

Preservation of Natural Diversity: The Problem of Extinction Prone Species



John Terborgh

BioScience, Vol. 24, No. 12. (Dec., 1974), pp. 715-722.

Stable URL:

<http://links.jstor.org/sici?sici=0006-3568%28197412%2924%3A12%3C715%3APONDTP%3E2.0.CO%3B2-6>

BioScience is currently published by American Institute of Biological Sciences.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/aibs.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact support@jstor.org.

Preservation of Natural Diversity: The Problem of Extinction Prone Species

John Terborgh

As concerned citizens and biologists we are anxious to understand how natural diversity can be maintained in a world of rapidly diminishing resources—resources that are important to the livelihood of human beings as well as to the 2 million or so other creatures with which we share this planet. Some day, of necessity, man must reestablish a steady state with nature. Where on the scale of population this steady state will lie and how we shall arrive there are difficult questions that are being forced upon us with an ever greater urgency by an accelerated pace of world events. With certainty the stressful transition period which we are entering now will impose extraordinary pressures on virtually all existing species, not the least on our own.

In developing a rational plan for the preservation of diversity we must be guided by an understanding of processes that unfold on an evolutionary time scale: the birth and death of species, the waxing and waning of whole faunas and floras, and the invasive replacement of archaic assemblages by more modern ones. Such dynamic facets of evolution have traditionally been the province of paleontologists and historical biogeographers. Biologists concerned with living organisms and present day distributions have too frequently assumed a static view of evolution. Only in the past decade or so with the rise of what might be called dynamic biogeography have we come to realize that these long-term processes can be successfully studied on a contemporary basis. The intellectual cornerstone of these advances is a paper entitled "An Equilibrium Theory of Island Biogeography" published by Robert MacArthur and

Edward Wilson in 1963. Since then the field has developed rapidly.

The diversity of any segment of the landscape is most simply represented by S , the number of species it contains. Recognizing that diversity is established and maintained by dynamic processes, it is an easy matter to express the flow and ebb of species in an elementary balance equation: $dS/dt = \text{rates of: (speciation + immigration) - (extinction + emigration)}$. Diversity remains constant only under the improbable condition that the gain and loss components of the equation are equal. In general this is not likely to be true because the gain and loss components are influenced by different sets of conditions and events, and because the feedback between them operates with a considerable time lag. The biologist who wishes to comprehend the regulation of diversity must carefully study the interlocking factors that control its component processes.

Our goal as conservationists is not to enforce a stasis of nature by somehow stopping the march of evolution; that is impossible. Rather, it is to prevent, over the period of transition to a steady state society, the processes of species loss from running too far ahead of the processes of species gain. On a world-wide basis the rate of species gain is constrained by the rate of genetic divergence of populations, and we know that this is slow with a time dimension on the order of thousands or tens of thousands of years. Extinctions, on the other hand, are not bounded by any such constraint as we know from many sources: the fossil record, the rapid disappearance of 30 genera of large mammals from North America with the advent of primitive man (Martin 1973), and, from more recent experience, with the decimation of the faunas of isolated oceanic islands (Greenway 1967). Given that our objective is to maintain diversity, it is evident that we must act to provide conditions that will retard the pace of extinction.

ESTIMATION OF EXTINCTION RATES

The day is rapidly approaching when the remnants of the natural environment will be contained in a patchwork of parks and reserves. Much of the world's biological endowment will then be locked into insular refugia that are surrounded by an inhospitable landscape, through which dispersal to the next refuge is slow or nonexistent. What are the prospects for natural communities that are removed from the mainstream of dispersal? Our best evidence comes from sets of "land-bridge" islands that formed at the conclusion of the Pleistocene when rising sea levels inundated low lying coastal regions. There are many such land-bridge islands around the world. Groups of them that are particularly suitable for the analysis of extinction are found in the Malay archipelago, in the New Guinea shelf region, and around the margin of the Caribbean sea. As my own experience as a naturalist has been primarily with birds in the New World tropics, I will focus on the latter group of islands and their birdlife.

When we compare the numbers of land bird species presently inhabiting land-bridge islands with those on oceanic islands (not connected with the adjacent mainland during the Pleistocene) we find that the larger land-bridge islands contain many more species than oceanic islands of the same size (Fig. 1). The effect of area is very marked. Below 250 km² the two classes of islands are indistinguishable. This is gratifyingly in agreement with what Diamond (1974) has found for a completely different fauna and set of islands in the southwest Pacific. Land-bridge islands 2,500 km² in area are estimated to contain three times as many species as occur on like-sized oceanic islands in the West Indies. This can be understood if we assume that land-bridge islands contained a full complement of continental

The author is with the Department of Biology, Princeton University, Princeton, NJ 08540. This paper was a contribution to the American Society of Zoologists symposium, "Toward a System of National Ecological Preserves," held in Houston, Texas, on 27 December 1973.

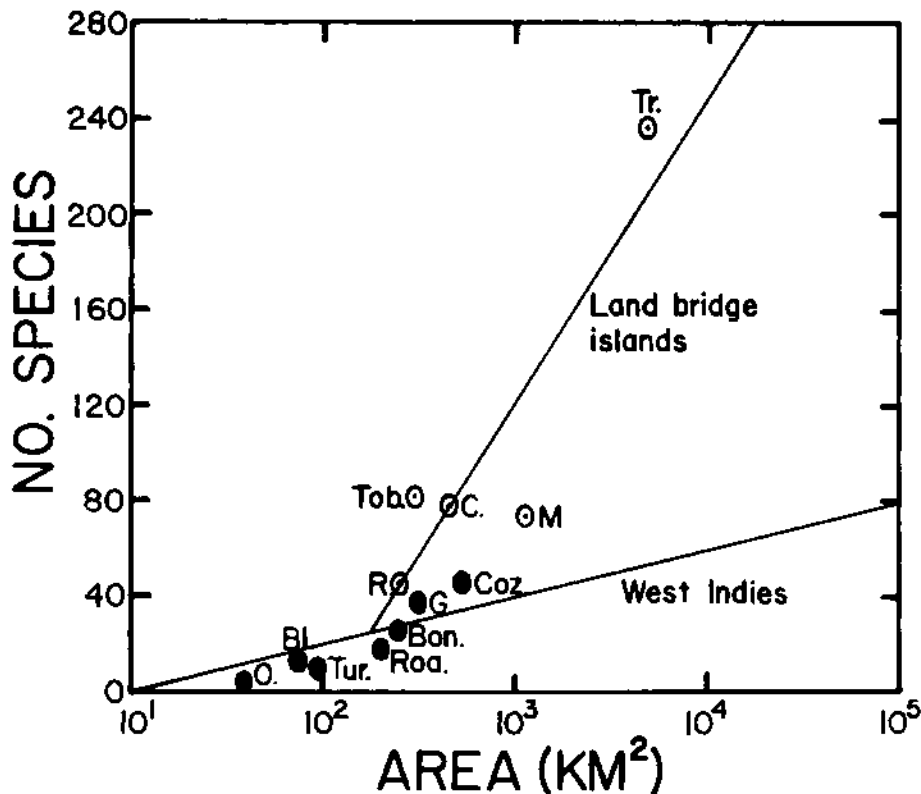


Fig. 1. Species-area regressions for neotropical land-bridge islands and the West Indies. Open circles pertain to land-bridge islands: Tr, Trinidad; M, Margarita; C, Coiba; Tob, Tobago; R, Rey. Solid dots represent oceanic islands near to the Central or South American mainlands. With the exception of Grenada, these were not used in computing the regression line for the West Indies. Coz, Cozumel; G, Grenada; Bon, Bonaire; Roz, Roatan; Tur, Turneffe; Bl, Blanquilla; O, Orchila.

species at the time of their separation and that their faunas have been slowly dwindling since then. Supporting this is the fact that the larger of these islands contain many species that have never been known to colonize oceanic islands. The smaller land-bridge islands, in contrast, have apparently lost most of their continental species and now support faunas composed largely of the same waif species that are found on oceanic islands.

A good example is Aruba in the Dutch Windward group, a 161 km² land-bridge island formerly connected to Venezuela. Today it harbors 34 breeding species, only one of which, the Burrowing Owl, is not found also on one or both of its two oceanic sister islands, Curaçao and Bonaire (Voous 1957). Even the presence of the Burrowing Owl does not betray Aruba's status as a former part of the mainland as this bird is an intrepid wanderer, having colonized a number of scattered islands in the Greater and Lesser Antilles and Bahamas. The avifauna of Aruba is thus indistinguishable from that of an oceanic island and consists entirely of widespread "weedy" species.

Minimum estimates of the post-Pleistocene losses from land-bridge islands are easily obtained by subtracting present day species numbers from the numbers presumed to have been present before separation. These are minimum estimates because they do not take into account any new colonizations, or recolonizations subsequent to prior extinctions. Present species numbers are known with a high degree of accuracy from recent faunal surveys. Initial species numbers can be estimated using the assumption that continental species densities have not changed greatly since the Pleistocene. Estimates appropriate to each island's size can then be derived by interpolation in a table giving the numbers of breeding land birds that today occupy defined areas of different size on the mainland (Table 1).

How can we be confident that this procedure is valid? The best evidence I have seen has kindly been put at my disposal by D. A. Hooijer who has been investigating the recent fossil mammals of the Greater Sunda Islands: Java, Sumatra, and Borneo. These are also land-bridge islands that were formerly

connected to each other and to the Malayan mainland. Collectively they support a fauna of 10 large mammals: primates, carnivores, and herbivores (Table 2). Presently Sumatra contains eight of these, Borneo five, and Java four. Pleistocene cave deposits indisputably show that each of these islands formerly contained more of the species. All 10 are known from Sumatra, 9 from Java, and 7 from Borneo. As only scanty remains are available from Borneo, and the probability of obtaining a complete faunal record from fossils is small anyway, it is likely that the Pleistocene ranges of all 10 large mammals included the regions that now comprise the three separate islands. In this one case at least we know that the missing species are more than just figments of the imagination of an overzealous population biologist.

Returning to the Caribbean and eastern Pacific land-bridge islands with bolstered confidence in our method, let us consider the kinetics of post-Pleistocene species loss. The model I shall use is the simplest one that is consistent with our knowledge of biological reality (Terborgh¹, Equation 1).

$$-\frac{dS}{dt} = kS^2 \quad (1)$$

It states that the rate of species loss is proportional to a constant times the square of the number of species present at any time. The square term acknowledges the fact of interspecific competition and assures that the survival expectancy of remaining populations increases as their competitors drop out. Using 10,000 years as a rough mean figure for the time elapsed since severance of the land bridges, the equation can be solved to give expressions for the extinction coefficient and the number of species present at any time in the intervening interval, S_t , in which S_0 is the initial species number and S_p is the present number (Equations 2).

$$k = -\frac{\frac{1}{S_p} - \frac{1}{S_0}}{t}; \quad S_t = \frac{S_0}{1 + kS_0t} \quad (2)$$

We shall neglect the complicating factor of immigration in the present group of islands because all of them still contain at least twice their equilibrium species numbers, as judged against the species area curve for oceanic islands displayed in Figure 1. Moreover, the

¹ Terborgh, J. Faunal equilibria and the design of wildlife preserves. *In* Trends in Tropical Ecology. Academic Press, New York, in press.

pool of potential transoceanic colonists is small in relation to the faunas of the land-bridge islands, a presumption we infer from the extremely limited number of species that have reached oceanic islands at similar distances from the New World mainland. A double log plot of the extinction coefficients for the several islands against their areas gives a line whose slope is rather tenuously determined by the largest and smallest, Trinidad and Rey, respectively (Fig. 2, Table 3). This line allows us to make somewhat precarious predictions of the rate of species loss in supracolombian insular avifaunas.

Increasingly heavy demands on the world's land resources threaten to convert many of our parks into supracolombian islands. An outstanding example of this is Barro Colorado Island, formerly a gently contoured hilltop that became an island about 1914 when Lake Gatun was formed in the central part of the Panama Canal by damming the Chagres River. In 1923 Barro Colorado was declared a natural reserve and placed under the administration of the Smithsonian Institution. The first thorough survey of the island's birdlife was conducted during the 1920's by the late Frank Chapman, who at the time was one of the world's leading ornithologists (Chapman 1938). Subsequently, Barro Colorado has been the site of numerous ornithological investigations, the results of which provide a running record of its bird populations. By far the most detailed data have been compiled by Edwin Willis who spent from 2 to 11 months on the island each year from 1961 to 1970. Through his farsighted work, some of which he has graciously permitted me to illustrate here, we have an unprecedented record of natural extinctions that have run their course without help or hinderance from man.

In the days of Chapman's earliest surveys, about 50 years ago, the island harbored 208 breeding bird species. By 1970, 45 of these had disappeared and several more were down to populations of one to a few individuals. The species that have disappeared fall into two nearly discrete ecological categories—those that inhabit open fields, edges, and early second growth and those that are found exclusively or most abundantly in mature forest. Barro Colorado was only partly in a natural state at the time of its separation from the mainland. About half of it was covered by abandoned farmsteads or seriously dis-

TABLE 1. Number of land bird species inhabiting various insular and continental land masses of defined area.

Island	Area (km ²)	No. Species		Reference
		10,000 yrs B.P. *	Now	
<i>Land-bridge islands</i>				
Trinidad	4,828	380	236	Herklots 1961
Margarita	1,150	320	74	Yepez and Benedetti 1940
Coiba	453	250	78	Wetmore 1957
Tobago	300	300	82	Herklots 1961
Rey	249	225	46	MacArthur, Diamond, and Karr 1972
Escudo de Veraguas	6	190	9	Wetmore 1959
<i>Oceanic islands</i>				
Cozumel	534		47	Paynter 1955, Bond 1961, 1963
Grenada	311		38	Bond 1971
Bonaire	246		26	Phelps and Phelps 1951
Roatan	202		18	Bond 1937
Turneffe	93		11	Bond 1954
Blanquilla	75		13	Phelps 1948
Orchila	39		5	Phelps and Phelps 1959
<i>Mainland Control Areas</i>				
Surinam	144,000		494	Haverschmidt 1968
Panama Canal Zone	938		330	Eisenmann and Loftin 1971
Rancho Grande Natl. Pk., Venezuela	873		401	Schafer and Phelps 1954
Barro Colorado Is., Panama	17		208	Willis 1974
Finca LaSelva, Costa Rica	6		221	Slud 1960
Hda. Luisiana, Peru	5		255	Terborgh and Weske 1969

*Before present

TABLE 2. Living and recently extinct large mammals in the Greater Sunda Islands. Unpublished data of D.A. Hooijer: + = presently occurs on island; E = extinct, known from fossil deposits; 0 = no definite evidence of occurrence.

Species	Java	Sumatra	Borneo
Orang-utan (<i>Pongo pygmaeus</i>)	E	+	+
Siamang Gibbon (<i>Symphalangus syndactylus</i>)	E	+	0
Tiger (<i>Felis tigris</i>)	+	+	E
Panther (<i>Felis pardus</i>)	+	E	0
Malay Bear (<i>Helactos malayanus</i>)	E	+	+
Elephant (<i>Elephas maximus</i>)	E	+	+
Malay Tapir (<i>Tapirus indicus</i>)	E	+	E
Java Rhino (<i>Rhinoceros sondaicus</i>)	+	+	0
Sumatran Rhino (<i>Dicerorhinus sumatrensis</i>)	0	+	+
Banteng (<i>Bibos javanicus</i>)	+	E	+

turbed forest. This land has subsequently returned to tall rain forest, except for a small clearing around the cluster of laboratory buildings. Most of the species loss from the island has been associated with successional changes in the habitat. These are extinctions of a trivial kind. Our real interest is in the species that have disappeared from the fauna of mature forest. Of these, there have been 13 to 18, depending on how

many of five species of borderline status are assigned to the forest community. (Table 4; Willis 1974).

Now let us return to the regression of extinction coefficients against island area (Fig. 2). As an adventure in scientific induction we can see how well it predicts the record of extinctions on Barro Colorado. Extrapolating beyond the cluster of points to the appropriate area, 17 km², we obtain a predicted

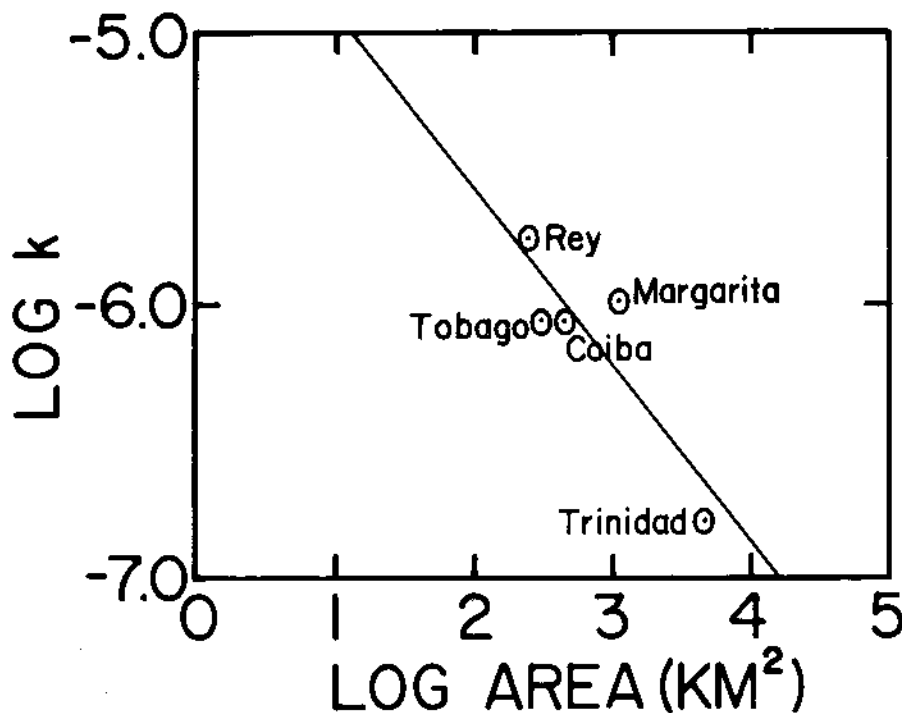


Fig. 2. Double log regression of extinction coefficient on area for five land-bridge islands. The extinction coefficients were calculated from equation 2 and are given in Table 3.

extinction coefficient of $10^{-5.1}$. Plugging this value and an elapsed time of 50 years into the formula we get a calculated estimate of 16.6 extinctions. Recall that the observed number is 13 to 18. The agreement with reality may be beginner's luck. Nevertheless, it does instill confidence in the method and I hope will encourage further analysis in a similar vein.

As a final comment on the prediction of extinction rates, I must warn against the application of island data to isolated patches of habitat on the mainland. The two situations are analogous but not equivalent. An island receives comparatively few immigrants of any kind, but the populations in an anomalous pocket of habitat are constantly exposed to the pressure of invasion from species in adjacent habitats. For this reason we can anticipate that supracommunity

pockets of habitat will suffer higher extinction rates than like-sized islands. The task of measuring these rates is a logical next step in putting theory to practical use.

PATTERNS OF EXTINCTION

Why have so many forest bird populations died out on Barro Colorado? In no case is there a definite answer to this question beyond the elementary truism that reproduction failed to keep up with mortality. There are, however, some striking consistencies in the pattern of extinction (Table 4). All but three of the 18 birds that have disappeared from the forest were either large for their trophic class, or were species that forage or nest on the ground. The remaining three species inhabit understory vegetation. A few of these extinctions took

place 20 or 30 years ago, and yet there has been no recorded instance of recolonization by a forest species, even though 16 out of the 18 species are still found on the nearby mainland, which at the closest is less than 500 meters away.

We can expect large species to be extinction prone when confined to a limited area because of their intrinsically low population densities. The disappearance of so many small ground dwelling and understory species is more puzzling, especially in view of the fact that there have been no extinctions recorded from the large canopy community. Forest understory species are known to be poor colonists (Terborgh and Weske 1969, Diamond 1971, 1973, Terborgh²), yet the pattern is so far from being random that there may be more involved than a difference in dispersal ability between canopy and understory species.

E. O. Willis has closely followed the populations of members of the ant following guild: birds that forage much or all of the time over raiding army ant swarms. His unique data show unambiguously for a small number of species that the declines leading to extinction are slow and inexorable (Fig. 3). Year after year reproduction fails to compensate for mortality, and as population levels fall lower, there is little to indicate the operation of density dependent responses. These are nontraumatic population declines compelled by unrelenting forces that are yet to be identified. Those of us who are accustomed to the fickle weather systems of temperate regions are conditioned to associate population crashes with catastrophic events: hurricanes, drought, a succession of severe winters, etc. Clearly we are witnessing a different class of phenomenon on Barro Colorado, one that may be typical of supracommunity faunas.

Although Barro Colorado has proven to be a valuable natural laboratory, it is clearly a failure as a faunal preserve. The pace of extinctions is unacceptably high. If they continue at the rate predicted by our model, we can anticipate that about 20% of the original forest bird community will have disappeared before the island's centennial. Trinidad (4,828 km²) has been a better preserve. According to our calculations, it lost only 2.3 species, or 0.6% of its avifauna, in its first 100 years as an island (Table 3). Though this performance is still no ideal, it is a vast improvement over

TABLE 3. Estimated species loss over first 100 and 1,000 years after isolation of five Neotropical land-bridge islands.

Island	No. Species lost in 10 ⁴ yrs	k	No. Species Lost		% of initial fauna lost 1st century
			1st 100 yrs	1st 1,000 yrs	
Trinidad	144	1.6×10^{-7}	2	22	0.6
Margarita	246	1.0×10^{-6}	10	80	3.2
Coiba	172	8.8×10^{-7}	5	45	2.2
Tobago	218	8.9×10^{-7}	8	63	2.6
Rey	179	1.7×10^{-6}	8	63	3.7

²See footnote 1, p. 716.

Barro Colorado. The moral is obvious: we must have large reserves in the size range of one to several thousand km² if we are to prevent a veritable rush of extinctions.

It is apparent in the record of extinctions on Barro Colorado that various definable groups of species become extinct at different rates and for different reasons. When the disruptive effects of human activities are superimposed on natural processes, it is usually the former that prevail in setting the pattern. Exploitation and widespread habitat destruction are the two dominant threats posed by burgeoning human populations and the entry of modern technology into the remaining primitive areas of the globe. The effects of these changes on natural communities are nothing less than cataclysmic. A minority of species, including pests and weeds, profit spectacularly in filling the void left in distorted or obliterated ecosystems. In developing a plan to protect the majority it is important to recognize the categories of species that are most vulnerable to decimation through the direct or incidental consequences of an expanded scale of human activity. In the following paragraphs I shall discuss six categories of species that have featured prominently in the history of extinction, and suggest for each a prescription for appropriate conservation action.

1. Species on the top trophic rung, and the largest members of guilds.

By virtue of a dispersed food supply and high metabolic demand these are animals which require large amounts of living space. Many are already widely extirpated in North America: Mountain Lion, Timber Wolf, Red Wolf, Bison, California Condor, Golden Eagle, Ivory-billed Woodpecker. Some of these have low reproductive rates and consequently cannot withstand hunting pressure, and when reduced are slow to make a comeback.

Prescription: Prohibit hunting except when individual animals are destroying livestock or where needed to cull surplus individuals from managed herds. Large parks are important for breeding refugia. Protection only in parks is not sufficient because an appreciable segment of any contained population will forage beyond park boundaries; witness the California Condor (Miller et al. 1965, Mertz 1971). As the species in

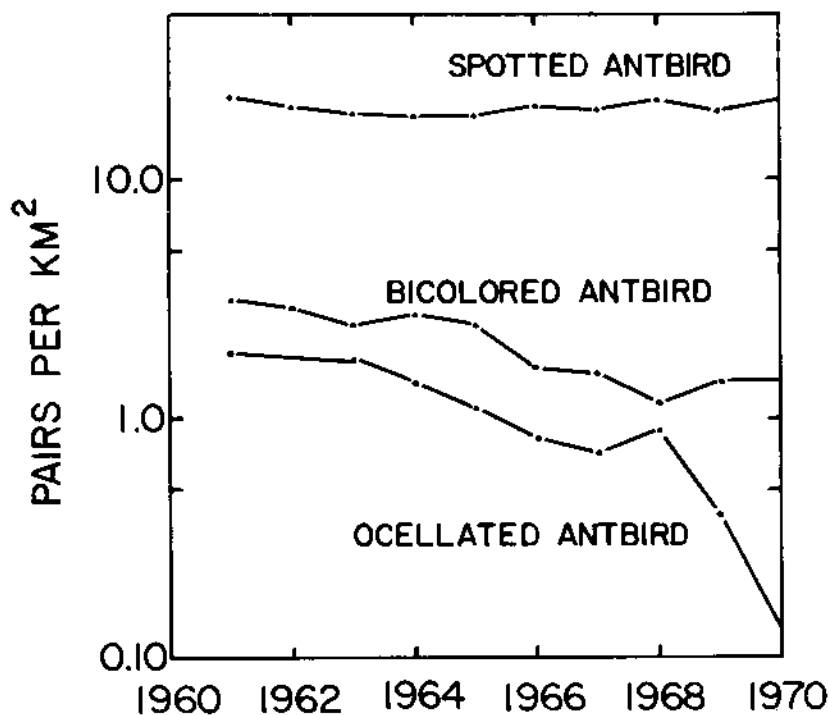


Fig. 3. Population trends in members of the guild of ant following birds on Barro Colorado Island, Panama. Source of data: Table 2 of Willis (1974). The largest member of this guild on the island, the Rufous-vented Ground-Cuckoo (*Neomorphus geoffroyi*), died out before 1960. The next largest, the Barred Woodcreeper (*Dendrocolaptes certhia*), was represented by two pairs in 1960 but had disappeared by 1970. The third largest, the Ocellated Antbird (*Phaenostictus mcleannani*), is illustrated in the figure. In 1960 the island contained 15 pairs, but by 1970 there remained only one female and several males. Two smaller species, the Bicolored Antbird (*Gymnophithys bicolor*) and the Spotted Antbird (*Hylophylax naevioides*), fared better, though the population of the former decreased from 50 to 20 pairs over the decade. A detailed account is given by Willis (1974).

TABLE 4. Nonsuccessional extinctions in the forest avifauna of Barro Colorado Island, Panama, 1920-1970. Adapted from Willis (1974).

Species	Large for guild	Ground nester	Ground forager
Little Tinamou (<i>Crypturellus soui</i>)*		+	+
Harpy Eagle (<i>Harpia harpyja</i>)	++		
Barred Forest-Falcon (<i>Micrastur ruficollis</i>)	+		
Red-throated Caracara (<i>Daptrius americanus</i>)	+		
Great Curassow (<i>Crax rubra</i>)	++		+
Marbled Wood-Quail (<i>Odontophorus gujanensis</i>)	+	+	+
Rufous-vented Ground Cuckoo (<i>Neomorphus geoffroyi</i>)	+		+
Rufous-breasted Hermit (<i>Glaucis hirsuta</i>)*			
Blue-crowned Motmot (<i>Momotus momota</i>)*	+	+	
Barred Woodcreeper (<i>Dendrocolaptes certhia</i>)	+		
Buff-throated Automolus (<i>Automolus ochrolaemus</i>)	+	+	
Black-faced Antthrush (<i>Formicarius analis</i>)	+		+
Thrushlike Manakin (<i>Schiffornis turdinus</i>)*			
Sulphur-rumped Flycatcher (<i>Myiobius sulphureipygeus</i>)			
Royal Flycatcher (<i>Onychorhynchus coronatus</i>)*			
White-breasted Wood-Wren (<i>Henicorhina leucosticta</i>)		+	+
Nightingale Wren (<i>Microcerculus marginatus</i>)			+
Song Wren (<i>Leucolepis phaeocephalus</i>)			+

*Species more numerous in second growth in some parts of its range.

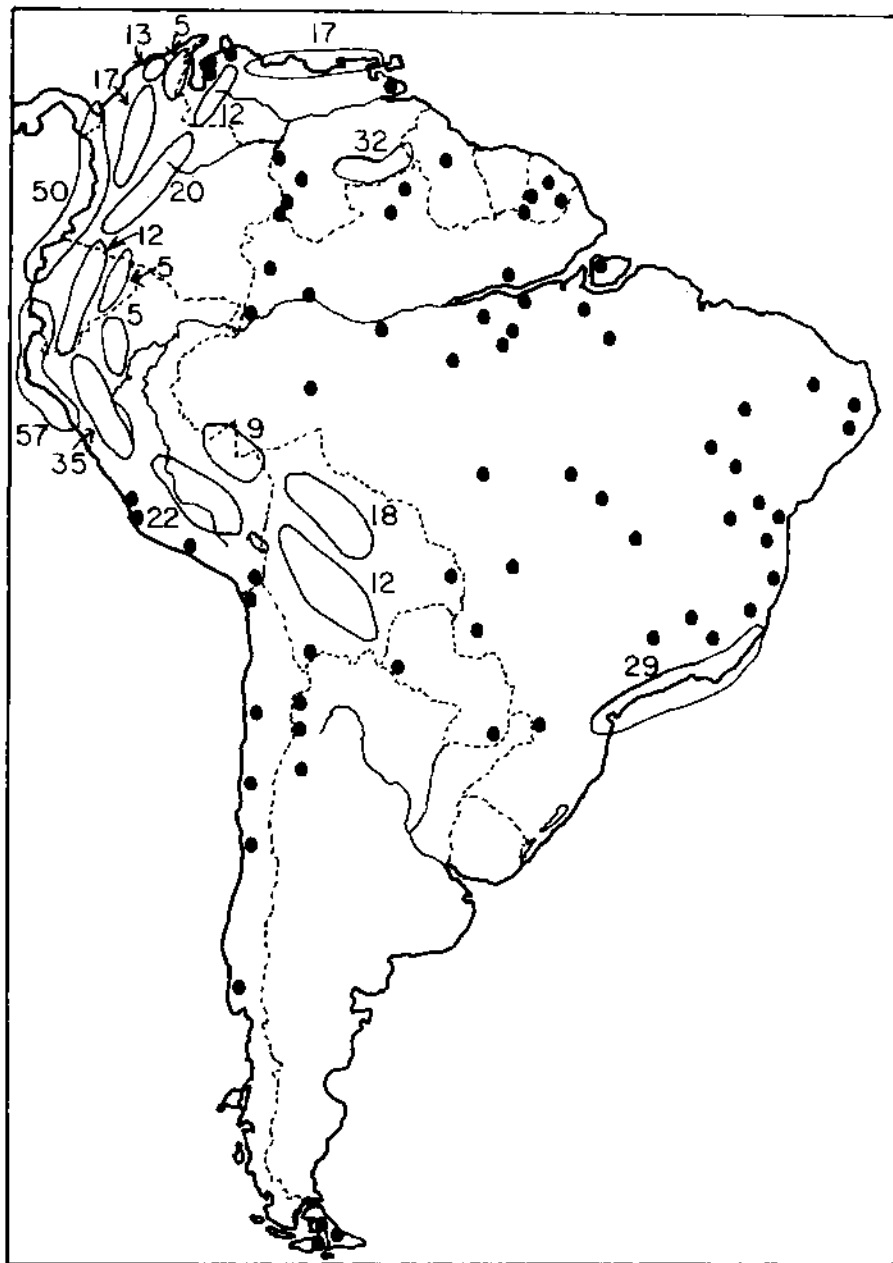


Fig. 4. Endemism in South American birds. Source: Meyer de Schauensee (1966). Any species having a range estimated to be less than 50,000 km² was considered endemic. South America contains roughly 440, North America only 8. Encircled areas are regions of concentrated endemism; dots give the locations of additional species. The circles include species found within a common topographic province, but in most cases the provinces are further subdivided to show the numbers of species occurring predominantly within each nation's boundaries.

this category tend to occupy a broad spectrum of habitats, the size of park is more critical than precise location.

II. Widespread species with poor dispersal and colonization ability.

This category includes a major fraction of the species that inhabited the pristine landscape. Their vulnerability to extinction is through habitat destruction rather than hunting or persecution.

Prescription: Along with the species in Category I above, they can be protected in a small number of medium to large parks, provided the habitat is intact. These parks should be located so as to include a maximum diversity of vegetation types, e.g., coastal habitats, lowland forests, bogs, oases, desert riparian woodlands, etc.

III. Continental endemics.

These are species which have unusually restricted distributions because of

historical conditions associated with their evolution. Some examples in the United States are Barbour's Map Turtle that inhabits a few rivers flowing into Florida's Gulf Coast, the Golden-cheeked Warbler of the Edward's Plateau of Texas, and several species of pup fish that live in desert springs in the southwest (Minckley and Deacon 1968). Endemics are usually common where they occur but often have rigid habitat requirements. Thus they are especially vulnerable to land development.

Endemics are often endangered unintentionally, simply because people are not aware of them. This problem is relatively slight in the United States for the reasons that our biota contains few endemics, the haunts and habits of most of them are being studied, and an influential segment of our society is concerned and acting to protect them. The problem is vastly more severe in other parts of the world where there are major concentrations of endemic species. South America, for instance, contains some 440 land bird species that occupy ranges of less than 50,000 km² (Fig. 4). Mexico also has a sizeable number. By the same criterion, the continental United States contains only eight.

Over much of the world, leaders are understandably more intent on pressing for rapid development than in protecting endangered species. As often as not, official apathy merely reflects ignorance that a country possesses unique forms of life. Appeals to nationalistic sentiments could have a favorable influence in persuading governments to set aside small but strategically located reserves. Such reserves need not be large because most endemics are small organisms with modest space and energy requirements.

Prescription: More research is needed to identify pockets of endemism and to define the ranges and habitat needs of the species. An effort should be mounted through international agencies such as the World Wildlife Fund to establish small parks in critical locations.

IV. Endemics of oceanic islands.

The communities of oceanic islands have proven to be extraordinarily fragile and have contributed a majority of the avian extinctions recorded in historical times. Many island ecosystems are already damaged beyond repair. As on continents, extinctions have resulted from systematic habitat destruction and

excessive hunting pressure, but in addition island populations have frequently succumbed to introduced diseases, predators, and competitors. As the problem of protecting island biotas is complex and poorly understood, I will not discuss it further.

Prescription: Reserves are important, especially in the remaining tracts of undisturbed vegetation. Introduction of exotic animals and plants should be prohibited except when cautiously undertaken for agricultural purposes. Populations of feral animals such as cats, mongooses, goats, pigs, etc., should be reduced or eliminated wherever practical. More research is needed to understand the extreme lability of island ecosystems.

V. Species with colonial nesting habits.

With a few exceptions, these are marine turtles, birds, and mammals that come to land to lay their eggs or to rear their young. Because eggs and young are easily harvested by predators, colonies are generally located on small offshore islets, though mainland beaches or promontories are used occasionally. Many former nesting grounds of gulls, shorebirds, and herons have been obliterated by waterfront development, both in the United States and elsewhere. Many others have been rendered unproductive by the casual introduction of rats and domesticated animals onto erstwhile predator-free islands.

A special problem is posed by a small number of land bird species that nest communally in large numbers. The Passenger Pigeon was one of these. Another is the White-crowned Pigeon, a beautiful and distinctively marked bird of the Caribbean region. Like the Passenger Pigeon, most of its population nests in a small number of giant colonies. The one on Isla Saona in the Dominican Republic I estimate to contain several tens of thousands of birds. There are only a few other colonies this large in existence in Cuba, the Bahamas, and in the islands east of Puerto Rico. Squabs are gathered by the barrelful from the Saona colony, and local promoters make handsome profits by guiding wealthy "sportsmen" to places where they can shoot a hundred birds or more in an afternoon. The Whitecrowned Pigeon will not long withstand this amount of pressure.

Prescription: Locate active nesting grounds and protect them. This is con-

servation on the cheap, for populations of hundreds or thousands of pairs can often be spared by setting aside only a few dozen acres. Predator removal is desirable on offshore islets.

VI. Migratory species.

Migratory species are exposed to double jeopardy because they are subject to the pressures of change at both ends of their routes, and may have to run a gauntlet of polluted waters and altered landscapes on the way. Two North American songbirds are on the brink of extinction today, and I believe the trouble in both cases is at least partly attributable to drastically altered conditions on their wintering grounds. They are the Bachman's Warbler and the Kirtland's Warbler which, of all North American migrants, have the most restricted winter ranges.

The Bachman's Warbler is known to have wintered only in the woodlands of western Cuba and the Isle of Pines (Barbour 1943). Flying over this region now one sees an unbroken expanse of sugarcane extending from coast to coast. It is safe to say that a minimum of three-quarters, and perhaps 90% or more, of the former winter range of the Bachman's Warbler no longer carries suitable habitat.

The situation is almost as serious for the Kirtland's Warbler which winters on two pine covered islands in the northern Bahamas: Grand Bahama and Abaco. American companies have almost totally ravaged the pine forests of Abaco in anticipation of large scale development, while some natural cover still remains in Grand Bahama. However zealously the Kirtland's Warbler and its habitat may be protected in Michigan, its fate probably lies at the mercy of commercial interests in the Bahamas. My prediction is that we shall see more changes in the status of our summer visitors as the remaining tracts of virgin rain forest in Central America and northern South America are converted to pasture and farmland. Species that winter in second growth and along edges will gain in abundance at the expense of those that require shady forests.

Prescription: More research is needed to define the winter ranges and habitats of our migrant species. Saving those that need undisturbed vegetation will require Americans to take an active interest in establishing suitable preserves in Latin America and in the Caribbean.

CONCLUSION

Preserving diversity in a world of rapidly shrinking land resources will require a prompt and universal response based on an appropriate application of ecological knowledge. Every nation should possess an inventory of its biological endowment. Agencies in charge of parks and wildlife should consciously adopt policies that are designed to minimize the pace of extinctions. The common practice of declaring parks in remote or unused portions of the landscape, or around scenic attractions, may fail to serve this purpose. Large reserves are needed to preserve natural vegetation formations, animals at the top of the trophic pyramid, and widespread species with sedentary habits and poor colonizing ability. Endemics or rare habitat types can frequently be protected with a relatively small investment in land, provided appropriate tracts can be identified and sequestered in time. The nesting grounds of colonial species can be spared with even less land withheld from production as they are usually located on offshore islets that are unsuitable for agriculture. Migratory species present more difficult problems in that appropriate action often requires international cooperation.

ACKNOWLEDGMENTS

I am profusely grateful to D. A. Hooijer and E. O. Willis for permission to use substantial amounts of their data. The paper draws especially on Willis' work, without which we would know a great deal less about island extinctions. My own research has been supported by the National Science Foundation.

REFERENCES

- Barbour, T. 1943. Cuban ornithology. *Memoirs of the Nuttall Ornithological Club* 9: 1-144.
- Bond, J. 1937. Resident birds of the Bay Islands of Spanish Honduras. *Proc. Acad. Nat. Sci. Phila.* 88: 353-364.
- _____. 1954. Birds of Turneffe and Northern Two Cays, British Honduras. *Not. Nat. (Phila.)* 260: 1-10.
- _____. 1961. Notes on the birds of Cozumel Island, Quintana Roo, Mexico. *Caribb. J. Sci.* 1: 41-47.
- _____. 1963. Eighth supplement of the check-list of birds of the West Indies. *Acad. Nat. Sci. (Phila.)* 11 pp.
- _____. 1971. *Birds of the West Indies*. 2nd ed. Houghton Mifflin Co., Boston, 256 pp.
- Chapman, F. 1938. *Life in an Air Castle*. Appleton Century, New York 250 pp.

Diamond, J. M. 1971. Ecological consequences of island colonization by southwest Pacific birds. I. Types of niche shifts. *Proc. Nat. Acad. Sci.* 67: 529-536.

_____. 1973. Distributional ecology of New Guinea birds. *Science* 179: 759-769.

_____. 1974. Extinction rates in isolated populations. American Society of Zoologists Symposium, "Toward a System of National Ecological Preserves." 27 December 1973, Houston, Texas.

Eisenmann, E., and H. Loflin. 1971. Field checklist of birds of the Panama Canal Zone Area. 2nd ed. Florida Audubon Soc. 38 pp.

Greenway, J. C., Jr. 1967. Extinct and vanishing birds of the world. 2nd ed. Dover, New York. 520 pp.

Haverschmidt, F. 1968. Birds of Surinam. Oliver and Boyd, London. 445 pp.

Herklots, B. A. C. 1961. The birds of Trinidad and Tobago. Collins, London. 287 pp.

MacArthur, R. H., J. M. Diamond, and J. R. Karr. 1972. Density compensation in island faunas. *Ecology* 53: 330-342.

MacArthur, R. H., and E. O. Wilson. 1963. An equilibrium theory of island biogeography. *Evolution* 17: 373-387.

Martin, P. S. 1973. The discovery of America. *Science* 179: 969-974.

Mertz, D. B. 1971. The mathematical demography of the California Condor population. *Amer. Natur.* 105: 437-453.

Meyer de Schauensee, R. 1966. The species of birds of South America and their distribu-

tion. Livingston, Narberth, Pa. 577 pp.

Miller, A. H., I. McMillan, and E. McMillan. 1965. The current status and welfare of the California Condor. *Nat. Audubon Soc. Res. Rep.* 6: 1-61.

Minckley, W. L., and J. E. Deacon. 1968. Southwestern fishes and the enigma of "endangered species." *Science* 159: 1424-1431.

Paynter, R. A., Jr. 1955. The ornithogeography of the Yucatan Peninsula. *Bull. Peabody Mus. Nat. Hist.* 9: 1-347.

Phelps, W. H., Jr. 1948. Las aves de la isla La Blanquilla y de los morros El Fondadero y La Horquilla del Archipelago de los Hermanos. *Bol. Soc. Ven. Cien. Nat.* 71: 85-118.

Phelps, W. H., and W. H. Phelps, Jr. 1951. Las aves de Bonaire. *Bol. Soc. Ven. Cien. Nat.* 77: 161-187.

_____. 1959. Las aves de la isla La Orchila. *Bol. Soc. Ven. Cien. Nat.* 93: 252-266.

Schafer, E., and W. H. Phelps. 1954. Las aves del Parque Nacional "Henri Pettier" (Rancho Grande) y sus funciones ecologicas. *Bol. Soc. Ven. Cien. Nat.* 83: 1-171.

Slud, P. 1960. The birds of finca "La Selva," Costa Rica: a tropical wet forest locality. *Bull. Amer. Mus. Nat. Hist.* 121: 55-148.

Terborgh, J., and I. S. Weske. 1969. Colonization of secondary habitats by Peruvian birds. *Ecology* 50: 765-782.

Voous, K. H. 1957. The birds of Aruba, Curacao and Bonaire. In P. W. Hummelinck, ed. *Studies on the Fauna of Curacao and Other Caribbean Islands, Vol. 7.* Martinus Nijhoff, The Hague. 260 pp.


Wetmore, A. 1957. The birds of Isla Coiba, Panama. *Smithsonian Misc. Coll.* 134(9): 1-105.

_____. 1959. The birds of Isla Escudo de Veraguas, Panama. *Smithsonian Misc. Coll.* 139(2): 1-27.

Willis, E. O. 1974. Populations and local extinctions of birds on Barro Colorado Island, Panama. *Ecol. Monog.* 44: 153-169.

Yepez, A. F., and F. L. Benedetti. 1940. Las aves de Margarita. *Bol. Soc. Ven. Cien. Nat.* 43: 91-132.

Practical new professional microscope for tomorrow's practitioners—SWIFT Model M1001



This SWIFT research quality microscope has specifically designed to meet all requirements of research, dental, and other advanced biological science usage. Optics are of particularly high caliber. Binocular head is rotatable 360 degrees to permit and forward and forward on pedestal and bearing with one hand movement. A built-in clutch mechanism operates automatically to prevent damage to finely polished lens surfaces. Coarse focusing for use by person of 12 years and older. Fine focus control operates continuously throughout the entire range of magnification.

View with 10x magnification are suitable for extended view and for and 10x magnification research studies. The M1001 is a highly modern instrument with wide range of accessories and features. Write today for literature and price list.

SWIFT INSTRUMENTS, INC.
 Technical Instrument Division
 P.O. BOX 562, SAN JOSE, CA 95106 • 408/293-2380
 (MAIN OFFICE: Boston, MA)

SWIFT AGENCIES are located throughout the U.S. and in most foreign countries.

MANUSCRIPTS FOR BIOSCIENCE

BioScience welcomes the submission of articles, news material about biologists, biological societies and departments, and meeting reports. Our interests are as broad as all of the life sciences and education. We no longer publish narrow research reports, and we welcome especially state-of-the-art articles on subjects with important new developments.

Send manuscripts to John A. Behnke, Editor, *BioScience*, Dept. of Biology, 952 Brown Bldg., New York Univ., Washington Sq., New York, NY 10003.

See Information for Contributors on page 726 in this issue.