Long-Term Changes in the Avifauna of Barro Colorado Island, Panama, a Tropical Forest Isolate

W. DOUGLAS ROBINSON*

Department of Ecology, Ethology, and Evolution, 515 Morrill Hall, University of Illinois, 505 S. Goodwin Avenue, Urbana, IL 61801, U.S.A., email songwren@pop.life.uiuc.edu

Abstract: *Since its isolation from the mainland more than 85 years ago, 65 bird species have disappeared from Barro Colorado Island, Panama. Because of these extinctions the island is often used as a model for the study of faunal relaxation, or loss of species through time. The most recent survey of the island's bird community was completed in 1970. Between June 1994 and May 1996 I surveyed the island and observed 218 species, including 5 species never before recorded. Three relatively sedentary species have experienced severe population declines since Willis's 1970 survey and may be on the brink of disappearing from the island. Willis estimated 500 Slate-colored Grosbeaks (*Pitylus grossus*), whereas I found only two pairs of this conspicuous midstory-dwelling finch. Two cotingas—Speckled Mourner (*Laniocera rufescens*) and Rufous Piha (*Lipaugus unirufus*)—have declined by 85–95%. I did not locate any individuals of 36 other species that were present during the 1970s. Most (21) of these are uncommon aquatic or nocturnal species, which I may have missed during my surveys, or are rare to uncommon edge species that probably move frequently to and from the island. Seven species, however, are primarily inhabitants of second-growth forest and have been lost probably because of continuing successional maturation of the forest, including changes in land use around the laboratory clearing. Seven forest-dwelling species disappeared during the 1970s and have not recolonized. I detected only one sedentary forest-dwelling species, Great Currasow (*Crax rubra*), that previously had been reported as missing from the island. The nearly complete lack of recolonizations by such forest-interior species suggests that local extinction from tropical forest isolates may be extremely persistent. Tropical forest reserves as small as Barro Colorado Island (1600 ha) may not preserve high levels of regional avian diversity over long periods of time.*

Cambios a Largo Plazo en la Avifauna de la Isla Barro Colorado, Panama, un Bosque Tropical Aislado

Resumen: *Desde su aislamiento del continente mas de 85 años atrás, 65 especies de aves han desaparecido de la isla Barro Colorado, Panama. Debido a estas extinciones, la isla es frecuentemente utilizada como un modelo, ejemplo para el estudio de relajamiento faunal, o pérdida de especies a travéz del tiempo. El estudio más reciente de la comunidad de aves de la isla fue completado en 1970. Entre Junio de 1994 y Mayo de 1996 estudié la isla y observé 218 especies, incluyendo 5 especies que nunca fueron registradas antes. Tres especies relativamente sedentarias han experimentado disminuciones poblacionales severas desde los estudios de Willis en 1970 y podrían estar muy cerca de su desapraición en la isla. Willis estimó 500 organismos de la especie* Pitylus grossus, *mientras que yo encontré solamente dos pares de esta llamativa especie. Las especies* Laniocera rufescens *y* Lipaugus unirufus *han disminuido entre un 85 y un 95%. No localicé un solo organismo de 36 especies que estuvieron presentes durante los 1970s. La mayoría (21) de estas son especies acuáticas o nocturnas poco comunes y es posible que hayan escapado a mis muestreos, o son especies raras en bordes que probablemente se mueven hacia y de la isla. Sin embargo, siete especies son principalmente habitantes de bosque de crecimiento secundario y posiblemente han sido perdidas debido a la maduración sucesional continua del bosque, incluyendo cambios de uso del suelo alrededor del clareado del laboratorio. Siete especies de moradores de bosque desaparecieron durante los 1970s y no han recolonizado. Detecté unicamente una especie sedentaria moradora de bosque (*Crax rubra*) que había sido reportada previamente como perdida en*

la isla. La casi nula carencia de recolonizaciones por estas especies de interiores de bosque sugiere que la extinción local en bosques tropicales aislados puede ser extremadamente persistente. Las reservas de bosques tropicales tan pequeñas como la isla Barro Colorado (1600 ha) pueden no preservar niveles altos de diversidad avícola local por periódos de tiempo largos.

Introduction

When extensive tracts of forest are converted to smaller, isolated patches, the populations of many species residing in the forest decline, sometimes to local extinction (Robbins 1980; Lovejoy et al. 1984; Andrén 1994). The magnitude of the negative effects of fragmentation depends on many factors, including the size of the remaining fragments, the distance separating the fragments from other forest patches or extensive forest tracts, and the magnitude of the biotic interactions with organisms that are more abundant in and along edges of small patches than inside large tracts of unfragmented forest (Rolstad 1991; Faaborg et al. 1995). In addition, the characteristics of the habitat surrounding the forest patches can have an important effect on the temporal persistence of populations through improving or impeding dispersal between patches (Stouffer & Bierregaard 1995*a*; Schmiegelow et al. 1997).

The effects of fragmentation on animal populations in temperate areas have been well documented (Whitcomb et al. 1981; Wilcove et al. 1986; Faaborg et al. 1995). Relatively few investigations, however, have been conducted in the tropics (Turner 1996). Several important factors suggest that investigations of the impacts of fragmentation on tropical communities deserve additional, immediate attention. First, tropical forests host a large percentage of global diversity, much of which has yet to be described (Pimm et al. 1995). Second, conversion of vast, formerly continuous expanses of tropical forest into disturbed, isolated forest remnants is occurring at an accelerating pace (Whitmore & Sayer 1992; Food and Agriculture Organization 1993). Third, the effects of fragmentation on tropical communities might be expected to be more severe than on temperate communities because the population densities of tropical species are frequently smaller on average than those of temperate species (Stotz et al. 1996). Because small populations are more vulnerable to extinction (Terborgh & Winter 1980; Pimm et al. 1988), tropical organisms may be at greater risk of extinction from fragmented landscapes.

Results from pre- and post-isolation surveys of bird communities in 1-, 10-, and 100-ha fragments near Manaus, Brazil, have shown rapid changes in population densities as well as local extinctions from forest patches (Bierregaard & Lovejoy 1989; Stouffer & Bierregaard 1995*a*). Immediately after excision from continuous for-est, bird abundances in new fragments increased, presumably as individuals displaced from the surrounding deforested areas sought appropriate habitat. Within 2–3 years after isolation, however, several species of ant-following birds and participants in mixed-species flocks began to disappear. Few of these species recolonized the fragments even up to 9 years after the fragments were isolated (Stouffer & Bierregaard 1995*a*). Thus, changes in community composition began soon after isolation of the forest fragments and lasted for many years. The small size of the patches, however, supported on average only one or two territories of most of the species involved, and thus the fragments were unlikely to allow the long-term persistence of many species (Bierregaard 1990).

Long-term preservation of biodiversity is a primary goal of conservation biologists. Unfortunately, long-term data from the tropics are scarce (Turner 1996). The only information available to address long-term changes in tropical bird communities are censuses separated by long time intervals, rather than continuous long-term census data. The few cases where censuses separated by long time intervals have been compared are from three sites censused four or fewer times at intervals of up to 130 years (Bogor Botanical Garden, Java [Diamond et al. 1987]; San Antonio, Colombia [Kattan et al. 1994]; and Lagoa Santa, Brazil [Christiansen & Pitter 1997]) and from Barro Colorado Island (BCI), Panama (Chapman 1938; Eisenmann 1952; Willis & Eisenmann 1979; Karr 1982*a*). Results from all these sites demonstrated a loss of 20–33% of the original avifauna after fragmentation. The most thoroughly studied of all the tropical forest fragments is Barro Colorado Island.

Study Area

Barro Colorado Island was formerly a hilltop in a lowland forest landscape along the Chagres River on the Atlantic slope of central Panama. Between 1911 and 1914, thousands of hectares of lowland forest were flooded to create Gatun Lake and the Panama Canal, which isolated the 1600-ha BCI hilltop from the surrounding mainland forest. In 1923 BCI was declared a biological reserve (Chapman 1929). Records of the avifauna were then kept by numerous visiting biologists.

The periods of greatest ornithological activity on BCI were 1923–1939 (Chapman 1929, 1938), 1944–1971 (Eisenmann 1952; Willis 1974; Willis & Eisenmann 1979),

and 1976–1996 (Gradwohl & Greenberg 1980; Greenberg 1981; Karr 1982*a*; Greenberg & Gradwohl 1986; G. Angehr, unpublished data). Although Chapman, Eisenmann, and Willis all compiled comprehensive lists of the island avifauna, only Willis (1980) presented results of a thorough island census in a single year (1970). Nevertheless, there were skilled observers (i.e., Chapman, Skutch, Wetmore, Eisenmann, Willis) present on the island for at least part of each year during all but 8 of the 74 years since 1923. Probably no other tropical location has been so well studied. The nearly continuous presence of ornithological activity on BCI provides an opportunity to evaluate the dynamics of the decline in species richness.

In particular, because so many skilled observers have kept records of birds on BCI, the dates of last sightings of many species are reasonably accurate; most disappearance dates can be placed in at least the proper decade. The fact that the island was losing species through time was noticed early (Eisenmann 1952), and special efforts were made to keep records of sightings of species whose numbers were dwindling (e.g., Willis 1974). Although the disappearances of some species that quickly declined immediately after isolation of the island may have been overlooked because of a lack of investigators or because of unfamiliarity with some species in the first 10 or 20 years (Willis & Eisenmann 1979; Karr 1982*a*), the disappearances of many of the more conspicuous species have been well documented (Willis 1974).

I report results from a recent, comprehensive inventory of the BCI avifauna. The main objectives of the study were to (1) survey the current species richness of BCI; (2) determine if any additional species had become locally extinct since the last survey; (3) determine if any species formerly reported to be locally extinct had recolonized; and (4) identify species with dramatic decreases in population size since 1970 that may be on the verge of disappearing from BCI. Finally, I evaluated the potential of BCI to preserve regional avian diversity over the long term.

Methods

I used three methods to inventory the species richness of the island: point counts, transects, and ad lib observations (Verner 1985). I censused birds at 129 points distributed across the entire island (Fig. 1). Sixty-four of the points were placed at randomly chosen locations, which were selected by superimposing a grid over a map of the island, numbering each grid point, then using a random number table to select the points. The remaining 65 points were supplemental and were located in series of 10 points along trails across the island or along transects between random points that were distant from trails. Each census point was separated by 200 m from the next nearest point.
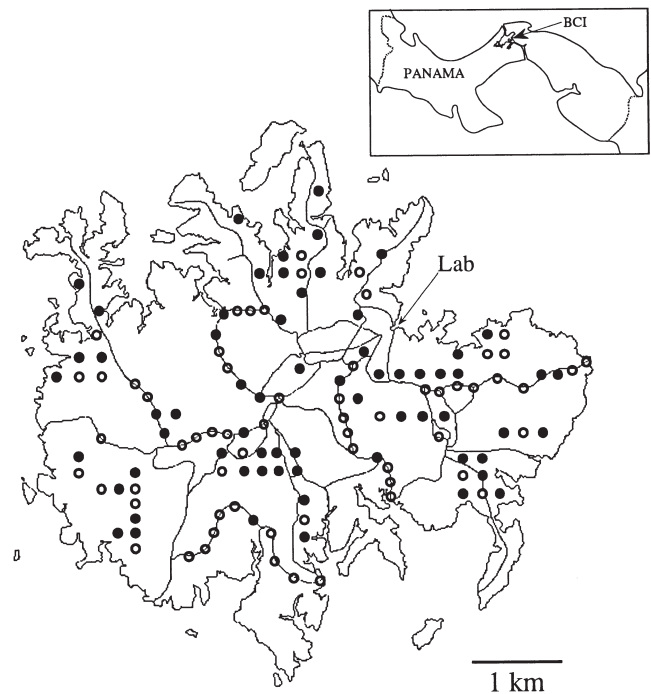

Figure 1. Locations of point counts across Barro Colorado Island. Solid circles denote randomly located points; open circles are supplemental points. Inset shows location of Barro Colorado Island within Panama.

Each point was visited once during the 4-hour period of peak song activity, which lasted from 30 minutes before dawn until 3.5 hours after dawn. At each visit, I noted all birds heard or seen, the direction and estimated distance (± 10 m) of each registration from the point, and the type of cue by which the bird was detected (song, call note, or visual sighting). Each point count lasted 8 minutes. During the 12 months prior to initiating counts on BCI, I conducted over 1000 similar point counts at other locations across central Panama, so I was familiar with all song or call notes of all species likely to be encountered on the island.

In addition to the point counts, I walked transects to maximize coverage of the entire island. These transects included walking all established trails and traversing areas of the island not well covered by the trails or point counts. During transect walks I noted the distance and direction from the nearest trail reference marker (or mapped grid point when doing off-trail transects) of all birds I encountered. I also recorded the time at which each bird was detected and the cue used to detect the bird. These transect counts were conducted from 30 minutes before dawn until bird activity reached its nadir during the early afternoon. Distances of 4.0–10.0 km were covered each day. I also conducted 10 pre-dawn (0330–0530) transect walks that traversed primarily the central portion of the island as an effort to improve de-

tection of nocturnal species. Finally, I conducted ad lib observations at flowering and fruiting trees to observe hummingbirds and canopy-dwelling frugivores, many of which are difficult to detect during point counts and transect walks (Karr 1981; Robinson 1998).

Because there is a strong seasonal effect on the song activity of most species in central Panama (W.D.R., unpublished data), I focused most of my efforts during the period of the year when song activity is highest: most of the dry season (December to late April) and the first 3 months of the wet season (May–July). I conducted censuses on the following dates: 16–18 June and 8–9 July 1994; 18 March and 30 November–4 December 1995; 3–7 January, 19–23 February, 18–27 March, 15–24 April, and 27–28 May 1996.

Because the focus of my surveys was to determine the current species richness of resident landbird species, detection of migrants and aquatic species was not a primary emphasis. Therefore, I did not conduct censuses during the late rainy season (September to mid-November), when peak numbers of Neotropical migrants occur on BCI (Willis 1980). I did, however, attempt to locate semi-aquatic resident species that utilize forest streams, such as Sunbittern (*Eurypyga helias*), Agami Heron (*Agamia agami*), and several kingfishers, by walking streams and portions of the island-lake interface, especially around the larger coves.

I characterized the residency status of each species as one of three classes: resident, migrant, or vagrant. Residents were species likely to or known to breed within central Panama, specifically within the habitats available on BCI (e.g., Crested Guan [*Penelope purpurascens*]). Migrants were species with an established pattern of seasonal occurrence on BCI. Although migrants did not breed on the island, some species spent long portions of the year there (e.g., Acadian Flycatcher [*Empidonax virescens*]). Vagrants, in contrast, were rare visitors with no established pattern of occurrence and for which fewer than three island records exist (e.g., Wood Stork [*Mycteria americana*]). I recorded only species observed on or flying above the island and aquatic species that could be seen from the island.

The habitat preference of each species was classified into one of four categories: forest, edge, open habitat, or aquatic habitat. Forest species were those detected within primary or secondary closed-canopy forest. Edge species were those detected along ecotonal boundaries of forest, such as at the forest-lake interface along the edge of BCI or in the lab clearing. Species occupying the upper portions of forest canopy at the canopy-air interface were classified as edge species. Species of open habitats were primarily those spending the majority of the time on the wing above the forest canopy, such as swifts and vultures, or in grassland. Aquatic species were those that used the lake or marshy habitats in coves around the island. Species using forest streams were classified as aquatic if they used the lake for foraging, but if all foraging was conducted along streams inside forest, the species were classified as forest-dwelling. I categorized species based on personal observations throughout central Panama and on published information (Ridgely & Gwynne 1989; Karr et al. 1990).

I further classified species as breeding or transient. Breeding species had established a pattern of continuous occurrence on the island, whereas transient species had not. Transient species were those detected only a few times and for which no evidence of breeding had been documented for BCI. Determination of breeding status for birds at tropical locations can be problematic because of the wide array of social systems and cryptic nest sites. Consequently, I use the term *recolonization* in a liberal sense. It was not feasible to determine if all species detected were actually breeding on BCI. I interpret the presence of a species classified as a resident forest breeder or resident edge breeder as indicative of potential breeding. By definition, transient species cannot be considered to have become locally extinct or to have recolonized.

Results

During 138 hours of censusing (Fig. 2), 218 species were detected on the island or in the waters surrounding BCI (for a complete list see Robinson 1998). The total number of species encountered was still increasing at the conclusion of the island inventory, but the numbers of forest-resident and edge-resident species had reached plateaus (Fig. 2). On-going detection of additional migrants and aquatic species accounted for the continuing increase in the total species accumulation curve. The total number of species detected on BCI over all 85 years is 394 (Willis & Eisenmann 1979; Karr 1982a; G. Angehr, unpublished data), which includes 220 resident breeders, 68 resident transients, 98 migrants, and 8 vagrants.

I found five species new to the island list, including three vagrants from edge or open habitats (White-tailed Kite [*Elanus leucurus*], Golden-fronted Greenlet [*Hylophilus aurantiifrons*], and Yellow-crowned Euphonia [*Euphonia luteicapilla*]), one Neotropical migrant (Yellow-rumped Warbler [*Dendroica coronata*]), and a parrot (Brown-hooded Parrot [*Pionopsitta haematotis*]). Small flocks of the parrots were encountered foraging in the canopy near the center of the island several times in 1994 and 1995, whereas the other new species were encountered only one time each. Thus, most of the species were vagrants to BCI rather than colonists establishing breeding territories; I found no evidence of breeding by the parrots and had no sightings during 1996. In addition, I encountered two migrant species suspected to occur on BCI but that were not yet confirmed (Willis &
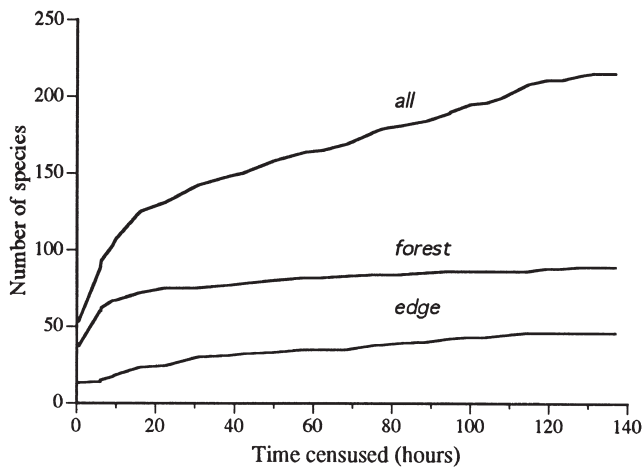
Figure 2. Species accumulation curves with respect to time spent censusing on Barro Colorado Island. The top curve represents data for all species, including migrants and transients. The middle curve represents data only for resident forest-breeding species. The bottom curve represents data for resident edge-breeding species. All curves begin at the origin, but the initial accumulation of species was rapid: within the first hour a total of 53 species was detected, which included 13 edge, 37 forest, and 3 aquatic species.

Eisenmann 1979): Mississippi Kite (*Ictinia mississippiensis*) and Common Nighthawk (*Chordeiles minor*). Snail Kites (*Rostrhamus sociabilis*) were numerous in the waters surrounding the island; their occurrence had not previously been noted in the literature, but small populations have been breeding near BCI since 1991 (G. Angehr, unpublished data).

Excluding migrants, I encountered 26 species that were not noted by Willis during the 1970s (Table 1). Four of these, plus Snail Kite, were new to the island list. The remaining species were primarily associated with edge, open, or aquatic habitats. Only 7, including Brown-hooded Parrot, were forest-dwelling species. Five of the forest species were associated with forest canopy, whereas one, Thrush-like Mourner (*Schiffornis turdinus*), was an understory species, and another, Great Currasow (*Crax rubra*), was terrestrial.

Many of the species found during 1994–1996 but not present in the 1970s represented island recolonizations (Table 2). Three forest species and 10 edge species previously were reported as extinct from BCI. An additional forest species that I did not detect, Sunbittern, was reported as missing by Willis and Eisenmann (1979) but had been encountered occasionally since 1979 (G. Angehr, unpublished data). Several of the recolonizing species were missing from BCI for many years. Wild Great Currasows were last reported nearly 70 years ago, although a pair, later found killed by a predator, was introduced in the 1960s (Willis & Eisenmann 1979). Half of the 14 species were last noted as breeding on the island during the 1960s. Most of the edge species have been detected as transients at irregular intervals after their disappearance as breeders.

Willis detected 36 species during the 1970s that I could not locate (Table 3). Some species may have been overlooked during my censuses because they are difficult to detect as a result of rarity or nocturnal habits. Despite efforts to survey streams and sections of the lake margin, several aquatic species, including Agami Heron, Sungrebe (*Heliornis fulica*), Sunbittern, and three species of kingfisher, could easily have been overlooked. One aquatic species, Least Bittern (*Ixobrychus exilis*), is likely to be missing now because marsh habitat along the island periphery is virtually absent. Seven edge species have disappeared, probably as a result of habitat maturation. At least three of the missing edge species (Gray-headed Chachalaca [*Ortalis cinereiceps*], White-bellied Antbird [*Myrmeciza longipes*], and Scrub Greenlet [*Hylophilus flavipes*]) were last known to occur in the youngest forest on the island (excluding the lab clearing), which is on the tip of Harvard peninsula, and on grassy islands just off the peninsular tip (Willis & Eisenmann 1979; G. Angehr, unpublished data). Importantly, none of the three forest-dwelling terrestrial insectivores that disappeared during the 1970s or 1980s (Pheasant Cuckoo [*Dromococcyx phasianellus*], Ocellated Antbird [*Phaenostictus mcleannani*], and Spectacled Antpitta [*Hylopezus perspicillata*]) had recolonized the island.

Several species not detected during the 1994–1996 surveys have not been encountered on BCI for many years and have not previously been reported as missing (Table 4). Two are large raptors whose home ranges are probably larger than the 1600-ha island. Crested Eagle (*Morphnus guianensis*) has not been reported from BCI since 1950, and it has been recorded only a few times from mainland areas of central Panama, most recently in 1989 (S. J. Wright, personal communication). Given its extreme rarity in central Panama, it seems unlikely that this large raptor still occurs regularly on BCI. Ornate Hawk-Eagle (*Spizaetus ornatus*) is also rare but still occurs infrequently in surrounding mainland forests (Robinson 1998). Pheasant Cuckoo was last detected by Willis in 1978, but it may have been overlooked until 1986 when the last record was obtained (G. Angehr, unpublished data). Long-tailed Tyrant (*Colonia colonus*) is a canopy-dwelling flycatcher that selects treefall gaps with standing dead trees for breeding sites (Wetmore et al. 1984); its absence from BCI since 1979 is enigmatic. The five edge species not previously reported as missing have not been found on BCI for 10 to more than 25 years. All prefer very open, edge habitats that are now generally lacking on the island. The list of newly extirpated species may be somewhat longer considering the

Table 1.   Species detected on Barro Colorado Island during the 1994–1996 survey that were not detected by Willis during the 1970s.[a]

Species	Habitat[b]	Stratum[c]	Notes
Little Tinamou	E	T	1 on western shore
Crypturellus soui			
White-tailed Kite	O		1 record
Elanus leucurus			
Snail Kite	W		recent immigrant
Rostrhamus sociabilis			
Bat Falcon	E	C	rare, mobile
Falco rufigularis			
Great Currasow	F	T	1–2 females; recolonized
Crax rubra			
Common Moorhen	W		in hydrilla in coves
Gallinula chloropus			
Limpkin	W		immigrant, 1985; now common
Aramus guarauna			
Wattled Jacana	W		in hydrilla in coves
Jacana jacana			
Blue Ground-Dove	E	T-M	pair observed
Claravis pretiosa			
Brown-hooded Parrot	F	C	a few small flocks
Pionopsitta haematotis			
Short-tailed Swift	O		forage over island
Chaetura brachyura			
White-vented Plumeleteer	F	C	2 at flowering trees
Chalybura buffonii			
Cinnamon Woodpecker	F	C	2 at disparate locations
Celeus loricatus			
Panama Flycatcher	E	M-C	bred in lab clearing, Harvard
Myiarchus panamensis			
Gray-capped Flycatcher	E	M	1 record on lake margin
Myiozetetes granadensis			
White-ringed Flycatcher	F	C	1 record on Wheeler
Conopias parva			
Thrushlike Mourner	F	U	1 male
Schiffornis turdinus			
Clay-colored Robin	E	T-C	1 transient
Turdus grayi			
Golden-fronted Greenlet	E	M-C	1 transient
Hylophilus aurantiifrons			
Bay-headed Tanager	F	C	1 record; with canopy tanagers
Tangara gyrola			
Thick-billed Euphonia	E	C	few records from lab clearing
Euphonia laniirostris			
Yellow-crowned Euphonia	E	C	1 transient
Euphonia luteicapilla			
Crimson-backed Tanager	E	U	bred at lab clearing
Ramphocelus dimidiatus			
Orange-billed Sparrow	E, F	T	1 record
Arremon aurantiirostris			
Great-tailed Grackle	E	T	5 transients in 2 groups
Cassidix mexicanus			
Giant Cowbird	E	T-C	bred at Yellow-rumped Cacique
Scaphidura oryzivora			(*Cacicus cela*) colonies

[a]*Migrants are excluded.*
[b]*E, edge; F, forest; O, open; W, water.*
[c]*Stratum is the vertical position of birds within forest or edge habitats: T, terrestrial; U, understory; M, midstory; C, canopy. Some species use more than one stratum, in which case more than one category is designated. Species of open and aquatic habitats are not assigned to strata.*

numerous species detected by Willis but not found by me. Even if some species were overlooked during the 1994–1996 inventory, given the extensive effort to survey the island, missed species will all be expected to be present in extremely low densities and thus highly susceptible to local extinction.

Populations of several formerly common species have declined conspicuously since Willis's (1980) survey and

Table 2.   Bird species formerly reported as extinct from Barro Colorado Island but present during the 1994–1996 survey.

Habitat and species	Last date recorded	Reference*	Notes
Forest species			
Great Currasow	1927	1, 2	1–2 females, Wetmore and Standley trails, 1996
Crax rubra			
Cinnamon Woodpecker	1976	2	2 at 2 locations
Celeus loricatus			
White-vented Plumeleteer	1960s	2	2 at flowering trees, 1996
Chalybura buffonii			
Edge species			
Little Tinamou	1966	2	1 along western shore, 1996
Crypturellus soui			
Blue Ground-Dove	1965	2	pair at Shannon 18, 1996
Claravis pretiosa			
Rufous-tailed Hummingbird	1971, 1979	2	transient at Barbour 24, 1996
Amazilia tzacatl			
Blue-crowned Motmot	1930s, 1961	1, 2	transient in lab clearing, 1994
Momotus momota			
Panama Flycatcher	1967, 1991	2, 3	recolonized 1991; now breeds in lab clearing and Harvard 21
Myiarchus panamensis			
Bat Falcon	1961	2, 3	transients in 1991, 1995
Falco rufigularis			
Gray-capped Flycatcher	1958	2	1 along eastern shore, north of Barbour 18, 1996
Myiozetetes granadensis			
Clay-colored Robin	1966	2, 3	transients in lab clearing 1986, 1996
Turdus grayi			
Thick-billed Euphonia	1930s	2, 3	transients 1991, 1994
Euphonia laniirostris			
Crimson-backed Tanager	1966	2, 3	recolonized 1991; now breeding in lab clearing; 1 along western shore 1996
Ramphocelus dimidiatus			

*1, Eisenmann (1952); 2, Willis & Eisenmann (1979); 3, G. Angehr (unpublished data).

appear to be on the brink of local extinction (Table 5). The largest decline involved Slate-colored Grosbeaks (*Pitylus grossus*) decreasing from an estimated population of 500 in 1970 to a minimum of only two pairs in 1994–1996. This conspicuous finch is difficult to overlook, so its virtual absence from the 1994–1996 inventory reflects a real change in population size. Willis (1980) also estimated 500 Sulphur-rumped Tanagers (*Heterospingus rubrifrons*) on BCI, but I found only three flocks of 2–5 individuals each (total of 12 birds). A relatively silent, canopy-dwelling frugivore, this species can be difficult to detect, and some individuals could have been overlooked by me, or population size could have been overestimated by Willis. Furthermore, like most tanagers foraging in the canopy, Sulphur-rumped Tanagers are probably highly mobile and could be absent from the island on a seasonal basis. Thus, my censuses may have been executed during times when few tanagers were present. The same explanation may hold true for Scarlet-thighed Dacnis (*Dacnis venusta*), which frequently accompanies flocks of Sulphur-rumped Tanagers on the mainland. Two species of cotinga were only rarely detected during my censuses. Only one Rufous Piha (*Lipaugus unirufus*), a species with a loud and distinctive call, was detected, which is a substantial decline from the estimate of 80 made by Willis. Only 2 Speckled

Mourners (*Laniocera rufescens*) were found, down from Willis's estimate of 30.

Two species, each represented by observations of a single male, were Thrush-like Mourner and Green Shrike-Vireo (*Vireolanius pulchellus*). Both individuals were located in the same locations where the last sightings of each species were made. The Thrush-like Mourner was found at the same location on the island as when last recorded in 1978 (N. Brokaw, unpublished data), and the shrike-vireo was at the same site as its last sighting in 1991 (G. Orians, unpublished data).

The rate of change in species richness has varied through time for both forest and edge species (Fig. 3). The richness of forest species has declined from 121 during the 1920s to 96 during 1996. The greatest changes in richness occurred during the 1930s, when 6 species were lost, and from 1950 to 1980, when approximately 6 species were lost per decade. Recent losses have slowed, however: only 1 species has been lost since 1980. The overall rate of forest species loss was 3.3 species per decade, which was identical to the loss of edge species. The richness of edge species declined from 72 in the 1920s to 47 in 1996. Losses of edge species peaked from 1950 to 1980, when 26 species disappeared. Since 1980 only 3 edge species have disappeared.

Table 3.   Bird species detected by Willis during the 1970s but not detected during the 1994–1996 survey of Barro Colorado Island.*

Species	Habitat	Stratum	Notes
Least Bittern	W		habitat changes
Ixobrychus exilis			
Great Blue Heron	W		uncommon; overlooked?
Ardea herodias			
Agami Heron	F	S	rare; overlooked?
Agamia agami			
Tiny Hawk	F	M-C	rare; mobile
Accipiter superciliosus			
Short-tailed Hawk	O		rare on Atlantic slope
Buteo brachyurus			
Zone-tailed Hawk	O		rare on Atlantic slope
Buteo albonotatus			
Crested Eagle	F	M-C	extremely rare
Morphnus guianensis			
Ornate Hawk-Eagle	F	M-C	extremely rare
Spizaetus ornatus			
Gray-headed Chachalaca	E	M-C	habitat maturation
Ortalis cinereiceps			
Sungrebe	W		rare; overlooked?
Heliornis fulica			
Sunbittern	F	S	rare; overlooked?
Eurypyga helias			
Pheasant Cuckoo	F	T	last record 1986
Dromococcyx phasianellus			
Smooth-billed Ani	E	T-U	habitat maturation
Crotophaga ani			
Crested Owl	F	M-C	nocturnal; overlooked? no records since 1986
Lophostrix cristata			
Mottled Owl	F	M-C	nocturnal; overlooked?
Ciccaba virgata			
Striped Owl	O		habitat maturation
Asio clamator			
Great Potoo	F	C	nocturnal; overlooked?
Nyctibius grandis			
White-collared Swift	O		rare
Streptoprocne zonaris			
Black-throated Mango	E	U-C	rare away from clearings
Anthracothorax nigricollis			
Rufous-crested Coquette	E, F	C	rare and difficult to detect
Lophornis delattrei			
Garden Emerald	E	M-C	rare on Atlantic slope
Chlorostilbon assimilis			
Long-billed Starthroat	E	U	rare
Heliomaster longirostris			
Green Kingfisher	W		overlooked?
Chloroceryle americana			
Amazon Kingfisher	W		overlooked?
Chloroceryle amazona			
Green-and-rufous Kingfisher	W		overlooked?
Chloroceryle inda			
Fasciated Antshrike	F, E	U-M	extinct 1951; transient 1977
Cymbilaimus lineatus			
White-bellied Antbird	E	T	habitat maturation
Myrmeciza longipes			
Ocellated Antbird	F	T	extinct since 1978
Phaenostictus mcleannani			
Spectacled Antpitta	F	T	extinct since 1971
Hylopezus perspicillata			
Yellow-bellied Elaenia	E	M	habitat maturation
Elaenia flavogaster			

Table 3.   (continued)

Species	Habitat	Stratum	Notes
Long-tailed Tyrant	F	C	uncommon
Colonia colonus			
Lance-tailed Manakin	E	U	habitat maturation; rare on Atlantic slope
Chiroxiphia lanceolata			
Black-chested Jay	F	M-C	very patchy distribution
Cyanocorax affinis			
Scrub Greenlet	E	M	habitat maturation
Hylophilus flavipes			
White-vented Euphonia	F	C	rare; easily overlooked
Euphonia minuta			
Yellow-tailed Oriole	E	M-C	inappropriate habitat?
Icterus mesomelas			

Migrants are excluded. Abbreviations as in Table 1, with addition of stream (S) for stratum used by species foraging along forest streams.

Discussion

Changes in the avifauna of Barro Colorado Island continue and include decreasing species richness and declining population sizes of some formerly common species. Since Willis's (1974) first tally of the number of species that disappeared from BCI, the total number of known extinctions has risen to 65. These include 30 forest species and 35 edge species. The number may be even higher (Karr 1982*a*), especially considering that newly isolated fragments often experience an initial crowding effect as forest birds displaced from nearby

Table 4.   Bird species now considered extinct from Barro Colorado Island but not previously reported as missing.

Habitat and species	Last date recorded	Reference*
Forest species		
Crested Eagle	1950	1
Morphnus guianensis		
Ornate Hawk-Eagle	1978	2
Spizaetus ornatus		
Pheasant Cuckoo	1986	2
Dromococcyx phasianellus		
Long-tailed Tyrant	1979	2
Colonia colonus		
Edge species		
Gray-headed Chachalaca	1980s	2
Ortalis cinereiceps		
Smooth-billed Ani	1980s	2
Crotophaga ani		
Black-throated Mango	1979	2
Anthracothorax nigricollis		
Scrub Greenlet	1970	2, 3
Hylophilus flavipes		
Variable Seedeater	1980s	2
Sporophila americana		

1, Willis & Eisenmann (1979); 2, G. Angehr (unpublished data); 3, Willis (1980).

destroyed habitat move into remaining refugia (Bierregaard & Lovejoy 1988, 1989). Thus, the species richness on BCI in the decade immediately after isolation, but before ornithological inventories began, could reasonably have been much greater. The data available from BCI may represent a conservative estimate of the influence of isolation on avifaunal change in this landscape.

Previous assessments of the patterns of species loss on BCI identified habitat maturation as a primary cause of species loss (Willis 1974; Willis & Eisenmann 1979; Karr 1982*a*). Forest and edge species, however, have disappeared at nearly identical rates (3.3 species per decade). Many of the edge species nevertheless have undoubtedly disappeared because of habitat change. Species such as White-bellied Antbird, Scrub Greenlet, and Gray-headed Chachalaca, which all prefer very young forest and forest edge, no longer have appropriate habitat on the island. A few individuals from a handful of edge species find small stretches of the shoreline, or the lab clearing, appropriate. Little Tinamou (*Crypturellus soui*) and Crimson-backed Tanager (*Ramphocelus dimidiatus*), for example, were found along the remote western shoreline, and the tanager was found breeding in the lab clearing. Many species that formerly bred in the lab clearing, such as Rosy Thrush-Tanager (*Rhodinocichla rosea*) and Black-striped Sparrow (*Arremenops conirostris*), have disappeared because succession in much of the former clearing has been allowed to proceed and the current clearing is kept manicured. Most of the island is now completely covered in tall, closed-canopy forest. The eastern and southern portions of the island where edge species formerly were most numerous (Willis & Eisenmann 1979) have matured.

The rate of species loss has slowed in the last two decades. Does this suggest that an equilibrium level of richness is being approached? Because island biogeography theory predicts a balance between extinctions and colonizations (MacArthur & Wilson 1967), an equilibrium value for edge species may be possible given their rela-

Table 5. Forest bird species rarely detected during the 1994–1996 survey that are perhaps near extinction from Barro Colorado Island.[a]

Species	Number detected	Willis's 1980 estimate	Island locations
Violaceous Quail-Dove *Geotrygon violacea*	4	100	Shannon 7, Van Tyne 0.5, Schneirla 2, Zetek 2 Zetek 2
Black-tailed Trogon *Trogon melanurus*	3	6	Schneirla 2, Shannon 7, Miller 11
Cinnamon Woodpecker *Celeus loricatus*	2	not estimated	Shannon 7, Fausto 0
Speckled Mourner *Laniocera rufescens*	2 (pair?)	30	Wetmore 18
Rufous Piha *Lipaugus unirufus*	1	80	Shannon 5
Thrush-like Mourner *Schiffornis turdinus*	1 male	not estimated	Shannon 18
Green Shrike-Vireo *Vireolanius pulchellus*	1 male	10	Drayton 7.5
Slate-colored Grosbeak *Pitylus grossus*	2 pair	500	Standley 7, Wetmore 3
Scarlet-thighed Dacnis *Dacnis venusta*	1[b]	40	Barbour 18
Sulphur-rumped Tanager *Heterospingus rubrifrons*	3[b]	500	Zetek 4, Standley 15, lab clearing

[a] *The number of individuals or pairs detected during the 1994–1996 survey is compared with Willis's (1980) estimate. Locations of sightings are referenced to the nearest established trail marker. For additional details see Robinson (1998).*
[b] *Observed in small flocks of two to five individuals.*

tively high vagility and colonization abilities (Faaborg 1979; Stouffer & Bierregaard 1995*b*). Among forest species, however, there appears to be much greater variability in colonization potential. Most forest species lost from BCI are terrestrial and understory species, whereas few canopy species have disappeared (Willis 1974; Karr 1997; Sieving & Karr 1997). Terrestrial insectivores in particular appear to be highly sensitive to nonforest openings and are unlikely to colonize forest patches separated by open areas (Willis 1974; Harper 1989; Stouffer & Bierregaard 1995*a*). Therefore, an equilibrium number of forest species on BCI would include only species that are able to cross the 200-m-or-more water gap between the island and the mainland.

Such a balance between extinction and colonization has yet to be attained because some species thought to be highly prone to extinction are still present. Leaftossers (*Sclerurus* spp.), for example, are uncommon on BCI but have been identified as extinction-prone in Amazonia (Stouffer & Bierregaard 1995*a*) and in southeastern Brazil (Willis 1979; Christiansen & Pitter 1997). Likewise, Bicolored Antbirds (*Gimnopithys leucaspis*), whose congeners are extinction-prone in South America (Willis 1979; Stouffer & Bierregaard 1995*a*), were identified as susceptible to extinction on BCI (Willis 1974). Willis (1974) noted a decrease in Bicolored Antbird populations from 3.2 pairs/km^2 in 1961 to 1.5 pairs/km^2 in 1970. He speculated that Bicolored Antbirds were unlikely to colonize BCI from nearby mainland populations and suggested that bicoloreds would soon follow the fate of the confamilial Ocellated Antbird and disappear from BCI. Bicolored Antbird populations appear to have remained relatively stable since 1970, however, because I estimated that about 40 individuals were present in 1996 (W.D.R., unpublished data), compared with 45 individuals in 1970. Several of the remaining species of understory antbirds are extremely common on BCI. All of these probably cross the water gap at least occasionally, because all occur on at least one of the smaller islands in Gatun Lake (Wright 1985) and all have been observed
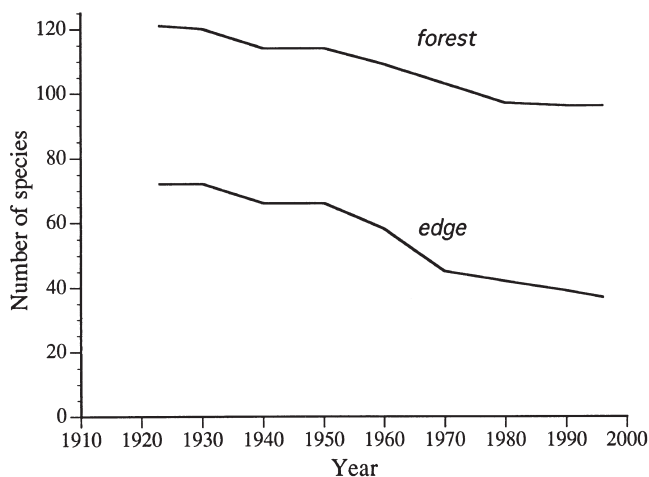

Figure 3. Loss of forest- and edge-dwelling resident species from Barro Colorado Island since its isolation in the early twentieth century.

crossing smaller gaps on the mainland (W.D.R., unpublished data).

In addition to the Scaly-throated Leaftosser (*Sclerurus guatemalensis*) and Bicolored Antbird, several other species may be at high risk of disappearing from BCI. The population of one conspicuous species in particular, the Slate-colored Grosbeak, has apparently declined from 500 in 1970 (Willis 1980) to approximately two pairs in 1996. Although the species appears to move readily within forest and across small (<25 m) gaps (W.D.R., unpublished data), no information about the effects of wider gaps is available. If it avoids open areas, extinction appears imminent. In contrast, two canopy-dwelling frugivorous tanagers that were rare during my censuses but uncommon to abundant during Willis's seem less likely to disappear permanently from BCI because of high mobility; both species fly long distances above the canopy between fruiting trees (Greenberg 1981) and should be able to recolonize BCI. The remaining rare forest species all occur below the high canopy of forest and may be less likely to move across open areas. Three species were represented on BCI during 1994–1996 by only a single individual male. It is unknown whether these three males had mates. Thus, the disappearance of several additional forest-dwelling species may be close at hand.

The prospect of BCI as an effective preserve of regional avian diversity is not promising. Willis (1974) suggested that if the surrounding mainland forests of central Panama were razed, the diversity of birds in the region would not be preserved by BCI alone. Extinction of certain species from BCI, especially terrestrial forest-dwelling species, appears to be extremely persistent. Despite the nearby presence of mainland populations of all terrestrial forest-dwelling species (Karr 1971; Robinson 1998), only one species has recolonized. All other similar species have remained absent after disappearance. Furthermore, several species that occur on the nearby mainland have never been detected on BCI (Karr 1982*a*). Thus, the isolation of the island may also prevent the founding of new populations by some species.

Although the lack of immigration has almost certainly prevented the persistence of many terrestrial forest-dwelling species, the relationship between immigration rates and island persistence by other species is less obvious. The necessary proximity of mainland sources of colonists for mid-story or canopy species is not known. Some species that persist on BCI may cross the water gap only rarely, but frequently enough to maintain island populations, whereas other species may commute to and from the island on a seasonal or even daily basis (e.g., pigeons, hummingbirds, and parrots). The impacts of regional forest clearance will therefore vary among species and will depend on species' differences in mobility (Wiens 1995).

The probability of regional forest clearance may be remote, however, given the importance of forest maintenance to the protection of the Panama Canal watershed. Nevertheless, forested areas larger in size than BCI will be required to maintain regional diversity. An important factor driving the need for large reserves is spatial and temporal variation in the reproductive success of populations. Evidence is mounting that populations may persist in small forest fragments even when reproduction in the fragments does not compensate for adult mortality, a situation referred to as a sink (Pulliam 1988; Pulliam & Danielson 1991). The negative rate of population growth in sinks does not mean local extinction is inevitable as long as immigration of individuals from other sites produces an excess of individuals (i.e., sources are sufficient to compensate for the shortage; Brawn & Robinson 1996). When immigration is eliminated, extinction is inevitable in the absence of self-maintaining productivity. On the other hand, if immigration rates are sufficiently high, individual species will remain present in preserves even if productivity is low. In these cases, the proximity of source areas will become important, and the differential abilities of species to disperse from source patches to sinks will affect long-term persistence. Those species that require forested habitat will need either forested connections between patches or very large preserves to persist over long time periods. Given the typically low densities and patchy distributions of tropical birds (Diamond 1980; Terborgh et al. 1990; Robinson 1998), isolated preserves will need to be extremely large. Large preserves will be more likely to contain a patchwork of internal sources and sinks that allow the free movement and redistribution of individuals within a preserve. Small preserves such as BCI will not be large enough to encompass such a matrix of subpopulations with varying levels of productivity for all species in the community. Species that do not move across unforested habitats therefore will be at greater risk of local extinction and also will be unable to recolonize once local populations have disappeared. In effect, isolated preserves such as BCI will become filled with species that disperse well and will lack a significant fraction of the regional avifauna (Janzen 1983; Diamond et al. 1987). For species that disperse across open areas, the landscape configuration of patches may be more important (Rolstad 1991). We are only beginning to quantify the variation in dispersal abilities and extinction proneness among tropical species.

Local extinctions in tropical fragments can mean a long-term, perhaps even permanent, change in avian community composition. Although the specific mechanisms causing local extinctions may vary greatly among species (Karr 1982*a*, 1982*b*, 1990; Schoener & Spiller 1992; Sieving 1992), the essential point for conservation biologists is that small, isolated tropical forest reserves such as Barro Colorado Island will not preserve the full complement of regional avian diversity over the long term.

Acknowledgments

Literature Cited

Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos **71:**355–366.

Bierregaard, R. O., Jr. 1990. Avian communities in the understory of Amazonian forest fragments. Pages 333–343 in A. Keast, editor. Biogeography and ecology of forest bird communities. Academic Publishing, The Hague.

Bierregaard, R. O., Jr., and T. E. Lovejoy. 1988. Birds in Amazonian forest fragments: effects of insularization. Proceedings of the International Ornithological Congress **19:**1564–1579.

Bierregaard, R. O., Jr., and T. E. Lovejoy. 1989. Effects of forest fragmentation on Amazonian understory bird communities. Acta Amazonica **19:**215–241.

Brawn, J. D., and S. K. Robinson. 1996. Source-sink population dynamics may complicate the interpretation of long-term census data. Ecology **77:**3–12.

Chapman, F. M. 1929. My tropical air castle. Appleton-Century, New York.

Chapman, F. M. 1938. Life in an air castle. Appleton-Century, New York.

Christiansen, M. B., and E. Pitter. 1997. Species loss in a forest bird community near Lagoa Santa in southeastern Brazil. Biological Conservation **80:**23–32.

Diamond, J. 1980. Patchy distributions of tropical birds. Pages 57–74 in M. E. Soulé and B. A. Wilcox, editors. Conservation biology: an evolutionary-ecological perspective. Sinauer Associates, Sunderland, Massachusetts.

Diamond, J. M., K. D. Bishop, and S. Van Balen. 1987. Bird survival in an isolated Javan woodland: island or mirror? Conservation Biology **1:**132–142.

Eisenmann, E. 1952. Annotated list of birds of Barro Colorado Island, Panama Canal Zone. Miscellaneous collections **117.** Smithsonian Institution, Washington, D.C.

Faaborg, J. 1979. Qualitative patterns of avian extinction on Neotropical land-bridge islands: lessons for conservation. Journal of Applied Ecology **16:**99–107.

Faaborg, J., M. Brittingham, T. Donovan, and J. Blake. 1995. Habitat fragmentation in the temperate zone. Pages 357–380 in D. M. Finch and T. E. Martin, editors. Ecology and management of Neotropical migratory birds: a synthesis and review of the critical issues. Oxford Unversity Press, Cambridge, United Kingdom.

Food and Agriculture Organization. 1993. Forest resources assessment 1990: tropical countries. Forestry paper no. 112. Madison, Wisconsin.

Gradwohl, J., and R. Greenberg. 1980. The formation of antwren flocks on Barro Colorado Island, Panama. Auk **97:**385–395.

Greenberg, R. 1981. The abundance and seasonality of forest canopy birds on Barro Colorado Island, Panama. Biotropica **13:**241–251.

Greenberg, R., and J. Gradwohl. 1986. Constant density and stable territoriality in some tropical insectivorous birds. Oecologia **69:**618–625.

Harper, L. H. 1989. The persistence of ant-following birds in small Amazonian forest fragments. Acta Amazonica **19:**249–263.

Janzen, D. H. 1983. No park is an island: increase in interference from outside as park size decreases. Oikos **41:**402–410.

Karr, J. R. 1971. Structure of avian communities in selected Panama and Illinois habitats. Ecological Monographs **41:**207–233.

Karr, J. R. 1981. Surveying birds in the tropics. Studies in Avian Biology **6:**548–553.

Karr, J. R. 1982*a*. Avian extinction on Barro Colorado Island, Panama: a reassessment. American Naturalist **119:**220–239.

Karr, J. R. 1982*b*. Population variability and extinction in the avifauna of a tropical land bridge island. Ecology **63:**1975–1978.

Karr, J. R. 1990. Avian survival rates and the extinction process on Barro Colorado Island, Panama. Conservation Biology **4:**391–397.

Karr, J. R. 1997. Extinction of birds on Barro Colorado Island, Panama. Pages 131–132 in G. K. Meffe and C. R. Carroll, editors. Principles of conservation biology. Sinauer Associates, Sunderland, Massachusetts.

Karr, J. R., S. K. Robinson, R. O. Bierregaard, Jr., and J. G. Blake. 1990. Birds of four Neotropical forests. Pages 237–269 in A. Gentry, editor. Four Neotropical rainforests. Yale University Press, New Haven, Connecticut.

Kattan, G. H., H. Alvarez-López, and M. Giraldo. 1994. Forest fragmentation and bird extinctions: San Antonio eighty years later. Conservation Biology **8:**138–146.

Lovejoy, T. E., J. M. Rankin, R. O. Bierregaard, Jr., K. S. Brown, Jr., L. H. Emmons, and M. E. Van Der Voort. 1984. Ecosystem decay of Amazon forest remnants. Pages 295–325 in M. H. Nitecki, editor. Extinctions. University of Chicago Press, Chicago.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey.

Pimm, S. L., H. L. Jones, and J. Diamond. 1988. On the risk of extinction. American Naturalist **132:**757–785.

Pimm, S. L., G. J. Russell, J. L. Gittleman, and T. M. Brooks. 1995. The future of biodiversity. Science **269:**347–350.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist **132:**652–661.

Pulliam, H. R., and B. J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. American Naturalist **137:**550–566.

Ridgely, R. S., and J. A. Gwynne, Jr. 1989. A guide to the birds of Panama with Costa Rica, Nicaragua, and Honduras. 2nd edition. Princeton University Press, Princeton, New Jersey.

Robbins, C. S. 1980. Effect of forest fragmentation on breeding bird populations in the piedmont of the mid-Atlantic region. Atlantic Naturalist **33:**31–36.

Robinson, W. D. 1998. Community structure, nesting success, and isolation effects in a tropical forest bird community. Ph.D. dissertation. University of Illinois, Urbana-Champaign.

Rolstad, J. 1991. Consequences of forest fragmentation for the dynamics of bird populations: conceptual issues and the evidence. Biological Journal of the Linnaean Society **42:**149–163.

Schmiegelow, F. K. A., C. S. Machtans, and S. J. Hannon. 1997. Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. Ecology **78:**1914–1932.

Schoener, T. W., and D. A. Spiller. 1992. Is extinction rate related to temporal variability in population size? An empirical answer for orb spiders. American Naturalist **139:**1176–1207.

Sieving, K. E. 1992. Nest predation and differential insular extinction among selected forest birds of central Panama. Ecology **23:**2310–2328.

Sieving, K. E., and J. R. Karr. 1997. Avian extinction and persistence mechanisms in lowland Panama. Pages 156–170 in W. F. Laurance

and R. O. Bierregaard, Jr., editors. Tropical forest remnants: ecology, management, and conservation of fragmented communities. University of Chicago Press, Chicago.

Stouffer, P. C., and R. O. Bierregaard, Jr. 1995*a*. Use of Amazonian forest fragments by understory insectivorous birds. Ecology **76:**2429–2445.

Stouffer, P. C., and R. O. Bierregaard, Jr. 1995*b*. Effects of forest fragmentation on understory hummingbirds in Amazonian Brazil. Conservation Biology **9:**1085–1094.

Stotz, D. F., J. W. Fitzpatrick, T. A. Parker III, and D. K. Moskovits. 1996. Neotropical birds: ecology and conservation. University of Chicago Press, Chicago.

Terborgh, J., and B. Winter. 1980. Some causes of extinction. Pages 119–133 in M. E. Soulé and B. A. Wilcox, editors. Conservation biology: an evolutionary-ecological perspective. Sinauer Associates, Sunderland, Massachusetts.

Terborgh, J., S. K. Robinson, T. A. Parker III, C. A. Munn, and N. Pierpont. 1990. Structure and organization of an Amazonian forest bird community. Ecological Monographs **60:**213–238.

Turner, I. M. 1996. Species loss in fragments of tropical rain forest: a review of the evidence. Journal of Applied Ecology **33:**200–209.

Verner, J. 1985. Assessment of counting techniques. Current Ornithology **2:**247–302.

Wetmore, A., R. F. Pasquier, and S. L. Olson. 1984. The birds of the Republic of Panama. Part 4. Smithsonian Institution Press, Washington, D.C.

Whitcomb, R. F., C. S. Robbins, J. F. Lynch, B. L. Whitcomb, M. K. Klimkiewicz, and D. Bystrak. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. Pages 125–292 in R. L. Burgess and D. M. Sharpe, editors. Forest island dynamics in man-dominated landscapes. Springer-Verlag, New York.

Whitmore, T. C., and J. A. Sayer. 1992. Deforestation and species extinction in tropical moist forests. Pages 1–14 in T. C. Whitmore and J. A. Sayer, editors. Tropical deforestation and species extinction. Chapman and Hall, New York.

Wiens, J. A. 1995. Habitat fragmentation: island v landscape perspectives on bird conservation. Ibis **137:**S97–S104.

Wilcove, D. S., C. H. McLellan, and A. P. Dobson. 1986. Habitat fragmentation in the temperate zone. Pages 237–256 in M. E. Soulé, editor. Conservation biology: the science of scarcity and diversity. Sinauer Associates, Sunderland, Massachusetts.

Willis, E. O. 1974. Populations and local extinctions of birds on Barro Colorado Island, Panama. Ecological Monographs **44:**153–169.

Willis, E. O. 1979. The composition of avian communities in remanescent woodlots in southern Brazil. Papéis Avulsos de Zoologia, Sao Paulo **33:**1–25.

Willis, E. O. 1980. Ecological roles of migratory and resident birds on Barro Colorado Island, Panama. Pages 205–225 in A. Keast and E. S. Morton, editors. Migrant birds in the Neotropics: ecology, behavior, distribution and conservation. Smithsonian Institution Press, Washington, D.C.

Willis, E. O., and E. Eisenmann. 1979. A revised list of birds of Barro Colorado Island, Panama. Contributions to zoology no. 291. Smithsonian Institution, Washington, D.C.

Wright, S. J. 1985. How isolation affects rates of turnover of species on islands. Oikos **44:**331–340.