

Effects of Hurricane Georges on the Resident Avifauna of Maricao State Forest, Puerto Rico

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Abstract.—Hurricane Georges crossed the island of Puerto Rico on 21-22 September 1998. Maricao State Forest, a montane reserve in southwestern Puerto Rico, was struck by Georges after being spared by hurricanes since 1932. I documented the changes in relative abundance of Maricao resident bird species caused by the impact of the hurricane by comparing baseline mist netting capture rates with data 33 days after the hurricane, and point counts records with data up to 22 months after Georges. Total capture rates increased after the storm (26.8 individuals/net hr pre-hurricane vs. 57.9 individuals/net hr post-hurricane). Capture rates classified according to foraging guilds did not differ, but showed significant increases according to foraging level (canopy vs. understory). Increases in capture rates were related to the displacement of birds into lower forest strata after canopy loss. While most species recorded in point counts declined after Georges (16/21), only the relative abundance of six species differed significantly among years. Just one species (Elfin Woods Warbler, *Dendroica angelae*) recovered by the end of the study. Two species were not observed after the hurricane, including one of the five most abundant (Ruddy Quail-Dove, *Geotrygon montana*) and a new species was observed in the study area after the hurricane (White-winged Dove, *Zenaidra asiatica*). Only the population of the Gray Kingbird (*Tyrannus dominicensis*) remained unchanged throughout the study. Results demonstrated that even common species in montane habitats can be highly susceptible to hurricanes, and thus, long-term monitoring of avian communities at different elevations is needed to understand the effects.

KEYWORDS.—bird populations, habitat disturbance, Hurricane Georges, mist netting, point counts

INTRODUCTION

Hurricane winds may impact bird populations by destroying the resources on which they depend. Effects involve the reduction or depletion of nectar, fruit, and animal prey, as well as the elimination of nesting and roosting sites (Wiley and Wunderle 1993). However, the consequences will depend on the foraging preferences and special habitat requirements of each species. Some species may cope with hurricane-induced changes by selecting different prey items while others may switch their foraging behavior and locations (Waide 1991; Wauer and Wunderle 1992; Wunderle et al. 1992).

Puerto Rico is frequently hit by hurri-

canes, but studies of their effects on bird populations are limited to the northeastern region (Waide 1991; Wunderle 1995; Wunderle 1999), and little is known about how bird species are affected elsewhere in the island. Hurricane Georges crossed the entire island of Puerto Rico from 21-22 September 1998 with sustained winds of 184 kph and wind gusts of up to 240 kph (category 3 on Saffir-Simpson scale of 5) (Bennett and Mojica 1998). Maricao State Forest, a montane reserve in southwestern Puerto Rico, was struck by Georges after being spared by hurricanes since 1932 (Salivia 1972; Scatena and Larsen 1991; Boose et al. 2004). This forest reserve has a high avian diversity, including isolated populations of the endemics Elfin Woods Warbler and Puerto Rican Tanager (Tossas and Delannoy 2001) (see Appendix for scientific names). Hurricane winds drastically altered the forest structure by opening the canopy

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through severe defoliation, tree uprooting, and stem and branch breakage (Tossas pers. obs.).

In this work I document the changes in relative abundance of resident bird species caused by the impact of Hurricane Georges in Maricao State Forest. Baseline capture rates are compared with data 33 days after the hurricane while point counts records are compared with data up to 22 months after the hurricane.

MATERIALS AND METHODS

Study area

Maricao State Forest comprises 4,150 ha in the western part of the Cordillera Central of Puerto Rico. Elevations range from 150 to 875 m above sea level, but study sites were established near the reserve's headquarters from 650 to 750 m. Annual precipitation and temperature average 2,326 mm and 21.7°C, respectively. Three life zones are present in the forest: subtropical wet forest (65.2%), subtropical moist forest (32.9%), and the lower montane wet forest (1.9%) (Silander et al. 1986). Dominant tree species in Maricao include *Micropholis chrysophylloides*, *Terebraria resinosa*, *Linociera dominguensis*, *Homalium racemosum*, *Tabebuia schumanniana*, and *Eugenia stahlii* (Silander et al. 1986).

Mist netting

Relative bird abundance was estimated in Maricao State Forest before and after Hurricane Georges using mist nets. Nine 12.5 m nets (30 and 36 mm mesh) were placed continuously on a trail in the subtropical wet forest, at an elevation of 650 m. Baseline data were collected during a mist netting session done from 28-31 July 1998 for 198 net-hours. I conducted the post-hurricane netting session from 25-27 October (33 days after the hurricane) in the same location for 103 net-hours. The nets were opened from dawn to noon in July but were closed before noon in the October session to avoid bird mortality due to the strong solar radiation caused by canopy loss. All captured individuals were marked with US

Fish and Wildlife Service aluminum bands and released. Capture rates were calculated for each session by dividing the number of new individuals captured per species by the number of net-hours. Migratory and transient species were not considered for analysis because they were not present in the summer session.

Point counts

Birds were also sampled with point counts before and after the hurricane along three trails, including the trail where the mist nets were placed. All trails were within the subtropical wet forest life zone and had similar floristic composition and vegetation structure. Point counts were conducted from February to July in each of three years ($n = 75$ in 1998; $n = 55$ in 1999; $n = 57$ in 2000). In each count, I stood in the center of the trail and during 10 min recorded all bird species seen or heard within a 25 m radius. On days with fair weather up to fifteen point counts were done in a single morning. Counts were not conducted on days with strong winds, thus causing variation in the total number of counts each year.

Statistical analyses

To determine the statistical significance of the post-hurricane change in the total mist net captures, I used a Wilcoxon's test for matched pairs, in which capture rates were compared for each species before and after the hurricane. I also tested the proportion of bird species captured in mist nets before and after the hurricane according to diet guilds and foraging level. For this analysis, I classified species as insectivore, omnivore, nectarivore, or frugivore, and as canopy or understory forager (see Table 1), following Waide (1996) and Wunderle (1995). Capture rates of species according to their foraging level and diet category before and after the hurricane were compared with a row x column test of independence using a G-statistic. The number of individuals detected in point counts was normalized with a logarithmic transformation

(value $x + 1$) and the means were compared among the three study years with a one-way ANOVA. Statistical tests followed Sokal and Rohlf (1981) and were performed in SPSS 13.0 for Windows (SPSS 2004).

RESULTS

Mist netting

Total capture rate for 17 species significantly increased (Wilcoxon's $T = 36$, $p = 0.004$) after Hurricane Georges (Table 1). I captured 53 individuals of 13 species before the hurricane and 73 individuals of 15 species after. Three species captured in July were not captured in October (Elfin Woods Warbler, Black-faced Grassquit, Puerto Rican Pewee). Five species captured after the hurricane were not captured previously (Greater Antillean Oriole, Gray Kingbird, Puerto Rican Woodpecker, Puerto Rican Lizard-Cuckoo and Green Mango).

Five species accounted for more than 70% of the net captures, but common species differed before and after the hurricane.

The five most frequently captured species before Georges were the Puerto Rican Bullfinch (18.9%), Bananaquit (15.1%), Red-legged Thrush (15.1%), Puerto Rican Vireo (13.2%) and Ruddy Quail-Dove (9.4%). In the post-hurricane netting session almost one third of all captures were individuals of the Bananaquit (31.5%), followed by Puerto Rican Spindalis (16.4%), Puerto Rican Tanager (12.3%), Puerto Rican Bullfinch (11%) and Puerto Rican Vireo (6.9%).

According to diet, omnivores were the most frequently captured birds before the hurricane, but were replaced by nectarivores after Georges. Although capture rates of all diet guilds increased after the hurricane (Fig. 1a), the proportional representation of the guilds did not differ significantly after the storm (row \times column test of independence, $G = 3.14$, $p = 0.37$). However, the proportion of canopy-forager captures significantly increased after the hurricane relative to the proportion of understory-forager captures ($G = 5.05$, $p = 0.024$) (Fig 1b).

TABLE 1. Capture rates (number of individuals capture/100 net hours) and proportion of sample of bird species in Maricao State Forest before (July 1998) and after (October 1998) Hurricane Georges with data on diet and foraging location.

Species	Diet and foraging location ¹	Capture Rate	
		Before (% of sample)	After (% of sample)
Ruddy Quail-Dove	F, U	2.5 (9.4)	0.8 (1.4)
Puerto Rican Lizard-Cuckoo	I, C	0	0.8 (1.4)
Green Mango	N, C	0	2.4 (4.1)
Puerto Rican Emerald	N, U	1.0 (3.8)	0.8 (1.4)
Puerto Rican Tody	I, C	1.0 (3.8)	3.2 (5.5)
Puerto Rican Woodpecker	O, C	0	0.8 (1.4)
Puerto Rican Pewee	I, U	0.5 (1.9)	0
Gray Kingbird	I, C	0	0.8 (1.4)
Puerto Rican Vireo	I, C	3.5 (13.2)	4.0 (6.8)
Red-legged Thrush	O, C	4.0 (15.1)	1.6 (2.7)
Elfin Woods Warbler	I, C	0.5 (1.9)	0
Bananaquit	N, C	4.0 (15.1)	18.3 (31.5)
Puerto Rican Tanager	O, C	2.0 (7.5)	7.1 (12.3)
Puerto Rican Spindalis	F, C	2.0 (7.5)	9.5 (16.4)
Black-faced Grassquit	F, U	0.5 (1.9)	0
Puerto Rican Bullfinch	F, C	5.1 (18.9)	6.3 (11.0)
Greater Antillean Oriole	I, C	0	1.6 (2.7)
Total capture rate		26.8	57.9
Total birds captured		53	73

¹I = insectivore, O = omnivore, N = nectarivore, F = frugivore, U = understory, C = canopy.

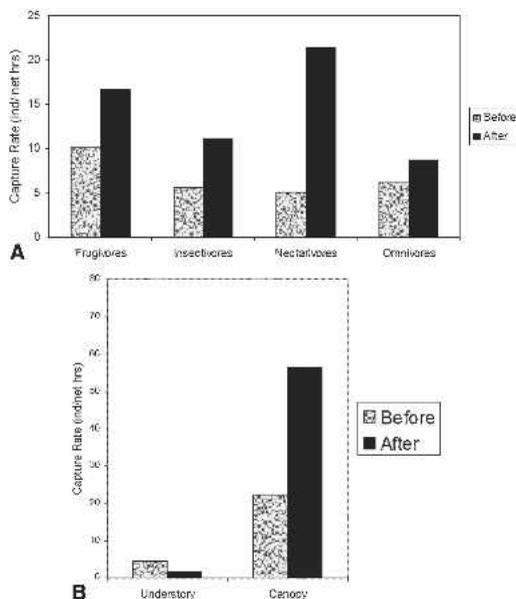


FIG. 1. Capture rate of bird species in Maricao State Forest before (July 1998) and after (October 1998) Hurricane Georges according to (a) foraging guilds, and (b) foraging level.

Point counts

While most species recorded in point counts declined after the hurricane (16/21), only the relative abundance of six species differed significantly among years (Table 2). Of these, only the population of the Elfin Woods Warbler returned to pre-hurricane levels by 2000. Two species disappeared, the Ruddy Quail-Dove and Antillean Euphonia, and a new species was observed in the study area after the hurricane, the White-winged Dove. Only the population of the Gray Kingbird remained unchanged among the three years.

DISCUSSION

Maricao State Forest provides important habitat for a diverse assemblage of avian species. Seventy-three species in 26 families have been reported in this forest reserve (Tossas and Delannoy 2001), including 13 of the 17 species endemic to Puerto Rico. Twenty-three species of breeding residents were reported in the present study. Based on data from mist netting captures and

point counts, all species showed fluctuations in their relative abundance following the passage of Hurricane Georges; the exception the Gray Kingbird. The kingbird is a species of forest edges and gaps thus was not affected by the main hurricane effect, canopy opening. However, even though their abundance remained unchanged, kingbirds appeared to forage closer to the ground as suggested by captures in the mist nets only after the storm. Twelve other species of canopy foragers were captured in the understory after the hurricane. Of these species, four were only captured in the nets after the hurricane, while the other eight species were more commonly captured in the nets after the hurricane. Overall, canopy-dwelling species were captured 2.3 times more frequently after than before the storm.

Only two canopy species, the frugivorous Red-legged Thrush and insectivorous Elfin Woods Warbler, declined in capture rates after Georges. Nevertheless, data from point count surveys showed that by 2000, the warbler had recovered to pre-hurricane population levels. The initial decline and subsequent recovery of the Elfin Woods Warbler may be attributable to the initial post-hurricane loss of foraging substrate (i.e., leaves), for arthropod gleaning and subsequent foliage re-growth. It is possible that the warblers abandoned defoliated sites immediately after the hurricane and shifted to protected patches with adequate foraging substrate and prey until the defoliated sites recovered. Movement from heavily damaged sites into protected areas is a frequently observed post-hurricane bird response (Wiley and Wunderle 1993), particularly since strong winds often result in the creation of a mosaic of sites showing different levels of disturbance even within the same forest (Wunderle et al. 1992; Wunderle 1995).

Other species that depend on fruits or seeds for their subsistence showed population declines as well (Scaly-naped Pigeon, Ruddy Quail-Dove, Puerto Rican Spindalis, Puerto Rican Bullfinch, Antillean Euphonia, Black-faced Grassquit). Of these, the quail-dove and euphonia were not reported again in point counts conducted in

TABLE 2. Mean number of individuals recorded per point count \pm SE, and proportion of sample (percentage within parenthesis) of bird species in Maricao State Forest before (1998) and after Hurricane Georges (1999; 2000). The relative abundance of each species was compared among years with an analysis of variance.

Species	Mean \pm SE (% of sample)		
	1998	1999	2000
Scaly-naped Pigeon	0.24 \pm 0.08 (4.5)	0.11 \pm 0.05 (3.7)	0.09 \pm 0.04 (2.2)
White-winged Dove	0	0	0.02 \pm 0.02 (0.4)
Ruddy Quail-Dove*	0.15 \pm 0.05 (2.7)	0	0
Puerto Rican Lizard-Cuckoo	0.01 \pm 0.01 (0.2)	0.04 \pm 0.03 (1.2)	0
Green Mango	0.08 \pm 0.03 (1.5)	0.16 \pm 0.05 (5.5)	0.25 \pm 0.07 (6.1)
Puerto Rican Emerald	0.32 \pm 0.06 (6.0)	0.20 \pm 0.07 (6.7)	0.44 \pm 0.09 (10.9)
Puerto Rican Tody*	0.79 \pm 0.09 (14.7)	0.42 \pm 0.09 (14.0)	0.37 \pm 0.09 (9.1)
Puerto Rican Woodpecker	0.11 \pm 0.05 (2.0)	0	0.02 \pm 0.02 (0.4)
Puerto Rican Pewee	0.15 \pm 0.05 (2.7)	0.02 \pm 0.02 (0.6)	0.09 \pm 0.05 (2.2)
Gray Kingbird	0.04 \pm 0.02 (0.7)	0.04 \pm 0.04 (1.2)	0.04 \pm 0.04 (0.9)
Puerto Rican Vireo	0.39 \pm 0.07 (7.2)	0.25 \pm 0.06 (8.5)	0.12 \pm 0.04 (3.0)
Black-whiskered Vireo	0.19 \pm 0.05 (3.5)	0.05 \pm 0.03 (1.8)	0.05 \pm 0.05 (1.3)
Red-legged Thrush*	0.19 \pm 0.05 (3.5)	0.07 \pm 0.04 (2.4)	0.05 \pm 0.03 (1.3)
Pearly-eyed Thrasher	0	0.02 \pm 0.02 (0.61)	0
Elfin Woods Warbler*	0.24 \pm 0.07 (4.5)	0.04 \pm 0.03 (1.2)	0.28 \pm 0.09 (7.0)
Adelaide's Warbler	0.15 \pm 0.05 (2.7)	0.04 \pm 0.03 (1.2)	0.07 \pm 0.06 (1.7)
Bananaquit	0.91 \pm 0.08 (16.9)	1.00 \pm 0.12 (33.5)	1.14 \pm 0.13 (28.3)
Puerto Rican Tanager	0.67 \pm 0.10 (12.4)	0.35 \pm 0.10 (11.6)	0.58 \pm 0.11 (14.3)
Puerto Rican Spindalis*	0.25 \pm 0.06 (4.7)	0.05 \pm 0.03 (1.8)	0.09 \pm 0.04 (2.2)
Antillean Euphonia	0.03 \pm 0.03 (0.5)	0	0
Black-faced Grassquit	0.04 \pm 0.03 (0.7)	0	0.07 \pm 0.05 (1.7)
Puerto Rican Bullfinch*	0.39 \pm 0.07 (7.2)	0.11 \pm 0.04 (3.7)	0.21 \pm 0.07 (5.2)
Greater Antillean Oriole	0	0	0.07 \pm 0.06 (1.74)
Total birds recorded	402	164	230
Number of point counts	75	55	57

* $p < 0.05$

1999 and 2000. These species may have dispersed in search of appropriate habitat outside the forest reserve, as occurred with strict frugivores in Jamaica after the passage of Hurricane Gilbert (Wunderle et al. 1992). In contrast, the Puerto Rican Tanager, a frugivore that complements its diet with a high proportion of invertebrate prey (Waide 1996), was able to rapidly increase its abundance after an initial post-hurricane decline.

The Ruddy Quail-Dove was probably the species most affected by the hurricane. After being one of the five most abundant species captured in mist nets before Hurricane Georges, only one quail-dove was mist netted in Maricao afterwards, but its weight was below the mean for the species (98 g vs. 137.5 g, $n = 3$ in July 1998, Tossas unpubl. data), suggesting difficulty in finding sufficient food resources. Previous studies have

indicated that *Geotrygon* spp. are especially susceptible to post-hurricane declines. In the El Verde rain forest in northeastern Puerto Rico, Ruddy Quail-Doves disappeared for over a year and a half following defoliation by Hurricane Hugo (Wunderle 1995). Similarly, Bridled Quail-Doves (*G. mystacea*) disappeared from a moist forest patch on St. Croix following defoliation by the same hurricane (Wauer and Wunderle 1992).

Point count surveys show declines in insectivorous species (Puerto Rican Woodpecker, Black-whiskered Vireo, Puerto Rican Vireo, Puerto Rican Pewee), including significant declines for the Puerto Rican Tody. Since previous studies have shown that the insectivorous guild is the less affected by hurricanes (Wiley and Wunderle 1993; Wunderle et al. 1992), their decline may have been caused by habitat changes

rather than to lack of prey. Habitat characteristics, such as microclimate or availability of foraging substrates (i.e., trunks, branches, foliage), may have been altered as a result of the canopy opening.

One of the species reported in this study, the White-winged Dove, was first found in Maricao State Forest five months following Hurricane Georges (Tossas and Delannoy 2001). This granivorous species prefers scrubland habitats and pastures interspersed with trees in coastal and urban areas (Raffaele et al. 1998). Previous to Georges it was only found in disturbed habitats around the forest reserve. It appears that forest structure changes caused by Hurricane Georges benefited this species. Similarly, in El Verde the seed-eating Black-faced Grassquit was only captured in mist nets after Hurricane Hugo following an invasion of grasses in forest gaps (Waide 1991).

According to Wunderle (1995), capture rates in El Verde returned to baseline levels within 198 days and point count detections showed no overall increases or decreases after Hurricane Hugo. However, in the present study the relative abundance of most bird species recorded in point count surveys (17/21 species, excluding two new species reported after the hurricane) were not recovered 22 months after the hurricane. Dissimilarities in recovery between the two sites could be related to stronger physical properties of Hurricane Georges or to the fact that Maricao was spared by hurricanes for several decades. Alternatively, the Maricao study area, being over 200 m higher than El Verde, could have gone through a slower recovery process characteristic of forests at high elevations (Weaver 1986) thus affecting its associated bird species. In Jamaica, Wunderle et al. (1992) found that new leaves were produced just several weeks after the passage of Hurricane Gilbert in lowland habitats in contrast to montane habitats which were still defoliated four months later. The authors also found that bird populations in montane habitats suffered more severe hurricane impacts than in the lowlands.

The slow recovery rates of Maricao's avifauna and the disappearance or population

declines of some of its common species after the passage of Hurricane Georges suggest that montane populations are highly vulnerable to these natural phenomena. While monitoring of the avian community is needed to understand the long-term consequences, particularly to species depending on plant resources, like nectar, fruits, or seeds, future work should also focus on hurricane effects related to elevation differences.

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APPENDIX

Scientific names of birds detected or captured in Maricao State Forest before and after Hurricane Georges.

Scaly-naped Pigeon (*Columba squamosa*), White-winged Dove (*Zenaida asiatica*), Ruddy Quail-Dove (*Geotrygon montana*), Puerto Rican Lizard-Cuckoo (*Saurothera vieilloti*), Green Mango (*Anthracothorax viridis*), Puerto Rican Emerald (*Chlorostilbon maugaeus*), Puerto Rican Tody (*Todus mexicanus*), Puerto Rican Woodpecker (*Melanerpes portoricensis*), Puerto Rican Pewee (*Contopus portoricensis*), Gray Kingbird (*Tyrannus dominicensis*), Puerto Rican Vireo (*Vireo latimeri*), Black-whiskered Vireo (*Vireo altiloquus*), Red-legged Thrush (*Turdus plumbeus*), Pearly-eyed Thrasher (*Margarops fuscatus*), Elfin Woods Warbler (*Dendroica angelae*), Adelaide's Warbler (*Dendroica adelaidae*), Bananaquit (*Coereba flaveola*), Puerto Rican Tanager (*Nesospingus speculiferus*), Puerto Rican Spindalis (*Spindalis portoricensis*), Antillean Euphonia (*Euphonia musica*), Black-faced Grassquit (*Tiaris bicolor*), Puerto Rican Bullfinch (*Loxigilla portoricensis*), Greater Antillean Oriole (*Icterus dominicensis*).