

OPTIMAL PREY SELECTION IN EASTERN GRAY SQUIRRELS

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ABSTRACT

The optimal prey selection hypothesis, a part of Optimal Foraging Theory, uses prey energy content and forager searching and handling times to predict when a forager will choose only the most profitable prey and when it will include less profitable prey in its diet. I tested the hypothesis using eastern gray squirrels as foragers and pairs of prey—sunflower fruits and seeds, and pumpkin seeds and embryos—that differed in handling time. In all foraging trials, the squirrels consumed both prey types, but showed a partial preference for the less profitable prey (sunflower fruit and pumpkin seed). For squirrels foraging on pumpkin seeds and embryos, the hypothesis, which predicts that the more profitable prey (embryos) alone would be selected, was not supported by a partial preference value significantly greater than 0.5 which would indicate that both prey types were consumed. The hypothesis may be limited to laboratory conditions in which prey are presented sequentially, a condition not met in the experiments described here where prey types were offered together and were constantly mixed as the squirrels searched for prey in a sand-containing dish. Instead, squirrels showed a slight preference for larger prey which may result from higher encounter rates or may result from squirrels using a “rule of thumb:” when hungry, consume prey as they are encountered.

Keywords

eastern grey squirrel, optimal foraging theory, optimal prey selection

INTRODUCTION

The optimal prey selection hypothesis is a component of Optimal Foraging Theory, which explains the food choice decisions of foragers (Charnov 1976; Krebs et al. 1977). It assumes that a forager will optimize its net energy gain when prey individuals are encountered sequentially and at random and when the forager can detect differences in prey profitability. It also predicts that food choices depend alone on the abundance of the most profitable prey (Krebs et al. 1977). The predictions were tested initially for caged tits (*Parus major* L.) who were sequentially offered individual mealworms (Krebs et al. 1977) and for caged mantids (*Hierodula crassa* Giglio-Tos) who could see all prey individuals

(Hollings' data in Charnov (1976)). Subsequently, most, but not all, experiments designed to test the optimal prey selection hypothesis have supported it (summarized in Stephens and Krebs 1986; Sih and Christensen 2001).

The optimal prey selection hypothesis (also called the optimal diet model) (Krebs et al. 1977; Davies et al. 2012) describes a means of testing the prey model of Optimal Foraging Theory by predicting forager choices for two prey types that differ in profitability. Profitability is determined by the energy gained per unit of handling time (E/H). If the profitability of the more profitable prey (Prey 1) is designated E_1/H_1 and the less profitable (Prey 2) by E_2/H_2 , then $E_1/H_1 > E_2/H_2$. A forager will always consume the more profitable prey, but will include the less profitable in its diet if $S_1 > [(E_1 \cdot H_2)/E_2] - H_1$, where S_1 is the searching time for Prey 1, E_1 is the energy content of Prey 1, E_2 is the energy content of Prey 2, H_1 is the handling time for Prey 1, and H_2 is the handling time for Prey 2 (Davies et al. 2012). Thus, choice of prey depends on the abundance of Prey 1 (as reflected in the searching time) and not on the abundance of Prey 2.

In previous foraging experiments, when fox squirrels (*Sciurus niger* L.) were offered two different prey, they showed a partial preference for the larger one even though it had higher energy costs (Tatina 2007). Their choice seemed not to support the optimal prey selection hypothesis. Consequently, eastern gray squirrels (*Sciurus carolinensis* Gmelin) were chosen to compare their prey choice decisions with those of fox squirrels. Like fox squirrels, gray squirrels are ideal foragers because they are generalist foragers (Steele and Koprowski 2001), readily accept foods from artificial patches, and are sufficiently abundant to permit replicated experimental designs. In addition, eastern gray squirrels can detect differences in prey profitability (Smith and Follmer 1972; Steele et al. 1996; Steele and Koprowski 2001; Steele et al. 2006; Sundaram et al. 2015).

To determine if the hypothesis could describe foraging outcomes outside the laboratory, I tested the prediction that a forager will always consume the more profitable prey, but will include the less profitable in its diet if $S_1 > [(E_1 \cdot H_2)/E_2] - H_1$, with eastern gray squirrels as foragers and confectioner sunflower (*Helianthus annuus* L.) fruits (= "shell"-enclosed seeds) and seeds (without "shells") and pumpkin (*Cucumis pepo* L.) seeds and embryos (= epicotyl, hypocotyl and cotyledons, but no seed coat), as prey. To do this I measured the time squirrels spent searching for and handling prey items and calculated their partial preference from giving up densities.

METHODS

All prey choice trials were run with randomly selected prey combinations scattered over the surface of approximately 600 cc of beach sand contained in a 2.8 L Pyrex dish (27.9 cm × 17.8 cm × 7.6 cm) and then covered with an additional 600 cc of sand. The dish was set on a platform 30 cm above ground in a yard in Sawyer, MI, approximately 3 m from a large white pine tree and 5 m from several large maple trees. Three, two-hour feeding trials were run each day at 0800 h, 1100 h, and 1400 h. Feeding trials began in December 2014, and ended in March 2017. A video recording was made of each feeding trial in all experiments

and viewed to determine which squirrel, based on fur color, ear color and fore foot color, was involved. All data were then sorted by squirrel before statistical analysis using Minitab 17.2.1 software (Minitab 2015) with $\alpha = 0.05$.

Prey type preference. A forager exhibits a partial preference for one prey type when the proportion of that prey type consumed is greater than the abundance of that prey type relative to all available prey types (Brown and Morgan 1995). To determine the prey preference of eastern gray squirrels, in February 2017, I presented mixtures of confectioner sunflower fruits and seeds (20, 40 or 60 fruits by 20, 40 or 60 seeds) in random order as determined from a table of random numbers, and pumpkin seeds and embryos (20, 30 or 40 seeds by 20, 30 or 40 embryos) in March 2017. At the end of each feeding trial, seeds and fruits or seeds and embryos were sifted from the sand and counted. The number of seeds, fruits and embryos equal their giving up densities (GUDs). To determine if one prey resource was preferred, I calculated the partial preference (PP) for one of the prey types (R) using the following formula from Chesson (1983) for tests without replacement of depletable resources:

$$PP_1 = (\log_e GUD_1 / R_1) / [(\log_e GUD_1 / R_1) + (\log_e GUD_2 / \log_e R_2)],$$

where GUD = giving up density, the number of uneaten prey items remaining after a foraging episode (Brown and Morgan 1995).

Mean partial preference values calculated for each feeding trial were subjected to a one-sample *t*-test to determine whether average values differed significantly from 0.5. Values significantly greater than 0.5 indicate a partial preference for prey type 1, values equal to 0.5 indicate no preference, and values less than 0.5 indicate a partial avoidance of prey type 1 (Brown and Morgan 1995).

Prey size preference. To determine if squirrels had a size preference when offered prey of only one type, I determined the average mass to the nearest 0.01g for 80, 100 or 120 sunflower fruits or seeds and the average mass for 30, 40 or 50 pumpkin seeds and the average mass for 100, 150 or 200 pumpkin embryos. One of the prey numbers was randomly selected to be offered. At the end of a feeding trial the number of remaining individuals was counted and then weighed to the nearest 0.01 g, after which the average mass was calculated. Thus, average mass equated to mass per item. For each squirrel, the average mass remaining was subtracted from the average mass offered. If the average difference was greater than zero, smaller prey items were preferred; if less than zero, large prey items were preferred. Differences were subjected to a one-tailed *t*-test of the statistical hypothesis that the difference was less than or equal to zero (i.e., larger prey item were preferred).

Foraging times. Squirrel foraging times are composed of searching times (average time to locate a prey item) and handling times (average time to ingest a prey item). To determine mean searching and handling times for prey items, I buried in sand 25 confectioner sunflower fruits or seeds (September – November 2015) or 25 pumpkin seeds or embryos (November – December 2016) and recorded squirrel foraging episodes using a small video camera and then viewed episodes

with a clock superimposed onto the video files. I assumed searching times started when a squirrel lowered its head to the sand and ended when it raised its head and started to put food to its mouth, at which time handling times started immediately and continued until the squirrel again lowered its head to the sand. I excluded intervals when a squirrel became motionless and stopped searching for or handling food items. Sums of searching and handling times for each prey type for each feeding trial for each squirrel were converted to the time in seconds to search for one prey item and to handle one prey item. I then compared searching times (seconds per item) and handling times (seconds per item) for pairs of prey types in two-tailed, two-sample t-tests.

Calculations for selectivity predictions. The variables used to predict the prey choice strategy of squirrels are those contained in the optimal selectivity models of Charnov (1976) and Krebs et al. (1977) as presented in Davies et al. (2012) as previously described in the Introduction. The energy content (E) of confectioner sunflower fruits and seeds was assumed to be equal since these two items differ only in the presence of the pericarp (“shell”) in the fruits, but absent from the seeds. Likewise, the energy content (E) of pumpkin seeds and embryos was assumed to be equal because these items differed only by the presence of the seed coat surrounding the seeds and not the embryos.

Partial preference changes over time. From December 2014, to March 2015, I offered sunflower fruits (0, 5, 10, and 15 g) and seeds (0, 10, 20, and 30 g) mixed in sand in random combinations from 800 h to 1000 h and 1500 h to 1700 h. At the end of each feeding trial, I weighed the fruits and seeds remaining and calculated the partial preference for fruits. To determine if squirrel preferences changed over time, I regressed partial preferences against time in days.

RESULTS

Prey preference for confectioner sunflower fruit/seed. In 34 foraging trials over 19 days, when squirrels were exposed to various random combinations of sunflower fruits and seeds, they consumed both, but had a low, albeit significant, partial preference for sunflower fruits ($PP_{\text{fruits}} = 0.5877 \pm 0.0524$ (\pm SD)); t ($\mu \leq 0.5$) = 4.10, $P = 0.005$, $n = 6$ squirrels).

Prey preference for pumpkin seed/embryo. Forty foraging trials over 26 days yielded a mean partial preference for pumpkin seeds ($PP_{\text{seeds}} = 0.5517 \pm 0.0278$ (\pm SD)), t ($\mu \leq 0.5$) = 3.17, $P = 0.017$, $n = 6$). Thus, eastern gray squirrels again consumed both prey types, but had a low, significant partial preference for pumpkin seeds over embryos.

Foraging times for confectioner sunflower fruit/seed. When presented with random sequences of 25 sunflower fruits or seeds in 38 foraging trials over 42 days, the average searching time per item of three eastern gray squirrels for fruits was significantly shorter than for seeds ($P = 0.001$), but the average handling time

per item was significantly longer ($P = 0.020$) (Table 1) because squirrels had to bite away the pericarp of the fruits before ingesting the seeds.

Foraging times for pumpkin seed/embryo. Eastern gray squirrels exhibited no difference in searching times ($P = 0.928$) when offered 25 pumpkin seeds or embryos (Table 1) in 40 foraging trials divided among three squirrels over 26 days, but had an approximately 2-1/2-fold increase in handling times for seeds due to having to remove first the seed coat before biting off and swallowing pieces of the embryo contained within.

Table 1. Eastern gray squirrel searching and handling times (seconds per prey item) for sunflower fruits and seeds and pumpkin seeds and embryos. Two-sample, two-tailed t-tests ($\mu = 0$) compared sunflower searching times for fruits to seeds, sunflower handling times for fruits to seeds and pumpkin searching times for seeds to embryos and pumpkin handling times for seeds to embryos. n = the number of squirrels.

	n	Mean ± SD	t	P ($\mu_1 = \mu_2$)
Searching Time—Sunflower Fruit (1)	3	6.47 ± 0.23		
Searching Time—Sunflower Seed (2)	3	8.64 ± 0.21	12.17	0.001
Handling Time—Sunflower Fruit (1)	3	3.54 ± 0.55		
Handling Time—Sunflower Seed (2)	3	1.86 ± 0.30	4.55	0.020
Searching Time—Pumpkin Seed (1)	3	5.77 ± 1.53		
Searching Time—Pumpkin Embryo (2)	3	5.87 ± 0.72	0.10	0.928
Handling Time—Pumpkin Seed (1)	3	15.47 ± 0.92		
Handling Time—Pumpkin Embryo (2)	3	6.03 ± 0.90	12.69	0.001

Optimal prey selection predictions. The profitability (E/H) of consuming sunflower fruits was 0.28 which was less than the 0.54 for seeds (Table 2). The searching time (S_{more}) for seeds of 8.64 s / item exceeded the 1.68 s / item calculated for $[(E_{\text{more}} \times H_{\text{less}}) / E_{\text{less}}] - H_{\text{less}}$, which suggests that the squirrels should consume both, which they did.

In the trial with pumpkin seeds and embryos, the embryos, with an E/H = 0.17, were almost 3 times more profitable for squirrels to consume (Table 2). However, their searching time (S_{more}) of 5.87 s / item was less than their 9.44 value for $[(E_{\text{more}} \times H_{\text{less}}) / E_{\text{less}}] - H_{\text{less}}$, suggesting that the squirrels should take only the more profitable embryos, but they included both, as indicated by a partial preference significantly greater than 0.5.

Table 2. Profitability (E/H) for pairs of prey items, search times (S_{more}) for the more profitable prey item, and the results of the calculation to predict if a forager will exhibit partial preference (i.e., when $S_{\text{more}} > [(E_{\text{more}} \times H_{\text{less}}) / E_{\text{less}}] - H_{\text{more}}$). E = relative energy gain and H = handling time. Boldface indicates preferred prey. Confectioner (Cnf) sunflower fruit and seed are commonly used for human consumption; whereas, oil sunflower fruit and seed are used for bird seed. Values for fox squirrels were calculated from data in Tatina (2007)

Prey	Forager	E/H (Profitability)	S_{more}	$[(E_{\text{more}} \times H_{\text{less}}) / E_{\text{less}}] - H_{\text{more}}$
Cnf sunflower fruit	Gray squirrel	1/3.54 = 0.28 (less)		
Cnf sunflower seed	Gray squirrel	1/1.86 = 0.54 (more)	8.64	1.68
Pumpkin seed	Gray squirrel	1/15.47 = 0.06 (less)		
Pumpkin embryo	Gray squirrel	1/6.03 = 0.17 (more)	5.87	9.44
Cnf sunflower fruit	Fox squirrel	1/4.55 = 0.22 (less)		
Cnf sunflower seed	Fox squirrel	1/2.53 = 0.40 (more)	6.25	2.22
Cnf sunflower fruit*	Fox squirrel	1.3/4.55 = 0.29 (less)		
Oil sunflower fruits	Fox squirrel	1/2.47 = 0.40 (more)	5.79	2.08
Cnf sunflower seed*	Fox squirrel	1.3/2.53 = 0.51 (more)	6.25	3.45
Oil sunflower fruit	Fox squirrel	1/2.47 = 0.40 (less)		

*The mean mass (\pm SD) of 13 sets of 25 confectioner (Cnf) sunflower seeds was 0.532 g (95% CI 0.492-0.572) per seed and for 10 sets of 25 oil sunflower seeds was 0.403 g (95% CI 0.370-0.436) per seed, making the confectioner seed 1.3 times heavier than the oil seed. Therefore, the energy content (E) of the confectioner fruit was estimated to be 1.3 times greater than that of the oil fruit. Mass differences are a reasonable substitute for energy content differences because the proximate analyses of the two seed types are very similar.

Prey selection based on size alone. When a single prey type was offered, the mean mass of the prey items consumed was not significantly greater than the mean mass of the same items offered (Table 3). This was true for confectioner sunflower fruits ($P = 0.818$) and seeds ($P = 0.097$) and pumpkin seeds ($P = 0.072$) and embryos ($P = 0.155$).

Table 3. Prey selection by eastern gray squirrels based on size. Paired t-test of difference (g) > 0 between the mean mass of food offered and the mean mass of food consumed. n = number of squirrels, Trials = number of feeding trials, Difference = mean \pm SD.

	Difference (g)	t	n	P	Trials
Confectioner Sunflower Fruits	-0.0307 \pm 0.0576	-1.07	4	0.818	20
Confectioner Sunflower Seeds	-0.0003 \pm 0.0003	-1.66	5	0.903	20
Pumpkin Seeds	0.0032 \pm 0.0033	1.96	4	0.072	26
Pumpkin Embryos	0.0515 \pm 0.0660	1.35	3	0.155	20

Partial preference changes over time. Partial preference values for sunflower fruits from 96 trials over 111 days regressed against time yielded a slope of -0.0005 ($R^2 = 0.0012$, $P = 0.275$).

DISCUSSION

Optimal Foraging Theory predicts, under a strict set of assumptions, that as foragers forage, they choose to consume prey that will optimize their energy gain. Energy gain is assumed to be a function of energy content minus foraging costs. Foraging costs include energy expended in searching for prey and in handling prey, as well as lost opportunities to engage in other essential life activities: escaping foragers, seeking mates, caring for offspring, etc. Assigning a value to each of these costs has been difficult, if not impossible. Instead, searching and handling times have been used as surrogates for costs (Brown 1988; Mitchell and Brown 1990), and handling time has been included in the optimal prey selection hypothesis to determine the profitability of prey items. Furthermore, the hypothesis assumes that a forager can assess energy content and handling time as it forages and was developed and tested under conditions in which prey were visible to foragers throughout foraging trials so that prey densities were known and forager encounter times, searching times, and handling times could be determined (Krebs et al. 1977). Under these conditions, the forager was shown to forage optimally as described by the hypothesis in that it always consumed the more profitable prey, but included the less profitable in its diet if the searching time for the more profitable prey was greater than the difference between handling time for the more profitable and the ratio of the product of the energy content of the more profitable prey and the handling time of the less profitable prey to the energy content of the less profitable prey, the $S_1 > [(E_1 \cdot H_2) / E_2] - H_1$ described in the Introduction (Krebs et al. 1977).

Under the conditions of my experiments in which prey items were buried in sand, eastern gray squirrels could not be shown to forage as described by the optimal prey selection hypothesis. Instead, when offered sunflower fruits and seeds, they showed a partial preference for the less profitable seeds. Similar results were obtained for fox squirrels in South Dakota (Table 2 and Tatina (2007)). When offered pumpkin seeds and embryos, eastern gray squirrels should have consumed only the more profitable prey, the embryos, but instead showed a partial preference for the less profitable seeds, consuming both seeds and embryos. When fox squirrels were offered a choice between confectioner sunflower fruits and the smaller oil sunflower fruits, they had a partial preference for the less profitable confectioner fruits (Table 2 and Tatina (2007)). When given a choice between confectioner sunflower seeds and oil sunflower fruits, the hypothesis predicted that fox squirrels would prefer the more profitable seeds, and would consume both; however, they showed no preference for either, consuming both depending on the amounts they were offered (Table 2 and Tatina (2007)).

Judging the profitability of a prey based on handling time seems not to be the strategy used by squirrels. Instead, they may use searching time as an indicator

of profitability because searching incurs more risk than handling (Makowska and Kramer 2007). As a squirrel is searching, its head is down and the amount of landscape it can view becomes less than when its head is elevated in the semi-erect posture it assumes when handling prey (Bednekoff and Lima 2002). The significantly shorter searching time for the larger prey item, the sunflower fruit in the trials with fruits and seeds, indicates a shorter time between prey encounters (Table 1). For pumpkin, the searching time was lower for the larger (seed) item, but the difference was not statistically significant (Table 1). The lack of a significant difference in searching times for pumpkin seeds and embryos may be due to the similarity in the ratio (1.8:1) of its seed to embryo masses (personal observation) compared to that (2.4:1) of sunflower fruits and seeds. When the average sizes of oil sunflower fruits and confectioner seeds were similar, fox squirrel searching times were similar and the squirrels showed no preference for either prey (Tatina 2007 and Table 2).

When eastern gray squirrels were offered two different prey items (fruits and seeds or seeds and embryos) that differed in size, they consistently showed a partial preference for the larger one. However, when they were offered prey items that differed in size only, I could not find support for the hypothesis that they selected the larger prey item, but size differences among prey in these foraging trials was much smaller than in the trials in which sunflower fruits and seeds or pumpkin seeds and embryos were offered, and squirrels may not have been able to detect such small differences.

The Optimal Foraging Theory assumes that foragers can detect differences in the energy content of potential prey and that they optimize the ratio of energy content to handling time. How they do this is not known. The theory claims that natural selection has molded the behavior of organisms such that when they make decisions about when to feed, where to feed, on what to feed, etc., they optimize energy gain. To do so, may involve complex interactions of sensory input, neural pathways, hormones, mental images and gene activation (Ydenberg et al. 2007). However, a forager may use some simple "rule of thumb" to make quick foraging decisions. Such rules of thumb may include prey characteristics of color, odor, and size or the strategy may be as simple as "if not satiated and prey is encountered, then attack and consume it." Such a strategy may indeed be optimal since failure to consume may be a missed opportunity that could not be compensated for by future encounters. Unfortunately, the design of my experiments did not allow for the measurement of encounter rates as did the experiments by Krebs et al. (1977).

If eastern gray squirrels can detect the size difference between prey items, how they accomplish this is not known; however, size has been a factor in other studies. For example, fox squirrels preferred the larger, less profitable prey when offered a choice between confectioner sunflower fruits (larger, less profitable) and seeds and between confectioner sunflower fruits (larger and less profitable) and oil sunflower fruits, but showed no preference when offered confectioner sunflower seeds and oil fruits whose size and profitability were more nearly equal (Table 2, and Tatina (2007)). Preferring the larger of prey items has been reported for fox squirrels on pine cones (Steele and Weigl 1992) and for gray squirrels on

insect galls (Shealer et al. 1999). As a generalist forager, eastern gray squirrels feed opportunistically on many types of prey (Steele and Koprowski 2001). To do so efficiently and not miss an opportunity to ingest food, these squirrels could apply a simple decision rule: when given a choice that can be perceived, select the larger prey. This was first suggested by O'Brien et al. (2005) for western crows feeding on whelks and clams, claiming that such a strategy is most effective when the difference in net energy gain is minimal. In the case of eastern gray squirrels feeding on pumpkin and sunflower prey, a negligible difference in net energy gain is not known.

Size may not be the only factor on which squirrels base prey selection. Other studies in which squirrels were the foragers have shown that preference may be based on prey digestibility (Smith and Follmer 1972; Schmidt 2000) and protein content (Lewis 1982).

A case could be made that the eastern gray squirrels preferred sunflower fruits over seeds because the black fruits were more conspicuous than the cream-colored seeds against the pale- yellow sand in which the seeds were mixed. But the white pumpkin seeds and the dark green pumpkin embryos would seem to be equally visible against the sand background. In addition, videos of foraging eastern gray squirrels show that they probably use visual cues to a lesser extent than they use tactile and olfactory cues to locate and select prey because a squirrel would usually encounter and select a prey item with its forepaws and muzzle.

Are squirrels showing a partial preference for the larger prey item (sunflower fruit or pumpkin seed) because they had developed a search image from past experience? It would be more usual for squirrels to encounter sunflower fruits than to encounter the smaller seeds because commercially available bird seed mixes contain sunflower fruits, and agricultural fields and roadsides provide sunflower fruits. For pumpkin seeds, which are usually available in late summer and fall as the contents of whole pumpkins in fields and as Halloween decorations, squirrels would have experience with seeds, but not with embryos. However, when fox squirrels in an urban setting in South Dakota were presented with a choice between confectioner sunflower fruits and oil fruits, they showed a partial preference for confectioner fruits even though they would probably have had more prior experience with oil fruits because these are what are sold for bird feeders (Tatina 2007). Finally, when partial preferences of eastern gray squirrels for sunflower fruits was regressed over time, the slope of the line was not different from zero, indicating that these squirrels had not changed their preference due to exposure to these two prey items during an extended set of feeding trials.

Eastern gray squirrels are scatter hoarders (Steele and Koprowski 2001) and may prefer sunflower fruits and pumpkin seeds because they can be cached because the pericarp of the sunflower fruits and the seed coat of the pumpkin seeds would protect these from decomposition. Squirrels were not observed to remove and bury the unprotected sunflower seeds or pumpkin embryos, nor were they observed to cache sunflower fruits. Instead, they consumed all three within the foraging trays. However, squirrels were seen removing some pumpkin seeds and burying them. Why they would bury pumpkin seeds and not sunflower fruits is not resolved, but squirrels are able to distinguish between high quality

and low quality prey (Hadj-Chikh et al. 1996; Steele et al. 1996) and, depending on their level of hunger, will consume low quality prey and cache high quality prey (Preston and Jacobs 2009). If this is the case with pumpkin seeds, then eastern gray squirrels must know that pumpkin seeds are cacheable, and pumpkin embryos are not.

Another possibility for the failure of the optimal prey selection hypothesis to correctly predict prey choice is that the experimental conditions of the current research do not satisfy one or more of the assumptions of the optimal prey selection hypothesis (Sih and Christensen 2001). First, if squirrels encounter more than one prey at a time, and there is no assurance that they do in the present experiments, especially after they have been searching in a feedings dish where they have been stirring the sand and the prey, the experiment violates the assumption that they encounter prey sequentially. Second, since the hypothesis was developed under conditions in which encounter rates and prey densities were known (Krebs et al. 1977), it may not describe outcomes where these two variables are not measured because they may be changing constantly. In the present research, these two variables may change constantly as the squirrel removes prey. Encounter rates are related to searching rates, but may not be the same because a squirrel may encounter a prey, but not capture it. Under the present experimental conditions in which prey were not visible, it was not possible to determine encounter rates. In addition, the density of prey is known at two times only—at the start of a feeding episode and at the end.

In foraging experiments in which prey are buried and not visible, a squirrel may be able to detect differences in profitability by measuring handling times and may be able to assess prey density by measuring searching times. But, as predicted by the optimal prey selection hypothesis, does a squirrel use these measures to make decisions about which prey to consume? From foraging trials described here, it would seem they do not. Instead, when they are hungry, they consume each prey they encounter. That they seem to prefer larger prey may be due to their encountering these more often simply because their larger size makes them more conspicuous. Such a simple foraging strategy may provide them with an optimal energy gain.

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