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GROWTH OF NESTLINGS OF THE BLUE-FRONTED AMAZON (*AMAZONA AESTIVA*) RAISED IN THE WILD OR IN CAPTIVITY

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Resumo. – Crescimento de filhotes de Papagaio-Verdadeiro (*Amazona aestiva*) criados em vida livre ou cativeiro. – De 1997 a 1999, analisamos o aumento do peso corporal e do comprimento da asa de ninhegos de uma população de Papagaio-Verdadeiro (*Amazona aestiva*), em vida livre no Pantanal Sul-Mato-Grossense e de um grupo criado no Centro de Reabilitação de Animais Silvestres (CRAS). Adicionalmente, examinamos os efeitos do fator "anos de coleta" (variável composta por vários fatores que não puderam ser individualizados), sexo, ordem de nascimento e infestação por ectoparasitas no crescimento dos papagaios. Utilizamos o modelo de Richard para estimar os parâmetros de crescimento (tamanho assintótico "A", tempo total de crescimento "T" e parâmetro que descreve a forma da curva "m"). Os dois grupos apresentaram pesos corporais assintóticos semelhantes, mas os filhotes de cativeiro necessitaram de um tempo maior para aproximar a assíntota. Os jovens de vida livre perderam peso próximo ao momento de deixar o ninho e o comprimento da asa continuou aumentando após deixarem o ninho. Nos ninhegos do cativeiro, as asas levaram 55% mais tempo para aproximar a assíntota do que o peso corporal. A análise dos resíduos dos pesos observados em relação a curva ajustada pelo modelo de Richards não revelou diferenças no crescimento corporal, entre sexos e entre local de criação, mas ANOVA revelou que os papagaios criados no CRAS, imediatamente antes de serem soltos na natureza, foram mais pesados que os animais criados em vida livre, imediatamente antes de deixarem os ninhos. O crescimento em peso variou entre anos nas aves de cativeiro, mas não nas de vida livre. A infestação por bernes e a ordem de nascimento afetaram negativamente o crescimento dos ninhegos de vida livre.

Abstract. – From 1997 to 1999, we analyzed growth in body mass and wing length of nestlings from a population of Blue-fronted Amazons (*Amazona aestiva*) living freely in the Pantanal of South Mato Grosso and nestlings raised in Centre for Rehabilitation of Wild Animals (CRAS). We studied whether sex, age, birth order and ectoparasite infestation affected their growth. To describe their growth, we used Richards' model to estimate the asymptotic size "A", total growth period "T" and a parameter, "m", which describes the form of the curve. The two groups presented similar asymptotic body masses. However, the nestlings raised in captivity took more time to attain their asymptotic mass and took 55% more time to attain their asymptotic wing length. Analysis of deviations from the mass predicted by the Richards' model did not reveal any differences between sexes or the manner in which they were raising. However, ANOVA revealed that immediately before being released the parrots at CRAS weighed more than those in their natural habitat before fledging into the wild. The rate of increase in mass varied among years for birds in captivity but not for birds in the wild. Infestation by ectoparasites, and nestling order negatively affected the growth of nestlings in the wild. *Accepted 15 October 2002.*

Key words: Blue-fronted Amazon, *Amazona aestiva*, growth curves, Richards' model, Pantanal.

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INTRODUCTION

Growth characteristics vary among bird species as a result of many selective pressures (Navarro & Bucher 1990). Intra-specific variations in growth parameters (i.e., between sexes or in relation to birth order) seem to have adaptive value (Ricklefs 1968, 1976) and are indicators of the organism's health and general body condition (Fendley & Brisbin 1977).

In general, parrots have relatively small eggs, long incubation periods and asynchronous clutches (Bucher 1983). Hatchlings are altricial and featherless, have their eyes closed, and are not able to hold their heads up. They grow slowly and fledge only after an extended period of time in the nest (Bucher 1983, Forshaw & Coopers 1989, Navarro & Bucher 1990). All this suggests that natural selection has not favored rapid growth and maturity in this group, but researchers have not found a convenient explanation for this unusual combination of characters (Bucher 1983). Very few data on parrot growth exist and most are from captive birds (Caccamise & Alexandro 1976, Caccamise 1980, Saunders 1982, 1986; Bucher 1983, Stamp *et al.* 1985). Although the Blue-fronted Amazon (*Amazona aestiva*) has a relatively wide distribution (northwest Brazil, eastern Bolivia, northern Argentina and southern Paraguay), little systematic information on the species' reproductive and growth characteristics are known to exist (Forshaw & Coopers 1989). All available information comprises nesting habitats and nest characteristics in the Province of Salta in Argentina (Sauad *et al.* 1991a, 1991b; Nunez *et al.* 1991). We did not find any study focused on Blue-fronted Amazon growth, in captivity or in the wild.

In the Brazilian state of Mato Grosso do Sul more than 3000 Blue-fronted Amazon nestlings illegally captured over the past 13 years have been seized and sent to the Wildlife Rehabilitation Centre/Secretariat of Environmental Affairs (SEMACT MS). This entity implemented a conservation and management programs for this parrot, focusing their efforts in the Pantanal region (Seixas & Mourão 2000). However, prior to the present study, the data on nesting ecology and growth of the species were sorely lacking.

This study aimed 1) to analyze growth parameters of Blue-fronted Amazon nestlings in the Pantanal of Mato Grosso do Sul and of captive nestlings raised at a Rehabilitation Center, 2) to evaluate Richard's model for growth, body weight and wing span analysis, and 3) to examine how the factors "year of collection", sex, birth order and an ectoparasite infestation (bot fly larvae) affect parrots' growth.

METHODS

Study area. We monitored Blue-fronted Amazon nestlings' growth during the reproductive seasons (August–December) of 1997 through 1999, in the farm Refúgio Ecológico Caiman (19º51'–19º58'S and 56º17'–56º24'W) in the Brazilian Pantanal wetlands. The Pantanal may be divided into sub regions with different hydrologic and biophysical characteristics. The study area is within the Miranda sub region, which is characterized by the presence of river depressions with sedimentary deposits (sandy and clay soils) belonging to the Paraguay River basin (Adámoli 1986). The farm covers a total area of 520 km^2 and consists of a mosaic of floodplains, grasslands, savannas, scrub savannas, arboreal savannas, forests of riparian vegetation, and man-made pastures (Pott 1997, Silva *et al.* 1998). The floodplains are covered by grasses and herbs, located in the seasonally flooded areas of the rivers, and the patches of forest are small geomorphological faces, slightly elevated (1–2 m), and free from inundation (Pott 1997, Silva *et al.* 1998).

Annual rainfall averages 1207 mm (Soriano 1997) and the dry (May–October) and wet seasons are well defined (November–April), with higher rainfall concentration between December and February.

In addition to free living nestlings, we also monitored the growth of parrot nestlings raised at the Wild Animal Rehabilitation Center (CRAS) of the State Secretariat for Environment of Mato Grosso do Sul, located in the state capitol Campo Grande, Brazil (20º27'S–54º33'W), during the reproductive seasons of 1997 through 1999. These birds, illegally captured, had been seized by police, and then brought to CRAS where they stayed until their reintroduction to the Pantanal areas of Mato Grosso do Sul.

Data collection on free-living animals. We monitored the growth of 86 nestlings from 44 nests located in the study area, i.e., 38 nestlings from 17 nests in 1997, 30 from 18 nests in 1998, and 18 from 9 nests in 1999. We weighed the birds (± 0.1 g) with a digital balance, and measured (± 0.5 mm) the length of folded left wing with a caliper.

The interval between visits to the nests varied between reproductive seasons and averaged 13 days (range of 7–17 days) in 1997 and 1999. In 1998, nest monitoring occurred, on average, every 8 days (range 3–16 days). We registered the number of ectoparasites, bot fly larvae (*Philornis* sp. larvae, Diptera: Muscidae), over the nestlings' bodies while they were in the nests. We estimated the age of 10 nestlings upon finding them in their nests (maximum 3-day error). For the 26 nestlings for which birth age determination was not possible, we estimated birth order based on physical characteristics (e.g., weight, feathering stage, etc.).

Data collection and management in captivity. We monitored the growth of 38 captive nestlings in 1997 and 86 in 1999. We measured the birds every eight days on average (range 3 to 22 days), beginning in September each year, until January in 1998 and February of 2000. At the CRAS, the nestlings were maintained in small-insulated cages for the first 4 weeks, being fed 3 times a day. Their initial diet was smashed fruits, vegetables, corn flour and puppy food. Thereafter, in order to train the birds to feed by themselves, nestlings were gradually provided with chopped fruit and vegetables, seeds and grains. When fully feathered, the birds were transferred to a bigger cage (2.5 x 2.5 x 2.5 m) exposed to weather conditions, and, in the last month, transferred to a wide cage (5 x 5 x 20 m) to give them the possibility to fly. During this last period, they were treated against parasites (Ivermectin). There was no ectoparasite infestation on captive birds.

Blood collection. In the last stage of feathering, we collected 0.1 ml of blood from 37 captive individuals (35 in 1997 and 2 in 1999) and of 21 free living birds in 1998 to determine their sex. Blood samples were collected through a nail cut, placed in a plastic tube with 0.5 ml absolute ethanol, and sent to the São Paulo University Biology Institute. The samples were analyzed through the polymerase chain reaction technique (Griffiths *et al.* 1998).

Statistical analysis. Theoretical growth models are especially useful to analyze growth data when the age of young is not accurately known. In many studies on nestlings' theoretical growth, e.g., Von Bertalanffy, Gompertz, or logistic models have been used to describe growth with three parameters (Ricklefs 1968, Pruitt *et al.* 1979, Ricker 1979). However, a common characteristic of these models, and also of monomolecular models, is the fixed shape of the curve, determined by the inflexion point (Ricklefs 1967, Zach *et al.* 1984) or by the parameter that defines the shape of the curve (m) (Brisbin *et al.* 1986). Thus, the monomolecular, von Bertalanffy, Gompertz or logistic models present inflexion points close to 0, 0.30, 0.37, and 0.50, and “m” values of 0.067, or close to 1 and 2, respectively (Brisbin *et al.* 1986). For these reasons they are considered to belong to the Richards’ model family which, by incorporating one more parameters (m), presents more flexibility (Zach *et al.* 1984, Brisbin *et al.* 1986). The advantages of using Richards’ model are discussed by many authors (White & Ratti 1977, Causton *et al.* 1978, Sugden *et al.* 1981), and questioned by many others who consider the adjusting techniques too complex, the values obtained for the parameters not directly comparable, and argue that simpler models of three parameters are adequate in most cases (Ricklefs 1967, 1973, Pruitt *et al.* 1979, Zach & Mayoh 1982). However, Zach *et al.* (1984) say that these assumptions were not properly tested and conclude that, in their experiment, the Richards’ method was adequate to describe body mass growth, but not useful to describe the growth of the primary feathers length.

Therefore, we used the Richards’ non linear asymptotic growth model, adapted by Brisbin (1988): $St = [A^{(1-m)}-(A^{(1-m)}-S_{t-1}{}^{(1-m)})e^{(-2dt/T(1+m))}]^{1/(1-m)}$, where “St” is mass or length measured at time “t”, “A” is asymptotic body mass or asymptotic length, “m” is the parameter that designs the curve, “St-1” is body mass or length measured at time “t-1”, “e” is the natural log base, “dt” is the interval between “t” and “t-1”, and “T” is the total growth time. That is, “T” is the period spent by the animal to reach asymptotic mass or asymptotic length.

This reparametering is desirable since it allows the estimation of total growth time (T) (Brisbin *et al.* 1986). This model is more flexible, and can usefully accommodate this situation when the estimated relationships between growth rate and body mass and wingspan suggest different functional forms (i.e., different “m”), indicating the need for more than one model of the relationships among the three parameters.

To avoid pseudo replication and ensure independence among observations in the dataset, we used only one growth measurement (the difference between one assessment and the subsequent assessment of the same bird is one growth measurement) for each bird. When data were available over several growth measurements or intervals for a particular bird, a random selection process was used to determine which of the intervals would be included in the analysis. Wild birds were seldom measured weighing less than 150 g and captive birds, seldom less than 250 g. As a result, we chose to include the “light” interval for a bird whenever the data were available in order to have a distribution of growth rates over the range of possible bird weights. A parallel process was imposed to manage the wing length dataset. Data from 6 wild and 18 captive birds that died in the nest were excluded from analysis.

We used the NONLIN module (modified Gauss-Newton method) of Systat 7.0 statistical software (Wilkinson 1997) to estimate A, m and T parameters of body growth in weight and wingspan, using the intervals of growth in body weight, or wingspan measured at the beginning and end of each time interval. We adjusted the size-age curve using the parameters estimated by the Richards’ model. In order to plot the body mass-age curve, and the wingspan-age curve we used the values 11 g and 10 mm for body mass and wingspan, respectively, as measurements registered for nestlings just after hatching.

We used analysis of variance (ANOVA), 1) to analyze deviations of observed measurements from the values estimated by the Richards’ model, and 2) to test the differences in the nestlings’ rate of weight gain between groups of birds, sexes and years. We used simple linear regression to investigate possible

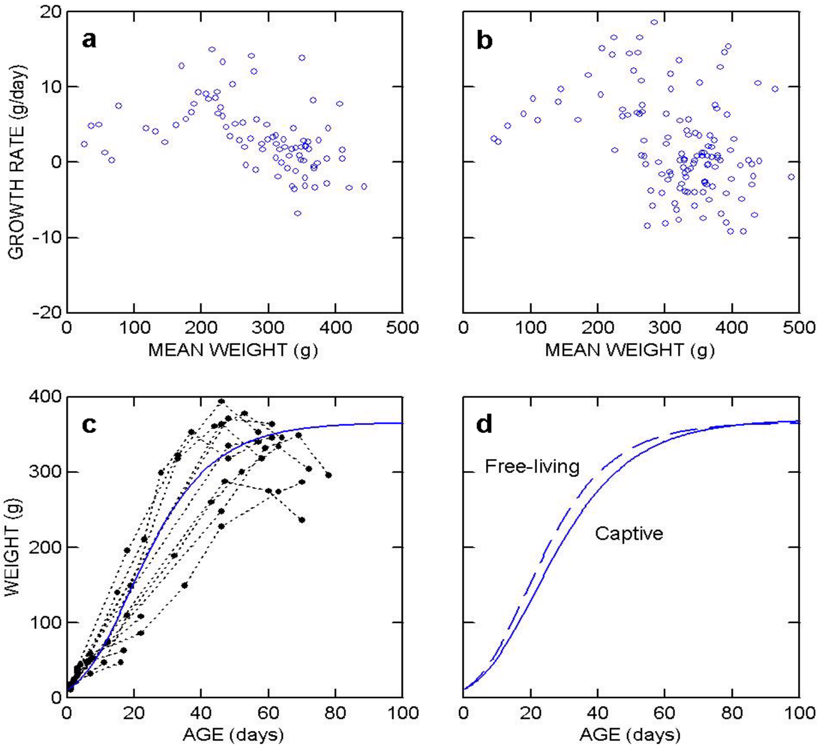

FIG. 1: Relationship between the growth rates and mean weight of wild (a) and captive-growing parrots (b). Adjusted size-age curve (continuous line) and individual growth of known aged (dotted lines) wild parrots (c), and (d) adjusted size-age curve for captive (continuous line) and wild parrots (broken line).

effects of bot fly larvae infestation and birth order over clutches with more than one hatchling for wild birds. "Year of collection" was considered a fixed variable to represent many other factors that could not be individualized (rainfall, temperature, etc.).

RESULTS

The observed change in body mass showed a convex relationship with average weight, both in wild parrots and those raised at CRAS. Maximum body mass increases of 10 to 20 g/day were reached when nestlings weighed around 200 to 300 g, and fell to zero or even were negative around 400 g (Figs 1A and 1B). The general shape of the curves suggested that a non-linear asymptotic model would be appropriate to describe growth under both raising conditions.

For wild nestlings, asymptotic weight was estimated as equal to 366 g and total growth time (T) as 56 days. The parameter that describes the "m" curve shape was 1.047. For captive nestlings the asymptotic weight was 370 g, "T" was 64 days, and "m" was 1.056. We estimated wingspan as 263 and 209 mm, total growth time (T) as 108 and 99 days, and the "m" curve parameter as 1.189 and 2.971 for wild and captive birds, respectively.

The graphical relationship between the known age of wild nestlings and their estimated rate of weight gain demonstrates a great deal of data variability. At about 50 days

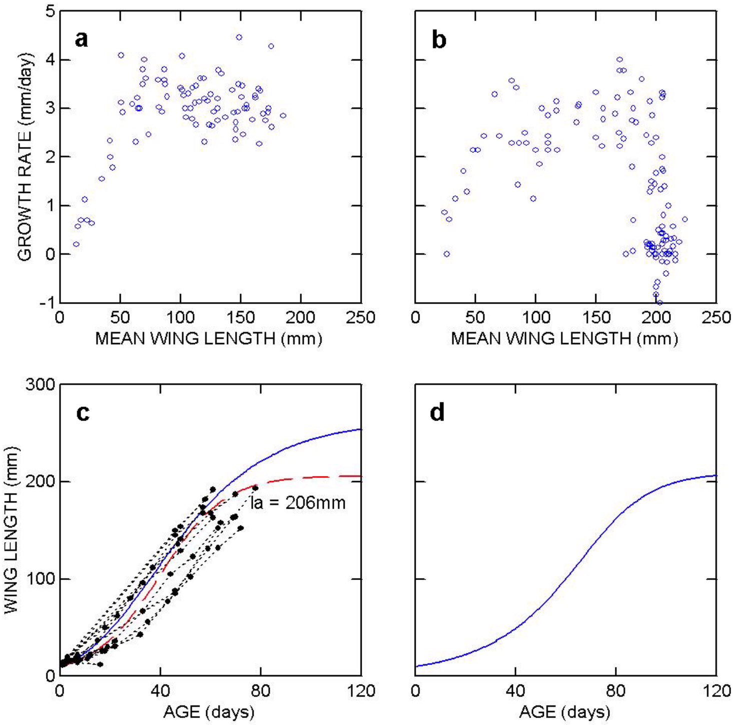

FIG. 2: Relationship between wing growth rates and mean wing length for wild (a) and captive parrots (b). Plot (c) shows the adjusted wing size-age curves of wild parrots estimated by fixing the asymptotic wing length at 206 mm (broken line), and by having the iteration algorithm estimating the asymptotic wing length (continuous line), overlaid with individual growth of known-aged parrots (dotted lines), and (d) adjusted wing size-age curve for the nestlings raised in captivity (continuous line).

TABLE 1: Mean and standard deviation (SD) of masses (g) of male and female fledglings of Blue-fronted Amazon raised in captivity or in the wild.

Groups	Sex	Mean	SD	n
Captive	Male	400.53	42.33	34
	Female	361.57	39.71	28
Wild	Male	364.22	38.81	9
	Female	343.08	56.57	12

of age, nestlings actually began to lose weight, according to our measurements (Fig. 1C).

Theoretical predictions of body weight gain for the two groups differed very little and, at 70–80 days, were practically the same (Fig. 1D). Although the curves adjusted by the Richards' model did not detect differences in asymptotic weight among captive and wild birds of both sexes, a two-way ANOVA indicates that nestlings raised at CRAS were heavier immediately before release (i.e., ages of 90–100 days) than wild fledglings (i.e., age of 60–70 days) (F_{1-80} = 5.875, P = 0.018, r^2 = 0.207). Males were heavier than females in both groups of birds (F_{1-80} = 12.987, P = 0.001, r^2 = 0.207) (Table 1).

Wing length increased at a low rate (4 mm/day) until reaching approximately 100 mm in length in both wild and captive nestlings (Figs 2A and 2B). There are no data for wild birds with wing length over 180 mm, since this is the size at which they left the nest. However, captive birds showed a clear decrease in wing length growth rates after reaching 180 mm, diminishing to zero at around 200 mm (Figs 2A and 2B). The wing-span-age curve for wild nestlings goes far beyond those figures reached by birds of known age until they left the nests (Fig. 2C) and follows a distinct pattern from the relationship estimated for captive nestlings (Fig. 2D). As a result, asymptotically similar sized birds across the two populations are biologically improbable. For this reason, we fixed wing asymptotic size at the estimated value for the captive group (206 mm) and re-analyzed the data. With the fixed asymptote, the "T" was estimated at 78 days and "m" = 2.088 for wing growth of wild birds.

An analysis comparing the deviation of the observed weights to the predicted weights taken from the curve adjusted with the Richards' model revealed no difference in body weight gain between males and females neither for wild ($F_{1-19} = 0.18$, $P = 0.68$) nor for captive nestlings ($F_{1-35} = 2.63$, $P = 0.11$). Year of collection affected weight gain in captive birds, but explained only a small proportion of the residual variation ($F_{1-103} = 4.16$, $P = 0.04$, $r^2 = 0.04$) and did not affect weight gain in wild birds ($F_{2-77} = 0.55$, $P = 0.58$). Bot fly larvae infestation negatively affected the growth of wild nestlings (residual = 31.06–14.01 number of bot fly larvae, $F_{1-13} = 6.61$, $P = 0.02$, $r^2 = 0.34$).

The effect of birth order on the relative weight of nestlings was similarly analyzed. The deviations of the observed weights from the estimated curve adjusted with the Richards' model were analyzed for 26 hatchlings, in 17 nests, with 7 "first" nestlings, 9 "second" nestlings, and 10 "third" nestlings. In eight (18%) clutches of two and three eggs it was possible to identify only the "third" nestling by its earlier feathering stage. The residual analysis indicated that there was variation in weight growth rates among wild birds, but it explained little of the variation in these growth rates (residual = 23.69–17.15 birth order, $F_{1-24} = 6.29$, $P = 0.02$, $r^2 = 0.21$). Unfortunately, there were not enough parrots with both bot fly larvae and birth order information to allow the statistical examination of the potentially interactive effect of these two factors on nestling weight gain.

DISCUSSION

The estimated asymptotic weight for wild Blue-fronted Amazons was close to that (~310 g) found for the Yellow-shouldered Amazon (*Amazona barbadensis*) (Rojas-Suárez 1994). Wild nestlings reached asymptotic body weight before leaving the nests. However, these birds lost, on average, 4% of their asymptotic weight before flying. Weight loss before leaving the nest was also observed in Monk Parakeets (*Myiopsitta monachus*) by Navarro & Bucher (1990) and seems to be common in many bird species. These losses can be associated with flying exercise, decreased food provided by parents at the final stages of growth (Bucher 1983), or energy consumption for thermoregulation (Ragusa-Netto 1998). Ydenberg (1989) suggested that some nestlings can "choose" to fly with lower body weight when the food provided by the parents decreases, and Piatt (1990) also associated the decrease of parental care with the end of the reproductive season. However, Blue-fronted Amazon nestlings of both sexes, raised in captivity, kept gaining weight and were, at 90–100 days of age, on average 3.5% heavier than their estimated asymptotic weight, and heavier than wild birds before leaving the nests ($P = 0.015$). This is possibly due to the fact that, in captivity, there was no food limitation at the final stages of growth and that cage conditions, with shade and ventilation, resulted in lower energetic consumption for thermoregulation than would otherwise be observed in the wild.

Nestlings raised in captivity showed slower growth than free living ones, needing approximately 8 additional days to reach asymptotic weight. This also has been observed in other birds such as gulls (Harris 1964) and corvids (Whitmore & Marzluff 1998). According to Bucher (1983), lower growth in captive birds may be associated to the frequency of food provision and food quality, and the long-term effects of this retarded growth are not yet clear. There is little information on Blue-fronted Amazon's natural feeding habits and nestlings' nutritional requirements are largely unknown.

Parrots' wings kept growing even after they left the nests. For the nestlings raised in captivity that were monitored for a longer period, we observed that the time spent to reach the wingspan asymptote was about 55% longer than the time required for body weight growth. Therefore, the data for wing growth of wild birds was not adequate to describe growth and the Richards' model estimated an asymptotic size that was biologically improbable. Leaving the nest before reaching full wing length seems to be a common fact among birds, and has been observed in swallows (Zach & Mayoh 1982) and in marine birds (Rodway 1997). Apparently, even nestlings of late-developing birds, like the Blue-fronted Amazon, cannot wait until the remiges are completely formed before for leaving the nest, as this means additional energy costs for the parents.

There were no difference in wild parrots' growth across the three years of observation, but slight differences were observed for captive animals. This can be explained by small changes in the diet composition served in captivity, or by temperature variations in insulated cages as observed in other studies (e.g., Johnson 1971).

Bot fly larvae infestation had linear and negative influence on body weight growth in wild parrots. During this study, two nestlings that had more than 25 bot fly larvae died before new data were collected and were excluded from the analysis. Guedes (1993) registered a high bot fly larvae infestation on a Hyacinth Macaw (*Anodorhynchus hyacinthinus*) nestling (~31 larvae), leading to slower growth, although the bird survived and flew. Marini *et al.* (1996) found that ticks and mallophaga are frequently found in cavity nests and that their occurrence is due to the non sterile conditions of their nests. We did not find ectoparasites on captive parrots, probably because of the hygienic conditions of their cages, which were cleaned daily, and where new substrate was provided.

Although the analysis of observed measurements deviations from the measurements predicted by the Richards' model did not detect the effect of sex on weight gain in parrots, feathered males weighed more than females ($P = 0.001$) at 60 and 100 days (for wild and captive birds, respectively). However, sex explained little of the weight variation.

In this study, birth order had an inverse linear effect on body weight growth of nestlings, although it explained only about 21% of residual variation. This is contrary to published findings with parakeets in Australia (Stamp *et al.* 1985) and in a 2-nestlings brood of Black-capped Donacobius (*Donacobius atricapillus*) (Ragusa-Netto 1996), but is consistent with observations in 3-nestlings broods of the Black-capped Donacobius, due to greater potential for asynchrony among nestlings. Many hypotheses suggest that birth order following nestling asynchrony, as observed in parrots, is an adaptive process that benefits parents (Stoleson & Beissinger 1997). Lack (1940) suggested that, when there is uncertainty about the future availability of food resources, parents produce more eggs that are immediately incubated, resulting in nestling asynchrony and, if food resources are limited, parents adjust clutches to the number of nestlings they can feed, eliminating the smaller. Thus, lower growth rates in younger birds may be a result of the competition for the food provided by the parents in periods of food scarcity (O'Connor 1978, Stamp *et al.* 1985). In this study, although the third nestlings had lower growth rates, there was no difference in the death rate of nestlings in the fledgling phase that could be attributed to birth orders. Apparently, nestlings' mortality during the fledgling phase was not directly related to birth order, but resulted from a combination of unidentified negative factors.

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