ORNITOLOGÍA NEOTROPICAL
SPECIAL ISSUE (2018) 29: S11–S18

ORIGINAL ARTICLE

TROPICAL FRUGIVOROUS BIRDS MOLT AND BREED IN RELATION TO THE AVAILABILITY OF FOOD RESOURCES

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ABSTRACT · Few studies have investigated how the abundance of food resources influences the phenology of the annual cycles of tropical birds. Frugivorous birds are good models for such investigation because the abundance of their main food types, fruits and arthropods, vary independently from each other. We investigated how the consumption and availability of fruits and arthropods are related to breeding and molt cycles of frugivorous birds in a fragmented landscape of the Brazilian Atlantic forest. We recorded the occurrence of brood patches and the molting of flight feathers in mist-netted birds, from which we also analyzed the contents of fecal samples. Using nonparametric and parametric correlation tests we investigated the relationships among breeding and molt stage with the availability of fruits and arthropods. We found that the availability of fruits and arthropods fluctuates temporally and independently, but both food sources have shortage periods, apparently more pronounced for fruits. During periods when fruit was scarce, birds relied more heavily on arthropods as food. Incubation occurred when fruit availability was high, whereas the molt period that followed was coincident with the availability of arthropods. Although our observational study does not permit definite conclusions regarding the relationship between food availability and the timing of the annual cycle events investigated, it is suggestive that avian breeding and molt cycles coincide with fruit and arthropod availability, respectively. Together with arthropods, fruits are important for nestlings of frugivorous birds, and protein from arthropods may be especially important for the development of new feathers.

RESUMO · Relação entre disponibilidade de alimento, muda de penas e reprodução de aves frugívoras
Poucos estudos abordaram a influência da abundância de recursos alimentares sobre a fenologia do ciclo anual de aves tropicais. Aves frugívoras são bons modelos para esse propósito porque as abundâncias dos seus principais alimentos, frutas e artrópodes, podem variar no tempo de maneira independente. Neste trabalho investigamos como os ciclos de muda de penas de voo e reprodução estão relacionados com a disponibilidade e o consumo de frutos e artrópodes em uma paisagem fragmentada de Mata Atlântica. Para isso registramos a ocorrência de placa de choco e mudas nas penas de voo de aves capturadas em redes de neblina e sua relação temporal com a disponibilidade de frutos e artrópodes amostrados nas áreas das redes. A disponibilidade de frutos e artrópodes apresentaram flutuações temporais independentes, porém ambos apresentaram períodos de escassez, aparentemente mais pronunciado para os frutos. Durante períodos de escassez de frutos, as aves consumiram mais artrópodes. O período de incubação ocorreu quando a disponibilidade de frutos era maior, enquanto a muda de penas coincidiu com o período de maior disponibilidade de artrópodes. Embora nosso estudo observacional não permita conclusões definitivas sobre a relação entre a disponibilidade de alimentos e os eventos de ciclo anual investigados, é sugestivo que os períodos de reprodução e muda tenham coincidido com maior disponibilidade de frutos e artrópodes, respectivamente. Juntamente com artrópodes, frutos podem ser importantes para a criação dos filhotes das aves frugívoras, enquanto proteína proveniente dos artrópodes pode ser especialmente importante para o desenvolvimento de novas penas.

KEY WORDS: Arthropod availability · Atlantic Forest · Brazil · Breeding cycle · Diet · Fecal samples · Flight feather molt · Fruit availability · Frugivorous birds · Thraupidae · Turdidae · Tyrannidae · Vireonidae

Receipt 29 July 2016 · First decision 30 September 2016 · Acceptance 18 July 2017 · Online publication 16 May 2018

Communicated by Rafael Rueda-Hernández, Angelina Ruiz-Sánchez, Santiago Guallar, Peter Pyle
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INTRODUCTION

The relationship between climatic factors (mainly rainfall and temperature) and the breeding and molt cycles of Neotropical birds has been the subject of many studies (Davis 1945, Diamond 1974, Foster 1975, Karr 1976, Cruz & Andrews 1989, Marini & Durães 2001, Wolfe et al. 2009, Durães, Johnson et al. 2012, Silveira & Marini 2012, Stouffer et al. 2013). Despite great geographic and temporal variation in the timing of breeding and molting among different taxonomic and functional groups of birds, most authors have concluded that breeding occurs in the most favorable season of the year in relation to climatic factors (hence food availability), being followed or preceded by molt (Skutch 1950, Diamond 1974, Karr 1976, Stiles 1980). The timing and the light overlap that normally exists between breeding and molting is interpreted as an evolutionary response to the high energetic demand required for both activities (Foster 1975). However, few studies actually have estimated the variations in the abundance of food resources (mainly fruits and arthropods) available for birds in the tropics and the phenology of their annual cycles despite the importance of investigating the simultaneous occurrence of such biological activities (Davis 1945, Karr 1976, Levey 1988, Blake et al. 1990).

Frugivorous birds are good models to investigate the relationship between breeding and molt cycles and food availability because, along with fruits, they often rely upon arthropods as a source of proteins (Moermond & Denslow 1983). With such a mixed diet, does breeding coincide with the peak availability of fruits and/or arthropods? And how does the molt period relate to the availability of fruits and arthropods? Previous studies have reached contrasting conclusions. Whereas some authors hypothesized that arthropods could be more important than fruit availability for breeding of frugivorous birds (Levey 1988, Loiselle & Blake 1991), others have argued the contrary (Snow & Snow 1964), while others have presented evidence showing that the peak availability of arthropods coincides with molt (Levey 1988, Poulin et al. 1992). In this study, we mist-netted birds in a fragmented landscape in Brazil recording the occurrence of brood patches, flight feather molt, and the presence of fruits and arthropods in feces. Concomitantly we evaluated the availability of fruits and arthropods to answer the following questions: (1) What is the composition of the diet of frugivorous birds, and how it is related to temporal variation and availability of fruits and arthropods?, and (2) How do temporal variations in the abundance of food resources affect the reproductive and molt cycles of frugivorous birds in a fragmented landscape?

METHODS

Study area. The study was conducted in an area of approximately 80 ha that included small rural properties located in Itatiba (22°57’S, 46°44’W; 800 m a.s.l.), São Paulo, southeastern Brazil (Figure 1). The region is part of the semi-deciduous Atlantic Forest (*sensu* Morellato & Haddad 2000). There is a dry, cold season extending from April to September, and a humid season from September to March (Figure 2A).

For decades, the landscape has been altered to make way for pastures and agriculture. Embedded by this matrix, four different types of anthropogenic habitats occur: (1) small, secondary forest fragments (1–20 ha) in different successional stages consisting mainly of pioneer plant species, (2) forest stands (i.e., small groups of trees < 0.05 ha) isolated in pastures; (3) hedgerows (140–450 m long, 6–12 m wide) or linear patches of regenerating native vegetation; (4) isolated trees in pastures. Previous observations on fruiting plants at the study area revealed 41 bird species feeding on fruit, including several of the 20 species (Table 1) that we sampled for the present study (Pizo 2004).

Sampling of birds. We sampled birds with mist-nets (36 mm mesh, 12 m length, 2.8 m height) set at nine stations distributed in three hedgerows and 15 stations located in five forest fragments. Each netting station was sampled once a month from October 2003 to December 2004, but samples from this last month were discarded from the analysis due to bad weather conditions. Nets were opened at sunrise, checked every hour and closed six hours later, except on days with rain and strong winds. The capture effort, calculated as the product of the number of nets used, the number of sampling hours, and the effective area of capture of mist nets (Straube & Bianconi 2002), was 54,750 m^2/h.

We considered as frugivorous all birds that, according to the literature (Wilman et al. 2014) and our field experience, consume fruits even in small proportions. We did not consider the family Columbidae due to the difficulty in identifying seeds found in fecal samples. Each bird captured was marked with a numbered metal band and released at the point of capture. Captured birds were kept in a cotton bag for 20 minutes or until they defecated. Feces were preserved in 70% alcohol for subsequent analysis in the laboratory under a stereomicroscope (10x magnification).

Fecal samples were classified using broad categories: “fruits only,” “fruits and arthropods,” and “arthropods only.” For graphical presentation and analysis, categories were combined and presented as proportion of fruits (all samples containing fruits) and proportion of arthropods (all samples containing arthropods). Arthropods were recognized by the remains of exoskeletons and articulated appendices, respectively. The presence of fruits was confirmed by the presence of residuals from fruit skin or pulp, sometimes accompanied by seeds.

Figure 1. Aerial photograph of the study area in Itatiba, São Paulo, southeastern Brazil showing the fragments and hedges (linear elements in the landscape) sampled.

Reproduction and molt. To determine the stage of breeding of our sampled birds, we recorded signs of incubation by observing and recording the presence of a brood patch or the vascularization, skin wrinkling, and pinkish-opaque staining on the abdominal region of captured birds. The presence of feathers on the abdomen, smooth dark red skin, and no vascularization were recorded as absence of incubation activity.

Molt was recorded by noting the presence of new remiges, rectrices, or contour (body) feathers. Molt was considered only when new feathers occurred symmetrically, to avoid recording adventitious molt, i.e., the replacement of missing feathers that occurred out of the molting period, generally following accidental shedding or forced removal (e.g., physical trauma or predation attempt), or indirect effects of feather loss, such as ectoparasitism (e.g., heavy mite or chewing louse infestations) (Marini & Durães 2001). To calculate the percentage of individuals in molt we considered only the molt of flight feathers, because for the birds we sampled it is a better indicator of the period of prebasic molt than molt of contour feathers, as some individuals can molt contour feathers throughout the year (Marini & Durães 2001). Immature birds were excluded from the molt analysis, because we analyzed only adult birds undergoing prebasic molt (Humphrey & Parkes 1959). Birds recaptured in different months were taken as independent records, but only the first record during the same month was considered (Marini & Durães 2001).

To reduce error estimates of the proportion of individuals incubating for species with different reproductive strategies, we adopted the following methods: (1) all adult individuals captured were included in the analysis for species in which both sexes incubate the eggs (e.g., Vireonidae); (2) for species that exhibit sexual dimorphism, only females

Table 1. Bird species sampled from October 2003 to December 2004 at rural properties located in Itatiba, São Paulo, Brazil (arranged in alphabetical order). Captures are the number of birds captured; Molt includes any individual molting flight feathers; Breeding denotes individuals with a brood patch; Fecal samples are the number of fecal samples analyzed.

Species	Captures	Molt	Breeding	Fecal samples
Cyclarhis gujanensis	4	0	2	1
Dacnis cayana	4	2	0	3
Elaenia flavogaster	1	0	0	1
Elaenia mesoleuca	1	0	0	1
Haplospiza unicolor	6	0	0	3
Myiarchus ferox	6	1	3	4
Myiarchus swainsoni	4	1	2	2
Myiodynastes maculatus	5	2	0	3
Myiozetetes similis	2	0	1	2
Pachyramphus validus	1	0	0	1
Pitangus sulphuratus	1	1	0	1
Saltator similis	4	0	0	1
Tachyphonus coronatus	20	1	1	12
Thlypopsis sordida	3	0	2	2
Thraupis sayaca	12	4	2	11
Trichothraupis melanops	1	1	1	0
Turdus amaurochalinus	10	1	0	6
Turdus leucomelas	41	12	12	31
Turdus rufiventris	39	12	11	32
Vireo olivaceus	1	0	0	0
Total	166	38	37	117

were considered (e.g., Thraupidae); (3) for monomorphic species, in which only females incubate (e.g., Turdidae), we considered all individuals caught since it is difficult to identify the sex of individuals incubating. Due to considerable variation in capture rates, the occurrence of reproductive activity and molt was expressed as the percentage of individuals incubating or molting each month (Poulin et al*.* 1992).

Availability of food resources. The availability of fruits was assessed monthly from October 2003 to December 2004 by monitoring the fruiting phenology of 85 bird-dispersed plants (17 plant species, 14 families) marked inside plots (2 x 4 m) that were established on each side (2 m away) of the 24 mist-nets, thus totaling an area of 16 m^2 per netting station. We sampled 18 plots (144 m^2) in hedgerows, and 30 plots in fragments (240 m^2), totaling 48 plots (384 m^2). Fruit production was estimated by counting the number of ripe fruits produced in as many as five randomly selected branches in different positions of the canopy of each marked plant. Fruit production per plant was then obtained by multiplying the average number of fruits on branches by the total number of branches on plants (Jordano & Schupp 2000). Fruits were considered ripe according to the previous experience of the authors, and changes in color, size, and hardness of the fruit coat.

The availability of arthropods was assessed monthly from September 2003 to August 2004 at the same plots used to monitor fruit availability. We used a non-destructive sampling method in which all arthropods found on the abaxial and adaxial surfaces of leaves and stems up to 2 m tall inside the plots were counted and identified to the level of taxonomic order: Araneae, Blattaria (suborder), Coleoptera, Diptera, Hemiptera, Homoptera, Hymenoptera, Orthoptera, Neuroptera, and Lepidoptera (categorized as larvae or adults). Other infrequent orders were classified as "other." Sampling took place at night following the protocol of Karr & Brawn (1990), and Develey & Peres (2000). Arthropod biomass was estimated based on body length and width (Johnson 2000). Measures of length and width of the arthropods were taken with the aid of a graduated rule to the nearest millimeter and a flash-light. Arthropods were measured from the forehead to the tip of the abdomen, and their widths were measured at the mesothorax. Biomass, used here as surrogate of arthropod availability, was derived from length and width of each arthropod by applying linear regressions developed for various arthropod taxa (except Orthoptera and Araneae) according to Sample et al. (1993). For the suborder Blattaria and "other" orders the equation for estimating the biomass of Insecta was used (Sample et al. 1993). For Araneae and Orthoptera we used the equation of Rogers et al. (1977). We assumed that the pattern of arthropod availability we found up to 2 m holds also higher in the vegetation, which is a reasonably assumption given the poorly-structured state of the vegetation in the hedgerows and forest fragments sampled.

Data analyses. The availability of ripe fruits was expressed in number of ripe fruits/m^2, which was obtained by summing all the ripe fruits of the plots and dividing the total by the pooled area of all plots sampled. The availability of arthropods was calculated in the same way and expressed in grams of arthropods/m^2.

Depending on data distribution, monthly relationships among rainfall, minimum and maximum temperatures (obtained at the House of Agriculture of Itatiba, São Paulo), fruit and arthropod availabilities, the proportions of fruits and arthropods in feces, and the proportions of incubating or molting individuals were investigated with one of two statistical tests: for arthropod availability correlations in a monthly basis, we used the parametric Pearson's correlation test that renders a product-moment correlation coefficient, or "Pearson's r." For fruit availability correlations, we used the nonparametric Spearman rank correlation test that produces the Spearman's rank correlation coefficient, or "Spearman's rho" ("r_s"). Angular transformations were applied to the proportions of individuals incubating or molting. For all analysis we used Statistica 6.0 (StatSoft 1999).

RESULTS

The availability of ripe fruits was positively correlated with rainfall (r_s = 0.66, P < 0.01, N = 15), both of which peaked in November–December and reached their lowest levels during the dry season (Figure 2B). *Lithraea molleoides* (Anacardiaceae), *Casearia sylvestris* (Salicaceae), and *Erythroxylum deciduum* (Erythroxylaceae) were the most productive plant species, together accounting for 96% of mature fruits produced during the study period. The availability of arthropods was also correlated with rainfall (r = 0.60, P = 0.05, N = 11) and minimum temperatures (r = 0.68, P = 0.02, N = 11), which were marginally correlated to each other (r = 0.48, P = 0.08, N = 14). The availability of arthropods peaked from January to March, a few months after the onset of the rainy season (Figure 2B). Araneae was by far the most common arthropod group in terms of dry biomass (0.68 g/m^2), followed by Lepidoptera (larvae and adults, 0.08 g/m^2) and Blattaria, Diptera, and Orthoptera (0.04 g/m^2 each). There was no correlation between the availabilities of fruits and arthropods (r = 0.04, P = 0.88, N = 11) (Figure 2B).

We captured 453 birds (56 species), 166 of which were frugivorous (20 species), representing 37% of the captured birds. Two thrushes (Pale-breasted *Turdus leucomelas*, Rufous-bellied Thrush *T. rufiventris*) and two tanager species (Flame-crested *Tachyphonus coronatus*, Sayaca Tanager *Thraupis sayaca*) were the most abundant frugivorous birds, together accounting for 68% of the captures of frugivores (Table 1). We examined 117 fecal samples from 20 bird species. In total, 68% of the samples contained fruit remains while 82% contained arthropods (Table 1). There was a positive correlation between the proportion of fruit-containing feces and the availability of fruits, which correlated strongly and negatively with the proportion of feces containing arthropods (Table 2, Figure 2C). No correlation was found between the availability of arthropods and the proportion of either arthropod- or fruit-containing feces (Table 2).

Only 2% of the birds (N = 117 birds for which incubation and molting could be unambiguously assessed) were concomitantly incubating and molting flight feathers. There was no correlation between rainfall, minimum or maximum temperatures, and the proportion of birds incubating (all P > 0.29) or molting flight feathers (all P > 0.10) (Figure 2). The proportion of incubating individuals was correlated with the availability of fruits, whereas the proportion of birds molting flight feathers was correlated with the availability of arthropods (Table 2, Figure 2D).

In sum, we found that the availability of fruits and arthropods fluctuates temporally independent from each other, but both food sources have shortage periods, apparently more pronounced for fruits. During periods of fruit scarcity, birds rely more heavily on arthropods as food. Incubation occurred when fruit availability was high, while the molt period that follows is coincident with the availability of arthropods.

DISCUSSION

Rainfall can indirectly influence the biological cycles of birds since it is generally positively correlated with the increase in food availability. Temporal fluctuations in arthropod availability, for instance, are closely linked to seasonal rains. Arthropods are more abundant in areas where annual rainfall is higher, whereas areas with seasonal rainfall tend to have greater fluctuations in the abundance of arthropods than areas where seasonality is less pronounced (Wolda 1978). Increases in rainfall are also positively related to the peak of fruit availability, especially in seasonal forests (Jordano 2000). In our study, the peaks of breeding and molt occurred during the rainy season, a pattern already described in other studies (Marini & Durães 2001, Piratelli et al. 2000). However, whereas the peak of breeding coincided with the peak of fruit availability, the peak of flight feather molt coincided with the period of greatest availability of arthropods. These results were similar to those

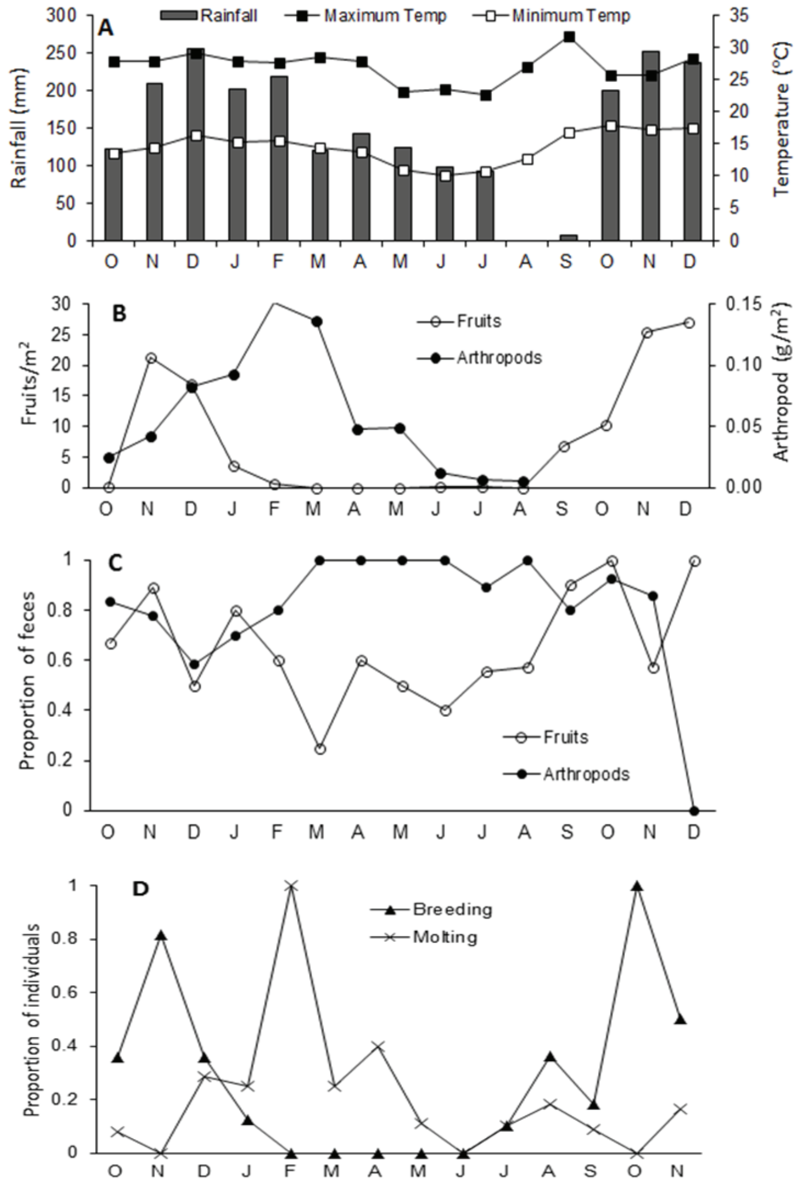

Figure 2. Monthly variation from October 2003 to December 2004 in rainfall, maximum, and minimum temperatures (A); availability of ripe fruits and arthropod dry biomass in sampled plots (384 m^2) (B); proportions of feces containing fruits and arthropods (C); and proportion of birds incubating or molting flight feathers (D). The dry season goes from April to September.

reported by Davis (1945) for forest birds in the state of São Paulo where the present study took place. Through analysis of gonadal development, Davis determined a well-defined reproductive period starting in August–September, with a peak in October. He also recorded two peaks in fruit production, July–September (end of rainy season and early dry season), and another small peak from December to January. Insect abundance was high from November to March, falling after April. Thus, the reproductive peak in Davis' (1945) study coincided with the peak of fruit production and peak availability of insects occurred during the time when most birds were taking care of nestlings or molting. As emphasized earlier, however, this is not a general pattern since much variation exists. For example, diet analyses by Poulin et al. (1992), revealed an increase of arthropods in the diet of birds during breeding seasons, followed by a decrease of vegetable matter. They concluded that abundance of arthropods is a crucial factor in determining the breeding cycles of birds, even in species that consume large amounts of nectar or fruits. It is noteworthy that Poulin et al. (1992) carried out their study in a region more arid than ours, which may have meant that food was temporally scarce as a result of drought conditions, thus influencing the response of birds to food supplies.

Though arthropods form the staple food of nestlings of many frugivorous birds, it is possible that fruits are also influencing the initiation of the breeding period, as suggested by Snow (1974). The importance of fruits in the development of nestlings of

Table 2. Pearson (r) and Spearman rank (r_s) correlations involving the monthly frequencies of occurrence of fruits and arthropods in feces of frugivorous birds, the monthly proportions of birds incubating or molting flight feathers, and the availability of fruits and arthropods. Significant correlations are in bold text.

	Fruit availability (ripe fruits/m^2)		Arthropod dry biomass (g/m^2)	
	r_s	*P*	r	*P*
Diet				
Fruits	**0.58**	**0.02**	-0.26	0.44
Arthropods	**-0.81**	**< 0.001**	-0.34	0.30
Incubation	**0.69**	**0.006**	-0.33	0.81
Molting	-0.24	0.41	**0.41**	**0.002**

frugivorous birds was rarely investigated in detail, but parents regularly offer fruits to them, especially in the later stages of the nestling period (Morton 1973). For instance, *Turdus leucomelas* gradually increases the proportion of fruits in the nestlings' diet up to 50% by the time they are 14–16 days old and ready to fledge (MAP unpubl. data). Contrary to arthropods, which were still available in periods of scarcity, albeit often in much reduced numbers, fruit availability dropped to zero during several months at our markedly seasonal study site, which also harbors a low diversity of fleshy-fruited plants. Therefore, breeding in the period of peak fruit availability may guarantee both a plentiful fruit supply and a crop of arthropods that are in greater abundance by that time and will serve as a rich supply of protein to help meet the ontogenetic demands of developing nestlings and recently fledged young (Young 1994, Stutchbury & Morton 2001).

While some experimental studies have found a positive influence of food availability on molt parameters, including molt initiation and feather growth (Class & Moore 2013, Swaddle & Witter 1997), others have not (Scheuerlein & Gwinner 2002). Although our observational study does not permit conclusions regarding this issue, it is suggestive that molt coincided with arthropod availability, a temporal overlap that may be important for the development of new feathers (Swaddle & Witter 1997). Definite conclusions regarding this relationship must wait for future experimental studies that supplement food for birds with diverse diets and inhabiting varied environments, since both environmental factors (e.g., rainfall seasonality) and food type have been shown to influence molt phenology (Johnson et al. 2012).

ACKNOWLEDGMENTS

We are grateful to Renan A. Bonança, Bruno Turbiani, and Rodrigo Neregato for the friendly help during the fieldwork, to Wayne J. Arendt, and an anonymous reviewer for comments on the manuscript, and to the Brazilian bird banding agency (ICMBio - CEMAVE) for providing metal bands. Special thanks to the landowners for allowing access to their lands. Financial support was furnished through a fellowship from the Brazilian Research Council to MSF (CNPq 101293/04-6).

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