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# Social constraints on the onset of incubation in a neotropical parrot: a nestbox addition experiment

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**Abstract.** We examined whether the early onset of incubation serves to protect eggs from the dangers imposed by conspecifics in the green-rumped parrotlet, *Forpus passerinus*, a small neotropical parrot that lays a large clutch and begins incubation on the first egg. Nestboxes with eggs were installed and their fate was followed for 72 h to determine whether egg destruction and nest site take-overs occurred as predicted by the Egg Protection and Limited Breeding Opportunities Hypotheses, or whether additional eggs appeared in the boxes as predicted by the Brood Parasitism Hypothesis. Eggs were destroyed at 40.6% of 69 experimental boxes but at only 4.5% of control nests occupied by laying pairs. No eggs were laid in the experimental boxes. Egg destruction at experimental nests occurred during daylight hours and all mortality was caused by green-rumped parrotlets. Over 75% of the nests were destroyed by male–female pairs prospecting for nest sites, and the remainder were destroyed by male–male pairs. Lone males never destroyed eggs, although they frequently visited experimental boxes. Two of three failures at control nests were the result of nocturnal predators, and the other nest was apparently destroyed by parrotlets. There was no significant difference between experimental and control boxes in the frequency of visitations by lone males, male–female pairs and male–male pairs. Although experimental boxes that parrotlets visited were discovered quickly after placement, parrotlets were usually slow to enter them ($\bar{X}$=5.8 h after discovery, range 0.3–23.5 h). Control nests were rarely left unattended: females spent nearly 75% of their time in the box, and pairs were typically absent for short intervals (median=7.5 min). Control females responded to intruding parrotlets by remaining in the box 94% of the time when alone, whereas males actively displaced and chased intruding parrotlets 66% of the time. Parrotlets that visited control nests approached the box significantly less often than those visiting experimental boxes. To ensure the survival of eggs, parrotlet parents must begin incubating eggs or guarding nests soon after laying to minimize destruction of clutches, loss of nest sites, a decline in the viability of their eggs and the time that all nestlings are exposed to predators.

Many species of birds initiate incubation before they complete egg-laying, which usually leads to asynchronous hatching (Lack 1968; Clark & Wilson 1981; Stoleson & Beissinger 1995). Hatching asynchrony results in offspring of different sizes (Bryant 1978; Viñuela 1996) and often leads to the death of the later-hatched young (Stokland & Amundsen 1988; Mock et al. 1990; Stoleson & Beissinger 1997). This illustrates the 'paradox of hatching asynchrony' (Stoleson & Beissinger 1995): avian parents are unusual among vertebrates in having some control over birthing intervals within a brood (since bird eggs usually do not develop until a parent warms them by initiating incubation), but many species opt for an incubation strategy that appears maladaptive. Current debate centres on whether early incubation leading to asynchronous hatching confers survival advantages for parents or selected offspring after hatching, such as adaptive brood reduction (O'Connor 1978; Magrath 1989; Harper et al. 1992) or minimizing exposure to predators (Clark & Wilson 1981; Hussell 1985), or is a result of physiological constraints, resource limitations and behavioural factors that affect the onset of incubation (Mead & Morton 1985; Amundsen &

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Slagsvold 1991; Stoleson & Beissinger 1995). It is likely that multiple causal factors interact to affect the onset of incubation and the resulting hatching pattern in birds, but the events surrounding the onset of incubation have been particularly ignored (Stoleson & Beissinger 1995).

Few studies have examined the role of social constraints on the onset of incubation. In some species, the early onset of incubation may serve a protective function from the dangers imposed by conspecifics. Parent birds may reduce the risk of infanticide on eggs by beginning incubation on the first egg (the Egg Protection Hypothesis; Dunlop 1910; Bollinger et al. 1990). Protection of eggs from conspecifics or predators has been proposed as the function of early incubation in colonially nesting gulls, terns and waterfowl (Parsons 1976; Thompson & Raveling 1987; Bollinger et al. 1990). Birds that use nest sites that are limited in number (e.g. cavities) may be forced to protect the site itself, especially if they do not defend an all-purpose territory. Initiating incubation on the first egg may be part of a tactic to defend the nest site and clutch from other pairs (the Limited Breeding Opportunities Hypothesis; Beissinger & Waltman 1991; Beissinger 1996). Initiating early incubation would not only allow the female to guard the nest site by occupying it, but would minimize (1) energy expenditures, which could be used for laying additional eggs (Beissinger 1987, 1996), and (2) the time that all young are exposed to predators in the nest (Clark & Wilson 1981). Some of the most extreme hatching asynchronies occur in hole-nesting species that do not defend all-purpose territories (Stamps et al. 1985; Wilson et al. 1986; Lessells & Avery 1989; Beissinger & Waltman 1991). Early incubation may also protect a clutch from brood parasitism (the Brood Parasitism Hypothesis), which often occurs before the onset of incubation (Lombardo et al. 1989) by either conspecific egg-dumping (Kendra et al. 1988; Romagnano et al. 1990) or by interspecific brood parasitism (Wiley & Wiley 1980). Thus, parents may compromise the survival of last-hatched young by initiating incubation early to secure the survival of first-laid eggs or to minimize the likelihood of raising young that they did not sire. In such instances, brood reduction would not be adaptive but would instead be an epiphenomenon of the nestling size hierarchy that resulted from the early onset of incubation (Stoleson & Beissinger 1995).

In this study, we examined the protective function of the early onset of incubation in a box-nesting population of Neotropical parrots. The green-rumped parrotlet, *Forpus passerinus*, a small parrot (24–36 g), lays a large clutch that hatches extremely asynchronously because females typically initiate incubation when the first egg is laid (Beissinger & Waltman 1991; Waltman & Beissinger 1992). Our experiment quantified the fate of unguarded parrotlet eggs in experimental nest sites that we installed. We predicted that there should be a high rate of egg destruction and nest site take-overs by other parrotlets at the experimental boxes if the early onset of incubation functions to reduce the loss of unguarded clutches or nest sites. Alternatively, if female green-rumped parrotlets initiate incubation early to protect against brood parasitism, then the presentation of an unguarded nest box containing a partially completed clutch should stimulate the laying of additional eggs by parrotlets in experimental boxes.

## METHODS

### Study Area

We conducted the study at Hato Masaguaral (8°34′N, 67°35′W), a cattle ranch in the llanos of Venezuela 45 km south of the town of Calabozo. This site is a seasonally flooded savanna with distinct wet and dry seasons (Troth 1979; Beissinger et al. 1988; O'Connell 1989). The rainy season, which commences in May and ends in December, coincides with the parrotlet breeding season (Waltman & Beissinger 1992).

We studied a banded population of *F. passerinus* from late May to November in 1994 and 1995. Approximately 3708 birds have been banded since the study began in 1988; each year all fledging young (400–600) and most newly immigrating adults (75–100) are given a unique combination of plastic and stainless steel or aluminium bands. The site contained 106 polyvinyl chloride (PVC) nestboxes, each about 1 m deep and fitted with a sleeve of hardware cloth that ran the length of the box, which allowed the birds to climb freely (Beissinger & Bucher 1992). Sawdust was placed at the bottom to act as a nesting substrate. In both years, 101 boxes were prospected by *F. passerinus* for breeding, and 94 and 87 received at least one egg during the 1994 and 1995 seasons, respectively. The duration of the breeding season usually allows for two and sometimes three breeding attempts to occur per box, although no more than two broods have been raised in a single season (Waltman & Beissinger 1992; Stoleson & Beissinger 1997).

### Study Species

The green-rumped parrotlet inhabits savannas in northern South America and feeds principally on the seeds of herbaceous plants or fruits (Forshaw 1989; Waltman & Beissinger 1992). It lays a very large clutch ($\bar{X}=7$ eggs, range=5–12) for a tropical bird and all eggs appear to be laid by a single female (Beissinger & Waltman 1991). Eggs are laid at 1–3-day intervals over 9–17 days. Only the female incubates, and the male provides her with food from well before the clutch is laid until about 1–2 weeks after hatching of the first young (Beissinger & Waltman 1991; Waltman & Beissinger 1992; Curlee & Beissinger 1995). Incubation is begun on the first egg, which results in a very asynchronous clutch hatching over 17 days. The female does all of the brooding, while the male does most of the foraging for her and the brood, until the oldest chick reaches 10–17 days of age. Thereafter, the female joins the male to forage together for the brood. Extreme hatching asynchrony leads to low survivorship of penultimate and last-hatched young, due mostly to starvation and other causes resulting from the size disparity among nestmates (Beissinger & Stoleson 1991; Beissinger & Waltman 1991; Stoleson & Beissinger 1997).

Understanding the factors that promote hatching asynchrony in the green-rumped parrotlet requires consideration of the distribution of this trait in birds and particularly in the order Psittaciformes (parrots, macaws, parrakeets and allied species). Hatching synchrony was the primitive condition in birds and asynchrony is a derived trait (Stoleson & Beissinger 1995). Although most parrots hatch their eggs asynchronously, the few studies that have been conducted on wild birds indicate that the degree of hatching asynchrony varies greatly among species. Galahs, *Eolophus roseicapillus*, do not begin incubation until the clutch of three to seven eggs is half completed, and 72% of their eggs hatch synchronously within 24 h (Rowley 1990). Similarly, the onset of incubation in the long-billed corella, *Cacatua pastinator pastinator*, occurs just before or after the second of two or three eggs is laid. In the genus *Amazona*, whose members typically lay three or four eggs, the Puerto Rican parrot, *A. vittata*, initiates incubation after laying the first or second egg (Snyder et al. 1987), and the Bahama parrot, *A. leucocephala bahamensis*, begins incubation on the first egg (Gnam 1991). Budgerigars, *Melopsittacus undulatus*, and macaws, *Ara* sp., both appear to start incubation on the first egg (Wyndham 1981; Munn 1992). Thus, initiating incubation before the clutch has been completed is a common trait in parrots, and although first egg incubation occurs often, the family displays variation in the degree of hatching asynchrony.

### Experimental Design and Data Collection

We selected 10 areas as sites to conduct experiments each year. We chose sites where parrotlet activity was frequently observed and where gaps of at least 20 m occurred between permanently placed nestboxes. We hung experimental boxes along a fence line no closer than 10 m to the nearest permanent nestbox. This distance represents the average distance between nestboxes at our site and is similar to distances observed between natural nest sites (Beissinger & Waltman 1991). Eight of the same sites were used in both 1994 and 1995, and two sites were changed between years due to interference by cattle ranching activities and changes in vegetative cover.

An experimental box was placed at each site for up to 3 days and was removed immediately upon completion of the experiment. In each experimental box, we placed three *F. passerinus* eggs that had been taken from abandoned or failed nests. Each egg had had its contents removed with a hypodermic needle and syringe, and had been dried at 105°C until completely desiccated. Drying the eggs ensured that they would not become rotten and accidentally break when used in the experiment. The eggs were placed at the bottom of the nestbox on a layer of sawdust to simulate nestboxes with an actively laying pair.

Upon placement, we watched the boxes continuously for 3 h. Occasionally, nest watches were shorter than 3 h when interrupted by heavy rain. Thereafter, we checked the nestboxes approximately every 4 h during daylight for 72 h. Contents were typically checked at 3, 6, 24, 27, 30, 33, 48, 51, 54, 57 and 72 h after the initial watch had been conducted. During checks, eggs were categorized as undisturbed, disturbed or destroyed since the box was last checked. Undisturbed eggs had not changed position from the previous nest check. Disturbed eggs were rearranged within the box, indicating that an individual had entered the box. Eggs were destroyed when they were missing, broken or buried under the layer of sawdust. Additional observations beyond the initial 3 h were recorded during the periodic nest checks if individuals were observed when we arrived.

In 1995 we used a video-camera to monitor experimental nests nearly continuously during daylight hours after we had finished nest watches. The camera was placed 10–15 m from the nest in a protected site. It was visited every 3–5 h to change the tape. We reviewed tapes on a full-sized colour television, and the sex and behaviour of individuals were recorded (see below). Although we could rarely determine complete band combinations of individuals from the video-camera, the camera did allow us to gather more precise information on the social status of individuals that destroyed the nest contents and the timing of destruction. When we were unable to determine the exact moment that a nest was first entered and the eggs were destroyed, the time elapsed until destruction was considered to be the midpoint between the time when we discovered that the nest had failed and the time when we had previously checked the nest.

During nest watches, the identity and behaviour of individual birds visiting the box were recorded, noting combinations of banded individuals. We recorded the location of the bird in relation to the experimental box as in the nest area (2–5 m from the box), near the box (<2 m from the box), in contact with the box, or inside the box. We also recorded whether visiting individuals were foraging in the area, perched in the area, on the box's perch looking into the nest cavity, in the nestbox but not out of sight of the researcher, or in the nestbox and out of sight of the researcher. We noted whether parrotlets arrived at nestboxes alone, in male–female pairs, in male–male pairs, or in a gang of individuals. Pairs of either type typically flew to and from the box together, often allopreened each other, and coordinated their movements so that one member would enter the nestbox while the other remained alert outside. Gangs ranged from four to 12 individuals and were composed mostly of males. Pair affiliations were sometimes evident in gangs, but little is known about gang cohesiveness or movements.

We established a control nest for each experimental replication. Control nests were in close proximity to experimental sites and contained pairs that were actively laying. We watched the control boxes for 3 h on the first day of the experiment and monitored them following the same protocol as experimental boxes, except that we did not use the video-camera for extended observations.

## Data Analyses

We completed 69 replications of the experiments during the two breeding seasons by conducting the experiment at each location three or four times each year. The replications were apportioned between the prospecting ($N$=40) and non-prospecting periods ($N$=29). Parrotlets are double-brooded, and nest initiations occur in two waves (Waltman & Beissinger 1992). Prior to the initiation of first and second broods, the majority of individuals were actively prospecting for nest sites to initiate egg laying or were in the process of egg laying. During the non-prospecting period, most individuals were incubating eggs and rearing young, and few were prospecting for new nest sites or initiating new nesting attempts. We delineated the prospecting and the non-prospecting periods of the breeding season by determining, as each experiment began, the phases of the breeding cycle (prospecting, laying, incubating, rearing or fledging) for the five nearest nestboxes.

Data analyses were conducted using SYSTAT (Wilkinson 1990) and SAS (1988). Chi-square and maximum likelihood analyses were used to test for: (1) differences between experimental and control nests in the factors affecting their fate, the social status of individuals visiting the boxes, and the occurrence of prospectors at different locations around the nest site; and (2) the responses of parents at control nests to prospecting males and females. When assumptions of normality and equal variances were met, analyses of variance and Tukey's HSD post hoc means separation test were used to compare the percentages of time that males and females spent in different locations around the nest site. Mean and 95% confidence intervals for the daily survivorship probability of experimental and control nests

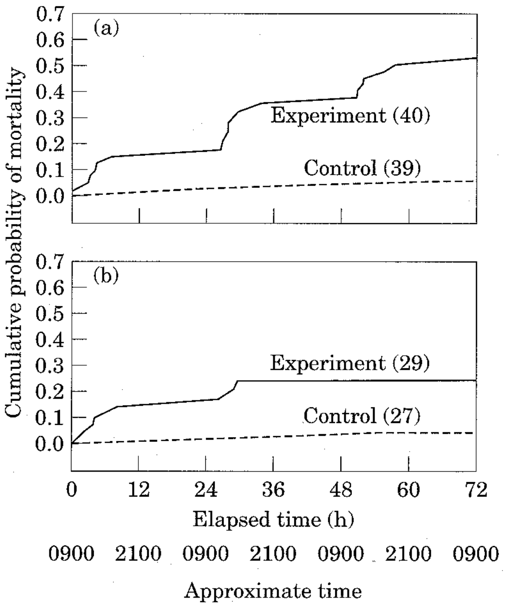

**Figure 1.** The cumulative probability of mortality of eggs at unattended experimental nests and control nests attended by laying pairs of green-rumped parrotlets during (a) prospecting and (b) non-prospecting periods of the breeding season. Sample sizes are in parentheses. The approximate time of day is indicated to show when mortality occurred in relation to daylight (0600–1900 hours) and darkness.

**Table I.** Maximum likelihood analysis indicating the effects of treatment (experiment and control), season (prospecting and non-prospecting), and year (1994 and 1995) on nest failure

| Factors | $\chi_1^2$ | $P<$ |
|---|---|---|
| Treatment | 11.33 | 0.0008 |
| Season | 0.03 | 0.8522 |
| Year | 1.94 | 0.1637 |
| Treatment*Season | 3.73 | 0.0534 |
| Treatment*Year | 0.38 | 0.5382 |
| Season*Year | 0.15 | 0.6951 |
| Treatment*Season*Year | 0.09 | 0.7629 |

were calculated using the Mayfield method (Mayfield 1975; Johnson 1979). Other means are presented with one standard deviation.

## RESULTS

### Fate of Experimental and Control Nests

Eggs were destroyed in the experimental boxes at a high rate (Fig. 1). Of the 69 replications of the nestbox addition experiment, 28 (40.6%) were destroyed within 72 h of installing the nestbox. Destruction occurred at 52.5% ($N=40$) of the experiments run during the prospecting period and 24% of the experiments run during the non-prospecting season ($N=29$). Only three (4.5%) of the control nests ($N=66$) had their eggs destroyed during the 72 h of the experiment. The probability of daily survival for experimental nests (0.8418 ± 0.0274) was significantly less than for control nests (0.9846 ± 0.0176).

Results of maximum likelihood analyses of the factors affecting the probability of nest destruction reflected these trends (Table I). Experimental or control treatment had an overwhelming effect on the likelihood of nest failure. A nearly significant interaction occurred between treatment and season, caused by higher failure rates during the prospecting than during the non-prospecting season for experimental nests (Fisher's exact test, $P=0.025$) but not for control nests (Fisher's exact test, $P=1.0$). Differences between years in the likelihood of nest destruction were not significant (Table I), so data from both years were pooled for subsequent analyses.

Destruction of experimental nests occurred rapidly and primarily during daylight hours (Fig. 1). Nests that were destroyed failed an average of 25.9 ± 18.6 h after experiments began (range= 0.42–54.2 h). Thirty-five percent of the failed nests were destroyed on the first day of the experiment, 35.7% on the second day, and 28.6% on the last day. Destruction occurred most frequently (78.6%) during the middle of the day (1000–1500 hours), and the remaining nests failed equally often in the morning (0600–1000 hours) and afternoon (1500–1900 hours). No experimental nests were destroyed during the night. The clumped timing of destruction of experimental nests during the middle of the day, accompanied by long periods of no destruction just prior to, during and after the evening, accounts for the step-like shape of the cumulative destruction function (Fig. 1). In comparison, two of the three control nests that were destroyed were lost during the night.

Prospecting pairs did not respond to the unguarded experimental box by parasitizing it.

**Table II.** The social status of green-rumped parrotlet individuals that destroyed experimental boxes and that prospected experimental and control boxes

| Social status | Destroyed experimental boxes | Visited experimental boxes | Visited control boxes |
|---|---|---|---|
| Mated male–female pairs | 16 | 30 | 16 |
| Male–male pairs | 5 | 9 | 12 |
| Lone males | 0 | 31 | 31 |
| Male gangs | 0 | 0 | 4 |
| Unknown | 7 | 0 | 0 |

No new eggs were laid in boxes during the experiments.

### Causes of Nest Destruction

Destruction by other green-rumped parrotlets caused egg mortality at all of the 28 experimental nests that experienced mortality. Parrotlets usually destroyed eggs by puncturing them with their bill. Occasionally eggs were not punctured but were buried at the bottom of the nest. Two of the three failures at control nests were the result of predators (probably snakes) that ate the eggs; punctured eggs were found in the other case, indicating parrotlets as the likely culprit.

In the cases where we were able to pinpoint which birds destroyed the experimental nests (Table II), 76.2% of the nests were destroyed by male–female pairs; male–male pairs destroyed the remainder. One male–female pair and one male–male pair were each responsible for destroying two nests. In only four cases were the destroyers completely banded. One was a male–female pair that had nested successfully earlier in the season but had lost its nestbox to another pair. Another male–female pair that destroyed an experimental nest later broke up, and the female paired and nested with another male. Finally, a male–female pair and a male–male pair that each destroyed an experimental nest did not nest in our study area throughout the entire breeding season.

### Social Status and Behaviour of Prospectors

Experimental nests were visited by up to 32 individuals during the first 3 h of observations ($\bar{X}$=2.5 visitors for all experiments; $\bar{X}$=4.8 for boxes that were discovered). The social status of individuals that visited experimental boxes (Table II) differed significantly from the status of individuals that destroyed eggs ($\chi^2_2=14.1$, $P<0.001$). Boxes were visited about as often by lone males as by mated pairs. Although lone males frequently visited experimental boxes, they were never observed destroying eggs. There was no significant difference between the social status of individuals that visited experimental and control boxes ($\chi^2_2=3.8$, $P=0.15$), excluding the occasional gangs of males that were observed at control nests.

Discovery of experimental nests by prospecting parrotlets often occurred rapidly, but prospectors varied in their willingness to enter boxes. Parrotlets discovered and began prospecting experimental nests as quickly as 12 min after they were installed, and 39.1% of the nests were discovered within the 3 h after placement. Complete coverage of the 1995 experiments using video-cameras enabled us to determine that the average time to discovery was 11.6 ± 15.5 h after placement ($N$=26; range=0.2–50.9 h) for nests that parrotlets visited. Only male–female and male–male pairs entered the boxes, except for one lone male that entered but did not disturb the eggs. The time interval from discovering to entering the box varied greatly among the eight pairs in 1995 that we could positively identify ($\bar{X}$=5.8 ± 9.5 h). Two male–female pairs entered the boxes within 2 min of discovery, but two waited 0.5–1.6 h, and two others prospected for nearly a day (18.5–23.5 h) before entering the box. Two male–male pairs prospected for 0.75–1.3 h before entering experimental boxes.

### Guarding Behaviours of Nesting Pairs

Nests were not often left unattended during the egg-laying period (Table III). Females at control nests spent 75% of their time out of sight in the

**Table III.** Mean ± SE percentage of time spent at different locations by male and female green-rumped parrotlets at 66 control nests during egg laying

| Location | Male | Female |
|---|---|---|
| In box | 7.0 ± 1.1 | 75.0 ± 3.0 |
| On box or perch by entrance | 7.8 ± 1.0 | 1.7 ± 0.5 |
| Near box (<2 m) | 5.6 ± 1.0 | 2.8 ± 1.1 |
| Near area (2–5 m) | 0.9 ± 0.3 | 0.5 ± 0.2 |
| Gone from area | 78.6 ± 2.0 | 20.0 ± 2.4 |

box, presumably incubating their eggs, while males spent over 75% of their time away from the nest area, presumably foraging for the pair (Waltman & Beissinger 1992). Incubation began on the first egg (see also Beissinger & Waltman 1991). The percentage of time that females spent in the box did not differ significantly (Tukey's HSD, $P>0.33$) among clutch sizes (one to eight eggs) except for three-egg clutches, which for some reason were incubated less regularly and differed only from seven-egg clutches (Tukey's HSD, $P=0.029$). Both parents were gone from the nest area about 20% of the time. The median time that nests were left unattended was only about 7.5 min ($\bar{X}=13.7 \pm 16.6$, $N=125$), although 12.8% of the nests were left vacant for more than 30 min, and one nest was left unattended for nearly 90 min.

Egg-laying females at control nests responded to prospectors more passively than did males, and differently when their mates were present than when alone (Fig. 2). If prospectors arrived when a female was alone, the female remained in the box and out of sight (presumably incubating or protecting the eggs) about two-thirds of the time and appeared at the box entrance about one-quarter of the time. Females actively defended their nest by displacing or chasing prospectors only 6% of the time. However, females were significantly more likely to chase or displace intruders and less likely to remain out of sight in the box if their mate was present ($\chi^2_3=17.1$, $P=0.001$). Males actively displaced and chased prospectors around the nest site more often than did females that were either in the presence of their mate ($\chi^2_3=11.4$, $P=0.01$) or alone ($\chi^2_3=40.9$, $P<0.001$). Although there was an overall tendency for control males, lone females and females in the company of their mate to displace and chase male–female and male–male prospectors more often (58%) than lone males or male gangs (42%), the difference was not significant (for all three tests: $\chi^2_1<2.1$, $P>0.14$).

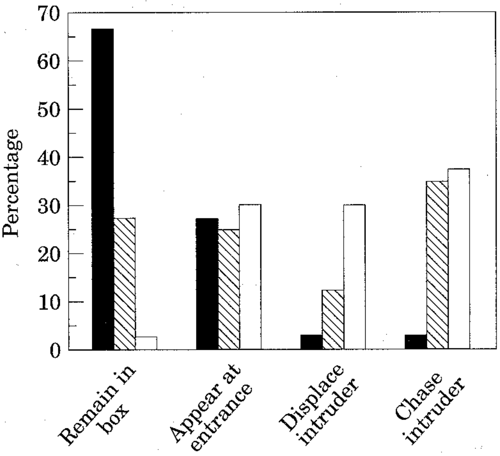

**Figure 2.** The strategies of nest defence used by control male and female green-rumped parrotlets when alone or with their mates, as indicated by the percentage of observations at different locations. ■, Female alone ($N=33$); ▧, female with male ($N=40$); □, male with female ($N=40$).

Prospectors were deterred by guarding behaviours of egg-laying pairs. Parrotlets that visited control nests were less frequently able to approach the box and land on the perch than those that visited unguarded experimental boxes (Table IV). The proportion of observations at various locations around the nest site differed significantly between control and experimental nests for both prospecting males ($\chi^2_3=42.5$, $P<0.001$) and females ($\chi^2_3=10.6$, $P=0.014$), but did not differ by the sex of the prospector ($\chi^2_3=4.65$, $P=0.20$).

## DISCUSSION

Our experiment was designed to examine the consequences of leaving nests unguarded on the survival of eggs. It mimicked a situation in which a pair remains away from the nest site for extended periods (perhaps to forage), and rarely returns to visit the nest (perhaps only to lay eggs). Thus, our experiment represents an extreme condition of no parental care or nest site defence. Absences of both members of a pair occur in nearly all bird species to some extent, although the

**Table IV.** The percentage of visits by location for prospecting male and female green-rumped parrotlets at control nests guarded by egg-laying pairs and unguarded experimental nests containing only eggs

| | Male visitors | | Female visitors | |
|---|---|---|---|---|
| Location | Control ($N$=222) | Experiment ($N$=462) | Control ($N$=72) | Experiment ($N$=148) |
| On perch by entrance | 14.4 | 35.7 | 13.8 | 31.1 |
| On box | 9.5 | 8.5 | 18.1 | 12.8 |
| Near box (<2 m) | 47.7 | 42.2 | 47.3 | 46.0 |
| Nest area (2–5 m) | 28.4 | 13.6 | 20.8 | 10.1 |

duration of absences from the nest area may be minutes to hours (e.g. Leffelaar & Robertson 1984; Gowaty et al. 1989) instead of full days as in our experiment.

Absences of both members of a pair from the nest area occur because of the conflicting demands of egg laying, nest defence, territorial defence and mate guarding. It is often not possible for a female to remain simultaneously in the proximity of her nest to guard against nest parasitism or destruction, and to forage for the food resources needed to lay a clutch of eggs (e.g. Gowaty et al. 1989). Demands on females made by nest defence and food acquisition especially conflict in species that do not defend all-purpose territories, that are colonial, that have large home ranges, or in which the female during egg laying receives little assistance from the male in the form of courtship feeding or nest guarding. Similarly, males also must choose among mate guarding to secure paternity, foraging for themselves or their mates, territorial defence and nest defence (e.g. Werschkul 1982; Leffelaar & Robertson 1984; Møller 1987; Westneat 1994). The conflicting demands on parents during egg laying lead to potential for conflict and cooperation between the sexes: (1) conflict betweeen the sexes over who will remain to guard the nest and who will leave to gather food, defend the territory or seek extra-pair copulations; and (2) cooperation to secure the safety of the nest, decrease the likelihood of parasitism and optimize clutch size. In relation to hatching asynchrony, consideration of conflict or cooperation between the sexes has been limited to the effects of asynchronous hatching on male and female behaviour during the nestling period (Slagsvold & Lifjeld 1989; Hebert & Sealy 1993; Nilsson 1995; Gowaty 1996); the conflicting demands of activities within, as well as between, each sex during the egg-laying period have been overlooked, with the exception of energy constraints (Nilsson 1993; Wiebe & Bortoliotti 1994). The outcome of conflict and cooperation results in either one member of the pair remaining to guard the nest site, or the pair risking the consequences of leaving it unprotected.

The consequences of not protecting a nest site for the green-rumped parrotlet were clear. Eggs left unguarded were destroyed at very high rates compared to control nests (Fig. 1), especially during the period when most parrotlets were prospecting for nest sites and laying eggs. The daily survivorship rate of experimental nests (0.8418 ± 0.0274) was far lower than daily survivorship of parrotlet nests from first laying until first hatching (0.9954 ± 0.0006), from first hatching until first fledging (0.9976 ± 0.0004), and from first to last fledging (0.9946 ± 0.0011; Stoleson 1996). Thus, laying may be a critical period of the nesting cycle that constrains reproductive success in the green-rumped parrotlet (Stoleson & Beissinger 1995).

Nest destruction during the laying period may be a potent source of mortality in many bird species. Egg destruction by conspecifics or competing species has been observed in wrens (Freed 1986; Pribil & Picman 1991; Kennedy & White 1996), thrashers (Arendt 1993) and swallows (Brawn 1990), and may be easily overlooked in other species. The consequences of not guarding nests successfully can be greater than just the loss of current reproductive effort: nest site or territory take-overs also occur (Freed 1986; Ingold 1989; Johnson & Kermott 1990; Munn 1992), and result in the loss of future reproduction.

Parrotlet eggs in experimental nestboxes were destroyed by other parrotlet pairs. There was no evidence of predators destroying unguarded eggs, although predation did occur at two of 66 control nests. It is possible that the lack of predation on experimental nests was the result of an absence of cues used by predators to locate nests (e.g. the odours or body heat of laying females). Nevertheless, rates of predation at control nests in this study (Fig. 1) and 943 parrotlet nests studied by Stoleson (1996) were extremely low compared to the high rate of visitation and destruction by parrotlets at unguarded experimental nests.

Three quarters of the eggs in experimental nestboxes were destroyed by male–female pairs of parrotlets that were not breeding elsewhere and were presumably prospecting for potential nest sites (Table II). Although we prevented marauding pairs from nesting by removing the experimental boxes after 72 h, it is likely that most pairs would have continued had the boxes stayed in place. The remainder of eggs were destroyed by male–male parrotlet pairs (Table II). Male–male pairs are commonly observed near nestboxes in our study area, and some behave like nesting pairs, entering boxes, allopreening each other and coordinating their flights to and from the boxes. What advantage males gain by destroying nests, other than spite (Harris 1979), is not clear. They may have the chance to obtain a female if nesting pairs break up after their eggs are destroyed. Lone males, however, did not destroy eggs even though they were the most frequent visitors to experimental boxes (Table II). Males rarely entered experimental boxes when they were alone, perhaps because of the risk of being predated (see below). More likely, lone males visited boxes in hopes of finding unmated females or perhaps to seek extra-pair copulations, although extra-pair copulations have yet to be observed in this species.

Nest guarding, even by lone females, was an effective way to safeguard eggs. Eggs were rarely destroyed by other parrotlets at control nests (Fig. 1). Prospecting parrotlets were less likely to approach the nest entrance at guarded control nests than at vacant experimental nests (Table IV). Even lone females were very effective in deterring conspecifics from the nest area. They often accomplished this by simply remaining inside their nestbox, compared to males, which vigorously chased or displaced intruders two-thirds of the time (Fig. 2). When in the company of their mates, however, females frequently left the nestbox to chase and displace intruders. Remaining in the box when alone may reassure the male of his paternity, and may be the least risky and most energetically efficient way for a female to defend the nest and eggs. Joining the male when he is present to chase other pairs may be more effective in repelling the threat than nest defence by a single bird and could serve to reinforce the pair-bond, since female parrotlets are dependent on males for most of their food from egg laying to hatching (Waltman & Beissinger 1992; Curlee & Beissinger 1995).

None of the experimental nests were parasitized by conspecifics. Furthermore, we have never recorded evidence for brood parasitism, in the form of two eggs appearing in a nestbox on the same day, during 8 years of daily nest checks at over 1000 parrotlet nests. Several factors make it unlikely that high rates of brood parasitism would occur in the green-rumped parrotlet. First, females typically begin laying eggs only after being fed extensively by their mates and occupying a box for 1–2 weeks (Beissinger & Waltman 1991; Waltman & Beissinger 1992; Curlee & Beissinger 1995). Thus, non-nesting females are probably incapable of quickly responding to unguarded nests by laying eggs. Second, neighbouring females that are in the middle of egg laying may be occupied defending their nests and incubating their eggs, and be unable to take advantage of opportunities to parasitize unguarded nests.

Boxes represent both opportunities to nest and threats to survival. Although cavities offer concealed sites and may afford greater nesting success than open nests (Lack 1968; Ricklefs 1969; Martin & Li 1992), cavities may contain predators capable of killing adults. Parrotlets were often hesitant to enter the experimental boxes upon encountering them, inspecting them on average for nearly 6 h before entering them. Given that the typical control pair left their nest unguarded for less than 8 min at a time, most prospecting individuals would probably have been discovered by a nesting pair and chased away before they would be able to enter the cavity. Nevertheless, some pairs entered boxes within 2 min of discovering them, and would have had ample opportunity to destroy eggs left unguarded or to lay additional eggs.

Our results are in accord with predictions from the Egg Protection and Limited Breeding Opportunities Hypotheses but not with those from the Brood Parasitism Hypothesis. Both the Egg Protection and Limited Breeding Opportunities Hypotheses posit that the early onset of incubation serves a protective function. The Limited Breeding Opportunities Hypothesis predicts protection of both the nest site and eggs from conspecifics or competitors that attempt to usurp it (Beissinger & Waltman 1991; Beissinger 1996). The Egg Protection Hypothesis is mainly concerned with protection against loss of eggs and makes no distinction about the desirability of the nest site or the motives and identity of the egg marauders. Of the two, the Limited Breeding Opportunities Hypothesis may be more apropos for the parrotlet, since eggs were mostly destroyed by male–female parrotlet pairs prospecting for nest sites.

In conclusion, the very early onset of incubation leading to extreme hatching asynchrony in the green-rumped parrotlet may be partly the result of social constraints imposed by nonbreeding parrotlets, which are capable of destroying eggs in unguarded nests at high rates during the laying period. Although protecting eggs and nest sites does not require females to begin incubating their eggs, early incubation may be selected for several reasons. First, guarding the nest by remaining outside the cavity would greatly increase: (1) the female's vulnerability to predation (Slagsvold & Dale 1996; Stoleson 1996); (2) the likelihood of her nest being discovered by conspecifics and predators; (3) the energetic costs of defending the nest or herself from males seeking copulations or pairs attempting to take over the nest; and (4) the female's vulnerability to forced copulations. By hiding inside the cavity, female parrotlets can cryptically secure the site and eggs by occupying the nest, while males gather food resources for them both. This allows females to reduce energetic expenditures through decreased locomotor activities (Walsberg 1983; Beissinger 1987) and lay large clutches (Beissinger & Waltman 1991; Beissinger 1996), since clutch size in the green-rumped parrotlet is positively related to the rate at which females are fed by males during egg laying (Waltman & Beissinger 1992; Curlee & Beissinger 1995). Encountering the female inside the nest may also serve to increase the male's confidence of paternity and ensure that he will continue to feed the female. Theoretically, females could occupy the deep nest cavity without incubating by holding onto the cavity wall above the eggs, but this would be energetically demanding, tiring and potentially devastating to the eggs if anything went wrong. Second, initiating incubation before the clutch is complete not only protects the eggs, but it minimizes the time that nestlings and females are exposed to predators during the nestling phase, when predation rates are highest (Stoleson 1996), since asynchrony reduces the time before the first chick fledges (Clark & Wilson 1981; Hussell 1985; Stoleson & Beissinger 1995). Third, eggs that are not incubated can lose their viability after several days if subjected to ambient air temperatures above physiological zero (25–27°C; Veiga 1992). Unincubated eggs are highly affected by exposure in warm tropical environments like the Venezuelan llanos, and hatching rates for green-rumped parrotlet eggs significantly decline after only 3 days of exposure to ambient temperatures (Stoleson 1996; S. H. Stoleson & S. R. Beissinger, unpublished data).

These three factors, defending the nest by hiding inside the cavity, minimizing the exposure of her young and herself to predation, and maintaining the viability of her eggs, may interact to select for the onset of incubation on the first egg, rather than on later eggs, in the green-rumped parrotlet. Thus, the nestling size hierarchy that results from asynchronous hatching in the green-rumped parrotlet may be an epiphenomenon of the benefits derived from early incubation itself, since asynchronous hatching appears to offer little benefit to parents or offspring (Stoleson & Beissinger 1997). It remains to be seen whether hatching asynchrony in other birds is caused by these factors, as the onset of incubation is a complex phenomenon (Clark & Wilson 1981; Stoleson & Beissinger 1995). Nevertheless, social constraints, predation and egg viability may affect the onset of incubation in many parrots: most species are highly social and nest in cavities (Forshaw 1989), which are often in short supply, many show aggressive competition and even attempt infanticide to obtain cavities (e.g. Snyder et al. 1987; Munn 1992), and the majority inhabit warm tropical climates (Forshaw 1989), which have high rates of predation and which make their eggs susceptible to a loss of viability from a delay in the onset of incubation (S. H. Stoleson & S. R. Beissinger, unpublished data).

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