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RESPONSES OF BIRD POPULATIONS IN A PUERTO RICAN FOREST TO HURRICANE HUGO: THE FIRST 18 MONTHS[1]

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Abstract. Bird populations in a subtropical wet forest were monitored every two to three weeks with mist nets and point counts beginning two weeks after the passage of Hurricane Hugo in September 1989. The results were compared with those of a pre-hurricane study in the same locations in which birds were sampled in forest understory and openings. Capture rates were initially higher than in the previous study, due to displaced canopy dwellers foraging in the understory. The shift of canopy dwellers may have obscured expected declines in nectarivores and fruit/seedeaters and contributed to increased detections of omnivores and insectivores. Bird captures and fruit production peaked 93–156 days after the storm in pre-existing gaps, where higher capture rates and a distinct assemblage of birds occurred in contrast to sites without fruit (forest understory and a powerline opening). Captures in pre-existing gaps decreased as fruit production ceased, and overall captures declined to baseline levels after 198 days. After one year of recovery, new gaps and forest understory became distinguishable on the basis of their unique foliage profiles. Although different bird assemblages had been found in forest understory and in gaps prior to the hurricane, these assemblages lost their distinctiveness after the storm. It may take many years after a hurricane for forest understory and gaps to become sufficiently distinct in structure and resources before birds differentiate between the two habitats.

Key words: Bird populations; Caribbean; habitat disturbance; Hurricane Hugo.

INTRODUCTION

Frequent hurricanes may directly and indirectly influence some of the characteristics of local avifaunas (reviewed in Wiley and Wunderle 1994). The high winds and rainfall associated with hurricanes directly cause mortality of some birds. However, the indirect effects of hurricanes may have even more profound and long-lasting effects on bird populations. These indirect effects include loss of food supplies or foraging substrates, loss of nests and nest or roost sites, increased vulnerability to predation, microclimate changes, and increased conflict with people. Before plant succession has had time to commence, birds may respond to hurricane damage by shifting their diet, foraging sites or habitats, and reproductive patterns. In the long-term, birds may respond to changes in plant succession as vegetation regenerates in storm-damaged forests.

Recently, some hurricane effects on birds have been documented in studies in which prior baseline data enabled quantitative before-and-after comparisons (Hooper et al. 1990, Lynch 1991, Askins and Ewert 1991, Waide 1991, Wunderle et al. 1992, Wauer and Wunderle 1992). However, most of these studies examined bird populations only once, shortly after a hurricane, and rarely have populations been continuously monitored for several months or years after a storm. Waide (1991) provides an example in which bird populations at El Verde were periodically sampled with point counts for one year after Hurricane Hugo hit subtropical moist forest in the Luquillo Mountains on the Caribbean island of Puerto Rico on 18 September 1989.

My study complements Waide's work by monitoring bird populations at El Verde using mist nets and point counts for 1.5 years after Hurricane Hugo. This study takes advantage of a pre-hurricane baseline netting study of bird populations that was conducted in three habitats from October 1983 through September 1984 (Wunderle et al. 1987) prior to the arrival of Hurricane Hugo in El Verde. This study replicates the netting methods, but in addition, extends the netting period by six months and includes point counts conducted in the same period. Birds were simultaneously monitored in three pre-existing habitats (gap, powerline opening and forest understory), thereby documenting population changes at a relatively small spatial scale com-

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pared to the larger area surveyed at the same time by point counts. Thus, this study documents the immediate effects of a hurricane on bird populations in a subtropical moist forest and describes subsequent population changes at different spatial scales over a year and a half in which substantial vegetation changes were documented.

STUDY SITE AND METHODS

This study was conducted at the El Verde field station in the Luquillo Experimental Forest in eastern Puerto Rico, described in Wunderle et al. (1987). The broad-leafed evergreen forest here at 350 m elevation is characterized by its dominant canopy species, tabonuco (*Dacryodes excelsa*), and is classified as subtropical wet forest in the Holdridge system (Odum and Pigeon 1970, Brown et al. 1983). Prior to the hurricane, a closed canopy existed at 20–24 m above an open understory.

Baseline netting methods are described in detail in Wunderle et al. (1987) and are only briefly described here. Birds were captured in mist nets (12 m length, 30-mm mesh, four shelves) placed in four treefall gaps (six nets), second growth in a powerline opening (six nets), and in nearby forest understory (six nets). A small stream (dry from March through May) ran through all three habitats and under a gap net (net C), a powerline net (net 3), and a forest understory net (net 8). The term pre-hurricane habitats is used throughout the remainder of the text to refer to the gap, powerline opening and forest understory as studied in the original baseline study.

Baseline netting occurred during a 12-month period from 8 October 1983 to 30 September 1984, and included all 16 nets, which were run for two days on each of 19 weekends (designated as netting sessions) at two or three-week intervals. Nets were open from dawn to dusk on Saturday and Sunday of each netting session, and were checked every 1–2 hr. All captured birds were given unique color-band combinations except for hummingbirds and todies in which tail feathers were clipped.

Post-hurricane netting sessions (two days each) began on 2 October 1989, two weeks after the passage of Hurricane Hugo, and were continued until 6 March 1991. The intervals between netting sessions corresponded with the baseline study, except during April–May, when netting was conducted at three week intervals rather than 2 week intervals. Nets were placed in the same locations as in the baseline study, except in two pre-existing gaps where the direction of net placement was changed to avoid fallen trees. All other post-hurricane netting procedures duplicated those of the baseline study.

For each captured bird, standard measurements were obtained as well as body mass and fat score. Subcutaneous fat in the furcular region was scored as follows: 0 (no fat), 1 (trace), 2 (fat filling bottom of furculum), 3 (fat filling furculum), 4 (fat mounded and spreading over pectoralis). Pre-hurricane body masses were obtained by placing birds in a plastic canister and weighting them on a triple beam balance. After the hurricane birds were weighed with Pesola spring balances. The two methods were compared and found to be equivalent (to the nearest 0.1 g) across the range of weights obtained in this study.

Birds were also surveyed using fixed-radius point counts (Hutto et al. 1986). A single observer recorded all birds seen and heard during a ten-minute period at each point. Counts were initiated at sunrise and 15 counts completed by 10:30 each morning for two consecutive days. The 30 points initially surveyed on 21 Feb. 1987, were re-sampled on 3 October 1989, two weeks after the passage of Hurricane Hugo and subsequently surveyed at intervals of two to three weeks until 11 March 1991. Each point was located 100 m from its nearest neighbor, with three points at net sites, and the remaining points both east and west of the nets. Point counts were made over a much greater area of the forest (25 ha) than were the mist nets (6.4 ha).

For each bird observed during a point count, I estimated the minimum distance between myself and the bird. 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, Wunderle and Waide (1993) determined that no individuals within a 25-m radius of the observer went undetected in this forest. For each species detected in a plot, I calculated the mean number of detections per 25 m radius plot. To examine changes in detectability, I 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 in which the species was recorded.

Foliage height profiles were used to quantify changes in vegetation structure surrounding each net, using the methods of Karr (1971) and Schemske and Brokaw (1981) as described in Wunderle et al. (1987). Profiles were obtained by establishing six 12-m long transects parallel to each net at 0.5 m intervals on each side of the net. The presence or absence of vegetation within each of 13 vertical height intervals was recorded at every 1 m along the transects. Height intervals above the ground (in meters) were 0–0.25, 0.25–0.50, 0.50–0.75, 0.75–1.00, 1.0–1.5, 1.5–2.0, 2–3, 3–5, 5–10, 10–15, 15–20, 20–25, and 25–30. For every profile at each net, we sampled at 156 points and calculated the percent cover for each height interval.

Foliage height profiles were obtained before the hurricane in September 1984, and after the hurricane in October 1989, April 1990, October 1990, and April 1991. Fallen trees and large branches were cut, but not removed in the powerline before the foliage profiles were made in October 1989. Trimming of live trees occurred in April 1991 along powerline nets 7, 9, and 11 and therefore, profiles associated with these nets are excluded at this period from analysis and Figure 1.

Post-hurricane fruiting phenology was monitored in belt transects along each net during each netting session. Only *Hirtella rugosa* was found fruiting in the gaps, and ripe fruit of this species was counted on both sides of a net in one meter strips parallel to each net (24 m^2 per net).

A percentage similarity (PS) matrix was used to make pairwise comparisons of foliage distributions associated with each net and to make pairwise comparisons of assemblages of birds captured in each net. The percent similarity derived from Bray and Curtis (1957) consisted of the following formulation:

$$PS = 100 - 1/2 \sum_{i=1}^{h} |P_{ai} - P_{bi}|$$

where P_{ai} and P_{bi} represent the percentage of individuals belonging to species i in samples a and b.

Statistical analyses followed Sokal and Rohlf (1981), unless otherwise noted. Possible hurricane-induced changes in the distribution of foliage were analyzed by comparing pre- and post-hurricane foliage-height profiles for each plot, using contingency chi-square tests. Chi-square tests were used to compare the observed number of net captures in stream nets with the expected number of captures within a pre-existing habitat (i.e., gap, powerline, or forest understory), and to compare the observed number of captures in two new habitats created by the hurricane and subsequent vegetation recovery with the expected number of captures in the new habitats. A row x column test of independence with a *G*-statistic was used to compare post-hurricane population changes in relation to pre-hurricane foraging site (canopy vs. understory). A Student's *t*-test (non-paired) was used to compare distributions that were normally distributed such as body mass of birds captured before and after the hurricane. The nonparametric Mann-Whitney *U*-test was used to compare two distributions which were not normally distributed which included: percentage similarities of foliage profiles; pre- and post-hurricane capture rates of individual species and groups of species; capture rates in gaps versus understory, and fat scores. The nonparametric Kruskal-Wallis test was used to compare the distribution of net captures in three habitats, because the distributions were not normally distributed. The association between two variables was quantified with a Spearman rank correlation coefficient, because the associations were found to be nonlinear for the ranked abundance of species in net samples, point count detections and net captures, and point count detections and detectability indexes. A K-means clustering technique (Wilkinson 1989) based on foliage profiles measured in October 1990 (one year post-hurricane) was used to distinguish two classes of foliage profiles (new gaps versus forest understory).

A Friedman rank sums test based on distribution-free multiple comparisons (Hollander and Wolfe 1973) was only used to compare the captures of a species among the three habitats when sample sizes were sufficient. This test makes all pairwise comparisons among the three habitats while controlling for the experimentwise error rate with each species. For all statistical tests, a probability of type I error of 0.05 or less was accepted as significant, but greater values are shown for descriptive purposes. Throughout the

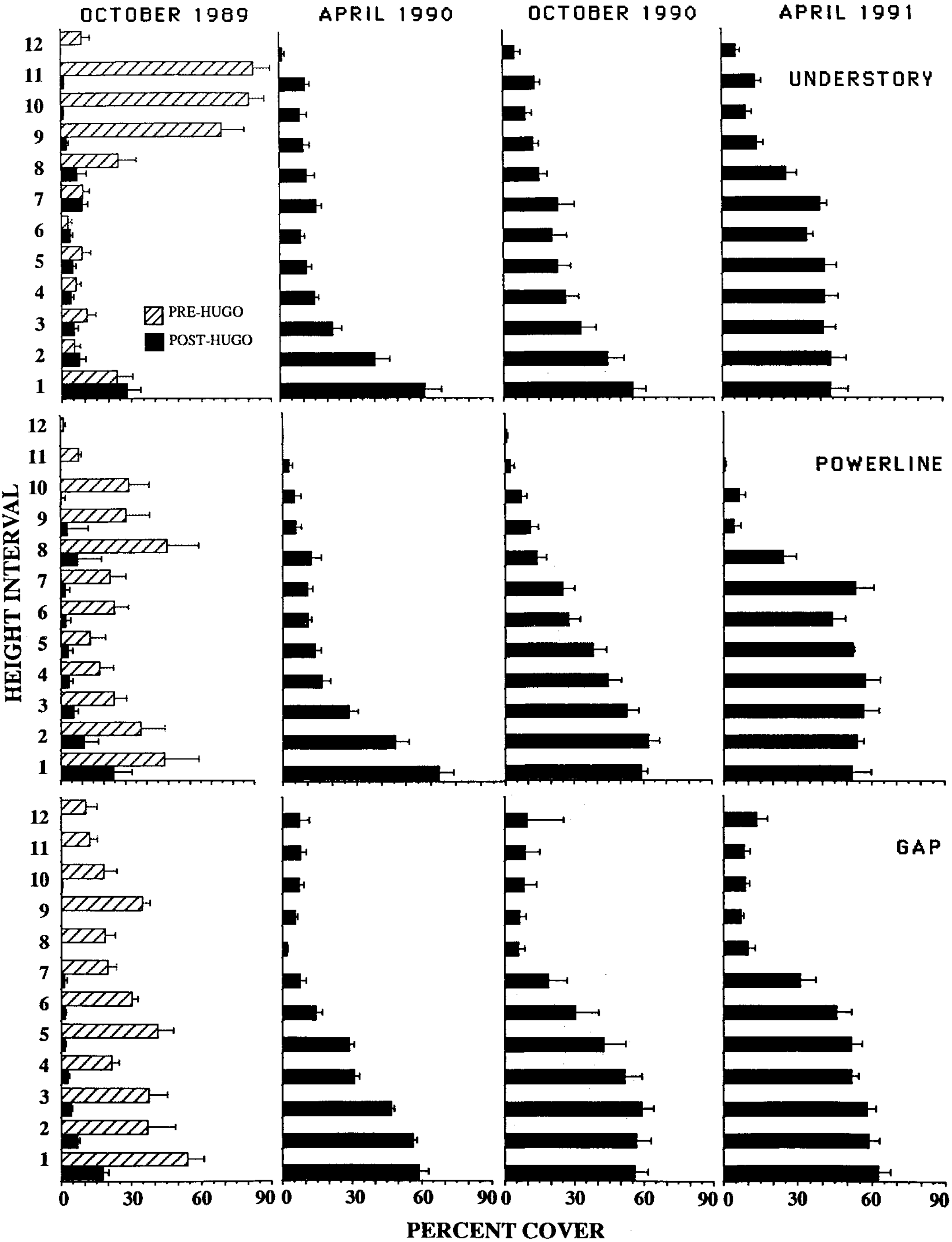

FIGURE 1. Foliage height profiles for forest understory (upper), powerline opening (center), and treefall gap (lower) nets before (September 1984) Hurricane Hugo struck El Verde (18 September 1989) and afterwards at four different dates. Percent cover represents the percent of vegetation touches in a given height interval. N = 156 sample points per net. Height intervals are in meters (1 = 0–0.25, 2 = 0.25–0.50, 3 = 0.50–0.75, 4 = 0.75–1.0, 5 = 1.0–1.5, 6 = 1.5–2.0, 7 = 2.0–3.8, 8 = 3–5, 9 = 5–10, 10 = 10–15, 11 = 15–20, 12 = 20–25).

TABLE 1. Mean (± SE) Percent Similarity (PS) values for foliage profiles of all net-pairs, net-pairs within the same pre-hurricane habitat, and net-pairs among different pre-hurricane habitats on different dates after Hurricane Hugo struck El Verde, Puerto Rico (18 September 1989). Comparison based on foliage height profiles associated with six nets each in forest understory, gap, and powerline opening shown in Figure 1. See text for description of methods.

Date	Mean ± SE percent similarity: All net-pairs	Net-pairs within same habitat	Net-pairs among different habitats
October 1989	0.59 ± 0.16	0.63 ± 0.16	0.57 ± 0.15
April 1990	0.68 ± 0.11	0.71 ± 0.90	0.66 ± 0.13
October 1990	0.70 ± 0.13	0.73 ± 0.11	0.69 ± 0.14
April 1991	0.74 ± 0.08	0.76 ± 0.06	0.73 ± 0.11

text, the standard error is used to describe variation around the mean.

RESULTS

VEGETATION

Foliage height profiles made at the end of the pre-hurricane baseline study in September 1984, indicated significant differences in foliage distribution among gap, understory, and powerline nets. At this time, foliage profiles from net-pairs within the same habitat were significantly more similar than profiles from net-pairs among habitats. This was evident from the mean percentage similarity (PS) of foliage profiles for all net-pairs within habitats ($\bar{x} = 0.71 \pm 0.09$) which differed significantly (Mann-Whitney $U = 4{,}229.5$, $P < 0.001$) from the mean PS for all net-pairs among habitats ($\bar{x} = 0.52 \pm 0.13$).

A dramatic loss of foliage was documented in all habitats after the hurricane, particularly in the canopy (Fig. 1). Significant differences were found between baseline foliage profiles and profiles obtained one month after the storm in October 1989 along nets in the understory (Contingency Chi-square = 652.54, df = 10, $P < 0.001$), powerline (Chi-square = 191.61, df = 10, $P < 0.001$), and gap (Chi-square = 264.92, df = 10, $P < 0.001$). Recovery of foliage was most rapid in the lower height zones primarily as a result of new herbaceous growth and resprouting of existing shrubs and trees. By the end of the study, this understory growth in the first seven height classes had resulted in greater foliage density than existed previously in the three habitats (Fig. 1). In contrast, the canopy never regained its original foliage density due to treefalls, trunk breaks, and numerous major branch breaks. As a result, Walker (1991) estimated that only about 50% of the original canopy had recovered by the end of the study (Fig. 2).

After the hurricane, foliage profiles associated with individual nets became increasingly similar as the vegetation recovered. Pairwise comparisons of foliage profiles indicated a significant increase ($y = 0.05x + 0.56$, $F = 21.44$, $P = 0.04$, $R^2 = 0.92$) in mean PS for profiles from all net-pairs taken at six month intervals from October 1989 to April 1991 (Table 1). Shortly after the hurricane (October 1989), foliage profiles from net-pairs within the same pre-hurricane habitat were significantly (Mann-Whitney $U = 2{,}972$, $P = 0.03$) more similar than profiles from net-pairs among habitats (Table 1), due to the high PS values of gap nets (0.78 ± 0.13). The pattern of higher PS values from profiles of net-pairs within habitats than among habitats persisted through the April 1990 measurements ($U = 2{,}946$, $P = 0.04$) and weakened by October 1990 ($U = 2{,}864$, $P = 0.08$) and finally disappeared by April 1991 ($U = 629$, $P = 0.249$). Thus as the vegetation recovered from the hurricane, foliage profiles which defined pre-hurricane habitats became less distinctive because variation within pre-hurricane habitats approached the variation among pre-hurricane habitats.

As a result of differential damage and re-growth of vegetation in the pre-hurricane habitats, new habitats (also defined on the basis of foliage profiles) became distinguishable. Two new foliage profile groups were identified by the K-means cluster technique from the profiles measured in October 1990. At one extreme were the "new gap" foliage profiles (associated with powerline nets 1, 3; pre-hurricane gap nets A, B) characterized by more foliage at ground and shrub level (0–3 m) in contrast to "new understory" profiles (associated with all remaining nets) with more

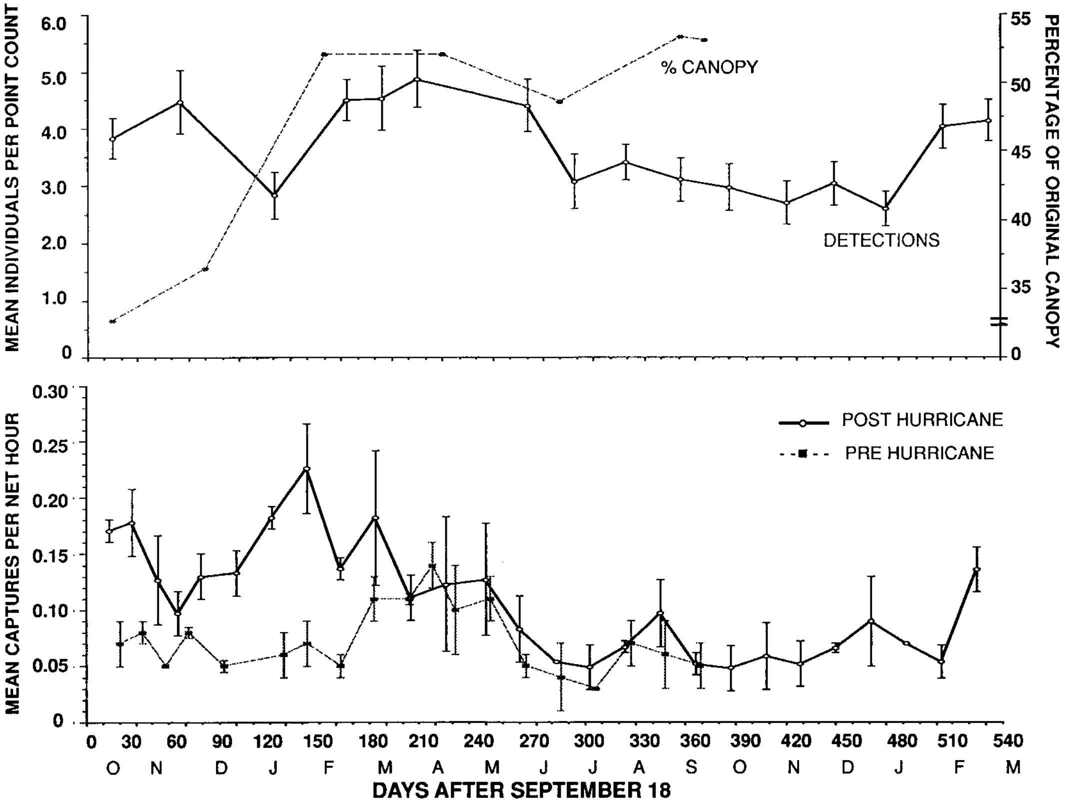

FIGURE 2. Mean (±SE) individuals per point counts conducted during 16 two-day sessions over a year and a half after Hurricane Hugo struck El Verde on 18 September 1989 (upper) and mean (±SE) captures per net hour during two-day netting sessions over a one-year period before (1983–1984) the hurricane and a one- and one-half-year period afterwards (lower). Also included in the upper graph is percentage of original canopy at different dates after the hurricane as reported by Walker (1991).

foliage from shrub layer through canopy (3–20 m). Profiles associated with net-pairs within the same "new" habitats in October 1990 were significantly more similar than profiles among "new" habitats ($\bar{x}$ = 0.76 ± 0.02 vs. $\bar{x}$ = 0.62 ± 0.02, Mann-Whitney U = 2,055, $P < 0.001$). This pattern persisted through the final foliage profiles measured in April 1991, so that profiles within "new" habitats were more similar than among "new" habitats ($\bar{x}$ = 0.76 ± 0.01 vs. $\bar{x}$ = 0.67 ± 0.02, U = 2,055, $P < 0.001$). Thus, by 378–534 days after the hurricane, two new foliage profile groups or habitats were distinguishable, but membership in these groups was not entirely congruent with the pre-hurricane foliage profile groups.

FIRST POST-HURRICANE NETTING SESSION

Ninety-one individuals of 12 species (see Appendix for scientific names) were captured in the first post-hurricane netting session (2–3 October 1991), in contrast to 26 individuals of eight species in the comparable baseline session (8–9 October 1983). The first session capture rate was more than twice the capture rate in the comparable baseline session (Fig. 2; Mann-Whitney U = 56.0, P = 0.001). Moreover, the first post-hurricane session capture rate was also significantly (U = 68.50, P = 0.003) higher than the highest baseline capture rate on 14–15 April 1984.

Increased capture rates shortly after the storm may have resulted from the presence of displaced canopy dwellers foraging in the understory. To test this hypothesis, birds were classified as either forest understory species, which forage exclusively in the forest understory, or as canopy and understory dwellers, which forage mostly in the forest canopy but at times follow the canopy contour into and out of forest openings (Wunderle et al. 1987). Based on this classification (see Appendix), it is evident that more canopy dwellers were captured after the hurricane (89% of captures, 81/91) than before in the comparable baseline session (65% of captures, 17/26) and in the entire baseline study (74%, 393/534). In both cases, the differences were significant ($G = 7.24$, df = 1, $P = 0.01$; $G = 5.81$, df = 1, $P = 0.03$, respectively). Despite the increased captures of canopy dwellers, the total captures of understory dwellers after the hurricane ($n = 10$) were nearly identical to those of the corresponding baseline session ($n = 9$). Thus, the immediate effect of the hurricane was to destroy the vertical stratification of the forest thereby forcing canopy dwellers to forage in the understory, where they faced a greater likelihood of capture.

Based on previous studies, population declines were expected to vary with diet, with those species relying directly on plants for food suffering most (reviewed in Wiley and Wunderle 1994). To test this hypothesis, birds were classified as either nectarivore, frugivore/seedeater, or omnivore (see Appendix) on the basis of Wetmore (1916), and Waide (1991). Despite predictions, this pattern was not evident in nectarivores (0.04 captures per net hr before vs. 0.5 captures per net hr after; Mann-Whitney $U = 139$, $P = 0.44$) nor in fruit/seedeaters (0.1 captures per net hr before vs. 0.3 captures per net hr after; $U = 134$, $P = 0.29$). However, post-hurricane increases were documented in both omnivores (0.002 captures per net hr before vs. 0.4 captures per net hr after; $U = 82.0$, $P = 0.002$) and insectivores (0.005 captures per net hr before vs. 0.07 captures per net hr after; $U = 50.00$, $P = 0.001$). The post-hurricane increase in omnivores is attributable primarily to significant increases in Pearly-eyed Thrashers ($U = 216.0$, $P = 0.008$), and Puerto Rican Tanagers ($U = 207.0$, $P = 0.02$). Post-hurricane insectivore increases are mostly due to increases in Puerto Rican Todies ($U = 52.0$, $P = 0.0001$) and Black-and-white Warblers ($U = 126$, $P = 0.04$). Thus, predicted decreases in nectarivore and fruit/seedeater captures were not detected shortly after the hurricane whereas omnivore and insectivore captures increased.

ALL NETTING SESSIONS

In 10,896 net hours after the hurricane, 1,428 individuals were captured representing 25 species, nine of which had not been captured previously. Most of the new species were represented by only one individual each (Scaly-naped Pigeon, Puerto Rican Lizard Cuckoo, Gray Kingbird, Wood Thrush, Ovenbird, Hooded Warbler), but some were represented by several individuals (Puerto Rican Woodpecker, $n = 3$; Stripe-headed Tanager, $n = 5$, Indigo Bunting, $n = 6$). Only one species from the baseline study was not captured after the hurricane, the Black-throated Green Warbler (*Dendroica virens*). This rare visitor to Puerto Rico was captured only once in the baseline study. Overall captures varied widely (Fig. 2) and averaged 44.1 ± 23.7 birds per netting session (range = 11–88) and 8.5 species per session (range = 2–14). After initially high capture rates, total bird captures declined to baseline levels 50 days (14–15 Nov. 1989) after the storm's passage. Bird captures reached their highest levels at 135 days after the storm (9–10 Jan. 1990) before returning again to baseline levels, at 198 days after the storm (3–4 April 1990), and remained at baseline levels through the end of the study. Post-hurricane capture rates declined to baseline levels as canopy cover reached an asymptote (Fig. 2).

Although the post-hurricane capture rates returned to baseline levels, the ranked abundance of species captured in a post-hurricane netting session was only rarely correlated with the ranked abundance of species captured on the corresponding date in the baseline study. There was no indication that the ranked abundance of species from a netting session captured after the storm became more similar to the original ranked abundances of the baseline sessions as the study progressed. For example, only in five of the 27 post-hurricane netting sessions were the ranked abundances of species significantly correlated with the ranked abundances from the corresponding baseline sessions (16–17 Oct. 1989, Spearman $r = 0.63$, df = 13, $P = 0.02$; 19–20 Feb. 1990, $r = 0.77$, df = 16, $P = 0.001$; 4–5 June 1990, $r = 0.96$, df = 7, $P < 0.001$; 26–27 June 1990, $r = 0.83$, df = 7, $P = 0.02$; 22–23 Jan. 1991, $r = 0.77$, df = 7, $P = 0.04$). However, as in the baseline study, Bananaquits were the predominant species, ranking first in abundance in 22 of 27 post-hurricane netting sessions and accounting for 16–79% of the captures per netting session.

For individual species the most prevalent capture pattern (Figures 4–8) was an initial high capture rate shortly after the hurricane followed by an eventual return to baseline levels. This was evident in permanent residents such as the Puerto Rican Tody, Pearly-eyed Thrasher, Red-legged Thrush, Puerto Rican Tanager, Stripe-headed Tanager, Puerto Rican Bullfinch, and Black-

TABLE 2. Mean (± SE) body mass (g) and fat scores of birds captured before (October–November 1983) and after (October–November 1989) Hurricane Hugo struck El Verde, Puerto Rico. Fat scores cover a range from 0–4 based on the quantity of subcutaneous fat in the furcular region, as described in the text. P values based on before and after comparisons of body mass with student's t-test and fat scores with Mann-Whitney U test.

Species	Period	Body mass (g)		Fat score	
		Mean ± SE	n	Mean ± SE	n
Ruddy Quail Dove	Before	152.0 ± 7.1	9	1.0 ± 0.0	8
	After	117.9 ± 4.3**	8	0.3 ± 0.2*	8
Puerto Rican Emerald	Before	2.9 ± 0.1	13	0.1 ± 0.1	12
	After	3.3 ± 0.1*	13	0.1 ± 0.1	13
Puerto Rican Tody	Before	6.2 ± 0.1	10	0.7 ± 0.2	10
	After	6.5 ± 0.1**	50	0.5 ± 0.1	43
Bananaquit	Before	9.7 ± 0.1	44	0.7 ± 0.1	44
	After	10.1 ± 0.1*	80	1.7 ± 0.0**	74
Black-throated Blue Warbler	Before	9.0 ± 0.3	7	0.4 ± 0.2	7
	After	9.3 ± 0.1	31	0.6 ± 0.2	24

* $P < 0.01$, ** $P < 0.001$.

faced Grassquit and in summer or winter residents including Black-whiskered Vireo, American Redstart, Black-and-white Warbler, Northern Parula, and Black-throated Blue Warbler. Only for the Louisiana Waterthrush did post-hurricane captures remain higher than baseline levels throughout the study. A post-hurricane decline from baseline capture rates appeared in Ruddy Quail-Doves in which initial post-hurricane captures were equivalent to the baseline, but decreased as netting continued. The nectarivores (Bananaquit, Puerto Rican Emerald, and Green Mango) showed no overall trend in post-hurricane captures, although the seasonal patterns of captures differed from the baseline patterns.

BODY MASS AND FAT

Comparisons of body mass and fat scores from birds captured in October and November 1983 with those captured in the same months after the hurricane indicated significant weight increases after the hurricane in Puerto Rican Emerald, Puerto Rican Tody, and Bananaquit, which also showed a significant increase in fat score (Table 2). Ruddy Quail-Doves displayed significant decreases in both body mass and fat score after the storm. The winter-resident Black-throated Blue Warblers showed no significant body mass or fat score changes after the hurricane.

HABITAT USE

After the storm, the average hourly capture rate per netting session differed significantly (Kruskal-Wallis value = 20.98, $P < 0.001$) among the three pre-hurricane habitats (gap $\bar{x} = 0.02 \pm 0.003$ birds/net hr; powerline $\bar{x} = 0.02 \pm 0.002$ birds/net hr; understory $\bar{x} = 0.01 \pm 0.001$). However, during most post-hurricane netting sessions captures did not vary consistently among the three pre-hurricane habitats (Fig. 3), except days 93–156. In this period, captures varied significantly among habitats during successive sessions including day 93 (Kruskal-Wallis value = 7.67, $P = 0.02$), day 114 (Kruskal-Wallis value = 8.26, $P = 0.02$), day 135 (Kruskal-Wallis value = 6.20, $P = 0.05$), and day 156 (Kruskal-Wallis value = 6.78, $P = 0.03$). In this period (day 93–156) captures were significantly higher in gaps than in understory (day 93, Mann-Whitney $U = 33.50$, $P = 0.008$; day 114, $U = 34.00$, $P = 0.01$; day 135, $U = 34.00$, $P = 0.01$; day 156, $U = 30.5$, $P = 0.04$). Higher gap captures at this time corresponded to the presence of *Hirtella rugosa* fruit in the gaps, in contrast to powerline and understory where fruit was absent (Fig. 3).

During the post-hurricane peak in gap captures (day 93–156), bird assemblages from each gap net were more similar to each other, than to assemblages from nets in the other habitats (i.e., gap vs. understory or gap vs. powerline). This was evident in the high mean PS value for all gap net-pairs ($\bar{x} = 0.74 \pm 0.01$) which was significantly different from the mean PS value for net-pairs that include a gap and powerline net ($\bar{x} = 0.48 \pm 0.03$, Mann-Whitney $U = 497.00$, $P < 0.001$), or a gap and understory net ($\bar{x} = 0.47 \pm 0.02$, $U = 537.00$, $P < 0.001$). The uniqueness of the gap assemblage during the post-hurricane peak in gap captures is attributed mostly to the

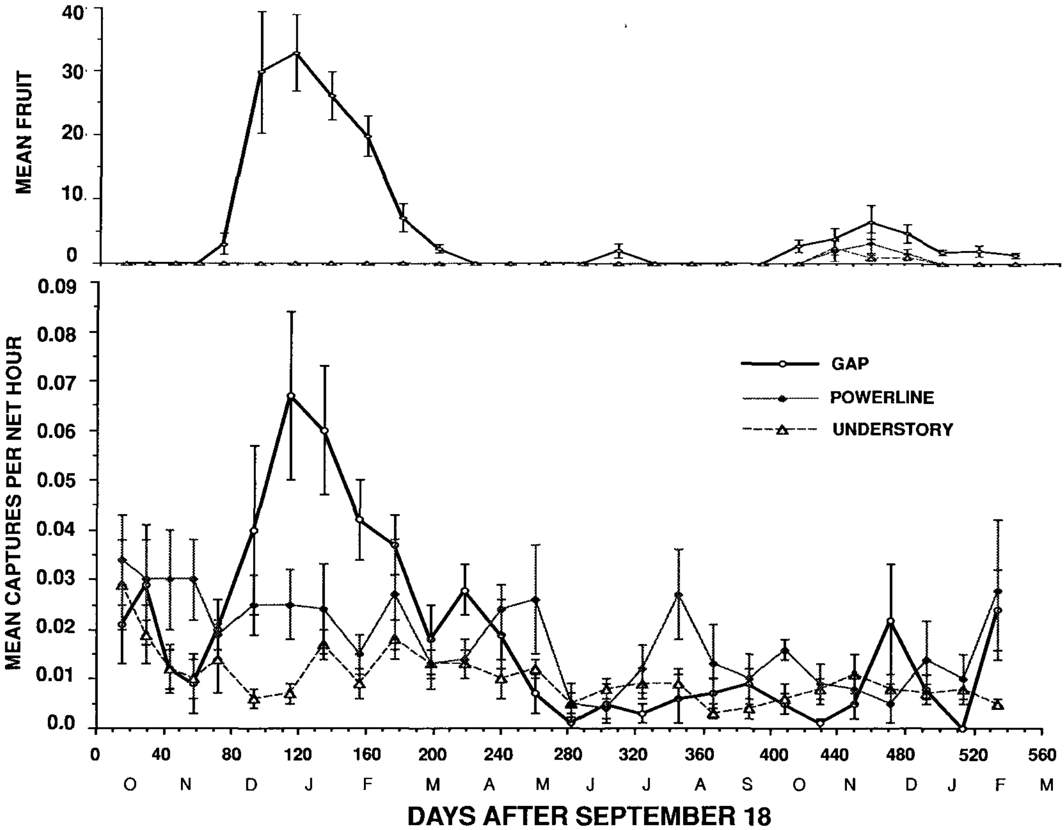

FIGURE 3. Upper: Mean (±SE) number of *Hirtella rugosa* fruits in 24 m^2 strip transects associated with each net in pre-existing forest understory, treefall gap, and powerline opening after Hurricane Hugo struck El Verde on 18 September 1989. Lower: Mean (±SE) captures per net hour during 29 two-day netting sessions in forest understory, treefall gap, and powerline opening after Hurricane Hugo struck El Verde.

preponderance of Puerto Rican Tanagers (45%, 14/31; 69%, 33/48; 51%, 27/53; and 16%, 5/33; of all gap captures) and Bananaquits (23%, 7/31; 8%, 4/48; 36%, 19/53; and 48%, 16/33; of all gap captures), and less so to the presence of species which were unique to gaps (Stripe-headed Tanager, $n = 4$; Red-legged Thrush, $n = 6$). During this peak in gap captures, Puerto Rican Tanagers were found significantly more often in gaps than in the understory (Friedman rank sum test $r = 7.0$, $P = 0.04$) while Stripe-headed Tanagers similarly showed a suggestive, but not quite significant preference for gaps over understory (Friedman rank sum test, $r = 4.5$, $P = 0.07$). Thus, approximately 3–5 months after the storm, a distinguishable assemblage of birds concentrated in pre-hurricane gaps at a time when fruit was available only in this habitat.

With the exception of this time period, total net captures after Hurricane Hugo did not differ among the pre-hurricane habitats, in contrast to the baseline study. For instance, total post-hurricane captures did not differ among the three habitats (374 in powerline, 350 in understory, 391 in gap), whereas baseline captures differed markedly among habitats (299 in powerline, 83 in understory, 149 in gap). The mean total captures per net did not differ significantly (Kruskal-Wallis statistic = 0.021, $P = 0.99$) among the three habitats (powerline net $\bar{x} = 62.3 \pm 29.6$; understory net $\bar{x} = 58.3 \pm 23.6$; gap net $\bar{x} = 65.2 \pm 41.5$).

After the hurricane, the total number of species captured in each pre-hurricane habitat was higher than in the baseline study, but as also found in the baseline did not differ among the habitats (18 vs. 13 in powerline, 20 vs. 11 in understory, 19 vs. 10 in gap). The average number of species captured per netting session did not vary significantly (Kruskal-Wallis statistic = 1.50, $P = 0.47$) among the pre-hurricane habitats (powerline $\bar{x}$ = 4.9 ± 2.3; gap $\bar{x}$ = 4.6 ± 2.8; understory $\bar{x}$ = 5.5 ± 2.6) in contrast to the baseline study in which the average number of species captured per session was higher in the powerline than in gaps.

Following the hurricane, only two of seventeen adequately sampled species showed evidence of habitat preference. Both Bananaquits and Black-whiskered Vireos had significantly (Friedman rank sums test, $r = 12.5$, $P = 0.05$; $r = 12.0$, $P = 0.01$, for the two species respectively) higher total captures in powerline nets than in gap nets (Bananaquits, 167 vs. 139; Black-whiskered Vireo, 24 vs. 13). Although the number of species showing habitat preference after the storm was higher than the value expected by chance (0.85), assuming a 5% level of significance, it was well below the baseline value (6 of 12 species). This indicates that few species showed differential habitat use among the pre-hurricane habitats after the storm.

Before the hurricane, bird assemblages from net-pairs within the same habitat were more similar than assemblages among habitats, suggesting that birds recognized differences among the three habitats. However, with the exception of the period including days 93–156, this was not the case after the hurricane. The mean PS for all net-pairs within habitats ($\bar{x}$ = 0.64 ± 0.11) was not significantly different (Mann-Whitney U = 2619.00, $P = 0.29$) from the mean PS for all net-pairs among habitats ($\bar{x}$ = 0.64 ± 0.94). The general absence of differential use of pre-hurricane habitats after the storm is not surprising, given that within habitat variation in foliage profiles approached the variation among habitats.

In the baseline study, the presence of a stream had a significant effect on the total number of captures in both the powerline and gap nets. However, in the storm's aftermath total captures in stream nets did not differ significantly (χ^2 test, P values > 0.05) from non-stream nets in powerline (14.2% of all captures), understory (13.4% of all captures), and gaps (13.6% of all captures).

To examine the possibility that birds responded to new foliage profile habitats created by the hurricane, I compared post-hurricane bird assemblages (9 October 1990–6 March 1991) from "new gap" and "new understory" nets previously identified by the K-means cluster analysis of foliage profiles. The PS values of bird assemblages from net-pairs within the new habitats were not significantly different from the PS values of net-pairs among habitats ($\bar{x}$ = 0.64 ± 0.02 vs. 0.61 ± 0.02, U = 3,145, $P = 0.28$). However, PS values of bird assemblages from net-pairs in the "new gap" were significantly higher than the PS values from net-pairs in the "new forest" ($\bar{x}$ = 0.79 ± 0.02 vs. 0.62 ± 0.01, U = 769.0, P = 0.002). The higher "new gap" PS values are attributable to the differential use of this habitat by Bananaquits, the only species to show a significant difference in use of the new habitats (39% of 152 captures in "new gap" nets vs. an expected 25% of captures, $\chi^2 = 15.48$, df = 1, $P < 0.01$). Although Bananaquits maintained predominance in the two new habitats, the ranked abundance of species captured in the two new habitats was not significantly correlated with the ranked abundance in the corresponding original habitats (gaps, Spearman's $r = 0.20$, df = 10, $P = 0.51$; understory, $r = 0.39$, df = 9, $P = 0.27$). Thus, although two new habitats were statistically distinguishable on the basis of foliage profiles after 378 days, the foliage differences were not associated with differences in bird assemblage, nor were the ranked abundances of species in these assemblages correlated with those in the corresponding habitat of the baseline study.

POINT COUNTS

The average number of individuals detected per point on 20–21 February 1990 ($\bar{x}$ = 4.5 ± 1.9), 156 days after the passage of Hugo, was significantly (Mann-Whitney U = 118.0, $P < 0.001$) higher than the average number of detections found before the storm on 21-22 February 1987 ($\bar{x}$ = 2.0 ± 1.6). As with the initial netting results, increases in average detections were attributable to increases in canopy individuals (1.84 ± 1.52 vs. 4.33 ± 2.02, U = 120.5, $P < 0.001$). However in contrast to the netting results, understory individuals decreased (0.76 ± 1.01 vs. 0.10 ± 0.31, U = 511.5, $P = 0.003$). Significant increases were detected in nectarivores (0.64 ± 0.15 vs. 1.57 ± 0.19, U = 183.5, $P = 0.001$), insectivores (0.76 ± 0.17 vs. 1.77 ± 0.22, U = 198.00, $P = 0.002$), and omnivores (0.32 ± 0.11 vs. 1.03 ± 0.23, U = 238.00, $P = 0.01$), but not frugivore/seedeaters (0.24 ± 0.11 vs. 0.10 ± 0.07, U = 423.5, P = 0.156). Between these dates, only Red-legged Thrushes showed a significant (U = 420.0, P = 0.05) decline in average detections per point (0.2

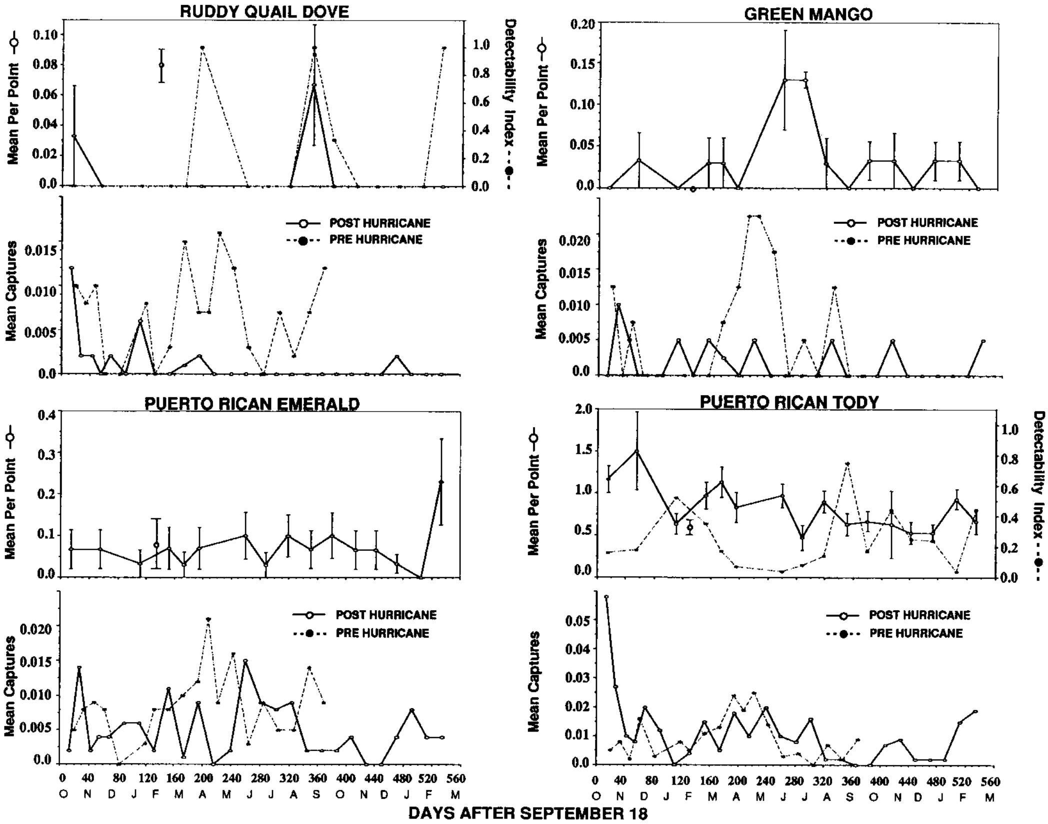

FIGURE 4. Mean (±SE) individuals of a specified species per point count and detectability index. Values are calculated for counts conducted during 16 two-day sessions over a year and one half after Hurricane Hugo struck El Verde on 18 September 1989 (upper). Also shown are mean (±SE) captures of that species per net hour during two-day netting sessions over a one-year period before (1983–1984) the hurricane and one- and one-half-year period afterwards (lower).

± 0.8 vs. 0.0) while significant increases in average detections were found in Bananaquits ($U = 173$, $P = 0.0003$, 0.6 ± 0.6 vs. 1.5 ± 1.0), Puerto Rican Tanagers ($U = 187.5$, $P = 0.00001$, 0 vs. 0.8 ± 1.2), and Black-whiskered Vireos ($U = 289.0$, $P = 0.02$, 0.04 ± 0.2 vs. 0.3 ± 0.6).

Detectability of some species could change with vegetation growth and refoliation and could possibly result in a perceived change in a species abundance over time. However, no consistent trend in detectability indexes over time was found in any species, despite increases in foliage density (Figs. 4–9).

POINT COUNTS AND NET CAPTURES

Post-hurricane netting and point count results combined for all species were not expected to be correlated, in part because the two methods do not sample equivalent vertical zones of vegetation. As expected, no significant correlation (Spearman's $r = 0.38$, $P > 0.1$) was found between the average number of detections of all individuals per point count and mean number of captures per net hour during the 16 weeks during which the community was simultaneously sampled by the two methods. Only 2 of 17 species (Puerto Rican Tody and Puerto Rican Tanager) showed significant correlations between mist net captures and mean detections per point ($r = 0.54$, $P < 0.05$, $r = 0.55$, $P < 0.05$, respectively).

The predominant post-hurricane netting trend (i.e., initial post-hurricane increase in abundance followed by decline to baseline levels) was also evident in point count results for canopy dwellers including Puerto Rican Tody, Puerto Rican Tan-

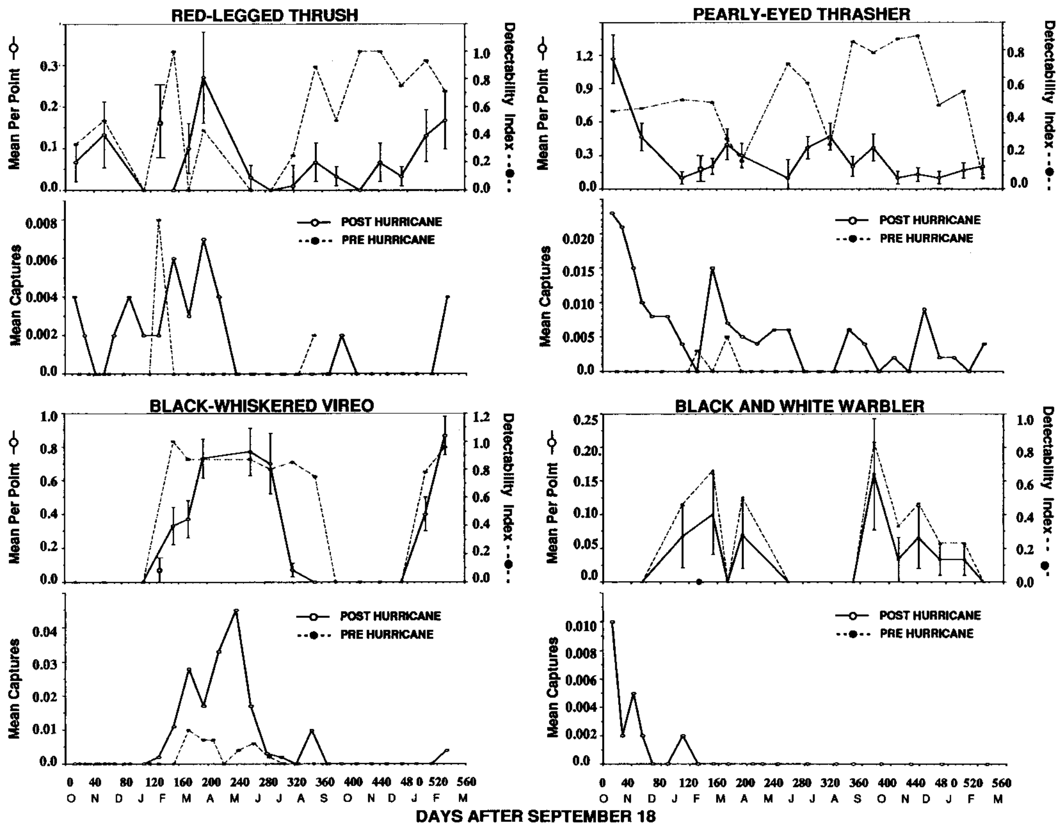

FIGURE 5. Mean (±SE) individuals of a specified species per point count and detectability index. Values are calculated for counts conducted during 16 two-day sessions over a year and one half after Hurricane Hugo struck El Verde on 18 September 1989 (upper). Also shown are mean (±SE) captures of that species per net hour during two-day netting sessions over a one-year period before (1983–1984) the hurricane and one- and one-half-year period afterwards (lower).

ager, Stripe-headed Tanager, Pearly-eyed Thrasher, and Puerto Rican Woodpecker. However, the predominant pattern in point counts was no overall increase or decrease in detections. Seasonal residents (Black-whiskered Vireo, American Redstart, Black-throated Blue Warbler, Northern Parula, Black-and-white Warbler) and some permanent residents (Red-legged Thrush, Puerto Rican Bullfinch) fit this pattern despite showing decreasing post-hurricane net captures which indicated that they remained in the forest, but were probably foraging above net level. Ruddy Quail-Dove was the only species to decline below baseline net capture rates, yet point counts indicate that it remained in the forest understory. Although nectarivores showed no overall post-hurricane trends in point count detections, as was also found in net captures, point counts revealed more seasonal variation in nectarivores than was found in net captures.

DISCUSSION

Hurricane Hugo remained over Puerto Rico for 4 hr, during which time maximum sustained winds of over 166 km/hr were recorded (Scatena and Larsen 1991). Severe defoliation occurred in 56 percent of the trees in study plots in El Verde, where 9% of the trees were uprooted and 11% of the tree trunks snapped, although overall tree mortality was only 7% (Walker 1991). Damage in Walker's study plots was patchy and most severe on north-facing sites, the same aspect in which nets in this study were located. Foliage profiles associated with the nets also demonstrated the severity of defoliation and its patchy distribution. However, overall damage to the 6.4

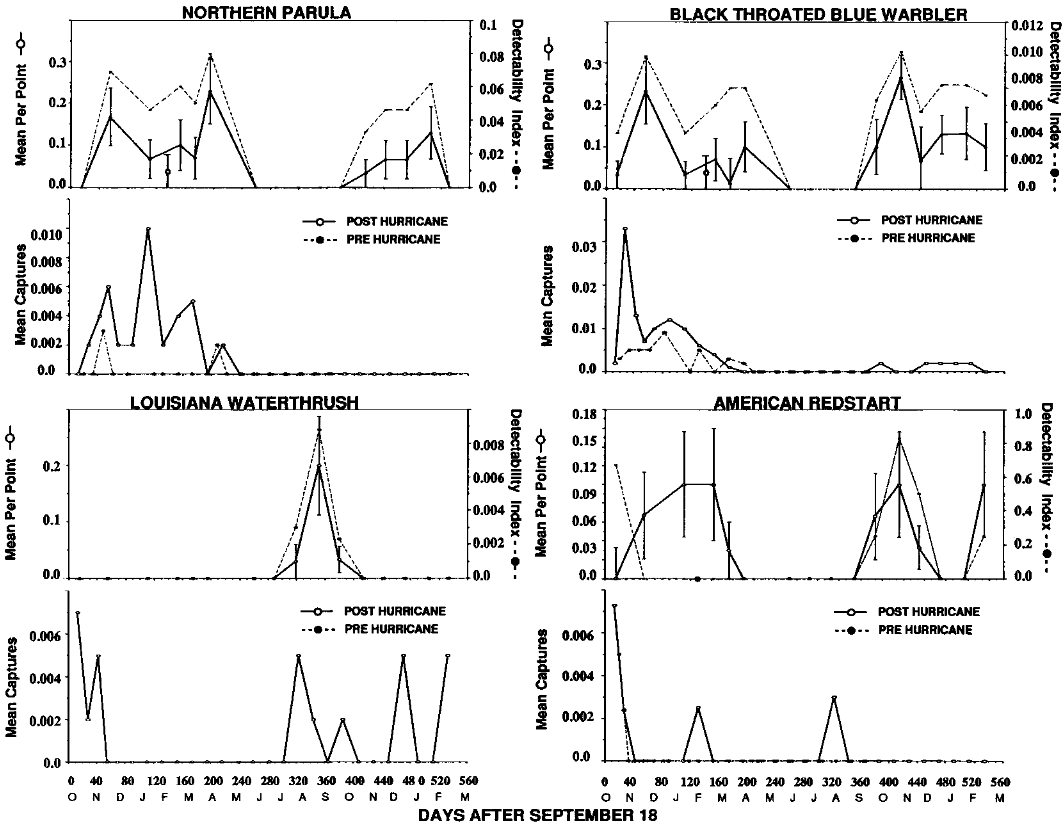

FIGURE 6. Mean (±SE) individuals of a specified species per point count and detectability index. Values are calculated for counts conducted during 16 two-day sessions over a year and one half after Hurricane Hugo struck El Verde on 18 September 1989 (upper). Also shown are mean (±SE) captures of that species per net hour during two-day netting sessions over a one-year period before (1983–1984) the hurricane and one- and one-half-year period afterwards (lower).

ha in which the nets were located was uniformly severe compared with the much larger area (25 ha) over which the point counts were conducted. Point count sites were located over a greater range of slope and aspect than netting sites, and presumably as a result, showed more variation in the severity of hurricane damage. Some point count sites appeared to suffer little defoliation or other canopy damage, and this variation in defoliation undoubtedly contributed to observed differences between net and point count results.

Despite differences in design, the results of this work are similar to the El Verde findings of Waide (1991). Waide's study spanned a year after the hurricane in which he monitored populations with fixed-radius point counts at four different periods starting 10 days after the storm, and compared them with baseline counts obtained in May 1989. Waide supplemented his point counts with mist netting results obtained in June 1990 and compared them with netting results obtained in March–July and September–October in 1981–1986. In contrast, I compared point counts conducted at 16 periods over 1.5 years after the storm with baseline counts obtained in February 1987. My mist netting efforts were also more intensive than those of Waide and involved a longer period of time (29 netting sessions over 1.5 yr) compared with one year of baseline netting (Wunderle et al. 1987). Despite these differences, and the fact that our censuses and netting were conducted in different parts of the forest near El Verde, our results for individual species are quite similar in terms of population response immediately after the hurricane and the pattern of population change in the following year. The larger

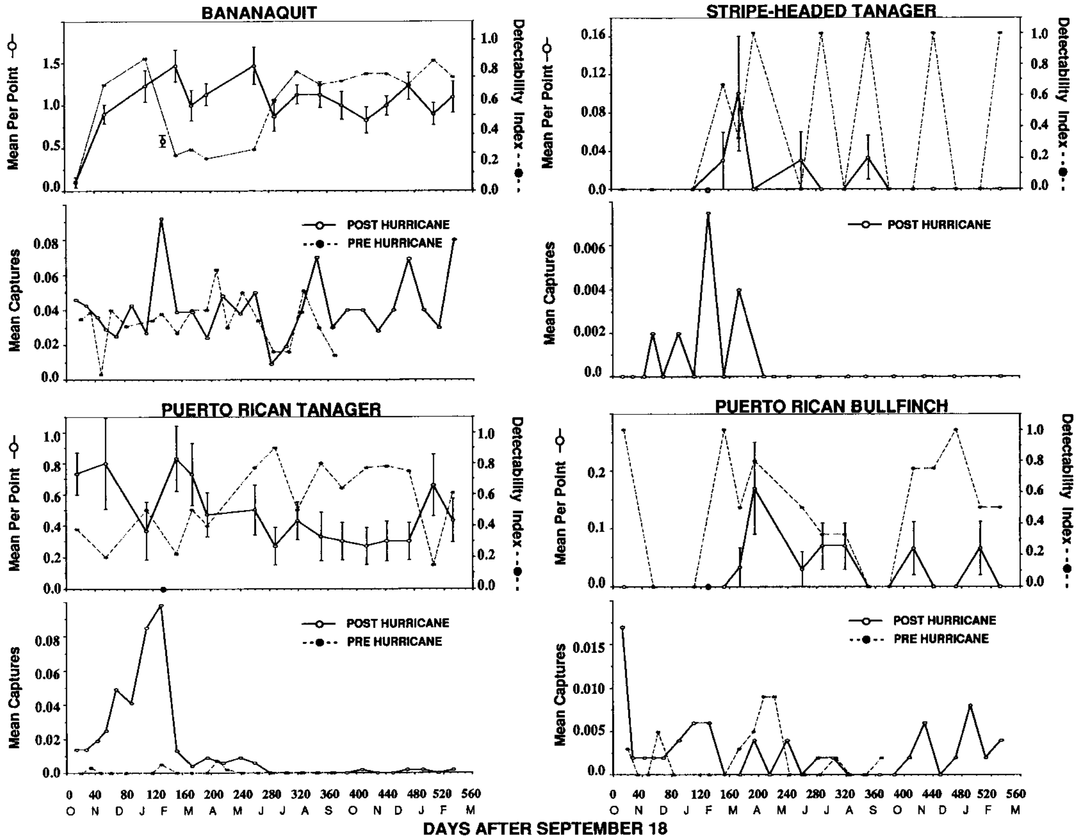

FIGURE 7. Mean (±SE) individuals of a specified species per point count and detectability index. Values are calculated for counts conducted during 16 two-day sessions over a year and one half after Hurricane Hugo struck El Verde on 18 September 1989 (upper). Also shown are mean (±SE) captures of that species per net hour during two-day netting sessions over a one-year period before (1983–1984) the hurricane and one- and one-half-year period afterwards (lower).

samples in my study permitted statistical verification of some trends described, but not tested, by Waide. The two studies mostly differ in their ability to detect local population changes and their documentation of use of pre-hurricane habitats.

I attribute the marked increase in bird captures shortly after the hurricane to a downward shift by canopy dwellers. Capture rates for understory dwellers were indistinguishable from pre-hurricane baseline rates. Although not demonstrated statistically, this same pattern of captures was also noted by Waide (1991), who also showed that Bananaquits and Black-whiskered Vireos spent a greater proportion of time foraging close to the ground after the hurricane than they had previously. Similarly, it was the canopy/understory species (62% of the species) rather than the understory species (38% of the species) which increased most in point count samples after Hurricane Gilbert struck tall-stature wet limestone forest in Jamaica (Wunderle et al. 1992). Thus, in tall-stature forests, increased captures and observations of canopy dwellers may be expected shortly after a hurricane impact.

The post-hurricane displacement of canopy dwellers to the understory, and the relatively slow regrowth of the canopy, would strongly select for species that are generalists in foraging height. As Waide (1991) and Wunderle et al. (1992) note, this may account for the findings of MacArthur et al. (1966) that birds in El Verde recognize only two vertical layers in the forest while those in mainland Panama recognize four layers. Also, frequent hurricanes may limit the height of Caribbean forests (Odum 1970), thereby restricting

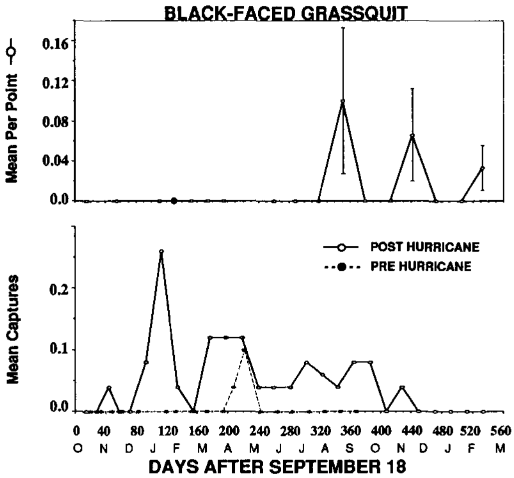

FIGURE 8. Mean (±SE) individual Black-faced Grassquits per point count and detectability index. Values are calculated for counts conducted during 16 two-day sessions over a year and one half after Hurricane Hugo struck El Verde on 18 September (upper) and mean (±SE) captures per net hour during two-day netting sessions over a one-year period before (1983–1984) the hurricane and one-half-year period afterwards (lower).

the vertical foliage profile on which segregation might occur. Therefore, it is perhaps not surprising that so few Caribbean species segregate on the basis of foraging height (J. Faaborg, pers. comm.). However, other traits which permit ecological co-existence (e.g., differences in morphology or body size) may be selected for by resource competition in the aftermath of hurricanes as forest birds are restricted to the same zone close to the ground.

Population changes shortly after Hurricane Hugo were not strongly related to diet, unlike the conclusions from previous studies of hurricane effects (reviewed in Wiley and Wunderle 1994). Expected population declines in nectarivores and fruit/seedeaters were not apparent in net captures and only weakly suggested in point counts. Nectarivores, such as Puerto Rican Emeralds and Green Mangos showed no decline in net captures or point counts. However, Bananaquit detections were lowest in point counts just after the hurricane while net captures at this time were indistinguishable from baseline rates. Given that Bananaquits are common canopy dwellers it might have been expected that their post-hurricane

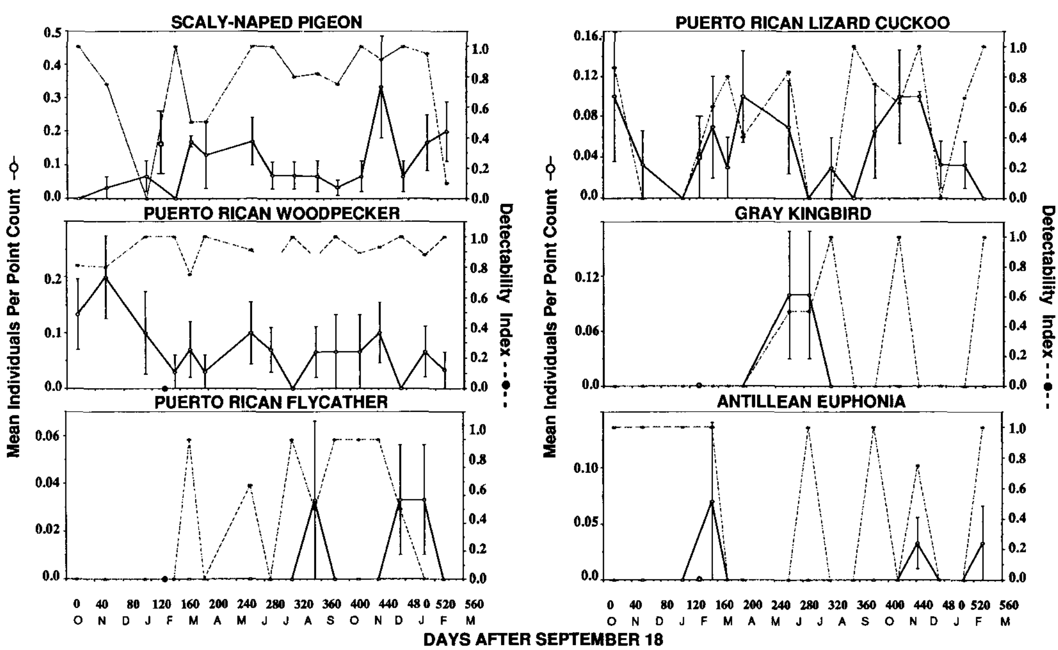

FIGURE 9. Mean (±SE) individuals of a specified species per point count and detectability index. Values are calculated for counts conducted during 16 two-day sessions over a year and one half after Hurricane Hugo struck El Verde on 18 September 1989.

capture rate would have increased above baseline levels. Thus, the lack of a post-hurricane increase in Bananaquit capture rates might actually indicate a decline in the total density of this species. Similarly, fruit/seedeater captures shortly after the hurricane were either slightly higher or comparable to baseline levels, while point counts indicated at least one possible fruit/seedeater decline after the storm. Detections of the fruit/seedeating Scaly-naped Pigeon were lowest shortly after the storm, but increased during the study. This was the only canopy-dwelling species which did not descend to the understory after the hurricane, but instead concentrated in the remaining patches of canopy foliage.

Both insectivores and omnivores showed significant increases in captures and point count detections shortly after the hurricane. However, point count detection rates then declined over the remainder of the study. The initial post-hurricane increase in insectivores and omnivores, is mostly attributable to high numbers of canopy dwellers represented in these diet groups. Therefore, the immediate post-hurricane shift of canopy dwellers to the understory in tall-stature forest may have obscured expected declines in some nectarivores and fruit/seedeaters and accentuated population counts of omnivores and insectivores.

The appearance of fruit of *Hirtella rugosa* in pre-existing treefall gaps coincided with high capture rates in gaps and the appearance of an assemblage of gap-associated species that was distinct from either the understory or powerline assemblages. Birds observed feeding on *H. rugosa* fruits in gaps included Puerto Rican Tanager, Bananaquit, Stripe-headed Tanager, and Red-legged Thrush. These species also showed high capture rates in gaps (Wunderle, unpubl. observ.). After the hurricane, fruit was more prevalent than before in stomach contents of birds collected in El Verde (Waide 1991). Although relatively high fruit production in gaps is well documented (e.g., Croat 1975, Opler et al. 1980, Denslow et al. 1986, Levey 1988) and attracts a disproportionate share of frugivores (Blake and Hoppes 1986, Martin and Karr 1986, Hoppes 1987, Levey 1988), this pattern was unexpected in the aftermath of a hurricane. However, *H. rugosa* was the only plant fruiting at this time and its distribution was restricted to pre-hurricane gaps. Gap plants were presumably able to quickly take advantage of high light levels for growth and fruiting after the hurricane while forest understory plants may have been initially light-shocked after the storm. Once fruit production ceased in gaps, capture rates in gaps declined to the level observed in the forest understory and powerline corridor. Thus, even in the aftermath of a hurricane, pre-existing gaps may serve as a "keystone habitat" (sensu Levey 1990) by maintaining frugivore populations through times of fruit scarcity.

With the exception of gap fruit production in the first 3–5 months, the major post-hurricane vegetation effect on bird populations resulted from vegetative growth of understory plants and refoliation of the canopy. As the canopy refoliated, overall net captures declined to baseline levels, presumably because birds returned to foraging in new canopy foliage above the nets. In addition, the foliage profiles which defined the pre-existing habitats lost their distinctiveness as a result of hurricane damage and subsequent plant regrowth in which foliage variation within and among habitats became equivalent. The loss of distinct foliage distributions of pre-existing habitats was associated with the absence of the distinguishable bird assemblages which characterized the three pre-hurricane habitats (Wunderle et al. 1987). After the hurricane, only two species differentiated among the three pre-hurricane habitats. In contrast, six species showed differential habitat use of the three habitats during the baseline period.

As the vegetation recovered following Hurricane Hugo, the pre-hurricane habitats lost their distinctiveness, but new gap and forest understory sites became statistically distinguishable on the basis of their unique foliage profiles after about one year. However, distinct bird assemblages were not apparent in the two post-hurricane habitats, presumably because foliage differences were insufficient to promote differential habitat use by most species (an exception was the Bananaquit). Most species probably do not respond directly to foliage differences between gap and mature forest understory, but rather to differences in food resources which were not yet sufficiently distinctive after one year to enable birds to distinguish between the two habitats. Given the relatively slow canopy recovery rate, it may take many years for the gap and understory to become sufficiently distinct in structure and resources before most bird species differentiate between these habitats.

The initial increase in mean individual body mass after the hurricane in Bananaquits, Puerto Rican Emeralds, and Puerto Rican Todies was unexpected. It is conceivable that directional selection resulted in lighter birds suffering higher mortality after the hurricane, possibly as a result of competition for limited food resources. Alternatively, the mean shift might result from post-hurricane immigration of heavier birds from high altitude sites where recovery of vegetation is slower as suggested for Jamaica after Hurricane Gilbert (Wunderle et al. 1992). This may have occurred in the Luquillo Mountains, at least for Bananaquits which are significantly heavier at higher altitudes than at El Verde (W. Arendt and J. Wunderle, unpubl. data). Obviously, future hurricane studies should focus on body condition and survival to resolve these possibilities.

Displacement, whether immigration or emigration, was the most obvious hurricane effect on bird populations in El Verde. This was evident in the increased numbers of canopy dwellers in the understory and the movement of fruit-eating birds into pre-existing gaps. However, it also includes the invasion by forest edge or shrubby second-growth species into the forest, as shown by species that were previously very rare (Black-faced Grassquit) or unknown in the forest (Indigo Bunting). This post-hurricane pattern was noted by Lynch (1991) in Yucatan and by Waide (1991) in the grassquit in El Verde. Only the Stripe-headed Tanager and Ruddy Quail-Dove appear to have disappeared from the netting sites in El Verde, although both were detected elsewhere in my point counts and those of Waide (1991). Stripe-headed Tanagers were not captured in the baseline study, but shortly after the hurricane they appeared in gaps, where they fed on fruit. Before the storm, Ruddy Quail-Doves avoided areas lacking a forest canopy, but with thick ground vegetation (Wunderle et al. 1987). Therefore, it is not surprising that this species disappeared from hurricane-damaged sites, as was also found in the Bridled Quail-Dove (*Geotrygon mystacea*) on St. Croix (Wauer and Wunderle 1992). The ability to shift habitats conveys a selective advantage to birds inhabiting hurricane-prone regions, and therefore it is not surprising that habitat breadth of island birds in the hurricane-prone Caribbean is on average greater than in continental forests where hurricane frequency is lower (e.g., Cox and Ricklefs 1977).

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APPENDIX

Scientific names of birds detected after Hurricane Hugo and diet and foraging site classification based on Wetmore (1916) and Waide (1991). Letters for diet indicate: F, fruit or seed; N, nectar; I, insect; O, omnivore. Letters for foraging site indicate: C, canopy; U, forest understory only.

Scaly-naped Pigeon (*Columba squamosa*) F, C; Ruddy Quail-Dove (*Geotrygon montana*) F, U; Puerto Rican Lizard-Cuckoo (*Saurothera vieilloti*) I, C; Puerto Rican Emerald (*Chlorostilbon maugaeus*) N, U; Green Mango (*Antrhracothorax viridis*) N, U; Puerto Rican Tody (*Todus mexicanus*) I, C; Puerto Rican Woodpecker (*Melanerpes portoricensis*) I, C; Gray Kingbird (*Tyrannus dominicensis*) I, C; Puerto Rican Flycatcher (*Myiarchus antillarum*) I, C; Red-legged Thrush (*Turdus plumbeus*) O, C; Wood Thrush (*Hylocichla mustelina*) I, U; Pearly-eyed Thrasher (*Margarops fuscatus*) O, C; Black-whiskered Vireo (*Vireo altiloquus*) I, C; Black-and-white Warbler (*Mniotilta varia*) I, C; Northern Parula (*Parula americana*) I, C; Black-throated Blue Warbler (*Dendroica caerulescens*) I, C; Ovenbird (*Seiurus aurocapillus*) I, U; Louisiana Waterthrush (*Seiurus motacilla*) I, U; Hooded Warbler (*Wilsonia citrina*) I, C; American Redstart (*Setophaga ruticilla*) I, C; Bananaquit (*Coereba flaveola*) N, C; Stripe-headed Tanager (*Spindalis zena*) F, C; Puerto Rican Tanager (*Nesospingus speculiferus*) O, C; Indigo Bunting (*Passerina cyanea*) O, C; Puerto Rican Bullfinch (*Loxigilla portoricensis*) F, C; Black-faced Grassquit (*Tiaris bicolor*) F, U.