

# **Effects of food type and patch location on foraging: a field test of optimal foraging predictions**

---

**Kathryn M. Frens**

**Thesis submitted  
in partial fulfillment of the requirements  
for the degree of Master of Science  
(Natural Resources and Environment)  
At the University of Michigan  
April 2010**

**Chair: Dr. Bobbi S. Low**

**Reader: Dr. Phil Myers**

## **Abstract**

Optimal foraging theory predicts that a foraging organism will maximize its fitness by maximizing its net energy intake per unit time, and will usually choose the available food type that yields the most calories for the effort it takes to locate, catch, or consume it. In an environment in which food is distributed in patches across different habitat types, foragers must decide which patch to visit and how long to forage there. These decisions can become complicated when competing foragers or predators are present. In this study, I compared the duration of visits of four species of overwintering passerines between bird feeders containing hulled and unhulled sunflower seeds, and also between feeders set up under forest cover and in an open field. Birds spent more time at feeders containing hulled sunflower seeds, which had a lower handling time, than at feeders containing unhulled seeds. They spent no more time at feeders in the forest than at feeders in the open, but did show a larger marginal preference for hulled seeds in the open habitat.

## Table of Contents

<b>Introduction</b> .....	<b>3</b>
<b>Study Site and Methods</b> .....	<b>7</b>
Study Site .....	7
Experimental Methods.....	7
Statistical Methods.....	8
<b>Results</b> .....	<b>9</b>
Food Type and Average Visit Length.....	9
Cover Type and Average Visit Length.....	10
Cover Type and Marginal Preference for Hulled Seeds.....	11
<b>Discussion</b>	
Food Type and Average Visit Length.....	12
Cover Type and Average Visit Length.....	14
Cover Type and Marginal Preference for Hulled Seeds.....	15
Future Research Directions.....	16
<b>Literature Cited</b> .....	<b>18</b>

## Introduction

Optimal foraging theory has become an important part of behavioral ecology since 1966, when Emlen and MacArthur and Pianka first developed mathematical models for ideal time allocation by a foraging organism. In its simplest form, optimal foraging theory predicts that animals in search of food will seek to optimize energy payoff per effort expended, or the net energy payoff (e.g. Alonso et al 2005, Grundel 1992, Snellen et al 2007). When prey is not evenly distributed across the environment, but instead occurs in patches or clumps, the organism's foraging decisions also have to take into account travel time to each patch, the type of food found in each patch, and the density of that food (Krebs and Cowie 1976, Cowie 1977, Werner and Hall 1974, Krebs et al 2004). Another model allows for optimization under constraints other than simple caloric intake, such as nutrients, gut capacity, or safety (Belovsky 1978, Ritchie 1990). This study will examine the foraging decisions of local, overwintering birds using the first two models by measuring birds' choices between two types of food with different net energy payoffs and birds' choices of patch between two environment types, which differed in predation risk.

In the simplest approach to optimal foraging theory, foraging organisms may be time minimizers or energy maximizers. When an individual requires some caloric minimum, and receives no benefit from extra calories, its fitness will be maximized when it spends as little time as possible gathering the food it needs, so it can spend its remaining time in a reproductively profitable way. Strategies might include preferentially choosing the largest prey (Werner and Hall 1974), the prey with the shortest handling time (Sauter et al 2006), or the prey that is easiest to find (Grundel 1992), if certain other criteria are met. It can then spend the rest of its time hiding from predators, defending a territory, or finding a mate—this is a time minimizing strategy. However, if an organism has a fixed amount of time in which to forage and it benefits from eating as many calories as it can, its fitness will be maximized by taking in as much energy as possible during the time it has to forage. This is an energy maximizing strategy. In both

energy maximizing and time minimizing organisms, the rate of net energy intake during the time the organism is foraging is maximized (Pyke et al 1977).

Net energy gain is a common proxy measurement of fitness in optimal foraging theory, and most authors assume that the fittest individuals are those who maximize their net energy gain, as measured in calories per unit time (e.g. Pyke et al 1977, Cezilly and Benhamou 1996). One of the few studies to measure the effects of optimal foraging on genetic fitness directly, a study of Columbian ground squirrels, found that individuals who optimize their energy intake do indeed have higher fitness than those who do not (Ritchie 1990). Ritchie showed that net energy intake is highly correlated with fitness in some cases, but the relationship between them has not been studied extensively in other species, and may vary across species and environments.

Energy maximization models of foraging assume the forager's knowledge of available food is perfect, but experimental testing has shown that many organisms do indeed forage optimally, at least from a qualitative point of view (e.g. Pyke 1984, Cezilly and Benhamou 1996). The quantitative predictions of the optimal foraging model are often not met (e.g. Nonacs 2001, Alonso et al 1995). Discrepancies can exist for a variety of reasons: the presence of predators, the possibility of danger from the prey itself, or the need to avoid parasites (Barette and Giraldeau 2008, Fleurance et al 2005, Rutten et al 2006).

The basic theory predicts that organisms should always choose the most profitable prey and should selectively ignore less profitable prey when the most profitable prey occurs at or above a certain density. However, two studies of Great Tits (*Parus major*) show that this is not always true. An early study in which small and large mealworm pieces were offered to great tits on a conveyor belt found that the birds did not discriminate between the two prey types when the density of both was low, and ignored the less profitable prey only when the density of the more profitable prey was very high. This

result was expected based on optimal foraging theory. Contrary to the predictions, however, the change between the “always attack” (nondiscriminatory) strategy and the “selective” (large prey preferred) strategy did not occur in one step. Instead, the birds made a gradual shift from one strategy to the other, suggesting that there may be a small energetic cost to gathering information about the availability and profitability of each food type (Krebs et al 1977).

In another study of Great Tits, again using pieces of mealworm presented on a conveyor belt, the birds nearly always attacked the most profitable prey, but even when the density of the most profitable prey was highest, they never completely excluded less profitable prey from their diet. These studies illustrate a real difficulty birds may have in making perfectly optimal foraging decisions: without perfect knowledge, a predator’s behavior cannot be perfectly optimal. While the most profitable prey should always be eaten, these birds’ behavior also indicates that they invest time in information-gathering, sometimes at the expense of maximizing their immediate energy intake (Berec et al 2003).

In patch choice models, predation risk is one of the most important factors, apart from food richness, that influences patch choice. While the vulnerability to predators varies across species and habitat types, in general, organisms appear to make trade-offs between feeding efficiency and safety. Black-capped chickadees foraging in open habitats often carry their prey to a safe place to eat it, and then return to the patch, lowering their energy intake per time, but spending less time exposed to predators (Lima 1985). Shochat (2004) showed that desert passerines leave food patches in an open habitat at a higher giving-up density (that is, the density of food in the patch at the time the bird leaves) than the same species of birds foraging in identical patches in bushy habitat (Shochat et al 2004). Since predation risk is higher in the open, predation appears to be the determining factor in when a bird decides to leave a given patch. In addition, the threat of predation forces organisms to spend more time on vigilance, and thus less time on food gathering (Altendorf et al 2001). Nonetheless, when

competition for food is stiff at the safer patches, some individuals will be forced to risk predation in order to get food (Koivula et al 1994). These individuals have a strong incentive to minimize their time spent gathering food, and organisms feeding in areas with high predation risk have been shown to be more discriminating in their food choice than organisms feeding in safety (Brown and Kotler 2004).

Here I report on the feeding behavior of several species of wild passerines foraging at experimentally established feeders in a protected area in southeastern Michigan. In this study, I tested three hypotheses relating to differences in food type choice and foraging location: first, that birds will spend more time foraging at a feeder that contains food with very low handling time than at a feeder containing food with a high handling time; second, that birds will spend more time foraging at feeders in a forest habitat than at feeders in an open field, and third, that the birds will discriminate more against the food with the highest handling time in the open habitat, where the threat of predation is high.

## **Study site and methods**

### *Study site*

The University of Michigan's Nichols Arboretum is a multi-habitat reserve near downtown Ann Arbor, Michigan. It contains patches of prairie, oak savannah, and oak-hickory habitats, as well as cultivated woody plants, and is home to a variety of species, including many native and a few introduced species of birds. The local birds are primarily generalist seed-eaters; there is also a resident pair of red-tailed hawks that live and over-winter in the Arboretum, and were occasionally seen from the study site. Other predators, including Cooper's hawks, falcons, and kestrels, are commonly seen in the area.

### *Experimental methods*

The experiment was done using two pairs of tube feeders, which had perches on the sides and a small platform at the bottom. I hung one pair of feeders from a pole under heavy cover in a patch of

maple-dominated forest, and one pair in a nearby open field, about 30 meters from the nearest cover. One feeder in each pair contained black oiled sunflower seeds, the other hulled sunflower seeds. Feeders were filled for two weeks before I began to collect data, to allow birds to acclimate to the new food resource. I observed the feeders for several months, from November 2008 to March 2009, at different times of day. I recorded each visit: the species of bird, the feeder and cover type visited, and the length of visit in seconds. I recorded nearly 1200 visits in all, and was able to record length of visit for 850 of those visits. Four species of birds (black-capped chickadee, American goldfinch, white-breasted nuthatch, and tufted titmouse) were recorded making 30 visits or more; these species were included in this analysis.

Beak depth has been shown to affect food choice in some seed-eating birds (Grant 1981). To obtain measurements of bill depth for the species studied, I measured 20 specimens (10 of each sex) of each species using a pair of digital calipers. The specimens were part of the University of Michigan Museum's Bird Division collection. In addition, for some museum specimens, exposed culmen measurements were recorded by the collector. For white-breasted nuthatches, no culmen measurements were available from the museum: I took this average measurement from the *Birds of North America* database.

### *Statistical methods*

The data on length of visit by seed type were analyzed in SPSS using one-way ANOVA, with time spent per visit designated as the dependent variable and food type as a non-continuous independent variable. The correlation between species and length of visit by seed type was calculated using a univariate model, with time as the dependent variable and species and food type designated as independent variables. To test food type preferences within each species, I filtered the data so that only



one species was tested at a time, and ran one-way ANOVAs with time spent per visit as the dependent variable and food type as the independent variable.

The correlation between cover and visit length was also analyzed in SPSS using one-way ANOVAs with time spent per visit as the dependent variable and cover type as the independent variable. The effect of cover length of visit by birds of each individual species was tested by filtering the data to test one species at a time.

To test for interactions between variables I used a univariate model, with time spent per visit as the dependent variable and food type, cover type, and species designated as independent variables. Estimated marginal means were calculated for each pair of independent variables.

## Results

### *1. Food type and average visit length*

All species studied, except black-capped chickadees, spent more time per visit on one feeder or the other. Both white-breasted nuthatches and tufted titmice spent much more time foraging at the hulled-seed feeders than at the natural-seed feeders ( $p < 0.001$ ). Visits by American goldfinches to the hulled seed feeders were marginally longer ( $p = 0.073$ ) than their visits to the natural seed feeders (Figure 1). For each species, variance in average visit length was higher for the hulled-seed feeders than for the oiled-seed feeders. High variance also corresponded with longer visit lengths. Variance was highest in goldfinches, which also spent the longest average time foraging per visit on both feeder types. Titmice showed a high variance in visit length on the hulled-seed feeders, but a lower variance in visit length on the natural-seed feeders. Chickadees and nuthatches each showed relatively low variance in visit length on both types of feeders (Table 1).

### *Frequency of visits*

Both chickadees and titmice visited the feeders of each food type approximately the same number of times. In contrast, goldfinches visited the hulled-seed feeders almost twice as often as the natural-seed feeders, and nuthatches visited natural-seed feeders marginally more often than the hulled-seed feeders (Table 2). Interestingly, nuthatches visited the unhulled-seed feeders more often (by a marginally significant degree:  $p=0.070$ ), but spent significantly more time foraging at the hulled-seed feeders ( $p<0.001$ ).

### *2. Cover type and average visit length*

The white-breasted nuthatch was the only species to show a significant preference for a particular cover type, spending more time per visit foraging in the open than under forest cover (Table 2). Titmice spent marginally more time per visit foraging at the feeders in the open than under forest cover. The other two species, chickadees and goldfinches, spent no more time foraging in the open than in heavy cover (Table 3).

### *3. Cover type and marginal preference for hulled seeds*

The third hypothesis, that the birds would show a more significant preference for hulled seeds over unhulled seeds in the open than in the forest, was supported for two of the four species: nuthatches and titmice. Both of these species showed a significantly larger difference in visit length to the hulled seed feeders over the natural seed feeders in the open habitat than they did under heavy cover. The other two species did not show a larger preference for hulled seeds in either habitat (Figure 2).

## **Discussion**

### *1. Food type and average visit length*

Three species of local birds spent more time per visit foraging at bird feeders containing hulled sunflower seeds than they did at feeders containing unhulled sunflower seeds, showing a clear preference for food with a lower handling time. This trend is consistent with previous studies (eg Pyke et al 1977, Sauter et al 2006). One species (Black-Capped Chickadees) showed no preference for either food type. Nuthatches visited the unhulled-seed feeders much more often than the hulled-seed feeders, and Goldfinches visited the hulled-seed feeders much more often than the unhulled-seed feeders. The other two species visited each feeder type approximately the same number of times. While some of this discrepancy may result from the relative novelty of the hulled seeds, the two-week period of acclimation at the beginning of the study was designed to familiarize the birds with both seed types.

While the birds spent significantly longer amounts of time foraging for hulled sunflower seeds, they never entirely excluded the unhulled seeds from their diet. This behavior is likely sub-optimal in terms of net caloric intake, because unhulled seeds have a higher handling time than hulled seeds, and it suggests that factors other than caloric intake may play a role in birds' food choice. For example, birds have been shown to invest time in "sampling" from different food sources to determine the type and density of available food (Krebs et al 1978). While each individual at first may spend some time foraging sub-optimally, this behavior may ultimately be beneficial, allowing individuals to ascertain where the most profitable food is located.

Nutrients may also play a key role in food choice. Several species will choose less energetically-optimal food if that food contains some limiting nutrient that a more energetically-optimal food does not (Belovsky 1978, Abrams and Schmitz 1999). However, it is unlikely in this experiment that the two types of sunflower seeds differed significantly in nutrient content.

I was unable to address the effects of competition on food choice in wintering birds, but competition may prove to be a profitable area of further research. Previous studies on flock-foraging

birds have shown that higher-status individuals are able to exclude lower-status individuals from the most profitable or safest feeding sites (Koivula et al 1994, Schneider 1984, Krams et al 2001). I observed fights many times when multiple birds attempted to forage at the same feeder, and it may have been more profitable for some less-competitive individuals to forage at the feeder containing unhulled seeds, rather than fighting for a place at the more crowded hulled-seed feeder.

#### *Within- species differences*

Although I predicted that all four bird species studied would spend more time per visit foraging at the hulled-seed feeders than at the unhulled-seed feeders, there were differences in feeding behavior across species. Black-capped chickadees spent no more time per visit foraging at hulled-seed feeders than at unhulled-seed feeders, and American goldfinches spent only marginally more time per visit foraging for hulled seeds. Tufted titmice and white-breasted nuthatches, as predicted, spent significantly more time per visit foraging at hulled-seed feeders compared to unhulled-seed feeders. Differences in behavior between species may be attributable to differences in life history or foraging behaviors; for example, birds such as chickadees that eat seeds from a wide variety of both prairie and forest plants may be more likely to 'sample' from different sites and to eat any food they can find than nuthatches, which are more reliant on insects (although they are still generalist feeders). In the case of goldfinches, the variance in average visit length was high, potentially obscuring the effects of food choice on average visit length.

All the species studied are generalists, feeding on a variety of seeds and insects (Sibley 2003), and all are commonly seen at bird feeders. However, their methods of obtaining natural foods differ. For example, chickadees often catch insects out of the air, while nuthatches typically pick them out of cracks in tree bark. These differences in habit, and more importantly the beaks that are adapted to each habit, may be at the root of differences in time allocation to seeds of different types. Beak morphology can be

important in food choice (e.g. Grant 1981): individuals with beaks of smaller depth generally specialize on smaller foods. I measured both beak depth and length in order to get an approximate measure of bill strength. Table 4 shows that beak morphology is not correlated with food choice in this case: chickadees and titmice have beaks of approximately the same depth-to-width ratio, and cracking the hulls of sunflower seeds should be equally difficult for both of them.

## *2. Cover type and average visit length*

White-Breasted Nuthatches spent more time foraging in the open cover than under heavy forest cover; the other three species showed no preference for cover type. Previous studies have shown a strong preference for forest cover over open areas, presumably due to a reduced risk of predation in cover. The arboretum in which I carried out this experiment is home to a pair of red-tailed hawks, and is often visited by other birds of prey, any of which could pose a threat to small songbirds. Organisms at risk of predation leave a patch earlier than birds foraging in a safer area (Shochat 2004, Lee 2005, Brown and Kotler 2004), and Nuthatches are primarily forest-dwellers. However, patch models of optimal foraging could explain this result. The length of time for which it is profitable for an individual to stay in a certain patch has been the subject of much study. In general, the further an individual must travel to get to a particular patch, the longer it must stay in order to make the trip energetically profitable (Cowie 1977, Nonacs 2001, Alonso et al 1995). Since birds had to fly farther from the nearest tree to reach the feeders in the open, as opposed to the feeders in forested cover, they had to obtain enough food to balance the energetic cost of travel.

Even with this in mind, it is difficult to explain why the birds seemed willing to expose themselves to the potential risk of predation. Several explanations are plausible. First, birds could be using increased vigilance when foraging in the open (as in Baker et al 2009). This would simultaneously increase the amount of time spent at the feeder (because the bird would have to spend less time

feeding and more time watching for predators) and decrease the bird's chance of being caught by a predator. Second, the birds, instead of being wary of the open cover due to the threat of predation from the air, could be acting to manage their risk from ground-based predators, such as cats, which are common in nearby neighborhoods (e.g. Lee et al 2005). Third, the risk of predation by birds of prey in the open could have been overestimated. The resident red-tailed hawks of the arboretum eat primarily squirrels (personal observation) and visiting birds of prey hunt mostly along the river rather than in the woods or fields nearby. Small birds of prey, such as Cooper's hawks, may also forage successfully under forest cover, and birds may be safer from these predators in the open.

### *3. Cover type and marginal preference for hulled seeds*

When white-breasted nuthatches and tufted titmice foraged in the open, the difference in the mean length of visit between hulled and unhulled seed feeders was larger than when they foraged in heavy cover. That is, in the open, these two species spent significantly more time foraging for hulled seeds than unhulled seeds, while in forested cover, the difference in average visit length between feeders containing hulled and unhulled seeds was much smaller. This is consistent with previous experiments (Brown and Kotler 2004), and also with the hypothesis that the risk of predation in the open would make it more important for birds to maximize their net energy intake. Based on the results discussed above, these two species of birds may be using a "time-minimizing" strategy while foraging in the open. Making one longer visit to the most profitable feeder could actually minimize the total amount of time the bird spends exposed to predators (aerial or terrestrial) while simultaneously fulfilling its energy needs (Lima 1985). However, black-capped chickadees and American goldfinches did not show a difference in marginal preference for one seed type between the two types of cover. The data on cover type preference suggests that these two species may not perceive a difference in predation risk or the tradeoff between travel time and caloric payoff in a more distant patch. Both species often are seen

foraging in prairie sites close to the study area, and may be better adapted to both open-area and forested-area foraging sites than nuthatches and titmice, which are less often seen foraging in the open.

*Future research directions*

The theory of optimal foraging has stood up to repeated tests, but there is much that is still unknown about specific foraging decisions made by organisms in the field. The effects of competition on food choice and patch choice could be a profitable avenue of research in the future. This study was not able to quantify the effects of competition, but it is likely that inter- or intra-specific interactions play a role in an individual's foraging decisions, and thus in determining an individual's fitness. In addition, although birds' preference for forest cover over more open cover has been well-documented, the reasons for this are unclear. Predation risk and patch choice could both be important, but, as different locations carry different risks for foraging birds, further research should be carried out on the relationship between cover type and choice of foraging location.

### Literature Cited

1. Abrams, Peter, and Schmitz, Oswald. 1999. The effect of risk of mortality on the foraging behavior of animals faced with time and digestive capacity constraints. *Evolutionary Ecology Research* 1: 3 285-301.
2. Alonso, JC, Alonso, JA, and Bautista LM. 1995. Patch use in cranes: A field-test of optimal foraging predictions. *Animal Behavior* 49:5 1367-1379
3. Altendorf, Kelly, Laundre, John, and Lopez-Gonzales, Carlos. 2001. Assessing effects of predation risk on foraging behavior of mule deer. *Journal of Mammology* 82 (2) 430-439.
4. Baker, DJ, Stillman, RA, and Bullock, JM. 2009. The effect of habitat complexity on the functional response of a seed-eating passerine. *Ibis* 151: 3 547-558.
5. Barette, S, and Giraldeau, L.A. 2008. Evidence against maximization of gross rate of seed delivery to the burrow in food-hoarding eastern chipmunks, *Tamias striatus*. *Animal Behavior* 75:2 655-661
6. Belovsky, GE. 1978. Diet optimization in a generalist herbivore: the moose. *Theoretical Population Biology* 14:1 105-134.
7. Berec, L, Krivan, V, and Berec, M. 2003. Are great tits (*Parus major*) really optimal foragers? *Canadian Journal of Zoology* 81:5 780-788
8. Brown, Joel S, and Kotler, Burt P. 2004. Hazardous duty pay and the foraging cost of predation. *Ecology Letters* 7(10) 999-1014.
9. Cezilly, F, and Benhamou, S. 1996. Optimal foraging strategies: a review. *Revue d'Ecologie: la terre et la vie* 51:1 43-86



10. Cowie RJ. 1977. Optimal foraging in the Great Tit (*Parus major*). *Nature* 268:5616 137-139
11. Emlen, JM. 1966. The role of time and energy in food preference. *The American Naturalist* 100:916 611-617.
12. Fleurance, G, Duncan, P, and Fritz, H. 2005. Importance of nutritional and anti-parasite strategies in the foraging decisions of horses: an experimental test. *Oikos* 110:3 602-612
13. Grant, PR. 1981. The feeding of Darwin's finches on *Tribulus cistoides* (L.) seeds. *Animal Behavior* 29:3 785-793.
14. Grubb, Jr., T. C. and V. V. Pravosudov. 2008. White-breasted Nuthatch (*Sitta carolinensis*), *The Birds of North America Online* (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online.
15. Grundel, R. 1992. How the mountain chickadee procures more food in less time for its nestlings. *Behavioral Ecology and Sociobiology* 31:4 291-300
16. Koivula, K, Lahti, K, Rytkonen, S, and Orell, M. 1994. Do subordinates expose themselves to predation—field experiments on feeding site selection by willow tits. *Journal of Avian Biology* 25:3 178-183.
17. Krams, IA, Krams, T, and Cernihovics, J. 2001. Selection of foraging sites in mixed Willow and Crested Tit flocks: rank-dependent survival strategies. *Ornis Fennica* 78:1 1-11
18. Krebs, JR, and Cowie, RJ. 1976. Foraging Strategies in Birds. *Ardea* 64:4 98-116
19. Krebs, JR, Erichsen, JT, Webber, M, and Charnov, EL. 1977. Optimal prey selection in the Great Tit *Parus-Major*. *Animal Behavior* 25:1 30-38
20. Krebs, JR, Kacelnik, A, and Taylor, P. 1978. Test of optimal sampling by great tits. *Nature* 275: 27-31
21. Lima, SL. 1985. Maximizing feeding efficiency and minimizing time exposed to predators—a trade-off in the black-capped chickadee. *Oecologia* 66:1 60-67
22. Lee, YF, Kuo, YM, and Bollinger, EK. 2005. Effects of feeding height and distance from protective cover on foraging strategies in birds. *Canadian Journal of Zoology* 83:6 880-890.
23. MacArthur, R, and Pianka, E. 1966. On optimal use of a patchy environment. *The American Naturalist* 100: 603-609.
24. Nonacs, P. 2001. State dependent behavior and the marginal value theorem. *Behavioral Ecology* 12: 71-83
25. Pyke, GH. 1984. Optimal foraging theory: a critical review. *Annual Review of Ecology and Systematics* 15: 523-575

26. Pyke, GH, Pulliam, HR, and Charnov, EL. 1977. Optimal Foraging: A selective review of theory and tests. *The Quarterly Review of Biology* 52:2 137-154
27. Ritchie, ME. 1990. Optimal foraging and fitness in Columbian ground squirrels. *Oecologia* 81:1 56-67.
28. Rutten, AL, Oosterbeek, K, Ens, BJ. 2006. Optimal foraging on perilous prey: risk of bill damage reduces optimal prey size in oystercatchers. *Behavioral Ecology* 17:2 297-302.
29. Sauter, A, Bowman, R, Schoech, SJ, and Passinelli, G. 2006. Does optimal foraging theory explain why suburban Florida scrub-jays (*Aphelocoma coerulescens*) feed their young human-provided food? *Behavioral Ecology and Sociobiology* 60:4 465-474
30. Schneider, KJ. 1984. Dominance, predation, and optimal foraging in white-throated sparrow flocks. *Ecology* 65:6 1820-1827
31. Shochat, E, Lerman, S, Katti, M, and Lewis, D. 2004. Linking optimal foraging behavior to bird community structure in an urban-desert landscape: Field experiments with artificial food patches. *American Naturalist* 164:2 232-243
32. Sibley, David Allen. 2003. *The Sibley Field Guide to Birds of Eastern North America*. Knopf. 296, 299, 300, 409
33. Snellen, CL, Hodum, PJ, and Fernandez-Juricic, E. 2007. Assessing western gull predation on purple sea urchins in the rocky intertidal using optimal foraging theory. *Canadian Journal of Zoology* 85:2 221-231.
34. Werner, EE, and Hall, DJ. 1974. Optimal foraging and size selection of prey by bluegill sunfish (*Lepomis macrochirus*). *Ecology* 55:5 1042-1052