PROPORTIONS OF WINTERING NORTH AMERICAN BIRDS IN DISTURBED AND UNDISTURBED DRY TROPICAL HABITATS

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Information on the ecology of temperate-zone birds on their tropical wintering grounds is scanty. Qualitative observations indicate that temperate-zone birds are most conspicuous in man-disturbed areas or in woodlands at high elevations. Lowland rain forests apparently contain very few temperate-zone migrants (Brosset 1968; Buechner and Buechner 1970).

Willis (1966) and Leck (1972a) have studied the relative impact of migrant and resident birds upon small portions of the available food resources of upland and lowland forests in Panamá. Otherwise, quantitative studies of the distribution and ecological importance of temperate-zone migrants in the tropics are virtually nonexistent. In particular, it is not clear whether migrants are scarce in all successionally mature lowland habitats or whether they merely avoid tracts of humid lowland forest. This paper represents a contribution toward answering that particular question.

STUDY AREAS AND PROCEDURES

Bird censuses used in this study were conducted by the author on nine different plots in the state of Yucatan, México, between 20°00′ and 21°00′ N. This region averages 50–70 cm of precipitation annually, most of it occurring between April and October. The censuses were taken during the period 23 December 1972–4 January 1973, in the midst of the dry season. During this time precipitation was nil, and temperatures ranged from 58 to 86°F. The plots were classified as either wholly man-disturbed (group A, 3 plots), partly disturbed (group B, 3 plots), or essentially undisturbed (group C, 3 plots). Brief descriptions of each census locality follow.

Group A: Plot I was located along the boulevard Paseo de Montejo in the city of Merida, Yucatan. The plot extended from Calle 41 northward to Calle 29 and encompassed a wide variety of urban and suburban habitats, including hotels, large homes with lawns and tall shade trees (many jacarina, figs, and palms), and one small vacant lot, partly overgrown with tall grasses, composites, legumes, and cecropia. Plot II consisted primarily of Parque los Americas in Merida, Yucatan, a small city park with trellises of bougainvillea and a number of young citrus and fig trees but virtually no undergrowth. In both plots I and II nearly 50% of the land surface was paved. Plot III was the grounds of the Hotel Mayaland in Chichen Itza, Yucatan. This small plot contained many trees including palms, one strangler fig, jacarina, and citrus, but virtually no undergrowth. In all three plots of group A, human visitation was intensive and continuous.

Group B: Plot I was part of a large abandoned sisal (*Agave* sp.) field just north of the city of Merida, Yucatan. The invading natural vegetation of thorny shrubs, grasses, and herbaceous plants averaged less than 1 m tall and constituted a fairly thick cover in low spots in the field. The flower stalks of sisal plants protruded above the other vegetation to a maximum height of 4 m. Human visitation was frequent, and the field was crisscrossed with paths. Plot II was a portion of the grounds of the archaeological site at Uxmal, Yucatan. The plot contained sections of mowed lawn, two patches of thick shrubby undergrowth 1 m high overgrown with morning glory vines (*Ipomoea* sp.), and four young trees. Plot III was a small area of low thickets and mowed weeds (mostly Compositae) next to a mangrove-lined bay east of Progreso, Yucatan. The plot also contained several tall coconut palm trees.

Group C: Plots I, II, and III were in dense thorny forest characteristic of undistrubed sites in Yucatan. Plot I was located near the archaeological site at Dzibilchaltun; the forest there contained numerous large cacti in addition to trees. C II and C III were not as dry, and cacti were absent. C II was a hilly tract near the Uxmal archaeological site, and C III was located on highway 269 5 km south of the town of Uman. At all three locations the canopy height averaged about 9 m. At the time of the censuses, the forest plots had about 80% of their foliage.

The size of seven of the nine census plots was 6 acres (2.43 ha). A I was extended to 40 acres (16.3 ha) because of its extreme heterogeneity; B I was also 40 acres because of the scarcity of birds there. Between 6 and 10 man-hours were spent in intensive bird censusing on each plot. Sampling exceeded 6 hr on all but two plots (A III and B I); on all the plots except two (A I and C III) all the species were found within 6 man-hours. Each plot was visited at least twice. Estimates of the number of birds using each plot were calculated as the mean number per visit, following the method used for winter censuses in the journal *American Birds* (no. 3 in each volume).

For each census the relative importance of North American migrants was determined. The parameters calculated were (1) percent of total species; (2) percent of total individuals; (3) percent of total biomass measured as grams live weight; and (4) percent of total consuming biomass in calories. Data on bird weights for the biomass calculation came from the tags of specimens in the collections at Princeton University, the University of Georgia, the U.S. National Museum, and the Museum of Zoology at the University of Michigan, as well as from Schoener (1968). Consuming biomass was calculated from formulas used by Karr (1971), in which the caloric requirement (M) in kcal/bird/day is related to weight (W) in grams by the equations

$$\log M = -0.1767 + 0.7321 \log W$$ (for nonpasserines), and

$$\log M = 0.2405 + 0.6119 \log W$$ (for passerines).

RESULTS

The bird censuses are summarized in table 1.

Only a few generalizations can be made from table 1. One is that total species richness was not correlated with the degree of human disturbance. One "disturbed" census tract (A I) had a high species count. This may be due in part to the large size of the tract, but more likely the heterogeneity of the area permitted the coexistence of many species in close proximity to one another. The trees lining Paseo de Montejo were invariably "alive" with birds of many species, especially in the early morning. Population densities were generally highest in the heavily disturbed areas and lowest in the structurally simple abandoned sisal field (B I). Other communities were intermediate. The three dry forest censuses (C I, II,

TABLE 1. Results of nine winter bird censuses in Yucatan, México. Estimates of the number of birds using each plot were calculated as the mean number per visit. North American migrant species are capitalized.

	Disturbed			Partly disturbed			Undisturbed		
	AI	II	III	BI	II	III	CI	II	III
FALCO SPARVERIUS American Kestrel	1				1				
Colinus nigrogularis Black-throated Bobwhite					10				
Columba livia Rock Dove	14	2							
Zenaida aurita Zenaida Dove							1		
Columbina passerina Common Ground-Dove	105	8	11	21	22	4	10	2	
Columbina talpacoti Ruddy Ground-Dove	88	14	3	7					
Leptotila jamaicensis Caribbean Dove								3	
Crotophaga sulcirostris Groove-billed Ani				9	21		2		
Nyctidromus albicollis Pauraque	1								
Chlorostilbon canivettii Fork-tailed Emerald					5			3	
Amazilia rutila Cinnamon Hummingbird	2		1	1		3			1
A. tzacatl Rieffer's Hummingbird	2	2				1			1
Doricha eliza Mexican Sheartail						5			
Trochilidae sp.			1				1		
Eumota superciliosa Turquoise-browed Motmot					1				1
Centurus aurifrons Golden-fronted Woodpecker	9	3	5	2			4	2	1
SPHYRAPICUS VARIUS Yellow-bellied Sapsucker	2	1							
Pachyramphus major Mexican Cotinga									1
Tyrannus melancholicus Tropical Kingbird	3		1		3	1	3	3	1
Megarhynchus pitangua Boat-billed Flycatcher								1	
Myiozetetes similis Social Flycatcher	2		3		1		4	2	8
Pitangus sulfuratus Kiskadee	5	1	1				1	1	
Myiarchus tyrannulus Brown-crested Flycatcher							1		
M. yucatanensis Yucatan Flycatcher								3	2
EMPIDONAX spp.[a]	7	2	1	1	1		3	1	1
Pyrocephalus rubinus Vermilion Flycatcher					1	2			
Cyanocorax yncas Green Jay	3								
Cissilopha yucatanica Yucatan Jay									8
Troglodytes musculus Tropical House Wren	2			4	1		2		2

[a] Probably the majority were *E. minimus*, Least Flycatcher, based on their vocalizations.

TABLE 1. *Continued.*

	Disturbed			Partly disturbed			Undisturbed		
	AI	II	III	BI	II	III	CI	II	III
Thryothorus albinucha White-browed Wren									4
Campylorhynchus yucatanicus Yucatan Wren						1			
Troglodytidae spp.			1					1	
DUMETELLA CAROLINENSIS Gray Catbird								1	2
Mimus gilvus Tropical Mockingbird	18	6	2	4	7	5	12	1	2
Turdus grayi Clay-colored Robin	7	2	6						
POLIOPTILA CAERULEA Blue-gray Gnatcatcher	11	5		5	1		4	2	
P. albiloris White-lored Gnatcatcher						1			2
VIREO GRISEUS White-eyed Vireo							1		
MNIOTILTA VARIA Black-and-White Warbler	1							2	1
VERMIVORA CELATA Orange-crowned Warbler		2							
PARULA AMERICANA Northern Parula		1						3	
DENDROICA PETECHIA Yellow Warbler	2								
D. erithachorides Mangrove Warbler						4			
D. MAGNOLIA Magnolia Warbler								2	
D. CORONATA Yellow-rumped Warbler	2		3						
D. DOMINICA Yellow-throated Warbler	8	7	1						
D. PENSYLVANICA Chestnut-sided Warbler	1								
D. PALMARUM Palm Warbler						1			
SEIURUS AUROCAPILLUS Ovenbird								1	1
Chaemaethlypis poliocephala Meadow Warbler				3	1				
SETOPHAGA RUTICILLA American Redstart								3	1
ICTERUS GALBULA Northern Oriole	1								
I. SPURIUS Orchard Oriole	2								
I. auratus Golden Oriole							1		
I. gularis Lichtenstein's Oriole			2	1			2		
I. cucullatus Hooded Oriole	6		4	4		2	2	4	
Cassidix mexicanus Great-tailed Grackle	240	75	16	15		4			
Tanagra lauta Yellow-throated Euphonia			10						

TABLE 1. *Continued.*

	Disturbed			Partly disturbed			Undisturbed		
	AI	II	III	BI	II	III	CI	II	III
Thraupis episcopus Blue Tanager	4								
PIRANGA RUBRA Summer Tanager	1								
Saltator atriceps Black-headed Saltator			2		3				
S. coerulescens Gray Saltator	4			2					
Cardinalis cardinalis Cardinal						4	2	2	2
PHEUCTICUS LUDOVICIANUS Rose-breasted Grosbeak					1				1
Cyanocompsa parellina Blue Bunting							2		
PASSERINA CYANEA Indigo Bunting	6		8	3	12				
Volatinia jacarina Blue-black Grassquit				6	9				
Spinus psaltria Lesser Goldfinch	13								
Arremonops rufivirgatus Olive Sparrow			1				4	4	6
Total species	32	15	21	16	18	14	20	22	21
Population density (birds/100 acres = 40.5 ha)	1433	2188	1386	153	1653	635	1035	818	818

III) were very similar in species richness and population density.

Table 2 summarizes the importance of wintering North American species in these communities. The results were somewhat ambiguous in the sense that variations within groups A, B, and C were in some cases greater than the differences between them—i.e., there was no clear-cut relationship between the importance of North American migrant birds and the degree of habitat disturbance. Five communities had rather high percentages of North American species (28–41%). The proportion of North American individuals was much smaller, in only one case exceeding 16% of the total avifauna. In addition, the importance of North American species computed as percent biomass and percent consuming biomass was small, exceeding 10% in only one census.

North American species had very low importance in plot B III, a disturbed coastal area bordered by mangroves. This site contained only a single migrant (*Dendroica palmarum*).

DISCUSSION

Table 2 supports the notion that the ecological importance of North American migrants on their tropical wintering grounds is small relative to the number of species involved. Although the percent of total species ranges as high as 41%, in all cases the importance of North American birds measured as percent of individuals is lower than the percent of species, and the percent of biomass and percent consuming biomass values are lower yet.

Thus, North American migrants are, on the average, less abundant and smaller than the native species. The percent of consuming biomass is somewhat higher than the percent of biomass because passerines have slightly higher metabolic rates than nonpasserines of the same weight (Karr 1971), and most of the North American migrants are passerines. In any case, it appears that wintering North American birds account for a rather small proportion of the total impact of the avifauna on the rest of the biotic community,

TABLE 2. Relative importance of North American species in the winter avifaunas of nine dry Neotropical localities.

	Disturbed			Partly disturbed			Undisturbed		
Parameter measured	AI	II	III	BI	II	III	CI	II	III
% of total species	41	40	19	19	28	7	15	36	29
% of total individuals	8	14	16	10	16	3	11	36	15
% of total biomass	1.4	1.5	3.3	1.7	5.7	0.6	3.0	12.2	7.0
% of consuming biomass	2.6	3.6	6.6	3.7	8.0	1.2	5.0	19.3	9.8

even in dry locations where migrants comprise a sizeable percentage of the total number of bird species.

Although the available data indicate that lowland rain forests contain few migrants, it is clear that in Yucatan undisturbed forest habitats of lower vegetation profile (CI, II and III) are not necessarily avoided by migrants.

These results reinforce the impressions of other investigators (e.g., Orians 1969; Karr, pers. comm.) that the Neotropics contain two rather distinct avifaunas: (1) that of wet lowland forests, containing a high proportion of families and genera endemic to the tropics and few wintering temperate-zone birds; and (2) the avifaunas of montane forests, disturbed areas, and dry forests of relatively low structural complexity, which contain a high proportion of temperate-zone families in the resident avifauna and moderate to high densities of migrants. Willis (1966), Brosset (1968), and Leck (1972b) have suggested some reasons for this pattern, but our information on the interactions between tropical forest residents and migrants remains too scanty to permit a definitive explanation.

SUMMARY

Bird populations were censused at nine Neotropical sites to investigate the importance of wintering North American migrants in the avifaunas of dry tropical localities. Census localities were designated as either highly disturbed, moderately disturbed, or undisturbed by man. The importance of North American migrants was highly variable within census groups. Importance calculated as percent of total species ranged as high as 41%, and always exceeded the percent of total individuals. The percent of total individuals in turn exceeded the measures of functional importance (percent of total biomass and percent of consuming biomass in calories). Thus migrant species are, on the average, smaller and scarcer than native species, and have a relatively small ecological impact. Migrants appeared to have similar importance values in all habitats, regardless of degree of disturbance; thus, migrants are relatively more abundant in dry tropical woodlands than in lowland rain forests.

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ALBINISM IN THE BLACK NODDY (*ANOUS TENUIROSTRIS*)

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Albinism apparently has not been recorded in the Black Noddy (*Anous tenuirostris*, here including *Anous minutus*). On 17 March 1968, while on Laysan Island, Northwestern Hawaiian Islands, I observed a strikingly marked albinistic Black Noddy (fig. 1) flying around the largest nesting colony on the island (see Berger 1973:68 for an illustration of this colony). Unlike other recently fledged noddies present, this bird flew weakly and was captured with a hand-net the following day. The specimen (USNM 543336), an immature female, weighed 69 g as compared with a mean of 100 g (range: 92–114 g) for three other immature females collected on Laysan and nearby Lisianski Island.

Albinism in which pigment is reduced or diluted in the plumage, eyes, or soft parts has been termed imperfect albinism (Gross 1965) or leucism (Harrison 1964) and has been shown experimentally to be related to diet in *Turdus merula* (Rollin 1959). Short and Laybourne (1967) cited instances in which white wing bars resulted from inadequate diet in corvids and in turkey (*Meleagris gallopavo*) poults. The marked symmetry in the leucism and the emaciated condition, of the aberrant noddy, suggest that in this instance, too, albinism may have arisen from dietary deficiencies.

Tens of thousands of adult and immature Black Noddies were observed during the course of the Pacific Ocean Biological Survey Program but only this individual showed such marked albinism. Instances of a lesser degree of albinism may well have been overlooked. During banding activities in August and September 1967 and in March 1968, C. A. Ely and I examined 232 Black Noddies for plumage aberrations on Laysan (180) and Lisianski (52) islands. In addition to the bird noted above, two adults on Laysan and one on Lisianski lacked pigment in one or more of the remiges. In one of the Laysan birds, both the web and vane of the outermost left secondary were white. In the other Laysan bird, the outer three primaries on each wing were mainly white with some pigmentation along the shaft. In the Lisianski albino, the innermost tertial of the right wing was white with a white vane, and the tertial next to it was mostly white with an elliptical dull grayish-brown center.

I examined 367 immature and adult Black Noddies (12 Atlantic, 24 Indian Ocean, 331 Pacific) in the collection of the U.S. National Museum of Natural History to determine how frequently such minor albinism may occur. Seven immatures showed faint to marked white edges on the tips of the rectrices. Of these, three also had faint white tips on some of the upper and lower tail coverts. Another bird, an adult female, is a partial albino. Numerous small feathers in the loral and malar areas, two of the greater secondary coverts on the right wing, one small covert on the left wing, and numerous small feathers on the carpal joint and on the leading edge of the wing are white.

In these samples, the incidence of albinism is 1.7%