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GROWTH OF SCARLET MACAW (ARA MACAO) CHICKS IN SOUTHEASTERN PERU

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Resumen. – Crecimiento de pichones de guacamayo escarlata (*Ara macao***) en el sudeste del Perú. –** Estudios de crecimiento aviar pueden incrementar el entendimiento acerca de las estrategias de desarrollo, tamaño de crías, calidad de progenie, y potencial para acciones de conservación de las especies. Medimos peso, culmen, ala y tarso en 45 pichones silvestres de guacamayo escarlata (*Ara macao***)** en Tambopata en la selva de Perú. De estos, 15 fueron primeros pichones, 15 fueron segundos pichones de nidadas de dos pichones (dobles) y 15 fueron pichones únicos en nidadas de un solo pichón (únicas). Los individuos volaron a los 86 ± 4 días de edad. En general, las tasas y curvas de crecimiento fueron similares a las elaboradas para otras especies del mismo orden. Los pichones en nidadas únicas aumentaron de peso significativamente más rápido que los pichones nueltadas dobles. Sin embargo, el pico de peso registrado, el peso asintótico y las edades de vuelo no difieren en miembros de diferentes tipos de nidadas, sugiriendo que para el momento en el que los pichones vuelan del nido, las diferencias en tasa de crecimiento ya no influyen significativamente en los individuos. Futuros estudios deben investigar las consecuencias de manipular tamaños de nidadas en psitácidos grandes como una técnica de manejo para determinar si es que criar individuos adicionales en una nidada deprime el crecimiento y sobrevivencia post vuelo de los compañeros de nidada.

Abstract. – Studying avian growth can provide insight in to developmental tradeoffs, offspring size, reproductive output and potential conservation actions. We measured body mass, culmen, wing, and tarsus growth of 45 wild Scarlet Macaw (*Ara macao*) chicks in the Tambopata region in lowland Peru. Of these, 15 were first chicks, 15 were second chicks in two chick broods, and 15 were only chicks in one chick broods. Chicks fledged in 86 ± 4 days. In general, the growth rates and curves were similar to those found for other members of the order. Chicks in one chick broods gained body mass significantly faster than chicks in two chick broods. However, the peak recorded body masses, asymptotic body masses, and fledging ages did not differ among the chicks in one and two chick broods, suggesting that by the time the chicks fledged, the different growth rates no longer had a significant influence on the birds. Future studies should look at the consequences of manipulating brood sizes of large psittacines as a management technique to determine if fostering additional chicks significantly depresses the growth and post fledging survival of brood mates. *Accepted 28 February 2010.*

Key words: Scarlet Macaw, Ara macao, chick growth, growth rate, logistic model, climatic variation, rainfall, Peru.

INTRODUCTION

Variations in avian growth and development are produced by interacting factors including phylogeny, environment, food supply, provisioning rates, hatching order, and others (Stark & Ricklefs 1998a, Krebs 1999). Studying the effects of these factors can provide insight in to avian life history evolution, limitations on reproductive rates, offspring quality and potential conservation actions to increase reproductive success. Hatching order also influences chick growth rates as younger chicks of many species receive less food and grow slower or die of starvation (Clark & Wilson 1981, Siikamaki 1996, Stoleson & Beissinger 1997).

The family Psittacidae is characterized by relatively slow growth and marked hatching asynchrony (Bucher 1983, Beissinger & Waltman 1991, Masello & Quillfeldt 2002). Parrots invest a great deal of effort in raising their young during both the long nestling period and the extensive period of postfledging care (Forshaw 1989) and many parrots have brood reduction through starvation (Smith 1991, Guedes & Harper 1995, Nycander et al. 1995, Stoleson & Beissinger 1997). The growth and development of relatively few psittacines have been studied in the wild, preventing family-wide conclusions about development strategies (see review in Renton 2002). However, most species studied to date raise broods in which all chicks fledge at similar sizes and body masses regardless of hatching order (Smith 1991, Guedes & Harper 1995, Stoleson & Beissinger 1997, Krebs 1999) but last hatched nestlings fledge significantly smaller and lighter than their siblings in a minority of species (Krebs 1999, Masello & Quillfeldt 2002, Renton 2002). These findings suggest that there may be important yet unappreciated variation in the nesting strategies of parrots.

The family Psittacidae contains more endangered species than any other bird family (Bennett & Owens 1997) and basic natural history information is sorely needed to aid in the conservation and management of this group. Knowledge of psittacine growth rates and the causes and consequences of varying brood sizes is also of practical importance because adding chicks to wild broods is an established management technique for augmenting populations of endangered parrots (Snyder *et al.* 1987, Snyder *et al.* 2000, Wunderle *et al.* 2003).

The Scarlet Macaw (Ara macao) is among the most widely distributed parrots in the Americas, ranging from southern Mexico through Bolivia and Brazil (Forshaw 1989). It is listed as "least concern" on the IUCN Red List, but is on Appendix I of CITES and classified as endangered by national governments throughout Central America (Collar 1997, Renton 2000, Birdlife International 2009). Nesting ecology of the species has been studied in Central and South America (Nycander et al. 1995, Iñigo-Elias 1996, Vaughan et al. 2003, Brightsmith 2005, Renton 2006, Guittar et al. 2009, Renton & Brightsmith 2009) and the species is the subject of ongoing conservation efforts (Brightsmith et al. 2005, Vaughan et al. 2005, Barcott 2008, Boyd & McNab 2008). In Peru the species breeds during the wet season. Chicks hatch asynchronously and the resulting development hierarchy leads to brood reduction through starvation of the younger chicks (Nycander et al. 1995). However, wild Scarlet Macaw chick growth and development remain undocumented.

Here we report on the growth rates of wild Scarlet Macaws chicks in the lowlands of southeastern Peru in an area free from large scale anthropogenic habitat modification and poaching (Foster *et al.* 1994, Brightsmith 2004). We also compare growth among chicks in one chick broods and first and second

chicks in two chick broods to determine if Scarlet Macaws raise broods in which all chicks are similar in size and body mass regardless of brood size and hatching order.

METHODS

Study site. The study was conducted at the Tambopata Research Center in the Department of Madre de Dios in southeastern Peru (13°8'S, 69°36'W). The center is on the border of the Tambopata National Reserve (275,000 ha) and the Bahuaja-Sonene National Park (537,000 ha) in the department of Madre de Dios in southeastern Peru. It lies in the tropical moist forest lifezone near the boundary with subtropical wet forest at 250 m elevation and receives 3200 mm of rain per year (Tosi 1960, Brightsmith 2004). The site is surrounded by a matrix of mature floodplain forest, successional floodplain forest, Mauritia flexuosa (Arecaceae) palm swamp, and upland forest (Foster et al. 1994).

Biometric data. We inspected about 35 potential nest sites each season (N = 8 seasons) using single rope climbing techniques (Perry 1978, Perry & Williams 1981). Of these, Scarlet Macaw chicks hatched and were accessible in 65 nests (7 \pm 3 nests per season, N = 8 seasons). Nests were checked every one to two days from approximately hatching to age 30 days for the youngest chick in the brood. After the youngest chick was at least 30 days old, nests were checked once per two to four days (approximately) until the oldest chick was 78 days old. After this, nests were checked every one to two days until the last chick fledged. During each nest inspection, all chicks in the nest were placed in a plastic bucket lined with towels, lowered to the ground, measured and returned to the nest. This entire process usually took less than 15 minutes. For chicks less than 25 days old, the bucket also contained a hot water bottle.

During our study a total of 137 chicks hatched. To ensure that our analysis would accurately describe the general growth patterns for the species we excluded chicks which did not fledge (N = 60), chicks which were measured < 25 times (N = 24), chicks without measurements during the first week of life (N = 4), chicks in two chick broods where the older sibling died (N = 3), and chicks that suffered severe dehydration episodes (N = 1). A total of 45 chicks met these requirements: 15 first chicks and 15 second chicks in two chick broods and 15 chicks in one chick broods (hereafter referred to as "lone" chicks). Throughout the study, the day of hatching was designated as day 0. While some broods contained up to four chicks, none of the third or fourth chicks fledged successfully, as reported for this site by Nycander et al. (1995). Of the 45 chicks included in this study 93% were from nests in PVC nest boxes, 7% were from wooden nest boxes and none were raised in natural nests (see Nycander et al. 1995 for a description of these nests).

We collected four measurements of each chick during each inspection: body mass, tarsus length, culmen length, and wing cord (not flattened). Data were collected from December 2000 through April 2008 (eight reproductive seasons). In addition, we measured eight adult Scarlet Macaws trapped near the research center.

To reduce disturbance at nests before hatching, we minimized nest checks during incubation as our data suggest that increased disturbance reduces hatching success (DJB unpubl. data). As a result we were unable to determine the exact hatch dates for all chicks. Hatch date was known within 24 hours for 19 chicks. For the remaining 26 chicks the hatch date was estimated using the time elapsed between the last check pre-hatch and the first check post-hatch and body mass of the chick when first

TABLE 1. Growth parameters for wild Scarlet Macaw chicks in southeastern Peru. The parameters were calculated using the combined data from 45 individuals. N (points) is the total number of measurements used to calculate the parameters. All parameters were calculated using the logistic growth model (Ricklefs 1968).

Biometric measurement	Asymptotic size	Growth rate	Age of maximum growth rate	R ²	N (points)
Body mass (g)	996	0.11	25.8	0.95	1845
Wing length (mm)	369	0.06	52.8	0.98	1823
Tarsus length (mm)	36	0.12	11.3	0.91	1762
Culmen length (mm)	60	0.05	24.8	0.97	1829

encountered compared to body mass of known age chicks.

Data analysis. We used iterative non-linear regression and the logistic, Gompertz and Bertalanffy model (Ricklefs 1968) to fit all four of the biometric variables collected. The logistic equation had the best fit (highest R²) for all variables, so only the results from the logistic model are presented here. The logistic growth curve used was W = A / $(1 + e^{(-B*(T-C))})$ where W = the morphological measurement collected in the field in grams or mm, T = age of the chick in days, A= the asymptotic size (body mass or length of measured body part), B = growth rate constant, C = age in days for which the growth rate is maximal, and e = the natural constant ~2.718. Curves were fitted using Datafit 8.1 (Oakdale Engineering, 2005, Oakdale, Pennsylvania, USA).

To model the general growth curves for Scarlet Macaws as a whole we fit logistic growth models to the combined raw data from all 45 chicks. To determine if growth differed among first chicks, second chicks, and lone chicks, we used the logistic equation (as described above) to calculate asymptotic size, growth rate constant, and age of maximum growth rate for the body mass, tarsus length, culmen length, and wing cord measurements to produce 12 growth parameters for each bird. We also determined three additional parameters for each chick: maximum body mass, age of maximum body mass, and fledging age. To test for difference among the three chick types we used two-way ANOVA with year and chick type as factors for each of the 15 parameters. For parameters where the ANOVA suggested a significant difference among chick types, we used multiple range tests to determine which chick types differed significantly.

RESULTS

We calculated growth rates for a total of 45 chicks which fledged successfully. Of these 15 were first chicks, 15 were second chicks and 15 were lone chicks in the brood. Of the 15 lone chicks, three were originally part of two chick broods and two were part of three chick broods. However the corresponding second chicks died at 8.5 \pm 5.2 days (range 2.5–16.5 days, N = 5) and the corresponding third chicks died at 4.3 ± 4.3 days (range 1–7.5, N = 2). Of the 15 two chick broods used, four began as three chick broods and three as four chick broods. The corresponding third chicks died at 7.2 \pm 3.2 days of age (range 6.5–10.5, N = 7) and the corresponding fourth chicks died at 3.8 ± 0.4 days of age (range 1.5-3.5, N = 3). The second chicks hatched on average 3.3 ± 1.2 days after the first chicks (range 1–5

SCARLET MACAW CHICK GROWTH



FIG. 1. Body mass increase of Scarlet Macaw chicks in southeastern Peru. Data are from 45 chicks. The solid line and the equation represent the logistic curve fitted by the method of Ricklefs (1968).

days, N = 15). Chicks fledged at 86.3 \pm 3.9 days of age.

General growth parameters. The combined data from all chicks gives the general logistic growth parameters for body mass, wing, tarsus, and culmen for Scarlet Macaws (Table 1). For body mass, the growth rate constant was 0.11, maximum growth rate was achieved at 25.8 days of age and predicted asymptotic body mass was 996 g (Fig. 1). The logistic equation did not model decline in body mass during the last 20 days before fledging. Actual peak body mass measured was 1082 ± 79 g (N = 45 chicks) at 63 ± 8 days of age. This body mass represents ~95 % of average adult body mass 1135 ± 64 g (N = 8). Chicks weighed 916 \pm 85 g (N = 40 chicks) just before fledging which is 81% of adult body mass. For wing length, the growth rate constant was 0.06, maximum growth rate was achieved at 52.8 days and predicted asymptotic wing size was 369 mm (Fig. 2). This length represents 84% of average adult wing length of 437 ± 46 mm (N = 3). For tarsus length, the growth rate constant was 0.12, maximum growth rate was achieved at 11.3 days of age and predicted asymptotic tarsus size was 36.5 mm (Fig. 3). This represents ~100% of average adult tarsus length of 35.0 ± 0.6 mm (N = 3). The culmen growth rate constant was 0.05, maximum growth was achieved on day 24.8 and the asymptotic maximum culmen size was 60 mm (Fig. 4). This length represents 86% of average adult culmen length of 69.4 ± 2 mm (N = 3).

Growth parameters by chick type. Body mass growth rate differed significantly among chick types (ANOVA: $F_{2,35} = 3.12$, P = 0.05 Table 2) with lone chicks' growth for body mass significantly more rapid than that of first chicks and second chicks (Multiple range test: P < 0.05 for both). Lone chicks achieved this higher growth rate at a younger age than second chicks in broods of two but the difference was not statistically significant (ANOVA $F_{2,42} = 2.9$, P = 0.06). The wings of



FIG. 2: Wing growth for Scarlet Macaw chicks from southeastern Peru. The data are from 45 chicks. The solid line and the equation represent the logistic curve fitted by the method of Ricklefs (1968).

second chicks grew slightly more rapidly than those of first chicks but this trend was not significant (ANOVA $F_{2,42} = 2.71$, P = 0.08). The maximum body mass measured, age of maximum body mass and fledging age did not vary significantly among first, second, and lone chicks (ANOVA $F_{2,42} < 1.2$, P > 0.3, Table 2).

DISCUSSION

Scarlet Macaw chicks had body mass gain curves typical of other parrots (Bucher 1983, Smith 1991, Stoleson & Beissinger 1997, Masello & Quillfeldt 2002, Renton 2002, Seixas & Mourão 2003, Pacheco *et al.* 2010). Growth was best fit by the logistic curve as has been found in most other studies of Psittaciformes (Bucher 1983, Smith 1991, Waltman & Beissinger 1992, Krebs 1999, Taylor & Perrin 2008, Pacheco *et al.* 2010). Chicks had a short stationary phase of two days in which body mass gain was minimal, apparently as they transition from consuming voke to consuming food from the parents (Bucher 1983, Abramson *et al.* 1995). Chicks then entered a logarithmic growth phase of 30 days, achieved peak body mass at age 63 days then slowly lost body mass until fledging (see Masello & Quillfeldt 2002 for a discussion of mass recession in Psittaciformes). Given that chicks fledge at only 81% of adult body mass, they continue to gain body mass post fledging as has been found for most parrots (Smith 1991, Masello & Quillfeldt 2002, Renton 2002) but see (Navarro *et al.* 1992).

Scarlet Macaws studied here have among the slowest body mass gain rates recorded for psittacines (Stark & Ricklefs 1998b, Renton 2002). However, the rate is similar to those recorded for other large macaws (*Ara* and *Anodorhynchus*) and altricial birds of similar body mass (Stark & Ricklefs 1998b, Renton 2002). Growth rates of the tarsus, culmen and wing vary greatly during chick development (Fig. 2–4). Consistent with the theory of compensatory growth (O'Connor 1977) chicks apparently prioritize growth of distinct body

SCARLET MACAW CHICK GROWTH



FIG. 3: Tarsus growth for Scarlet Macaw chicks from southeastern Peru. The data are from 45 chicks. The solid line and the equation represent the logistic curve fitted by the method of Ricklefs (1968).



FIG. 4: Culmen growth for Scarlet Macaw chicks from southeastern Peru. The data are from 45 chicks. The solid line and the equation represent the logistic curve fitted by the method of Ricklefs (1968).

parts based on the part's importance in facilitating immediate survival and future growth. The tarsus reaches its maximum growth rate at only 11 days and is almost adult size by 35 days of age. Early tarsus growth may be selected for as strong feet may allow the

TABLE 2: Growth parameters among chick types for Scarlet Macaws from southeastern Peru. "Only chicks" are chicks in one chick broods, "First chicks" are older chicks in two chick broods and "Second chicks" are younger chicks in two chick broods. N = 15 for all measurements for all chick types. Within a row, values followed by different superscript letters differed significantly using a one way ANOVA.

	Growth parameter	"Only chicks"	"First chicks"	"Second chicks"
Body mass (g)	Asymptotic size	1003 ± 74	1020 ± 57	996 ± 80
	Growth rate	0.12 ± 0.01 ^A	0.11 ± 0.01 ^B	0.11 ± 0.01 ^B
	Age of maximum growth rate	25.1 ± 2.4	26.1 ± 2.2	27.0 ± 2.0
Wing length (mm)	Asymptotic size	360 ± 10	371 ± 22	353 ± 25
wing length (min)	Crowth rate	0.063 ± 0.005	0.050 ± 0.005	0.061 ± 0.005
		0.003 ± 0.003	0.039 ± 0.003	0.001 ± 0.003
	Age of maximum growth rate	49.5 ± 3.9	52.7 ± 5.5	51./ ± 5.2
Tarsus length (mm)	Asymptotic size	37.8 ± 2.4	37.1 ± 2.8	36.5 ± 3.2
	Growth rate	0.127 ± 0.021	0.115 ± 0.022	0.110 ± 0.021
	Age of maximum growth rate	11.4 ± 1.4	11.7 ± 1.9	11.9 ± 2.2
Culmen length (mm)	Asymptotic size	60.6 ± 2.6	597 ± 31	58.7 ± 3.0
	Growth rate	0.052 ± 0.005	0.054 ± 0.005	0.054 ± 0.007
	Age of maximum growth rate	24.2 ± 2.1	24.3 ± 3.2	24.4 ± 3.1
		1105 100		1070 1 01
Maximum body mass (g)	-	1105 ± 103	1107 ± 65	1079 ± 91
Age of maximum	-	64.2 ± 8.0	60.4 ± 7.0	62.3 ± 7.3
body mass (days)				
Fledging age (days)	-	86.3 ± 4.2	86.9 ± 4.2	85.7 ± 3.3

chicks to minimize contact with the substrate and compete with siblings for food (O'Connor 1977, Pacheco *et al.* 2010).

The culmen is the second to reach its maximum growth rate (~25 days). A larger bill may simultaneously enhance ability to consume food from the parents (O'Connor 1977) and self-defense against predators. The upper mandible continues to grow post fledging (Koenig 2001, Renton 2002, Pacheco *et al.* 2010). The wing cord is the last to reach its maximum growth rate as primary feathers are developing. At fledging, primary feathers are still shorter than those of adults and usually still sheathed at the base (GV pers. observ.) confirming that wing growth continues post fledging as found for other psittacines (Smith 1991, Krebs 1999, Koenig 2001, Renton

2002, Seixas & Mourão 2002, Pacheco et al. 2010).

Relative growth among brood mates. We recorded only slight differences among growth parameters for first, second, and lone chicks in our study, as found for wild Hyacinth Macaws (Guedes & Harper 1995). Growth rates (for body mass) for chicks in one chick broods were greater compared to both the first and second chicks in two chick broods. This suggests that lone chicks receive more food at a younger age than chicks in two chick broods. However, the peak recorded body masses, asymptotic body masses, and fledging ages did not differ among chicks in one and two chick broods, suggesting that by fledging, these differential growth rates no longer had a significant influence on the birds. This is similar to Green-rumped Parrotlets (*Forpus passerinus*), Lilac-crowned Parrots (*Amazona finschi*), and Monk Parakeets (*Myiopsitta monachus*) where later hatching chicks grew slower but were not significantly lighter at fledging (Navarro & Bucher 1990, Stoleson & Beissinger 1997, Renton 2002) but contrasts with Burrowing Parrots (*Cyanoliseus patagonus*) where younger chicks were smaller and lighter upon fledging (Masello & Quillfeldt 2002).

Many altricial birds are more vulnerable to predation immediately after fledging and this appears to be the case for Scarlet Macaws (Naef-Daenzer et al. 2001, Myers & Vaughan 2004). For many bird species, increased body body mass and size at fledging are positively correlated with survival (Tinbergen & Boerlijst 1990, Magrath 1991, Jeugd & Larsson 1998, Naef-Daenzer & Keller 1999). However, the few studies of psittacines conducted to date have found no correlation between fledgling size and survival (Smith 1991, Stoleson & Beissinger 1997, Krebs 1999). How to interpret this finding is unclear as chicks with greatly reduced growth and malnourishment should show reduced probability of survival to adulthood. However, the studies of fledgling size and survival suggest that parents do not commonly fledge such undernourished chicks with reduced chance of survival. The reasons for this remain unknown but some parrots may adjust brood size according to their ability to adequately provision young (Smith 1991).

Our results suggest that lone chicks were not consistently larger than either first or second chicks in two chick broods. Future studies should look at the consequences of manipulating brood sizes of large psittacines to determine if fostering additional chicks significantly depresses the growth and post fledging survival of brood mates. Such work would not only be of theoretical interest, but would also provide much needed insight in to the potential consequences of using such techniques to manage threatened parrot populations (Snyder *et al.* 2000).

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REFERENCES

- Abramson, J., B. L. Spear, & J. B. Thomsen. 1995. The large macaws: their care, breeding and conservation. Raintree Publications, Fort Bragg, California, USA.
- Barcott, B. 2008. Last flight of the Scarlet Macaw: one woman's fight to save the world's most beautiful bird. Random House, New York, New York, USA.
- Beissinger, S. R., & J. R. Waltman. 1991. Extraordinary clutch size and hatching asynchrony of a Neotropical parrot. Auk 108: 863–871.
- Bennett, P. M., & I. P. F. Owens. 1997. Variation in extinction risk among birds: chance or evolutionary predisposition? Proc. R. Soc. B. 264: 401–408.
- BirdLife International. 2009. Species factsheet: Ara macao. Accessed on 9 March 2010 at http:// www.birdlife.org.
- Boyd, J., & R. B. McNab. 2008. The Scarlet Macaw in Guatemala and El Salvador: 2008 status and future possibilities. Findings and recommendations from a Species Recovery Workshop 9–15 March 2008. Wildlife Conservation Society -Guatemala Program, Guatemala City and Flores, Peten, Guatemala.

- Brightsmith, D. J. 2004. Effects of weather on avian geophagy in Tambopata, Peru. Wilson Bull. 116: 134–145.
- Brightsmith, D. J. 2005. Parrot nesting in southeastern Peru: seasonal patterns and keystone trees. Wilson Bull. 117: 296–305.
- Brightsmith, D. J., J. Hilburn, A. Del Campo, J. Boyd, M. Frisius, R. Frisius, D. Janik, & F. Guillén. 2005. The use of hand-raised psittacines for reintroduction: a case study of Scarlet Macaws (*Ara macao*) in Peru and Costa Rica. Biol. Conserv. 121: 465–472.
- Bucher, T. L. 1983. Parrot eggs, embryos, and nestlings: patterns and energetics of growth and development. Physiol. Zool. 56: 465–483.
- Clark, A. B., & D. S. Wilson. 1981. Avian breeding adaptations: hatching asynchrony, brood reduction, and nest failure. Q. Rev. Biol. 56: 253–277.
- Collar, N. J. 1997. Family Psittacidae. Pp. 280–479 in d. Hoyo, J., A. Elliott, & J. Sargatal (eds). Handbook of the birds of the world. Volume 4: Sandgrouse to cuckoos. Lynx Edicions, Barcelona, Spain.
- Forshaw, J. M. 1989. Parrots of the world. 3rd ed. Landsdowne Editions, Melbourne, Australia.
- Foster, R. B., T. Parker, A, A. H. Gentry, L. H. Emmons, A. Chicchón, T. Schulenberg, L. Rodríguez, G. Larnas, H. Ortega, J. Icochea, W. Wust, M. Romo, C. J. Alban, O. Phillips, C. Reynel, A. Kratter, P. K. Donahue, & L. J. Barkley. 1994. The Tambopata-Candamo Reserved Zone of southeastern Peru: a biological assessment. Conservation International, Washington, DC, USA.
- Guedes, N. M. R., & L. H. Harper. 1995. Hyacinth macaws in the Pantanal. Pp. 395–422 in Abramson, J., B. L. Spear, & J. B. Thomsen (eds). The large macaws: their care, breeding and conservation. Raintree Publications, Fort Bragg, California, USA.
- Guittar, J. L., F. Dear, & C. Vaughan. 2009. Scarlet Macaw (*Ara macao*, Psittaciformes: Psittacidae) nest characteristics in the Osa Peninsula Conservation Area (ACOSA), Costa Rica. Rev. Biol. Trop. 57: 387–393.
- Iñigo-Elias, E. E. 1996. Ecology and breeding biology of the Scarlet Macaw (*Ara macao*) in the Usumacinta drainage basin of Mexico and Guatemala. Ph.D. dissertation, Univ. of Florida, Gainesville, Florida, USA.

- Jeugd, H. P. v. d., & K. Larsson. 1998. Pre-breeding survival of Barnacle Geese *Branta leucopsis* in relation to fledgling characteristics. J. Anim. Ecol. 67: 953–966.
- Koenig, S. E. 2001. The breeding biology of Blackbilled Parrot Amazona agilis and Yellow-billed Parrot Amazona collaria in Cockpit Country, Jamaica. Bird Conserv. Int. 11: 205–225.
- Krebs, E. A. 1999. Last but not least: nestling growth and survival in asynchronously hatching Crimson Rosellas. J. Anim. Ecol. 68: 266– 281.
- Magrath, R. D. 1991. Nestling body mass and juvenile survival in the Blackbird, *Turdus merula*. J. Anim. Ecol. 60: 335–351.
- Masello, J. F., & P. Quillfeldt. 2002. Chick growth and breeding success of the burrowing parrot. Condor 104: 574–586.
- Myers, M. C., & C. Vaughan. 2004. Movement and behavior of Scarlet Macaws (*Ara macao*) during the post-fledging dependence period: implications for in situ versus ex situ management. Biol. Conserv. 118: 411–420.
- Naef-Daenzer, B., & L. F. Keller. 1999. The foraging performance of Great and Blue Tits (*Parus major* and *P. caeruleus*) in relation to caterpillar development, and its consequences for nestling growth and fledging weight. J. Anim. Ecol. 68: 708–718.
- Naef-Daenzer, B., F. Widmer, & M. Nuber. 2001. Differential post-fledging survival of Great and Coal Tits in relation to their condition and fledging date. J. Anim. Ecol. 70: 730–738.
- Navarro, J. L., & E. H. Bucher. 1990. Growth of Monk Parakeets. Wilson Bull 102: 520–525.
- Navarro, J. L., M. B. Martella, & E. Bucher. 1992. Breeding season and productivity of monk parakeets in Cordoba, Argentina. Wilson Bull. 104: 413–424.
- Nycander, E., D. H. Blanco, K. M. Holle, A. d. Campo, C. A. Munn, J. I. Moscoso, & D. G. Ricalde. 1995. Manu and Tambopata: nesting success and techniques for increasing reproduction in wild macaws in southeastern Peru. Pp. 423–443 *in* Abramson, J., B. L. Spear, & J. B. Thomsen (eds). The large macaws: their care, breeding and conservation. Raintree Publications, Fort Bragg, California.
- O'Connor, R. J. 1977. Differential growth and body composition in altricial passerines. Ibis

119: 147–166.

- Pacheco, M. A., S. R. Beissinger, & C. Bosque. 2010. Why grow slowly in a dangerous place? Postnatal growth, thermoregulation, and energetics of nestling Green-Rumped Parrotlets (*Forpus passerinus*). Auk 127: 558–570.
- Perry, D. R. 1978. A method of access into the crowns of emergent and canopy trees. Biotropica 10: 155–157.
- Perry, D. R., & J. Williams. 1981. The tropical rain forest canopy: a method providing total access. Biotropica 13: 283–285.
- Renton, K. 2000. Scarlet Macaw. Pp. 253–257 in Reading, R. P., & B. Miller (eds). Endangered animals: a reference guide to conflicting issues. Greenwood Press, Westport, Connecticut, USA.
- Renton, K. 2002. Influence of environmental variability on the growth of Lilac-crowned Parrot nestlings. Ibis 144: 331–339.
- Renton, K. 2006. Diet of adult and nestling Scarlet Macaws in Southwest Belize, Central America. Biotropica 38: 280–283.
- Renton, K., & D. J. Brightsmith. 2009. Cavity use and reproductive success of nesting macaws in lowland forest of southeast Peru. J. Field Ornithol. 80: 1–8.
- Ricklefs, R. E. 1968. Patterns of growth in birds. Ibis 110: 419–451.
- Seixas, G. H. F., & G. Mourão. 2002. Nesting success and hatching survival of the Blue-fronted Amazon (*Amazona aestiva*) in the Pantanal of Mato Grosso do Sul, Brazil. J. Field Ornithol. 73: 399–409.
- Seixas, G. H. F., & G. M. Mourão. 2003. Growth of nestlings of the Blue-fronted Amazon (*Amazona aestiva*) raised in the wild or in captivity. Ornitol. Neotrop. 14: 295–305.
- Siikamaki, P. 1996. Nestling growth and mortality of pied flycatchers *Ficedula hypoleuca* in relation to weather and breeding effort. Ibis 138: 471– 478.
- Smith, G. T. 1991. Breeding ecology of the Western Long-billed Corella, *Cacatua pastinator pastinator*. Wildl. Res. 18: 91–110.
- Snyder, N. F. R., P. Mc Gowan, J. Gilardi, & A. Grajal. 2000. Parrots. Status survey and conservation action plan 2000–2004. IUCN, Gland,

Switzerland and Cambridge, UK.

- Snyder, N. R. R., J. W. Wiley, & C. B. Kepler. 1987. The parrots of the Luquillo: natural history and conservation of the Puerto Rican Parrot. Western Foundation of Vertebrate Zoology, Camarillo, California, USA.
- Stark, J. M., & R. E. Ricklefs (eds). 1998a. Avian growth and development. Oxford Univ. Press, New York, New York, USA.
- Stark, J. M., & R. E. Ricklefs. 1998b. Data set of avian growth parameters. Pp. 381–415 *in* Stark, J. M., & R. E. Ricklefs (eds). Avian growth and development. Oxford Univ. Press, New York, New York, USA.
- Stoleson, S. H., & S. R. Beissinger. 1997. Hatching asynchrony, brood reduction, and food limitation in a Neotropical parrot. Ecol. Monogr. 76: 131–154.
- Taylor, S., & M. R. Perrin. 2008. Application of Richards's growth model to Brown-headed Parrot *Poicephalus cryptoxanthus* nestlings. Ostrich 79: 79–82.
- Tinbergen, J. M., & M. C. Boerlijst. 1990. Nestling body mass and survival in individual Great Tits (*Parus major*). J. Anim. Ecol. 59: 1113–1127.
- Tosi, J. A. 1960. Zonas de vida natural en el Perú. Memoria explicativa sobre el mapa ecológico del Perú. Instituto Interamericano de las Ciencias Agricolas de la Organización de los Estados Americanos, Lima, Peru.
- Vaughan, C., N. Nemeth, J. Cary, & S. Temple. 2005. Response of a Scarlet Macaw *Ara macao* population to conservation practiced in Costa Rica. Bird Conserv. Int. 15: 119–130.
- Vaughan, C., N. Nemeth, & L. Marineros. 2003. Ecology and management of natural and artificial scarlet macaw (*Ara macao*) nest cavities in Costa Rica. Ornitol. Neotrop. 14: 381–396.
- Waltman, J. R., & S. R. Beissinger. 1992. Breeding behavior of the Green-rumped Parrotlet. Wilson Bull. 104: 65–84.
- Wunderle, J. M., N. R. R. Snyder, B. Muiznieks, J. W. Wiley, & J. M. Meyers. 2003. Histories of Puerto Rican Parrot nests in the Caribbean National Forest/Luquillo Experimental Forest, 1973–2000. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.