

THE INFLUENCE OF FOOD ON REPRODUCTIVE STRATEGIES IN A MONOGAMOUS KINGFISHER (*CHLOROCERYLE AMAZONA*)

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ABSTRACT.—We examined the influence of food accessibility on the reproductive behavior of the Amazon Kingfisher (*Chloroceryle amazona*) in Panama. Both sexes invested equally in nest building, but females incubated the eggs more often than males. Foraging performance (time elapsed between successful dives) differed between mates because they often used different foraging patches within the breeding territory. Male foraging performance was significantly correlated to fish biomass sampled from preferred foraging patches. Furthermore, the level of a male's foraging determined the number of fish he fed to his mate: more successful foragers courtship-fed their mates more fish than less successful males. In turn, the rate of courtship feeding influenced whether a female would lay eggs and the date of laying. Pre-laying foraging performance of both sexes was a predictor of the number of fish fed to nestlings. We conclude that disparities in the amount of food delivered to ovulating females by males, and to nestlings by both parents, are determined by the distribution of food within the territory. Received 14 June 1990, accepted 24 February 1991.

FOOD abundance can affect the timing and success of breeding in birds (Kallander 1973, Murton and Westwood 1977, Drent and Daan 1980, Davies and Lundberg 1985). Furthermore, food distribution will influence mating patterns (Oring 1982, Wittenberger and Tilson 1980) and may determine the relative contribution of each parent to feeding nestlings (Reyer and Westertep 1985). In plentiful years when females can adequately provision young without help from the male, the value and level of paternal care decreases. In suboptimal years, however, male contribution is believed to be critical to offspring survival (Bart and Tornes 1989). The argument that there are periods when paternal care is essential implies that food availability is an important determinant of parental feeding patterns. The relationship between food availability and reproductive behavior is seldom quantified.

The issue is not simply overall abundance of food, but also whether food is equally available to each parent. If not, one parent may contribute less than its mate in feeding young, independent of any sex differences due to anisogamy or a prior investment in caring for the young (Trivers 1972, Beissinger 1987). Analysis of pa-

rental behavior using game theory shows that conflicts of interest between parents can account for the occurrence of multiple parental investment strategies (see reviews Maynard Smith 1977, Wittenberger 1979, Oring 1982). Such conflicts may arise if parents have an unequal access to essential resources such as food (Beissinger 1986). We propose that the reproductive behavior of both sexes can be strongly affected by their relative access to food. To test this hypothesis, we examined the relationship between food distribution, foraging, and courtship feeding rates of male Amazon Kingfishers (*Chloroceryle amazona*). We also examined the parental roles of males and females based on the relative food availability to each parent.

METHODS

Distribution and ecology.—The Amazon Kingfisher resides along lowland streams from southern Mexico into the Amazonian region of South America. The species is monogamous, with pairs often remaining mated for several years. Nests are excavated in exposed earthen banks along streams or in banks close to fresh water. Amazon Kingfishers eat fish, freshwater shrimp, and occasionally frogs and aquatic insect larvae (Davis unpubl. data). Typically, there is one brood per season; nestlings remain in the nest for a minimum of 21 days (Skutch 1957, Davis pers. obs.). Breeding occurs in the dry season, which along the Caribbean coast in Panama may extend from late December to July. The end of the breeding season coincides with flooding, which can destroy occupied nests. A pair defends a breeding territory that con-

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tains a nest bank and foraging patches, with territorial aggression directed primarily towards birds of the same sex (Remsen 1978, Davis unpubl. data).

We observed 12 mated pairs of *C. amazona* from mid-December to mid-May, 1987 and 1988, along the Cascajal River in Portobelo National Park, Panama. The moist rain forest along the banks of this lowland stream have been largely converted to cattle pastures. In early December in both years just before breeding began, we mist-netted and marked birds with colored leg bands and paint on the rectrices. We recorded changes in weather and water level throughout the breeding season. Nests located in earthen banks were opened from the top to allow access to the eggs and nestlings (Davis 1980). To assess breeding-population sizes, we counted the number of kingfishers and active nest burrows along several streams in the same general area as the Cascajal.

We observed individuals through binoculars or spotting scopes, and used focal sampling to record behavior (mean observation period [\pm SD] = 156 \pm 71 min). We timed specific behaviors (Table 1) to the nearest 5 seconds. Observations were made between 0700 and 1200. We recorded location and outcome of foraging events, prey size and type, and courtship feedings. Prey size was estimated to the nearest centimeter by comparing prey with the length of the bird's bill (which was known for all tagged individuals). The kingfishers' habit of beating their food before swallowing provided an opportunity to identify species of most prey items.

Prey abundance.—We estimated the number of fish accessible to *C. amazona* by recording the success of birds as they foraged at specific locations (foraging patches), and by counting the number of fish swimming within these patches. Because most foraging dives occurred in water <10 cm deep along edges of the river or in pools, we counted all fish that entered a half-circle of 2-m radius as measured from the edge of the stream. We adopted a sampling period of 5 min/count, because the average resident time of actively foraging kingfishers ($n = 33$ observations) in a patch was 5.7 \pm 3.7 min. Care was taken to approach the stream slowly so as not to disturb the fish. Once the observer was in position, counts began after 5 min to allow time for fish to habituate. We recorded the identity of species when possible, size (within the following categories: 0–3, 3.1–6, 6.1–9, and >9.1 cm), and swimming depth estimated to the nearest cm. We made 2–6 counts at most foraging locations. We analyzed only data from the 10 most frequently visited patches within a male's territory, because other patches were used infrequently (≤ 2 visits recorded per patch).

We converted fish counts into biomass (g) available per patch by extrapolating from regression equations that related length vs. wet weight for each species (water content of different species varied between 15% and 25% of body weight after drying at 100°C for

TABLE 1. Behavior categories.

Category (abbrev.)	Description
Active foraging (AFOR)	Bird stands alertly on a perch or hovers; attention directed toward a foraging area.
Passive foraging (PFOR)	Bird's attention is directed toward foraging area while bird sits low on its perch.
Total foraging (TFOR)	Combined time bird spent actively (AFOR) and passively foraging (PFOR).
Inactive (INACT)	Bird is perched; few body movements; attention directed away from stream; eyes periodically closed (sleeping).

24 h). Fish used to calculate regression equations were caught by seining. Most (>95%) fish caught by Amazon Kingfishers were 3–9 cm long and swam within 10 cm of the surface. Calculations of biomass from fish counts include only specimens that met these criteria. We also used regression equations to calculate biomass of prey captured by kingfishers.

Parental investment.—In 1987 we recorded the time and effort (number of visits) that adults spent on nest excavation and incubation. In 1987 and 1988 we recorded occurrences of courtship feeding (CF) and copulation. Courtship feedings included (1) voluntary feeding of females by males when the fish was offered head first; (2) involuntary feeding when a female wrestled a fish from a male; and (3) reversed feeding when the female fed the male (<1% of total number of courtship feedings observed).

In 1988, six females on contiguous territories failed to lay eggs by 4 March, the middle of the breeding season. We conducted supplemental feeding experiments to determine if low fish numbers contributed to this failure. On alternating territories ($n = 3$), we stocked a plastic-lined pool (45 cm in diameter and 12 cm deep) with a minimum 30 fish between 0700 and 0900. Supplemental feedings continued on a territory until the female laid her first egg or 28 days had elapsed. We recorded the number of courtship feedings and copulations for a period of 30–60 min after a pool was stocked.

Also in 1988, we conducted an experiment to determine whether the accessibility of food or number of nestlings would affect the amount of food parents brought to the nest. Seven nests with 12–15-day-old nestlings were tested. We observed feedings from blinds during three 5-h periods on consecutive mornings starting at 0700. During the first period, we recorded feeding rates without manipulating food or number of nestlings; at four nests, two control periods were run. At the start of the second period, we constructed a temporary pool within 20 m of the nest

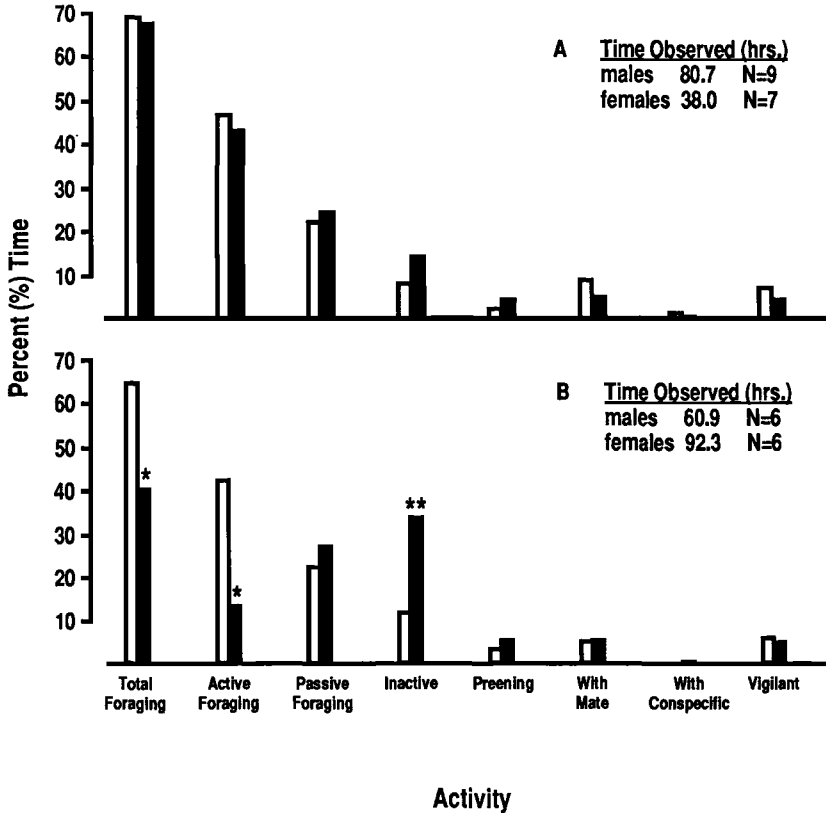


Fig. 1. Percent time spent by males and females in various activities before the first courtship feeding (A) and during the period of courtship feeding (B). Open bars represent males; closed bars, females. Asterisks indicate levels of significance of two-tailed, independent sample *t*-tests between values in A and B; * = $P < 0.05$ and ** = $P < 0.01$. Differences in the number of hours that males and females were observed are due to sampling bias. Early in the breeding season (A), we were preferentially following males. After the start of courtship feeding (B), we followed both sexes, but female activity decreased and females were in view more often than males.

and stocked it with fish. Fish were readily taken from the pools. At the start of the third period, we increased brood size by 50% by adding chicks taken from nests located along other streams (food was not supplemented). Age and weight of nestlings were matched to those of the resident chicks.

RESULTS

In 1988 we recaptured 18 of 24 individuals banded in 1987. Eight pairs remained intact and on their original territories, while one male and one female acquired new mates (unbanded). The fate of the remaining 6 birds is unknown. These data indicate a high degree of site fidelity by both sexes. We recorded 3 cases of females switching mates: 1 case after the pair's eggs had hatched (the male fledged their 4 young) and 2 cases before eggs were laid.

Both mates participated in nest excavation. We found no difference between the sexes in the number of digging bouts per observation period during 17 periods at 10 nests (male $\bar{x} [\pm SD] = 5.4 \pm 6.6$, female $\bar{x} = 3.7 \pm 3.8$; paired *t*-test, $t = 0.8$, $P > 0.1$) or in the total amount of time spent digging per observation period (male $\bar{x} = 701 \pm 942.1$ s, females $\bar{x} = 606.2 \pm 741.7$ s; paired *t*-test, $t = 0.3$, $P > 0.3$). We confirmed Skutch's (1957) report that only females incubate at night and both sexes share incubation duties during the day ($n = 6$ nests).

Before courtship feeding, the sexes spent equal percentages of time foraging (Fig. 1A), but after the start of courtship feeding, females significantly decreased their foraging time and increased their time sitting inactive (Fig. 1B). Furthermore, females who subsequently laid eggs

showed a more dramatic drop in percent time foraging (TFOR) than nonlaying females (Fig. 2: linear regression coefficients for laying females 4, 9, and 11 are $r = -0.96$ [$P < 0.001$], $r = -0.78$ [$P < 0.003$], and $r = -0.7$ [$P < 0.02$], respectively; for nonlaying females 8, 7, 6, and 12, $r = -0.42$ [$P > 0.08$], $r = -0.59$ [$P > 0.07$], $r = -0.47$ [$P > 0.6$], and $r = 0.08$ [$P > 0.7$], respectively). We obtained similar results with percent time actively foraging (AFOR); all r values for layers were statistically significant at $P < 0.05$, while all r values for nonlayers were nonsignificant ($P > 0.05$).

Foraging performance and resource availability.—Individual foraging performance of males varied substantially (Table 2). We defined *foraging performance* as the time a bird spends actively foraging (AFOR) divided by the number of successful dives. High numbers indicate poor performance. Mean fish biomass varied substantially both within and across territories (Table 3). Thus, variability in male foraging may be due to an unequal distribution of good foraging patches. In fact, we found a greater biomass of fish in territories of males who displayed the best foraging performance (territories 4, 9, 2, and 12; $\bar{x} = 104.7$ g) than in territories of males with the poorest record (territories 8, 7, and 6; $\bar{x} = 37.8$ g; two-tailed t -test, $t = 2.39$, $P < 0.05$; territory 11 was not included in the t -test because of the extremely low fish count on this territory). The results of a Spearman rank correlation between male foraging performance and total fish biomass per territory ($n = 7$, $r = 0.75$, $P < 0.05$, one-tailed) further indicate that fish biomass within a territory influenced the resident male's performance.

Foraging performance data are available for 4 birds in both 1987 and 1988 (females 4 and 7; males 8 and 3). A cross-year comparison shows that performance was significantly better in 1987 than in 1988 (paired t -test, one-tailed: in 1987, $\bar{x} = 51.7$; in 1988, $\bar{x} = 68.8$; $t = -2.6$, $P < 0.05$). Assuming that an individual's fishing skill does not decrease with experience, we believe that patch quality on average decreased between years and was responsible for the observed differences in performance across breeding seasons. Therefore, we consider the variability in patch quality—not the bird's fishing ability—to be an important factor affecting breeding success of *C. amazona*; all pairs in 1987 that laid eggs did so at earlier dates than the same pairs in 1988 (Fig. 3).

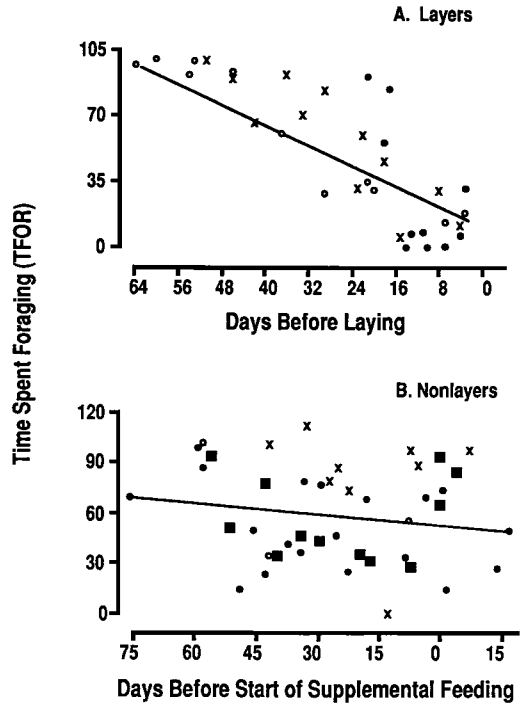


Fig. 2. Percent time that females spent foraging (TFOR). Layers (A) laid eggs unaided: females 4 (○), 9 (×), and 11 (●). Nonlayers (B) were supplied with food: females 8 (●), 7 (×), 6 (○), and 12 (■). In A, zero corresponds to the date when laying began. In B, zero corresponds to the day when supplemental feedings started. See text for values of regression coefficients.

We had insufficient data to assess the impact of patch quality on female foraging performance. However, our data indicate that mates partition foraging sites within their territory (Table 4). The fact that only one parent used supplemental feeding pools during our experiments is further indication that the sexes used separate foraging areas.

Courtship feeding.—Courtship feeding performance (minutes between feedings) of males varied substantially (Table 2). There was no significant correlation between courtship feeding performance and percent capture rate (number of successful dives per number of dives; Spearman rank correlation, $r = -0.48$, $df = 8$, $P > 0.05$), but there was a significant correlation between courtship feeding performance and foraging performance (Spearman rank correlation, $r = 0.63$, $df = 7$, $P < 0.05$; males 7 and 8 shared the last rank and male 6 was excluded because no courtship feedings were observed; see Table

TABLE 2. Male foraging and courtship feeding (CF) performance.

Pair	Year ^a	Time in view (min)	Courtship feeding performance (min/CF)	Foraging ^b performance (min/success)	No. of dives	Capture rate (%)
4	1987	191.9	64.0	—	0	—
	1988	623.3	105.4	28.7	14	35.7
9	1987	232.5	67.7	24.5	8	62.3
	1988	1,145.5	95.5	26.3	31	45.2
3	1987	406.3	65.7	37.9	4	33.3
2	1987	413.9	88.9	26.6	7	28.6
	1988	404.9	101.0	62.4	21	23.8
11	1987	102.6	102.6	—	4	0.0
	1988	1,164.8	77.7	12.6	32	59.4
8	1988-B	491.0	NA ^b	64.2	12	33.3
	1988-A	345.1	26.5	NA	NA	NA
7	1988-B	975.2	NA ^b	207.4	11	18.2
	1988-A	259.0	51.8	NA	NA	NA
6	1988-B	575.0	NA ^c	82.1	22	31.8
	1988-A	NA	NA	NA	NA	NA
12	1988-B	652.9	108.8	28.2	7	33.3
	1988-A	263.0	65.8	NA	NA	NA

^a Data from both 1987 and 1988; the time period BEFORE (B) and AFTER (A) the start of supplemental feeding in 1988 is given. Other values were calculated from data collected between the dates of the first recorded courtship feeding and egg laying. Data were not systematically collected for pairs 8, 7, 6, 12 in 1987 or pair 5.

^b Not Available (NA) because only 1 courtship feeding was observed.

^c Not Available because no courtship feedings were observed.

2). This implies that courtship feeding performance of a male is determined by his foraging performance.

Mates of males with poor performance laid few eggs or none. In 1988, when fish counts, foraging performance, and courtship feeding performance were low, females on territories 8, 5, 7, 6, 12, and 13 failed to lay eggs by the mid-point (early March) of the 1987 breeding season (Table 5). The failure to lay eggs may be due to the males' inability to adequately feed their mates. Specifically, a minimum feeding rate may be necessary to support egg laying (courtship feeding performance of males 8, 5, 7, 6, and 12 before the start of supplemental feedings were all <1 feeding/108 min). This hypothesis is

supported by the facts that males increased the number of courtship feedings when supplied with fish (Table 5), and that females on food-supplemented territories (8, 7, and 12) laid eggs while females on nonsupplemented territories (5, 6, and 13) failed to lay.

Feeding nestlings.—We observed a large variability in nestling feeding rate in both 1987 and 1988. In all but one pair both parents fed nestlings, although contributions were seldom equal (Fig. 4). In every instance where adults exploited the supplemental food, feeding rates increased above that of the control period (Fig. 5; average number of fish fed to each nestling during control periods was: 2, 2, 1.3, 1.7, 3.5, 2, 3; during food supplemented periods: NA, NA, 4,

TABLE 3. Estimated fish biomass from patches most frequently visited by males.

	Territory ^a							
	4	2	9	11	8	7	6	12
Mean biomass (g)	19.5	13.0	7.8	0.0	4.1	5.2	2.0	6.3
No. of patches	8	10	9	10	9	10	10	10
Coefficient of variation ^b	142	155	121	0.0	173	152	220	189

^a A continuum between territory 4, the farthest upstream, and territory 12, the farthest downstream.

^b Expressed as percent of the mean: CV = (SD × 100)/ \bar{x} .

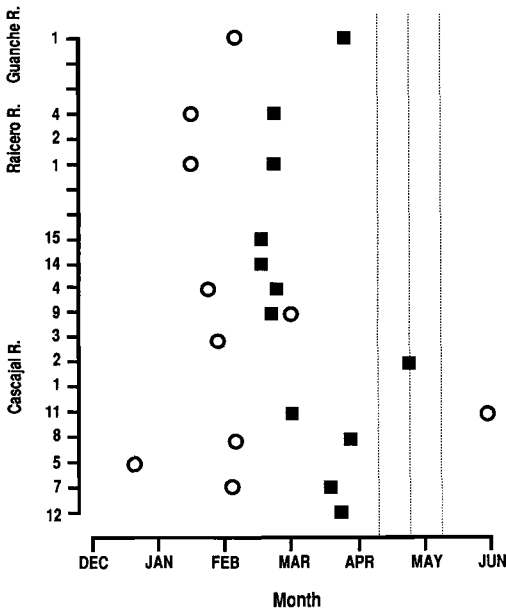


Fig. 3. Laying dates during 1987 (○) and 1988 (■). Territories (y-axis) are arranged with respect to location along the stream. Dates of flooding events that destroyed nesting banks are indicated by vertical dotted lines. Data from territories on the Raicero and Guanche rivers are shown for comparison.

4, 4.5, 3, 4 on territories 15, 4, 9, 11, 8, 7, and 1g, respectively [NA indicates that data are not available]). In contrast, when nestlings were added to a nest in absence of supplemental food, parents did not increase food deliveries to meet the increase in demand (Fig. 5; average number of fish fed to each nestling during chick supplemental periods was 0.8, 1, 1.8, 0.4, NA, 0.67, 0.8). Presumably access to food affects nestling feeding rates for each parent.

Logically, nestling feeding rates should be positively correlated with foraging performance of parents, but we could not test this deduction because it was impractical to record feeding activity at a nest and at the same time

follow parents as they foraged for food. We did compare prenesting data on foraging performance of parents that fed nestlings the most (\bar{x} = 86.7 min) vs. parents that fed the least (\bar{x} = 158.2 min) (one-tailed matched *t*-test; t = -2.13, df = 4, P = 0.05). Within a pair, the parent with the best early foraging performance will most likely become the best provider (i.e. display the highest feeding rate).

DISCUSSION

The accessibility of fish is of utmost importance for successful reproduction in *C. amazona*. Because foraging patches vary in quality and patch distribution is unlikely to be uniform, access to fish across territories will differ. Access to food affects foraging performance, which in turn determines the number of fish that males feed their mates before egg laying, which influences whether females lay eggs. Furthermore, because the sexes partition the available foraging sites within their territories, mates may have unequal access to food. Such resource partitioning can potentially lead to a disparity in parental investment (e.g. the amount of food fed to nestlings by each sex).

Variable foraging performance.—Variability in foraging performance is best explained by differential individual access to prey as opposed to differences in individual foraging ability. Prey accessibility is a function of fish density within a patch, as well as patch characteristics such as water depth, flow rate, turbidity, and substrate type (Davis 1982, Reyer and Westerterp 1985, Davis in prep.). Physical properties of a patch can change dramatically following moderate to heavy rainfall (Davis 1980) or by changes in the silt load. In fact, the rainy season in late 1987 (July to December) was particularly severe and of long duration (communication with local residents). This caused water levels to be consistently higher by 50 cm in 1988 than in 1987

TABLE 4. Percent similarity^a of patch use by mates.

	Pairs in 1987		Pairs in 1988						
	4	9	4	9 ^b	11 ^b	8	7	6	12 ^b
No. of visits	12	22	44	49	53	55	59	52	59
Time foraging	—	—	35	42	27	48	54	32	52

^a Percent similarity (PS): $PS = 1 - 0.5 \sum |p_1 - p_2|$ where p_1 and p_2 reflect the use of a specific patch by the male and female of a breeding pair respectively. Use was measured by both the percentage of the total number of visits to all patches and by the percentage of time spent in a patch.

^b One member of a pair foraged a proportion of its time in secluded backwaters or side tributaries.

TABLE 5. (A) Pre-laying supplemental food experiment conducted after 4 March in 1988. Results are shown relative to *Before* and *After* the start of the experiment. Pairs marked with an asterisk received supplemental feedings. (B) Comparable data on pairs laying eggs before 4 March. NA = not available.

Pair	Eggs laid?		Male CF performance (min/CF) After	No. of CFs		Observation time (h[days])	
	Before	After		Before	After	Before	After
A. Pairs included in experiment							
8*	No	Yes	26.5	1	20	44.2 [30]	[10] ^a
5	No	No	—	0	NA	NA	NA
7*	No	Yes	51.8	1	6 ^b	37.7 [23]	[3]
6	No	No	—	1	NA	16.6 [11]	NA
12*	No	Yes	65.8	6	17	20.9 [20]	[14]
13	No	No	—	NA	NA	NA	NA
B. Pairs laying eggs without help from supplemental feeding							
4	Yes	—	105.4	7	—	32.9 [23]	—
9	Yes	—	95.5	12	—	72.0 [38]	—
2	Yes	—	101.0	3	—	6.7 [9]	—
11	Yes	—	77.7	14	—	43.3 [26]	—

^a Behavior was not systematically recorded after food was supplied, therefore hours of observation are not reported.

^b Female foraged from supplemental feeding pond more than male.

along the Cascajal River. In 1988, frequent removal of gravel for road repair along the upper section of territory 11 produced large quantities of silt during periods of low water level. Siltation could account for no fish in territory 11 (Table 3) and the lower fish counts and foraging performances recorded from territories downstream (8, 5, 7, 6, and 12) as compared with territories upstream (2, 9, 4, and 15).

Disparity in territory quality is further increased by the use of foraging sites along tributaries or backwater pools. Although smaller tributaries offer an abundant food supply, Amazon Kingfishers seldom nested along them because nests located in low banks, typically found along tributaries, are more vulnerable to predators and flooding (Brooks and Davis 1987). The demand for safe nesting banks may result in habitat saturation along larger rivers, where fish availability is not necessarily greater than along their tributaries. An irregular distribution of nesting banks could produce a mosaic of territories that differ in size and vary substantially in foraging site quality (Davis 1982).

Patch partitioning and patch quality within a territory may produce unequal access to food and, subsequently, a significant disparity in foraging performance between sexes. One possible advantage of patch partitioning by mates is an increase in total yield from their territory. This is because a significant recovery period exists after a dive during which fish are inaccessible within a patch (5–10 min; unpubl. data). Hence,

if mates fished from the same limited number of sites, each bird may unknowingly waste time in a patch that has not recovered from its last disturbance. Partitioning of foraging sites has also been reported in the Belted Kingfisher (*Ceryle alcyon*; Davis 1982).

Courtship feeding.—Two hypotheses have been developed regarding courtship feeding: (1) courtship feeding is not critical to egg production but plays a vital role in the initiation or maintenance of bonds between mates (Lack 1940, Morley 1949, Tasker and Mills 1981) and (2) courtship feeding provides essential nutrients required by females to lay eggs (Royama 1966, Krebs 1970, Nisbet 1973). Both hypotheses have merit. When food is abundant and needs are low (or in large birds that lay a few small eggs), courtship feeding appears to be nutritionally nonessential for laying females (Poole 1985). On the other hand, in species for which foraging is energetically expensive, the energy gained from courtship feeding by males may trigger egg laying (Hunt 1980). Female Amazon Kingfishers who received few courtship feedings in 1988 failed to lay eggs until fish were made available in artificial pools. When prey became available, courtship feedings substantially increased, and eggs were laid within 3 to 4 weeks (Table 5).

The nutrition hypothesis assumes that the female's energy budget is insufficient for both self-maintenance and egg formation. If so, one would expect ovulating females to minimize

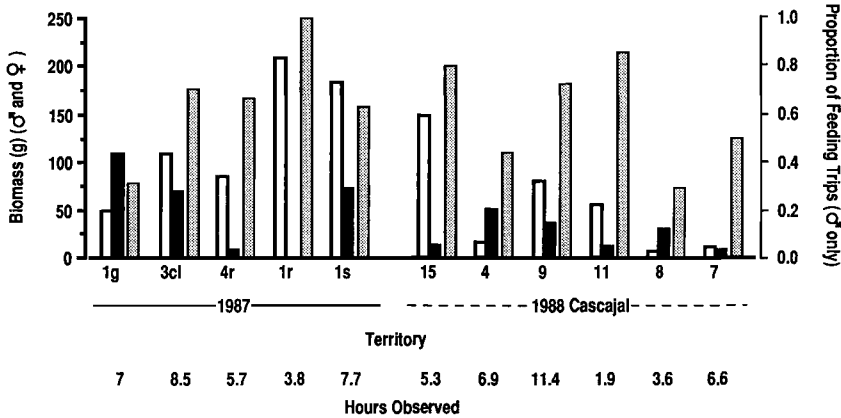


Fig. 4. Nestling feeding rates. Right scale (proportion of total feeding trips) refers to the stippled bars (males only). Left scale (biomass delivered; wet wt.) refers to the open (male) and solid (female) bars. Data from 1987 are shown along the left while data from 1988 are shown on the right. The number of hours each nest was observed is shown along the bottom.

unnecessary activities to conserve energy. In this study we observed that as the date of egg laying approached, female kingfishers who were fed by their mates progressively decreased the time spent foraging and increased time spent inactive. We proposed that an energy saving is realized by females who stop foraging and rely on their mates for food (see Krebs 1970). Decreased foraging by ovulating females may also have functions other than energy conservation. For example, an ovulating female may stop foraging because the act of diving to catch a fish could damage a developing egg. This possibility, the "gravid female" hypothesis, has been used to explain reduced activity levels in other birds (Nisbet 1977, Newton 1979, Wheeler and Greenwood 1983).

Males who display high courtship feeding performance are more likely to sire offspring than poor performers for several reasons. First, a female may desert a male who is a poor provider. We observed two cases in which a female switched to a neighboring bachelor male. A skewed sex ratio favoring males in our population (unpubl. data), may promote female desertion. Second, poor courtship feeding performance apparently inhibits egg laying. In 1988, downstream pairs failed to lay eggs until they were provided with supplemental food (which males readily used to increase their feeding rates; Table 5). Apparently, during periods when fish are readily available, courtship feeding is restricted to a period of 2-3 weeks followed by egg laying, but when food is difficult to catch,

courtship feeding may occur over a period of months at levels too low to initiate laying. Low rates of courtship feeding delay laying and may reduce fledgling survival. Delayed nesting can increase the chicks' vulnerability to floods that come at the end of the breeding season. In 1987 and 1988 we recorded both egg and nestling

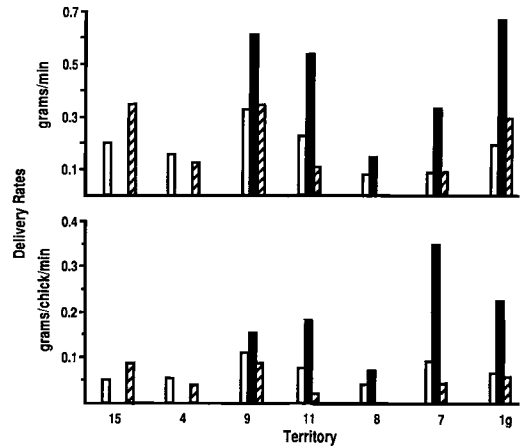


Fig. 5. Delivery rate of fish during nestling augmentation. Open bars: control period; solid bar: food added; hatched bar: nestlings added. Missing bars indicate that neither parent fed from the artificial pool or that chicks were not added to the nest. Both sexes were involved in feeding young, except female 11. Data from both sexes were pooled to calculate rates for each pair tested. See text for data on the number of fish fed to nestlings.

mortality due to late flooding (also see Davis 1980). Because laying occurred 3–4 weeks later in 1988 than 1987 (Fig. 3), it was the first nests that were destroyed by flooding in 1988, whereas only second attempts were destroyed in 1987.

Variable nestling feeding rate.—The effect of food availability on parental behavior has been studied in the Pied Kingfisher (*Ceryle rudis*; Reyer 1980, 1984; Reyer and Westerterp 1985). Reyer and Westerterp (1985) report that the amount of food delivered to nestlings by males was strongly influenced by accessibility to high-quality prey. In our study, accessibility to prey also appears to affect parental behavior. For example, we observed a dramatic rise in feeding rates when food was made available during the nestling augmentation experiment. On the other hand, an increased demand achieved by adding chicks to nests did not significantly affect either the proportion or amount of food delivered to nestlings by parents. Feeding rate apparently is controlled more by vagaries in food availability than nestling demand. We concluded that the large variability observed in nestling feeding rate (Fig. 4) was likely caused by a heterogeneous distribution of fish within territories, such that parents had unequal access to fish.

We propose that food constraints imposed by a variable and unpredictable environment is the principal factor selecting to maintain monogamy in *C. amazona*. Before laying, for example, low or unpredictable food supply may limit a male's ability to courtship-feed his mate, as well as restrict his ability to attend to additional females. Later in the season, vagaries in food supply coupled with a patchy distribution of foraging sites can lead to low foraging performance by one or both parents. If energy demands of young are high, low foraging performances may force both parents to provide food to nestlings as opposed to searching for additional mating opportunities.

Parental investment theory cites various reasons for differences in parental roles of males and females. These include physiological sex differences, differences in additional mating opportunities, scarcity of breeding habitat, and difference in prior investment in offspring (Trivers 1972, Silver et al. 1985; also see references in Winkler 1987). We propose that unequal access to food resources should be added to this list. The fact that mates exploit different foraging patches within their territory could

have a profound effect on their respective abilities to catch fish and, hence, feed their young.

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LITERATURE CITED

- BART, J., & A. TORNES. 1989. Importance of monogamous male birds in determining reproductive success: evidence for House Wrens and a review of male-removal studies. *Behav. Ecol. Sociobiol.* 24: 109–116.
- BEISSINGER, S. R. 1986. Demography, environmental uncertainty, and the evolution of mate desertion in the Snail Kite. *Ecology* 67: 1445–1459.
- . 1987. Anisogamy overcome: female strategies in Snail Kites. *Am. Nat.* 129: 486–500.
- BROOKS, R. P., & W. J. DAVIS. 1987. Habitat selection by breeding Belted Kingfishers (*Ceryle alcyon*). *Am. Midl. Nat.* 117: 63–70.
- DAVIES, N. B., & A. LUNDBERG. 1985. The influence of food on time budgets and timing of breeding of the Dunnock *Prunella modularis*. *Ibis* 127: 100–110.
- DAVIS, W. J. 1980. The Belted Kingfisher: its ecology and territoriality. MS thesis. Cincinnati, Ohio, Univ. Cincinnati.
- . 1982. Territory size in *Megaceryle alcyon* along a stream habitat. *Auk* 99: 353–362.
- DRENT, R. H., & S. DAAN. 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea* 68: 225–252.
- HUNT, G. L. 1980. Mate selection and mating systems in seabirds. Pp. 113–144 in *Behavior of marine animals*. Vol. 4, Marine birds (J. Berger, B. Olla, and H. Winn, Eds.). New York, Plenum Press.
- KALLANDER, H. 1973. Advancement of laying of Great Tits by the provision of food. *Ibis* 116: 365–367.
- KREBS, J. R. 1970. The efficiency of courtship feeding in the Blue Tit *Parus caeruleus*. *Ibis* 112: 108–110.
- LACK, D. 1940. Courtship feeding in birds. *Auk* 57: 169–178.
- MAYNARD SMITH, J. 1977. Parental investment: a prospective analysis. *Anim. Behav.* 25: 1–9.
- MORLEY, A. 1949. Observations on courtship-feeding and coition of the Marsh-tit. *Br. Birds* 42: 233–239.

- MURTON, R. K., & N. J. WESTWOOD. 1977. Avian breeding cycles. Oxford, U.K., Clarendon Press.
- NEWTON, I. 1979. Population ecology of raptors. Vermillion, South Dakota, Buteo Books.
- NISBET, I. C. T. 1973. Courtship-feeding, egg size and breeding success in Common Terns. *Nature* 241: 141-142.
- . 1977. Courtship-feeding and clutch size in Common Terns *Sterna hirundo*. Pp. 101-109 in *Evolutionary ecology* (B. Stonehouse and C. Perrins, Eds.). London, University Park Press.
- NUR, N. 1987. Parents, nestlings and feeding frequencies: a model of optimal parental investment and implications for avian reproductive strategies. Pp. 457-475 in *Foraging behavior* (A. Kamil, J. R. Krebs, and R. H. Pulliam, Eds.). New York, Plenum Press.
- ORING, L. W. 1982. Avian mating systems. Pp. 1-92 in *Avian biology* (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). New York, Academic Press.
- POOLE, A. 1985. Courtship feeding and Osprey reproduction. *Auk* 102: 479-492.
- REMSEN, J. V. 1978. Geographical ecology of Neotropical kingfishers. Ph.D. dissertation. Berkeley, California, Univ. California.
- REYER, H. U. 1980. Flexible helper structure as an ecological adaptation in the Pied Kingfisher (*Ceryle rudis*). *Behav. Ecol. Sociobiol.* 6: 219-227.
- . 1984. Investment and relatedness: a cost/benefit analysis of breeding and helping in the Pied Kingfisher (*Ceryle rudis*). *Anim. Behav.* 32: 1163-1178.
- , & K. WESTERTERP. 1985. Parental energy expenditure: a proximate cause of helper recruitment in the Pied Kingfisher (*Ceryle rudis*). *Behav. Ecol. Sociobiol.* 17: 363-369.
- ROYAMA, T. 1966. A re-interpretation of courtship feeding. *Bird Study* 13: 116-129.
- SILVER, R., H. ANDREWS, & G. F. BALL. 1985. Parental care in an ecological perspective: a quantitative analysis of avian subfamilies. *Am. Zool.* 25: 823-840.
- SKUTCH, A. F. 1957. Life history of the Amazon Kingfisher. *Condor* 59: 217-299.
- TASKER, C. R., & J. A. MILLS. 1981. A functional analysis of courtship feeding in the Red-billed Gull (*Larus novaehollandiae*). *Behaviour* 77: 222-241.
- TRIVERS, R. L. 1972. Parental investment and sexual selection. Pp. 136-179 in *Sexual selection and the descent of man, 1871-1971* (B. Campbell, Ed.). Chicago, Aldine.
- WHEELER, P., & P. J. GREENWOOD. 1983. The evolution of reversed sexual size dimorphism in birds of prey. *Oikos* 40: 145-149.
- WINKLER, D. W. 1987. A general model for parental care. *Am. Nat.* 130: 526-543.
- WITTENBERGER, J. F. 1979. The evolution of mating systems in birds and mammals. Pp. 271-349 in *Handbook of behavioral neurobiology*. Vol. 3, Social behavior and communication (P. Marler and J. Vandenbergh, Eds.). New York, Plenum Press.
- . 1982. Factors affecting how male and female Bobolinks apportion parental investments. *Condor* 84: 22-39.
- , & R. L. TILSON. 1980. The evolution of monogamy: hypotheses and evidence. *Annu. Rev. Ecol. Syst.* 11: 197-232.