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Influence of environmental variability on the growth of Lilac-crowned Parrot nestlings

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Growth rate parameters were analysed for Lilac-crowned Parrot *Amazona finschi* nestlings in the tropical dry forest of the Reserva de la Biosfera Chamela-Cuixmala, Mexico. Growth rates for psittacine species follow the inverse relation with body mass observed for neotropical landbirds, with larger parrot species exhibiting slower growth rates. There was significant variation between years in size and growth rates of Lilac-crowned Parrot nestlings with nestlings exhibiting slower growth rates in 1996 than in 1997. Food abundance for parrots also varied significantly between years, with greater food availability during the 1997 breeding season than that of 1996. The increased size and growth rates of nestlings in 1997 may have reflected this, and suggests the potential influence of environmental variability on parrot reproduction, particularly in such a markedly seasonal habitat.

Growth rates of nestling birds may be adapted to environmental factors such as the energetic requirements of the young and food availability (Case 1978, Martin 1987). The influence of food supply on growth has been most easily demonstrated for aerial insectivores, with growth rate corresponding to fluctuations in insect abundance (Bryant 1975, 1978a, 1978b, Quinney *et al.* 1986, Blancher & Robertson 1987, Emlen *et al.* 1991, Rodenhouse & Holmes 1992, Adams *et al.* 1994, McCarty & Winkler 1999). Nestling birds of prey exhibit flexible growth rates in response to food variability (Lacombe *et al.* 1994, Negro *et al.* 1994), while fluctuations in food supply for seabirds may also influence nestling growth and survival (Bukacinski *et al.* 1998, Tveraa *et al.* 1998). There have been few studies on the influence of food supply on growth of frugivorous or granivorous birds. Species with long nestling periods may also be expected to alter their growth patterns adaptively with fluctuations in food availability.

Nestling parrots hatch asynchronously, are highly altricial, and have long nestling periods, all of which may increase the potential for growth processes to respond to environmental conditions. Most studies on nestling growth rates for psittacines have been conducted on Australian parrots (Saunders 1982, 1986, Rowley 1990, Rowley & Chapman 1991, Smith 1991, Krebs 1999, Krebs *et al.* 1999), while few studies have determined growth rates for neotropical parrot species (Navarro & Bucher 1990, Waltman & Beissinger 1992, Stoleson & Beissinger 1997). No data on growth rates are available for larger neotropical psittacines, although it is known that nestlings of both the Red-crowned Parrot *Amazona viridigenalis* in north-eastern Mexico (Enkerlin-Hoeflich & Hogan 1997), and the Puerto Rican Parrot *Amazona vittata* (Snyder *et al.* 1987), attain asymptotic mass half-way through the nestling phase.

Growth rates of Monk Parakeet *Myiopsitta monachus* nestlings varied significantly between years, while asymptotic values remained relatively constant, suggesting that growth rate is affected by environmental factors (Navarro & Bucher 1990). Understanding the influence of environmental factors such as food availability on reproduction and nestling growth may be important in the conservation of threatened populations of many parrot species. Food limitation as a result of habitat destruction may have been a principal factor in the poor growth and survival of cockatoo nestlings in agricultural areas of Australia, leading to the extirpation of local populations (Saunders 1986, 1990, 1991). Data on nestling development are necessary to determine the standard pattern of growth, and to evaluate

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the factors influencing the reproductive success of threatened species (Saunders 1986).

The family Psittacidae contains more threatened species than any other bird family (Bennett & Owens 1997), with the majority of threatened psittacines occurring in the neotropics. The genus *Amazona* is the most diverse of neotropical psittacines consisting of 31 species, almost two-thirds of which are currently threatened by pressures of habitat destruction and the wildlife trade (Collar & Juniper 1992, Snyder *et al.* 2000, Wright *et al.* 2001).

The Lilac-crowned Parrot *Amazona finschi* is endemic to the Pacific coast of Mexico, and is a nationally threatened species of conservation concern (Collar *et al.* 1994, INE 1994). Tropical dry deciduous forest along the Pacific coast is a highly threatened forest type, which exhibits marked seasonality in precipitation and plant phenology (Bullock 1986, Bullock & Solis-Magallanes 1990). This paper presents growth rate parameters of a neotropical amazon parrot, and evaluates the influence of fluctuations in rainfall and food availability on nestling growth.

METHODS

Study site

The study was conducted at 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. The study site has a dry tropical climate exhibiting a marked seasonality in precipitation, with 85% of the 748 mm mean annual rainfall occurring in June to October, and a prolonged drought from mid-February to late May (Bullock 1986). Precipitation varied between the study years with 780 mm in the rainfall year of June 1995–May 1996, and 1099 mm in June 1996–May 1997. During 1997, rainfall occurred in March for the second time, and in April for the first time since 1977 (Bullock 1986).

The reserve has a hilly topography varying in elevation from 20 m to 520 m asl. The dominant vegetation type on the slopes is tropical dry deciduous forest, with a canopy height of 8–12 m, in which the majority of trees drop their leaves for 5–8 months of the year (Rzedowski 1994). By comparison, small areas of semi-deciduous forest occur in larger, more humid valleys. This forest type has a canopy height of 15–30 m, and most tree species retain their leaves throughout the year (Rzedowski 1994). Species composition of semi-deciduous forest is also distinct from that of deciduous forest (Lott *et al.* 1987, Lott 1993, Rzedowski 1994).

Food availability

In total, 45 phenology transects of 200 m × 6 m were established, with 15 transects in three habitat types: (1) deciduous forest; (2) semi-deciduous forest; (3) along watercourses. Transects were positioned away from main road or trail systems to avoid recording edge species, and were monitored by the same observer during the second and third weeks of each month from January to June in 1996 and 1997. Fruit- or seed-bearing trees > 10 cm in diameter at breast height (dbh) were recorded when detected within a 3-m band on either side of the transect line in order to determine canopy variation in resource availability (Bullock & Solis-Magallanes 1990, Chapman *et al.* 1994). Where a tree occurred on the boundary of the 3-m transect width, the tree was included if the mid-point of the trunk was rooted within the transect area.

Tree species were identified by comparison with material in the herbarium at the Estación de Biología Chamela, Instituto de Biología, Universidad Nacional Autónoma de México. The dbh of each fruit- or seed-bearing tree was measured as a correlate of fruit crop abundance (Chapman *et al.* 1992, 1994). Where the trunk was branched below breast height (1.3 m), the dbh of each trunk branch was measured and summed to give a total dbh for that tree.

The number of fruiting trees and their dbh were summed over all transects in each of the three habitat types in order to obtain habitat-wide estimates of resource abundance. Only tree species which provide food resources for Lilac-crowned Parrots were recorded on the transects, and fruit or seed crops were included in the analysis at the stage of ripeness when they are consumed by parrots (Renton 2001). Preliminary analysis using the Kolmogorov–Smirnov statistic with Lilliefors significance level determined that the data did not deviate significantly from the normal distribution required for parametric analysis. Between-year variation in food resource abundance for Lilac-crowned Parrots was tested by two-way ANOVA on the number of trees and sum of dbh of fruiting trees in each habitat type during the dry season of 1996 and 1997. Pairwise comparisons between habitat types were conducted using the Newman–Keul test (Zar 1996).

Nestling growth and development

Lilac-crowned Parrots are not sexually dimorphic, though males may be 2–3% larger than females (Forshaw 1989). Lilac-crowned Parrot diet comprises 82% seeds and 9% fruit, during both the breeding and the non-breeding seasons (Renton 1998, 2001). Nesting occurs during the dry season from February to May, and Lilac-crowned Parrots exhibit high synchrony between nesting pairs in the timing of nest initiation (Renton & Salinas-Melgoza 1999). Egg-laying takes place at the beginning of February, and females lay two or three eggs, with an incubation period of 28 days (Renton 1998). Nestlings hatch asynchronously, and brood sizes are small (two or three young) compared with the large brood sizes reported in other psittacine studies (Navarro & Bucher 1990, Rowley & Chapman 1991, Smith 1991, Stoleson & Beissinger 1997, Krebs 1999). The main period of chick rearing occurs during March–April, with all nestlings fledging by early to mid-May (Renton & Salinas-Melgoza 1999).

After the eggs hatched, inspections of six nests in 1996 and five nests in 1997 were conducted during the mid-day lull in parental activity (Renton & Salinas-Melgoza 1999). Access to nest cavities was achieved using both single-rope ascending techniques (Perry 1978, Perry & Williams 1981), and a tree bole-climbing technique (Donahue & Wood 1995). All nestlings were measured on average every 3 days; however, growth parameters and analysis were only determined for 14 nestlings which fledged successfully, comprising two broods of two nestlings and one brood of three nestlings in both 1996 and 1997. Nestling growth was evaluated using the length of the left wing and culmen, measured to the nearest 0.1 mm with dial callipers. Body mass was also determined by weighing nestlings individually with 1.0 g and 2.0 g precision *Pesola* balances depending on chick size (Saunders 1982, 1986, Rinke 1989, Rowley & Chapman 1991).

All growth variables were measured by the same method and researcher in both years, with the exception that in 1996 length of open left wing was measured, while in 1997 it was found more reliable to measure length of folded left wing. Each nestling was marked with indelible ink on one foot to identify hatching sequence as first, second and third hatched. All measurements were conducted at the nest entrance to minimize handling time and potential stress for the nestlings. Disposable gloves and a face mask were used when handling nestlings to avoid potential disease transmission between nestlings and researcher.

The pattern of nestling growth was described using Ricklefs' (1967) logistic equation:

$$G_t = A/(1 + \exp[-k(\text{age} - t_i)])$$

where, A = the asymptote (normally the adult value), k = the rate of growth and t_i = the inflection point of the growth curve (i.e. time to attain 50% of the asymptote). Growth parameters for the logistic curve were fitted to nestling weights and wing and culmen lengths using the SPSS non-linear regression procedure (Norusis 1994).

Many nestling birds exhibit a pattern of body mass recession prior to fledging, due to the loss of water from maturing feathers (Ricklefs 1968a). Zach (1988) recommends the use of three-parameter growth models which are less sensitive to small fluctuations in data, as well as statistical analysis of observed measures to evaluate growth. Lilac-crowned Parrot nestlings peaked in mass half-way through the nestling phase, exhibited fluctuations in mass during the second month of the nestling phase and declined in mass prior to fledging. This creates fluctuations in data and makes interpretation of the logistic curve difficult, as the point of inflection (t_i) and the rate constant (k) depend on the value of the asymptote. Culmen length varied less than mass between measurements, and provided more reliable estimates of the asymptote. Due to variability of the logistic curve with the asymptote, and its susceptibility to fluctuations in data, statistical analysis was conducted using observed measures of chick size and the growth rate over the linear portion of the growth curve.

The rate of nestling growth was compared between years by linear regression with use of the F-test (Zar 1996) for both mass increment and increase in culmen length between 5 and 30 days of age, when the growth curve approached a straight line. Between-year differences in nestling size were evaluated by comparison of observed values for the growth variables: culmen length of nestlings at 6 days, 40 days and 60 days after hatching; nestling mass 6 days after hatching; maximum nestling mass; and fledging mass. Analysis of covariance (ANCOVA) incorporating hatching sequence as a factor was applied to linear growth between 5 and 30 days, and chick sizes with age. The general linear model was applied where data sets were unbalanced. Between-year variation in chick sizes at different stages of development were further analysed by two-sample *t*-test. Descriptive statistics are presented with means, value ranges and standard deviations.

RESULTS

Interannual variation in food resources

Food availability during the dry season was greater in 1997 than in 1996 (Fig. 1). This difference was significant for number of trees fruiting, and sum of dbh of fruiting trees (Table 1). Habitats also differed significantly within the dry season for both number of trees, and sum of dbh of fruiting trees (Table 1). Semi-deciduous forest provided more food during the dry season than both deciduous forest (Trees: $q_{30,3} = 5.50$, $P < 0.01$; dbh: $q_{30,3} = 9.52$, $P < 0.001$) and watercourses (Trees: $q_{30,2} = 3.04$, $P < 0.05$; dbh: $q_{30,2} = 7.45$, $P < 0.001$). Furthermore, significantly more species of food trees were available during the dry season of 1997 than of 1996 (one-way ANOVA: $F_{1,10} = 7.34$, $P = 0.022$; Fig. 1).

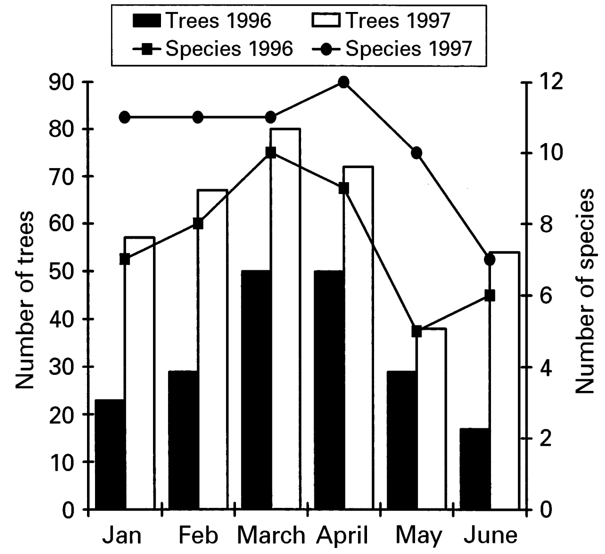


Figure 1. Total number of food trees and species available over all transects during the dry season of 1996 and 1997.

Table 1. Two-way ANOVA on the number of food trees and sum of dbh of fruiting trees from phenology transects in three habitat types during the dry season of 1996 and 1997.

		Number of trees		Sum of dbh	
Source	*df*	*F*-value	*P*-value	*F*-value	*P*-value
Year	1, 30	15.74	0.0001	13.14	0.001
Habitat	2, 30	7.58	0.002	25.09	0.0001
Year × habitat	2, 30	0.38	0.685	0.38	0.684

Pattern of nestling growth and development

Lilac-crowned Parrot nestlings weighed 11–19 g on hatching, and spent a mean (± sd) 64 ± 2.8 days (range 60–69 days, $n = 13$) in the nest. Nestlings hatched with eyelids fused together, and a light covering of feather down. The eyelids began to separate at 18 ± 2.3 days of age (range 15–23, $n = 15$), and were not fully open until 22.5 ± 2.3 days (range 18–26 days, $n = 15$). Nestlings underwent a rapid increase in body mass during the first 4 weeks of the nestling phase (Fig. 2) and completed 90% of their growth at 32 ± 3.9 days after hatching (range 25–38 days, $n = 14$). Mean maximum body mass was 327 ± 8.5 g (range 309–338 g, $n = 14$), and weight recession occurred 10–14 days prior to fledging. Mean fledging mass of nestlings was 280 ± 15.1 g (range 254–302 g, $n = 13$), 14% less than the mean maximum body mass.

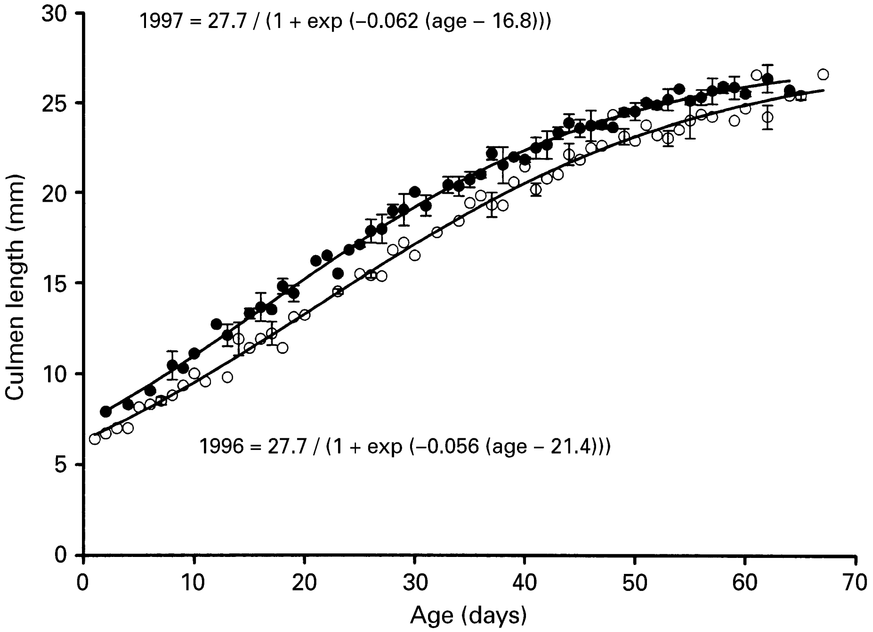
Primary wing feathers erupted by 26 ± 1.6 days of age (range 23–29 days, $n = 17$), and development during the second month of the nestling phase consisted principally of feather growth. Increase in wing-length was slow during the first 2–3 weeks after hatching, but increased linearly once the feather pins began to emerge. Increase in culmen length was regular during the first month after hatching, but began to plateau towards the end of the nestling phase.

The most frequent ectoparasites found on parrot nestlings were red mites and bot fly *Philornis* sp. larvae, though the average maximum bot fly load was low with 3 ± 4.2 bot fly larvae per nestling (range 0–13 larvae, $n = 23$).

Interannual variation in nestling growth

Growth parameters of the logistic curve for body mass and culmen length are presented with mean values for nestlings in 1996 and 1997 (Fig. 2). The linear rate of nestling growth from days 5 to 30 differed significantly between the years for both body mass increment (ANCOVA: $F_{1,55} = 22.6$, $P < 0.001$) and increase in culmen length (ANCOVA: $F_{1,55} = 94.97$, $P < 0.001$), with nestlings exhibiting faster growth in 1997 than in 1996 (Fig. 3). Hatching sequence did not influence rate of growth of culmen

(a) Culmen length



(b) Body mass

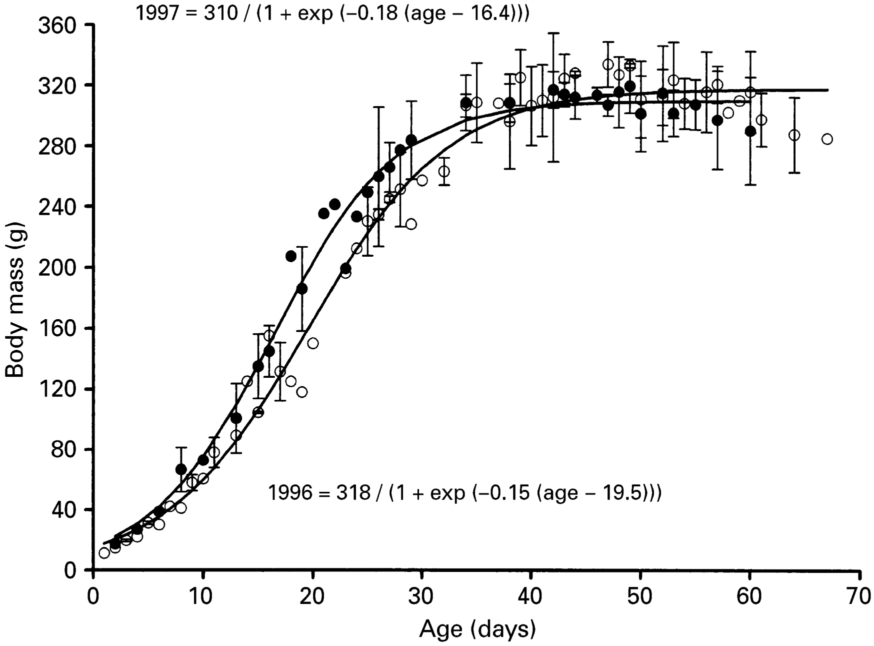


Figure 2. Growth of Lilac-crowned Parrot nestlings in 1996 (○) and 1997 (●). Error bars represent standard deviations of mean values.

length, but was slightly significant for body mass increment (ANCOVA: $F_{2,55} = 3.24$, $P = 0.047$), particularly with respect to third-hatched nestlings, which were smaller and exhibited slightly slower growth than first- or second-hatched nestlings ($q_{55,3} = 3.74$, $P < 0.05$).

Nestling sizes also differed between the years (Table 2, Fig. 2). The culmen length of nestlings was significantly shorter in 1996 than in 1997 at both 6 days and 40 days after hatching, and differed slightly at 60 days after hatching when culmen length approaches an asymptote (ANCOVA for culmen

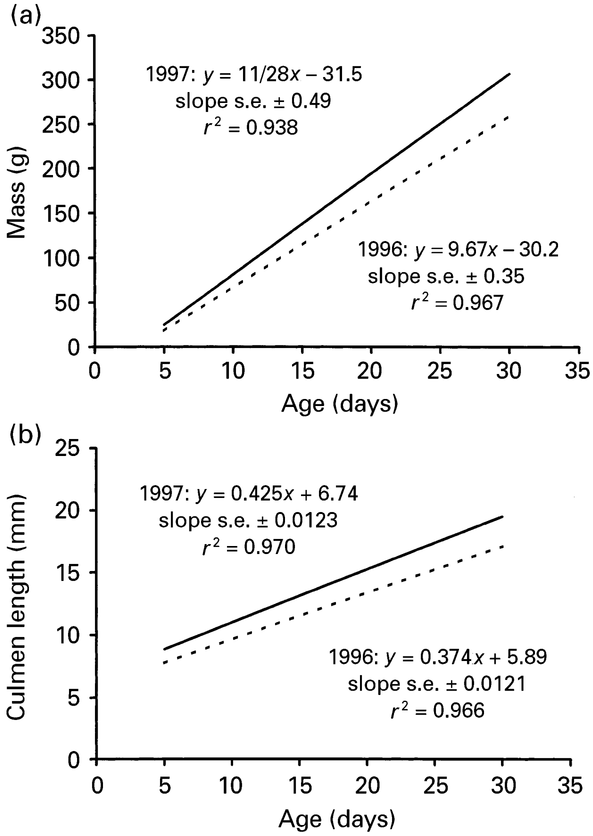


Figure 3. Linear regression lines of nestling growth between day 5 and day 30 for 1996 (stippled lines) and 1997 (solid lines). (a) Body mass increment, and (b) increase in culmen length.

length, incorporating hatching sequence, $F_{1,33} = 7.98$, $P < 0.01$). Differences in body mass between years or by hatching sequence were not significant, though body mass of nestlings 6 days after hatching was slightly lower in 1996 than in 1997 (Table 2). Maximum body mass did not differ between years (Table 2), though nestlings took longer to attain maximum body mass in 1996 than in 1997 (Fig. 2). Nestlings fledged at 65 ± 2.2 days (range 62–68, $n = 7$) in 1996, and 63.7 ± 2.9 days (range 60–69, $n = 6$) in 1997. Fledging mass of nestlings was slightly lower in 1997 than in 1996 (Table 2). The more rapid growth of nestlings during 1997 means that feather maturation may have been more advanced at the time of fledging, resulting in a greater weight recession owing to the loss of water from feather tissues than in 1996.

Comparison between Psittacine species

Growth rate constants and asymptotic values of the logistic curve are summarized for various psittacine species in Table 3. This shows greater variation between parrot species in the growth rate constant (k) for body mass (coefficient of variation = 26.9%) than for wing length (coefficient of variation = 11.7%). Growth rate for body mass was also inversely correlated with adult size ($r^2 = 0.75$, $F_{1,6} = 18.26$, $P = 0.005$), with larger parrot species exhibiting slower growth rates. However, wing growth was fairly constant between parrot species and was unrelated to adult wing length.

DISCUSSION

Tropical forests in Central America may experience climatic variability between years which influences the production of fruits and seeds, and in turn limits densities of frugivorous and granivorous mammals (Foster 1982, Wright *et al.* 1999). Interannual fluctuations in environmental factors may influence the condition of nestling birds (McCarty & Winkler 1999), particularly in seasonal habitats. Lilac-crowned Parrot nestlings grew more quickly in 1997, corresponding with an increase in food availability in tropical dry forest as a result of the higher rainfall.

Hatching sequence also influenced body mass increment, with third-hatched nestlings being slightly smaller than first- or second-hatched nestlings. The clutch size of Lilac-crowned Parrots in tropical dry forest is low compared with similarly

Table 2. Comparison of nestling sizes in 1996 and 1997. Results presented are means with standard error, and two-sample *t*-test significance level.

Variable	1996	1997	Significance test
Culmen length at 6 days (mm)	8.4 ± 0.15	9.3 ± 0.51	$t_8 = 3.4$, $P = 0.015$
Culmen length at 40 days (mm)	20.6 ± 0.5	22.1 ± 0.25	$t_{12} = 2.82$, $P = 0.022$
Culmen length at 60 days (mm)	24.9 ± 0.34	25.9 ± 0.24	$t_{11} = 2.29$, $P = 0.045$
Mass at 6 days (g)	36.4 ± 1.9	44.2 ± 3.2	$t_8 = 2.07$, $P = 0.084$
Maximum mass (g)	330 ± 3.0	323 ± 3.0	$t_{12} = 1.73$, $P = 0.11$
Fledging mass (g)	285 ± 4.0	276 ± 6.9	$t_{11} = 1.03$, $P = 0.33$

Table 3. Comparison of Ricklefs' (1967) growth rate constant (*k*) for psittacines.

Variable	Asymptote	Constant (*k*)	Source
Body mass (g)			
Hyacinth Macaw, captive bred, *Anodorhynchus hyacinthinus*	1500	0.11	data from Abramson (1991)
Scarlet Macaw, Belize, *Ara macao*	1135	0.139	Renton (unpubl. data)
Scarlet Macaw, captive-bred *Ara macao*	1111	0.149	data from Abramson (1991)
Lilac-crowned Parrot *Amazona finschi*	314	0.17	This study
Red-shining Parrot *Prosopeia tabuensis*	277	0.162	Rinke (1989)
Long-billed Corella *Cacatua pastinator pastinator*	275	0.23	Smith (1991)
Monk Parakeet *Myiopsitta monachus*	103.9	0.24	Navarro and Bucher (1990)
Green-rumped Parrotlet *Forpus passerinus*	23.7	0.23	Waltman and Beissinger (1992)
Length of folded left wing (mm)			
Scarlet Macaw, Belize, *Ara macao*	399	0.066	Renton (unpubl. data)
White-tailed Black Cockatoo *Calyptorhynchus funereus*	366	0.074	Saunders (1982, 1986)
Long-billed Corella *Cacatua pastinator pastinator*	285	0.087	Smith (1991)
Red-shining Parrot *Prosopeia tabuensis*	239.5	0.086	Rinke (1989)
Lilac-crowned Parrot *Amazona finschi*	190	0.073	This study

sized Amazon parrots (Gnam & Rockwell 1991, Enkerlin-Hoeflich & Hogan 1997), and variations in growth rate for third-hatched nestlings may suggest a limitation for brood size in this habitat, which could place third-hatched nestlings at a disadvantage in extreme years of low food availability. However, the sample is small and the sex of nestlings was unknown, though size differences between males and females are not large in this species (Forshaw 1989). In psittacine species that demonstrate sex differences in growth, males are on average 10–15% larger than females (Rinke 1989, Krebs 1999). Nevertheless, an unequal distribution of males and females between years may influence the results.

The energetically costly activities associated with breeding may coincide with periods of relative food abundance (Perrins 1970, Martin 1987). The main growth period of Lilac-crowned Parrot nestlings in March–April coincides with an increase in food abundance during the mid-dry season, and may enable young to fledge before the end of the dry season when food availability declines (Renton 2001).

Parrot nestlings can survive temporary food shortages and exhibit flexible growth trajectories (Stoleson & Beissinger 1997). This, combined with the length of the nestling period and parental effort (Drent & Daan 1980, Cucco & Malacaren 1995, Krebs *et al.* 1999, Krebs & Magrath 2000), may enable Lilac-crowned Parrot nestlings to reach asymptotic size prior to fledging, even in poor years. Variations in growth rate, even in the absence of differences in eventual asymptotic size, would be advantageous to nestlings in such a seasonal environment by enabling them to adapt to fluctuations in food availability, and complete the energetically demanding phase of growth prior to the decline in food resources at the end of the dry season. Rapid growth early in development also reduces the vulnerability of nestlings to predation risks which may be greater towards the end of the dry season (Sieving 1992).

The pattern of growth exhibited by Lilac-crowned Parrot nestlings corresponds with that observed for similarly sized Australian parrots (Rowley & Chapman 1991, Smith 1991), which reach asymptotic mass half-way through the nestling phase. However, this contrasts with the slow growth exhibited by larger cockatoo species (Saunders 1982). Larger bird species tend to have slower growth rates for body mass (Ricklefs 1968b). This inverse relation between body mass and growth rate is supported for psittacine species ($r^2 = 0.75$), and is similar to the inverse relation obtained by Ricklefs (1976) for tropical landbirds ($r^2 = 0.73$).

Between-year variations in growth rate of Lilac-crowned Parrot nestlings corresponded with fluctuations in food availability in tropical dry forest. Flexible growth rates may enable nestling parrots to exploit periods of increased food availability and withstand periods of food shortage. Tropical dry forest is a highly seasonal habitat, which is influenced by climatic El Niño events in the Pacific (Bullock 1986). Seasonal forests in Central America may exhibit cycles of years of fruit abundance followed by years of fruit scarcity (Foster 1982, Wright *et al.*

1999), though little is known of the impact of this environmental variability on animal populations. Tropical dry forest also has one of the highest rates of deforestation in Mexico (Masera *et al.* 1997), making it essential to determine the impact of this increased habitat fragmentation on animal populations, particularly in extreme years of climatic variability. Very few data are available on growth rates of neotropical parrots, or the influence of food resource availability on reproduction, which is essential to understand the potential impacts of environmental variability and habitat fragmentation on wild populations of threatened species.

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