

SHORT-TERM EFFECTS OF HURRICANE GILBERT ON TERRESTRIAL BIRD POPULATIONS ON JAMAICA

JOSEPH M. WUNDERLE, JR.,¹ D. JEAN LODGE,² AND ROBERT B. WAIDE²

¹*Institute of Tropical Forestry, Southern Forest Experiment Station, USDA Forest Service, P.O. Box B, Palmer, Puerto Rico 00721; and*

Department of Biology, University of Puerto Rico, Cayey, Puerto Rico 00633, USA; and

²*Terrestrial Ecology Division, Center for Energy and Environment Research, GPO Box 363682, University of Puerto Rico, San Juan, Puerto Rico 00936, USA.*

ABSTRACT.—Four months after Hurricane Gilbert we resampled 10 habitats that were sampled previously in December 1987. Overall, we found no change in the total number of species nor in the mean number of individual birds detected. The mean number of individuals declined in three montane habitats (cloud forest, pine plantation, and coffee plantation), where structural damage to tree trunks and branches was often severe, and trees were still defoliated. In the mountains, higher proportions of nectarivores and fruit/seed eaters declined than insectivores. We found increased mean numbers of individuals in two lowland sites (wet limestone forest and mangroves), where structural damage to trees was also severe, but where new foliage was present. Mean numbers of individuals did not change in five other lowland habitats, despite varying levels of vegetation damage. Populations of several species declined in some habitats and increased in others, a pattern consistent with interhabitat migration. Population declines in montane habitats were related to diet, suggesting that Hurricane Gilbert's greatest stress on Jamaica's montane bird populations occurred after its passage rather than during its impact. Frequent hurricanes may contribute to some of the commonly observed characteristics of the Caribbean avifauna. *Received 5 March 1991, accepted 10 July 1991.*

IN SOME tropical regions, hurricanes occur with sufficient frequency to be important factors in determining the structure and species composition of biotic communities (e.g. Wadsworth and Englerth 1959, Odum 1970). For bird populations in particular, hurricanes can have both direct and indirect effects (for recent review, see J. Wiley, unpubl. manuscript). Direct hurricane effects include death from exposure to high winds and rain (Kennedy 1970). Indirect effects of hurricanes on bird populations include destruction of food supplies (or nesting, roosting, and foraging substrates) by the storm's high winds (Jeggo and Taynton 1980). Furthermore, storm-weakened birds may be at greater risk to predation, particularly in the absence of vegetative cover or roosting sites for protection (Engstrom and Evans 1990). Hurricanes can disrupt normal migration patterns and, in some instances, change the geographic distributions of species (Thurber 1980). Following hurricanes, humans may kill weakened birds and accelerate the rate of habitat destruction (Thompson 1900).

The difficulty with much of the previous literature on hurricane effects on bird populations is its anecdotal nature and the absence of prior

baseline data for quantitative comparison after the storm's impact (but see Lynch 1991a, b, Askins and Ewert 1991, Waide 1991). Another problem is that a variety of habitats or sites is rarely surveyed and, thus, it is difficult to assess overall population or community changes after a hurricane. Our study takes advantage of baseline samples of bird populations and vegetation structure gathered in 10 habitats in December 1987, prior to the arrival of Hurricane Gilbert in Jamaica. We replicated our baseline measurements in these same sites in January 1989, four months after the storm's passage, to evaluate the short-term effects of the hurricane on vegetation structure and terrestrial bird populations. Vegetation measurements provided us with an indication of the storm's damage at each of the sites where we counted birds. Here we describe the effects of a hurricane on avian populations before major plant successional changes took place.

Hurricane Gilbert reached hurricane force on 10 September 1988 approximately 363 km southeast of the Dominican Republic. It side-swiped Puerto Rico and Hispaniola, and then struck Jamaica on 12 September. Hurricane Gilbert arrived at 1700 with minimum sea-level

pressure of 960 mbars and sustained winds of 205 kph, with gusts of up to 226 kph. Over 700 mm of rain fell over the interior mountains of the island from 10–12 September. After leaving Jamaica, Hurricane Gilbert became the most powerful storm recorded in the Western Hemisphere in this century (Lawrence and Gross 1988). Damage caused by Gilbert to Jamaican forests was widespread and severe (Jamaica Natural Resources Conservation Department, unpubl. report; Varty 1991, Bellingham et al. 1992), causing local observers to believe that bird populations might have been seriously reduced (Haynes-Sutton 1988, Gosse Bird Club 1989). Although Gilbert was an intense hurricane, Gupta (1975, 1988) has shown that storms of this magnitude are common, and even larger ones have occurred in Jamaica's past.

METHODS

Vegetation.—We sampled 10 typical Caribbean habitats (Appendix 1). We used two to four 16-m-diameter circular plots (0.02 ha) to quantify vegetation in each habitat. Two plots were placed in vegetation representative of areas in which bird point counts were made. Occasionally, additional plots were located near the mist nets or in areas representing the extremes of vegetation structure in variable habitats. After the hurricane, we attempted to measure vegetation in the same locations as the prehurricane plots. Pre- and posthurricane plots were considered to be well matched when the original center tree could be found or, alternatively, if: (1) there was greater than 80% similarity in the number of trees in every diameter class; (2) the number and diameters of trees recorded by species or life form were the same (e.g. standing dead, palms, tree ferns, miscellaneous, dicots); and (3) the understory species or life forms were the same (i.e. grasses, forbs, ferns, bamboo, ginger and cacti). We obtained matched pairs of pre- and posthurricane plots in montane cloud forest (4 of 4 sites), montane pine plantation (1 of 2 sites), montane coffee (2 of 2 sites), dry limestone forest (2 of 2 sites), dry limestone ruinata (1 of 3 sites), wet limestone forest (1 of 3 sites), lowland coffee with mimosaceous overstory (2 of 2 sites), lowland second growth forest (1 of 3 sites), and mangroves (2 of 4 sites).

Stems of all standing and hurricane-felled trees and saplings greater than or equal to 3 cm diameter were measured 1.3 m from the base (dbh) and were recorded in diameter classes (dbh) of: 3–8 cm; >8–15 cm; >15–23 cm; >23–38 cm; and >38 cm. We also classified each tree according to life form or species as noted above, and according to the type of structural damage from the hurricane. Damage classes (from most to least severe) were: trunk broken; trunk down

(uprooted with trunk or branches on the ground); trunk leaning (partially uprooted); and presence of major branch breaks (branches >10 cm diameter; branch breaks recorded in all habitats except montane cloud forest). If an individual tree had more than one type of damage, then only the most severe damage was used in the analysis. Damage data were pooled from all posthurricane plots in each habitat, except in wet limestone forest where damage varied significantly among plots.

Foliage-height profiles were determined at 20 points located at 1.6-m intervals along the north, south, east and west radii of the circular plot (after Schemske and Brokaw 1981). A 3-m pole (2.0 cm diameter) marked at 0.5-m intervals was placed vertically at each sample point. We recorded the presence or absence of foliage touching the pole within each height class. For height intervals above 3 m, we sighted along the pole and recorded the presence/absence of foliage in each of the following estimated height intervals: 3–4, 4–6, 6–8, 8–10, 10–12, 12–15, 15–20, 20–25, and 25–30 m. We measured heights of 10 canopy trees in the plot with optical range finders. According to these measurements, we overestimated the heights of the tallest trees using the canopy-profile method in 2 of the 42 plots; the data from the upper two categories of the canopy-height profiles in those plots, therefore, were moved to the next-lower height interval. For each height interval, we calculated percent cover by dividing the number of points in which foliage was present in that height interval by the total number of sample points ($n = 20$) and multiplying by 100. Pre- and posthurricane foliage-height profiles are shown on the same graph only if they represent a matched pair. When there was more than one matched pair of pre- and posthurricane measurements, only one plot is shown as determined by a coin toss.

Foliage-height profiles were used to analyze changes in both the amount of foliage and its distribution. Friedman tests (nonparametric equivalent of an ANOVA) were used to determine if there were differences among all plots in the amount of foliage present for a given habitat, including pre- and posthurricane measurements (two-tailed tests). If significant or suggestive differences ($P < 0.1$) in the amount of foliage were found, then we quantified possible hurricane-induced changes in the amount of foliage by comparing the number of height intervals in which the frequency of foliage intercepts increased or decreased in a plot. We used one-tailed sign tests for each plot (matched pre- and posthurricane pairs) to evaluate the null hypothesis that there was no decrease in the amount of foliage after the hurricane. Understory vegetation was somewhat weighted in this analysis, because there were more height classes in the understory than in the overstory. Possible hurricane-induced changes in the distribution of foliage within a plot were analyzed by comparing pre- and posthurricane foliage-height profiles for each plot,

using contingency chi-square tests. This test is insensitive to the amount of foliage present.

Bird censuses.—We surveyed from 5–23 December 1987 before the hurricane, and 22 January to 2 February 1989 after the hurricane. We modified the fixed-radius point count method of Hutto et al. (1986) after taking preliminary counts to determine the effectiveness of the technique in three different habitats in Puerto Rico. A single observer recorded all birds seen and heard during a 10-min period at each point. Counts were initiated at sunrise and terminated before 1200, with most counts completed before 1100. Each point was at least 100 m from all others and not closer than 25 m from a habitat edge. We attempted to complete 30 point counts per habitat, but frequently the size of the habitat limited the number of point counts (summarized in Appendix 2). Two observers, moving in opposite directions, each independently made 15 point counts on the same morning in the same habitat. In dense habitats, we sampled from trails or roads and, frequently, used trails to travel through a habitat. In open habitats, we used a compass to follow a transect.

For each bird observed during a point count, we estimated the minimum distance from the observer. Those birds that were heard but not seen were tallied in one of two categories: ≤ 25 m from the observer; or > 25 m from the observer. Before sampling in Jamaica, we chose 25 m as the radius within which we could detect all individuals in all but the most dense habitats.

We calculated the mean number of detections per 25-m-radius point count for each species in each habitat both before and after the hurricane. We compared the before and after samples for each species in each habitat with a Mann-Whitney *U*-test. For each habitat we tallied the number of species that increased, showed no change, or decreased after the hurricane. The diet of each species was classified as either nectar, fruit/seeds, or insects on the basis of Lack (1976) and Faaborg (1985). This information was analyzed in a three-way table using a log-linear model (Sokal and Rohlf 1981) to test for the presence of a three-factor interaction among habitat (10 habitats), diet (two diet types: plant or insect), and population trend (two trend categories: increase/no change or decrease). The log-linear model was then used to test for conditional independence, as well as two-factor interaction. A probability of type I error of 0.05 or less was accepted as significant, but we show greater values for descriptive purposes. Throughout the text, we use standard errors to describe variation around the mean.

Appropriate control sites to monitor changes in bird populations in the absence of a hurricane between 1987 and 1988 could not be located on Jamaica, because all sites on the island sustained at least some hurricane damage. Therefore, as a control to examine changes in bird populations in the absence of a hurricane between 1987 and 1988, we used two sites on

the island of Puerto Rico. Wunderle conducted point counts in a Puerto Rican lowland pasture and montane second-growth forest in November 1987 and 1988. Point counts in the control sites were run in the same manner as in Jamaica, except that two consecutive mornings were required per site (15 counts/morning).

The lowland-pasture control site located in Salinas, Puerto Rico, was drier and contained more mesquite (*Prosopis juliflora*) than the lowland pasture in Jamaica. However, the two pasture sites have similar avifaunas, with 12 genera and 8 species in common. The montane second-growth forest site at 720 m near Carite, Puerto Rico, was at a lower elevation and had more shrubby vegetation than the montane cloud forest at Hardwar Gap, Jamaica. Similarities exist in the avifauna of the two montane sites in that they share 16 genera and 8 species.

Mist-net sampling supplemented the point counts in 6 of the 10 habitats in Jamaica. We used 12-m nets with 30-mm mesh and four shelves, set to a height of 2.5 m, usually in a continuous line. The number of nets ranged from 15 to 20 per site. We usually set nets during the afternoon and then opened them at sunrise on the following day; nets were kept open until late afternoon (with the exception of the mangrove site after the hurricane). Morning netting was simultaneous with point counts in each habitat. After the hurricane, we attempted to set nets in the exact location as earlier, but this was impossible in some cases because of extensive damage to the site. In wet limestone forest and mangroves, we set nets 15–20 m from their prehurricane positions.

We used mist-netting data to estimate population abundance before and after the hurricane in each of the sampled habitats using a modification of the method of Terborgh and Faaborg (1973). For each habitat and each netting session, we regressed the number of new captures per 15 net hours against the cumulative net hours of sampling effort. From the *Y*-intercept we obtained an estimate of the projected capture rate. In addition, we show the slopes of the regression before and after the hurricane in each habitat. The slope of the regression provides a measure of overlap in foraging range; a steep negative slope indicates little overlap. We compared the mist-netting results with those of the point counts, but did not analyze them statistically because of small sample sizes.

RESULTS

Damage to vegetation.—Hurricane Gilbert swept the length of Jamaica. The eye of the storm passed over all sampled habitats except for the dry limestone forest at Portland Ridge (Fig. 1), where damage to structure (branches and trunks) was slight. Among the sites crossed by the eye of the storm, second-growth lowland

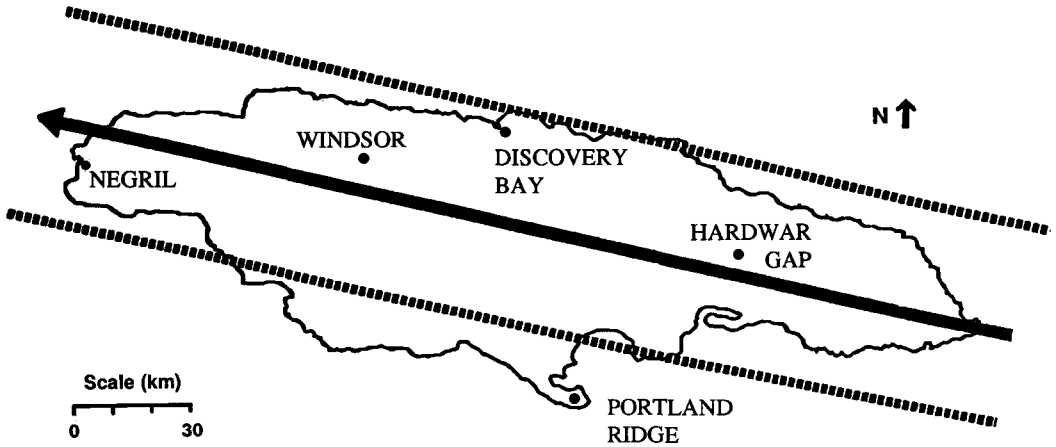


Fig. 1. Path of Hurricane Gilbert over Jamaica on 12 September 1988. Dashed lines indicate approximate width of hurricane eye, and names indicate approximate locations of sampled habitats: Hardwar Gap, montane cloud forest, montane pine plantations, and montane coffee; Portland Ridge, dry limestone forest; Discovery Bay, dry limestone ruinate; Windsor, wet limestone forest and lowland coffee; Negril, lowland secondary forest, lowland pasture, and mangroves.

habitats with short stature were least damaged (dry limestone ruinate, Fig. 2A; lowland secondary forest, Fig. 2E). Structural damage was most variable in the hilly limestone karst area around Windsor, where damage to the wet limestone forest was most severe in the floodplain (Fig. 2H), and least severe in a saddle between two hills (Fig. 2G). Coffee trees were relatively undamaged compared to the shade overstory trees in the lowland coffee plantation, in contrast to the montane open-grown coffee in which an estimated 60–80% of the coffee trees were blown over. The most severe structural damage to large-diameter trees was in mangroves (Fig. 2F) and montane pine plantations (Fig. 2J). Thus, topography, tree stature, and species differences contributed to the variation in plant structural damage among habitats.

Structural damage accounted for most of the reduction in foliage in the lowland habitats, as these habitats had refoliated by the time of our survey (Figs. 2 and 3). In the lowlands, significant reductions in the total amount of foliage were found in only one plot each in lowland coffee and mangroves (Table 1). Although total amounts of foliage were unchanged in most lowland plots, significant changes in the distribution of foliage indicate that regrowth of understory foliage compensated for loss of canopy foliage in wet limestone forest, lowland coffee, mangroves, and dry limestone ruinate. In contrast, we found significant reductions in

the amount of foliage in all plots in montane cloud forest and montane coffee, and a suggestive ($P = 0.07$) but statistically nonsignificant decrease in montane pine plantations (Table 1). Most of the foliage loss in montane habitats also was attributed to structural damage, with the exception of montane cloud forest. The severe foliage reduction in montane cloud forest (Fig. 3B) was due primarily to the absence of new foliage as damage to branches and trunks was moderate (Fig. 2B).

Control sites.—At our two control sites in Puerto Rico, we detected little change in the bird populations over a one-year period (November 1987 to November 1988). For example, the average number of individuals per point count did not change significantly in montane second-growth forest or lowland pasture (Table 2). Only slight decreases were noted in total numbers of species in each control habitat after one year, and the species turnover also was low (Table 2). None of the species in the control habitats had significant or suggestive population changes between censuses.

Species turnover.—On Jamaica, we detected 58 species of birds in the point counts before the hurricane and 58 species afterwards. Of these, 50 species were encountered before and after, leaving a turnover of 8 species observed only before and 8 species observed only after the hurricane. Species observed only before the hurricane were infrequent (Crested Quail Dove,

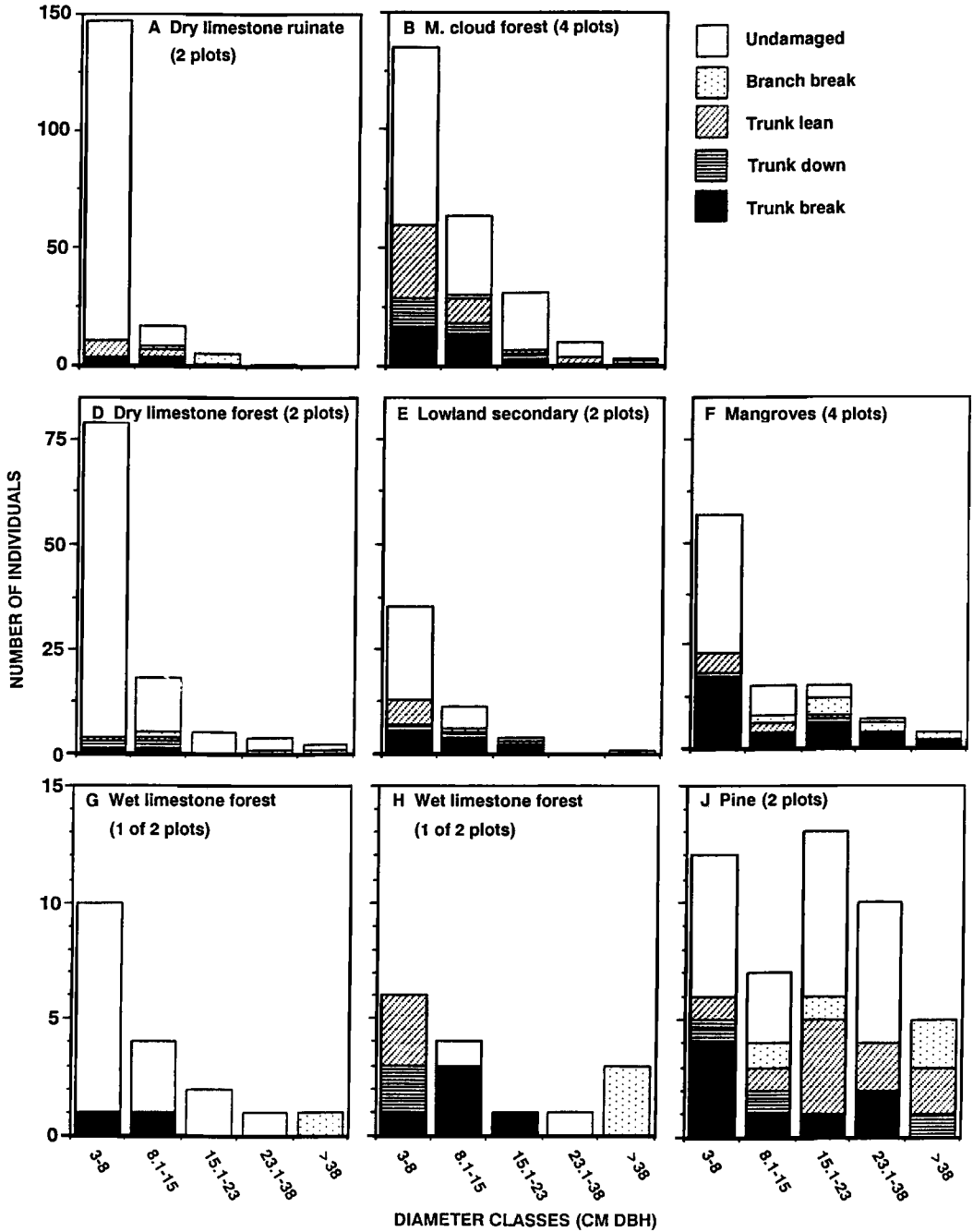


Fig. 2. Major structural damage to trees in Jamaica caused by Hurricane Gilbert by diameter class. Trees classified by most severe damage sustained in following order: trunk break; trunk down (completely uprooted); trunk lean (partially uprooted); branch breaks (only those >10-cm diameter); and undamaged. (A) Dry limestone ruinate (Discovery Bay); (B) montane cloud forest (Hardwar Gap); (D) dry limestone forest (Portland Ridge); (E) lowland secondary forest (Negril); (F) mangroves (Negril); (G-H) wet limestone forest (Windsor); (J) montane pine plantation (Hardwar Gap). Data pooled for similar 16-m-diameter circle plots; number of plots noted. Data not pooled in wet limestone forest because of heterogeneity in damage. Number of trees on Y-axis shows pooled sample sizes of trees in each diameter class.

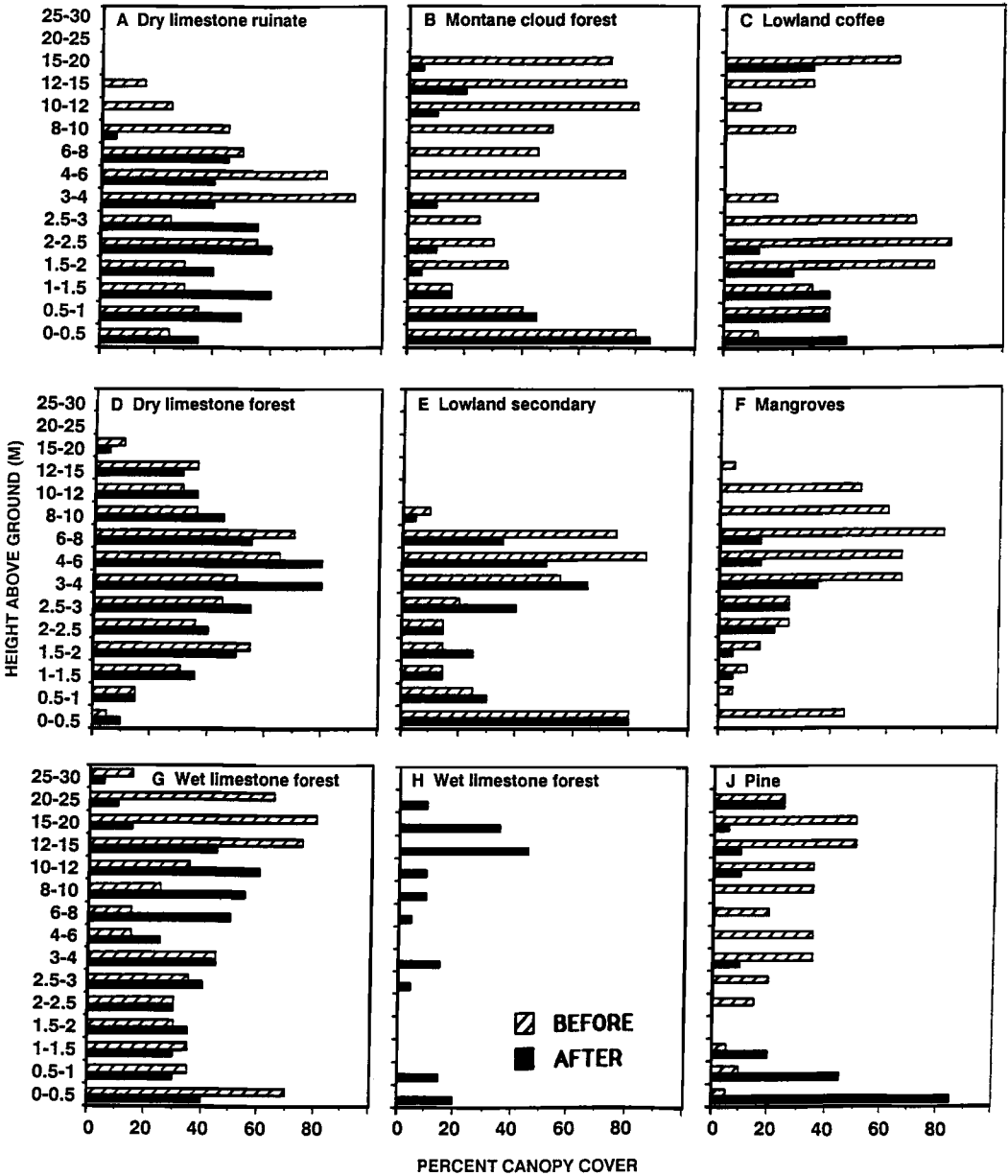


Fig. 3. Representative foliage-height profiles for various vegetation types throughout Jamaica before and after Hurricane Gilbert. (A) Dry limestone ruinate (Discovery Bay); (B) montane cloud forest (Hardwar Gap); (C) lowland coffee (Windsor); (D) dry limestone forest (Portland Ridge); (E) lowland secondary forest (Negril); (F) mangroves (Negril); (G-H) wet limestone forest (Windsor); (J) montane pine plantation (Hardwar Gap). For each 16-m-diameter plot shown (except in H), canopy-height profiles recorded along 20 vertical transects in December 1987 and again in January 1989. Percent cover (X-axis) shown for each height interval in meters on Y-axis. Height intervals increase with height on (Y-axis).

TABLE 1. Summary of probability values for tests of similarity in amount and vertical distribution of foliage before and after Hurricane Gilbert in Jamaica. Changes analyzed by tallying number of increases or decreases in foliage present in 15 height classes for each plot. Changes in vertical distribution of foliage analyzed by comparing overall vertical pattern of foliage distribution. Total numbers of vegetation plots shown, but comparisons of foliage before and after hurricane restricted to matched-plot pairs.

| Habitat | Number of plots (before : after) | Foliage amount | | Foliage distribution |
|--------------------------|----------------------------------|------------------------------|-------------------------------|-------------------------------|
| | | Among all plots ^a | Before vs. after ^b | before vs. after ^c |
| Montane cloud forest | 4:4 | <0.001 | <0.001 | >0.100 |
| | | | 0.020 | <0.005 |
| | | | 0.020 | <0.005 |
| | | | <0.001 | >0.500 |
| Montane pine plantations | 2:2 | 0.068 | 0.073 | <0.005 |
| Montane coffee | 2:2 | <0.001 | 0.004 | >0.100 |
| | | | 0.004 | <0.005 |
| Wet limestone forest | 2:2 | <0.001 | 0.500 | <0.020 |
| Lowland coffee | 2:2 | 0.056 | 0.254 | <0.005 |
| | | | 0.054 | <0.005 |
| Lowland secondary forest | 2:2 | 0.175 | 0.500 | >0.500 |
| Mangroves | 2:4 | 0.087 | <0.001 | <0.010 |
| | | | 0.508 | <0.050 |
| Dry limestone ruinate | 2:2 | 0.552 | 0.500 | <0.005 |
| Dry limestone forest | 2:2 | 0.140 | 0.131 | >0.500 |
| | | | 0.194 | >0.975 |

^a Two-tailed Friedman test.

^b One-tailed sign test.

^c Contingency chi-square.

$n = 2$; Zenaida Dove, $n = 1$; Red-necked Pigeon, $n = 1$; Vervain Hummingbird, $n = 1$; White-eyed Thrush, $n = 1$; Tennessee Warbler, $n = 1$; Hooded Warbler, $n = 1$; Chestnut-sided Warbler, $n = 6$). Most species observed only after the hurricane were also rare and foraged alone (Ring-tailed Pigeon, $n = 1$; Ruddy Quail Dove, $n = 1$; Mangrove Cuckoo, $n = 3$; Greater Antillean Elaenia, $n = 1$; Cape May Warbler, $n = 1$; Yellow-throated Warbler, $n = 3$), but two species were found in flocks (Guiana Parrotlet, $n = 4$; European Starling, $n = 5$). The mean detections per habitat for each bird species are summarized in Appendix 2.

Species turnover within individual habitats after the hurricane was frequently high (Table 2). For instance, 12 species were lost from lowland-coffee and dry-limestone-ruinate habitats. Fewer were lost in the following habitats: montane coffee (11 species), montane cloud forest (10 species), and montane pine plantation (10 species). On average, the loss of species from a habitat was greater than the addition of new species to the same habitat following the hurricane, though this difference was only suggestive (paired t -test, $t = 1.95$, $P = 0.08$; Table 2). The average number of species per habitat also

showed a suggestive, but not significant, decline (paired t -test, $t = 1.95$, $P < 0.08$; Table 2). The average number of habitats occupied by a species declined significantly (paired t -test, $t = 2.41$, $P = 0.02$) from 3.7 ± 0.4 habitats per species before the hurricane to 3.2 ± 0.4 habitats per species afterward. Despite the high spatial variation in damage within some habitats, the variance in individuals detected per point count was generally similar in the pre- and posthurricane counts. Only in the montane pine plantations were significant differences ($F_{\max} = 3.13$, $P < 0.01$) found in the variance of individuals detected per point count before (9.4) and after (3.0) the hurricane.

Abundance.—The mean number of individuals detected per point count changed significantly after the storm's passage in 5 of the 10 habitats (Table 2). We found significantly fewer individuals per point count in the three montane habitats—cloud forest, pine, and coffee plantations. Netting results in montane cloud forest and montane coffee were consistent with the point counts as indicated by dramatic declines in total captures. The projected capture rates, consequently, were low within the two habitats (Table 3). In contrast, we detected sig-

TABLE 2. Changes in mean number of individuals, total number of species, and species turnover in fixed-radius point counts in 2 habitats in Puerto Rico (Controls) and 10 habitats in Jamaica before and after Hurricane Gilbert. Comparison of mean values before and after hurricane for each habitat made with a Mann-Whitney *U*-test. Paired *t*-test used to determine significance level for total means.

| Habitat | Individuals per point count ($\bar{x} \pm SE$) | | Total no. species | | Species turnover | |
|-------------------------------|---|----------------------------|-------------------|-------------------|------------------|------------------|
| | Before | After | Before | After | Before only | After only |
| Controls (Puerto Rico) | | | | | | |
| Montane second-growth forest | 5.6 \pm 0.3 | 6.1 \pm 0.4 | 21 | 18 | 4 | 1 |
| Lowland pasture | 4.8 \pm 0.4 | 4.7 \pm 0.3 | 18 | 17 | 5 | 4 |
| Treatments (Jamaica) | | | | | | |
| Montane cloud forest | 3.3 \pm 0.3 | 2.3 \pm 0.4 ^b | 27 | 21 | 10 | 4 |
| Montane pine plantation | 5.0 \pm 0.6 | 2.1 \pm 0.3 ^a | 23 | 19 | 9 | 5 |
| Montane coffee | 2.9 \pm 0.3 | 1.5 \pm 0.3 ^a | 18 | 9 | 11 | 2 |
| Wet limestone forest | 3.8 \pm 0.6 | 5.0 \pm 0.6 ^c | 28 | 32 | 3 | 7 |
| Lowland coffee | 3.0 \pm 0.4 | 2.5 \pm 0.6 | 26 | 20 | 12 | 6 |
| Lowland secondary forest | 4.8 \pm 0.5 | 4.8 \pm 0.4 | 27 | 29 | 7 | 9 |
| Mangroves | 4.4 \pm 0.3 | 5.5 \pm 0.4 ^c | 22 | 23 | 5 | 6 |
| Lowland pasture | 4.5 \pm 0.6 | 4.3 \pm 0.6 | 25 | 23 | 7 | 5 |
| Dry limestone ruinat | 3.7 \pm 0.4 | 3.4 \pm 0.5 | 24 | 20 | 12 | 8 |
| Dry limestone forest | 3.0 \pm 0.4 | 3.5 \pm 0.4 | 21 | 20 | 4 | 3 |
| Mean total | 3.7 | 3.4 | 24.1 | 21.6 ^d | 8.0 | 5.5 ^d |
| SE | 0.3 | 0.4 | 1.0 | 1.9 | 1.0 | 0.7 |

^a $P = 0.001$, ^b $P = 0.003$, ^c $P = 0.05$, ^d $P = 0.08$.

nificantly more individuals per point count in the wet limestone forest and mangroves. Netting results supported the point-count results in the wet limestone forest, but not in the mangroves. This inconsistency in the mangrove results may occur because the 1987 netting was initiated in the late afternoon and the 1989 netting was initiated in the early morning. The mist-net and point-count results were consistent in lowland secondary forest and dry limestone forest, where we found no significant changes.

When making a large number of statistical comparisons, some observations are expected to deviate significantly from expected values by chance alone. For example, we performed 211 individual tests for population changes after the hurricane, of which 10% (21.1) and 5% (10.6) were expected to differ by chance at significance levels of 0.10 and 0.05, respectively. However, we found that 56 populations changed at $P \leq 0.10$ and that 37 populations changed at $P \leq 0.05$ (Table 4). Furthermore, eight populations showed changes at the level of 0.001—a very unlikely random event. We conclude that the majority of the population changes after the hurricane were not artifacts of the large number of statistical comparisons.

Eighteen species showed significant or sug-

gestive declines in mean number of individuals per point count in one or more habitats (Table 4). These declines could result from either hurricane-induced mortality, movement to other habitats, or decreased detectability. Sixteen species showed significant or suggestive increases in mean number of individuals per point count in one or more habitats (Table 4). These increases could result from movement into a habitat, because the birds were easier to detect as a result of increased foraging activity, or because previously obscured canopy dwellers became more apparent. Eight species decreased in some habitats and increased in other habitats (Table 4). Such observations are consistent with a between-habitat migration, but factors such as changes in detectability could also be involved.

To examine changes in detectability, we used the methods of Hutto et al. (1986) to calculate detectability ratios for each species both before and after the hurricane. The ratio is equivalent to the number of point counts at which a given species was recorded only beyond the 25-m radius, divided by the total number of counts at which the species was recorded. Of 48 species with adequate sample sizes before and after the storm, 23 species were more detectable after the storm, 17 species were less detectable, and 8 species were unchanged. The number of species

TABLE 3. Summary of mist-net capture results before and after Hurricane Gilbert in six Jamaican habitats. Slope and Y-intercept derived from regression of captures per net hour against net hours.

| Habitat | Net hours | Total | | Individuals/ 100 net h | Slope | Y-intercept |
|--------------------------|-----------|---------|----------|---------------------------|--------|-------------|
| | | Species | Captures | | | |
| Montane cloud forest | | | | | | |
| Before | 195.5 | 23 | 130 | 66.5 | -0.001 | 0.79 |
| After | 293.7 | 16 | 54 | 18.4 | -0.001 | 0.34 |
| Montane coffee | | | | | | |
| Before | 176.9 | 18 | 74 | 41.8 | -0.002 | 0.59 |
| After | 200 | 10 | 32 | 16.0 | -0.001 | 0.24 |
| Wet limestone forest | | | | | | |
| Before | 170.5 | 17 | 56 | 32.8 | -0.002 | 0.50 |
| After | 178.0 | 27 | 89 | 50.0 | -0.004 | 0.91 |
| Lowland secondary forest | | | | | | |
| Before | 192.5 | 21 | 79 | 41.0 | -0.005 | 0.91 |
| After | 148.5 | 23 | 80 | 53.8 | -0.004 | 0.98 |
| Mangroves | | | | | | |
| Before | 121.0 | 20 | 122 | 100.8 | -0.019 | 2.67 |
| After | 172.6 | 25 | 151 | 87.5 | +0.002 | 0.86 |
| Dry limestone forest | | | | | | |
| Before | 283.8 | 16 | 46 | 16.2 | -0.001 | 0.32 |
| After | 140.0 | 17 | 39 | 27.9 | -0.001 | 0.37 |

that were more detectable was not significantly different from the number of species that were less detectable (chi-square goodness-of-fit test, $X^2 = 0.90$, $df = 1$, $P < 0.50$).

Four species were significantly ($P < 0.05$) more detectable after the hurricane—Streamertail, Greater Antillean Bullfinch, Yellow Warbler, and Arrow-headed Warbler. The Olive-throated Parakeet and Jamaican White-eyed Vireo were significantly less detectable. However, no obvious relationship was found between changes in a species' detectability ratio and changes in the average number of individuals per point count after the hurricane. Thus, significant changes in detectability ratios were found in some species after the hurricane, but it is unlikely that these changes caused a consistent bias.

Overall patterns.—We found a strongly suggestive ($G = 16.64$, $df = 9$, $P = 0.055$) three-way interaction of habitat, diet, and population trend based on the log-linear analysis. Tests for conditional independence were run on two factors at a time given the level of a third factor. For instance, a significant interaction was found between diet and population trend for specific habitats ($G = 21.18$, $df = 10$, $P = 0.02$). A significant interaction was found between habitat and population trend for a given diet type (G

$= 35.39$, $df = 18$, $P = 0.008$). There was no significant interaction between habitat and diet for a given population trend ($G = 20.86$, $df = 18$, $P = 0.34$). However, a test of independence indicated a significant ($G = 42.68$, $df = 27$, $P < 0.05$) interaction between diet and population trend.

Previous hurricane studies have suggested that montane bird populations are affected more than lowland populations (J. Wiley, unpubl. manuscript). To test this possibility, we compared the trends (i.e. decrease versus increase/no change) of each species' population in each montane habitat (habitats above 700 m; $n = 3$) with the trends of populations in the lowland habitats ($n = 7$). This comparison indicated a significant difference ($G = 4.45$, $df = 1$, $P = 0.04$) in which 63% (49 of 78) of the montane populations declined compared to 48% (100 of 210) of the lowland populations. As noted previously, this pattern was also evident in the average number of individuals per point count (Table 2).

We expected the pattern of population decline in the montane regions to vary with diet, with those species relying directly on plants for food suffering most (J. Wiley, unpubl. manuscript). To examine this possibility, we categorized species into four diet categories (nectari-

TABLE 4. Species that declined or increased ($P \leq 0.10$) in mean detections per point count after passage of Hurricane Gilbert in Jamaica. Habitats where declines or increases detected are listed, as are significance levels based on comparison of pre- and posthurricane point counts using Mann-Whitney U -test.

| Location of decline (P) | Location of increase (P) |
|----------------------------------|------------------------------------|
| | Caribbean Dove |
| Dry limestone forest (0.063) | |
| | Streamertail |
| Montane cloud forest (0.001) | |
| Montane coffee (0.006) | |
| Montane pine plantation (0.001) | |
| Lowland secondary forest (0.10) | |
| | Loggerhead Kingbird |
| Lowland coffee (0.08) | |
| | Black-faced Grassquit |
| Montane cloud forest (0.03) | |
| Montane coffee (0.001) | |
| Montane pine plantation (0.013) | |
| | Yellow-shouldered Grassquit |
| Dry limestone ruinate (0.04) | |
| | Gray Catbird |
| Lowland secondary forest (0.086) | |
| | Black-throated Blue Warbler |
| Montane coffee (0.03) | |
| | Ovenbird |
| Wet limestone forest (0.08) | |
| Lowland coffee (0.08) | |
| Dry limestone forest (0.08) | |
| | Black-and-white Warbler |
| Montane pine plantation (0.02) | |
| Lowland coffee (0.04) | |
| | Chestnut-sided Warbler |
| Lowland coffee (0.08) | |
| | Bananaquit |
| Montane pine plantation (0.001) | Wet limestone forest (0.001) |
| Montane coffee (0.04) | Lowland coffee (0.020) |
| Lowland pasture (0.05) | Dry limestone forest (0.018) |
| | Orangequit |
| Montane pine plantation (0.001) | Wet limestone forest (0.09) |
| Montane coffee (0.04) | |
| | Stripe-headed Tanager |
| Montane cloud forest (0.10) | Lowland coffee (0.02) |
| | Dry limestone forest (0.018) |
| | Greater Antillean Bullfinch |
| Montane coffee (0.04) | Montane pine plantation (0.09) |
| Lowland secondary forest (0.09) | |
| | White-chinned Thrush |
| Montane coffee (0.04) | Lowland coffee (0.04) |
| Lowland secondary forest (0.02) | |
| | Blue Mountain Vireo |
| Montane pine plantation (0.09) | Montane cloud forest (0.06) |
| | Jamaican Oriole |
| Montane cloud forest (0.07) | Dry limestone ruinate (0.04) |
| Montane pine plantation (0.08) | |

TABLE 4. Continued.

| Location of decline (<i>P</i>) | Location of increase (<i>P</i>) |
|----------------------------------|-----------------------------------|
| | Prairie Warbler |
| Lowland coffee (0.02) | Montane cloud forest (0.09) |
| Lowland pasture (0.006) | Mangroves (0.003) |
| Dry limestone ruinate (0.04) | |
| | Jamaican Woodpecker |
| | Dry limestone forest (0.05) |
| | Mangrove Cuckoo |
| | Mangroves (0.08) |
| | Dusky-capped Flycatcher |
| | Wet limestone forest (0.09) |
| | Lowland secondary forest (0.001) |
| | Dry limestone ruinate (0.08) |
| | Dry limestone forest (0.04) |
| | Jamaican Euphonia |
| | Lowland secondary forest (0.05) |
| | Jamaican White-eyed Vireo |
| | Dry limestone forest (0.03) |
| | Yellow Warbler |
| | Mangroves (0.001) |
| | Northern Parula |
| | Lowland pasture (0.08) |
| | Yellow-faced Grassquit |
| | Dry limestone ruinate (0.04) |

vore, fruit/seedeater, resident insectivore, migrant insectivore), and the number of populations that decreased was compared to those that either increased or showed no change. We found a significant interaction between diet type and population trend in montane habitats ($G = 10.69$, $df = 1$, $P = 0.01$), indicating that nectarivores and fruit/seedeaters were more likely to have declining populations than insectivores in montane habitats. For instance, declines in montane habitats occurred in 80% of the nectarivore populations ($n = 10$), 83% of the fruit/seedeater populations ($n = 23$), 50% of the resident insectivore populations ($n = 22$), and 44% of the migrant insectivore populations ($n = 23$). Even with the exclusion of nonnative montane habitats (pine and coffee), the pattern of population decline and diet remained. For example, in montane cloud forest 67% of the nectarivore populations ($n = 3$), 90% of the fruit/seedeater populations ($n = 10$), 50% of the resident insectivore populations ($n = 10$), and 29% of the migrant insectivore populations ($n = 7$) declined.

Population decline in these montane habitats

may be related to foraging height within the habitat. Therefore, we used the observations of Lack (1976) to classify the montane species into those confined to the forest understory and those that are primarily canopy dwellers. It was difficult to find canopy-only species, because many canopy dwellers frequently descend to the understory via gaps and edges (e.g. Wunderle et al. 1987). Our analysis of population trends based on foraging location indicated that 60% of montane populations confined to the understory ($n = 20$) had declining population trends. The remaining 40% had trends indicating increase or no change. The same pattern (i.e. 60% declining, 40% increase/no change) was also found for canopy dwellers ($n = 58$), suggesting that the pattern of population decline in montane habitats was unrelated to foraging height.

We examined the possibility that the observed increases in the number of individuals in two lowland habitats (wet limestone forest and mangroves) after the hurricane might be attributed to an influx of montane nectarivores and fruit/seedeaters. The number of lowland populations that changed (decrease/no change

versus increase only) was tallied for species in different diet categories. Fifty percent of the lowland nectarivore populations increased, 54% of the fruit/seed-eater populations increased, and both the resident (67%) and migrant (47%) insectivores increased. No significant interaction occurred between diet type and population trend in the two lowland habitats ($G = 0.13$, $df = 3$, $P = 0.99$). Thus, nectarivores and fruit/seed-eaters were not any more likely than insectivores to have increasing populations after the hurricane in the two lowland habitats.

Increases in bird populations in the two lowland habitats after the hurricane might also be attributed to increased detectability of canopy species that were foraging at ground level. We found that 62% of the canopy/understory populations ($n = 47$) had increased in contrast to 38% of the understory populations ($n = 16$). Although this trend was suggestive, it was not possible to test statistically because of the confounding effect of diet on foraging location. For instance, 56% of the species relying upon plants for food ($n = 27$) were canopy species, in contrast to 80% of the insectivores ($n = 40$), a significant difference ($G = 4.50$, $df = 1$, $P < 0.05$).

DISCUSSION

Altitude and diet.—The hurricane's impact on bird populations was much less severe in lowland habitats than in the montane habitats. Although the storm's intensity was probably greatest in the uplands, damage to trunks and branches of trees in some lowland habitats (e.g. mangroves and wet limestone forest) was actually greater than in the montane cloud forest. Furthermore, many of the lowland habitats (wet limestone forest, lowland secondary forest, mangroves, lowland pasture, dry limestone ruinate) reportedly had been extensively defoliated (including loss of flowers and fruit). However, a major difference between lowland and montane vegetation was the rapidity with which the vegetation recovered. For example, most of the lowland sites had reportedly refoliated within several weeks, yet montane trees were still defoliated and showed the greatest differences between pre- and posthurricane canopy profiles four months later. Even after 10 months, many of the trees at high altitude were just beginning to produce new leaves (Varty 1991). Slower recovery of montane vegetation also was reported in Puerto Rico after hurricanes San

Felipe (Bates 1930) and Hugo (pers. observ.), and in Dominica following Hurricane David (Lugo et al. 1983). Slow rates of recovery from disturbance may be typical of montane cloud forests (Weaver 1986).

Our findings that population declines in montane habitats were related to diet suggest that the greatest impact of Hurricane Gilbert on Jamaica's montane bird populations was from indirect effects that occurred after its passage, rather than from direct exposure to the storm. It seems unlikely that resident insectivores in the mountains were somehow less vulnerable to the hurricane's high winds and rains than most fruit/seed-eaters and nectarivores residing in the same place. It is possible that hummingbirds, because of their small mass and high metabolic rate, suffered considerable mortality from exposure to the hurricane. Indeed, Streamertails (6 g) decreased significantly in more habitats ($n = 4$) than any other species, but the larger nectarivorous Bananaquits (11 g) and Orangequits (16 g) also declined significantly in some habitats. Moreover, the small (6.4-g) insectivorous Jamaican Tody showed no population changes after the storm, despite its prehurricane abundance. These findings are more consistent with a posthurricane-food-stress explanation than with the possibility of differential mortality arising from different vulnerabilities to hurricane exposure. Furthermore, most migrants were probably absent when Gilbert struck on 12 September (Lack and Lack 1972), yet both resident and migrant insectivores displayed similar population declines (50% and 44%, respectively). This also indicates that the indirect effects of Gilbert on terrestrial birds were greater than the direct impact of the storm. Gilbert's most important direct effect apparently was on the vegetation, which affected bird populations secondarily by limiting food after the storm's passage.

In the montane region the degree of damage inflicted by the hurricane on bird populations varied among the different food-resource types. The winds which defoliated most habitats undoubtedly also stripped flowers and fruits from plants, as reported in other hurricanes (Bates 1930; N. F. R. Snyder and H. A. Snyder, unpubl. 1979 report; Wunderle, unpubl. data). Indeed, flower and fruit abundance still appeared low in the montane sites at the time of our surveys, four months after the hurricane. Arthropod populations were probably reduced by the

storm, but because of their shorter life cycles and rapid reproductive rates, they may have recovered more quickly than the vegetation. In addition, portions of some insect populations (e.g. Diptera, Lepidoptera, Coleoptera) likely survived the storm as larvae or pupae in relatively protected sites in the soil, in leaf litter, and under bark (Wolcott 1932; B. Freeman, pers. comm.). Also, some insect populations might increase after the storm due to decreased predation and increases in their resources (J. Torres, pers. comm.). Thus, a reliance on a food source with a high diversity and turnover rate (i.e. arthropods) could buffer montane insectivorous birds from hurricane-induced food shortages.

The decline in montane nectarivores and fruit/seedeaters could have resulted from movement out of the montane habitats into other less damaged sites. As foragers on patchily distributed and temporarily available food resources, tropical nectarivores and frugivores range widely and often migrate seasonally and altitudinally in some tropical regions (e.g. Stiles 1983). Tropical insectivores, which feed on more predictable resources, tend to wander less than nectarivores, frugivores and seedeaters. For instance, under drought conditions in the Caribbean, insectivorous birds tend to have the most stable populations while nectarivores and fruit/seedeaters are most likely to decline (Faaborg et al. 1984). Presumably, some of these declines result from migration or nomadism. The reliance on widely distributed and temporary food resources could preadapt nectarivores and fruit/seedeaters to respond to localized hurricane-induced food shortages through emigration.

Despite potentially higher levels of flowering and fruiting in the lowlands, there was no detectable overall influx of montane nectarivores and fruit/seedeaters into the lowlands. Our inability to detect an increase in these foraging types in the lowlands may have resulted from surveys in the wrong lowland habitats or locations, or the inability of point counts to accurately detect relatively small increases (5–10%). The montane sites were in east-central Jamaica, whereas most of the lowland sites were in western Jamaica. Furthermore, montane habitats above 1,000 m elevation comprise only 4–6% of the total land area in Jamaica, and it would be difficult to detect an influx from the relatively small montane populations into such an extensive lowland area. However, some species

decreased in some habitats and increased in others. This implies localized movements, where birds moved from a damaged to a less-damaged site. For example, the Bananaquits probably emigrated from montane habitats (significant declines in two habitats) and into lowland habitats (significant increases in three habitats). Bananaquits feed on nectar from a high diversity of flowers (Snow and Snow 1971, Lack 1976) and may be very sensitive to flower abundance, as evidenced by drastic declines in dry forest under drought conditions (Faaborg et al. 1984). The White-chinned Thrush, a widespread frugivore, also fit a pattern consistent with interhabitat movement. They disappeared from montane coffee and lowland secondary forest, and increased in lowland coffee. Local interhabitat movements within the lowlands also occurred. For example, the Prairie Warbler, an overwintering migrant insectivore, decreased significantly in three lowland habitats and increased markedly in mangroves. Prairie Warblers appeared after the hurricane in the middle of the defoliated montane cloud forest, a habitat in which they had not been encountered previously. Several other species had posthurricane population shifts consistent with an interhabitat movement pattern, though the differences were not as marked.

Foraging substrates and cover.—Whereas posthurricane food loss explains most observed population declines, factors such as changes in foliage profiles and vegetation structure could affect certain species. For example, loss of high-canopy foraging substrates undoubtedly explains the absence of Black-and-white Warblers from montane pine plantations and their decline in lowland coffee plantations. The overstory trees in both of these habitats suffered substantial loss of branches and twigs, where this migrant warbler normally gleans insects. Extensive damage to mimosaceous trees in the overstory of lowland coffee, lowland pasture, and dry limestone rinate scrub probably contributed to the decline of overwintering migrant Prairie Warblers, which commonly glean insects from their leaves (Lack and Lack 1972). Many forest-floor species are accustomed to foraging in a dark forest understory and are likely to leave areas with reduced canopy cover. Such a response was suggested by the declining posthurricane Ovenbird populations in wet limestone and lowland coffee. Ovenbirds are insectivorous migrants that normally feed on the

forest floor only where a canopy is found overhead (Lack and Lack 1972). Thus, structural damage to vegetation produced by hurricanes could eliminate foraging substrates, as well as the vegetation characteristics used by some species as proximal cues for habitat selection.

Hurricane-induced changes in foliage distributions could also disrupt the stratification of foraging normally associated with different foliage layers (e.g. MacArthur et al. 1966). This disruption should be most apparent in forests of tall stature in which prehurricane separation of canopy and understory foraging zones was most distinct. Such was the case in the aftermath of Hurricane Hugo in Puerto Rico, where canopy destruction caused many former canopy dwellers to forage at ground level (Wunderle unpubl. data). Increased numbers of individuals in Jamaican mangroves and wet limestone forest may have resulted from displacement of canopy dwellers, although we were unable to test this hypothesis statistically. Furthermore, frequent hurricanes may, over the long term, make it difficult for Caribbean forest-dwelling species to segregate on the basis of foraging height (J. Faaborg, pers. comm.). This may account for the findings of MacArthur et al. (1966), in which Puerto Rican species appeared to recognize two vertical layers in the forest while those in Panama recognized four layers.

The tremendous loss of overstory canopy and the overall reduction of foliage in some patches of mangroves may account for the apparent posthurricane increase in Yellow Warblers. Although this resident warbler will sometimes forage in dry scrub bordering mangroves, we found them only in mangroves. Yellow Warblers have one of the narrowest habitat breadths of any Jamaican species (Lack 1976), and their "reluctance" to use other habitats may have compressed their populations into the remaining mangrove fragments. Density increases in remnant mangrove fragments also could explain the increased number of aggressive interactions and vocalizations detected after the hurricane. Thus, some species with narrow habitat preferences may respond to hurricane damaged habitats by remaining at higher densities in remnants of their original habitat rather than by moving into other nearby habitats. The consequences of remaining in fragments of original habitat, at higher than normal densities, as opposed to moving into other habitat types are unknown. However, in the case of Yellow War-

blers, the high primary productivity of mangroves (Lugo and Snedaker 1974) may have allowed a rapid recovery of insects, their primary food source. This may have allowed the warblers to remain in their traditional habitat despite substantial vegetation damage.

Some characteristics of Caribbean birdlife.—It is reasonable to expect that species restricted to a single habitat type are most at risk of extinction from habitat damage by hurricanes. Our results indicate that this is even more likely for nectarivores and fruit/seed eaters restricted to high montane forests, particularly when undamaged lowland habitats are unavailable. This could occur on mountainous islands with a limited coastal plain, or on islands in which lowland vegetation has been destroyed for agriculture. This was the situation on St. Kitts, where all but the mountain summit was planted in sugar cane in the late 19th century (Beard 1949). The Puerto Rican Bullfinch (*Loxigilla portoricensis grandis*), a fruit/seed eater, was abundant on that island in the late 1800s, but it was confined to high-elevation forest on one mountain. In 1899, two hurricanes hit the island and may have reduced the bullfinch population to a level from which it could not recover (Raffaele 1977). After the hurricanes, the bullfinches were probably unable to find food in the sugar-cane dominated lowlands and, as our study suggests, it is likely that the montane fruit and seed crops were destroyed. Although the population persisted until at least 1929 (Olson 1984), it is likely that it was no longer viable. Thus, in this instance, a combination of hurricane destruction of a food resource in an area with slow recovery and an absence of alternative habitats or food sources may have contributed to extinction of a bird species. Perhaps montane nectarivores and fruit/seed eaters in the Caribbean face higher risks of hurricane-induced extinctions, particularly as more lowland forests are destroyed for agriculture.

If the slower recovery of hurricane-damaged montane vegetation places stress on montane bird populations for longer periods than lowland populations, then hurricanes may contribute to some of the commonly observed patterns of avian distribution in the Caribbean. For example, throughout the Caribbean, montane forests support fewer bird species than lowland forests (e.g. Kepler and Kepler 1970, Ricklefs and Cox 1972, Lack 1976). Also, more endemic species are found in montane forests than in

the lowland forests of the Caribbean (Ricklefs and Cox 1972, Lack 1976). Hurricane-related extinctions of one or several disjunct montane populations may contribute to endemism among montane species. In addition, island birds tend to use a wider range of habitats than continental species (e.g. Crowell 1962, MacArthur et al. 1966), and this trait appears to favor posthurricane survival. Thus, hurricanes could contribute to these avifaunal characteristics on Caribbean islands by reducing the number of species surviving in montane habitats, increasing endemism and extinction rates of montane species, and favoring the survival of species capable of using a broad range of habitats.

ACKNOWLEDGMENTS

Ariel Diaz Perez and Luis E. Migenis Lopez provided excellent field assistance and suffered a variety of indignities with good humor. Marcel Anderson and Elaine Foster of the Natural Resource Conservation Division (Ministry of Agriculture) and Roy Jones of the Department of Forestry kindly provided permits and assistance. Erroll Ziadie and R. Campbell provided assistance and permission to work on their land. Advice was provided by Alexander Cruz, Audrey Downer, Brian Freeman, Richard Holmes, Chandler Robbins, Robert Ross, Ann Haynes-Sutton, Robert Sutton, and Jeremy Woodley, and members of the Gosse Bird Club. The manuscript benefited from the comments of Robert Askins, John Faaborg, James Lynch, Fred Scatena, Noel Snyder, Juan Torres, Peter Weaver, James Wiley, Michael Willig, and Glen Woolfenden. Financial support was provided by the World Wildlife Fund-U.S., University of Puerto Rico, and the National Science Foundation (BSR-8811902) through the Luquillo Long-term Ecological Research program.

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APPENDIX 1. Site descriptions. All sites have been described previously in detail (Lack 1976, Kapos 1986, Proctor 1986, Tanner 1986, Anonymous 1987).

Montane cloud forest.—Very Wet Ridge Forest (Tanner 1983) on Mt. Horeb and Mt. Oatley in Port Royal Mountains (1,350 m elevation; mean annual rainfall 1,900 mm). Nets set along Shelter Trail in Hardwar Gap Forest Reserve, and vegetation measured in two plots near Shelter Trail and two near Mt. Horeb Trail. Overstory (up to 20 m tall) dominated by *Cyrtilla racemiflora*, *Podocarpus urbanii*, *Hedyosmum arborescens*, *Mecranium purpurascens*, *Clethra occidentalis*, *Alchornea latifolia*, and *Dendropanax pendulus*, with tree ferns (*Cyathea* spp.) understory.

Montane coffee.—Shadeless coffee (3–4 m height) with an understory of grasses and forbs on Mt. Horeb near Hardwar Gap (ca. 1,300 m) in Port Royal Mountains.

Montane pine plantations.—Small plantations sampled between Hardwar Gap and Irish Town on south side of Port Royal Mountains (ca. 1,000–1,300 m elevation; mean annual rainfall 1,900 mm). Even-aged *Pinus caribaea* plantations (canopy 12–25 m) had a few *Eucalyptus*, with an understory of ginger, bamboo, and ferns, as sampled in vegetation plots at Woodside Estate in Greenwich.

Wet limestone forest.—Forest sampled at Windsor (ca. 300–600 m elevation; mean annual rainfall 2,000–2,500 mm) in limestone karst region known as Cockpit Country. Vegetation plots located near mist nets in floodplain forest (property of Mr. Campbell), and in saddle next to Windsor Cave. Canopy height reached 15–20 m in uplands and 25–35 m in lowlands. Cockpit Country has list of 46 tree species, including many in the Sapotaceae and Lauraceae with prominent endemics such as *Terminalia arbuscula* and *Manilkara excisa*.

Lowland coffee.—Small plantations with a shade overstory (Mimosaceae: 15–20 m canopy) and coffee understory (2–3 m) at Windsor.

Lowland secondary forest.—Mist netted and sampled vegetation at site

APPENDIX 1. Continued.

near Negril Cabins in Negril (<10 m elevation; mean annual rainfall 1,900–2,540 mm); point counts made here and to north along main road. Canopy heights of 6–10 m for dominant *Pithecellobium* sp. in these disturbed second-growth forests.

Mangroves.—Nets and two vegetation plots located in mangroves near Negril Municipal dump, and two additional vegetation plots in Green Island. Point counts made in both areas. Overstory (canopy 12–15 m) dominated by *Avicennia nitida* and *Rhizophora mangle*, while *Hibiscus tiliaceus* and coconut palms common on higher ground.

Lowland pasture.—Point counts made in pastures east of Green Island (near sea level), but no vegetation or mist-net samples obtained. Pasture contained scattered large leguminous trees (*Pithecellobium* sp. and *Haematoxylum* sp.). Diversity of large (10–15 m tall) leguminous trees in fence rows bordering pastures.

Dry limestone ruinate.—Censuses taken at Discovery Bay (10–30 m elevation; mean annual rainfall 1,000–1,500 mm). Censuses and vegetation plots located south of Columbus Park and at University of the West Indies Marine Biology Station. Dry scrub vegetation disturbed by cutting (canopy 6–10 m). Common tree species include *Bursera simaruba*, *Metopium brownii*, *Fagara spinosa*, *Coccoloba* sp., and *Tabebuia* sp.; a columnar cactus (*Stenocereus hystrix*) also common.

Dry limestone forest.—Relatively undisturbed dry forest sampled at Portland Ridge (100–150 m elevation; mean annual rainfall 1,270–1,900 mm). Mist nets and vegetation plots located in well-developed forest (canopy 10–16 m), but canopy height lower in many of point-count areas on ridges. Flora similar but more diverse than at Discovery Bay. Largest trees (up to 80 cm dbh) were *Bursera simaruba*, while *Tecoma stans*, *Thrinax parviflora*, and *Bauhinia divaricata* present in understory.

APPENDIX 2. Mean number of individuals per point count before (upper row) and after (lower row) Hurricane Gilbert for 10 habitats in Jamaica. Acronyms for habitats and number of point counts in each as follows: MCF, montane cloud forest ($n = 43$); MPP, montane pine plantations ($n = 30$); MC, montane coffee ($n = 33$); WLF, wet limestone forest ($n = 30$); LC, lowland coffee ($n = 28$); LSF, lowland secondary forest ($n = 30$); Ma, mangroves ($n = 30$); LPa, lowland pasture ($n = 30$); DLR, dry limestone ruinate ($n = 30$); DLF, dry limestone forest ($n = 30$). Letters for diet indicate: F, fruit or seed; N, nectar; I, insects. Significance level for before-and-after comparisons indicated by footnotes.

| Species | Diet | Habitats | | | | | | | | | |
|---|------|----------|------|------|------|------|------|------|------|------|-------|
| | | MCF | MPP | MC | WLF | LC | LSF | Ma | LPa | DLR | DLF |
| White-crowned Pigeon (<i>Columba leucocephala</i>) | F | 0.00 | 0.00 | 0.00 | 0.00 | 0.04 | 0.00 | 0.07 | 0.00 | 0.00 | 0.00 |
| | | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.07 | 0.00 | 0.00 | 0.00 |
| Red-necked Pigeon (<i>C. squamosa</i>) | F | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.03 | 0.00 | 0.00 |
| | | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Ring-tailed Pigeon (<i>C. caribaea</i>) | F | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| | | 0.00 | 0.00 | 0.00 | 0.03 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Zenaida Dove (<i>Zenaida aurita</i>) | F | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.03 | 0.00 | 0.00 | 0.00 |
| | | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| White-winged Dove (<i>Z. asiatica</i>) | F | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.07 | 0.00 |
| | | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.03 | 0.00 | 0.00 | 0.00 |
| Common Ground Dove (<i>Columbina passerina</i>) | F | 0.00 | 0.00 | 0.03 | 0.00 | 0.00 | 0.00 | 0.00 | 0.10 | 0.03 | 0.00 |
| | | 0.00 | 0.00 | 0.00 | 0.00 | 0.14 | 0.07 | 0.03 | 0.10 | 0.00 | 0.00 |
| Caribbean Dove (<i>Leptotila jamaicensis</i>) | F | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.03 | 0.00 | 0.00 | 0.00 | 0.37 |
| | | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.07* |
| Ruddy Quail Dove (<i>Geotrygon montana</i>) | F | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| | | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.03 | 0.00 | 0.00 | 0.00 | 0.00 |
| Crested Quail Dove (<i>G. versicolor</i>) | F | 0.02 | 0.00 | 0.00 | 0.03 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| | | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Olive-throated Parakeet (<i>Aratinga nana</i>) | F | 0.00 | 0.00 | 0.00 | 0.30 | 0.00 | 0.07 | 0.07 | 0.13 | 0.30 | 0.00 |
| | | 0.00 | 0.00 | 0.00 | 0.33 | 0.07 | 0.20 | 0.10 | 0.10 | 0.00 | 0.00 |

APPENDIX 2. Continued.

| Species | Diet | Habitats | | | | | | | | | |
|---|------|---------------------------|---------------------------|---------------------------|---------------------------|---------------------------|---------------------------|---------------------------|---------------------------|---------------------------|---------------------------|
| | | MCF | MPP | MC | WLF | LC | LSF | Ma | LPa | DLR | DLF |
| Guiana Parrotlet (<i>Forpus passerinus</i>) | F | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.13 | 0.00 0.00 |
| Mangrove Cuckoo (<i>Coccyzus minor</i>) | I | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.10 ^b | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 |
| Chestnut-bellied Cuckoo (<i>Hyetornis pluvialis</i>) | I | 0.02 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.03 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 |
| Jamaican Lizard Cuckoo (<i>Saurothera vetula</i>) | I | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.67 0.67 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 |
| Smooth-billed Ani (<i>Crotophaga ani</i>) | I | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.04 0.07 | 0.03 0.00 | 0.00 0.03 | 0.43 0.43 | 0.00 0.00 | 0.00 0.00 |
| Jamaican Mango (<i>Anthracothonax mango</i>) | N | 0.00 0.00 | 0.00 0.00 | 0.03 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.03 0.00 | 0.00 0.03 | 0.03 0.00 | 0.27 0.13 |
| Streamertail (<i>Trochilus polytmus</i>) | N | 0.77 0.15 ^f | 0.67 0.17 ^f | 0.24 0.00 ^d | 0.57 0.57 | 0.25 0.32 | 0.27 0.10 ^b | 0.07 0.13 | 0.00 0.03 | 0.40 0.07 ^a | 0.17 0.13 |
| Vervain Hummingbird (<i>Mellisuga minima</i>) | N | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.04 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 |
| Jamaican Tody (<i>Todus todus</i>) | I | 0.09 0.11 | 0.03 0.10 | 0.06 0.09 | 0.23 0.47 | 0.25 0.18 | 0.00 0.07 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.03 0.07 |
| Jamaican Woodpecker (<i>Melanerpes radiolatus</i>) | I | 0.02 0.00 | 0.03 0.00 | 0.00 0.00 | 0.23 0.43 | 0.04 0.00 | 0.20 0.27 | 0.07 0.13 | 0.03 0.03 | 0.00 0.00 | 0.07 0.30 ^c |
| Jamaican Becard (<i>Platyparus niger</i>) | I | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.13 0.03 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 |
| Loggerhead Kingbird (<i>Tyrannus caudifasciatus</i>) | I | 0.00 0.02 | 0.07 0.00 | 0.03 0.03 | 0.03 0.03 | 0.14 0.00 ^b | 0.13 0.13 | 0.03 0.13 | 0.47 0.37 | 0.13 0.17 | 0.00 0.03 |
| Stolid Flycatcher (<i>Myiarchus stolidus</i>) | I | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.07 0.10 | 0.00 0.00 | 0.03 0.00 | 0.00 0.00 | 0.07 0.00 | 0.03 0.00 | 0.20 0.33 |
| Dusky-capped Flycatcher (<i>M. barbirostris</i>) | I | 0.02 0.02 | 0.03 0.03 | 0.00 0.00 | 0.03 0.20 | 0.00 0.04 | 0.03 0.40 ^f | 0.07 0.07 | 0.00 0.03 | 0.00 0.10 ^b | 0.00 0.13 ^c |
| Rufous-tailed Flycatcher (<i>M. validus</i>) | I | 0.00 0.00 | 0.00 0.03 | 0.00 0.00 | 0.07 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.03 0.10 |
| Greater Antillean Pewee (<i>Contopus caribaeus</i>) | I | 0.02 0.00 | 0.07 0.03 | 0.00 0.00 | 0.00 0.07 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 |
| Greater Antillean Elaenia (<i>Elaenia fallax</i>) | I | 0.00 0.02 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 |
| Yellow-crowned Elaenia (<i>Myiopagis cotta</i>) | I | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.07 | 0.04 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 |
| Gray Catbird (<i>Dumetella carolinensis</i>) | F | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.37 0.10 ^b | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 |
| Northern Mockingbird (<i>Mimus polyglottos</i>) | F | 0.00 0.00 | 0.00 0.00 | 0.03 0.00 | 0.00 0.00 | 0.00 0.00 | 0.03 0.10 | 0.03 0.10 | 0.37 0.47 | 0.07 0.00 | 0.07 0.23 ^a |
| Rufous-throated Solitaire (<i>Myadestes genibarbis</i>) | F | 0.02 0.00 | 0.07 0.00 | 0.00 0.00 | 0.03 0.03 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 |
| White-chinned Thrush (<i>Turdus aurantius</i>) | F | 0.07 0.09 | 0.00 0.03 | 0.12 0.00 ^c | 0.10 0.20 | 0.04 0.25 ^c | 0.17 0.00 ^c | 0.03 0.00 | 0.03 0.00 | 0.00 0.07 | 0.00 0.00 |
| White-eyed Thrush (<i>T. jamaicensis</i>) | F | 0.02 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 |
| Yellow-faced Grassquit (<i>Tiars olivacea</i>) | F | 0.02 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.03 | 0.00 0.10 | 0.00 0.00 | 0.37 0.30 | 0.03 0.33 ^c | 0.00 0.00 |
| Black-faced Grassquit (<i>T. bicolor</i>) | F | 0.26 0.04 ^c | 0.47 0.10 ^c | 0.70 0.18 ^f | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.07 0.43 ^a | 0.00 0.03 | 0.00 0.00 |
| Yellow-shouldered Grassquit (<i>Loxipasser anoxanthus</i>) | F | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.04 0.00 | 0.07 0.00 | 0.00 0.00 | 0.00 0.00 | 0.17 0.00 ^c | 0.07 0.03 |
| Greater Antillean Bullfinch (<i>Loxigilla violacea</i>) | F | 0.16 0.07 | 0.03 0.20 ^b | 0.12 0.00 ^c | 0.10 0.07 | 0.00 0.00 | 0.20 0.03 ^b | 0.00 0.00 | 0.00 0.00 | 0.07 0.43 ^c | 0.53 0.43 |
| Stripe-headed Tanager (<i>Spindalis zena</i>) | F | 0.51 0.30 ^b | 0.30 0.07 | 0.03 0.00 | 0.07 0.07 | 0.00 0.29 ^c | 0.00 0.00 | 0.00 0.00 | 0.00 0.00 | 0.23 0.47 | 0.00 0.10 ^b |
| Jamaican Euphonia (<i>Euphonia jamaica</i>) | F | 0.02 0.02 | 0.03 0.00 | 0.00 0.00 | 0.00 0.00 | 0.07 0.00 | 0.13 0.33 ^c | 0.00 0.00 | 0.07 0.03 | 0.00 0.03 | 0.00 0.00 |
| Orangequit (<i>Euneornis campestris</i>) | N | 0.26 0.21 | 1.00 0.03 ^f | 0.18 0.00 ^c | 0.03 0.20 ^b | 0.07 0.00 | 0.00 0.03 | 0.00 0.00 | 0.00 0.00 | 0.10 0.03 | 0.00 0.00 |

APPENDIX 2. Continued.

| Species | Diet | Habitats | | | | | | | | | | |
|---|------|----------|------|------|------|------|------|------|------|------|------|------|
| | | MCF | MPP | MC | WLF | LC | LSF | Ma | LPa | DLR | DLF | |
| Tennessee Warbler (<i>Vermivora peregrina</i>) | I | 0.00 | 0.00 | 0.00 | 0.03 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Northern Parula (<i>Parula americana</i>) | I | 0.00 | 0.03 | 0.00 | 0.07 | 0.07 | 0.10 | 0.20 | 0.00 | 0.00 | 0.00 | 0.03 |
| Yellow Warbler (<i>Dendroica petechia</i>) | I | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.33 | 0.00 | 0.00 | 0.00 | 0.00 |
| Chestnut-sided Warbler (<i>D. pensylvanica</i>) | I | 0.00 | 0.00 | 0.00 | 0.00 | 0.11 | 0.00 | 0.00 | 0.03 | 0.03 | 0.03 | 0.00 |
| Magnolia Warbler (<i>D. magnolia</i>) | I | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.03 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Cape May Warbler (<i>D. tigrina</i>) | N | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Black-throated Blue Warbler (<i>D. caerulescens</i>) | I | 0.30 | 0.47 | 0.49 | 0.27 | 0.29 | 0.13 | 0.03 | 0.07 | 0.03 | 0.03 | 0.03 |
| Yellow-rumped Warbler (<i>D. coronata</i>) | I | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Black-throated Green Warbler (<i>D. virens</i>) | I | 0.00 | 0.00 | 0.00 | 0.00 | 0.21 | 0.03 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Yellow-throated Warbler (<i>D. dominica</i>) | I | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Prairie Warbler (<i>D. discolor</i>) | I | 0.00 | 0.00 | 0.09 | 0.00 | 0.18 | 0.07 | 0.03 | 0.30 | 0.17 | 0.07 | 0.07 |
| Palm Warbler (<i>D. palmarum</i>) | I | 0.00 | 0.00 | 0.00 | 0.00 | 0.04 | 0.00 | 0.00 | 0.27 | 0.03 | 0.03 | 0.00 |
| Arrow-headed Warbler (<i>D. pharetra</i>) | I | 0.07 | 0.13 | 0.91 | 0.10 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Black-and-white Warbler (<i>Mniotilta varia</i>) | I | 0.07 | 0.17 | 0.00 | 0.10 | 0.29 | 0.07 | 0.40 | 0.13 | 0.03 | 0.10 | 0.10 |
| American Redstart (<i>Setophaga ruticilla</i>) | I | 0.21 | 0.07 | 0.09 | 0.17 | 0.11 | 0.57 | 0.57 | 0.10 | 0.10 | 0.13 | 0.13 |
| Worm-eating Warbler (<i>Helminthos vermivorus</i>) | I | 0.00 | 0.03 | 0.00 | 0.07 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.03 | 0.03 |
| Ovenbird (<i>Seiurus aurocapillus</i>) | I | 0.05 | 0.03 | 0.00 | 0.10 | 0.21 | 0.07 | 0.07 | 0.03 | 0.10 | 0.10 | 0.10 |
| Northern Waterthrush (<i>S. noveboracensis</i>) | I | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.87 | 0.00 | 0.00 | 0.00 | 0.00 |
| Common Yellowthroat (<i>Geothlypis trichas</i>) | I | 0.07 | 0.10 | 0.46 | 0.00 | 0.07 | 0.27 | 0.37 | 0.33 | 0.03 | 0.00 | 0.00 |
| Hooded Warbler (<i>Wilsonia citrina</i>) | I | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.03 |
| Bananaquit (<i>Coereba flaveola</i>) | N | 0.07 | 0.77 | 0.12 | 0.07 | 0.00 | 0.83 | 0.37 | 0.33 | 1.23 | 0.23 | 0.23 |
| European Starling (<i>Sturnus vulgaris</i>) | I | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Jamaican White-eyed Vireo (<i>Vireo modestus</i>) | I | 0.00 | 0.00 | 0.00 | 0.17 | 0.00 | 0.30 | 0.07 | 0.03 | 0.20 | 0.13 | 0.13 |
| Blue Mountain Vireo (<i>V. osburni</i>) | I | 0.23 | 0.20 | 0.00 | 0.07 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Jamaican Oriole (<i>Icterus leucopteryx</i>) | I | 0.07 | 0.10 | 0.03 | 0.10 | 0.04 | 0.27 | 0.13 | 0.10 | 0.00 | 0.10 | 0.10 |
| Jamaican Blackbird (<i>Nesopsar nigerrimus</i>) | I | 0.07 | 0.00 | 0.00 | 0.03 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Greater Antillean Grackle (<i>Quiscalus niger</i>) | I | 0.00 | 0.00 | 0.00 | 0.00 | 0.14 | 0.00 | 0.23 | 0.03 | 0.03 | 0.00 | 0.00 |

^a $P < 0.15$. ^b $P < 0.10$. ^c $P < 0.05$. ^d $P < 0.01$. ^e $P < 0.005$. ^f $P < 0.001$.