AVIAN EXTINCTIONS IN AN ISOLATED TROPICAL WET-FOREST PRESERVE, ECUADOR

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ABSTRACT.—The avifauna of a small forest island in lowland Ecuador was surveyed to detect recent extinctions. The 87-ha national forest, at Rio Palenque, has had serious declines in bird species numbers, even within the relatively short period of 1973–78. Among the 170 species of forest-dwelling birds, I found no recent records for 19 species, 25 had been last noted in 1975, and 15 presently have precariously low populations. Attributes of the species that had local extinctions included, in order of importance, large body size (predatory habits), general rarity (specialization), or declining populations throughout their range. Illegal hunting was related to the loss of two species at the preserve. The importance of large refuges is reaffirmed by this study. *Received 5 July 1978, accepted 19 December 1978.*

SHORTLY after island biogeography showed the importance of large island size for the maintenance of species richness, ecologists applied the concept to isolated habitat patches or "islands" in the terrestrial landscape. Studies of birds particularly have contributed to discussion of the importance of size in forest preserves (e.g. Terborgh 1976, Diamond 1975). Comparative field surveys of forest islands have been done for breeding birds of northeastern temperate woodlands (Galli et al. 1976, MacClintock et al. 1977) and have yielded dramatic evidence of the inability of small patches to act as effective preserves. Few tropical studies have yet to survey such a series of forest patches because of logistic difficulties, lack of appropriate forest islands, or limitations of single observers where species richness is extremely high. Nevertheless, we can measure size stress in a single tropical forest by looking at local extinctions in the time since the forest became isolated as an island. Willis (1974) did this for Barro Colorado Island Preserve, Panama and noted a loss of 22% of the original resident avifauna since 1925.

In 1978 I made an ornithological survey of a small tropical wet-forest on the west side of the Ecuadorian Andes to evaluate the sensitivity of tropical species to the pressures of habitat size. My study area, at Centro Cientifico Rio Palenque, was a national forest that has been well studied by field ornithologists since its establishment, so documentation of local extinctions through time was possible. Here I report the extent of avian extinctions at Rio Palenque and their rapidity and causes, particularly as they might reflect the dynamics of the small forest patches that are becoming so common in the neotropics today.

STUDY SITE AND METHODS

Centro Cientifico Rio Palenque (approximately ½°S, 79½°W) is located on the west side of the Ecuadorian Andes (about 17 km from the foothills), at an elevation of 200 m. The station is 65 km south of the equator and 47 km south of Santo Domingo de los Colorados, on the Rio Palenque (Rio Quevedo). The area has an average annual rainfall of over 380 cm, the majority of which occurs during the December–May wet season. Temperatures average 17°–24°C in the dry season, and 23°–32°C in the wet season.

The property itself includes 167 ha, 87 of which are still mature forest (80 ha are planted in the African oil palm, *Elaeis guineensis*). The mature forest is exceptionally rich in plants. Gentry (1977) indicates that the "almost 600 species per km^2 recorded from Rio Palenque is probably the highest recorded plant diversity in the world." At least 800 species have been recorded, on the natural forest study area while

the 1.7 km² of the entire Centro Cientifico property has yielded 1,100 species of plants (Dodson and Gentry, in press). The vegetation benefits from alluvial soil deposits that are far superior to the common tropical lateritic soils.

Within the forest, canopy is dense (30–42 m), with 59 species of trees. Families of importance are Moraceae, Lauraceae, and Bombacaceae. Epiphytes (266 species) and large lianas are also important. Middle story trees, 10–20 m, include 74 species of Moraceae, Palmae, and other families. Small trees, 3–9 m, include 49 species, mostly in Piperaceae, Rubiaceae, and Melastomaceae. Shrubs and herbaceous plants (<1 m) include more than 100 additional species. (See Dodson and Gentry, in press, who provide an exhaustive review of the flora of Rio Palenque.)

The mature forest has apparently not undergone any significant successional change in recent years, nor has it suffered any unnatural disturbances, except for the removal of a small number of large *Balsa* trees. The critical local change has been simply the isolation of the Rio Palenque forest: by 1978 the entire surrounding area was agricultural. This isolation has accelerated greatly since 1970 with recent improvements in the Pan American Highway. Marked improvements in regional transportation continue even today, and the agricultural exploitation surrounds Rio Palenque with banana plantations, corn fields, and oil palm plantations (a government diversification). Gentry (1977) provides an important description of this area's development:

> "Moreover, the narrow strip of wet forest extending south along the base of the Andes is currently the country's fastest-disappearing habitat. It has been opened up within the last decade by road construction . . . and in the last five or six years formerly extensive wet forest vegetation has been converted to almost solid banana and oil palm plantations. Perhaps the only unthreatened area of this vegetation . . . is the minuscule (less than 2 km²) Rio Palenque Field Station."

Putney (1976) maps sections of natural vegetation remaining in Ecuador. He shows that Rio Palenque is well isolated (more than 50 km from another large forested area) and that there are only small forest patches widely scattered along this western bottom edge of the Andes. The lower slopes of the Andean foothills provide some nearby (20 km) forests, but it is unclear if these are secondary habitats or remanents of natural vegetation. In any case, the foothills themselves are rapidly being cleared with burning and subsequent farming.

Since 1973, many field ornithologists have visited the Rio Palenque station and contributed to our knowledge of the local avifauna (see Acknowledgments), but particular recognition should be given to several. Oscar Owre began studies of Rio Palenque birds when the preserve was first established; he directed class studies there and made a good representative collection of avian specimens (University of Miami collection), which provided essential groundwork. Fernando Ortiz of the Universidad Catolica, Quito, has visited the site more frequently than any other ornithologist; his records include notes on nesting activity and unusual species. Richard Webster has been an indefatigable observer at Rio Palenque. His period of longest residence was between 9 June and 3 September 1975, from which he produced an excellent review of the 257 species he observed (unpublished MS). His 1975 report provides many comments on the status of individual species to which I compare current trends. My fieldwork at the station took place between 21 February and 6 April 1978, during which time I observed almost 200 species (including nonforest species). My censusing included daily fieldwork at virtually all hours of the day and irregular periods of mist-netting (usually in the early morning).

STATUS OF FOREST BIRDS AT RIO PALENQUE

In the following pages I review the status, from 1973 to 1978, of the 170 species at Rio Palenque that I consider "forest birds." They are birds that are primarily forest-dwelling at the station, even if they frequent other habitats in other geographical areas. Meyer de Schauensee (1970) includes "forest" as a habitat note for almost all of these species. They are birds that would probably be sensitive to forest isolation.

I have not included forest edge species or open habitat species that might increase with forest disturbance or reduction. An annotated checklist of *all* 336 species recorded from the Rio Palenque property has been prepared (Leck et al. MS). Our annotated list indicates species abundances, habitat preferences, and some population changes (long-term and seasonal).

In the review below, birds are discussed by families, and each family name is followed by two numbers in parentheses—the total number of species at Rio Palenque and the number of these considered to be "forest species." In the text I occasionally refer to non-forest species when appropriate for a comparison with the forest birds.

TINAMIDAE (3, 3)

The largest species (*Tinamus major*) has a remanent population of only a few individuals (1978). *Crypturellus soui* is common, and *C. cinereus* is uncommon but nesting.

ACCIPITRIDAE (13, 5)

The largest predatory bird, the Harpy Eagle (*Harpia harpyja*), was formerly present but is now locally extinct. There are almost no records for this species on the west side of the Ecuadorian Andes in recent years (F. Ortiz pers. comm.). Two other forest hawks (*Accipiter superciliosus* and *Geranospiza caerulescens*) were last reported in 1975. The Semiplumbeous Hawk (*Leucopternis semiplumbea*) remains evident with several resident birds, and the Gray-headed Kite (*Leptodon cayanensis*) is still seen.

FALCONIDAE (4, 2)

There are no recent records of *Daptrius americanus,* and *Micrastur ruficollis* was last reported in 1975. (Two falcon species of the forest edge are still regularly seen.)

CRACIDAE (2, 1)

The guan (*Penelope purpurascens*) is apparently gone. (The smaller *Ortalis erythroptera,* of open areas, remains.)

PHASIANIDAE (1, 1)

The small wood-quail (*Odontophorus erythrops*) continues as a regular breeding bird.

RALLIDAE (5, 1)

The large wood-rail (*Aramides wolfi*) will soon be extirpated; only one or two individuals remained in 1978.

COLUMBIDAE (8, 4)

All four forest pigeons (*Columba subvinacea, C. goodsoni, C. cayennensis,* and *Leptotila pallida*) are seen regularly.

PSITTACIDAE (14, 9)

Four forest parrots (*Ara ambigua, Touit dilectissima, Pionopsitta haematotis,* and *Pionus sordidus*) have not been recorded in recent years, and one (*Amazona festiva*) has not been seen since 1975. I found four other species (*Ara severa, Pionus menstruus, P. Chalcopterus,* and *Amazona farinosa*) still frequent at Rio Palenque in 1978. The macaw (*Ara*) was usually seen overhead; all four species appeared to fly to nearby Andean foothills each evening. (The foothills provide a more continuous forest, or "source area.") The daily visiting flocks were often interspecific (with a species maximum of 20 *P. chalcopterus*). Courtship was noted in *Amazona*, but it seems unlikely that there is nesting at the preserve itself.

CUCULIDAE (6, 1)

The only forest-frequenting cuckoo (*Piaya cayana*) is seen daily.

STRIGIDAE (2, 2)

Both local forest owls (*Pulsatrix perspicillata* and *Otus guatemalae*) are present. For the former species, the larger of the two, only one or two individuals are recorded.

NYCTIBIIDAE (1, 1)

The nocturnal *Nyctibius griseus* has not been recorded in recent years; it could easily be overlooked.

TROCHILIDAE (20, 15)

Two forest hummingbirds (*Ocreatus underwoodii* and *Acestrura bombus*) have not been seen in recent years. The remaining 12 species have been noted regularly to the present: *Glaucis aenea, Threnetes ruckeri, Phaethornis yaruqui, P. superciliosus, P. longuemareus, Eutoxeres aquila, Popelairia conversii, Thalurania furcata, Damophila julie, Amazilia amabilis, A. franciae* (rare), *Heliodoxa jacula,* and *Heliothryx barroti.* The more common of these are associated with forest undergrowth and flowering *Heliconia* (Musaceae) clumps.

TROGONIDAE (4, 3)

The trogons (*Trogon melanurus, T. viridis,* and *T. collaris*) are regularly observed but vary in detectability. Richard Webster (pers. comm.) had found them less common in 1977 than in 1975, while I found them common again in March 1978 but much less conspicuous in April.

MOMOTIDAE (3, 3)

Electron platyrhynchum and *Baryphthengus ruficapillus* remain as residents; *Momotus momota* has disappeared, and there are no recent records.

BUCCONIDAE (4, 4)

The puffbirds appear to be doing poorly—*Notharchus tectus* and *Nystalus radiatus* have not been reported since 1975. There are some recent sightings of *Notharchus macrorhynchus* and *Malacoptila panamensis,* but they do not suggest viable populations. I recorded none of the four species in 1978.

RAMPHASTIDAE (4, 4)

Records suggest the recent loss of one species, *Aulacorhynchus haematopygus* (in the past it may only have been a visitant). *Ramphastos brevis* and *R. ambiguus* remain evident in small numbers. I saw several individuals of *Pteroglossus sanguineus* at the station for the first time in April 1978.

PICIDAE (10, 9)

Most of the forest woodpeckers (*Picumnus olivaceus, Piculus rubiginosus, Celeus loricatus, Melanerpes pucherani, Veniliornis kirkii*) are regularly seen, although one (*Piculus leucolaemus*) is distinctly uncommon. Two large woodpeckers (*Dryocopus lineatus* and *Phloeoceastes guayaquilensis*) are present. The latter was found nesting in 1977, and both species were evident in 1978. (*Phloeoceastes melanoleucos*? was reported here in 1973; there were no other records.)

DENDROCOLAPTIDAE (5, 4)

Two small woodcreepers (*Dendrocincla fuliginosa* and *Glyphorhynchus spirurus*) are common. The two larger species (*Xiphorhynchus erythropygius* and *Campylorhamphus trochilirostris*) are less common but still regularly recorded.

FURNARIIDAE (12, 9)

Two forest furnariids (*Premnoplex brunnescens*? and *Sclerurus mexicanus*) have not been recorded in recent years. Other species are regularly reported: *Hyloctistes subulatus, Philydor erythrocercus, Automolus rubiginosus, A. ochrolaemus, Xenops rutilans, X. minutus,* and *Sclerurus guatemalensis.* Of these, only *Philydor* and the *Xenops* species are common.

FORMICARIIDAE (19, 18)

The only antbird not recorded since 1975 is *Pittasoma rufopileatum.* The most common species are

Thamnophilus punctatus, Myrmotherula axillaris, Microrhopias quixensis, and *Myrmeciza exsul.* Also regularly reported are *Cymbilaimus lineatus, Dysithamnus mentalis, Myrmotherula surinamensis, M. fulviventris, Cercomacra tyrannia, Pyriglena leuconota, Myrmeciza immaculata, Gymnopithys leucaspis,* and *Formicarius nigricapillus.* Uncommon or rare species are *Taraba major, Myrmotherula schisticolor, Hylophylax naevioides,* and *Grallaria perspicillata* (only recorded in 1977).

COTINGIDAE (9, 6)

Two large forest cotingids (*Carpodectes hopkei,* and *Cephalopterus penduliger*) are rare. Small groups of *Querula purpurata* still nest. Two becards are regular, *Pachyramphus cinnamomeus* (common) and *P. albogriseus. Lipaugus unirufus* has not been recorded since 1975.

PIPRIDAE (5, 5)

As a group, manakins are doing very poorly, with the single exception of the common *Manacus manacus* (many courting individuals, February–March 1978). Three species (*Pipra mentalis, Schiffornis turdinus*, and *Allocotopterus deliciosus*) have not been recorded since 1975 and then only as a few birds. *Pipra coronata* is rarely reported to the present.

TYRANNIDAE (46, 26)

The most common flycatchers are species of the edge and open habitats. Ten of 26 forest flycatchers at Rio Palenque are no longer reported. Species not reported in recent years are *Colonia colonus* and *Tyranniscus nigrocapillus*?. Species last reported in 1975 (all of these were uncommon or rare) are *Sirystes sibilator, Attila torridus, Platyrinchus coronatus, Rhynchocyclus fulvipectus, Poecilotriccus ruficeps, Pogonotriccus ophthalmicus, Tyranniscus viridiflavus,* and *Mionectes olivaceus.*

Of the 16 species remaining, the more commonly reported are *Myiodynastes maculatus, Myiobius barbatus, Tolmomyias assimilis, Lophotriccus pileatus, Rhynchocyclus brevirostris, Leptopogon superciliaris,* and *Pipromorpha oleaginea.* Species irregularly or rarely reported are *Attila spadiceus, Terenotriccus erythrurus, Myiotriccus ornatus, Myiophobus fasciatus, Platyrinchus mystaceus, Todirostrum nigriceps, Tyrannulus elatus,* and *Ornithion semiflavum. Myiobius atricaudus* was recorded once, in 1977. We have insufficient data to evaluate or predict population trends in the rarer flycatchers.

TROGLODYTIDAE (7, 2)

Both forest wrens remain evident; *Microcerculus marginatus* (common) and *Cyphorhinus arada.*

TURDIDAE (6, 3)

There have been no reports of *Platycichla leucops* since 1975 and only two reports in recent years of *Turdus obsoletus.* The migrant forest thrush, *Catharus ustulatus,* was common in March 1978. (*Turdus nudigenis* of the forest edge and open areas is common.)

SYLVIIDAE (4, 3)

Microbates cinereiventris and *Polioptila schistaceigula* are present; *Ramphocaenus melanurus* has not been recorded since 1975.

VIREONIDAE (3, 2)

The resident *Hylophilus minor* is uncommon; the possibly migrant *Vireo olivaceus* is common.

ICTERIDAE (6, 2)

Two forest icterids (*Cacicus uropygialus* and *Icterus mesomelas*) are irregularly reported.

PARULIDAE (6, 2)

One forest parulid, *Parula pitiayumi,* appears to be declining (none in 1978), while the terrestrial *Basileuterus rivularis* remains common.

COEREBIDAE (8, 5)

As a family, the Coerebidae are doing very poorly, and the only common forest species is *Chlorophanes spiza*. *Cyanerpes caeruleus* was common and declined, *C. cyaneus* is irregular, *Iridophanes pulcherrima* has not been seen in recent years, and *Dacnis venusta* was last seen in 1975.

THRAUPIDAE (24, 13)

Forest tanagers are also doing poorly. Species not recorded in recent years are: *Tangara lavinia, T. nigroviridis,* and *Buthraupis eximia* (specimen). Last recorded in 1975 were *Euphonia minuta* and *Tangara icterocephala*. *Euphonia saturata* had nested in the past but was not recorded in 1978. Other species (*Heterospingus xanthopygius, Hemithraupis guira, Tangara gyrola, Tachyphonus luctuosus,* and *T. delatrii*) are regularly recorded. The only common forest tanager, *Mitrospingus cassinii,* is a species that also exploits second growth. (Many other clearing thraupids are common.)

FRINGILLIDAE (14, 2)

Most members of the family are of open and disturbed habitats. Only two are truly forest birds at Rio Palenque, *Pitylus grossus* (uncommon) and *Arremon aurantiirostris* (probably the most common forest bird).

DISCUSSION OF POPULATION LOSSES

The declines in forest avifauna at Rio Palenque are reviewed in Table 1, using the information presented in the previous section. We see that 44 forest birds have been lost, and a further 15 species are in such low numbers as to be unstable and likely to be lost in the near future. What characteristics make species candidates for extirpation? We cannot assume, a priori, that all or even most of the declines are directly related to "size stress" of the forest island. I will describe at least five classes of factors contributing to the declines, with the realization that my goal is primarily the explanation of *local* changes at the forest. In contrast, if a species is decreasing throughout its South American range, this widespread decline is a probable reason for its observed decline at Rio Palenque, although we clearly have another biological question remaining for the overall change. For example, *Daptrius americanus* and *Nystalus radiatus* are declining species at the property (Table 1), but they have also recently decreased in large parts of their range (Ridgely 1976).

Large birds (nine species) were prone to decline. Generally, we find a good ecological correlation between body size and territory size in forest birds (Schoener 1968), so larger birds rapidly feel the spatial limitations of habitat patches. This greater territorial demand of larger species is, of course, related to greater food intake and often to the higher trophic positions of large birds. It should be noted, however, that "large" can also be applied relatively; that is, within a family the (locally) largest member is likely to have greater area demands and to be rarer than smaller species, even though all members of the family can be considered small. At Rio Palenque, losses and declines of big birds include the predatory eagle (*Harpia harpyja*) and owl (*Pulsatrix perspicullata*), neither of which has ever been represented by more than one pair. In fact, the eagle undoubtedly had to include formerly adjacent forest within its foraging area. Other large species in decline are *Tinamus major, Penelope purpurascens* (see also comments on hunting), *Aramides wolfi, Ara ambigua, Ramphastos brevis, R. ambiguus,* and *Phloeoceastes melanoleucos*.

Not surprisingly, loss of large predatory species was also noted for mammals at Rio Palenque. The station notebooks indicate, for example, that *Felis concolor* was noted a few years ago (of the four local cats in this genus, only the ocelot is still

TABLE 1. Population declines at Rio Palenque.

Family (number of forest species)	No recent records	Last seen 1975	Low Population	Factors contributing to decline[a], comments
Tinamidae (3)			1	Largest species, hunting
Accipitridae (5)	1	2		Largest species, rare species (2)
Falconidae (2)	1	1		Declining species, rare species
Cracidae (1)	1			Largest species, hunting
Rallidae (1)			1	Largest species
Psittacidae (9)	4	1	[b]	Largest species, unknown (4)
Strigidae (2)			1	Largest species
Nyctibiidae (1)			1	Difficult to census
Trochilidae (15)	2			Unknown (2)
Momotidae (3)	1			Killed by domestic cats
Bucconidae (4)		2	2	Declining species, unknown (3)
Ramphastidae (4)		1	2	Large species (2), unknown
Picidae (9)	1			Large species
Furnariidae (9)	2			Difficult to census, unknown
Formicariidae (18)		1		Unknown
Cotingidae (6)		1	2	Rare species (2), unknown
Pipridae (5)		3	1	Difficult to census, unknown (3)
Tyrannidae (26)	2	8	[c]	Difficult to census (2), unknown
Turdidae (3)		1	1	Unknown (2)
Sylviidae (3)		1		Unknown
Parulidae (2)			1	Unknown
Coerebidae (5)	1	1	1	Unknown (3)
Thraupidae (13)	3	2	1	Unknown (6)
TOTALS (149)	19	25	15	Total 44 species no longer present
PERCENTAGES OF TOTAL FOREST SPECIES[d] (170)	11%	15%	9%	Total species decline, 35%

[a] Factors apply to one species unless more are indicated in parenthesis.
[b] Four forest species are common but maintained only by commuting flocks from Andean foothills.
[c] There is insufficient data for analysis of eight rare flycatchers.
[d] Total forest species include 21 additional species for families with no noted population declines. The families are: Phasianidae (1), Columbidae (4), Cuculidae (1), Trogonidae (3), Dendrocolaptidae (4), Troglodytidae (2), Vireonidae (2), Icteridae (2), and Fringillidae (2).

regularly seen). Similarly, the mustelids *Eyra barbara* and *Grison canaster* are no longer recorded.

Another class of sensitive species includes those birds that are generally rare. At Rio Palenque such rarities may be ephemeral because of the small forest's limitation on their numbers. Species I include in this group are three predatory birds (*Accipiter superciliosus, Geranospiza caerulescens,* and *Micrastur ruficollis*) and two large fruit-eating cotingids (*Carpodectes hopkei* and *Cephalopterus penduliger*). The rarity of such birds may be related to diet specializations that cause the type of large territorial demands discussed earlier.

Six species of birds that are included as decreasing may simply reflect censusing difficulties. One is the nocturnal *Nyctibius griseus*. Five others are inconspicuous birds, which are better detected by mist-netting than by observation (Ridgely 1976). They are: *Premnoplex brunnescens, Schiffornis turdinus, Sclerurus mexicanus, Platyrinchus coronatus,* and *Mionectes olivaceus*. Mist-netting is the only form of censusing that was done more thoroughly at Rio Palenque in earlier years (the work of Fred Sibley).

Hunting is prohibited on the property, but we still found shooting and poaching in 1978 (pers. obser.). Species that may well have part of their local decline attributable to local hunting include *Tinamus major* and *Penelope purpurascens*. A wounded, immature *Harpia harpyja* was found on the property in the early 1970's,

and people poaching mammals occasionally shoot toucans! Such human pressures are expected in a forest island that is surrounded by developed agricultural land.

Finally, domestic cats account for one local extinction. *Momotus momota* formerly nested near the station building until cat predation eliminated them. Accounts of such cat-induced extinctions are not infrequent, particularly on oceanic islands (examples in Welty 1975).

The declines of 23 species have been considered above; 36 declines remain unexplained. In this latter group I have searched for factors without clear success, and suggest that the reasons for these declines may often be more subtle than those considered above. The set includes some species that are widespread or even common elsewhere (e.g. *Pionopsitta haematotis, Pipra mentalis*). Some are difficult to census because of high foraging (e.g. *Platycichla leucops, Parula pitiayumi*) or shyness (e.g. *Turdus obsoletus, Ramphocaenus melanurus*), but still they are detectable when present. For interested readers, the remaining species are listed below.

Touit dilectissima, Pionus sordidus, Amazona festiva, Ocreatus underwoodii, Acestrura bombus, Notharchus tectus, N. macrorhynchus, Malacoptila panamensis, Aulacorhynchus haematopygius, Pittasoma rufopileatum, Lipaugus unirufus, Pipra coronata, Allocotopterus deliciosus, Colonia colonus, Tyranniscus nigrocapillus, Attila torridus, Sirystes sibilator, Rhynchocyclus fulvipectus, Poecilotriccus ruficeps, Pogonotriccus ophthalmicus, Tyranniscus viridiflavus, Cyanerpes caeruleus, Iridophanes pulcherrima, Dacnis venusta, Tangara lavinia, T. nigroviridis, T. icterocephala, Euphonia minuta, E. saturata, and *Buthraupis eximia.*

For certain of the rarer species in this group, particularly the members of Tyrannidae, I think it is probable that they were not actually established elements of the Rio Palenque avifauna but simply rare visitors. Certainly the isolation of this forest from former nearby woodlands would reduce the frequency of regional wandering to Rio Palenque for many, if not most, forest birds. Two other broad suggestions for declines of some of the above species warrant future consideration. Intensive airplane spraying of pesticides on croplands adjacent to the preserve might effect losses of birds, either directly or indirectly. And Willis (MS), from studies of woodlots in Sao Paulo, believes that frugivorous birds may be lost if small forest isolation deprives them of a continuous (year around) availability of trees in fruiting condition (through the loss of critical tree species).

TROPICAL FOREST ISLAND DYNAMICS

The avian losses in small forest islands show the sensitivity of predatory species in both a tropical situation, as discussed above, or in temperate forests (e.g. Forman et al. 1976). Even small insectivores appear to share this "predator sensitivity" to small patch size. Large body sizes or top trophic position and concomitant large territory requirement can clearly lead to local extinctions (Terborgh 1974). Thus, Willis (1974) found three of the largest of seven original species of ant-following birds essentially lost since the establishment of Barro Colorado Island. Large body size was the most important explanation (nine species) for the avian declines at Rio Palenque.

Rates of extinction can be appreciable within small preserves. For the total 209 breeding forest birds at Barro Colorado, Willis (1974) found that 45 species (22%) disappeared without replacement in the period 1923–71. Some of these losses were of successional species, but at least 13 were forest birds. Extinction of the forest-

dwelling birds there was about 0.3 species per year. At Rio Palenque we found the loss of 44 species (26% of the forest species) in the short period of 6 years, 1973–78. At Rio Palenque some, or even most, of the lost species may have already been declining from the forest isolation well before the formal establishment of the forest as a preserve. Also, a high rate of extinction was expected, as the forest (87 ha) is very small compared with 15-km^2 Barro Colorado Island. In fact, Rio Palenque must be considered an extreme example of small preserves, and apparently it will be unsatisfactory as a refuge for many types of birds and mammals. [It may be more meaningful in its role as a national forest of preserving some of the last lowland wet-forest vegetation of Ecuador (Gentry 1977), although certain avian losses could negatively effect plant diversity.] Whitcomb (1977) makes clear arguments to support his conclusion that "thousands of contiguous acres may be required to assure the long-term survival of the forest-interior bird species," even in the temperate zone. Further, Pickett and Thompson (1978) suggest that the internal successional dynamics of natural disturbance within patches may well require larger reserve sizes than previously predicted. I now suspect that rainforest refuges will not be reasonably successful at sizes less than 25–30 km^2; often more than 100 km^2 may be required.

While this paper has concerned itself with species in decline, mention should be made of those species that are common in spite of the forest isolation. On the entire property of Rio Palenque only half the total 336 species are forest dwellers. Many birds of the second growth, open areas, and forest edge remain plentiful and are probably even increasing within the region as forests are cleared or isolated (e.g. *Molothrus bonariensis, Geothlypis semiflava, Thraupis episcopus,* and several fringillids). Forest species that remain common included those that are generally widespread (geographic range), have broad diets, and are characteristically common wherever they occur. Some birds that show seasonal movements also remain frequent visitors at Rio Palenque, whether their movements involve regional (e.g. *Ictinia plumbea*) or distant migration (e.g. *Catharus ustulatus*). The numbers of such species can be independent of the condition or size of a local habitat patch, which may be occupied only briefly. A seasonal influx could help *reestablish* residents for certain fruit- and nectar-feeding birds at the preserve.

Rarely do we know species' natural history in sufficient detail to explain continued survival, but Oniki (1975) provides such a case from Barro Colorado Island. While other species of Formicariidae were declining, the Slaty Antshrike (*Thamnophilus punctatus*) remained common—it showed versatile foraging abilities and repeated nesting almost all year (Oniki 1975), in contrast to the specializations of other species (Willis 1974). At Rio Palenque, therefore, it is not surprising that the Slaty Antshrike is one of the most common Formicariidae and is not showing the decline of so many forest birds. Interestingly, both Webster and I found birdlife at Rio Palenque to be particularly evident; we independently described it as one of the best tropical bird-watching localities. Thus even small refuges will retain some valuable variety of bird species, and conservationists should not disregard a potential preserve just because it might be smaller than ideal. Certain birds, particularly diet generalists, may increase as other species drop out, therby relieving some of the pressure on food supplies. For example, Willis (MS) found smaller insectivores in the understory increasing as larger insectivores declined. It also seems possible that for a short time (i.e. the current decade), some forest species may be common or even increasing locally because of an influx of regional birds from other forests that have been

recently cleared. This temporary effect would simply be "crowding on the ark," an ark that is already inadequate.

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