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ANNUAL PATTERNS OF MOLT AND REPRODUCTIVE ACTIVITY OF PASSERINES IN SOUTH-CENTRAL BRAZIL

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Abstract. We analyzed the occurrence of molt and brood patches in resident passerines from four localities in south-central Brazil. The annual patterns of molt and reproductive activity were very similar among the sites. Brood patches first appeared in August, but were most common between October and January, with a peak in November, early in the rainy season. Molt started in October but was most widespread from the middle to the end of the rainy season, between December and April, with a peak in February. Timing of the appearance of brood patches was not related to trophic guild (insectivores, frugivores, omnivores). Molt of flight feathers started at the end of the reproductive period, which varied slightly among trophic guilds. Molt and brood patch overlap occurred in little more than 4% of individual birds, or in less than 2% considering just those molting flight feathers. This overlap occurred mostly between November and February. Regional environmental factors, instead of local factors, seem to be responsible for the annual breeding and molt patterns of the considered species.

Key words: Atlantic forest, Brazil, cerrado region, molt, passerine birds, reproduction.

INTRODUCTION

The biology of molt and reproduction are intimately related in the annual cycles of birds (Snow 1976, Poulin et al. 1992). The extra energy demanded by these activities exerts an evolutionary pressure for their occurrence during the most favorable time of the year and for the minimization of overlap between them (Foster 1975). The timing of both events during the annual cycle of birds is obtained by a mutual adjustment, in which breeding affects molt as molt affects breeding (Langston and Rohwer 1996). Our understanding, however, of how this fine and complex adjustment takes place is far from complete, since different patterns have evolved among species and regions (Payne 1972).

Long-term studies about molt of Neotropical birds are rare, and most of them emphasize observations about molt sequence (Wagner 1955), occasional molt records (Oniki 1981, Dyrcz 1987), or records for single species (Miller 1961, Davis 1971, Mallet-Rodrigues et al. 1995, Valente 2000). Reproduction of Neotropical birds also has received relatively little attention.
(Skutch 1968, Oniki and Willis 1982, Cruz and Andrews 1989). In addition, molt and reproduction rarely have been studied together in the annual cycles of bird communities (Snow 1976, Poulin et al. 1992, Piratelli et al. 2000).

Studies of the occurrence of molt and reproduction at the community level may indicate general patterns on the annual cycle of birds at a local level, and may help us to understand how these activities relate to each other and to local environmental characteristics. Here, we describe the annual patterns of molt and breeding activity, indicated by the occurrence of brood patches, in passerines residing mostly in forests within the cerrado region of south-central Brazil. Trophic guilds are compared to evaluate whether these patterns are affected by diet. Finally, by comparing four sites, we evaluate whether molt and breeding patterns are determined at a local or regional level.

METHODS

STUDY AREA

We conducted this study in gallery, semi-deciduous, and mesic forests of Minas Gerais State and the Federal District of Brazil. In Minas Gerais, three regions were sampled: (1) Belo Horizonte: forest fragments within the Water Management Areas of Barreiro, Mutuca, and Taboães owned by the Companhia de Saneamento de Minas Gerais (21°00' S, 44°00' W, 800–900 m elevation); (2) Uberlândia: forest fragments within private cattle farms (18°57' S, 48°12' W, 800 m); and (3) Canastra: two study sites 65 km apart, including a gallery forest owned by the Companhia Elétrica de Minas Gerais (20°40' S, 46°19' W, 900 m), and natural forest patches within the Parque Nacional da Serra da Canastra (22°00' S, 46°45' W, 1033–1493 m). Three gallery forests were sampled in the fourth region, Brasília, including two at the Fazenda Água Limpa, owned by the Universidade de Brasília (15°58' S, 47°56' W, 1100 m), and one at the Reserva Biológica do Instituto Brasileiro de Geografia e Estatística (IBGE; 15°56' S, 47°54' W, 1100 m; Fig. 1).

The cerrado biome is a savanna-like ecosystem of open vegetation formations, from grasslands to dense scrub, as well as gallery forests in wetter areas and dry forests in rich-soil areas (Eiten 1978, Ferri 1981). All localities sampled lie within the cerrado biome, except for the Belo Horizonte sites, which lie at the transition between the cerrado and the Atlantic Forest biome (Velo 1966, Ab’Saber 1977).

Climate of the cerrado region is seasonal, with a rainy warm season between October and March and a dry cool season between April and September. The rainiest months are December and January and the driest are June, July, and August. Temperature ranges from 18–24°C, with a mean of 21°C. Monthly precipitation ranges from 9 to 320 mm, with mean annual total of
DATA COLLECTION

Data were collected between March 1986 and February 2000, with different efforts in each site, varying from nine months over four years up to 34 months over six years (Table 1). Birds were captured with 36-mm, 12 × 2.5 m mist nets, opened usually between 06:00 and 13:00 along transects in the interior and at the edge of the forests. Each bird caught received a metal band provided by the official Brazilian banding agency (CEMAVE/IBAMA). Birds were checked for the presence of molt and brood patch. Molt was divided into three types: (1) contour feathers: molt of any type of feather, except the flight feathers of the wings and the tail, with a minimum of 10 feathers growing in one or more body regions; (2) wing flight feathers or remiges, and (3) tail flight feathers or rectrices. Wing and tail feathers were considered in molt only when the replacement was symmetrical. Immature birds and migratory species were excluded. Species sampled were mostly forest dwelling, but open-area species were considered as well. Birds recaptured in different months were considered as independent records, but only the first record of an individual during each month was considered.

Brood patch was scored as present or absent. A brood patch was considered present when well characterized with evident vascularization and wrinkled, opaque-rose skin. The presence of a brood patch was taken as an indication that the bird was reproductively active. In order to minimize error in our estimation of the proportion of birds with brood patches, we adopted the following method for species with different incubation strategies: (1) We included in the analyses all captured individuals for species in which both sexes incubate the eggs (families Rhyndocryptidae, Formicariidae, Conopophagidae, Vireonidae, Dendrocolaptidae, and Furnariidae); (2) for sexually dimorphic species in which only the females incubate the eggs, only the females were considered (families Tyrannidae, Emberizidae, and Cotingidae). For manakins (Pipridae) whose immature males resemble females, all “green” (female-plumaged) individuals were included; and (3) for monomorphic species in which only the females incubate the eggs (families Tyrannidae, some Pipridae, Muscicapidae [Turdinace], Emberizidae, and Trogodytidae), the

<table>
<thead>
<tr>
<th>Study sites</th>
<th>Sampling period</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brasilia (1986–1990)</td>
<td></td>
<td>2518 (2315)</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>470 (368)</td>
</tr>
</tbody>
</table>

**TABLE 1.** Number of birds analyzed by month and study site in forests of south-central Brazil. Individuals recaptured in different months were considered independent samples (number of individuals in parentheses).
TABLE 2. Number of species (individuals) of analyzed passerines by study site. Taxonomy follows Sick (1997).

<table>
<thead>
<tr>
<th>Family</th>
<th>Uberlândia</th>
<th>Brasíla</th>
<th>Canastra</th>
<th>Belo Horizonte</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rhinocryptidae</td>
<td>0</td>
<td>0</td>
<td>1 (1)</td>
<td>0</td>
<td>1 (1)</td>
</tr>
<tr>
<td>Formicariidae</td>
<td>6 (29)</td>
<td>1 (9)</td>
<td>2 (26)</td>
<td>4 (124)</td>
<td>8 (188)</td>
</tr>
<tr>
<td>Conopophagidae</td>
<td>1 (3)</td>
<td>1 (7)</td>
<td>1 (13)</td>
<td>1 (64)</td>
<td>1 (87)</td>
</tr>
<tr>
<td>Furnariidae</td>
<td>6 (18)</td>
<td>4 (33)</td>
<td>4 (25)</td>
<td>8 (64)</td>
<td>14 (140)</td>
</tr>
<tr>
<td>Dendrocolaptidae</td>
<td>2 (5)</td>
<td>2 (34)</td>
<td>3 (11)</td>
<td>3 (67)</td>
<td>5 (117)</td>
</tr>
<tr>
<td>Tyrannidae</td>
<td>9 (71)</td>
<td>7 (62)</td>
<td>14 (98)</td>
<td>14 (331)</td>
<td>22 (562)</td>
</tr>
<tr>
<td>Pipridae</td>
<td>3 (72)</td>
<td>2 (77)</td>
<td>2 (27)</td>
<td>4 (135)</td>
<td>6 (311)</td>
</tr>
<tr>
<td>Cotingidae</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1 (1)</td>
<td>1 (1)</td>
</tr>
<tr>
<td>Trogloidyidae</td>
<td>1 (7)</td>
<td>1 (16)</td>
<td>0</td>
<td>0</td>
<td>1 (23)</td>
</tr>
<tr>
<td>Muscicapidae (Turdinidae)</td>
<td>2 (19)</td>
<td>3 (27)</td>
<td>2 (20)</td>
<td>3 (94)</td>
<td>3 (160)</td>
</tr>
<tr>
<td>Vireonidae</td>
<td>1 (2)</td>
<td>1 (2)</td>
<td>0</td>
<td>2 (14)</td>
<td>2 (18)</td>
</tr>
<tr>
<td>Emberizidae</td>
<td>7 (134)</td>
<td>17 (203)</td>
<td>22 (156)</td>
<td>23 (417)</td>
<td>37 (910)</td>
</tr>
<tr>
<td>Total</td>
<td>38 (360)</td>
<td>39 (470)</td>
<td>51 (377)</td>
<td>63 (1311)</td>
<td>101 (2518)</td>
</tr>
</tbody>
</table>

total number of captured individuals was divided by two. These percentages were calculated monthly, for each year and study area. This method may have produced small errors by including a few non-incubating males or excluding a small number of incubating females, but a separate analysis using only evidently incubating individuals produced similar results, indicating that this error did not alter overall conclusions.

The classification of the reproductive behavior of males and females was based on Willis (1995) and Sick (1997). For Vireonidae, we followed Sick, who reports that for all species of the family both sexes incubate the eggs. Species nomenclature, classifications, and diet characterization follow Sick (1997).

STATISTICAL ANALYSES
We compared brood patch frequency by month between pairs of regions using Spearman rank correlation (Sokal and Rohlf 1981). We compared molt frequency by month between pairs of regions using Pearson correlation coefficients. Non-normal data were normalized using arcsine transformation (Sokal and Rohlf 1981). Only months with at least 10 individuals for each site were included. Results were considered statistically significant at $P \leq 0.05$.

RESULTS
Our analyses are based on 2518 records from 2315 individuals belonging to 101 species in 12 families of Passeriformes. The numbers of individuals and species sampled were similar for three regions, and larger for the Belo Horizonte region (Table 2). The number of bird families was similar among the four regions sampled (Table 2).

Brood patches were recorded in 349 (21%) of 1649 individuals considered for this analysis. Reproductive activity, as indicated by the presence of brood patches, began in August, and was more frequent in November in all four regions (Fig. 2a). All regions showed high correlation ($r$, values = 0.58–0.87) between monthly molt frequency, even though two of the six comparisons were not significant ($P > 0.2$), probably due to the small number of months included in
these analyses. We therefore pooled data from the four regions to evaluate the regional reproductive-period pattern for south-central Brazil. As above, brood patches began to appear in August, at the end of the dry season, and reached the highest frequencies between October and December with a peak in November, early in the rainy season (Fig. 3).

Molt was recorded in 774 (31%) of 2518 birds, most of them replacing contour feathers separately ($n = 437$) or together with flight feathers ($n = 274$), while 63 individuals were molting just flight feathers. Molt of remiges was recorded in 254 (10%) of the assessed individuals and molt of rectrices was recorded in 208 (8%) of these individuals.

Molt was concentrated between January and March in all regions sampled, diminishing or stopping completely in the other months (Fig. 2b). This period corresponds to the second half of the rainy season in the region. Molt frequency was highly correlated between regions (all $r > 0.65$) and the comparisons were significant in all cases but two ($P = 0.07$ and 0.16), so we pooled data to evaluate the existence of a general molt pattern for south-central Brazil. The pooled data for the four regions revealed higher molt frequency between December and April, with a molt peak in February–March, late in the rainy season (Fig. 3). Molt of all types of feathers (wing, tail, and contour) occurred mostly in this period, but $>15\%$ of birds replaced contour feathers even during dry-season months, revealing a year-round replacement of body feathers not necessarily related to post-nuptial molt (Fig. 4). The peak of rectrix molt occurred in March, a month after the peak of remige and body molt (Fig. 4).

Comparison of molt and brood-patch timing among trophic guilds revealed small differences related to diet within the general pattern (Fig. 5). Insectivores and frugivores started to breed in August. Although omnivores also showed some breeding activity in August, it increased substantially in September. For all three guilds, however, the reproductive period was most pronounced ($>40\%$ of individuals with brood patch) from October to December or January. Insectivores had high frequencies of brood...
patches between October and December, with a peak in November, and their molt was most frequent between December and March. Frugivores also had a high frequency of brood patches between October and December, but without a very pronounced peak. Molt frequency began to increase in January, but peaked in February–March. Omnivores had a high frequency of brood patches from October to January, with a peak in December–January, later than the other guilds. Their molt was more frequent between January and March, with a peak in February.

Overlap between molt and breeding was recorded in 4.1% (n = 66) of the 1620 individuals assessed for both molt and brood patch. These 66 individuals represent 26 species from six families. Overlap occurred from August until May, but was most frequent from November to February. When we considered only those individuals molting flight feathers, whether or not in conjunction with body feather molt, the rate of overlap dropped to 1.8% (n = 29), in 13 species and five families (Table 3). The overlap between breeding and molt of flight feathers was shorter, occurring mostly between December and February (Fig. 3).

**DISCUSSION**

Reproduction and molt are two activities that demand a high amount of energy, are generally concentrated in a period of high food productivity, and overlap minimally (Cruz and Andrews 1989, Poulin et al. 1992, Piratelli et al. 2000). In seasonal tropical regions, the time of the year with the greatest food availability is the end of the dry season and the rainy season (Davis 1945, Diamond 1974, Poulin et al. 1992). Matching this pattern, brood patches began to appear at late dry season–early rainy season in all four sampled regions, while molt was more pronounced from the middle to the end of the rainy season.

The observed cycle of breeding activity is very similar to that reported by Davis (1945) for forest birds in São Paulo state, south of our study sites. Through analyses of gonadal develop-
Determine the periods of reproduction and molt in birds instead of local variations, are more likely to agree with studies conducted in two other Brazilian states, São Paulo (molt period from December to February, Oniki 1981) and Mato Grosso do Sul (molt period from November to April, Piratelli et al. 2000).

Differences in timing of reproduction and molt between trophic guilds were slight. Contrary to other studies (Skutch 1950, Snow and Snow 1964), but in agreement with Poulin et al. (1992), frugivores did not start reproduction before insectivores; both guilds started to breed in August. Noticeable reproductive activity for omnivores began later, in September, and had a very sharp decrease in January. Insectivores also concluded the reproductive period in January, while frugivores extended reproduction until February. The start of the molting period varied with the end of the incubation period for each guild, but the end of molt coincided with the end of the rainy season. Omnivores, for example, which had a longer period with high frequencies of brood patches, presented a shorter period of molt than frugivores and insectivores. On the other hand, insectivores had the frequency of brood patches largely reduced by January and started to molt earlier, in December.

Regional climatic patterns in south-central Brazil, instead of local variations, are more likely to determine the periods of reproduction and molt of forest passerines. The latitudinal difference of 5° between Brasília and the other regions was not enough to cause major changes in reproduction and molt periods. Altitude, also, did not strongly interfere in the determination of reproduction and molt periods over the 300–600 m difference between Canastra and the other three regions.

Molt of flight feathers indicate better the period of postnuptial molt than the molt of contour feathers, since at least 15% of individuals were replacing contour feathers year round. The peak of molt of remiges preceded the peak of molt of rectrices by about one month. However, there was high overlap, suggesting that birds have little time to molt before the onset of the dry season.

Foster (1974) stated that the proportion of overlap between molt and reproduction is higher in tropical than in temperate habitats, due to a prolonged breeding period in the tropics. The low proportion of individuals overlapping molt and breeding that we observed is similar to or smaller than the frequencies recorded in other tropical regions. Piratelli et al. (2000) registered a 3.2% overlap between birds presenting brood patches and any type of molt in southern Brazil. Payne (1969) reported a 3.8% overlap between gonads in reproductive stage and feather replacement in a collection of African birds, but this rate dropped to 1.5% when only individuals molting flight feathers were considered. In Costa Rica, Foster (1975) observed overlap between high gonadal development or active brood patch and molt in approximately 9% of individuals. Ralph and Fancy (1994) registered overlap of 3.2% between brood patch or well-developed cloacal protuberance and molt of flight feathers in six Hawaiian finch species. The comparison between these studies, however, must be made carefully. Many tropical species show incomplete regression of gonads (Payne 1972), which probably explains the higher proportion of overlap observed in studies based on gonadal stage in relation to studies based on occurrence of brood patches. In addition, while our study considers only incubating species and sexes, both Foster and Payne included in their analyses birds with different life histories. For example, brood parasites (Icterinae) certainly have smaller costs of reproduction and could overlap breeding and molt to a larger extent.

Molt demands energy not only for the production of new feathers, but also to compensate for the loss of insulation and flight efficiency (Ginn
and Melville 1995, Swaddle and Witter 1997). Payne (1972) pointed out that even a small increase in metabolic rate associated with an increase in protein demand and reduced flight efficiency may be ecologically restrictive when a bird is reproducing. Birds overlapping breeding and molt can incur reduced clutch size, nest success, and survivorship of nestlings and adults (Nilsson and Svensson 1996, Svensson and Nilsson 1997).

Even considering that the frequency of overlap may be higher in tropical than temperate regions, the proportion of overlap observed in this and the other mentioned studies is still low. This low overlap and the concentration of the molting and reproductive cycles in a period of high food availability suggest that, even in the tropics, these activities may represent an energetic constraint and that there may be selection against the simultaneous occurrence of both.

Our results support previous studies from tropical regions showing that reproduction and molt cycles of forest resident passerines are intimately associated with the rainy season, but have little overlap with each other. Small adjustments of the periods of reproduction and molt occur in different trophic guilds, and the regional climate influences the annual molt and breeding patterns more than the local climate.

ACKNOWLEDGMENTS


Ralph, C. J., and S. G. Fancy. 1994. Timing of breed-