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VARIATION IN THE ONSET OF INCUBATION IN A NEOTROPICAL PARROT¹

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Abstract. We studied the onset of incubation in the Green-rumped Parrotlet (*Forpus passerinus*), a cavity-nesting species with female-only incubation starting on the first egg and asynchronous hatching. We quantified how the onset of incubation varied among individual females, with stage of egg-laying and by ultimate clutch size. We then examined whether this variation affected the incubation period and hatching success of individual eggs. Female parrotlets initiated incubation in three characteristic patterns: slowly rising, rapidly rising, and pulsed. The diurnal incubation rate of the first egg was 80.0% and increased as the laying cycle progressed, but was not affected by ultimate clutch size. Females that were fed more often by their mates during laying had lower incubation rates. First-laid eggs had longer incubation periods than later-laid eggs, but nearly all eggs hatched in the order they were laid. Hatching success was not affected by laying order. Despite the strong hatching asynchrony and consistent first-egg incubation exhibited by this species, we found significant variation in the onset of incubation, although no serious fitness consequences of this variation were detected.

Key words: *Forpus passerinus*, *Green-rumped Parrotlet*, *hatching asynchrony*, *hatching success*, *incubation patterns*, *incubation period*, *onset of incubation*.

INTRODUCTION

Hatching asynchrony in birds has puzzled researchers for decades. Whereas the cost to young chicks of competing with older sibs has been well documented, the benefits of asynchronous hatching remain unclear (Clark and Wilson 1981, Stoleson and Beissinger 1995). Hatching patterns of eggs within a clutch are thought to be determined by incubation patterns during egg-laying (Bortolotti and Wiebe 1993) and may operate under phylogenetic constraints (Stoleson and Beissinger 1995). Although incubation of completed clutches has been well studied (White and Kinney 1974), behavior of parents during the onset of incubation is poorly understood. Published accounts are problematic because they often fail to distinguish the onset of incubation from incubation following clutch completion (Jones 1987, Coleman and Whittall 1988), ignore or only briefly mention variation among individuals in the onset of incubation (Wilson and Verbeek 1995), use indirect techniques that may be imprecise indicators of parental behavior during the onset of incubation (Enemar and Arheimer 1989), or focus on continuous incubation without addressing the details or importance of

partial incubation (Drent et al. 1985, Banbura and Zielinski 1995).

The onset of incubation can vary among individuals and may be affected by stage of the laying cycle, ultimate clutch size, and food supply. In many birds, clutches may be partially incubated before laying has been completed, and incubation often slowly increases to a maximum, steady rate (Haftorn 1981). Females may differ by up to several days in the onset of partial, nocturnal, and maximum incubation (Banbura and Zielinski 1995, Anderson 1997). Wiebe et al. (1998) found that individual kestrels increased incubation from partial to maximum attendance in three distinct patterns: rising, steady, and pulsed. The interaction between clutch size and laying date also may contribute to variation in the onset of incubation (Potti 1998). In some temperate species, clutches laid late in the breeding season are smaller and are incubated earlier and more intensely than clutches laid earlier in the year (Haftorn 1981, Meijer et al. 1990). Lastly, abundant food during the laying period may increase (Wiebe and Bortolotti 1994) or decrease (Nilsson 1993) hatching synchrony, presumably by altering the onset of incubation.

In this paper, we characterize variation in the onset of incubation and the resulting effects on hatching patterns in the Green-rumped Parrotlet (*Forpus passerinus*). This Neotropical parrot

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lays a large clutch ($\bar{x} = 7$ eggs) and begins incubation on the first egg (Beissinger and Waltman 1991). Only the female incubates, and she is fed regurgitated seeds by her mate during laying (Waltman and Beissinger 1992). Clutches hatch over a variable period of 2 to 14 ($\bar{x} = 8.7$) days (Beissinger and Waltman 1991). Early initiation of incubation is typical in parrots, but species differ greatly in degree of hatching asynchrony (Beissinger et al. 1998). We quantified intraspecific variation in incubation behavior during egg-laying and describe common patterns adapted from Wiebe et al. (1998). Because parrotlets appear to begin incubation on the first egg and consistently show strongly asynchronous hatching, we expected to find little variation in the rate of incubation during egg-laying among individuals, in relation to the number of eggs in the nest or to ultimate clutch size. We also examined whether male feeding rate and intruder pressure influenced female incubation patterns. We predicted that females fed more frequently by their mates would spend more time on the eggs and less time away from the nest foraging. We had no clear prediction about the effect of intruder pressure, because female nest defense behavior differs greatly according to the presence or absence of her mate (Beissinger et al. 1998). Lastly, we investigated whether variation in the onset of incubation affected the incubation period, hatching order, and hatching success of individual eggs. Because we expected to find little variation, we predicted that the length of the incubation period, hatching order, and hatching success would not be affected by variation in the onset of incubation.

METHODS

STUDY SITE AND SPECIES

We studied parrotlets at the Hato Masaguaral (8°31'N, 67°35'W), a cattle ranch 45 km south of Calabozo in the state of Guarico, Venezuela. The area is a highly seasonal llanos with small patches of brush and forest (Troth 1979). Nearly all adult parrotlets in the population as well as young produced in our nest boxes are permanently marked with colored leg-bands. We conducted intensive observations from June–August 1997 on parrotlet pairs nesting in nest boxes (Beissinger and Bucher 1992) and report data for first-attempt nests that were successful through the laying phase. For analyses of hatch-

ing patterns, we used data collected from 1988–1997. The laying and hatching order of eggs within a clutch were determined by visiting nests daily and using indelible ink to mark eggs as they were laid and nestlings as they hatched.

Green-rumped Parrotlets are small, sexually dimorphic, cavity-nesting parrots native to northern South America (Forshaw 1989) that feed mainly on the seeds of forbs and grasses (Waltman and Beissinger 1992). Parrotlets breed in the rainy season from late May to December. The laying interval between successive eggs averages 1.5 days (range 1–3 days; Beissinger and Waltman 1991). Unattended eggs may be destroyed by prospecting conspecifics (Beissinger et al. 1998).

SAMPLING FEMALE INCUBATION BEHAVIOR FROM NEST TEMPERATURES

Full sets of temperature data were collected from nine nests that survived into the post-laying incubation phase. Temperatures were recorded once per minute inside nest boxes using a Hobo Data Logger in a waterproof case hung outside the box that was attached to a thermister placed under a thin layer of wood shavings directly below the eggs. Thermisters were usually installed on the afternoon that the first egg was laid and no later than the next day. Females sometimes destroyed thermisters that protruded from the shavings, so thermisters were tied in place with cotton thread. Damaged thermisters were replaced as soon as possible, but some gaps in data occurred.

We initially learned how to interpret nest temperature data by comparing records of nest temperature with direct observations of female incubation behavior conducted simultaneously for a 3-hr period ($n = 4$ females, 5 nest watches). These comparisons indicated that relative changes in temperature worked better than absolute temperature to distinguish incubation from recesses off the nest. Diagnostic temperature profiles for female trips off the eggs showed rapid cooling that slowed as the nest neared ambient temperatures, and extremely rapid warming as soon as the female recommenced incubation. Female departure produced a characteristic dip on the temperature graph with a curved initial down-slope, a gradually flattening bottom as she remained away, and a sharp, nearly vertical up-slope when she returned to the eggs. While females incubated, nest temperatures fluctuated

0.5–1°C around a constant temperature or temperature trend. This relatively small magnitude of fluctuation, compared to the pronounced drop in temperature when the female left the eggs, allowed recesses to be distinguished from a shift in the position of the incubating female. Nest temperatures varied greatly by nest, day, and time of day, due to diurnal fluctuations in ambient temperature, degree of shade around the box, aspect of the box, and chance irregularities in the placement of the thermister (Stoleson and Beissinger, 1999). Generally, morning nest temperatures were in the range of 32–34°C and dropped to as low as 24°C when the female took a long recess from incubation. Afternoon nest temperatures were usually 34–38°C during incubation and dropped about 3–4°C when the female was away.

We conducted a separate set of nest watches to test the accuracy of our assignment of female incubation behavior from nest temperature graphs. Thirty nest watches on nine nests totaling 85.8 hr were compared to a simultaneously recorded set of nest temperature data. The percent of time that females spent incubating determined by direct observation ($86.2 \pm 12.1\%$) did not differ significantly from the percent calculated from thermister data ($84.8 \pm 13.0\%$; Wilcoxon signed rank, $Z = 0.52$, $P = 0.61$). Our error rate for assigning females as either incubating or off of the eggs was $4.9 \pm 5.6\%$ as calculated by the difference between the percent of time females incubated determined from nest temperatures and from nest watch data. Over- and under-estimations were nearly equal, however, which resulted in an overall difference of only $1.3 \pm 7.3\%$.

NEST WATCHES OF MALE, FEMALE, AND EXTRA-PAIR BEHAVIOR

Thirteen nests were observed for continuous 3-hr periods at least three times during laying and once during post-laying incubation. We tried to sample each nest immediately subsequent to the laying of the first, third, and sixth eggs, and 3 or 4 days after the clutch was complete. In some cases, nests were not sampled until 1 or 2 days after the target day, by which time another egg had sometimes been laid. We excluded the nests of females that exhibited unusual shyness or avoidance of the nest during observation. Observations were conducted during light rains but were discontinued during heavy rains. During

each nest watch, a single observer sat 20–40 m from the nest box with a direct line of sight to the entrance hole and perch. We used 10× binoculars and 15–60× spotting scopes to identify each banded individual.

We gathered behavioral data during nest watches on the incubating female, her mate, and intruding conspecifics. We recorded the location of each parrotlet relative to the nest box as inside, on top, less than 5 m away, or outside the nest area. We assumed that females inside the box were incubating. We recorded the number of male feeding visits to the nest per hour. Because males rarely regurgitate to their mates in view of the observer, we followed Beissinger and Waltman's (1991) definition of a feeding visit as when the male joined his mate after having been away from the nest area and unaccompanied by the female for ≥ 10 min. We also recorded the percent of time extra-pair birds were present in the nest area and the number of vigilance visits that the breeding male made to the nest per hour. A vigilance visit occurred when the male perched in the nest area and left without visiting the female.

DATA ANALYSIS

We divided the continuous 24-hr temperature data into day (06:00–19:00) and night (19:00–06:00). Unless otherwise stated, only the daylight incubation rates are referred to in this paper, because nearly all females incubate continuously at night beginning with the first egg (Beissinger and Waltman 1991). We defined the laying phase as beginning the day the first egg was laid and ending the day the last egg was laid, and the post-laying incubation phase as beginning the day after the last egg was laid and ending the day before the first egg hatched. When nest temperature and nest watch data were recorded on the same day, we used the nest temperature data, because they encompassed a greater number of hours. We used nest watch data for analyses of incubation behavior when no concurrent temperature data were available. We adapted individual female incubation patterns from Wiebe et al. (1998).

All statistical analyses were conducted with SYSTAT 7.0 (SPSS 1997). Percent incubation was arcsine transformed to approximate normality. When data were normal and variances homogenous, analysis of variance (ANOVA) was used with post-hoc Tukey's HSD pairwise

comparisons. When data could not be normalized through transformations, we employed Spearman rank correlations (r_s), Kruskal-Wallis ANOVA (H), and Wilcoxon sign rank tests (Z). To examine changes in female incubation behavior over the course of laying, we used repeated measures ANOVA (F) to eliminate pseudoreplication from sampling the same female over time. When we compared these univariate F -tests to analyses, such as the Greenhouse-Geiser Epsilon and multivariate tests (Wilks' Lambda), that allowed relaxation of the compound symmetry assumption for the covariance matrix (Nemec 1996), results from all approaches were the same, so we report only the univariate test results.

To prevent empty cells in repeated measures ANOVA procedures, we sometimes grouped data into time periods of 2–4 days and averaged the values for each nest within a time period to prevent pseudoreplication. For repeated measures analyses, we divided time after the first egg was laid into intervals of 0–2 days, 3–5 days, 6–9 days, and 10–14 days, and post-laying incubation. Similarly, number of eggs was grouped into 1–2 eggs, 3–4 eggs, 5–6 eggs, and 7–8 eggs, and post-laying incubation. Because of the sampling regime of our nest watches, number of eggs was grouped slightly differently (1–2 eggs, 3–5 eggs, 6–8 eggs, and post-laying incubation) for correlations between the percentage of time females incubated and the behavior of their mates, the presence of extra-pair birds, and the frequency and duration of female recesses off the nest.

We used data collected from 1988–1997 to examine variation in hatching patterns. We selected only eggs from unmanipulated nests for which both the date of laying and hatching were certain ($n = 1,084$ eggs from 276 nests) to study variation in the incubation period, defined as the time from the laying of an egg to when it hatched. We then examined these nests to determine how often eggs in a clutch hatched on the same day or in an order other than they were laid. We investigated the relationship between hatching success and laying order, using only eggs from unmanipulated nests that survived through the hatching period ($n = 2,363$ eggs from 363 nests). We also excluded eggs that failed for reasons other than insufficient incubation, such as predation, parental neglect, or

parental death. Values presented are means \pm SD.

RESULTS

FEMALE INCUBATION BEHAVIOR

We characterized incubation behavior using 1,138 daylight hours ($n = 105$ days) of nest temperature data from nine nests, representing an average of 88.2% percent of each female's laying period. On average, females spent 84.5% of daylight hours incubating. When night hours were included, females spent 91.6% of their total time on the eggs. Females incubated eggs all night long ($n = 94$ nights) during laying with two exceptions. One female spent an entire night off her first egg following the morning that a thermister was placed in her nest, although she had spent several hours earlier that day on the egg after the thermister was installed. Her entire clutch of eight hatched successfully. Another female took a 4-hr recess from incubating her first four eggs in the middle of one night during a period when she was switching mates, which was associated with a very high level of male parrotlet aggression at the nest during daylight hours. Although two of these eggs failed before hatching due to infanticide, the first two eggs did hatch, but they had unusually long incubation periods of 22–23 days (See Relationship Between Laying Order, Incubation Period, and Hatching Success below).

Females exhibited three general incubation patterns during laying (Fig. 1) based on nest temperature and nest watch data. The most common was a slowly rising pattern ($n = 5$ females) where the female gradually increased the percentage incubation until reaching the maximum around the sixth egg (Fig. 1A). A rapidly rising onset of incubation was the next most common pattern ($n = 4$ females, Fig. 1B). Rapidly rising incubation tended to increase a greater absolute percentage and more quickly than the slowly rising pattern, reaching the maximum percent incubation by the third egg. Slightly fewer females ($n = 3$) began incubation in a pulsed pattern, where the percent incubation rose, fell, and then rose again (Fig. 1C).

The percentage of daylight hours that eggs were incubated increased as the laying cycle progressed (Fig. 2). The percent of time females incubated increased both with days after the first egg was laid (repeated measures ANOVA, $F_{3,24}$

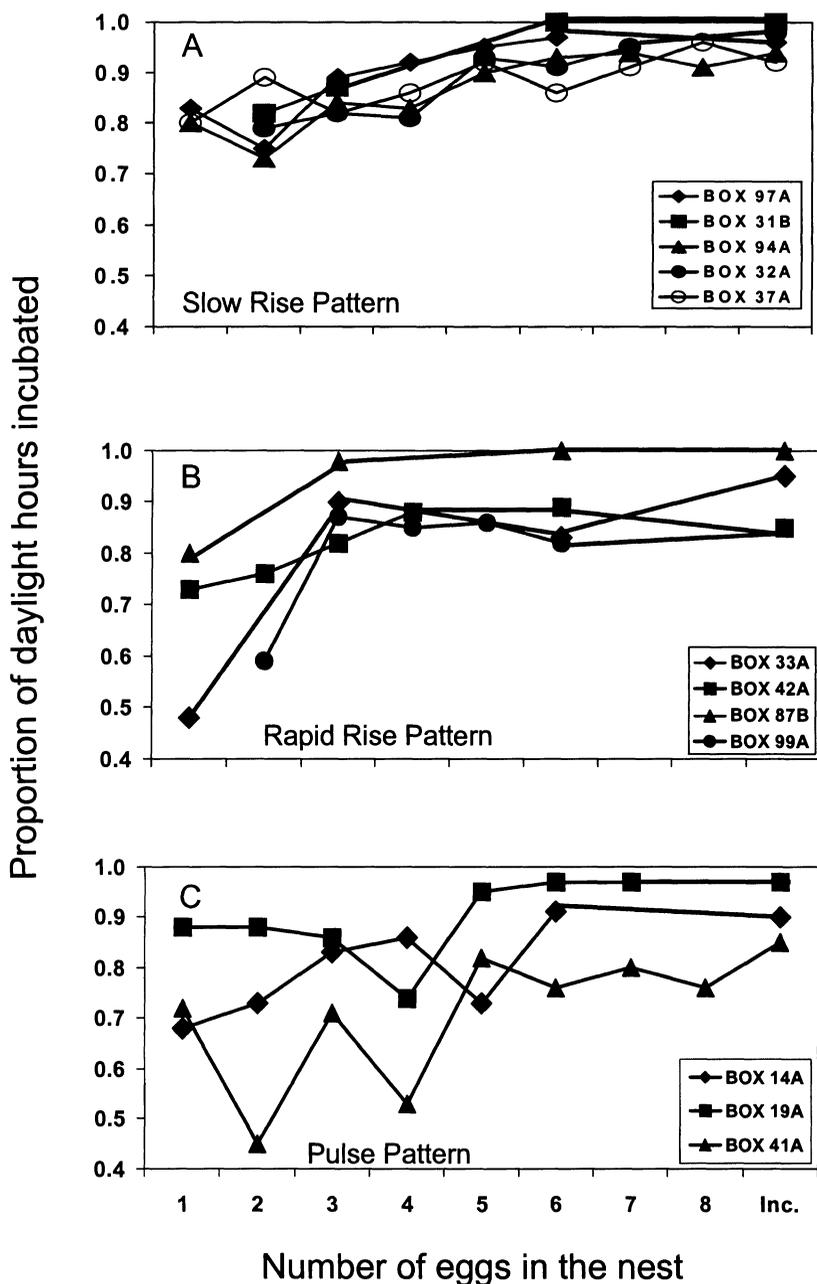


FIGURE 1. Individual patterns of incubation during the laying period and shortly after clutch completion (Inc.) adapted from Wiebe et al. (1998). In the slowly rising pattern (A), the female gradually increased the percentage incubation until reaching a maximum around the sixth egg. In the rapidly rising pattern (B), incubation tended to increase a greater absolute percentage and more quickly than in the slowly rising pattern, reaching the maximum percent incubation by the third egg. In the pulse pattern (C), the percent incubation rose and fell before continuous incubation began.

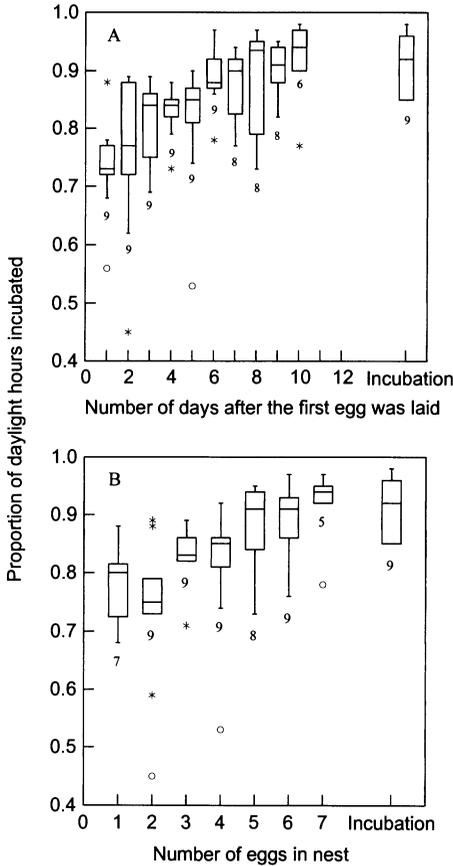


FIGURE 2. Proportion of daylight hours that females incubated eggs during the laying period and shortly after the clutch was completed in relation to (A) number of days after the first egg was laid and (B) number of eggs in the nest. Numbers under boxes are sample sizes of females, bars within each box are medians, and the bottom and top of each box indicate first and third quartiles, respectively. Whiskers encompass points falling from the nearest edge of the box up to 1.5 times the interquartile range (IQR). Outliers falling 1.5–3 and > 3 times the IQR are denoted by asterisks and open circles, respectively. In (A), day 1 includes both the day the first egg was laid and the following day, and day 10 combines days 10 through 14. In (B), egg 7 is an average of eggs 7 and 8 for three nests that had eight eggs.

= 32.2, $P < 0.001$) and with number of eggs in the nest (repeated measures ANOVA, $F_{3,24} = 24.4$, $P < 0.001$). A linear model fit the average increase in percent incubation over the course of laying better ($F_{1,8} \geq 150.5$, $P < 0.001$) than quadratic or cubic models ($P > 0.25$). The percentage of time females incubated increased significantly from days 0–2 to 3–5, from days 3–5 to

6–9, from eggs 1–2 to 3–4, and from eggs 3–4 to 5–6 (Tukey's HSD, all $P < 0.05$). However, incubation rate did not increase significantly during the latter half of the laying period, from days 6–9 to 10–14 and from eggs 5–6 to 7–8.

Female incubation behavior was not related to ultimate clutch size. Ultimate clutch size was unrelated to the percent of time that females incubated when one ($F_{1,5} = 1.0$, $P > 0.3$) or two ($F_{2,6} = 0.2$, $P > 0.5$) eggs were in the nest, or when the clutch was complete ($F_{2,6} = 2.5$, $P > 0.1$).

FACTORS AFFECTING FEMALE INCUBATION BEHAVIOR

Female incubation behavior was related to the behavior of their mates and to the presence of other parrotlets. Over the laying period as a whole, percent incubation was negatively correlated with male feeding rates ($r_s = -0.39$, $n = 47$, $P < 0.01$) and the rate of male vigilance visits ($r_s = -0.26$, $n = 47$, $P = 0.04$), and showed a nearly significant negative relationship with the percent of time that extra-pair parrotlets were near the nest ($r_s = -0.22$, $n = 47$, $P = 0.07$). None of these correlations were significant ($n = 12$, $P > 0.10$) when 1–2 or 3–5 eggs were in the nest. Male feeding rates were negatively related to percent incubation when 6–8 eggs were present ($r_s = -0.53$, $n = 12$, $P < 0.05$). After the clutch was complete, both male feeding rates ($r_s = -0.56$, $n = 11$, $P < 0.05$) and male vigilance visits ($r_s = -0.67$, $n = 11$, $P < 0.03$) were negatively related to the percent of time females spent on the nest.

The rhythm of female recesses from incubation changed over the course of laying. The number of recess trips per hour did not change significantly over time ($H_2 = 1.6$, $P > 0.4$), but trip duration decreased as the number of eggs in the nest increased ($H_2 = 12.5$, $P < 0.01$). Female recesses lasted significantly longer when 1–2 ($\bar{x} = 967 \pm 950$ sec) or 3–5 eggs ($\bar{x} = 617 \pm 681$ sec) were in the nest than when 6–8 eggs were present ($\bar{x} = 196 \pm 376$ sec; Wilcoxon, $Z \geq 2.5$, $P \leq 0.01$).

RELATIONSHIP BETWEEN LAYING ORDER, INCUBATION PERIOD, AND HATCHING SUCCESS

We examined whether laying order affected incubation period. The incubation period ranged from 17 to 24 days, but over 80% of eggs

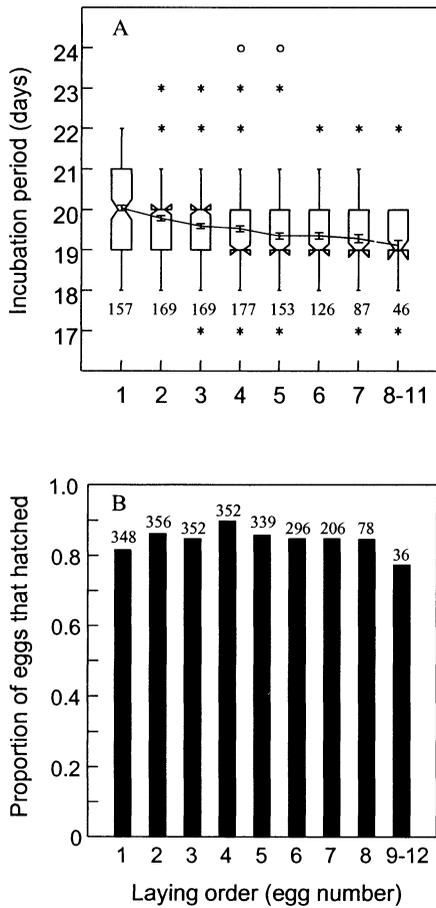


FIGURE 3. Effect of laying order on incubation period (A) and hatching success (B) of individual eggs. Numbers under boxes or above bars are sample sizes of eggs. In (A), eggs 8–11 are pooled due to small sample sizes, and box plot symbols are as described in Figure 2, with the addition of notches indicating 95% confidence intervals for the median incubation period. The line between boxes connects the means for each egg number, and vertical bars denote \pm SE. In (B), eggs 9–12 are pooled due to small sample sizes.

hatched in 19 or 20 days (Fig. 3A). Incubation period differed significantly by laying order ($F_{7,1076} = 13.1, P < 0.001$). Eggs 1–3 tended to hatch in 20 days, whereas later eggs usually hatched in 19 days. Significant differences among incubation periods only occurred between egg 1 and eggs 3–11 (Tukey's HSD, $P < 0.001$), between egg 2 and eggs 5–11 ($P \leq 0.001$), and between egg 3 and eggs 8–11 ($P = 0.03$).

Despite some variation in the incubation period related to laying order, nearly all eggs

hatched in the order they were laid. In no cases did earlier-laid eggs hatch after later-laid eggs. Sixteen (7.3%) of the 219 clutches analyzed had one pair of consecutively-laid eggs hatch on the same day ($n = 658$ pairs of eggs total). Thus, pairs of eggs laid consecutively within a clutch had only a 2.4% chance of hatching on the same day. These consecutively-laid eggs that hatched on the same day occurred throughout the laying cycle, with no clear bias toward earlier- or later-laid eggs.

We also examined whether hatching success was affected by laying order (Fig. 3B). Hatching success was high, averaging 85.5% ($n = 2,363$ eggs from 363 nests). First eggs showed a slightly lower hatching success than subsequent eggs, egg 4 had the greatest success, and eggs 9–12 the least. However, these differences were not significant, and the percentage of eggs that hatched did not differ by laying order ($\chi^2_8 = 12.22, P = 0.14$), despite our large sample sizes.

DISCUSSION

The onset of incubation in Green-rumped Parrotlets varied among females and in relation to time during laying (Fig. 1 and 2). Only our prediction that ultimate clutch size would not affect incubation behavior during laying was correct. These results were somewhat surprising, given the consistent first-egg incubation and strong asynchronous hatching exhibited by parrotlets (Beissinger and Waltman 1991, Stoleson and Beissinger 1997). The unexpected increase in incubation as laying progressed may have caused slightly shorter incubation periods for later-laid eggs (Fig. 3A). However, the vast majority of eggs hatched in the order of laying, and we found no differences in hatching success with laying order (Fig. 3B).

FACTORS AFFECTING VARIATION IN THE ONSET OF INCUBATION

Females exhibited individual variation in the onset of incubation, but the magnitude of the differences was not great (Fig. 1). All females began partially incubating on the first egg at a fairly high rate (50–90% of daylight hours) and gradually increased incubation to a constant, maximum level over several days. However, individuals differed qualitatively in the rapidity, magnitude, and consistency of the increase in incubation (Fig. 1). The percent time spent incubating rose either a small amount and slowly,

to a greater degree and more rapidly, or in pulses. The extent of these individual differences during the onset of incubation was much less than in Great Tits (*Parus major*; Haftorn 1981) and kestrels (Bortolotti and Wiebe 1993, Wiebe et al. 1998), which varied up to several days in the initiation of partial and maximum incubation as well as in the intensity of each. Despite these interspecific differences in the magnitude of individual variation, Eurasian Kestrels (*Falco tinnunculus*) and parrotlets displayed similar incubation patterns during laying (Wiebe et al. 1998). Female parrotlet incubation profiles required slight modification of Wiebe et al.'s (1998) patterns because incubation began earlier in parrotlets than in kestrels. Individual females incubated in three distinct patterns: slowly rising, rapidly rising, and pulsed. These patterns reflect subtle differences among individuals during the first few days of laying, rather than pronounced variation throughout the onset of incubation. Pulsed incubation was associated with poor body condition in the Eurasian Kestrel (Wiebe et al. 1998), but such data were not available for parrotlets.

Female parrotlets spent more time on the nest as the laying cycle progressed (Fig. 2). Most of this variation occurred during laying of the first few eggs, and later eggs were incubated at the maximum rate. The general trend of increasing incubation over time during laying is common in birds (Meijer et al. 1990, Anderson 1997). Parrotlets differed from other birds in that their incubation regime varied much less over time. Other species exhibit from none to less than 50% incubation at the onset of incubation (Haftorn 1981, Bortolotti and Wiebe 1993). Kestrels reached maximum levels of incubation that were similar to parrotlet levels (85–100%; Wiebe et al. 1998), whereas full incubation in the Great Tit comprised less than 80% of the birds' active hours (Haftorn 1981). The relatively high incubation rate of parrotlets throughout laying, their lack of individual variation after the first few eggs, and the resulting strongly asynchronous hatching patterns suggest a powerful selective pressure for the early onset of intense incubation leading to hatching asynchrony.

Ultimate clutch size had no effect on parrotlet incubation during laying, which contrasts with the behavior of Great Tits (Haftorn 1981), Eurasian Kestrels (Meijer et al. 1990), and Pied Flycatchers (*Ficedula hypoleuca*; Potti 1998). Tit

and kestrel clutches laid late in the breeding season were smaller and were incubated earlier and more intensely. Flycatchers tended to incubate larger clutches earlier, regardless of when in the season they were laid (Potti 1998). Our sample included only parrotlet nests with 6–8 eggs laid early in the breeding season. Because parrotlets typically lay eggs from June–November and clutch sizes range from 5–13 eggs, our sample may have been insufficient to detect differences in the onset of incubation related to ultimate clutch size. However, it seems likely that ultimate clutch size may influence the onset of incubation mainly in species with greater intraspecific variation in behavior during laying.

The importance of food and nest defense in determining incubation regimes is often postulated, but has rarely been demonstrated (Wiebe and Bortolotti 1994, Beissinger et al. 1998). Contrary to our prediction regarding male feeding rate, females that were fed more often by their mates incubated less frequently. Because females usually leave the nest in order to be fed by their mate, this relationship may simply reflect the time necessary to receive food. Wiebe and Bortolotti (1994) found that kestrels with greater food supplies hatched their eggs more synchronously. Well-fed female parrotlets may also have been increasing the hatching synchrony of their clutches, but only very slightly, because they spent so much time on the nest during laying (Fig. 1 and 2). Females at nests with high intruder pressure tended to incubate less, suggesting that they leave the eggs to defend the nest. Females are more likely to leave the eggs to defend the nest if their mates are present, and nesting parrotlets displace intruding male-female pairs, male-male pairs, male gangs, and lone males with equal frequency (Beissinger et al. 1998). An effect of harassment on female care of eggs supports the suggestion by Birkhead et al. (1995) that failure of embryos to hatch may often be due to egg neglect caused by conspecific social interactions rather than infertility. The influence of intruder pressure on the onset of incubation may be more pronounced in species that, unlike the parrotlet, defend territories larger than the immediate nest area.

Female parrotlets increased incubation rate over the course of laying by decreasing the duration of their recesses off of the eggs rather than by decreasing the number of trips. Prospecting parrotlet pairs destroy eggs in unattend-

ed nests, but they often delay a minimum of 20 min before entering the nest box of another pair (Beissinger et al. 1998). As reproductive investment grows with the number of eggs in a clutch, female parrotlets may increase their nest defense later in laying by shortening their absences so that conspecifics do not have time to enter unguarded nests. Taking many short recesses is feasible for female parrotlets because the warm tropical climate makes reheating eggs energetically inexpensive after an absence.

FITNESS CONSEQUENCES OF VARIATION IN THE ONSET OF INCUBATION

Any fitness consequences of partial incubation of the first few eggs compared to later-laid eggs should be detectable in the hatching patterns. Although we could not directly examine the fitness effects of variation in the onset of incubation, we were able to test for the influence of laying order, which is related to variation in the onset of incubation (Fig. 2). Partial incubation of early-laid eggs slightly retarded their time to hatching relative to later-laid eggs (Fig. 3A), despite high ambient temperatures that may allow eggs to develop when the female is not incubating (Drent 1973, Stoleson and Beissinger 1999). Nevertheless, the maximum difference in incubation period by laying order was only one full day, which can only slightly ameliorate the effects of hatching asynchrony in parrotlets because hatching spreads are so large ($\bar{x} = 8.7$ days; Beissinger and Waltman 1991). Variation in incubation period with laying order in parrotlets was similar to Black Kites (*Milvus migrans*; Vinuela 1997), but was much more pronounced in Spur-winged Plovers (*Vanellus spinosus*; Yogeve et al. 1996), and American (*Falco sparverius*) and Eurasian Kestrels (Bortolotti and Wiebe 1993, Wiebe et al. 1998). Interspecific differences in the effect of incubation delays on the time to hatching may be partly due to differences in breeding season temperatures. Exposed eggs of parrotlets in tropical Venezuela and kites in southern Spain may have experienced warmer ambient temperatures than exposed eggs of kestrels in Saskatchewan and Scandinavia, where cool temperatures most likely halted egg development completely when the female was not incubating (Drent 1973). In addition, the greater variation exhibited by kestrels in the onset of incubation (Wiebe et al. 1998) probably accounted for much of the variability

in time to hatching by laying order. Exposed plover eggs, however, probably experienced ambient temperatures in Israel similar to those for kite and parrotlet eggs. The onset of incubation in Black Kites and Spur-winged Plovers is poorly known, so its influence on incubation period cannot be analyzed.

Although variation in the onset of incubation related to laying order affected the incubation period of individual parrotlet eggs, it caused very few eggs to hatch out of order and did not alter the probability of hatching (Fig. 3B). Because parrotlets incubate early and intensely, the close fidelity between laying order and hatching order suggests that females have a great deal of control over hatching patterns via their incubation behavior, which parallels findings for kestrels (Wiebe et al. 1998). Because partial incubation of early eggs did not reduce their hatching success, variation in the onset of incubation in parrotlets appears to have only minor fitness consequences, if any. Similarly, Potti (1998) found no fitness differences between Pied Flycatcher females who began incubating before or after completing the clutch. Lower initial incubation rates in parrotlets may slightly shift hatching patterns toward synchrony and may even occasionally cause consecutively-laid eggs to hatch on the same day, but the constraint or benefit that promotes hatching asynchrony appears to greatly outweigh the effects of variation in incubation during laying.

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