

FORAGING PATTERNS OF NESTING GILA WOODPECKERS

by

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TABLE OF CONTENTS

	Page
LIST OF TABLES	v
LIST OF ILLUSTRATIONS	vi
ABSTRACT	vii
1. THE FORAGING PATTERNS	1
Methods	2
Behavioral Observations	3
Monitoring Deliveries	4
Results	5
Itineraries and Substrate Use	6
Effects of Distance from the Nest	17
Discussion	25
Substrate Selection	25
Central Place Foraging	28
2. NEST DEFENSE, CENTRAL PLACE FORAGING, AND THE PARENTAL TEAM	32
Theory: Nest Defense and Central Place Foraging	34
The Nest Attack Experiment	41
Methods	42
Results	43
Parental Role Switching in Gila Woodpeckers	48
Discussion	55
REFERENCES	63

LIST OF TABLES

Table	Page
1. Delivery transition probabilities for males and females	9
2. Substrate transition probabilities for males and females	10
3. Direction transition probabilities for males and females	12
4. Substrate use by 3 pairs of birds in 1979	15
5. Behaviors used by the birds on each substrate	16
6. Behaviors on saguaros at different distances from the nest	20
7. Effects of distance from the nest on saguaro fruit density and visitation by the birds	21
8. Type of food delivered from different distances	22
9. Sizes of insects delivered from different distances	23
10. Delivery distances before and after experimental nest attacks	45
11. Sizes of insect loads delivered to the nests before and after experimental attacks	46
12. Type of food delivered to the nest before and after experimental attacks	47

LIST OF ILLUSTRATIONS

Figure	Page
1. Distribution of stops per trip	7
2. Distribution of saguaro fruits on cactus tops available in study area, and on tops visited by the woodpeckers	13
3. The effects of travel time on patch use by an optimal forager	35
4. The effects of nest defense on patch use by a central place forager	38
5. The predicted effects of increasing the attack rate at the nest	40
6. Rates of nest deliveries for a pair of mated Gila Woodpeckers on 8 mornings of observation in 1979	50
7. Rates of nest deliveries for the pair on an hourly basis	52
8. Indifference curves showing the tradeoffs of foraging effort and nest defense for parental teams	58

ABSTRACT

I document the movement patterns and nest deliveries of Gila Woodpeckers (Melanerpes uropygialis) in nature, in an attempt to reveal the decisions made by these birds as they feed and defend the nestlings. In particular, I consider substrate selection, the effects of distance from the nest, and teamwork among mates. The woodpeckers selected substrates partly on the basis of recent foraging success, but the ambient temperature was also important. The birds spent much of their time resting on the shady sides of saguaro cacti, even though they had very low rates of prey capture there.

Orians and Pearson (1979) showed that to maximize the delivery rate to nestlings, foragers using small prey should select higher quality patches, search longer, and deliver larger items when farther from the nest. From greater distances, the woodpeckers did deliver larger insects, and selected saguaro tops with more fruit. Visit duration increased only slightly with delivery distance, but at greater distances, foraging effort was greater. Thus, the qualitative predictions of the delivery rate maximization model were upheld.

The woodpeckers spent much time simply guarding their nests, however, and I present a graphical model to show that nest defense tends to reverse the above predictions about the effects of delivery distance on foraging behavior. If the attack rate at the nest is increased, a parent should stay closer and deliver smaller items. Experimental attacks with stuffed specimens at woodpecker nests produced the

predicted changes in the foraging of males, but not of females. Females simply increased their delivery rates to compensate for the decrease in the male rate. Observations indicate that mated pairs often coordinate their activities, so that one bird guards the nest while the other feeds the young, and that roles are switched back and forth between the sexes. Parents may work as a team to increase their joint effects on the survivorship of the young.

The results show that physiological constraints, nest defense, and interactions among mates are crucial to an understanding of the foraging patterns of these birds. I suggest we direct more of our theoretical efforts toward decision processes with multiple objectives, rather than building more complex models based solely on maximizing the food acquisition rate.

CHAPTER 1

THE FORAGING PATTERNS

Foraging animals must continually make decisions about which of several possible patches or substrates to visit, how long to search, what items to eat, and so on. Based on the assumption that natural selection operates so as to produce efficient animals, ecological theories of behavior have flourished over the last fifteen years (McFarland 1977, Pyke et al. 1977). For animals delivering small prey items to young in a nest, Andersson (1978), Orians and Pearson (1979), and Schoener (1979) pointed out that in order to maximize the delivery rate, a predator's behavior should depend on the travel time from the foraging location to the nest. In this chapter, I document the foraging patterns of nesting Gila Woodpeckers (Melanerpes uropygialis), discuss the decision processes involved in substrate selection by these birds, and test the qualitative predictions of the delivery rate maximization model. Nesting Gila Woodpeckers are particularly appropriate for testing behavioral hypotheses, since the Sonoran desert in which they live is open enough to allow continuous observation of their locations. These woodpeckers are bill-loaders, and when delivering food to the nest, they land by the entrance hole for several seconds, so an observer can photograph or categorize the load.

Although insect distributions were not sampled, I make inferences about the search strategies of the birds by considering their itineraries, the distribution of stops per round trip from the nest, the sequencing of deliveries, and the effects of recent foraging success on subsequent locations and substrates. These woodpeckers also eat (and deliver) saguaro fruits, which were censused, and I document their selection of cactus tops. The birds perform various activities besides foraging, however, and I show that substrate selection is based to a large extent on the avoidance of heat stress rather than on prey capture rates. I then turn to the effects of delivery distance from the nest. I present data not only on visit duration and delivery load sizes, but also on foraging effort, the selection of saguaro tops, and the delivery diet. I discuss search strategies for hidden prey, and briefly consider the problem of multiple foraging currencies.

Methods

The field work was performed during the 1979 and 1980 nesting seasons, from mid-April through mid-July. The study area was in Saguaro National Monument (Tucson Mountain Unit), 25 km. west of Tucson, Arizona. The perennial vegetation there is typical of the lower Sonoran desert (Lowe 1964) and consists of saguaro cactus (Carnegieia gigantea), foothill paloverde (Cercidium microphyllum), ironwood (Olneya tesota), and various other cacti and desert shrubs. A photograph of my study area appears in Steenbergh and Lowe (1977, p. 8, Fig. 5A).

I or an assistant observed individual birds throughout their foraging bouts, as we sat on a nearby hill or rock about 100 m. from

the nest. We were able to track the birds successfully for about 50% of the time spent watching. We verbally recorded behavioral observations with cassette tape recorders, and I transcribed the tapes later, using a stopwatch to measure durations. In the 1979 season, we observed 3 pairs of birds, and monitored the nest deliveries of 2 of these pairs. In 1980, we observed behaviors and monitored nest deliveries at 9 nests. Since the woodpeckers were generally inactive from 1200 to 1600 hours, we observed nest deliveries only in the mornings. The local air temperature was recorded every half hour.

I censused the number of fruits on saguaro cacti in the vicinity of the three nests studied in 1979. At each nest, I counted all the fruits on each saguaro top in four strips radiating out from the nest in arbitrary directions. Each strip was 10 m. wide and 300 m. long. I also counted fruits on the tops actually visited by the birds. It was not possible to sample adequately the insect distributions available to these Gila Woodpeckers.

Behavioral Observations

The observational data included a bird's foraging substrate, direction from the nest estimated to the nearest 30°, and distance from the nest estimated to the nearest 25 m. When possible, the behavior of the woodpecker was sampled at fixed time intervals of 5 seconds, and categorized as one of the following: scan, search, peck, or rest. These categories were mutually exclusive and exhaustive of the foraging related behaviors on a substrate. During a "scan", the bird's bill was directed upward or outward from the substrate, and the

bird was apparently looking at the sky, into the desert, or at another bird, rather than for insects on or in the substrate. During a "search" the bill was directed down toward the substrate and the bird was hunting for food. When searching, the woodpeckers often walked or hopped every few seconds, whereas they were stationary when scanning. "Peck" included hammering and probing wood, cactus tissue, or the ground for food. "Rest" indicated that the bird was perched, and neither scanning, searching, nor pecking. This category included all maintenance behaviors, such as preening and bill-wiping, as well as actual resting.

Monitoring Deliveries to the Nest

When delivering food to the young, an adult Gila Woodpecker would land on the side of the saguaro at the nest entrance hole, then quickly feed the contents of his or her bill to the young in the nest cavity. To make these deliveries generally took 5 to 10 seconds, long enough for an observer near the nest to photograph or categorize the contents of the bill.

In the 1979 season, I photographed about 400 deliveries at one nest and about 100 deliveries at another nest. The setup was a standard 35 mm. camera with a 300 mm. telephoto lense and 2x teleconverter, placed about 5 m. from the nest cactus (8 m. from the nest hole itself). I or an assistant manually operated the camera and kept notes on the type, color, and size of the items delivered. All the pictures were developed as transparencies, and projected so I could categorize them.

In most cases, I could identify the item delivered as being either an insect larva, insect adult, or mass of ripe saguaro fruit pulp. I could also usually categorize the size of the load as small, medium, or large. Small loads filled one-fourth of the bill or less (were ≤ 7 mm. long), medium items filled one-fourth to three-fourths (were 7-21 mm. long), and large ones were larger than three-fourths of a bill length (> 21 mm. long).

After studying the photographs, I found that I could identify the loads and categorize their sizes equally well by direct observation, using binoculars from a location 5 to 10 m. away from the nest cactus. To simplify the data collection process in 1980, I categorized the deliveries in the field, independently of the other observer's data on where the woodpecker had been foraging.

Results

Both males and females actively delivered food to the nestlings. For several of the foraging patterns discussed in this chapter, there were no statistically significant differences between the sexes; these data have been lumped to simplify the presentation. Where significant differences between the sexes occurred, I present the data separately, but the primary purpose here is to document the foraging behavior of individuals, not to demonstrate sexual dimorphism or differences among individuals. I explore the dimorphism in Chapter 2 and elsewhere (Martindale and Lamm, in prep.). Unless otherwise specified, data are lumped for all 12 males and 12 females studied in both field seasons.

As pointed out in the discussion, saguaro fruit is a fundamentally different type of resource than insects. Also, insect larvae are generally less mobile and less chitinous than insect adults, so these two categories may represent very different food types. In several of the tables, I present tests of the a priori hypotheses that the effects depend on prey type. "Overall" tests are for the entire table as given; "insect only" tests are for the subtables consisting of insect rows and columns only. Incidentally, over 90% of the deliveries were of a single item, so when referring to insect deliveries, I use item, insect, and load as synonyms.

Itineraries and Substrate Use

Both male and female Gila Woodpeckers visited an average of 4.2 different plants in a foraging trip before returning to the nest with a load ($n = 654$ round trips, $sd = 5.0$ locations). In 58% of these trips, the birds worked outward; that is, they started close to the nest and ended up farther away. In only 5% of the trips did the birds work toward the nest. In the remaining 37% of the trips, all locations visited were the same distance from the nest (± 25 m.).

Figure 1 shows the distribution of the number of stops made before the bird returned to deliver a load. If at each foraging location the birds had a constant probability of finding an item worth returning to the nest, then one would expect a geometric distribution of the number of stops per trip (see DeGroot 1970, p. 36). A mean of 4.2 stops and standard deviation of 5.0 stops implies the parameters $p = .20$ and $q = .80$, that is, a probability of .20 of finding a

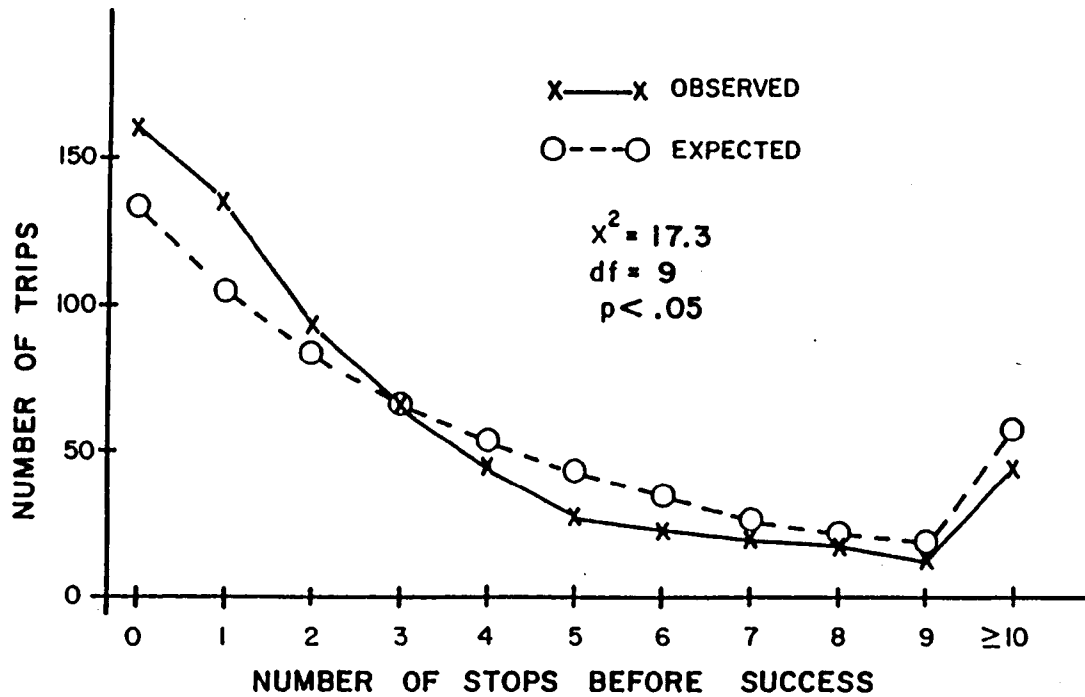


Figure 1. Distribution of stops per trip.

Expected values are based on the null hypothesis that prey captures are random and independent, with a constant probability of success at each location (a geometric distribution of parameters $p = .20$ and $q = .80$).

suitable prey item at each location. Figure 1 shows that the deviations between expected and observed distributions were significant; the birds made short trips (0-2 stops before success) more often than expected, and longer trips less often than expected. This pattern of deviations could arise because prey were clumped. The birds often returned to the same exact spot to make a second delivery. In some cases, they spent considerable time and effort (20 minutes or more) pecking and digging at a saguaro rot or desert shrub, then made 5 or more single-stop deliveries from that location.

The prey item that a woodpecker delivered on a given trip depended in part on what the bird delivered on its previous trip to the nest. Table 1 shows the transition matrices for delivery composition. If load compositions were sequentially independent, the transition probabilities would equal the total proportions of prey types. For example, females would deliver an insect adult 37% of the time, regardless of what had been delivered on the previous trip. But the departures from sequential independence were highly significant. All the entries on the main diagonals of each matrix are greater than expected, so the birds tended to deliver in runs of the same type of prey. For example, after delivering an insect adult, females delivered another one 56% of the time, instead of the 37% expected by the null hypothesis of sequential independence.

Table 2 shows the transition matrices for substrates visited by the woodpeckers. If no delivery to the nest was made, the probability of a bird visiting the same substrate type twice in a row during a

Table 1. Delivery transition probabilities for males and females.

Each entry in the transition matrix is the probability of an item being delivered to the nest, given the item delivered on the previous delivery. Numbers in parentheses are the total proportions of items delivered. Males overall $X^2 = 24.1$, $df = 4$, $p < .001$; insects only $X^2 = 22.1$, $p < .001$.

LAST ITEM DELIVERED	NEXT ITEM DELIVERED			Number of Deliveries
	Insect Adult	Insect Larva	Saguaro Pollen/Fruit	
MALES				
Insect adult	.42	.40	.19	144 (.31)
Insect larva	.24	.54	.22	207 (.45)
Saguaro pol/fruit	.35	.28	.36	110 (.24)
FEMALES				
Insect adult	.56	.30	.13	145 (.37)
Insect larva	.31	.57	.14	156 (.39)
Saguaro pol/fruit	.21	.22	.57	95 (.24)

Table 2. Substrate transition probabilities for males and females.

Entries are the probabilities that the substrate visited immediately after a nest delivery was the same as (or different from) the one visited immediately before the nest visit (where capture was made).

"None" means that no capture was made, and the bird visited another plant instead of returning to the nest. Males overall $X^2 = 27.9$, $df = 3$, $p < .001$; insects only $X^2 = 0.4$, n.s. Females overall $X^2 = 49.4$, $p < .001$; insects only $X^2 = 17.5$, $p < .001$.

PREY DELIVERED	NEXT SUBSTRATE VISITED		Sample Size
	Same as last	Different from last	
MALES			
Insect adult	.43	.57	72
Insect larva	.48	.52	113
Saguaro pollen/fruit	.55	.45	62
None	.27	.73	271
FEMALES			
Insect adult	.18	.82	66
Insect larva	.55	.45	55
Saguaro pollen/fruit	.71	.29	51
None	.29	.71	267

foraging trip was only about 0.3. After making a delivery, however, there was a significant tendency for the birds to return to the same substrate type as the one where the capture was made. For the females only, the response depended on what had just been delivered. After delivering an insect adult, the females switched substrate type as often as when no delivery was made ($\chi^2 = 3.3$, $df = 2$, n.s.), but after delivering an insect larva or saguaro pollen/fruit, females returned to the same substrate.

As Table 3 shows, the woodpeckers tended to return in the same direction as the last trip, regardless of the item delivered (all rows are significantly different from the 25% same directions and 75% different directions expected for sequentially independent trips). For the females, but not the males, the magnitude of the tendency depended on what type of prey had just been delivered. After delivering an insect adult, females switched directions more often than after delivering insect larvae or saguaro pollen/fruit.

When foraging on saguaro tops, the woodpeckers tended to select those with many fruits (Figure 2). The mean number of fruits on cactus tops visited by the birds was about twice the average on available tops in the area. Since the fruits are bright red and can be seen from a distance, it is not surprising that the birds were attracted to these tops.

It is clear from these results that the birds selected substrates where they were likely to have a high foraging rate. After delivering an insect, the woodpeckers tended to return to the same

Table 3. Direction transition probabilities for males and females.

Entries are the probabilities that the direction of a foraging trip from the nest was the same as, or different from, the direction of the trip immediately preceding the delivery. "Same" means within 45° of each other. Males overall $X^2 = 0.27$, n.s.; insects only $X^2 = 0.22$, n.s. Females overall $X^2 = 14.9$, $df = 2$, $p < .001$; insects only $X^2 = 8.7$, $df = 1$, $p < .005$.

PREY DELIVERED	NEXT DIRECTION FROM NEST		Sample Size
	Same as last	Different from last	
MALES			
Insect adult	.49	.51	72
Insect larva	.52	.48	115
Saguaro pollen/fruit	.49	.51	55
FEMALES			
Insect adult	.41	.59	70
Insect larva	.67	.33	61
Saguaro pollen/fruit	.73	.27	52

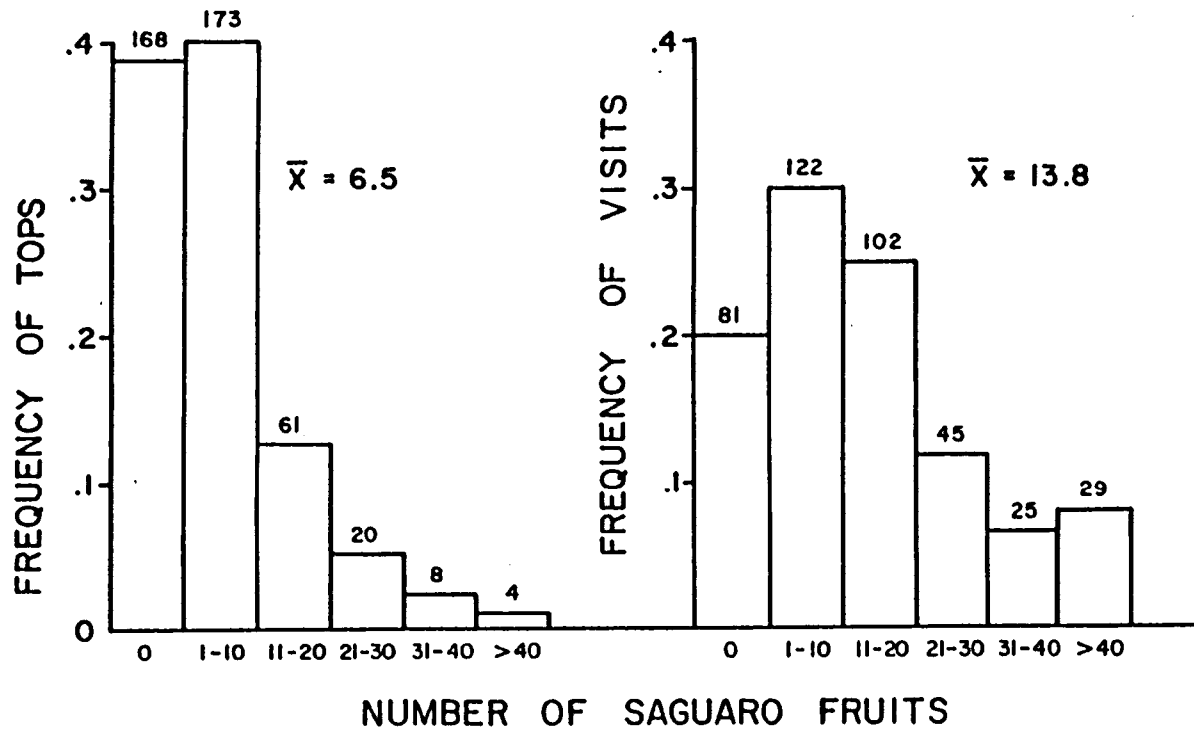


Figure 2. Distribution of saguaro fruits on cactus tops available in study area, and on tops visited by the woodpeckers.

Data are for the 3 pairs of birds studied in 1979.

substrate where the capture had been made, and when using saguaro fruits, they visited cactus tops with large numbers of ripe fruit. Over a long period of time, such behavior should result in visitation rates proportional to the capture rates on each substrate. But as Table 4 shows, the woodpeckers did not visit substrate types in the same proportions as they delivered food from them. These birds visited paloverdes and ironwoods, which yielded the highest capture rate, considerably less often than they visited saguaros, where the capture rate was lowest. If time per visit to a substrate is included, the disparity is even more pronounced (Table 4). The males spent nearly half their total time on saguaro sides despite a very low probability of delivering an item from there.

The differences between observed substrate use and that expected for foraging success arise in part because the birds perform many activities on a substrate besides hunting for food. As Table 5 shows, behavior was highly dependent on the substrate type. The "search" and "peck" categories together constitute foraging behaviors, as opposed to "scan" and "rest" which include all other behaviors. Thus, when on paloverdes, the males spent 90% of their time actually foraging, but when on saguaro sides, they spent only 39% of their time foraging. To calculate the foraging effort on the substrates, then, the total time spent on each type should be weighted by the proportion of time spent on that substrate searching and pecking. But even when the times are weighted in this way, the birds spent much more time on saguaro sides than expected on the basis of delivery rates (Table 4, last column).

Table 4. Substrate use by 3 pairs of birds in 1979.

P(capt) is the probability that a bird captured and delivered a prey item from the given substrate, based on a sample of 591 foraging locations for males and 688 locations for females, where all locations visited in the round trip were observed. P(visit) is the probability of visiting the substrate, based on the total sample of 1,659 male locations and 2,062 female locations. Duration statistics are based on the total sample. P(tot) is the proportion of total observation time on the given substrate. P(for) is the proportion of foraging time only (total time weighted by percent of time spent foraging on the substrate).

SUBSTRATE	P(capt)	P(visit)	Average duration of visit (seconds)	sd duration of visit (seconds)	P(tot)	P(for)
MALES						
Saguaro top	.19	.33	36.9	35.3	.24	.23
Saguaro side	.13	.33	72.5	101.5	.47	.34
Paloverde	.26	.13	45.3	44.7	.12	.21
Ironwood	.25	.08	66.9	67.8	.11	.13
Other	.21	.13	24.1	23.0	.06	.09
FEMALES						
Saguaro top	.16	.32	23.8	24.7	.25	.21
Saguaro side	.16	.37	28.9	36.9	.35	.34
Paloverde	.20	.11	43.8	40.1	.15	.20
Ironwood	.32	.07	57.0	52.6	.13	.17
Other	.21	.14	27.1	30.2	.13	.08

Table 5. Behaviors used by the birds on each substrate.

For the same 3 pairs as in Table 4. Entries are the proportions of observations in each behavioral category for the given substrate type. Temperature range: 30-39°C. Males $X^2 = 815.7$, $df = 12$, $p < .001$. Females $X^2 = 493.4$, $p < .001$.

SUBSTRATE	BEHAVIORS				Sample size
	Scan	Search	Peck	Rest	
MALES					
Saguaro top	.41	.19	.31	.09	1113
Saguaro side	.26	.17	.22	.35	587
Paloverde	.02	.80	.10	.07	348
Ironwood	.08	.30	.36	.27	105
Other	.18	.34	.11	.37	124
Total	.28	.29	.25	.18	2277
FEMALES					
Saguaro top	.34	.29	.32	.06	974
Saguaro side	.14	.49	.19	.18	782
Paloverde	.08	.86	.05	.00	205
Ironwood	.08	.78	.13	.02	112
Other	.46	.42	.04	.09	125
Total	.24	.45	.22	.09	2198

When not actively foraging, the woodpeckers spent considerable time guarding the nest. This is reflected by the scanning and resting time on saguaros (Table 5). The males, in particular, would often spend several minutes on a saguaro top near the nest without foraging. I explore nest defense in more detail in Chapter 2.

Much of the time the Gila Woodpeckers spent on saguaro sides, however, may represent the behavioral avoidance of heat stress. Local air temperatures were usually above 30°C, and often above 40°C. When it was hot, the birds increased their time spent resting on the shady sides of saguaros, the coolest places available. On an hourly basis, the proportion of time spent on saguaro sides (arcsin transformed) was positively correlated with temperature for both sexes ($r = .85$, $n = 42$ hours, $p < .01$). Also, the proportion of time spent resting (on all substrates, and also on saguaro sides alone) was positively correlated with temperature ($r = .82$, $n = 42$ hours, $p < .01$).

Effects of Distance from the Nest

The flight speed of both sexes was on average 11.6 m/sec. ($n = 200$ flights, $sd = 2.5$ m/sec.). Thus, a round trip to a foraging location 300 m. or so from the nest required about 1 min. travel time. In the same amount of time, the bird could search at least one or two locations close to the nest (see average durations in Table 4). Since only four stops were made on an average trip, this travel effort represented a genuine cost in terms of lost foraging time, and possibly in terms of water loss as well (see Torre-Bueno 1978).

A prediction of the Orians and Pearson (1979) and Schoener (1979) models is that to maximize the delivery rate, foraging time should be positively correlated with distance from the nest. When on paloverdes, the birds spent virtually all of their time foraging (Table 5), so I used only the data for that substrate type to test the prediction. Durations of visits to paloverdes were exponentially distributed, so I used log-transformed times for the significance tests. For males, the correlation of duration of visit with distance from the nest was not constant. At the nest intensively studied (and described in more detail in Chapter 2), the male made many deliveries to the nest for the first two days of observation, then decreased his delivery rate. During the two days of the high rate, foraging times on paloverdes were positively and significantly correlated with distance from the nest ($r = .24$, $n = 72$, $p < .05$). Thereafter, and for all other males studied, the correlation was not significantly different from zero. For the females, durations of visits to paloverdes were consistently correlated with distance from the nest ($r = .29$, $n = 144$, $p < .01$). But even when significant, the correlations were low; less than 10% of the variance in durations can be accounted for by distance from the nest.

As the birds went farther from the nest, however, their behavior on the substrates changed. To document this change, I have used only the observations from saguaro tops and sides, since the birds were most observable there. I did not consider observations beyond 200 m. because of the difficulty of observing behaviors at such great distances. Table 6 shows that when on saguaros, both sexes spent more time searching and

pecking for food when far from the nest, and more time scanning and resting when close to the nest. In addition, the birds selected saguaro tops with more fruits when farther from the nest, as Table 7 shows. There was no significant effect of distance on number of fruits per saguaro top, so this pattern does not result from local resource depletion close to the nest. It appears, then that foraging effort was greater at farther distances from the nest, not only in the behaviors used on a substrate, but in the selection of plants as well.

The composition of deliveries to the nest was strongly dependent on delivery distance. Table 8 shows that most saguaro fruit deliveries were made from within 100 m. of the nest. Since saguaro fruits were abundant, this result is not surprising, but might indicate that the birds are responsive to the cost of delivery. There was no significant effect of distance on the proportion of insect larvae versus insect adults delivered.

Perhaps the most interesting prediction arising from the delivery rate maximization models is that load size should be positively correlated with delivery distance. Table 9 shows that, as predicted, Gila Woodpeckers did deliver fewer small insects and more large ones from greater distances. There was not enough variation in saguaro fruit load size or delivery distance for a meaningful test of fruit deliveries.

In sum, these woodpeckers dramatically changed their foraging behaviors as they traveled farther from the nest. At greater distances, the birds spent more time searching and pecking for food instead of

Table 6. Behaviors on saguaros at different distances from the nest.

Entries are the proportions of observations in each behavioral category for the given distance. Saguardo tops: Males $X^2 = 49.1$, $df = 3$, $p < .001$; Females $X^2 = 58.0$, $p < .001$. Saguardo sides: Males $X^2 = 49.1$, $p < .001$, Females $X^2 = 37.3$, $p < .001$.

DISTANCE FROM NEST (meters)	BEHAVIORS				Sample Size
	Scan	Search	Peck	Rest	
SAGUARO TOPS					
MALES					
1-100	.57	.11	.24	.08	369
101-200	.23	.23	.49	.04	107
FEMALES					
1-100	.52	.18	.27	.04	176
101-200	.19	.56	.22	.03	144
SAGUARO SIDES					
MALES					
1-100	.42	.09	.17	.33	248
101-200	.12	.18	.43	.28	112
FEMALES					
1-100	.19	.27	.15	.40	75
101-200	.07	.78	.05	.11	73

Table 7. Effects of distance from the nest on saguaro fruit density and visitation by the birds.

Entries are the proportions of saguaro tops in each density category for the given distances. Distribution of fruit $X^2 = 1.0$, $df = 4$, n.s. Male use: $X^2 = 22.2$, $p < .001$; Female use $X^2 = 20.1$, $p < .001$.

DISTANCE FROM NEST (meters)	NUMBER OF FRUITS PER TOP			Sample Size
	0-10	11-30	>30	
DISTRIBUTION OF FRUIT				
0-99	.80	.17	.03	174
100-199	.79	.20	.02	112
200-299	.77	.20	.03	148
MALE VISITS				
0-99	.67	.28	.05	78
100-199	.50	.33	.17	52
200-299	.38	.43	.19	21
FEMALE VISITS				
0-99	.68	.29	.03	75
100-199	.11	.35	.22	108
200-299	.43	.33	.23	90

Table 8. Type of food delivered from different distances.

Entries are the proportions of deliveries of each type for the given distance category. Males overall $X^2 = 63.1$, $df = 4$, $p < .001$, insects only $X^2 = 3.2$, $df = 2$, n.s. Females overall $X^2 = 55.3$, $p < .001$, insects only $X^2 = 317$, n.s.

DISTANCE FROM NEST (meters)	FOOD DELIVERED			Sample Size
	Insect larva	Insect adult	Saguaro pollen/fruit	
MALES				
0-99	.33	.26	.40	201
100-199	.50	.39	.11	148
≥ 200	.42	.50	.08	103
FEMALES				
0-99	.34	.26	.40	207
100-199	.41	.49	.10	108
≥ 200	.46	.54	.00	46

Table 9. Sizes of insects delivered from different distances.

Entries are the proportions of deliveries of each size for the given distances.

Males: $\chi^2 = 11.0$, $df = 4$, $p < .05$. Females: $\chi^2 = 12.0$, $p < .025$.

DISTANCE FROM NEST (meters)	SIZE OF INSECT DELIVERED			Sample Size
	Small	Medium	Large	
MALES				
0-99	.51	.37	.12	120
100-199	.40	.44	.17	133
≥ 200	.36	.38	.26	95
FEMALES				
0-99	.47	.38	.15	124
100-199	.35	.41	.24	97
≥ 200	.20	.52	.28	46

scanning or resting, selected saguaro tops with more fruits, and delivered a greater proportion of insects (instead of fruit). From greater distances these woodpeckers also delivered larger insects.

Discussion

Substrate Selection

The probability of delivering a food item from a particular foraging location was low - about .2 per visit (Table 4) - and depended on the substrate type. The Gila Woodpeckers apparently did not often know where prey were located, and usually had to search 4 or more plants before finding an item worth returning to the nest. The search component of foraging thus appears to be of fundamental importance in this system. Although foraging theorists have long recognized the importance of search times in determining optimal diets (see, e.g., MacArthur and Pianka 1966, Schoener 1971), they are just beginning to explore search strategies as such, for predators confronted with random prey distributions of unknown parameters. Oaten (1977) showed that to the extent which prey are clumped, a predator gaining information about patch structure should employ different decision rules (stay longer after a capture in a patch) than a predator harvesting patches of known quality. Using a more tractable model, Green (1980) demonstrated the process by which a predator should update its assessment of the capture probabilities, and use this information to decide when to leave a patch and where to search next. Koopman (1980) recently reviewed the operations research literature on search strategies. His results are couched primarily in terms of military problems, but have many biological applications for predators searching

for hidden prey. The approach throughout these theoretical works is for the predator to update its subjective probability distribution of prey items, using Bayes' Theorem to include new information gained from sampling (see DeGroot 1970). Under a fairly wide range of assumptions, the predator should next search the location with the highest probability of capture, assuming all prey items are of equal value. If detection is not certain the search effort in each patch should be proportional to the capture probabilities (or their logarithms, as in Koopman 1980, p. 149). Krebs et al. (1978) were able to show that Great Tits (Parus major) in the laboratory did indeed employ optimal sampling effort when deciding between two patches.

The search problem faced by Gila Woodpeckers in nature, however, is complicated by the fact that the capture probabilities change rapidly over time. Once a clump of prey had been located, the birds would return for several deliveries, so that they made more short trips and fewer long ones than expected for constant and independent capture probabilities (Figure 1). Also, prey items were delivered in runs (Table 1), indicating that the birds were either harvesting clumped prey or forming search images, either of which would alter subsequent probabilities of prey capture. After a successful delivery from a substrate, these woodpeckers were more likely to return to the same plant species than if no capture was made (Table 2), and they also tended to return to the same general foraging area (Table 3). Although insect distributions were not sampled, a plausible inference from the movement patterns is clearly that Gila Woodpeckers learn where prey are

to be found momentarily, and select foraging locations partly on the basis of very recent foraging success. The tendency to search in areas of recent foraging success has been demonstrated for several other bird species as well (e.g., Croze 1970, Smith 1973, Zach and Falls 1979).

Another complication is that at least two fundamentally different types of items were sought by the birds - insects and saguaro fruits. Insects were presumably the primary source of protein, but saguaro flowers and fruits provided water and carbohydrates. The evaporative water loss of these birds is considerable at typical desert temperatures (Braun 1969, see also Torre-Bueno 1978), and I have shown above that the avoidance of heat stress is important in substrate selection. There was no free water in my study area, so saguaro nectar and fruit may be of critical importance to survival there. In most foraging models, the currency to be maximized is assumed to be energy (Pyke et al. 1977), but in this system there may well be a tradeoff between energy and water. Bivariate utility theory provides a way to combine qualitatively different items, like fruits and insects, into a common currency for measuring the tradeoffs (Caraco et al. 1980). Sibly and McFarland (1976) discussed the optimal strategies for acquiring both food and water, basing their arguments on the motivational changes occurring as a result of deprivation (or satiation) of each. They showed that the choice of which to pursue should depend on whether the product of deficit \times availability \times the limiting attempt rate is greater for food or water.

Central Place Foraging

Orians and Pearson (1979) presented graphical arguments on how foraging behavior should change as a function of distance from the nest, assuming that the foragers seek to maximize the delivery rate of energy to the nestlings. They showed that the quantitative predictions differ depending on whether the predator is a single or multiple-prey loader, but in either case the qualitative predictions are the same. If one assumes that the patches are identical except for their distance from the nest, the forager should stay in a patch longer and deliver larger items from farther away.

There has been little published evidence in support of the model. Orians (1980, p. 135) presented estimated data suggesting that Brewer's Blackbirds (Euphagus cyanocephalus) did tend to deliver larger loads from greater distances. Kramer and Nowell (1980) showed that the loading times of Eastern Chipmunks (Tamias striatus) increased with foraging distance from the nest, and for fledglings rather than a fixed nest, Davies (1976) showed that Spotted Flycatchers (Muscicapa striata) did deliver larger insects from greater distances.

My results show not only that the predicted size-distance relationship holds for Gila Woodpeckers, but also that an entire suite of other foraging-related behaviors change as the birds travel farther from the nest. Although distances explained very little of the variance in time spent on a substrate, the other behavioral changes were such that the birds increased their foraging effort at greater distances. They spent a greater proportion of time searching and

pecking for insects or fruit rather than scanning the surroundings or resting when farther from the nest. The birds also changed the delivery diet to include more insects and less saguaro fruit, and when using saguaro tops they selected tops with more fruit.

The observed patterns can be explained by an alternate hypothesis, however, which should be more fully explored in future work of this sort. The woodpeckers (and many other species as well) spend much time close to the nest mostly guarding it, but while doing so, may deplete the resources in the local vicinity. If they prefer large prey items over small ones, the resulting distribution of insects may be smaller around the nest than farther away. As the parent travels farther from the nest, it switches from guarding primarily to foraging (so selects higher quality patches), and might deliver larger prey simply because they are more readily available, rather than to minimize the cost of delivery as assumed in the above model. I could not sample insect distributions completely enough to test this alternative, but suggest that future workers consider the possibility of resource depletion around the nest.

Orians and Pearson (1979) also reasoned that predators should work toward the nest rather than away from it, but my results were exactly opposite. Gila Woodpeckers were 10 times more likely to work outward than inward. Working toward the nest would be advantageous only in an environment where the resources are completely known to the forager. If prey captures are random, the forager can not know beforehand how far to go to accumulate a full load just as it reaches

the nest. In a random environment, a forager could fail to find any prey items at all on an inward journey, and thus waste the entire trip. The effects of stochasticity on central place foraging patterns need further theoretical work, although Andersson (1978) did include random elements in his model.

Schoener (1979) showed the Orians and Pearson results were a special case of his more general model of central place foraging. The results should apply for predators like insectivorous birds which use relatively small prey, so that provisioning time is not longer for the larger items. But if larger loads cost more to transport, as in the case of beavers dragging trees to their nests, then the size-distance effect can be reversed. Jenkins (1980) confirmed this prediction: from farther away, the beavers he studied did deliver smaller rather than larger trees.

All these models assume that the goal of the predator is to maximize the delivery rate of food to the young in the nest. The assumption is reasonable in light of Lack's (1968) work showing that survivorship of young birds (and hence the fitness of their parents) increased with the delivery rate of food. The approach apparently works for qualitative predictions about the size-distance relationship of several species, but most biological systems are far more complex than reflected by models based solely on food acquisition by individual predators. I showed above that the avoidance of heat stress was important in substrate selection, and in Chapter 2, I show that if other important components are operating, such as predation or intrusion at

the nest, the Orians and Pearson predictions about the effects of distance can be easily reversed. I point out there that in species where both parents (or several helpers) provision the nestlings, the effects of all the foragers on the survivorship of the young must be considered jointly rather than individually.

CHAPTER 2

NEST DEFENSE, CENTRAL PLACE FORAGING, AND THE PARENTAL TEAM

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). In Chapter 1, I presented data indicating that Gila Woodpeckers foraging during the breeding season do satisfy the major predictions of the delivery rate maximization model. When farther from the nest, these birds selected richer saguaro tops, increased their foraging effort, and delivered larger loads. In the course of that 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, nests are vulnerable to attacks by other birds. On several occasions, I witnessed foreign Gila Woodpeckers apparently trying to usurp nest sites. Intruders sometimes flew directly to a nest saguaro from over 200 meters away, then immediately began exploring the nest cavities in the cactus. In all conspecific attacks, the residents were able to repel the intruder, though the ensuing fights often lasted several minutes, and entailed aerial chases to more than 300 meters from the nest. On one occasion,

a Common Flicker (Colaptes auratus chrysoides) actually evicted a pair of adult woodpeckers from their nest cavity, and I presume that if undeterred, intruding woodpeckers would expel the young and start their own brood. Hence, the cost of leaving the nest unguarded is potentially great: the residents could lose not only their nest site, but also their young. When viewed in this light, it is not surprising that the Gila Woodpeckers spend considerable time in the vicinity of the nest simply guarding it, rather than foraging and delivering food to the young, but such behavior is beyond the scope of the delivery rate maximization model. In this chapter, I present a graphical model which does include the costs of leaving the nest unattended, and show that nest defense can lead to different predictions about foraging behavior than delivery rate maximization alone. The predicted effects of increasing the attack rate at the nest are tested directly with data from a field experiment using mounted woodpecker specimens to mimic attacks.

The second aspect I consider here is 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 both major goals simultaneously. I present data from Gila Woodpeckers in nature to demonstrate the division of labor among the sexes and the occurrence of parental role switching, and discuss the advantages and implications of team foraging by parents raising young.

Theory: Nest Defense and Central Place Foraging

Orians and Pearson (1979) developed a graphical model to show how behavior should change as a 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. Hence, as Figure 3 shows, the prey acquisition curves, E_n and E_f , have negative second derivatives. The abscissa is total time away from the nest. T_n is the time it takes the forager to make a round trip to the near patch (during which no food is acquired) and T_f is the round trip travel time to the far patch. The expected rate of food acquisition at any point in time is just the slope of the line tangent to the curves E_n or E_f at that time, but the rate of food delivered to the nest is the slope of the line from the origin to a point on the curve at that time. The maximum possible delivery rate to the nest is the slope of the line from the origin to a point of tangency with the curve, R_n for the near patch and R_f for the far patch. Note that the slope of R_n is greater than that of R_f , so the maximum delivery rate from the near patch is greater than that of the far patch. The tangency points determine the optimal foraging times per trip (including

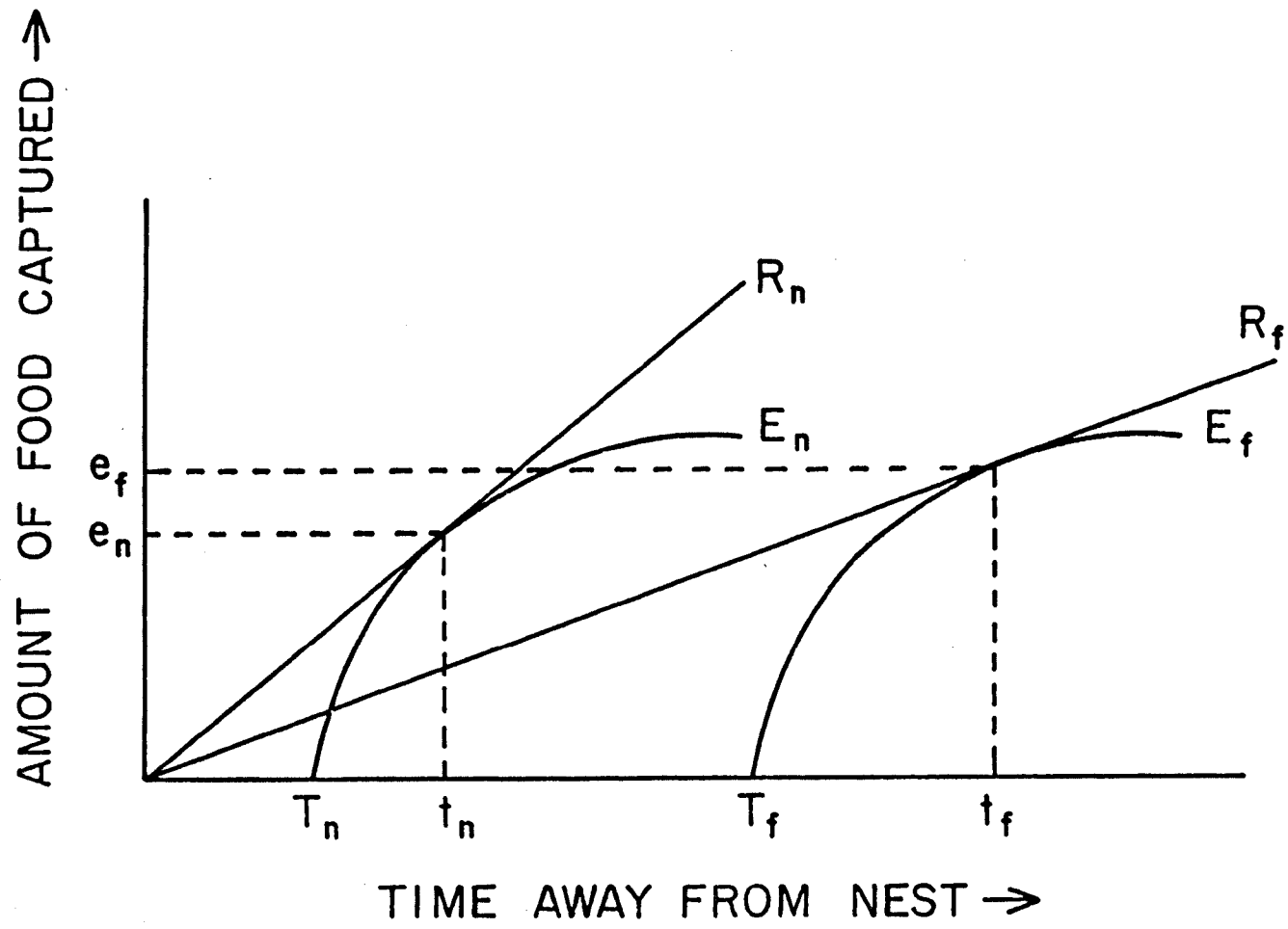


Figure 3. The effects of travel time on patch use by an optimal forager. See text for explanation.

travel), t_n in the near patch and t_f in the far patch, and also the optimal delivery load sizes, e_n and e_f . The optimal foraging time in the near patch is less than that in the far patch, since $t_n - T_n < t_f - T_f$. Also, the optimal load size from the near patch is smaller than that from the far patch ($e_n < e_f$).

This model strictly applies only to multiple-prey loading foragers, but Orians and Pearson (1979) show that the same qualitative results hold for single prey loaders which deliver just one prey item per trip (as Gila Woodpeckers usually do). Their model for single-prey loaders is similar to the one presented above, but requires a somewhat detailed proof, which they provide. To gain energy at a given average rate, a single loader should only pursue prey which are greater than or equal to some minimum size. The actual relationship between acceptable prey size and the resulting average rate depends on prey densities, but does not effect the qualitative results. For the single-prey loader to maximize the overall delivery rate to the nest, its minimum acceptable prey size must increase with delivery distance. That is, larger items (insects in the case of Gila Woodpeckers) should be delivered from farther away from the nest. As the minimum acceptable prey size increases, it takes longer to find one worth delivering, so again foraging time should increase with distance from the nest. As in the multiple-prey loader case, the maximum possible rate decreases with distance from the nest.

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 derived above can thus be converted to fitness units and represented as the benefit curves shown in Figure 4. As before, 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 simply 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 shown above, the maximum delivery rate is greater for the near patch. Since the optimal forager should stay in the far patch longer, $t_n - T_n < t_f - T_f$.

Now consider the decrease in production of the young caused by attacks at the nest while the forager is away. This cost function must depend not only on the probability of an attack occurring, but also on 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 most probably repelled. At great distances, though, attacks cannot even be detected. Hence the cost function must approach an asymptote equal to the loss in fitness of sacrificing the entire nest and young. I assume that the maximum possible cost from a single foraging bout is much greater than the maximum possible benefit, but that the probability of an attack occurring during a single foraging bout is low. Most foraging takes place within the high detectability area.

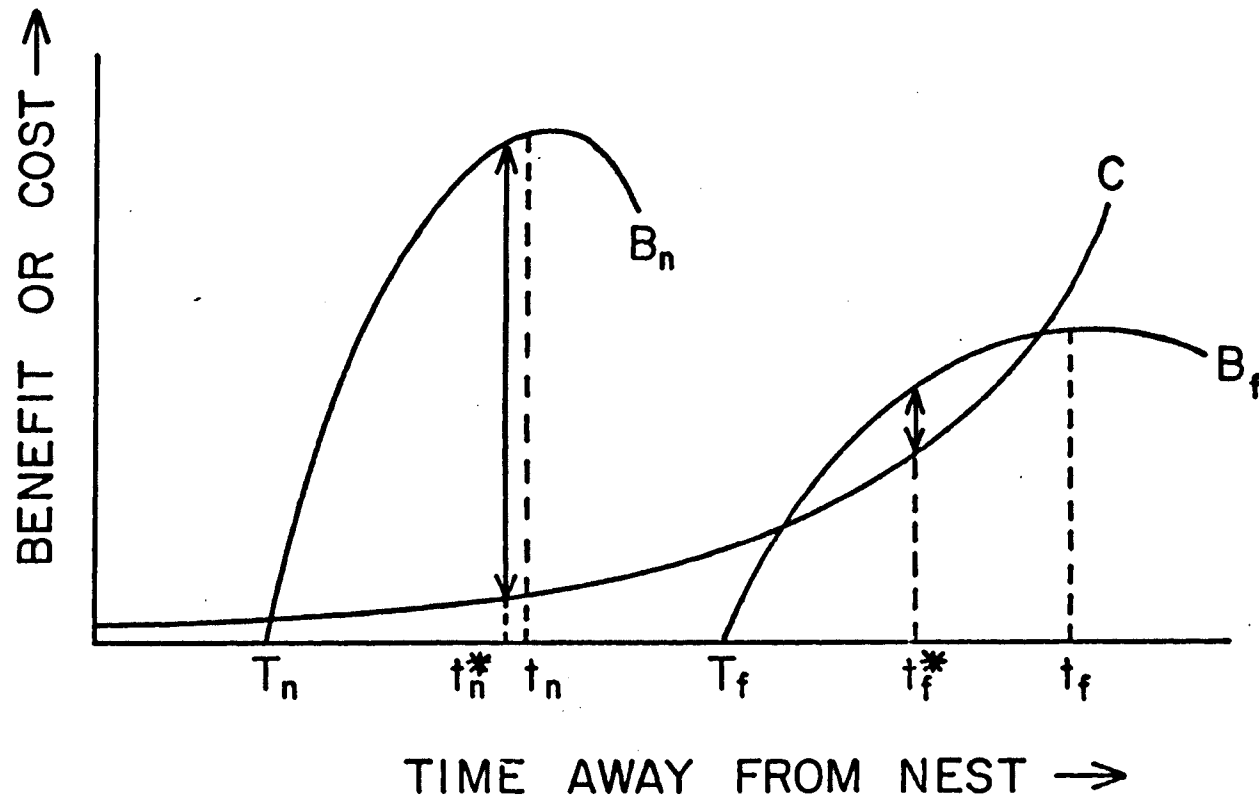


Figure 4. The effects of nest defense on patch use by a central place forager.

See text for explanation.

Hence, the patches of interest are 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 (C in Figure 4).

Natural selection should produce animals which behave such that their net fitness, not just their delivery rate, is maximized. I assume the benefits from delivering food and costs from leaving the nest unguarded are additive, so the objective is to maximize the quantity (Benefit-Cost). The optimal foraging times, t_n^* and t_f^* , now occur at the points at which the first derivatives of the benefit and cost functions are equal, as indicated by the arrows in Figure 4. 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 $t_n^* < t_n$ and $t_f^* < t_f$. 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 ($t_n - t_n^* < t_f - t_f^*$). 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 Figure 4 shows, $t_f^* - T_f$ can be less than $t_n^* - T_n$, 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, as Figure 5 shows. The patches and the benefits are the same as before, but now C_1 is the cost function associated with a low attack rate, and C_h is the cost

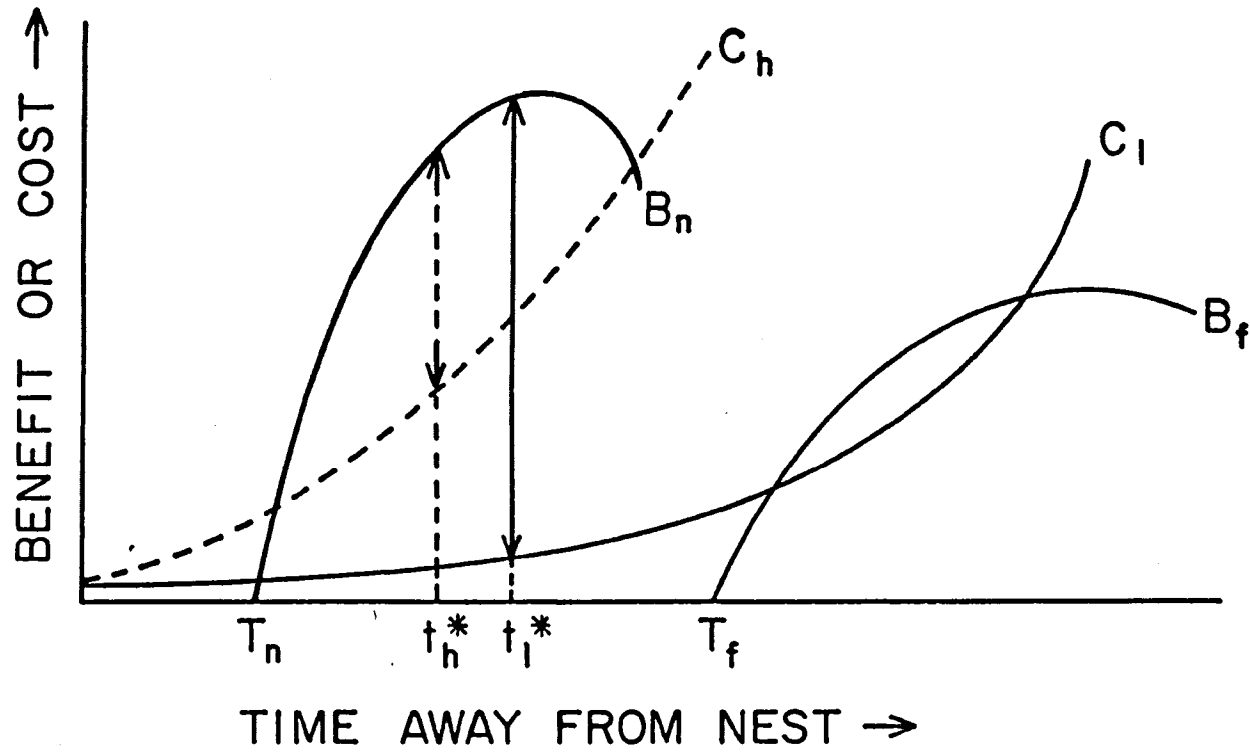


Figure 5. The predicted effects of increasing the attack rate at the nest.

See text for explanation.

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, $t_h < t_l$, 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 the trip. But if defense of the young is more important, the animal should return to guard the nest as soon as possible.

The Nest Attack Experiment

To evaluate the relevance of the nest defense model, I used stuffed specimens to increase the attack rate experimentally at Gila Woodpecker nests. The design was intended to mimic an intrusion by a foreign woodpecker, since I observed such encounters on several occasions. Foraging distances and delivery load sizes were observed in the field before and after the experimental attacks, to test directly for the effects predicted in the theory section.

Methods

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 Chapter 1 for details). The desert vegetation is quite open, so that during the nesting season (mid-April to mid-July), 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 detail the events there.

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 minutes after the residents had apparently 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 deliveries for at least one hour before and one hour after each trial. During this time, one observer tracked the movements of the birds, while the other independently monitored deliveries to the nest. 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. An observer sitting about 10 m. from 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). These Gila Woodpeckers delivered a single prey item on over 90% of their trips.

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 knock 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: $X^2 = 11.00$, $df=1$, $p < .001$).

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 10 shows that the males foraged closer to the nest after the attacks, as predicted by the nest defense hypothesis. No statistically significant change occurred in the females' foraging distances. Males delivered smaller loads after the attacks, again as predicted, but females did not change (Table 11). Further, males changed the composition of deliveries to include more saguaro pollen or fruit, as Table 12 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.

In Chapter 1, I showed that 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. 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

Table 10. Delivery distances before and after experimental nest attacks.

Entries are proportion of deliveries from each distance.

Males: $\chi^2 = 8.96$, $df = 2$, $p < .025$. Females: $\chi^2 = 2.15$, n.s.

	DISTANCE FROM NEST (METERS)			Sample Size
	0-9	100-199	≥ 200	
MALES				
Before	.54	.27	.19	122
After	.74	.15	.11	104
FEMALES				
Before	.56	.30	.14	57
After	.67	.20	.14	87

Table 11. Sizes of insect loads delivered to the nests before and after experimental attacks.

Entries are proportions of deliveries of each size category.

Males: $\chi^2 = 25.6$, $df = 2$, $p < .001$. Females: $\chi^2 = 3.08$, n.s.

	SIZE OF LOAD			Sample Size
	Small	Medium	Large	
MALES				
Before	.15	.68	.16	104
After	.48	.45	.07	98
FEMALES				
Before	.15	.62	.24	55
After	.24	.48	.28	86

Table 12. Type of food delivered to the nest before and after experimental attacks.

Entries are proportion of deliveries of each type.

Males: $X^2 = 7.29$, $df = 2$, $p < .05$. Females: $X^2 = 2.1$, n.s.

	TYPE OF DELIVERY			Sample Size
	Insect adult	Insect larva	Fruit	
MALES				
Before	.23	.43	.33	129
After	.18	.32	.50	137
FEMALES				
Before	.37	.31	.32	72
After	.30	.40	.30	121

vs. experimental insect sizes: $X^2 = 9.23$, $df=2$, $p < .01$). 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 ($X^2 = 0.84$, $df=2$, n.s.).

Parental Role Switching in Gila Woodpeckers

The results of the experiment indicate that males decreased their delivery rates and primarily guarded the nest after the attacks, while females increased their foraging rates to compensate. This was hardly the only time males behaved in a complimentary fashion; indeed, they often divided the labor involved in raising the young, and coordinated their activities. In this section, I present various observations to demonstrate some of the parental roles normally adopted, and the frequent occurrence of facultative role switching between the sexes. I focus on tradeoffs of feeding versus guarding the young.

The observations are taken from a study of 14 nests in the 1979 and 1980 field seasons. At one nest in 1979, two observers simultaneously followed both parents as they foraged on a total of ten days (eight mornings and two afternoons). Only the morning data are presented here, since the birds were mostly inactive in the heat of the afternoon. We observed 4 other nests in 1979 and 9 nests in 1980 for two mornings each. We kept records of the birds' foraging distances from the nest (estimated to the nearest 25 m.), and their delivery rates.

Most of the woodpeckers immediately habituated to the presence of the observers. At the site most intensively studied in 1979, however, the female was exceptionally wary of the observer by the nest, and made no deliveries during the first morning of observation, and only one the second morning. Instead, she stayed close to the nest (mean distance = 51 m, $n = 156$ plants visited, $sd = 50.8$ m), repeatedly giving the low-intensity alarm call ("call 2" of Brenowitz 1978). On the third day of observation, the female began delivering again, and subsequently increased her rate each day. During this period, she went much farther from the nest than before (mean distance = 148 m, $n = 350$ visits, $sd = 96.9$ m). Since the variances in distance from the nest were correlated with the means, I used log-transformed data for significance tests (see Sokal and Rohlf 1969, p. 382). The change in distance by the female after she resumed delivering was highly significant ($t = 14.7$, $df = 504$, $p < .001$). Figure 6 shows that the male compensated for the changes in the female's rate by changing his own rate of feeding the young. When the female initially stopped delivering, the male maintained a very high foraging rate and went farther from the nest (mean distance on 6/17 and 6/19 = 126 m, $n = 200$ visits, $sd = 75.9$ m). As the female increased her rate, however, the male decreased his rate, and stayed closer to the nest (mean distance after 6/26 = 73 m, $n = 200$ visits, $sd = 63.9$). Again, this change in distance was significant ($t = 219$, $df = 398$, $p < .01$). When not actively foraging and delivering, the birds just guarded the nest; they spent most of their time scanning and resting rather than searching or pecking for food.

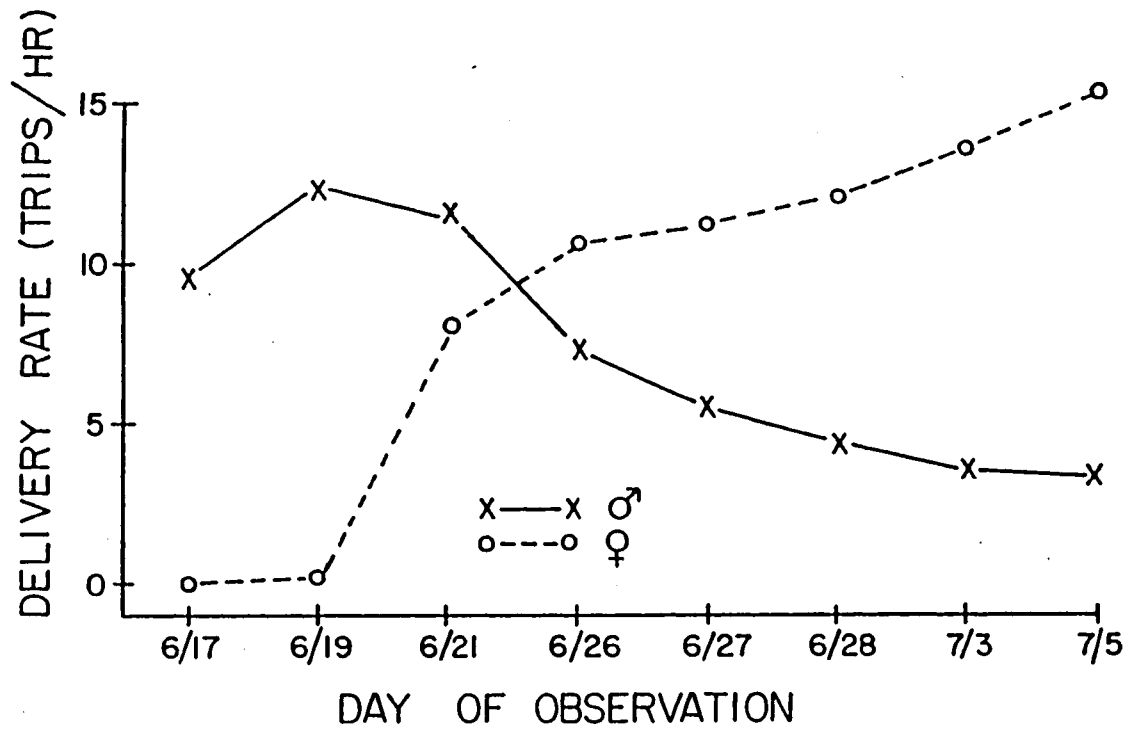


Figure 6. Rates of nest deliveries for a pair of mated Gila Woodpeckers on 8 mornings of observation in 1979.

See text for explanation.

The compensatory rate changes by the male occurred within an hour of changes in the female rate, as Figure 7 shows for the day the female resumed delivering. On average, males maintained a rate of about 8 trips/hr. and females a rate of about 12 trips/hr. from 0700 until 1200, so the pattern does not reflect a circadian rhythm. Over all mornings, there was a significant negative correlation in the hourly delivery rates of the two sexes ($r = -.54$, $n = 28$ hours, $p < .01$). I do not know if the male was responding to the female's activities per se or to the hunger level of the nestlings, who are exceptionally vocal. It is remarkable that about thirty percent of the variance in delivery rates by an individual could be accounted for by the behavior of its mate, since the environmental conditions usually considered important in determining foraging rates (prey availability, temperature, tec.) were undoubtedly similar for both sexes.

At a nest observed in 1979, the female disappeared altogether; the male then stayed much closer to the nest guarding it, and also increased his delivery rate. At one nest observed in 1979 and another in 1980, the males spent long periods of time (20 min. or more per bout) preparing secondary nest cavities. During such times, the females did all of the feeding of the young in the active nest, and increased their foraging rates.

Parental role switching was common. At one of the 1980 nests, the pair actually incubated a second set of eggs while feeding the first brood. The nest cavities were on different arms of the same saguaro cactus. Both the male and female incubated, as usual. While one was on the eggs, the other actively delivered food to the nestlings

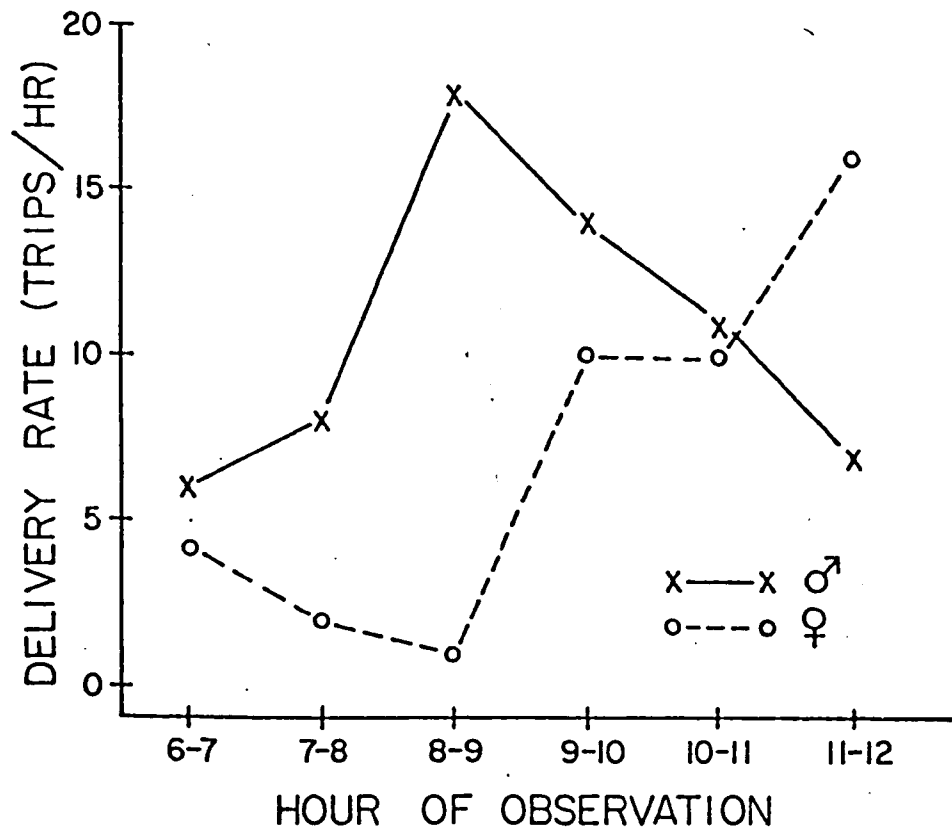


Figure 7. Rates of nest deliveries for the pair on an hourly basis.

Data are for 21 June 79, the day the female resumed delivery.

See text for explanation.

in the primary cavity. After twenty minutes or so per hour, the forager would relieve the incubator, who would immediately resume delivering food to the primary nest.

I observed another nest in 1980 after an immature bird from the first brood had already fledged. In this case, the adult female did not deliver food to the nest, but instead, guarded and fed the fledgling, while the male provisioned the young in the nest. As an experiment, I approached and harassed the fledgling and mother. The adult female gave several alarm calls, and the male joined the fledgling, guarding and feeding it for the next half hour or so. During this time, the female switched back to feeding the young still in the nest.

The facultative division of labor among sexes extended to the chore of removing fecal sacs from the nest cavities. At 11 of the 12 nests observed, the males alone performed this task. Only at one nest where the male was engaged in preparing a second nest cavity did the female clean the nest.

Male Gila Woodpeckers are considerably larger and more aggressive than the females, so it is not surprising that they assumed aggressive and defensive duties when the females could not successfully repel an invasion. On one occasion, for instance, the female was guarding the nest when it was vigorously attacked by a foreign adult male Gila Woodpecker. The intruder displaced the female several times, and explored a secondary nest cavity in the nest saguaro. The female gave several alarm calls, until the resident male returned from his foraging

location, some 200 m. away. The resident male then immediately attacked the intruder, chasing him to more than 300 m. from the nest.

The observations summarized above indicate that mated Gila Woodpeckers coordinate their activities so that one bird primarily searches for food while the other guards the nest. Roles are by no means exclusive; both sexes perform both (and other) tasks, and even switch back and forth. In general, the males take over nest defense when serious attacks occur, while females do more of the feeding of the young.

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 1980, 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. The data presented support the nest defense hypothesis; Gila Woodpeckers often decreased their foraging rate and distances for the sake of protecting the nest, and males foraged closer and delivered smaller prey when confronted with an increase in the perceived attack rate. Hence, at least one other dimension in addition to food - defense of the nest - appears necessary for a more complete model of foraging behavior during the breeding season.

The relative importance of nest defense may depend on the cost of starting a new nest if the current one is destroyed or usurped. Hole nesters like woodpeckers have an enormous investment in their nest cavities, which can take weeks to excavate (Short 1979). Open nesting species which can build a new nest in a few days may be less influenced by the attack rate, but they should also be responsive to this variable.

A corollary is that central place foraging patterns should depend on population density. At higher densities, the intrusion rate is higher, so the residents should move closer to the nest and deliver smaller items. Results supporting the delivery rate maximization model (e.g., Chapter 1 of this dissertation, Orians 1980) may be obtained only in years of relatively low population density, or early in the breeding season, since as the season progresses, the rate of invasions by fledglings from other nests increases.

Because the two objectives require different optimal behavior sets, an individual can not 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 (or many helpers) raise the young, the situation is complicated by the fact that individuals need not forage independently (as I have shown above for Gila Woodpeckers). Instead,

mates can work as a team simultaneously to pursue two objectives. 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.

Figure 6 illustrates the advantage to specializing when mates forage as a team. The figure shows indifference curves for various levels of nest defense and foraging effort; survivorship of the young increases in the direction indicated by the arrow (see Caraco 1979). I assume the curves to be concave because the effects on fitness of a unit increase in either variable should depend inversely on the amount of effort already being invested. For instance, if very little time is being spent foraging, the young would be in dire need of food. In this condition, the forager should be willing to sacrifice a relatively large amount of nest defense for only a small increase in foraging time, to save the young from starving. If a great deal of time is already being spent foraging, however, the young would be satiated, or nearly so, and a small increase in foraging effort would have little effect on their survivorship, so the parent should not be willing to forego nest defense in order to feed the young more.

The optimal behavior for an individual clearly depends on what its mate is doing. For simplicity assume that when the pair forages simultaneously, the effects on survivorship of the young are additive. If one partner is primarily foraging, as is A in the figure, its mate should defend the nest, B in the figure, since doing so maximizes the

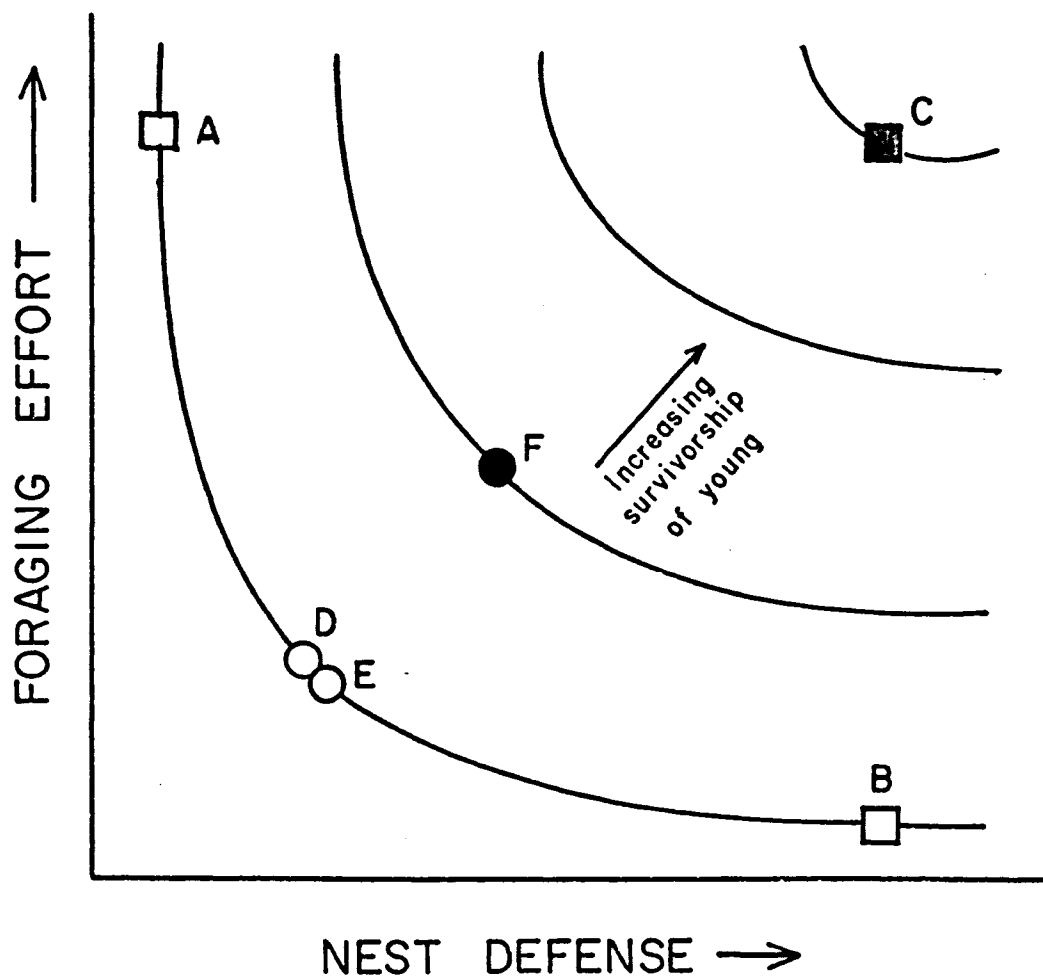


Figure 8. Indifference curves showing the tradeoffs of foraging effort and nest defense for parental teams.

All points on a curve confer the same survivorship on the young in the nest. Square symbols are specialists, round ones are generalists. Open symbols are individuals considered alone, closed ones are parental teams.

See text for explanation.

joint effect on survivorship, C. Points D and E correspond to a team of generalists who pursue both goals nearly equally; F is their combined effect on the young. Even though the foragers all have the same individual fitness if considered alone (A, B, D, and E are all on the same indifference curve), the young from the team of specialists have much higher survivorship than those of the generalists. Complete partitioning of the roles need not occur for the specialists to do better than generalists; in the figure, for instance, the specialists perform both foraging and defense tasks, but in unequal proportions.

The results for Gila Woodpeckers indicate that the males do tend to specialize on nest defense, while the females concentrate on nest deliveries. Since the male is larger, he can fend off intruders more successfully. 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 (Snyder and Wiley 1976).

Sexual dimorphism in birds, melanerpine woodpeckers in particular, has long been considered a mechanism for the reduction of ecological competition among the sexes. In a seminal paper, Selander (1966) showed that insular woodpeckers have less overlap in size and foraging behaviors than continental forms, presumably because there are

fewer other competitors on the islands. Christensen (1971) showed for Gila Woodpeckers that the degree of niche overlap among sexes also varied seasonally. In the winter when resources are scarce, the sexes overlapped less in their use of substrates than in the summer. But this effect depended to a large extent on the fact that in summer, both sexes heavily used the superabundant saguaro flowers and fruits, resulting in a high overlap value. In studies of this sort, interaction among the sexes is assumed to be primarily competition for food. It is certainly true that food eaten on a common territory by one member of the pair is unavailable to the other. But these birds apparently mate for life, and must spend much of their time together guarding their young as well as foraging, so sexual dimorphism may result in part from the joint benefits of cooperation on the survivorship of the young.

By emphasizing behavioral cooperation among mates, I do not mean to imply that individuals are sacrificing their own fitness for the sake of their partner. Taylor (1979) and the authors cited by him have considered the questions of if and when to desert a mate. The decision to help raise the young should depend not only on how much parental behaviors can benefit current offspring, but also on how much helping detracts from the parent's chances of reproducing in the future with the same or possibly a different mate. For the Gila Woodpeckers, new mates and nest sites may be difficult or impossible to find in the breeding season, and there may be advantages to remaining with one mate on the same territory since prime foraging locations must be learned and remembered. In addition, nestlings and fledglings probably

have a very low survival rate when tended by only one parent. I observed just one nest from which the female disappeared; in this case the male attempted, but failed, to raise the young.

For those species in which parents do cooperate, one must consider mated pairs (rather than individuals) to be competing against other pairs in the population in a race to produce healthy offspring. I believe we should increase our efforts to elucidate the extent to which parental (or helper) behaviors are complimentary and coordinated. Which of the several proximal goals should an individual pursue when it is a member of a parental (or helper) team? To what extent should (and do) species in various life history and environmental settings divide the labor between the sexes and between defense versus foraging?

The results for Gila Woodpeckers showed that the same sexes often switched between nest defense and feeding the young. Facultative adjustments of parental behaviors have been noted for several other species as well. Chase (1980) recently reviewed the literature, and formulated the problem of parental investment as a set of decisions on whether to engage in cooperative or noncooperative behavior at each moment (rather than simply when to desert forever). Chase interpreted graphs like the feeding rates in Figures 4 and 5 as indicating various combinations of cooperative behaviors of the male and female. But Gila Woodpeckers not actively delivering food were generally guarding the nest or fledglings, or preparing a secondary nest cavity - such behaviors hardly qualify as noncooperative.

Currently, much theoretical work is being directed toward increasingly complex models based on maximizing an individual's foraging rate, but it is clear that an adequate explanation of behavior must include several objectives. In Chapter 1, I showed that many of the decisions made by nesting Gila Woodpeckers were consistent with the foraging model predictions, so feeding theories are useful as a first approximation. But I also showed that physiological constraints, not prey capture rates, were crucially important in the selection of substrates. In Chapter 2, I have shown that the foraging patterns of Gila Woodpeckers depend on the attack rate at the nest, which they closely defend. Moreover, pairs apparently work as a team to accomplish several tasks simultaneously, so models based on individuals alone are too simplistic. I hope that over the next several years, theorists devote more of their efforts toward developing predictive models of behavior with multiple goals. We should try to elucidate the ways in which various factors interact, rather than continuing to dissect but a single dimension.

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