

## CLIMATIC VARIABILITY, NEST PREDATION, AND REPRODUCTIVE OUTPUT OF LILAC-CROWNED PARROTS (*AMAZONA FINSCHI*) IN TROPICAL DRY FOREST OF WESTERN MEXICO

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**ABSTRACT.**—For 1996–2003, we determined reproductive output and success of 70 Lilac-crowned Parrot (*Amazona finschi*) nests in tropical dry forest of the Chamela-Cuixmala Biosphere Reserve in western Mexico. Only 42% of nests had young that fledged; predation was the main cause of nest failure. Low brood survival in 2000 and 2003 caused significant between-year variation in the probability of nest success during the nestling phase of the nest cycle. Reproductive output of Lilac-crowned Parrots was low, with females producing an average of 0.99 fledglings on an initial investment of 2.6 eggs. The fecundity component of clutch size varied significantly between years, because of the high median clutch size recorded in 2000. Nestling survival also varied significantly between years, creating large interannual fluctuations in reproductive output. The most productive breeding season was 1999, with an average output of 1.7 fledglings on an investment of 2.7 eggs; whereas the poorest breeding season was 2000, with an output of 0.57 fledglings from 3.3 eggs. Loss of reproductive potential was greatest in 2000 and 2003, because of brood reduction through starvation of later-hatched nestlings, with hatching order influencing the probability of nestling survival. Mean number of nestlings per egg-laying female was associated with interannual fluctuations in precipitation resulting from the El Niño–La Niña weather cycle in the Pacific Ocean. Both nest predation and food availability may limit parrot reproduction in tropical dry forests, with populations of threatened species in dry habitats being vulnerable to effects of climatic variability and habitat fragmentation. Received 4 September 2003, accepted 24 June 2004.

**RESUMEN.**—El éxito de nidificación y la productividad reproductiva del loro *Amazona finschi* fueron determinados para 70 nidos durante 1996–2003 en el bosque tropical seco de la Reserva de la Biosfera Chamela-Cuixmala, en el oeste de México. Sólo el 42% de los nidos produjeron volantones, y la principal causa que ocasionó que los nidos fallaran fue la depredación. La alta mortandad de pollos durante los años 2000 y 2003 produjo variación significativa entre años en la probabilidad de éxito de nidificación durante la fase de crianza de los pollos. La productividad reproductiva de *A. finschi* fue baja, ya que a partir de una inversión promedio inicial de 2.6 huevos las hembras produjeron 0.99 volantones. El tamaño de la nidada varió significativamente entre años, debido a una alta nidada en el año 2000. La supervivencia de los pollos también varió significativamente entre años, lo cual creó grandes fluctuaciones interanuales en la productividad reproductiva. La temporada reproductiva más productiva fue la de 1999 con una productividad promedio de 1.7 volantones a partir de una inversión de 2.7 huevos, mientras que la temporada menos productiva fue la del año 2000 con una producción de 0.57 volantones a partir de 3.3 huevos. La pérdida en el potencial reproductivo fue mayor en los años 2000 y 2003 debido a una elevada reducción en la nidada por inanición de los pollos que eclosionaron tardíamente, de modo que la probabilidad de supervivencia de los pollos estuvo asociada con el orden de eclosión. El número promedio de pollos por hembra estuvo asociado con las variaciones interanuales en la precipitación que resultan de los ciclos de El Niño–La Niña en el Océano Pacífico. Tanto la depredación de los nidos como la disponibilidad de alimento pueden limitar la reproducción de los loros en el bosque tropical seco, siendo las poblaciones de especies amenazadas en los hábitat secos muy vulnerables a los impactos de la variabilidad climática y la fragmentación del hábitat.

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CLIMATIC VARIABILITY CAN affect avian reproduction, particularly in arid environments where breeding success may be sensitive to precipitation (Gibbs and Grant 1987, Curry and Grant 1989, Li and Brown 1999, Christman 2002). The El Niño Southern Oscillation over the Pacific creates strong environmental variability (Taylor et al. 1998), which affects rainfall patterns and reproductive success of bird populations (Gibbs and Grant 1987, Grant and Grant 1987, Christman 2002). Rainfall may affect breeding success in arid environments, given that many bird species initiate reproduction in the rainy season and use arthropod resources while raising young (Dittami and Gwinner 1985, Gibbs and Grant 1987, Wrege and Emlen 1991). Few studies have examined the effects of climatic variability on bird species that breed in the dry season (Brown and Li 1996, Li and Brown 1999, Christman 2002) or that depend on either fruit or seed resources during the breeding season. Between-year climatic variability may also affect fruit and seed production in tropical forests of Central America (Foster 1982, Wright et al. 1999). However, we know little of the effect of such cycles on reproduction of granivorous or frugivorous birds in seasonally dry tropical forests.

Predation affects nest success and limits production of young in birds, with tropical birds experiencing higher predation and lower nest success than temperate birds (Ricklefs 1969, Skutch 1985, Robinson et al. 2000). Cavity nests are less vulnerable to predation than open nests (Alerstam and Högstedt 1981). Cavity-nesting birds generally have >60% nest success (Martin and Li 1992, Johnson and Kermott 1994, Purcell et al. 1997). Most parrot species have nest-success rates equivalent to those of cavity-nesting birds (Saunders 1982, 1986; Rowley 1990; Rowley and Chapman 1991; Smith 1991; Munn 1992; Robinet and Salas 1999; Masello and Quillfeldt 2002; Monterrubio et al. 2002; Seixas and Mourão 2002), though many parrot species produce few young despite high nest success (Masello and Quillfeldt 2002).

Low fecundity makes bird species vulnerable to decline (Bennett and Owens 1997). The family Psittacidae contains more threatened species than any other bird family (Bennett and Owens 1997). Most parrot species employ conservative breeding strategies of small clutches, high parental investment, and few offspring (Forshaw

1989, Masello and Quillfeldt 2002). The genus *Amazona* is the most diverse in the parrot family and contains more threatened species, two-thirds of which are currently under pressure from habitat destruction and the wildlife trade (Snyder et al. 2000). Parrot species inhabiting seasonally dry forests are among those most susceptible to habitat loss (Snyder et al. 2000). A large number of threatened Neotropical parrots occur in such habitats (Collar and Juniper 1991). However, we have little information on factors that limit parrot reproduction in dry forest habitats. The Lilac-crowned Parrot (*Amazona finschi*) is a threatened species, endemic to the Pacific coast of Mexico, where it inhabits tropical dry forest (Forshaw 1989, Diario Oficial de la Federación 2002). Here, we present information, from an eight-year study, on the potential effects of nest predation and climatic variability on reproductive success of Lilac-crowned Parrots in a tropical dry forest in western Mexico.

#### METHODS

We conducted our nest studies in the 13,142-ha Reserva de la Biosfera Chamela-Cuixmala (19°22'N, 104°56'W to 19°35'N, 105°03'W) on the Pacific coast of Mexico, from January to June (1996–2003). The study site has a dry tropical climate that exhibits a marked seasonality in precipitation, with 85% of the 748-mm mean annual rainfall occurring in June to October, followed by a prolonged drought from mid-February to late May (Bullock 1986). The dominant terrain is tropical dry deciduous forest, with semi-deciduous forest in the larger drainages and more-humid valleys (Lott 1993).

Lilac-crowned Parrots nest during the dry season, with nest initiation and egg laying starting at the beginning of February (Renton and Salinas-Melgoza 1999). Egg incubation period lasts 28 days (Renton 1998), followed by a 60-day period of nestling growth, with all nestlings fledging in May (Renton and Salinas-Melgoza 1999, Renton 2002). Lilac-crowned Parrots are predominantly granivorous and do not supplement nestling diets with arthropod prey (Renton 1998, 2001). Nesting pairs make only two foraging trips to the nest per day (Renton and Salinas-Melgoza 1999).

We conducted nest searches from January to February; we located all nests during the nest prospecting and early incubation period of the nesting cycle. We did not find additional nests later in the nesting cycle, because the behavior of breeding pairs made nest detection difficult. We monitored parrot nests at regular intervals during the nesting cycle to determine clutch and brood size and causes of nest

failure. We accessed nest cavities using both single-rope ascending (Perry 1978, Perry and Williams 1981) and tree-bole climbing techniques (Donahue and Wood 1995).

To reduce the risk of clutch abandonment by females, we inspected nests only once during incubation, to determine clutch size. In 1996 and 1997, we measured egg length and width to the nearest 0.1 mm with dial calipers, and egg weight to the nearest 1.0 g with Pesola scales. We used disposable gloves when handling eggs, to prevent contamination through the permeable shell. We discontinued egg measurements in following years, because of the risk of inducing clutch abandonment by females. Following hatching, we inspected nests every 3–5 days during the mid-day lull in parental activity (Renton and Salinas-Melgoza 1999) to determine hatching order, brood size, and causes of nest failure. We recorded evidence of nest predation where possible; human poaching of nests was easily identified from signs of human activity around the nest and through confirmation by local informants. During 1996–2001, we marked nestlings with indelible ink on one foot to identify hatching order. From 2002 onwards, we banded nestlings with numbered steel bands.

We evaluated nest success by estimating daily survival rates for nests during the incubation, early nestling (1–30 days after hatching), and late nestling (31–60 days after hatching) phases. We divided the nestling stage into early and late phases, given that Lilac-crowned Parrot nestlings attain 90% of their adult body weight by 30 days after hatching (Renton 2002), which may increase their survival probabilities. We defined successful nests by the presence of at least one egg or nestling at each stage. We calculated success rates using the maximum-likelihood estimate modification of Mayfield (1975), to resolve potential biases in survival estimates when nests are inspected at irregular intervals (Johnson 1979, Bart and Robson 1982, Krebs 1989).

We determined reproductive potential at major stages of the nesting cycle by clutch size, brood size at hatching, and brood size at fledging for successful nests. Actual reproductive output was determined for each egg-laying female, taking into account the loss of reproductive potential through mortality of eggs or nestlings.

*Analysis.*—We used the Kolmogorov-Smirnov (KS) test of normality with Lilliefors significance correction (Zar 1999) to determine whether the data deviated significantly from the normal distribution required for parametric analysis. Nonparametric analysis was employed where the data did not present a normal distribution. Proportions from the modified Mayfield estimate of finite nest success were arcsine transformed prior to analysis (Zar 1999), and presented a normal distribution (KS = 0.11, df = 4,  $P = 0.20$ ). Yearly variation in finite probabilities of nest success

at different stages of the nesting cycle was evaluated by log-ratio chi-square, with Bonferroni correction to  $P < 0.01$  for multiple analyses (Zar 1999).

Components of reproductive potential did not present a normal distribution, and nonparametric analysis was applied. We evaluated between-year differences in productivity of Lilac-crowned Parrot females by Kruskal-Wallis analysis of variance on the fecundity components of clutch size, brood size at hatching, and brood size at fledging for successful nests. Where a significant difference was determined, we conducted pairwise comparisons, using the Dunn multiple-comparison test for unequal sample sizes (Zar 1999). Proportions for egg and nestling survival were arcsine transformed prior to analysis. Log-ratio chi-square was applied to evaluate between-year variation in survival of eggs (KS = 0.18, df = 8,  $P = 0.20$ ) and nestlings (KS = 0.23, df = 8,  $P = 0.20$ ), and the arcsine transformed proportions for the influence of hatching order on nestling survival (KS = 0.27, df = 5,  $P = 0.20$ ).

We used linear regression to evaluate the relation between precipitation during the preceding rainy season (KS = 0.17, df = 8,  $P = 0.20$ ) and mean number of eggs, nestlings, and fledglings per egg-laying female (KS = 0.15, df = 24,  $P = 0.15$ ). We compared breeding parameters for Lilac-crowned Parrots with those for 33 psittacine species by fitting observed values to the allometric equations presented by Masello and Quillfeldt (2002) for the relation between adult body mass and egg mass ( $y = 5.4 + 0.03x$ ), clutch size ( $y = 2.2 + 5.5 \exp[-0.006x]$ ), and relative clutch mass ( $y = 7.9 + 61.1 \exp[-0.007x]$ ). We used  $P < 0.05$  significance level in our statistical analysis; values are presented as mean  $\pm$  SE, with range.

## RESULTS

*Nest success and productivity.*—For 1996–2003, we calculated Mayfield maximum-likelihood estimates of nest success at different phases of the nesting cycle for 70 nests (Table 1). Lilac-crowned Parrots demonstrated a low (42%) overall nest success, with greatest nest success in 1999 (59%), and lowest in 2000 (31%). The period of lowest probability of nest success was the early nestling phase, with 68% nest survival; followed by the incubation (76%) and late-nestling (82%) phases. Natural predation, the main cause of clutch failure (71%; Fig. 1), caused one-third of all nest failures (32%). Natural predation was also the main cause of brood failure (52% brood failures; 29% all failures), followed by human poaching of nestlings (19% brood failures; Fig. 1).

Probability of nest success varied significantly between years during the early, late, and

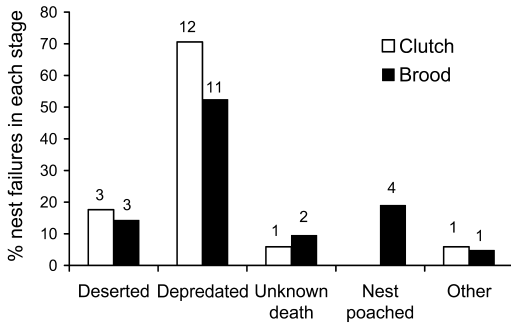


FIG. 1. Causes of total nest failure for Lilac-crowned Parrot clutches and broods, 1996-2003. Number of failed nests above bars.

combined nestling phases. Lowest success for those phases occurred in 2000 and 2003 (Table 1). There was no significant between-year variation in nest success during incubation or over the entire nesting cycle.

We determined clutch size in 60 nests, with a total of 162 eggs and average clutch size of  $2.6 \pm 0.07$  eggs (range = 2-4 eggs; Fig. 2). Median clutch size was three eggs, and 2000 was the only year that females laid four eggs. Mean egg length was  $37.6 \pm 0.33$  mm (range = 35.7-39.7 mm,  $n = 19$ ), and width was  $28.6 \pm 0.19$  mm (range = 27.5-30 mm,  $n = 19$ ). Mean egg weight was  $14.8 \pm 0.43$  g (range = 12-18.5 g,  $n = 19$ ). Hatching success was 90.2% (119 of 132 surviving eggs hatched young), with 73% of all eggs laid producing nestlings. Average brood size was 2.38 nestlings in 50 nests (range = 1-4 nestlings; Fig. 2), though 2000 was the only year in which 4 nestlings were hatched in 2 broods. Majority of nests produced 2 fledglings, with an average of 2.27 fledglings (range = 1-3; Fig. 2) in successful nests.

The most productive clutch size for Lilac-crowned Parrot females was three eggs. A total of 13 fledglings were produced from clutches of 2 eggs, giving 0.52 fledglings per egg-laying female; 53 fledglings were produced from 3-egg clutches (1.66 fledglings per egg-laying female); and 2 fledglings were produced from 4-egg clutches (1 fledgling per egg-laying female). Number of chicks hatched in successful nests was significantly related to clutch size ( $r = 0.999$ ,  $F = 573$ ,  $df = 1$  and 1,  $P = 0.027$ ), though that includes a small number of four-egg clutches ( $n = 2$ ). However, successful two- and three-egg clutches also varied significantly in

TABLE 1. Mayfield maximum-likelihood estimates of finite nest success during each phase of the nesting cycle.

Nesting phase	Year										$\chi^2$ comparison (df = 7)
	1996	1997	1998	1999	2000	2001	2002	2003	1996-2003		
Incubation (28 days)	0.90	0.59	0.73	0.90	0.86	0.71	0.52	0.89	0.76	11.9, NS	
Early nestling (30 days)	0.67	0.83	0.53	0.67	0.38	0.83	1.0	0.58	0.68	28.9, $P < 0.001^a$	
Late nestling (30 days)	0.68	0.81	1.0	1.0	1.0	0.80	0.86	0.62	0.82	24.8, $P < 0.001^a$	
Combined nestling (60 days)	0.46	0.67	0.48	0.64	0.28	0.66	0.86	0.36	0.55	19.9, $P < 0.001^a$	
Entire nest cycle (88 days)	0.44	0.36	0.36	0.59	0.31	0.47	0.43	0.37	0.42	4.62, NS	
Number of nests	9	8	8	10	7	8	12	8	70		

<sup>a</sup>Significant difference between years after Bonferroni correction to  $P < 0.01$ ; NS = not significant.

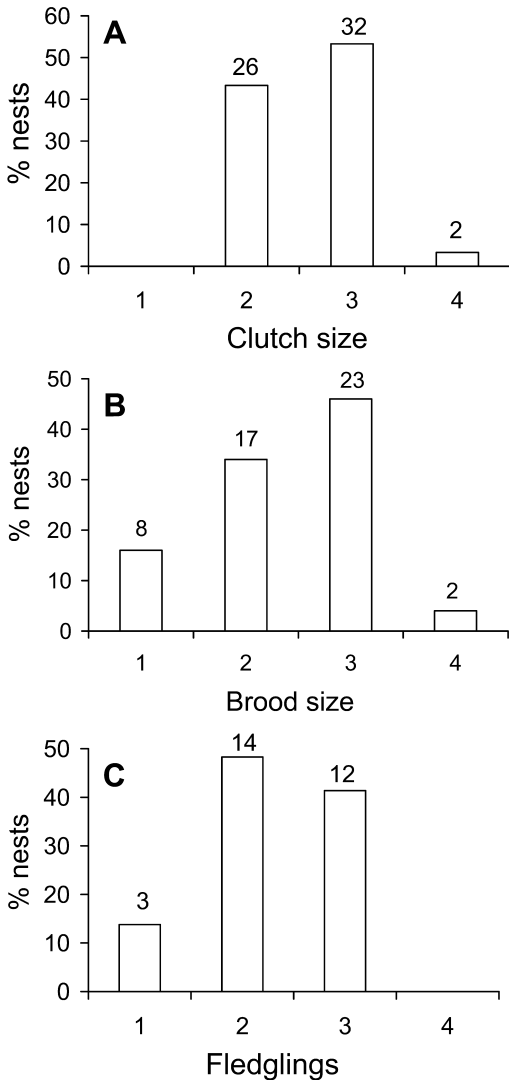


FIG. 2. Relative distribution of (A) clutch size, (B) brood size, and (C) number of fledglings for Lilac-crowned Parrot nests, 1996–2003. Numbers of nests are presented above bars.

number of chicks hatched (2 eggs: mean =  $1.65 \pm 0.12$  hatch; 3 eggs: mean =  $2.74 \pm 0.09$  hatch;  $H = 26.1$ ,  $df = 1$ ,  $P < 0.001$ ) and number of chicks fledged (2 eggs: mean =  $1.86 \pm 0.14$  fledge; 3 eggs: mean =  $2.41 \pm 0.16$  fledge;  $H = 4.13$ ,  $df = 1$ ,  $P = 0.04$ ). Over the eight-year study, 97% of three-egg clutches hatched at least one egg, with 69% fledging at least one chick; whereas 68% of two-egg clutches hatched at least one egg, and only 28% fledged at least one chick.

*Fitness components and reproductive output.*—Fitness components and actual reproductive output of Lilac-crowned Parrots at each stage of the nesting cycle are presented in Table 2. Over eight years, Lilac-crowned Parrot females had an annual reproductive output of 0.99 fledglings per female on an initial investment of 2.6 eggs (Table 2). The most productive breeding season was 1999, with a reproductive output of 1.67 fledglings per female on an investment of 2.7 eggs. The poorest breeding seasons were 2000, with an output of 0.57 fledglings per female on an investment of 3.3 eggs; and 2003, with 0.63 fledglings per female on an investment of 2.8 eggs (Table 2).

The fecundity component of clutch size varied significantly between years ( $H = 14.7$ ,  $df = 7$ ,  $P = 0.04$ ), because of the high clutch recorded in 2000 (2000 vs. 2001:  $Q = 3.59$ ,  $df = 8$ ,  $P < 0.01$ ; Table 2). However, there was little between-year variation in successful nests for fecundity components of brood size at hatching and brood size at fledging. Overall, there was 74% survival of eggs, with no between-year variation in egg survival. The major losses in reproductive potential occurred at the nestling stage, with a low 56% nestling survival.

Nestling survival varied significantly between years ( $\chi^2 = 24.1$ ,  $df = 7$ ,  $P = 0.001$ ), because of the high brood reduction recorded in 2000 and 2003 (Table 2). Those two years were the only breeding seasons in which we recorded mortality attributable to starvation of fourth-hatched (2000: two nestlings), third-hatched (2000: one nestling, 2003: four nestlings), and second-hatched (2003: two nestlings) nestlings. All nestlings were found dead in the nest with empty crops, and had shown a decline in weight or been registered with empty crops on prior nest inspections. Fourth-hatched nestlings died at  $6.5 \pm 4.5$  days after hatching, third-hatched nestlings at  $8.0 \pm 3.3$  days, and second-hatched nestlings at  $22.5 \pm 1.5$  days. Three additional broods were abandoned by females  $11 \pm 4.5$  days after hatching (2000: 2 broods, 2003: 1 brood). Probability of nestling survival varied significantly, depending on hatching order ( $\chi^2 = 98.3$ ,  $df = 4$ ,  $P < 0.001$ ), with poor survival of fourth-hatched and single-brood nestlings, and lower survival of third-hatched nestlings (Table 3).

*Relation to precipitation.*—Mean number of nestlings per egg-laying female was significantly related to the amount of precipitation

TABLE 2. Fitness components and productivity of Lilac-crowned Parrots at each stage of the nest cycle.

Fitness component	1996	1997	1998	1999	2000	2001	2002	2003	1996–2003
Number of eggs	19	20	17	24	20	15	25	22	162
Mean clutch size	2.5 ± 0.22	2.5 ± 0.19	2.5 ± 0.22	2.7 ± 0.17	3.3 ± 0.21	2.1 ± 0.14	2.5 ± 0.17	2.8 ± 0.16	2.6 ± 0.07
Egg survival	0.79	0.60	0.59	0.79	0.90	0.80	0.72	0.73	0.74
Number of nestlings	14	12	10	19	18	12	18	16	119
Nestling survival	0.57	0.67	0.70	0.79	0.22	0.58	0.78	0.31	0.57
Brood size per egg-laying female	1.8 ± 0.41	1.5 ± 0.5	1.4 ± 0.48	2.1 ± 0.39	2.6 ± 0.53	1.5 ± 0.38	1.5 ± 0.4	2.0 ± 0.42	1.8 ± 0.15
Number of fledglings	8	8	7	15	4	7	14	5	68
Fledglings per egg-laying female	0.89 ± 0.46	1.0 ± 0.5	0.88 ± 0.44	1.67 ± 0.47	0.57 ± 0.37	0.88 ± 0.35	1.17 ± 0.39	0.63 ± 0.32	0.99 ± 0.15

during the preceding rainy season ( $r = 0.74$ ,  $F = 7.03$ ,  $df = 1$  and  $6$ ,  $P < 0.05$ ), though mean numbers of eggs and fledglings were not related to precipitation. The high clutch size recorded in 2000 followed two years of high precipitation during the rainy seasons for 1998 (1,292 mm) and 1999 (1,162 mm), with almost double the average annual rainfall (Fig. 3). The high precipitation during those two years resulted from the strong 1998–2000 cold episode (La Niña) of the El Niño Southern Oscillation. The highly successful parrot breeding season of 1999 also occurred during that weather event (Fig. 3). However, the low nestling survival in 2000 suggests that nesting pairs were unable to maintain their initial reproductive investment through the period of nestling growth. Equally, the disastrous reproductive season of 2003, with a high rate of brood reduction through starvation of later-hatched nestlings, occurred following three successive seasons of low precipitation (2000: 551 mm, 2001: 368 mm, and 2002: 582 mm; Fig. 3).

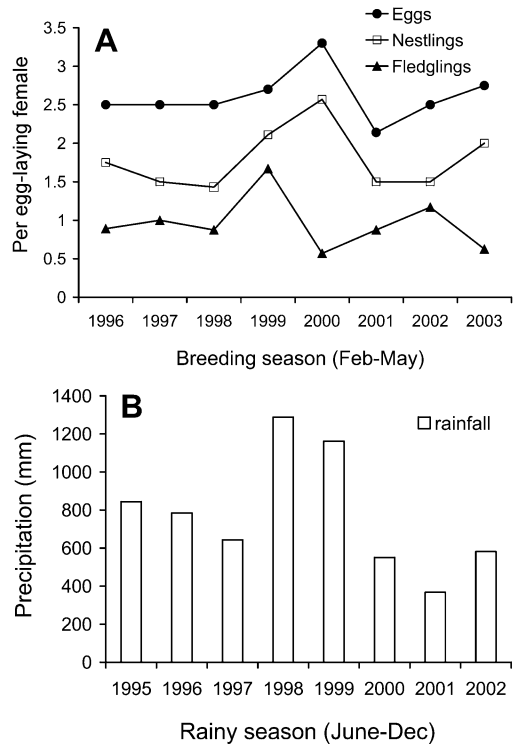


FIG. 3. (A) Productivity of Lilac-crowned Parrot females in relation to (B) precipitation during the preceding rainy season.

TABLE 3. Hatching order and Mayfield likelihood estimate of survival for Lilac-crowned Parrot nestlings, 1996–2003.

Hatching order	Number hatched	Number fledged	Survival (%)	Daily survival ( $\pm$ SE)	Finite survival (60 days)
First	42	27	64	0.993 $\pm$ 0.002	0.67
Second	42	27	64	0.994 $\pm$ 0.002	0.68
Third	25	13	52	0.989 $\pm$ 0.003	0.51
Fourth	2	0	0	0.823 $\pm$ 0.115	0.00
Single brood	8	1	12.5	0.965 $\pm$ 0.014	0.12

*Comparison with other psittacines.*—Lilac-crowned Parrots have a relatively low clutch size in relation to body mass. The closely related Red-crowned Parrot (*A. viridigenalis*) in northeastern Mexico has a similar body mass but a higher mean clutch size (3.4 eggs) and range (2–5 eggs; Enkerlin-Hoeflich and Hogan 1997) than the Lilac-crowned Parrot (Table 2; Fig. 2). Observed clutch size, egg mass, and relative clutch mass (12%) for Lilac-crowned Parrots were fitted to the regression equations for allometric relationships of 33 psittacine species presented by Masello and Quillfeldt (2002). Lilac-crowned Parrots, with an average body mass of 314 g (Renton 2002), had a predicted clutch size of 3 eggs, egg mass of 14.8 g, and relative clutch mass of 14.7%. Observed clutch size and relative clutch mass were 14% and 17% lower than predicted, though egg mass was equal to the predicted value. Among psittacine species, the Lilac-crowned Parrot had one of the lowest rates of overall nest success (42%). Only four species presented lower rates of nest success (Masello and Quillfeldt 2002), and those are principally red-listed species of high conservation concern (Snyder et al. 2000). Average number of young produced per egg-laying female was also lower than that for most parrot species of similar size (Masello and Quillfeldt 2002), with species that have lower reproductive rates tending to have larger body sizes (mean mass = 622  $\pm$  114 g,  $n = 11$ ).

#### DISCUSSION

*Nest success and predation.*—The 42% nest success for Lilac-crowned Parrots was lower than that predicted for cavity-nesting species (Skutch 1976, Martin and Li 1992, Johnson and Kermott 1994). The early nestling phase had the lowest probability of success, possibly because nestlings are smaller, less developed, and left unguarded when females join males

on foraging trips (Renton and Salinas-Melgoza 1999). Eggs may also be highly vulnerable; however, the high nest attendance exhibited by Lilac-crowned Parrot females during incubation (Renton and Salinas-Melgoza 1999) may confer additional protection for eggs, resulting in the higher probability of nest success during the incubation than the nestling phase. In the late nestling phase, nestlings have approached asymptotic body mass (Renton 2002) and therefore may be less vulnerable to losses through predation, thermoregulatory failure, or lack of food.

Natural predation of eggs or chicks caused 61% of all nest failures and was the main cause of nest loss in all years. Predation was also a significant cause of nest loss for three amazon parrot species in disturbed habitat of northeastern Mexico (Enkerlin-Hoeflich 1995). However, nest success was generally higher for parrot species in relatively intact forest habitats (Saunders 1982, Munn 1992, Monterrubio et al. 2002).

The high rate of nest predation may be attributable to characteristics of the tropical dry forest during the dry season. Potential predators of parrot nests include snakes (*Boa constrictor* and *Drymarchon corais*), rats (*Oryzomys couesi* and *Xenomys nelsoni*), Virginia opossum (*Didelphis virginiana*), and white-nosed coati (*Nasua narica*) (Enkerlin-Hoeflich and Hogan 1997). A decrease in food availability for most animal species toward the end of the dry season may result in a temporal increase in predation risks at that time (Sieving 1992). Moreover, Lilac-crowned Parrot nest sites were almost exclusively located in semideciduous forest (Renton and Salinas-Melgoza 1999), most of which occurs in narrow bands (<200 m wide) along valleys and dry stream beds. During the dry season, environmental conditions can become harsh in deciduous forest; prey species, such as arthropods and small mammals, are more abundant in semideciduous forest

along stream beds (Janzen and Schoener 1968, Miranda 2002, Pescador-Rubio et al. 2002). Potential predators, such as the white-nosed coati, also preferentially forage in forest along stream beds during the dry season (Valenzuela and Ceballos 2000).

Hence, high predation rates may be due to greater activity of predators in small patches of semideciduous forest during the dry season. That may be compounded by the high deforestation rates for semideciduous forest and increasing fragmentation of forest patches (A. Miranda pers. comm.). High predation rates may be a factor affecting the infrequent, brief nest visitation employed by Lilac-crowned Parrots (Renton and Salinas-Melgoza 1999), and may also limit the reproductive success of other bird species in that habitat.

*Climatic variability and reproductive output.*—Amount of precipitation prior to the breeding season may affect reproductive success of Lilac-crowned Parrots through its potential effect on the water table and plant resources during the dry season. Fluctuations in precipitation at the study site influence the phenology of plant resources (Bullock and Solis-Magallanes 1990) and availability of food resources for Lilac-crowned Parrots (Renton 2001, 2002). Between-year variation in precipitation and food availability has also been shown to affect nestling size and growth rate (Renton 2002). Tropical dry forest is a highly seasonal forest type, influenced by climatic El Niño events in the Pacific (Bullock 1986). Central American forests go through cycles of years of fruit abundance followed by years of fruit scarcity, with associated fluctuations in densities and rates of mortality of frugivorous and granivorous mammals (Foster 1982, Wright et al. 1999).

The eight-year productivity data for Lilac-crowned Parrots suggests that such cycles may influence parrot reproductive success. High rainfall during the 1998–2000 La Niña cycle may have resulted in an increase in food resources for Lilac-crowned Parrots, with a corresponding high nest success and reproductive output during the 1999 breeding season, and elevated clutch size in 2000. However, in dry forests of Central America, excessive rainfall in one season may result in a crash in fruit production in the following season, with annual fruiting rhythms of tropical forests being seriously disrupted every 5–10 years (Foster 1982).

Hence, an overabundance of fruit resources during the dry season in 1999 may have been followed by a year of fruit scarcity in 2000 (Wright et al. 1999). The low nest success, high nestling loss, and starvation of later-hatched nestlings observed during the breeding season in 2000 suggests that nesting parrots may have experienced food scarcity. That pattern was observed again in 2003, which followed three successive years of low rainfall and coincided with low food availability, as well as a two- to three-month delay in fruiting of *Astronium graveolens* (K. Renton pers. obs.), which forms the major component of nestling diets (Renton 1998). Hence, the low nest success observed in 2000 and 2003 may be attributable to food limitation.

Hatching order may influence nestling survival, particularly in years of low food availability. Third-hatched nestlings are smaller and have slower growth rates than first- or second-hatched nestlings, which may put them at a disadvantage in extreme years of food limitation (Renton 2002). That was the case in 2000 and 2003, with starvation of later-hatched nestlings resulting in lower survival probabilities for third-hatched nestlings as compared with first- and second-hatched nestlings. Fourth-hatched nestlings had negligible probabilities of survival, and four-egg clutches or broods were observed in only one of the eight years of study. Single-brood nestlings also had low probabilities of survival, and 75% of single broods were lost during the first few weeks after hatching, mainly from illness, thermoregulatory failure, or brood abandonment by females. The need for female parrots to leave young chicks to forage with males may make single-brood nestlings more vulnerable to thermoregulatory failure because of the lack of nest mates.

The high brood loss of 2000 and 2003, despite higher clutch sizes, suggests that female Lilac-crowned Parrots are unable to predict the availability of food resources throughout the nesting cycle. Food supply for Lilac-crowned Parrots in tropical dry forest varies from month to month and between years (Renton 2001, 2002), and phenological responses of vegetation to rainfall may be rapid in that habitat (Gibbs and Grant 1987, Bullock and Solis-Magallanes 1990). The long, three-month nesting period of Lilac-crowned Parrots means that environmental variability during the nesting cycle may



influence reproduction. Rapid, flexible growth rates of nestling parrots may enable them to adapt to fluctuations in food availability (Renton 2002), whereas brood reduction may be the most appropriate strategy for nesting pairs where food resources prove to be unreliable (Lack 1954, Skagen 1988), particularly in years of climatic variability.

*Reproductive strategies and conservation.*—Birds subjected to a high rate of nest failure may be expected to lay smaller clutches (Slagsvold 1984, Skutch 1985). However, Robinson et al. (2000) found substantial variation in nest success between tropical bird species in Panama, with little variation in clutch size. On average, female Lilac-crowned Parrots laid smaller clutches than predicted by body size, though the most frequent clutch size was the most productive, and females increased clutch size in exceptional years of high rainfall. Hence, number and quality of eggs laid by females may depend on food availability and the female's nutritional condition at time of laying (Martin 1987).

High nest predation in tropical dry forest means that most years have low nest success. Therefore, to successfully fledge sufficient young, breeding pairs may need a number of nesting attempts. The unpredictable nature of food resources in dry forest may also preclude Lilac-crowned Parrot females from varying the production of eggs, other than in exceptional years. Parrots are long-lived species with many opportunities to breed. Although Lilac-crowned Parrots demonstrate low reproductive output, they may have occasional years of high success in a lifetime of breeding efforts.

Low nest success and low reproductive output of Lilac-crowned Parrots in tropical dry forest makes these populations vulnerable to additional human or environmental pressures. Human poaching of Lilac-crowned Parrot nests is widespread and occurs at greater frequency outside the reserve (K. Renton and A. Salinas-Melgoza pers. obs.). Hence, nest success and reproductive output is likely to be lower for parrot populations in unprotected areas (Wright et al. 2001). In Mexico, tropical dry forests also have one of the highest rates of deforestation (Masera et al. 1997), which may affect reproduction of threatened species. Low nesting and reproductive success rates have been reported for parrot populations in disturbed habitat, where the main cause of

nest failure is food limitation (Saunders 1986, 1990) or predation (Enkerlin-Hoeflich 1995). Both predation and food availability may limit parrot reproduction, even in conserved areas of tropical dry forest. Those factors are likely to be exacerbated by increased habitat fragmentation, with parrot populations becoming susceptible to environmental fluctuations and highly vulnerable to decline under the dual pressures of capture for trade and habitat loss.

Parrot species restricted to dry or seasonally dry habitats in Central and South America are of conservation concern, because of the threat of habitat destruction (Collar and Juniper 1991, Snyder et al. 2000). However, potential high nest predation and food limitation in tropical dry forests may also make parrot populations highly vulnerable to climatic variability and El Niño events in the Pacific, with implications for the conservation of threatened species in dry habitats.

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