Gulliver travels to the fragmented tropics: geographic variation in mechanisms of avian extinction

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Irrespective of geography, forest destruction and fragmentation lead to lower avian species richness. The underlying mechanisms causing local extirpations have been studied most thoroughly in northern temperate landscapes, where higher levels of brood parasitism, nest predation, and possibly decreased food availability are responsible for the loss of some species. Tropical landscapes are being similarly altered, but studies of responses by tropical birds remain relatively scarce. Predicting how tropical birds respond to habitat loss and fragmentation should not be extended directly from the results of temperate investigations. Tropical birds possess different evolutionary and life histories, which make them vulnerable to a different suite of threats than those normally considered for birds from temperate regions. These same traits, including greater physiological and sensory specialization, reduced dispersal capabilities, and much lower local and regional population densities, indicate that strategies for conserving bird diversity will be different in tropical landscapes than those for temperate regions.


In a nutshell:

- Bird diversity declines in landscapes altered by habitat loss and fragmentation, but most studies have been done in northern temperate areas
- Tropical birds are also declining in disturbed landscapes, but as a result of different threats
- Lower tolerance of microclimatic changes or light environments in fragmented habitats and lower dispersal abilities are factors generally not considered for temperate birds
- Preservation of tropical diversity will improve if these traits are considered during reserve design

Differences in life histories and behaviors between temperate and tropical birds have been recognized for a long time (Skutch 1949). Alexander Skutch, during a famous series of debates with David Lack about the latitudinal gradient in avian clutch sizes (Lack 1947; Skutch 1949), remarked that if most biologists had been raised in the tropics they would ask why temperate birds lay unusually large clutches, rather than asking, as did temperate biologists, why tropical clutches are so small. Similarly, Ricklefs (2002) noted that his time in the neotropics was pivotal in cementing the idea that many neotropical bird lineages are distinct from North American ones in both their evolutionary and life histories. The degree to which such differences influence the conservation of bird populations in human-dominated landscapes remains unappreciated.

Nevertheless, two present-day commonalities exist between tropical and temperate birds. First, species in both realms are confronted with destruction and conversion of forests (Faaborg et al. 1995; Laurance et al. 2000). Areas of high endemism, such as the Atlantic rainforests of Brazil, the northern and central Andes, and Amazonia, are particularly at risk (Balmford and Long 1994). Secondly, many species respond negatively to such disturbances and their populations decline or disappear in fragmented landscapes. Local extinction of species from fragmented forests is well documented across northern temperate areas (Whitcomb et al. 1981) as well as in the neotropics (Stouffer and Bierregaard 1995; Robinson 1999, 2001). Thus, temperate and tropical birds face similar challenges. Yet the mechanisms producing the observed declines in species richness may differ between
the two regions. Conservation strategies applied in temperate North America may therefore be less effective in the neotropics.

Here, we briefly review currently accepted hypotheses for bird extirpations as a result of forest fragmentation. We also identify several hypotheses that should be considered and studied in detail for neotropical birds. Our goal is not to provide an exhaustive review of the hypotheses proposed to explain declines or local extinctions of birds, but rather to highlight the salient differences in responses to environmental change by tropical and temperate birds. We focus largely on comparing results from northern temperate areas with those from tropical ones. Further study is needed to understand the degree to which factors operating in northern temperate landscapes also operate in southern temperate areas.

### Northern temperate extinction mechanisms

#### Brood parasitism

Of the primary factors responsible for population declines in the temperate zone, brood parasitism (the laying of eggs in nests of other bird species and subsequent abandonment of offspring to be raised by foster parents) by cowbirds has received perhaps the most attention, at least in eastern and midwestern North America (Smith *et al.* 2000). Brown-headed cowbirds (*Molothrus ater*) increase in abundance in disturbed landscapes, particularly fragmented forests in an agricultural matrix (Robinson *et al.* 1995). High levels of cowbird parasitism can cause population declines, which increases the risk of local extirpations (Hoover 2003), and even extinctions for a few extremely vulnerable species, such as Kirtland's warbler (*Dendroica kirtlandii*) (Kepler *et al.* 1996).

In contrast, brood parasitism appears to be a minor risk to forest birds in most mainland neotropical landscapes. Although two generalist brood parasites, shiny (*M bonaniensis*) and bronzed cowbirds (*M aeneus*), occur in Central and South American landscapes, current levels of brood parasitism in fragmented forests are generally low (Figure 1). The risks of brood parasitism can be greater in more subtropical landscapes, such as Mexico, Argentina, and the West Indies, where cowbirds tend to be more numerous, and have caused major declines in some species, such as the yellow-shouldered blackbird (*Agelaius xanthomus*) (Wiley *et al.* 1991). Furthermore, where brood parasites do occur regularly in equatorial areas, they tend to parasitize only a few specific host species with whom they may be tightly coevolved, such as the giant cowbird (*Scaphidura oryzivora*) and its hosts, oropendolas and caciques (Payne 1997). Thus, one of the primary threats to forest birds living in temperate fragments is currently of little or no consequence to most tropical species. How neotropical cowbird distributions might change as landscapes become deforested has not, to our knowledge, been evaluated.

#### Nest predation

Reproductive failure in forest fragments may also be caused by abnormally elevated nest predation (Robinson *et al.* 1995). Some edge-loving nest predators, such as skunks, raccoons, and snakes, are more abundant in human-altered landscapes (Chalfoun *et al.* 2002). Nests in forest fragments may be easier for predators to detect, especially those located along edges, where predator activity is greater (Chalfoun *et al.* 2002). Other characteristics of the habitat remnant, such as vegetation structure or food supply, may nevertheless remain attractive to birds. In such instances, forest birds may be common, but fail at reproduction because of brood parasitism or nest predation, a situation sometimes referred to as an ecological trap (Misenhelter and Rotenberry 2000).

Nest predation has yet to be studied rigorously in tropical landscapes, fragmented or not, largely because of the difficulty of finding sufficient numbers of nests of comparatively rare species (Robinson *et al.* 2000). Extinctions of birds from Barro Colorado Island, Panama, a former hill-top of lowland rainforest isolated during flooding of the Panama Canal, have been explained by elevated levels of nest predation (Terborgh 1974). The island, at 1562 ha, is too small to maintain populations of top carnivores, such as big cats and raptors, which may have allowed...
numbers of medium-sized mammalian nest predators to increase unchecked. Studies using artificial bird nests suggested that predation was greater on Barro Colorado Island than nearby mainland sites (Sieving 1992). However, the accuracy with which artificial nests measure predation of real bird nests is questionable (Moore and Robinson 2004). Furthermore, mammalian nest predators appear not to be abundant on Barro Colorado compared with nearby mainland forest where big cats and eagles are extant (Wright et al. 1994). Finally, video evidence of predators attacking understory bird nests on the island indicated that 80% of attacks were by snakes, not mammals (Figure 2; Robinson et al. in press).

Despite such concerns, can results from Barro Colorado be generalized to other tropical landscapes? Because they are surrounded by water and are therefore relatively protected from invasions that threaten fragments surrounded by agricultural and suburban habitats (such as spread of edge-loving nest predators), islands are good models for understanding ecosystem disintegration (Leigh et al. 2002). Yet, most fragments occur in areas where access by species from surrounding habitats is much easier. As discussed above, birds in temperate regions suffer because of this. In tropical landscapes, however, many of which are inhabited by small farmers, ease of access is also greater for humans, who commonly persecute snakes and larger mammals (Redford 1992). In a sense, then, top-down control of nest predators could be greater in tropical fragmented landscapes, allowing bird populations greater opportunity to breed successfully. Apart from various artificial nest studies, no other data from tropical landscapes allow an evaluation of the effects of fragmentation on predation risk.

**Prey abundance**

Forest fragmentation has been associated with decreased prey abundance for near-ground or ground-foraging insectivorous birds (Burke and Nol 1998). Declines in food availability may be a consequence of microclimatic changes such as increased temperature and decreased humidity near fragment edges (Williams-Linera 1990; Saunders et al. 1999). In the neotropics, arthropod population responses to fragmentation are complex and poorly understood. As might be expected, the effects of habitat fragmentation differ across arthropod taxa and through time as the edge changes in structure (Didham 1997). Rainforest fragmentation does alter the composition of arthropod communities, but the applicability of the reduced prey abundance hypothesis is currently in doubt because many species of potential arthropod prey can become more abundant after fragmentation (Didham 1997). Indeed, in Costa Rica, Sekercioglu et al. (2002) did not find any differences in prey biomass between forested and fragmented sites.

**Suggested additional mechanisms for neotropical bird extinctions**

Nest predation, brood parasitism, and prey abundance are the three hypotheses commonly proposed to explain local extinctions in temperate and neotropical landscapes (Figure 3). Yet there is either no data to support these hypotheses in the tropics, or the evidence suggests that fragmentation has the opposite effect there. How, then, can we explain why neotropical birds in forest fragments become extinct? Instead of explanations that focus on biotic interactions, we suggest that the evolutionary histories of neotropical birds have resulted in physiologies and behaviors that make them less tolerant of environmental variation.

**Physiological constraints**

Microclimatic changes in fragments may affect birds directly if altered temperature and humidity levels in forest remnants expose them to evapotranspiration rates that cause physiological stress. The idea of greater habitat specialization in the tropics is an old one (Janzen 1967; Karr and Freemark 1983), but has received less attention than it deserves (Marra and Renssen 1997). It is under-
standable that ornithologists studying birds in temperate regions tend to look elsewhere for useful hypotheses. Many of these species are probably more tolerant, given the wide range of conditions they encounter during a calendar year; migratory species, for example, must endure highly variable climatic conditions as they journey thousands of kilometers. Non-migratory species must survive temperatures varying from winter to summer by an order of magnitude more than a resident rainforest species would experience in its entire lifetime, and more than some tropical species’ ancestors might have experienced in thousands of generations. Unlike species from temperate areas, many neotropical species may be much less physiologically tolerant of climatic variation, particularly if those species inhabit the relatively stable understories of closed-canopy mature forest.

Evaluations of this hypothesis are lacking, because of the rarity of measurements of metabolic rates, particularly with respect to ranges of thermal tolerance in neotropical birds. However, some indirect evidence is available. Resident insectivorous birds in Panama move to sites with higher humidity during the heat of dry season days (Karr and Freemark 1983). Two common understory species near Manaus, Brazil, exhibit slower feather growth rates in forest fragments compared to the feather growth rates of birds in continuous forest (Stratford and Stouffer 2001). In the Afrotropics, feather asymmetries of birds captured in small fragments were more severe than those of birds birds in larger fragments, suggesting developmental problems in the birds from small fragments (Lens et al. 2002).

Phylogenetically controlled comparisons of temperate and tropical bird physiological tolerances are needed. If the metabolic constraint hypothesis is valid, many tropical species should have narrower thermoneutral zones and be less tolerant of small changes in temperature and humidity. Predicting the size of those small changes could be accomplished by measuring annual ranges of temperatures and humidities experienced in the interior of unfragmented forests (Figure 4). We also predict that the fraction of bird communities disappearing in fragmented landscapes will be negatively correlated with the degree of annual and daily climatic variation. For example, bird communities in more seasonal tropical environments, such as seasonally dry forests, some deserts, and higher altitude habitats, should be more tolerant to fragmentation, whereas relatively aseasonal lowland forest bird communities are likely to contain a greater proportion of fragmentation-sensitive species.

Bird species whose habitat use is restricted to the most unvarying microhabitats, such as the floor of old-growth forests, should be more sensitive to habitat fragmentation than birds inhabiting forest microhabitats with wider climatic fluctuations, such as canopy- and edge-dwelling species (Figure 4). Species distribution data are consistent with this prediction, revealing that gap specialists and edge-loving species (eg many types of humming-birds) are tolerant of fragmentation (Stouffer and Bierregaard 1995).
tion, the area available to a sensitive understory species should be lower than the actual physical size of the fragments. Since edges are often exposed to sun and drying winds, they will tend to experience more microclimatic variation than interior sites, which are protected from such forces. Sensitive species would, therefore, drop out of fragments earlier than would be predicted based solely on habitat patch area. The role of physiological tolerances or metabolic constraints as mechanistic explanations for tropical bird extinctions is ripe for further evaluation.

Visual constraints

Just as deforestation and forest fragmentation may present abiotic conditions that stress thermoregulatory processes, visual constraints may also limit habitat use (Canaday 1996). We know that some neotropical birds, such as manakins and cotingas, are highly sensitive to the light environments they select for sexual displays (Endler and Théry 1996). Likewise, many other species may be sensitive to changes in light levels. In mature tropical forest, less than 5% of the light striking the canopy penetrates to the ground (Shuttleworth et al. 1984). Bird species foraging exclusively in the lower understory or on the ground of evergreen tropical forests must therefore see well in low-light conditions. To do so, some species may have unusually large eyes to enhance light gathering or have internal structural modifications that otherwise enhance visual acuity in poorly lit situations.

A potential cost of such specialization is an inability to use brightly lit habitats such as large forest gaps, edges, or canopies. Although such constraints will probably not lead directly to higher extinction risk, they could explain low rates of recolonization after local extirpation by retarding the progress of light-sensitive species across brightly lit habitat gaps. It is also possible that species sensitive to bright light may be unable to detect the presence of distant habitat patches in a landscape. That is, their perceptual range could be limited compared to species that forage regularly in gaps, edges, and other brighter habitats.

Given the general absence of such light-limited habitats for diurnal birds in temperate areas, this degree of specialization is unlikely to be an important component of extinction risk for these species. Particular groups of neotropical birds that might be more sensitive to light conditions are the ground antbirds (Formicariidae) and some ovenbirds (Sclerurus leaftossers). Tests of the light-sensitivity hypothesis should include histological comparisons of ocular structural components and cell sensitivities between fragmentation-sensitive and fragmentation-tolerant species. Comparisons could be done in a phylogenetically controlled manner, given the occurrence within some families (eg Thamnophilidae) of both forest-interior and gap-specialist species. Additional experiments could include habitat choice tests in chambers where light environments are manipulated and bird use of those environments is quantified.

Dispersal ability

Another hypothesis that was previously dismissed as basically irrelevant to temperate breeding birds is that some species could experience difficulties colonizing isolated habitat remnants. Given that birds are generally very mobile, the inability or unwillingness of neotropical birds to traverse gaps seems surprising to many temperate-zone biologists (Harris and Reed 2002). This attitude might be changing, since more recent evidence suggests that some species from temperate regions may be more inhibited from crossing gaps than others (Bélisle et al. 2000; Gobeil and Villard 2002). Considering that many temperate-zone species fly thousands of kilometers during migration, it is particularly interesting that we are discovering how some species settle for a breeding season and then appear to restrict what types of landscapes they will move through (Bélisle and St. Clair 2001).

In contrast, dispersal limitation is a longstanding hypothesis among tropical ornithologists (Wallace 1853; Willis 1974; Mayr and Diamond 2001). Within the tropics, there may be hundreds of forest-dwelling species that will not move across non-forested habitats (Figure 5). For instance, Develey and Stouffer (2001) found that many mixed-flock species were unlikely to cross a road of only...
Conclusions

The unusually specialized lives of tropical birds, relative to temperate species, subjects them to greater risk of extinction in altered landscapes. The most sensitive species are highly adapted to environments of the understory and forest floor, where variations in humidity, temperature, and light are very small. Furthermore, at least over recent evolutionary time, the continuous distribution of mature forest means that year-round resident species rarely, if ever, had to cross non-forest habitats, resulting in morphological specializations for walking and reduced abilities for sustained flight. Although many of these hypotheses still require intensive evaluation by experimental and observational studies, the pace at which tropical landscapes are being fragmented demands may not be as difficult as flights across open water if some species are willing to leave forest but need stopping points along the way to ensure a successful journey.

Low population densities and large home ranges

The average abundance of most forest-dwelling, neotropical species is an order of magnitude lower than their north temperate ecological counterparts (Terborgh et al. 1990; Robinson et al. 2000). In Amazonian Peru, 35% of species occur in densities of <1 pair/100 ha and median abundance is 2.5 pairs/100 ha (Terborgh et al. 1990). In other Amazonian sites, median abundance may be even lower (Stouffer and Bierregaard 1995). Low abundance goes hand in hand with much larger home ranges in the tropics, establishing a greater degree of area-sensitivity than is normally seen in bird species from northern temperate zones. The smallest territories of passerines in Amazonia are 3 to 4 ha, whereas many breeding season territories of birds in temperate areas are less than 1 ha (Terborgh et al. 1990). When forests are fragmented, the rarity of most tropical species will result in a low probability of occurrence. Likewise, large territory sizes and patchy distributions will ensure that few individuals of most species will be present even in 100-ha fragments, a size that many biologists studying northern temperate species would consider to be large. The probability of long-term persistence in all but fragments of hundreds to thousands of hectares is expected to be small unless recolonizations are frequent.
that we move forward and design tropical reserve systems with these specialized lives of tropical birds in mind. We suggest the following approaches.

First, given the very large home ranges and the general rarity of most species, every effort must be made to preserve the largest habitat remnants still extant. In many cases, this should include the preservation of many small forest patches in a region, followed by the reforestation of surrounding disturbed habitats. Some dispersal-limited species may not move across pastures, but will move through young second-growth forest, which will facilitate passive recolonization of smaller fragments.

Second, when protection of the matrix surrounding fragments is impossible, corridors connecting isolated remnants are essential. Reducing the isolation of patches by reconnecting them is absolutely critical to promote dispersal in the tropics, although it may not be necessary in many temperate landscapes (Hannon and Schmiegelow 2002).

Third, the effective area of remnants will be increased if microclimatic variability is reduced and the light environment is carefully regulated (Figure 7). Three strategies will help here. One is to construct vegetative buffers around edges of new fragments to reduce wind and light penetration. In many neotropical locations, the creation of buffer zones can be accomplished relatively quickly and passively by allowing second-growth trees to grow around the margins of forest fragments. Additional considerations are to exclude cattle and other grazers which defoliate the ground and understories of forests and to exclude, or carefully limit, timber extraction, as the removal of timber permits increased solar penetration by opening up canopies.

These approaches will also benefit conservation of birds in temperate regions, but many tropical birds lack the same levels of resilience to disturbance because of their evolutionary and life histories. Gulliver would also have found the lives of tropical birds to be very peculiar. Understanding these peculiarities will lead to effective conservation.

**Acknowledgements**

We thank the Brazilian and Panamanian natural resource agencies for allowing us to study birds in their countries. The work was supported by the Auburn University Center for Forest Sustainability and National Science Foundation grants 0212587, 0408186, and 0422233.

**References**


![Figure 7. An abandoned pasture surrounding a forest fragment in Brazil. Revegetation along margins of fragments provides some insulation against effects of drying winds and solar penetration. As regrowth of trees in the pasture continues, more fragmentation-sensitive bird species will disperse across the landscape and recolonization of fragments will increase.](image-url)
Robinson WD, Rompét GR, and Robinson TR. Videography of Panama bird nests shows snakes are principal predators. Ornithologia Neotropical. In press.
Skutch AF. 1949. Do tropical birds rear as many young as they can nourish? Ibis 91: 430–55.
Swift J. 1726. Travels into several remote nations of the world. London, UK: Benjamin Motte.
Waller AR. 1853. A narrative of travels on the Amazon and Rio Negro with an account of the native tribes, and observations on the climate, geology, and natural history of the Amazon Valley. London, UK: Reeve & Co.