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# Bird Species' Tolerance of Secondary Forest Habitats and Its Effects on Extinction

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**Abstract:** *Intense deforestation causes massive species losses. These losses occur because the habitats supplanting primary forest are inadequate to sustain viable populations of forest-dependent species. Despite this, certain species do seem to persist within the secondary habitats that replace original forest. This implies that there is a special class of species that might survive the loss of primary forest. Such a result would significantly influence conservation plans and extinction predictions. We tested whether species that tolerate secondary habitats survive extensive habitat loss and whether the same degree of loss threatens species that are forest obligates. To identify purported "survivors," we compared the remaining range sizes of endemic birds, their abundances, and their degree of extinction threat. We did this within the remaining Atlantic Forest of Brazil, a region extremely rich in endemics but with only approximately 10% of its forest remaining. We found no survivors. Habitat loss threatens forest-obligate birds and those using secondary habitats equally.*

**Key Words:** Brazil's Atlantic Forest, deforestation, extinction, secondary habitat

Tolerancia de Especies de Aves a Hábitats de Bosque Secundario y sus Efectos sobre Extinción

**Resumen:** *La deforestación intensiva provoca pérdidas masivas de especies. Estas pérdidas ocurren porque los hábitats que suplantán al bosque primario son inadecuados para sustentar poblaciones viables de especies dependientes de bosque. A pesar de esto, parece que ciertas especies persisten en los hábitats secundarios que reemplazan al bosque original. Esto implica que hay una clase especial de especies que puede sobrevivir a la pérdida de bosque primario. Tal resultado podría influir significativamente en los planes de conservación y en las predicciones de extinción. Probamos si especies que toleran hábitats secundarios sobreviven a la pérdida de hábitat y si el mismo nivel de pérdida amenaza a especies que son exclusivas de bosques. Para identificar a "sobrevivientes" aparentes, comparamos el tamaño del rango restante de aves endémicas, sus abundancias y el grado de amenaza de extinción. Hicimos esto para lo que queda de Bosque Atlántico de Brasil, una región extremadamente rica en endémicas pero con solo ~10% de su bosque original. No encontramos sobrevivientes. La pérdida de hábitat amenaza por igual a aves exclusivas de bosque y a aquellas que utilizan hábitats secundarios.*

**Palabras Clave:** Bosque Atlántico de Brasil, deforestación, extinción, hábitat secundario

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## Introduction

Deforestation is rarely total or completely permanent (e.g., Collins et al. 1991; Myers 1992; Sayer et al. 1992; Harcourt & Sayer 1996; Food and Agriculture Organization of the United Nations [FAO] 1999). Small patches of original habitat remain and, in time, secondary forests,

gardens, or plantations replace some cleared areas. To varying degrees, these habitats hold some of the original forests' species. Acknowledging this, we asked, how well do some species survive in habitats left by deforestation? Are some species in deforested areas "survivors," able to persist in deforested landscapes, or is their presence in secondary areas temporary or conditional on remaining

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primary forest elsewhere? The answer is important. The loss of tropical forests is the principal driver of modern extinctions (Pimm et al. 1995; Myers et al. 2000; Pimm & Raven 2000). How successfully species use secondary habitats affects the number of extinctions that follow tropical forest clearing. Survivors might be species of lesser concern for immediate conservation action.

Some species seem ecologically plastic and often appear in highly modified habitats. Perhaps they use adaptations gained from past selection pressures—those provided by frequent habitat disturbances or the existence of natural habitat edges, for example. Yet the simple presence of species in secondary habitats is ambiguous. How essential is the presence of nearby primary forest? Secondary habitats might be population sinks, with individuals spilling in from primary forest nearby (Pulliam 1988). Such species may not persist in its absence.

In their compilation of Neotropics birds, Parker et al. (1996) identified a distinct group of species that regularly breed in, or use, secondary habitats, even in the absence of locally adjacent undisturbed forest. Parker et al. (1996) acknowledged that many forest-obligate species also visit second-growth areas opportunistically (for reasons including their capitalization on briefly abundant food resources), but they doubt that such transient guests could survive there permanently. Conservative in assigning species to a secondary habitat category, they reserved this distinction for species that are “clearly adapted” to secondary forests. Species present in edge habitats but unable to survive away from primary forest comprise another group.

Additional support for species surviving in habitats left by deforestation comes from considering species endangerment. Building on the species-area relationship, Brooks and Balmford (1996) and Brooks et al. (1999c) compared the numbers of predicted extinctions with the numbers of species threatened with extinction following deforestation in Brazil's Atlantic Forest (the Mata Atlântica). By necessity, their species-area analyses considered only the region's endemic species (Pimm & Askins 1995). In this context, *threatened* has a specific, official meaning. In the opinion of the World Conservation Union (IUCN), it describes species facing extreme to high risks of extinction (IUCN 2003). The designation of “threat” is based on expert opinions proffered one species at a time.

Brooks et al. (1999c) found a good fit between the predicted number of threatened species and those species that are actually threatened. They obtained the best fit, however, by excluding those endemic species—identified by Parker et al. (1996)—that use secondary habitats. Brooks et al. (1999c) argued that these are survivors that can survive the complete removal of primary forests, whereas forest-obligate species cannot.

Other explanations exist. Apparent survivors might have unusually large geographical ranges or occur across areas where deforestation has been comparatively low.

Additionally, they may be unusually locally abundant within their ranges or may have escaped the many factors that cause species endangerment.

There is also an unresolved issue of spatial scale. Primary forest may not be adjacent to the secondary forest, but it may be present regionally. Apparent survivors may simply be those species that, fortuitously, have a relative abundance of primary forest regionally.

The key question is what happens when secondary habitat users and primary forest obligates are exposed to the same set of challenges to their survival. Are the former less threatened under conditions that threaten the latter? To answer this, we created a set of criteria (rules) that predict the expert opinions on whether a forest-obligate species is threatened or not threatened. These rules could be complicated and multifactorial, but we demonstrate they are not, by showing that the following variables classify the status of almost all the species: location (montane vs. lowland); local abundance (rare, uncommon, fairly common, and common); and range size (original and remaining contemporary forest cover). Next, we asked whether species tolerant of secondary habitats follow a different, more relaxed set of rules—ones that might allow them to suffer further insults before experts consider them threatened.

We could apply our methods to any taxon in any region. However, with claims of survivors amid the birds of Brazil's Atlantic Forest, we focused our efforts on these birds. Globally, this region ranks sixth in the number of endemic bird species and has <10% of its original forest remaining (Myers et al. 2000). It also contains the most threatened passerine species within the Americas (Manne et al. 1999). If some species can now tolerate and live in deforested landscapes (i.e., be survivors), we expected to find them here.

## Methods

### The Birds of Brazil's Atlantic Forest

The boundary of the original Atlantic Forest is necessarily arbitrary. We based our estimate on the terrestrial habitats that the World Wildlife Fund (WWF) classifies into ecoregions, areas with distinct species assemblages and environmental conditions (Olson et al. 2001). Combining several of these ecoregions forms the Atlantic Forest (Fig. 1): Pernambuco coastal and interior forests, Bahia coastal and interior forests, Alta Paraná interior forests, Serra do Mar coastal forests, and *Araucaria* moist forests. We considered restinga (white sand forest) part of the Atlantic Forest only for the particular endemics using this habitat. We did not include mangroves. Based on the WWF's framework, we estimated the Atlantic Forest's original extent (with restinga) at 1,197,170 km<sup>2</sup>. Encouragingly, this

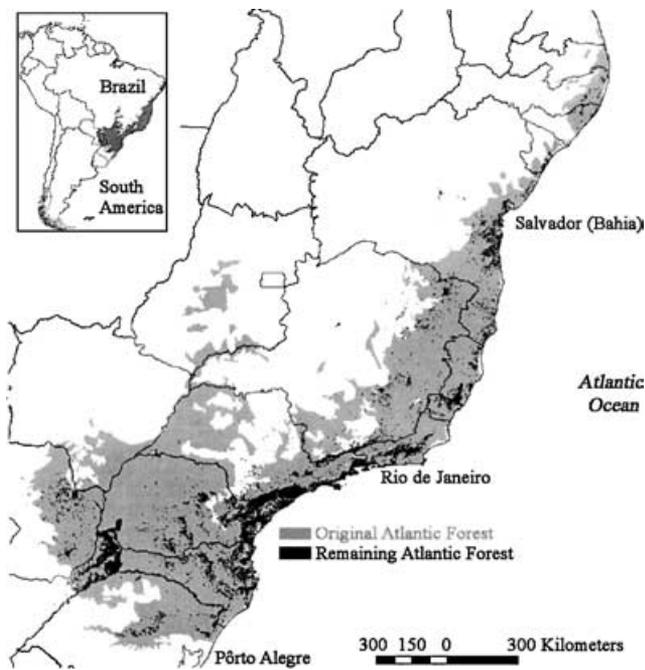


Figure 1. The Atlantic Forest of Brazil. Remaining forest was estimated by using satellite imagery analysis with Satellite Pour l'Observation de la Terre Vegetation (SPOT VGT) images ( $1 \times 1$  km). The original forest is a prediction based on uniting the World Wildlife Fund ecoregions representing the historical extent of the Atlantic Forest with our estimate of remaining forest cover.

is similar to Myers et al.'s (2000) estimate of 1,227,600 km<sup>2</sup>.

This region hosts 688 species (Goerck 1997), of which 199 are endemic (Parker et al. 1996). Brooks et al. (1999c) relied on habitat categories set by Parker et al. (1996) and considered 124 species to be forest dependent. Our analysis included 176 endemics: 127 species that are forest dependent and 49 species that are tolerant of secondary habitats. Some 121 of the forest dependent species come from Brooks et al. (1999c) and are unequivocally forest dependent. We removed three from their total. One species, *Oreophylax moreirae* (Itatiaia Spinetail), inhabits montane scrub, so we excluded it. We counted two others, *Pyrrhura cruentata* (Blue-throated Parakeet) and *Thraupis cyanoptera* (Azure-shouldered Tanager), as secondary-habitat tolerant, although Parker et al. (1996) considered this characterization uncertain and Brooks et al. (1999c) ranked them as forest dependent. We considered *Aramides saracura* (Slaty-breasted Wood-rail) a forest-dependent species, although Brooks et al. (1999c) did not because of its need for streams. Finally, *Neopelma aurifrons* (Wied's Tyrant-manakin) is now considered a forest obligate, whereas *N. chrysolophum* (Serra do Mar

Tyrant-manakin) remains tolerant of secondary habitats (Whitney et al. 1995).

We included an additional 50 birds, 42 of which Brooks et al. (1999c) believed are tolerant of secondary habitats. This total includes *Conopophaga lineata* (Rufous Gnateater), because although it also occurs in deciduous forest, its predominant habitat is Atlantic Forest. The other 8 species have been described since Sibley and Monroe (1990, 1993), which is the taxonomy Brooks et al. (1999c) followed. Four of these forest species also use secondary habitats (two determined by the IUCN [2003]).

The IUCN catalogs all birds currently threatened in the Americas. We used a more current version (IUCN 2003) than Brooks et al. (1999c). This resulted in 27 status changes from Brooks et al. (1999c), only 3 of which involve switching between threatened and not threatened status. (Pimm 2004).

### Factors Determining Threat of Extinction

Manne et al. (1999) predicted threat for 2287 species of passerine birds in the New World. They derived a rule based on two factors: original range size and location. Species with small ranges are considerably more likely to be threatened than species with larger ranges. Location matters, and in a way contrary to previous thought. Continental species are more likely to be threatened than island species with the same range size. (One might expect that island species, naive when exposed to species introduced from the mainland, would be more vulnerable.) Species on "islands" of montane habitats on continents follow the same pattern as species on oceanic islands, and they are less often threatened than species of continental lowlands with the same range size.

Manne et al. (1999) posited the importance of a third factor: local abundance. This poses a complication, because birds with small ranges tend to be locally rare within them (Gaston et al. 1997). Thus, Manne et al. (1999) postulated that species on oceanic and montane islands tend to be more abundant, relative to species in continental lowlands with the same range sizes. Manne and Pimm (2001) verified this assertion. They further showed that locally rare species are more likely to be threatened than those that are locally abundant, other things being equal. The combination of small range and local rarity greatly increase the chance of being threatened. Purvis et al. (2000) obtained similar results for mammals.

The rules based on abundance and original range size better predict threat than range size and location. However, Manne and Pimm (2001) also found that montane species are consistently less threatened than lowland species, even when considering range size and abundance. This likely results from the perception of fewer threats to montane habitats. In contrast, lowland species with small ranges often have strong specializations that limit their range and increase their extinction risk (D.

Stotz, personal communication). In short, the rules have to include all three factors—range size, abundance, and location.

Manne et al.'s (1999) estimates of range size are too large in three obvious ways. First, not all the area within a given range is within the elevational limits a species utilizes. We modified ranges by correcting for elevation.

Second, not all the area within an original range is suitable habitat. Although habitat destruction is the leading cause of species endangerment, Manne et al. (1999) did not measure it directly. They assumed that deforestation is more or less constant across all species' ranges. A novel feature of our research is the incorporation of remaining range size as a predictor of threat. This provides a measure of the extent to which deforestation challenges individual species.

Third, we found that approximately 28% of the remaining Atlantic Forest comprises individual forest fragments of <math><100\text{ km}^2</math>. (We choose this benchmark because Ferraz et al. [2003] found that below it, bird populations become locally extinct on a time scale of less than a century.) A species might have a relatively large remaining range, but through bad luck it may be composed of many small forest fragments, each too small to allow the populations to persist. In a final modification, we calculated the remaining range of each species that occurs in fragments of >math>100\text{ km}^2</math>.

### Location

As with range delineations, determining elevational limits is difficult and somewhat arbitrary. These limits depend on a given location and many other factors (Hartshorn 2001). To simplify our comparison, we grouped birds by elevation, relying on data found mostly in Parker et al. (1996) but also BirdLife International (2001) (4 species), Stattersfield et al. (1998) (1 species), and Whitney et al. (1995) (2 species). We considered montane species to be those that live at a minimum elevation of 200 m above sea level (all but 7 species have minima above 500 m). Lowland species occur to sea level, even if they sometimes reach high elevations (all but 25 are found below 1500 m).

### Abundance

Parker et al. (1996) used four categories of local abundance: rare, uncommon, fairly common, and common. Additionally, these investigators coded some species as patchily distributed. These we included within their parent group (e.g., a species deemed both rare and patchy were included with other rare species). For only one species (*Dysithamnus [plumbeus] plumbeus* [Plumbeous Antvireo]), did we rely on IUCN abundance data (IUCN 2003). Abundances for seven other species are unknown. That fact, in itself, implies rarity.

### Calculating a Species' Original Range Size

Before European contact, primary forest likely covered most of the Atlantic Forest ecosystem (Dean 1995), and all forest endemic birds were associated with this habitat. We generated this original forest extent by uniting the relevant WWF ecoregions with our own recent forest-cover prediction (details follow). Although our recent forest-cover prediction should not extend beyond the original WWF forest prediction, the WWF ecoregions miss some current forest that our recent forest-cover prediction identifies. Uniting the WWF Atlantic Forest ecoregions and our estimate increased the amount of original forest based solely on WWF's data by only 0.71%. Our estimate for the size of the original Atlantic Forest (without restinga) was 1,193,030 km<sup>2</sup> (Fig. 1).

To obtain birds' historic ranges, we digitized range maps from Ridgely and Tudor (1989, 1994) on a 1° scale (Manne et al. 1999 supply details). We also used data from World Map, Wings of the Americas (on CD-ROM; Mehlman et al. 1999), which has digitized ranges for threatened passerine and nonpasserine birds on a 15-minute grid. Finally, we mapped 37 endemic species based on information found in BirdLife's World Bird Database (2001). When possible, we used multiple sources and averaged the estimates. These ranges were further modified according to birds' specific elevation requirements by subsetting them in a 1-km digital elevation map (Hastings et al. 1999).

We superimposed range maps (Manne et al. 1999; Mehlman et al. 1999; BirdLife International 2001) for each species on our original Atlantic Forest prediction. Then we trimmed them to fit within the original forest boundary. Each species' estimated original range is an averaging of values, in those cases for which multiple sources map the same species range.

### Remaining Range

Although the Fundação SOS Mata Atlântica and the Instituto Nacional de Pesquisas Espaciais (INPE) jointly map the remaining Atlantic Forest multiple times, the numbers differ widely between reports. The foundation's Atlantic Forest estimate of 216,624 km<sup>2</sup> (17%) forest remaining in 2000 is more than double its 1998 estimate of 81,821 km<sup>2</sup> (8%) forest remaining in 1995 (Fundação SOS Mata Atlântica/INPE/Instituto Socioambiental 1998; Fundação SOS Mata Atlântica/INPE 2002). In the updated 2002 report, the 1995 estimate changes to 164,424 km<sup>2</sup> without explanation (Fundação SOS Mata Atlântica/INPE 2002). Changes in methodology, specifically a finer mapping scale, may account for some of this increase but not for a doubling of total area. All states previously mapped appear to lose forest, with some discrepancies resulting from the addition of two large states to the mapping area.

Uncomfortable with the SOS data, we generated an estimate of remaining forest by mapping the evergreen

Atlantic Forest with Satellite Pour l'Observation de la Terre Vegetation (SPOT VGT) satellite imagery. This imagery has a 1-km<sup>2</sup> resolution and contains four spectral bands specifically geared toward discerning vegetation. To minimize cloud interference, we used five dry-season images taken from 1998, 1999, and 2000. In our analyses, approximately 1.5% of original forest extent is masked by cloud and shadow. Sites in "key areas for threatened birds in the Neotropics" (Wege and Long 1995) provide the coordinates of sites with primary (or at least good quality) forest. (We have visited some, but not all, of the sites.) The book identifies the most important known places for conserving the 290 globally threatened birds in the Neotropics. Fifty of Wege and Long's (1995) listed Atlantic Forest sites formed the basis of our "primary forest signatures." We generated our forest-cover classification by using a supervised classification and maximum likelihood decision rules. The remaining Atlantic Forest exists in a multitude of fragments, with a cumulative area of 119,540 km<sup>2</sup> (not including restinga), about 10% of its original extent (Fig. 1).

We evaluated the accuracy of our Atlantic Forest prediction based on SPOT VGT by comparing it with five different Landsat Enhanced Thematic Mapper Plus (ETM+) scenes from 2000. One hundred random points were generated on our classification map, 50 in areas coded as forest and 50 in nonforested areas, excluding water. These same points were overlaid on the Landsat ETM+ scenes. An independent observer counted points as forest only if a 1-km box around a point encompassed more than 50% forest. Otherwise, points were scored as nonforest. Our Atlantic Forest classification generated by SPOT VGT agreed with the ETM+ scenes in 87 of the 100 cases. Most of the 13 errors were in extremely fragmented areas, which the 1-km sensor had difficulty resolving.

We calculated current estimates of bird ranges with the same method we used to calculate their original ranges. We adjusted the historical range estimates according to each species' preferred elevation with the 1-km resolution digital elevation map (Hastings et al. 1999). Then we overlaid ranges onto our current forest estimate. Only the intersection between each species range and the forest cover was retained—creating a map of each bird's remaining range. Final estimates for each endemic's remaining range are the averaged predictions of the different data sets when available.

### Restinga

Restinga is a part of the Atlantic Forest (Ab'Saber 1977). These white sand forest habitats hold few bird species (Reis & Gonzaga 2000) and are spatially restricted. Nine Atlantic Forest endemics utilize them, with eight birds occupying other Atlantic Forest habitats. We analyzed the

sole restinga endemic (*Formicivora littoralis* [Restinga Antwren]) as if it spilled into bordering Atlantic Forest. In satellite imagery, restinga is extremely difficult to classify because of sand reflectance. Fortunately, the WWF includes this habitat within its ecoregion analysis, a prediction that we incorporated (Olson et al. 2001). The amount is small, increasing the overall area of the Atlantic Forest by 0.3% for a total of 1,197,170 km<sup>2</sup>.

Although the WWF's original restinga prediction probably overestimates what currently remains, we did incorporate it into the remaining range for these nine birds. Again, the effect is minimal, increasing our remaining range prediction by 3% for a final amount of 123,717 km<sup>2</sup>. We based all range calculations for restinga species on these original and remaining Atlantic Forest predictions.

### Remaining Range Size: Effects of Forest Fragmentation

As a final step in our model, we explored the contribution of habitat fragmentation on threat. For each species, we filtered out all remaining forested range in fragments of <100 km<sup>2</sup>. We proceeded as before with these modified remaining ranges, which now contain only large forest fragments.

### Errors in Estimates of Remaining Range Sizes

The estimate of remaining forest includes primary forest and undoubtedly some secondary forests, plantations, gardens, and other special cover types (including bamboo). The task of completely classifying all the forest types of this region based on remote sensing is daunting. Almost certainly, we overestimated the remaining ranges for forest-obligate species.

Conversely, we underestimated the remaining ranges for species that use secondary habitats. Such birds likely persist in forest edges and small forest patches. As noted, our remaining forest predictions based on SPOT VGT (1-km<sup>2</sup> resolution) underestimated remaining forest compared with more finely resolved Landsat ETM+ images (30 × 30 m). The latter method picks up smaller forest fragments and more edges than the former.

The inability to distinguish forest types, along with the discounting of edges and small fragments, increases the chances of finding differences between forest-obligate species and secondary habitat users. Remaining range size predictions for the former are too high; those for the latter are likely correct (or too low). This weighed our analysis toward identifying not-threatened, secondary-habitat birds with small remaining ranges that are not threatened—the survivors. Had we found differences between the two groups of species, this would be an issue, but we did not find any differences, as we show in the next section.

**Table 1.** Counts for lowland forest-obligate birds endemic to Brazil's Atlantic Forest in various abundances, original range and remaining range size categories, separated by threatened status.

Range size (km <sup>2</sup> )	Abundance			
	rare	uncommon	fairly common	common
<b>Original</b>				
threatened				
<150,000	15 <sup>a</sup>	5 <sup>a</sup>	2 <sup>a</sup>	0 <sup>a</sup>
150,000–350,000	3 <sup>a</sup>	6 <sup>a</sup>	0	0
>350,000	6 <sup>a</sup>	0	0	0
not threatened				
<150,000	0 <sup>a</sup>	0 <sup>a</sup>	1 <sup>a,b</sup>	0 <sup>a</sup>
150,000–350,000	0 <sup>a</sup>	4 <sup>a,b</sup>	1	2
>350,000	2 <sup>a,b</sup>	18	17	6
<b>Remaining</b>				
threatened				
<21,000	14 <sup>a</sup>	8 <sup>a</sup>	2 <sup>a</sup>	0 <sup>a</sup>
21,000–56,000	8 <sup>a</sup>	3 <sup>b</sup>	0	0
>56,000	2 <sup>a</sup>	0	0	0
not threatened				
<21,000	0 <sup>a</sup>	0 <sup>a</sup>	1 <sup>a,b</sup>	0 <sup>a</sup>
21,000–56,000	1 <sup>a,b</sup>	6	2	2
>56,000	1 <sup>a,b</sup>	16	16	6

<sup>a</sup>Species expected to be threatened according to our model.

<sup>b</sup>Model exceptions.

## Results

### Rules for Forest-Obligate Lowland Species

Threatened species (1) were locally rare, (2) had original ranges of <150,000 km<sup>2</sup>, and (3) were locally uncommon with original ranges of <350,000 km<sup>2</sup> (Table 1). Of 88 species, this three-factor system misclassified only 7 species. Two locally rare species were not threatened; they had large original ranges. Six other locally rare species with large original ranges were threatened. Of locally uncommon birds with original ranges between 150,000 and 350,000 km<sup>2</sup>, 6 were threatened and 4 were not. Two fairly common species with original ranges of <150,000 km<sup>2</sup> were threatened and 1 was not.

For 88 species, the three-factor-based system (lowland species, local abundance, remaining range size) misclassified 6 species (Table 1). Again, all but 2 locally rare species were threatened. Although birds with remaining ranges below 21,000 km<sup>2</sup> were threatened (one exception), the rule for locally uncommon species with intermediate ranges was reversed. Now, the majority of locally uncommon species were not threatened (three exceptions). Finally, 2 locally fairly common species with remaining ranges of <21,000 km<sup>2</sup> were threatened and 1 was not.

In our examination of the effects of forest fragment size, we considered only the amount of remaining range found in fragments of <100 km<sup>2</sup>. This did not resolve any

**Table 2.** Counts for montane forest-obligate birds endemic to Brazil's Atlantic Forest in various abundances and original range size categories, separated by threatened status.

Range size (km <sup>2</sup> )	Abundance			
	rare	uncommon	fairly common	common
<b>Original</b>				
threatened				
<2600	3 <sup>a</sup>	2 <sup>a</sup>	0 <sup>a</sup>	0 <sup>a</sup>
>2600	7 <sup>a</sup>	1 <sup>b</sup>	0	0
not threatened				
<2600	0 <sup>a</sup>	0 <sup>a</sup>	0 <sup>a</sup>	0 <sup>a</sup>
>2600	1 <sup>a,b</sup>	14	7	4

<sup>a</sup>Species expected to be threatened according to our model.

<sup>b</sup>Model exceptions.

more exceptions, although it could have, had the remaining ranges for the three threatened species our method misclassified (Table 1) consisted of only small forest fragments.

### Rules for Forest-Obligate Montane Species

Generally, original ranges for montane species were much smaller than for lowland bird ranges. Regardless of local abundance, species with original ranges smaller than 2600 km<sup>2</sup> were threatened (no exceptions). With one exception, locally rare species were threatened, irrespective of their range size. Locally uncommon species with original ranges of >2600 km<sup>2</sup> were not threatened, also with one exception (Table 2). We obtained no improvement when we considered remaining ranges, although the range values were smaller (200 km<sup>2</sup> instead of 2600 km<sup>2</sup>).

### Species Tolerant of Secondary Habitats

We analyzed all lowland and montane species that use secondary habitats according to the same rules derived for the forest-obligate birds (Table 3). Because analyzing remaining range clarified species threat, we report only these values. For species that use secondary habitats, there were no misclassifications among lowland and montane species (Table 3).

If species that use secondary habitats survived forest loss better than the others, they would not be threatened in the combinations of low abundance and small geographical range that threaten forest-obligate species, but we did not see this result. The majority of birds that tolerate secondary habitats had large ranges and high abundances within those ranges. These factors cushion them from deforestation's harm. Lowland secondary-habitat-using birds that were rare or had remaining ranges of <21,000 km<sup>2</sup> were threatened like the forest obligates. A parallel result occurred for montane species (Table 3).

**Table 3.** Counts for lowland and montane secondary-forest-tolerant birds endemic to Brazil's Atlantic Forest in various abundances, and remaining range size categories, separated by threatened status.

Location, status, range size (km <sup>2</sup> )	Abundance			
	rare	uncommon	fairly common	common
Lowland				
threatened				
<21,000	2*	3*	2*	0*
21,000–56,000	0*	0	0	0
>56,000	0*	0	0	0
not threatened				
<21,000	0*	0*	0*	0*
21,000–56,000	0*	1	7	3
>56,000	0*	3	8	11
Montane				
threatened				
<200	3*	0*	0*	0*
>200	0*	0	0	0
not threatened				
<200	0*	0*	0*	0*
>200	0*	3	2	1

\*Species expected to be threatened according to our model.

### Rule Exceptions

Six lowland species broke the rules. Two were lowland birds that are locally rare, yet they were not considered threatened. One, *Platyrinchus leucoryphus* (Russet-winged Spadebill), was considered threatened by Collar et al. (1994), but has since been downlisted to the not-threatened category. For the other, *Amaurospiza moesta* (Blackish-blue Seedeater), the IUCN (2003) disagreed with Parker et al. (1996) on local abundance, considering the bird “relatively common.” D. Stotz (personal communication) disputes this strongly and believes that it is at risk. These birds had the fourth largest and largest remaining range sizes, respectively, for rare, lowland species. The second- and third-largest remaining range sizes of rare, lowland species are *Pipile jacutinga* (Black-fronted Piping-guan) and *Claravis godefrida* (Purple-winged Ground-dove). Both were classified as threatened and the guan is hunted, increasing its vulnerability. It seems likely that large remaining range sizes protect the spadebill and the seedeater from threat, but not the hunted guan (Owens & Bennett 2000). The dove and the seedeater depend on bamboo fruiting (D. Stotz, personal communication), although we found no relationship between this specialization and the degree of threat. In short, both passerine species had relatively large remaining ranges, and there are doubts either about whether the species should be threatened or its local abundance. Neither our rules nor the IUCN criteria seemed problematic.

This was not the case, however, with another lowland species, *Phaethornis idaliae* (Minute Hermit) with an abundance of “fairly common.” We suggest that the

IUCN misclassified it as not threatened. Although its original range was once large (108,810 km<sup>2</sup>), it has been reduced to only 8% of the original. This amount of remaining range (8530 km<sup>2</sup>) ranked only third within a suite of 16 other threatened species. Conversely, *Lipaugus lanioides* (Cinnamon-vented Piha) and *Carpornis melanocephalus* (Black-headed Berryeater) were considered threatened, although both these locally uncommon species had relatively large remaining ranges (approximately 46,000 km<sup>2</sup> and 36,000 km<sup>2</sup>, respectively). Both birds rely heavily on fruit throughout the year and probably explore large areas to acquire it.

The final lowland exception is *Leucopternis lacernulata* (White-necked Hawk). This hawk was also locally uncommon, had a remaining range of approximately 56,000 km<sup>2</sup>, and was considered threatened, whereas its congener *L. polionota* (Mantled Hawk) has about twice the remaining range and was not threatened. Hawks are often shot and, in any case, locally uncommon for a predatory hawk likely implies a lower absolute density in the Parker et al. (1996) classification than for a small passerine.

There were two rule breakers within the montane category. One species, *Cercomacra brasiliana* (Rio de Janeiro Antbird), was not threatened but ranked seventh for the smallest remaining range in a set of 14 rare and threatened species. The IUCN believes that this species uses secondary habitats, and BirdLife (2001) specifically mentions its tolerance of secondary habitats as a reason for not considering it threatened. Conversely, *Piprites pileatus* (Black-capped Piprites) was exceptional by remaining threatened among 30 other species that were not threatened. It retained 21% of its original range, a sizable amount for a montane species (21,514 km<sup>2</sup>).

Idiosyncratic factors of natural history—such as being large-bodied or frugivorous—almost surely increase the risk of extinction (Owens & Bennett 2000). Nevertheless, our rules classified the majority of other, broadly similar species correctly. In short, there were no obvious and simple patterns demanding an expansion of our rules based on remaining range, local abundance, and location.

### Discussion

Extensive habitat loss threatens species tolerant of secondary habitats and forest-obligate species equally. This simple conclusion raises four questions. First, our results classified the species-by-species expert opinions on whether a species should be threatened. How confident are we that these classifications predict true threat? Our hypotheses consider the relative likelihoods of extinction, not the surrogate measure of expert opinions. Second, do large-ranged species get this way—and subsequently become less vulnerable to habitat loss—because of their potential to use a wider range of habitats over their evolutionary history? Third, if there is no special class of

secondary-habitat-using survivors, why do Brooks et al. (1999c) need to posit such exceptions to improve species-area predictions of future extinctions? Fourth, to what extent can we generalize these results to other places?

### Threat to Species

One view of our method is that we merely uncovered the algorithm employed by the IUCN experts to determine whether a species should be labeled threatened. Even if true, our results allow the designation of threat based merely (and simply) on location (montane vs. lowland), remaining range size, and local abundance. The key issue is that designations of threat lack independent validation. Only enough time—and a lack of conservation action—will determine whether threatened species do become extinct in the interval expected by the IUCN experts. Importantly, many experts throughout the world proffer opinions on whether a particular species should be threatened. This is a consensus of multiple experts, one deserving considerable weight.

Should these experts have considered whether a species uses secondary habitats in making their determinations? There is no evidence that those who classify species deliberately excluded this factor or simply forgot it. As noted previously, there is some evidence to the contrary.

Whether the putative IUCN algorithm is correct in giving little or no importance to the use of secondary habitats is unknown. If the algorithm is in error, the seven lowland species using secondary habitats that are classified as threatened should not be. Their small remaining ranges (<21,000 km<sup>2</sup>) and low abundances confirm their vulnerability. For example, one of these species, *F. erythronotos* (Black-hooded Antwren), is a secondary-habitat-tolerant species so rare that it was not recorded for more than 100 years until its rediscovery in 1987 (BirdLife International 2001).

The decisions to list some secondary-habitat-using species as threatened were sensible. Species considered not threatened were those expected from our knowledge of forest-obligate species. Another reason to reject our conclusion would be if the experts misclassified the many forest-obligate species that are not threatened. The number of such species alone makes this implausible.

### Secondary Habitat Use and Range Size

We recognize that birds tolerant of secondary habitats might be better at dispersing across the landscape. As habitats changed throughout recent millennia (and, especially, dried out), the species we characterized as tolerant of secondary habitats might have been more able to survive in the drier forests that acted as barriers for more forest-obligate species. In some evolutionary sense, secondary habitat tolerance may confer less risk of threat if it generates larger ranges and greater local abundance.

Even if that argument is true, it does not alter the conservation message—which is that for the species present in this area with their given ecological attributes (however obtained), secondary habitat use does not confer an added protection against deforestation.

### Implications for Predicting Extinctions

In a series of papers, we and our colleagues employ the species-area relationship to predict the number of species that will become threatened and, in time, extinct, following the loss of forest habitats (Pimm & Askins 1995; Brooks & Balmford 1996; Brooks et al. 1997; Brooks et al. 1999a; Brooks et al. 1999b). These predictions generally match the observed numbers of threatened or extinct species, and the exceptions are few but interesting. Brooks et al.'s (1999c) analysis of the birds of the Atlantic Forest suggests that to improve their predictions, it is necessary to identify and exclude a special class of survivors. We found no special class of survivors. So why do Brooks et al. (1999c) need to posit one to improve their predictions of the numbers of threatened species? If the presumption of a special class is in error, does this mean that there is a flaw in the predictions derived from the species-area relationship? Seemingly paradoxically, we argue that although there is no need for a special class of survivors, its absence does not refute the utility of species-area predictions. To resolve the paradox, consider the connection between the rules for endangerment we have derived for individual species and the community-wide predictions that the species-area relationship provides.

The mechanism that underlies extinction is that habitat loss can eliminate the entire range of a species, or just some of it, but leaves the remnant populations too small to persist. Often overlooked is that, in his classic papers on the species ( $S$ ) to area ( $A$ ) relationship, Preston (1962) first derives a relationship of species to total number of individuals of all species ( $I$ ). The substitution of area,  $A$ , for individuals,  $I$ , is late in the argument and follows in an algebraically trivial way by assuming a constant density of individuals. That  $S$  decreases as  $I$  decreases is not, in itself, surprising. Preston's first crucial insight is that species are lost in a way that maintains the empirically—and independently—observed statistical distribution of individuals per species. His second insight is that this could only happen if there is a minimum population size ( $m$ ). Below  $m$ , a species cannot survive. If this were not the case, the rare species would simply become rarer, but the number of species would remain constant.

This digression matters. Some have argued (Harte et al. 1999) that the mechanism of species loss following habitat loss is that some unfortunate species are just in the wrong place and lose their entire habitat. This is not the mechanism postulated here, and it is not the method invoked in the other papers we quote at the start of this section. Nearly all the species we examined have some

remaining habitat. The question is whether it is enough to support their continued persistence.

It follows that what dooms a species is that habitat destruction reduces a species' total numbers to below the persistence threshold. Whether that happens depends on a species' local abundance and the size of its remaining range. The latter depends in turn on fate: whether a species lived in an area that suffered moderate or extensive habitat destruction. Simply, our results are entirely in accord with Preston's (1962) theory. Then why do Brooks et al. (1999c) find the theory to give a less than perfect answer?

Preston gets his species-to-area result because of the constraint of a special ("canonical") distribution of the number of individuals per species. The result extends to predictions of the species lost from habitat destruction through the assumption that deforestation affects all species equally. Obviously, if the damage is geographically uneven, the extension will fail to some extent. Brooks et al.'s (1999c) predictions of too few threatened species could arise if species with small ranges live, by good fortune, in areas where deforestation is relatively light. This is the case within this region (G.M.H. & S.L.P., unpublished data). Indeed, such a result is obvious in Brooks & Balmford (1996), a paper in which the authors regionally subdivide their predictions. (Globally, however, the pattern is one of bad fortune: the areas richest in endemic species have disproportionately high levels of deforestation; Myers et al. 2000.)

Simply, the species-area predictions provide general insights on the number of species likely to become extinct, but one must turn to underlying mechanisms to understand specific exceptions. Our results support those mechanisms.

### Generalizing Results

We attach no level of statistical significance to our simple conclusion. Statistics allow inferences from samples. Here, we evaluated *all* the endemic forest bird species in the Atlantic Forest, not a random sample. (Manne et al. [1999] provides further discussion.)

Does our conclusion extend to other hotspots or to other species? This region is not a random pick from the set of all hotspots and its endemics are not a random sample of the global set of endemics. Had we selected endemics randomly from that global set, statistics would permit us to derive global implications. This approach would require estimates of remaining habitat for each species, a much more difficult task. These facts mean that, at a minimum, our conclusion that the use of secondary habitats does not reduce the chance of being designated threatened applies only to these species in this place. Nonetheless, there is no a priori reason to think that the species discussed here are exceptional.

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