

BREEDING BEHAVIOR OF THE GREEN-RUMPED PARROTLET

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ABSTRACT.—We studied the breeding behavior of Green-rumped Parrotlets (*Forpus passerinus*) using nest boxes in the llanos of Venezuela. Aggressive and courtship displays, and nest prospecting behavior are described. Females occupied nest boxes for about 80% of daylight hours from shortly before egg laying through hatching (30–40 days), and did all incubating and brooding. Males spent nearly 80% of the time away from the nest, presumably foraging for their mates and chicks. Clutch sizes of females were correlated positively with the rate at which they were fed by males during egg laying. Clutches hatched asynchronously, and nestling growth and development was slow. Females stopped brooding when oldest chicks were one to two weeks of age to join their mates in feeding young, though the youngest chicks were at most a few days old. Food delivery rates by parents to young were related positively to brood size after all eggs had hatched. Most pairs (91%) remained mated throughout the breeding season. Mate replacement between years was more common ($\geq 31\%$). More than half of the females that nested in the first part of the breeding season attempted second nests. Intervals between nesting attempts ($\bar{x} = 22$ days) were correlated positively with the number of young fledging from first nests. Over three-quarters of the pairs that remained together and renested used the same nest box, even though intruders constantly attempted to obtain nest sites. Results are discussed in relation to the division of parental care and the high degree of pair cohesion exhibited by parrots. Received 9 April 1991, accepted 1 Oct. 1991.

Little is known about the breeding biology of the Green-rumped Parrotlet (*Forpus passerinus*), one of seven species in the Neotropical genus *Forpus*. Green-rumped Parrotlets inhabit lowland wet and dry forests, savannah, and farmlands (Friedman and Smith 1950, Forshaw 1989). During the rainy season, nests are made in unlined natural tree cavities in holes excavated in arboreal termitaria (Belcher and Smooker 1936, Friedman and Smith 1950, Forshaw 1989), and in cavities in wooden fence posts (Beissinger and Bucher 1991). One unusual nest was in a hole at the base of a palm frond (Belcher and Smooker 1936) and another was in the cross-arm of a clothesline support (Friedman and Smith 1955). Clutches of captive pairs usually range between four and six eggs, but up to 10 eggs have been recorded (Wildeboer 1926, Enehjelm 1951, Noble 1984). During the dry season, breeding appears to cease and flocks of more than 100 birds can be seen (Morton 1979).

This paper presents new information on the breeding biology and food

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habits of the Green-rumped Parrotlet in the llanos of Venezuela. We also present some information on the bird's behavior in the dry season.

STUDY AREA AND METHODS

We studied Green-rumped Parrotlets on the cattle ranch Hato Masaguaral, 45 km south of Calabozo, in Guarico, Venezuela (8°34'N, 67°35'W). The study area is mostly flat natural savanna, or llanos, with scattered clumps of mature trees. Vast areas flood seasonally in the wet season (June–November) and dry out in the dry season (December–May) (Troth 1979, Beissinger et al. 1988). We conducted field work from June to December, 1988, and during the last two weeks of March, 1989. Additional sightings of banded birds were made from June to December, 1989 as part of other studies (Beissinger and Stoleson, in press). Rainfall measured 139 cm during the study in 1988 and there was no rain during the fieldwork in March, 1989.

Forty nest boxes, made from polyvinyl-chloride plastic, were attached to fence posts frequently used by nesting Green-rumped Parrotlets (Beissinger and Bucher 1991). The boxes were opened and observations were begun on 21 June, 1988. At that time no active nests were found but about 15 to 20 pairs were prospecting for nest sites in fence posts. Adult birds were caught in 12-m mist nets near active nests along fencelines, and uniquely banded with plastic color and aluminum bands.

Nest boxes were checked every one to two days for activity and contents. Eggs were uniquely marked with indelible ink, weighed to the nearest 0.1 g with a 10-g Pesola scale, and measured for length and width to the nearest 0.01 mm with dial calipers. Egg volume was calculated from Hoyt's (1979) equation: $\text{volume} = (0.51) \times (\text{egg length}) \times (\text{egg width})^2$. Hatchlings were weighed to the nearest 0.1 g with a 10-g Pesola scale and marked on their toe nails with a unique color of fingernail polish. Nestlings were reweighed to the nearest 0.1 and 0.5 g with 10-g and 30-g Pesola scales every two–five days until fledging. We banded nestlings near day 20 with a unique combination of colored plastic and aluminum bands. Nestlings were considered to have fledged if they survived in the nest until at least 25 days of age.

We observed nests from 30 to 50 m with a 15–40× telescope and 10× binoculars for two to four hour periods throughout the nesting cycle between 07:00 and 13:00 h. Sex of parents was differentiated by plumage dichromatism (Forshaw 1989). The locations of parents were noted as “inside the nest cavity,” “in the nest area” (within a ten-m radius of the nest), or “outside the nest area.” The presence of conspecifics and other birds in the nest area was recorded. Courtship, parental and nest defense behaviors were recorded for each parent. Twenty-five active nests were observed at least once and sixteen nests were observed at least four times, generally at 7 to 10 day intervals. We made a total of 99 nest watches totaling 295 h.

During our watches, *F. passerinus* often disappeared from view, either outside the nest area or inside the nest cavity, and it was difficult to be sure if birds fed their mates or young when feedings were not in view. However, males often had seeds on their bills after emerging from the cavity or after returning to the nest area with their mates. Therefore, we assumed that males fed egg-laying, incubating, and brooding females whenever the male returned after at least 10 minutes away from the nest area and then disappeared with the female either into the cavity or away from the nest. Females were assumed to have foraged for themselves if they were seen foraging or disappeared from the nest area for more than ten minutes. When nests contained young, parents often had seeds on their bills and frequently shook their heads in a pre-regurgitation motion before entering the box. Occasionally, nestling begging calls could be heard from inside the boxes. Thus, we assumed that nestlings

were fed whenever a parent returned from a trip away from the area of at least 10 min duration, and then entered the nest or passed food to a mate which subsequently entered the nest. Visits by each parent to nests with young were scored as separate feeding bouts.

Observations of diet, vocalization, flocking, and roosting behavior were made ad libitum during nest observations, nest checks, mist netting, and periodic walks through the study area.

Clutch sizes were categorized as small (5–6 eggs), medium (7–8 eggs), and large (9–10 eggs). Likewise, brood sizes were defined as small (1–5 young), medium (6–7 young), and large (8–10 young). The nesting cycle was divided into six periods: courtship, egg laying, incubation, hatching, nestling, and fledging.

Data were analyzed using SYSTAT (Wilkinson 1990). Means are reported with standard deviations. Percentages were arcsin-transformed to normalize the distribution. When data were normally distributed and variances were equal, analyses of variance (ANOVA), and *t*-tests were used to compare behaviors of parents among different periods and among different-sized clutches and broods. The Spearman rank correlation was used with non-parametric data. Logistic curves and growth parameters were fit to weights from chicks of known age with empty or nearly empty crops using the SAS NLIN procedure (SAS 1988).

RESULTS

Nest prospecting.—Individual pairs prospected at up to six nest sites before deciding on a cavity. Pairs flew to potential nest sites together up to 10 times per hour. Upon arriving at a potential nest site, prospecting pairs were usually very vocal, emitting a loud “rapid chatter” of indistinct notes, similar to the twittering of Budgerigars (*Melopsittacus undulatus*) (Forshaw 1989).

While prospecting at nest sites, pairs were often accompanied by and fought with additional pairs and unmated males. Birds gave a threat display by spreading wings, expanding plumage, and crouching with bills opened and tails fanned. Birds lunged at one another, usually with bills opened wide and feet clutching at a perch and occasionally grasped one another with bills or feet. A penetrating “tsup-tsup” call, described by Snyder (1966), often accompanied these encounters. *F. passerinus* occasionally behaved aggressively towards other species at nest sites, particularly Saffron Finches (*Sicalis flaveola*). Saffron Finches, Straight-billed Woodcreepers (*Xiphorhynchus picus*), Spot-breasted Woodpeckers (*Chrysomitris punctigula*) and Dusky-capped Flycatchers (*Myiarchus tuberculifer*) all nested in fence posts. *S. flaveola* and *M. tuberculifer* occasionally nested in the *Forpus* nest boxes.

Courtship behavior.—Several ritualized head, tail, and wing movements were initiated by both sexes throughout the nesting cycle, but occurred most frequently during the courtship period. These courtship displays, described below, often preceded or followed the entrance of one or both members of a pair into the cavity. In the early stages of prospecting, it was usual for birds to enter cavities singly while their mates waited outside.

During “head bowing” displays, the body was bent forward and the head was rocked up and down, usually but not always into or towards an opening of a potential nest cavity. The tail was sometimes tipped into the air as the head was directed downward. Bouts of head bowing typically lasted from a few seconds to 1.5 min ($\bar{x} = 23.8 \pm 13.3$ sec, range = 5–100 sec, $N = 62$). Birds bowed alone or facing their mate, alternating downstrokes between pair members.

“Tail fanning” usually accompanied head bowing. Tail feathers were spread in a fan-like manner for up to 30 sec, or were alternately fanned and relaxed for only a second or two at a time. Tail fanning bouts averaged 18.2 ± 11.2 sec (range = 2–100 sec, $N = 48$).

“Wing flashing” was performed almost exclusively by males in the presence of females or other males, usually, but not always, at a potential nest site or before copulation. Three types of wing flashing were discernible: quick flicks, full spread and shake, and slow lifts. During “quick flicks,” described by Arman and Arman (1980) and Snyder et al. (1987), the wings were quickly spread and refolded, revealing a flash of blue underwing color for less than a second. Bouts of “quick flicks” ranged from 1 to 129 sec ($\bar{x} = 18.1 \pm 32.1$ sec, $N = 56$). Females occasionally performed “quick flicks” when fighting with conspecifics at a nest site, even though females lack the contrasting blue underwing of males. “Full spread and shake” was observed on only six occasions, always performed by males before a group of one or more females and one or more other males. Wings were fully extended to the sides and then rapidly moved forward and back, no more than a few centimeters, for 6 to 250 sec ($\bar{x} = 120.8 \pm 115.4$ sec, $N = 6$). This action produced a blur of brilliant blue from the underwing.

“Slow lifts” were also performed by solitary males perched in trees often within 20 m of an active nest. The folded wings were slowly lifted a few centimeters and rotated outward slightly, revealing the blue underwing. Wings were extended in this manner for only 2 or 3 sec at a time. “Slow lift” bouts ranged from 1 to 58 sec ($\bar{x} = 21 \pm 21.3$ sec, $N = 8$). “Slow lifts” were usually accompanied by a shrill “chee . . . chee . . . chee,” consisting of three to seven notes (Friedman and Smith 1950). Males called in this way to females in a nest cavity. We believe that females may recognize their mates’ calls because females usually climbed to the cavity opening when their own mates called but not when other males called.

Two types of bill contact were observed within pairs. Pairs often engaged in “nipping bouts” at a potential nest site, especially during agonistic encounters. Pairs typically lunged at one another’s bills, legs, and feet, poking and nipping at the flesh in a manner suggesting heightened allo-

preening. Nipping bouts lasted between 4 and 24 sec ($\bar{x} = 10.7 \pm 5.5$ sec, $N = 38$). Pair members often "allopreened" their mates in the head and neck regions. Allopreening bouts often were mutual preening bouts and ranged from 4 to 309 sec ($\bar{x} = 45.4 \pm 53.2$ sec, $N = 102$).

"Courtship feeding" was observed on fence lines within 5 m of the nest cavity and in vegetation within 40 m of nests. Females begged to initiate courtship feeding by crouching forward, fully opening their bills, and rocking their heads up and down rhythmically. Feeding bouts lasted between 6 and 88 sec ($\bar{x} = 26.5 \pm 19.9$ sec, $N = 33$) and were occasionally punctuated with a high pitched scream emitted by the female. Prior to feeding females, males began regurgitation by rotating their heads in an elliptical manner from side to side. Food was delivered with bills clasped at right angles. Afterwards, regurgitated seeds were frequently observed on the male's bill.

F. passerinus fed mostly on forbs and grasses, especially *Croton hirtus*, *Hyptis suaveolens*, *Wissadula* sp., *Cyperus* spp., *Scoparia dulcis*, and *Melochia parviflora*. *C. hirtus* occurred most often in the crops of nestlings. Parrotlets also occasionally fed on seeds from the fruits of trees, such as *Anona* sp. and guava (*Psidium guava*). Most birds foraged in small flocks of 3–20 individuals, but in the dry season, *F. passerinus* foraged in flocks of over 100 individuals.

Sometimes pair members locked their bills together as if courtship feeding but without the preceding male regurgitation or female begging motions characteristic of feeding bouts. These "bill clasping" episodes were witnessed only during the courtship and egg-laying periods and lasted between 28 and 168 sec ($\bar{x} = 53.6 \pm 55.5$ sec, $N = 9$). It was difficult to determine whether food passage occurred at these times or whether "bill clasping" was another courtship behavior. Bouts of "bill clasping" were distinct from normal courtship feeding bouts, which were usually composed of a series of short bill grasps separated by regurgitation and begging.

Copulation occurred in trees within 40 m of the nest and rarely on fence lines. Begging and courtship feeding often preceded copulation. Males typically "quick flicked" or "full spread" their wings while walking towards the female, and often engaged in "nipping bouts" before mounting. Copulation behavior was typical for New World parrots (Smith 1975, Skeate 1984, Snyder et al. 1987), except that the male often grasped the female's primaries while mounting rather than placing one foot passively on her back. Copulations lasted between 63 and 205 sec ($\bar{x} = 91.9 \pm 34.3$ sec, $N = 17$), and occurred from seven days before egg laying began until six days after egg laying had ceased. After copulation, a pair often engaged in allopreening before returning to the nest cavity.

Nest site attachment and occupancy.—Ownership of a nest site was

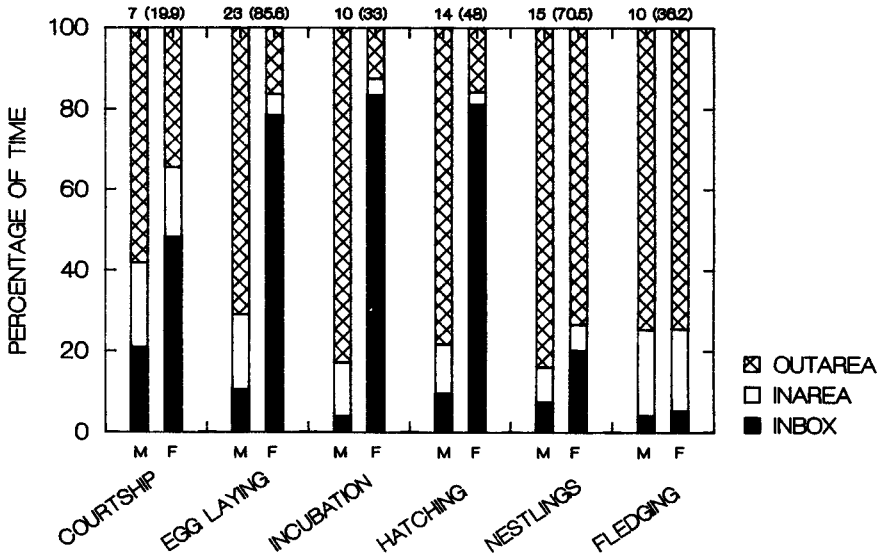


FIG. 1. Percentage of daylight hours that male (M) and female (F) *Forpus passerinus* parents spent in three locations during the six periods of the nesting cycle. Dark bars represent time spent in nest cavities, open bars represent time spent in the nest area and crosshatched bars represent time spent out of the nest area. Number of observation periods (total h of observation) are depicted by numbers above the bars.

established when both members of a pair entered the cavity together and remained inside for minutes at a time. Time budgets of males and females became quite different as egg laying approached and remained different well into the nestling period. Males spent progressively more time away from their nests while females spent most of their time in the nest until all of their eggs hatched (Fig. 1). A three-way ANOVA (Table 1) showed that the percentage of time that parents spent in, near, and away from the nest (location) differed significantly. Location interacted with sex and nesting period, indicating that the sexes differed in their locations during some periods of the nesting cycle but not during others (Table 1, Fig. 1).

A few days before egg laying, females began spending about 75% of the time in the cavity (Fig. 1) and roosted alone there at night. Males made solitary flights away from the cavity at this time, presumably to forage, and continued roosting in large trees near nesting areas in groups of 7 to 43 ($N = 8$ roosts). The number of individuals at roosts during the nesting season was small compared to dry season roosts, attended by up to 159 individuals of both sexes ($\bar{x} = 64 \pm 61$ individuals, $N = 4$ roosts).

Egg laying and incubation.—In 1988, egg laying began on 12 July, three

TABLE 1
ANOVA OF THE ARCSIN-TRANSFORMED PERCENTAGE OF TIME THAT MALE AND FEMALE *FORPUS PASSERINUS* PARENTS SPENT IN THREE LOCATIONS DURING THE SIX DIFFERENT PERIODS IN THE NESTING CYCLE (FIG. 1)

Effect	df	F	P
Sex of parent	1	0.3	0.60
Location ^a	2	266.5	0.01
Period ^a	5	0.3	0.92
Sex · location	2	231.5	0.01
Sex · period	5	0.2	0.98
Period · location	10	32.4	0.01
Sex · period · location	10	26.0	0.01
Error ^b	408		

^a See methods section for definition of periods of the nesting cycle and location.

^b See Figure 1 for sample sizes.

weeks after pairs were first seen entering nest cavities. The last clutch was initiated on 10 November (Fig. 2), although two pairs were prospecting for nest sites on 6 December, the last day of the study. Sixty-three nesting attempts were observed: 58 in nest boxes and five in fence posts.

Eggs were white and spherical to elliptical in shape, with one end slightly more pointed than the other. Egg lengths averaged 18.0 ± 0.8 mm (range = 16.1–20.7 mm, N = 280), egg widths averaged 15.1 ± 0.5 mm (range = 13.4–16.1 mm, N = 280), and egg volumes averaged 2084 ± 184.1 mm³ (range = 1479–2621 mm³, N = 280). Egg masses, taken up to two days after laying, averaged 2.2 ± 0.3 g (range = 1.6–2.8 g, N = 42).

Clutches averaged seven eggs and were laid over a seven to 16 day period (Beissinger and Waltman 1991). Eggs were usually laid on successive days or every other day, but occasionally at intervals up to five days. Females initiated incubation with their first egg (Beissinger and Waltman 1991) and during the egg-laying period spent over three-fourths of the day inside the cavity ($\bar{x} = 79 \pm 21\%$, range = 4–100%, N = 85.6 h at 23 nests, Fig. 1).

Males visited females up to three times an hour to feed, preen, and copulate with them. Pairs continued courtship behaviors during these visits. On average, males fed females 0.97 ± 0.44 times per hour (N = 85.6 h at 23 nests) during the egg-laying period (Fig. 3). The rate at which males fed females during this period (Fig. 4) was positively correlated with the eventual clutch size of their mates (Spearman $r = 0.5$, $P < 0.05$, N = 21 nests).

Incubation was performed exclusively by females. Females spent $84 \pm$

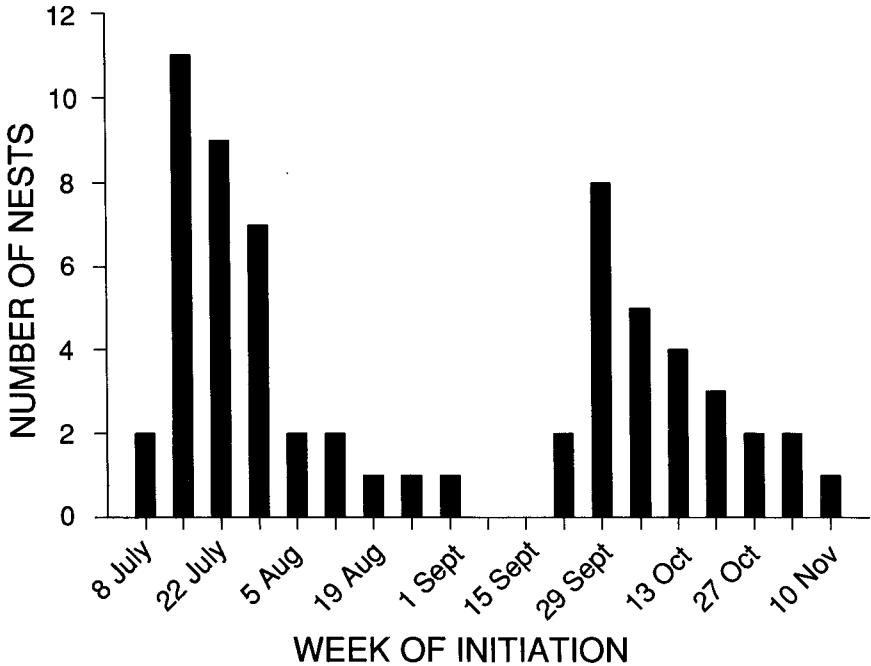


FIG. 2. The number of *Forpus passerinus* nests initiated during each week of the study. Nests were initiated when the first egg was laid.

15% of the daytime in nests during this period (range = 60–100%, $N = 33$ h at 10 nests, Fig. 1) and developed large brood patches. Males were seen at nests less frequently than in the preceding periods (Fig. 1) and fed their females slightly less often ($t = 1.5$, $P = 0.15$) during incubation ($\bar{x} = 0.74 \pm 0.36$ feeds per hour, $N = 33$ h at 10 nests, Fig. 3) than during egg laying. The rate of food deliveries by males to their mates did not correlate with clutch size during the incubation period (Spearman $r = 0.20$, $P > 0.5$, $N = 10$ nests).

Parental care.—Eggs hatched asynchronously 18 to 22 days after laying (Beissinger and Waltman 1991). Two to fourteen days passed between the hatching of first and last nestlings and an average of 5.7 chicks hatched per brood (Beissinger and Waltman 1991). Egg shells were not removed from nests after hatching and were often found buried under nest material.

Parental feeding rates differed significantly between the sexes, by nesting periods, and for brood sizes (Table 2, Fig. 3). Males apparently did all or most of the foraging for the nestlings in the hatching period, and passed food either directly to their young or to their mates. Males made almost

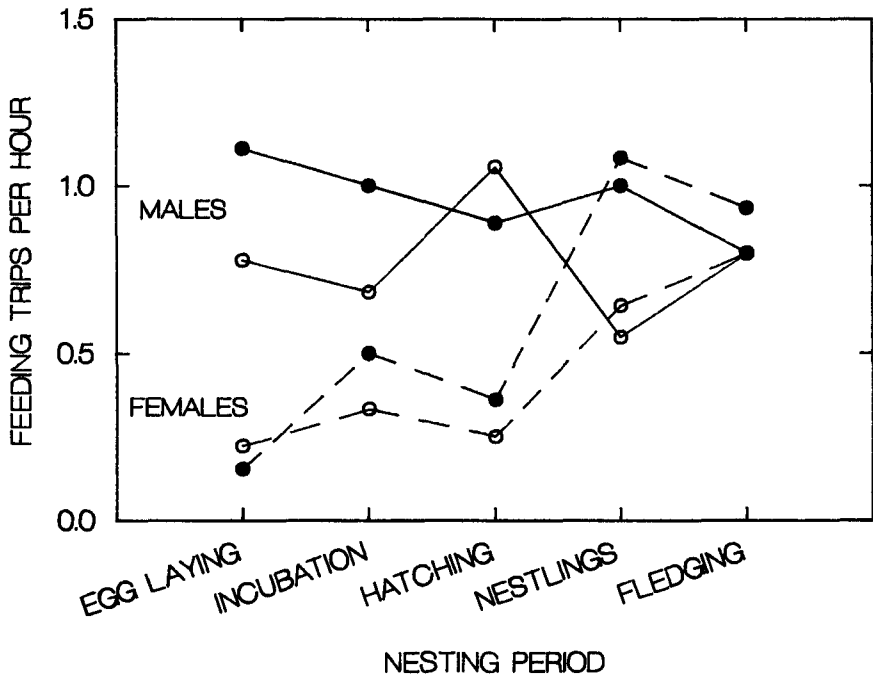


FIG. 3. Feeding rate by *Forpus passerinus* males (solid lines) and females (broken lines) at nests containing medium (solid circles) and small (open circles) broods during five periods of the nesting cycle.

one feeding trip to the nest each hour during this period ($\bar{x} = 0.93 \pm 0.23$ feedings/h, $N = 48$ h at 14 nests) (Fig. 3). Females fed nestlings infrequently during the hatching period ($\bar{x} = 0.28 \pm 0.22$ feedings/h, $N = 48$ h at 14 nests) (Fig. 3). Females brooded nestlings most of the day ($\bar{x} = 81.2 \pm 10.4\%$, $N = 48$ h at 14 nests) until the oldest chick was between one and two weeks old (Figs. 1 and 5). Females continued roosting in nests overnight until the youngest chick was in its second week.

After brooding was completed, males and females nearly always visited nests together. Both sexes spent a majority of time away from the nest area (Fig. 1). On average, males and females fed their young just less than once an hour during the nestling period (males: $\bar{x} = 0.76 \pm 0.27$ feedings/h; females: $\bar{x} = 0.86 \pm 0.31$ feedings/h, $N = 70.5$ h at 15 nests) (Fig. 3). The number of feeding visits per hour at 15 nests by males (Spearman $r = 0.75$, $P < 0.01$), females ($r = 0.69$, $P < 0.01$), and pairs (male + female rate; $r = 0.77$, $P < 0.01$) were positively correlated with brood size during the nestling period. During the fledging period, parents continued to show

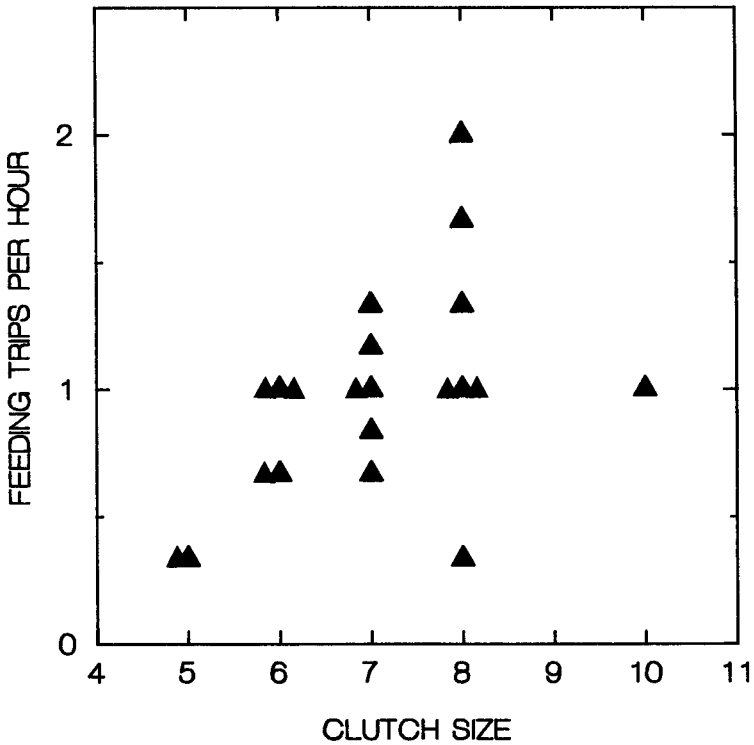


FIG. 4. Food delivery rates by *Forpus passerinus* males to females during the egg-laying period as a function of ultimate clutch size.

TABLE 2
ANOVA OF PRESUMED FEEDING RATE AT NESTS BY MALE AND FEMALE *FORPUS PASSERINUS* PARENTS HATCHING SMALL AND MEDIUM-SIZED BROODS

Effect	df	F	P
Brood size ^a	1	9.4	0.01
Sex of parent	1	29.3	0.01
Period ^a	4	3.6	0.02
Size·sex	1	0.1	0.72
Size·period	4	2.0	0.11
Sex·period	4	10.3	0.01
Size·sex·period	4	1.5	0.21
Error	98		

^a See methods section for definition of brood sizes and periods of the nesting cycle.

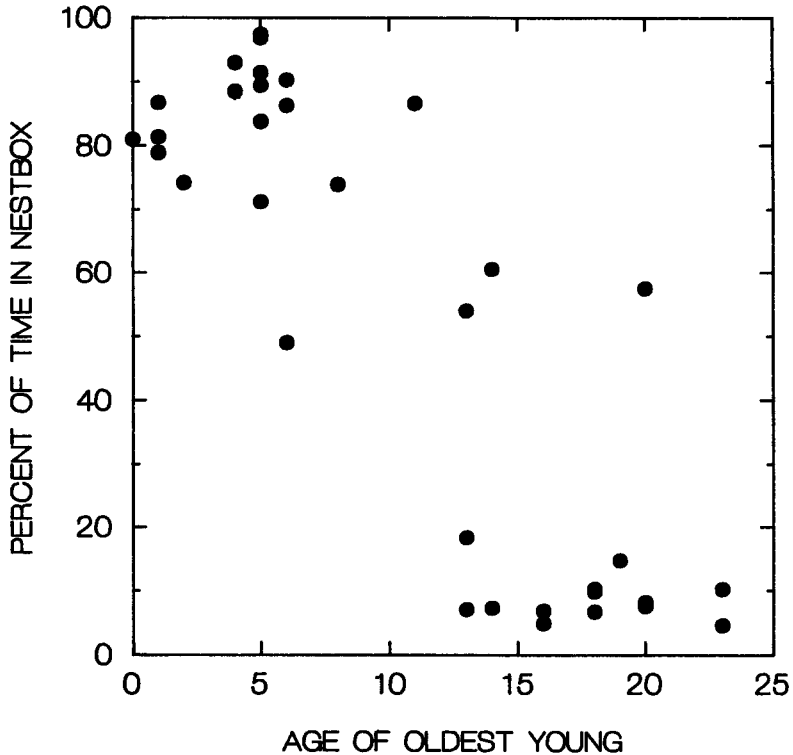


FIG. 5. Percentage of daylight hours that *Forpus passerinus* females spent in the nest cavity in relation to age of the oldest nestling.

the same pattern of nest visitation and feeding (Figs. 1 and 3). Adults may also have been feeding fledged young away from the nest at this time.

Nestling growth and development.—At hatching, nestlings weighed between 0.8 and 2.8 g ($\bar{x} = 1.8 \pm 0.3$ g, $N = 170$). Chicks were born with eyelids fused and only a small amount of yellow or white down. Eyes did not begin to open until six to eight days after hatching, and were not fully opened until day 8–10. Primary feather shafts began to emerge on day 8–10 and feathers began erupting on day 15–20. Green feather coloration was visible, and blue color was seen in male nestlings on or about day 16–23. After about 25 days, plumage of nestlings was nearly indistinguishable from that of adults.

Nestling growth was quite slow (Fig. 6) and resembled the logistic curve reported for other parrots (Bucher 1983, Navarro and Bucher 1990). The average daily growth increment (K) for all chicks was 0.233 ± 0.005 g,

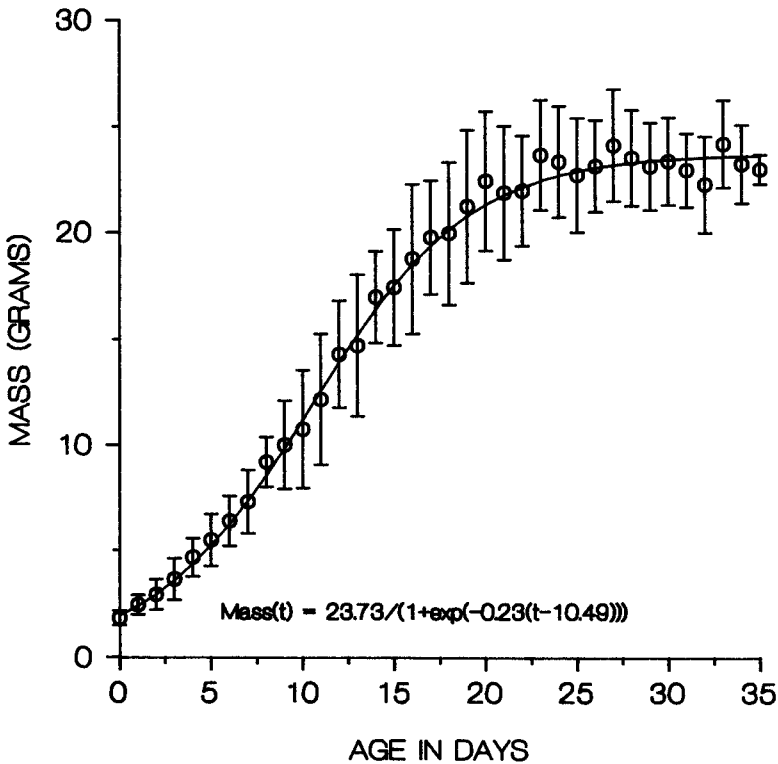


FIG. 6. Mean and standard deviation of mass for *Forpus passerinus* nestlings with empty or nearly empty crops. Sample sizes (totalling 1128 masses) vary from 2 to 165 and averaged 41 ± 28 . The logistic curve was plotted using the parameters given in the equation on the figure.

the inflection point (I) was reached at age 10.48 ± 0.12 days, and the asymptotic mass (A) averaged 23.7 ± 0.2 g based on 1128 masses. Growth parameters did not differ between males ($K = 0.236 \pm 0.008$ g, $I = 10.16 \pm 0.16$ days, $A = 23.7 \pm 0.2$ g, $N = 480$) and females ($K = 0.235 \pm 0.007$ g, $I = 10.17 \pm 0.15$ days, $A = 23.9 \pm 0.2$ g, $N = 466$).

Nestlings remained in the bottom of the cavity until their third week, when they began to climb to the nest opening to receive food. Often, some nestlings would beg at the cavity opening while others remained inside. Parents often fed the young at the cavity entrance but would also enter the cavity to feed nestlings inside.

Fledging occurred 28 to 35 days after hatching, and the interval between the fledging of first and last chicks averaged 9.1 days (Beissinger and Waltman 1991). Three times we observed first flights of fledglings. In

each case, the parents urged the young out of the nest by flying from the nest opening back and forth to a perch a short distance away. Fledglings flew about 10–30 m to perch in a tree, accompanied in each case by the parents.

We occasionally witnessed parents feeding fledged young. Fledglings rarely followed their parents back to the nest. We observed only one female feed a fledgling while nestlings remained in her nest. This fledgling was 32 days old and had fledged two days earlier. On three occasions we observed parents being pursued by their entire post-fledged brood away from the nesting area. In each case, the parents fed at least one of the young. The young were 37 to 56 days old and had fledged seven to 22 days earlier. More often, fledglings were resighted in small flocks foraging with five to 20 other birds, including other yearlings. They also appeared occasionally at other nests and begged to the parents there.

Nestling mortality.—Of the 63 nesting attempts that we observed in this study, 23 failed before at least one young fledged. Probable causes of these failures include: predation (five nests), abandonment due to harassment from a neighboring pair (three nests), abandonment caused by human interference (three nests), flooding of the nest structure (two nests), and death or disappearance of one parent (two nests). Eight nests were abandoned for unknown reasons. Snakes, lizards, and rodents were common in the study area and could have accounted for nest predation. We also found a small marsupial (*Marmosa robinsoni*) in nest boxes on three occasions.

Causes of mortality of nestlings at successful nests were difficult to determine. Starvation may have killed all last and penultimately hatched nestlings, which were found dead in nests with empty crops. In contrast, only 60% of the earlier hatched nestlings died with empty crops (Beissinger and Waltman 1991). Three chicks were found dead in a nest with very full crops and wet plumage. Because these nestlings were between 17 and 25 days old, it is possible that they had put their heads out of the nest opening to beg for food, were rained on, and died of hypothermia. Three nestlings were found dead with punctures on the head, neck and back, and with broken, twisted wings. Similar wounds have been observed when invading pairs commit infanticide (S. H. Stoleson, pers. comm.). On average, 4.7 nestlings fledged from successful nests (Beissinger and Waltman 1991).

Renesting.—Nest initiations occurred in two waves during the 1988 breeding season (Fig. 2). The initial period lasted from 12 July through 2 September and the later period, defined by the first renesting attempt of a banded pair, lasted from 22 September through 10 November. Of 27 nesting attempts in the second half of the 1988 season, at least 14 were

by females that had bred successfully in the first half of the season. Of 37 banded birds that nested successfully in the first half of the breeding season (17 fully banded pairs, three partially banded pairs), 23 (62%) nested again in the second period.

Clutches laid in the initial period of the season ($\bar{x} = 7.3 \pm 1.1$ eggs, $N = 27$) were significantly larger ($t = 2.2$, $df = 46$, $P < 0.05$) than clutches laid in the later period ($\bar{x} = 6.7 \pm 1.0$ eggs, $N = 21$). There were no significant differences between the two periods in the number of young hatching ($t = 0.6$, $df = 42$, $P = 0.6$) or fledging ($t = 0.3$, $df = 28$, $P = 0.8$) per successful nest.

An average of 22.0 ± 9.2 days (range = 11–40 days, $N = 10$ pairs) elapsed from the fledging of the last chick at first nests until the laying of the first egg at second nests. This interval was positively correlated with the number of young fledged from the first nest (Spearman $r = 0.62$, $P < 0.05$, $N = 10$), but was not correlated with the size of the first clutch ($r = 0.23$, $P > 0.10$, $N = 10$).

Pairbonds.—Pairs generally remained mated throughout the breeding season. Of 11 fully banded pairs that bred successfully in the first period and were resighted in the second period, 10 renested together (91%) and one changed mates (the female from this nest renested with a new mate).

Mate fidelity was more variable between breeding seasons. At least one member of 16 banded pairs that nested in 1988 nested again in 1989. Five members from these 16 pairs were resighted in 1989 with new partners, although in only two cases were the 1988 mates seen in 1989. Of the remaining 11 pairs from 1988, six remained together and nested in 1989; at least one member of the other five pairs nested in 1989 but with a partner who's identity could not be unequivocally confirmed due to partial band loss. In total, 37–69% of pairs remained mated for consecutive years and 31–63% changed mates between years.

Mate loss and replacement.—Three nesting attempts in 1988 were disrupted when one member of a pair disappeared or was found dead. The banded mate of one banded female disappeared after she had laid three eggs. The next day 12 males were present, displaying, vocalizing and fighting at her nest. The female discontinued laying but continued partial incubation for three days before abandoning the nest. Twelve days after ending incubation, this female initiated a new clutch with a new male. At another nest, containing six nestlings aged 10 to 19 days, the male disappeared. This female was pursued by four males and began to associate closely with one of them five days later. The new suitor followed the female to the nest and attempted to enter on many occasions, but the female always chased this new male away from the entrance. The female successfully raised six young. Predation might explain the disappearance of both of these parents; we witnessed an Aplomado Falcon (*Falco fe-*

moralis) flying with an adult parrotlet in its talons. At another nest, the female was found dead from unknown causes in the bottom of her nest box. The male stopped feeding his five nestlings (5–12 days old), and they died shortly thereafter.

Nest site fidelity.—Of the ten fully banded pairs that renested together in 1988, eight renested in the same cavity and two renested elsewhere. In addition, the female that switched mates renested in a new site, and the two banded birds that nested twice with unbanded birds renested in the same cavity. Therefore, 18 of 23 banded birds (78%) that nested twice, reused the same cavity.

However, holding possession of a nest site for a second attempt required a dedicated effort by the pair. After one or more young had fledged from a nest, other pairs, males, and groups of males began inspecting the cavity, perhaps anticipating its impending vacancy. Agonistic interactions occurred between the resident pair, intruding pairs, and other individuals. Parents displaced more intruders in this period than in any other period (egg laying: 0.47/h; incubation: 0.36/h; hatching: 0.17/h; nestling: 0.24/h; fledging: 1.0/h).

DISCUSSION

Green-rumped Parrotlets are highly aggressive towards conspecifics at nest sites. Agonistic behaviors observed in *F. passerinus* are common to many parrots (Brockway 1964b, Wyndham 1980, Skeate 1984, Snyder et al. 1987). High rates of nest box occupancy (Beissinger and Bucher 1991) and frequent interactions between pairs at nest sites suggests that breeding in *F. passerinus* may be limited by the availability of nest sites. In contrast, populations with an abundance of available nest sites exhibit agonistic behavior less often (Lanning and Shiflett 1983, Snyder et al. 1987), although agonistic behavior at nests was common for Budgerigars (Wyndham 1981) and White-tailed Black Cockatoos (*Calyptorhynchus funereus latirostris*) (Saunders 1982).

The head bowing, tail fanning and wing flicking courtship displays observed in *F. passerinus* are similar to those described for Puerto Rican Parrots (*Amazona vittata*) (Snyder et al. 1987), Thick-billed Parrots (*Rhynchopsitta pachyrhyncha*) (Lanning and Shiflett 1983), White-tailed Black Cockatoos (Saunders 1974), White-fronted Amazons (*A. albifrons*) (Skeate 1984), Budgerigars (Brockway 1964a) and African parrots of the genus *Agapornis* (Dilger 1960). Snyder et al. (1987) suggested that head bowing is specifically related to pair formation in parrots and was seldom exhibited by established pairs of Puerto Rican Parrots. However, we observed this display in *F. passerinus* in all periods of the nesting cycle and during defense of nest areas from conspecifics. Thus, the display may help enhance, or reaffirm pair cohesion.

Nipping bouts occurred among pairs in *F. passerinus* especially during agonistic encounters with other pairs. This activity also appeared to reaffirm pair cohesion. Nipping bouts were observed in a different context in Puerto Rican Parrots as a highly aggressive activity between pairs (Snyder et al. 1987).

Bill clasping resembled a ritualized version of courtship feeding in which no food is actually transmitted. White-fronted Amazons exhibit a similar activity in which bills are gently locked while flicking tongues (Skeate 1984).

Allopreening and copulation bouts of Green-rumped Parrotlets were of long duration as described for other parrots. We saw male *F. passerinus* feeding females up to three weeks before the initiation of egg laying. Males began feeding females up to 26 days before initiation of egg laying in Puerto Rican Parrots (Snyder et al. 1987) and White-tailed Black Cockatoos (Saunders 1982), and fed females year-round in White-fronted Amazons (Skeate 1984) and *Agapornis* sp. (Dilger 1960). Allopreening, copulation and courtship feeding may serve to affirm pair cohesion.

Courtship feeding rates by male Green-rumped Parrotlets during egg laying were positively correlated with eventual clutch sizes laid by their mates (Fig. 4). Egg production by females may depend on the amount of nourishment they receive at this time (Dilger 1960, Nesbit 1977, Smith 1980). Alternatively, females may use male feeding rates as an honest indicator of paternal feeding in later stages of the nesting cycle (Smith 1980, Beissinger 1987). This may be particularly important in parrots because females do nearly all of the incubation and are almost completely dependent on males for food for long periods (Wyndham 1981, Saunders 1982, Skeate 1984, Snyder et al. 1987). Feeding rate was not correlated with clutch size during incubation, suggesting that males responded to the variable needs of their females.

The decision by females to switch from brooding to feeding young may be particularly difficult in parrots. Parrot nestlings are extremely altricial, growing and developing thermoregulatory capacity very slowly (Brockway 1964a, Bucher 1983). Because parrot broods typically are extremely asynchronous in hatching, the needs of the youngest nestlings to be brooded and of the oldest nestlings to be fed may conflict. Female Green-rumped Parrotlets shift their behavior from all day brooding to feeding nestlings when the oldest chick is about one to two weeks old (Figs. 3 and 5), a pattern also displayed in other parrots (Snyder et al. 1987, Saunders 1982, Stamps et al. 1985, Lanning and Shiflett 1983). This change in female behavior may occur quickly (Fig. 5), suggesting that nestling requirements change discretely. For example, nestlings may reach a stage when they no longer require brooding, or when the food demands of the brood reaches

a level that the male alone cannot fulfill. Especially in large broods, females may switch to feeding nestlings before the last hatched young can thermoregulate, when they are less than a week old. Unless they are incidentally brooded by older nestlings, last hatched chicks in large broods could possibly die of hypothermia on cool, rainy days, probably an unusual cause of mortality in tropical lowland birds (Skutch 1987).

Despite difficulties inherent in successfully raising a full brood, one *F. passerinus* female managed to fledge six young after her mate died. Puerto Rican Parrot (Snyder et al. 1987) and Budgerigar adults (Stamps et al. 1985) are also capable of rearing young alone. Widowed females of all three species began to choose a new mate immediately, even if he did not assist directly in raising her brood. The pairbond may be important to survival or for defending a nest from infanticide or replacement by other pairs, and may explain why females accept mates that do not appear to assist in feeding their young (Dilger 1960, Saunders 1974).

Although captive studies have noted that *Forpus* parrotlets are self-feeding at fledging (Mobbs 1981, Noble 1984), we occasionally saw fledglings fed by their parents up to 22 days after fledging. The duration of post-fledging care appears to be quite variable in parrots. Neither parent of wild Budgerigars was likely to feed young after fledging (Wyndham 1981) but in captivity young of this species did not become independent until two weeks after fledging (Brockway 1964b). After fledging, Thick-billed Parrots roamed in family groups and parents fed the young (Lanning and Shiflett 1983). Young White-tailed Black Cockatoos stayed with their parents until the next breeding season (Saunders 1982), while captive juvenile White-fronted Amazons did not feed themselves until 72 days after fledging (Skeate 1984). The extent of post-fledging care in parrots appears to be variable, and may depend in part on whether pairs can nest more than once during a breeding season and on the intensity of competition for nest sites in the population.

Inter-clutch intervals were not correlated with clutch size in *F. passerinus* or in Budgerigars (Stamps et al. 1985), but were correlated in both species with the number of young fledged. This suggests that either egg laying may not be as costly to females as rearing young, or that larger broods require longer periods of post-fledging care. Reproductive effort increased with brood size in Green-rumped Parrotlets, since feeding rates were positively related with the number of young in the nest.

Pair cohesion is very strong in most parrots (Dilger 1960, Brockway 1964a, Saunders 1974, Skeate 1984, Snyder et al. 1987). Aviculturalists have reported that pairs of Green-rumped Parrotlets mate for life and that females often kill new males that are placed in their cages (Noble 1984). In our population, most pairs remained mated throughout the

breeding season, but fewer pairs remained mated between years. Mate switching has also been recorded in Puerto Rican Parrots (Snyder et al. 1987), but not in White-tailed Black Cockatoos (Saunders 1974, 1982).

In conclusion, parrot reproduction is characterized by a long incubation period, a high degree of hatching asynchrony, very altricial nestlings, and slow growth of young. These characteristics may have resulted in the extreme division of parental care roles that parrots exhibit for much of the breeding cycle. Females depend on males to feed them and their young for prolonged periods and must develop confidence that their mates will not desert them (Beissinger 1987). Furthermore, in populations with a shortage of available nest sites, a high degree of intraspecific aggression and competition for nest sites may result in coordination of activities by members of a pair to protect their nest site. These factors may require a high degree of cooperation between mates and may account for the high degree of pair cohesion in many parrot species.

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