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# Reduced Feather Growth Rates of Two Common Birds Inhabiting Central Amazonian Forest Fragments

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**Abstract:** *Forest fragmentation may negatively affect populations typically found within continuous forest tracts. Some effects, such as absence from small fragments, are obvious, but other effects may be subtle and easily overlooked. We evaluated the hypothesis that forest birds dwelling in fragments, where microclimatic conditions have been shown to be hotter and drier than in continuous forest, may be in poorer physiological condition than those in the forest interior. We studied two bird species, the Wedge-billed Woodcreeper (*Glyphorhynchus spirurus*) and the White-crowned Manakin (*Pipra pipra*), common to the fragmented landscape north of Manaus, Brazil. We analyzed feather growth rates in *Pipra* and *Glyphorhynchus* captured in 1-, 10-, and 100-ha forest fragments and continuous forest. Mean daily feather growth rates of the outer right rectrix of birds captured in fragments were significantly slower than feather growth rates of birds captured in continuous forest. Based on recapture data, Wedge-billed Woodcreepers probably grew their feathers in sites where they were first captured. White-crowned Manakins, however, were highly mobile and were recaptured rarely. Although we cannot conclusively show that fragmentation caused birds to be in poorer physiological condition, the data indicate that birds in poorer physiological condition were more likely to be captured in fragments than in continuous forest. Thus, our data suggest that forest fragmentation may have subtle but important effects on species that are relatively common after landscape alteration.*

Reducción de la Tasas de Crecimiento de Lumas de Dos Aves Canoras de Fragmentos de la Amazonía Central

**Resumen:** *La fragmentación de bosques puede afectar negativamente a poblaciones que típicamente habitan en bosques continuos. Algunos efectos, como la ausencia en algunos fragmentos, son obvios; pero otros son sutiles y fácilmente pasan desapercibidos. Evaluamos la hipótesis de que las condiciones fisiológicas de aves que habitan en fragmentos, donde las condiciones microclimáticas son más calientes y secas que en bosques continuos, son más pobres que las de aves del interior de los bosques. Estudiamos a dos especies, *Glyphorhynchus spirurus* y *Pipra pipra*, comunes en el paisaje fragmentado al norte de Manaus, Brasil. Analizamos las tasas de crecimiento de plumas en *G. spirurus* y *P. pipra* capturados en fragmentos de 1-, 10- y 100 ha y en bosque continuo. La tasa media de crecimiento de la rectriz externa derecha de las aves capturadas en fragmentos fue significativamente menor que la de aves capturadas en bosque continuo. Con base en datos de recaptura, es probable que *G. spirurus* desarrolló sus plumas en los sitios donde fueron capturados la primera vez. Sin embargo, *P. pipra* fueron altamente móviles y raramente fueron recapturados. Aunque no podemos mostrar concluyentemente que la fragmentación provocó condiciones fisiológicas pobres en las aves, los datos indican que las aves con condiciones fisiológicas pobres tenían mayor probabilidad de ser capturadas en fragmentos que en bosques continuos. Por tanto, nuestros datos sugieren que la fragmentación de bosques puede tener efectos sutiles, pero importantes, sobre especies relativamente comunes después de la alteración del paisaje.*

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## Introduction

The negative effects of forest fragmentation on avian communities are well documented. Forest fragmentation may affect populations through increased nest predation (Small & Hunter 1988; Andr en 1992; Robinson et al. 1995) and increased exposure to brood parasites and predators of adults (Ambuel & Temple 1983; Brittingham & Temple 1983; Robinson et al. 1995). At the community level, the consequences of forest fragmentation may include reduced species richness (Galli et al. 1976; Ambuel & Temple 1983; Howell 1984; Soul e et al. 1988; Keller & Anderson 1992; McCoy & Mushinsky 1994), reduced densities (Askins et al. 1987; M oller 1987; Wenny et al. 1993), or interruption of normal social interactions such as mixed-species flocks (Stouffer & Bierregaard 1995a).

Field studies investigating the effects of fragmentation have been conducted primarily in North America and Europe. The majority of these studies rely on abundance data to test hypotheses concerning the effects of forest fragmentation on bird communities (Lynch & Whigham 1984; Wilcove 1985; Robbins et al. 1989; Askins et al. 1990; Matthysen et al. 1995). Fewer data on fragmentation are available for tropical forests (but see Willis 1974, 1979; Leck 1979; Bierregaard & Lovejoy 1989; Bierregaard 1990; Stouffer & Bierregaard 1995a, 1995b; Robinson 1999; Stratford & Stouffer 1999), even though tropical species are thought to be more sensitive to fragmentation (Terborgh 1974; Remsen & Parker 1984; Karr et al. 1990). Moreover, generalizations of the effects of fragmentation from North American and European studies may be inappropriate because many Neotropical taxa are phylogenetically and ecologically distinct from taxa occurring in North America (Hansen & Urban 1992). More comprehensive studies of habitat fragmentation in the tropics have consisted of monitoring abundance changes over several years (e.g., Stouffer & Bierregaard 1995a, 1995b). Other studies in the Neotropics have compared bird abundance among fragments or between fragments and nearby continuous forest during a single sampling episode (e.g., Willis 1974, 1979; Leck 1979; Karr 1982). More direct measurements of the effects of fragmentation, such as effects on reproductive success (e.g., Robinson et al. 1995), are logistically difficult in tropical forests due to a number of factors, including highly concealed nests and low densities of species (Karr 1981).

We used ptilochronology (Grubb 1989) to examine the relationship between landscape and feather growth. In ptilochronology, the width of the growth bars on feathers is used to infer the bird's nutritional condition while the feather was growing (reviewed in Grubb 1995; cf. Murphy & King 1991). Healthy birds are assumed to grow their feathers faster and hence have

wider growth bars. Grubb (1989) originally used ptilochronology to determine the effects of supplemental food supplies on Downy Woodpeckers (*Picooides pubescens*). He found that female woodpeckers with supplemented winter food supplies had higher feather growth rates than those females without extra food. Subsequent studies have further demonstrated the validity of ptilochronology in both the laboratory (Grubb 1991; Zuberbier & Grubb 1992; Brodin 1993; Grubb & Pravosudov 1994) and in the field for an array of applications, including quantifying the effects of social foraging (Grubb 1989; Cimprich & Grubb 1994), food caches (Waite 1990), brood size (White et al. 1991), habitat quality (Grubb & Yosef 1994), and territory size (Yosef & Grubb 1992).

Studies of birds in Amazonian forest fragments have revealed dramatic negative effects of fragmentation in many forest understory birds (Stouffer & Bierregaard 1995a). Nevertheless, many species persisted in fragments as small as 1 ha. This is 25% of the territory size of even the most common Amazonian forest birds (Powell 1989; Terborgh et al. 1990). We hypothesized that forest birds in small fragments would be affected negatively by fragmentation and that ptilochronology could be used to reveal differences in condition among birds in different-sized fragments. Possible mechanisms influencing the nutritional condition of the birds include microhabitat change associated with edge effects, reduced prey availability, changes in vegetation structure, or increased vigilance for predators. We examined abundance patterns and feather growth in two species of understory birds that occur in fragments and continuous forest.

## Study Species and Site

We chose two bird species common in Amazonian forest fragments and continuous forest. The White-crowned Manakin (*Pipra pipra*) is a dispersed-lekking member of the Pipridae. It can be found from Costa Rica to southern Brazil (Ridgely & Tudor 1994). It forages for fruit and insects in the understory of mature forest (Stotz & Bierregaard 1989), but is also found in secondary habitats, especially *Cecropia*-dominated areas (Borges 1995). We considered only green individuals—immature males and females—in the analysis of feather growth. Sample sizes of adult males were too low to be included in the analyses.

The Wedge-billed Woodcreeper (*Glyphorhynchus spirurus*) is a diminutive, widespread member of the Dendrocolaptidae (Ridgely & Tudor 1994). It is distributed from southern Mexico to eastern Brazil (Ridgely & Tudor 1994). This species was one of the most common birds in a number of studies conducted in wet Neotropical forests (Levey 1988; Karr et al. 1990; Thiollay 1994).

*Glyphorynchus* is a scansorial bark forager that feeds alone or in pairs and is often found in mixed flocks (Munn & Terborgh 1979; Stotz & Bierregaard 1989; Stotz 1993). *Glyphorynchus* will also use secondary growth areas and treefall gaps (Levey 1988; Karr et al. 1990; Loiselle & Blake 1994), especially those areas dominated by *Cecropia* (Borges 1995).

Our study was conducted in 1991–1992, approximately 80 km north of Manaus in the Brazilian state of Amazonas (lat. 2°30'S, long. 60°W). We collected data from five 1-ha, four 10-ha, and two 100-ha fragments and a continuous-forest reference site. See Lovejoy et al. (1986) for a more detailed description of the site and Stratford and Stouffer (1999) for a map. The area is a mosaic of terra firme forest, active cattle ranches, early successional areas, and fragments of primary forest. The fragments are located on three adjacent cattle ranches with approximately 50 km separating the most distant fragments.

Fragments were created by cattle ranchers clearing land in collaboration with the Biological Dynamics of Forest Fragments Project (BDFFP) (reviews by Lovejoy & Bierregaard 1990; Bierregaard et al. 1992). The fragments were created between 1980 and 1990 (10 of the 11 fragments were isolated by 1984). Fragments were separated by distances ranging from 70 to 650 m to the nearest continuous forest. At three 1-ha and two 10-ha fragments, the vegetation surrounding the fragments was burned, and cattle were allowed to graze around the fragments. After several years, plant growth dominated by trees in the genera *Vismia* (Clusiaceae) and *Bellucia* (Melastomataceae) appeared in these areas. By 1991 this growth was 3–7 m high around the fragments. At the two other 1-ha and two 10-ha sites, the felled vegetation was not burned and *Cecropia sciadophylla* (Cecropiaceae) quickly dominated. By 1991 this growth was 12–15 m high. The 100-ha fragments were partially surrounded by both *Cecropia* and *Vismia*. Apart from the cattle ranches, sites are embedded in continuous forest unbroken for hundreds of kilometers.

In the continuous forest, canopy height averages 30–35 m, with occasional emergents up to 55 m. The understory is relatively open and dominated by palms. Understory fruiting shrubs are comparatively uncommon, possibly because of poor soils (Gentry & Emmons 1987). Rainfall at Reserva Ducke, approximately 50 km south of the study site, averaged 2500 mm/year from 1966 to 1990, with the greatest amount of rainfall from January to April and a pronounced dry season from June to September (Stouffer & Bierregaard 1993).

Reviews of the site avifauna have been provided by Cohn-Haft et al. (1997). The understory bird community at this site has been analyzed for the short- and long-term effects of fragmentation (Bierregaard 1990; Bierregaard & Lovejoy 1989; Bierregaard et al. 1992; Stouffer & Bierregaard 1995a, 1995b).

## Methods

### Mist Netting

*Glyphorynchus* and *Pipra* were captured in mist nets as part of a larger study examining the effects of fragmentation on understory species (Stouffer & Bierregaard 1995a; Bierregaard & Stouffer 1997). Before isolation, trails were cut through the areas that were to be sampled. Lines of 8 mist nets (NEBBA-type ATX, 36-mm mesh, 12 × 2 m), set with the bottom of the net at ground level, were used to sample 1-ha fragments. One line of 16 nets was used in 10-ha fragments, three lines of 16 nets were used in the 100-ha fragments, and four lines of 16 nets were used in the reference area. Each line was opened for 1 day at a time from 0600 to 1400 hours. Sites were sampled approximately once every 2 months from before isolation until about 3 years after isolation, less frequently until 1991, and every 6 weeks from 1991 to 1992. We used capture rate (captures/1000 net hours) as a standard estimator of abundance. *Glyphorynchus* and *Pipra* are active understory species, and mist netting is probably an efficient method for sampling these species. At times their foraging heights may have been higher than the mist nets but this potential bias (Remsen & Good 1996) should be equal across fragments and continuous forest. Same-day recaptures were not included in the analysis. Birds were banded and released at the point of capture.

Our long-term analysis of bird abundance in response to fragmentation was based on 11,208 net hours before isolation and 54,315 net hours 9 years after isolation. For this analysis, we partitioned time into five periods: pre-isolation (time 0); 0–1 year after isolation (time 1); 1–3 years after isolation (time 2); 3–6 years after isolation (time 3); and 6–9 years after isolation (time 4). Some fragments had been isolated for more than 9 years, but 9 years was the maximum balanced sample. The long-term data included 1- and 10-ha fragments from preisolation through 1991. Fragments of 100 ha were excluded from the analysis, because only one 100-ha fragment was isolated until 1990. The long-term analysis dataset ended after August 1991 because the matrix surrounding seven of the 1- and 10-ha fragments was recut in 1991–1992.

For the long-term data, we used repeated-measures analysis of variance (ANOVA) to analyze time trends, fragment-size effects, and second-growth effects (either *Cecropia*- or *Vismia*-dominated). These data are well suited to repeated-measures analysis because the same sites were sampled repeatedly with the same protocol. (For more complete details of the analysis, see Stouffer & Bierregaard 1995a). We report the *p* values from univariate test of within-fragment effects of time and its interactions with the main effects (Stevens 1990). We used natural log-transformed capture rates in all para-

metric analyses to reduce the correlation between the variance and mean within samples (Sokal & Rohlf 1981).

We analyzed capture-rate data from 1991–1992 separately. These data include two 100-ha fragments, four 10-ha fragments, four 1-ha fragments, and a continuous forest site. All sites were sampled eight times, for a total of 14,336 net hours. We tested for heterogeneity in capture rates among size classes of fragments using log-likelihood ratio tests of the null hypothesis of equal abundance in all fragments based on netting effort. Expected captures were based on the total number of captures and the netting effort for each size class multiplied by the number of replicates for each of the size classes. Because the netting effort was the same for all size classes, the expected number of captures was equal except for the 1-ha fragments, which had half the expected value because the effort was also half. For all these tests,  $df = 3$ .

### Ptilochronology

We collected feathers for ptilochronology from birds netted in continuous forest and 1-, 10-, and 100-ha fragments in 1991 and 1992, using the procedure outlined by Grubb (1989). We removed only the sixth right rectrix to control for interfollicular variation in growth rates. We then placed the feather in a glassine envelope until analysis. When possible we used an induced feather; when birds were captured only once, however, we used feathers that were not induced because of constraints of sample size. We marked growth bars on an index card by poking through the feather with a small mounting pin at the distal edge of the dark growth bar along the feather rachis. We considered only feathers for which we could find a minimum of eight adjacent growth bars. The mean daily growth rate (MDG) was found by dividing the aggregate width of the growth bars by the number of bars.

Fragments of equivalent sizes were pooled in our analysis. We used analysis of covariance (ANCOVA) with species effect as a block, because we knew a priori that species of different mass grow feathers at different rates. Wing length was entered as the covariate. We tested the homogeneity of slopes by testing the interaction between fragment and wing length. We then followed the ANCOVA with an orthogonal contrast of the three fragment size classes versus the reference area (1,1,1,-3).

## Results

### Capture Rates

Repeated-measures ANOVA indicated no significant long-term trends in capture rates of *Glyphorhynchus* (all  $p > 0.109$ ) in 1-ha and 10-ha fragments (Fig. 1). Fragment size and type of second growth were not signifi-

cant as main effects ( $p > 0.53$ ) and did not have significant interactions ( $p > 0.09$ ). Repeated-measures ANOVA for all fragments also indicated no significant long-term trends in capture rates of *Pipra* ( $p = 0.10$ ). Fragment size and type of secondary growth were not significant main effects ( $p = 0.07$ ), and their interaction was not significant ( $p > 0.10$ ). Although not statistically significant, both species showed a decline in capture rates, followed by a return to pre-isolation abundance (Fig. 1).

These two species were among the 10 most abundant captured in continuous forest and all fragment size classes. Despite their overall ubiquity, capture rates of these two species were lower in smaller fragments in the 1991–1992 data. Observed capture rates differed significantly from the expected values for *Glyphorhynchus* ( $G = 26.1$ ,  $df = 3$ ,  $p < 0.001$ ) and *Pipra* ( $G = 11.4$ ,  $df = 3$ ,  $p < 0.01$ ). *Pipra* was most abundant in the 100-ha fragments, and *Glyphorhynchus* was most abundant in continuous forest (Fig. 2). The number of captures was lowest in the 1-ha fragments and intermediate in the 10-ha fragments for both species (Fig. 2).

### Feather Growth Rates

The interaction between fragment and wing length was not significant in the first ANCOVA model ( $p = 0.818$ ). This interaction was dropped, and the second model resulted in significant species effects ( $p < 0.001$ ) and body-size effects ( $p < 0.001$ ) and a fragment effect ( $p =$

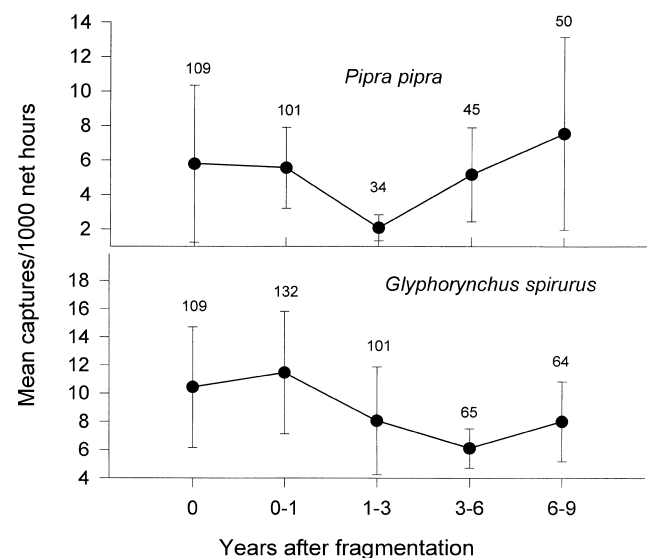


Figure 1. Long-term, mist-net capture rates (mean  $\pm$  2 SE) of *Pipra pipra* and *Glyphorhynchus spirurus* in forest fragments near Manaus, Brazil. Year (0) refers to the fragment before isolation. Numbers associated with error bars indicate sample size.

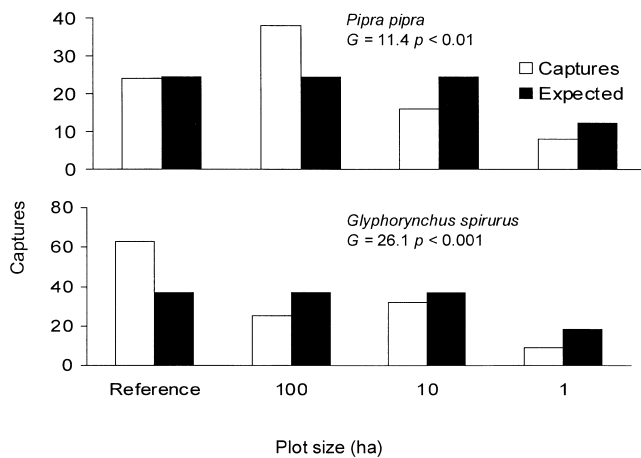


Figure 2. Comparison of expected and observed mist-net captures of *Pipra pipra* and *Glyphorynchus spirurus* in forest fragments and a reference plot near Manaus, Brazil.

0.063) that was not significant. When we used the residuals after the effect of bird size was removed, the orthogonal contrast of fragments versus reference resulted in a significant fragment effect ( $p = 0.023$ ), indicating that feathers from the birds captured in fragments grew more slowly than feathers from birds captured in continuous forest (Fig. 3). Generally, *Glyphorynchus* was more likely captured before and after a feather was pulled than was *Pipra* (Table 1).

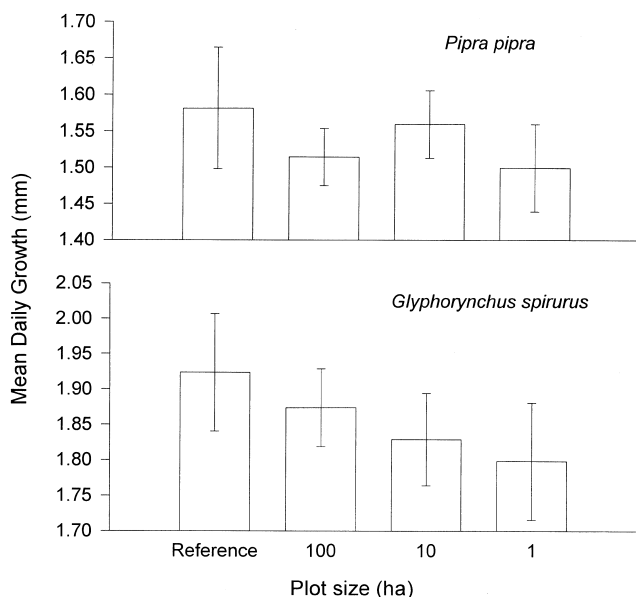


Figure 3. Mean daily feather growth rates (mean  $\pm$  2 SE) of *Pipra pipra* and *Glyphorynchus spirurus* in forest fragments and a reference plot near Manaus, Brazil. See Fig. 1 for sample sizes.

Table 1. *Glyphorynchus spirurus* and *Pipra pipra* recaptured north of Manaus, Brazil.\*

	Fragment			Reference plot
	1 ha	10 ha	100 ha	
<i>Glyphorynchus spirurus</i>				
previously captured	3	7	8	0
recaptured	1	4	6	2
no recaptures	7	1	6	11
no data	2	1	0	0
total	13	13	20	13
<i>Pipra pipra</i>				
previously captured	0	1	3	2
recaptured	0	4	7	1
no recaptures	13	13	17	6
no data	0	0	0	0
total	13	18	27	9

\*Capture data are presented in relation to when a rectrix was pulled. Previous captures and recaptures took place at least 6 weeks before and after a feather was pulled, respectively.

## Discussion

There were no appreciable long-term changes in the capture rates of *Glyphorynchus* and *Pipra* over as many as 12 years in some fragments, despite habitat fragmentation and subsequent successional changes around and within fragments. After isolation there was not the dramatic decrease in capture rates that has been found for the majority of understory species (Stouffer & Bierregaard 1995a; Stratford & Stouffer 1999). There does, however, appear to be a trend toward lower abundance after a few years. This is probably a complex interaction between an initial lack of recruitment into the fragments and succession of the matrix which allowed new individuals to colonize fragments. The disparity of reaction to fragmentation between the two species considered here and other species at the site (e.g., Stratford & Stouffer 1999) suggests that reaction to fragmentation is species-specific and should not be generalized for forest-interior species. Perhaps it is the ability of *Glyphorynchus* and *Pipra* to utilize the second growth around the fragments that buffers the effect of isolation. This could also explain the reduced abundance in 1-ha fragments in 1991–1992 (Fig. 2) because three of the four fragments had been reisolated during that period, probably reducing movements into and out of the fragments.

These data suggest that there are no long-term effects of fragmentation on *Pipra* and *Glyphorynchus* abundance, except in small, isolated fragments. But, analysis of the feather-growth data show that birds in forest fragments grew their feathers more slowly than birds in continuous forest. Mean growth rates of the feathers were lower for individuals of both species residing in the smallest fragments and were higher in continuous forest. Feather growth rates of these two species were negatively affected by fragmentation, even though we cap-

tured these species after the second growth around the fragments was developed enough for many fragmentation-sensitive species to return to the fragments (e.g., Stouffer & Bierregaard 1995a).

How does fragmentation affect feather growth? The increased temperatures and decreased humidity in the smaller fragments (Kapos 1989) may affect feather growth directly, although experimental evidence to date suggests that this is unlikely. Zuberbier and Grubb (1992) failed to find a correlation between ambient temperatures and feather growth, although their experiments were restricted to cold temperatures and water was provided ad libitum. Weathers (1997) suggests that tropical species have high rates of evaporative water loss, which would be exacerbated in small fragments (Kapos 1989). For *Glyphorhynchus*, the collapse of flocks in small fragments may mean that the loss of vigilance against predators or other advantages of social foraging lead to reduced foraging efficiency and slower feather growth.

Insect abundance may be reduced in fragments as a result of drier conditions (Lovejoy et al. 1986; Kapos 1989). Shelly (1988) found that day-flying insects were more common in the more humid understory than in treefall gaps. It is not known, however, how fragmentation may affect insects that are available for *Glyphorhynchus*, a bark gleaner, or for the partially frugivorous *Pipra*. Fruit availability may actually increase along edges (Levey 1988), even though overall foraging area is reduced. This suggests that factors other than food availability may be affecting feather growth. Malcolm (1994) showed that canopy cover decreases and shrub cover increases in fragments and that these changes may affect birds directly by changing the foraging substrate.

Birds with slower-growing feathers may have grown their feathers in continuous forest then emigrated to fragments. This is probably the case for *Pipra pipra*, which was rarely recaptured in fragments. Even for *Glyphorhynchus spirurus*, socially dominant individuals in continuous forest may push juveniles or birds in poorer physiological condition into fragments (Fretwell & Lucas 1970). Several temperate species show despotic distributions in relation to habitat quality (e.g., Andr n 1990; Holmes et al. 1996). Despotic distributions may be even more common in tropical birds, which tend to be longer-lived and have stable year-round territories (Greenberg & Gradwohl 1986; Terborgh et al. 1990).

Regardless of the causes of reduced feather growth, our results suggest that fragments represent inferior habitat, even for birds that are relatively unaffected numerically. Thus there may be subtle effects of fragmentation that are overlooked by abundance data. The next step is to determine if these birds in fragments are making a positive demographic contribution to the population at a larger scale or if they are marooned in a sink. Although more direct, mechanistic examinations of the effects of

forest fragmentation in the tropics will remain difficult, we encourage researchers to develop techniques that will more accurately assess how bird populations are faring in fragmented landscapes.

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## Literature Cited

- Ambuel, B., and S. A. Temple. 1983. Area-dependent changes in the bird communities and vegetation of southern Wisconsin forests. *Ecology* **64**:1057-1068.
- Andr n, H. 1990. Despotic distribution, unequal reproductive success, and population regulation in the jay *Garrulus glandarius* L. *Ecology* **71**:1796-1803.
- Andr n, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. *Ecology* **73**:794-804.
- Askins, R. A., M. J. Philbrick, and D. S. Sugeno. 1987. Relationship between the regional abundance of forest and the composition of forest bird communities. *Biological Conservation* **39**:129-152.
- Askins, R. A., J. F. Lynch, and R. Greenberg. 1990. Population declines in migratory birds in eastern North America. *Current Ornithology* **7**:1-57.
- Bierregaard, R. O., Jr. 1990. Avian communities in the understory of Amazonian forest fragments. Pages 333-343 in A. Keast, editor. *Biogeography and ecology of forest bird communities*. SPB Academic, The Hague, The Netherlands.
- Bierregaard, R. O., Jr., and T. E. Lovejoy. 1989. Effects of forest fragmentation on understory bird communities. *Acta Amazonica* **19**: 215-241.
- Bierregaard, R. O., Jr., T. E. Lovejoy, V. Kapos, A. A. dos Santos, and R. W. Hutchings. 1992. The biological dynamics of tropical rainforest fragments. *BioScience* **42**:859-866.
- Bierregaard, R. O., Jr., and P. C. Stouffer. 1997. Understory birds and dynamic habitat mosaics in Amazonian rainforests. Pages 138-155 in W. F. Laurance and R. O. Bierregaard, Jr., editors. *Tropical forest remnants: ecology, management, and conservation of fragmented communities*. University of Chicago Press, Chicago.
- Borges, S. H. 1995. Comunidade de aves em dois tipos de vegeta o secund ria da Amaz nia central. Masters thesis. Instituto Nacional de Pesquisas de Amazonia, Amazonas, Brazil.
- Brittingham, M. C., and S. A. Temple. 1983. Have cowbirds caused forest songbirds to decline? *BioScience* **33**:31-35.
- Brodin, A. 1993. Radio-pitochronology: tracing radioactively labeled food in feathers. *Ornis Scandinavica* **24**:167-173.
- Cimprich, D. A., and T. C. Grubb Jr. 1994. Consequences for Carolina Chickadees of foraging with Tufted Titmice in winter. *Ecology* **75**: 1615-1625.
- Cohn-Haft, M., A. Whittaker, and P. C. Stouffer. 1997. A new look at

- the "species-poor" central Amazon: the avifauna north of Manaus, Brazil. *Ornithological Monographs* **48**:205-235.
- Fretwell, S. D., and H. L. Lucas Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* **19**:16-36.
- Galli, A. E., C. F. Leck, and R. T. T. Forman. 1976. Avian distribution patterns in forest islands of different sizes in central New Jersey. *Auk* **93**:356-364.
- Gentry, A. H., and L. H. Emmons. 1987. Geographic variation in fertility, phenology, and composition of the understory of Neotropical forests. *Biotropica* **19**:216-227.
- Greenberg, R., and J. Gradwohl. 1986. Constant density and stable territoriality in some tropical insectivorous birds. *Oecologia* **69**:18-25.
- Grubb, T. C., Jr. 1989. Ptilochronology: feather growth bars as indicators of nutritional status. *Auk* **106**:314-320.
- Grubb, T. C., Jr. 1991. A deficient diet narrows growth bars on induced feathers. *Auk* **108**:725-727.
- Grubb, T. C., Jr. 1995. Ptilochronology: a review and prospectus. *Current Ornithology* **12**:89-114.
- Grubb, T. C., Jr., and V. V. Pravosudov. 1994. Ptilochronology: follicle history fails to influence growth of induced feather. *Condor* **96**:214-217.
- Grubb, T. C., Jr., and R. Yosef. 1994. Habitat-specific nutritional condition in Loggerhead Shrikes (*Lanius ludovicianus*): evidence from ptilochronology. *Auk* **111**:756-759.
- Hansen, A. J., and D. L. Urban. 1992. Avian response to landscape pattern: The role of species' life histories. *Landscape Ecology* **7**:163-180.
- Holmes, R. T., P. P. Marra, and T. W. Sherry. 1996. Habitat-specific demography of breeding Black-throated Blue Warblers (*Dendroica caerulescens*): implications for population dynamics. *Journal of Animal Ecology* **65**:183-195.
- Howell, R. W. 1984. Local dynamics of bird assemblages in small forest habitat islands in Australia and North America. *Ecology* **65**:1585-1601.
- Kapos, V. 1989. Effects of isolation on the water status of forest patches in the Brazilian Amazon. *Journal of Tropical Ecology* **5**:173-185.
- Karr, J. R. 1981. Surveying birds in the tropics. *Studies in Avian Biology* **6**:548-553.
- Karr, J. R. 1982. Avian extinction on Barro Colorado Island, Panama: a reassessment. *The American Naturalist* **119**:220-239.
- Karr, J. R., S. Robinson, J. G. Blake, and R. O. Bierregaard Jr. 1990. Birds of four Neotropical rainforests. Pages 237-269 in A. H. Gentry, editor. *Four Neotropical forests*. Yale University Press, New Haven, Connecticut.
- Keller, M. E., and S. H. Anderson. 1992. Avian use and habitat configurations created by forest cutting in southeastern Wyoming. *Condor* **94**:55-65.
- Leck, C. F. 1979. Avian extinctions in an isolated tropical wet-forest reserve, Ecuador. *Auk* **96**:343-352.
- Levey, D. J. 1988. Tropical wet forest treefall gaps and distributions of understory birds and plants. *Ecology* **69**:1076-1089.
- Loiselle, B. A., and J. G. Blake. 1994. Annual variation in birds and plants of a tropical second growth woodland. *Condor* **96**:368-380.
- Lovejoy, T. E., and R. O. Bierregaard Jr. 1990. Central Amazonian forests and the minimum critical size of ecosystems project. Pages 60-71 in A. H. Gentry, editor. *Four Neotropical rainforests*. Yale University Press, New Haven, Connecticut.
- Lovejoy, T. E., R. O. Bierregaard Jr., A. B. Rylands, J. R. Malcolm, C. E. Quintela, L. H. Harper, K. S. Brown Jr., A. H. Powell, G. V. N. Powell, H. O. R. Schubart, and M. B. Hayes. 1986. Edge and other effects of isolation on Amazon forest fragments. Pages 257-285 in M. E. Soulé, editor. *Conservation biology: the science of scarcity and diversity*. Sinauer Associates, Sunderland, Massachusetts.
- Lynch, J. F., and D. F. Whigham. 1984. Effects of forest fragmentation on breeding bird communities in Maryland, USA. *Biological Conservation* **28**:287-324.
- Malcolm, J. R. 1994. Edge effects in central Amazonian forest fragments. *Ecology* **75**:2438-2445.
- Matthysen, E., F. Adriaensen, and A. A. Dhondt. 1995. Dispersal distances of nuthatches, *Sitta europaea*, in a highly fragmented habitat. *Oikos* **72**:375-381.
- McCoy, E. D., and H. R. Mushinsky. 1994. Effects of fragmentation on the richness of vertebrates in the Florida scrub habitat. *Ecology* **75**:446-457.
- Møller, A. P. 1987. Breeding birds in habitat patches: random distribution of species and individuals? *Journal of Biogeography* **14**:225-236.
- Munn, C. A., and J. W. Terborgh. 1979. Multi-species territoriality in Neotropical foraging flocks. *Condor* **81**:338-347.
- Murphy, M. E., and J. R. King. 1991. Ptilochronology: a critical evaluation of assumptions and utility. *Auk* **108**:695-704.
- Powell, G. V. N. 1989. On the possible contribution of mixed species flocks to species richness in Neotropical avifaunas. *Behavioral Ecology and Sociobiology* **24**:387-393.
- Remsen, J. V., Jr., and D. A. Good. 1996. Misuse of data from mist-net captures to assess relative abundance in bird populations. *Auk* **113**:381-398.
- Remsen, J. V., Jr., and T. A. Parker III. 1984. Arboreal dead-leaf searching birds of the Neotropics. *Condor* **86**:36-41.
- Ridgely, R. S., and G. Tudor. 1994. *The birds of South America*. Volume 2. University of Texas Press, Austin.
- Robbins, C. S., D. K. Dawson, and B. A. Dowell. 1989. Habitat area requirements of breeding forest birds of the Middle Atlantic States. *Wildlife Monographs* **103**:1-34.
- Robinson, S. K., F. R. Thompson III, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science* **267**:1987-1990.
- Robinson, W. D. 1999. Long-term changes in the avifauna of Barro Colorado Island, Panama, a tropical forest isolate. *Conservation Biology* **13**:85-97.
- Shelly, T. E. 1988. Relative abundance of day-flying insects in treefall gaps vs. shaded understory in a Neotropical forest. *Biotropica* **20**:114-119.
- Small, M. F., and M. L. Hunter Jr. 1988. Forest fragmentation and avian nest predation in forested landscapes. *Oecologia* **76**:62-64.
- Sokal, R. R., and F. J. Rohlf. 1981. *Biometry*. W. H. Freeman, New York.
- Soulé, M. E., D. T. Bolger, A. C. Alberts, J. Wright, M. Sorice, and S. Hill. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conservation Biology* **2**:75-92.
- Stevens, J. 1990. *Intermediate statistics: a modern approach*. Erlbaum, Hillsdale, New Jersey.
- Stotz, D. F. 1993. Geographic variation in species composition of mixed species flocks in lowland humid forests in Brazil. *Papéis Avulsos de Zoologia* **38**:61-75.
- Stotz, D. F., and R. O. Bierregaard Jr. 1989. The birds of the fazendas Porto Alegre, Esteio, and Dimona north of Manaus, Amazonas, Brazil. *Revista Brasileira de Biologia* **49**:861-872.
- Stouffer, P. C., and R. O. Bierregaard Jr. 1993. Spatial and temporal abundance pattern of Ruddy Quail-Doves (*Geotrygon montana*) near Manaus, Brazil. *Condor* **95**:896-903.
- Stouffer, P. C., and R. O. Bierregaard Jr. 1995a. Use of Amazonian forest fragments by understory insectivorous birds. *Ecology* **76**:2429-2445.
- Stouffer, P. C., and R. O. Bierregaard Jr. 1995b. Effects of forest fragmentation on understory hummingbirds in Amazonian Brazil. *Conservation Biology* **9**:1085-1094.
- Stratford, J. A., and P. C. Stouffer. 1999. Local extinction of terrestrial insectivorous birds in a fragmented landscape near Manaus, Brazil. *Conservation Biology* **13**:1416-1423.
- Terborgh, J. 1974. Preservation of natural diversity: the problem of extinction prone species. *BioScience* **24**:715-722.
- Terborgh, J., S. K. Robinson, T. A. Parker III, C. A. Munn, and N. Pierpont. 1990. Structure and organization of an Amazonian forest bird community. *Ecological Monographs* **60**:213-238.
- Thiollay, J. 1994. Structure, density, and rarity in an Amazonian rainforest bird community. *Journal of Tropical Ecology* **10**:449-481.

- Waite, T. A. 1990. Effects of caching supplemental food in induced feather regeneration in wintering Gray Jays *Perisoreus canadensis*: a ptilochronology study. *Ornis Scandinavica* **21**:122-128.
- Weathers, W. W. 1997. Energetics and thermoregulation by small passerines of the humid, lowland tropics. *Auk* **113**:341-353.
- Wenny, D. G., R. L. Clawson, H. Faaborg, and S. L. Sheriff. 1993. Populations density, habitat selection, and minimum area requirements of three forest-interior warblers in central Missouri. *Condor* **95**:968-978.
- White, D. W., E. D. Kennedy, and P. C. Stouffer. 1991. Feather regrowth in female European Starlings rearing brood of different sizes. *Auk* **108**:889-895.
- Wilcove, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* **66**:1211-1214.
- Willis, E. O. 1974. Populations and local extinctions of birds on Barro Colorado Island, Panama. *Ecological Monographs* **44**:153-169.
- Willis, E. O. 1979. The composition of avian communities in remanent woodlots in southern Brazil. *Papéis Avulsos de Zoologia* **33**: 1-25.
- Yosef, R., and T. C. Grubb Jr. 1992. Territory size influences nutritional condition in nonbreeding Loggerhead Shrikes (*Lanius ludovicianus*): a ptilochronology approach. *Conservation Biology* **6**: 447-449.
- Zuberbier, G. M., and T. C. Grubb Jr. 1992. Ptilochronology: wind and cold temperatures fail to slow induced feather growth in captive White-breasted Nuthatches *Sitta carolinensis* maintained on ad libitum food. *Ornis Scandinavica* **23**:139-142

