

AVIAN EXTINCTIONS FROM TROPICAL AND SUBTROPICAL FORESTS

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■ **Abstract** Tropical forests are being lost at an alarming rate. Studies from various tropical locations report losses of forest birds as possibly direct or indirect results of deforestation. Although it may take a century for all the sensitive species to be extirpated from a site following habitat loss, species with larger or heavier bodies and those foraging on insects, fruits, or both are particularly extinction prone. Larger- or heavier-bodied species may occur at low densities, increasing their vulnerability to habitat alterations. Insectivores are vulnerable for reasons such as the loss of preferred microhabitats, poor dispersal abilities, and/or ground nesting habits that make them susceptible to predation. The lack of year-round availability of fruits may make survival in deforested or fragmented areas difficult for frugivores. Extirpation of large predators, superior competitors, pollinators, and seed dispersers may have repercussions for tropical ecosystem functioning. Large tropical reserves that adequately protect existing forest avifauna are needed. Sound ecological knowledge of tropical forest avifauna for biodiversity-friendly forest management practices is also needed but sorely lacking.

INTRODUCTION

Despite extremely high species diversity and endemism of existing tropical forests, 16 million ha are lost annually (Achard et al. 2002). The speed of tropical deforestation is unprecedented in evolutionary history (Bierregaard et al. 1992). A large proportion of current biotas may have originated from tropical climates, so tropical extinctions have repercussions for the preservation of current as well as future biodiversity (Myers & Knoll 2001).

Globally, one in eight bird species may become extinct over the next 100 years—99% of the extinctions owing to human activities such as deforestation and hunting (BirdLife International 2000). Therefore, there is an urgent need to understand the

patterns and processes of avian extinctions. We review extinctions of forest avifauna from the tropics and subtropics, lying largely between the Tropics of Cancer and Capricorn, 23.5° north and south of the equator. These forests are typically found in aseasonal or semiseasonal climates, and they harbor a disproportionate share of the planet's biodiversity (Whitmore 1980, Myers et al. 2000). Ninety-three percent of 902 threatened forest birds are found in the tropics (Birdlife International 2000). Tropical forest birds are particularly sensitive to deforestation compared with other taxa such as vascular plants (Brook et al. 2003). They may be inherently vulnerable to habitat perturbations owing to relatively low population sizes, patchy distributions, poor dispersal abilities, and high habitat specificity (Terborgh et al. 1990, Turner 1996, Laurance et al. 1997).

We do not review extinctions on the basis of fossil records, as they have been dealt with elsewhere (e.g., Milberg & Tyrberg 1993, Pimm et al. 1994). We are concerned with local extinctions (hereafter extinctions) or extirpations. Local (population) extinctions are determined by comparing results from recent surveys with those made in the past (historical approach). Alternatively, they are inferred by making comparisons among differently sized fragments (fragmentation approach). We review evidence from both empirical approaches. However, for the fragmentation approach, we include only studies that provided quantitative data on species extirpations.

We present the current state of knowledge on avian extirpations from tropical forests by exploring these questions: Are populations at the distributional edges rather than centers of their ranges more vulnerable to extinction? Are large-sized species more vulnerable to extinction than small ones? Have extinctions occurred disproportionately in certain foraging guilds? Does certain behavior(s) make a species more extinction-prone? Is there any evidence that inbreeding depression causes extinctions? Are certain families more prone to extinctions? Do extinctions affect ecosystem functioning? Can any conservation efforts reverse or halt the extinctions? We also highlight areas where future research and resources should be focused.

PATTERNS

Anthropogenically driven extinctions have occurred on tropical and subtropical islands for thousands of years (e.g., Diamond 1989, Milberg & Tyrberg 1993, Steadman 1995). Mechanisms for prehistorical extinctions may be similar to those for current extinctions: overhunting, introduced predators and diseases, and habitat destruction (Milberg & Tyrberg 1993). Further, forest maturation can render habitats unsuitable for some species and cause local extinctions (e.g., Bush & Whittaker 1991). Although "natural" or human-caused prehistoric extinctions have occurred, probably owing to accelerating habitat destruction and burgeoning human populations, extinction rates have soared recently (Balmford 1996, Kerr & Burkey 2002).

Most studies reporting bird extirpations are Neotropical (12 out of 16). Extirpations reported ranged from 1% (Costa Rica, minimum estimate; see Daily et al. 2001) to 67% (Singapore; see Castelletta et al. 2000) of the original forest avifauna. There are important patterns to note from these studies. First, the existence of refuges can probably dampen the effects of deforestation (Brash 1987). Second, habitat flexibility seems to aid survival. For example, in experimentally fragmented areas (1 and 10 ha) of Manaus (Brazil), mixed-species flocking species that used forest edges and secondary forests survived (wedge-billed woodcreeper, *Glyphorhynchus spirurus*; chestnut-rumped woodcreeper, *Xiphorhynchus pardalotus*; and white-flanked antwren, *Myrmotherula axillaris*), whereas species restricted to the forest interior (e.g., cinereous antshrike, *Thamnomanes caesius*) perished (Stouffer & Bierregaard 1995a). Similarly, because of abilities to use forest edges and gaps, predominantly nectivorous understory hummingbirds suffered few negative effects from fragmentation and maintained species composition and abundance similar to those occurring prior to isolation in the same area (Stouffer & Bierregaard 1995b). Last, observed recolonizations of altered areas remain few, suggesting poor colonization abilities of most extirpated species. These poor colonization abilities may be due to variables such as low initial population density and/or reluctance to cross even small gaps (e.g., 80 m; see Bierregaard et al. 1992). Out of the eight forest-dwelling species missing from Barro Colorado Island (Panama) since the 1970s, only one (great currawong, *Crax rubra*) appeared to have recolonized (Robinson 1999). In some studies (e.g., Karr 1982a) nearby continuous forests are assumed to be a population source area. In light of possible poor dispersal abilities of most tropical bird species (see above), such an assumption needs verification.

LAG TIME IN AVIAN EXTINCTIONS

Possibly because of comparatively low reproductive effort and high environmental stability, tropical bird species should have low adult mortality. Adult mortality of only 10% to 30% per year has been estimated for birds from various tropical locations (Trinidad, Sarawak [Malaysia], and Barro Colorado Island; see Willis 1974). This fact suggests that it may take some time for a tropical bird species to disappear following habitat loss unless such habitat loss decreases adult longevity. The Puerto Rican parrot (*Amazona vittata*, longevity in captivity is 23 years), for example, had about 2000 individuals around 1900 in the Caribbean National Forest. Their numbers declined to 20 over the next 60 years, despite a halt in deforestation (Brash 1987). This result indicates that it may take decades for the extinction of some species, and once the decline starts it may be difficult to halt even if habitat degradation ceases. For such species, management actions (see below), in addition to stopping deforestation, may be required to halt or reverse the decline.

Brooks et al. (1999b) found that a plausible half-life (time taken to lose half of the species) for avifaunal extinctions in fragmented forests in Kenya was 50 years. Half-life decreased with fragment size and isolation from nearby forested areas

(e.g., 23 years for a 100 ha fragment 9.0 km from the nearest patch). Because the smallest fragment was also the most isolated, it was not possible to tease apart independent effects of fragment size and isolation in this study. Smaller fragments may contain small populations, and isolation may reduce immigration and thus result in zero or minimal “rescue effect” (immigration by unrelated individuals into isolated populations; Brown & Kodric-Brown 1977). Half-lives may be further shortened in fragments by indirect factors, such as high predation, parasitism, and damage in case of catastrophic events such as fires and storms (Brooks et al. 1999b). In fact, 100 ha fragments may lose half of their species in less than 15 years (Ferraz et al. 2003). Therefore, there may be decades, even if remaining forests are large, in which to halt the extinctions of at least a large proportion of tropical forest bird species following initial habitat loss. Further, ability to tolerate habitat deterioration and dispersal capability may vary among species and affect their persistence within a disturbed landscape (Lens et al. 2002).

MECHANISMS

Ultimately, decreased survival, fecundity, or both may result in extinction of a species. Mechanisms causing extirpations may act independently or synergistically (Figure 1). Pinpointing a single cause of an extinction may be difficult (Pimm 1996, Reed 1999). Habitat loss may directly cause some extinctions, but it also facilitates colonization by invasive species and infiltration by disease vectors and parasites, and it opens up habitats for hunters. For example, in Hawaii, avian extinctions were higher than predicted by habitat loss alone (Scott et al. 1988, Pimm 1996), suggesting collective effects by a myriad of factors.

Habitat destruction is considered a major cause of species losses (e.g., Tilman et al. 1994, Pimm & Raven 2000, Gaston et al. 2003). However, some authors argue that there has been little *direct* empirical evidence that tropical deforestation causes extinctions (Heywood & Stuart 1992). Such direct evidence has come from well-designed experiments that compare data before and after deforestation, as has been done in Manaus, Brazil (Bierregaard et al. 1992). Mounting evidence also suggests that deforestation is one of the prime direct or indirect causes of reported bird extirpations. Brook et al. (2003), using the species-area equation, projected that if the current rate of deforestation continues in Southeast Asia, there will be 16% to 32% extirpations of forest birds by 2100. Similarly, Brooks et al. (1997) used deforestation data and the species-area equation to predict the number of threatened endemic species in Southeast Asia. In more detailed analyses, Brooks et al. (1999a) determined the correlation between degree of deforestation and the existence of threatened endemic species in the lowland and montane forests of Southeast Asia. Broadly, more threatened bird species were in heavily deforested areas. However, there were some regional and habitat differences. The number of threatened species in montane areas was underestimated by the species-area equation, possibly because their restricted ranges made them disproportionately more vulnerable to habitat loss (Brooks et al. 1999a). Conversely, lowland avifauna

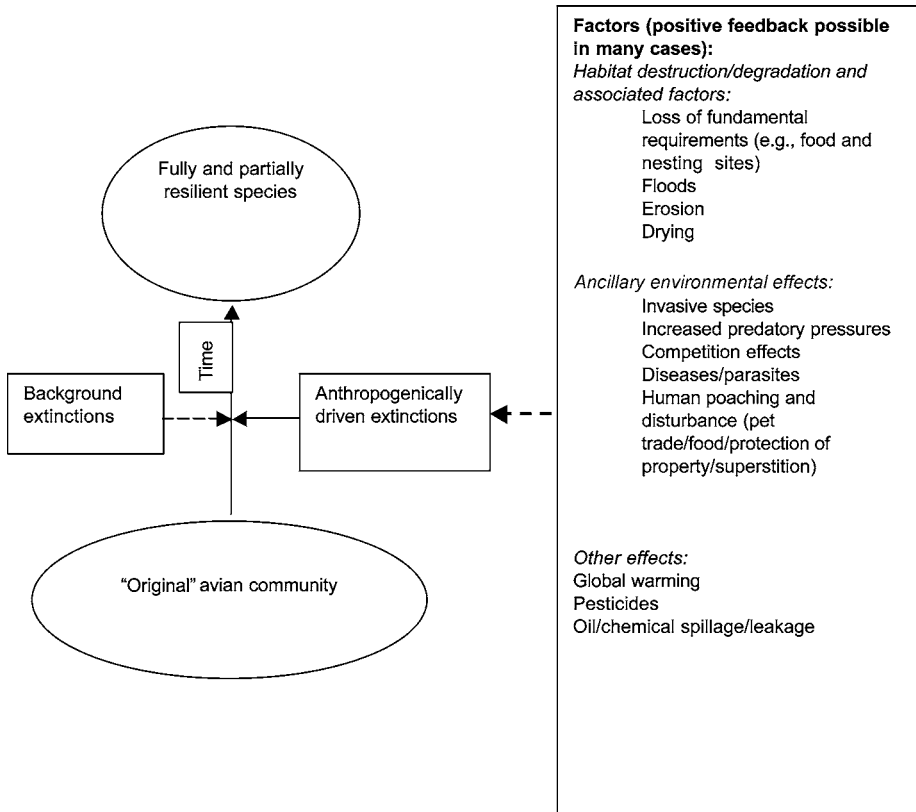


Figure 1 A generalized diagram showing the possible pathway and factors causing bird extinctions. (Background extinctions refer to extinctions from natural causes, e.g., catastrophic events such as hurricanes.)

of areas such as Lesser Sundas and Java were less threatened than predicted by the same equations. Because of centuries of habitat loss, these areas may either have lost their more sensitive endemics before any scientific surveys were conducted or they may contain inherently tolerant species. Brooks et al.'s (1999a) analyses did not demonstrate a direct link between deforestation and species endangerment but did show that deforested areas generally harbor more threatened species, because of either habitat loss or degradation or associated causes (e.g., hunting).

Deforestation can cause the loss of preferred habitats of some forest bird species. Only one or two woodpecker species occurred in fragments smaller than 2500 ha in Java, possibly because of the lack of suitable nesting trees (Van Balen 1999). Loss of forest streams in the western Andes might have caused the extinction, for instance, of the Andean cock-of-the-rock, *Rupicola peruviana*, and the crested ant-tanager *Habia cristata* (Kattan et al. 1994). Similarly, mesic forests are preferred by forest-dependent endemic and quasi-endemic bird species in the cerrado region

of Brazil (Marini 2001), suggesting that loss of such forests may be detrimental to them.

As mentioned above, roads and trails make deforested areas more accessible to hunters (hunting for food and/or the cage; see Milner-Gulland et al. 2003). In the 1980s, 2–5 million birds were captured for the international trade (Beissinger 2001). There is little monitoring of the international bird trade, but half a million birds traded between 1991 and 1996 were listed in CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) appendices (Beissinger 2001). Almost all these birds originated from the tropics.

In many cases, human persecution may have caused the extirpation or decline of forest species. For example, in Ecuador hunting may have partly caused the decline of species such as the great tinamou (*Tinamus major*) and crested guan (*Penelope purpurascens*; Leck 1979). Similar cases have been reported elsewhere (Brash 1987, Christiansen & Pitter 1997, Van Balen 1999, Marini 2001). Not all hunting is for meat, as some large birds are shot because it is believed they eat domestic animals (see Gillespie 2001).

Increased accessibility of forests to people may have other negative effects on birds. Diamond et al. (1987) speculated that increased human-mediated disturbance (e.g., nest predation by domestic dogs, *Canis familiaris*) might have been one factor contributing to the extinction of ground-dwelling species such as the banded pitta (*Pitta guajana*) and black-capped babbler (*Pellorneum capistratum*) in Bogor Botanical Garden (Java, Indonesia). The use of pesticides may also be detrimental to forest birds. The extirpation of two Mauritian carnivorous forest bird species, the Mauritius kestrel (*Falco punctatus*) and Mauritius cuckoo-shrike (*Coracina typica*) before the 1950s from some areas was probably due to the use of organochlorines (Safford & Jones 1997). Both species seem to have recovered since 1970, after use of organochlorines decreased. Helped by the reintroduction program and provision of nest boxes, the kestrel seems to have recolonized all the previously occupied areas. Owing to the poor dispersal abilities of the cuckoo-shrike, its reintroduction into all previously occupied areas may be needed (Safford & Jones 1997).

Deforestation may also facilitate the spread of invasives (plants and animals) into previously forested areas (e.g., Brash 1987, Diamond et al. 1987). The magnitude of the impact of invasives on extirpations remains unclear. The introduced brown tree snake (*Boiga irregularis*) was likely responsible for the loss of 12 (at least 8 forest species) of 18 native bird species from Guam (Fritts & Rodda 1998, Wiles et al. 2003). Similarly, ground-nesting birds are negatively impacted by feral cats (*Felis catus*) and domestic dogs (Leck 1979, Diamond et al. 1987, Kattan et al. 1994). However, some ground-nesting bird species may be able to counter cats because of adaptations to native ground predators (e.g., rodents and land crabs) (Mayr & Diamond 2001).

On French Polynesian islands, monarchs (*Pomarea* spp.) were rarely found on islands with the brown rat (*Rattus rattus*) (Seitre & Seitre 1992), suggesting either that they were avoiding this potential nest predator or that this rat was one

of the possible reasons causing the extirpation. In a recent study, Thibault et al. (2002) reported that the rat probably caused the decline and extinction of monarchs from Polynesian islands. This decline was likely caused by nest predation and was exacerbated by a larger, superior, invasive competitor, the red-vented bulbul (*Pycnonotus cafer*).

EXTINCTION PRONENESS

Extinction proneness may depend on the level and type of threat and interactions among multiple factors (e.g., biogeographical, morphological, and behavioral).

Biogeography

Whether populations at the edges of their ranges are more vulnerable to deforestation remains unclear (Brooks 2000). Populations may be at their physiological and ecological limits at their distributional edge. In addition, because of low densities, populations at the edges of their ranges could be particularly vulnerable to genetic (e.g., inbreeding depression) and/or environmental stresses (e.g., pesticides; see Møller 1995). Nineteen of 29 species at the upper or lower limit of their elevational distributions were extirpated from the western Andes (Kattan et al. 1994). Similar instances have been reported elsewhere (Christiansen & Pitter 1997, Gillespie 2001). However, in the Colombian Andes, Renjifo (1999) found that species beyond their usual elevational limits were not disproportionately likely to become extinct, suggesting, in some cases, resilience even at distributional limits.

Rare species may be more extinction prone than common species, but rarity is not an independent factor and correlates with variables such as body size, habitat specificity, and geographic distribution (Kattan 1992, Goerck 1997). In Ecuador, some inherently rare species such as the tiny hawk (*Accipiter superciliosus*) and crane hawk (*Geranospiza caerulescens*) were possibly extirpated (Leck 1979). Small initial population size, requirement for large territories, and diet specialization may be factors in their elimination. Similarly, rare and uncommon species were more likely to be extirpated than common species in the Colombian Andes (Renjifo 1999). In tropical moist rainforests of eastern Queensland (Australia), rare species were negatively affected by fragmentation (Warburton 1997).

However, rare species are not always more extinction prone than common species. Karr (1982b) sampled the understory fauna of Limbo Hunt Club (Panama) 9 km east of Barro Colorado Island (BCI), presumed to be the source fauna for BCI. The species that were extirpated from BCI were not less abundant at Limbo Hunt Club (e.g., song wren, *Cyphorhinus phaeocephalus*). Species with higher annual population variability in the Limbo Hunt Club were the ones that disappeared from BCI. Karr hypothesized that such species track variable food resources and may require larger areas for their local movements. Similarly, apparently widespread and common species are sometimes extirpated, for example, the brown-hooded parrot

(*Pionopsitta haematotis*) and red-capped manakin (*Pipra mentalis*) in Ecuador (Leck 1979).

Extinction proneness can also be affected by the size of a species' range (Ribon et al. 2003). Small ranges may make species more vulnerable to stochastic perturbations even if local abundance is high. Proportionally, more passerines with small geographic ranges in the Americas are threatened than those with large geographic ranges (Manne et al. 1999). Deforestation may reduce habitat sizes for species requiring large home ranges. Four canopy frugivores likely requiring large home ranges (e.g., the scaly-naped parrot, *Amazona mercenaria*) disappeared from San Antonio, Ecuador (Kattan et al. 1994). Assuming that home range scales positively with body mass, Beier et al. (2002) determined that threshold patch size in Ghana for a 24 g and 920 g species was 10 ha and 8000 ha, respectively. Renjifo (1999) suggested that for some species large home ranges may not be a constraint, as such species could be adapted to track variable food resources and thus be able to travel even through the matrix (areas surrounding the forest).

Body Size

Large-bodied vertebrates are considered more extinction prone than small-bodied ones (e.g., Kattan 1992, Gaston & Blackburn 1995, Brook et al. 2003, but see Gotelli & Graves 1990 for island extinctions). A common explanation for this trend is that body size is inversely correlated with population size (Pimm et al. 1988), making large-bodied animals particularly vulnerable to environmental perturbations. The extinction proneness of large-bodied animals is further enhanced because of other correlated traits such as large area requirements, greater food intake, high habitat specificity, and low reproductive rates (Terborgh 1974, Leck 1979, Kattan 1992, Sieving & Karr 1997).

Large bird species are generally more vulnerable to human persecution, whereas small species are generally more vulnerable to habitat loss (Owens & Bennett 2000). However, we should be cautious in generalizing about the role of body size in the extinction process. Owing to a slower reproductive rate, larger parrots are more vulnerable than smaller finches, despite lesser numbers being captured for the pet trade (estimated 70% and 25% of 1.6–3.2 million birds annually, respectively) (Beissinger 2000). However, some smaller bird species (e.g., Muscicapinid flycatchers) with small population sizes can also be vulnerable owing to heavy pet trade, suggesting that in certain cases factors other than body size may enhance extinction proneness.

Many studies report the disproportionate loss of large-bodied or heavier species from avian communities (Leck 1979, Karr 1982a, Diamond et al. 1987, Christiansen & Pitter 1997, Renjifo 1999, Castelletta et al. 2000). Species that were lost from Barro Colorado Island were heavier than extant species, on the basis of sampling of the understory of nearby Limbo Hunt Club (Panama; Karr 1982b). However, there was no correlation between body mass and rarity, suggesting that larger species may not always be rare. Species extirpated between 1911

and 1997 from the Colombian Andes were heavier than extant species (Renjifo 1999). However, this relationship was not manifested for the missing species from smaller fragments, indicating resilience in some extant large-bodied species. On the same note, Castelletta et al. (2000) showed that larger species suffered more extirpations than smaller species initially, but this was not the case in recent losses (i.e., during the past 50 years). This result shows that body size may be important in early extirpations, but other factors may become more critical as the extinction process proceeds.

There may be an interaction between foraging habits and body size. Large canopy frugivores and large understory insectivores are extinction-prone guilds in the Neotropics (Willis 1979, Bierregaard & Lovejoy 1989). Extinct large canopy frugivores had significantly longer body lengths (mode 30 versus 10 cm) than extant species in San Antonio, Colombia (Kattan et al. 1994). Such species depend on fruits that typically vary spatially and temporally and may be difficult to locate in isolated forests. This was not the case for smaller canopy frugivores such as tanagers, because they supplement their diet with insects. Also, tanagers use a variety of habitats, such as the forest canopy, edges, and gaps, making them more resilient to habitat loss.

A minority of studies indicate no clear relationship between body size and extinction proneness. Newmark (1991) found that body mass was not correlated with bird occurrences. However, this result should be carefully interpreted because of relatively small variation in the body masses (7–138 g) and small sample sizes (22 out of 26 species had fewer than 30 captures). Body size also did not predict abundance in the forests of Sumba and Buru, Indonesia (Jones et al. 2001).

In addition to body size, other morphological variables may also affect extinction proneness. High investment in sexual traits may render some species less adaptable to changing environments. However, Jones et al. (2001) found that sexual dimorphism was not one of the predictors of forest bird abundance on the islands of Sumba and Buru. The effect of sexual dimorphism on extirpation of forest bird species remains unclear.

Behavioral Characteristics

Foraging habits can affect a species' ability to persist in an altered habitat. Many studies show that either frugivores or insectivores or both are more extinction prone than other guilds (Leck 1979, Willis 1979, Brash 1987, Newmark 1991, Kattan et al. 1994, Christiansen & Pitter 1997, Goerck 1997, Stratford & Stouffer 1999, Castelletta et al. 2000, Jones et al. 2001, Beier et al. 2002, Lambert & Collar 2002, Raman & Sukumar 2002, Ribon et al. 2003). The lack of year-round availability of fruit plants in smaller forests may cause the extinction of frugivores (Leck 1979).

A number of hypotheses are proposed for the disappearance of insectivores from deforested or fragmented areas. First, deforestation may impoverish the insect fauna and reduce preferred insectivore microhabitats (e.g., dead leaves). Second, insectivores may be poor dispersers and/or have near-ground nesting habits where

they may be more vulnerable to nest predators. The insectivorous guild was more depauperate in small fragments (4–5 ha) than in a large fragment (227 ha) near Las Cruces (Costa Rica; Sekercioglu et al. 2002). Most large and specialized insectivorous bird species (e.g., the black-faced antthrush, *Formicarius analis*) were probably absent from small fragments. Invertebrate abundance, average length, and dry biomass were similar among the fragments. Fragment size also had little effect on the diet composition, prey biomass, and prey items per sample of most sampled bird species. This fact led Sekercioglu et al. (2002) to conclude that absence of some insectivorous bird species from small fragments may not be related to food scarcity but likely to their poor dispersal abilities.

Other guilds may be more extinction prone in some areas. In Bogor Botanic Garden, proportionally more extirpations were of carnivores than of any other foraging guild (Diamond et al. 1987). Similarly, carnivorous species were more vulnerable than other guilds in Nicaragua because of their lower population densities and susceptibility to hunting (Gillespie 2001). Are species with generalist foraging habits safe? In Singapore, mono-diet species were more vulnerable initially, but as the extinctions proceeded, multi-diet species also were extirpated, suggesting that with heavy forest loss even generalist species are affected (Castelletta et al. 2000). Two other studies showed no effect of dietary habits on extinction proneness (Karr 1982a, Renjifo 1999).

In Singapore, 30% of extinctions occurred in species that fed in the canopy (Castelletta et al. 2000). There may be an interplay of factors, as these canopy feeders were frugivores with large bodies, such as hornbills. Such species may have low population densities and may be affected by lack of adequate fruits, among other things (e.g., lack of nesting sites), in shrunken forests (Terborgh 1974).

Behaviors other than specialized foraging habits or sites also affect extinction proneness. Species forming mixed-species flocks disappeared more frequently from smaller fragments (1 and 10 ha) in Manaus (Brazil; Stouffer & Bierregaard 1995a). Some of the mixed-species flock members (e.g., the cinereous antshrike, *Thamnomanes caesius*) may have high foraging success in mixed flocks or have large territories and high territory fidelity (Munn & Terborgh 1979, Powell 1985). The latter two may be eroded in isolated fragments. Similarly, obligate army-ant followers, restricted to the Neotropics, also disappeared from smaller fragments, probably because of large area requirements (Bierregaard & Lovejoy 1989, Bierregaard et al. 1992). These species (e.g., the white-rumped antbird, *Rhegmatorhina hoffmannsi*) may have home ranges between 1 and 5 km in diameter (Willis & Oniki 1978, Harper 1989, Bierregaard & Lovejoy 1989), an area not available in smaller fragments (≤ 10 ha). Harper (1989) demonstrated that obligate ant-followers (e.g., the rufous-throated antbird, *Gymnopithys rufigula*) disappeared from fragments not containing army ant colonies but were more likely to persist if such colonies were made experimentally available. In addition to mixed-species flocking and army-ant following birds, colonial nesting Icterids may also be vulnerable because they cannot form viable colonies in small fragments (Renjifo 1999).

A majority of tropical forest bird species have poor dispersal abilities (Terborgh 1974, Bierregaard et al. 1992, but see Terborgh et al. 1997). Ability to disperse may depend on morphology (e.g., wing loading) and physiology (e.g., intolerance to sunlight) (Johns 1992). Poor dispersal abilities may make certain bird species vulnerable because they cannot colonize new areas (Tilman et al. 1994, Lens et al. 2002). Indirect results show that species with superior colonization abilities and those that can exploit secondary habitats may be less extinction prone (Stouffer & Bierregaard 1995a, Gascon et al. 1999, Sekercioglu et al. 2002).

Habitat loss may also disrupt some behaviors of bird species (e.g., mating), thus making them particularly vulnerable to extinction (Reed 1999), but such data are lacking for tropical forest birds.

Life History Traits and Genetics

Habitat loss affects species regardless of their life history traits (Beissinger 2000, Purvis et al. 2000). Species with high fecundity, short generation time, low to moderate survival rate, and small body size are predicted to be vulnerable because they can succumb to large stochastic population fluctuations. Alternatively, species with low fecundity, long generation time, high survival, and large body size may also be susceptible because they would recover slowly from reductions in population size.

Attempts to understand the role of life-history traits in the extinction process of tropical birds have been rare. This is mainly because heavily concealed nests and breeding throughout the year make sound demographic data from tropical birds difficult to collect. Although artificial nest experiments do show that undisturbed areas may suffer less predation pressure than disturbed areas (Wong et al. 1998, Sodhi et al. 2003), results are difficult to generalize. For example, in the forests of the cerrado region of Brazil, the predation pressure estimated by artificial nest experiments did not vary with fragment size (Marini 2001).

Deforestation can also be one of the major factors in the loss of genetic variability within populations (Heywood & Stuart 1992). Because of poor dispersal abilities, patchy distributions, and generally low population densities, genetic diversity for some tropical bird species may be difficult to maintain. However, empirical evidence for this hypothesis is lacking. Overall, the role of inbreeding in avifaunal extinctions from isolated tropical populations remains unclear and requires scientific attention.

Taxonomy and Phylogeny

It is well known that controlling for phylogenetic effects is important in comparative behavioral ecological studies (Harvey & Pagel 1991). Lockwood (1999) correctly pointed out that phylogenetic effects are commonly measured as taxonomic effects (i.e., families or genera are taken as monophyletic). Despite the practical ease of considering taxonomy (a proxy for phylogeny) and the nonrandom nature of extinctions with respect to phylogeny (e.g., Bennett & Owens 1997, McKinney & Lockwood 1999), most studies concerning extinction vulnerability of tropical

birds do not take this problem into account. A phylogenetic approach should be used more regularly for tropical birds because practical conservation measures take place in the context of local or regional avifaunas. Most of the studies concerned with phylogenetic biases have been done on a global scale (see Bennett & Owens 2002 for a review and summary), and the practical usefulness of these studies for management decisions in the tropics is not high. Another concern is that studies determining the role of phylogeny in bird extinctions rely heavily on Sibley & Ahlquist (1990), and in the absence of an independent source of information the conclusions should be drawn with caution.

Researchers have repeatedly pointed out that saving species is not enough; we must save evolutionary history (e.g., reviewed briefly in Vazquez & Gittleman 1998). But this has not been practiced in the tropics as far as we know. Poorly studied taxa are in general at higher direct risk of extinction (McKinney 1999). Because tropical areas are much less well studied than temperate areas, even for a comparatively well-studied taxon such as Aves, one can predict that tropical birds are even more at risk, owing to lower professional and public awareness (see Stutchbury & Morton 2001).

Although some authors suggest that phylogenetics should be incorporated into conservation decisions (Heard & Mooers 1999), others argue that species richness can be an adequate surrogate of phylogenetic diversity (Rodrigues et al. 2004). However, it is unclear how far theoretical considerations can go in practice, especially in the tropics. Practical tests of management of vulnerable species in the tropics need to be carefully carried out with scientific rigor to test the available (and conflicting) models (Nee & May 1997, Heard & Mooers 1999). Results thus far have been mixed. For instance, Fjeldså & Lovett (1997) pointed out that younger species of African birds are more patchily distributed and hence relatively more vulnerable to extinction. However, Lockwood et al. (2000) found that the age of a lineage does not seem to affect community homogenization (i.e., if particular lineages are lost and the community gets swamped by only a few invasive lineages).

Few specific tropical case studies deal with phylogenetic effects. Among those that exist, which primarily examine extinctions and the numbers of congeners, results are conflicting. Thiollay (1997) suggested that the presence of congeners may lead to competitive pressure, narrower niches, and lower abundance of at least some potential competitors. However, Terborgh & Winter (1980), with data from Trinidad and Venezuela, and Jones et al. (2001), with data from Sumba and Buru, suggest that congeners did not affect survivorship of their relatives.

Terborgh & Winter (1980) found that families containing disproportionately more susceptible species in Fernando Po, Trinidad, Hainan, Sri Lanka, and Tasmania (temperate island) were: Bucerotidae, Cracidae, Falconidae, Phasianidae, Picidae, Timaliidae, Tinamidae, and Ramphastidae, although patterns for other families were mixed (containing similar numbers of both susceptible and resilient species). In the Colombian Andes, only Icteridae, as a family, was more prone to extinctions (Renjifo 1999). In Las Cruces, Sekercioglu et al. (2002) found a positive correlation between the number of species of a bird family present in nonforested habitats and their presence in small fragments. They seemed to

suggest that family-level dispersal characteristics and abilities to exploit deforested habitats may assist in species persistence in small fragments.

ECOLOGICAL IMPACTS OF EXTINCTIONS

The extinction of some species (e.g., large predators and pollinators) may have higher ecological consequences than extinction of others (Terborgh 1992, Crooks & Soulé 1999). Because of the loss of larger predatory species from tropical communities, avian vulnerability to predation is often exacerbated. These larger predators (e.g., jaguars, *Panthera onca*) do not prey on birds directly but prey on smaller predators such as medium-sized and small mammals (mesopredators). In the absence of their predators, mesopredators become more abundant and prey upon adult birds, their young, and/or eggs (Terborgh 1992). Although this mesopredator release hypothesis has been applied largely to mammals, loss of birds such as raptors (e.g., the harpy eagle, *Harpia harpyja*) may cause similar effects in the ecosystem.

Does the disappearance of a competitor result in niche expansion and higher densities of subordinate species? In the undergrowth of Barro Colorado Island, the disappearance of a larger and probably superior competitor, the black-faced antthrush (*Formicarius analis*) appeared to have allowed the chestnut-backed antbird (*Myrmeciza exsul*) to become more densely and evenly distributed (Sieving & Karr 1997). Extinction of forest bird species, coupled with habitat changes (i.e., increased edge), may result in the thriving of edge species in isolated areas. Leck (1979) suggested that increased forest edge in Ecuador may have contributed to the commonness and possible increase of species such as the shiny cowbird (*Molothrus bonariensis*) and olive-crowned yellowthroat (*Geothlypis semiflava*). More than two thirds of the species that increased over time near Lagoa Santa (Brazil) live in the understory (Christiansen & Pitter 1997). These understory-dwellers are small-bodied insectivores, and their increase could be related to the increase in abundance of insects in remnants owing to an increased amount of edge.

Following deforestation, more nonforest or edge species (e.g., the rufous-collared sparrow, *Zonotrichia capensis*) can colonize new areas (Renjifo 1999). But this change is more likely due to the creation of optimal habitats than to the extinction of forest bird species. The loss of insectivorous species from experimentally isolated fragments in Manaus did not facilitate the increase of nonforest or previously uncommon species even after nine years of isolation (Stouffer & Bierregaard 1995a).

Therefore, the role of *direct* interspecific competition in the extinction process remains unclear. Similarly, how competitive release affects the extant species remains to be clearly demonstrated. The extinction of insectivorous birds from scrubs of West Indian islands correlated with the subsequent higher biomass of competing *Anolis* lizards (Wright 1981). It would have been interesting to determine whether bird reintroductions reversed the observed pattern (i.e., lowered the biomass of *Anolis* lizards).

Parasitism may also be affected by extinctions. The parasitic brush cuckoo (*Ca-comantis variolosus*) disappeared from Bogor Botanic Garden, possibly because of the decline in the abundance of its likely hosts, the pied fantail (*Rhipidura javanica*) and hill blue flycatcher (*Cyornis banyumas*). In contrast, the parasitic plaintive cuckoo (*C. merulinus*) survived in this isolate because of high abundance of its primary host, the ashy tailorbird (*Orthotomus ruficeps*; Diamond et al. 1987).

Because many tropical trees produce large, lipid-rich fruits adapted for animal dispersal (Howe 1984), the demise of bird frugivores may have consequences for forest regeneration. One of the dominant fruiting trees in Puerto Rico, *Dacryodes excelsa*, failed to reestablish in areas it previously occupied, possibly because of the extinction and decline of frugivores (Brash 1987). Some late successional montane tree species (e.g., *Canarium asperum*) rely heavily on frugivorous bird species such as hornbills and fruit pigeons for seed dispersal (Hamann & Curio 1999). These bird species are under heavy hunting pressure and their likely extinction may disrupt the recruitment of the trees. A similar predicament has been found for African trees that rely heavily on birds for seed dispersal (Cordeiro & Howe 2001, 2003).

RESILIENCE

Despite our focus on tropical extinctions, not all tropical species are extinction prone. The species-area relationship leads to a rule of thumb that a 90% loss in habitat leads approximately to a 25% to 50% loss of species (Simberloff 1992a). The predictive power of this relationship may be weak because it does not account for either habitat diversity or fragmentation (Simberloff 1992b), but it is the only such existing model and is still used to make crude predictions of the extent of biotic extinctions. Thus far, tropical bird extinctions largely seem to be fewer than predicted by the species-area equation (Brooks et al. 2002). This fact indicates temporary or permanent resilience in some of the species and/or a time lag in the extinction process.

Since European colonization about 500 years ago, the Atlantic coastal rainforest of Brazil has been reduced to 12% of its approximated original size but with no recently reported avian extirpations (Brown & Brown 1992). The above results may reflect genuine resilience in some of the species. Alternatively, extinctions of species unknown to science may have already happened or there may be a time lag in extinctions following habitat loss (Balmford 1996, Brooks & Balmford 1996, Brooks et al. 1999c).

In a 15-km² remnant forest (0.3%) of Cebu Island (Philippines), 7 of 14 forest endemic bird species/subspecies survived (Magsalay et al. 1995). Fragmented landscape containing mature forest can retain as much as 96% of the original avifauna several decades after isolation (Renjifo 1999). Many other examples show that a proportion of forest avifauna can be found in disturbed habitats (e.g., Johns 1986, Thiollay 1992, Mitra & Sheldon 1993, Warkentin et al. 1995, Woltmann 2003). Few data are available, however, on whether persisting species in

degraded areas are reproducing and surviving as well as their counterparts in pristine areas.

THE FUTURE

Establishment of appropriate protected areas is critical in halting future extinctions. About 23% of existing tropical humid forests are officially protected (Chape et al. 2003). However, it is not known if these reserves receive adequate protection (e.g., against illegal logging and poaching). In the tropics, the extent of protected areas does not correspond well with the number of threatened species (Kerr & Burkey 2002). Effective forest reserves should have viable populations of the threatened species, as mere presence cannot guarantee survival. Although population viability remains a controversial aspect, ecological data such as population size, survival, and recruitment are needed and should be collected to evaluate adequately the population viability of a given species (see Caughley & Gunn 1986, Coulsen et al. 2001, Brook et al. 2002).

Because of typically patchy distributions among tropical bird species, care should be taken in reserve selection (Diamond 1980, Van Balen 1999). Lists of threatened species must be consulted because a large reserve may fail to protect all or even most vulnerable species. For example, in the Albertine Rift Mountains in Central Africa, 9 of 15 threatened bird species do not occur in any of the protected reserves (Bibby 1994). In addition to reserve location, reserve size is also critical. Small reserves may (a) not contain enough resources, (b) facilitate the infiltration and spread of parasites and invasives from the surrounding matrix, and (c) contain tiny populations that may be vulnerable to environmental stochasticity, such as hurricanes. In fact, a 198 ha remnant failed to contain vulnerable species such as the black-necked aracari (*Pteroglossus aracari*) and spot-billed toucanet (*Selenidera maculirostris*) near Lagoa Santa (Brazil; Christiansen & Pitter 1997). Therefore, larger protected areas may be necessary, but there is no consensus about the minimum reserve size in tropics. Leck (1979) recommended reserves as large as 20–30 km² but preferred those as large as 100 km². Other authors also have suggested that reserves of several thousand km² may be needed in the tropics to halt or diminish the chances of mass extinctions (Terborgh 1974, 1992; Whitmore 1980; Myers 1986; Thiollay 1989). Such large reserves may be possible in areas such as the Congo and French Guiana where large undisturbed forests still exist (Whitmore 1997). In areas where large forested tracts are unavailable, forests around the existing reserves could be restored (Whitmore & Sayer 1992a).

The abundance of potential predators should not be unnaturally high in reserves (Terborgh et al. 1997). Ideally, mature and/or high-quality forests should be protected. Renjifo (1999) showed that fragments with mature forest can sustain an avifauna for decades after isolation. Sodhi (2002) found that a reserve with poor-quality mature forest (i.e., heath forest) contained fewer rare species than one with high-quality, similar-sized mature forest.

Habitat links (e.g., fence rows and windbreaks) between patches or reserves may facilitate dispersal and prevent local extinctions or population declines in

fragmented landscapes (Lovejoy et al. 1997, Sekercioglu et al. 2002). Data on efficacy and adequacy of habitat corridors in the tropics are limited, however. Vegetation cover (both native and non-native) can enhance the abilities of corridors to attract forest species such as the short-tailed babbler, suggesting either movement through these areas or use of such edge habitats (Sodhi et al. 1999). On the negative side, corridors can be expensive to create and maintain, may not serve well in heavily fragmented landscapes, and may be counter-productive by facilitating the spread of predators and diseases (Simberloff & Cox 1987, Simberloff 1992b).

Although our review shows that a proportion of avifauna does not adapt to habitat change and will be extirpated, 26% of 144 species recorded in the countryside of Las Cruces (Costa Rica) were forest species (restricted to forest habitat including edges of the small fragments; Hughes et al. 2002). Edges with vertically complex vegetation (tree-tangle-shrub) had at least 100 species. It is unknown if the forest species in this anthropogenic habitat were maintaining sustainable populations, but this study showed adaptability in certain species (e.g., collared aracari, *Pteroglossus frantzii*). Removal of tall trees and edge habitats, even from degraded landscapes, may lower avian richness (Hughes et al. 2002, Petit & Petit 2003). These results cannot be generalized yet, as resilience will likely be species- or site-specific. For example, some endemic species, e.g., elegant sunbird (*Aethopyga duyvenbodei*), rarely use secondary forests even though congeneric species do (Whitten et al. 1987).

Habitat preservation may be a better approach as it can conserve many bird species simultaneously, but specific management may be needed to save individual species (Temple 1986). Conservation programs should not be directed solely at preventing population declines of vulnerable species but should also bring about recovery. To increase the population size of species headed toward extinction, researchers can envision habitat restoration, reintroduction, elimination of invasive predators and competitors, and captive breeding (Heywood & Stuart 1992). Eradication techniques for invasive species have been well developed over the years (Conover 2002). However, management must proceed carefully, using detailed ecological understanding to avoid failure (e.g., failed reintroduction of song wrens on Barro Colorado Island owing to high predation; Morton 1978). Above all, unsustainable forestry practices in the tropics must be curtailed (Laurance 2000). More emphasis is needed to integrate sound biology into forestry practices. For example, there is no consensus on how many years of logging rotation cycle are required to preserve the avian diversity. Research to realize biodiversity-friendly forestry practices is urgently needed.

When one considers that natural tropical forests occupy an area of 1756 million ha containing different forest types (e.g., lowland and montane; Whitmore 1997), little ground has been covered on the effects of deforestation on avifauna. Data are also insufficient to evaluate whether different types of disturbance (e.g., agriculture and urbanization) yield similar negative effects on the avifauna. Some tropical areas remain poorly surveyed and the status of their biodiversity uncertain (Whitten et al. 1987). Detailed biological understanding may be needed for proper conservation/management (Reed 1999), but such an understanding may be poor for

certain tropical areas (Diamond 1987, Sodhi & Liow 2000). Systematic surveys to determine faunal vulnerability and to collect ecological data are needed throughout the tropics in order to practice educated conservation. Life-history variables (e.g., clutch size, reproductive output, and dispersal abilities) and diet of a large proportion of tropical bird species remain unknown. This lacuna makes the generalization of extinction proneness of tropical bird species ecologically shallow.

Studies determining the effects of deforestation on tropical avifauna must be better designed (Bierregaard et al. 1997, Crome 1997, Danielsen 1997). These studies must (a) obtain adequate sample sizes, (b) have adequate sampling periods with multiple visits, (c) use more than one sampling method (e.g., point counts and mist-netting) for adequate sampling, (d) estimate species abundances or densities, (e) validate local extinctions using playback surveys and present species accumulation curves (see Gotelli & Colwell 2001), and (f) have adequate controls (e.g., larger "original" forests). Data sets from the studies should be published or, better still, made available on the Internet for a wide access. We also recommend that individuals making bird lists rank species according to their abundance and clearly define their ranking system. This ranking will assist in determining whether a species is declining in abundance and whether rare species are more extinction prone than common species. Last, scientists must collect data showing whether applied conservation measures (e.g., establishment of reserves) are abating extinctions.

Our review shows that deforestation and its associated effects are permanently altering tropical forest bird communities. Extirpated species may or may not share similar characteristics across the tropics. Idiosyncrasies among species and sites and poor ecological knowledge make widely applicable extinction proneness rules for tropical forest bird species elusive. In general, biology is not properly integrated into tropical forestry practices. More ecological research is needed to evaluate the status and to increase our understanding of the biology of tropical birds.

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