Changes in abundance of birds in a Neotropical forest fragment over 25 years: a review

W. D. Robinson

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Abstract

Changes in abundance of birds in a Neotropical forest fragment over 25 years: a review.— Few data are available to evaluate the long term effects of habitat isolation on species richness or abundances in the tropics. Barro Colorado Island (BCI), Panama, has been studied for more than 80 years since its isolation from surrounding lowland forest when the Panama Canal was constructed. Thirty-five percent of the originally present 200 resident species have disappeared. Although the loss of species is well–studied, changes in abundance that might help predict future losses have not been evaluated. One study in 1970 and the present study conducted 25 years later estimated abundances of most bird species on BCI. Comparisons indicate at least 37 species have declined by at least 50%. Twenty–six species of edge habitats are expected to decline as forest maturation proceeds, yet 11 forest species that are now rare may be lost soon. All 26 species that were present in 1970 but not detected in the mid–1990s were rare in 1970. Thus, rarity appears to be a good predictor of extinction risk in this tropical habitat fragment.

Key words: Barro Colorado Island, Extinction, Faunal relaxation, Habitat fragmentation, Neotropics, Panama.

Resumen

Cambios en la abundancia de aves en un fragmento de bosque neotropical durante un período de 25 años: una revisión.— Hay pocos datos disponibles para evaluar los efectos a largo plazo que supone el aislamiento del hábitat con respecto a la riqueza o la abundancia de especies en el trópico. La Isla de Barro Colorado (BCI), Panamá, se ha estado estudiando durante más de 80 años, desde que la construcción del Canal de Panamá la dejara aislada de los bosques de las tierras bajas circundantes. El treinta y cinco por ciento de las 200 especies residentes inicialmente presentes ha desaparecido. Aunque la pérdida de especies se ha estudiado a fondo, no se han evaluado los cambios en abundancia que podrían ayudarnos a predecir pérdidas futuras. Un estudio de 1970 y el presente estudio, realizado 25 años después, han estimado la abundancia de la mayoría de especies de aves presentes en la BCI. Las comparaciones indican que al menos 37 especies han disminuido en un 50%, como mínimo. Se prevé que 26 especies pertenecientes a hábitats de las orillas vayan disminuyendo con la maduración del bosque, si bien 11 especies del bosque que ahora son poco frecuentes podrían extinguirse muy pronto. La totalidad de las 26 especies existentes en 1970, pero que no se detectaron a mediados de la década de 1990, ya eran raras entonces. Así pues, el hecho de que una especie sea rara parece constituir un buen indicador del riesgo de extinción en este fragmento de hábitat tropical.

Palabras clave: Isla de Barro Colorado, Extinción, Relajamiento de la fauna, Fragmentación del hábitat, Neotrópico, Panamá.

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W. Douglas Robinson, Dept. of Fisheries and Wildlife, 104 Nash Hall, Oregon State Univ., Corvallis, OR 97331, U.S.A.

E–mail: wdrobins@acesag.auburn.edu

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Introduction

The dynamics of species communities in habitat patches have been a focus of interest among ecologists and conservation biologists (MacArthur & Wilson, 1967; Simberloff, 1995; Laurance & Bierregaard, 1997; Terborgh et al., 2002). In particular, the process of species loss from human–created habitat patches, such as forest fragments, has been of interest because understanding that process may allow predictions of the size of reserves necessary to maintain viable populations (Zimmerman & Bierregaard, 1986). A common pattern observed among recently isolated habitat patches is where an initially high species richness relaxes through time to some lower level of species richness (Diamond, 1972; Soulé et al., 1979). This process of species loss, also called faunal relaxation, apparently occurs most quickly immediately after isolation, but may continue to occur for an indeterminate amount of time (Lovejoy et al., 1984), possibly until an equilibrium between extinction and immigration is reached (MacArthur & Wilson, 1967). Because of a lack of long–term data sets, however, efforts to understand the process of faunal relaxation have been impeded. Consequently, conservation biologists trying to preserve habitat remnants in regions threatened by further habitat destruction lack sufficient information from which to understand how the size of nature preserves may influence persistence of species over long time periods. Such problems are particularly acute in the tropics where species abundance patterns are very different from temperate sites; that is, a greater proportion of species in the tropics are rare, and thus may be more likely to be lost from habitat remnants by stochastic effects of population fluctuations (Karr, 1982a; Lande, 1987) or by environmental variation (Leigh 1981).

Of particular interest to conservation biologists is predicting which species are at greatest risk of being lost from preserves so that steps might be taken to reduce risks of extinction. A key predictor of extinction risk is population size (Terborgh & Winter, 1980; Davies et al., 2000); species with low population sizes tend to have greater risks of extinction (Pimm et al., 1988; Belovsky et al., 1999). One useful method, therefore, for predicting the extinction risk of a population would be to assess temporal changes in population size within a conservation reserve. Ideally, long–term monitoring of population sizes would allow conservation biologists to examine long temporal series of annual population size estimates and then to evaluate statistically the probability of extinction resulting from stochastic or deterministic factors. However, in most cases, such long–term data remain scarce or non–existent. In the Neotropics, for example, loss of bird species from isolated conservation reserves or forest fragments is common, with local extinctions often exceeding 35% of the species originally present (Kattan et al., 1994; Christiansen & Pitter, 1997; Stouffer & Bierregaard, 1995; Robinson, 1999), yet no temporal sequence of community–wide bird census data spanning more than five years is available. Several sites have been surveyed through use of mistnets for 15 to 30 years (Karr et al., 1990a; Brawn et al., 1995; 1999; Stouffer & Bierregaard, 1995), but such studies only effectively sample the understory of forest bird communities (Karr, 1971, 1981). Notwithstanding the limitations of presently available data, pressing conservation needs require use of extant data to help predict species that are sensitive to anthropogenic disturbances of Neotropical habitats, particularly forest fragmentation (Brawn et al., 1998).

The objective of this study was to assess changes in population sizes of forest birds on Barro Colorado Island (BCI), Panama, over the last 25 years. Studies of the BCI avifauna provide the longest–running data set on the process of species loss from a tropical habitat fragment (Robinson, 1999). BCI is a 1,562 ha land–bridge island in Gatun Lake, which forms part of the Panama Canal. Originally isolated from the mainland in 1914 by creation of the Canal, BCI has been inventoried repeatedly by ornithologists since 1923. The island hosted as many as 200 resident species of the forest and forest edge (Willis & Eisenmann, 1979; Karr, 1982b; Robinson, 1999). Although the exact number of species lost is debated, positively known extinctions represent at least 35% of the species present at the first inventory in the 1920s. Furthermore, the extinctions were not concentrated in the time period immediately after isolation; rather, they have occurred throughout the 80 years since the first inventories (Chapman, 1929; Willis & Eisenmann, 1979; Robinson, 1999). Although species inventories were conducted several times, only once were population sizes for most species on the island estimated. Willis (1980) spent the entire year of 1970 working on BCI and estimated population sizes for most species he encountered that year. An extensive series of point counts on BCI were conducted from 1994 to 1996 to generate population estimates for comparison with Willis's, so that species experiencing large changes in population size could be identified, the tendency for rare species to disappear could be evaluated, and predictions could be made regarding which currently extant species might be most likely to disappear from BCI in the future.

Methods

Willis (1980) generated island population estimates by studying intensively several species of understory birds on BCI from 1960 to 1971. By 1970, he knew all calls and songs of all species on the island and generated island–wide estimates

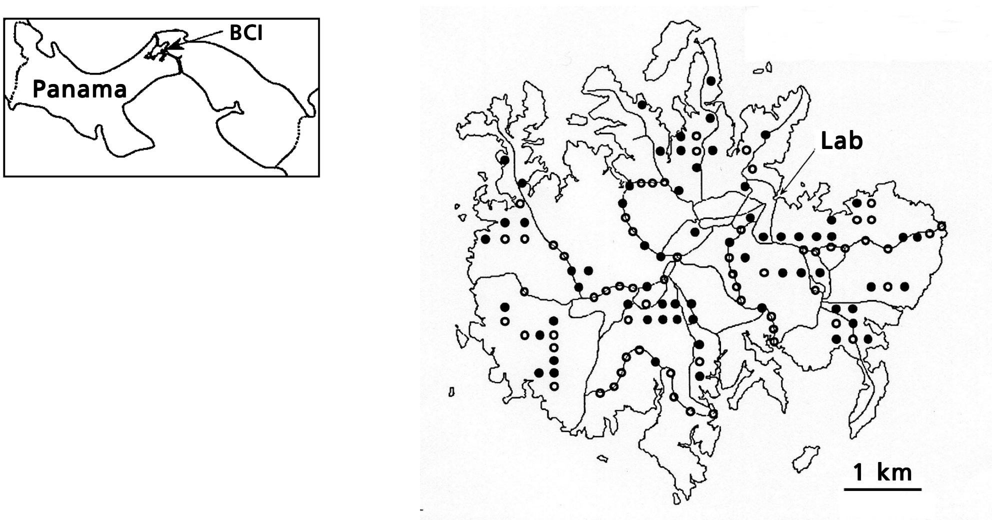

Fig. 1. Distribution of point count locations across Barro Colorado Island, Panama. Random (closed circles) and supplemental (open circles) points are all separated by at least 200 m: BCI. Barro Colorado Island.

Fig. 1. Distribución de los emplazamientos de recuento de la Isla de Barro Colorado, Panamá. Los puntos al azar (círculos negros) y los suplementarios (círculos blancos) distan entre sí un mínimo de 200 m: BCI. Isla de Barro Colorado.

of abundance for that year. Those estimates were generated from spending hundreds of hours in the field and gauging abundances of all species relative to the antfollowing species for which he knew abundances rather precisely because of following color–marked birds and mapping their territories (WILLIS, 1980). Thus, if certain species were encountered twice as often as a focal antfollower species which had an abundance of 200 pairs, Willis estimated the BCI population to be 400 pairs. Although this method is not repeatable and error can not be estimated, given the enormous time spent in the field to generate the numbers reasonable confidence can be had that the numbers are probably in the general vicinity of actual population sizes for most species.

An exhaustive inventory of bird species on BCI from 1994 to 1996 was conducted using three methods: point counts, line transects, and ad lib observations (ROBINSON, 1999). To generate estimates of population sizes, the point count data was used for several reasons. First, the location of points was randomized, improving my ability to extrapolate results from the subset of island space actually surveyed during point counts. Sixty–four points were randomly distributed across the island so that no point was closer than 200 m to the next nearest point. In addition, the random points were supplemented with 65 other points distributed between the random points, sometimes along established foot paths and sometimes between random points that were distributed off the trail system. To determine if the random and supplemental points differed in the number of individuals of each species detected, the mean number of individuals detected for each resident bird species at random and supplemental points were compared with ANOVA. In 7 of 199 resident species, number of detections differed ($p < 0.05$) between random and supplemental points. This is no different than expected by chance ($p = 0.035$) when so many tests are involved. Therefore, the results from random and supplemental points were combined and used all 129 to generate estimates of abundance (fig. 1).

Each point was visited for 8 minutes between January and July, the period of the year during which peak singing activity occurs (ROBINSON et al., 2000a). Eight–minute visits were used extensively during surveys on the nearby mainland (ROBINSON et al., 2000a) and are of sufficient duration that few new individuals are detected during the last two minutes of point counts. Points were conducted within four hours of dawn. Although some supplemental points were visited more than once, no random point was, so only data from the first visit to each point were used. During point counts, each bird seen or heard was identified and its distance and direction from the observer estimated. Distances were calibrated based on experience conducting more than 1,000 similar point counts throughout central Panama in the previous 2 years (Robinson et al., 1999, 2000a; Condit et al., 2001). Briefly, a series of point counts were conducted over a six–month period in 1993 and early 1994 where distances to vocalizing birds were paced off to ensure accuracy of distance estimation. Distance estimates were also frequently checked during line transect surveys conducted on BCI. Although accuracy of distance estimates diminishes with distance from the observer, distances to most species can be accurately judged within 200 m. No birds detected more than 200 m from the observer were included in analyses.

Not all species can be heard as far as 200 m. For example, several small insectivores have weak voices that carry no more than 30 to 50 m in tropical forest (e.g., Southern bentbill [see table 1 for scientific names] and Golden–crowned spadebill; Robinson et al., 2000a). Therefore, when calculating the area that was surveyed at each point count location, the maximum detection distance for each species was used as the radius of the circular area being inventoried. The maximum distance at which an individual of each species was noted was considered the maximum radius of the circular area for which surveys of that particular species could be considered effective.

To estimate island population size for each species, the area surveyed for each species was calculated separately because maximum detection distance varied among species. Thus, the area surveyed during point counts was calculated as the number of points surveyed times the area per point (π x [maximum detection distance]^2). Because points were distributed randomly, a proportional relationship between the number of birds detected at points and number of birds on the entire island was assumed. Therefore, to estimate abundances, the mean number of birds of a species detected per point was multiplied by the island area (1,562 ha) and then that product divided by the area surveyed at the 129 points. That quotient equals the mean number of birds on the island. An important assumption of this simple approach is that all species are equally detectable; in other words, the assumption is made that probability of detection if a bird is within detectable range of a point equals one. Given the wide range of behaviors among tropical birds, this is clearly not the case. Nearly 98% of detections during point counts in Panama are from auditory cues (Robinson et al., 2000a). Some species vocalize several times per minute during the morning, whereas others may vocalize much less regularly. Thus, probability of detecting a species when it is within detectable range is not always high. To adjust for such detectability differences among species would involve a huge effort to assess how vocalization patterns of each species vary with respect to time of day, season, and breeding phenology. In a tropical bird community with nearly 200 resident species, such data are not yet available. Therefore, I have taken the conservative approach in this study and assumed probability of detection is equal across species. For most species, the approach will lead to an underestimate of total island population size. Because extreme changes in abundance over the 25 years since Willis' survey were assessed and not minor changes, evaluations of population declines should still be of interest. Any dramatic increases in population size should be of even greater interest because of the likelihood that the method employed here underestimates population sizes. A better method for analyzing temporal changes in abundance would be to institute a standardized point count scheme where particular points are surveyed each year in the same season by the same or comparable observers (Verner, 1985). That design would be statistically more robust, would allow assessment of temporal trends within a species so that detectability issues would be minor, and would provide the most precisely repeatable protocol currently available for monitoring bird populations.

Residency status, preferred habitat, and ecological guild membership of bird species were categorized according to criteria established by Robinson et al. (2000a). Here, migratory species were excluded and only population estimates of year–round residents were compared.

Results and Discussion

Population increases. Population estimates of fifteen species increased by 100% or more (table 2). Four species (Plain xenops, Checker–throated antwren, Dot–winged antwren and White–shouldered tanager) associate with one another in mixed–species foraging flocks. Two other species that forage with them also increased: Slaty antshrike increased by 40% and White–flanked antwren by 50%. Several canopy species (Paltry tyrannulet, Lesser greenlet and Blue dacnis) increased by 100–150%. Since 1970, the number of colonial icterids foraging on the island increased from 40 to 175 birds, presumably because of the locations of several nesting colonies in dead trees standing in lake coves around the island. Another lake margin species, Common tody–flycatcher, which builds its pendant nest from a branch tip hanging over water, increased from 6 to 100 individuals. Whether this increase is real or if lake margin habitats were under–surveyed by Willis is unclear. Crested guan populations tripled since 1970 as protection of BCI from hunters has increased in effectiveness over the last few decades. Guans have been hunted nearly to extirpation in mainland forests of the Canal watershed (Robinson et al., 2000a). Lastly, the increase in numbers of three hummingbird species is enigmatic.

Table 1. Resident bird species detected on Barro Colorado Island, Panama, by Willis (1980) and Robinson (1999). Habitat affinities, guilds, and body masses are reported in addition to island–wide population size estimates. Species (names and sequence follow Ridgely & Gwynne (1989): nd. Not detected; ne. Abundance not estimated). Habitat (H): f. Forest; e. Edge or open habitats such as the island–lake interface, canopy edge, or aerial space above the island. Mass (M, in g): data from mistnet captures in Soberania National Park (Robinson et al. [1999b, 2000a]; Stiles & Skutch [1989]; Karr et al. [1978, 1990]; Willis [1980]). Guilds (assignments are based on personal observations and data in Karr et al. (1990b): Aquat. Aquatic species found primarily along forest streams or, in the case of some vagrants, near larger bodies of water; Carr. Carrion consumers; FA. Arboreal frugivores; FAS. Sallying arboreal frugivores; FT. Terrestrial frugivores; GA. Arboreal granivores; GT. Terrestrial granivores; IADL. Arboreal insectivores that search primarily dead leaf clusters; IAer. Aerial insectivores (species that capture and consume insect while in flight); IAF. Army ant followers; IAG. Gleaning arboreal insectivores; IAS. Sallying arboreal insectivores; IBI. Insectivores that extract food from the interior of bark substrates (e.g., woodpeckers); IBS. Insectivores that glean food from the surface of bark (e.g., woodcreepers); ITG. Gleaning terrestrial insectivores (e.g., leaftossers); ITS. Sallying terrestrial insectivores (e.g., common pauraque); N. Nectarivores; most species also consume some small arthropods; OA. Arboreal omnivores; OAG. Gleaning arboreal monivores; OAS. Sallying arboreal omnivores; OT. Terrestrial omnivores; OTG. Gleaning terrestrial omnivores; RD. Raptors diurnal; RN. Raptors nocturnal.

Tabla 1. Especies de aves residentes detectadas en la Isla de Barro Colorado, Panamá, por Willis (1980) y Robinson (1999). Se informa de afinidades de hábitats, agrupaciones y masas corporales, además de estimaciones en cuanto al tamaño de la población presente en toda la isla. Las especies (nombres y orden según Ridgely & Gwynne (1989): nd. No detectadas; ne. Abundancia no estimada). Hábitat (H): f. Bosque; e. Orillas o hábitats abiertos, como la interfase entre el lago y la isla, el extremo de la bóveda o el espacio aéreo que cubre la isla. Masa (M, en g): datos obtenidos en capturas mediante redes en el Parque Nacional Soberanía (Robinson et al. [1999b, 2000a]; Stiles & Skutch [1989]; Karr et al. [1978, 1990]; Willis [1980]). Agrupaciones (las asignaciones se basan en observaciones personales y datos de Karr et al. (1990b): Aquat. Especies acuáticas encontradas principalmente a lo largo de arroyos del bosque o, en el caso de algunas especies vagabundas, cerca de masas de agua de mayor tamaño; Carr. Carroñeros; FA. Frugívoros arbóreos; FAS. Frugívoros arbóreos que cazan insectos al vuelo; FT. Frugívoros terrestres; GA. Granívoros arbóreos; GT. Granívoros terrestres; IADL. Insectívoros arbóreos que buscan principalmente acumulaciones de hojas muertas; IAer. Insectívoros aéreos (especies que capturan y consumen insectos durante el vuelo); IAF. Rastreadores de hormigas–ejército; IAG. Insectívoros arbóreos que rebuscan; IAS. Insectívoros arbóreos que cazan insectos al vuelo; IBI. Insectívoros que extraen alimento del interior del sustrato de las cortezas (por ej.: los pájaros carpinteros); IBS. Insectívoros que recogen alimentos de la superficie de las cortezas (por ej.: los pájaros trepadores); ITG. Insectívoros terrestres que rebuscan (por ej.: la hojarasca); ITS. Insectívoros terrestres que cazan insectos al vuelo (por ej.: los tapacaminos picuyos); N. Nectarívoros; la mayor parte de las especies también consumen pequeños artrópodos; OA. Omnívoros arbóreos; OAG. Omnívoros arbóreos que rebuscan; OAS. Omnívoros arbóreos que cazan insectos al vuelo; OT. Omnívoros terrestres; OTG. Omnívoros terrestres que rebuscan; RD. Aves de rapiña diurnas; RN. Aves de rapiña nocturnas.

Species	H	M	Robinson	Willis	Guild
Tinamidae					
Great tinamou – *Tinamus major*	f	1,160	100	200	FT / GT
Little tinamou – *Crypturellus soui*	e	250	2	nd	FT / GT
Ardeidae					
Rufescent tiger–heron – *Tigrisoma lineatum*	e	840	10	10	Aquat
Cathartidae					
Black vulture – *Coragyps atratus*	e	1,800	20	70	Carr
Turkey vulture – *Cathartes aura*	e	1,300	10	50	Carr
King vulture – *Sarcoramphus papa*	e	3,200	2	10	Carr

Table 1. (Cont.)

Species	H	M	Robinson	Willis	Guild
Accipitridae					
Gray–headed kite – *Leptodon cayenensis*	f	500	4	5	RD
Hook–billed kite – *Chondrohierax uncinatus*	e	270	< 1	10	RD
Double–toothed kite – *Harpagus bidentatus*	f	185	20	30	RD
Tiny hawk – *Accipiter superciliosus*	f	100	nd	1	RD
Crane hawk – *Geranospiza caerulescens*	f	377	< 1	2	RD
Semiplumbeous hawk – *Leucopternis semiplumbea*	f	278	4	20	RD
White hawk – *Leucopternis albicollis*	f	736	2	20	RD
Short–tailed hawk – *Buteo brachyurus*	e	495	nd	1	RD
Zone–tailed hawk – *Buteo albonotatus*	e	565	nd	1	RD
Crested eagle – *Morphnus guianensis*	f	1,750	nd	2	RD
Black hawk–eagle – *Spizaetus tyrannus*	f	1,005	2	10	RD
Ornate hawk–eagle –*Spizaetus ornatus*	f	1,305	nd	5	RD
Falconidae					
Collared forest–falcon – *Micrastur semitorquatus*	f	1,325	2	1	RD
Bat falcon – *Falco rufigularis*	e	150	1	nd	RD
Cracidae					
Gray–headed chachalaca – *Ortalis cinereiceps*	e	536	nd	20	OAG
Crested guan – *Penelope purpurascens*	f	1,000	150	50	FA
Great currasow – *Crax rubra*	f	3,800	1	nd	FT / GT
Rallidae					
Gray–necked wood–rail – *Aramides cajanea*	f	405	20	20	IT
Eurypygidae					
Sun bittern – *Eurypyga helias*	f	210	nd	5	Aquat
Columbidae					
Pale–vented pigeon – *Columba cayennensis*	e	210	12	10	FA
Scaled pigeon – *Columba speciosa*	e	259	20	5	FA
Short–billed pigeon – *Columba nigrirostris*	e	160	100	300	FA
Blue ground–dove – *Claravis pretiosa*	e	69	2	nd	FA / GA
White–tipped dove – *Leptotila verrauxi*	e	130	2	6	FT
Gray–chested dove – *Leptotila cassinnii*	f	155	400	400	FT
Violaceous quail–dove – *Geotrygon violacea*	f	102	6	100	FT
Ruddy quail–dove – *Geotrygon montana*	f	128	100	200	FT
Psittacidae					
Orange–chinned parakeet – *Brotogeris jugularis*	e	63	60	400	FA / GA
Brown–hooded parrot – *Pionopsitta haematosis*	f	145	5	nd	GA
Blue–headed parrot – *Pionus menstruus*	e	235	50	150	GA
Red–lored amazon – *Amazona autumnalis*	f	416	150	200	GA
Mealy amazon – *Amazona farinosa*	f	687	150	250	GA
Cuculidae					
Squirrel cuckoo – *Piaya cayana*	f	105	150	300	IAG
Pheasant cuckoo – *Dromococcyx phasianellus*	f	86	nd	5	ITG
Greater ani – *Crotophaga major*	e	170	50	50	IADL
Smooth–billed ani – *Crotophaga ani*	e	110	nd	15	IAG

Table 1. (Cont.)

Species	H	M	Robinson	Willis	Guild
Strigidae					
Vermiculated screech–owl – *Otus guatemalae*	f	100	ne	100	RN
Crested owl – *Lophostrix cristata*	f	510	nd	20	RN
Spectacled owl – *Pulsatrix perspicillata*	f	850	16	40	RN
Mottled owl – *Ciccaba virgata*	e	300	nd	30	RN
Black–and–white owl – *Ciccaba nigrolineata*	e	458	ne	10	RN
Striped owl – *Rhinoptynx clamator*	e	420	nd	1	RN
Caprimulgidae					
Short–tailed nighthawk – *Lurocalis semitorquatus*	e	75	5	5	IAer
Common pauraque – *Nyctidromus albicollis*	e	53	2	2	ITS
Nyctibiidae					
Great potoo – *Nyctibius grandis*	f	585	nd	10	IAS
Apodidae					
White–collared swift – *Streptoprocne zonaris*	e	80	nd	1	IAer
Short–tailed swift – *Chaetura brachyura*	e	19	7	5	IAer
Band–rumped swift – *Chaetura spinicauda*	e	15	20	20	IAer
Lesser Swallow–tailed swift – *Panyptila cayennensis*	e	20	5	10	IAer
Trochilidae					
Long–tailed hermit – *Phaethornis superciliosus*	f	6	200	60	N
Little hermit – *Phaethornis longuemareus*	f	3	150	10	N
White–necked jacobin – *Florisuga mellivora*	e	6.3	100	60	N
Black–throated mango – *Anthracothorax nigricollis*	e	7	nd	5	N
Rufous–crested coquette – *Lophornis delattrei*	f	3	nd	5	N
Garden emerald – *Chlorostilbon canivetii*	e	4	nd	1	N
Crowned woodnymph – *Thalurania colombica*	f	5	200	100	N
Violet–bellied hummingbird – *Damophila julie*	f	4	100	100	N
Sapphire–throated hummingbird – *Lepidopyga coeruleogularis*	e	4	1	nd	N
Blue–chested hummingbird – *Amazilia amabilis*	f	3.3	100	150	N
Rufous–tailed hummingbird – *Amazilia tzacatl*	e	5	2	5	N
White–vented plumeleteer – *Chalybura buffoni*	f	6.0	5	nd	N
Purple–crowned fairy – *Heliothryx barroti*	e	6	5	50	N
Long–billed starthroat – *Heliomaster longirostris*	e	6	nd	1	N
Trogonidae					
White–tailed trogon – *Trogon viridis*	f	80	40	100	OA
Violaceous trogon – *Trogon violaceus*	f	57	60	100	OA
Black–throated trogon – *Trogon rufus*	f	52	250	300	OA
Black–tailed trogon – *Trogon melanurus*	f	115	2	6	OA
Slaty–tailed trogon – *Trogon massena*	f	140	175	200	OA
Momotidae					
Blue–crowned motmot – *Momotus momota*	e	105	ne	nd	OA
Rufous motmot – *Baryphthengus martii*	f	162	300	200	OA
Broad–billed motmot – *Electron platyrhynchum*	f	62	100	100	OA
Alcedinidae					
Ringed kingfisher – *Ceryle torquata*	e	290	2	10	Aquat

Table 1. (Cont.)

Species	H	M	Robinson	Willis	Guild
Green kingfisher – *Chloroceryle americana*	e	25	nd	30	Aquat
Amazon kingfisher – *Chloroceryle amazona*	e	130	nd	4	Aquat
Green–and–rufous kingfisher – *Chloroceryle inda*	f	59	nd	2	Aquat
American pygmy kingfisher –*Chloroceryle aenea*	f	16	5	20	Aquat
Bucconidae					
Black–breasted puffbird – *Notharchus pectoralis*	f	68	150	600	IAS
Pied puffbird – *Notharchus tectus*	f	33	25	50	IAS
White–whiskered puffbird – *Malacoptila panamensis*	f	44	300	200	IAS
Ramphastidae					
Collared aracari – *Pteroglossus torquatus*	f	65	125	300	FA
Keel–billed toucan – *Ramphastos sulfuratus*	f	375	200	300	FA
Chestnut–mandibled toucan – *Ramphastos swainsoni*	f	750	150	300	FA
Picidae					
Black–cheeked woodpecker – *Melanerpes pucherani*	f	54	150	150	IBI
Cinnamon woodpecker – *Celeus loricatus*	f	74	2	nd	IBI
Lineated woodpecker – *Dryocopus lineatus*	e	180	24	20	IBI
Crimson–crested woodpecker – *Campephilus melanoleucos*	f	225	30	50	IBI
Furnariidae					
Plain xenops – *Xenops minutus*	f	11	800	400	IBS
Scaly–throated leaftosser – *Sclerurus guatemalensis*	f	34	100	150	ITG
Dendroccolaptidae					
Plain–brown woodcreeper – *Dendrocincla fuliginosa*	f	41	90	100	IAF / IBS
Wedge–billed woodcreeper – *Glyphorynchus spirurus*	f	15	500	800	IBS
Buff–throated woodcreeper – *Xiphorhynchus guttatus*	f	47	175	250	IBS
Black–striped woodcreeper – *Xiphorhynchus lachrymosus*	f	51	200	500	IBS
Formicariidae					
Fasciated antshrike – *Cymbilaimus lineatus*	f	37	nd	5	IAG
Slaty antshrike – *Thamnophilus punctatus*	f	22	3,500	2,500	IAG
Spot–crowned antvireo – *Dysithamnus puncticeps*	f	15	175	200	IAG
Checker–throated antwren – *Myrmotherula fulviventris*	f	10	4,000	1,500	IADL
White–flanked antwren – *Myrmotherula axillaris*	f	8	3,000	2,000	IAG
Dot–winged antwren – *Microrhopias quixensis*	f	8	4,000	1,000	IAG
Dusky antbird – *Cercomacra tyrannina*	e	17	20	20	IADL / IAG
White–bellied antbird – *Myrmeciza longipes*	e	28	nd	5	ITG
Chestnut–backed antbird – *Myrmeciza exsul*	f	27	1,500	1,050	IAG / ITG
Spotted antbird – *Hylophylax naevioides*	f	17	750	700	IAF / ITG
Bicolored antbird – *Gymnopithys leucaspis*	f	30	60	60	IAF
Ocellated antbird – *Phaenostictus mcleannani*	f	51	nd	6	IAF
Streak–chested antpitta – *Hylopezus perspicillata*	f	42	nd	4	ITG
Tyrannidae					
Paltry tyrannulet – *Tyranniscus vilissimus*	e	9	2,500	1,000	OAS
Brown–capped tyrannulet – *Ornithion bruneicapillum*	f	7	250	600	IAS
Southern beardless–tyrannulet – *Camptostoma obsoletum*	e	8.5	6	150	IAS
Yellow–crowned tyrannulet – *Tyrannulus elatus*	e	8	700	400	OAS

Table 1. (Cont.)

Species	H	M	Robinson	Willis	Guild
Forest elaenia – *Myiopagis gaimardii*	f	14	90	80	IAS
Yellow–bellied elaenia – *Elaenia flavogaster*	e	25	nd	1	IAS
Ochre–bellied flycatcher – *Mionectes oleaginea*	f	13	100	100	OAS
Black–capped pygmy–tyrant – *Myiornis atricapillus*	f	5	125	300	IAS
Southern bentbill – *Oncostoma olivaceum*	f	7	800	400	IAS
Common tody–flycatcher – *Todirostrum cinereum*	e	7	100	6	IAS
Olivaceous flatbill – *Rhynchocyclus olivaceus*	f	22	200	300	IAS
Yellow–margined flycatcher – *Tolmomyias assimilis*	f	14	400	500	IAS
Golden–crowned spadebill – *Platyrinchus coronatus*	f	9	200	200	IAS
Ruddy–tailed flycatcher – *Terenotriccus erythrurus*	f	7	400	400	IAS
Bright–rumped attila – *Attila spadiceus*	f	38	25	50	IAS
Speckled mourner – *Laniocera rufescens*	f	49	4	30	OAS
Rufous mourner – *Rhytipterna holerythra*	f	38	50	70	OAS
Dusky–capped flycatcher – *Myiarchus tuberculifer*	f	20	1,000	1,000	IAS
Panama flycatcher – *Myiarchus panamensis*	e	33	8	nd	IAS
Lesser kiskadee – *Philohydor lictor*	e	25	100	100	IAS
Great kiskadee – *Pitangus sulphuratus*	e	50	50	nd	IAS
Boat–billed flycatcher – *Megarhyncus pitangua*	e	60	100	150	IAS
Rusty–margined flycatcher – *Myiozetetes cayanensis*	e	28	75	70	IAS
Social flycatcher – *Myiozetetes similis*	e	24	300	600	IAS
Streaked flycatcher – *Myiodynastes maculatus*	e	45	20	50	IAS
Piratic flycatcher – *Legatus leucophaius*	e	26	10	2	OAS
Tropical kingbird – *Tyrannus melancholicus*	e	40	400	500	IAS
White–winged becard – *Pachyramphus polychopterus*	e	18	nd	ne	IAS
Masked tityra – *Tityra semifasciata*	e	80	40	300	OAS
Black–crowned tityra – *Tityra inquisitor*	e	41	15	50	OAS
Cotingidae					
Rufous piha – *Lipaugus unirufus*	f	86	1	80	OAS
Blue cotinga – *Cotinga nattererii*	f	55	50	80	FA
Purple–throated fruitcrow – *Querula purpurata*	f	104	180	250	OAS
Pipridae					
Thrushlike mourner – *Schiffornis turdinus*	f	33	2	nd	OAS
Golden–collared manakin – *Manacus vitellinus*	e	17	50	150	FAS
Red–capped manakin – *Pipra mentalis*	f	15	800	1,000	FAS
Hirundinidae					
Gray–breasted martin – *Progne chalybea*	e	39	25	10	IAer
Mangrove swallow – *Tachycineta albonotata*	e	15	100	ne	IAer
Southern rough–winged swallow – *Stelgidopteryx serripennis*	e	16	ne	10	IAer
Corvidae					
Black–chested jay – *Cyanocorax affinis*	f	220	nd	1	OAG
Troglodytidae					
Plain wren – *Thryothorus modestus*	e	18	2	20	IAG
Sylvinae					
Long–billed gnatwren – *Ramphocaenus rufiventris*	f	10	30	100	IAG

Table 1. (Cont.)

Species	H	M	Robinson	Willis	Guild
Tropical gnatcatcher – *Polioptila plumbea*	f	7	300	200	IAS
Turdinae					
Clay–colored thrush – *Turdus grayii*	e	80	1	nd	OTG
Vireonidae					
Yellow–green vireo – *Vireo flavoviridis*	e	17	nd	5	OAG
Scrub greenlet – *Hylophilus flavipes*	e	13	nd	5	IAG
Lesser greenlet – *Hylophilus decurtatus*	f	10	3,000	1,500	IAG
Green shrike–vireo – *Vireolanius pulchellus*	f	25	1	10	IAG
Coerebinae					
Bananaquit – *Coereba flaveola*	e	9	100	300	OAG
Thraupinae					
Plain–colored tanager – *Tangara inornata*	e	18	100	200	OAG
Bay–headed tanager – *Tangara gyrola*	e	22	ne	nd	OAG
Golden–hooded tanager – *Tangara larvata*	e	19	50	100	OAG
Scarlet–thighed dacnis – *Dacnis venusta*	e	16	5	40	OAG
Blue dacnis – *Dacnis cayana*	e	13	1,000	500	OAG
Green honeycreeper – *Chlorophanes spiza*	e	18	200	400	OAG
Shining honeycreeper – *Cyanerpes lucidus*	e	12	75	50	FAG
Red–legged honeycreeper – *Cyanerpes cyaneus*	e	13	200	300	FAG
Yellow–crowned euphonia – *Euphonia luteicapilla*	e	12	1	nd	FAG
Thick–billed euphonia – *Euphonia laniirostris*	e	15	2	nd	FAG
Fulvous–vented euphonia – *Euphonia fulvicrissa*	f	11	250	1,000	OAG
White–vented euphonia – *Euphonia minuta*	e	11	nd	2	FAG
Blue–gray tanager – *Thraupis episcopus*	e	30	20	150	OAG
Palm tanager – *Thraupis palmarum*	e	35	10	100	OAG
Gray–headed tanager – *Eucometis penicillata*	f	30	40	ne	OAF / OAG
White–shouldered tanager – *Tachyphonus luctuosus*	e	15	300	100	OAG / OAS
Red–throated ant–tanager – *Habia fuscicauda*	e	39	50	40	OAG
Crimson–backed tanager – *Ramphocelus dimidiatus*	e	28	6	nd	OAG
Cardinalinae					
Slate–colored grosbeak – *Pitylus grossus*	f	43	4	500	OAG
Blue–black grosbeak – *Cyanocompsa cyanoides*	f	32	80	300	OAG
Emberizinae					
Orange–billed sparrow – *Arremon aurantiirostris*	e	31	ne	nd	OTG
Variable seedeater – *Sporophila aurita*	e	10	2	30	GT
Yellow–bellied seedeater – *Sporophila nigricollis*	e	10	ne	2	GT
Icterinae					
Giant cowbird – *Scaphidura oryzivora*	e	187	4	nd	OTG
Yellow–backed oriole – *Icterus chrysater*	e	43	40	40	OAG
Yellow–rumped cacique – *Cacicus cela*	e	68–113	100	20	OAG
Chestnut–headed oropendola – *Zarhynchus wagleri*	e	113–214	75	20	OAG

Table 2. Species for which island population sizes increased at least 100% between 1970 and the mid–1990s. (See table 1 for scientific names.

Tabla 2. Especies cuya población en la isla aumentó al menos en un 100% desde 1970 hasta mediados de la década de 1990. (Para los nombres científicos, véase la tabla 1.)

Species	1970	1995	%
Crested guan	50	150	200
Long–tailed hermit	60	200	233
Little hermit	10	150	1,400
Crowned woodnymph	100	200	100
Plain xenops	400	800	100
Checker–throated antwren	1,500	4,000	167
Dot–winged antwren	1,000	4,000	300
Paltry tyrannulet	1,000	2,500	150
Southern bentbill	400	800	100
Common tody–flycatcher	6	100	1,567
Lesser greenlet	1,500	3,000	100
Blue dacnis	500	1,000	100
White–shouldered Tanager	100	300	200
Yellow–rumped cacique	20	100	400
Chestnut–headed oropendola	20	75	275

Population declines. Thirty–seven species and four species groups (hawks, vultures, owls, and kingfishers) declined by at least 50% (table 3). Those species represent an ecologically diverse subset of the island avifauna. Several major patterns are apparent.

First, consumers of vertebrates declined as a whole. Hawks declined by at least two–thirds; owls by 92%; carrion–eating vultures by 75%; and piscivorous kingfishers by 89%. Despite extensive pre–dawn surveys (Robinson, 1999), extremely few owls were detected on the island, with only 3 of the 5 forest species Willis detected being found by me in the mid–1990s. A single Striped owl was observed by Willis on a small satellite island near the BCI laboratory facilities, which was dominated by grass and shrubs at that time. By the mid–1990s the habitat had matured and was unsuitable for that species. Similarly, 5 species of hawk found by Willis were not found by me, although Double–toothed kite continued to be the most numerous raptor. The paucity of hawks and owls is curious. The lack of kingfishers has been explained by the introduction of Peacock

Table 3 Species, or species groups, for which island population sizes declined at least 50% between 1970 and the mid–1990s. (See table 1 for scientific names.)

Tabla 3. Especies, o grupos de especies, cuya población en la isla disminuyó al menos en un 50% desde 1970 hasta mediados de 1990. (Para los nombres científicos, véase la tabla 1.)

Species	1970	1995	%
Great tinamou	200	100	50
Hawks	108	<37	66
Vultures	130	32	75
Short–billed pigeon	300	100	67
Violaceous quail–dove	100	6	94
Ruddy quail–dove	200	100	50
Orange–chinned parakeet	400	60	85
Blue–headed parrot	150	50	67
Squirrel cuckoo	300	150	50
Owls	>200	>16	92
Purple–crowned fairy	50	5	90
White–tailed trogon	100	40	60
Black–throated trogon	6	2	67
Kingfishers	66	7	89
Black–breasted puffbird	600	150	75
Pied Puffbird	50	25	50
Black–striped woodcreeper	500	200	60
Brown-capped tyrannulet	600	250	58
Southern beardless tyrannulet	150	6	96
Black–capped pygmy–tyrant	300	125	58
Bright–rumped attila	50	25	50
Speckled mourner	30	4	87
Social flycatcher	600	300	50
Streaked flycatcher	50	20	60
Masked tityra	300	40	87
Black–crowned tityra	50	15	70
Rufous piha	80	1	99
Golden–collared manakin	150	50	67
Plain wren	20	2	90
Long–billed gnatwren	100	30	70
Green shrike–vireo	10	1	90
Bananaquit	300	100	67
Plain–colored tanager	200	100	50
Scarlet–thighed dacnis	40	5	90
Green honeycreeper	400	200	50
Fulvous–vented euphonia	1,000	250	75
Blue–gray tanager	150	20	87
Palm tanager	100	10	90
Slate–colored grosbeak	500	4	99
Blue–black grosbeak	300	80	73
Variable seedeater	30	2	93

bass (*Cichla* sp.) into Gatun lake, which are predaceous on smaller, native fishes (ZARET & PAINE, 1973). The hypothesis suggests that as bass populations rose, native fishes were driven locally extinct and the food resource base of kingfishers was reduced. However, strong tests of the hypothesis have not been conducted.

Second, 11 species are usually commonest in edge or young forest habitats: Orange–chinned parakeet, Southern beardless–tyrannulet, Golden–collared manakin, Plain wren, Long–billed gnatwren, Plain–colored tanager, Fulvous–vented euphonia, Blue–gray tanager, Palm tanager, Blue–black grosbeak, and Variable seedeater. Nearly all those species are now most frequently observed near the laboratory clearing or along the island–lake interface and go virtually undetected within the interior of the island. Continued successional maturation of the forest probably explains the declines of those species.

Third, several species commonly nest in standing trees in Gatun lake. Such trees were numerous after lake waters rose to isolate the island in the early 1900s and have steadily disappeared as they have rotted and fallen into the lake. Social flycatchers commonly build their bulky nests in the branches of such trees, whereas the tityras and Streaked flycatcher usually occupy cavities in dead trees.

Fourth, several frugivorous or granivorous species are highly mobile and numbers on the island could fluctuate from year to year depending on fruit availability so much that comparisons of two point estimates may not indicate long–term declines in numbers. Short–billed pigeon, Ruddy quail–dove, Blue–headed parrot, and Green honeycreeper all move easily across long distances and may track resource abundance (WRIGHT, 1985). Violaceous quail–dove has declined the most precipitously, by 94%, but this decline may reflect a real regional decline. Nowhere in central Panama can one now find population densities like the 100 individuals Willis estimated on BCI in 1970. Instead, the species is rare and sparsely distributed (Robinson, unpublished data).

Fifth, including Violaceous quail–dove, six species of forest interior birds have declined so dramatically that they are on the brink of extinction from BCI. Speckled mourner, which is a persistent singer and is easy to detect has dropped to four individuals on BCI. Rufous piha, a loud and formerly common species with an estimated 80 birds in 1970, was down to one individual in 1994; none have been seen or heard since then. Green shrike–vireo, also a very loud and persistent singer that vocalizes all day long, was never common, but is now represented by one singing male; it is unknown if a female accompanied the male. Scarlet–thighed dacnis was rarely found in the mid–1990s and its total island population size was estimated at five individuals. That species remains high in the canopy with other tanager and honeycreeper species, however, and could have been underestimated. Slate–colored grosbeak, however, has a very distinctive song uttered at regular intervals as it forages in the mid–story of tall forest. Its population collapsed from 500 to four (two pairs).

Finally, in contrast to increases in numbers of guans, Great tinamous, another species often hunted in Panama, declined on BCI by about 50%. Given the level of protection from hunting, an increase would be expected; however, it is possible that this ground–nesting species has experienced elevated levels of nest predation. Tinamou nests have low survival rates on the mainland (ROBINSON et al., 2000b) and their eggs are consumed by snakes and monkeys (ROBINSON et al., 2001). BCI has somewhat higher densities of monkeys than nearby mainland forests (WRIGHT et al., 1994), suggesting that predation on tinamou nests might be greater. A handful of canopy species, such as Black–breasted and Pied puffbirds, Black–striped woodcreeper, Brown–capped tyrannulet and Black–capped pygmy–tyrant have declined for unknown reasons.

Extinctions and colonizations. Nineteen species were detected on BCI during the mid–1990s but not found by Willis in 1970 (table 4). Great curassow, Brown–hooded parrot, Cinnamon woodpecker and Thrush–like mourner are all forest–dwelling species, whereas the remaining species all prefer edge habitats. ROBINSON (1999) provides details on these colonizations.

Twenty–seven species were found by Willis but not the author of this study. ROBINSON (1999) discusses possible reasons for the loss of those species. Rarity, however, appears to be strongly related to extinction probability. The maximum estimated abundance of any species lost since 1970 was 30, which was Green kingfisher, a species that utilizes only the margins of the island. Island–wide abundance for 21 of the 27 species not found in the mid–1990s was 5 or fewer individuals. Although KARR (1982b) argued that rarity is not a good predictor of extinction probability among birds on BCI, his conclusions were based on comparisons of mainland and BCI species lists built from general impressions of abundance on the mainland only; no abundance estimates derived from censuses, on either the mainland or island, were used. Evidence supporting the hypothesis that rarity increases extinction risk has come from the British island avifauna, where population size was the most important predictor of risk of extinction (PIMM et al., 1988).

If rarity is defined as any species whose population size is less than 10, then 26 of the rare species present in the mid–1990s were species of edge habitats (table 1). Losses of those species could occur naturally as forest maturation continues, but many may not disappear permanently from the island. As ROBINSON (1999) indicated, edge species disperse well and

Table 4. Resident species not detected in both 1970 and the mid–1990s. Those undetected in 1970 probably colonized by the mid-1990s and those detected in 1970 but not found in the mid–1990s had probably disappeared from Barro Colorado Island: A. Present in 1970, absent in 1995; B. Absent in 1970, present in 1995. (See table 1 for scientific names, habitat affiliations, and abundance estimates.)

Tabla 4. Especies residentes no detectadas, ni en 1970 ni a mediados de la década de 1990. Las especies que no se detectaron en 1970 probablemente se establecieron en colonias a mediados de la década de 1990, y aquellas que se detectaron en 1970, pero que no pudieron encontrarse a mediados de la década de 1990, probablemente habían desaparecido de la Isla de Barro Colorado: A. Presentes en 1970, ausentes en 1995; B. Ausentes en 1970, presentes en 1995. (Para los nombres científicos, afiliaciones de hábitat y abundancias estimadas, véase la tabla 1.)

A	B
Tiny hawk	Little tinamou
Short–tailed hawk	Bat falcon
Zone–tailed hawk	Great curassow
Crested eagle	Brown–hooded parrot
Ornate hawk–eagle	Sapphire–throated hummingbird
Gray–headed chachalaca	Long–billed starthroat
Sunbittern	White–vented plumeleteer
Pheasant cuckoo	Blue–crowned motmot
Smooth–billed ani	Cinnamon woodpecker
Great potoo	Panama flycatcher
White–collared swift	Great kiskadee
Black–throated mango	Thrush–like mourner
Rufous–crested coquette	Clay–colored robin
Garden emerald	Bay–headed tanager
Green kingfisher	Yellow–crowned euphonia
Amazon eingfisher	Thick–billed euphonia
Green–and–rufous kingfisher	Crimson–backed tanager
Fasciated antshrike	Orange–billed sparrow
White–bellied antbird	Giant cowbird
Ocellated antbird	
Streak–chested antpitta	
Yellow–bellied elaenia	
White–winged becard	
Black–chested jay	
Yellow–green vireo	
Scrub greenlet	
White–vented euphonia	

recolonize when appropriate habitat becomes available. Thus, their disappearances from BCI, despite local rarity, may typically be temporary. In contrast, rare species of the forest may be absent for long time intervals after local extinction from BCI. Many forest species appear to disperse poorly and have difficulties recolonizing isolated forest remnants (WILLIS, 1974; ROBINSON, 1999). ROBINSON (1999) showed that most forest species that had disappeared from BCI were never encountered on the island again. Thus, the 11 forest species currently present in very low numbers may disappear from BCI permanently once they become locally extinct. That total excludes six forest raptor species whose abundances are less than 10, but whose home ranges are so large that they must forage off the island as well.

If the remaining forest species are common enough that they are relatively unlikely to disappear over the next 25 years, the rate at which forest species are being lost from BCI may be slowing. BCI may now be acting as a reserve for common species and failing to preserve many rare species that comprise a significant proportion of the species in the bird community of central Panama. Thus, with continued loss of bird species from the island, BCI will be filled with common and widely distributed species and, like other small tropical reserves (DIAMOND et al., 1987), will not act as an effective preserve of regional avian diversity.

Future directions

No method of surveying tropical birds is perfect or complete. The great diversity and variety of life histories causes some species to be much more easily detected than others so that complete community surveys must involve multiple methods (TERBORGH et al., 1990; ROBINSON et al., 2000a). However, for many species, a simple point count scheme, where points are surveyed annually by the same or comparable observers at the same season, will provide the best information for detecting long–term population trends with a minimum of bias (VERNER, 1985). Such schemes are now possible in some Neotropical locations such as Panama where knowledge of bird vocalizations is reasonably complete. With the accumulation of such information, conservation biologists will be better able to predict accurately the long–term effects of habitat fragmentation on bird communities, particularly the likelihood of extinction as a function of population fluctuations.

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