GENERAL NOTES

Wilson Bull., 97(3), 1985, pp. 356–365

An ecological comparison of the avifaunas of Grenada and Tobago, West Indies.—Low numbers of species and the absence of many neotropical families are characteristics of the bird faunas of West Indian islands. Although the West Indian avifauna is partly a subset of both the Neotropical and Nearctic avifaunas, it does have distinctive elements and has been described as a separate avifauna (Bond, Proc. Acad. Nat. Sci. Phila. 115:79–98, 1963; Lack, Island Biology, Univ. California Press, Berkeley, California, 1976). The southeastern boundary of this avifaunal region lies between the islands of Grenada and Tobago. The difference in the avifaunas of these adjacent (120 km) islands is so dramatic that Lack (1976) proposed calling this boundary "Bond's Line" in honor of James Bond, the avian zoogeographer of the West Indies. The avifauna of Tobago is South American, while that of Grenada is primarily West Indian with a strong South American element. Common South American families that occur on Tobago, but are absent from Grenada and the rest of the Lesser Antilles, include Nyctibiidae, Trogonidae, Momotidae, Galbulidae, Dendrocolaptidae, Furnariidae, Formicariidae, Cotingidae, and Pipridae. The most striking difference between the two islands, however, is the presence of twice as many species of land birds on Tobago as on Grenada (70 vs 35; Lack 1976). Eighteen terrestrial species are common to both islands.

Despite the differences in avifaunas, the islands of Grenada and Tobago are similar in size (310 km and 300 km respectively), climate, cultivated crops, area under cultivation, and recent disturbance by hurricanes (Grenada, Hurricane Janet 1955; Tobago, Hurricane Flora 1963). Maximum elevations are less on Tobago than Grenada (580 m and 840 m respectively). Also, Tobago's forests are floristically richer than those of Grenada (Beard, Ecol. Monogr. 14:135–163, 1944; Beard, The Natural Vegetation of the Windward and Leeward Islands, Clarendon Press, Oxford, England, 1949). Both islands are located about 130 km from South America, although Tobago is only 35–40 km from the island of Trinidad. Tobago is a continental island, and was connected to the mainland until early in the Pleistocene (Lack 1976). Grenada is an oceanic island that arose as a volcano from the sea. Here, I report a preliminary survey of both habitat use and frequency of occurrence of birds on the two islands and investigate some aspects of ecological release.

From the earlier literature (e.g., Crowell, Ecology 42:75–88, 1962; Keast, Biotropica 2: 61–75, 1970; Diamond, Proc. Natl. Acad. Sci. 67:529–536, 1971; Cox and Ricklefs, Oikos 28:113–122, 1977), I predicted that the relatively depauperate Grenadian avifauna would show greater ecological release (e.g., a wider variety of habitats used and higher frequencies of occurrences within habitats) than the larger avifauna of Tobago. In addition, I hypothesized that those species that have successfully colonized other islands in the Lesser Antilles would show more ecological release than species from South America restricted to only Grenada and Tobago.

Methods.—Bird communities in nine different habitats—grassland, scrub, young secondary forest, old secondary forest, mature lowland forest, cloud forest, savanna, mangrove forest, and residential parklands—were censused on both Grenada and Tobago. Foliage height profiles were made for all habitats on both islands except residential parklands. I was able to match most of my habitats with those studied in Trinidad, Jamaica, and St. Lucia by Cox and Ricklefs (1977) on the basis of foliage height profiles (using their technique) and their published descriptions. I also tried to study sites with matching rainfall and altitude on the two islands. With the exception of mature lowland forest (see below), the habitat types appeared to be roughly equivalent in size, and were contiguous with other habitats of similar foliage profiles. The habitat types and localities selected for study sites on Grenada and Tobago are described below:

(1) *Secondary grassland.*—Dry pasturelands containing a mixture of predominantly perennial grasses, some herbs, and an occasional woody shrub were censused at Calliste (SW Grenada) and near Crown Point Airport (W Tobago). Both sites were grazed, and 99% of the vegetation was below 3 m covering an area of about 150 ha.

(2) *Secondary scrub.*—Old farmland with shrubs, saplings, and scattered patches of herbs were censused near the golf course, Grenada, and near Mt. Irvine, Tobago. Both sites were located in hilly areas, with 90% of the plant foliage below 9 m covering an area of about 250–300 ha.

(3) *Young secondary forest.*—The young forest on both islands had an open canopy at approximately 6 m with a few individual trees reaching 10 m. The understory contained a dense growth of shrubs and scattered patches of herbs. Both sites covering about 175–350 ha were located on hilly locales: Halifax Harbor, Grenada, and Grafton Estate, Tobago (both approximately 150 m above sea level).

(4) *Old secondary forest.*—This forest contained a closed canopy 18–22 m high, with occasional trees reaching 24 m. The open understory contained only a few scattered shrubs and a few herbs. The secondary forest sites were located at Mt. Granby, Grenada, and southwest of Kings Bay, Tobago, both on steep slopes and covering areas of about 125–225 ha.

(5) *Mature lowland forest.*—This is probably the rarest habitat on both islands because of recent hurricanes and agricultural clearing. Both sites had a closed canopy at a height of 20–25 m, with an occasional tree exceeding 26 m. Except for scattered second growth in tree falls, the understory was open and consisted of small tree seedlings. Remnants of lowland moist forest were found on the slopes of Morne Delice at an altitude of 300 m on Grenada and on slopes at 200 m at Kings Bay, Tobago. The Grenada site of about 75 ha was completely surrounded by cultivated land and young forest, whereas the Tobago site was larger (about 150 ha) and surrounded by old secondary forest.

(6) *Cloud forest.*—Both sites were located on ridges at 590 m at Grand Etang, Grenada, and at 550 m in the forest reserve just north of Roxborough, Tobago. The trees were covered with epiphytes, and scattered palms were present in the understory and lower forest canopy. The 15–18 m canopy was closed on Grenada, but partially open (25–40%) on Tobago. Cloud forests covered the higher regions on both islands covering about 500–700 ha.

(7) *Savanna.*—Both sites were at sea level in the drier parts of the islands (Calliste, Grenada; Crown Point, Tobago). Both were heavily grazed with scattered trees and shrubs, mostly <4 m high in an area of about 150–250 ha.

(8) *Mangrove forest.*—Red (*Rhizophora mangle*) and black mangroves (*Avicennia nitida*) with open canopies at a height of about 8–10 m dominated the sample sites at Levera Beach, Grenada, and Bucco, Tobago. On both islands the two habitats were very limited in size (about 50–75 ha).

(9) *Residential parklands.*—This habitat consisted of extensive lawn areas with ornamental herbs, shrubs, and trees, surrounding private homes or hotels at Westerhall Point, Grenada, and at Mt. Irvine, Tobago, covering about 250–400 ha.

Vegetation density profiles of all habitats except residential parkland were made directly from measurements of the basal area per hectare of plant stems by dividing the area into fractions associated with foliage at different heights. A nested quadrat method, in which woody and herbaceous plants with various circumferences at breast height were counted on plots of different sizes, was used to sample representative vegetation in each habitat. The basal area per ha for trees in each circumference class was allocated to estimated height zones according to the percent of the canopy estimated in each height zone for a specific sample tree. The height profile is thus based on basal area. For details of this technique see Cox and Ricklefs (1977).

I calculated similarity coefficients using the following equation (after Cox and Ricklefs, 1977):

$$C = \frac{2W}{a + b}$$

Similarity coefficients (C) were computed from the distribution among the 9 height zones of basal area per hectare. W indicates the sum, over the various height zones, of the smaller of the basal area component values ($m^2\ ha^{-1}$) for corresponding heights in the compared habitats, and a and b represent the basal area totals for the two habitats. The coefficient varies from 0 to 1, with 1 representing complete overlap of height profiles.

Field work was conducted on Grenada from 16 to 25 November 1981 and on Tobago from 1 to 22 December 1981. Both islands were sampled during the wet season after the peak of breeding, although some species were still nesting. I used a census technique developed by Blondel et al. (Alauda 38:55–71, 1970), which was used in the West Indies by Cox and Ricklefs (1977). The technique gave a high correlation with other counts based on number of individuals seen per hour on the island of St. Lucia. On Grenada, I found that the technique gave a high correlation with both mist-net results and number of individuals seen per hour in residential areas, savanna, and scrub habitats (Wunderle, unpubl. data). The census technique consisted of observations at 10 points: all species (except raptors, migrants, and nocturnal species) heard or seen were recorded during 20-min periods at each point (see Appendixes 1 and 2). All observations were made in the morning, and all 10 observation points within a habitat were made on the same day. Observations were stopped only during heavy rains. The observation points within a habitat were at least 100 m from each other, and it is unlikely that individuals were recorded at more than one point. From the 10 observation periods per habitat, I determined the number of species per habitat, the number of times a species was present in each of the 10 observation periods within a habitat (designated as occurrences per habitat), and the number of times a species was present in each of the 10 periods, given that it occurred in at least one of the 10 periods (designated as the number of occurrences per habitat occupied). The resulting index of abundance calculated from these observations is valuable for comparing the same species within the same habitat on different islands. Comparisons between different species or between different habitats represent differences in conspicuousness as well as abundance.

Results. —Many of the 9 habitats found on both Grenada and Tobago had closely matching vegetation profiles (Table 1). The basal areas and the distribution of foliage in the different height zones fall within the range of corresponding Caribbean habitats sampled by Cox and Ricklefs (1977). For the same habitats on the two islands, I found high similarity coefficients for the mature lowland forest (0.86), savanna (0.85), and grasslands (0.85). Less similarity was found between the scrub (0.69), mangrove forest (0.69), cloud forest (0.57), old secondary forest (0.54), and young secondary forest (0.52). The mean coefficient of similarity for the same habitats on Grenada and Tobago was 0.70. These findings indicate that the corresponding habitats on the two islands were at least as similar in basal area and foliage profiles as the most similar habitats on the same island. In addition, the habitat matchings were based on features other than foliage profiles that may be even more important to the birds.

Thirty species of birds were found on Grenada compared with 53 on Tobago, representing 88.2% and 77.9%, respectively, of the known terrestrial nonraptorial species for the two islands (Table 2). The Grenada findings are comparable to those of Cox and Ricklefs (1977) for St. Lucia (N = 34 species observed, 85% of known species in counts). The Tobago results fall between those obtained by the same authors for Trinidad (N = 108, 58%) and Jamaica (N = 55, 86%).

TABLE 1

BASAL AREA PER HECTARE AND PERCENTAGES OF TOTAL BASAL AREA ASSOCIATED WITH MAJOR FOLIAGE HEIGHT ZONES FOR WOODY AND HERBACEOUS PLANTS SAMPLED ON GRENADA AND TOBAGO

	Basal area (m^2ha^{-1})		Basal area % association with successive foliage height zones (m)			
Community	Woody plants	Herbaceous plants	0–3	3–9	9–23	23–45
Secondary grassland						
Grenada	0.1	45.8	100	0	0	0
Tobago	0.0	62.4	100	0	0	0
Secondary scrub						
Grenada	28.9	13.5	75.9	23.3	0.8	0
Tobago	20.7	16.9	66.1	31.3	2.6	0
Young secondary forest						
Grenada	25.7	1.7	36.4	41.6	23.0	0
Tobago	34.3	1.2	37.7	47.9	14.4	0
Old secondary forest						
Grenada	41.1	3.2	10.0	16.4	65.2	8.4
Tobago	43.9	0.1	0.2	13.1	76.5	10.2
Mature lowland forest						
Grenada	81.3	0	2.9	20.9	49.1	27.1
Tobago	87.2	0	1.1	2.7	66.6	29.6
Cloud forest						
Grenada	55.8	8.6	15.0	31.2	50.7	3.1
Tobago	52.8	11.1	18.1	7.8	74.1	0
Savanna						
Grenada	4.6	52.1	97.6	2.4	0	0
Tobago	3.3	49.7	99.9	0.1	0	0
Mangrove forest						
Grenada	27.6	0	7.0	57.4	35.6	0
Tobago	24.7	0	4.7	72.4	22.9	0

Besides a lower number of total species, Grenada also had a significantly (Mann-Whitney U Test, $U = 65$, $P < 0.05$) lower average number of species per habitat when compared with Tobago (15.6 vs 21.4). On Tobago, the number of species per habitat ranged from 10 in secondary grassland to 30 in secondary scrub. Variability was less on Grenada, ranging from 11 species in secondary grassland to 20 species in secondary scrub and savanna. These differences are consistent with those for other Caribbean islands (Cox and Ricklefs, 1977).

The total number of observations was 758 on Grenada and 916 on Tobago. The variation in these values fell within the range (621–934) found by Cox and Ricklefs (1977), despite the fact that all my observations were made past the peak of breeding at a time when

TABLE 2

SUMMARY OF STANDARDIZED OBSERVATIONS OF BIRDS IN NINE HABITATS ON GRENADA AND TOBAGO[a]

	Grenada	Tobago
Terrestrial species in fauna (excluding owls)	34	68
Terrestrial species in counts	30	53
Number of species/total occurrences of all species		
Secondary grassland	11/61	10/55
Secondary scrub	20/101	30/150
Young secondary forest	19/112	28/137
Old secondary forest	14/79	22/99
Mature lowland forest	11/55	21/93
Cloud forest	15/78	25/103
Savanna	20/127	19/106
Mangrove forest	12/49	18/65
Residential	18/96	20/108
Total all habitats	140/758	193/916
Mean	15.5/84.2	21.4/101.8
Mean habitats per species	4.63	3.63
Mean occurrence per habitat occupied	5.36	4.71
Mean occurrences per species	24.80	17.22
Relationship of number of species to total occurrences		
Correlation coefficient	0.95[b]	0.91[b]
Slope	0.13	0.18
Intercept	4.29	3.29

[a] Based on 10, 20-min observation periods in each habitat.
[b] $P < 0.01$.

conspicuousness might be low. Variation in these values represent differences in conspicuousness or abundance.

On both islands, a positive correlation was found between the number of species in a habitat and number of occurrences. A positive correlation was also found between the number of habitats and average number of occurrences per habitat on both islands (Table 2). This indicates that species that are widespread on an island tend to be abundant in the habitats they occupy (cf. Ricklefs and Cox, Am. Nat. 112:875–895, 1978). Locally distributed species, however, are not necessarily rare in the habitats they occupy.

Associated with Grenada's lower number of species was an increase in the mean number of habitats used by each species, an increase in mean occurrences per habitat occupied, and an increase in mean occurrences per species (Table 2). These findings are consistent with previous studies (e.g., Crowell 1962, MacArthur et al., Am. Nat. 100:319–332, 1976; Cox and Ricklefs 1977) that showed that bird populations respond to smaller number of bird species both by expanding through different habitats and increasing local population density.

A better understanding of ecological release might be obtained by examining both number of habitats and number of occurrences for individual species and groups of species on the two islands. To examine the possibility that species common to both islands might show greater ecological release on species-poor Grenada, I made the following comparisons for

16 of the 18 species found on both islands: the mean number of habitats per species (4.75 ± 2.44 SD Grenada; 4.58 ± 2.10 Tobago), mean number of occurrences per species (26.94 ± 19.85 Grenada; 28.14 ± 19.51 Tobago), and mean occurrences per habitat occupied (5.12 ± 2.18 Grenada; 5.18 ± 2.34 Tobago). No significant differences were found between these parameters in the species common to the two islands, supporting the statement of Ricklefs and Cox (1977:889), regarding island colonists, that "the degree of ecological release appears to be unrelated to the number of co-occuring species on islands." Thus, while the total avifauna of Grenada appears to show characteristics of ecological release when compared with Tobago, species common to both islands do not demonstrate ecological release.

Do species that have colonized other islands in the Lesser Antilles (LA) show more ecological release than species from South America (SA) restricted to only Grenada or Tobago in the Caribbean? To answer this question, I compared the ecological release parameters of species belonging to these two groups. Lack (1976:390) lists six SA species that have colonized only Grenada in the Lesser Antilles. He also suggested that *Leptotila wellsi* is in the same superspecies as *L. verreauxi* of South America, which increases the SA list to seven on Grenada. The five SA species (*Leptotila wellsi, Chaetura cinereiventris, Glaucis hirsuta, Sporophila nigricollis, Volatinia jacarina*) that I observed on Grenada had a mean number of habitats per species of 2.8 ± 1.48 vs 5.0 ± 2.31 for 25 L.A. species on Grenada (one-tailed Mann-Whitney U test, $U = 2.27$, $P < 0.01$). A suggestive, but not significant, difference was found between SA and LA groups on Grenada in the average number of occurrences per species (14.0 ± 13.98 vs 26.9 ± 19.10; $U = 1.530$, $P < 0.10$). No significant difference (one-tailed Mann-Whitney U test, $U = 0.498$, $P > 0.10$) was found between SA and LA groups in the average number of occurrences per habitat occupied (4.16 ± 2.07 vs 4.98 ± 2.29).

On Tobago, I observed 14 species common to the Lesser Antilles and 35 species restricted to Tobago, Trinidad, and South America. Significant differences between SA and LA groups were found in the mean number of habitats per species (3.14 ± 5.81 vs 4.57 ± 4.42; $U = 1.94$, $P < 0.05$), mean number of occurrences per species (13.57 ± 16.11 vs 28.14 ± 1.95; $U = 3.13$, $P < 0.01$), and mean occurrences per habitat occupied (3.32 ± 1.89 vs 5.18 ± 2.34; $U = 2.91$, $P < 0.005$). Data from Tobago, as well as those from Grenada, suggest that the successful Caribbean colonizers (LA species) occupy more habitats and maintain higher population densities than the SA species restricted to Grenada or Tobago. As these census results are also a measure of relative conspicuousness, it is also possible that the LA species are more conspicuous or are found in habitats where they might be more apparent than the SA species.

Which avian communities on Grenada are most and least similar to communities on Tobago? To answer this question, I calculated bird community similarity coefficients for each of the nine habitats, comparing one habitat with the corresponding habitat on the other island. The most similar bird communities of the two islands were grassland (0.50), savanna (0.46), mangrove forest (0.45), and residential parkland (0.44). The least similar were cloud forest (0.21), young secondary forest (0.22), old secondary forest (0.22), mature lowland forest (0.28), and scrub (0.31). These findings are consistent with Lack's (1976) observations that the species common to the two islands were abundant in the human-disturbed sites of Tobago, but not in the woodland areas. There was a significant correlation ($r = 0.74$, $P < 0.05$) between the bird-community similarity coefficients and vegetation-community similarity coefficients for the respective habitats on the two islands.

It is possible to investigate the similarities of communities in more detail by examining the species composition within those communities. On Tobago, the LA species are most abundant in open human-disturbed sites, with scrub sites having the most LA species (N = 13) and cloud forest having the least (N = 3). The SA species restricted to Tobago were most common in the forested habitats (young secondary forest, N = 18; old secondary forest, N = 16; mature lowland forest, N = 15; cloud forest, N = 18), and least common in the open disturbed sites (residential, N = 8; savanna, N = 10; scrub, N = 13, grassland, N = 2). On Grenada, the SA species with a limited Caribbean distribution (Grenada only) are most abundant in open areas (scrub, N = 3; young secondary forest, N = 3; grassland, N = 2; savanna, N = 2). The presence of the geographically widespread island species in human-disturbed habitats is consistent with previous observations (see review by MacArthur and Wilson, The Theory of Island Biogeography, Princeton Univ. Press, Princeton, New Jersey, 1967).

Discussion. — Despite the two-fold difference in number of species between the two islands, there was no difference in parameters of ecological release (number of habitats or number of occurrences) for the 16 species observed on both islands. This suggests that the carrying capacities for these species are similar on the two islands, even though the number of potential competitors is quite different. Also, high levels of gene flow between the island populations or a short history in isolation might explain why species common to both islands have similar habitat preferences (and occurrence levels) and fail to show signs of ecological release. Hence the difference in ecological release of the avifaunas of the two islands is attributable largely to differences between the SA species and the LA species. On Tobago, the SA species were most common in the forested regions and showed the least ecological release, while on Grenada the SA species were most abundant in open or disturbed sites. The LA species on Tobago showed the most ecological release and were most abundant in open or human-disturbed sites.

These findings suggest that "ecological release" within the Caribbean avifauna is an artifact of the species composition rather than actual ecological release by the individual species. While the total avifauna might appear to show ecological release, none or few of the individual species actually change their habitat breadth or population density. Instead, species with low density populations and narrow habitat preferences disappear, leaving only those species with high density populations and wide habitat preferences. For example, as one proceeds from larger to smaller islands or from continental to more distant islands, one would expect the number of montane rainforest species (with narrow habitat tolerances) to decrease, leaving an avifauna with only generalist species having wide habitat tolerances. Montane rainforest species might be absent from many Caribbean islands for several reasons. For instance, Pregill and Olson (Annu. Rev. Ecol. Syst. 12:75–98, 1981) provide evidence suggesting that arid xerophitic habitats were the predominate habitat of the West Indies during the late Pleistocene. Thus, montane rainforests were much reduced in area and, therefore, more difficult to colonize and less likely to maintain viable populations. This, together with the fact that rainforest species are poor dispersers, would explain why rainforest species are absent from smaller and more distant islands.

Evidence from the fossil record indicates that environmental conditions in the West Indies during the last Pleistocene glaciation differed from those of the present by the predominance of arid habitats (Pregill and Olson 1981). Xeric scrub vegetation was more abundant on all low lying West Indian islands at that time than it is now. The Lesser Antillean avifauna consists mainly of xeric scrub-adapted species that have invaded mesic habitats (Terborgh et al., Auk 95:59–72, 1978), probably as a result of the earlier climatic conditions (Pregill and Olson 1981). In my study, the highest mean avian community similarity coefficient occurred in secondary (xeric) scrub on Grenada and savanna on Tobago, which is consistent with the paleoclimatic evidence. In other words, on Grenada and Tobago the habitats having the avifauna most similar to the remaining habitats are the drier habitats. As neotropical forest birds have relatively low dispersal abilities, the mesic forests may have been historically depauperate and hence available for colonization by island species from nearby xeric scrub areas.

Acknowledgments.—Hospitality and housing on Grenada was provided by J. Andersen, P. Arnold, C. Doyle, and I. VanDerhorst. I am also grateful to my wife, D. J. Lodge, for providing logistic support and encouragement. In addition, R. Askins, G. Cox, J. Diamond, J. Faaborg, P. Feinsinger, D.Petit, R. Ricklefs, and R. Wade provided critical comments and suggestions on the manuscript. Funding was provided by the Frank M. Chapman Memorial Fund of the American Museum of Natural History, the National Geographic Society, and a Stewart Award from the Wilson Ornithological Society.—JOSEPH M. WUNDERLE, JR., *Departamento de Biología, Colegio Universitario de Cayey, Universidad de Puerto Rico, Cayey, Puerto Rico 00633, U.S.A.* *Accepted 18 Mar. 1985.*

APPENDIX 1

HABITAT OCCURRENCES OF BIRDS ON GRENADA[a]

Species	Habitats								
	G[b]	SC	YSF	OSF	ML	CF	SA	MA	R
Columba squamosa	—	—	2	—	6	6	—	1	1
Zenaida auriculata	4	3	7	—	—	—	6	—	4
Z. aurita	—	—	—	—	2	—	2	3	2
Columbina passerina	6	7	7	—	—	—	8	—	8
Leptotila wellsi	—	2	5	—	—	—	—	—	—
Geotrygon montana	—	—	—	—	—	3	—	—	—
Coccyzus minor	—	4	4	2	1	2	1	—	3
Crotophaga ani	2	1	—	—	—	—	6	—	—
Chaetura cinereiventris	—	—	2	—	—	—	—	—	—
Glaucis hirsuta	—	—	7	10	10	10	—	—	1
Eulampis holosericeus	—	—	1	2	—	1	—	—	—
Orthorhyncus cristatus	—	9	6	10	7	10	9	3	10
Tyrannus dominicensis	4	4	6	3	1	1	5	3	3
Myiarchus tyrannulus	—	4	9	4	—	4	6	4	3
Elaenia flavogaster	—	6	4	—	—	—	10	—	1
E. martinica	—	—	—	1	—	2	—	—	—
Progne subis	1	—	—	—	—	—	2	—	—
Troglodytes aedon	—	1	5	—	—	—	7	—	10
Mimus gilvus	5	10	9	—	—	—	10	3	10
Turdus nudigenis	—	8	8	2	1	—	7	7	8
T. fumigatus	—	—	—	10	—	6	—	—	—
Vireo altiloquus	—	—	—	8	9	8	—	3	—
Coereba flaveola	—	9	10	10	10	9	8	10	10
Tangara cucullata	—	7	4	10	5	8	—	3	—
Molothrus bonariensis	5	—	—	—	—	—	6	—	4
Quiscalus lugubris	6	9	9	2	1	1	10	7	6
Volatinia jacarina	7	1	—	—	—	—	4	—	—
Sporophila nigricollis	4	2	—	—	—	—	5	—	—
Loxigilla noctis	—	7	7	5	—	4	5	2	10
Tiaris bicolor	9	6	—	—	—	—	10	—	3

[a] Each number represents the number of 20-min observation periods in which a species was present during 10 observation periods in each habitat.

[b] Acronyms for habitats are as follows: G = Secondary grassland, SC = Secondary scrub, YSF = Young secondary forest, OSF = Old secondary forest, ML = Mature lowland forest, CF = Cloud forest, SA = Savanna, MA = Mangrove forest, R = Residential.

APPENDIX 2

HABITAT OCCURRENCES OF BIRDS ON TOBAGO[a]

Species	Habitats								
	G[b]	SC	YSF	OSF	ML	CF	SA	MA	R
Columba cayennensis	—	—	—	—	2	5	—	—	—
Zenaida auriculata	3	7	1	—	—	—	8	4	10
Columbina talpacoti	4	4	1	—	—	—	5	—	2
Leptotila verreauxi	—	7	9	7	9	2	7	5	2
Amazona amazonica	—	—	—	3	—	10	—	—	—
Coccyzus minor	—	—	—	—	—	—	—	1	—
Crotophaga ani	5	2	—	—	—	—	3	1	3
Chaetura brachyura	—	1	5	—	—	—	—	—	—
Glaucis hirsuta	—	—	—	8	9	10	—	—	—
Florisuga mellivora	—	—	—	—	—	4	—	—	—
Anthracothroax nigricollis	—	3	—	—	—	—	—	—	5
Chrysolampis mosquitus	—	2	—	—	—	—	1	2	—
Amazilia tobaci	—	9	9	9	10	10	7	3	3
Trogon collaris	—	—	—	—	—	3	—	—	—
Momotus momota	—	—	5	1	3	4	—	—	—
Galbula ruficauda	—	—	4	—	—	4	—	—	—
Melanerpes rubricapillus	—	4	7	1	2	—	—	3	6
Veniliornis kirkii	—	—	—	—	2	—	—	—	—
Dendrocincla fuliginosa	—	—	—	—	—	1	—	—	—
Sittasomus griseicapillus	—	—	3	—	1	—	—	—	—
Xiphorhynchus guttatus	—	—	8	7	4	3	—	—	—
Synallaxis cinnamomea	—	—	4	1	—	4	—	—	—
Thamnophilus doliatus	—	10	9	8	7	9	8	3	5
Dysithamnus mentalis	—	—	—	—	—	1	—	—	—
Formicivora grisea	—	6	8	7	6	—	8	1	—
Pachyramphus polychopterus	—	2	—	—	—	—	—	—	—
Chiroxiphia pareola	—	—	2	6	3	4	—	—	—
Tyrannus melancholicus	7	4	2	2	2	1	1	1	3
T. dominicensis	1	3	—	—	—	—	—	—	—
Myiodynastes maculatus	—	—	—	—	—	1	—	—	—
Myiarchus tyrannulus	—	2	1	—	1	—	—	5	—
M. venezuelensis	—	—	—	—	—	—	1	—	—
Cnemotriccus fuscatus	—	—	1	—	—	—	—	—	—
Tolmomyias flaviventris	—	—	10	4	6	3	—	—	—
Elaenia flavogaster	—	9	5	2	1	2	7	—	8
Mionectes oleagineus	—	—	—	2	—	—	—	—	—
Thryothorus rutilus	—	—	5	2	1	2	—	—	—
Troglodytes aedon	—	7	6	5	—	—	—	—	3
Mimus gilvus	6	10	2	—	—	—	10	2	10
Platycichla flavipes	—	—	—	—	—	3	—	—	—
Turdus nudigenis	—	6	4	2	3	—	3	8	8
Vireo chivi	—	—	—	—	1	—	—	—	—
Hylophilus flavipes	—	5	4	4	—	—	5	4	—

APPENDIX 2
CONTINUED

Species	Habitats								
	G[b]	SC	YSF	OSF	ML	CF	SA	MA	R
Molothrus bonariensis	—	2	—	—	—	—	—	—	—
Scaphidura oryzivora	—	2	—	—	—	—	—	—	—
Psarocolius decumanus	—	5	3	2	4	5	—	2	1
Quiscalus lugubris	6	1	—	—	—	—	4	9	6
Sturnella militaris	3	—	—	—	—	—	—	—	—
Coereba flaveola	—	10	10	10	10	10	9	10	10
Thraupis episcopus	—	6	4	4	6	—	2	2	5
Tachyphonus rufus	—	2	—	—	—	1	—	—	—
Volatinia jacarina	10	9	3	—	—	—	9	—	8
Tiaris bicolor	10	5	—	—	—	—	8	—	10

[a] For acronyms and explanation see footnote of Appendix 1.

Wilson Bull., 97(3), 1985, pp. 365–366

Seasonal distribution of subadult Bald Eagles in three Minnesota habitats.—Although the biology of breeding and wintering Bald Eagles (*Haliaeetus leucocephalus*) has been much studied, little is known of the biology of subadults during the breeding season. In this note we describe seasonal changes in abundance of subadult Bald Eagles in three types of shoreline habitat.

The study was conducted on a 1500 km^2 area in the center of the Chippewa National Forest (CNF) in north central Minnesota. The area is mostly glacial outwash and lacustrine plain and has numerous rivers, creeks, and lakes. We observed segments of shoreline from fixed-wing aircraft at approximately weekly intervals (6–10 days) from 21 March to 30 September in 1977 and 1978. We flew at 30–60 m above the ground and recorded the plumage and location of all eagles observed. The area surveyed on each flight included approximately 39 km of river shoreline (Mississippi and Leech Lake rivers), 26 km of small (1–210 ha) lake shoreline, and 128 km of large (370–44,280 ha) lake shoreline. In this note, subadult eagles refers to those with off-white to brown heads and tails (Southern's plumages A–E, Jack-Pine Warbler 45:70–80, 1967). Counts are reported as means $\pm$ 1 SE.

We recorded 1159 observations of subadult Bald Eagles on 56 aerial surveys. The mean number of birds observed per flight was 20.7 $\pm$ 1.7 (range 0–62). Few birds were observed in March, September, and October; peak counts occurred in mid-April, and intermediate numbers were seen in May–August (Fig. 1). The mean number of subadults per flight in September–October was lower than for any other month except March. We observed 860 birds on large lakes, 83 on small lakes, and 216 on rivers. These frequencies differed from the numbers expected (769, 156, and 234, respectively) based on the relative amounts of the three types of shoreline surveyed ($\chi^2 = 46$, df = 2, $P < 0.001$).

Most lakes in the study area were ice-covered until early or mid-May, and eagles exhibited greater use of rivers in March through May than during the balance of the year ($\chi^2 = 115$, df = 1, $P < 0.001$) (Fig. 1). Eagles observed on lakes before ice-out often were near fish discarded by ice fishermen.