Behav Ecol Sociobiol (1982) 10:85–89

Behavioral Ecology and Sociobiology

Nest Defense and Central Place Foraging: A Model and Experiment

Steven Martindale*

Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721, USA

Received April 22, 1981 / Accepted December 8, 1981

Summary. A graphical model presented here indicates that a nest-defending forager should stay closer to its nest, forage for shorter times per patch, and deliver smaller loads than predicated for delivery rate maximization. The effect is more pronounced farther from the nest, so that if nest defense is especially important, the predator should leave far patches sooner than near ones, and deliver smaller loads from farther away. Moreover, if the attack rate at the nest is increased, the defending forager should move closer and deliver smaller prey.

Experimental attacks with stuffed specimens at Gila woodpecker (*Melanerpes uropygialis*) nests produced the predicted changes in the foraging behavior of males, but not of females.

Mated pairs may work as a team to pursue simultaneously two conflicting goals – food delivery and nest protection – both of which affect the survivorship of the young. Sexual dimorphism in monogamous species may result in part from specialization in these roles.

Introduction

A parent or helper provisioning nestlings must travel to a foraging patch, search for and accumulate food, then return to the nest to deliver the load. Assuming such an animal's goal to be one of maximizing the delivery rate of food to the young, theorists have recently developed predictions on the use of time, space, and resources (see Andersson 1978; Orians and Pearson 1979; Schoener 1979). Martindale (1980) presented data indicating that Gila woodpeckers (*Melanerpes uropygialis*) foraging during the breeding season did satisfy the major predictions of the delivery rate maximization model. When farther from the nest, these birds selected saguaro cacti (*Carnegiea gigantea*) with more fruits, increased their foraging effort, and delivered larger loads. In the course of the initial study, however, it became clear that at least two important aspects of the system were being ignored, and here I consider these complications.

First, while the parents are away foraging, nestlings are vulnerable to attacks by intruders or predators. On several occasions, I witnessed foreign Gila woodpeckers apparently trying to usurp nest sites, and once, a common flicker (*Colaptes auratus chrysoides*) actually evicted a pair of woodpeckers from their nest cavity. Hence, the cost of leaving the nest unguarded is potentially great: the young could well be hurt or lost altogether. It is thus not surprising that the Gila woodpeckers spent considerable time in the vicinity of the nest simply guarding it, rather than foraging and delivering food to the young (Martindale 1980), but such behavior is beyond the scope of the delivery rate maximization model.

In this paper, I present a graphical model which includes nest defense, and show that this can lead to different predictions about foraging behavior than delivery rate maximization alone. The predicted effects of increasing the number of attacks at the nest are tested directly with data from a field experiment using mounted woodpecker specimens to mimic attacks. In the Discussion, I introduce the second complicating factor, cooperation among mates. The above models are couched in terms of individuals feeding and guarding the young. But mates need not behave independently; they can work as a team to pursue multiple goals.

The Model

Orians and Pearson (1979) developed a graphical model to show how behavior should change as a

---

* Present address: Department of Biological Sciences, State University of New York at Albany, 1400 Washington Avenue, Albany, New York 12222, USA

forager travels farther from the nest, in order to maximize the delivery rate of food. In this section, I briefly recapitulate their approach, then incorporate their results into a different model which includes nest defense.

Consider two foraging patches which are identical except for their distance from the nest. For the sake of simplicity, assume that the forager is a multiple-prey loader, i.e., that more than one prey item is captured in a patch before a load is delivered to the nest. In each patch, prey can initially be seized very quickly, but the capture rate decreases with time since prey become scarce and harder to locate, and because prey already held make capture more difficult. The rate of food delivery depends not only on the capture rate within a patch, but also on the round trip travel time from the patch to the nest. When travel time is added to foraging time, the maximum possible delivery rate is greater for the near patch than the far patch. This maximum occurs at shorter foraging times and smaller load sizes for the near patch than the far patch. Orians and Pearson (1979) further showed that the same qualitative results hold for single prey loaders which deliver just one prey item per trip (as Gila woodpeckers often do).

For central place foragers to increase their fitness, they must produce healthy young in the nest, and it is reasonable to assume that the survivorship of the young increases with the delivery rate of food. The optimal foraging results can thus be converted to fitness units and represented as the benefit curves shown in Fig. 1. T_N and T_F are the round trip travel times to the near and far patches, respectively. The benefits B_N and B_F are proportional to the delivery rates resulting from foraging in each patch. In the absence of risk to the nest, the optimal foraging times, t_N and t_F are those which maximize the benefits, that is, the times at which the slopes of the benefit curves are zero. Even though the patches are identical except for their distance from the nest, the maximum possible benefit for the near patch is greater than for the far patch, since as indicated above, the maximum delivery rate is greater for the near patch. The optimal forager should stay in the far patch longer, so $(t_N - T_N) < (t_F - T_F)$.

Now consider the decrease in production of the young caused by attacks at the nest while the forager is away. This cost function depends on the probability of an attack occurring times the probability of the forager repelling the invader, given that an attack has occurred. Any attack occurring while the forager is within a certain distance of the nest will be detected and probably repelled. At great distance, though, attacks cannot even be detected. Hence the cost function must approach an asymptote equal to the lost in fitness of sacrificing the entire nest and young, and I assume it to be sigmoidal. The maximum possible cost from a single foraging bout (loss of the young) is much greater than the maximum possible benefit (delivery of one load of food), but the probability of an attack occurring during a single foraging trip is low. Also, most foraging probably takes place within the range of high detectability of attacks on the nest. Hence, the foraging patches of concern are assumed to be closer to the nest than the inflection point of a sigmoidal cost function, and I treat the function as monotone increasing with positive second derivative. The cost function associated with low attack rates at the nest is represented by C_L in the figure.

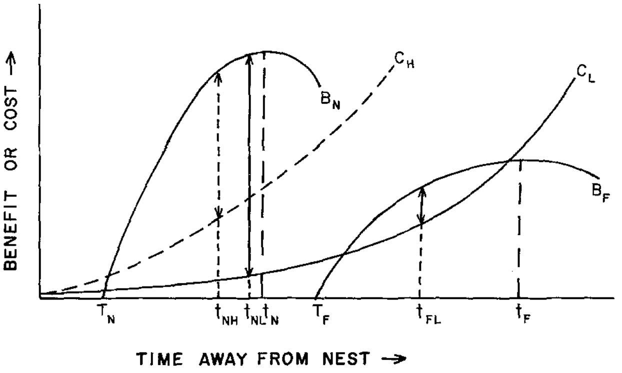

Fig. 1. The hypothetical effects of nest defense on central place foragers. N and F index two food patches which are identical except for their distance from the nest, with travel times T_N and T_F. The benefit curves, B_N and B_F, are proportional to the rate at which food can be delivered to the nest; $(t_N - T_N)$ and $(t_F - T_F)$ are the foraging times which maximize delivery rate. Cost functions are proportional to the probability that a successful attack on the nest occurs; C_L for a low attack rate and C_H for a high attack rate. $(t_{NL} - T_N)$ and $(t_{FL} - T_F)$ are the foraging times which maximize the net benefit (i.e., survivorship of the young) at the low attack rate. Nest defense results in leaving all patches sooner than expected for delivery rate maximization, and affects the use of far patches more than near ones. $(t_{NH} - T_N)$ is the optimal time in the near patch at the high attack rate, when the far patch no longer confers a positive net benefit. As attack rate is increased, the defending forager should move closer to the nest, leave patches sooner, and hence deliver smaller loads

Natural selection should produce animals which behave so as to maximize their net fitness, not just their delivery rate. I assume that in terms of fitness units, the benefits from delivering food and costs from leaving the nest unguarded are additive, so the forager's objective is to maximize the quantity (Benefit-Cost). The optimal foraging times, t_{NL} and t_{FL}, now occur at the points at which the first derivatives of the benefit and cost functions are equal, as indicated by the arrows in Fig. 1. Since the cost function has a positive slope throughout, these times must occur before the slopes of the benefit curves drop to zero, so that $t_{NL} < t_N$ and $t_{FL} < t_F$. That is, the nest defending animal should always return to the nest sooner than predicted by the delivery rate maximization model. The slope of the cost function is greater for the far patch, so the effect is more pronounced there: $(t_N - t_{NL}) < (t_F - t_{FL})$. The magnitude of this effect depends on the actual slopes of the benefit and cost functions, but these slopes can be such that the delivery rate maximization predictions are reversed. As Fig. 1 shows, $(t_{FL} - T_F)$ can be less than $(t_{NL} - T_N)$, so that the nest defending forager should stay in the near patch longer and hence deliver larger loads than when foraging in the far patch.

The decisions on how far to forage from the nest and how long to stay in a patch depend on the attack rate. Increasing the attack rate corresponds to increasing the slope of the cost function; C_H in the figure is the cost function associated with a high attack rate. Note that the far patch confers a net benefit to the forager only at low attack rates. That is, as nest defense becomes more important, the forager should stop using patches far from the nest, and move in closer. Also, $t_{NH} < t_{NL}$, so at the high attack rate, the forager should leave the acceptable patch sooner, and hence deliver smaller loads than at low attack rates. These results are particularly robust, since the cost function need only be weakly monotone increasing for them to apply.

In summary, efficient defense of the nest tends to reverse the relationships between distance, foraging time, and load size predicted for delivery rate maximizers. An increase in the attack rate should result in closer foraging distances and smaller load sizes. The results of the nest defense model are intuitively plausible, as are those of the delivery rate maximization model. In essence, if delivery time is more important, the animal should deliver larger loads from farther away to pay for the cost of traveling. But if defense of the young is more important, the animal should return to guard the nest as soon as possible.

Materials and Methods

To evaluate the relevance of the nest defense model, I used stuffed specimens to increase the attack rate experimentally at Gila woodpecker nests. I performed the experiment a total of 12 times at 9 different nests in the 1980 breeding season. The study area was in Saguaro National Monument (Tucson Mountain Unit), 25 km west of Tucson, Arizona (see Martindale 1980 for details). The desert vegetation is quite open, so that I or an assistant could sit on a rock or hill about 100 m from a nest and observe Gila woodpeckers throughout their foraging bouts. A second observer sat about 10 m from the nest to monitor the deliveries.

The experimental design was intended to mimic an intrusion by a foreign woodpecker, since I observed such encounters on several occasions. I mounted a stuffed specimen of an adult Gila woodpecker on a metal pole, 2 cm in diameter and adjustable in length, then positioned this decoy on the side of the nest cactus within 1 m of the entrance hole. Real intruders rarely stayed in the nest area for more than a few minutes, since the resident woodpeckers would vigorously attack and chase them to distances of 300 m or more from the nest. Hence, I removed the decoy about 5 min after the residents discovered it. In each experiment, I presented both male and female skins in random order, waiting half an hour between trials.

We observed the resident woodpeckers' foraging movements and monitored nest delivers for at least one hour before and one hour after the first trial. During this time, one observer tracked the movements of the birds, while the other independently monitored the deliveries. Gila woodpeckers carry the prey items back to the nest in their bills, then land on the side of the nest saguaro for several seconds before poking their heads into the nest cavities to feed the young. The observer sitting near the nest cactus could usually identify the load at least as consisting of an insect larva, insect adult, or saguaro pollen or fruit, and estimate the size of the load as small (less than 1/4 of a full bill-load), medium (1/4 to 3/4 of a bill), or large (more than 3/4 of a full bill-load).

Results

The responses of residents to the stuffed Gila woodpecker specimens were quite variable, and depended on the sex of the decoy – only decoys of the same sex were attacked. In 10 out of the 12 cases, males vigorously pecked at the male decoys (in some cases hard enough to known down the entire pole assembly), but they never pecked female decoys. Female residents often just vocalized to alert the males. In 4 trials, the females vigorously pecked the female decoy, but they never attacked male decoys. After the decoys were removed, males spent much of the next hour guarding the nest, while females continued foraging. In 11 of the 12 trials, males decreased their rate of delivery to the nest in the hour after the attacks (compared to the hour before the experiment), while in 9 of the 12 trials, the females increased their delivery rate (male vs female rate changes: $\chi^2 = 11.0$, $df = 1$, $P < 0.001$).

Each trial produced only a small number of observations on the foraging distances, sizes and types of food delivered by each sex in the hour after the experiment. Hence, I have combined the data from all 12 trials and for both sexes of decoys. In the tables, the data are presented as proportions of the deliveries observed, but the corresponding contingency tests are based, of course, on the actual counts in each cell. Sample sizes vary from table to table because of incomplete observations. For a given delivery, for example, the observer at the nest may have been unable to see the load well enough to categorize it, even though the other person did observe the delivery distance.

Table 1 shows that the males foraged closer to the nest after the attacks, as predicted by the nest defense hypothesis. No statistically significant change

Table 1. Delivery distances before and after experimental nest attacks. Entries are proportion of deliveries from each distance. Males: $\chi^2=8.96$, $df=2$, $P<0.025$. Females: $\chi^2=2.15$, n.s.

	Distance from nest (m)			Sample size
	0–99	100–199	≧200	
Males				
Before	0.54	0.27	0.19	122
After	0.74	0.15	0.11	104
Females				
Before	0.56	0.30	0.14	57
After	0.67	0.20	0.14	87

Table 2. Sizes of insect loads delivered to the nests before and after experimental attacks. Entries are proportions of deliveries of each size category. Males: $\chi^2=25.6$, $df=2$, $P<0.001$. Females: $\chi^2=3.08$, n.s.

	Size of load			Sample size
	Small	Medium	Large	
Males				
Before	0.15	0.68	0.16	104
After	0.48	0.45	0.07	98
Females				
Before	0.15	0.62	0.24	55
After	0.24	0.48	0.28	86

Table 3. Type of food delivered to the nest before and after experimental attacks. Entries are proportion of deliveries of each type. Males: $\chi^2=7.29$, $df=2$, $P<0.05$. Females: $\chi^2=2.1$, n.s.

	Type of delivery			Sample size
	Insect adult	Insect larva	Fruit	
Males				
Before	0.23	0.43	0.33	129
After	0.18	0.32	0.50	137
Females				
Before	0.37	0.31	0.32	72
After	0.30	0.40	0.30	121

occurred in the females' foraging distances. Males delivered smaller loads after the attacks, again as predicted, but females did not change (Table 2). Further, males changed the composition of deliveries to include more saguaro pollen or fruit, as Table 3 shows, but females did not. The blooms occur on the tops of these cacti, so that one advantage of harvesting them is that the bird can maintain surveillance of the surrounding area. Insect prey, on the other hand, require greater search time, during which the bird cannot watch the nest.

When unperturbed by experimental attacks to the nest, both male and female woodpeckers deliver larger items from greater delivery distances, and saguaro pollen and fruit mostly from close to the nest (Martindale 1980). Hence, the changes in size and diet following the experimental attacks may have been effects simply of the males' closer foraging distances, rather than added results of defending the nest. But comparison of load sizes blocked for the same distances shows that the experiment did have a significant added effect on insect prey size (for deliveries within 100 m, unperturbed vs. experimental insect sizes: $\chi^2=9.2$, $df=2$, $P<0.01$). After the attacks, males did deliver smaller items than before, even from the same distances. Load composition, however, was not significantly different from the unperturbed diet delivered from the same distances ($\chi^2=0.84$, $df=2$, n.s.).

Discussion

Following the principle of parsimony, one should try to explain the behavior of animals in nature with as few variables as possible. Recently, central place foraging theorists (Orians and Pearson 1979; Schoener 1979; Andersson 1978) have done so in the extreme, and considered only one dimension, food, to be important in determining movement patterns. In his model, Rosenzweig (1974) did include the risk of predation to the forager, but he was concerned with the proportion of time spent away from a protected nest rather than the effects of distance on foraging patterns. Covich (1976) also considered the risk of predation to the forager, but in his model, total rewards were assumed a function of distance, so that no predictions could be made about foraging time per bout or delivery load size. In the theory section above I showed that guarding the nest can result in smaller load sizes, shorter foraging times, and closer distances to the nest than those which maximize the delivery rate of food. After the experimental attacks, male Gila woodpeckers decreased their foraging rates and distances, and delivered smaller prey as predicted by the nest defense model. Hence, at least one other dimension in addition to food – defense of the nest – appears necessary for a more realistic model of foraging behavior during the breeding season.

Because the two objectives require different optimal behavior sets, an individual cannot maximize both nest defense and delivery rate. Caraco (1979) and McCleery (1978) discussed the notion of an indifference set for individuals faced with conflicting demands (see also Keeney and Raiffa 1976). An indifference set consists of all combinations of defense effort and foraging effort which result in the same fitness for the individual. A forager should pursue the set of behaviors which gives the highest possible fitness. For monogamous species in which both parents raise the young, the situation is complicated by the fact that individuals need not forage independently. Instead, mates can work as a team to pursue two objectives simultaneously. If both foragers are the true parents, or at least closely related helpers, their fitness is reflected in part by the survivorship of the young, and one must consider the joint effects of both foragers on this survivorship. That is, the optimal behavior for an individual depends on what its mate is doing.

Size dimorphism in monogamous species may result in part from the combined benefits of simultaneously guarding and feeding the young. When confronted with attacks at the nest, male Gila woodpeckers tended to specialize on defense, while females concentrated on delivering food. Males are considerably larger than females, and attack large birds more frequently and more successfully than females do, so it is not surprising that the male is the primary nest defender. Also, the energetic cost of traveling and foraging is lower for the female, so she may be more efficient at feeding the young, since she need not eat as many of the insects that she finds while searching. Male birds in general tend to be more concerned with nest defense and sanitation than in feeding the young (see Skutch 1976). An interesting exception occurs in hawks, in which males are smaller than the females. In these species, the males do nearly all the feeding of the young in the early nesting stages, while females vigorously defend the nest (Snyder and Wiley 1976). But while size dimorphism influences the behaviors of the sexes, role are apparently not fixed. I show elsewhere that the Gila woodpeckers often switched roles back and forth between mates. If the male was away foraging, the female often guarded the nest, but used an alarm call to summon the male if a serious attack occurred.

Considerable work is now being directed toward complex models of individual foraging rates, but during the breeding season, defense of the young from intruders or predators is clearly important in determining movement patterns. Moreover, models based on individuals alone are too simplistic for those species in which both parents help raise the young. For these species, one must consider mated *pairs* to be competing against other *pairs* in the population in a race to produce healthy offspring. I hope that over the next few years, behavioral ecologists will increase their efforts to model cooperative behavior with multiple goals. We must elucidate the interactions of several behavioral components rather than simply dissect a single dimension, food acquisition by individuals.

Acknowledgements. I thank Ron Pulliam, Thomas Whittam, and Thomas Caraco for numerous insights. Michael Rosenzweig, James Brown, Gordon Orians, Stephen Russell, Astrid Kodric-Brown, and David Vleck made valuable comments on the manuscript. Special thanks go to Nancy Ares for helping in the field and to Judy Spencer for drafting the figure. This paper constitutes part of my Ph.D. dissertation submitted to the University of Arizona. While engaged in the research, I was supported by U.S. NSF Grant DEB77-0341 awarded to H. H. Ronald Pulliam and by the Graduate School of the University of Arizona.

References

Andersson M (1978) Optimal foraging area: size and allocation of search effort. Theor Popul Biol 13:397–409

Caraco T (1979) Time budgeting and group size: a theory. Ecology 60:611–617

Covich AP (1976) Analyzing shapes of foraging areas: some ecological and economic theories. Annu Rev Ecol Syst 7:235–257

Keeney RL, Raiffa H (1976) Decisions with multiple objectives: preferences and value tradeoffs. Wiley, New York

Martindale S (1980) Foraging patterns of nesting Gila woodpeckers. PhD dissertation, University of Arizona

McCleery RH (1978) Optimal behavior sequences and decision making. In: Krebs JR, Davies NB (eds) Behavioural ecology, an evolutionary approach. Sinauer, Sunderland, MA

Orians GH, Pearson NE (1979) On the theory of central place foraging. In: Horn DJ, Staris GR, Mitchell RD (eds) Analysis of ecological systems. Ohio State University Press, Columbus, OH

Rosenzweig ML (1974) On the optimal aboveground activity of bannertail kangaroo rats. J Mammal 55:193–199

Schoener TW (1979) Generality of the size-distance relation in models of optimal foraging. Am Nat 114:902–914

Skutch AF (1976) Parent birds and their young. University of Texas Press, Austin, TX

Snyder NFR, Wiley JW (1976) Sexual dimorphism in hawks and owls of North America. Ornithol Monogr 20:1–96