EXTRAORDINARY CLUTCH SIZE AND HATCHING ASYNCHRONY OF A NEOTROPICAL PARROT

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ABSTRACT.—We studied the nesting biology of the Green-rumped Parrotlet (*Forpus passerinus*) in the llanos of Venezuela. Clutch size averaged 7 eggs (range: 5–10), and eggs were typically laid daily or every other day over 7–16 days ($\bar{x}$ = 10). Incubation began with the first egg. Clutches hatched over 2–14 days ($\bar{x}$ = 8.6) and fledged over 4–17 days ($\bar{x}$ = 9.7). An average of 5.7 chicks hatched (range: 2–10) and 4.7 chicks fledged (range: 1–8) per successful nest. The number of young fledging increased slightly with clutch size, but parents that hatched more eggs were able to fledge significantly more young. Chicks fledged at 28–35 days of age, and chicks that hatched later and in nests with larger broods took significantly longer to fledge.

Hatching success was significantly lower for last eggs in large clutches than for eggs laid earlier or in smaller clutches. However, fertility and volume of last eggs were similar to other eggs. Fledging success was uniformly high for nestlings in small broods, declined slightly for the last two chicks in medium sized broods, and declined sharply for the last two nestlings in large broods. Last-hatched and penultimately hatched chicks were found dead with empty crops significantly more often than earlier-hatched chicks, which implies death by starvation.

We evaluated these results in relation to current hypotheses for the evolution of clutch size in tropical birds and the causes of hatching asynchrony. We propose the *limited breeding-opportunities hypothesis* to explain both the large clutch size and hatching asynchrony in *F. passerinus.* When opportunities to nest are limited through intra- or interspecific competition, females might be expected to invest heavily in reproductive effort and guard their clutches from nest-site takeovers. This could lead to large clutches, incubation beginning with the first egg, and a large hatching interval. *Received 30 August 1990, accepted 23 March 1991.*

TROPICAL birds usually lay smaller clutches than similarly sized temperate counterparts (Lack 1968, Klomp 1970, Skutch 1985). We present data on a Neotropical parrot that lays a large clutch that hatches very asynchronously.

Forpus passerinus, the Green-rumped Parrotlet, is one of seven species in a genus of small Neotropical parrots (Forshaw 1978). Among Neotropical birds, parrots are one of the least studied groups, with the exception of the Puerto Rican Parrot (*Amazona vittata*) (Snyder et al. 1987). Unlike many other Neotropical parrots, *F. passerinus* inhabits open habitats like savannah or pastures, the sexes are plumage dimorphic (Forshaw 1978), and adults are small (24–36 g).

We present detailed information on the large clutch size and hatching asynchrony of *F. passerinus* and evaluate these data in relation to current hypotheses for the evolution of clutch size in the tropics and the evolution of hatching asynchrony.

METHODS

Our study site is in the llanos of Venezuela at Hato Masaguaral (8°34′N, 67°35′W), a working cattle ranch 45 km south of Calabozo in the state of Guarico. The habitat is seasonally flooded savannah broken by small patches of denser forest. Rains usually commence in May and end in December. Troth (1979) and O'Connell (1989) present descriptions of the study area. During our studies (June through December 1988) total rainfall was 1,390 mm.

On the ranch, *F. passerinus* nested in three locations: very rarely in natural cavities in trees, more commonly in seminatural cavities in hollow fence posts cut from trees and, since 1987, very commonly in nest boxes. Beissinger and Bucher (in press) describe the construction and use of these boxes. Forty nest boxes were attached to fence posts and opened during the last week of June 1988. At that time, parrotlet courtship behavior was observed but no active nests were found. Eggs were laid from mid-July through mid-

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Table 1. Reproductive effort and development of *Forpus passerinus* in Venezuela. The number of nests is in parentheses following the mean value.

Reproductive characteristic	$\bar{x}$ ± SD (n)	Range
Clutch size	7.0 ± 1.1 (48)	5-10
Laying period (days)	10.1 ± 2.1 (31)	7-16
Incubation period (days)	19.7 ± 0.8 (39)[a]	18-22
Number of young hatched	5.7 ± 1.7 (44)	2-10
Hatching interval (days)	8.7 ± 2.6 (31)	2-14
Number of young fledged	4.7 ± 2.0 (30)	1-8
Age at fledging (days)	30.9 ± 1.7 (31)[b]	28-35
Fledging interval (days)	9.7 ± 3.2 (21)	4-17

[a] Incubation period of 151 eggs at 39 nests.

[b] Mean based on 121 young fledged from 31 nests.

November. We observed 63 nesting attempts: 58 in nest boxes and 5 in fence posts. Adult birds were mist-netted near active nests along fencelines and banded with unique combinations of colored plastic and aluminum bands.

Nest boxes were checked every 1-2 days. Eggs were uniquely marked with indelible ink and weighed to the nearest 0.1 g with 10-g pesola scales. Egg length and width were measured using dial calipers to calculate egg volume (Hoyt 1979): Volume = 0.51 × (Egg length) × (Egg width)^2. Hatchlings were color-marked on their toenails with fingernail polish, weighed with 10- or 30-g pesola scales, and crop contents noted. Wetness and color of down were used to determine hatching sequence if two unmarked chicks were found on the same day. Unhatched eggs were broken and examined for evidence of development. Nestlings were reweighed every 2-5 days until fledging and were banded near day 20. Nestlings were considered to have fledged if they survived 25 days of age. Age at fledging was calculated only for birds for which the exact dates of hatching and fledging were known.

After hatching, nests were observed from 30 to 50 m with spotting scopes and binoculars to determine feeding rates. Parrotlets often disappeared from view inside the nest box. We assumed that feedings occurred whenever a parent either entered the box or passed food to its mate who subsequently entered the box upon return from a trip away from the nesting area of 10 or more minutes duration. Waltman and Beissinger (in press) give detailed descriptions of feeding behavior and sequences. Fifteen nests were observed at least once and 12 nests were observed 3 times, for a total of 155 hours of observations.

We grouped clutch sizes into small (5-6 eggs), medium (7-8 eggs), and large (9-10 eggs) clutches. Likewise, brood sizes were defined as small (1-5 young), medium (6-7 young), and large (8-10 young). Laying and hatching-order data were examined for position effects and then categorized as first, middle (from second to third-to-last), penultimate, or last. Nesting periods were based on nest contents. Hatching period nests contained hatched young and eggs. During the nestling period, nests had nestlings and sometimes inviable eggs. The fledging period began after one or more nestlings fledged from the nest. Data were analyzed using SYSTAT and SAS programs. Analysis of variance (ANOVA) was used when data were normally distributed and variances were equal. Multiple-contingency models with maximum likelihood estimates (Sokal and Rohlf 1981) were employed to an-

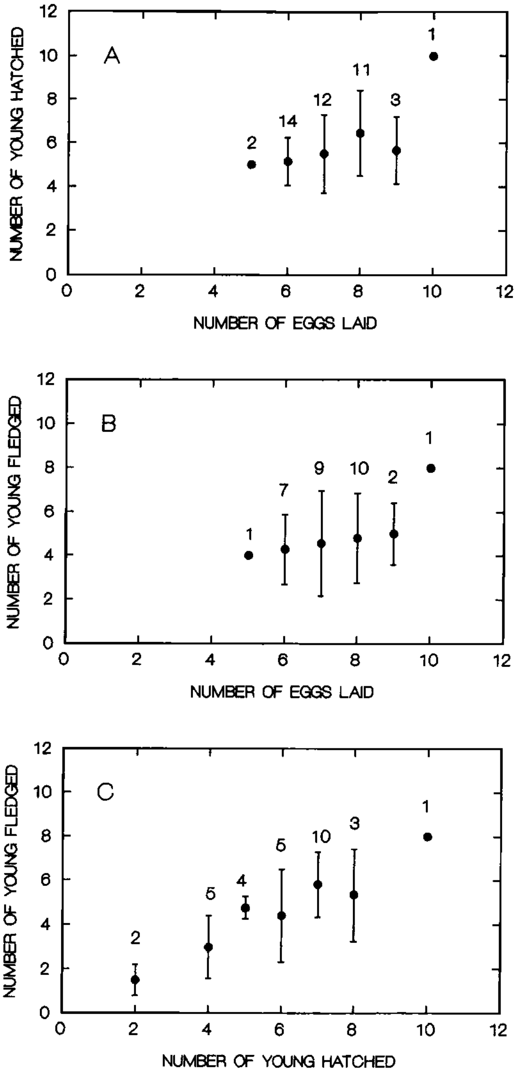

Fig. 1. The relationship between (A) clutch size and the number of young hatching, (B) clutch size and the number of young fledging, and (C) the number of young hatching and fledging at successful Green-rumped Parrotlet nests in Venezuela. Means are given with sample sizes above standard deviation bars.

TABLE 2. The age (days) of *Forpus passerinus* young at fledging in relation to hatching sequence and brood size. The number of eggs is in parentheses following the mean (±SD) value.

Hatching order	Brood size		
	Large	Medium	Small
First egg	30.7 ± 2.1 (3)	30.2 ± 1.1 (11)	30.3 ± 1.3 (8)
Middle eggs	31.9 ± 1.9 (9)	30.5 ± 1.6 (48)	30.2 ± 1.4 (10)
Penultimate egg	33.0 ± 0.0 (1)	31.5 ± 1.4 (12)	30.8 ± 1.3 (4)
Last egg	—	32.7 ± 2.1 (10)	31.3 ± 1.5 (4)

alyze the effects of laying or hatching sequence and clutch or brood size on hatching or fledging success.

RESULTS

Parrotlets laid very large clutches. Clutch size in 48 nests averaged 7 eggs and ranged from 5 to 10 eggs (Table 1). One exceptional banded female apparently laid 12 eggs over a 28-day period. When her original 8-egg clutch was reduced to 2 eggs, presumably by predation, she began laying 4 additional eggs just as her first egg hatched. All of the last 4 eggs laid hatched but only the middle two young survived; the others died shortly after hatching.

Three lines of evidence suggest that most clutches were laid by only one female. First, during nearly 100 hours of observations at 23 nests during egg laying, only one banded female was seen entering each nest. Second, females spent most daylight hours in the boxes, beginning several days before egg laying, and they occupied the boxes almost continuously from egg laying through hatching (Waltman and Beissinger in press). During this time females were fed by their mates. Finally, clutches of up to 8 eggs have been routinely reported for captive pairs in isolation (Wildeboer 1926, Enehjelm 1951, Noble 1984).

Clutches were laid over a relatively long period (7–16 days) (Table 1). On average, 10 days were required to complete a clutch. Eggs (n = 146) were usually laid on successive days (35%) or every other day (63%), but occasionally at 3-day intervals (2%).

Behavioral clues suggested that most females initiated incubation with their first egg. For 3-h watches, we observed 8 nests, each containing one egg. In 7 of these nests, females spent an average of 81.5 ± 1.3% of the time in the box. The eighth female behaved differently; she spent only about one third of the time in the box. In 19 nests with one egg, checked after dark, all had incubating females. Finally, in only 4 of 44 nests did the first two eggs hatch on the same day.

Eggs hatched very asynchronously, 18–22 days after they were laid (Table 1). For example, one brood of 8 chicks hatched over a 12-day period. By the time the last chick hatched, weighing 1.8 g, the oldest nestling was partially feathered and weighed 15.0 g. On average, 8.7 days elapsed between the hatching of the first and last nestling (Table 1), but hatching was as asynchronous as 14 days. The interval between hatching of first and last eggs correlated positively with clutch size ($r = 0.37$, $n = 31$, $P = 0.04$).

Pairs hatched an average of 5.7 chicks, about one fewer than clutch size, but occasionally hatched as many as 10 nestlings (Table 1). The number of young fledged averaged 4.7 per nest but ranged up to 8 young (Table 1). Although the number of young hatching increased ($r = 0.39$, $n = 43$, $P < 0.05$) with increasing clutch size, the result was strongly affected by a few very small (5-egg, $n = 2$) or large (10-egg, $n = 1$) clutches (Fig. 1A). Among clutch sizes most frequently laid (6–9-egg clutches), there was no significant difference in the number of young fledged per nest ($F = 1.4$; df = 3, 36; $P = 0.26$). Likewise, large clutches fledged slightly more young ($r = 0.34$, $n = 34$, $P < 0.06$) than small clutches at successful nests (Fig. 1B). But again this difference was not significant for common clutch sizes (6–9 egg clutches: $F = 0.1$; df = 3, 24; $P = 0.95$). However, pairs with large clutches were capable of hatching all the eggs and fledging most of their young (Fig. 1: A and B). Parents that hatched large broods were able to fledge significantly more ($F = 4.1$; df = 5, 23; $P < 0.01$) young than parents hatching fewer eggs (Fig. 1C).

Nestlings fledged at 28–35 days after hatching (Table 2). A two-way ANOVA found that both hatching order ($F = 7.2$; df = 3, 114; $P < 0.001$) and brood size ($F = 4.3$; df = 2, 114; $P =$

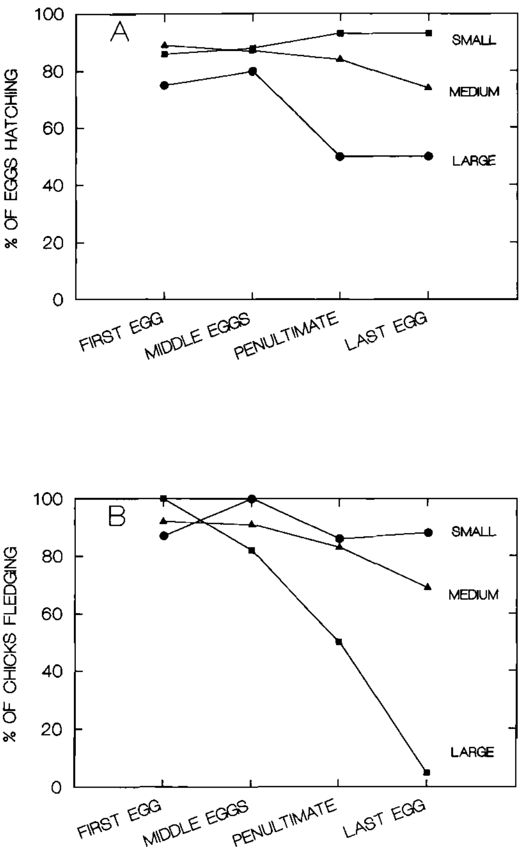

Fig. 2. The relationship between (A) laying order and hatching success for small ($n = 14$), medium ($n = 19$), and large ($n = 4$) clutches, and (B) hatching order and fledging success for small ($n = 8$), medium ($n = 13$), and large ($n = 4$) broods. Only *Forpus passerinus* nests that successfully fledged young were included.

0.016) influenced the time to fledging. Fledglings that hatched later and at nests with larger broods spent slightly more time in the nest before fledging. Fledging asynchrony was also great. The interval between the fledging of first and last young averaged 9.7 days but ranged up to 17 days (Table 1), and the interval was positively related to the number of young that hatched ($r = 0.45$, $n = 21$, $P = 0.04$) and fledged ($r = 0.65$, $n = 21$, $P < 0.01$).

Hatching success of individual eggs was affected by both clutch size and laying order (Fig. 2A). Hatching success was generally high in small and medium sized clutches, and lower in large clutches. Hatchability was affected by laying order only in large clutches: while most eggs hatched in small clutches, last eggs tended to hatch less frequently in medium-sized clutches and the last two eggs hatched only half of the time in large clutches. Maximum likelihood analysis found that clutch size ($\chi^2 = 6.4$, df = 2, $P = 0.04$) but not laying order ($\chi^2 = 1.1$; df = 3, $P = 0.78$) or the interaction of the two ($\chi^2 = 3.4$, df = 6, $P = 0.76$), significantly affected the probability of hatching. Differential fertility could not explain this pattern of hatchability (Table 3). Maximum likelihood analysis found that the percentage of eggs that did not develop was similar among clutch sizes ($\chi^2 = 1.1$, df = 2, $P = 0.58$) and by laying order ($\chi^2 = 0.7$, df = 3, $P = 0.88$), but small sample sizes prevented testing for an interaction.

TABLE 3. Percentage of fertile *Forpus passerinus* eggs by clutch size and laying order. Sample size is in parentheses.

	Clutch size		
Hatching order	Large	Medium	Small
First egg	100 (3)	95 (22)	87 (15)
Middle eggs	95 (23)	90 (94)	93 (42)
Penultimate egg	100 (4)	94 (18)	93 (15)
Last egg	100 (4)	94 (18)	93 (15)

The survival of nestlings to fledging strongly resembled the pattern of hatching success, but the effects of brood size and hatching sequence were more pronounced (Fig. 2B). Fledging success was uniformly high for nestlings in small broods, declined slightly for the last two chicks in medium-sized broods and declined sharply for the last two nestlings in large broods. Young which hatched last never fledged in our sample of four large broods. Maximum likelihood analysis yielded significant effects for both brood size ($\chi^2 = 8.4$, df = 2, $P < 0.02$) and hatching order ($\chi^2 = 12.4$, df = 3, $P = 0.006$). Small samples precluded testing for interaction effects.

The mechanisms of nestling mortality at successful nests are poorly understood. A two-way ANOVA found that egg volume (Table 4) did not differ by laying order ($F = 0.5$; df = 3, 268; $P = 0.69$) or by clutch size ($F = 1.6$; df = 2, 268; $P = 0.20$), and no interaction occurred ($F = 0.3$; df = 6, 268; $P = 0.92$). We suggest that mass at hatching for later-hatched nestlings was similar to earlier-hatched chicks, because egg volume was highly correlated ($r = 0.90$, $n = 66$, $P < 0.001$) with fresh-egg weight. However, all penultimately hatched ($n = 4$) and last-hatched ($n = 9$) nestlings from nonpredated nests that were

TABLE 4. Mean (±SD) for *Forpus passerinus* egg volumes (mm^3) calculated from Hoyt (1979) by clutch size and laying order. The number of eggs measured is in parentheses following the mean (±SD) value.

Hatching order	Clutch size Large	Medium	Small
First egg	2,031 ± 78 (3)	2,047 ± 240 (20)	2,123 ± 151 (13)
Middle eggs	2,073 ± 134 (25)	2,094 ± 204 (94)	2,099 ± 154 (43)
Penultimate egg	1,984 ± 247 (5)	2,083 ± 231 (21)	2,089 ± 117 (15)
Last egg	1,987 ± 144 (5)	2,079 ± 209 (21)	2,098 ± 97 (15)

found dead had empty crops, while 40% of the earlier-hatched nestlings ($n = 10$) that died had at least some food in their crops (excluding chicks that disappeared or that died of bodily injuries caused by apparent infanticide; see Discussion). This pattern suggests that last-hatched and penultimately hatched chicks died significantly more often from apparent starvation than earlier-hatched young (Fisher's exact test, $P = 0.03$).

The rate that parents visited nests to regurgitate seeds to nestlings indicates that food demand increased with brood size only during the nestling phase (Fig. 3). A two-way ANOVA for small and medium-sized broods showed that the total number of trips to the nest with food by parents increased slightly with brood size ($F = 3.7$; df = 1, 27; $P < 0.07$) but not by period after hatching ($F = 2.4$; df = 2, 27; $P = 0.11$). However, a significant interaction occurred ($F = 3.5$; df = 2, 27; $P < 0.05$), because delivery rates differed between brood sizes during the nestling period but not between brood sizes among other periods (Fig. 3).

DISCUSSION

Green-rumped Parrotlet clutches were large (Table 1), and most clutches were likely to be laid by single females. This clutch size is among the largest recorded for tropical bird species (Lack 1968, Klomp 1970, Skutch 1985), including most parrots (Smith 1975, Forshaw 1978, Saunders et al. 1984). In addition, *F. passerinus* nestlings hatch and fledge much more asynchronously (Table 1) than most other tropical and temperate birds (Clark and Wilson 1981, Slagsvold 1986, Lessells and Avery 1989). Although both life history characteristics may be related to the hole-nesting habits of this parrot (Klomp 1970, Clark and Wilson 1981, Saunders et al. 1984; but see Slagsvold 1986), *F. passerinus* appears to have pushed them to the extreme. To the best of our knowledge, only small parrots (including other *Forpus* species), the Barn Owl (*Tyto alba*), and a few ducks lay equally large clutches in the tropics (Forshaw 1978, Hilty and Brown 1986) or hatch them over such a prolonged period (Stamps et al. 1985, Wilson et al. 1986, Voous 1988).

The adaptive significance of the large clutch size of Green-rumped Parrotlets is unclear, because the number of young fledging did not increase greatly with clutch size at successful nests (Fig. 1B). When clutch size exceeded 7 eggs, females appeared to be unable to incubate all eggs simultaneously. Eggs could usually be seen protruding from under the female's abdomen and sometimes were cradled under her wings. Thus, female body size could constrain reproductive success by limiting the number of eggs capable of development (Klomp 1970, Andersson 1976). Although the percentage of *F. passerinus* eggs that hatched declined significantly in large clutches, females were capable of hatching all eggs in large clutches (Fig. 1A). Because *F. passerinus* eggs have no markings and did not differ in size (Table 4), it seems unlikely that females would be able to identify later-laid eggs in a dimly lit nest cavity and actively choose not to incubate them.

Low hatchability and fledging success of last-laid eggs (Fig. 2) in large clutches could result from egg or chick neglect by females. Green-rumped Parrotlet chicks are born with very little down and are continuously brooded by the female. Males do nearly all of the foraging for the nestlings and their mates through the first week of hatching (Waltman and Beissinger in press). Shortly afterwards, females discontinue brooding and join their mates to feed the nestlings. In large broods at this time, later-laid eggs may not have hatched yet; if the eggs hatched, the youngest nestlings are only a few days old. Unless later-laid eggs or chicks are brooded in-

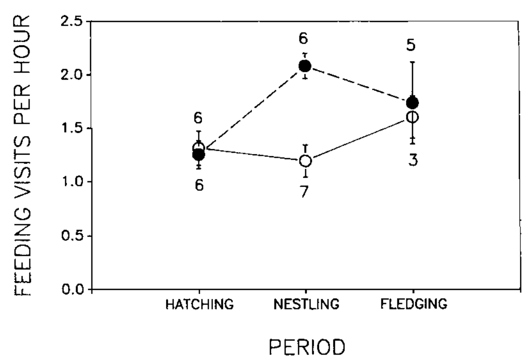

Fig. 3. The number of feeding visits to the nest per hour by *Forpus passerinus* parents in relation to nesting period (see Methods) for small and medium-sized broods. Means are given with standard error bars. Sample size placed above (medium-sized broods) or below bars (small broods) is the number of nests observed.

cidentally by older nestlings, they might die of hypothermia on cool, rainy days, which is probably an unusual cause of mortality in tropical lowland birds (Skutch 1985). Thus, decreased survivorship of later-laid eggs in large broods could be a consequence of the female's joining the male to forage for the brood rather than remaining on the nest to incubate or brood.

Last-laid eggs could represent a hedge against earlier-laid eggs that do not hatch or die as young chicks (the *insurance hypothesis*; Stinson 1979). Fertility rates of all eggs were high (Table 3) and did not differ by laying order. However, older chicks frequently died while the rest of the brood survived, and parents might have increased clutch size by one or two eggs just to cover such circumstances. Mock and Parker (1986) developed a method to partition the reproductive value (RV) of a chick into RV_e or *extra RV* (the probability of a chick fledging if all earlier hatched siblings fledged), and RV_i or *insurance RV* (the probability of a chick fledging if, or perhaps because, it was predeceased by an older sibling). Reproductive value components varied for last- and pentultimately laid *F. passerinus* eggs (Table 5). Insurance RV was the dominant component of the total RV for these eggs in all brood sizes except large broods, where none of the later-hatched chicks fledged. Although later-laid eggs may function mostly as insurance against failure of earlier-laid eggs, our sample sizes are too small to allow us to draw strong inference, especially for large broods.

Tropical birds may lay smaller clutches than temperate counterparts to decrease the probability of detection by predators (Skutch 1985) or as insurance against high rates of nest predation (Stearns 1976, Slagsvold 1982). We hesitate to use our nest-box data for inference about nesting success (Møller 1989). However, the success rate of nests in seminatural sites (fence post) appears to be relatively high (44%; Beissinger and Bucher in press) compared with other tropical birds (Ricklefs 1969, Skutch 1985). Low rates of predation may also lead to asynchronous hatching (the *nest failure hypothesis*; Clark and Wilson 1981, Slagsvold 1986).

Few investigators have manipulated brood sizes of tropical land birds. Most found that parents were incapable of raising enlarged broods (Beissinger 1990), and support Lack's (1968) contention that food may limit clutch

TABLE 5. Estimates of Mock and Parker's (1986) components of reproductive value (RV) for last-laid and penultimately laid *F. passerinus* eggs by clutch size. Total reproductive value (RV_T) is the sum of extra reproductive value[a] ($RV_e = q \times P_e$) or success for parents, and insurance reproductive value[b] ($RV_i = (1 - q) \times P_i$) that functions only as a replacement in the case of the death of earlier-laid eggs.

			Components of success[a,b]			Components of RV		
Hatch order	Clutch size	*n*	q	P_e	P_i	RV_e	RV_i	RV_T
Last	Small	7	0.29	0.50	0.60	0.15	0.43	0.58
	Medium	18	0.28	0.60	0.38	0.17	0.27	0.44
	Large	3	0.00	0.00	0.00	0.00	0.00	0.00
	All	28	0.25	0.57	0.38	0.14	0.29	0.43
Penultimate	Small	8	0.38	0.67	0.80	0.25	0.50	0.75
	Medium	17	0.35	0.83	0.64	0.29	0.42	0.71
	Large	3	0.33	0.00	0.00	0.00	0.00	0.00
	All	28	0.36	0.70	0.61	0.25	0.39	0.64

[a] q = proportion of broods in which the youngest chick was not predeceased by an elder sibling; P_e = proportion of q in which the youngest chick fledges.

[b] P_i = proportion of youngest chicks fledging in $(1 - q)$ broods where they were predeceased by an older sibling.

size of tropical birds. Because *F. passerinus* lays a large clutch, it might appear to be the exception. However, the high rate of starvation of later-hatched offspring in larger parrotlet broods implies that food could limit reproductive success. Starvation of last-hatched young was not found in captive Budgerigars (*Melopsittacus undulatus*)(Stamps et al. 1985). In this species, survival and growth of young were independent of hatching order because females fed smaller chicks preferentially over larger ones. Offspring mortality patterns in *F. passerinus* suggest that parents do not feed last-hatched chicks preferentially (Beissinger and Stoleson in press). Thus, it is not clear whether food quantity or the unequal distribution of food among nestlings limits fledging success for *F. passerinus.*

If food limits reproduction, a high degree of hatching asynchrony might enable parents to raise more young and would select for larger clutches either by facilitating brood reduction if food supply varies unpredictably (Lack 1954, Skagen 1988) or by spreading out the peak periods of food demand (Hussell 1972). Lack's hypothesis might not apply to *F. passerinus* because parrotlets eat a wide variety of seeds. Seed availability—unlike insect availability (Blancher and Robertson 1987)—may be unlikely to be affected by rapid changes in rainfall or temperature after the young have hatched. Hussell's hypothesis could apply to *F. passerinus* because the hatching asynchrony is large enough that Green-rumped Parrotlets may be one of the few species that could benefit by spreading out peak food demands (Mock and Schwagmeyer 1990).

In the preceding discussion, we considered the large clutch size and hatching asynchrony in the Green-rumped Parrotlet as coadapted traits. A large clutch size is required to achieve a larger hatch spread and a very asynchronous hatching may allow more young to fledge from larger broods. On the other hand, the very asynchronous hatching may simply be a constraint of laying a large clutch, because hatching asynchrony is often related positively to clutch size (e.g. Smith 1988, this study). To discriminate between these two explanations, we must understand why female parrotlets initiate incubation after laying their first eggs which results in very asynchronous hatching. Many birds start to incubate only when the penultimate egg is laid (Clark and Wilson 1981, 1985).

We offer another hypothesis to account for both the large clutch size and asynchronous hatching found in *F. passerinus.* Limited opportunities to breed could also promote large clutches that hatch asynchronously (the *limited breeding-opportunities hypothesis*), because reproductive effort should be high when residual reproductive value is low (Williams 1966, Stearns 1976). If nesting opportunities are limited (e.g. nest sites limited through intra- or interspecific competition), then females might be expected to invest heavily in reproductive effort by laying large clutches, if the food supply permits, when the chance to nest arises. Females that occupied their nest sites to defend them from other pairs should initiate incubation early (leading to a very asynchronous hatching), because this would also promote rapid fledging of some young (*the nest failure hypothesis*) and would minimize the time that females are exposed to predators (Macgrath 1988). For species like *F. passerinus* that do not defend territories, consistent occupancy of a cavity may be the most effective way for a single individual to defend a cavity against intruding pairs. Thus, one mate would be free to forage, for itself and its mate, while the other mate defended the cavity by initiating incubation. The female constantly occupies the nest cavity in *F. passerinus,* as in most other parrots (Waltman and Beissinger in press). Such behavior by females minimizes their energetic expenditures during egg laying and decreases the cost of clutch production (Beissinger 1987), which in the case of *F. passerinus* could allow females to lay more eggs. Female Green-rumped Parrotlets that were fed more often by their mates during egg laying laid larger clutches (Waltman and Beissinger in press). Hence, both clutch size and hatching spread are influenced by male reproductive efforts.

Several forms of evidence suggest that limited breeding opportunities might exist for *F. passerinus.* First, the rapid acceptance and high degree of nest-box occupation in our study population implies that nest sites are limited (Beissinger and Bucher in press). Second, competition occurred for nest sites and invading pairs have been observed to destroy unguarded eggs and young (Beissinger and Stoleson in press, Waltman and Beissinger in press).

The *limited-breeding opportunities hypothesis* might only explain hatching asynchrony in hole-nesting birds that do not defend territories, as territories might be defended more successfully by actively patrolling or duetting pairs rather than by single individuals. But, nonterritorial hole nesters, like *F. passerinus,* other psittacines and Barn Owls (Forshaw 1978, Stamps et al. 1985, Wilson et al. 1986), provide some of the most extreme cases of hatching asynchrony (Clark and Wilson 1981, Lessells and Avery 1989). Asynchronous hatching in species that exhibit extreme asynchrony may represent a true adaptation rather than an incidental consequence of egg-laying behavior (Mead and Morton 1985). Piciformes are the exception to the trend of very asynchronous hatching in hole nesters; they lay average-sized clutches with little hatching asynchrony (Klomp 1970, Clark and Wilson 1981). However, nest sites might not be as limiting for many piciforms as they are for other cavity-nesting birds, because many piciforms excavate their own cavities (Bent 1939, Graber et al. 1977).

Further work will be required to determine which of the many functional hypotheses (Lessells and Avery 1989) are likely to account for the evolution of asynchronous hatching in the Green-rumped Parrotlet. Like Mock and Parker (1986), we believe that asynchronous hatching can not be evaluated alone without understanding its relationship to clutch-size evolution. In the extraordinarily large clutch size and hatching asynchrony of *F. passerinus,* it is not clear if these elements are independent of each other or are coadapted. Understanding female parrotlet egg-laying and incubation behavior may be the key to understanding the causes and consequences of this staggering phenomenon.

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LITERATURE CITED

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