The phenology of molting, breeding and their overlap in central Amazonian birds

Erik I. Johnson, Philip C. Stouffer and Richard O. Bierregaard, Jr


Annual life history events in birds that demand especially high energy expenditure include breeding, molting, and migration, and these are typically separated temporally to minimize their overlap (Drent and Daan 1980, Kjellén 1994, Murphy 1996). Because energy available to birds is limiting, trade-offs between successful breeding, molting, and migration are often apparent. For example, high reproductive investment can delay molt, decrease feather quality, and reduce parental survival (Siikamäki et al. 1994, Nilsson and Svensson 1996, Dawson et al. 2000). Conversely, molting early can reduce fecundity, but increase parental survival (Morales et al. 2007). Furthermore, costs associated with molting are believed to prevent overlap with migration; some migratory species even temporarily arrest molt until migration is completed (Stresemann and Stresemann 1966, Pyle 1997, Leu and Thompson 2002, Pérez and Hobson 2006). Thus, the timing of these life-history events is presumably subject to strong evolutionary pressures and is optimized through natural selection to maximize fitness (Dawson et al. 2000, Ricklefs and Wikelski 2002, Moreno 2004). Little is known about the timing of these events in tropical communities, especially in contrast to temperate communities (Pyle 1997, Dawson 2008).

For tropical species that do not migrate, temporal constraints on molting and breeding should be reduced. Paradoxically, individuals of many tropical species are thought to regularly molt and breed simultaneously, referred to as molt–breeding overlap (Snow and Snow 1964, Foster 1975, Avery 1985, Astheimer and Buttemer 1999, Marini and Duraes 2001). It is not clear what drives increased molt–breeding overlap in tropical birds, but reduced physiological demands due to a slower-paced lifestyle appears to correlate with its occurrence (Foster 1974, Franklin et al. 1999, Wingfield 2005). Tropical birds typically lay fewer eggs per clutch (usually just two; Skutch 1969, Kulesza 1990, Young 1994, Martin et al. 2000), have reduced maximum gonad size and hormonal concentrations (Stutchbury and Morton 2001, Wikelski et al. 2003a, Goymann et al. 2004, Hau et al. 2010), a lower metabolic rate (Ricklefs 1976, Weathers 1979,
of molt-breeding overlap would correlate with longer molting frequencies with the expectation that increased frequency ing to their ecology and taxonomy if this trait was adap-

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Alternatively, if molt-breeding overlap to occur only at the beginning of the weeks and that molt often follows breeding (Jones 1971, Del Hoyo 1992–2010, Pyle 1997), we predicted molt-breeding overlap may not severely reduce fecundity or fitness in tropical species compared to temperate species (Foster 1974, Slagsvold and Dale 1996, Hemborg and Lundberg 1998, Hemborg 1999, Hemborg et al. 2001).

Tropical forest birds show great variation in foraging strategy, social system, and microclimate use (Karr 1977, Terborgh et al. 1990, Stutchbury and Morton 2001). The humid lowland rainforests of the central Amazon contain a diverse avian community with great variation in life history strategies, providing an ideal opportunity to study within-community variation in molting and breeding phenology (Cohn-Haft et al. 1997, Johnson et al. 2011). For example, in a single 100-ha patch of undisturbed central Amazonian forest, over 200 species have been found (Johnson et al. 2011). Such diversity in life history strategies may also result in variation in molt-breeding overlap frequency among species, but few large datasets (Poulain et al. 1992, Marini and Durães 2001, Wolfe et al. 2009) are available to examine the variation of molting and breeding phenologies within a tropical community.

In this paper, we present the phenology of breeding using brood patch data, molting using primary feather molt data, and their overlap in a near-equatorial community of understory forest birds in Amazonian Brazil, as well as explore ecological factors that covary with these patterns. We first predicted that the frequency of molt-breeding overlap among species would vary among species according to their ecology and taxonomy if this trait was adaptive. We then examined correlates of molt-breeding overlap frequencies with the expectation that increased frequency of molt-breeding overlap would correlate with longer molt duration and decreased flexibility in timing of molt initia-

We also predicted that individual birds would increase their probability of having molt-breeding overlap when they experienced relatively slow molts. Finally, for two bird families with frequent molt-breeding overlap and large sample sizes, we examined when molt-breeding overlap occurs in the molt cycle, providing insight into how molt and breeding may be regulated. Given that brood patches for single-brooded birds may last no longer than four weeks and that molt often follows breeding (Jones 1971, del Hoyo 1992–2010, Pyle 1997), we predicted molt-breeding overlap to occur only at the beginning of the molt cycle (i.e. when molting primary 1) if a physiological mechanism was activated to defer the initiation of molt until after breeding. Alternatively, if molt-breeding overlap were to occur haphazardly throughout the molt cycle, we would instead conclude that molt and breeding are physiologically decoupled, in contrast to conclusions drawn from many studies of temperate species.

Methods

Study site

We conducted our study at the Biological Dynamics of Forest Fragments Project (BDFFP), which is located about 80 km north of Manaus, Brazil (2°30’S, 60°W). This landscape contains largely undisturbed terra firme lowland tropical rainforest, especially to the north of our study site. The forest canopy is 30–37 m tall with emergents reaching 55 m. The understory is relatively open and is dominated by palms. Annual rainfall is approximately 2500 mm (ranging from 2000 to 3500 mm) with a dry season typically lasting from June to November (Stouffer and Bierregaard 1993, Laurance 2001). The site has some topography, especially near streams, and varies in elevation from 50 to 100 m. Soils are generally nutrient-poor sandy or clay-rich ferrasols, typical of the region (Sombroek 2000).

The BDFFP is well-known for its studies of forest fragmentation (Bierregaard et al. 2001) including considerable efforts to document the natural avian community in mature undisturbed forest (Cohn-Haft et al. 1997, Johnson et al. 2011), but also includes extensive monitoring and research at intact continuous forest that act as control sites. Here we use a long-term mist-netting database of this research from 1979 through 2009 that includes over 60,000 captures and 324,860 mist-net hours. This database has been accrued from 11 forest fragments, including 1/4 to 10 yr of pre-isolation sampling (median 1 yr; Bierregaard et al. 2001), as well as 34 continuous forest sites. Mist-nets were typically open from 08:00 to 14:00 and the number of 12 x 2-m mist nets used at each site was dependent on plot or fragment size with eight mist nets in 1-ha plots, 16 nets in 10-ha plots, and 48 nets in 100-ha plots. Beginning in 1991, an additional 16 nets were placed around the borders of fragments and interior forest plots. Fragments were sampled year-round 1–16 times (median 5 times) per year in 1979–1992, and 2000, and during the dry seasons of 2007 and 2009. Each continuous forest site has been sampled less consistently than the fragments, but collectively account for 62% of mist-net hours and 67% of all captures. Although some uncertainty remains about how fragmentation potentially impacts the phenology of molting, breeding, and their overlap (Results), the majority of our data are derived from continuous forest sites. Beginning in 1991 we collected a rectrix from each bird. Taxonomy follows Gill and Donsker (2011).

Assessing breeding, molting, and their overlap

Since 1979, molt status was determined by the occurrence (yes-no) of primary feather molt, while molt extent was determined by the number of the most recently molted primary feather (primary 1 to primary 10). Breeding status of captured birds, defined as the presence or absence of an active brood patch, indicated by a featherless oedematous hyper-vascularized belly region, was assessed since 1982. The presence of a vascularized brood patch is indicative of incubation, and typically disappears during the nestling stage (Jones 1971). We excluded captures with asymmetrical molt, defined as only one wing undergoing primary
molt, and molting and breeding records for within-month recaptures. We considered molt–breeding overlap to occur when molting primary feathers on the wing occurred simultaneously with an active brood patch. Although other metrics have been used in the literature to assess molt–breeding overlap, including gonad size, body molt, and molt overlapping fledging (Foster 1975, Nilsson and Svensson 1996, Marini and Durães 2001), our assessment is among the most conservative and least subjective. We define the frequency of molt–breeding overlap as the proportion of all breeding birds that are simultaneously molting. This, by definition, eliminates age and sex classes that do not develop brood patches from the study sample.

**Taxonomic groupings and guild classification**

To test whether there is a phylogenetic component to molt–breeding overlap, we grouped passerines into three major categories, the suboscines (suborder Tyranni), 10-primaried oscines (suborder Passeri, Muscicapoidae and Corvoidea [Vireonidae only]), and 9-primaried oscines (suborder Passeri, Passeroidea; Cracraft and Barker 2009). Although 9-primaried oscines are more correctly referred to as oscines with nine visible primaries and a clear phylogenetic boundary with oscines with 10 visible primaries (Hall 2005), our groupings here are used for convenience as they reflect three distinct phylogenetic groups among our study species.

Species were also categorized into one of eight ecological groups, or guilds, according to their diet and mode of foraging (Stouffer and Bierregaard 1995, Stouffer and Borges 2001, Stouffer et al. 2006, Johnson et al. 2011). All non-forest species were categorized together based on their previously identified dependence on second growth at the study site (Stouffer and Bierregaard 1995). Frugivores were species that regularly consumed fruit. Insectivores were split into six remaining categories: obligate ant-followers (those that depended on Eciton army-ant swarms), gap specialists (those that were dependent on tree fall gaps), terrestrial (those that foraged by walking or hopping on the ground), flock-specialists (those that spent most of their time among Thamnomanes-led mixed-species flocks), flock dropouts (those that often associated with mixed-species flocks, but were could establish territories in the absence of these flocks), and other insectivores (those that did not fall into the above five insectivore guilds, but collectively were found in the forest understory).

We tested the difference in molt–breeding overlap frequency among the three taxonomic groups, between suboscines and oscines, among families within each major taxonomic group, and among ecological guilds using Chi-square contingency tests.

**Molting and breeding phenology**

We assessed the frequency of captures either breeding or molting for each month, pooling across all years and study plots. Although we suspected some annual variation in the timing of molting and breeding, sample sizes for any given species in any given month and year were relatively low, with some years more effectively sampled than others.

**Frequency of molt–breeding overlap**

We quantified the proportion of captures with molt–breeding overlap among all 87 passerines by species, sub-family, family, and suborder. We did not examine non-passerines because they collectively represent few captures and because some have ambiguous (e.g. Trochilidae and Columbidae) or unknown brood patch development. We compared molt–breeding overlap frequencies at family- and suborder-levels, and among ecological guilds (Stouffer et al. 2006) using Chi-square contingency tests (Proc Freq, SAS ver. 9.1).

**Correlates of molt–breeding overlap**

Focusing on 31 species with ≥ 15 observed brood patches, we asked four questions to understand correlates in the frequency of molt–breeding overlap among study species.

1) **Does molt duration affect molt–breeding overlap frequency?**

We estimated molt duration (MD; the average length of time an individual takes to molt for each species) by examining recaptured individuals as they progressed through their wing molt. By noting which feather was actively molting when captured and dividing the number of feathers molted by the number of days between captures, we could therefore estimate molt duration for each individual. We then averaged molt duration among individuals to estimate molt duration for each species. These data allowed us to test the hypothesis that longer average molt duration increases the frequency of molt–breeding overlap using a simple linear regression.

A potential source of bias with our estimates is that the primary feather molt duration is not constant throughout the molting process and slows down as molt completes because of the increased length of outer primary feathers (Pimm 1976, Summers et al. 1983, Underhill and Zucchini 1988, Dawson and Newton 2004), but we expect this to have minimal impact on our conclusions. Specifically, by using recaptured birds to estimate molt duration, some birds will be equally likely to be early in the molt sequence (with relatively fast molt progression) as late in the molt sequence (with relatively slow molt progression), with the most frequent estimate of molt duration centering on the middle of the molt sequence. Further, because our study species are non-migratory understory species, the difference in feather length between the inner- and outer-most primaries is typically relatively small (Therény 1997, Lockwood et al. 1998, Claramunt et al. 2012). Finally, our use of this metric is primarily to compare the duration among species, thus if there is bias in this estimate, it should be similar among species.

2) **Can birds adjust the timing of molt to minimize molt–breeding overlap?**

We assessed the variability in the timing of molt initiation using the same birds as the previous analysis, but extrapolating back to estimate the date of wing molt initiation. We also estimated the length of the molting season (MS), which we define as the number of months that ≥ 16% of captures were molting, and the length of the breeding
season, defined as the number of months that ≥4% of captures were breeding. These molting and breeding season metrics indicate seasonality at the population level, whereas molt duration offers the duration of an individual molt within this season (we do not have data to show breeding duration on the individual level). We then explored how variation in molt initiation date, the ratio of molt duration to length of the molting season (MD/MS), and the overlap over the breeding and molting seasons predicted the frequency of molt–breeding overlap using generalized linear models (simple linear regression and 1-factor ANOVA).

3) Do feather growth rates of individual birds predict their probability of exhibiting molt–breeding overlap?
For birds with brood patches for which we also collected an outer rectrix, we measured the rate of feather growth and multiplied by the length of the feather to determine the number of days it took to completely grow an outer tail feather. We measured rectrix growth rate by measuring the distance between at least six consecutive visible growth bars, each of which are perpendicular to the rachis and indicate 24 h of growth (Michener and Michener 1938, Jovani et al. 2011). We then divided this measurement by the number of growth bars to get an average daily growth rate, known as ptilochronology (Grubb 1989). We standardized feather growth across species by constructing residuals around each species’ mean feather growth rate and then pooled residual growth rates at the guild level for a logistic regression analysis using nine species, each with at least 10 feather growth rate samples. These data test whether individual birds that molted feathers more slowly had an increased probability of molt–breeding overlap.

4) When in the molt sequence does breeding overlap?
For species in the Thamnophilidae, Formicariidae, and Furnariidae, we counted the number of individuals with brood patches according to the extent of primary feather molt (primary 1 to primary 10). If molt extent differed on each wing, we added a ‘half’ bird to each feather molt category. This tests the hypothesis that molt–breeding overlap would predominantly only at the beginning of the molt cycle (i.e. when molting primary 1) if a physiological mechanism attempts to defer the initiation of molt until after breeding. Alternatively, if the data reveal that breeding occurs haphazardly throughout the molt cycle, we would instead conclude that molt and breeding are physiologically decoupled, in contrast to conclusions drawn from many studies of temperate species.

Percentage data were arcsine-transformed and other variables were log-transformed to meet assumptions of parametric statistics where necessary. We present least-square means and standard errors unless otherwise stated.

Results
Molting and breeding phenology
Pooling across all 87 species of passerines, breeding occurred year-round at our study sites near Manaus, Brazil, but peaked in the late dry season and early wet season (September–January; Fig. 1). The frequency of molt began to increase in September and peaked in December to March. The proportion of birds molting while breeding (i.e. exhibiting molt–breeding overlap) among all captures was <2% in every month and did not correlate with monthly brood patch frequency (Pearson’s \( r = 0.24, p = 0.46 \); Fig. 1). However, when brood patch (i.e. breeding) frequency increased, proportionally fewer birds were simultaneously molting and breeding (Pearson’s \( r = -0.65, p = 0.022 \)). In other words, molt–breeding overlap appeared to be present at low frequencies throughout the year, but most breeding birds...
apparently avoided simultaneously molting and breeding during the peak of the breeding season.

Variation was considerable in the breeding and molting phenologies among 31 frequently captured species with ≥15 individuals captured with active brood patches (Table 1, 2). For many species, the breeding season was strongly seasonal and most pronounced during the dry season from June or July through January (e.g., *Certhiasomus stictolaemus*, *Xiphorhynchus pardalotus*, and *Myiobius barbatus*), whereas for other species breeding was occasionally extended into March or April, well into the wet season (e.g., *Dendrocincla merula* and *Pipa pipra*). Breeding seasons for some other species peaked during the dry season, between December and June (e.g., *Formicarius colma*, *Sclerurus ruficollis*, and *Mionectes macconnelli*). Another strategy appeared to be the presence of two breeding peaks, one during the dry season from about September to December, and a second in March and April (e.g., *Myrmeciza ferruginea* and perhaps also *Percnostola rufifrons*). Other species appeared to breed year-round, although breeding peaked at various times of the year depending on the species (e.g., *Gymnopithys rufigula*, *P. rufifrons*, and *Glyphorynchus spirurus*). Peaks of molting frequency often followed peaks of breeding (Table 1, 2), but many species had individuals molting in every month of the year, especially within Thamnophilies, but also some Furnariidae. Oscines typically had more strongly seasonal breeding and molting seasonality.

### Molt–breeding overlap by taxonomy and ecological guild

Our dataset includes 26,871 records of 87 species of Passeriformes from 1979 to 2009 for which the presence–absence of wing molt and brood patch was assessed (Supplementary material Appendix 1). Most of these records were for suboscines (90.4%), with only 6.9% from 10-primaried oscines and 2.7% from 9-primaried oscines. The most frequently captured species were in the Thamnophilidae (41.9%), followed by Furnariidae (27.5%), Pipridae (9.1%), and Tyrannidae (7.3%). An active brood patch was observed in 1472 (5.5%) of captured individuals, and of these, 187 (12.7%) were simultaneously undergoing symmetrical primary feather molt, which we considered to be molt–breeding overlap apparently avoided simultaneously molting and breeding during the peak of the breeding season.

Table 1. The proportion of captured birds (n = number of total captures) in breeding condition by species and month near Manaus, Brazil. The degree of shading corresponds to breeding frequency (none: <2.0%, light: 2–3.9; medium: 4.0–7.9; dark: >8.0). Months in bold (June–December) indicate the dry season.

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Table 2. The proportion of captured birds (n = number of total captures) with wing molt by species and month near Manaus, Brazil. The degree of shading corresponds to molting frequency (none: < 4.0%, light: 4–7.9; medium: 8.0–15.9; dark: > 16.0). Months in bold (June–December) indicate the dry season.

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(Supplementary material Appendix 1). The occurrence of molt–breeding overlap varied among species and higher-level taxa, and was significantly more frequent in suboscines (13.3%) than in oscines (6.4%; χ² = 4.6, p = 0.032; Fig. 2). The frequency of molt–breeding overlap differed significantly among suboscine families, not including families with < 15 individuals observed with brood patches (χ² = 98.2, p < 0.001; Fig. 2). Among suboscines, molt–breeding overlap was most frequent in the Thamnophilidae (23.0%) and least frequent in the Tyrannidae (4.4%), Tityridae (0.0%) and Pipridae (1.5%). Within oscines, molt–breeding overlap was more frequent in 10-primaried oscines (7.9%), especially in the Polioptilidae (15.2%), than 9-primaried oscines (2.5%), but differences between 10- and 9-primaried oscines were not significant (χ² = 1.8, p = 0.19), nor were pairwise differences among oscine families (Fig. 2). In only one occasion was molt–breeding overlap observed in a 9-primaried oscine (Cyanocompsa cyanoides; Supplementary material Appendix 1).

Molt–breeding overlap frequency differed among ecological guilds (χ² = 78.1, p < 0.001; Fig. 3). Ant-followers had the highest frequency of molt–breeding overlap (31%), followed by gap specialists, terrestrial insectivores, other insectivores, and flock obligates with 13–17%. The remaining guilds included flock dropouts, frugivores, and non-forest species, and had <7% molt–breeding overlap frequency.

Correlates of molt–breeding overlap

We focus subsequent analyses on 31 species with ≥ 15 observed brood patches. The proportion of these populations either breeding or undergoing wing molt in each month from 1979 to 2009 indicated substantial variation in the timing and duration of the molting and breeding seasons among species (Table 1, 2). Of these 31 species, 20 (65%) had substantially prolonged breeding and molting seasons that each lasted ≥ 6 months of the year. These prolonged breeding and molting seasons set the stage for molt–breeding overlap to occur at the individual-level. We asked four questions to understand how the timing and duration of life history events, like molting and breeding, affected molt–breeding overlap frequency.
Figure 2. Frequency of molt-breed overlap by order (black bars) and family (gray bars) near Manaus, Brazil. Numbers inside bars indicate the sample size (number of individuals captured with brood patches). Letters above bars represent differences using post hoc pairwise comparisons; comparisons are made across the three suborders and among families within suboscines and within 10- and 9-primaried oscines.

Figure 3. Frequency of molt-breed overlap for eight ecological guilds near Manaus, Brazil. Letters above bars represent differences among post hoc pairwise comparisons and the numbers within the bars represent the sample size (number of individuals with brood patches).
1) Does molt duration affect molt–breeding overlap frequency?

We used molt duration estimates obtained by documenting molt extent of individual birds recaptured while progressing through a complete wing molt. We obtained reasonable molt duration estimates for 27 of the 31 focal species (average ± SE: $21.2 ± 7.5$ birds examined per species; Supplementary material Appendix 2). For these 27 species, molt duration positively correlated with molt–breeding overlap frequency ($R^2 = 0.69, F_{1,25} = 56.9, p < 0.001$; Fig. 4).

2) Can birds adjust the timing of molt to minimize molt–breeding overlap?

Three strategies emerged with respect to variation in molt initiation dates. First were species with short molt duration (MD) relative to their molting season (MS; MD/MS < 0.61), hereafter called Strategy 1. These species showed a trend for the greatest variation in initial molt date and a low frequency of molt–breeding overlap (Table 3, Fig. 5), suggesting they were capable of adjusting the timing of their molt to avoid overlap with breeding. Second were species with MD more similar in length to MS: Strategy 2. These species still had a shorter MD than MS ($0.61 < MD/MS < 0.84$), intermediate variation in molt initiation date, the longest molt duration, and the greatest proportion of birds with molt–breeding overlap (Table 3). Species with these first two strategies had a higher frequency of molt–breeding overlap as MD approached MS ($R^2 = 0.56, F_{1,16} = 20.8, p < 0.001$; Fig. 5). Third were species with non-overlapping molting and breeding seasons: Strategy 3. These species had MD lasting approximately as long as MS ($0.84 < MD/MS < 1.16$), little variation in molt initiation date, and a low frequency of molt–breeding overlap (Table 3, Fig. 5) because the molting and breeding seasons were relatively distinct (Table 1, 2).

These three life history strategies appear to have a phylogenetic basis. Woodcreepers and antbirds (but also one tanager and one gnateater) typically exhibited the first two strategies, whereas Strategy 3 species were largely flycatchers, manakins, a vireo, and a thrush, but also two woodcreepers and an antthrush (Table 3).

3) Do feather growth rates of individual birds predict their probability of exhibiting molt–breeding overlap?

We used logistic regression to test whether individual birds that molted more slowly had an increased probability of molt–breeding overlap. Although guilds differed in their response (Wald’s $\chi^2_4 = 15.5, p = 0.004$), more slowly grown feathers did not increase the probability of molt–breeding overlap pooling across all nine species (Wald’s $\chi^2_1 = 2.4, p = 0.12$), although there may have been an interaction between feather growth rate and guild (Wald’s $\chi^2_4 = 7.9, p = 0.096$; Fig. 6). When we conducted the analysis using only females, the interaction became nearly significant (Wald’s $\chi^2_4 = 8.8, p = 0.066$), indicating guild-specific responses affect the influence of feather growth rates.

Table 3. Three strategies among average molt duration (MD; the length of time an individual takes to molt), variation in molt initiation date (MI; the variance of when individuals begin molting), and molt–breeding overlap (MBO) frequency near Manaus, Brazil for three strategies. Species are placed in strategies defined by the ratio of individual molt duration to the population’s molting season (MD/MS). Average MD (in days), MI (in days), and MBO (% frequency) are given ± SE, as well as the species comprising each strategy. Each of these three variables was tested for differences among strategies with a 1-factor ANOVA; letters indicate Tukey-adjusted comparisons of variable means across strategies.

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<th>Strategy 3 (distinct molting and breeding seasons)</th>
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1 Tukey-adjusted A–B difference: $p = 0.083$. 

Figure 4. The relationship between the average estimated duration of primary feather molt and the frequency of molt–breeding overlap in 27 species near Manaus, Brazil. A simple linear regression line with 95% confidence intervals is also illustrated.
our study species (Poulin et al. 1992, Pyle 1997, Marini
serines, a complete post-nuptial (‘pre-basic’ sensu Humphrey
during the wet season, and others apparently bred year-
February – April), whereas a few species bred most frequently
a secondary breeding peak during the wet season (often
and Durães 2001, Verea et al. 2009). Some species also had
Species at our study sites near Manaus, Brazil, similar to other
seasons (Strategy 3; open circles; Table 3).

4) When in the molt sequence does breeding overlap?
Among Furnariidae with molt–breeding overlap, brood
patches were observed mainly when molting primaries 1–4
and 9–10, but among Thamnophilidae with molt–breeding
overlap, brood patches were observed throughout the molt
cycle (Table 4).

Discussion
Breeding and molting seasonality near Manaus
Among all species combined, molt frequency rose and
fell about one or two months after similar rises and falls
in breeding frequency (Fig. 1). The breeding season, as
measured by brood patches, peaked during the late dry
and early wet season (October–January; Fig. 1) for many spe-
cies at our study sites near Manaus, Brazil, similar to other
Amazonian bird communities (Poulin et al. 1992, Marini
and Durães 2001, Verea et al. 2009). Some species also had
a secondary breeding peak during the wet season (often
February–April), whereas a few species bred most frequently
during the wet season, and others apparently bred year-
round (Table 1). Typical of most temperate and tropical pas-
erines, a complete post-nuptial (‘pre-basic’ sensu Humphrey
and Parkes 1959, Howell et al. 2003) follows breeding in
our study species (Poulin et al. 1992, Pyle 1997, Marini
and Durães 2001, Wolfe et al. 2009). This variation in
phenology has been demonstrated in other lowland tropical
forest communities, suggesting it may be widespread
(Chapman 1995, Wikelski et al. 2003a, b).

Molt–breeding overlap frequency
For all captured passerines, 12.7% of individual birds that
were breeding were also molting, i.e. were undergoing molt–breeding overlap. The frequency of molt–breeding
overlap varied considerably among well-sampled species,
and was highest in P. albifrons (38.8%), but at or near
0.0% in many other species (Supplementary material
Appendix 1). Antbirds in general were frequently breeding
and molting simultaneously, whereas oscines, and in par-
ticular thrushes and tanagers, rarely or never were seen with
molt–breeding overlap (Fig. 2).

Variation in molt–breeding overlap not only varied by
family but also varied according to foraging guild (Fig. 3).
In particular, ant-followers, gap specialists, terrestrial inse-
cctivores, other insectivores, and obligate flock members had
relatively frequent molt–breeding overlap compared to flock
dropouts, nonforest species, and frugivores. We acknowl-
edge confounding phylogenetic effects when sorting by for-
aging guild, because guilds with thamnophilids had greater
molt–breeding overlap than guilds without antbirds. Even
so, many other taxa contributed to at least some of these
guilds with frequent molt–breeding overlap (Supplemen-
tary material Appendix 1). Future studies should evaluate
variation in molt–breeding overlap among foraging guilds
in the Afrotropics, tropical Australasia, and Oceania to
determine whether our observed patterns are consistent
when taxonomic contributions to each guild are consider-
ably different.

Correlates of molt–breeding overlap
The duration of molt at least partially explained molt–
breeding overlap frequency. Species with greater molt–
breeding overlap frequency were those with prolonged
molds, often taking at least 150 d to complete primary
feather replacement (Fig. 4). From an energy budget per-
spective, it may be particularly costly to molt and breed
simultaneously if energetic resources are dedicated to a rapid
molt (Foster 1974). By slowing the rate of molt, daily ener-
getic demands may be reduced and would minimize costs
of molt–breeding overlap. A slow molt that decreases gaps
among flight feathers may also reduce predation risk, espe-
cially during take-off, and may ensure greater feather quality
or allow resources to be diverted to increased immunological
vigor (Slagsvold and Dale 1996, Hedenström and Sunada
1999). Gymnopithys rufifrons and P. albifrons represented
the extreme in seasonal strategies, with at least 36% in
G. rufifrons and 46% in P. albifrons molting year-round and
individuals taking 9–10 months to complete their wing
molt. These species may not maintain an annual cycle,
but instead breed when highly unpredictably local condi-
tions are suitable (i.e. when enough ant swarms in their
home range are simultaneously swarming [J. Chaves-
Campos pers. comm.]). These ant-followers, as well as
terrestrial insectivores, and flock obligates, all are most

Figure 5. The relationship between molt–breeding overlap fre-
quency and the ratio of average individual molt duration (MD)
to molting season length (MS). MD/MS indicates the relative
amount of time an average individual takes to molt relative to the
length of time that species’ population has molting individuals near
Manaus, Brazil. The simple linear regression line and 95% confi-
dence interval only includes species with Strategies 1 (black dots;
short individual molts that temporally overlap with the popula-
tion’s breeding season) and 2 (gray dots; long individual molts that
temporally overlap with the population’s breeding season), i.e.
excluding species with temporally distinct molting and breeding
seasons (Strategy 3; open circles; Table 3).
closely associated with the forest understory among our study species and had among the highest rates of molt-breeding overlap. This microhabitat is climactically the most predictable within tropical forest (Kapos et al. 1993), thus may have the lowest consequences for molt-breeding overlap from an energetic perspective. There may be additional advantages to having a prolonged molt in the understory, such as developing more structurally robust feathers, which would reduce wear and abrasion (Dawson et al. 2000); this may help explain why gap specialists also have relatively high levels of molt-breeding overlap.

When breeding and molting seasons overlap (Strategies 1 and 2), the ability to vary the timing of molt initiation appears to correlate with reduced molt-breeding overlap frequency. Other species minimize molt-breeding overlap by temporally separating the breeding and molting season (Strategy 3; Table 3, Fig. 5). Individuals of species that take the longest time to molt typically use the entire molting season to molt and are therefore less flexible in when they initiate molt (Strategy 2). This group of species in Strategy 2 also exhibits the most frequent molt-breeding overlap, but the trade-off between molt duration and energy expenditure may minimize fitness costs otherwise associated with molt-breeding overlap (Foster 1974, Slagsvold and Dale 1996, Hemborg and Lundberg 1998, Hemborg 1999, Hemborg et al. 2001).

We showed that decreased feather growth rates increased an individual bird’s probability of having molt-breeding overlap in five of nine species (Fig. 6). To our knowledge, this has not been demonstrated before and provides a unique insight into how individual birds may be forced to breed and molt simultaneously. Decreased feather growth rates can be caused by nutritional deficiencies (Grubb 1989) suggesting that depressed body condition in some birds can increase their probability of having molt-breeding overlap, which in turn may depress fecundity (Slagsvold and Dale 1996, Hemborg and Lundberg 1998, Hemborg 1999, Hemborg et al. 2001).

Individuals of some species, particularly slow-molting species like *P. albifrons*, *G. rufigula*, and *Percnostola rufigula*, did not show a relationship between feather growth rates and the probability of experiencing molt-breeding overlap, suggesting that molt-breeding overlap is not always a consequence of body condition. Many antbirds can breed and molt simultaneously at any stage of the wing molt sequence (Table 4). Even in some furnariids, molt-breeding overlap occurred nearly throughout the molting cycle, although more frequently in the beginning or end of the molt cycle.

Figure 6. The relationship between feather growth rate (residual of the average number of days for a tail feather to complete molting) and the frequency of molt-breeding overlap (MBO) for five guilds representing nine species near Manaus, Brazil illustrated by solid lines (all individuals) and dotted lines (females only) from logistic regression models. Larger residuals represent slower growing feathers. Individuals are represented by dots (females) and open circles (males) with 1.0 = experiencing molting breeding overlap and 0.0 = breeding, but not molting. Species in guilds are as follows: ant followers (*Pithys albifrons*, *Gymnopithys rufigula*), flock obligates (*Thamnomanes ardeiacus*, *T. caesius*), flock dropouts (*Glyphorynchus spirurus*, *Myrmotherula axillaris*), gap specialists (*Hypocnemis cantator*, *Percnostola rufigula*), other insectivore (*Williornis poecilinota*).
Table 4. The number of birds with brood patches, by stage of primary feather molt (primary 1 to primary 10 [p1–p10]) by species and family. Half birds are a result of asymmetry in the extent of primary molt between wings. Unk indicates birds that exhibited molt–breeding overlap (MBO), but the extent of molt was not recorded. No. MBO is sample size (the total number of birds) used for each species and family.

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>Molting primary feather</th>
<th>No. MBO</th>
</tr>
</thead>
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<tr>
<td></td>
<td></td>
<td>p1 p2 p3 p4 p5 p6 p7 p8 p9 p10 Unk No. MBO</td>
<td></td>
</tr>
<tr>
<td>Thamnophilidae</td>
<td>Fredericena viridis</td>
<td>16 17 17.5 16 10.5 13.5 11 13.5 12 22 19 171</td>
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<tr>
<td></td>
<td>Thamnophilus muniinus</td>
<td>0.5 0.5 1 2</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Thamnomanes ardesiacus</td>
<td>2.5 1.5 2 1.5 1 5.5 2.5 0.5 2 1 1 21</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Thamnomanes caesius</td>
<td>1 3.5 1 0.5 1 0.5 2.5</td>
<td></td>
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<tr>
<td></td>
<td>Epinecrophylla gutturalis</td>
<td>2</td>
<td></td>
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<tr>
<td></td>
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<td>0.5 0.5</td>
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<td></td>
<td>Myrmotherula axillaris</td>
<td>1 1</td>
<td></td>
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<tr>
<td></td>
<td>Myrmotherula longipennis</td>
<td>1 1 1 1 1 1 2 1 1 1 9</td>
<td></td>
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<tr>
<td></td>
<td>Hypocnemis cantator</td>
<td>0.5 1.5 1 1 3 3</td>
<td></td>
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<tr>
<td></td>
<td>Peruncostola rufifrons</td>
<td>2 3</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Myrmeciza ferruginea</td>
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<td></td>
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<tr>
<td></td>
<td>Myrmornis turcata</td>
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<td></td>
<td>Hylornis naevius</td>
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<tr>
<td></td>
<td>Willisonis poecilinotus</td>
<td>1.5 4 1.5 1 0.5 1.5 0.5 0.5 4 1 16</td>
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<tr>
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<td></td>
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<td></td>
<td>Automolus infuscatus</td>
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<tr>
<td></td>
<td>Xenops minutus</td>
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<tr>
<td></td>
<td>Dendrocincla fuliginosa</td>
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<tr>
<td></td>
<td>Dendrocincla merula</td>
<td>1 2</td>
<td></td>
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<tr>
<td></td>
<td>Glyphorynchus spirurus</td>
<td>0.5 1.5 2</td>
<td></td>
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<tr>
<td></td>
<td>Dendrocolaptus picumnus</td>
<td>1</td>
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<td></td>
<td>Dendrocolaptus certhia</td>
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<tr>
<td></td>
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<td>2 1 1 1 1 5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Campylorhamphus procurvoides</td>
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</table>

Brood patches for a single brood may last up to four weeks and these taxa take 15–30 d to grow a primary flight feather (Supplementary material Appendix 2). Therefore, even when primary 1 or 2 is molting, the physiological mechanisms that regulate breeding have been long activated, suggesting a minimal effort to temporally separate molting and breeding in contrast to many temperate species (Murphy 1996, Dawson 2006, Hau et al. 2008).

Across-study comparisons

Using brood patch and wing molt data from captured birds is a highly conservative metric and can easily be replicated across sites, although not all studies have assessed molt–breeding overlap in this manner. For example, Foster’s (1975) seminal paper highlighting the frequency of molt–breeding overlap among tropical birds in Costa Rica was largely based on specimens and examination of their reproductive organs. Variation among tropical birds in the degree to which they regress their gonads after breeding ranges from nearly complete, as in temperate birds, to nearly absent (Moreau 1936, Miller 1962, Snow and Snow 1964, Davis 1971, Astheimer and Buttemer 1999, Wikelski et al. 2003a). Thus, it becomes difficult to accurately determine breeding condition across many study species using reproductive organs.

Comparisons to other studies are further complicated because of inconsistencies in how to molt–breeding overlap is reported. Its frequency is in some cases measured by calculating the proportion of birds simultaneously molting and breeding among all individuals captured or otherwise sampled (Ralph and Fancy 1994, Yap 2005, Verea et al. 2009), rather than among only individuals in breeding condition. At our study sites near Manaus, Brazil, molt–breeding overlap among all individuals using this metric would be 0.7% (Supplementary material Appendix 1). This, however, includes non-breeding-season captures and demographic groups that do not typically develop brood patches, such as males of some species or subadults, and therefore is strongly dependent on the context of the study. Molt–breeding overlap reported as the number of birds breeding and molting, divided by the total number of birds breeding, as we have done, would facilitate greater comparison among studies.

Despite the limitations outlined above, some general patterns emerge across studies. First, molt–breeding overlap is widespread in the Neotropics (Foster 1975, Avery 1985, Piratelli et al. 2000, Marini and Durães 2001, Rohwer et al. 2009) and can occur in tropical regions around the world (Moreau 1936, Payne 1969, Ralph and Fancy 1994, Yap 2005). Second, molt–breeding overlap is apparently rarely pervasive in any given species, usually with <20% of breeding individuals also molting (Marini and Durães 2001, Supplementary material Appendix 1). Third, studies conducted in the wet Neotropics suggest some consistency in the frequency of molt–breeding overlap. At 18–22°S, Marini and Durães (2001) found 8.3% molt–breeding overlap when expressed as the percentage of breeding birds simultaneously molting. This is consistent with Foster (1975)
with 8.1% at 10°N and this study near Manaus, Brazil with 12.7% at 2°S. Geographical patterns, such as latitudinal and environmental gradients in molt–breeding overlap, remain difficult to confidently discern, however, because so few community-level datasets are available, and because molt–breeding overlap frequencies likely depend on the biome, region, and taxonomic composition of the avian community (Poulin et al. 1992, Mallet-Rodrigues 2005, Magalhães et al. 2007). For example, we primarily studied understory passerines, and molt–breeding overlap frequency of the community may increase or decrease as other members of the community are included.

Although the physiology underlying molt–breeding overlap and the role of the environment on molt–breeding overlap remains largely untested, our research suggests that it is an important component of life history events in some tropical birds. Future studies documenting molt–breeding overlap should report both the proportion of total birds with molt–breeding overlap as well as the proportion with breeding evidence that are simultaneously molting. This will facilitate cross-regional comparisons to understand the frequency, extent, and variation of breeding, molting, and their overlap among tropical birds.

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Supplementary material (Appendix J5574 at <www.oikos office.lu.se/appendix>). Appendix 1–2.