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Effects of Hurricane Gilbert on Birds in a Dry Tropical Forest in the Yucatan Peninsula[1]

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ABSTRACT

On 14 September 1988 Hurricane Gilbert, the strongest tropical storm ever recorded in the Western Hemisphere, passed through an area of tropical forest in Quintana Roo, Mexico, where I had been studying winter bird populations since 1984. The hurricane defoliated the forest, and created a nearly impenetrable tangle of fallen branches and vines at ground level. Point counts and mist-netting conducted 5–6 mo after the storm revealed an influx of field- and shrub-associated bird species. Most previously common insectivores and feeding generalists were present in February–March 1989, but many had declined significantly in abundance. Resident frugivores and nectarivores were especially scarce after the hurricane. Wildfires that swept through northeastern Quintana Roo in the summer of 1989 had a greater effect on birds than did the storm itself. By late winter 1990 the bird community within unburned forest was clearly converging toward its prehurricane composition. In contrast, the bird community in burned forest resembled that associated with recently abandoned agricultural fields and pastures. As a group, overwintering nearctic migrants appeared to be more resilient than year-round residents to the effects of both the hurricane and the associated fires.

RESUMEN

El 14 de septiembre de 1988 de huracán Gilberto, la tormenta tropical más fuerte registrada hasta ahora en el hemisferio occidental, pasó a través de un área de bosque tropical en Quintana Roo, México, donde se habían estado estudiando poblaciones de pájaros de invierno desde 1984. El huracán defolió el bosque, creando un maraña casi impenetrable de ramas caídas y bejucos a nivel del suelo. El "conteo en puntos" y la captura con redes realizadas de 5–6 meses luego del huracán demostró una entrada de especies relacionadas a arbustos y plantaciones. La mayoría de los insectívoros comunes y generalistas estuvieron presentes en febrero–marzo de 1989, pero la abundancia de muchos disminuyó significativamente. Los frugívoros y nectarívoros escasearon especialmente luego del huracán. Los incidendios naturales que se extendieron a través del noreste de Quintana Roo en el verano de 1989 tuvieron un mayor efecto en los pájaros que la tormenta en sí. Al final de invierno de 1990, la comunidad de pájaros en el bosque no quemado se estaba acercando evidentemente a su composición antes del huracán. En contraste, la comunidad de pájaros en el bosque quemado era semejante a la asociada a plantaciones agrícolas abandonadas recientemente y a pastizales. Como grupo, los migratorios invernales neárticos aparentemente son más resistentes a los efectos del huracán y los fuegos asociados que los residentes de todo el año.

In the past century more than 30 hurricanes and other major tropical storms have swept the Caribbean coastline of Quintana Roo, the most hurricane-prone region in Mexico (Jauregi *et al.* 1980, Lopez Ornat 1983). Hurricane Gilbert's arrival on the Quintana Roo coast on 14 September 1988 was therefore not a freak occurrence, although this storm was unusually severe. NOAA aircraft measured wind speeds aloft of more than 300 km/hr and internal barometric pressures as low as 885 mb, making Gilbert the strongest cyclonic storm ever recorded in the Western Hemisphere (Clark 1989). Since 1984 D. F. Whigham and I had been conducting studies of bird and plant communities in an area of northeastern Quintana Roo, Mexico that received the full impact of this hurricane.

Fueled by hurricane debris (cf. Whigham *et al.* 1991), wildfires swept through northeastern Quintana Roo during the unusually dry summer of 1989. Burned and unburned tracts of forest were juxtaposed, making it possible to directly compare hurricane effects with those of fire. In this paper I describe the winter bird community of the prehurricane forest, then document changes that occurred over the 18 mo following Hurricane Gilbert.

STUDY SITE AND METHODS

Studies were conducted near the fishing village of Puerto Morelos (Fig. 1). Data on bird communities had been gathered prior to Hurricane Gilbert using point counts and mist-netting. Because these two survey methods yield very different results in the Yucatan region (Lynch 1989), and because most other investigators have employed only one method

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(but see Waide 1991), results of point counts and mist-netting are discussed separately.

As part of a regional survey of winter bird communities in the Yucatan Peninsula, I conducted unlimited-radius point counts between February 1987 and March 1988 at 52 forested locations within a 15 km radius of Puerto Morelos. Lynch (1989) describes the methodology in detail. Post-hurricane counts were conducted in the same region (though not at the same points) in February–March 1989 and February–March 1990. The 1990 counts were equally divided among sites that burned in summer 1989 and unburned sites. All counts were conducted in mature stands of medium-stature (canopy height = 10–18 m) semievergreen tropical forest, the *selva mediana subperennifolia* of Miranda (1958). Results were summarized as percent occurrences for individual species and for groups of species (*e.g.*, migrants, residents, frugivores). Occurrence rates from posthurricane surveys were compared with prehurricane rates, using *t*-tests of arcsine transformed percentages (Sokal & Rohlf 1969: 607–608). The statistical technique of rarefaction was employed to estimate species richness (±1 SD) in standard samples of 100 detections, using the FORTRAN program of Simberloff (1978).

The second set of prehurricane data derives from 5559 net-hr of mist-netting (Lynch 1989, in press) at Rancho San Felipe, 6 km SSW of Puerto Morelos (Fig. 1). Netting took place during winter months between February 1984 and March 1988 in an extensive tract of mature forest and an adjacent 6 ha patch of brushy second-growth (*acahual*) that was 5–7 years into secondary succession. Posthurricane mist-netting was conducted at the forested site in February–March in 1989 and 1990. In the latter year netting effort was divided between unburned forest and areas where >80 percent of all trees had been killed by wildfires during the previous summer. The *acahual* could not be studied after the hurricane, as it had been cleared for farming. At each site 15–24 nylon mist-nets (12 m × 2 m; mesh size: 3.2–3.8 cm) were operated between first light and midday for 2–4 consecutive mornings each winter. Rarefaction was used to estimate the number of species (±1 SD) expected in standard samples of 100 captures.

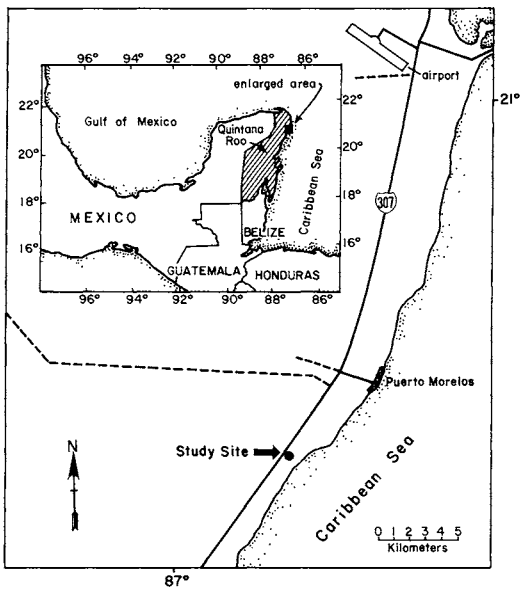

FIGURE 1. Location map showing the Yucatan Peninsula, the Mexican state of Quintana Roo, and the study site where mist-netting was conducted.

RESULTS AND DISCUSSION

PREHURRICANE POINT COUNTS.—Point counts conducted in *selva mediana* during the 2 winters prior to Hurricane Gilbert yielded 69 bird species and 446 species detections, termed "occurrences" (Table 1). Overwintering North American migrants made up 23 percent of all species and 37 percent of all occurrences. Four of the ten most frequently detected species were nearctic migrants (scientific names are given in Appendix): Hooded Warbler, Magnolia Warbler, Wood Thrush, and American Redstart. The most frequently recorded resident species were Brown Jay, Red-throated Ant-Tanager, Lesser Greenlet, Keel-billed Toucan, Dusky-capped Flycatcher, and Olivaceous Woodcreeper. Forest-associated resident frugivores and nectarivores (15 species of tinamous, chachalacas, pigeons and doves, parrots, toucans, hummingbirds, and trogons) contributed 18 percent of all detections in the prehurricane sample (Table 1).

EFFECTS OF HURRICANE GILBERT ON THE FOREST.—Whigham *et al.* (1991) have analyzed the impact of the hurricane on the forest at Rancho San Felipe. Briefly, the storm completely defoliated most trees and destroyed all arboreal fruit and flowers. Large numbers of branches and vines were blown down, but relatively few trees were windthrown or otherwise killed outright. Extensive regrowth of leaves had occurred by February 1989, at which time vines, downed tree limbs, and invading weeds formed an almost impenetrable tangle in a forest whose understory previously had been relatively open.

TABLE 1. *Summary statistics for point counts and mist-netting conducted before and after Hurricane Gilbert struck Puerto Morelos, Quintana Roo, Mexico. The number of species per 100 detections and per 100 captures (±1 SD) are estimated by rarefaction (see text). Capture rate = 100 × no. new captures per net-hour. In 1990 surveys were divided between unburned (U) and burned (B) sites. In all three posthurricane samples the percentage of frugivores and nectarivores was significantly lower than the prehurricane value (*** P < .001; ** P < .01)*

	Prehurricane		Posthurricane forest		
	Forest	*Acahual*	1989	1990 (U)	1990 (B)
Point counts					
Number of counts	52	—	45	36	36
Detections/pt.	8.6	—	5.1	7.7	4.4
Total species	69	—	59	63	46
Spp/100 detections	43 ± 3	—	41 ± 3	43 ± 3	37 ± 2
Migrant species (%)	16 (23)	—	13 (29)	15 (24)	17 (37)
Migr. detections/pt.	3.2	—	2.0	2.9	2.8
% Frugivore & nectarivore detections	18	—	6***	10**	5***
Mist-netting					
Net-hrs	4213	1346	396	662	424
Total captures	527	559	130	162	171
Capture rate	11.9	41.3	32.8	24.5	40.3
Total species	54	81	46	42	41
Spp/100 captures	30 ± 2	40 ± 3	41 ± 3	35 ± 2	32 ± 2
Migrant species (%)	12 (22)	22 (27)	14 (30)	13 (31)	13 (32)
Migr. captures (%)	161 (30)	240 (43)	51 (39)	53 (33)	98 (57)

POINT COUNTS 5–6 MONTHS AFTER HURRICANE GILBERT.—The number of species detected in point counts 5–6 mo after Hurricane Gilbert was about 15 percent below the prestorm value, reflecting both a lower number of detections per point and a somewhat smaller sample of counts in 1989 (Table 1). The hurricane had no apparent effect on the underlying dominance/diversity pattern of the community. Rarefaction of the point count data indicates that about the same number of species would be expected per 100 detections before and after the storm. Nearctic migrants made up about the same proportion of all species and occurrences as they had before the hurricane, but the number of migrant occurrences per point decreased by more than one-third (Table 1). However, only two migrant species showed substantial posthurricane shifts in both relative and absolute abundance. Wood Thrush, which had ranked fifth among all species in frequency, was not detected 5–6 mo after the storm. In contrast, White-eyed Vireo doubled its prehurricane occurrence rate (Table 2).

The number of resident species detected per count declined by 44 percent after the hurricane, and occurrence rates of many individual resident species were reduced by more than 75 percent (Table 2). As a group, resident frugivores and nectarivores (see above) declined by more than one-half ($P < .001$; Table 1). On the other hand, a number of resident species (*e.g.*, Lesser Greenlet, White-throated Spadebill, Golden-fronted Woodpecker, Bright-rumped Attila, Rose-throated Tanager) occurred at approximately their prehurricane frequencies 5–6 months after the storm, and several previously scarce edge/shrub species (*e.g.*, White-bellied Wren, Spot-breasted Wren) were common in the forest interior (Table 2).

POINT COUNTS 17–18 MONTHS AFTER HURRICANE GILBERT.—By late winter of 1990, the forest bird community had begun to return to its prestorm abundance and composition. The total number of occurrences per point count in unburned *selva mediana* increased by 50 percent over the 1989 value, and the number of migrant occurrences per point increased by 45 percent (Table 1). The most frequently encountered migrants were Magnolia Warbler, White-eyed Vireo, Hooded Warbler, American Redstart, and Black-and-white Warbler. By 1990 canopy regrowth had begun to shade out the dense understory, and the ground-foraging Wood Thrush was detected in 6 percent of the 1990 counts. Some resident species (*e.g.*, Red-throated Ant-tanager, Dusky-capped Flycatcher) had reversed their

TABLE 2. *Responses of 35 bird species (plus all hummingbirds) to Hurricane Gilbert and subsequent fire disturbance, based on results of point counts conducted near Puerto Morelos, Quintana Roo. Entries are the percentage of counts in which a species was detected. Nearctic migrants are indicated by (m). Last column gives data for forest that burned in summer 1988. Statistical significance of changes is based on comparisons with prehurricane occurrence rates (* P < .05; ** P < .01, *** P < .001).*

	Pre-hurricane ($N = 52$)	Posthurricane		
		1989 ($N = 45$)	1990 ($N = 36$)	1990 (Burn) ($N = 36$)
Initial decline—little or no recovery by 1990				
Hooded Warbler (m)	81	42***	44***	33***
Brown Jay	56	16***	14***	14***
Wood Thrush (m)	29	0***	6**	0***
Pale-billed Woodpecker	14	4	0***	3*
Ferruginous Pygmy-Owl	14	0***	0***	0***
Blue-winged Warbler (m)	12	0***	0**	6
Initial decline—substantial or full recovery by 1990				
Hummingbirds (4 species)	64	11***	22***	17***
Red-throated Ant-Tanager	33	12*	31	22
Dusky-capped Flycatcher	19	6*	11	6
Keel-billed Toucan	19	2**	6	0***
Olivaceous Woodcreeper	17	4*	14	0***
Carolina Wren	17	4*	14	0***
Yucatan Flycatcher	10	0**	11	6
Red-crowned Ant-Tanager	6	0*	11	0*
No significant response to hurricane in unburned or burned forest				
American Redstart (m)	29	24	39	44
Golden-fronted Woodpecker	17	18	17	8
Black-and-white Warbler (m)	17	22	19	33
Black-throated Green Warbler (m)	12	8	14	11
Melodious Blackbird	12	6	3	3
Roadside Hawk	10	2	8	6
No response in unburned forest—significant reduction in burned forest				
Lesser Greenlet	27	20	31	0***
White-throated Spadebill	23	20	11	0***
Bright-rumped Attila	17	8	22	0***
Northern Bentbill	12	13	22	0*
Citreoline Trogon	12	4	17	0***
Gray Catbird (m)	10	4	17	3**
Initial increase in unburned forest—no change in 1990				
Spot-breasted Wren	4	18*	22**	3
White-bellied Wren	0	13**	11**	6*
Continued increase in unburned forest in 1990				
Magnolia Warbler (m)	50	38	75*	36
White-eyed Vireo (m)	17	36*	53***	36*
Rose-throated Tanager	17	22	36*	14
Green-backed Sparrow	0	4*	11**	0
Increased in burned forest in 1990				
Least Flycatcher (m)	4	4	11	19*
Yellow-rumped Warbler (m)	0	0	0	19***
Common Yellowthroat (m)	0	2	3	17***
Northern Waterthrush (m)	2	0	0	11

posthurricane declines, but others, particularly frugivores and nectarivores, still had not rebounded (Tables 1 and 2).

EFFECTS OF FIRE.—In February 1990, six months after late summer rains finally extinguished the wildfires that had swept northeastern Quintana Roo, extensive tracts of forest in the study area were charred beyond recognition. Few or no live trees or shrubs were present in some stands, the only living ground cover consisting of freshly sprouted bracken fern (*Pteridium aquilinum*). However, natural and man-made firebreaks had preserved pockets of intact or only partially burned forest in close proximity to tracts that had been completely burned.

Compared with unburned *selva mediana,* burned forest had 27 percent fewer bird species, 43 percent fewer occurrences per point, and 13 percent fewer expected species per sample of 100 detections (Table 1). Migrants occurred at very high relative frequencies in burned forest, where they comprised nearly two-thirds of all detections, but the absolute number of migrant occurrences per point was virtually identical in burned and unburned forest (Table 1). The same five species dominated the migrant assemblage in burned and unburned forest. Forest-floor migrants that require shaded, humid conditions (*e.g.,* Wood Thrush) were absent from burned forest. In contrast, migratory species whose normal winter habitat in the Yucatan Peninsula (*cf.* Lynch 1989, in press) includes fields, pastures, and early successional scrub (*e.g.,* Least Flycatcher, Yellow-rumped Warbler, Yellow-throated Warbler, Palm Warbler, Common Yellowthroat, Indigo Bunting, Painted Bunting) contributed 17 percent of all detections in burned forest (*vs.* 2% in unburned forest).

Resident species were disproportionately affected by fire. In comparison with unburned forest, burned forest yielded 40 percent fewer resident species and 67 percent fewer resident detections per point (Table 1). Only one of the ten most frequent species in burned forest was a permanent resident (Table 2).

PREHURRICANE MIST-NETTING RESULTS.—The prehurricane capture sample from *selva mediana* consisted of 516 individuals that belonged to 54 species (Table 1). The capture rate (CR = 100 × no. new captures/net-hr) in forest was relatively low, and rarefaction predicts only 30 species per 100 captures. This reflects the fact that a mere five species accounted for half of all captures in the prehurricane forest (Table 3).

Migrants contributed 22 percent of the species and 31 percent of the individuals in the sample, and five of the ten most frequently captured species were migrants. Although the ranked abundance of some individual migrant species were comparable in netted samples and point counts, the abundances of most species showed little correlation between the two survey methods (Table 3). Among residents, only Red-throated Ant-tanager ranked highly in both the mist-net and point count samples.

Although the netting effort for the prehurricane old-field was less than one-third that for the forest, the *acahual* yielded 16 percent more captures and 50 percent more species (Table 1). The high species richness of the old-field sample is not simply an artifact of the large number of captures, as rarefaction of both samples to 100 captures yields a 30 percent higher predicted species richness of the *acahual* sample (Table 1). Migrants made up a higher proportion of the species and captures in the *acahual* than in the forest (Table 1). In the Yucatan region, many forest-associated migrants also occur in brushy second-growth (Lynch 1989, in press), and some such species were quite common in the netted sample from the *acahual.* On the other hand, many of the migrants and residents that are most characteristic of the *acahual* habitat in northeastern Quintana Roo (*e.g.,* Caribbean Elaenia, Gray Catbird, Black Catbird, Mangrove Vireo, Blue Bunting) were rarely or never netted in the prehurricane forest.

MIST-NETTING RESULTS 5–6 MONTHS AFTER THE HURRICANE.—The posthurricane forest combined the tree stature and tree density of the intact forest with the dense understory and high light levels typical of *acahuales* and other low-stature habitats. The 1989 sample of captures reflects this hybrid quality of the posthurricane vegetation. The capture rate in the posthurricane forest (Table 1) was closer to the prestorm rate for the *acahual* than to the prestorm rate for forest. Similarly, rarefaction of the posthurricane sample yields an expected species richness per 100 captures that greatly exceeds the prehurricane value for the forest, but is virtually identical to the corresponding value for the *acahual* (Table 1).

An influx of scrub and field-edge species (*e.g.,* Spot-breasted Wren, Indigo Bunting, Bananaquit, Orchard Oriole, and Orange Oriole) was balanced by continued high numbers of forest-associated species that forage in dense, leafy understory vegetation (*e.g.,* Red-throated Ant-Tanager, Tawny-crowned Greenlet) or that are relatively indifferent to understory characteristics (*e.g.,* Ivory-billed Woodcreeper). However, numerous previously common

TABLE 3. *Capture rates (CR = 100 × individuals/net-hr) for 32 resident and migrant (m) bird species before and after Hurricane Gilbert. Data for 1990 are from unburned and burned (B) forest. Figures in parentheses (R_p) are ranks of species in prehurricane point counts.*

Species	N	R_p	Pre-hurricane	Posthurricane		
				1989	1990	1990(B)
Red-throated Ant-Tanager	136	(4)	2.5	2.8	2.9	0.2
Ruddy Woodcreeper	59	(60)	1.2	0.2	1.4	—
Hooded Warbler (m)	55	(1)	1.0	1.3	0.9	0.5
Ovenbird (m)	40	(24.5)	0.7	0.8	0.8	0.7
Wood Thrush (m)	26	(5.5)	0.6	—	—	—
Kentucky Warbler (m)	28	(36)	0.5	0.5	0.8	—
Tawny-crowned Greenlet	31	(60)	0.5	1.0	0.9	—
Ivory-billed Woodcreeper	38	(36)	0.5	2.0	1.2	0.5
Black-and-white Warbler (m)	22	(12)	0.4	0.2	0.3	—
Wedge-tailed Sabrewing	22	(36)	0.4	—	1.1	—
Royal Flycatcher	14	—	0.3	0.5	—	0.2
Bright-rumped Attila	16	(12)	0.3	0.5	0.6	—
Blue Bunting	17	—	0.3	0.8	1.4	0
White-bellied Emerald	11	(20.5)	0.2	0.5	0.4	—
Olivaceous Woodcreeper	21	(12)	0.2	1.8	0.6	0.2
Magnolia Warbler (M)	15	(3)	0.2	1.5	—	0.2
White-throated Spadebill	12	(8)	0.1	1.3	0.2	—
Northern Bentbill	11	(19)	0.1	0.5	0.6	—
White-eyed Vireo (m)	42	(12)	0.1	3.3	2.6	1.9
Gray Catbird (m)	11	(23)	0.05	0.8	0.8	0.2
Common Yellowthroat (m)	6	—	0.02	—	0.4	0.5
Green-backed Sparrow	5	—	0.02	0.2	0.4	—
Common Ground Dove	6	—	—	—	—	1.4
Ruby-throated Hummingbird (m)	13	—	—	0.8	—	2.4
Spot-breasted Wren	7	(48.5)	—	1.0	0.4	—
Bananaquit	11	—	—	1.0	0.6	0.7
Indigo Bunting (m)	61	—	—	1.3	0.9	11.8
Painted Bunting (m)	15	—	—	0.2	0.3	2.8
Blue-black Grassquit	9	—	—	—	0.2	4.2
Altamira Oriole	4	—	—	—	—	0.9
Orchard Oriole (m)	5	—	—	1.3	—	—
Orange Oriole	4	—	—	1.0	—	—

species were rare or absent in the mist-netted sample after the hurricane (Table 3).

Migrants continued to make up approximately 30 percent of all species and 40 percent of all captures after Hurricane Gilbert, but the relative and absolute capture frequencies of some migrant species changed dramatically. In agreement with the point count results, the capture data (Table 3) show a dramatic increase in the relative and absolute abundance of the previously uncommon White-eyed Vireo, disappearance of the formerly common Wood Thrush, and first appearances in the forest of several field-shrub species (*e.g.*, Indigo Bunting, Painted Bunting).

MIST-NETTING RESULTS 17–18 MONTHS AFTER THE HURRICANE.—In late winter of 1990 the capture rate fell slightly below the 1989 level, but remained more than double the prehurricane rate (Table 1). In other respects, however, the capture data agree with the point count results in indicating a rapid return of the forest bird community toward its pre-hurricane composition. Rarefaction of the 1990 data yields an expected species richness midway between the 1989 and prestorm values (Table 1). Most of the field-shrub species that had invaded the forest following the hurricane were rare or absent in winter 1990, and there was a concomitant resurgence of several forest-associated species that had initially declined (*e.g.*, Wedge-tailed Sabrewing, Ruddy Woodcreeper). On the other hand, some forest birds that prefer a dense, leafy shrub layer (*e.g.*, White-eyed Vireo, Tawny-crowned Greenlet) maintained or even augmented the increases they had shown after the storm (Table 3).

Migrants continued to contribute about the same proportion of species and individuals in the netted sample from late winter of 1990 (Table 1). White-

eyed Vireo remained the most commonly netted migrant, but Magnolia Warbler, the second most frequent migrant in 1989, was not captured in 1990. This warbler was abundant in the 1990 point counts (Table 2), and is a good example of a canopy-foraging species that is under-sampled by netting in undisturbed forest (Lynch 1989).

FIRE EFFECTS.—The capture data are consistent with the point counts in indicating a major effect of the 1989 wildfires on the local avifauna. In 1990, capture rates in burned forest greatly exceeded those in the 1990 unburned forest or in the prehurricane forest, and approximated capture rates in the prehurricane *acahual* and in the 1989 unburned forest (Table 1). Numerous field-associated species (*cf.* Lynch 1989, in press) were netted in burned forest, but were absent from unburned forest (Table 3). However, nearly one-half of the captures from burned forest were contributed by only three species: Indigo Bunting, Painted Bunting, and Blue-black Grassquit (Table 3). Due to this low equitability, the species richness of a rarefied sample of captures from burned forest is considerably lower than equivalent estimates for either the 6 mo or 18 mo unburned forest (Table 1). Numerical dominance of early successional communities by one or a few bird species is widespread in the Yucatan area (*cf.* Waide 1980; Lynch 1989, in press).

CONCLUSIONS

Given the unusual severity of Hurricane Gilbert, and the resulting loss of virtually all arboreal fruit, flowers, and foliage from the forest, the immediate effects of the storm on birds must have been much more drastic than was evident 5–6 mo later. By then, the forest vegetation had begun to regenerate, and most of the usual species of forest-associated birds were present, though generally in low numbers. As a group, specialized forest-associated frugivores and nectarivores declined dramatically after the hurricane, and still had not fully recovered 18 mo later (Table 2). Recent studies in Puerto Rico (Waide 1991) and the U.S. Virgin Islands (Askins & Ewert 1991) also have documented especially severe impacts of hurricanes on frugivorous and nectarivorous birds.

Hurricane-damaged forest was invaded by bird species that are normally associated with forest-edge, dense scrub, or even open-field habitats. The resulting anomalous mixture of forest- and field-adapted species proved to be transitory, and present evidence suggests that within a very few years the bird community in unburned hurricane-damaged forest will resemble that associated with intact forest, at least with respect to major patterns of diversity, abundance, and species composition. The effects of wildfires, which historically have followed in the wake of major hurricanes in Quintana Roo (Perez Villegas 1980), appear to be more severe and long-lasting than the effects of wind damage. The fires that swept through tens of thousands of hectares of Quintana Roo in the summer of 1989 obliterated the effects of initial forest regeneration and pushed back secondary succession to the earliest stages associated with active or very recently abandoned pastures and agricultural fields (Lynch 1989, in press). In terms of bird community composition, the closest natural analog of hurricane- and fire-perturbed forest communities in the northeastern Quintana Roo may be the coastal dune-scrub assemblage. This vegetation type is also strongly influenced by hurricanes, and its flora and avifauna contain many Caribbean elements (López Ornat & Lynch 1991). Some birds whose main natural habitat in the Yucatan is coastal dune scrub invaded the hurricane-impacted and (especially) the fire-impacted forest (*e.g.*, Yellow-rumped Warbler, Palm Warbler, Yellow-throated Warbler).

Major perturbations by hurricanes and fire must have characterized the northern Yucatan Peninsula for many thousands of years, although the frequency and intensity of fires have increased in the past few centuries due to human activities (Perez Villegas 1980). At a very general level, the Peninsula's entire biota can be considered to be adapted to irregular, but relatively frequent, major disturbances, as has been suggested for the Caribbean region as a whole (Lugo 1988).

With some notable exceptions (*e.g.*, Wood Thrush), overwintering nearctic migrants appear to be relatively well adapted to survive in naturally disturbed landscapes such as those produced by the effects of hurricanes and fire. This seems to be true despite the fact that intact forest is the vegetation type where many migrants reach their maximum abundance during winter (Lynch 1989, in press). Species that can cope with a natural mosaic of disturbance may be preadapted to accommodate human-induced changes in the tropical landscape. This ecological resiliency may be expressed as the ability to inhabit land that is heavily disturbed by farming or grazing, to quickly colonize early successional vegetation after human disturbance ceases, or to make use of an unusually broad spectrum of natural and exotic vegetation. Finally, the results of the present study underscore an important, but often

neglected, point: even degraded landscapes can provide a reservoir of habitat for species of conservation significance.

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APPENDIX

Scientific names of bird species mentioned in the text and tables.—Acciptridae: Roadside Hawk (*Buteo magnirostris*); Columbidae: Common Ground Dove (*Columbina passerina*); Strigidae: Ferruginous Pygmy-Owl (*Glaucidium brasilianum*) Trochilidae: Ruby-throated Hummingbird (*Archilochus colubris*), Wedge-tailed Sabrewing (*Campylopteris curvipennis*), White-bellied Emerald (*Amazilia candida*); Trogonidae; Citreoline Trogon (*Trogon citreolus*); Ramphastidae: Keel-billed Toucan (*Ramphastos sulfuratus*); Picidae: Golden-fronted Woodpecker (*Centurus aurifrons*), Pale-billed Woodpecker (*Campephilus guatemalensis*); Dendrocolaptidae: Ivory-billed Woodcreeper (*Xiphorhynchus flavigaster*), Olivaceous Woodcreeper (*Sittasomus griseicappilus*), Ruddy Woodcreeper (*Dendrocincla homochroa*); Tyrannidae; Least Flycatcher

(*Empidonax minimus*), Caribbean Elaenia (*Elaenia martinica*), Bright-rumped Attila (*Attila spadaceus*), Dusky-capped Flycatcher (*Myiarchus tuberculifer*), Yucatan Flycatcher (*Myiarchus yucatanensis*), Royal Flycatcher (*Onychorhynchus coronatus*), White-throated Spadebill (*Platyrinchus mystaceus*), Northern Bentbill (*Oncostoma cinereigulare*); Corvidae: Brown Jay (*Cyanocorax morio*); Troglodytidae: Carolina Wren (*Thryothorus ludovicianus*), Spot-breasted Wren (*Thryothorus maculipectus*), White-bellied Wren (*Uropsila leucogastra*); Muscicapidae: Wood Thrush (*Hylocichla mustelina*); Mimidae: Black Catbird (*Melanoptila glabirostris*); Gray Catbird (*Dumatella carolinensis*); Vireonidae: Lesser Greenlet (*Hylophilus decurtatus*), Tawny-crowned Greenlet (*Hylophilus ochraceiceps*), Mangrove Vireo (*Vireo pallens*), White-eyed Vireo (*Vireo griseus*); Emberizidae (Parulinae): Black-throated Green Warbler (*Dendroica virens*), Magnolia Warbler (*Dendroica magnolia*), Yellow-throated Warbler (*Dendroica dominica*), Yellow-rumped Warbler (*Dendroica coronata*), Common Yellowthroat (*Geothlypis trichas*), Black-and-white Warbler (*Mniotilta varia*), Kentucky Warbler (*Oporornis formosus*), Ovenbird (*Seiurus aurocapillus*), Northern Waterthrush (*Seiurus noveboracensis*), American Redstart (*Setophaga ruticilla*), Blue-winged Warbler (*Vermivora pinus*), Hooded Warbler (*Wilsonia citrina*); (Thraupinae): Bananaquit (*Coereba flaveola*), Red-throated Ant-Tanager (*Habia fuscicauda*), Red-crowned Ant-Tanager (*Habia rubica*), Rose-throated Tanager (*Piranga roseogularis*); (Cardinalinae): Blue Bunting (*Cyanocampsa parellina*), Indigo Bunting (*Passerina cyanea*), Painted Bunting (*Passerina ciris*); (Emberizinae): Green-backed Sparrow (*Arremenops chloronotus*), Blue-black Grassquit (*Volatinia jacarina*); (Icterinae): Altamira Oriole (*Icterus gularis*), Orange Oriole (*Icterus auratus*), Orchard Oriole (*Icterus spurius*), Melodious Blackbird (*Dives dives*).