

## MOLT-REPRODUCTION OVERLAP IN BIRDS OF CERRADO AND ATLANTIC FOREST, BRAZIL

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**Resumo.** – **Sobreposição entre reprodução e muda de penas em aves do Cerrado e da Mata Atlântica, Brasil.** Através de programas de marcação e recaptura, foram estudadas comunidades de aves nos estados de Mato Grosso do Sul (Cerrado - 1994 a 1996) e Rio de Janeiro (Mata Atlântica - 2001 a 2005), Brasil, com o propósito de determinar períodos de muda de penas e de reprodução, bem como sua sobreposição temporal nas comunidades. Foram considerados como em muda os adultos que apresentavam crescimento simétrico de penas novas, e aqueles que apresentavam placa de incubação foram definidos como em atividades reprodutivas. No Cerrado, com 713 capturas (89 espécies), observou-se que a reprodução ocorreu de agosto a janeiro, sendo mais intensa entre setembro e outubro. As atividades de muda de vô começaram em novembro e terminaram em maio (asa) e junho (cauda); ambos foram mais comuns de dezembro a fevereiro. As mudas de vô ocorreram principalmente no final da estação chuvosa, logo após a reprodução, e somente em novembro houve sobreposição temporal de eventos de mudas e de reprodução. Pelos 794 indivíduos amostrados na Mata Atlântica (91 espécies), ficou caracterizado que a estação reprodutiva começou um mês depois (setembro), prolongando-se até abril. As mudas também se iniciaram em setembro, reduzindo-se fortemente em maio. Neste bioma a duração dos dois eventos, bem como sua sobreposição, foi bem mais extensa (quase seis meses do ano). Apenas 10 indivíduos capturados no cerrado tinham muda de penas de vô e placa ao mesmo tempo, enquanto na Mata Atlântica, 32 foram detectados com as duas atividades simultâneas. Os dois eventos ocorreram na época mais chuvosa do ano nos dois biomas, e nossos dados apontam que a sobreposição entre mudas e reprodução é muito restrita no nível de indivíduos, e que o estresse hídrico e possível menor oferta de recursos alimentares, provavelmente regula a sazonalidade destes eventos nas comunidades de aves tropicais estudadas.

**Abstract.** – Through bird banding programs, I studied bird communities in the states of Mato Grosso do Sul (Cerrado -1994 to 1996) and Rio de Janeiro (Atlantic forest - 2001 to 2005), Brazil, aiming to determine the periods of molts and reproduction, as well as their temporal overlap in the communities. Molts were considered in adults having symmetrical growth of new feathers, and those with brood patch were defined as in reproductive activities. In Cerrado, after 713 captures (89 species), I found that reproduction occurred from August to January, being more intense between September and October. Flight feathers molts began in November and ended in May (wing) and June (tail), and both were more common from December to February. Flight feathers molts occurred mostly at the end of the rainy season, after breeding, and only in November, there was temporal overlap across species. For the 794 captured birds in the Atlantic forest (91 species), it was characterized that the breeding season began a month later (September) and lasted until April. Molts also started in September, lasting until May. In this biome, the duration of both events, as well as their overlap, was more consistent across different species (almost six months of the year). Only 10 individuals were captured in Cerrado having both molts and brood patch; while in the Atlantic forest these two simultaneous events were detected in 32 individuals. Both events occurred in the rainiest season of the year in each biome, and our data indicate that the overlap between molts and breeding is very limited at the individual level, and the water stress and possible restrictions in resource availability, may play an important role in the seasonality of these events in the studied tropical bird communities.

**Key words:** Atlantic forest, Birds, Brazil, Cerrado, Molt-reproduction overlap.

## INTRODUCTION

Molting and breeding are high-energetic events, either by the need to compensate the reduction of thermal insulation, the loss of aerodynamics, or by the production of new feathers, eggs and parental care (Watson, 1962, Lustik 1970, An-kney 1984, Hemborg & Lundber 1998, Hedenström & Sunada 1999), leading to an evolutionary trend in reducing temporal overlap between these two events (Foster 1974).

Many ecological and biological aspects might be crucial for determining the seasonal cycles of molting and breeding and the frequency of temporal overlap. Among the ecological factors, the availability of food resources (Hemborg & Lundberg 1988) is critical, and in temperate regions the overlap would be infrequent, due to temporal limitation in food availability (Payne 1969, Moreno 2004). In the tropics, where a larger availability of resources is likely year-round (Begon *et al.* 2006), the co-occurrence would be more common (Foster 1975), being more frequent in males that have fewer investments on parental care (Jenni & Winkler 1994).

Payne (1969) had examined 1050 specimens of 190 species collected in south-central Africa, where only 41 individuals of 24 species showed overlap between the two events (maximum 3.8%). Foster (1975) found about 10% of overlap in 960 individuals of Neotropical birds, and stated some adaptive advantages for this temporal coincidence including the completeness of both cycles in the rainy season when resources were abundant. In south-central Brazil, Marini & Durães (2001) found 29 of 1620 individuals (1.8%) from 13 passerine species overlapping breeding with flight feathers molt. In southeastern Brazil, Mallet-Rodrigues (2005) recorded 940 captures of 56 species, and non-accidental molts was observed in 358 individuals; none of them having brood patch at the same time (here used as an indicator of reproductive activity). Piratelli *et al.* (2000) studied molts across 76 species of

central Brazil, founding a strong relationship between molting of flight and contour feathers, stressing a well-defined seasonal period for these events, soon after the breeding season and having few individual overlap.

Many birds change their feathers at least once a year (Humphrey & Parkes 1959, Dawson *et al.* 2000) and there exists a direct relationship between body size and extension of flight feathers molts, where the larger the bird, the longer its period of replacement of feathers (Rohwer 2008). Thus, considering that time required to raising young also increases with body size, it could be a limiting factor in the annual cycle of larger birds, leading to a tradeoff between molt and reproduction (Rohwer *et al.* 2011).

This paper assumes that molting and breeding are well-defined seasonal events in birds, having a trend for most individuals and species in a Neotropical community to focus these activities in the warmer and rainy seasons, thereby ensuring greater availability of food resources. Being highly energetically activities, very few overlap between them is likely.

To test these assumptions, my questions are: 1) at the community level, when do birds change their feathers and reproduce?, 2) does it vary in different biomes? How frequently they overlap? In Brazil, the Cerrado is likely to have lower rainfall and higher water stress than the Atlantic forest, thus, I predicted a larger time for both molting and breeding in Atlantic forest, and larger overlap between them in Cerrado.

## METHODS

*Study sites.* Using the stations of the bird banding programs, I studied bird communities in the states of Mato Grosso do Sul (Cerrado, central Brazil) from 1994 to 1996, and in the Atlantic forest (Rio de Janeiro, southeastern Brazil) from 2001 to 2005 using 6 to 16 mist-nets (36- and 61-mm mesh, 12 x 2 m) (Table 1 and Fig. 1).

TABLE 1. Summary of the studied sites, including coordinates, date and sample efforts (See Piratelli *et al.* 2000; Piratelli & Pereira 2002; Piratelli & Blake, 2006; Piratelli *et al.* 2008 and Piña-Rodrigues *et al.* 2009 for detailed descriptions of the studied areas).

Biome	Vegetation	Geographic localization	Date	Sample effort (net-hours)
Cerrado	Cerrado <i>strictu sensu</i>	20°20'S; 51°40'W - 20°59'S; 51°46'W - 21°00'S; 51°50'W	Jul-94 to Dec-96	3,676.2
Cerrado	Dry forest (cerradão)	20°50'S; 51°40'W 20°40'S; 51°40' W,	Aug-94 to Dec-96	6,007.9
Cerrado	Gallery forest	20°59'S; 51°46'W	Jul-94 to Oct-95	2,378.0
Cerrado	<i>Eucalyptus</i>	20°50'S; 51°40'W 20°59'S; 51°46' W	Aug-94 to Dec-96	1,403.3
Atlantic forest	Montane semi deciduous forest	22°30'S 42°23'W	May-02 to Jan-04	2,686.67
Atlantic forest	Atlantic pluvial forest	22°24'S 42°58'W	Jul-04 to Jun-05	1,905.00
Atlantic forest	Fragments of second-growth forest	(22°17'S - 42°52'W and 22°16'S - 42°51'W)	Dec-03 to Aug-05	3,529.00
			Total	21,582.07

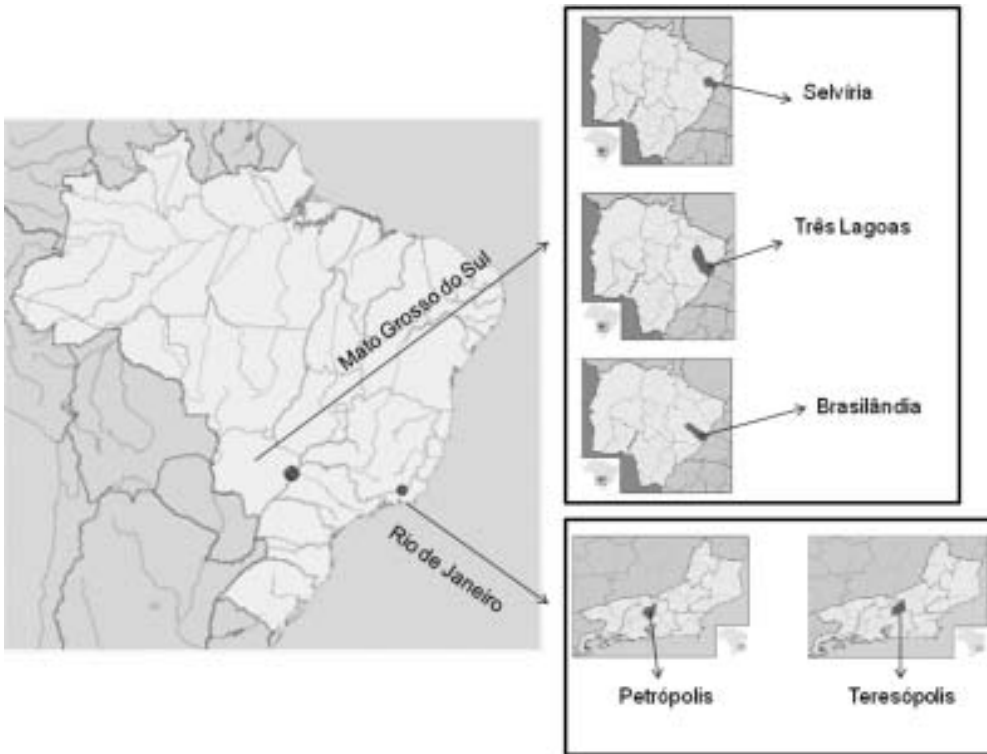


FIG. 1. Sampled areas in Mato Grosso do Sul and Rio de Janeiro, Brazil. (Modified from <http://pt.wikipedia.org>).

Mato Grosso do Sul was sampled through 14 study sites, outside the cities of Brasilândia (21°25'S; 52°25'W), Selvíria (20°22'S; 51°22'W) and Três Lagoas (20°45'S; 51°40'W), in areas having mixture of native and non-native (*Eucalyptus* spp.) vegetation.

Based on the climate data collected in the region of Três Lagoas from 1961 to 1990 (Embrapa 2011; Tempo Agora 2011), the climate may be characterized by two well-defined seasons: dry - (April to September), and wet - (October to March), with June been the driest month and December and January the rainiest. July is the coldest month and December the hottest.

In the state of Rio de Janeiro, I worked in three areas. Miguel Pereira (22°30' S; 42°23' W), in a 440-ha of montane semi decidu-

ous pluvial forest (Rizzini, 1997), Teresópolis (a 10,600 ha-continuous forest); Serra dos Órgãos National Park (22°24'S; 42°58'W); and four small fragments - 4 to 64 ha - in agricultural areas surrounded by pastureland for raising cattle. For further descriptions of the studies sites see Piratelli & Blake (2006) and Piratelli *et al.* (2008).

According to climatic data collected from 1961 to 1990 in the region of Teresópolis (Tempo Agora, 2011), which represents the studied region, the wet season goes from September to February or March, and dry season starts in March and finishes in August. July is the driest and coldest month, with December been the rainiest and January the hottest.

*Study methods.* In order to determine the periods of breeding and molts, as well as their

overlap, captured birds were banded with metallic rings supplied by CEMAVE/ICMBio. All same-day recaptures were taken off the analyses. Age (categorized as young or adult), was defined considering the presence of gape and skull ossification, and all young or uncertain aged individuals were also excluded from these analyses.

I looked for evidences of molts in the contour and flight (wing and tail) feathers, recognized by the presence of sheathed feathers, which I assumed to be growing following Foster (1975). For flight feathers, I always looked at primaries in both wings and sides of the tail, and I have considered a bird as in molt only when this was found in symmetry; therefore accidental molts were not considered.

Captured birds were visually inspected for the presence of brood patch. It is characterized by the loss of contour feathers on the belly and sub-dermal hypervascularity, facilitating the transfer of heat to the eggs and nestlings. The brood patch can begin developing before (e.g. Passeriformes) or during (e.g. Galliformes) laying eggs (Jones 1971) and can therefore be used as an indicator of reproductive activity.

For the two studied biomes, it was estimated the means ( $\pm$  SD) of individuals captured each month. From this average, I calculated the monthly percentage of individuals having wing and tail molts, brood patch, and simultaneously flight feathers molts and brood patch. Months having only one capture were removed before analysis. In both study sites, I compared monthly means and standard deviation of captured individuals having molts and brood patch in order to elucidate temporal extension of these events, as well as their overlap. A two tailed t-test was used to check for statistical differences between wet and dry seasons. Data were transformed using square root before analysis to assure the assumption of homogeneity of variances. All statistical tests were done using BioEstat 5.3 (Ayres *et al.* 2008).

I also clustered birds in trophic guilds, following Willis (1979), Piratelli & Pereira (2002) and Piña-Rodrigues *et al.* (2009). Thus, the following groups were determined: frugivorous, granivorous, insectivorous (ground), insectivorous (trunk-twig), nectar-eating, omnivorous, piscivores, insectivorous (aerial), insectivorous (foliage-gleaner) and carnivorous. I calculated monthly percentile of captured individuals in each guild having flight feathers molts and brood patch, and then got monthly average of occurrence of these events per each guild. To have a more robust source of data, I grouped all types of insectivores in a single group (insectivores), and used only this group and frugivore for the guild analysis presented here.

To verify relationships among molts and breeding events with environmental variables (temperature and rainfall), I calculated the Spearman rank correlation coefficient with a significance level of 0.05. I used monthly mean data of captured individuals having flight feathers molts and brood patch in the two study sites, which were correlated with average climate data from their respective regions, obtained from meteorological stations as described above. All analyses were performed in BioEstat 5.3 (Ayres *et al.* 2008) and the free software Past (Hammer *et al.* 2001).

## RESULTS

A total of 2191 captures corresponds to the sampling universe of this study (for all captured species in Cerrado see Piratelli & Blake 2006; for most captured species in Atlantic forest, see Piratelli *et al.* 2008), excluding from the analysis all individuals considered young or of uncertain age ( $n = 680$ ), plus all same-day recaptures, the total number for these analysis was 1507, 713 in Cerrado (from 89 species) and 794 in Atlantic forest (from 91 species), with both biomes sharing 20 species. From these, 146 (9.8 %) were replacing their wing feathers and 144 (9.7%) their tail feathers. Overall 354

TABLE 2. Total of individuals (and percentage) of birds having molts in wing, tail, wing/tail, Flight and contour feathers molts, brood patch and flight feathers molts/brood patch in Cerrado and Atlantic forest, Brazil.

	Cerrado	Atlantic forest	Total
Wing molts	71 (10%)	75 (9.6%)	146 (9.8%)
Tail Molts	70 (9.9%)	74 (9.5%)	144 (9.7%)
Wing and tail molts	28 (3.9%)	41 (5.3%)	69 (4.6%)
Flight and contour feathers molts	38 (5.3%)	59 (7.6%)	97 (6.4%)
Brood patch	148 (20.9%)	206 (26.8%)	354 (24.0%)
Flight feathers molts and brood patch	10 (1.4%)	32 (4.0%)	42 (2.8%)

individuals had brood patch (20.4%), and 42 (2.8%) were captured with flight feathers molts and brood patch at the same time (Table 2).

In the community of birds in Cerrado, incubation started in August and was more intense in September, October and November (Fig. 2a). The higher percentile of individuals having brood patch was in September 1994 (50% of captured individuals).

For 76 species, flight feathers molts started in November and up to April for wings and May for tail) (Fig. 2b). The percentile of individuals having both flight feathers molts and brood patch at the same time was very small, not exceeding 2% in November and April (mean of 3.1 and 5.1 individuals respectively). As a total, only 10 individuals from nine different species (all Passeriformes, except *Nyctidromus albicollis*) had both activities at the same time representing 1.4% of captures in this biome.

In Cerrado, there were positive and significant correlations between flight feathers molts and temperature ( $r_s = 0.69$ ;  $p < 0.013$ ) and rain ( $r_s = 0.78$ ;  $p = 0.003$ ). Such correlations were not present with regards to the presence of brood patch, whose correlations were not significant with both climate variables (respectively  $r_s = 0.09$ ;  $p = 0.77$  and  $r_s = -0.07$ ;  $p = 0.83$ ).

In the Atlantic forest, the beginning of the reproductive season was one month later (September), and was prolonged until March and even April (Fig. 3a). Of the 794 individuals sampled here, 223 (24.61%) had brood patch and 26 (11.65%) were also molting wing feathers, 31 (13.9%), tail, 52 (23.32%), contour feathers and 21 (9.41%) both wings and tails. In September, records of flight feathers molts also have began, which lasted until May. At this site, I obtained in February a maximum of 26.5% of captured individuals (over a mean of 23 individuals sampled in this time of the year) changing flight feathers and having brood patch at the same time. Nevertheless, only 32 (4.03%) of the total individual captures (17 Passeriformes; two non-Passeriformes species) had simultaneously both events.

In this biome, there was a significant positive correlation between molting and temperature ( $r_s = 0.70$ ;  $p = 0.01$ ), but not with rain ( $r_s = 0.44$ ;  $p = 0.15$ ). The correlations were significant for presence of brood patch and temperature ( $r_s = 0.77$ ;  $p = 0.003$ ), as well as with precipitation ( $r_s = 0.71$ ;  $p = 0.009$ ).

In Cerrado, there was no significant difference between wet and dry seasons for brood patch occurrence ( $t = -1.004$ ;  $p = 0.32$ ), but significant for molts ( $t = -3.167$ ;  $p =$

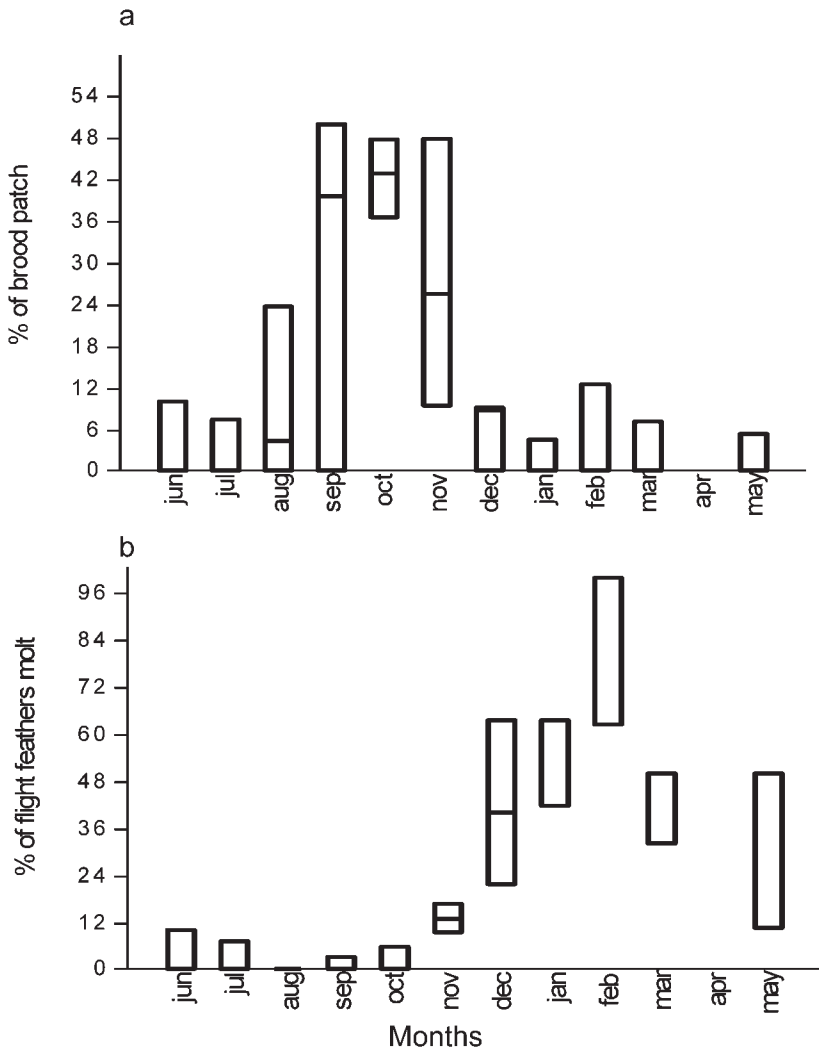


FIG. 2. Box plots for monthly variation of captured birds having (a) brood patch and (b) flight feathers molts in Cerrado, Brazil.

0.004). For the Atlantic forest the difference was significant for brood patch ( $t = -5.57$ ;  $p < 0.0001$ ), but not significant for molts ( $t = 1.03$ ;  $p = 0.31$ ).

When considering the presence of brood patch by trophic guilds, frugivorous had the highest mean incidence in September ( $6.4 \pm 6.0$ ) in Cerrado, and November ( $5.6 \pm 6.3$ ) in the Atlantic forest. For insectivores, incubation

took place mainly in November ( $10.4 \pm 4.0$ ) in Cerrado and March ( $13.4 \pm 9.5$ ). Atlantic forest. A small number of frugivores (max.  $n = 3$ ) molting in Cerrado from December to May were detected ( $0.6 \pm 1.0$ ). They were also few in the Atlantic forest ( $1.2 \pm 2.0$ ), but more often throughout the year. Insectivorous having molts were more numerous in both Cerrado ( $2.3 \pm 2.8$ ) and Atlantic forest ( $2.8 \pm 3.0$ ).

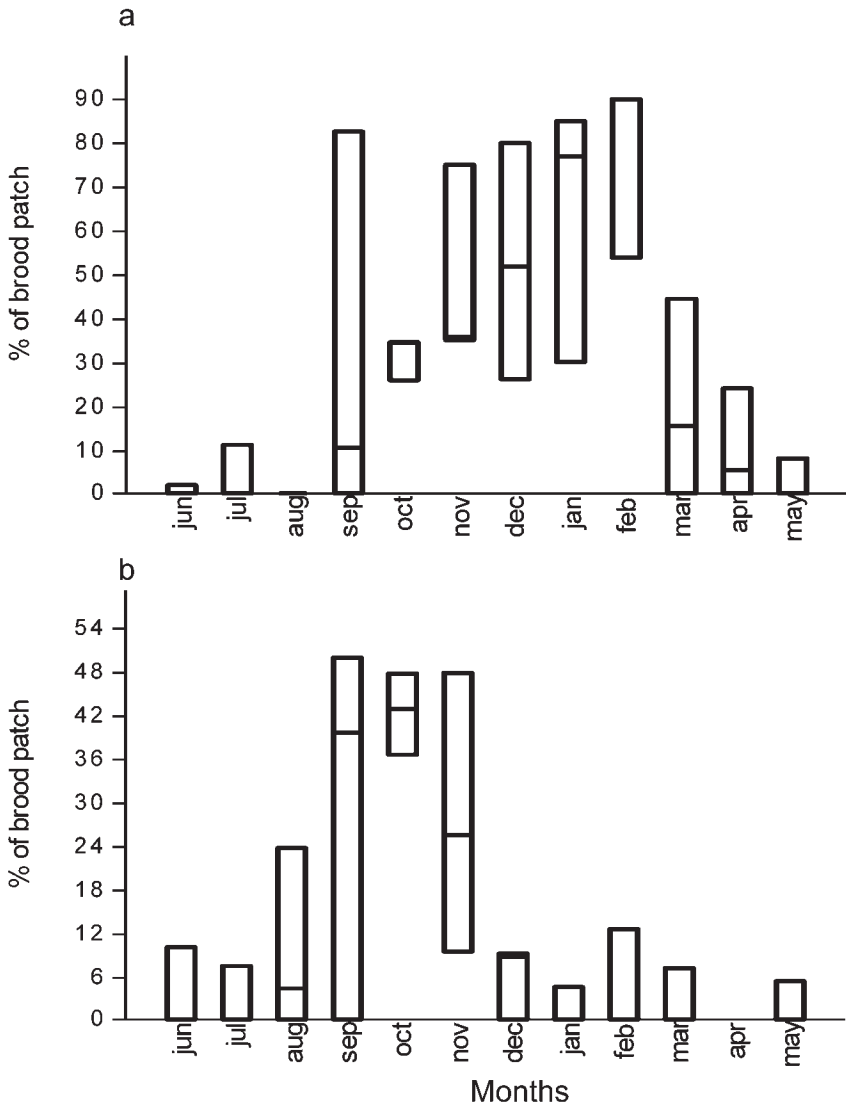


FIG. 3. Box plots for monthly variation of captured birds having (a) brood patch and (b) flight feathers molts in Atlantic forest, Brazil.

DISCUSSION

High-costly activities are expected to occur under favorable environmental conditions and with least interference from others (Foster 1975). Thus, physiological and ecological trade-offs be-

tween molt and breeding are likely (Hemborg & Lundberg 1998, Rohwer *et al.* 2011), which might lead to a temporal separation between them. Nevertheless, overlap has been reported in the tropics (eg. Payne 1969, Foster 1975) and the seasonal food supply has been claimed to be a key



factor in solving this paradigm (e.g. Poulin *et al.* 1992). This overlap however, would be costly in terms of fitness, which could reduce the reproductive success and even the individual survival (Swaddle & Witter 1997).

There are specific situations when overlap seems to be more common. In the aseasonal environment in the Amazon, Tallman & Tallman (1997) found 33% of individuals of antbirds molting and breeding at the same time. This seems to be a quite uncommon situation, due to the locally aseasonality of breeding for these species, which behave seasonally in other areas, as stressed by the authors.

I observed that birds from Cerrado incubated their eggs and changed their flight feathers in a shorter time that did the Atlantic forest birds, which was probably associated with an increased rainfall in the latter biome. Molts were correlated to temperature in the two biomes, but only to rainfall in Cerrado. However, incubation was linked with both climatic variables in Atlantic forest, but none in the Cerrado. The lowest rainfall of central Brazil may be crucial for time and length of molting, which would lead to a larger synchronization between the species in this biome.

With flight feathers molts occurring at the end of the rainy season, and playing a tendency of non-overlapping, breeding also would take place in a shorter period of time. In the states of Goiás and Minas Gerais, also in Cerrado region, Marini & Durães (2001) found brood patches from the late dry season-early rainy season, and molts being more evident from the middle to the end of the rainy season. The authors have agreed to Poulin *et al.* (1992) to link their results to the time of the year having maximum food offer in seasonal tropical regions.

Two main costs are involved in molts, the reduction in the efficiency of feathers functions and an increase in metabolic demand. For flight feathers, losses in aerodynamic and in efficiency of social interactions are the most

obvious consequences. In relation to metabolism, since molt may involve up to 10% of the total body mass of a passerine, a high energetic demand is required (Jenni & Winkler 1994). These may have contributed to the evolution of matching these activities to the warmer and rainy season, even in tropical regions.

The sequence reproduction-molt that I and others authors have found at the community level in tropical regions (e.g. Foster 1975, Marini & Durães 2001) embeds several variations to the species level from one year to another, and so on for different populations and sexes (Foster 1975 and references herein). For a broader scale, this may reflect a larger pattern of temporal distribution, especially if environmental constraints are reduced. In the regions here studied, the overlap between the two events was restricted, both in terms of individuals and communities. Payne (1969), Foster (1975) and Marini & Durães (2001) had already observed this tendency in studies in Africa and Central and South America (up to 3.8-, 10- and 1.8% respectively). Recently in Brazil, Reppenning & Fontana (2011) found only two Tyrant individuals (1.11% of their records) having temporal overlap.

Food has been largely considered as key factor in determining time of molt and reproduction in tropical birds (Echeverry-Galvis & Córdoba-Córdoba 2008 and references herein). No information on insect abundance and its relation to rainfall is available for the studied Atlantic forest, but for Cerrado, Piratelli & Pereira (2002) found more proportion of insect in birds' fecal samples either in rainy or in the dry season. In this biome, Piratelli (1999) pointed out more prevalence of ripe fruits on September, when brood patch occurrence was also well established (but not molt).

Insectivorous might have less food limitations than frugivorous (Poulin *et al.* 1992), and thereby may invest energy in their life cycles of molting and breeding over a larger time of the year. Poulin *et al.* (1992) stressed that the abun-

dance of arthropods may be critical for reproductive activities, even for birds that consume higher proportions of fruit and nectar. Loiselle & Blake (1991) observed that frugivorous birds when ripe fruit was in short supply in all forest sites that they studied in Costa Rica, and one explanation would rely on the need of fruits available for adult birds along with the importance of protein supply (arthropods) for production of eggs and feeding young. For molts, the protein requirements involved also lead to a tendency of replacing feathers in periods of higher supply of arthropods and/or caloric fruits (Gomes *et al.* 2010).

Here I have not measured the photoperiod, which is considered a conservative adaptive response that may adjust the biological cycles of birds better than environmental conditions of food and temperature, at least in temperate regions (Trivedi *et al.* 2006). In the tropics, evidence also suggests its importance in determining long-term patterns related to reproduction (Wikelski *et al.* 2000). Indeed, the photoperiod varies between different latitudes and seasons (Trivedi *et al.* 2006); however, the latitudinal differences between the two areas here studied were not larger than three degrees, which does not seem to be significant in determining different patterns.

In conclusion, I found for most birds a tendency for molting and reproduction in the warmer and rainy months, both in Cerrado and Atlantic forest, with few overlaps, as stated. A larger time for molting and breeding did happen in Atlantic forest, where I also found larger overlaps, different from my initial prediction. The climate seasonality and thereby fluctuations in the availability of fruits and arthropods may explain the differences in cycles and durations of molt and reproduction between Cerrado and Atlantic forest.

There are still not many long-term and large-scale studies monitoring and describing patterns of molting and its degree of overlap with reproduction in Brazilian continental birds.

These studies are more important if joined to information on reproductive biology and availability of food resources, which could better characterize these events and elucidate some key ecological components for their occurrence. I agree with Repenning & Fontana (2011) that we are just in the begging of our knowledge.

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