

Management and Conservation of Migratory Landbirds Overwintering in the Neotropics

Daniel R. Petit¹, James F. Lynch², Richard L. Hutto³,
John G. Blake⁴, and Robert B. Waide⁵

Abstract — Loss of tropical broadleaved forests and concurrent population declines of long-distance migratory birds in temperate breeding areas have been closely linked in both scientific and popular literature; however, little evidence of a causal association currently exists. We review the current land use situation in the neotropics, the projected outcome of deforestation early in the 21st century, and the extent of knowledge of migratory bird habitat use on the wintering grounds. From that information, we assess the likely current and future impact of deforestation on migratory birds, and examine land use practices that may be compatible with the concept of conservation of those species.

At least 40% of the original tropical forests have been converted to other land uses. Most remaining tropical forests lie in the vast Amazon Basin, where few neotropical migrants spend winter. Permanent pasture and agriculture each presently comprise 10-30% of land area in many countries. Reasons for the rapid pace of deforestation are deeply rooted in socioeconomic problems of developing nations; solutions to those issues must be realized and implemented before forest conversion will slow. Early in the 21st century, once-forested landscapes will most likely be a mosaic of agricultural lands, cattle pastures, and secondary forests in various stages of

regeneration. Large tracts of mature forest will probably be restricted mainly to national parks and reserves. Thus, tropical landscapes will be changing increasingly toward "agroscares". Migratory birds as a group are most abundant in tropical habitats that are: (1) disturbed; (2) of medium stature (5-20 m); found at (3) low (m) elevations, and (4) high latitudes (15° N); and located (5) on the mainland. Slight to moderate levels of disturbance enhance numbers of migrants occupying broadleaved forest sites. However, species vary considerably in their preferences for winter habitats, such that broad generalizations may have limited use for actual on-site management and conservation plans. We examined habitat use by 123 species of migratory landbirds through an extensive literature review. Based upon the apparent reliance of species on undisturbed, broadleaved habitats, we identified 23 species that may be highly vulnerable to alteration of tropical forests.

Use or conversion of natural vegetation associations in the tropics as it relates to impacts on native flora and fauna can be placed under three broad categories: "conservative", "sustainable", and "destructive". "Conservative" land uses, such as protected parks and reserves, will play a major role in maintaining biodiversity. However, future economic growth and retention of natural resources in Latin America rest upon the concept of "sustainable" development. Several examples of sustainable forestry, such as strip clearcutting, appear highly compatible with goals of management of neotropical migratory

¹Daniel R. Petit, Department of Biological Sciences, Arkansas Cooperative Fish and Wildlife Research Unit, University of Arkansas, Fayetteville, Arkansas 72701. Present address: Smithsonian Environmental Research Center, P.O. Box 28, Edgewater, Maryland 21037.

²James F. Lynch, Smithsonian Environmental Research Center, P.O. Box 28, Edgewater, Maryland 21037.

³Richard L. Hutto, Division of Biological Sciences, University of Montana, Missoula, Montana 59812.

⁴John G. Blake, Department of Biology, University of Missouri—St. Louis, 8001 Natural Bridge Road, St. Louis, Missouri 63121.

⁵Robert B. Waide, Center for Energy and Environment Research, University of Puerto Rico, G.P.O. Box 3682, San Juan, Puerto Rico 00936.

birds. Finally, "destructive" practices, such as heavily grazed or managed pastures and extensive monocultures, are the greatest threat to migratory birds in Latin America and the Caribbean.

Several measures need to be enacted within all national boundaries to ensure viability of migratory bird populations is not threatened by events on wintering grounds. These include: (1) assessment and monitoring of bird populations; (2) identification of both present and future threats; (3) identification of critical areas and habitats; (4) incorporation of sustainable development into land use planning; and (5) development of a system of protected reserves. Because neotropical migrants as a group are more tolerant of forest disruption and artificial environments than are resident species, conservation of migrants could be accomplished within plans devised for resident species.

INTRODUCTION

Loss of tropical broadleaved forests (Myers 1980, Lanly 1982) and concurrent population declines of migratory landbirds that breed in temperate North America and overwinter in the tropics (Robbins et al. 1986, Sauer and Droege 1992) have been closely linked in both the scientific and popular literature. Conversion and fragmentation of moist, tropical forests has been convincingly implicated in population declines or extirpation of permanent resident tropical bird species (e.g., Willis 1974, Lovejoy et al. 1984, Scott and Brooke 1985, Thiollay 1992), but impacts of tropical deforestation on migratory species that breed in North America are more dubious. The overwintering period could be a time of intense selective pressure on neotropical migrants because of mortality associated with stress from migratory flights, occupation of unfamiliar habitats by juvenile birds, and increased competition for food due to inflated densities of potential competitors (Morse 1980). Because these pressures should be exacerbated in the face of widespread alteration of native vegetative associations, a conceptual basis exists for a causal relationship between habitat changes on tropical wintering grounds and breeding populations of migrants. However, firm evidence for such a causal relationship remains obscure because of limited knowledge of ecologies of migrants during the boreal winter. Indeed, basic information on habitat distributions of migrants during winter (including habitat-specific survival rates) would greatly reduce the present-day gap between speculation and sound inference.

Threat of loss of biological diversity has been an impetus for the global conservation effort during the past several decades. In this light, recognition of potential future ecological catastrophes, such as extinction of plants and animals, is central to developing a coherent strategy for conserving natural communities for future generations. If tropical forest destruction and conversion are potentially responsible for estimated declines of certain migratory birds, then efforts must be initiated to identify, preserve, and manage appropriate tropical habitats for those species.

Development of pragmatic conservation plans for overwintering migratory landbirds requires assessment of several pertinent questions related to tropical forest alteration and its potential impact on migratory birds: What are the sociological and economical correlates of tropical forest destruction? What is the current extent of forests and other vegetation associations in the neotropics? What is the likely scenario for change in these natural resources as we enter the 21st century? What geographic regions and habitat types do migratory landbirds use and does overall habitat use reflect relative suitability? In this chapter, we briefly review these topics to lay the foundation for our assessment of present and future problems faced by migrants in the neotropics and the potential management and conservation solutions to those issues. Such an analysis is timely in light of the desire of both North American and Latin American governments to prevent further loss of biological diversity, including migratory birds, in the neotropics (Canadian Minister of the Environment 1983; U.S. Fish and Wildlife Service 1990; U.S. Congress, Office of Technology Assessment 1992).

FOREST DESTRUCTION AND THE STATUS OF TROPICAL FOREST ASSOCIATIONS

Migratory birds are found in nearly all natural vegetation associations in the neotropics, but several vegetation types are particularly important: wet/moist broadleaved forests, dry broadleaved forests, pine or mixed-pine forests, and mangrove forests. These categories are used here to develop a basis for understanding the extent and reasons for tropical deforestation and are discussed in further detail below; vegetation groupings are broad, but information on rates of conversion of specific vegetation associations in the tropics is not readily available. Accurate rates of deforestation are difficult to determine because of limited and conflicting data and variable use of such vocabulary as "deforestation" (Hamilton 1991). The terms "deforestation", "removal", and "conversion" (Melillo et al. 1985) of tropical forests are used synonymously throughout this paper to represent transformation of forested land to shifting cultivation, permanent crops, pasture, or extensive clear-cuts. Selective logging and other relatively minor disturbances to forests (e.g., collection of firewood) are generally not included under these headings.

Direct and Indirect Causes of Tropical Deforestation

Forests in the New World Tropics are typically cut to create agricultural or grazing lands, or to provide timber products (Myers 1981) that are often marketed overseas (e.g., Parsons 1976). Direct and indirect causes of deforestation are varied and complex, but most can be attributed to socioeconomic inequalities, both within developing countries and between

developing and industrialized countries. That is, demand from industrialized nations for inexpensive agricultural products, as well as unequal distribution of land and resources among citizens of Latin American nations, have created a social and economic system where the bulk of the populace is poor and dependent upon subsistence agriculture (Leonard 1987, Ascher and Hubbard 1989). Examined slightly differently, wholesale depletion of natural forest resources in the neotropics can be viewed as a result of the inability of locally available technology to keep pace with population growth (Myers 1987). However, conservation biologists and sociologists believe that widespread implementation of available forest management practices would greatly relieve mounting pressures on tropical forests (e.g., World Resources Institute 1985, Anderson 1990, Thelen 1990). Outlined below are four major forest types and their current status within the neotropics.

Moist Broadleaved Forest

Moist and wet tropical forests (popularly termed "rain forests") occur in areas that receive 150-500 cm precipitation/year. Although the rapid removal of moist broadleaved forests from the neotropics during the past thirty years is an indisputable fact (Myers 1980, Lanly 1982, Sader and Joyce 1988), the exact rate of cutting and ultimate fate of deforested lands is difficult to assess (Melillo et al. 1985). At least 40% of the area originally covered by tropical moist forest has been converted to other land uses, with the bulk of remaining forests situated in the vast Amazon Basin (Myers 1980, 1991; World Resources Institute 1985; Mahar 1989). Mexico and most Central American nations contain (% of their original moist forest (Leonard 1987, Myers 1991, and projected trends from above sources). Because of the historical pattern of settlement and land use in tropical landscapes, a greater fraction of mid-to-high elevation moist forests are intact compared to coastal and other low elevation forests (Holdridge 1970, Janzen 1988). The relentless pace of forest cutting is especially alarming to conservation biologists, who fear that mass extinctions may occur before the full extent of biological diversity in the neotropics can even be evaluated (Leonard 1987).

Dry Broadleaved Forest

Most attention to tropical deforestation has focussed on moist/wet forests. However, dry forest associations, which comprised 42% of the total area of all tropical and subtropical forests (Brown and Lugo 1982), have been subjected to the greatest pressures from human populations. Tropical dry forests occur most extensively in western Mexico and Central America, northern and western South America, and on the Yucatan Peninsula and several Caribbean islands. A combination of low precipitation (usually <150 cm/yr), pronounced dry season(s), and stressful edaphic conditions often produce climax forest

types represented by short (<20 m), sclerophyllous trees or thorn forests (Murphy and Lugo 1986). Dry, semi-deciduous forests are also more open and less complex structurally than wet, evergreen forests (Holdridge et al. 1971). These climatic conditions allow dry forests to be easily cleared and maintained by fire and often produce more productive soil for agriculture and grazing than do moist forests (Murphy and Lugo 1986, Janzen 1988). Moreover, the relatively dry climate is more conducive to human settlement (Murphy and Lugo 1986). For all these reasons, areas supporting dry forest are usually the first to be cleared and settled in the tropics (Holdridge 1970, Hartshorn 1992). Janzen (1988) suggested the critical period for conservation of tropical dry forests was 100 years ago and that most of the dry forest biome has now been reduced to scattered fragments.

Mangroves

Mangroves, a group of unrelated tree species occupying sites within the bounds of high and low tides (Simberloff 1983), fringe many salt and brackish water ecosystems in tropical and subtropical regions. Information on the status of mangrove forests is even more sparse than that for upland forests, but all indications suggest these forests are declining due to pollution, unrestricted collection of firewood and timber, and coastal development (Christensen 1983, Leonard 1987). For example, country environmental profiles summarized in Leonard (1987) indicate that <10% of the original mangrove forests remain in Guatemala, and that mangroves have been significantly reduced in Costa Rica (half of original mangroves harvested), Panama, and El Salvador. Overall, mangroves do not provide primary winter habitat for many migratory land birds, but they are important in certain regions and for certain species (see below).

Pine Forest

Pine and mixed pine-hardwood forests occur naturally in scattered regions throughout northern Central America, Mexico, and the Caribbean and have been introduced for plantation harvesting as far south as Ecuador (e.g., Garrison and Pita 1992). Many migrants associated with conifers during the breeding season also overwinter in pine-dominated habitats (see below). Pine forests have not been depleted to the same extent as broadleaved forests because pines are fast-growing and more easily managed than tropical broadleaved trees. Indeed, fire control and management schemes have allowed commercial production to expand dramatically in recent years, while still maintaining relatively constant acreage (e.g., see references in Leonard 1987; also see Salazar 1990). A proportion of these stands representing mature and old growth forest, however, appears to be declining due to accelerated harvesting schedules (Leonard 1987).

Future Scenario For Tropical Forests

Projections of tropical broadleaved forest resources surviving into the first several decades of the 21st century are dismal, but clearly dependent upon the level of conservation and management initiated by individuals, corporations, and governments during the next decade (e.g., Myers 1979, Janzen 1986, Gradwohl and Greenberg 1988, Wilson 1988). Currently, approximately half the area is capable of sustaining broadleaved forests in the neotropics actually supports closed-canopy forest, but most of this is in the Amazon Basin (Myers 1980, 1991; Mahar 1989). Most deforested land has been converted to permanent pasture and agricultural land, each comprising approximately 10-30% of the area in most Central American countries (Leonard 1987:Table A.33). Many surviving closed forests are not old-growth, but represent advanced secondary forests that probably have not yet reached their former levels of biological diversity and ecological function (Opler et al. 1977, Mabblerley 1992). Moist forests in Latin America and the Caribbean as a whole are being destroyed at a rate of approximately 0.5-1.0% per annum (Lanly 1982, Grainger 1983). However, deforestation is nearly three times higher within the area encompassing the winter ranges of most migratory species (Mexico to Colombia). Caribbean islands already have been so extensively altered that little natural forest remains to be cut (Myers 1980, Lugo 1990, McElroy et al. 1990, Arendt 1992).

The following scenario of the probable fate of forested neotropical biomes is based upon a compendium of published data and projections of conservation biologists. It assumes that current rates of deforestation will not be substantially reduced in the near future (Simberloff 1986). By the early 21st century, once-forested neotropical landscapes will mostly be a mosaic of agricultural lands, cattle pastures, and secondary forests in various stages of regeneration (Terborgh 1980, Melillo et al. 1985, Janzen 1986). In all regions except Amazonia, extensive tracts of primary or advanced secondary forest will probably be restricted mainly to national parks and reserves, as in present-day Costa Rica (Stiles 1985, Sader and Joyce 1988). In much of Mesoamerica and the Caribbean, forests will be reduced to disturbed, isolated fragments that occur predominantly at higher elevations (Rappole et al. 1983, Rubinoff 1983, Janzen 1986). The Brazilian Amazon will contain the bulk of the remaining undisturbed moist forest in the New World Tropics (Myers 1980, Lanly 1982). Mangrove and other wetland ecosystems will also be degraded, but to what extent is difficult to predict. Although the extent of upland pine forests may remain essentially unchanged, intensified timber management is likely to cause major changes in age structure and floristic composition. Management-oriented forestry, including agroforestry, is projected to be integrated into many forest ecosystems in the ensuing decades (National Research Council 1982, Anderson 1990, Kiernan et al. 1992). Estimations of extinctions of tropical flora and fauna due to this rapid conversion of forested landscapes to "agroscares" (*sensu* Janzen 1986) range from

catastrophic to relatively mild (Simberloff 1986, Raven 1988, Wilson 1988). How might these dramatic changes in landscape composition affect migratory landbirds? To begin to address that question, we need to critically examine habitat use, survival, and behavioral ecology of migrants during the overwinter period and then place this information into the context of widespread removal of primary tropical forests.

HABITAT AND GEOGRAPHIC DISTRIBUTION OF MIGRANTS IN THE NEOTROPICS

Conventional wisdom holds that migratory landbirds in the neotropics are most abundant (1) at higher tropical latitudes and (2) in disturbed habitats, such as secondary growth and edges (Karr 1976, Terborgh 1980, Willis 1980). A third generality, that overwintering migrants occur disproportionately at middle elevations (1000-2500 m), has also received some support during the past 30 years (Karr 1976; for review, see Terborgh 1980). Research conducted in the past 15 years allows a more quantitative assessments of these and other generalizations. Furthermore, application of information on general patterns of habitat use by target species groups can help conservationists identify areas and habitats that warrant special protection (Margules and Usher 1981, Diamond 1985).

We compiled data from nearly 50 studies (>300 study sites) to identify those habitats and regions in the tropics supporting the greatest numbers of migratory birds during winter. Only reports that met the following criteria were included in analyses: (1) study was conducted largely or entirely during the winter period (as opposed to autumn or spring migration); (2) sites were located between the Tropics of Capricorn and Cancer, with the exception of one study located in southern Florida and the Bahamas; (3) data on habitat use were gathered through a scientifically acceptable procedure, such as visual/auditory surveys or mist-netting (simple species lists based upon informal surveys were not included); and (4) data were collected within defined individual vegetation types (survey results pooled over several habitats were not acceptable). Several types of information were extracted from each study: (1) percent of individuals surveyed that were North American migrants; (2) percent of species surveyed that were migrants; and (3) total number of migratory species detected. Because all three of those variables were significantly correlated (percent individuals vs. percent species, Spearman's $r = 0.83$; percent individuals vs. number of species, $r = 0.55$; percent species vs. number of species, $r = 0.64$; $P < 0.0001$) and exhibited similar trends in our analyses below, only results based upon numbers of migratory species detected will be presented. Habitat, topographic and geographic information were taken from descriptions provided by each author or from other relevant sources. Environmental data were grouped in broad categories for statistical analyses (Table 1). Analysis of variance (or Kruskal-Wallis test) was used to detect statistically significant

Table 1. — Habitat and geographical information used in analyses of migrant distribution in the neotropics.

Variable	Category	Description
HABITAT TYPE	Moist forest	Semi-evergreen to evergreen forests >10 m tall in regions generally receiving >150 cm rain/yr. Examples include wet, moist, montane, and cloud forests.
	Dry forest	Semi-evergreen to deciduous forests > 5-10 m tall in regions generally receiving <150 cm rain/yr with a pronounced dry season. Examples include dry, oak, and sclerophyll, as well as arid limestone, forests.
	Pine forest	Habitats dominated by coniferous trees. Examples include pine and pine-oak-fir forests and pine-savanna.
	Scrub	Early successional or naturally-occurring broadleaved habitats <5-8 m tall. Examples include early successional dry and moist forests, thornscrub, and savanna-scrub.
	Open	Natural or human-altered habitats low in stature with few woody plants. Examples include open field, pasture, coastal dunes, marsh, and savanna.
	Artificial	Vegetation types heavily altered for agricultural or residential uses, but with vegetation >4 m tall. Examples include urban areas/parks and citrus or coffee plantations.
HABITAT HEIGHT	<5 m	
	6 - 10 m	
	11 - 20 m	
	>20 m	
DISTURBANCE	Disturbed	Moderate to heavy disturbance. Examples of disturbances include logging, fragmentation, agriculture, residential, and clearing of forest understory.
	Undisturbed	Very slight to nonexistent disturbance.
ELEVATION	≤200 m	
	201 - 500 m	
	501 - 1000 m	
	1001 - 2000 m	
	>2000 m	
INSULARIZATION	Mainland	
	Island	
LATITUDE	≤5° N	
	6 - 15° N	
	16 - 25° N	
	>25° N	

(P) differences in distribution of migrants across gradients or categories of the environmental variables. Below, we present a synopsis of those results; more details can be found in Petit et al. (unpubl. ms.).

disturbed than in undisturbed, vegetation types (Karr 1976, Terborgh 1980). However, no habitat association exhibited a highly depauperate migratory bird assemblage, which indicates that migrants as a group use a broad array of vegetation types during winter (see Lynch 1992).

Habitat Type

On average, migratory species richness reached its peak in residential and agricultural habitats (fig. 1A). Those artificial habitats supported approximately 50% more species than vegetation types dominated by natural woody vegetation associations and more than twice the number of species found in open areas, such as pastures and grasslands. These analyses support the belief that more migratory species overwinter in

Habitat Height

More species per study were observed in habitats of intermediate height (5-20 m) than in habitats of shorter or taller stature (fig. 1B). Because many habitat types attain heights of 5-20 m, this analysis cannot directly equate habitat heights with particular vegetation types. However, these data suggest that most migrants avoid tall, moist forests, the only habitat that

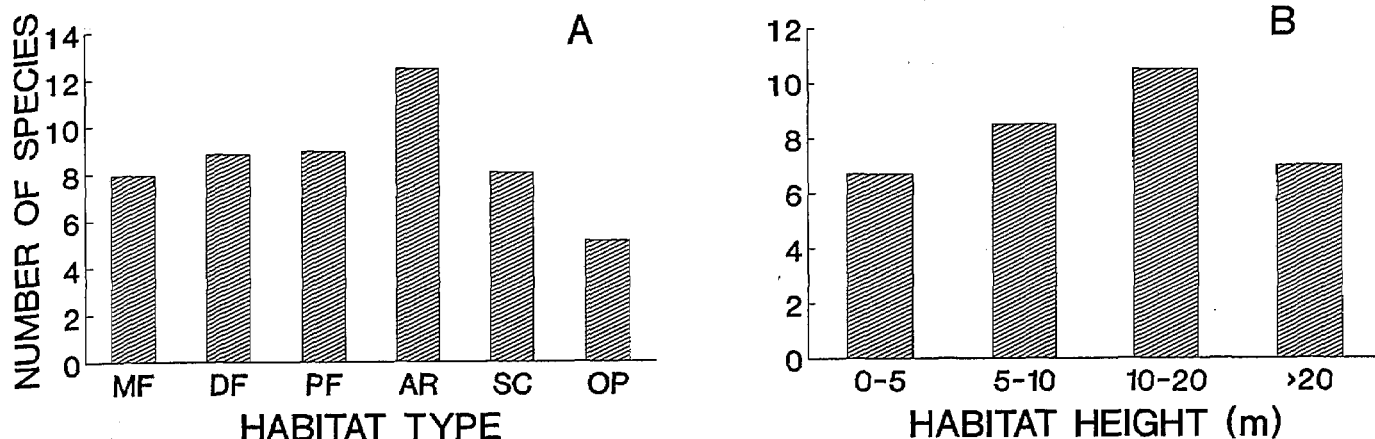


Figure 1. — Average number of migratory species detected per study plot (A) for different habitat types and (B) across habitats of various canopy heights. MF = moist (wet) forest; DF = dry forest; PF = pine forest; AR = artificial habitats, such as urban parks, residential areas, and citrus groves; SC = scrub or early second-growth; and OP = open habitats, such as grassland and pasture. See text and Table 1 for details.

typically exceeds 20 m in height. This interpretation is supported by the fact that migrants were twice as abundant in shorter (≤ 20), regenerating moist forest plots (average of 13 species detected) than in mature forests (6 species).

Disturbance Level

The number of migratory species was greatest in disturbed habitats (fig. 2A). Because this result could reflect use of artificial habitats (all of which are classified as disturbed) as opposed to disturbed natural forest, we examined the effect of disturbance within each forested vegetation type. Disturbed moist and dry forests supported 100% and 37% more species (respectively) than their undisturbed counterparts, although this difference was not statistically significant for dry forests. Disturbance level did not greatly influence use of pine forests by migratory birds as a group.

In general, then, more migratory species at a given site occur in disturbed habitats than in natural vegetation types, confirming patterns recognized by Karr (1976), Terborgh (1980) and many ornithologists before them. However, our analyses show that natural forests also support a diverse assemblage of migrants. Moreover, not all types of disturbance provide suitable habitat for migratory birds. Most migratory birds require that some woody vegetation persists, often in the form of canopy or subcanopy trees (Saab and Petit 1992). One exception appears to be citrus groves, where migratory bird abundance and richness can sometimes exceed that of most other nearby habitats (Mills and Rogers 1992, Robbins et al. 1992).

Elevation

Migrants were under-represented at elevations above ca. 500 m (fig. 2B), contradicting the previously cited generalization that migrants prefer middle elevations (Leck 1972a, Karr 1976). Even within a given forest type, lowland sites supported at least as many, and usually more, species as did higher elevations.

Insularization

Migratory bird assemblages were nearly twice as species-rich on continental sites compared with island habitats (fig. 3A), contrary to patterns described by Leck (1972b) and Karr (1976). Migratory birds comprised similar proportions (individuals and species) of the total avifauna on islands and the mainland (Petit et al., unpubl. ms.), but this result was due to a latitudinal effect (see below) associated with the fact that most Caribbean islands are located at more northerly latitudes within the tropics. The relative paucity of migrants within habitats on islands may be due to increased energetic costs and mortality risks associated with flying long distances over unsuitable (water) habitat in search of relatively small land masses (Moreau 1972, Terborgh and Faaborg 1980).

Latitude

The number of migratory species detected per study reached its peak between 16° N and 25° N (northern Central America and southern Mexico), which was twice the number of species present in southern Central America and South America (fig. 3B; also see

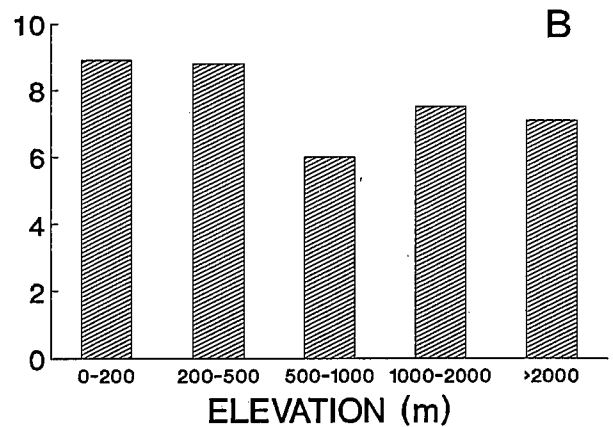
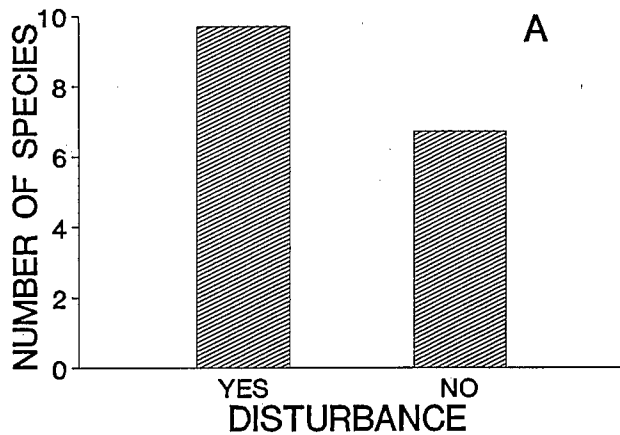


Figure 2. — Average number of migratory species detected per study plot that varied in (A) level of disturbance and (B) elevation. See text and Table 1 for details.

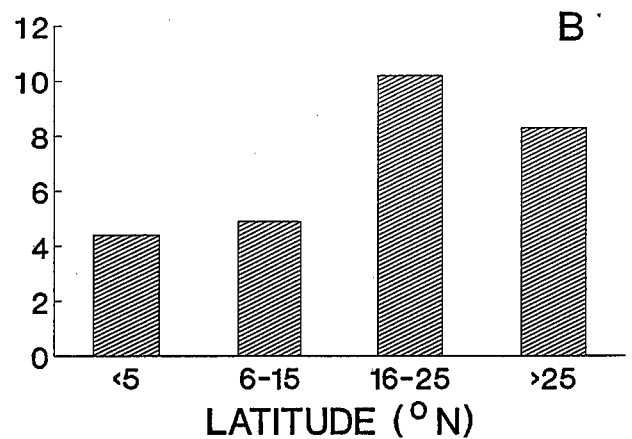
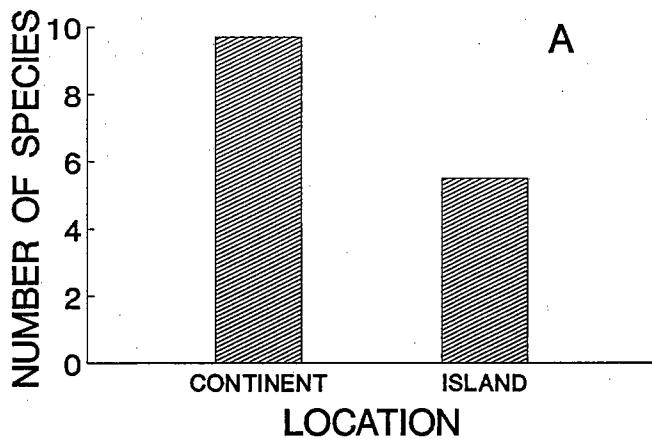


Figure 3. — Average number of migratory species detected per study plot on (A) islands vs. mainland sites and (B) at different latitudes. See text and Table 1 for details.

Rappole et al. 1983). Again, this distribution may reflect costs and risks of migration (Greenberg 1980, Terborgh and Faaborg 1980).

MOIST AND DRY FORESTS: TWO THREATENED TROPICAL ASSOCIATIONS

Taken together, the above analyses suggest that the greatest number of migratory species are found in disturbed, low elevation habitats at high tropical latitudes in Mexico and

northern Central America. These geographic and ecological patterns may provide general preliminary guidelines for identification of important habitat for migratory birds as a group. However, we recognize that bird-habitat relationships are both complex and species-specific. Identification of the most appropriate potential reserves, for example, may be best served by considering each area on a site-by-site basis and by taking into account individual species of particular interest. Moreover, not all habitats that support migrants are of primary interest to conservation biologists because some represent habitats (e.g., early successional growth, plantations) that are being created, not threatened, by forest conversion. However, several forest

associations are of special importance to conservation efforts in the neotropics. Here, we examine ecological correlates of migratory bird use of moist and dry forest associations using the data set outlined above.

The most widely-recognized formations of moist (including wet) tropical forest are based upon Holdridge's (1947) Life Zone concept as they relate to elevation (also see Whitmore 1991). Here, we consider four broad categories of moist forest: coastal (<200 m), lowland evergreen (200-500 m), lower montane (500-2000; includes premontane), and upper montane (2000 m) forests. Coastal forests were distinguished from lowland evergreen forests because of often higher human populations along coastlines compared to more upland areas (e.g., Myers 1980:150, Janzen 1986). Because the level of forest disturbance was related to habitat occupancy by neotropical migrants (see above), disturbed and undisturbed sites were examined separately.

In disturbed moist forests, numbers of migratory species showed a weak (nonsignificant) tendency to decline with elevation. Migratory birds in undisturbed moist forests, on the other hand, showed a significant decline in number of species across the elevational gradient. Undisturbed coastal and lowland evergreen forests contained 35% and 125% (respectively) more migratory species than undisturbed, montane (>500 m) forests. Upper montane (cloud) forests supported fewest migratory species in both disturbed and undisturbed forests. In nearly all moist forest associations, disturbed sites supported more migratory species than more pristine sites. Thus, migrants as a group appear to prefer lowland (<500 m) evergreen forests to montane forests, but this relationship is weaker where forests are disturbed. Migrants may increase use of habitats along an elevational gradient in response to slight or moderate levels of forest perturbation if disturbances enhance suitability of wet forests for those species (Petit 1991).

Although the general pattern of moist forest use suggests disturbed and lowland forests support the greatest number of migratory bird species, all moist forest associations were used by migrants. Information on body condition (e.g., fat scores) and overwinter survival rates are necessary to gain better insight into suitability of each forest association, but moist tropical forest clearly represents an important habitat for overwintering migrants. On average, eight migratory species were detected within each plot of evergreen forest (fig. 1A), representing about one-fifth the total winter bird community on those sites (Petit et al., unpubl. ms.). Moreover, disturbed and undisturbed mature, evergreen forests are principal winter habitats for >40 migratory species (Petit et al., unpubl. ms.; see below). In summary, despite the fact that migrant diversity tends to be highest in disturbed forests, conservation of many migratory species, in addition to hundreds of species of resident tropical species, is dependent upon preservation of undisturbed moist evergreen forests.

Dry forests contained similar numbers of migratory species as found in moist forests, although migrants comprised a larger proportion of the local avifauna in dry forests (Petit et al., unpubl. ms.). Disturbance may have an important effect on

numbers of migrants occupying dry forests, as disturbed sites contained nearly 60% more species than undisturbed sites. However, this trend was not statistically significant. More migratory species were detected on plots situated within coastal and lowland dry forests (average of 9.5 species) than in upland forests (8 species), but the difference was not significant. Migrants were significantly more abundant in taller (>10 m) dry forests and on mainland sites.

Dry forests represent an important habitat for migrants during winter, especially at more northerly latitudes. Little is known about use of dry forest habitats in South America by migrants (Bosque and Lentino 1987). Because the Pacific slope of Mexico and Central America is comprised largely of dry forest associations and because a large proportion of species that breed in western North America overwinter there (Hutto 1980, Terborgh 1980), retention of dry forest is especially important for migratory bird conservation. Additionally, dry forest associations are significant for species overwintering on the Yucatan Peninsula (Lynch 1989) and Caribbean islands (Arendt 1992).

MIGRANTS MOST LIKELY TO BE IMPACTED BY TROPICAL DEFORESTATION

Analysis of overall patterns of habitat use by migrants on a regional or continental level is important in determining those habitats and geographic locations that support the greatest number of individuals and species, an especially critical need during the initial stages of identification and development of prospective biological reserves (Diamond 1986, Jenkins 1988). This type of conservation plan, similar to both gap analysis (Burley 1988) and the "coarse filter" approach to species management (Noss 1987a), is aimed at maximizing the number of species that gain protection, while minimizing acreage to be acquired. However, equally important is assessment of habitat needs of individual species to identify those migrants that may not be adequately protected under a general management plan. Furthermore, interpreting observed population declines of migrants requires a firm understanding of year-round ecologies of those species. Habitat-dependent factors (e.g., probability of nest predation or survival) during both breeding and nonbreeding seasons are thought to be the root causes of those declines (Aldrich and Robbins 1970, Terborgh 1980, Greenberg 1986). Not surprisingly, obtaining quantitative information on habitat association of neotropical migrants is frequently cited as a primary research priority by conservation biologists (Rappole et al. 1983, Hutto 1989, Lynch 1989, Blake and Loiselle 1992).

Abundant qualitative information exists on winter habitat use by neotropical migrants, but summarizing those data is difficult because of the divergent goals of each study as well as different ways in which data were collected, presented, and interpreted. We summarized this information in a quantitative, objective manner by extracting data from the literature and

Table 2. — Projected vulnerability of neotropical migratory landbirds to anthropogenic alteration of tropical, broadleaved forests. See Appendix A for details.

HIGHLY VULNERABLE		VULNERABLE BUT OCCUPY SITES OF MODERATE DISTURBANCE	
Chuck-will's-widow (<i>Caprimulgus carolinensis</i>)	Worm-eating Warbler (<i>Helmitheros vermivorus</i>)	Black-billed Cuckoo (<i>Coccyzus erythrophthalmus</i>)	Northern Parula (<i>Parula americana</i>)
Olive-sided Flycatcher (<i>Contopus borealis</i>)	Swainson's Warbler (<i>Limnithlypis swainsonii</i>)	Yellow-billed Cuckoo (<i>Coccyzus americanus</i>)	Magnolia Warbler (<i>Dendroica magnolia</i>)
Western Wood-Pewee (<i>Contopus sordidulus</i>)	Northern Waterthrush (<i>Seiurus noveboracensis</i>)	Broad-tailed Hummingbird (<i>Selasphorus platycercus</i>)	Black-throated Blue Warbler (<i>Dendroica caerulescens</i>)
Veery (<i>Catharus fuscescens</i>)	Louisiana Waterthrush (<i>Seiurus motacilla</i>)	Yellow-bellied Sapsucker (<i>Sphyrapicus varius</i>)	Black-throated Gray Warbler (<i>Dendroica nigrescens</i>)
Blackburnian Warbler (<i>Dendroica fusca</i>)	Kentucky Warbler (<i>Oporomis formosus</i>)	Eastern Wood-Pewee (<i>Contopus virens</i>)	Townsend's Warbler (<i>Dendroica townsendi</i>)
Blackpoll Warbler (<i>Dendroica striata</i>)	Scarlet Tanager (<i>Piranga olivacea</i>)	Acadian Flycatcher (<i>Empidonax virens</i>)	Hermit Warbler (<i>Dendroica occidentalis</i>)
VULNERABLE BUT TOLERANCE TO SLIGHT DISTURBANCE		Willow Flycatcher (<i>Empidonax traillii</i>)	Black-throated Green Warbler (<i>Dendroica virens</i>)
Whip-poor-will (<i>Caprimulgus vociferus</i>)	Golden-winged Warbler (<i>Vermivora chrysoptera</i>)	Least Flycatcher (<i>Empidonax minimus</i>)	Black-and-white Warbler (<i>Mniotilta varia</i>)
Yellow-bellied Flycatcher (<i>Empidonax flaviventris</i>)	Chestnut-sided Warbler (<i>Dendroica pensylvanica</i>)	Hammond's Flycatcher (<i>Empidonax hammondi</i>)	American Redstart (<i>Setophaga ruticilla</i>)
Great Crested Flycatcher (<i>Myiarchus crinitus</i>)	Bay-breasted Warbler (<i>Dendroica castanea</i>)	Gray Flycatcher (<i>Empidonax wrightii</i>)	Ovenbird (<i>Seiurus aurocapillus</i>)
Wood Thrush (<i>Hylocichla mustelina</i>)	Cerulean Warbler (<i>Dendroica cerulea</i>)	Western Kingbird (<i>Tyrannus verticalis</i>)	Connecticut Warbler (<i>Oporomis agilis</i>)
White-eyed Vireo (<i>Vireo griseus</i>)	Prothonotary Warbler (<i>Protonotaria citrea</i>)	Blue-gray Gnatcatcher (<i>Polioptila caerulea</i>)	MacGillivray's Warbler (<i>Oporomis tolmiei</i>)
Yellow-throated Vireo (<i>Vireo flavifrons</i>)		Gray-cheeked Thrush (<i>Catharus minimus</i>)	Hooded Warbler (<i>Wilsonia citrina</i>)
		Swainson's Thrush (<i>Catharus ustulatus</i>)	Wilson's Warbler (<i>Wilsonia pusilla</i>)
		Solitary Vireo (<i>Vireo solitarius</i>)	Canada Warbler (<i>Wilsonia canadensis</i>)
		Warbling Vireo (<i>Vireo gilvus</i>)	Yellow-breasted Chat (<i>Icteria virens</i>)
		Blue-winged Warbler (<i>Vermivora pinus</i>)	Black-headed Grosbeak (<i>Pheucticus melanocephalus</i>)
		Virginia's Warbler (<i>Vermivora virginiae</i>)	Hooded Oriole (<i>Icterus spurius</i>)
		Lucy's Warbler (<i>Vermivora luciae</i>)	

applying it to an index which estimates vulnerability of a species to population decline due to alteration of tropical forest. Derivation of this index is outlined in Appendix A. It is important to keep in mind this vulnerability index is based upon only one of several factors (Rabinowitz et al. 1986) that could influence a species' susceptibility to extinction.

Of 123 migratory species considered, 23 (19%) were mainly restricted to undisturbed broadleaved forests during winter (top two sections of Table 2). These species should be most sensitive to forest alteration. Thirty-seven additional species (30%) were often associated with forested habitats, although they also used certain types of disturbed vegetation (e.g., tree crops, forest

openings, fragmented forest; Table 2). That migratory birds utilize broadleaved forests during winter is not surprising, but this analysis provides direction as to which species are likely to be highly impacted by forest conversion, and suggests that at least 19% of migratory landbirds fall into that category. In fact, the 23 species most closely-tied to broadleaved forests (Table 2) possibly have already been affected by current levels of deforestation. Those 23 species exhibited average population declines >8 times that estimated for the 37 species less dependent upon close-canopied forests (1978-1988 population data taken from Sauer and Droege 1992). Furthermore, this trend is independent of nesting habitat (log-likelihood ratio test; $G =$

1.21, $P > 0.50$). This last point is important because migrants that overwinter in broadleaved forests also tend to breed in forests in temperate areas, thereby confounding attempts to separate events during these two seasons (also see Robbins et al. 1989b, Sauer and Droege 1992). Our list of species in greatest danger of undergoing dramatic population changes should be considered conservative because only 123 of the approximately 200 species of neotropical migrant landbirds were considered in the above analysis. Furthermore, we incorporated only one aspect of the ecology of species (habitat use) that makes them vulnerable to extinction. Certainly, our inventory will expand when information on relative global population sizes and geographic winter ranges are incorporated (Rabinowitz et al. 1986, Kattan 1992, Reed 1992).

Many alarming predictions have been made (mostly in the popular and semi-technical literature) about the ultimate effect of tropical deforestation on migratory bird populations. Those assessments may well prove to be correct, but at the same time they often are not based on rigorous application of available scientific literature (also see perspectives of Hutto 1988). Several excellent overviews of migrant vulnerability to tropical forest conversion have been published and species lists derived from those studies correspond reasonably well with what we have produced (for example, see Rappole et al. 1983, Diamond 1991). Because these sensitive species exhibit varied responses to available habitat types, ecologies of individual species need to be embodied within future conservation plans. Finally, our list of species, like others, is based upon multiple assumptions and incomplete data; it is therefore open to further research and revision.

SUMMARY OF HABITAT USE

Data presented here are general and preliminary because most analyses considered only one or two habitat and geographic variables. Relative importance of each factor must be considered in the context of all other variables. These analyses, however, do provide an indication of use of different tropical habitats by migratory birds.

Clearly, all tropical habitats contained some migratory birds. Disturbed habitats, whether natural (e.g., regenerating or selectively logged wet forest) or unnatural (citrus plantation), supported the greatest number of migratory species. However, caution must be used when relating relative abundance of organisms to suitability because local high densities could reflect highly rigid dominance relationships and distributions based upon relative suitability of habitats (e.g., Van Horne 1981). For example, are young birds or females forced into suboptimal, disturbed habitats, where they overwinter in high densities relative to undisturbed forest (see below)? If so, mere distributions of individuals across habitat types does not give an accurate picture of relative suitabilities of those habitats, or indeed of habitat "preference" patterns. Information on physical

condition of individuals, along with survival, is necessary to accurately assess value of each habitat to migrants (Holmes et al. 1989).

On the other hand, distributions of individuals among habitats may indeed provide a reliable indication of relative suitabilities of those vegetation types (Orlans and Wittenberger 1991). For example, physical condition (Greenberg 1992) and survival rates (estimated indirectly through recapture rates; Rappole and Warner 1980, Robbins et al. 1987, Blake and Loiselle 1992) are not necessarily improved in undisturbed forests relative to disturbed forests (but, see Rappole et al. 1989). If the classical interpretation that habitat use reflects habitat suitability is, in fact, approximately correct, then our results and those of others suggest that migratory birds as a group are not being adversely affected by at least some current land use practices in Latin America and the Caribbean. The task for future researchers is to determine how much disturbance (and in what form) can a tropical forest withstand and still be suitable as winter habitat for neotropical migrants (also see Lynch 1992).

DEVELOPMENT OF EFFECTIVE MANAGEMENT AND CONSERVATION PLANS: LIMITATIONS OF GENERALIZATIONS ABOUT MIGRANT HABITAT USE

Limitations in funding and control over land use force resource managers and conservation biologists to strive for management plans that maximize number of species and individuals protected. While we recognize that habitat requirements and population biology of each species are unique, there is nevertheless a practical need to develop useful generalizations about the requirements necessary for survival of migrant birds in the neotropics. Above, we attempted to categorize preferred habitats of migrants as a group, as well as requirements for individual species dependent upon broadleaved forests. Even at the species level, however, broad management plans may be difficult to formulate due to variation in winter habitat use exhibited by different individuals and populations. Habitat models must be applied cautiously for wildlife species across their North America ranges (Bart et al. 1984, Stauffer and Best 1986), and this concern may hold for wintering grounds as well. Thus, unrecognized intraspecific variation in habitat use and life history traits can lead to dysfunctional management guidelines. Below, we briefly discuss three sources of variation in winter habitat use critical for conservation of migratory bird populations.

Geographic Variation in Habitat Use

Some disagreement among avian ecologists about habitat requirements of certain migrant species in the tropics probably reflects geographic variation in habitat use (Greenberg 1986,

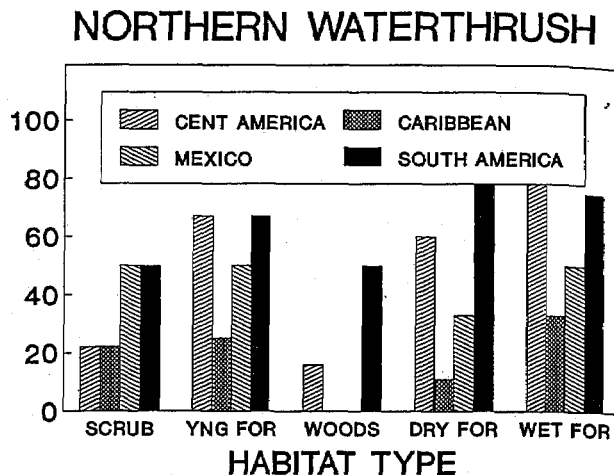
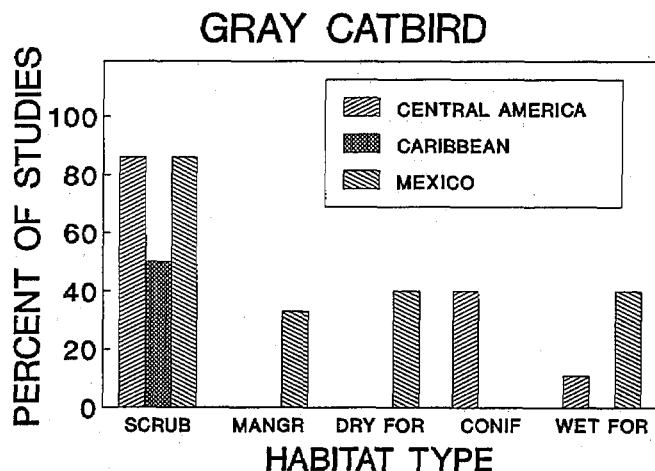


Figure 4. — Geographic variation in habitat use by Gray Catbirds and Northern Waterthrush. The ordinate represents the number of studies in which a species was found to occur in a given habitat type divided by the number of studies in which each species could have occurred in that habitat. See Appendix A for details.

Martin 1992, Morton 1992). For example, Gray Catbirds (*Dumetella carolinensis*) and Northern Waterthrushes (scientific names of some species are listed in Table 2) exhibit pronounced regional differences in habitat use (fig. 4). This may result from either disparate availability of habitats, regional differences in preference for certain habitat types, or a combination of both. Black-throated Green Warblers are commonly found in pine stands in northern Central America and on Caribbean islands, but occupy broadleaved forest associations in eastern Mexico and southern Central America, where pines are scarce (this study). This interpretation is complicated, however, by the fact that Black-throated Green Warblers at the edge of their winter range in western Mexico prefer montane broadleaved forest even though mixed-pine forests are present at similar elevations (Hutto 1992). Louisiana and Northern waterthrushes provide additional examples of how availability of a given habitat type in a region might influence habitat use. In continental areas, waterthrushes generally do not occupy residential areas during winter, but on densely-populated and developed Caribbean islands (compare Leonard 1987:Table A.2 with McElroy et al. 1990:Table 21.1) they use gardens as secondary habitats (this study; also see Arendt 1992).

Geographic variability in habitat preferences also may indicate either localization of different subspecies (see Ramos and Warner 1980) that respond to distinct habitat cues, or a manifestation of selective pressures that vary regionally. For example, geographic differences in habitat use could reflect differences in (1) assemblages of competing species (e.g., Bennett 1980, Keast 1980), (2) characteristics of the food base supported by vegetation associations (Janzen 1973), (3) predation pressure (Buskirk 1976) or other factors. Comparative studies of habitat use, and factors affecting that use, are needed to help determine the ecological basis of geographic variation

in habitat occupancy. For the migratory bird community as a whole, certain habitats are of high regional importance, e.g., mangroves in the Caribbean and cloud forests in western Mexico and South America (fig. 5). Whether geographic differences in habitat use reflect variation in these factors, or others (e.g., population density, climate), is unknown. However, for present conservation efforts, the mechanism for geographic shifts may be less important than knowledge of their mere existence. Geographic variation in habitat use by individual species and

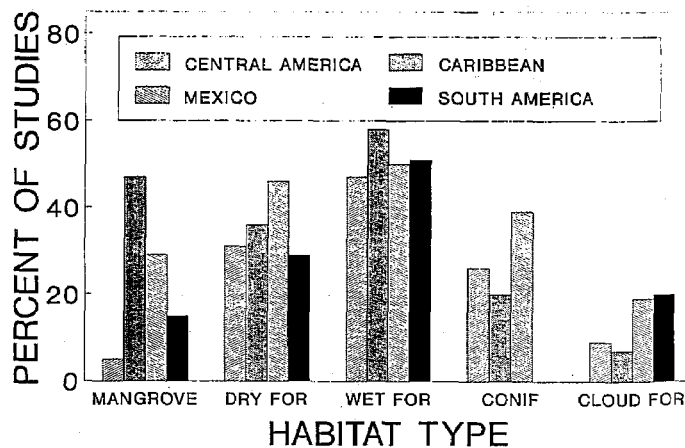


Figure 5. — Example of geographic variation in habitat use by migratory birds. The ordinate represents the number of studies in which a species was found to occur in a given habitat type divided by the number of studies in which each species could have occurred in that habitat, summed over all migratory species. See Appendix A for details.

regional assemblages may dictate a more localized (i.e., region-specific) approach to designing conservation plans for migratory birds in the tropics.

Sex- and Age-Specific Habitat Use

Habitat use by some migrants varies by sex, such that overall habitat distribution of a species reflects the combined, unique preferences of each sex. Lynch et al. (1985) showed that male and female Hooded Warblers in the Yucatan region differed in selection of winter habitat: males tended to occur in relatively tall, closed-canopy forest, while females were most often found in old-fields, native coastal scrub, treefall gaps, and other disturbed, low-stature vegetation. Sex-specific habitat selection has subsequently been documented for about 10 other migratory parulines (Lopez Ornat and Greenberg 1990, Wunderle 1992) and, in most cases, males occur at higher than expected frequencies in more mature habitats. Age-related exclusion of some individuals from certain habitats also may occur on wintering grounds, although evidence is sparse. In Belize, young (≥ 2 yr) male American Redstarts occupied habitats intermediate between those of females and older (> 2 yr) males (Petit and Petit, unpubl. data). Pearson (1980) described a possible latitudinal gradient of age classes for overwintering Summer Tanagers (*Piranga rubra*).

Sex- and age-specific habitat use has important ramifications for conservation of neotropical migrants. First, partitioning of winter habitats could lead to differential, habitat-based mortality rates either due to intrinsic factors or to more extensive loss of certain habitats than others. The resulting skewed sex-ratios would reduce the effective size of breeding populations and could dramatically enhance probability of local extirpation or extinction (Shaffer 1981). Second, placement of reserves must incorporate potential sex-based dichotomies in habitat use by assuring that appropriate habitat for both sexes is adequately represented. Finally, if innate or dominance-based habitat use is manifested in distinct geographic winter ranges for sex or age classes (e.g., Ketterson and Nolan 1983), then development of protected reserves or application of appropriate land use practices must be implemented throughout entire winter ranges of species.

Habitat Use During Migration

Migration to and from tropical areas is energetically stressful (Blem 1980) and mortality during this period may substantially limit size of breeding populations (Moore et al. 1990). Species use of available habitats during migration is largely unknown (but see Parnell 1969), especially in the tropics. Generally, though, migrants appear to be highly plastic (*sensu* Morse 1971) in their use of habitats during migration. Because migration habitats overlap extensively with winter habitats for many species, conservation of winter habitats may be an

appropriate means of preserving vegetation types occupied during migration. However, there are certain situations where special consideration may need to be directed towards habitat requirements of migrants during migration. First, forest patches and other vegetation associations along coastal areas may represent significant habitats for birds initially arriving to a land mass after having flown over a large body of water (the same argument holds for birds preparing to leave a land mass). Migratory birds often are stressed after such flights and require rapid replenishing of fat reserves (Moore and Kerlinger 1987, Moore et al. 1990). Access to fresh water may be equally important.

Second, forested corridors (MacClintock et al. 1977, Noss 1987b) may be especially useful landscape components for birds during migration. Although the value of corridors to migrating birds is unknown, strips of remnant vegetation connecting larger patches are thought to be directly related to persistence of populations that make widespread movements throughout their annual cycle, such as migratory birds (e.g., Saunders 1990). Furthermore, some migrants wander extensively even during mid-winter in the neotropics (often associated with frugivorous habits) and those individuals may suffer higher mortality than sedentary counterparts (Rappole et al. 1989). Thus, corridors could be an effective management tool for both migrating and overwintering migratory birds (as well as for resident species; Loiselle and Blake 1991). The migratory period needs special consideration in design and placement of tropical reserves, as well as identifying agricultural, forestry, and other land uses that provide adequate habitats for birds in migration.

FINE FILTERS AND CONSERVATION OF RESTRICTED SPECIES AND HABITATS

Most migratory species overwinter in various types and seral stages of broadleaved forest (see above) and, therefore, conservation efforts clearly need to be directed towards those widespread habitats. However, whereas a "coarse-filter" approach is designed to protect the majority of the target fauna in a region, "fine-filter" management practices are aimed at catching those species that passed through the coarse filter because of special habitat or ecological requirements (Noss 1987a). Restricted habitats or ecosystems especially sensitive to anthropogenic disturbances need to be considered in migratory bird conservation efforts because several of those habitats, specifically mangrove swamps and pine forests, are pivotal in the winter ecologies of certain migrants.

Mangroves are declining due to unrestricted collection of firewood, pollution, and development along coastal areas (e.g., Leonard 1987). In general, mangroves are not a primary habitat for migrants, but within certain regions, particularly the Caribbean, mangroves provide important winter habitats for migratory birds. For example, several parulines, such as American Redstart, Louisiana Waterthrush, Ovenbird and

Black-and-white, Hooded and Magnolia warblers, use mangroves extensively on Caribbean islands, but are found much less commonly in such swamps in Central and South America. Thus, mangroves may provide an important alternative forested habitat in areas where deforestation has claimed much of the native upland vegetation. Sustainance of regional overwintering populations could be important in maintaining the diversity of species' gene pools (e.g., Franklin 1980), as well as the regional breeding populations in North America (Ramos and Warner 1980, Atwood 1992). Furthermore, mangrove forest is a principal habitat for at least three long-distance migrants (Prothonotary and Swainson's warblers and Northern Waterthrush) throughout those species' wintering ranges. Maintenance of mangrove ecosystems requires determined intervention by national governments.

More than a dozen species of migratory birds rely heavily on pine-dominated forests as a principal habitat during winter (Petit et al., unpubl. ms.). Pine forests, including pine-savanna and pine-oak woodlands, constitute widely-dispersed habitats in Mexico, northern Central America, and the Caribbean. Given the patchy nature of pine forests and the value of the pine resources to national economies, special attention needs to be devoted to this vegetation type to ensure that forests remain not only sustainable, but also ecologically viable for wildlife, including migratory birds. For instance, prescribed burning is often used to control broadleaved understory and reduce fuel loads in pine stands (Salazar 1990). However, loss of broadleaved understory causes a severe reduction in quality of those sites for most migratory and resident birds (D.R. Petit, unpubl. data). Wildlife management principles need to be incorporated into the rotational and management schemes of tropical pine forests (*sensu* Harris 1984).

Another important component of the fine-filter approach is identification of species with restricted geographic ranges, as those species may be highly susceptible to extinction due to isolated, local events (Rabinowitz et al. 1986). Migratory species that have extremely limited winter ranges, for example Black-capped Vireo (*Vireo atricapillus*), and Kirtland's (*Dendroica kirtlandii*), Swainson's, and Mourning (*Oporornis philadelphia*) warblers, are likely to be overlooked in broad, multinational attempts to develop parks and reserves.

EFFECTS OF LAND USE PRACTICES ON MIGRATORY BIRD HABITAT

The fate of tropical ecosystems ultimately lies in ability of governments and local tropical communities, as well as economists, sociologists, biologists, and other professionals, to identify, devise and implement land use practices that provide an increasing standard of living for citizens, while at the same time preserving viable populations of diverse flora and fauna. These two goals should be central issues for all groups mentioned above. Use or conversion of natural vegetation

associations in the tropics as it relates to impacts on native flora and fauna can be placed under one of three broad categories: "conservative", "sustainable", and "destructive". These classifications are not discrete, but rather represent overlapping regions along a continuum from preservation to decimation of natural ecosystems (a continuum can also be envisioned for short- or long-term economic development). Below we discuss examples of each type of land use and how they might affect migratory birds. We then place land-use into the context of the conservation goals outlined above. Because cutting of tropical forests for alternative land uses necessarily leads to fragmentation of forest biomes, we begin this section with a brief overview of impacts of forest fragmentation on neotropical migratory birds during winter.

Effects of Forest Fragmentation on Migrants

Extensive research in North America has shown that presence of migratory birds breeding in temperate forests is intricately related to tract size (Whitcomb et al. 1981, Lynch and Whigham 1984, Blake and Karr 1987, Robbins et al. 1989a). Similar information on effects of insularization in Latin America, however, is meager. Fragmentation and isolation of tropical broadleaved forests have pronounced biological ramifications not only for plants and animals that are directly displaced, but also for individuals that remain after isolation. For example, the microclimate of fragments can be substantially altered within several hundred meters of edges, such that a concomitant change in plant species often results, which, in turn, is partly responsible for redistribution or local extinction of the fauna inhabiting the forest island (e.g., Lovejoy et al. 1984, Williams-Linera 1990, Laurance 1991, Laurance and Yensen 1991, Saunders et al. 1991). Forest fragments do not contain as many resident tropical bird species as contiguous tracts during either the breeding or nonbreeding season (Terborgh 1974, Willis 1979, Robbins et al. 1987). Most long-distance migrants, however, do not appear to exhibit such pronounced sensitivity to reduced forest area during the boreal winter (Robbins et al. 1987). In fact, many migrants that are area-sensitive on the breeding grounds show no such relationship, or are found at higher densities in forest remnants than in larger tracts, during winter (Robbins et al. 1987, 1992; Askins et al. 1992). These few studies support our previous conclusions that migrants as a group are most abundant in disturbed and fragmented habitats (see above). Despite the apparent lack of fragmentation effects on most migratory birds, so few data have been collected that results must be viewed as strictly preliminary. Indeed, several migratory species have exhibited disproportionate use of large forest tracts in the neotropics (Robbins et al. 1987) and some migratory species identified as highly susceptible to forest disturbance (Table 2) may also prove sensitive to the area of forest tracts.

"Conservative" Land Use Practices

All things being equal, preservation of extensive tracts of native vegetation would be the most acceptable conservation practice for many conservation biologists. In reality, socioeconomic considerations are often of overriding priority, such that limitations are placed on the extent of pristine ecosystems that can be protected from anthropogenic disturbances. Examples of conservative land use practices are well-known throughout the world, under the form of Biosphere Reserves, Wilderness Areas, National Parks, and World Heritage Sites. A system of such reserves is thought to play a critical role in the long-term preservation of tropical diversity (e.g., Rubinoff 1983, Wilson and Peter 1988, Cornelius 1991).

The concept of nature reserves also is highly compatible with conservation of migratory birds. As outlined above, several dozen migratory species occupy tropical broadleaved forests during winter (also see Petit et al., unpubl. ms.) and those most reliant upon undisturbed forests will be particularly susceptible to severe population declines in the future. Because tropical landscapes will undergo increased deforestation in coming decades, protected natural areas is one important approach for maintaining numbers of forest-dwelling, migratory birds, as well as resident species.

"Sustainable" Land Use Practices

The future economies and natural resources of Latin America are believed to rest upon the concept of "sustainable development", defined as "economic development that meets the needs of the present without compromising the ability of future generations to meet their own needs" (WCED 1987). This definition, as applied to forests, explicitly or implicitly identifies three components of sustainable development: competitive productivity, renewability of resources, and maintenance of ecological diversity (Maini 1992). Contained within the bounds of sustainable development are a myriad of land use practices which vary in their regard for "maintenance of ecological diversity". For example "extractive reserves" (Fearnside 1989) allow indigenous communities to remove certain highly-renewable products (e.g., Brazil nuts, rubber latex, medicinal plants, and fruits) from the reserve, but prohibit alteration of the natural structure or function of the forest. Clearly, this type of plan, if implemented properly, would provide suitable habitat for many species. At the other end of the continuum are certain types of "agroforestry" (von Maydel et al. 1982), in which native overstory trees are replaced with exotic species and understories are stripped clean by grazing cattle (e.g., Combe 1982). Despite substantial variation in the quality of "sustainable" lands for migratory birds (and other wildlife), some forms of sustainable development are relatively benign from the viewpoint of migratory bird conservation. Here,

we outline several examples of sustainable development projects that take into account preservation of wildlife and appear to be compatible with survival of many migratory bird species.

One of the most promising forestry practices in the neotropics appears to be strip clearcutting (Hartshorn 1990, Ocana-Vidal 1992). This method of managing natural forests, conceived by the Tropical Science Center of Costa Rica, is designed to harvest wood from long (100-500 m), narrow (30-50 m) strips through forest. The width of a strip is meant to mimic natural treefall gaps, thereby allowing natural regeneration to occur rapidly. Several strips are harvested each year and cuts made in successive years are at least 100 m apart. The projected rotation period is currently set at 30-50 years. By reducing the area of each strip, detrimental effects associated with logging, such as erosion and alteration of local microclimate, are minimized. Extraction of logs is made with the aid of oxen to reduce disturbance and soil compaction. This design is similar in concept to that proposed by Harris (1984), whereby a certain proportion of a given tract remains in mature forest and areas in similar stages of regeneration are overdispersed. Few neotropical migrants that utilize forested habitats during winter appear to avoid sites that have undergone such small-scale disturbances (see above and Petit et al., unpubl. ms.). In fact, many forest-dwelling migrants are more common along forest edges than interior (Petit et al. 1992). Because strip clearcutting results in no net loss of forest cover and is economically beneficial to rural communities, it may prove to be an important forest management technique in the future.

A number of demonstration projects are currently underway evaluating economic feasibility of selective logging in rural communities as well as new approaches to minimize impacts of cutting and extraction of trees (e.g., Kiernan et al. 1992). Selective logging of highly marketable timber has been practiced in the neotropics for >200 years. However, in many instances, large national or multinational corporations have extracted timber, and little profit remains to be distributed among local landowners. One recent approach has been to form cooperatives, whereby local landowners pool their resources and make informed decisions (often with the aid of government and foreign consultants) about which and how many trees to harvest in a given year. In this way, local people derive the bulk of the economic benefit. Even extraction of single trees from tropical forests often results in major collateral damage to surrounding forest. Recently, though, harvesting practices have been implemented to reduce this extraneous damage and enhance value of sustainable forests (Dykstra and Heinrich 1992, Kiernan et al. 1992). Formation of cooperatives and implementation of environmentally-sound harvesting techniques has several implications for conservation of migratory birds. First, because income derived from cooperatives improves the local standard of living, fewer demands should be placed on surrounding forests. Second, reduced environmental damage from logging operations keeps the structural and microclimatic environment of the forest interior relatively intact.

Clearly, the more closely agroecosystems mimic natural vegetation associations the more suitable those systems are for forest-dependent wildlife. Many types of agroforestry strategies provide habitat for migratory birds. For example, Mayan cultures have incorporated concepts of sustainable forestry into their "forest gardens" for centuries (Alcorn 1990). These small plots of land surrounding family dwellings are comprised of native trees and shrubs that produce fruit, wood, nuts, and other products for sustaining the local community (Gomez-Pompa and Kaus 1990). Scattered among these woody plants are small patches of annual crops (e.g., corn, beans). There also may be regular management of nearby moist forest. Here, some undesirable trees are selectively removed to allow certain species to mature or fruit at faster rates (Anderson 1990, Gomez-Pompa 1991). Another form of agroecosystem that is widespread throughout the New World Tropics consists of low-stature tree crops (e.g., cacao, coffee) cultured under a canopy of shade trees (an unfortunate trend in recent years is to grow these crops without shade trees). Shifting-cultivation, one major cause of conversion of tropical forests, can be considered a form of sustainable development provided the proportion of landscape farmed at any one time is relatively small (Uhl et al. 1990). Shifting-cultivation realizes its greatest potential as a type of sustainable use when local farmers are able to incorporate sound management practices, thereby increasing the productive life of a plot and decreasing the pressure on surrounding forest. However, when population pressure results in shorter fallow periods and a higher proportion of the landscape being cultivated, the neutral or beneficial effects of shifting cultivation tend to become negative. These small-scale systems mentioned often result in more open, disturbed forests, habitats that support many species of migratory birds (see above).

Agroforestry is often manifested as a combination of cattle and overstory trees (for shade or timber) or trees crops, such as *Citrus* (Combe 1982, Shane 1986). These forms of land use are detrimental to many migratory species (e.g., forest specialists), but do have potential to provide habitat for certain neotropical migrants, depending mainly on the extent and complexity of woody cover that is maintained (Lynch 1989, Saab and Petit 1992). Incorporation of agroforestry practices into pasture development could provide a viable alternative to barren pasture, due to economic benefits to landowners and to use of these habitats by wildlife.

"Destructive" Land Use Practices

Destructive types of land use by definition provide few bird species with suitable habitat. Heavily-grazed pasture with few trees or shrubs is perhaps the most conspicuous form of tropical land use that is not readily occupied by migratory birds (Karr 1976, Saab and Petit 1992). Likewise, active rice (Robbins et al. 1992), corn, and bean fields probably support few species of migrants. Extensive monocultures, such as banana plantations (Stiles and Skutch 1989, Robbins et al. 1992) appear also to be

avoided by migrants. Most migratory birds using these agricultural lands are habitat generalists (e.g., Yellow-rumped Warbler [*Dendroica coronata*]) or are characteristic of highly-disturbed vegetation types (e.g., Common Yellowthroat [*Geothlypis trichas*], Indigo Bunting [*Passerina cyanea*]) in their wintering areas. Suitable winter habitat is not presently limited for such species. *Citrus* monocultures, however, have been reported to contain extremely dense concentrations of migrants, including some species considered to be typical of forested habitats (Mills and Rogers 1992, Robbins et al. 1992).

Conversion of native vegetation to pasture and some types of non-woody monocultures, such as cash crops, are clearly the most imminent threats to wildlife in the neotropics. We have noted throughout this paper the potential detrimental impacts of tropical agriculture and cattle industries on forest-dwelling migratory birds. However, with increasing land area being devoted to cash crops and pasture, patches of second growth, which harbor large numbers of migratory birds, are also likely to be increasingly converted to those land uses. Thus, although our immediate concern for forest-dwelling species (Table 2) is clearly justified, we cannot discount the future threat that may face the dozens of migratory species that occur mainly in disturbed second growth in wintering areas (L.J. Petit, pers. comm.).

GUIDELINES FOR CONSERVATION OF MIGRATORY BIRDS IN THE NEOTROPICS

Several measures need to be enacted within all Latin American and Caribbean countries to ensure that viability of migratory bird populations is not threatened by events in wintering areas. These include: (1) assessment and monitoring of bird populations in different habitats; (2) identification of both present and future threats to migrants; (3) incorporating sustainable development into land use planning; (4) identification of critical areas and habitats needed for protection of migratory birds; and (5) development of a system of protected reserves based upon firm biological and sociological foundations.

Assessment and Monitoring

We presented a broad overview of winter habitat use by migratory birds. However, because of scant data and the great geographic variability in habitat use exhibited by many species, this preliminary assessment must be viewed with caution. Indeed, the validity of applying general information presented here to specific local field situations is dubious. What is needed is a comprehensive, quantitative survey of migrant habitat use in each of the major physiographic regions (or life zones) of each country. Within each such region, many potential habitats (e.g., different seral stages) should be assessed for their

suitability (occupation) for each species. These data are already available for certain regions of some countries (e.g., Yucatan Peninsula and high-elevation life zones of western Mexico). The product of these efforts would be an abundance-weighted habitat and geographic analysis of the winter distributions of migratory birds, a central component necessary to build a conservation strategy for migratory birds in the neotropics (Greenberg 1986).

To assess habitat use and changes in long-term abundances of migratory birds, we recommend surveys based upon point counts (Hutto et al. 1986). The exact method needs to be worked out, but would probably require distinguishing individuals that are both within and beyond some threshold distance from the observer (see Hutto et al. 1986). Mist-netting could be used to supplement visual/auditory surveys and may provide important information about habitat-based survival rates. However, because of biases associated with mist-netting, comprehensive visual/auditory surveys should also be conducted in all regions.

Long-term monitoring of populations also would provide information on the temporal stability of habitat associations during winter and the relative importance of certain habitats as refugia for migrants during "bottleneck" (*sensu* Wiens 1977) years. For example, during drought years migrants may be unable to find sufficient food in some habitats, such as dry forests, and be forced to relocate to moister habitats (Faaborg et al. 1984). In this case, the benefit of access to moist forest in sustaining long-term populations is clear, although in most years moist forests may contain relatively few individuals.

Identification of Present and Future Threats

An important component of species conservation is identification of potential future sources of anthropogenically-induced mortality. To this end, broad-scale threats other than outright habitat destruction have been recognized by Rappole and co-workers (1983), who concluded that pollution (including pesticides) is an imminent problem. For example, migrants may face serious problems because of lax regulations on pesticide application in many developing countries (see references in Rappole et al. [1983]). Because some migratory birds occur in high densities in agricultural areas (see above), ecologists need to assess detrimental effects of pesticide ingestion on birds. Some areas where migrants presently abound may prove to be "ecological traps", where induced mortality is higher than in "preferred" habitats. Direct exploitation (e.g., for food or for the pet trade) and other sources of human-induced mortality are minor problems for most neotropical migrant landbirds.

A system needs to be implemented in Latin American and Caribbean countries that allows monitoring of point sources of pollution, areas that are undergoing unrestricted deforestation, and certain "development" projects that may threaten important areas or ecosystems. For example, the social and economic pressures in many developing countries lead to cutting of government-controlled forests by squatters for subsistence

farming, who then apply (often successfully) to the government for ownership rights to that "developed" land. An effective system for monitoring illegal encroachment on forest and enforcing existing laws might greatly reduce conversion of pristine forests, but socioeconomic conditions that drive this type of forest cutting (Hough 1988, Gow 1992) have to be rectified before monitoring and enforcement can be fully effective. More responsible land use practices, however, may be the most effective means of conserving limited natural resources and promoting conservation of overwintering migratory birds.

The Need for Sustainable Development

Economists, ecologists, and conservationists need to stress the potential importance and compatibility of certain sustainable land uses and wildlife populations. However, few detailed research projects have focussed on the relationship between sustainable forestry or agroforestry and bird populations. Such information is necessary before definitive conservation plans can be drafted for regional or local use within the neotropics. Nevertheless, in principal, sustainable land uses offer the most promising alternatives for long-term stability of tropical economies and wildlife populations. An important area of future tropical research for avian ecologists is to determine relative benefits and costs of different modes of sustainable forestry. Furthermore, as agricultural lands expand throughout Latin America, wildlife management practices (e.g., maintenance of hedgerows and woodlots; Gradwohl and Greenberg 1991) need to be incorporated into landscape planning. It is also important to note that, while the current conservation emphasis is on forest-associated species, development of permanent pasture and agricultural plots consumes both mature forest and early second-growth. Thus, the current conservation status of nonforest birds could easily be reversed as disturbed second-growth areas are converted to permanent agriculture.

Identification of Sensitive Areas and Ecosystems and Development of a System of Protected Reserves

Increasing the frequency and accuracy of forest and land inventories would improve our ability to monitor the current status of natural ecosystems. Those data could be used to identify habitats and geographic areas in greatest need of conservation. Little biological basis exists for the current placement of many national parks and reserves in the neotropics, and political and economic considerations often determine where parks are located. As a result, key habitats in certain areas may be overlooked, with potentially disastrous effects on threatened species. As outlined above, national land inventories along with information on distribution of migrants among regions and habitats could provide the necessary insight into identification of the most appropriate locations for reserves. Moist and dry

forests are clearly the associations most threatened by forest conversion. Protected areas should be dispersed among life zones in each region, not necessarily concentrated in the extensive tracts remaining in highlands. A useful approach to planning of tropical forest reserves is that devised by The Nature Conservancy: attempt to have all ecosystems represented within a region. This approach is believed to secure habitat for 80-90% of the species in temperate regions (Noss 1987a). Fine-filter (see above) guidelines could then be established to identify any unique species and habitats not adequately protected by a comprehensive reserve system. Although a system of reserves may be most easily accomplished within countries because of complications of multinational cooperation, long-term stability would be enhanced by coordination and integration of all planning and placement of national reserves into an overall Latin American network. Realistically, we must recognize the political "clout" of migratory land birds is very limited within Latin America and the Caribbean, except insofar as migratory bird issues can be used to attract outside resources into the region. A comprehensive, regional approach to conservation and land-use planning will, however, tend to improve long-term prospects for overwintering migrants, even if the impetus for such planning derives from the preservation of "local" resident (i.e., nonmigratory) birds and other wildlife.

CONCLUSIONS

The most imminent threat to migratory landbirds in the neotropics is destruction of forest ecosystems. Most migratory species appear tolerant of light-to-moderate levels of landscape alteration, and many may actually prefer disturbed sites to pristine vegetation. However, at least a dozen species of migratory landbirds are strongly associated with relatively undisturbed tracts of forest; these species may require individual attention in any regional conservation strategy. The long-term economic and sociological stability of Latin America is dependent upon rapid development and implementation of sustainable land use practices; rates of deforestation apparently have not slowed appreciably in recent years, and it is probable that little undisturbed forest will remain outside the Amazon Basin after several more decades of cutting and burning. Because neotropical migrants as a group are substantially more tolerant of forest disruption and artificial environments than are resident species, conservation of migrants could be accomplished within comprehensive conservation plans devised for resident bird species. The latter strategy will be more attractive to local people than a strategy that unduly emphasizes the welfare of what are commonly regarded as "North American" species. Perhaps our conservation strategy for overwintering migratory birds should focus on increasing the welfare of rural human populations, while simultaneously preserving habitats for resident wildlife species. If these twin efforts are successful, preservation of neotropical migrants on the wintering grounds will follow as a matter of course.

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Appendix A. Methods used to estimate vulnerability of migratory species due to destruction of tropical broadleaved forests.

We used approximately 50 publications that examined habitat use by individual species across at least two habitat types. Reports derived from study of single vegetation types were not used, as those provided no information as to habitat "selection", which we define operationally as differential abundance of a species in one habitat relative to others. Data from some studies were presented qualitatively (e.g., Land 1970, Stiles and Skutch 1989) and others quantitatively (e.g., Waide 1980, Lynch 1989, Blake and Loiselle 1992, Hutto 1992). Habitats used outside the wintering period (for example during migration) were excluded when possible. Thus, for each species observed in a given study, two types of information were extracted: (1) all "possible" habitats where the species could occur in the study area (defined by the author), and (2) the habitat(s) that contained a disproportionate number of individuals or that were stated by the author to be "preferred" by the species. A total of 11 habitats were identified for this study: moist forest, wet forest, cloud forest, mangroves, advanced second-growth, forest edge, open woodlands/forest, coniferous/mixed-coniferous forest, early second-growth, residential, and grassland/pasture. Thus, for each species we derived the number of both "available" and "used" sites for each habitat type; the proportion of available sites that were used (used/available) provided an indication of the extent of use of each habitat type. For each habitat type for each species, proportions ranged from 0 (species never occurred there or was less common than expected) to 1.0 (species always occurred there). Habitats with indices between 0.5 and 1.0 were considered "primary" habitats, those between 0.25 and 0.49 "secondary" habitats, and those used in <25% of the studies by a given species were regarded as marginal habitats.

Most species exhibited a wide range of habitat occupancy during winter, with only 25% of the migrants restricted to <4 categories. Here, we concentrate on those migratory species that are most likely to be impacted by moderate (current?) alteration and fragmentation of tropical broadleaved forests. (Effects of complete or nearly complete deforestation is a moot point since it will affect nearly all species dependent upon trees.) A simple ranking scheme was devised that accounted for both the distribution and relative abundance (primary or secondary habitat) of each species in broadleaved habitats and the number of habitats in which each species occurred. All undisturbed and lightly disturbed broadleaved, forested habitats (i.e., moist forest, dry forest, cloud forest, and mangroves) were given scores (S) of 2; disturbed forested habitats (advanced second-growth, forest edge, open woodlands/forest) received scores of 1. Open or nonbroadleaved habitats (residential, coniferous, early second-growth, grassland) were not used in calculations here (but, see below). Each forested association (broadleaf) that represented a primary habitat for a given species was weighted by a factor (W) of 2 (large factor because we assumed that this was a preferred habitat and that a greater proportion of individuals occurred there); secondary habitats were weighted by a factor of 1; habitats classified as marginal (see above) were weighted by 0. Thus, for each of the h species, we calculated a measure (F_h) reflecting the species' use of undisturbed forests: $F_h = \sum (S_i \times W_i)$, where i equals the ijth habitat type. In this analysis, F_h could take values from 0 (no forested habitats used) to 22 (all forested habitats were primary).

Because breadth of habitat use can influence the impact of habitat loss on population demographics (Rabinowitz et al. 1986), we devised a simple weighted measure of habitat breadth (B_h). B_h was calculated as the sum of the weights of all habitats (not only forested habitats) used by each of the h species (that is primary habitats = 2, secondary habitats = 1): $B_h = \sum (W_i)$. Theoretically, B_h could range between 1 (only one secondary habitat used) and 22 (all habitats were primary). The ratio F_h/B_h , then, describes the extent to which each species was restricted to undisturbed, broadleaved habitats and could range between 0 (species not dependent upon forests or woodland) and 2 (species dependent upon undisturbed, broadleaved forests). Finally, we incorporated F_h/B_h into an index of vulnerability (V_h): $(F_h/B_h) \times (1 - \log_{10}[n_h])$, where n is the number of habitats occupied by species h (for analyses, n was given values from 1 to 5 which represented 1-2, 3-4, 5-6, 7-8, and >8 habitats). The latter term in the equation was added to account for the absolute number of habitats used by each species. F_h/B_h reflects only how narrowly a species was restricted to undisturbed, broadleaved habitats, not how many distinct habitats it occupied. As habitat breadth increases probability of extinction decreases (Rabinowitz et al. 1986). $(1 - \log_{10}[n_h])$ was chosen to estimate the probability of severe population decline because this inverse, decelerating function places the greatest significance (i.e., most rapid declines) between successive numbers of habitats when few habitats are occupied. For instance, this relationship implies that the change in the probability of extinction should be less between 7 and 8 habitats occupied compared to 2 and 3 habitats occupied. A linear function would have resulted in equal changes in extinction probabilities for all successive habitat breadths (i.e., number of habitats occupied).