.011	100.281	4.608	11.111	0.956	1.523	4	0.02	32	-0.149	-0.214	0.052	0.998	0.314	2	1.09
FR10	E(B)	1.272	0.030	-3.512	11.111	0.748	2.683	7	33.84	512	-0.326	-32.479	0.037	0.993	0.595	2	-
FR10	E(B)	0.101	0.233	-1.455	11.111	0.915	1.573	2	54.35	16	-	-	-	-	-	-	-
FR10	E(B)	0.016	0.242	-1.417	11.111	0.923	1.435	6	333.34	256	-0.261	-0.212	0.030	0.998	-	0	61.21
FR10	E(B)	0.015	0.402	-0.910	11.111	0.966	0.477	5	217.63	128	-0.098	-3.519	0.025	0.999	-	0	-
FR10	E(B)	0.032	0.271	-1.305	11.111	0.988	0.598	5	148.55	128	-0.016	-14.735	0.020	0.997	-	0	31.58
FR10	E(B)	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
FR30	E(B)	0.050	0.122	-2.108	11.111	0.975	0.731	4	2.90	64	-0.010	-0.374	0.010	0.998	-	0	40.98
FR30	E(B)	0.034	0.230	-1.471	11.111	0.945	1.282	5	166.40	128	-0.069	-6.590	0.011	1.000	0.193	1	42.17

Condition	PR(FR)	α	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{max}	BP	l	θ	Q_{alone}	VAC	SE	df	Xpt
FR30	E(B)	0.031	0.241	-1.421	11.111	0.979	0.627	4	2.34	64	-	-	-	-	-	-	-
FR30	E(B)	0.017	0.447	-0.805	11.111	0.924	1.437	5	168.21	128	-0.182	-1.169	0.014	0.999	0.327	1	51.26
FR30	E(B)	0.025	0.313	-1.160	11.111	0.985	0.624	5	2.25	128	-	-	-	-	-	-	-
FR30	E(B)	0.020	0.185	-1.686	11.111	0.880	1.983	6	348.34	256	-0.287	-2.563	0.021	0.998	0.000	2	70.03
FR10	M(C)	1.420	0.041	-3.187	11.111	0.874	1.516	5	0.30	64	-	-	-	-	-	-	-
FR10	M(C)	0.024	1.263	0.233	11.111	0.998	0.189	4	0.58	32	-33.56	17.254	0.037	0.993	-	0	36.49
FR10	M(C)	1.285	0.042	-3.169	11.111	0.717	2.597	5	0.33	64	-1.485	-18.746	0.028	0.936	-	0	-
FR10	M(C)	0.163	0.060	-2.821	11.111	0.884	1.670	3	1.83	16	-	-	-	-	-	-	-
FR10	M(C)	0.031	0.545	-0.606	11.111	0.978	0.733	5	1.06	64	-0.473	-1.822	0.011	0.991	-	0	31.40
FR10	M(C)	0.042	0.267	-1.319	11.111	0.860	1.892	4	1.58	32	-0.030	-27.356	0.055	1.000	-	0	-
FR30	M(C)	0.031	0.171	-1.768	11.111	0.996	0.267	4	3.40	64	-	-	-	-	-	-	-
FR30	M(C)	0.049	0.296	-1.219	11.111	0.959	1.048	5	1.22	64	-0.939	-2.638	0.006	0.977	-	0	36.13
FR30	M(C)	0.045	0.122	-2.101	11.111	0.921	1.311	4	3.25	64	-	-	-	-	-	-	-
FR30	M(C)	0.059	0.691	-0.370	11.111	0.953	0.985	3	0.44	16	-	-	-	-	-	-	-
FR30	M(C)	0.031	0.046	-3.078	11.111	0.909	1.483	3	12.38	32	-	-	-	-	-	-	-
FR30	M(C)	0.103	0.116	-2.156	11.111	0.942	1.110	4	1.49	32	-2.926	52.108	0.018	1.000	-	0	21.90

Note: B = Berries, C = Chicken, E = Egg & M = Mushrooms.

Table E8. Parameter estimates for initial demand, Q_0 ; essential value, α ; P_{\max} , interaction, I , and sensitivity, β ; break point and cross point data for P2 in Experiment 4 for the PR FR 30 and PR FR 10 conditions.

Condition	PR(FR)	α	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{\max}	BP	I	β	Q_{alone}	VAC	SE	df	Xpt
FR10	B(E)	0.092	0.724	-0.323	9.255	0.967	0.923	3	0.32	16	-	-	-	-	-	-	-
FR10	B(E)	0.108	0.089	-2.424	9.255	0.977	0.609	3	2.22	16	-	-	-	-	-	-	-
FR10	B(E)	0.108	0.283	-1.263	9.255	0.972	0.858	4	0.70	32	-	-	-	-	-	-	-
FR10	B(E)	0.232	0.045	-3.098	9.255	0.956	1.218	5	2.04	64	-0.202	-21.90	0.023	0.996	0.563	1	-
FR10	B(E)	0.366	0.077	-2.564	9.255	0.947	1.465	4	0.76	32	-0.305	-42.33	0.046	0.996	0.399	2	3.35
FR10	B(E)	0.135	0.053	-2.944	9.255	0.939	1.440	6	2.99	128	-0.079	-27.05	0.031	0.998	0.305	2	-
FR30	B(E)	-	-	-	-	-	-	0	-	4	-	-	-	-	-	-	54.60
FR30	B(E)	0.064	0.572	-0.558	9.255	0.977	0.902	5	0.59	64	-	-	-	-	-	-	-
FR30	B(E)	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
FR30	B(E)	0.540	0.022	-3.817	9.255	0.968	1.222	5	1.80	64	-0.461	-85.77	0.015	0.997	0.568	1	8.80
FR30	B(E)	-	-	-	-	-	-	0	-	4	-	-	-	-	-	-	-
FR30	B(E)	0.195	0.075	-2.587	9.255	0.868	2.229	5	1.46	64	-0.636	0.031	0.008	0.990	1.090	1	101.45
FR10	C(M)	0.071	0.147	-1.921	9.255	0.957	0.802	4	2.05	32	-	-	-	-	-	-	-
FR10	C(M)	0.057	1.358	0.306	9.255	0.953	1.319	4	0.28	32	-	-	-	-	-	-	-
FR10	C(M)	0.076	0.322	-1.133	9.255	0.879	1.612	4	0.88	32	-	-	-	-	-	-	-
FR10	C(M)	0.022	17.891	2.884	9.255	0.940	1.521	5	0.05	64	-	-	-	-	-	-	-
FR10	C(M)	0.862	0.047	-3.060	9.255	0.867	2.622	3	0.53	16	-	-	-	-	-	-	-
FR10	C(M)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
FR30	C(M)	-	-	-	-	-	-	0	-	4	-	-	-	-	-	-	-
FR30	C(M)	0.056	0.340	-1.078	9.255	0.972	0.817	5	1.12	64	-	-	-	-	-	-	-
FR30	C(M)	-1.01	0.001	-6.847	9.255	0.984	1.117	3	26.73	16	-	-	-	-	-	-	-
FR30	C(M)	0.075	0.245	-1.407	9.255	0.974	0.830	5	1.16	64	-	-	-	-	-	-	-
FR30	C(M)	0.184	5.621	1.727	9.255	0.992	0.778	3	6.76	16	-	-	-	-	-	-	-
FR30	C(M)	0.306	0.096	-2.345	9.255	0.978	0.886	4	0.73	32	-	-	-	-	-	-	-
FR10	E(B)	0.837	0.104	-2.266	9.255	0.772	2.699	3	1.33	32	-	-	-	-	-	-	-
FR10	E(B)	0.250	0.026	-3.633	9.255	0.951	1.423	4	17.42	64	-0.079	-89.32	0.021	0.997	0.366	2	4.97
FR10	E(B)	0.056	0.330	-1.108	9.255	0.981	0.606	3	6.22	32	-	-	-	-	-	-	-
FR10	E(B)	0.061	0.204	-1.588	9.255	0.969	0.554	5	9.17	128	-	-	-	-	-	-	-
FR10	E(B)	-	-	-	-	-	-	0	-	4	-	-	-	-	-	-	-
FR10	E(B)	0.040	0.170	-1.775	9.255	0.976	0.756	5	17.18	128	-	-	-	-	-	-	-
FR30	E(B)	0.047	2.739	1.008	9.255	0.982	1.017	3	0.14	32	-0.106	-16.50	0.018	0.999	-	1	6.11
FR30	E(B)	0.082	0.152	-1.886	9.255	0.904	1.759	4	9.27	64	-	-	-	-	-	-	-

Condition	PR(FR)	α	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{max}	BP	l	θ	Q_{alone}	VAC	SE	df	Xpt
FR30	E(B)	0.502	0.091	-2.402	9.255	0.989	0.806	2	0.52	16	-0.204	-5.461	0.027	0.917	2.344	2	8.50
FR30	E(B)	0.049	0.159	-1.840	9.255	0.980	0.742	5	14.76	128	-	-	-	-	-	-	-
FR30	E(B)	0.061	5.687	1.738	9.255	0.995	0.853	1	0.05	8	-	-	-	-	-	-	-
FR30	E(B)	0.066	0.354	-1.038	9.255	0.953	1.303	4	4.94	64	-	-	-	-	-	-	-
FR10	M(C)	3.881	0.038	-3.275	9.255	0.850	1.957	3	0.15	16	-	-	-	-	-	-	-
FR10	M(C)	0.085	2.610	0.959	9.255	0.990	0.656	2	0.10	8	-	-	-	-	-	-	-
FR10	M(C)	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-
FR10	M(C)	-	-	-	-	-	-	0	-	4	-	-	-	-	-	-	-
FR10	M(C)	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-
FR10	M(C)	0.995	23.069	3.138	9.255	0.865	3.429	2	0.00	8	-	-	-	-	-	-	-
FR30	M(C)	0.042	0.100	-2.305	9.255	0.979	0.731	7	5.76	256	-	-	-	-	-	-	178.50
FR30	M(C)	0.069	0.385	-0.955	9.255	0.978	0.652	4	0.81	32	-	-	-	-	-	-	-
FR30	M(C)	0.033	0.096	-2.343	9.255	0.950	1.073	7	7.37	256	-	-	-	-	-	-	-
FR30	M(C)	0.054	0.338	-1.084	9.255	0.957	0.651	3	1.16	16	-	-	-	-	-	-	-
FR30	M(C)	0.037	0.046	-3.079	9.255	0.909	1.284	4	12.38	32	-	-	-	-	-	-	-
FR30	M(C)	0.055	0.585	-0.536	9.255	0.914	1.700	5	0.66	64	-	-	-	-	-	-	-

Note: B = Berries, C = Chicken, E = Egg & M = Mushrooms.

Table E9. Parameter estimates for initial demand, Q_0 ; essential value, α ; P_{\max} , interaction, I , and sensitivity, β ; break point and cross point data for P3 in Experiment 4 for the PR FR 30 and PR FR 10 conditions.

Condition	PR(FR)	α	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{\max}	BP	I	β	Q_{alone}	VAC	SE	df	Xpt
FR10	B(E)	2.833	0.143	-1.943	15.747	0.888	-	0	0.03	4	-	-	-	-	-	-	-
FR10	B(E)	0.059	0.055	-2.907	15.747	0.821	3.270	4	3.91	16	-	-	-	-	-	-	-
FR10	B(E)	0.060	0.685	-0.379	15.747	0.912	1.931	1	0.30	8	-	-	-	-	-	-	-
FR10	B(E)	0.176	0.027	-3.618	15.747	0.930	1.789	2	2.66	16	-	-	-	-	-	-	-
FR10	B(E)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
FR10	B(E)	0.040	0.037	-3.288	15.747	0.986	0.619	5	8.38	128	-	-	-	-	-	-	-
FR30	B(E)	0.077	0.453	-0.791	15.747	0.988	0.763	2	0.36	16	-	-	-	-	-	-	-
FR30	B(E)	5.266	0.022	-3.812	15.747	0.761	3.196	3	0.11	32	-	-	-	-	-	-	-
FR30	B(E)	0.150	0.136	-1.992	15.747	0.915	1.986	2	0.61	16	-	-	-	-	-	-	-
FR30	B(E)	0.105	0.124	-2.089	15.747	0.978	0.934	3	0.96	32	-0.087	-36.892	0.035	0.999	-	0	-
FR30	B(E)	0.022	1.893	0.638	15.747	0.975	1.021	2	0.31	16	-	-	-	-	-	-	-
FR30	B(E)	0.032	0.269	-1.314	15.747	0.923	1.676	4	1.44	64	-0.516	1.925	0.033	0.996	0.486	1	19.53
FR10	C(M)	0.043	0.062	-2.787	15.747	0.928	1.400	6	4.70	128	-0.793	-11.411	0.051	0.987	0.928	2	27.66
FR10	C(M)	0.039	0.085	-2.468	15.747	0.965	0.797	5	3.84	64	-	-	-	-	-	-	-
FR10	C(M)	0.047	0.110	-2.207	15.747	0.973	0.760	5	2.43	64	-0.307	-47.669	0.032	0.937	-	0	-
FR10	C(M)	1.168	0.076	-2.576	15.747	0.794	1.727	5	0.14	64	-	-	-	-	-	-	-
FR10	C(M)	0.047	0.093	-2.379	15.747	0.958	0.671	5	2.85	64	-0.793	-11.411	0.036	0.956	1.883	1	31.99
FR10	C(M)	0.027	0.150	-1.895	15.747	0.894	1.383	5	3.05	64	-	-	-	-	-	-	-
FR30	C(M)	0.038	0.062	-2.788	15.747	0.964	0.996	5	5.41	128	-0.720	-12.787	0.062	0.985	0.782	2	23.32
FR30	C(M)	0.028	0.976	-0.024	15.747	0.954	1.329	4	0.45	32	-0.043	-13.954	0.032	1.000	-	0	9.10
FR30	C(M)	0.140	0.152	-1.886	15.747	0.934	1.222	4	0.59	64	-9.564	1.058	0.016	0.994	-	0	-
FR30	C(M)	0.102	0.168	-1.786	15.747	0.975	0.933	4	0.73	32	-0.001	-155.63	0.032	1.000	-	0	-
FR30	C(M)	0.050	0.082	-2.497	15.747	0.986	0.597	4	3.03	64	-9.564	1.058	0.016	0.994	-	0	34.66
FR30	C(M)	0.681	0.012	-4.395	15.747	0.963	1.401	4	1.49	32	-0.149	-1735.6	0.052	0.998	0.314	2	11.98
FR10	E(B)	0.034	0.204	-1.591	15.747	0.929	1.467	4	273.17	64	-0.523	-1.872	0.008	0.990	-	0	37.88
FR10	E(B)	0.104	0.156	-1.856	15.747	0.986	0.806	3	118.24	64	-3.026	25.572	0.031	0.999	-	0	-
FR10	E(B)	0.052	0.124	-2.089	15.747	0.935	1.462	4	299.64	64	-0.236	-15.250	0.017	0.985	-	0	-
FR10	E(B)	0.139	0.788	-0.238	15.747	0.983	1.547	1	17.53	8	-	-	-	-	-	-	-
FR10	E(B)	0.058	0.071	-2.641	15.747	0.946	1.498	5	460.42	128	-0.645	-5.255	0.010	0.983	1.036	2	-
FR10	E(B)	0.044	1.313	0.273	15.747	0.927	1.944	1	33.04	8	-	-	-	-	-	-	-
FR30	E(B)	0.088	0.050	-2.995	15.747	0.966	1.011	3	2.85	32	-	-	-	-	-	-	-

Condition	PR(FR)	α	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{\max}	BP	l	β	Q_{alone}	VAC	SE	df	Xpt
FR30	E(B)	0.033	0.067	-2.709	15.747	0.975	0.790	5	861.79	128	-	-	-	-	-	-	-
FR30	E(B)	0.019	0.131	-2.032	15.747	0.946	1.101	5	4.92	128	-	-	-	-	-	-	-
FR30	E(B)	0.146	0.132	-2.027	15.747	0.974	1.038	2	99.68	16	-	-	-	-	-	-	-
FR30	E(B)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
FR30	E(B)	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
FR10	M(C)	0.058	0.657	-0.419	15.747	0.936	1.478	3	0.33	16	-	-	-	-	-	-	-
FR10	M(C)	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
FR10	M(C)	0.047	0.120	-2.122	15.747	0.957	0.212	5	2.24	64	-	-	-	-	-	-	-
FR10	M(C)	0.057	0.415	-0.880	15.747	0.887	1.609	3	0.53	16	-	-	-	-	-	-	-
FR10	M(C)	0.035	0.119	-2.124	15.747	0.974	0.046	5	3.00	64	-	-	-	-	-	-	-
FR10	M(C)	0.043	0.558	-0.584	15.747	0.928	1.185	3	0.52	16	-	-	-	-	-	-	-
FR30	M(C)	0.016	1.108	0.103	15.747	0.898	2.814	4	0.71	64	-	-	-	-	-	-	-
FR30	M(C)	0.050	0.184	-1.695	15.747	0.976	0.557	3	1.35	16	-	-	-	-	-	-	-
FR30	M(C)	0.044	0.382	-0.961	15.747	0.948	1.361	3	0.74	32	-1.417	-3.435	0.754	0.896	1.873	1	3.33
FR30	M(C)	0.066	0.417	-0.875	15.747	0.981	0.684	3	0.46	16	-0.962	18.361	0.034	1.000	-	0	7.77
FR30	M(C)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
FR30	M(C)	0.042	0.363	-1.014	15.747	0.973	0.789	4	0.83	32	-0.016	-19.694	0.022	1.000	-	0	-

Note: B = Berries, C = Chicken, E = Egg & M = Mushrooms.

Table E10. Parameter estimates for initial demand, Q_0 ; essential value, α ; P_{\max} , interaction, I , and sensitivity, β ; break point and cross point data for P4 in Experiment 4 for the PR FR 30 and PR FR 10 conditions.

Condition	PR(FR)	α	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{\max}	BP	I	β	Q_{alone}	VAC	SE	df	Xpt
FR10	B(E)	0.062	0.130	-2.042	10.856	0.898	2.194	5	2.26	4	-0.403	-3.027	0.031	0.995	-	1	-
FR10	B(E)	0.039	0.039	-3.240	10.856	0.934	1.386	6	12.04	16	-	-	-	-	-	-	-
FR10	B(E)	0.091	0.075	-2.592	10.856	0.911	1.174	5	2.67	8	-0.427	-8.966	0.039	0.987	1.026	1	-
FR10	B(E)	0.043	0.031	-3.470	10.856	0.964	1.025	6	13.67	16	-	-	-	-	-	-	-
FR10	B(E)	0.103	0.040	-3.223	10.856	0.940	1.495	5	4.43	64	-0.425	-20.24	0.038	0.981	1.026	2	-
FR10	B(E)	0.042	0.108	-2.230	10.856	0.881	2.328	5	4.07	128	-	-	-	-	-	-	-
FR30	B(E)	0.179	0.062	-2.784	10.856	0.986	0.763	4	1.62	64	-	-	-	-	-	-	-
FR30	B(E)	0.042	0.056	-2.885	10.856	0.895	1.935	6	7.79	32	-0.045	-14.18	0.012	0.999	-	2	-
FR30	B(E)	0.131	0.047	-3.057	10.856	0.978	0.963	5	2.87	128	-	-	-	-	-	-	-
FR30	B(E)	0.108	0.053	-2.934	10.856	0.936	1.635	5	3.17	32	-0.004	-44.87	0.012	1.000	0.157	1	-
FR30	B(E)	0.136	0.062	-2.775	10.856	0.871	2.202	5	1.16	128	-	-	-	-	-	-	-
FR30	B(E)	0.195	0.043	-3.152	10.856	0.945	1.531	4	2.18	64	-0.005	-114.5	0.019	0.999	0.347	1	11.56
FR10	C(M)	0.061	0.008	-4.869	10.856	0.912	1.814	6	38.64	128	-	-	-	-	-	-	-
FR10	C(M)	0.042	0.032	-3.436	10.856	0.877	1.945	7	13.40	64	-	-	-	-	-	-	-
FR10	C(M)	0.016	0.041	-3.201	10.856	0.886	1.695	7	28.57	256	-0.296	0.043	0.072	0.815	3.779	1	0.00
FR10	C(M)	0.019	0.075	-2.592	10.856	0.913	1.614	7	13.12	512	-	-	-	-	-	-	-
FR10	C(M)	0.044	0.055	-2.906	10.856	0.897	1.729	7	7.65	256	-1.317	-4.360	0.057	0.957	1.535	3	65.97
FR10	C(M)	0.020	0.096	-2.348	10.856	0.931	1.160	7	9.47	256	-	-	-	-	-	-	-
FR30	C(M)	0.026	2.228	0.801	10.856	0.988	0.491	3	0.30	16	-	-	-	-	-	-	-
FR30	C(M)	0.061	0.024	-3.717	10.856	0.933	1.428	7	12.38	256	-0.744	-10.02	0.029	0.991	0.936	1	51.10
FR30	C(M)	0.013	21.789	3.081	10.856	0.986	0.790	4	23.00	32	-	-	-	-	-	-	-
FR30	C(M)	0.010	0.112	-2.185	10.856	0.889	1.602	7	16.42	256	-0.304	-2.725	0.016	0.994	0.243	2	100.80
FR30	C(M)	0.860	0.138	-1.982	10.856	0.995	0.572	2	0.15	8	-	-	-	-	-	-	-
FR30	C(M)	0.067	0.033	-3.425	10.856	0.934	1.461	7	8.32	256	-0.903	-15.78	0.034	0.987	0.754	4	48.41
FR10	E(B)	0.084	0.119	-2.128	10.856	0.973	0.923	4	99.45	64	-	-	-	-	-	-	-
FR10	E(B)	0.151	0.025	-3.703	10.856	0.963	1.248	5	268.04	128	-0.436	-59.51	0.024	0.993	0.657	2	-
FR10	E(B)	0.145	0.061	-2.792	10.856	0.906	1.955	4	112.46	64	-0.442	-22.91	0.019	0.997	0.561	1	19.53
FR10	E(B)	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
FR10	E(B)	0.052	7.348	1.994	10.856	0.964	-	0	2.62	4	-	-	-	-	-	-	-
FR10	E(B)	0.025	0.042	-3.162	10.856	0.961	0.842	6	938.30	8	-	-	-	-	-	-	-
FR30	E(B)	0.110	0.048	-3.036	10.856	0.980	0.876	5	3.39	128	-	-	-	-	-	-	-
FR30	E(B)	0.047	0.107	-2.236	10.856	0.903	1.757	5	198.21	128	-	-	-	-	-	-	-

Condition	PR(FR)	α	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{max}	BP	l	θ	Q_{alone}	VAC	SE	df	Xpt
FR30	E(B)	0.065	0.239	-1.432	10.856	0.937	1.507	4	1.22	64	-	-	-	-	-	-	-
FR30	E(B)	0.054	0.060	-2.814	10.856	0.969	1.048	6	310.75	256	-	-	-	-	-	-	-
FR30	E(B)	0.056	0.175	-1.740	10.856	0.957	1.317	5	1.74	128	-0.442	-22.42	0.012	0.926	2.398	2	28.42
FR30	E(B)	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
FR10	M(C)	0.046	0.159	-1.837	10.856	0.983	0.672	6	2.49	128	-0.001	-19.70	0.012	0.999	0.328	1	35.95
FR10	M(C)	0.095	0.200	-1.608	10.856	0.971	0.814	4	0.96	32	-	-	-	-	-	-	-
FR10	M(C)	0.044	0.123	-2.094	10.856	0.977	0.427	6	3.40	64	-	-	-	-	-	-	-
FR10	M(C)	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
FR10	M(C)	0.026	0.332	-1.103	10.856	0.968	0.880	6	2.12	128	-	-	-	-	-	-	-
FR10	M(C)	0.057	0.039	-3.234	10.856	0.988	0.575	7	8.17	256	-0.897	-13.31	0.103	0.983	-	2	-
FR30	M(C)	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-
FR30	M(C)	0.044	0.088	-2.433	10.856	0.940	0.957	6	4.75	128	-	-	-	-	-	-	-
FR30	M(C)	0.088	0.118	-2.134	10.856	0.991	0.477	5	1.73	64	-	-	-	-	-	-	-
FR30	M(C)	0.028	0.130	-2.043	10.856	0.933	1.064	6	4.98	16	-	-	-	-	-	-	-
FR30	M(C)	0.041	0.717	-0.333	10.856	0.916	1.616	4	0.60	32	-	-	-	-	-	-	-
FR30	M(C)	0.026	0.488	-0.718	10.856	0.846	1.564	5	1.41	64	-	-	-	-	-	-	-

Note: B = Berries, C = Chicken, E = Egg & M = Mushrooms.

Table E11. Parameter estimates for initial demand, Q_0 , essential value, α ; P_{max} , interaction, I , and sensitivity, β ; break point and cross point data for P5 in Experiment 4 for the PR FR 30 and PR FR 10 conditions.

Condition	PR(FR)	α	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{max}	BP	I	β	Q_{alone}	VAC	SE	df	Xpt
FR10	B(E)	0.006	356.789	5.877	9.567	0.852	2.112	3	0.01	32	-	-	-	-	-	-	-
FR10	B(E)	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-
FR10	B(E)	0.114	0.456	-0.786	9.567	0.800	3.131	2	0.40	16	-	-	-	-	-	-	-
FR10	B(E)	1.868	0.077	-2.569	9.567	0.822	1.931	3	0.14	32	-	-	-	-	-	-	-
FR10	B(E)	-0.075	0.056	-2.890	9.567	0.781	3.066	1	-4.96	8	-	-	-	-	-	-	-
FR10	B(E)	-0.17	0.023	-3.778	9.567	0.745	3.390	2	-5.18	16	-	-	-	-	-	-	-
FR30	B(E)	-	-	-	9.567	-	-	0	-	4	-	-	-	-	-	-	-
FR30	B(E)	0.041	0.119	-2.128	9.567	0.911	1.314	4	4.26	64	-	-	-	-	-	-	-
FR30	B(E)	0.230	0.325	-1.123	9.567	0.982	1.030	2	0.28	16	-	-	-	-	-	-	-
FR30	B(E)	0.031	0.014	-4.259	9.567	0.910	1.808	4	47.72	64	-	-	-	-	-	-	-
FR30	B(E)	-	-	-	-	-	-	0	0.56	4	-	-	-	-	-	-	-
FR30	B(E)	-	-	-	-	-	-	0	-	2	-	-	-	-	-	-	-
FR10	C(M)	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
FR10	C(M)	-	-	-	-	-	-	0	-	4	-	-	-	-	-	-	-
FR10	C(M)	-	-	-	-	-	-	0	-	4	-	-	-	-	-	-	-
FR10	C(M)	0.141	0.204	-1.588	9.567	0.967	0.350	32	0.72	512	-	-	-	-	-	-	-
FR10	C(M)	-	-	-	-	-	-	0	-	2	-	-	-	-	-	-	-
FR10	C(M)	-	-	-	-	-	-	0	-	2	-	-	-	-	-	-	-
FR30	C(M)	-	-	-	-	-	-	0	-	4	-	-	-	-	-	-	-
FR30	C(M)	4.030	0.013	-4.352	9.567	0.998	0.348	2	0.40	8	-	-	-	-	-	-	-
FR30	C(M)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
FR30	C(M)	-	-	-	-	-	-	0	-	1	-	-	-	-	-	-	-
FR30	C(M)	-	-	-	-	-	-	0	-	2	-	-	-	-	-	-	-
FR30	C(M)	-	-	-	-	-	-	0	-	2	-	-	-	-	-	-	-
FR10	E(B)	-	-	-	-	-	-	0	-	2	-	-	-	-	-	-	-
FR10	E(B)	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
FR10	E(B)	-	-	-	-	-	-	0	-	2	-	-	-	-	-	-	-
FR10	E(B)	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
FR10	E(B)	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
FR10	E(B)	-	-	-	-	-	-	0	-	1	-	-	-	-	-	-	-
FR30	E(B)	0.382	0.180	-1.715	9.567	0.940	9.875	5	3.32	128	-	-	-	-	-	-	-
FR30	E(B)	-	-	-	-	-	-	2	-	4	-	-	-	-	-	-	-

Condition	PR(FR)	α	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{\max}	BP	l	β	Q_{alone}	VAC	SE	df	Xpt
FR30	E(B)	0.039	4.545	1.514	9.567	0.887	7.680	4	1.17	64	-0.323	-0.042	0.012	0.993	0.722	2	-
FR30	E(B)	-	-	-	-	-	-	2	-	4	-	-	-	-	-	-	-
FR30	E(B)	0.059	0.205	-1.585	9.567	0.962	6.001	5	1.62	128	-0.323	-0.042	0.012	0.993	0.722	2	32.50
FR30	E(B)	-	-	-	-	-	-	0	-	4	-	-	-	-	-	-	-
FR10	M(C)	0.033	0.179	-1.721	9.567	0.954	0.764	5	3.51	64	-	-	-	-	-	-	-
FR10	M(C)	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
FR10	M(C)	-	-	-	-	-	-	0	-	1	-	-	-	-	-	-	-
FR10	M(C)	-	-	-	-	-	-	0	-	4	-	-	-	-	-	-	-
FR10	M(C)	0.074	0.285	-1.254	9.567	0.911	1.113	3	0.98	16	-	-	-	-	-	-	-
FR10	M(C)	-	-	-	-	-	-	0	-	1	-	-	-	-	-	-	-
FR30	M(C)	0.103	0.108	-2.229	9.567	0.963	0.971	5	1.88	64	-	-	-	-	-	-	-
FR30	M(C)	0.077	0.400	-0.917	9.567	0.891	1.358	3	0.67	16	-	-	-	-	-	-	-
FR30	M(C)	0.125	0.245	-1.408	9.567	0.938	0.848	5	1.56	64	-	-	-	-	-	-	-
FR30	M(C)	0.002	0.025	-3.690	9.567	0.968	0.870	3	338.74	16	-	-	-	-	-	-	-
FR30	M(C)	-	-	-	-	-	-	0	-	1	-	-	-	-	-	-	-
FR30	M(C)	0.213	2.073	0.729	9.567	0.959	2.064	1	0.05	4	-	-	-	-	-	-	-

Note: B = Berries, C = Chicken, E = Egg & M = Mushrooms.

Table E12. Parameter estimates for initial demand, Q_0 , essential value, α ; P_{\max} , interaction, I , and sensitivity, β ; break point and cross point data for P6 in Experiment 4 for the PR FR 30 and PR FR 10 conditions.

Condition	PR(FR)	α	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{\max}	BP	I	β	Q_{alone}	VAC	SE	df	Xpt
FR10	B(E)	0.045	0.242	-1.418	9.770	0.964	0.752	3	1.85	32	-	-	-	-	-	-	-
FR10	B(E)	0.019	4.278	1.454	9.770	0.933	1.804	6	0.24	256	-0.449	-0.270	0.032	0.593	6.125	1	-
FR10	B(E)	-	-	-	-	-	-	0	-	2	-	-	-	-	-	-	-
FR10	B(E)	0.126	0.025	-3.705	9.770	0.843	2.619	5	6.50	128	-0.955	-25.41	0.051	0.984	0.573	2	-
FR10	B(E)	0.190	0.304	-1.190	9.770	0.957	1.441	2	0.35	16	-	-	-	-	-	-	-
FR10	B(E)	0.096	0.048	-3.029	9.770	0.868	2.235	5	4.34	128	-1.475	-8.165	0.050	0.959	1.753	2	40.74
FR30	B(E)	0.070	0.421	-0.865	9.770	0.967	1.014	3	0.70	32	-	-	-	-	-	-	-
FR30	B(E)	0.585	0.081	-2.519	9.770	0.916	2.548	1	0.43	8	-	-	-	-	-	-	-
FR30	B(E)	0.039	0.377	-0.977	9.770	0.976	0.774	4	1.41	64	-	-	-	-	-	-	-
FR30	B(E)	0.044	0.571	-0.561	9.770	0.966	1.110	4	0.81	64	-	-	-	-	-	-	-
FR30	B(E)	0.080	0.245	-1.408	9.770	0.980	0.710	3	1.06	32	-	-	-	-	-	-	-
FR30	B(E)	0.055	0.692	-0.369	9.770	0.972	0.982	3	0.54	32	-	-	-	-	-	-	-
FR10	C(M)	0.261	0.139	-1.973	9.770	0.954	1.398	4	0.56	32	-1.215	-16.27	0.064	0.966	-	1	-
FR10	C(M)	0.028	0.715	-0.335	9.770	0.988	0.240	1	1.00	4	-	-	-	-	-	-	-
FR10	C(M)	0.216	0.209	-1.567	9.770	0.959	1.341	4	0.45	32	-0.598	-27.50	0.067	0.978	1.474	1	4.72
FR10	C(M)	0.036	0.366	-1.005	9.770	0.968	0.971	6	1.53	128	-	-	-	-	-	-	-
FR10	C(M)	0.051	0.209	-1.564	9.770	0.940	1.077	5	1.90	64	-0.081	-14.19	0.016	0.999	0.293	1	31.42
FR10	C(M)	0.081	0.037	-3.296	9.770	0.898	1.888	7	6.75	256	-0.980	-14.06	0.042	0.974	1.655	1	36.73
FR30	C(M)	0.145	0.319	-1.144	9.770	0.966	1.120	4	0.50	32	-	-	-	-	-	-	-
FR30	C(M)	-	-	-	-	-	-	0	-	2	-	-	-	-	-	-	-
FR30	C(M)	0.139	0.232	-1.463	9.770	0.966	1.051	4	0.70	32	-	-	-	-	-	-	-
FR30	C(M)	0.227	0.581	-0.543	9.770	0.981	0.893	2	0.15	8	-	-	-	-	-	-	-
FR30	C(M)	0.247	0.180	-1.715	9.770	0.783	2.315	3	0.49	16	-	-	-	-	-	-	-
FR30	C(M)	0.019	37.762	3.631	9.770	0.964	-	1	0.03	4	-	-	-	-	-	-	-
FR10	E(B)	0.133	0.124	-2.086	9.770	0.977	0.964	4	115.23	64	-	-	-	-	-	-	-
FR10	E(B)	0.073	0.059	-2.826	9.770	0.905	1.998	6	437.70	256	-0.282	-20.24	0.029	0.825	3.779	2	25.23
FR10	E(B)	0.239	0.248	-1.393	9.770	0.955	1.535	1	31.93	8	-	-	-	-	-	-	-
FR10	E(B)	0.058	0.082	-2.507	9.770	0.973	0.996	6	398.57	256	-	-	-	-	-	-	-
FR10	E(B)	0.806	0.036	-3.324	9.770	0.974	1.289	2	65.42	16	-	-	-	-	-	-	-
FR10	E(B)	-	-	-	-	-	-	0	-	4	-	-	-	-	-	-	-
FR30	E(B)	0.416	0.032	-3.440	9.770	0.956	1.450	3	1.53	32	-0.214	-12.82	0.029	0.945	1.827	2	5.06
FR30	E(B)	1.216	0.018	-4.010	9.770	0.989	0.900	3	86.11	32	-	-	-	-	-	-	-

Condition	PR(FR)	α	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{max}	BP	l	β	Q_{alone}	VAC	SE	df	Xpt
FR30	E(B)	0.056	0.345	-1.066	9.770	0.918	0.681	3	2.61	32	-	-	-	-	-	-	-
FR30	E(B)	0.150	3.520	1.259	9.770	0.996	0.758	1	3.59	8	-	-	-	-	-	-	-
FR30	E(B)	0.036	0.471	-0.752	9.770	0.936	0.709	3	0.84	32	-	-	-	-	-	-	-
FR30	E(B)	0.040	0.618	-0.481	9.770	0.999	0.081	4	76.86	64	-	-	-	-	-	-	-
FR10	M(C)	0.134	0.065	-2.728	9.770	0.814	2.490	5	2.31	64	-	-	-	-	-	-	-
FR10	M(C)	0.051	0.331	-1.106	9.770	0.989	0.505	5	1.21	64	-	-	-	-	-	-	-
FR10	M(C)	0.099	0.070	2.654	9.770	0.986	0.662	6	2.89	128	0.583	-6.892	0.006	0.984	-	1	55.16
FR10	M(C)	0.066	0.221	-1.510	9.770	0.952	0.362	4	1.39	16	-	-	-	-	-	-	1.00
FR10	M(C)	-	-	-	-	-	-	0	-	2	-	-	-	-	-	-	-
FR10	M(C)	0.051	0.176	-1.737	9.770	0.878	1.880	6	2.25	128	-	-	-	-	-	-	-
FR30	M(C)	0.064	0.483	-0.728	9.770	0.937	1.252	4	0.66	32	-	-	-	-	-	-	-
FR30	M(C)	0.247	0.375	-0.981	9.770	0.944	1.403	2	0.22	8	-	-	-	-	-	-	-
FR30	M(C)	0.066	0.151	-1.893	9.770	0.997	0.194	4	2.05	32	-	-	-	-	-	-	-
FR30	M(C)	0.096	0.090	-2.411	9.770	0.947	0.261	4	2.34	32	-	-	-	-	-	-	-
FR30	M(C)	0.037	0.187	-1.677	9.770	0.990	0.366	5	2.96	64	-	-	-	-	-	-	-
FR30	M(C)	0.033	0.527	-0.641	9.770	0.943	0.853	4	1.16	32	-	-	-	-	-	-	-

Note: B = Berries, C = Chicken, E = Egg & M = Mushrooms.

Table E13. Parameter estimates for a , b , L , P_{\max} , y_0 , a (FR) break point and cross point data averaged over five days for each possum in Experiment 5 as derived by Equation 1 (Hursh et al., 1988) and non-linear least squares regression for the FR data.

Possum	PR(FR)	a	b	L	$\ln L$	VAC	SE	df	P_{\max}	BP	y_0	a	VAC	SE	df	Xpt
P1	B(E)	0.040	0.229	0.026	-3.644	0.859	0.343	5	30.51	128	-4.775	-0.001	0.010	0.901	7	-
	CM(I)	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-
	E(B)	0.005	-0.227	0.068	-2.692	0.731	0.485	6	169.76	512	-3.164	-0.001	0.034	0.464	7	208.48
	M(C)	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-
P2	B(E)	-0.674	-3.139	0.037	-3.298	0.732	1.047	1	3.17	16	-5.874	0.056	0.198	0.861	3	-
	CM(I)	0.017	0.867	0.001	-6.621	0.425	1.259	6	110.04	256	-7.070	-0.002	0.014	1.903	4	-
	E(B)	0.001	-0.345	0.034	-3.394	0.741	0.599	6	971.20	512	-5.529	-0.009	0.154	1.801	6	-
	M(C)	0.329	2.155	0.002	-6.498	0.419	1.451	2	9.58	16	-	-	-	-	-	-
P3	B(E)	0.025	-0.789	0.054	-2.928	0.925	0.385	1	8.54	16	-7.099	0.002	0.088	1.166	5	-
	CM(I)	0.008	-0.538	0.274	-1.296	0.613	1.431	6	58.33	256	-7.595	0.003	0.050	1.579	4	178.05
	E(B)	0.001	-0.748	0.114	-2.170	0.864	0.692	6	199.83	256	-	-	-	-	-	261.09
	M(C)	0.354	0.201	0.019	-3.963	0.927	0.776	2	3.39	16	-4.178	-0.005	0.003	0.590	4	-
P4	B(E)	0.008	-0.440	0.056	-2.890	0.969	0.292	6	73.78	256	-6.686	0.003	0.373	0.950	3	-
	CM(I)	0.003	-0.375	0.081	-2.518	0.820	0.683	6	233.93	512	-6.529	0.001	0.049	1.036	8	416.57
	E(B)	-0.001	-0.861	0.242	-1.419	0.873	0.781	6	-122.2	512	-5.090	0.002	1.000	0.006	2	287.10
	M(C)	0.010	-0.335	0.036	-3.311	0.976	0.259	6	65.37	256	-4.351	0.000	0.001	0.547	7	14.41
P5	B(E)	-0.019	-0.838	0.033	-3.417	0.504	1.097	4	-8.66	64	-	-	-	-	-	-
	CM(I)	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-
	E(B)	0.042	-0.223	0.002	-6.162	0.229	1.283	2	18.38	4	-6.891	0.017	0.004	1.886	3	5.52
	M(C)	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-
P6	B(E)	0.095	-0.191	0.045	-3.099	0.781	0.926	3	8.52	32	-6.447	0.009	0.432	0.289	3	17.80
	CM(I)	0.159	0.108	0.003	-5.914	0.917	0.366	2	6.97	16	-	-	-	-	-	-
	E(B)	0.065	0.343	0.028	-3.579	0.568	0.463	3	20.75	32	-5.739	-	0.038	1.298	4	-
	M(C)	-0.015	-0.369	0.036	-3.337	0.589	0.465	2	-41.80	16	-	-	-	-	-	-

Note: B = Berries, C = Chicken, E = Egg & M = Mushrooms.

Table E14. Parameter estimates for initial demand, Q_0 ; essential value, α ; P_{\max} , interaction, I , and sensitivity, β ; break point and cross point data averaged over five days for each possum in Experiment 5 as derived by Equation 2 (Hursh & Silberberg, 2008) and Equation 5, the cross-price demand model (Hursh et al., 2013).

Possum	PR(FR)	α	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{\max}	BP	I	β	VAC	SE	df	Xpt
P1	B(E)	0.175	0.036	-3.311	6.230	0.994	0.450	5	4.98	256.00	-3.117	1187.0	0.989	0.440	5	3.53
	CM(I)	-	-	-	-	-	-	-	-	2.00	-	-	-	-	-	-
	E(B)	0.037	0.052	-2.950	6.230	0.977	0.809	6	16.44	512.00	-1.448	-0.014	0.974	0.971	6	196.10
	M(C)	-	-	-	-	-	-	-	-	2.00	-	-	-	-	-	-
P2	B(E)	1.101	0.043	-3.154	5.666	0.959	1.702	1	0.74	16.00	-4.681	1029.0	0.994	0.838	1	7.12
	CM(I)	0.030	0.006	-5.123	5.666	0.936	1.815	5	192.78	256.00	-7.118	3830.2	0.943	2.491	3	14.83
	E(B)	0.446	2.331	0.846	5.666	0.971	1.124	5	0.03	512.00	-1.938	-0.008	0.938	2.127	5	-
	M(C)	12.880	1.120	0.114	5.666	0.955	1.903	2	0.00	16.00	-	-	-	-	-	-
P3	B(E)	0.822	0.059	-2.829	8.138	0.988	0.850	1	0.50	16.00	-	-	-	-	-	-
	CM(I)	0.091	0.066	-2.713	8.138	0.986	0.727	5	5.15	256.00	-1.673	2.230	0.970	1.840	3	-
	E(B)	0.105	0.041	-3.191	8.138	0.950	0.343	5	5.62	256.00	-1.279	3.683	0.980	1.314	4	132.73
	M(C)	3.132	0.029	-3.530	8.138	0.991	0.938	2	0.34	16.00	-0.549	-25.56	0.988	0.723	2	-
P4	B(E)	0.116	0.032	-3.454	6.901	0.994	0.349	5	7.78	256.00	-2.085	13.372	0.985	1.337	1	79.14
	CM(I)	0.034	0.043	-3.149	6.901	0.978	0.148	5	19.84	512.00	-1.456	2.624	0.979	1.108	7	364.84
	E(B)	0.040	0.062	-2.773	6.901	0.943	1.479	5	11.53	512.00	-2.980	368.87	0.996	0.754	1	198.07
	M(C)	0.153	0.024	-3.737	6.407	0.996	0.431	5	7.85	256.00	-0.952	-0.801	0.988	0.083	5	27.74
P5	B(E)	0.434	0.015	-4.225	5.911	0.960	1.310	4	5.27	64.00	-	-	-	-	-	-
	CM(I)	-	-	-	-	-	-	-	-	4.00	-	-	-	-	-	-
	E(B)	7.962	0.415	-0.878	5.911	0.982	1.363	2	0.01	4.00	-1.470	1.673	0.956	1.511	2	5.49
	M(C)	-	-	-	-	-	-	-	-	4.00	-	-	-	-	-	-
P6	B(E)	0.675	0.055	-2.902	5.565	0.984	0.842	3	0.96	32.00	-0.764	-22.67	0.988	1.137	1	12.84
	CM(I)	8.542	0.157	-1.851	5.250	0.991	1.020	2	0.03	16.00	-	-	-	-	-	-
	E(B)	0.165	0.035	-3.345	5.565	0.990	0.531	3	6.10	32.00	-0.736	281.9	0.999	0.258	4	-
	M(C)	0.356	0.047	-3.059	5.250	0.997	0.322	2	2.25	16.00	-	-	-	-	-	-

Note: B = Berries, C = Chicken, E = Egg & M = Mushrooms.

Table E15. Parameter estimates for initial demand, Q_0 ; essential value, α ; P_{\max} , interaction, I , and sensitivity, β ; break point and cross point data for three days and averaged for each possum in Experiment 6 under the geometric PR FR schedule for the 'wet' foods.

Possum	PR(FR)	Day	α	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{\max}	BP	I	β	VAC	SE	df	Xpt
P1	B(E)	1	0.079	0.228	-1.479	11.870	0.971	0.948	3	0.926	32	-	-	-	-	-	-
		2	-	-	-	11.870	-	-	-	-	4	-	-	-	-	-	-
		3	0.084	0.101	-2.296	11.870	0.763	2.792	3	1.961	32	-	-	-	-	-	-
		Average	0.042	0.189	-1.666	11.870	0.933	1.083	3	2.085	32	-398.88	312.894	0.993	0.788	1	18
	E(B)	1	0.021	0.206	-1.580	11.870	0.851	1.881	5	3.911	128	-	-	-	-	-	-
		2	0.014	0.495	-0.704	11.870	0.888	1.583	6	2.329	128	-0.121	-1.821	0.998	0.398	1	46
		3	0.012	0.200	-1.609	11.870	0.903	1.829	7	6.839	512	-0.059	-5.470	0.998	0.359	1	101
		Average	0.015	0.655	-0.423	11.870	0.943	0.745	7	1.700	512	-0.129	-1.403	1.000	0.121	2	38
	P2	B(E)	1	0.014	0.179	-1.719	11.132	0.974	0.701	6	7.243	256	-	-	-	-	-
2			0.088	0.064	-2.756	11.132	0.791	2.732	6	3.172	256	-	-	-	-	-	-
3			0.020	0.087	-2.441	11.132	0.948	1.061	6	10.151	256	-	-	-	-	-	-
Average			-0.001	0.222	-1.503	11.132	0.539	2.912	6	-88.21	256	-267.17	31.469	0.992	1.004	1	-
E(B)		1	0.014	0.526	-0.642	11.132	0.914	1.724	5	2.462	128	-	-	-	-	-	-
		2	0.031	0.069	-2.680	11.132	0.913	0.476	5	8.338	256	-	-	-	-	-	-
		3	0.024	0.103	-2.271	11.132	0.952	1.096	6	7.075	256	-	-	-	-	-	-
		Average	-0.0003	0.302	-1.196	11.132	0.544	3.281	5	-221.4	256	-	-	-	-	-	-
P3	B(E)	1	0.064	0.264	-1.331	10.065	0.970	0.811	3	1.153	32	-	-	-	-	-	-
		2	0.062	0.088	-2.431	10.065	0.888	1.575	4	3.598	64	-	-	-	-	-	-
		3	0.085	0.218	-1.524	10.065	0.956	1.344	4	1.062	64	-	-	-	-	-	-
		Average	0.019	0.226	-1.486	10.065	0.826	1.480	4	4.581	64	-1.185	-2.328	0.956	2.333	1	-
	E(B)	1	0.086	0.067	-2.705	10.065	0.935	1.540	5	3.394	64	-	-	-	-	-	-
		2	0.055	0.291	-1.235	10.065	0.944	1.356	4	1.232	64	-	-	-	-	-	-
		3	0.091	0.054	-2.925	10.065	0.991	0.535	5	4.038	128	-	-	-	-	-	-
		Average	-0.010	0.121	-2.115	10.065	0.831	1.171	5	-16.209	128	-0.477	-14.851	0.995	0.837	1	-

Possum	PR(FR)	Day	α	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{\max}	BP	l	β	VAC	SE	df	Xpt
P4	B(E)	1	0.044	0.088	-2.428	9.234	0.943	0.364	6	5.495	256	-	-	-	-	-	-
		2	0.090	0.147	-1.921	9.234	0.964	0.178	6	1.619	256	-	-	-	-	-	-
		3	0.086	0.188	-1.672	9.234	0.967	1.054	4	1.328	64	-	-	-	-	-	-
		Average	0.045	0.092	-2.384	9.234	0.955	0.336	6	5.163	256	-0.313	-6.084	0.999	0.344	1	125
	E(B)	1	0.079	0.038	-3.263	9.234	0.898	2.021	6	7.113	256	-	-	-	-	-	-
		2	0.084	0.115	-2.164	9.234	0.942	1.273	4	2.224	64	-	-	-	-	-	-
		3	0.065	0.014	-4.272	9.234	0.933	1.544	5	23.524	128	-	-	-	-	-	-
Average	0.055	0.051	-2.979	9.234	0.953	1.220	6	7.613	256	-0.444	-14.798	0.994	0.831	1	-		
P5	B(E)	1	0.047	0.157	-1.849	11.104	0.857	1.769	3	2.388	32	-	-	-	-	-	-
		2	0.029	0.143	-1.945	11.104	0.913	1.306	5	4.249	128	-	-	-	-	-	-
		3	0.059	0.060	-2.811	11.104	0.943	1.182	4	5.026	64	-	-	-	-	-	-
		Average	0.032	0.137	-1.985	11.104	0.959	0.977	5	4.024	128	-	-	-	-	-	-
	E(B)	1	0.854	0.026	-3.647	11.104	0.945	2.057	3	0.800	32	-0.776	-149.26	0.985	1.429	1	6
		2	0.850	0.025	-3.685	11.104	0.858	3.359	2	0.833	16	-0.756	-203.30	0.986	1.305	1	5
		3	-	-	-	11.104	-	-	-	-	4	-	-	-	-	-	-
Average	0.614	0.035	-3.345	11.104	0.906	2.632	3	0.821	32	-0.919	-113.96	0.985	1.103	2	9		
P6	B(E)	1	0.027	1.295	0.259	8.899	0.971	1.056	6	0.634	256	108.374	473.624	0.843	3.862	2	-
		2	6.059	0.000	-9.210	8.899	0.814	3.224	4	36.635	128	-	-	-	-	-	-
		3	0.063	0.263	-1.335	8.899	0.958	1.088	4	1.342	64	-	-	-	-	-	-
		Average	0.032	0.805	-0.217	8.899	0.980	0.869	6	0.869	256	-1.533	2.095	0.950	1.850	3	34
	E(B)	1	0.241	0.052	-2.963	8.899	0.976	1.004	4	1.783	64	-1.332	-22.048	0.981	1.771	1	21
		2	0.047	0.430	-0.844	8.899	0.993	0.439	4	1.092	64	-0.569	-1.092	0.995	0.795	1	32
		3	0.027	1.036	0.035	8.899	0.974	0.930	5	0.791	128	101.944	241.121	0.904	2.934	2	-
Average	0.033	0.914	-0.090	8.899	0.978	0.939	6	0.745	256	-1.666	-0.273	0.997	0.362	3	27		
P7	B(E)	1	1.159	0.016	-4.134	11.491	0.836	3.841	2	0.926	32	-	-	-	-	-	-
		2	0.148	0.040	-3.217	11.491	0.943	1.391	3	2.897	32	-	-	-	-	-	-
		3	0.273	0.124	-2.085	11.491	0.926	1.993	2	0.506	16	-	-	-	-	-	-
		Average	0.152	0.067	-2.708	11.491	0.960	1.150	3	1.695	32	-	-	-	-	-	-
	E(B)	1	0.235	0.145	-1.932	11.491	0.955	1.501	1	0.506	8	-	-	-	-	-	-
		2	0.112	0.120	-2.117	11.491	0.994	0.502	4	1.270	64	-0.720	0.183	0.982	1.315	1	-
		3	0.159	0.138	-1.983	11.491	0.953	1.452	3	0.785	32	-	-	-	-	-	-
Average	0.126	0.114	-2.173	11.491	0.990	0.679	4	1.199	64	0.000	-268.04	0.991	0.954	1	-		

Possum	PR(FR)	Day	α	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{max}	BP	l	θ	VAC	SE	df	Xpt	
P8	B(E)	1	0.238	0.067	-2.703	8.081	0.981	0.879	4	1.534	64	-	-	-	-	-	-	
		2	0.073	0.088	-2.435	8.081	0.814	2.181	5	3.811	128	-	-	-	-	-	-	
		3	0.111	0.146	-1.923	8.081	0.964	1.059	4	1.507	16	-	-	-	-	-	-	
		Average	0.072	0.072	-2.633	8.081	0.966	0.950	5	4.747	128	-	-	-	-	-	-	
	E(B)	1	0.087	0.540	-0.616	8.081	0.984	0.709	3	0.520	8	-	-	-	-	-	-	-
		2	0.097	2.054	0.720	8.081	0.959	1.546	4	0.123	64	-0.393	-0.557	0.996	0.710	2	12	
		3	0.151	0.451	-0.796	8.081	0.973	1.122	3	0.360	32	-	-	-	-	-	-	
		Average	0.076	0.856	-0.155	8.081	0.995	0.458	4	0.376	64	-0.418	-1.333	0.998	0.570	1	-	
P9	B(E)	1	1.773	0.038	-3.264	8.677	0.873	3.987	1	0.336	8	-	-	-	-	-	-	
		2	0.049	5.779	1.754	8.677	0.931	1.897	3	0.080	32	-	-	-	-	-	-	
		3	0.009	0.030	-3.507	8.677	0.807	3.365	3	87.708	32	-	-	-	-	-	-	
		Average	0.285	0.072	-2.632	8.677	0.989	0.643	3	1.111	32	-	-	-	-	-	-	
	E(B)	1	-0.147	0.008	-4.847	8.677	0.865	3.002	2	-19.76	16	-	-	-	-	-	-	
		2	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	
		3	0.570	0.064	-2.746	8.677	0.967	1.345	2	0.622	16	-	-	-	-	-	-	
		Average	0.410	0.034	-3.382	8.677	0.978	0.982	2	1.636	16	-	-	-	-	-	-	
P10	B(E)	1	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	
		2	12.859	0.002	-6.223	10.537	0.989	1.501	1	0.735	8	-	-	-	-	-	-	
		3	2.102	-0.001	-	10.54	0.002	-	0	-8.738	4	-	-	-	-	-	-	
		Average	3.966	0.003	-5.809	10.537	0.968	2.520	1	1.576	8	-0.504	-6518.0	0.985	1.156	1	0	
	E(B)	1	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	
		2	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	
		3	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	
		Average	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	
P11	B(E)	1	0.137	0.073	-2.622	9.931	0.949	1.354	4	2.004	64	-0.515	-2.228	0.990	0.942	1	-	
		2	0.072	1.259	0.231	9.931	0.989	0.733	2	0.218	128	-	-	-	-	-	-	
		3	0.253	0.457	-0.782	9.931	0.937	2.357	1	0.172	16	-0.169	-135.09	0.999	0.242	1	3	
		Average	0.105	0.128	-2.056	9.931	0.954	1.270	4	1.486	64	-1.217	-0.618	0.991	0.500	3	22	
	E(B)	1	0.044	0.136	-1.996	9.931	0.963	0.982	5	3.298	128	-0.188	-9.832	0.999	0.279	1	59	
		2	0.070	0.058	-2.843	9.931	0.957	1.287	6	4.900	256	-0.262	-1.288	0.996	0.434	3	107	
		3	0.059	0.156	-1.856	9.931	0.977	0.884	5	2.144	128	-0.484	-3.981	0.997	0.586	1	41	
		Average	0.047	0.106	-2.249	9.931	0.967	1.080	6	3.980	256	-0.103	-5.965	1.000	0.125	2	63	

Possum	PR(FR)	Day	α	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{\max}	BP	l	θ	VAC	SE	df	Xpt	
P12	B(E)	1	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	
		2	0.074	0.106	-2.244	7.808	0.922	1.235	3	3.221	32	-	-	-	-	-	-	
		3	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	
		Average	0.079	0.100	-2.305	7.808	0.985	0.536	3	3.199	32	-	-	-	-	-	-	
	E(B)	1	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-
		2	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-
		3	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-
		Average	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-

Note: B = Berries & E = Egg.

Values in the 'average' rows are based on fits to consumption rates fit over three days shown in Figures 26 - 27.

Table E16. Parameter estimates for initial demand, Q_0 ; essential value, α ; P_{\max} , interaction, I , and sensitivity, β ; break point and cross point data for three days and averaged for each possum in Experiment 6 under the arithmetic PR FR schedule for the 'wet' foods.

Possum	PR(FR)	Day	α	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{\max}	BP	I	β	VAC	SE	df	Xpt
P1	B(E)	1	0.022	1.347	0.298	11.870	0.920	1.703	2	0.550	21	-	-	-	-	-	-
		2	0.027	0.378	-0.974	11.870	0.888	1.695	8	1.621	51	-0.078	-19.605	0.994	0.742	1	27
		3	0.027	0.350	-1.050	11.870	0.924	1.503	11	1.765	66	-0.015	-22.764	0.999	0.164	2	-
		Average	0.027	0.289	-1.241	11.870	0.943	0.013	11	2.130	66	-0.064	-19.917	0.998	0.129	4	28
	E(B)	1	0.023	0.306	-1.184	11.870	0.908	1.818	17	2.322	51	-0.920	-1.265	0.932	1.672	9	-
		2	0.049	0.047	-3.061	11.870	0.942	0.427	20	7.226	111	-0.426	-37.474	0.989	0.649	6	61
		3	0.024	0.124	-2.086	11.870	0.940	1.085	20	5.677	111	-0.119	-21.034	0.995	0.475	3	1
		Average	0.026	0.095	-2.359	11.870	0.941	1.181	26	6.778	141	-0.119	-21.034	0.995	0.475	3	-
	P2	B(E)	1	0.073	0.201	-1.605	11.132	0.966	1.040	5	1.215	36	-	-	-	-	-
2			0.075	0.067	-2.706	11.132	0.928	1.330	5	3.524	36	-	-	-	-	-	-
3			-	-	-	11.132	-	-	-	-	11	-	-	-	-	-	-
Average			-0.114	0.051	-2.973	11.132	0.494	3.566	5	-3.053	36	-0.057	-106.85	0.999	0.339	1	-
E(B)		1	-0.460	0.005	-5.391	11.132	0.799	3.161	5	-8.469	36	-	-	-	-	-	-
		2	0.035	0.201	-1.604	11.132	0.841	1.974	14	2.538	71	-4.560	23.206	0.885	3.954	1	-
		3	0.047	0.034	-3.377	11.132	0.901	1.523	7	11.014	46	-	-	-	-	-	2
		Average	0.033	0.113	-2.181	11.132	0.847	2.219	12	4.747	106	-	-	-	-	-	-
P3		B(E)	1	0.029	1.177	0.163	10.065	0.978	0.393	8	0.580	51	-0.661	-0.897	0.975	1.589	1
	2		0.017	2.351	0.855	10.065	0.964	1.125	3	0.486	26	-	-	-	-	-	-
	3		0.061	0.193	-1.645	10.065	0.965	0.935	6	1.679	41	-	-	-	-	-	-
	Average		0.021	0.802	-0.221	10.065	0.902	1.638	8	1.158	51	-1.112	-0.152	0.974	1.319	2	-
	E(B)	1	0.073	0.773	-0.257	10.065	0.976	1.294	3	0.347	26	-	-	-	-	-	-
		2	0.036	0.156	-1.859	10.065	0.944	1.114	14	3.486	111	-	-	-	-	-	-
		3	0.064	0.229	-1.473	10.065	0.982	0.773	8	1.329	111	-	-	-	-	-	1
		Average	0.055	0.085	-2.466	10.065	0.953	1.059	14	4.200	81	-	-	-	-	-	-

Possum	PR(FR)	Day	α	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{max}	BP	l	β	VAC	SE	df	Xpt	
P4	B(E)	1	0.153	0.064	-2.749	9.234	0.929	1.645	10	2.192	61	-0.465	-15.815	0.994	0.609	3	35	
		2	0.054	0.166	-1.798	9.234	0.939	1.300	13	2.386	76	-0.023	-36.234	0.999	0.369	1	-	
		3	0.104	0.036	-3.333	9.234	0.942	1.318	17	5.791	96	-0.205	-72.567	0.997	0.792	1	-	
		Average	0.070	0.078	-2.545	9.234	0.975	0.836	17	3.893	96	-0.397	-24.493	0.993	0.617	9	-	
	E(B)	1	0.136	0.119	-2.128	9.234	0.987	0.672	11	1.317	56	-0.146	-44.088	0.995	0.552	4	-	
		2	0.060	0.001	-6.908	9.234	0.550	2.638	19	357.835	61	0.000	-	0.945	2.166	2	-	
		3	0.043	0.355	-1.036	9.234	0.960	1.055	9	1.395	56	-	-	-	-	-	1	
		Average	0.057	0.214	-1.543	9.234	0.979	0.767	10	1.746	61	-	-	-	-	-	-	
P5	B(E)	1	0.032	0.385	-0.956	11.104	0.963	1.014	9	1.443	56	-	-	-	-	-	-	
		2	0.061	0.088	-2.426	11.104	0.988	0.551	11	3.291	66	-	-	-	-	-	-	
		3	0.121	0.051	-2.980	11.104	0.963	1.120	10	2.899	61	-	-	-	-	-	-	
		Average	0.050	0.149	-1.906	11.104	0.991	0.495	11	2.384	66	-	-	-	-	-	-	
	E(B)	1	-	-	-	11.104	-	-	-	-	-	-	-	-	-	-	-	-
		2	-	-	-	11.104	-	-	-	-	-	6	-	-	-	-	-	-
		3	-	-	-	11.104	-	-	-	-	-	1	-	-	-	-	-	-
		Average	-	-	-	11.104	-	-	-	-	-	6	-	-	-	-	-	-
P6	B(E)	1	0.048	0.580	-0.545	8.899	0.963	1.203	8	0.795	51	-	-	-	-	-	-	
		2	0.054	0.493	-0.707	8.899	0.958	1.062	2	0.838	21	-	-	-	-	-	-	
		3	0.046	0.681	-0.384	8.899	0.959	1.300	8	0.705	51	-	-	-	-	-	-	
		Average	0.044	0.634	-0.456	8.899	0.976	0.940	8	0.796	51	-0.872	-1.270	0.989	1.439	1	48	
	E(B)	1	0.072	0.248	-1.393	8.899	0.961	1.071	11	1.239	56	-0.153	-13.928	0.987	0.990	3	-	
		2	0.028	0.878	-0.130	8.899	0.992	0.227	3	0.899	16	-	-	-	-	-	45	
		3	0.052	0.366	-1.006	8.899	0.942	1.395	9	1.167	56	-0.016	-19.948	0.997	0.622	2	1	
		Average	0.043	0.432	-0.838	8.899	0.961	1.146	11	1.195	66	-0.016	-19.948	0.997	0.622	2	88	
P7	B(E)	1	11.310	0.024	-3.723	11.491	0.955	1.079	6	2.242	41	-	-	-	-	-	-	
		2	-	-	-	11.491	-	-	-	-	1	-	-	-	-	-	-	
		3	0.127	0.023	-3.774	11.491	0.993	0.993	3	5.904	21	-	-	-	-	-	-	
		Average	0.052	0.028	-3.587	11.491	0.981	0.678	6	12.010	41	-	-	-	-	-	-	
	E(B)	1	-0.045	0.023	-3.769	11.491	0.951	1.170	3	-16.730	26	-0.634	116.972	0.993	0.670	1	-	
		2	0.285	0.042	-3.162	11.491	0.923	2.513	1	1.424	16	-	-	-	-	-	-	
		3	-0.020	0.025	-3.671	11.491	0.932	1.183	6	-33.823	41	-	-	-	-	-	1	
		Average	-0.016	0.028	-3.580	11.491	0.969	0.770	6	-37.623	41	-	-	-	-	-	-	

Possum	PR(FR)	Day	α	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{max}	BP	l	β	VAC	SE	df	Xpt
P8	B(E)	1	0.088	0.688	-0.374	8.081	0.996	1.274	3	0.403	21	-	-	-	-	-	-
		2	0.076	1.056	0.055	8.081	0.989	2.044	5	0.305	31	-9.124	2.174	0.990	1.276	1	-
		3	0.202	0.040	-3.226	8.081	0.974	0.930	9	3.049	56	-1.307	5.560	0.973	1.101	5	-
		Average	5.201	0.000	-9.210	8.081	0.005	5.652	9	46.999	56	-4.707	244.433	0.601	2.431	4	4
	E(B)	1	0.167	0.122	-2.101	8.081	0.975	1.018	8	1.199	51	-0.099	-53.244	0.991	0.653	7	-
		2	0.079	0.281	-1.270	8.081	0.984	0.826	13	1.096	76	-0.737	-5.507	0.978	0.935	12	17
		3	0.249	0.033	-3.399	8.081	0.957	1.324	13	2.943	76	-0.943	-34.876	0.984	0.780	10	1
		Average	0.164	0.103	-2.271	8.081	1.000	1.055	12	1.444	76	-0.943	-34.876	0.984	0.780	10	-
P9	B(E)	1	0.038	0.010	-4.626	8.677	0.994	1.575	4	61.371	26	-	-	-	-	-	-
		2	0.632	0.021	-3.849	8.677	0.995	1.134	5	1.693	31	-	-	-	-	-	-
		3	0.052	0.030	-3.507	8.677	0.974	3.089	3	14.590	21	-	-	-	-	-	-
		Average	0.456	0.019	-3.987	8.677	0.938	1.733	4	2.689	31	-	-	-	-	-	-
	E(B)	1	-	-	-	-	-	-	-	-	11	-	-	-	-	-	-
		2	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
		3	-	-	-	-	-	-	-	-	6	-	-	-	-	-	-
		Average	-	-	-	-	-	-	-	-	11	-	-	-	-	-	-
P10	B(E)	1	-	-	-	-	-	-	-	-	6	-	-	-	-	-	-
		2	-	-	-	-	-	-	-	-	6	-	-	-	-	-	-
		3	-	-	-	-	-	-	-	-	6	-	-	-	-	-	-
		Average	-	-	-	-	-	-	-	-	6	-	-	-	-	-	-
	E(B)	1	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
		2	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
		3	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
		Average	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
P11	B(E)	1	0.218	0.016	-4.165	9.931	0.999	1.341	12	5.880	66	-0.575	-	0.983	1.225	2	32
		2	0.130	0.084	-2.479	9.931	0.932	1.681	10	1.822	61	-0.642	172.765	0.975	1.656	2	-
		3	0.121	0.069	-2.671	9.931	0.919	1.699	10	2.379	61	-	-34.572	-	-	-	-
		Average	0.124	0.048	-3.039	9.931	0.944	1.353	11	3.343	66	-0.664	-54.972	0.982	2.391	1	213
	E(B)	1	0.114	0.026	-3.636	9.931	0.956	1.302	17	6.598	111	-1.121	-21.884	0.988	0.815	1	212
		2	0.072	0.049	-3.011	9.931	0.975	1.027	20	5.637	141	-0.570	-21.699	0.994	0.667	6	84
		3	0.049	0.040	-3.208	9.931	0.968	1.110	26	10.015	186	-	-	-	-	-	-
		Average	0.942	0.033	-3.409	9.931	0.942	1.200	13	10.254	186	-0.027	-18.562	1.000	1.585	9	32

Possum	PR(FR)	Day	α	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{max}	BP	l	θ	VAC	SE	df	Xpt	
P12	B(E)	1	-	-	-	-	-	-	-	-	6	-	-	-	-	-	-	
		2	0.455	0.046	-3.069	7.808	0.870	2.898	2	1.197	21	-	-	-	-	-	-	
		3	0.141	0.067	-2.705	7.808	0.915	1.560	6	2.684	41	-	-	-	-	-	-	
		Average	0.166	0.050	-2.995	7.808	0.924	1.319	6	3.044	41	-	-	-	-	-	-	
	E(B)	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
		2	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
		3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		Average	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-

Note: B = Berries & E = Egg.

Values in the 'average' rows are based on fits to consumption rates fit over three days shown in Figures 26 - 27.

Table E17. Parameter estimates for initial demand, Q_0 ; essential value, α ; P_{\max} , interaction, I , and sensitivity, β ; break point and cross point data for three days and averaged for each possum in Experiment 6 under the geometric PR FR schedule for the 'dry' foods.

Possum	PR(FR)	Day	α	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{\max}	BP	I	β	VAC	SE	df	Xpt	
P1	BA(O)	1	0.018	0.031	-3.471	11.870	0.953	1.071	4	30.004	64	-	-	-	-	-	-	
		2	0.034	0.118	-2.138	11.870	0.989	0.407	3	4.137	32	-	-	-	-	-	-	
		3	-0.158	0.029	-3.526	11.870	0.907	1.641	2	-	16	-	-	-	-	-	-	
		Average	0.031	0.076	-2.578	11.870	0.999	0.148	4	7.137	64	-	-	-	-	-	-	
	O(BA)	1	0.018	0.182	-1.703	11.870	0.979	0.308	6	4.952	256	-	-	-	-	-	-	-
		2	0.121	0.070	-2.657	11.870	0.926	1.711	4	1.959	64	-	-	-	-	-	-	-
		3	0.029	0.120	-2.124	11.870	0.934	1.066	4	4.785	64	-	-	-	-	-	-	-
		Average	0.023	0.135	-2.004	11.870	0.989	0.559	6	5.346	256	-0.946	-1.406	0.993	1.341	1	221	
		1	0.067	0.117	-2.146	11.132	0.927	1.159	11	2.250	128	-0.478	-1.730	0.990	0.761	1	23	
P2	BA(O)	2	0.060	0.263	-1.335	11.132	0.977	0.576	10	1.133	64	-	-	-	-	-	-	-
		3	0.032	0.080	-2.531	11.132	0.982	0.708	6	7.075	64	-	-	-	-	-	-	-
		Average	-0.068	0.400	-0.916	11.132	0.964	0.743	12	-	256	-0.131	-1.498	0.994	0.472	3	53	
		1	0.025	0.114	-2.168	11.132	0.944	0.105	6	6.263	256	-0.358	-3.217	0.985	1.240	1	75	
	O(BA)	2	0.026	0.542	-0.612	11.132	0.972	0.855	4	1.245	64	-	-	-	-	-	-	-
		3	0.021	0.770	-0.261	11.132	0.917	1.945	4	1.073	64	-	-	-	-	-	-	-
		Average	0.019	0.190	-1.659	11.132	0.896	1.303	12	4.881	256	-0.206	-0.019	0.999	0.191	2	69	
		1	0.115	0.569	-0.564	10.065	0.972	0.807	4	0.301	16	-	-	-	-	-	-	-
		2	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-
P3	BA(O)	3	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	
		Average	0.212	0.400	-0.916	10.065	0.633	2.210	7	0.231	16	-0.019	-29.113	0.999	0.180	1	-	
		1	0.020	0.229	-1.475	10.065	0.937	1.083	5	4.287	128	-	-	-	-	-	-	-
	O(BA)	2	0.036	0.273	-1.297	10.065	0.927	1.492	5	2.014	128	-	-	-	-	-	-	-
		3	0.058	0.387	-0.950	10.065	0.983	0.790	4	0.871	64	-	-	-	-	-	-	-
		Average	0.027	0.213	-1.546	10.065	0.950	0.708	11	3.418	128	-1.000	-0.856	0.980	1.464	1	-	
		1	0.055	0.103	-2.270	9.234	0.988	0.455	3	3.739	32	-	-	-	-	-	-	-
		2	1.028	0.044	-3.134	9.234	0.710	6.079	1	0.478	8	-	-	-	-	-	-	-
	P4	BA(O)	3	0.082	0.154	-1.873	9.234	0.977	0.818	4	1.688	64	-	-	-	-	-	-
Average			0.028	0.700	-0.356	9.234	0.973	0.824	4	1.080	64	-3.259	0.126	0.742	3.718	3	28	
1			0.281	0.057	-2.862	9.234	0.944	1.314	4	1.333	64	-	-	-	-	-	-	-
2			0.051	0.085	-2.470	9.234	0.936	1.524	6	4.912	8	-	-	-	-	-	-	-
O(BA)		3	0.043	0.078	-2.557	9.234	0.979	0.761	6	6.417	256	-	-	-	-	-	-	-
		Average	0.044	0.068	-2.683	9.234	0.958	1.268	7	7.177	512	-0.289	-2.638	0.999	0.241	1	143	

Possum	PR(FR)	Day	α	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{max}	BP	l	β	VAC	SE	df	Xpt	
P5	BA(O)	1	0.793	0.014	-4.238	11.104	0.945	1.885	3	1.554	32	-0.364	147.525	0.992	0.536	2	-	
		2	0.135	0.334	-1.097	11.104	0.975	1.053	2	0.395	16	-	-	-	-	-	-	
		3	0.080	0.205	-1.584	11.104	0.865	2.703	4	1.086	64	-0.499	0.941	0.989	0.793	1	-	
		Average	-0.177	0.551	-0.596	11.104	0.941	1.667	4	-0.182	64	-0.502	1.432	0.991	0.498	3	10	
	O(BA)	1	0.827	0.046	-3.082	11.104	0.712	6.064	1	0.469	8	-	-	-	-	-	-	
		2	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	
		3	0.143	0.061	-2.799	11.104	0.930	1.681	4	2.041	64	-	-	-	-	-	-	
		Average	0.141	0.063	-2.770	11.104	0.890	1.529	8	2.008	64	-0.205	-32.216	0.998	0.256	3	13	
	P6	BA(O)	1	0.030	0.092	-2.391	8.899	0.986	0.454	4	7.994	64	-	-	-	-	-	-
			2	0.019	0.095	-2.355	8.899	0.989	0.535	1	12.482	8	-	-	-	-	-	-
3			0.048	0.152	-1.885	8.899	0.967	0.916	5	3.039	128	-	-	-	-	-	-	
		Average	4.9E-	0.400	-0.916	8.899	0.998	0.083	5	113.494	128	-	-	-	-	-	-	
O(BA)		1	0.058	0.660	-0.415	8.899	0.973	1.002	4	0.580	64	-	-	-	-	-	-	
		2	0.066	0.479	-0.736	8.899	0.932	1.414	3	0.700	32	-	-	-	-	-	-	
		3	0.030	0.303	-1.195	8.899	0.985	0.371	2	2.447	16	-	-	-	-	-	-	
		Average	0.053	0.638	-0.449	8.899	0.967	1.112	4	0.661	64	-	-	-	-	-	-	
P7		BA(O)	1	0.315	0.062	-2.787	11.491	0.964	1.408	1	0.886	8	-	-	-	-	-	-
			2	0.361	0.061	-2.802	11.491	0.979	1.109	1	0.784	8	-	-	-	-	-	-
	3		0.337	1.534	0.428	11.491	0.934	4.554	1	0.033	8	-1.176	0.503	0.984	1.896	1	-	
		Average	0.315	0.127	-2.067	11.491	0.991	0.721	1	0.432	8	-3.574	111.255	0.991	1.072	1	8	
	O(BA)	1	0.037	0.203	-1.595	11.491	0.972	0.755	4	2.307	64	-	-	-	-	-	-	
		2	0.094	0.530	-0.635	11.491	0.997	0.336	1	0.344	8	-	-	-	-	-	-	
		3	0.071	0.595	-0.519	11.491	0.991	0.652	3	0.408	32	-0.461	-2.847	0.991	0.812	1	8	
		Average	0.048	0.171	-1.768	11.491	0.977	0.746	4	2.097	64	-0.394	-15.996	-0.829	8.425	2	27	
	P8	BA(O)	1	0.084	0.112	-2.190	8.081	0.980	0.786	5	2.607	128	-0.547	4.278	0.992	0.485	2	40352
			2	0.086	0.347	-1.060	8.081	0.966	1.090	4	0.818	64	-	-	-	-	-	-
3			0.087	0.243	-1.416	8.081	0.984	0.694	4	1.159	64	-	-	-	-	-	-	
		Average	0.069	0.241	-1.425	8.081	0.981	0.795	5	1.478	128	-0.111	0.493	1.000	0.105	2	-	
O(BA)		1	0.109	0.468	-0.760	8.081	0.982	0.875	4	0.478	64	0.000	-18.755	0.996	0.379	2	8	
		2	0.005	0.024	-3.738	8.081	0.657	2.616	5	205.355	128	-0.528	-7.784	0.958	1.633	1	-	
		3	0.046	0.883	-0.125	8.081	0.990	0.616	5	0.598	128	-0.005	-3.067	1.000	0.031	1	-	
		Average	0.053	0.728	-0.317	8.081	0.995	0.446	5	0.630	128	-0.202	-0.716	0.996	0.319	3	13	

Possum	PR(FR)	Day	α	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{max}	BP	l	β	VAC	SE	df	Xpt
P9	BA(O)	1	0.116	0.093	-2.374	8.677	0.957	1.141	4	2.108	64	-	-	-	-	-	-
		2	0.107	0.183	-1.697	8.677	0.953	1.299	4	1.161	64	3.567	0.003	0.027	0.011	1	-
		3	0.053	1.488	0.397	8.677	0.990	0.672	4	0.288	64	-0.156	-0.544	0.998	0.364	1	-
		Average	0.090	0.198	-1.621	8.677	0.957	1.185	4	1.278	64	-0.350	0.732	0.997	0.413	1	17
	O(BA)	1	0.162	0.017	-4.083	8.677	0.977	1.004	6	8.349	256	-0.885	-3.473	0.981	0.753	6	-
		2	0.079	0.053	-2.934	8.677	0.982	0.795	6	5.394	256	-0.807	3.475	0.990	0.738	2	57
		3	0.073	0.062	-2.784	8.677	0.980	0.844	6	5.060	256	-0.575	2.146	0.997	0.376	2	50
		Average	0.081	0.048	-3.027	8.677	0.993	0.499	6	5.766	256	-0.826	-0.962	0.990	0.538	6	128
	P10	BA(O)	1	0.330	0.086	-2.458	10.537	0.985	0.567	8	0.663	32	-	-	-	-	-
2			0.289	0.137	-1.987	10.537	0.961	1.438	2	0.474	16	-	-	-	-	-	-
3			0.365	0.089	-2.420	10.537	0.971	1.293	1	0.578	8	-	-	-	-	-	-
		Average	0.266	0.121	-2.115	10.537	0.992	0.379	9	0.585	32	-0.001	-95.937	0.999	0.310	1	7
O(BA)		1	0.034	0.033	-3.423	10.537	0.973	0.804	5	17.008	128	-	-	-	-	-	-
		2	-0.040	0.032	-3.434	10.537	0.999	0.170	1	-14.462	8	-	-	-	-	-	-
		3	0.046	0.041	-3.190	10.537	0.994	0.361	4	9.864	64	-	-	-	-	-	-
		Average	0.039	0.035	-3.355	10.537	0.992	0.427	5	13.818	128	-	-	-	-	-	-
P11		BA(O)	1	0.060	0.264	-1.332	9.931	0.944	1.361	4	1.262	64	-	-	-	-	-
	2		0.115	0.248	-1.394	9.931	0.953	1.342	3	0.699	32	-	-	-	-	-	-
	3		0.107	0.234	-1.453	9.931	0.949	1.331	3	0.793	32	-	-	-	-	-	-
		Average	0.078	0.214	-1.542	9.931	0.973	0.970	4	1.200	8	-	-	-	-	-	-
	O(BA)	1	0.044	0.272	-1.302	9.931	0.974	0.788	4	1.651	64	-	-	-	-	-	-
		2	0.044	0.469	-0.757	9.931	0.915	1.144	1	0.954	8	-	-	-	-	-	-
		3	0.032	0.815	-0.204	9.931	0.929	1.372	3	0.761	32	-	-	-	-	-	-
		Average	0.033	0.395	-0.929	9.931	0.975	0.921	5	1.545	128	-0.136	-0.684	0.999	0.232	1	31
	P12	BA(O)	1	0.870	0.009	-4.690	7.808	0.954	1.669	4	3.166	64	-0.129	-175.16	0.999	0.113	4
2			0.131	0.083	-2.487	7.808	0.975	0.963	5	2.331	128	0.000	-65.999	0.991	0.814	1	-
3			0.084	0.055	-2.902	7.808	0.957	1.088	5	5.461	128	-1.365	6.369	0.981	1.257	1	54
		Average	0.121	0.043	-3.138	7.808	0.965	1.057	5	4.810	128	-0.306	-9.603	0.995	0.333	5	14
O(BA)		1	-0.075	0.017	-4.052	7.808	0.886	2.020	3	-19.315	32	-	-	-	-	-	-
		2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		3	0.164	0.232	-1.460	7.808	0.978	0.894	3	0.663	32	-	-	-	-	-	-
		Average	0.131	0.094	-2.363	7.808	0.997	0.246	3	2.059	32	-	-	-	-	-	-

Note: B = Barley mix & O = Oats

Values in the 'average' rows are based on fits to consumption rates fit over three days shown in Figures 28 - 29.

Table E18. Parameter estimates for initial demand, Q_0 ; essential value, α ; P_{\max} , interaction, I , and sensitivity, β ; break point and cross point data for three days and averaged for each possum in Experiment 6 under the arithmetic PR FR schedule for the 'dry' foods.

Possum	PR(FR)	Day	α	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{\max}	BP	I	β	VAC	SE	df	Xpt
P1	BA(O)	1	-0.625	0.004	-5.449	11.870	0.701	3.563	8	-	51	-	-	-	-	-	-
		2	0.310	0.015	-4.214	11.870	0.731	4.018	9	3.632	56	-0.126	-285.833	1.000	0.147	1	-
		3	0.172	0.020	-3.912	11.870	0.689	3.927	8	4.837	51	-	-	-	-	-	-
		Average	0.038	0.068	-2.681	11.870	0.991	0.396	9	6.454	56	-1.523	-24.038	0.988	1.062	5	-
	O(BA)	1	0.126	0.068	-2.684	11.870	0.852	2.708	11	1.928	66	-1.756	-21.568	0.987	0.969	5	51
		2	0.088	0.109	-2.216	11.870	0.935	1.932	17	1.727	96	-1.345	-12.506	0.997	0.434	13	-
		3	0.044	0.143	-1.945	11.870	0.877	2.015	15	2.673	86	-0.247	-20.911	0.998	0.369	3	-
		Average	0.054	0.126	-2.071	11.870	0.891	2.112	17	2.437	96	-1.631	-9.606	0.995	0.553	14	-
P2	BA(O)	1	0.028	0.667	-0.405	11.132	0.967	1.089	8	0.936	51	-16393.15	1037.336	0.990	0.662	2	-
		2	0.028	0.833	-0.182	11.132	0.912	1.817	6	0.759	41	0.149	-26.224	0.989	0.829	1	-
		3	0.031	1.287	0.253	11.132	0.977	1.100	5	0.442	36	-0.020	-8.450	0.991	0.551	3	-
		Average	0.031	0.550	-0.597	11.132	0.982	0.784	8	1.027	56	-0.115	-6.180	0.997	0.277	5	-
	O(BA)	1	0.052	0.054	-2.920	11.132	0.926	1.445	23	6.362	126	-0.415	-16.627	0.989	0.576	10	84
		2	0.025	0.519	-0.656	11.132	0.990	0.591	13	1.348	76	-0.373	0.174	0.996	0.317	8	32
		3	0.036	0.187	-1.676	11.132	0.941	1.329	17	2.649	96	-0.189	-7.211	0.997	0.292	10	38
		Average	0.044	0.074	-2.598	11.132	0.933	1.318	20	5.386	111	-0.166	-17.854	0.997	0.257	13	63
P3	BA(O)	1	-	-	-	-	-	-	-	-	6	-	-	-	-	-	
		2	-	-	-	-	-	-	-	-	1	-	-	-	-	-	
		3	-	-	-	-	-	-	-	-	-	6	-	-	-	-	-
		Average	-	-	-	-	-	-	-	-	-	6	-	-	-	-	-
	O(BA)	1	0.045	0.563	-0.575	10.065	0.834	2.590	4	0.766	31	-	-	-	-	-	-
		2	0.078	0.222	-1.503	10.065	0.932	1.568	6	1.129	41	0.000	-123.470	0.992	0.519	3	12
		3	0.044	0.177	-1.734	10.065	0.951	1.153	14	2.549	81	-	-	-	-	-	-
		Average	0.049	0.152	-1.883	10.065	0.941	1.304	14	2.626	81	-0.227	-21.559	0.984	0.252	4	37

Possum	PR(FR)	Day	α	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{max}	BP	l	β	VAC	SE	df	Xpt	
P4	BA(O)	1	0.033	0.382	-0.962	9.234	0.955	0.145	13	1.719	5	-23.610	14.102	0.990	0.011	2	52	
		2	-	-	-	-	-	-	-	-	6	-	-	-	-	-	-	-
		3	-	-	-	-	-	-	-	-	6	-	-	-	-	-	-	-
		Average	0.048	0.211	-1.556	9.234	0.953	1.157	13	2.116	4	-0.554	-1.852	0.984	0.734	5	77	
	O(BA)	1	0.083	0.038	-3.281	9.234	0.962	0.019	35	6.889	146	-5.559	44.072	0.987	0.005	6	97	
		2	0.035	0.087	-2.440	9.234	0.979	0.718	33	6.971	176	-	-	-	-	-	-	-
		3	0.041	0.069	-2.670	9.234	0.939	1.266	31	7.506	166	-168.169	77.311	0.999	0.391	1	-	
		Average	0.034	0.092	-2.381	9.234	0.988	0.543	33	6.815	5	-1.462	-0.668	0.978	0.944	9	132	
P5	BA(O)	1	0.012	6.509	1.873	11.104	0.972	1.370	3	0.228	26	-0.001	-2.997	1.000	0.114	1	-	
		2	0.060	0.201	-1.606	11.104	0.939	1.172	17	1.481	61	-0.488	-0.498	0.988	0.531	7	20	
		3	0.029	0.450	-0.798	11.104	0.947	1.521	13	1.376	76	-0.403	-2.283	0.981	0.662	9	25	
		Average	0.047	0.206	-1.581	11.104	0.598	1.313	13	1.855	76	-0.215	-8.946	0.989	0.478	11	22	
	O(BA)	1	0.082	0.040	-3.226	11.104	0.956	1.186	20	5.431	111	-0.046	-81.192	0.940	1.313	11	-	
		2	0.056	0.045	-3.101	11.104	0.968	0.992	29	7.095	156	-0.373	-10.837	0.994	0.386	22	50	
		3	0.055	0.043	-3.138	11.104	0.981	0.745	30	7.408	161	-0.576	4.240	0.992	0.454	22	60	
		Average	0.054	0.044	-3.127	11.104	0.982	0.730	30	7.477	161	-0.528	-3.269	0.995	0.353	26	56	
P6	BA(O)	1	0.037	0.298	-1.209	8.899	0.915	1.263	11	2.011	66	-	-	-	-	-	-	
		2	0.034	0.437	-0.827	8.899	0.947	0.802	11	1.506	66	0.000	-40.065	0.939	1.979	2	-	
		3	0.040	0.231	-1.467	8.899	0.947	1.160	15	2.433	86	-0.465	-3.404	0.980	1.059	2	46	
		Average	0.037	0.224	-1.497	8.899	0.953	1.058	15	2.658	86	-0.409	-5.840	0.987	0.665	5	48	
	O(BA)	1	0.032	0.953	-0.048	8.899	0.901	1.852	6	0.723	41	-2.5E-04	-21.620	0.999	0.275	1	76	
		2	0.082	0.417	-0.875	8.899	0.874	2.401	3	0.651	26	-	-	-	-	-	-	
		3	0.022	1.001	0.001	8.899	0.957	0.813	2	0.997	21	-	-	-	-	-	-	
		Average	0.030	1.094	0.090	8.899	0.908	1.807	6	0.670	41	-0.060	-7.211	0.965	1.428	3	22	
P7	BA(O)	1	0.461	0.118	-2.133	11.491	0.986	1.516	1	0.315	16	-0.214	-101.930	0.983	1.182	1	-	
		2	0.368	0.076	-2.576	11.491	0.990	0.528	6	0.614	21	0.000	-421.206	1.000	0.148	1	-	
		3	0.265	0.033	-3.403	11.491	0.980	1.221	1	1.952	16	-	-	-	-	-	-	
		Average	0.292	0.099	-2.317	11.491	0.990	0.879	2	0.598	21	-0.299	-64.579	0.993	0.543	2	-	
	O(BA)	1	0.056	0.980	-0.020	11.491	0.953	2.080	4	0.312	31	0.000	-125.324	0.811	4.742	2	-	
		2	0.067	0.763	-0.271	11.491	0.957	1.906	5	0.336	36	-0.527	-7.021	0.993	0.795	3	6	
		3	0.046	0.432	-0.839	11.491	0.869	2.693	9	0.873	56	-0.049	-15.504	0.998	0.477	2	-	
		Average	0.047	0.452	-0.794	11.491	0.903	0.349	9	0.804	56	0.000	-128.553	0.881	2.838	7	17	

Possum	PR(FR)	Day	α	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{max}	BP	l	β	VAC	SE	df	Xpt
P8	BA(O)	1	0.203	0.054	-2.918	8.081	0.992	0.544	12	2.232	71	-7.290	155.679	0.998	0.187	9	20
		2	0.069	0.235	-1.448	8.081	0.991	0.562	14	1.496	81	-18.752	49.850	0.983	0.518	11	24
		3	0.050	0.306	-1.183	8.081	0.992	0.512	16	1.586	91	-483.095	70.138	0.986	0.475	11	29
		Average	0.076	0.180	-1.712	8.081	0.993	0.483	16	1.778	91	-7.400	46.856	0.995	0.299	13	25
	O(BA)	1	0.059	0.231	-1.467	8.081	0.991	0.539	16	1.800	91	-2993.912	-0.500	0.941	1.073	13	25
		2	0.048	0.282	-1.265	8.081	0.995	0.412	17	1.807	96	-9.312	25.304	0.999	0.146	13	34
		3	0.062	0.190	-1.659	8.081	0.992	0.507	16	2.078	91	0.000	-52.408	0.962	0.964	9	-
		Average	0.049	0.273	-1.298	8.081	0.998	0.224	17	1.812	96	-815.459	110.142	0.986	0.503	14	26
P9	BA(O)	1	0.379	0.055	-2.904	8.677	0.948	1.686	3	1.095	26	-0.208	-46.772	0.997	0.353	2	-
		2	0.089	0.145	-1.929	8.677	0.965	1.078	11	1.765	66	-0.166	-25.110	0.904	2.463	2	16
		3	3.257	0.000	-9.210	8.677	0.258	5.900	6	69.903	41	-0.010	1797.815	0.884	3.310	1	-
		Average	0.093	0.160	-1.836	8.677	0.968	1.091	11	1.536	66	-0.723	-4.686	0.995	0.387	7	-
	O(BA)	1	0.145	0.029	-3.550	8.677	0.983	0.005	21	0.145	116	-0.722	-15.805	1.000	1.251	19	39
		2	0.103	0.058	-2.840	8.677	0.980	0.817	20	3.834	111	-1.031	-9.088	0.971	0.964	0	46
		3	1.796	0.000	-9.210	8.677	-0.335	4.639	26	126.797	141	-0.563	41.290	0.992	0.450	21	0
		Average	0.093	0.046	-3.075	8.677	0.991	0.547	26	5.310	141	-0.868	-7.182	0.994	0.397	25	47
P10	BA(O)	1	0.119	0.102	-2.287	10.537	0.960	1.202	2	1.546	16	-	-	-	-	-	-
		2	0.120	0.038	-3.268	10.537	0.998	0.281	2	4.098	21	-	-	-	-	-	-
		3	0.205	0.246	-1.403	10.537	0.927	2.981	1	0.373	16	-	-	-	-	-	-
		Average	0.117	0.106	-2.245	10.537	0.988	0.646	2	1.508	21	-	-	-	-	-	-
	O(BA)	1	-1.647	0.002	-6.383	10.537	0.892	2.222	9	-6.738	56	-0.897	-351.097	0.991	0.851	3	-
		2	0.054	0.067	-2.699	10.537	0.951	1.097	17	5.169	36	-	-	-	-	-	-
		3	0.025	0.294	-1.223	10.537	0.933	1.300	15	2.543	86	-	-	-	-	-	-
		Average	0.041	0.095	-2.350	10.537	0.971	0.814	17	4.839	96	-0.426	-18.525	0.990	0.786	7	-
P11	BA(O)	1	0.036	0.747	-0.291	9.931	0.977	0.922	6	0.733	41	-149.977	158.478	0.983	0.730	2	16
		2	0.059	0.189	-1.665	9.931	0.927	0.557	14	1.784	46	-	-	-	-	-	-
		3	0.052	0.450	-0.800	9.931	0.952	1.333	6	0.856	41	-0.0001	-40.618	1.000	0.089	1	-
		Average	0.046	0.353	-1.042	9.931	0.985	0.648	7	1.214	46	-1641.059	81.962	0.998	0.269	3	26
	O(BA)	1	0.084	0.044	-3.126	9.931	0.941	0.605	18	5.383	101	-0.284	-41.515	0.992	0.549	6	44
		2	0.037	0.203	-1.595	9.931	0.975	0.843	18	2.644	101	-1.851	5.521	0.988	0.661	5	56
		3	0.040	0.455	-0.787	9.931	0.977	0.877	9	1.091	56	-0.549	-0.836	0.990	0.588	5	26
		Average	0.049	0.114	-2.169	9.931	0.978	0.383	18	3.555	101	-0.299	-12.563	0.990	0.130	12	51

Possum	PR(FR)	Day	α	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{max}	BP	l	β	VAC	SE	df	Xpt
P12	BA(O)	1	0.288	0.017	-4.094	7.808	0.959	1.259	14	5.273	81	-0.483	-72.754	0.988	0.539	12	-
		2	0.145	0.088	-2.431	7.808	0.981	0.117	11	1.989	66	-1.617	51.082	0.985	0.619	9	25
		3	0.098	0.033	-3.412	7.808	0.963	1.003	20	7.830	111	-0.340	-49.872	0.976	1.459	2	-
		Average	0.127	0.024	-3.741	7.808	0.971	0.171	20	8.363	111	-1.185	96.807	0.994	0.378	7	23
	O(BA)	1	0.073	0.208	-1.569	7.808	0.950	1.313	14	1.654	81	-1.116	-1.845	0.971	1.655	2	-
		2	0.074	0.422	-0.862	7.808	0.933	1.524	5	0.807	36	-	-	-	-	-	-
		3	0.086	1.853	0.617	7.808	0.960	1.517	6	0.160	41	-0.483	-0.537	0.983	0.745	5	-
		Average	0.096	0.146	-1.924	7.808	0.957	1.236	14	1.814	81	-0.338	-18.976	0.988	0.640	6	25

Note: B = Barley mix & O = Oats

Values in the 'average' rows are based on fits to consumption rates fit over three days shown in Figures 28 - 29.

Table E19. Parameter estimates for initial demand, Q_0 ; essential value, α ; P_{\max} , interaction, I , and sensitivity, β ; break point and cross point data for each possum in Experiment 6 under the geometric PPR FR schedule for the 'wet' foods.

Possum	PR(FR)	α	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{\max}	BP	I	β	VAC	SE	df	Xpt
P1	B(E)	0.341	0.008	-4.808	5.948	0.982	0.913	5	11.93	256	-5.059	0.059	0.985	0.648	5	9.30
	E(B)	0.311	0.013	-4.334	5.948	0.978	1.017	6	8.13	512	-1.549	0.004	0.984	0.495	5	89.05
P2	B(E)	0.114	0.135	-2.004	11.163	0.990	0.191	6	2.31	256	-	-	-	-	-	-
	E(B)	0.483	0.012	-4.394	5.338	0.978	0.039	7	5.93	512	-	-	-	-	-	-
P3	B(E)	0.292	5.814	1.760	8.138	0.972	1.613	2	0.01	16	-	-	-	-	-	-
	E(B)	0.217	0.035	-3.352	8.138	0.947	0.409	5	3.20	256	-1.110	0.001	0.986	1.265	3	-
P4	B(E)	0.114	0.135	-2.004	5.580	0.990	0.191	6	2.31	256	-	-	-	-	-	-
	E(B)	0.483	0.012	-4.394	5.580	0.978	0.039	7	5.93	512	-	-	-	-	-	-
P5	B(E)	1.861	0.328	-1.115	6.507	0.980	1.368	3	0.02	32	-	-	-	-	-	-
	E(B)	0.261	0.000	-8.140	6.507	0.996	0.809	2	398.47	16	-0.202	0.000	0.999	0.425	2	-
P6	B(E)	1.342	1.050	0.049	6.054	0.976	1.265	3	0.02	32	-4.884	0.006	0.994	1.072	1	18.47
	E(B)	0.289	0.007	-5.008	6.054	0.992	0.650	3	16.87	32	-1.698	0.002	0.987	1.247	3	-
P7	B(E)	4.004	0.086	-2.448	5.984	0.985	1.224	3	0.10	32	-	-	-	-	-	-
	E(B)	3.495	0.289	-1.242	5.984	0.985	1.161	3	0.03	32	-	-	-	-	-	-
P8	B(E)	0.703	0.880	-0.128	6.506	0.954	1.502	6	0.05	128	-1.294	0.006	0.989	0.809	6	4.48
	E(B)	0.215	0.008	-4.865	6.506	0.996	0.422	6	18.33	256	-1.045	0.002	0.987	0.973	5	160.22
P9	B(E)	-	-	-	5.624	-	-	0	-	4	-	-	-	-	0	-
	E(B)	9.495	0.035	-3.365	5.624	0.995	0.623	4	0.11	32	-	-	-	-	-	-
P10	B(E)	-	-	-	5.841	-	-	-	-	2	-	-	-	-	-	-
	E(B)	-0.427	0.002	-6.458	5.841	0.938	2.171	4	-50.49	64	-0.850	0.001	0.994	1.048	2	-
P11	B(E)	0.507	0.039	-3.251	6.085	0.949	1.254	4	1.65	32	-	-	-	-	-	-
	E(B)	0.168	0.021	-3.865	6.085	0.994	0.457	6	9.22	256	-2.965	0.002	0.996	0.728	2	214.86
P12	B(E)	1.125	1.110	0.105	6.288	0.984	1.046	3	0.03	32	-	-	-	-	-	-
	E(B)	0.001	0.000	-8.361	6.288	0.995	1.150	1	137066.12	8	-	-	-	-	-	-

Note: B = Berries & E = Egg.

Values in the 'average' rows are based on fits to consumption rates fit over three days shown in Figures 26 - 27.

Table E20. Parameter estimates for initial demand, Q_0 ; essential value, α ; P_{\max} , interaction, I , and sensitivity, β ; break point and cross point data for each possum in Experiment 6 under the arithmetic PPR FR schedule for the 'wet' foods.

Possum	PR(FR)	α	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{\max}	BP	I	β	VAC	SE	df	Xpt
P1	B(E)	0.981	0.018	-4.034	5.948	0.993	1.224	5	1.91	101	-0.846	31.401	0.989	0.908	7	12.97
	E(B)	0.433	0.011	-4.486	5.948	0.991	0.423	5	6.81	156	-1.627	222.566	0.996	0.455	6	67.38
P2	B(E)	1.337	0.003	-5.656	5.337	0.990	0.718	17	7.92	96	-1.577	3.973	0.988	1.274	8	116.99
	E(B)	0.298	0.008	-4.810	5.337	0.992	0.079	54	15.25	276	-1.089	2.494	0.987	1.754	8	84.38
P3	B(E)	0.442	0.012	-4.417	8.138	0.998	0.441	23	4.55	126	-1.383	287.099	0.978	0.786	24	27.99
	E(B)	0.427	0.013	-4.325	8.138	0.990	1.146	5	4.30	91	-7.575	26.091	0.511	0.000	6	229.52
P4	B(E)	0.769	0.007	-4.910	0.004	0.997	0.391	22	6.24	121	-0.286	-194.17	0.992	0.956	7	16.82
	E(B)	0.404	0.021	-3.871	0.045	0.994	0.533	32	1.12	176	-1.021	18.357	0.994	1.118	7	69.10
P5	B(E)	0.986	0.011	-4.548	6.507	0.996	0.004	5	2.91	51	-	-	-	-	-	-
	E(B)	0.323	6.915	1.934	6.507	0.996	0.013	3	0.01	21	-0.153	-0.116	0.120	1.000	2	-
P6	B(E)	0.398	0.113	-2.184	6.054	0.989	0.835	33	0.73	176	-3.912	7.498	0.984	1.897	6	36.88
	E(B)	0.374	0.007	-4.900	6.054	0.988	0.721	39	11.70	211	-2.059	12.345	0.988	1.798	7	127.93
P7	B(E)	3.179	0.019	-3.947	5.984	0.998	0.389	5	0.54	36	-1.714	217.942	0.994	0.822	4	17.46
	E(B)	0.834	0.037	-3.289	5.984	0.995	0.621	25	1.06	136	-1.922	16.153	0.988	0.827	19	35.05
P8	B(E)	1.626	0.080	-2.526	6.506	0.986	0.964	15	0.28	86	-0.916	27.095	0.998	0.238	16	6.72
	E(B)	3.559	1.007	0.007	6.506	0.991	0.560	26	0.01	146	0.000	-6.496	0.982	0.869	27	-
P9	B(E)	2.138	0.007	-4.974	5.624	0.998	0.405	4	2.38	31	-	-	-	-	-	-
	E(B)	-	-	-	5.624	-	-	0	-	11	-	-	-	-	-	-
P10	B(E)	0.001	0.00023	-8.363	5.841	0.995	1.150	1	126739.13	11	-	-	-	-	-	-
	E(B)	-	-	-	5.841	-	-	0	-	11	-	-	-	-	-	-
P11	B(E)	-	-	-	6.085	-	-	-	-	6	-	-	-	-	-	-
	E(B)	0.247	0.040	-3.210	6.085	0.976	0.920	15	2.13	86	-0.441	-48.641	0.991	0.173	13	-
P12	B(E)	3.005	0.496	-0.701	6.288	0.971	1.832	2	0.02	21	-	-	-	-	-	-
	E(B)	-	-	-	6.288	-	-	-	-	-	-	-	-	-	-	-

Note: B = Berries & E = Egg.

Values in the 'average' rows are based on fits to consumption rates fit over three days shown in Figures 26 - 27.

Table E21. Parameter estimates for initial demand, Q_0 ; essential value, α ; P_{max} , interaction, I , and sensitivity, β ; break point and cross point data for each possum in Experiment 6 under the geometric PPR FR schedule for the 'dry' foods.

Possum	Food Pair PR(FR)	PR	FR		k	VAC	SE	df	P_{max}	BP	I	β	VAC	SE	df	Xpt
		α	Q_0	$\ln Q_0$												
P1	BA(O)	1.935	0.004	-5.428	5.948	0.994	0.577	5	3.91	64	-0.860	296.092	0.993	0.440	5	-
	O(BA)	0.227	0.040	-3.218	5.948	0.983	0.703	6	3.66	128	-4.897	96.124	0.998	0.419	3	-
P2	BA(O)	-	-	-	11.163	-	-	-	-	4	-	-	-	-	-	-
	O(BA)	0.171	0.031	-3.475	5.338	0.994	0.447	6	6.99	256	-4.405	30.491	0.996	0.537	5	97.86
P3	BA(O)	0.710	0.012	-4.464	8.138	0.991	0.634	5	2.97	64	-2.929	225.391	0.925	0.588	3	21.14
	O(BA)	0.070	0.195	-1.634	8.138	0.947	1.530	6	1.79	256	-0.767	2.854	0.999	0.426	1	54.31
P4	BA(O)	0.424	0.012	-4.453	5.580	0.998	0.324	6	7.17	256	-4.255	39.474	0.989	1.186	3	124.55
	O(BA)	2.013	0.021	-3.857	5.580	0.966	1.520	3	0.83	32	-0.868	101.306	0.995	0.806	1	-
P5	BA(O)	0.528	0.010	-4.607	6.507	0.917	2.138	5	5.76	128	-2.313	1294.989	0.993	0.295	6	3.31
	O(BA)	0.084	0.107	-2.239	6.507	0.998	0.204	6	3.40	128	-11.74	66.932	0.998	0.372	2	48.36
P6	BA(O)	0.272	0.024	-3.723	6.054	0.997	0.392	6	4.96	256	-2.235	34.405	0.973	1.010	6	33.64
	O(BA)	0.302	0.045	-3.093	6.054	0.999	0.113	6	2.38	32	-1.336	16.814	0.993	0.260	6	38.52
P7	BA(O)	0.974	0.034	-3.396	5.984	0.965	1.028	3	1.01	32	-	-	-	-	-	-
	O(BA)	0.245	0.050	-2.995	5.984	0.994	0.417	4	2.70	64	-3.895	47.405	0.984	1.017	1	43.13
P8	BA(O)	0.237	0.055	-2.904	6.506	0.995	0.212	6	2.34	256	-26.794	1433.658	0.989	0.620	5	6.50
	O(BA)	0.103	0.101	-2.292	6.506	0.995	0.404	6	2.92	256	-3.139	23.765	0.988	0.702	6	40.35
P9	BA(O)	5.640	0.069	-2.675	5.624	0.997	0.562	3	0.09	32	-0.296	31.876	1.000	0.115	5	-
	O(BA)	0.890	0.020	-3.912	5.624	0.986	0.827	5	1.97	128	-1.099	22.504	0.995	0.439	6	28.28
P10	BA(O)	1.048	0.029	-3.544	5.841	0.990	0.597	3	1.12	16	-	-	-	-	-	-
	O(BA)	0.066	0.043	-3.158	5.841	0.999	0.161	5	11.98	128	-4.930	55.585	0.981	1.375	2	-
P11	BA(O)	1.402	0.032	-3.438	6.085	0.936	1.516	4	0.72	64	-1.765	37.736	0.968	1.052	6	7.92
	O(BA)	0.161	0.058	-2.854	6.085	0.999	0.170	5	3.50	128	-2.691	69.671	0.987	0.844	6	52.13
P12	BA(O)	0.084	0.035	-3.356	6.288	0.982	0.646	6	10.78	256	-2.907	7.764	0.921	2.051	5	142.50
	O(BA)	0.152	0.042	-3.181	6.288	0.982	0.738	5	4.98	128	-2.931	58.128	0.960	1.514	5	56.37

Note: B = Barley mix & O = Oats

Values in the 'average' rows are based on fits to consumption rates fit over three days shown in Figures 28 - 29.

Table E22. Parameter estimates for initial demand, Q_0 ; essential value, α ; P_{max} , interaction, I , and sensitivity, β ; break point and cross point data for each possum in Experiment 6 under the arithmetic PPR FR schedule for the 'dry' foods.

Possum	PR(FR)	α	Q_0	$\ln Q_0$	k	VAC	SE	df	P_{max}	BP	I	β	VAC	SE	df	Xpt
P1	BA(O)	2.346	0.015	-4.229	5.948	0.977	1.400	3	0.97	46	-1.316	13.018	0.954	0.015	1	3.61
	O(BA)	1.315	0.016	-4.135	5.948	0.993	0.663	7	1.58	51	-0.366	-22.48	0.998	0.030	0	-
P2	BA(O)	1.346	0.141	-1.962	5.337	0.977	1.400	3	0.20	46	-0.610	-8.514	0.933	0.017	1	251.00
	O(BA)	0.224	0.035	-3.343	5.337	0.976	0.892	22	0.00	126	-1.666	3.091	0.932	0.006	1	92.53
P3	BA(O)	-	-	-	8.138	-	-	0	-	11	-	-	-	-	-	-
	O(BA)	0.151	0.115	-2.166	8.138	0.975	0.788	9	1.40	56	-4.884	20.618	0.973	0.002	2	47.87
P4	BA(O)	1.773	0.002	-6.158	0.004	0.976	1.195	17	9.44	96	-0.869	5.030	0.974	0.879	0	-
	O(BA)	0.205	0.030	-3.510	0.045	0.987	0.350	34	5.77	51	-1.868	61.000	0.987	0.857	0	198.80
P5	BA(O)	0.221	0.082	-2.507	6.507	0.992	0.596	17	1.69	96	-3.131	33.050	0.973	0.021	1	24.62
	O(BA)	0.169	0.085	-2.463	6.507	0.990	0.184	29	2.11	161	-3.372	20.958	0.972	0.010	1	43.17
P6	BA(O)	0.194	0.075	-2.596	6.054	0.979	0.000	18	2.25	206	-2.046	18.651	0.988	0.600	18	36.84
	O(BA)	0.183	0.108	-2.229	6.054	0.979	0.861	16	1.66	91	-6.650	43.713	0.938	0.025	1	30.61
P7	BA(O)	1.039	0.022	-3.827	5.984	0.975	1.215	8	1.46	51	-0.607	77.789	0.997	0.024	0	-
	O(BA)	0.136	0.058	-2.848	5.984	0.971	0.831	11	4.18	66	-4.734	34.647	0.955	0.005	3	-
P8	BA(O)	0.151	0.369	-0.996	6.506	0.986	0.846	19	0.54	106	-0.509	3.847	0.995	0.031	0	9.33
	O(BA)	0.171	0.046	-3.068	6.506	0.983	0.746	24	3.81	121	-1.753	37.102	0.997	0.010	0	28.80
P9	BA(O)	1.513	0.008	-4.797	5.624	0.991	0.717	12	2.81	71	-1.455	17.429	0.954	0.014	1	7.08
	O(BA)	0.342	0.040	-3.224	5.624	0.988	0.718	18	2.58	101	-2.624	42.253	0.979	0.005	0	44.75
P10	BA(O)	-	-	-	5.841	-	-	-	-	6	-	-	-	-	-	-
	O(BA)	0.199	0.064	-2.749	5.841	0.980	0.847	18	2.66	101	-2.973	14.169	0.989	0.002	0	82.17
P11	BA(O)	0.228	0.091	-2.392	6.085	0.971	0.149	9	1.56	46	-4.472	21.742	0.977	0.001	2	-
	O(BA)	0.151	0.096	-2.340	6.085	0.984	0.753	19	2.23	106	-7.053	80.540	0.997	0.008	0	34.66
P12	BA(O)	0.174	0.106	-2.245	6.288	0.983	0.838	18	1.70	101	-3.921	26.351	0.926	0.025	1	27.90
	O(BA)	0.181	0.076	-2.575	6.288	0.979	0.894	18	2.28	101	-1.969	17.417	0.987	0.009	0	38.47

Note: B = Barley mix & O = Oats

Values in the 'average' rows are based on fits to consumption rates fit over three days shown in Figures 28 - 29.

Appendix F.*Table F23. Schedule of Experiments.*

Experiment	Date
Body weight (Appendix A)	April 2010 – April 2011
Body weight stability (Appendix B)	May 2011 – June 2011
Experiment 1	June 2010 – July 2010
Experiment 2 (P7-12)	April 2011
Experiment 2 (P1-6)	March 2012
Experiment 3	May 2011 – February 2012
Experiment 4	April 2012 – May 2012
Experiment 5	August 2012 – March 2013
Experiment 6	June 2013 – February 2014