Application of Extinction and Conservation Theories for Forest Birds in Nicaragua

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Abstract: An increasing number of empirical studies have been done on the effects of tropical forest fragmentation on avian communities, but few researchers have applied these theories to assess the vulnerability of birds in poorly researched countries such as Nicaragua. I used a logistic regression to determine which natural-bistory characteristics were most important in predicting a list of threatened birds known to occur in Nicaragua. The best model included five macroecological variables (body weight, babitat specificity, trophic group, forest preference, and biogeography within Nicaragua). I used this model to generate predicted probabilities of extinction for all forest birds in Nicaragua. The predicted probability of extinction from the best model ranked 63% of the extinction-prone birds from La Selva, Costa Rica, and 59% of the extinction-prone birds from Barro Colorado, Panama, in the first quartile of all forest birds recorded in Nicaragua. This method provides a first-order approximation of which species deserve global and national priorities for conservation. The central and Atlantic regions of Nicaragua deserve high priority for conservation at a global scale, whereas the Atlantic region deserves the highest priority for conservation at a national scale. The Nicaraguan Ministry of Natural Resources and the Environment has done an adequate job of identifying areas for conservation based on the proportion of decreed nature reserves in each biogeographic region and the distribution of forest birds with a high predicted probability of extinction. Forest birds in central Nicaragua, however, may currently be the most vulnerable to local extinction because of low forest cover within decreed reserves.

Aplicación de Teorías de Extinción y Conservación en Aves de Bosque de Nicaragua

Resumen: Hay un incremento en el número de estudios empíricos sobre el efecto de la fragmentación de bosques tropicales sobre las comunidades de aves, pero pocos estudios han aplicado estas teorías para evitar la vulnerabilidad de aves en países poco investigados como Nicaragua. Utilicé regresión logística para determinar características de la historia natural de importancia para predecir una lista de aves amenazadas en Nicaragua. El mejor modelo incluyó cinco variables macroecológicas (peso corporal, especificidad de bábitat, grupo trófico, preferencia de bosque y biogeografía en Nicaragua). Utilicé este modelo para predecir la probabilidad de extinción de todas las especies de bosque de Nicaragua. La probabilidad de extinción del mejor modelo incluyó al 63 % de las especies expuestas a extinción en La Selva, Costa Rica y al 59 % de las de Barro Colorado, Panamá en el primer cuartil de todas las aves de bosque registradas en Nicaragua. Este modelo proporciona una primera aproximación a las especies que merecen prioridades de conservación a nivel global y nacional. Las regiones Central y Atlántica de Nicaragua tienen una alta prioridad de conservación en la escala global, mientras que la región Atlántica tiene la más alta prioridad nacional. El Ministerio Nicaragüense de Recursos Naturales y Ambiente ha desempeñado un trabajo adecuado al identificar áreas de conservación con base en la proporción de áreas naturales decretadas en cada región biogeográfica y en la distribución de aves de bosque con una alta probabilidad de extinción. Sin embargo, las aves de Nicaragua central pueden ser más vulnerables a la extinción local debido a la baja cobertura forestal en las reservas decretadas.

Introduction

Nicaragua is the second poorest and arguably one of the most poorly studied countries in Latin America (Nietschmann 1990). Although 424 species of terrestrial breeding birds have been recorded in Nicaragua, there is no consensus as to which or how many species are threatened with extinction at global, national, and local scales (Gillespie & Nicholson 1997). Global conservation priorities generally focus on endemic or restrictedrange species that are in decline. The World Conservation Union (IUCN) Red Book recognizes two resident forest birds as vulnerable in Nicaragua, whereas the International Council for Bird Preservation (ICBP)/IUCN Red Data Book identifies one resident forest bird as in danger of extinction (Collar et al. 1992; Groombridge 1993). National conservation priorities are generally based on species in danger of becoming locally extinct within a country's political boundaries, whereas local conservation priorities are based on species going extinct in a biogeographic region of the country or habitat type (Long et al. 1996; Stotz et al. 1996). Although there is no official government list of national- or local-scale priorities for Nicaragua, the official Costa Rican endangered species list identified eight resident forest birds that occur in Nicaragua as endangered (Stiles 1985). There is no overlap in species between these three lists, making it difficult to summarize the actual conservation status of Nicaraguan birds.

Birds are the most thoroughly studied taxonomic group with respect to the effects of tropical forest fragmentation (Turner 1996). Empirical studies have identified a number of natural-history characteristics associated with extinction-prone birds, including small population size (Karr 1982; Diamond et al. 1987; Pimm et al. 1988); restricted geographic range (Faaborg 1979; Terborgh & Winter 1980); habitat specificity and forest preference (Diamond et al. 1987; Newmark 1991; Kattan et al. 1994); trophic group (Leck 1979; Kattan et al. 1994; Christiansen & Pitter 1997); elevational range (Kattan et al. 1994; Christiansen & Pitter 1997); and large body size (Willis 1974; Leck 1979; Terborgh & Winter 1980; Karr 1982). In countries such as Nicaragua for which few population data exist, data on natural-history characteristics correlated with extinction may be used to identify potentially vulnerable forest birds (Brown 1995). Once these species are identified, an assessment of how adequately they are protected under Nicaragua's decreed nature reserve system at different spatial scales can be undertaken (Scott et al. 1995).

This study uses a macroecological approach to (1) identify and rank potentially threatened forest birds in Nicaragua based on natural-history characteristics associated with extinction, (2) test how accurately it predicts extinction-prone birds from well-researched sites in Central America, and (3) assess the current status of for-

est birds under Nicaragua's nature reserve system over different spatial scales. This assessment can aid in the prioritization of species and conservation areas in Nicaragua until the necessary time and resources for extensive inventories are available.

Study Area

Nicaragua is located at the crossroads of the Nearctic and the Neotropic realms, with representative avifauna from both regions (Howell 1969). The country can be divided into three general biogeographic regions based on physiography, climate, vegetation, and zoogeography (Taylor 1963; Howell, unpublished data) (Fig. 1). The Pacific region contains tropical dry forest, gallery forest, and savanna below 400 m on the western side of Nicaragua. The central region contains upland pine-oak forest, montane evergreen forest or cloud forest, and elfin forest on the tops of mountain ranges and volcanoes above 400 m. The Atlantic region contains pine savanna and lowland rainforest in eastern Nicaragua below 400 m. My study includes all terrestrial breeding birds recorded from each biogeographic region of Nicaragua.

Methods

Three lists of threatened birds were combined and used as a dependent variable in a logistic regression model. The first list is the official endangered species list from Costa Rica, which contains eight terrestrial breeding birds known to occur in Nicaragua (Stiles 1985). All spe-

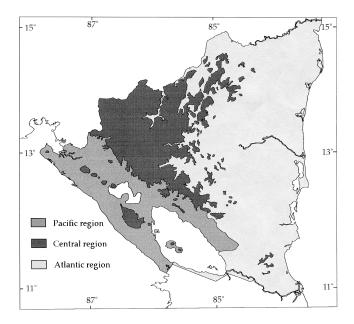


Figure 1. Biogeographic regions in Nicaragua.

cies are moderately to exceedingly rare, with only small populations persisting in Costa Rican national parks. The second list is from the IUCN Red Book, which recognizes two birds vulnerable to extinction in Nicaragua, and the final list is from the ICBP/IUCN Red Data Book, which identified one bird as endangered in Nicaragua (Collar et al. 1992; Groombridge 1993).

I used sets of biogeographic and life-history characteristics correlated with extinction as independent variables in a logistic regression model. I collected data on biogeography within Nicaragua, elevational extent, elevational location, forest preference, habitat specificity, trophic group, and body weight for all recorded terrestrial breeding birds in Nicaragua.

Biogeography within Nicaragua identifies species presence in one or more of Nicaragua's three biogeographic regions: Pacific, central, and Atlantic. Terrestrial breeding birds were categorized as species recorded in only one biogeographic region, species recorded in two biogeographic regions, and species recorded in all three biogeographic regions. The majority of the data came from personal field notes from 17 months of field work in 1995, 1996, and 1997 and unpublished data provided by T. R. Howell and other professional ornithologists. Elevational extent for all terrestrial breeding birds was calculated in meters above sea level to 1800 m, which is the highest point in Nicaragua. Elevational location identified terrestrial breeding birds that do not occur below 300 m. All species were classified into two categories: species restricted to elevation above 300 m and species not restricted to high elevations. All data for elevational variables came from Stotz et al. (1996).

Forest preference follows the classification system of Stiles (1985), which is based on a species' dependence on forest. Species were classified as requiring almost solid forest, patchy forest, or not needing forest. All species not needing forest were excluded from the final analysis. Eight habitat types used by terrestrial resident birds occur in Nicaragua: lowland evergreen forest, montane evergreen forest, elfin forest, tropical deciduous forest, gallery forest, lowland pine forest, upland pine-oak forest, and secondary forest (Taylor 1963). All resident birds were classified as occurring in one to eight habitat types that occur within Nicaragua (Stotz et al. 1996). Trophic group classifications followed those of Karr et al. (1990), with slight modifications. All species were classified as carnivore, frugivore, granivore, insectivore, nectarivore, or omnivore. Body weights were given in grams and were averages from mist-net data from Stiles and Skutch (1989) and Dunning (1992).

I used logistic regression (SPSS 1997) to determine which variables were most important in predicting the list of 11 threatened birds and to generate the predicted probability of extinction for all forest birds in Nicaragua. A logistic regression estimates the coefficients of a probabilistic model from a binary dependent variable and a set of independent variables (SPSS 1997). It has the advantage of using both categorical and continuous data and requires few assumptions about the distribution of the independent variables. The dependent variable was coded as 1 for species identified from the list of potentially threatened birds and 0 for species not identified from any list. The independent variables of body weight and elevational extent were entered as continuous variables; longitudinal extent, habitat specificity, elevational location, trophic group, and forest preference were entered as categorical variables.

Individual variables and their combinations were used to create logistic regression models. Two criteria were used to select the best model for generating a predicted probability of extinction for all forest birds. First, a classification table estimated the overall percent accuracy of the model based on individual and combined variables. The best model had the highest percent accuracy. Second, goodness of fit was used to assess how well the estimated model fits the data. The best models had a small value for goodness of fit.

Once the best model was identified, the diagnostic statistics of the predicted probabilities ranging from 1.0 to 0.0 were generated for all resident forest birds in Nicaragua. These statistics were called the predicted probability of extinction. Two lists of extinction-prone species in Central America based on long-term empirical observations were compared to the predicted probability of extinction to test the accuracy of the model. The first list came from the La Selva Biological Station located on the Atlantic side of Costa Rica, 50 km from the Nicaraguan border. La Selva is one of the oldest and most intensively studied tropical research stations in the world. Stiles and Levey (1994) identified 24 forest birds that have disappeared or possibly decreased in number due to forest conversion around the La Selva research station since 1968. The second list came from Pipeline Road and Barro Colorado, Panama (Karr 1982). This list (Karr 1982) includes 20 resident forest birds present or formerly present on Pipeline Road, but not present on Barro Colorado, in 1980. Seventeen of these birds have also been recorded in Nicaragua.

An assessment of global, national, and local conservation priorities in Nicaragua was undertaken for resident forest birds based on their predicted probability of extinction. Birds that deserve a global priority for conservation were identified as species with a latitudinal extent of 10° or less. Latitudinal extent was calculated as the straight-line distance between the northern and southern extremes of a species' breeding range, with migratory ranges excluded (Gaston 1996). It was expressed as the number of degrees within which a species is known to breed historically and determined with a number of range maps and breeding records (Gillespie & Nicholson 1997). National conservation priorities were based on the predicted probability of extinction for all resident forest birds recorded in Nicaragua. Local conservation priorities were based on the forest birds restricted to one biogeographic region within Nicaragua.

Forest birds were divided into groups based on their predicted probability of extinction over different spatial scales. Natural breaks in the predicted probability of extinction were used to identify gaps between groups. Hypothetical IUCN classifications of critical, endangered, and vulnerable categories were assigned to individual and combined groups to aid in the analysis (Groombridge 1992). Although IUCN the classification system has specific criteria for each category based on population data, this system was used to provide a first-order approximation of what a vulnerability index in Nicaragua should look like.

The ARC/INFO software was used to calculate areas of each biogeographic region and decreed reserves in Nicaragua (Environmental Systems Research Institute 1997). Topographic maps, Holdridge's life-zone map, and decreed nature reserves were digitized as vector-based map layers (Holdridge 1962; Instituto de Rescursos Naturales y del Ambiente 1992; Instituto Nicarguense de Estudios Terrestriales 1995). Overlays of topographic and Holderidge's life-zone maps were used to calculate the total land area of the Pacific, central, and Atlantic biogeographic regions. All areas above 400 m were classified as the central region. The boundaries between tropical dry and tropical moist forest according to the Holdridge life-zone system delineated the Pacific and Atlantic regions. The size and frequency of reserves in each region were calculated from overlays of reserve boundaries and Nicaragua's biogeographic regions. All reserves were assigned to individual regions based on 85% of the reserve area occurring in one region.

Aerial photos (1987) and maps (1:50,000) from the Nicaraguan Institute of Terrestrial Studies were used to estimate the extent of forest cover in terrestrial reserves within each biogeographic region. Following van Wyngaarden (1988), outlines of decreed reserve boundaries were overlaid on aerial photos to calculate the area of forest cover within reserves with terrestrial forest. Percent forest cover within each reserve for the purpose of this study was classified into two broad categories because of partial cloud cover in aerial photos: 100–50% forest cover and 50–0% forest cover.

Results

Nicaragua has 424 species of terrestrial breeding birds, 325 of which require patchy or solid forest. I identified 11 species as threatened in Nicaragua by combining the IUCN list, ICBP list, and the endangered species list of Costa Rica. When these threatened birds were used as a dependent variable in a logistic regression, body weight was the best individual variable for predicting the threatened bird list, followed by habitat specificity (accuracy = 96.2, goodness of fit = 270.0), biogeography within Nicaragua (accuracy = 96.2, goodness of fit = 279.0), and trophic group (accuracy = 96.2, goodness of fit = 292.0) (Table 1). Combinations of two or more variables further improved the model by increasing the overall percent accuracy and lowering the goodness of fit. The best model included the five variables of trophic group, habitat specificity, body weight, forest preference, and biogeography within Nicaragua. This model contained the highest percent accuracy and a low goodness-of-fit value. The inclusion of elevational extent or elevational location resulted in either a lowering of percent accuracy or an increase in goodness of fit.

I generated the predicted probabilities of extinction for all resident forest birds based on the best logistic regression model and compared it with empirical lists of extinction-prone birds from La Selva, Costa Rica, and Barro Colorado, Panama. The predicted probability of extinction for all forest birds in Nicaragua ranked 63% of the extinction-prone birds from La Selva in the first quartile and 21% in the second quartile (Fig. 2). The predicted probability of extinction ranked 59% of the extinction-prone birds from Pipeline Road in the first quartile and 29% in the second quartile. Four species from La Selva and Barro Colorado were ranked in the third and fourth quartile.

Of the resident forest birds with a latitudinal extent of 10° or less, 49 of them should be of interest when global conservation priorities are assessed within Nicaragua. Five natural groups were identified and assigned conservation categories based on the ranking of the predicted probability of extinction (Tables 2 & 3). Only the Black Guan (*Penelopina nigra*) clearly had the highest probability of extinction in Nicaragua and was classified as critical (Table 3). There were four birds assigned to the

Table 1. The best (1–7) variable models for predicting the list of threatened forest birds in Nicaragua.

	Number of variables in logistic regression model							
	1	2	3	4	5	6	7	
Characteristics* Accuracy (%) Goodness of fit	G 96.9 225.7	T,H 96.9 214.7	T,H,B 97.2 228.0	T,H,B,G 97.9 192.8	T,H,B,G,F 97.9 176.2	T,H,B,G,F,L 97.9 207.1	T,H,B,G,F,L,E 97.5 170.8	

*Natural bistory characteristics: G, body weight; T, trophic group; H, habitat specificity; B, biogeography within Nicaragua; F, forest preference; L, elevational location; E, elevational extent.

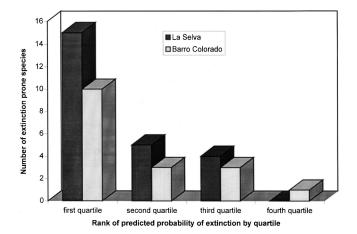


Figure 2. Ranking of all resident forest birds in Nicaragua based on the predicted probability of extinction by quartile and the number of species identified as extinction-prone from La Selva, Costa Rica, and Barro Colorado, Panama.

endangered category and 13 birds assigned to the vulnerable category. Within Nicaragua, the Atlantic and central region both contained a similar number of birds with a high predicted probability of extinction and a similar number of species restricted to one region. The Atlantic region had 11 species in conservation categories, 8 of which were restricted to the region, whereas the central region contained 8 species in conservation categories, of which 6 were restricted to the region.

National- and local-scale conservation priorities were compared for all 325 resident forest birds recorded in Nicaragua. Eight naturally occurring groups were identified based on gaps in the predicted probability of extinction for all resident forest birds and were again assigned conservation categories (Table 4, Appendix 1). There were 6 species in the critical category, 16 species in the endangered category, and 49 species in the vulnerable category. Nearly twice as many forest birds with a high predicted probability of extinction occurred in the Atlantic region than in the central region. The Pacific region contained fewer threatened species (10%) with a predicted probability of extinction of >0.200 than ei-

 Table 3.
 Global-scale conservation priorities for forest birds in

 Nicaragua based on predicted probability of extinction.*

Conservation category and scientific name	Latitudinal extent	Predicted probability of extinction
Critical		
Penelopina nigra	2	0.253
Endangered		
Procnias tricarunculata	8	0.097
Carpodectes nitidus	8	0.086
Myadestes unicolor	6	0.080
Manacus candei	9	0.079
Vulnerable		
Geotrygon albifacies	7	0.039
Ortalis leucogastra	4	0.035
Ortalis cinereiceps	10	0.030
Neomorphus geoffroyi	9	0.030
Piprites griseiceps	6	0.029
Pharomachrus mocinno	9	0.028
Amazona auropalliata	7	0.027
Crypturellus boucardi	9	0.024
Melozone leucotis	6	0.023
Cyanerpes lucidus	10	0.022
Lanio leucothorax	7	0.021
Microcerculus philomela	8	0.021
Dysithamnus striaticeps	5	0.021

*Common names given in Appendix 1.

ther the Atlantic (24%) or central region (15%). The Atlantic region had the most species restricted to one region, and 37 of these birds had a predicted probability >0.200. The central region had one-third as many forest birds restricted to one region as the Atlantic region. The Pacific region had the fewest species (2%) restricted to the region.

The Ministry of Natural Resources and the Environment designated 71 conservation areas for protection, 57 of which contain terrestrial ecosystems used by resident forest birds (Table 5). The Atlantic biogeographic region is the largest region with the greatest area (21%) of decreed reserves. The central biogeographic region includes the highest frequency of decreed reserves and has the second highest area (18%) of decreed reserves. The Pacific region is the smallest in total land area and has the fewest and smallest decreed reserves (2%). Only

Table 2. Global-scale conservation priority for resident forest birds by biogeographic region in Nicaragu	Table 2.	Global-scale conservation	priority for resident	forest birds by bioge	eographic region in Nicaragua.
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Predicted probability of extinction	Conservation categories	Number of species	Pacific region	Central region	Atlantic region
0.999-0.253	critical	1	0	1(1)	0
0.097-0.079	endangered	4	0	2 (2)	2 (2)
0.039-0.021	vulnerable	13	2(1)	5 (3)	9 (6)
0.016-0.014		9	2 (0)	6(2)	2 (0)
0.011-0.000		22	10(0)	20 (8)	9 (4)
Total		49	14 (1)	34 (16)	22 (12)

*Number of species restricted to each region in parentheses.

Table 4.	National and local-scale pr	viorities for forest birds by	y biogeographic region	in Nicaragua.*
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Predicted probability of extinction	Conservation category	Number of species	Pacific region	Central region	Atlantic region
0.994-0.555	critical	6	0	4 (0)	6(2)
0.423-0.210	endangered	7	1 (0)	3(1)	6 (3)
0.186-0.120	endangered	9	0	4(1)	8 (5)
0.104-0.073	vulnerable	8	0	3 (2)	6 (5)
0.047-0.020	vulnerable	41	8(1)	15(6)	30 (22)
0.018-0.010		78	8(0)	41 (17)	54 (36)
0.008-0.007		32	5(1)	13 (5)	24 (16)
0.004-0.000		144	71 (0)	113 (24)	100 (26)
Total		325	93 (2)	196 (56)	234 (115)

*Number of species restricted to each region in parentheses.

39% of the decreed terrestrial conservation areas in Nicaragua have >50% forest cover within the decreed reserve boundaries. The Atlantic region maintains the most forest cover; most reserves within the central and Pacific region contain <50% forest cover.

Discussion

Identifying natural-history characteristics associated with extinction-prone species has long been a central theme in conservation biology (Terborgh 1974; Laurance 1991; Groombridge 1992; Meffe et al. 1997). I identified body weight, habitat specificity, trophic group, biogeography within Nicaragua, and forest preference as important predictors of threatened birds.

Body weight is often cited as one of the most important variables in predicting extinction-prone species (Brown 1995; Gaston & Blackburn 1995). In general, large-bodied birds in Nicaragua have low population densities and low reproductive rates, and they occur at the top of the trophic pyramid. Weight is also an important surrogate variable for identifying vulnerable birds based on the effects of hunting (Redford 1992). Large birds, such as guans, tinamous, and quail, are relentlessly hunted in Nicaragua, and many large-bodied birds are birds of prey that are shot on site because rural Nicaraguans believe they eat domestic animals (Stiles 1985; Martinez-Sanchez 1986; Stiles & Skutch 1989).

Habitat specificity, measured as the number of habitats in which a species occurs, is also an important macroecological variable for identifying habitat specialists that occur in only one vegetation type. Sixty forest birds within Nicaragua occur in one habitat type, and these birds will not be able to persist if their respective habitats are significantly reduced or degraded. Nicaragua's three biogeographic regions are closely correlated with habitat and forest type (i.e., tropical dry forest, lowland rainforest), so this variable also identifies species intolerant to different climatic and vegetation regimes. There are 197 species restricted to one biogeographic region that are also important to the setting of regional conservation priorities.

Trophic group is often cited to identify extinctionprone species (Leck 1979; Willis 1974; Terborgh & Winter 1980; Kattan et al. 1994). The carnivores clearly are some of the most threatened birds; as previously mentioned, members of this trophic group, which have high body weights, are generally rare in Nicaragua because of low population densities and hunting. Trophic group was the fourth best individual variable for predicting threatened birds, but when it was combined with other variables such as habitat specificity, weight, or forest preference, overall accuracy and goodness of fit improved significantly. This concurs with the findings of a number of researchers who combined trophic group with other variables such as body weight or forest preference (i.e., "large frugivores" or "understory insectivores") to identify extinction-prone specialized guilds (Newmark 1991; Kattan et al. 1994).

Following Stiles (1985), I found forest preference to be a useful variable for identifying a number of threat-

Table 5.	Characteristics of three	e biogeographic regions and	l decreed conservation areas	used by forest birds in I	Nicaragua.
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Biogeographic regions	Region area (km²)	Reserve area (km²)	Number of reserves	Number of reserves with forest cover of >50%
Pacific	21,528	362	7	3
Central	26,570	4,745	36	8
Atlantic	70,219	14,872	15	10
Total	118,317	19,979	57*	21

*One reserve bas over 15% of its area in two regions, so it is included twice by region but not in the total number of reserves.

ened species at this macroecological scale. Birds that require solid forest to persist have a higher probability of extinction than birds that require patchy forest. Birds that require solid forest will only decline as deforestation continues in Nicaragua, whereas birds that require either patchy forest or nonforest habitats will most likely expand (Newmark 1991; Warburton 1997). Most important, the forest-preference category excludes nonforest birds that are not "core" members of forest communities and should not be included when theories of forest fragmentation are applied (Remsen 1994).

Elevational extent identified species with limited elevational ranges, and elevational location identified species restricted to high elevations. Both of these variables have been correlated with extinction-prone species (Terborgh & Winter 1980; Kattan et al. 1994), but these natural-history characteristics were not as valuable as other variables in this study, possibly because Nicaragua has relatively little relief, little variation in species' elevational distribution, and few species with narrow bands of elevational distribution (Taylor 1963). The use of elevational extent and location may be more significant in countries with a more pronounced elevational gradient such as Colombia or Costa Rica.

A number of studies have found that theoretical generalizations of extinction are often too weak to be predictive and that models of extinction are too simplistic and untestable (Gibbons 1992; Doak & Mills 1994; Simberloff 1994). But surrogate lists, a species database (based on natural-history research), and a logistic regression model can provide a working and testable hypothesis concerning which species are the most vulnerable based on current theories of extinction and natural-history characteristics. This method provides resource managers and biologists with a first-order approximation of which species and regions deserve the highest priority for conservation.

At a global scale, my study suggests that the Black Guan should also be included on a global conservation priority list, because it has natural-history characteristics similar to those of other threatened birds, this species, which has a latitudinal extent of only 2°, may be vulnerable to extinction in both Nicaragua and Costa Rica. Other forest birds with a small latitudinal extent and a high predicted probability of extinction should also be considered when globally threatened species are assessed in Nicaragua. The fact that few of these species with a small latitudinal extent have a high predicted probability of extinction (i.e., >0.100), may suggest that Nicaragua deserves a relatively low priority for conservation compared to other Neotropical countries with high endemism.

In well-researched temperate countries, such as the United States, England, and Australia, national- and localscale endangered species lists are based heavily on population size, population trends, current distribution, distributional trends, reproductive potential, and ecological specialization (Millsap et al. 1990; Lunney et al. 1996). These lists are created and modified by specialists and are subject to intense peer review. In most tropical countries with high diversity, however, few quantitative or comparative data exist on any aspect of population size or trends, and only the most general distributional and ecological data are available (Diamond 1987). Although the IUCN Red Books are a valuable resource for identifying endangered taxa on a global scale, these lists underestimate the number of endangered species by country, region, or habitat; hence, other methods may be warranted.

This research may provide an important first-order approximation of which species deserve national priority for conservation. First, the predicted probability of extinction did an adequate job of ranking endangered birds from Costa Rica in the critical conservation category. Of the six forest birds included in the critical category, five occur on the official endangered species list for Costa Rica (Stiles 1985). It is also interesting that the predicted probability of extinction identified the Harpy Eagle (Harpia harpyja) as the most extinction-prone bird in Nicaragua. This bird has not been seen in Costa Rica or Nicaragua for over 20 years (Stiles & Skutch 1989). Second, when general abundance data from eight sites in Costa Rica are compared with the next group of forest birds with a high predicted probability, all are "rare" or "uncommon" with the exception of the last two, the Mealy Parrot (Amazona farinosa), which can be abundant at certain sites, and the Purple-throated Fruitcrow (Querula purpurata), which has been recorded only once in Nicaragua (Stiles 1983, 1985; M. Cody, personal communication; J. Martinez-Sanchez, personal communication). Although abundance data do not necessarily indicate that the species are in decline, it may indicate that further research is warranted on the abundance and distribution of these species in Nicaragua.

The logistic regression model, with 11 globally and nationally threatened species as a dependent variable, ranked a majority of the species that are rare or that have gone locally extinct in other sites in Central America in the first quartile of all forest birds. It may be the case that although conservation priorities differ significantly with spatial scale, the extinction process for forest birds and natural-history characteristics associated with the process remain relatively constant over different spatial scales. In a recent study from Barro Colorado, Robinson (1999) found that three species have experienced a severe decline since early surveys and are at the brink of disappearing from the island. These three species, the Slate-colored Grosbeak (Pitylus grossus), Speckled Mourner (Laniocera rufescens), and Rufous Piha (Lipaugus unirufus), all had a high predicted probability of extinction due to their natural-history characteristics and were therefore included in national conservation categories (*Pitylus grossus*, endangered; *Laniocera rufescens* and *Lipaugus unirufus*, threatened).

Although the methods I employed did a relatively good job of identifying and ranking extinction-prone birds, my results should be interpreted with caution. First, there can be no substitute for intensive field studies on avian abundance and distribution within Nicaragua and intense peer review for creating a final vulnerability index. Data on species' abundance in individual reserves are desperately needed and this should be one of the highest priorities for avian research in Nicaragua. Second, the predicted probability of extinction did not always place species identified as globally, nationally, or locally threatened into appropriate hypothetical conservation categories. At a global scale, this method did not rank the Keel-billed Motmot (Electron carinatum) into any conservation category because it had a low predicted probability of extinction. This bird was the only bird in Nicaragua identified as endangered by the ICBP/ IUCN Red Book (Collar et al. 1992).

At a national scale, two birds identified as endangered in Costa Rica, the Scarlet Macaw (*Ara macao*) and the Resplendent Quetzal (*Pharomachrus mocinno*), were included in conservation categories as threatened. These species should be placed in the endangered category. At a local level, 15 species included in the list from La Selva or Barro Colorado were not included in the hypothetical conservation categories (Appendix 2). This group contains various families, with the only common variable being that they require patchy forest. Finally, my study focused only on forest birds and completely ignored species that do not require forest, such as grassland and aquatic birds. A complete and accurate vulnerability index should include these species.

It appears that the Ministry of Natural Resources and the Environment has done an adequate job of identifying areas for conservation based on the proportion of decreed nature reserves in each region and the distribution of forest birds with a high predicted probability of extinction. At a global scale, both the central and Atlantic regions deserve a similar priority for conservation based on their number of restricted-range species with a high predicted probability of extinction. At a national scale, the Atlantic region deserves and appears to have received the highest priority for conservation within Nicaragua. The Atlantic region has some of the largest reserves and largest intact lowland rainforest in Central America (Nietschmann 1990). A majority of these reserves maintain over 50% forest cover and can significantly contribute to the conservation of species that occur in the lowland evergreen rainforest of Central America.

Although the Pacific region appears to be the most inadequately preserved based on forest cover, and percentage protected, this region has the lowest number of forest birds. Only two forest birds are restricted to the region, and few species in the region have a high predicted probability of extinction. The Pacific region may prove to deserve a higher priority for conservation if an assessment of aquatic or migratory birds is undertaken. The central region occupies 22% of Nicaragua but contains a number of species that are of global importance and, to a lesser extent, national importance. Although there are 36 decreed reserves in this region which on paper appear protected, 77% have <50% forest cover because many occur on active volcanoes or have been converted to agriculture, leaving only elfin forest intact on the summits. Forest birds in the central region may currently be the most vulnerable to local extinction in Nicaragua, and establishment of these reserves deserves a high priority.

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Literature Cited

- Brown, J. H. 1995. Macroecology. University of Chicago Press, Chicago. Christiansen, M. B., and E. Pitter. 1997. Species loss in a forest bird
- community near Lagoa Santa in southeastern Brazil. Biological Conservation **80:**23-32.
- Collar, N. J., L. P. Gonzaga, N. Krabbe, N. Madroño, L. G., Naranjo, T. A. Parker III, and D. C. Wege. 1992. Threatened birds of the Americas: the ICBP/IUCN red data book. Part 2. International Council for Bird Preservation and World Conservation Union, Cambridge, United Kingdom.
- Diamond, J. M. 1987. Extant unless proven extinct? Or extinct unless proven extant. Conservation Biology 1:77–79.
- Diamond, J. M., K. D. Bishop, and S. van Balen. 1987. Bird survival in an isolated Javan woodland: island or mirror? Conservation Biology 1:132-142.
- Doak, D. F., and L. S. Mills. 1994. A useful role for theory in conservation. Ecology 75: 615–626.
- Dunning, J. B., Jr. 1992. CRC handbook of avian body masses. CRC Press, Boca Raton, Florida.
- Environmental Systems Research Institute. 1997. Arc/Info user's manual. Redlands, California.
- Faaborg, J. 1979. Qualitative patterns of avian extinction on Neotropical land-bridge islands: lessons for conservation. Journal of Applied Ecology 16:99–107.

- Gaston, K. J. 1996. Species-range-size distributions: patterns, mechanisms and implications. Trends in Ecology and Evolution **11:**197–201.
- Gaston, K. J., and T. M. Blackburn 1995. Birds, body size and the threat of extinction. Philosophical Transactions of the Royal Society of London B 347:205-212.
- Gibbons, A. 1992. Conservation biology in the fast track. Science **225**: 20-22.
- Gillespie, T. W., and K. Nicholson. 1997. Checklist, biogeography, and natural history characteristics of herpetofauna, avifauna, and mammals in Nicaragua. Technical publication 14. Ministry of Natural Resources and the Environment, Managua.
- Groombridge, B. 1992. Global biodiversity: status of the earth's living resources. Chapman and Hall, London.
- Groombridge, B. 1993. 1994 IUCN Red lists of threatened animals. World Conservation Union, Gland, Switzerland.
- Holdridge, L. R. 1962. Ecological map of Nicaragua, Central America from 1:1,000,000 scale maps. U.S. Agency of International Development, Managua.
- Howell, T. R. 1969. Avian distribution in Central America. The Auk 86: 293–326.
- Instituto de Rescursos Naturales y del Ambiente. 1992. El sistema de areas silverstres protegidas de Nicaragua from 1:500,000 scale maps. Managua.
- Instituto Nicaraguense de Estudios Terrestriales. 1995. Mapa de la Republica de Nicaragua from 1: 525,000 scale maps. Managua.
- Karr, J. R. 1982. Avian extinction on Barro Colorado Island: a reassessment. The American Naturalist 119:220–239.
- Karr, J. R., S. K. Robinson, J. G. Blake, and R. O. Bierregaard. 1990. Birds of four Neotropical forests. Pages 237-269 in A. H. Gentry, editor. Four Neotropical rainforests. Yale University Press, New Haven, Connecticut.
- Kattan, G. H., H. Alvarrez-Lopez, and M. Giraldo. 1994. Forest fragmentation and bird extinctions: San Antonio eighty years later. Conservation Biology 8:138–146.
- Laurance, W. F. 1991. Ecological correlates of extinction proneness in Australia tropical rainforest mammals. Conservation Biology 5: 79-89.
- Leck, C. 1979. Avian extinction in an isolated tropical wet-forest preserve, Ecuador. The Auk 96:343-352.
- Long, A. J., M. J. Crosby, A. J. Stattersfield, and D. C. Wege. 1996. Towards a global map of biodiversity: patterns in the distribution of restricted-range birds. Global Ecology and Biogeography Letters 5: 281–304.
- Lunney, D., A. Curtin, D. Ayers, H. G. Gogger, and C. R. Dickman. 1996. The biological scores used in the evaluation of the status of all fauna of New South Wales. Environmental heritage monograph series no. 2. National Parks and Wildlife Service, Hurstville, New South Wales, Australia.
- Martinez-Sanchez, J. C. 1986. Causes affecting the survival of birds of prey in Nicaragua. Birds of Prey Bulletin **3**:43-47.
- Meffe, G. K., et al. 1997. Principles of conservation biology, 2nd Edition. Sinauer Associates, Sunderland, Massachusetts.
- Millsap, B. A., J.A. Gore, D. E. Runde, and S.I. Cerulean. 1990. Setting the priorities for the conservation of fish and wildlife in Florida. Journal of Wildlife Management 54:5–57.

- Newmark, W. D. 1991. Tropical forest fragmentation and the local extinction of understory birds in the eastern Usambara Mountains, Tanzania. Conservation Biology 5:67–78.
- Nietschmann, B. 1990. Conservation by conflict in Nicaragua. Natural History November:42-49.
- Pimm, S. L., H. L. Jones, and J. M. Diamond. 1988. On the risk of extinction. The American Naturalist 132:757–785.
- Redford, K. 1992. The empty forest. BioScience 42:412-422.
- Remsen, J. V., Jr. 1994. Use and misuse of bird lists in community ecology and conservation. The Auk 111:225-227.
- Robinson, W. D. 1999. Long-term changes in avifauna of Barro Colorado Island, Panama, a tropical forest isolate. Conservation Biology 13:85-97.
- SPSS. 1997. SPSS: statistics. Version 6.1.1. Chicago.
- Scott, M., B. Csuti, D. Jacobi, and J. Estes. 1995. Species richness, a geographic approach to protecting future biological diversity. Bioscience 37:782–788.
- Simberloff, D. 1994. Habitat fragmentation and population extinction of birds. IBIS 137:105-111.
- Stiles, F. G. 1983. Birds: introduction and checklist. Pages 502–544 in D. H. Janzen, editor. Costa Rican natural history. University of Chicago Press, Chicago.
- Stiles, F. G. 1985. Conservation of forest birds in Costa Rica: problems and perspectives. Pages 141–168 in W. A. Diamond and T. E. Lovejoy, editors. Conservation of tropical forest birds. Technical publication 4. International Council for Bird Preservation, Cambridge, United Kingdom.
- Stiles, F. G., and A. F. Skutch. 1989. A guide to the birds of Costa Rica. Cornell University Press, Ithaca, New York.
- Stiles, F. G., and D. J. Levey. 1994. Birds of La Selva and vicinity. Pages 384–393 in L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn, editors. La Selva: ecology and natural history of a Neotropical rain forest. University of Chicago Press, Chicago.
- Stotz, D. F., J. W. Fitzpatrick, T. A. Parker III, and D. K. Moskovits. 1996. Neotropical birds: ecology and conservation. The University of Chicago Press, Chicago.
- Taylor, B. W. 1963. An outline of the vegetation of Nicaragua. Journal of Ecology 51:27-54.
- Terborgh, J. 1974. Preservation of natural diversity: the problem of extinction prone species. BioScience 24:715-722.
- Terborgh, J., and B. Winter. 1980. Some causes of extinction. Pages 119-134 in M. Soule, editor. Conservation biology: the science of scarcity and diversity. Sinauer Associates, Sunderland, Massachusetts.
- Turner, I. M. 1996. Species loss in fragments of tropical rain forest: a review of the evidence. Journal of Applied Ecology 33:200-209.
- van Wyngaarden, W. 1988. Low-level aerial survey techniques. Pages 209–213 in A. W. Küchler and I. S. Zonneveld, editors. Vegetation analysis. Volume 2. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Warburton, N. H. 1997. Structure and conservation of forest avifauna in isolated rainforest remnants in tropical Australia. Pages 190–206 in W. F. Laurance and R. O. Bierregaard, editors. Tropical forest remnants. University of Chicago Press, Chicago.
- Willis, E. O. 1974. Population and local extinction of birds on Barro Colorado Island, Panama. Ecology Monographs 44:153-169.



Appendix 1

National-scale conservation priorities for forest birds in Nicaragua based on predicted probability of extinction.

	TB ^a	LS ^b	BC^{c}	Predict probability of	Discountly
Conservation category, common and scientific name	IB	LS	BC	extinction	Biogeography ^d
Critical Harry Faclo (Hartia hartuia)				0.004	
Harpy Eagle (<i>Harpia barpyja</i>)	X	X	X	0.994	A CA
Great Currasow (<i>Crax rubra</i>)	х	X	X	0.905 0.786	CA CA
King Vulture (<i>Sarcorhamphus papa</i>) Ornate Hawk-Eagle (<i>Spizaetus ornatus</i>)	v	X		0.780	CA
Orange-breasted Falcon (Falco deiroleucus)	x x	х		0.612	A
Black-and-white Hawk-Eagle (<i>Spizastur melanoleucus</i>)	X X	v		0.555	CA
Endangered	А	х		0.)))	CA
Green Macaw (Ara ambigua)	х	х		0.423	Α
Tiny Hawk (Accipiter superciliosus)	А	1		0.363	A
Barred Forest-Falcon (<i>Micrastur ruficollis</i>)			х	0.294	CA
Great Black-Hawk (Buteogallus urubitinga)				0.259	PA
Black Guan (<i>Penelopina nigra</i>)				0.253	C
Mealy Parrot (Amazona farinosa)				0.235	ČĂ
Purple-throated Fruitcrow (Querula purpurata)				0.210	A
Endangered					
White Hawk (Leucopternis albicollis)				0.186	CA
Black Hawk-Eagle (<i>Spizaetus tyrannus</i>)	х			0.183	CA
Chestnut-mandibled Toucan (Ramphastos swainsonii)				0.163	Α
Slate-colored Grosbeak (Pitylus grossus)				0.153	A
Blue-crowned Chlorophonia (Chlorophonia occipitalis)				0.149	С
Red-capped Manakin (<i>Pipra mentalis</i>)				0.148	Α
Olive-backed Euphonia (Euphonia gouldi)				0.148	Α
Yellow-eared Toucanet (Selenidera spectabilis)		х		0.130	Α
Bicolored Hawk (Accipiter bicolor)				0.120	CA
Vulnerable					
White-crowned Pigeon (Columba leucocephala)				0.104	Α
Three-wattled Bellbird (Procnias tricarunculata)	х			0.097	С
Brown-hooded Parrot (Pionopsitta haematotis)				0.092	Α
Snowy Cotinga (Carpodectes nitidus)				0.086	Α
Lovely Cotinga (Cotinga amabilis)				0.083	Α
Slate-colored Solitaire (Myadestes unicolor)				0.080	С
White-collared Manakin (Manacus candei)				0.079	Α
Ochre-bellied Flycatcher (Mionectes oleagineus)				0.073	CA
Vulnerable					
Great Tinamou (<i>Tinamus major</i>)				0.047	CA
Scarlet Macaw (Ara macao)	х			0.043	PA
White-faced Quail-Dove (Geotrygon albifacies)				0.039	С
White-bellied Chachalaca (Ortalis leucogastra)				0.035	Р
Rufous Piha (<i>Lipaugus unirufus</i>)				0.033	A
Plain Chachalaca (Ortalis vetula)				0.033	PC
Speckled Mourner (<i>Laniocera rufescens</i>)				0.032	A
Gray-headed Chachalaca (Ortalis cinereiceps)				0.030	A
Rufous-vented Ground-Cuckoo (Neomorphus geoffroyi)		х	Х	0.030	A
Gray-headed Manakin (<i>Piprites griseiceps</i>)		х		0.029	CA
Red-throated Caracara (<i>Daptrius americanus</i>)		х	Х	0.028	A
Resplendent Quetzal (<i>Pharomachrus mocinno</i>)	Х			0.028	С
Yellow-naped Parrot (<i>Amazona auropalliata</i>)				0.027 0.025	PA
Scaled Pigeon (<i>Columba speciosa</i>) Band-tailed Pigeon (<i>Columba fasciata</i>)				0.025	A C
Slaty-breasted Tinamou (<i>Crypturellus boucardi</i>)				0.023	CA
Pale-vented Pigeon (Columba cayennensis)		v		0.024	A
White-eared Ground Sparrow (Melozone leucotis)		х		0.023	C A
Red-crowned Ant-Tanager (<i>Habia rubica</i>)				0.023	C
Orange-billed Sparrow (Arremon aurantiirostris)				0.023	A
Gray-headed Kite (Leptodon cayannensis)		х		0.023	PA
Shining Honeycreeper (<i>Cyanerpes lucidus</i>)				0.025	A
White-fronted Parrot (Amazona albifrons)				0.022	PC
Black-faced Antthrush (Formicarius analis)			х	0.022	A

Appendix 1 (continued)

Conservation category, common and scientific name	TB ^a	LS ^b	BC ^c	Predict probability of extinction	Biogeography ^d
Ocellated Antbird (Phaenostictus mcleannani)		x	х	0.022	Α
Spectacled Antpitta (Hylopezus perspicillatus)			х	0.021	Α
Plain-brown Woodcreeper (Dendrocincla fuliginosa)				0.021	Α
Spotted Wood-Quail (Odontophorus guttatus)				0.021	С
White-throated Shrike-Tanager (Lanio leucothorax)		х		0.021	Α
Striped-headed Sparrow (Aimophila ruficauda)				0.021	PC
Wing-banded Antbird (Myrmornis torquata)				0.021	Α
Olive Sparrow (Arremonops rufivirgatus)				0.021	PC
Song Wren (Cyphorbinus phaeocephalus)			х	0.021	Α
Chestnut-colored Woodpecker (Celeus castaneus)				0.021	CA
Rufous-fronted Wood-Quail (Odontophorus erythrops)		х		0.021	Α
Nightingale Wren (Microcerculus philomela)			х	0.021	Α
Streaked-crowned Antvireo (Dysithamnus striaticeps)				0.021	Α
Tawny-faced Gnatwren (Microbates cinereiventris)				0.021	Α
Golden-crowned Spadebill (Platyrinchus coronatus)				0.020	Α
White-crowned Parrot (Pionus senilis)				0.020	CA
Olive-throated Parakeet (Aratinga nana)				0.020	Α

^aResident forest birds identified as threatened by the World Conservation Union, the International Council of Bird Preservation, and lists of endangered species of Costa Rica.

^bResident forest birds that have disappeared or possibly decreased in number because forest conversion around the La Selva research station since 1968.

^cResident forest birds present or formerly present on Pipeline Road, but not present on Barro Colorado, in 1980.

^dBiogeography within Nicaragua: P, Pacific region; C, central region; A, Atlantic region.

Appendix 2 Species identified as extinction-prone from La Selva and Barro Colorado but not included in national conservation categories.*

Common and scientific name	LS	BC	Predicted probability of extinction
Cinnamon Woodpecker (Celus loricatus)		X	0.016
Barred Woodpecker (Dendrocolaptes certhia)		х	0.015
Buff-throated Foliage-gleaner (Automolus ochrolaemus)		х	0.014
White-breasted Wood-Wren (Henicorbina leucosticta)		х	0.007
Sulphur-rumped Flycatcher (<i>Myiobius sulphureipygius</i>)	х	х	0.002
Spotted-crowned Woodcreeper (Lepidocolaptes affinis)		х	0.002
Band-tailed Barbthroat (Threnetes ruckeri)		х	0.000
Bare-crowned Antbird (Gymnocichla nudiceps)	х		0.015
Checker-throated Antwren (Myrmotherula fulviventris)	Х		0.015
Chestnut-headed Oropendola (Psarocolius wagleri)	х		0.013
Olive Tanager (Chlorothraupis carmioli)	х		0.011
Russet Antshrike (Thamnistes anabatinus)	Х		0.007
White-flanked Antwren (Myrmotherula axillaris)	х		0.007
Bat Falcon (Falco rufigularis)	х		0.000
Collared Forest-Falcon (Micrastur semitorquatus)	X		0.000

*Abbreviations are the same as those in Appendix 1.