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# Optimal Foraging in Eastern Fox Squirrel: Food Size Matters for a Generalist Forager

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**ABSTRACT** -- Classical optimal foraging theory (OFT) predicts that an animal forages optimally when it chooses foods with the highest energy benefit or minimizes time searching for and handling food. I evaluated OFT by presenting eastern fox squirrel (*Sciurus niger*) multiple food items (i.e., sunflower seeds and fruits) in various density combinations. When the choice was between foods of equal energy benefits but different costs, they chose forage items with greater costs, seemingly not foraging optimally. However, individuals showed a partial preference for food items which minimized search time, but not handling time. The eastern fox squirrel also was found to be a generalist forager with a preference for larger food. Thus, food size might be a cue that usually leads to optimal foraging.

**Key words:** Eastern fox squirrel, optimal foraging theory, *Sciurus niger*, sunflower.

Based on the theory of natural selection, optimal foraging theory (OFT) attempts to explain feeding strategies of herbivores and carnivores. According to MacArthur and Pianka (1966), natural selection produces feeding strategies (e.g., food selection, feeding location, time, and duration) that optimize energy gains. Several reviews of OFT have been published, the latest by Cézilly and Benhamou (1996), who describe the classical model of OFT as food choices which minimize search and handling time, while maximizing average energy gained. Under the classical model, rate of energy gain is a function of  $E_f / (T_s + T_h)$ ; where  $E_f$  is net energy gain,  $T_s$  is search time, and  $T_h$  is handling time (Stephens and Krebs 1986).

The classical OFT model predicts that if a forager is offered two food types containing equal energy but differing in average search and handling time, food

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types with lower search and handling times will be selected. Except for studies by Steele and Weigel (1992) and Smith and Briggs (2001), who reported handling times for different foods, no eastern fox squirrel (*Sciurus niger*) study has included both search and handling times in assessing food choice decisions.

Pyke (1984) reported that foragers might not always optimize energy gains as they make food choices. Instead they might be avoiding toxins, or seeking essential nutrients. In such cases, the classical OFT model might be an oversimplification. In fact, Brown and Morgan (1995) categorize the classical OFT model into three general feeding strategies: 1) an expanding specialist -- a forager who specializes on one food type until it falls below some threshold value at which point it begins to include other food types in its diet; 2) a micropatch partitioner -- one who has the ability to subdivide its feeding patches into smaller areas than were intended by the researcher; and 3) a generalist -- one who consumes any food type it encounters. Knowledge of eastern fox squirrel foraging behavior might lead to increased understanding of how distribution and abundance of artificial foraging sites might influence survival of urban eastern fox squirrel populations. Thus, the objective of my study was to evaluate optimal foraging theory in an urban eastern fox squirrel population in eastern South Dakota.

## METHODS

To determine whether individuals of the eastern fox squirrel made optimal foraging decisions when offered foods of equal energy but different search and handling times, I exposed randomly selected combinations of confectioner sunflower (*Helianthus annuus*) fruits and seeds to foraging individuals from 0700 to 1700 hr between 19 August 2002 and 15 May 2003 and between 29 August 2003 and 30 April 2004. I assumed fruits and seeds contained equal energy because they differed only in the presence of the pericarp (i.e., present in fruits and absent in seeds). Combinations of fruits and seeds (in grams) respectively were 0 to 10, 0 to 20, 0 to 30, 5 to 0, 5 to 10, 5 to 20, 5 to 30, 10 to 0, 10 to 20, 10 to 30, 15 to 0, 15 to 10, 15 to 20, and 15 to 30; fruits and seeds were combined to yield approximately equivalent volumes at 15 to 30g. I placed food combinations over 250 cc of beach sand and covered each combination with 250 cc of sand in a 2.0 L Pyrex dish (27.9 cm X 17.8 cm X 7.6 cm). I placed food combinations on an elevated stand approximately 30 cm above ground level in a residential backyard in Mitchell, South Dakota. At the end of each day, I sifted beach sand to remove uneaten food; uneaten food was then weighed by type. Remaining food mass became the giving up density (GUD; Brown and Morgan 1995) for each type.

I determined how the eastern fox squirrel made food choices between forage items that differed in size by conducting a set of foraging experiments from 30 August 2004 until 5 May 2005. I paired confectioner fruits with seeds and with oil

sunflower fruits (i.e., oil fruits = smaller, black fruits grown for oil and bird feed) in the following 15 combinations of confectioner fruits and oil fruits or seeds: 0 to 10, 0 to 20, 0 to 30, 5 to 0, 5 to 10, 5 to 20, 5 to 30, 10 to 0, 10 to 10, 10 to 20, 10 to 30, 15 to 0, 15 to 10, 15 to 20, and 15 to 30 g, respectively. Also, I paired confectioner seeds and oil fruits in the following eight combinations: 0 to 10, 0 to 20, 10 to 0, 10 to 10, 10 to 20, 20 to 0, 20 to 10, and 20 to 20 g, respectively. I scattered combinations of fruits and seeds over 450 cc of beach sand in a 2.8 L Pyrex baking dish (33.0 cm X 22.9 cm X 5.1 cm) and then covered the combinations with 900 cc of sand. Equivalence of seed and oil fruit size was judged from a Student's t-test of the mean mass of 100 food items.

I used log transformed GUDs and initial food mass to calculate partial preference for food types by using the following formula from Brown and Morgan (1995): partial preference for food type 1 =  $\log_e(N_1/R_1) / [\log_e(N_1/R_1) + \log_e(N_2/R_2)]$  where  $N_1$  was the GUD for food type 1,  $R_1$  was the initial mass of food type 1,  $N_2$  was the GUD for food type 2, and  $R_2$  was the initial mass of food type 2. I used in calculations only the combinations in which both food types were present. I subjected daily partial preference values to a one-sample z-test to determine whether average values differed from 0.5; values greater than 0.5 indicated a partial preference for food type 1, values equal to 0.5 indicated no preference and values less than 0.5 indicated avoidance of food type 1 (Brown and Morgan 1995). A forager exhibits partial food preference when the proportion consumed is greater than that food's abundance relative to all available foods (Brown and Morgan 1995).

I determined mean search and handling times for forage items by placing 100 fruits or seeds in 2.8 L Pyrex dishes and burying forage items in beach sand by using the same procedure described for the 2004 to 2005 experiments. I recorded eastern fox squirrel foraging episodes on VHS tape and subsequently viewed episodes with a clock superimposed onto videotapes. I assumed search times started when an eastern fox 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 eastern fox squirrel again lowered its head to the sand. I excluded time intervals when an eastern fox squirrel became motionless and stopped searching or handling food items. I compared search times, handling times, and combined search and handling times for pairs of food types by using a Student's t-test.

To determine if food density influenced food choice, I calculated ratios of GUD mass to initial food mass for dishes that contained only confectioner fruits. I compared the ratios between smaller dishes (surface area = 486.6 cm<sup>2</sup>) used in 2002 to 2003 and 2003 to 2004 and larger dishes (surface area = 755.7 cm<sup>2</sup>) used in 2004 to 2005 by using a Student's t-test.

I performed sodium ion analysis of water extracts of confectioner fruits and seeds and oil fruits by using flame atomic absorption spectrophotometry (Olson Biochemical Laboratories at South Dakota State University, Brookings, South Dakota)

to determine if eastern fox squirrel forage preference was associated with greater amounts of sodium ions. I prepared extracts by swirling 25 g of a food type in 100 mL of demineralized water for 1-minute followed by vacuum filtration through an acid-washed 0.45  $\mu\text{m}$  Millipore filter. I compared sodium ion concentrations for the three foods by using a one-way ANOVA.

I determined general foraging strategies of the eastern fox squirrel by regressing partial preference values for confectioner fruits on initial mass of confectioner fruits and seeds and oil fruits by using criteria from Brown and Morgan (1995). Statistical analyses were performed by using Minitab Release 12 software (Minitab 1997).

## RESULTS

Individuals of the eastern fox squirrel showed a partial preference for confectioner fruits in all foraging experiments. During the 2002 to 2003 foraging experiment, 61 days yielded non-zero GUD values that could be used in calculating partial preference values. Mean partial preference for confectioner fruits with confectioner seeds was  $0.537 \pm 0.010$  (SE) ( $z = 3.59$ ,  $P = 0.0004$ ,  $n = 61$ ). A similar preference ( $z = 8.02$ ,  $P = 0.00001$ ,  $n = 69$ ) was noted in 2003 to 2004 in which a mean partial preference for confectioner fruits with confectioner seeds was  $0.597 \pm 0.012$  (SE). Individuals of the eastern fox squirrel exhibited shorter search times for confectioner fruits than seeds ( $t = 4.92$ ;  $df = 2342$ ,  $P = 0.0001$ ), but longer handling times ( $t = 19.71$ ;  $df = 2890$ ,  $P = 0.00001$ ) (Table 1). Individuals also spent more total time searching for and handling fruits than seeds ( $t = 2.42$ ;  $df = 2509$ ,  $P = 0.015$ ) (Table 1).

The eastern fox squirrels had a mean partial preference value ( $0.679 \pm 0.005$  (SE)) for the larger confectioner fruits when paired with the smaller oil fruits that was significantly greater than 0.500 ( $z = 35.19$ ,  $P = 0.00001$ ,  $n = 97$ ). Mean search time for oil fruits ( $5.79 \text{ sec} \pm 0.32$  (SE)) was longer ( $t = 2.41$ ,  $df = 744$ ,  $P = 0.016$ ), mean handling time ( $2.47 \text{ sec} \pm 0.07$  (SE)) shorter ( $t = 19.28$ ,  $df = 1868$ ,  $P = 0.000001$ ), and total search and handling time ( $8.25 \text{ sec} \pm 0.33$  (SE)) shorter ( $t = 3.30$ ,  $df = 812$ ,  $P = 0.001$ ) than for confectioner fruits (Table 1).

I documented no difference ( $P > 0.05$ ) in size for confectioner seeds and oil fruits (Table 1) and that partial preference values for oil fruits ( $0.486 \pm 0.008$  (SE)) was not significantly different from 0.500 ( $z = -1.76$ ,  $P = 0.079$ ,  $n = 42$ ). In addition, I found no differences in search ( $t = 1.21$ ,  $df = 1019$ ,  $P = 0.23$ ) and handling times ( $t = 0.71$ ,  $df = 1262$ ,  $P = 0.48$ ) (Table 1). Similarly, no differences ( $t = 0.38$ ,  $df = 31$ ,  $P = 0.71$ ) between high food density dishes in years 2002 to 2003 and 2003 to 2004 and low food density dishes in 2004 to 2005 were documented. High food density dishes had a mean ratio of  $0.067 \pm 0.015$  (SE), and low food density dishes a mean ratio of  $0.051 \pm 0.040$  (SE).

**Table 1.** Mean ( $\pm$  SE) food sizes (g per 100 items) and search and handling times (in sec) for confectioner sunflower fruit (CF), confectioner sunflower seed (CS), and oil sunflower fruit (OF) fed to *Sciurus niger* in Mitchell, South Dakota for 9 months in 2002 to 2003 and 8 months in 2003 to 2004 and 2004 to 2005. S + H Time = Sum of Search Time + Handling Time. Statistically significant differences ( $P < 0.05$ ) are indicated by a common superscripted letter in a column.

Food	Mass	Search time	Handling time	S + H time
CF	13.06 $\pm$ 0.11 <sup>ab</sup> n = 66	4.94 $\pm$ 0.15 <sup>ab</sup> n = 1750	4.55 $\pm$ 0.22 <sup>ab</sup> n = 1713	9.50 $\pm$ 0.18 <sup>ab</sup> n = 1713
CS	5.51 $\pm$ 0.19 <sup>a</sup> n = 12	6.25 $\pm$ 0.22 <sup>a</sup> n = 1269	2.53 $\pm$ 0.60 <sup>a</sup> n = 1259	8.79 $\pm$ 0.23 <sup>a</sup> n = 1259
OF	4.08 $\pm$ 0.03 <sup>b</sup> n = 19	5.79 $\pm$ 0.32 <sup>b</sup> n = 506	2.47 $\pm$ 0.07 <sup>b</sup> n = 506	8.25 $\pm$ 0.33 <sup>b</sup> n = 506

Extractable sodium ion amount for each food did not differ ( $F = 1.07$ ;  $df = 2, 4$ ;  $P = 0.447$ ) between duplicate samples. Mean ( $\pm$  SE) sodium ion concentration ( $\mu\text{g Na/g food}$ ) for confectioner fruits, confectioner seeds, and oil fruits was  $1.53 \pm 1.14$ ,  $0.92 \pm 0.47$  and  $3.33 \pm 1.73$ , respectively. When partial preferences for confectioner fruits paired with seeds and oil fruits were regressed onto initial food mass, no slopes were significantly different from zero ( $P > 0.05$ , Table 2); values of  $r^2$  ranged from 0.001 to 0.22 for 18 regressions.

## DISCUSSION

When offered a choice between confectioner fruits and seeds or between confectioner fruits and oil fruits, the eastern fox squirrel chose confectioner fruits -- the larger item with shorter search time, but longer handling time and longer combined search and handling times. A preliminary attempt to determine if shorter search time was due to food density as it affects distance between food items indicated it was not. When presented choices between confectioner seeds and oil fruits, food items of equivalent size and search and handling times, eastern fox squirrel showed no preference, supporting the hypothesis that eastern fox squirrel food choice is based on food size. Thus, urban individuals of the eastern fox squirrel in my study did not appear to optimally forage.

**Table 2.** Slopes of regression line when average partial preference values ( $PPV_{CF}$ ) of *Sciurus niger* for confectioner sunflower fruits are regressed on initial food density (D). The food types are CF = confectioner fruit, CS = confectioner seed, and OF = oil seed. No slopes were significantly different from zero ( $P > 0.05$ ), which indicated that eastern fox squirrel was a generalist forager.

Year	Variables Regressed	Slope	$r^2$	P	n
2002-03	$PPV_{CF} \times D_{CF}$ (when CS = 10g)	-0.002	0.009	0.662	23
2002-03	$PPV_{CF} \times D_{CF}$ (when CS = 20g)	0.007	0.120	0.166	18
2002-03	$PPV_{CF} \times D_{CF}$ (when CS = 30g)	0.007	0.001	0.884	20
2002-03	$PPV_{CF} \times D_{CS}$ (when CF = 5g)	-0.004	0.220	0.105	15
2002-03	$PPV_{CF} \times D_{CS}$ (when CF = 10g)	0.002	0.052	0.320	22
2002-03	$PPV_{CF} \times D_{CS}$ (when CF = 15g)	-0.003	0.038	0.396	24
2003-04	$PPV_{CF} \times D_{CF}$ (when CS = 10g)	0.001	0.001	0.913	21
2003-04	$PPV_{CF} \times D_{CF}$ (when CS = 20g)	0.004	0.017	0.594	19
2003-04	$PSV_{CF} \times D_{CF}$ (when CS = 30g)	-0.006	0.001	0.893	22
2003-04	$PPV_{CF} \times D_{CS}$ (when CF = 5g)	-13.64	0.30	0.575	16
2003-04	$PPV_{CF} \times D_{CS}$ (when CF = 10g)	-0.003	0.071	0.218	22
2004-05	$PPV_{CF} \times D_{CS}$ (when CF = 15g)	-0.006	0.002	0.839	29
2004-05	$PPV_{CF} \times D_{CF}$ (when OF = 10g)	-0.004	0.034	0.344	28
2004-05	$PPV_{CF} \times D_{CF}$ (when OF = 20g)	-0.003	0.022	0.384	37
2004-05	$PSV_{CF} \times D_{CF}$ (when OF = 30g)	-0.002	0.007	0.650	32
2004-05	$PSV_{CF} \times D_{OF}$ (when CF = 5g)	-0.002	0.025	0.401	30
2004-05	$PPV_{CF} \times D_{OF}$ (when CF = 10g)	-0.001	0.002	0.789	37
2004-05	$PSV_{CF} \times D_{OF}$ (when CF = 15g)	-0.002	0.046	0.281	27

Eastern fox squirrel preference for confectioner fruits over oil fruits might have been due to higher lipid content of confectioner fruits, which contain about 49% lipid (National Sunflower Association) compared to oil fruits, which contain about 42% (National Sunflower Association 2006). However, eastern fox squirrels showed no preference for the higher lipid-containing item when confectioner seeds were paired with oil fruits, which suggested that lipid content was not a proximate factor used by eastern fox squirrel in making food choices.

Confectioner fruits and seeds and oil fruits are locally available for feeding. Oil fruits are the least expensive, specifically sold for feeding birds, and are probably fed upon more often by the eastern fox squirrel than the other two foods. In my study, the eastern fox squirrel never showed a preference for oil fruits; instead it preferred confectioner fruits or had no preference. Therefore, the eastern fox squirrel did not prefer the test food that it would most often encounter in an urban environment.

Although birds forage on sunflower fruits and seeds but were not excluded intentionally from feeding dishes, birds were not observed in VHS tapes and were rarely observed at forage sites prior to and at the time of experiments. Additionally, the experiment was terminated before avian migrants and summer residents returned to the area in the spring. Hence, the effects of birds on GUD's was likely minimal.

Brown and Morgan (1995) found that when sunflower fruits and seeds were exploited by eastern fox squirrel, individuals foraged as generalists by consuming whatever foods they encountered. These observations are supported by Steele and Koprowski (2001), whose list of foods consumed suggested that the eastern fox squirrel was an opportunistic and omnivorous forager.

My results indicated that the eastern fox squirrel might not be maximizing energy gains as predicted by the classical formulation of OFT (Pulliam 1974, Cézilly and Benhamou 1996), which assumes that foragers can assess rate of energy gain for multiple variables (i.e., energy content, search time, and handling time). Instead, the eastern fox squirrel might be able to assess only one variable while foraging. Eastern fox squirrel has been found to maximize food size (present study, Brown and Morgan 1995, Shealer et al. 1999), minimize search time (present study, Stapanian and Smith 1984), minimize handling time (Smith and Briggs 2001), maximize digestibility (Smith and Follmer 1972), or maximize energy content (Havera and Smith 1979). When individuals could assess one of these parameters, their foraging behavior changed (Stapanian and Smith 1984), or they made fewer optimal foraging errors (Schmidt and Brown 1996).

Classical formulation of OFT also might oversimplify foraging decisions. For example, specific nutrient requirements such as for sodium and/or phosphorous might override rate of energy gain (Steele and Koprowski 2001). The eastern fox squirrel must supplement its diet with sodium because this element is nearly absent from foods it consumes. Thus, squirrels often obtain sodium by licking streets and sidewalks (Weeks and Kirkpatrick 1978). However, food choices were not altered by sodium need during my study because surface sodium ion concentration did not differ among food types. The eastern fox squirrel also has been found to base foraging decisions on safety of food location (Brown and Morgan 1995), spatial distribution of forage items (Brown and Morgan 1995), balancing predator risk and food toxin avoidance (Schmidt 2000), or present and future value of a food (Steele and Weigel 1992, Kotler et al. 1999).

While the results of my study appeared to indicate that the urban eastern fox squirrel did not forage optimally, it did not include travel time between food patches. Thus, it remains unclear how travel time influences optimal foraging decisions by the eastern fox squirrel. Nearly daily visits to food sources in my study suggested that the eastern fox squirrel remembered food-rich locations and consumed all foods. Additionally, urban eastern fox squirrel populations were possibly food limited, especially during winter months when food was covered with snow and relatively unavailable for consumption by foraging eastern fox squirrel. During these months the eastern fox squirrel might become more dependent on food placed in bird feeders than at other times during the year. Perhaps its optimal foraging strategy was to minimize travel time to food-rich sites and consume all food types (i.e., as generalist foragers) at the site, but with a bias for larger food items.

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