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The Role of Habitat Disturbance in the Ecology of Overwintering Migratory Birds in the Yucatan Peninsula

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ABSTRACT

The Yucatan Peninsula harbors an unusually large concentration of nearctic/neotropical migrants during the north-temperate winter. Historically, the Yucatan region has been subjected to relatively frequent, intense natural disturbances (hurricanes, wildfire, drought), as well as several cycles of major anthropogenic disturbance. Recent studies of the responses of birds and vegetation to natural and human-caused perturbations support the hypothesis that the Yucatan's biota, like that of the Caribbean basin generally, is relatively resilient and well-adapted to disturbance. Recovery of forest structure and function and of avian abundance and community composition, was unexpectedly rapid following the impact of an unusually severe tropical storm (Hurricane Gilbert). Significant numbers of forest-associated migrants were present within a few weeks of the storm's passage, and many community properties had converged to their pre-hurricane values within three years after the storm. Recovery from the effects of wildfire has been slower, but substantial numbers of forest-associated migrant and resident bird species colonized fire-razed habitats within two years. Even migratory species that reach their greatest abundance in mature forest also occur in early successional vegetation. With some exceptions, overwintering migratory species appear especially well-buffered against habitat disturbance, and the ratio of migrants-resident individuals and species increased greatly after hurricane and fire. These and other findings suggest that (1) a long association with habitats subjected to severe natural disturbances may have pre-adapted overwintering migrants in the Yucatan to tolerate anthropogenic disturbance, and (2) early successional growth and other non-pristine woody vegetation constitute an important reservoir of habitat for overwintering migrants in northern Mesoamerica and the Caribbean.

RESUMEN

La Península de Yucatán alberga una concentración grande de aves migratorias neotropicales durante el invierno boreal. Históricamente, la región de Yucatán ha sido sometida a perturbaciones naturales intensas (huracanes, incendios, sequía) relativamente frecuentes, así como también a varios ciclos de mayor perturbación antropogénica. Estudios recientes de las respuestas de pájaros y de la vegetación a las perturbaciones naturales y a las ocasionadas por humanos, apoyan a la hipótesis que la bióta de Yucatán, como la de la cuenca Caribeña en general, es relativamente elástica y bien adaptada a la perturbación. La recuperación de la estructura y función del bosque y de la abundancia y composición comunitaria de la avifauna, fue inesperadamente rápida después del impacto de una tormenta tropical severa (Huracán Gilberto). Cantidades importantes de aves migratorias asociadas al bosque fueron presentes entre unas pocas semanas después del paso de la tormenta y muchas características comunitarias habían regresado a sus valores pre-huracán tres años después de la tormenta. La recuperación de los efectos de los incendios ha sido más lenta, pero cantidades considerables de aves migratorias y residentes asociadas al bosque colonizaron los hábitats destruidos por el incendio entre dos años. Aun especies migratorias que alcanzan su mayor abundancia en el bosque maduro también occurren en la fase temprana de la regeneración de la vegetación. Con algunas excepciones, las especies migratorias que invernan en la región parecen ser especialmente inmune ante la perturbación del hábitat, y la proporción de especies e individuos migratorias entre la avifauna total aumentó mucho después del huracán e incendio. Estos y otros hallazgos sugieren que (1) una asociación larga con hábitats sometidas a perturbaciones naturales severas puede haber resultado en que las aves que invernan en Yucatán estén preadaptadas para tolerar la perturbación antropogénica, y (2) la sucesión vegetal temprana y otros tipos de vegetación leñosa no prístina constituyen un depósito importante de hábitat para las aves migratorias invernando en la porción norteña de Mesoamérica y el Caribe.

INTRODUCTION

For many years overwintering nearctic/neotropical migrant landbirds were thought to be associated mainly with disturbed, ephemeral, or marginal tropical habitats (e.g., Slud 1960; Willis 1966; Beuchner and Beuchner 1970; Morse 1971; Karr 1976; Fitzpatrick 1980; Hutto 1980; Tramer and Kemp 1980), possibly due to competitive exclusion of migrants from mature lowland tropical forest by better-adapted resident species (e.g., Willis 1966; DesGranges and Grant 1980; Johnson 1980). Freed from the spatial and energetic constraints of the breeding season (cf. Morton 1980; Cox 1985), overwintering migrants might be well suited to exploit spatially and temporally patchy food resources. Proponents of this view, while acknowledging that some migrants occur in mature tropical forest, have emphasized the importance of disturbed and marginal tropical vegetation to migrants. We term this

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view the "disturbance-associated" paradigm for overwintering migrants.

Publication of the symposium volume *Migrant Birds in the Neotropics* (Keast and Morton 1980) signalled the ascendancy of a very different view of the winter ecology of migrants. By 1980 it was known that migrants can be quite common in mature lowland tropical forest, where some species occupy stable feeding territories for the entire winter (Rappole and Warner 1980; Schwartz 1980) and join resident species in mixed flocks (e.g., Powell 1980; Tramer and Kemp 1980). Such observations led to the characterization of overwintering migrants as "full-fledged" members of lowland tropical forest communities (e.g., Morton 1980, 1992; Schwartz 1980; Stiles 1980, 1983; Terborgh 1980; Rappole et al. 1983, 1992). It has been asserted that most migratory species that breed in temperate forests require tropical forest as winter habitat and that the vast majority of migrant individuals overwinter in tropical forest (Terborgh 1980). Proponents of this view readily acknowledge that some migratory species, especially those that breed in fields or scrub, are common in disturbed tropical vegetation. However, they strongly emphasize the importance of mature tropical forest to overwintering migrants, thereby adopting what we term a "disturbance-averse" paradigm for the winter ecology of migrants. Some proponents of this view have attempted to reconcile the idea that mature tropical forest is the main habitat for overwintering migrants with the observation that many forest-breeding migrant species are extraordinarily abundant in highly disturbed tropical vegetation. Terborgh (1980) noted that most comparisons of migrant abundance in different tropical habitats had not included severely disturbed vegetation (e.g., overgrazed pasture, intensively managed crops). He argued that intensively managed fields and pastures support only grossly depauperate avifaunas, that migrant-rich "edge" habitats make up only a tiny fraction of tropical landscapes, and that the significance of successional vegetation to migrant conservation is minimal.

Another perspective on overwintering migrants in second growth has been presented by Rappole et al. (1989) and Winker et al. (1990), who argue that the quality of second growth is inferior to that of primary forest for at least some migrant species. In a study conducted in Veracruz, Mexico, these authors concluded that most overwintering Wood Thrushes (*Hylocichla mustelina*) found in secondary vegetation (as well as many in forest) were non-territorial "floaters" that were prevented from occupying stable home ranges in lowland forest by established territorial Wood Thrushes. Based on a higher observed mortality rate and a lower rate of relocating banded and radio-tagged birds in second growth, Rappole et al. (1989) concluded that floaters suffered higher overwinter mortality than did territorial birds. This interpretation is plausible, but is complicated by the fact that non-territorial Wood Thrushes inhabiting second growth made significantly longer daily movements than did forest-dwelling territorial individuals (Rappole et al. 1989). Birds that move greater distances may be more difficult to recapture or relocate, independent of their mortality rate. That is, Wood Thrushes could use different exploitation strategies in primary forest versus secondary scrub, yet still experience similar survivorship in both habitats (cf. Blake and Loiselle 1992; Staicer 1992).

Since 1980 many studies have examined the abundance and diversity of overwintering migrants in relation to habitat disturbance (e.g., Hutto 1985, 1989, 1992; Martin 1985; Rappole and Morton 1985; Lynch 1989, 1991, 1992; Askins et al. 1992; Blake and Loiselle 1992; Greenberg 1992; Kricher and Davis 1992; Petit et al. 1992, 1993; Powell et al. 1992; Rappole et al. 1992; Robbins et al. 1992). All of the cited field studies demonstrate that overwintering migrants, including many forest-breeding species, are abundant in a wide variety of disturbed tropical vegetation. Many of these same species also occur in mature tropical forest during the northern winter, but are not necessarily more abundant there. No overwintering migrant species is restricted to mature tropical forest, though some disturbance-averse species reach their highest densities in forest. On the other hand, many disturbance-prone migrant species are essentially restricted to disturbed vegetation and native scrub, and avoid closed canopy tropical forest.

Neither the disturbance-associated nor the disturbance-averse paradigms adequately expresses the relationship between the winter ecology of migrants and habitat disturbance. We suggest a more inclusive viewpoint that considers the occurrence of individual migrant species in relation to the entire available continuum of mature through highly disturbed vegetation. Such a perspective downplays the artificial discontinuity between human-altered habitats, many of which retain many natural features, and "natural" vegetation types, all of which are subject to some degree of non-anthropogenic disturbance. For example, in the Yucatan Peninsula successional stages of semievergreen forest and mature semideciduous forest are similar in structural and floristic features, as well as in the composition of their associated bird communities

(Paynter 1955; Lynch 1989). The fact that thorn-scrub, savannah, and other semiarid vegetation was much more widespread in Mesoamerica in the recent geological past (Greenberg et al., this volume) also argues for a more comprehensive view of the roles of natural and secondary "scrub" in migrant ecology.

We have focused on the Yucatan Peninsula in our field studies of overwintering nearctic-neotropical migrants. There, we have compared migrant communities in a range of intact, naturally disturbed, and anthropogenically disturbed habitats. By understanding the responses of migrants to a wide spectrum of disturbances, we should be better able to anticipate future trends in migrant abundance. We also hope to gain a firmer factual basis for recommending management interventions that will benefit migrants and still allow much-needed improvement of the living standards for the people who populate Mesoamerica.

STUDY AREA

The Yucatan Peninsula (240,000 km$^{2)}$ encompasses the Mexican states of Yucatan, Quintana Roo, and Campeche, all of Belize, and the Peten region of northern Guatemala. Limited areas in southern Belize receive more than 3000 mm rainfall each year and support wet tropical forest. However, annual precipitation throughout most of the Peninsula is 900–1400 mm, and the predominant natural vegetation consists of deciduous, semideciduous, and semievergreen forest (Lynch 1989). These forests are subjected to a four- to six-month winter-spring dry season, and are considered to be subcategories of dry tropical forest, sensu Holdridge (1967).

Dry tropical forests have been subjected to particularly intense human disturbance worldwide (Lerdan et al. 1991), and the Yucatan has been no exception. Even areas that are presently forested were intensively exploited by a sizable Maya population from ca. 3000 years ago until ca. 1000 years ago. Another cycle of land clearing began with the Spanish conquest of the region in the mid-16th century. The Yucatan is also disrupted by frequent large-scale natural disturbances, notably hurricanes and associated wildfires (Lynch 1991; Whigham et al. 1991). A long history of human and natural disturbance has been superimposed on a regional gradient in annual rainfall to produce a complex mosaic of natural and anthropogenic vegetation. This habitat diversity, together with the Peninsula's relative proximity to the North American Gulf Coast, probably accounts for the unusually large number of migrant species and individuals that overwinter in the Yucatan (Lynch 1989, 1992). Our assessment of the role of habitat disturbance in the winter ecology of migrants in the Yucatan is based our field studies and those of others in the region (e.g., Waide 1980; Lopez Ornat 1990; Lopez Ornat and Greenberg 1990; Lopez Ornat and Lynch 1991; Greenberg 1992; Morton 1992; Morton et al. 1993; Robbins et al. 1992; Whitacre et al. 1993; D. Niven pers. comm.).

MODES AND INTENSITIES OF HABITAT DISTURBANCE IN THE YUCATAN

White and Pickett (1985:7) define ecological disturbance as "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment." Here, we consider only modes of disturbance that potentially influence the distribution or abundance of migratory landbirds in the Yucatan region: natural treefalls, logging, agriculture, ranching, hurricanes, wildfire, and construction of human habitations. We focus on the similarities between the effects of natural and anthropogenic disturbances on migrants. We characterize disturbances (Table 1) according to their intensity (the degree to which a specified unit of habitat is perturbed from its original structural and/or floristic composition), duration (the temporal extent of the disruptive phase), recovery time (the time required for a perturbed system to return to its pre-disturbance state), patch size (the spatial extent of an individual disturbance event), recurrence interval (the average time between disturbance events at a given site), and density (number of disturbance foci per large area of landscape). Real landscapes are usually patchworks of different disturbance states.

In some parts of the Yucatan the area covered by successional vegetation exceeds the combined coverage of all other land use categories. For example, in 1977 approximately 50% of Quintana Roo was covered by secondary regrowth (Cabrera Cano et al. 1982). In such landscapes, successional dynamics are obviously highly relevant to migrant distribution and abundance.

Treefall Gaps

In all forests small canopy openings are continually created by the death of mature trees. These gaps should be viewed as intrinsic features of the forest, unless their frequency is substantially increased by external forces (Denslow and Hartshorn 1994). In typical tropical forests ca. 1% of the canopy trees die each year (Brokaw 1985), and the mean time interval between the creation of gaps at a given

Table 1. Characteristics of major classes of habitat disturbance in the Yucatan Peninsula. Disturbance categories are ranked from least disruptive to most disruptive, based on their effects on overwintering migrants.

Disturbance Type	Intensity	Duration	Recovery Time	Recurrance Rate	Patch Area	Regional Density
Treefalls	Low	Short-Mod.	Rapid	Low	Small	High
Selective Logging	Medium	Short	Rapid	Low	Small	High
Hurricane	Medium	Short	Rapid	Medium	V. Large	Low
Milpa Agriculture	High	Moderate	Medium	Low-Med.	Medium	Variable
Wildfire	High	Short	Medium	Medium	Large	Low
Cattle Ranching	High	Moderate	Medium	Low	Large	Variable
Residential	High	Long	Slow	Low	Variable	Variable

site is ca. 80–140 years (Denslow 1987). Lowland forests in Mexico and Central America contain 300–1200 treefall gaps km^{-2}. Our data for semievergreen forests in northeastern Quintana Roo indicate an annual tree death rate of ca. 0.5% in years without hurricanes or major fires (Whigham et al. 1991). In southeastern Quintana Roo the rate of gap formation may be somewhat lower (M. Dickenson unpubl. data).

Selective Logging

Although large tracts of forest in the Yucatan are clearcut to prepare sites for farming or ranching, clearcutting for timber production is not practiced. Historically, most commercial logging has entailed selective extraction of a few valuable hardwood species, notably mahogany (*Swietenia macrophylla*) and Spanish cedar (*Cedrela mexicana*). Other species are sometimes cut for railroad ties and other specialized uses, and understory trees and palms are used for local construction.

A progressive silvicultural system has recently been adopted by most of the rural logging communities in the heavily forested southern half of the state of Quintana Roo (Richards 1991; Lynch 1992; Snook 1993). This system, originally termed the "Plan Piloto Forestal" (PPF), begins with a detailed forest inventory, then designates annual cutting blocks of several hundred hectares, and harvests <5% of the mature trees within a given cutting block every 25 years. Skid tracks are as narrow as possible, and collateral damage to nontarget trees and understory vegetation is kept to a minimum. The incidental destruction of nontargeted vegetation is the most detrimental aspect of most so-called selective logging operations in the tropics (Johns 1988).

The mean area of canopy gaps created by PPF logging operations is somewhat larger than the mean for natural treefall gaps ($59\ m^2$ versus $33\ m^2$), and the total area of forest canopy that is opened increases from 0.2% yr^{-1} to 1.2% yr^{-1} (M. Dickenson unpubl. data). Nevertheless, the impact of the PPF method on forest structure is minimal compared with that of other logging methods. Careful analysis of the impact of the PPF on wildlife is appropriate, as forestry officials in Belize and Guatemala have expressed interest in adopting similar systems.

Traditional Agriculture

Some high-rainfall areas in the southern Yucatan were terraced and irrigated by the pre-Columbian Maya, and much of the semiarid north was devoted to intensive cultivation of henequen in the 19th and early 20th century. With these exceptions, "milpa" agriculture (the shifting cultivation of maize and associated crops) has been the principal human land use in the Yucatan for approximately 3000 years. Features of the milpa system include (1) small plot size (1–5 ha), (2) felling and burning of most trees and shrubs, but not removal of boles and roots, (3) little active management of the plot other than occasional weeding, (4) abandonment of plots after two to three years of cultivation, and (5) a fallow period of ten to 50 years, depending mainly on the local availability of land. In recent decades the extent of milpa agriculture has declined in the Mexican portion of the Peninsula (Lynch 1992), but is rapidly expanding in the Peten of Guatemala (Whitacre et al. 1993).

Ranching

Over the past half-century cattle ranching has come to dominate much of the Mesoamerican landscape (Hartshorn 1992). Despite the unprofitability of ranching in most of Mexico's portion of the Yucatan, government subsidies encouraged conversion of forest to pasture from the 1960s until the mid-1980s. The prevalence of ranching in the northern half of the Yucatan has declined with the recent elimination of these subsidies, but active and abandoned cattle pastures still account for most of the anthropogenically disturbed vegetation in this area (Lynch 1992). To the south, the Peten region of Guatemala has experienced an exponential increase in cattle ranching since the early 1970s (Whitacre et al. 1993).

Initial site preparation is similar for pastures and milpas, but pastures are much larger (typically 10–500 ha). Depending on economic and cultural factors, pasture maintenance may involve mowing, manual removal of invading trees, application of herbicides, periodic burning, or introduction of exotic forage grasses, or a combination of these. In the northern Yucatan, where ranching is economically marginal, little effort is expended on pasture maintenance and stocking rates are low. As a result, pastures tend to contain tall, rank grasses, weedy herbs, pioneering shrubs and trees (e.g., *Cecropia obtusifolia*), and relict canopy trees (e.g., *Manilkara zapota*). In sharp contrast, pastures in some areas of Belize are regularly mowed, and emergent woody vegetation is virtually absent (Saab and Petit 1992). Just southwest of the Yucatan, in the Ocosingo Valley of Chiapas, Mexico, cattle ranchers rotate their land between pasture grasses and *Acacia* woodland. The latter is a source of wood and cattle fodder, and incidentally serves as habitat for many migratory birds (Greenberg et al. this volume). These three management styles have dramatically different impacts on bird communities, even though the results of all three would be lumped under the category "pasture" in most land use tabulations.

Hurricanes

Hurricanes are a recurring source of widespread habitat disturbance in the eastern Yucatan, where a given site is expected to experience a major tropical storm approximately every ten to 20 years (Jauregi et al. 1980; Snook 1993). Although a hurricane may affect hundreds or thousands of square kilometers, the intensity of storm damage varies dramatically, even over short distances. Caribbean ecosystems may possess general adaptations that enable them to withstand, or rapidly recover from, hurricane effects (Lugo 1988; Loope et al. 1994). As an example, a forested site in northeastern Quintana Roo that was devastated by an unusually severe hurricane in 1988 required only three to four years to converge on predisturbance values for tree growth, litter production, canopy closure, and many characteristics of the bird community (Lynch 1991; Whigham et al. 1991).

Wildfire

In the Yucatan, wildfires typically occur in the wake of hurricanes (Juaregi et al. 1980; Snook 1993). The massive quantities of coarse woody debris produced by Hurricane Gilbert in September 1988 fueled fires that ravaged more than 200,000 ha of forest in northern Quintana Roo during the following dry season. In much of the fire-affected area, 80%–90% of the canopy trees were killed, the forest floor was denuded of vegetation, the standing crop of woody debris was significantly decreased, and organic matter in the shallow soil was reduced to ash. Patches of unburned forest survived where the spread of fire was stopped by natural or artificial barriers, but contiguous stands of up to several thousand hectares of forest were reduced to the earliest stage of secondary succession.

Buildings, Roads, and Other Permanent Construction

This category encompasses intense anthropogenic disturbances whose persistence is measured in decades. Although permanent human construction can have severe local impacts on birds, its total areal extent in the Yucatan is limited. Moreover, some of the more extensive forms of permanent construction (e.g., residential areas) retain significant amounts of vegetation that is utilized by a variety of migrants (Tramer 1974; Arendt 1992). In the eastern Yucatan, the narrow, fragile strip of coastal dune vegetation is at extreme risk due to development for tourism (Lopez Ornat and Lynch 1991; Lynch 1992).

RESPONSES OF MIGRATORY BIRDS TO DISTURBANCE

We have conducted mist netting and point counts in pastures, milpas, old fields ("acahuales") of various ages, forest disturbed by selective logging, hurricane, and wildfire, and undisturbed mature forest. Tables 1 and 2 summarize habitat occurrence data for overwintering migrants in the northern Yucatan (Lynch 1989, 1991, 1992, unpubl. data). To a first approximation, the responses of overwintering migrants to all of these modes of disturbance falls along a single continuum. At one extreme are birds associated with floristically depauperate habitats with low, simple physiognomy (e.g., burns, quarries, exposed roadsides, beaches). At the other end of the disturbance continuum are birds associated with structurally and floristically diverse evergreen and semievergreen forests. These endpoints are linked by an array of "climax" scrub habitats, successional stages, and land use types which, despite their heterogeneity, support one graded sequence of migrant communities. Most migrant species can be characterized as disturbance-associated (most abundant in herb/grass-stage or shrub-stage of succession, or in analogous pristine vegetation types; mature forest avoided), or disturbance-resistant (similar abundance across a wide range of natural and anthropogenic scrub and forest habitats, or disturbance-averse most abundant in mature forest and late stages of succession; early regrowth and other highly disturbed vegetation avoided) (Table 2).

Response of Migrants to Treefall Gaps

The tall, wet lowland forests of Central America and Amazonia harbor a number of resident bird species whose primary or sole habitat is treefall gaps and other small forest clearings (Schemske and Brokaw 1981). However, the lower, drier, and less shaded forests of the northern Yucatan do not appear to support obligate gap specialists. There, migrants and residents found in treefall gaps are mostly species that also occur in continuous forest, forest-edge, or advanced second growth. However, treefall gaps may be important in that they allow the expression of age- or sex-based intraspecific habitat segregation in tracts of continuous forest. In the northern Yucatan, for example, wintering male Hooded Warblers (*Wilsonia citrina*) are usually associated with closed canopy forest, but females tend to occur in acahuales, forest edge, seasonally flooded deciduous forest, and other "scrubby" vegetation (Lynch et al. 1985; Lopez Ornat and Greenberg 1990). Within continuous tracts of semievergreen forest, treefall gaps are the main microhabitats where female Hooded Warblers regularly occur (J. Lynch unpubl. data). Migrant

Table 2. Mist net capture data for 25 migrant species in disturbed and undisturbed habitats in Quintana Roo, Mexico. Tabled entries are captures per 100 net-hrs. Data from Lynch (1989, 1991, 1992, unpubl.).

	Burned				F/P	Acahual	Forest: Hurricane-impacted					Forest: Logged		Forest: Intact	
Years since disturbance	0.5	1.5	2.5	3.5	1.0	6–8	0.5	1.5	2.5	3.5	4.5	0.5	2.5	PM	NB
Disturbance-associated Species															
A. Early successional (herb/grass stage)															
Ruby-throated Hummingbird	**2.4**	0.6	**3.0**	1.3	—	—	0.7	—	—	—	—	—	—	—	—
Yellow-rumped Warbler	**0.5**	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Blue Grosbeak	**0.2**	—	0.5	—	0.1	—	—	—	—	—	—	—	—	—	—
Indigo Bunting	**12.2**	**13.9**	**9.5**	—	8.5	0.7	1.2	1.2	0.2	0.3	—	—	—	—	—
Painted Bunting	**2.8**	**10.3**	**4.6**	**2.1**	0.6	0.3	0.2	0.3	0.2	0.2	—	—	—	—	—
Northern Parula	0.7	**1.4**	**1.1**	0.5	0.2	0.3	—	—	—	—	—	—	—	—	—
Yellow Warbler	—	**0.8**	0.3	—	0.1	0.3	—	—	—	—	—	—	—	—	—
Common Yellowthroat	0.5	**4.4**	0.5	**2.3**	**3.5**	1.4	—	0.4	0.2	—	—	—	—	.02	—
B. Mid-successional (shrub stage)															
Least Flycatcher	0.5	0.6	**1.4**	**1.8**	0.9	1.0	0.5	0.2	0.2	—	0.5	—	—	—	—
Yellow-breasted Chat	—	—	0.5	**0.8**	**0.7**	0.2	—	—	—	—	0.2	—	—	.02	—
Orchard Oriole	—	—	**0.5**	—	0.2	.05	**1.2**	—	—	—	—	—	—	—	—
Gray Catbird	0.2	0.8	**1.9**	**3.9**	1.1	**2.7**	0.7	0.8	—	1.0	0.2	0.6	0.3	.05	0.4
Disturbance-resistant Species															
White-eyed Vireo	1.9	**5.0**	**7.0**	**6.5**	1.4	2.3	3.2	2.3	2.1	2.0	1.3	—	0.6	0.1	0.1
Blue-winged Warbler	—	0.6	—	—	—	0.2	0.2	0.2	0.2	0.3	0.2	—	—	—	—
Magnolia Warbler	0.2	**2.8**	**3.0**	**2.1**	0.7	1.0	1.5	0.5	0.5	0.3	0.7	0.3	—	0.2	—
Ovenbird	0.7	**1.4**	**1.4**	1.3	0.4	**1.6**	0.2	0.3	0.9	1.1	1.0	0.9	0.3	0.7	0.5
Hooded Warbler	0.5	1.1	0.5	1.0	0.4	**1.2**	**1.2**	1.1	1.0	1.1	**1.3**	**2.0**	1.1	1.0	0.8
Summer Tanager	—	—	**0.3**	—	0.2	0.2	—	—	—	**0.3**	—	—	—	—	—
Northern Waterthrush	—	0.3	—	—	0.2	—	—	—	—	—	—	0.3	—	—	—
Disturbance-averse Species															
Black-and-white Warbler	—	—	—	0.5	0.1	0.1	0.2	0.3	0.9	**1.1**	0.3	**2.0**	**1.1**	0.4	0.4
American Redstart	—	—	—	—	0.1	—	—	0.3	—	**0.8**	—	—	—	—	0.1
Worm-eating Warbler	—	—	—	0.5	—	0.2	0.2	0.3	**0.9**	0.5	0.4	**0.6**	—	0.1	0.4
Swainson's Warbler	—	—	**0.3**	—	—	0.1	—	—	0.2	**0.3**	0.2	—	—	.02	—
Kentucky Warbler	—	0.6	0.5	0.3	—	0.3	0.5	0.8	**1.2**	**1.5**	0.4	0.9	**2.5**	0.5	**1.2**
Wood Thrush	—	0.3	0.3	0.3	—	1.5	—	—	0.8	1.6	1.9	**3.7**	**5.3**	0.6	**7.5**

Bold-face entries represent preferred habitats. Values are individuals captured per 100 net-hours.
Burned = forest burned after hurricane; F/P = field and pasture sites; Acahual = abandoned cornfield; Logged = mature semi-evergreen forest selectively logged under Plan Piloto Forestal system; Intact = unlogged mature semievergreen forest; PM = Puerto Morelos forest site.
The entry for intact forest at Noh-Bec (NB) is based on data from three separate tracts of forest.

species that are adapted to low, open vegetation (e.g., fields, early successional regrowth) rarely occur in individual treefall gaps, but may temporarily invade forest when hurricane or other intense disturbance increases the density of treefall gaps and opens the forest canopy (Lynch 1991).

A Generalized Successional Sequence for Migrants in the Yucatan

In the northern half of the Yucatan, where we have conducted most of our field work, few migrants occur at the very earliest stage (0–0.5 year) of succession after burning or other severe disturbance. Palm Warbler (*Dendroica palmarum*) and Yellow-rumped Warbler (*Dendroica coronata*), both ground-foraging species, are commonly observed around quarries, roadsides, overgrazed or burned fields, and other sparsely vegetated sites, especially where bare substrate is exposed. These species also temporarily colonize forest whose canopy and ground cover have been destroyed by wildfire, but disappear when dense continuous ground cover regenerates (Lynch 1989, 1991). Where living trees, dead snags, buildings, or other tall emergent structures are present, the Yellow-throated Warbler (*Dendroica dominica*) gleans elevated substrates. In Belize, this warbler is also widespread in open pine savanna (Russell 1964). All three species are common in coastal dune scrub, which may be the closest natural analogue of the most highly disturbed anthropogenic habitats (Lopez Ornat and Lynch 1991; Lynch 1992).

As a tall (1–4 m), dense cover of grasses, forbs, and shrubs develops during years 1–3 after abandonment, Ruby-throated Hummingbird, (*Archilochus colubris*) Yellow Warbler (*Dendroica petechia*), Common Yellowthroat (*Geothlypis trichas*), Indigo Bunting (*Passerina cyanea*), and Blue Grosbeak (*Guiraca caerulea*) colonize old fields, while the Palm Warbler and Yellow-rumped Warbler tend to disappear (Lynch 1989, 1992). Once shrubs becomes prominent (normally two to five years into succession), Least Flycatcher (*Empidonax minimus*), Gray Catbird (*Dumetella carolinensis*), White-eyed Vireo (*Vireo griseus*), Yellow-breasted Chat (*Icteria virens*), Yellow Warbler, Northern Parula (*Parula americana*), Ovenbird (*Seiurus aurocapillus*), Painted Bunting (*Passerina ciris*), and Orchard Oriole (*Icterus spurius*) are typical species. Forest-associated species (e.g., Wood Thrush, Magnolia Warbler [*Dendroica magnolia*], Hooded Warbler, Kentucky Warbler [*Oporornis formosus*]) begin to appear three to four years into succession (Lynch 1989, 1992; Whitacre et al. 1993), and may be present in even younger seral vegetation if remnant trees or shrubs are present (Greenberg 1992).

By the time succession has reached the shrub-sapling stage (five to ten years after abandonment), forest-associated species such as Wood Thrush, American Redstart (*Setophaga ruticilla*), Black-throated Green Warbler (*Dendroica virens*), Magnolia Warbler, Northern Parula, Hooded Warbler, Kentucky Warbler, and Ovenbird are typically present, and are no longer restricted to remnant patches of the original forest (Lynch 1989, 1992). Some of these species (e.g., Wood Thrush) reach higher densities in forest than in early second growth (Lynch 1992; Whitacre et al. 1993), but a surprising number (e.g., Black-throated Green Warbler, Magnolia Warbler, Hooded Warbler, Kentucky Warbler, Ovenbird, American Redstart) occur with approximately the same frequency in mid-successional scrub as in mature forest. Thus, most successional turnover of the migrant community already has occurred within the first ten years of abandonment, long before the acahaul has converged on mature forest in structure and floristic composition.

None of the common forest-associated migrants in the Yucatan are absent from five- to ten-year-old successional scrub. On the other hand, several field- or scrub-associated migrants (e.g., Ruby-throated Hummingbird, Least Flycatcher, Common Yellowthroat, Yellow-breasted Chat, Indigo Bunting, Painted Bunting, Blue Grosbeak, Orchard Oriole) avoid closed-canopy forest, though they occasionally occur in clearings (Lynch 1989).

Effects of Selective Logging

Preliminary results of a study initiated in 1993 near the village of Noh-Bec, in southern Quintana Roo, indicated few if any impacts of the PPF system of selective logging on the occurrence of migrants (Table 2). Migrant numbers and species composition were similar at three unlogged control sites and two sites that were logged in 1992 and 1990. The only major difference in migrant capture rates among these five sites was an anomalously high number of Wood Thrushes at one of the control sites. This species has occasionally been captured in unusually high numbers at other sites in Quintana Roo (J. Lynch pers. obs.), perhaps reflecting local population movements during the overwintering period. Migrant and resident species typical of open fields or other highly disturbed habitats were not encountered in the small clearings created by selective logging. From the viewpoint of overwintering migrants (and apparently most resident species as well), the PPF logging system appears to be benign.

Effects of Hurricanes

In September 1988 our forest study site near Puerto Morelos, in northeastern Quintana Roo, was struck by Hurricane Gilbert. This unusually severe tropical storm generated wind speeds up to 300 km hr^{-1}. The mature semievergreen tropical forest was totally defoliated and ca. 10% of the canopy trees were wind-thrown. Enormous amounts of standing and downed coarse woody debris were produced, and the crowns of surviving trees were severely damaged (Whigham et al. 1991). By February 1989, leaves had begun to re-sprout in the canopy, but the forest floor remained an impenetrable tangle of downed trees, branches, and vines. Pioneer plant species characteristic of abandoned fields (e.g., *Cecropia schreberiana, Carica papaya)* had germinated on the forest floor. In effect, Hurricane Gilbert superimposed certain structural and floristic elements of early secondary succession onto a mature semievergreen tropical forest.

Six months after the hurricane, mist net capture rates for migrants were triple their prestorm levels, and approximated capture rates in a nearby five- to eight-year-old acahual (Table 3a; Lynch 1991). The proportion of migrant individuals in our netted samples increased after the hurricane (Lynch 1991). The post-hurricane migrant community consisted of the usual forest migrants (e.g., Hooded Warbler, Kentucky Warbler, Ovenbird, Black-and-white Warbler [*Mniotilta varia*]), with an admixture of early successional species (e.g., Indigo Bunting, Painted Bunting, Common Yellowthroat, Orchard Oriole). Based on point counts and mist net captures, the most common migrant after the hurricane was the White-eyed Vireo, a shrub-forest generalist that favors dense leafy vegetation. The Wood Thrush was the only previously common migrant species that was completely absent from our study site after the storm. Wood Thrushes remained abundant to the south, just outside the area severely affected by the hurricane (Greenberg 1992; J. Lynch pers. obs.).

Even these limited effects of Hurricane Gilbert on the migrant bird community proved to be short-lived. Two winters after the hurricane, field-associated migrants had mostly disappeared from the forest, though the White-eyed Vireo and several resident shrub-forest generalists remained abundant (Table 3a). Small numbers of Wood Thrushes re-appeared in the second winter after the hurricane, and by the fourth winter capture rates for this species exceeded pre-storm levels. By the sixth winter, the overall migrant capture rate and community composition in the hurricane-damaged forest were very close to their pre-hurricane values (Table 3a).

Effects of Wildfire

We sampled bird communities in burned forest nearly six to seven months after post-hurricane wildfires swept northeastern Quintana Roo. Although extensive areas remained unvegetated, the area already had been colonized by dense thickets of bracken fern (*Pteridium aquilinum*), as well as various herbs and fast-growing shrubs (e.g., *Solanum verbacifolium).* The effects of wildfire on the migrant community were neither as catastrophic nor as long-lasting as the devastated appearance of the landscape would have suggested. Capture rates initially increased after the wildfire (Table 3b), but this mainly reflected the shift of many arboreal species from the denuded canopy down to the densely vegetated forest floor. Point counts conducted six to seven months after the fire revealed no significant differences between burned and unburned forest in the number of migrant species or detections per point (Lynch 1991). In contrast, the numbers of resident species and detections declined by about two-thirds in burned forest. Fire had a disproportionate impact on resident frugivores and nectarivores (Lynch 1991). Largely as a result of declines shown by resident species, migrants contributed a much higher proportion (64%) of point count detections in recently burned hurricane-damaged forest than in unburned hurricane-damaged forest (38%,) or pre-disturbance forest (37%).

Species normally associated with field and scrub habitats (e.g., Indigo Bunting, Painted Bunting, Common Yellowthroat) initially dominated the post-fire migrant community. In the first winter after the fire, a few forest-associated migrants (notably Wood Thrush and Kentucky Warbler) were absent from sites where they had been common.However, otherforestspecies (e.g., Hooded Warbler, Magnolia Warbler, American Redstart) persisted at near-normal numbers even in areas where >80% of the trees had been killed and the understory consisted mainly of thickets of newly sprouted bracken fern. In the second and third winters after the fires, Indigo Buntings were extraordinarily abundant, accounting for more than half of all migrant captures in mist net samples (Table 3b).

The migrant community quickly converged toward its pre-disturbance composition. Wood Thrushes and Kentucky Warblers reappeared in the second winter after the fire, and field-adapted species had begun to decline by the third winter.

Table 3. Mist netting data for migrant species at Puerto Morelos, Quintana Roo, showing impact of Hurricane Gilbert (September 1988) and wildfires (summer 1989). Entries are numbers of individuals captured and (in brackets) capture rates (CR = 100 × individuals/net-hr). Pre-hurricane CR given in first column

	Pre-H	1989	1990	1991	1992	1993	1994
A. Hurricane-damaged Forest (Unburned)							
Ruby-throated Hummingbird	—	3 (0.7)	—	—	—	—	—
Least Flycatcher	—	2 (0.5)	1 (0.2)	1 (0.2)	—	2 (0.5)	—
Wood Thrush	0.6	—	—	22 (3.8)	10 (1.6)	6 (1.9)	1 (0.2)
Gray Catbird	0.05	3 (0.7)	5 (0.8)	—	6 (1.0)	1 (0.2)	—
White-eyed Vireo	0.1	13 (3.2)	15 (2.3)	12 (2.1)	12 (2.0)	9 (1.3)	2 (0.3)
Hooded Warbler	1.0	5 (1.2)	7 (1.1)	6 (1.0)	7 (1.1)	9 (1.3)	4 (0.6)
Kentucky Warbler	0.5	2 (0.5)	5 (0.8)	7 (1.2)	9 (1.5)	3(0.4)	2 (0.3)
Ovenbird	0.7	1 (0.2)	2 (0.3)	5 (0.9)	7 (1.1)	7 (1.0)	4 (0.6)
Yellow-breasted Chat	0.02	—	—	—	—	1 (0.2)	—
Common Yellowthroat	0.02	—	3 (0.4)	1 (0.2)	—	—	—
Worm-eating Warbler	0.1	1 (0.2)	2 (0.3)	5 (0.9)	3(0.5)	3(0.4)	1 (0.2)
Swainson's Warbler	0.02	—	—	1 (0.2)	2 (0.3)	1 (0.2)	—
Black-and-white Warbler	0.2	2 (0.3)	5 (0.9)	7 (1.1)	2 (0.3)	4 (0.6)	4 (0.6)
Northern Parula	—	—	—	—	—	—	—
Magnolia Warbler	0.2	6 (1.5)	3 (0.5)	3(0.5)	2 (0.3)	5 (0.7)	1 (0.2)
Blue-winged Warbler	—	1 (0.2)	1 (0.2)	1 (0.2)	2 (0.3)	1 (0.2)	1 (0.2)
American Redstart	—	2 (0.3)	—	5 (0.8)	—	—	—
Summer Tanager	—	—	—	—	1 (0.2)	—	—
Indigo Bunting	—	5 (1.2)	8 (1.2)	1 (0.2)	2 (0.3)	—	—
Painted Bunting	—	1 (0.2)	2 (0.3)	1 (0.2)	1 (0.2)	—	—
Orchard Oriole	—	5 (1.2)	—	—	—	—	—
Total Net-Hours (H)	4,213	405	662	572	612	678	618
Migrant Species	12	14	14	14	15	13	9
Migrant Individuals (N)	161	49	58	71	76	48	20
Capture Rate (=100 × N/H)	3.8	12.1	8.8	12.4	12.4	7.1	3.4

	Pre-H	1990	1991	1992	1993	1994
B. Burned Hurricane-damaged Forest						
Ruby-throated Hummingbird	—	10 (2.4)	2 (0.6)	11(3.0)	5(1.3)	2(0.4)
Least Flycatcher	—	2(0.5)	2(0.6)	5(1.4)	3(1.8)	3(0.6)
Wood Thrush	0.6	—	1(0.3)	1(0.3)	1(0.3)	1(0.2)
Gray Catbird	0.05	1(0.2)	3(0.8)	7(1.9)	15(3.9)	4(0.8)
White-eyed Vireo	0.1	8 (1.9)	18(5.0)	26(7.0)	25(6.5)	19(3.9)
Hooded Warbler	1.0	2 (0.5)	4(1.1)	2(0.5)	4(1.0)	1(0.2)
Kentucky Warbler	0.5	—	2(0.6)	2(0.5)	1(0.3)	1(0.2)
Ovenbird	0.7	3 (0.7)	5(1.4)	5(1.4)	5(1.3)	6(1.2)
Northern Waterthrush	—	—	1(0.3)	—	—	—
Yellow-breasted Chat	0.02	—	—	2(0.5)	3(0.8)	—
Common Yellowthroat	0.02	2 (0.5)	16(4.4)	2(0.5)	9(2.3)	6(1.2)
Worm-eating Warbler	0.1	—	—	—	2(0.5)	—
Swainson's Warbler	0.02	—	—	1(0.3)	—	—
Black-and-white Warbler	0.2	—	—	—	2(0.5)	2(0.4)
Northern Parula	—	3 (0.7)	5(1.4)	7(1.1)	2(0.5)	2(0.4)
Palm Warbler	—	—	—	—	2(0.5)	1(0.2)
Yellow-rumped Warbler	—	2(0.5)	—	—	—	—
Yellow Warbler	—	—	3(0.8)	1(0.3)	—	—
Magnolia Warbler	0.2	1 (0.2)	10 (2.8)	11(3.0)	8(2.1)	7(1.4)
Blue-winged Warbler	—	—	2(0.6)	—	—	2(0.4)
Summer Tanager	—	—	—	1(0.3)	—	1(0.2)
Indigo Bunting	—	52 (12.2)	50(13.9)	35(9.5)	—	1(0.2)
Painted Bunting	—	12 (2.8)	37(10.3)	17(4.6)	8(2.1)	7(1.4)
Blue Grosbeak	—	1 (0.2)	—	2(0.5)	—	—
Orchard Oriole	—	—	—	2(0.5)	—	—
Total Net-Hours (H)	4,213	424	360	370	386	485
Migrant Species	12	13	16	19	16	17
Migrant Individuals (N)	161	99	161	140	95	66
Capture Rate (= 100 × N/H)	3.8	23.4	45.0	37.8	24.6	13.4

By the fourth winter, Indigo Buntings had completely disappeared from the site. In the fifth winter after the fire, migrant capture rates in burned forest were less than a third of their 1991 maximum, though they still somewhat exceeded capture rates in undisturbed forest (Table 3b).

Effects of Ranching

In the Yucatan, the impact of ranching on migrants is highly dependent on the style of pasture management. In three mowed, heavily grazed pastures in Belize where vegetation height was <1 m, the Yellow-rumped Warbler was the only common migrant species (Saab and Petit 1992). Three similar pastures that had been abandoned for two to four years supported vegetation that was taller (to 3 m) and structurally more heterogeneous, and contained significant numbers of several migrant species, including Least Flycatcher, Gray Catbird, Yellow Warbler, Magnolia Warbler, Common Yellowthroat, and Yellow-breasted Chat. Yellow-rumped Warblers were absent from the three abandoned pastures (Saab and Petit 1992).

In Quintana Roo, active pastures are less intensively managed and therefore more heterogeneous than those studied in Belize, and a richer migrant community is present (Lynch 1989). In Quintana Roo the number of migrant individuals tends to increase in the first few years following pasture abandonment, but there is not a marked change in species richness (Table 4).

DISCUSSION

Migrant species that reach their highest local abundance in the Yucatan within milpas, rough pasture, and early (1–5 year) successional regrowth include Ruby-throated Hummingbird, Least Flycatcher, Common Yellowthroat, Yellow Warbler, Yellow-rumped Warbler, Yellow-throated Warbler, Orchard Oriole, Blue Grosbeak, Painted Bunting, and Indigo Bunting. Some migrants can be extraordinarily abundant in severely disturbed habitats, including sites recently impacted by hurricane and/or wildfire (Lynch 1991), early herbaceous second growth (Waide 1980; Lynch 1989, 1992; Kricher and Davis 1992; Petit et al. 1992), and intensively managed croplands (Robbins et al. 1992). However, in low-stature disturbed habitats that lack significant woody vegetation, the migrant community tends to be dominated by only one or two species. In overgrown weedy fields the Indigo Bunting sometimes outnumbers all other migrants combined in mist net capture samples (Table 3a, 3b; Waide 1980). The Yellow-rumped Warbler is often the most common migrant in very low, patchy herba-

Table 4. Capture rates (CR = 100 × captures/net-hr) for migrants in active and recently abandoned cattle pastures in Quintana Roo, Mexico. The active pasture and five- to seven-year-old acahual were studied in 1985–1986 in the Sian Ka'an Biosphere Reserve; the one-year-old abandoned pasture was studied in 1985 near Puerto Morelos.

	Years since abandonment		
	Active	1 yr	5–7 yrs
Least Flycatcher	0.9	1.0	—
Gray Catbird	—	—	3.0
Wood Thrush	—	—	0.4
White-eyed Vireo	0.3	1.0	3.0
Ovenbird	—	—	1.5
Hooded Warbler	0.6	—	2.6
Kentucky Warbler	—	—	0.4
American Redstart	—	—	1.1
Magnolia Warbler	1.2	—	1.1
Northern Parula	—	—	1.1
Yellow-breasted Chat	0.3	—	0.4
Swainson's Warbler	0.3	—	—
Indigo Bunting	0.9	4.5	—
Painted Bunting	—	1.0	—
Common Yellowthroat	1.2	1.0	—
Net-hrs	336	310	264
Total migrant individuals	19	26	36
Total migrant species	8	5	10
Total Migrant CR	5.6	8.4	13.6

ceous vegetation where extensive bare substrate is exposed (e.g., coastal scrub). However, Yellow-rumped Warblers never reach the abundance shown by the Indigo Bunting in the latter's preferred habitat.

A few migrants (e.g., Gray Catbird, Painted Bunting, Yellow-breasted Chat), appear to be most abundant in mid-successional (3–10 year) scrub. Others (e.g., Wood Thrush, Kentucky Warbler, Worm-eating Warbler [*Helmitheros vermivorus*]) are common in forest, less so in mid-successional scrub, and essentially absent from very early (i.e., herb-grass stage) successional vegetation. Finally, a number of ecological generalists (e.g., White-eyed Vireo, Magnolia Warbler, Hooded Warbler, Ovenbird) are almost equally as common in all but the very earliest stages of succession (Lynch 1989, 1991, 1992). There are strong similarities between the migrant communities associated with acahuales and those found in low-stature, relatively open natural forest types, including deciduous forest and semideciduous forest (Paynter 1955; Lynch 1989) and seasonally flooded "bajo" forest (Lopez Ornat 1990; Whitacre et al. 1993).

Migrants versus Residents

Nearctic migrant landbirds constitute a nonrandom subset of the neotropical terrestrial avifauna. Compared with sympatric residents, migrants average smaller in body size, are less specialized in morphology and food habits, and are taxonomically biased toward the Parulinae, Vireonidae, and Tyrannidae (Willis 1980; Lynch 1992; Ricklefs 1992). Nevertheless, Yucatan migrants are fairly similar to their resident counterparts in average habitat niche breadth, a reflection of the fact that migrants and residents show similar tendencies to utilize both disturbed and undisturbed vegetation (Stiles 1980; Willis 1980; Lynch 1989, 1992). Contrary to what would be predicted if overwintering migrants competed strongly with residents, the abundance of the two groups is positively correlated in the Yucatan (Waide 1980; Lynch 1992).

Despite these ecological similarities, migrants and residents do appear to differ in their responses to major habitat disturbance. On the whole, migrants are more resilient than are residents to major perturbations such as habitat fragmentation (Greenberg 1992; Robbins et al. 1992), hurricane, and wildfire (this study). The responses of most migrant species to the latter two disturbance types in Quintana Roo involved relatively minor changes in abundance. The forest migrant community required only about three to four years to return to its previous composition after the impact of Hurricane Gilbert. Recovery was slower in forest that was swept by wildfire after the hurricane, but most forest-associated migrant species persisted after the fire. The few species that initially disappeared (Wood Thrush, Kentucky Warbler) recolonized the site within two to three years. In contrast, populations of many resident species (particularly frugivores and nectarivores) plummeted or disappeared completely after the forest was affected by hurricane or (especially) fire, and their recovery has been slow (Lynch 1991, unpubl. data).

In a field study conducted in Quintana Roo, Greenberg (1992) found that forest migrants were more likely than forest residents to use small, isolated patches of trees or brush in open fields. Many common resident species never were observed to occupy even fairly large forest patches. Greenberg concluded that forest migrants "might present a distinct and complementary conservation problem to those faced by resident birds," an assessment with which we concur.

Regional Comparisons

Although comparative data are few, there appear to be geographical differences in the responses of migrants to disturbance. Thus, as one moves from higher to lower latitudes within the northern Neotropics, migrants not only become scarcer and less diverse (Terborgh 1980; Petit et al. 1993), but also show a greater tendency to occupy disturbed, peripheral, and montane habitats, and to avoid the interior of primary lowland forest. In southeastern Mexico migrants are about as abundant in mature lowland forest as in secondary vegetation (Lynch 1989, 1992; Rappole et al. 1992). Migrants appear to be more concentrated in "edge" and secondary habitats in Belize (Kricher and Davis 1992; Petit et al. 1992), Panama (Willis 1980), Costa Rica (Stiles 1980; Blake and Loiselle 1992; Powell et al. 1992), Colombia (Hilty 1980), and Peru (Fitzpatrick 1980). In the dry lowlands of western Mexico migrant individuals and species are strongly concentrated in disturbed vegetation (Hutto 1980, 1992). In none of these regions are any migrant species restricted to mature forest, although some species reach their maximum density there.

The Significance of Disturbed Vegetation to Overwintering Migrants

In a recent review of the role of disturbed vegetation in the distribution of overwintering migratory landbirds, Petit et al. (1993) found that disturbed tropical habitats tend to contain more migrant species than do undisturbed tropical forests. Quantitative surveys (e.g., Hutto 1980; Blake and Loiselle 1992; Petit et al. 1992; Powell et al. 1992; Robbins et al. 1992) reveal that the abundance of migrant individuals also is considerably higher in many secondary habitats than in mature forest. Although many migrants avoid intensively managed croplands and pastures and the earliest stages of second growth (Lynch 1989,1992; Saab and Petit 1992; Whitacre et al. 1993), most species are able to occupy rough pastures, woody scrub, thinned forest, fruit and coffee plantations, and other disturbed habitats that contain trees, shrubs, or tall herbaceous vegetation. Importantly, a sizeable minority of migrant species, including some whose population status should concern conservationists, avoids mature tropical forest. If one's goal is to preserve the maximum abundance and diversity of migrants, the entire spectrum of disturbed and undisturbed vegetation in tropical landscapes must be considered.

Our point is not that mature tropical forest is unimportant to migrants. On the contrary, approximately 20% of all migrant landbird species overwinter mainly in mature tropical forest, and about half of all migrants make significant use of this habitat (Petit et al. 1993). Nor do we believe that overgrazed pastures, sugarcane fields, and other highly managed agro-ecosystems have significant conservation value for any but a handful of migrant species. However, concern for the preservation of mature tropical forests should not blind conservationists to the significance of tree plantations, orchards, abandoned pastures, fallow fields, immature woodlands, and other managed and secondary habitats. These non-pristine habitats will become increasingly critical to the future survival of migratory birds and other wildlife in the Mesoamerican landscapes of the future. Although high rates of tropical deforestation are widely cited, it is exceedingly difficult to obtain quantitative information on the prevalence of various stages of secondary regrowth and the extent of disturbed (as opposed to obliterated) primary forest (Sader and Joyce 1988). A few preliminary studies have combined remote sensing technology and habitat-specific ground surveys to project migrant abundance at the regional scale (e.g., Green et al. 1987; Powell et al. 1992). Our data for the Yucatan strongly suggest that most successional turnover in migrant communities occurs within the first few years after farm or pasture abandonment, long before the regenerating vegetation resembles mature forest in stature, canopy structure, or floristic composition. To exploit the full potential of remote sensing technology, we need to map various stages of early- to mid-successional communities that traditionally have been either ignored, or else lumped together as "scrub" or "second growth". Ground truth information on the occurrence of migrants in the various classes of disturbed and undisturbed vegetation then can be used to assess migrant distribution and abundance at a regional scale.

Conservation and Disturbed Vegetation

Conservationists should pay more attention to secondary and disturbed tropical habitats. Where second growth makes up a significant proportion of the landscape, as in the Yucatan Peninsula, successional vegetation may harbor a high proportion of the total populations of many of the species we wish to preserve. This applies not only to overwintering migrants, but to many resident birds and other wildlife as well. Even where second growth is not the preferred habitat, it may serve a useful role in linking more desirable habitat patches, buffering primary forest against change, or simply increasing the carrying capacity of the entire landscape. We may decry the fact that most of Mesoamerica, the Caribbean islands, and huge areas of South America already have been converted to fields, pastures, plantations, and second growth, but all indications are that this trend will only intensify in the future. It would be inexcusably shortsighted if we were to ignore the crucial role that non-pristine habitats can play in the struggle to preserve neotropical biodiversity.

Scarce conservation resources are often expended to preserve fragments of primary forest that are too small and too isolated to maintain viable populations of the wildlife species they contain. It might be better to devote some of those resources to the protection or outright purchase of much larger areas of cheaper secondary habitat, and to focus more attention on the wise management of tropical lands that are not devoted primarily to conservation (e.g., selectively logged forest). Given the choice of preserving 100 ha of scrubby successional vegetation or an equal area of magnificent old growth tropical forest, most of us would opt for the latter. But what if 1000 ha of secondary forest could be obtained for the same price as 100 ha of old growth? For many migrant birds (and, we suspect, many other species as well), the second growth alternative would not necessarily be second best.

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APPENDIX. Scientific and common name of bird species mentioned in the tables and text.

Family—Subfamily	Common Name	Scientific Name
Trochilidae		
	Ruby-throated Hummingbird	*Archilochus colubris*
Tyrannidae		
	Least Flycatcher	*Empidonax minimus*
Muscicapidae		
	Wood Thrush	*Hylocichla mustelina*
Mimidae		
	Gray Catbird	*Dumetella carolinensis*
Vireonidae		
	White-eyed Vireo	*Vireo griseus*
Emberizidae—Parulinae		
	Hooded Warbler	*Wilsonia citrina*
	Kentucky Warbler	*Oporornis formosus*
	Ovenbird	*Seiurus aurocapillus*
	Northern Waterthrush	*Seiurus noveboracensis*
	Yellow-breasted Chat	*Icteria virens*
	Common Yellowthroat	*Geothlypis trichas*
	Worm-eating Warbler	*Helmitheros vermivorus*
	Swainson's Warbler	*Limnothlypis swainsonii*
	Black-and-white Warbler	*Mniotilta varia*
	Northern Parula	*Parula americana*
	Black-throated Green Warbler	*Dendroica virens*
	Magnolia Warbler	*Dendroica magnolia*
	Yellow-rumped Warbler	*Dendroica coronata*
	Yellow Warbler	*Dendroica petechia*
	Blue-winged Warbler	*Vermivora pinus*
	American Redstart	*Setophaga ruticilla*
Emberizidae—Thraupinae		
	Summer Tanager	*Piranga rubra*
Emberizidae—Cardinalinae		
	Indigo Bunting	*Passerina cyanea*
	Painted Bunting	*Passerina ciris*
	Blue Grosbeak	*Guiraca caerulea*
Emberizidae—Icterini		
	Orchard Oriole	*Icterus spurius*