J. Carib. Ornithol. 21:7-17, 2008

BIRD ABUNDANCE AND SPECIES RICHNESS IN MANGROVE FOREST AT SUGAR BAY, ST. CROIX, US VIRGIN ISLANDS: LONG-TERM COMPARISON BEFORE AND AFTER HURRICANE HUGO

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Abstract: I surveyed landbirds and waterbirds during winter 2002-2003 at the Sugar Bay mangrove forest on St. Croix, U. S. Virgin Islands, to compare pre- and post-hurricane species richness and abundance 13 yr after Hurricane Hugo. The number of Nearctic-Neotropical migrants decreased by half after Hugo, from 16 to eight species and the number of individuals decreased by one order of magnitude. The insectivorous Northern Waterthrush (*Seiurus noveboracensis*), a specialist of mangrove wetlands, declined. This species is recovering more quickly than other Nearctic-Neotropical migrants because it occurs on or near the ground, unlike most migrants and several resident landbirds that require mature forest. The number of resident landbird species was similar before and after the hurricane. However, the number of individuals after Hugo decreased 25%. The number of waterbirds after Hugo increased from four to 19 and the number of individuals increased one order of magnitude. This long-term response to habitat change wrought by destruction of over 90% of the mature mangrove forest (11-15 m high, pre-Hugo) at Sugar Bay has not been documented before in mangrove forests in other parts of the Caribbean.

Key words: abundance, distribution, Hurricane Hugo, management, mangrove forest, Nearctic-Neotropical migrants, resident birds, St. Croix, surveys, U. S. Virgin Islands, waterbirds

Resumen: ABUNDANCIA Y RIQUEZA DE ESPECIES DE AVES DE UN MANGLAR EN SUGAR BAY, ST. CROIX, ISLAS VIRGENES DE EEUU: COMPARACIONES A LARGO PLAZO ANTES Y DESPUÉS DEL HURACAN HUGO. Durante el invierno de 2002-2003, muestre las aves forestales y acuáticas en manglares en Sugar Bay, St. Croix, Islas Vírgenes estadounidenses para comparar la riqueza y abundacia de especies pre y post-huracán luego de 13 años del paso del Huracán Hugo. El número de migrantes neárticos-neotropicales disminuyó a la mitad luego del paso de Hugo, de 16 a ocho especies y el número de individuos disminuyó en un orden de magnitud. La especie insectívora *Seiurus noveboracensis*, un especialista presente en los manglares, disminuyó. Está especie se está recuperando más rápidamente que otros migrantes neárticos-neotropicales debido a que se le encuentra en el suelo o cerca de este, a diferencia de la mayoría de las aves forestales migratorias y muchas especies residentes que requieren de bosques maduros. El número de especies de aves forestales residentes fue similar antes y después del huracán. Sin embargo, el número de individuos disminuyó 25% después de Hugo. El número de especies de aves acuáticas se incrementó de cuatro a 19 después del paso del huracán y el número de individuos se incrementó en un orden de magnitud. La respuesta a largo plazo al cambio de hábitat producto de la destrucción de más de 90% de los manglares maduros (11-15m de altura, antes de Hugo) en Sugar Bay no ha sido documentada antes en manglares en otras partes del Caribe.

Palabras clave: abundancia, distribución, huracán Hugo, manejo, manglar, migrantes neárticos-neotropicales, aves residentes, St. Croix, muestreos, Islas Vírgenes EEUU, aves acuáticas

Résumé : ABONDANCE ET RICHESSE SPÉCIFIQUE DE L'AVIFAUNE D'UNE FORÊT DE MANGROVE À SUGAR BAY, ST. CROIX, ILES VIERGES AMÉRICAINES : ANALYSE TEMPORELLE AVANT ET APRÈS L'OURAGAN HUGO. J'ai étudié l'avifaune terrestre et aquatique dans la forêt de mangrove de Sugar Bay à St. Croix pendant l'hiver 2002-2003, afin de comparer la richesse spécifique et l'abondance pré et post cyclonique 13 ans après l'Ouragan Hugo. Le nombre de migrateurs néarctiques- néotropicaux a diminué de moitié après Hugo, de 16 à 8 espèces et le nombre d'individus a diminué d'un facteur 10. La Paruline des ruisseaux (*Seiurus noveboracensis*), une espèce spécialiste des zones humides des mangroves, a diminué. Cette espèce a récupéré plus rapidement que les autres espèces migratrices car c'est une espèce vivant à terre ou près du sol au contraire de la plupart des migrateurs et de certaines espèces terrestres sédentaires qui ont besoin de forêt mature. Le nombre d'espèces terrestres sédentaires était proche avant et après le cyclone alors que le nombre d'individus a diminué de 25 %. Le nombre d'espèces aquatiques a augmenté après Hugo de 4 à 19 et le nombre d'individus d'un facteur 10. Cette réponse à long terme au changement d'habitat qui résulte de la destruction de plus de 90 % de la forêt de mangrove (hauteur avant Hugo : 11-15 m) observée à Sugar Bay n'avait pas été documentée auparavant ailleurs dans la Caraïbe.

Mots-clés : abondance, distribution, études, gestion, forêt de mangrove, Iles Vierges américaines, migrateurs néarctiques-néotropicaux, oiseaux aquatiqu, oiseaux sédentaires, Ouragan Hugo, St. Croix

Bird abundance and species richness in mangrove forests were generally undersampled in the West Indies (Lack and Lack 1972, Terborgh and Faaborg 1980, Gochfeld 1985, Arendt 1992) before Wunderle and Waide's (1993) survey of numerous islands. In the U. S. Virgin Islands, Robertson (1962) documented eleven species of resident landbirds and five species of Nearctic-Neotropical migrants (Parulidae) in a red mangrove (*Rhizophora mangle*) swamp, probably of high stature (canopy height not given), during winter 1957 on St. John. The abundance and frequency of Nearctic-Neotropical migrants in mangrove forest generally declines with distance from Florida within the Greater Antilles (Wunderle and Waide 1993). However, migrants were numerous in tall mangrove forest in Sugar Bay, St. Croix (Wauer and Sladen 1992), at the eastern fringe of the Greater Antilles, regardless of deleterious anthropogenic habitat change (dredging and filling) in the Salt River Estuary from 1968 to 1975. In mangrove forests of the Greater Antilles, Nearctic-Neotropical migrants species richness and abundance during the non-breeding season is higher in tall forests (11-20 m high) than in low forests <3 m high (Wunderle and Waide 1993).

Most studies of hurricane impacts on avian communities in the West Indies have focused on short-term effects (≤ 1-2 yr) on landbirds (Askins and Ewert 1991, Waide 1991, Wunderle *et al*. 1992, Rivera-Milan 1995, Faaborg *et al*. 2000, Tossas 2006). In St. Croix, roadside survey routes did not adequately cover mangrove habitats (Wauer and Wunderle 1992). In Jamaica, the number of landbirds, including Nearctic-Neotropical migrants in tall mangrove forest, increased with major damage to these forests by Hurricane Gilbert (Wunderle *et al*. 1992). However, long-term effects (>2 yr) of hurricane impacts on birds in mangrove forests have not been assessed, despite the importance of tall mangrove forests for overwintering migrants in the Caribbean (Lack and Lack 1972, Arendt 1992, Wauer and Sladen 1992, Wiley and Wunderle 1993, Wunderle and Waide 1993, 1994, Confer and Holmes 1995, Wallace *et al*. 1996, Murphy *et al*. 1998). Severe structural damage of habitat by hurricanes should reduce species to those capable of using a broad range of microhabitats (Latta and Wunderle 1998, Tossas 2006). Even though mangrove forests in the Greater Antilles are species-poor in resident landbirds (Wunderle and Waide 1993), these species have evolved to use a variety of disturbed habitats and a broad spectrum of vegetative structure types that have facilitated their survival (Robertson 1962, Wauer and Wunderle 1992, Wallace *et al*. 1996). In contrast, migrants are largely forest-dwelling gleaning insectivores that have little dietary overlap with resident landbirds (Robertson 1962, Faaborg and Terborgh 1980, Latta and Wunderle 1998, Steadman *et al*. in press), at least in the U. S. Virgin Islands, so they would be expected to be more constrained foragers, requiring taller mangrove forests. Mature mangrove forests can take over 50 yr to recover following devastation by a major hurricane because taller forests are less resistant to structural damage and require more time for replacement (Brokaw and Walker 1991, Smith *et al*. 1994, Wunderle and Wiley 1996).

In this study I surveyed birds at the Sugar Bay mangrove forest to compare bird abundance and species richness 13 yr after Hurricane Hugo, a category 4 storm (on the Saffir-Simpson scale of 5) in 1989, to surveys conducted 3 yr before the hurricane (Wauer and Sladen 1992). I recorded all species although the focus was on landbirds, particularly Nearctic-Neotropical migrants (cf., Wauer and Sladen 1992). Many factors other than the widespread destruction of foraging and roosting substrates that may influence a change in the short-term status of landbirds (cf., Wunderle *et al*. 1992) should not apply to their long-term status. Following Robertson (1962), Wunderle and Waide (1993), and other sources I postulated the following hypotheses: (1) abundance and species richness of Nearctic-Neotropical migrants at Sugar Bay in 2002-2003 in the low to medium-height mangrove forest should be generally low; (2) migrants generally prefer mature moist forest (including mangrove forest) so they should have a greater proportional decrease after Hugo compared to resident landbirds, which generally prefer or tolerate a variety of habitats; (3) the effects of habitat change on abundance and species richness of many landbirds, especially Nearctic-Neotropical migrants, should be greater than the influence of diet; this includes assessment of whether insectivores declined less than nectarivores and frugivores/granivores in the long-term aftermath of a severe hurricane with outright tree mortality; and (4) abundance and species richness of waterbirds should increase at Sugar Bay.

Methods

Study Site

Before Hurricane Hugo, the closed canopy red mangrove forest at Sugar Bay, St. Croix, was 11-15 m tall (corresponding to tall mangrove forest; Wunderle and Waide 1993) and the black mangroves (*Avicennia germinans*) were 7-10 m (Gladfelter 1988, Wauer and Sladen 1992, B. Gladfelter pers. comm.). Hurricane Hugo snapped trunks or uprooted >90% of the red mangroves and most black mangroves at Sugar Bay on 17-18 September 1989 (Wauer 1990, Wauer and Wunderle 1992, Tobias 1996; see before and after hurricane photographs in Fig. 1 of Wauer and Wunderle 1992). Over 9,000 seedling red mangroves have been planted in Sugar Bay since 1997 (≤1 m high; all black mangrove seedlings died; M. Walsh pers. comm.) to restore this forest in areas where massive mortality occurred. Much of this area in 2002-2003 was characterized by these red mangrove seedlings and open water choked with remnant basal skeletons of dead mangroves, mostly below the surface. The extant mangrove forest (with a semi-open canopy) is restricted to the head of Sugar Bay (mainly black mangroves ≤9 m), with contiguous remnants of riverine forest where Salt River used to flow. A low (3-3.5 m) fragmented fringe of red mangroves also occurs along Sugar Bay which in the northeastern section partially encloses a small (ca. 1 ha) salt pond that is nonetheless contiguous with the mangrove forest and largely open to the bay. Otherwise, only isolated manglars (islets of one or more red mangroves without solid land) occur in Sugar Bay, apart from manglars in the western arm at the Salt River Marina.

Survey Protocols

Wauer and Sladen (1992) conducted their 12 surveys by walking in an area of approximately 6 ha in closed canopy red and black mangrove forest at the head of Sugar Bay. This included the most extensive understory of swamp fern (*Acrostichum danaeifolium*) of ca. four extant sites on St. Croix (see Fig. 34 *in* Imsand and Philibosian 1987; McNair pers. obs.). They conducted their surveys over a 6-month period (October-March) and sampled autumn more than winter. Survey times ranged from 2-2.5 hr. These observers entered their survey area from the main paved highway to the west, and walked across the forest to the northern tip of a narrow (10 m) old diked road which divides the forest along the southeastern side of Sugar Bay (for directions, see Imsand and Philibosian 1987:103-104; for a map, see Fig. 55 in Gladfelter 1988). Wauer and Sladen (1992) did not provide a detailed description of their survey area, nor did they measure the habitat.

I conducted 17 surveys from October to April (at least once a month; more in autumn than winter or spring), duplicating the area search method (Dieni and Jones 2002) used by Wauer and Sladen (1992), by walking in this approximate 6-ha area block they sampled where black mangroves were now ≤9 m tall (corresponding to medium canopy height, 4-10 m; Wunderle and Waide 1993). The tallest red mangroves were ≤ 2.5 m, including some fringing vegetation along the old diked road which also contained low (1-2.5 m) scrub. I enlarged the survey area (to facilitate comparisons to future surveys) to include additional decimated red mangrove forest as well as fringing mangroves along a portion of the salt pond. I accessed the study area by canoe and began the route along these fringing red mangroves near the tip of the northeastern shore of Sugar Bay. I paddled south, with one stop on the sandy berm to examine the salt pond from its northwestern corner, before canoeing farther south and debarking near the northern tip of the old diked road. I then walked south into the tallest extant mangrove forest at the head of Sugar Bay along a meandering trail I created and marked with red flagging. This area was the core of the approximate 6-ha study site of Wauer and Sladen (1992). I retraced this route back to the canoe and returned to Salt River Marina (not included in the survey area because of anthropogenic changes) along the western shoreline, where the route ended at an impacted area where the first break in the fringing mangroves began (Tobias 1996). Total survey time during each visit was similar to the observation periods for Wauer and Sladen (1992), 2-2.5 h (including at least 1.5 h in the approximate core 6-ha area), between 0630-0930 under conditions of no rain and reduced wind (≤ 4 on the Beaufort scale). Thus, I sampled a larger area that included a salt pond over a longer time (April included) with greater effort (17 vs 12 visits) compared to Wauer and Sladen (1992). I also sampled after a hurricane at a site where detectability of landbirds and waterbirds were expected to increase.

Analysis

I examined or allowed for the following potential biases. First, I assessed the potential bias of having a different number of survey visits in 1986-1987 and 2002-2003 by examining accumulation plots for species richness. Species richness on accumulation plots for 1986-1987 compared to 2002-2003 had stabilized for Nearctic-Neotropical migrant landbirds, resident landbirds, waterbirds, and all species by 9 vs 8 visits, 8 vs 10 visits, 6 vs 12 visits, and 9 vs 12 visits, respectively, none greater than the 12 surveys conducted by Wauer and Sladen (1992). Consequently, I used data from all 17 surveys in 2002-2003.

Secondly, differences in detectability among most migrants on the winter range at St. Croix are ordinarily minor (Pashley 1988; also see Wiley and Wunderle 1993). However, detectability of birds before and after a hurricane is an issue in this study because of the change from a tall closed canopy habitat to a shorter, semi-open or open habitat. Increased detectability of landbirds in 2002-2003 would underestimate the severity of declines, as expected, at least for Nearctic-Neotropical migrants. Hence, detectability differences between the two periods and the larger area surveyed after the hurricane that included most extant mangrove forest in Sugar Bay would facilitate the most parsimonious comparison if declines for landbirds (especially Nearctic-Neotropical migrants) occurred after the hurricane. In contrast, increased detectability of waterbirds in 2002-2003 plus the larger area surveyed and inclusion of a salt pond would overestimate an expected increase.

Following Wauer and Wunderle (1992), I categorized species into two classes (waterbirds, landbirds), then divided landbirds into two groups, residents and Nearctic-Neotropical migrants, to assess general trends within these categories. I categorized the Osprey and the Belted Kingfisher (see Table 2 for scientific names) as waterbirds. I categorized the Yellow Warbler as a resident landbird because a resident subspecies (*D. p. cruciana*) is numerous in mangrove forests on St. Croix (following Pashley and Martin 1988 and Askins *et al*. 1992), even though migrant races of the *aestiva* group probably occur there (cf., McNair *et al.* 1999). Finally, each species of Nearctic-Neotropical migrant and resident landbird was categorized according to their preferred diet (using simple foraging guilds) and habitat in the U. S. Virgin Islands (Table 2).

I summed the total number of individuals for each species by category within each survey period (before and after Hugo), even though the data may represent pseudo-replicates, from the raw data presented in Wauer and Sladen (1992) and from my surveys. Counts of unidentified "blue" pigeons (either Scaly-naped or White-crowned) and hummingbirds (either the Green-throated Carib or Antillean Crested Hummingbird) on my surveys were assigned according to the proportion of certain identifications of these two pairs of species. I used chi-square tests with Yates' correction to compare changes in the proportion of species richness of classes and groups before and after Hugo. I used non-parametric Mann-Whitney *U* tests to compare differences in the median relative abundance of all birds, classes, and groups before and after Hugo, as well as each species when sample sizes from each survey period permitted. I also calculated the mean relative abundance of each species for each survey period to qualitatively compare changes in the rank abundance of each species before and after Hugo; using median relative abundance was less useful for all species because of many tied ranks for scarce migrants and waterbirds. Using results from the foregoing analyses and following Wauer and Wunderle (1992), I used a chi-square test with Yates' correction to compare changes in the proportion of migrants and resident landbirds after Hugo (including species detected during only one survey period) that had increased, declined, or showed no change (defined as <20% change in mean relative abundance). I then examined whether these changes were associated with preferred diet or habitat (citations for diet and habitat provided in Table 2).

RESULTS

ALL BIRDS

A total of 54 species were detected over both surveys in the Sugar Bay mangrove forest, including 19 waterbirds and 35 landbirds. Of the latter class, 17 species were residents and 18 were Nearctic-Neotropical migrants. Species richness observed before and after Hurricane Hugo was not significantly different (pre-Hugo: 35 species, post-Hugo: 44 species; $\chi^2 = 0.81$, $P > 0.05$). However, the difference in proportion of waterbirds and landbirds observed before and after the hurricane was highly significant, primarily because of the disparity between the number of waterbirds (pre-Hugo: four waterbirds, 31 landbirds; post-Hugo: 19 waterbirds, 25 landbirds; $\chi^2 = 8.05$, $P < 0.01$). The proportion of Nearctic-Neotropical migrants and resident landbirds observed before and after the hurricane was not significantly different even though twice as many species of migrants occurred in the Sugar Bay mangrove forest before Hurricane Hugo (pre-Hugo: 15 resident, 16 migrant species; post-Hugo: 17 resident, 8 migrant species; $\chi^2 = 1.45$, $P > 0.05$). Ten migrants detected before Hugo were undetected after Hugo. Two migrants detected after Hugo were undetected before Hugo, including the rare Yellow-bellied Sapsucker. Two resident landbirds detected after Hugo were undetected before Hugo, including

Table 1. The median number per survey period of individuals of Nearctic-Neotropical migrants, resident landbirds, all landbirds, waterbirds, and all birds during migration and winter from a pre-hurricane Hugo (1986-1987) survey (12 visits; Wauer and Sladen 1992) and a post-hurricane Hugo (2002-2003) survey (17 visits; this study) in mangrove forest at Sugar Bay, St. Croix, United States Virgin Islands.

	Median Count		Mann-Whitney *U* test	
Class or Group	Pre-Hugo	Post-Hugo	*U*	*P*
Nearctic-Neotropical migrants	27	5	2	<0.001
Resident landbirds	62.5	46	49	0.02
All landbirds	87	54	26	<0.001
Waterbirds	2	31	0	<0.001
All birds	89	83	82.5	0.39

the locally scarce Lesser Antillean Bullfinch.

Median counts of individuals of Nearctic-Neotropical migrants, resident landbirds, all landbirds, and waterbirds during migration and winter in mangrove forest at Sugar Bay were significantly different before and after Hurricane Hugo (Mann-Whitney *U* tests; Table 1); only the comparison of all birds was not significant. The abundance of waterbirds was much greater after the hurricane. Thirteen of 22 (59%) comparisons of changes in abundance for particular species of all birds before and after the hurricane were significantly different (Table 2). Seven of these species declined (three migrants, four resident landbirds), whereas six species increased (three resident landbirds, three waterbirds). Five of the seven landbirds that declined preferred moist forest, whereas all three resident landbirds that increased preferred dry forest and scrub. These ten landbirds represented a variety of preferred diets (Table 2). The proportion of migrants that declined was significantly more than expected after the hurricane, whereas resident landbirds increased or did not change (migrants: 15 declined, three increased/stable; residents: six declined, 11 increased/stable; $\chi^2 = 6.52$, $P < 0.05$). All but four migrants preferred moist forest (including mangrove wetlands) and all were insectivores (Table 2). In contrast, resident landbirds represented a variety of preferred habitats and diets; three species that increased were insectivores whereas four species that increased were frugivores and/or seed-eaters.

Nearctic-Neotropical Migrants

The proportion of individual migrants compared to resident landbirds decreased from 35.6% before Hugo to 11.6% after Hugo. The Northern Waterthrush, which usually occurred on or near the ground, was the most abundant migrant during both survey periods (Table 2). However, it was three times more numerous before the hurricane. Disregarding the Northern Waterthrush, the average number of 20.8 (250/12) migrants per survey before Hugo was 13 times more numerous than the 1.6 (27/17) migrants after Hugo. The three next most abundant species before Hugo, the canopy or mid-canopy dwellers Black-and-white Warbler, Northern Parula, and American Redstart, accounted for 182 of these birds. Only two migrants other than Northern Waterthrush even approached comparable abundance before or after the hurricane. The Prairie Warbler, also three times less numerous after Hugo (and whose decline was almost significant; Table 2), occupied semi-open low scrub to medium high young forest and forest edge. The Hooded Warbler, whose abundance was similar both periods regardless of its large positive change in rank, was restricted to mangrove forest with a dense understory of swamp fern.

Resident Landbirds

The Yellow Warbler and Bananaquit were the two most numerous resident landbirds during both survey periods, with no significant differences in abundance before and after Hurricane Hugo (Table 2). The next two most abundant species before Hugo, Pearly-eyed Thrasher and Scaly-naped Pigeon, both typically most abundant in tall mature forest (Table 2), were three to four times less numerous after Hugo and dropped in rank. The six species that increased in rank after Hugo (and all but one increased in abundance as well) are most abundant in semi-open scrub, low dry forest, and edge habitats. The remaining resident landbirds are

Table 2. Total number, mean (and median) number per visit, rank order of abundance, preferred diet, and preferred habitat of Nearctic-Neotropical migrants, resident landbirds, and waterbirds during migration and winter from a pre-hurricane Hugo (1986-1987) survey (12 visits; Wauer and Sladen 1992) and a post-hurricane Hugo (2002-2003) survey (17 visits; this study) in mangrove forest at Sugar Bay, St. Croix, United States Virgin Islands.

	1986-1987			2002-2003				Mann-Whitney *U* test			
Species	Total number	Number per visit	Rank[a]	Total number	Number per visit	Rank	Change in rank	*U*	*P*	Diet[b]	Habitat[c]
NEARCTIC-NEOTROPICAL MIGRANTS											
Northern Waterthrush *Seiurus noveboracensis*	162	13.5 (12.5)	1	76	4.5 (4)	1	0	18	<0.001	I	M
Black-and-white Warbler *Mniotilta varia*	71	5.9 (5)	2	2	0.1 (0)	5	-3	9.5	<0.001	I	M
Northern Parula *Parula americana*	66	5.5 (4.5)	3	6	0.1 (0)	4	-1	11.5	<0.001	I	M
American Redstart *Setophaga ruticilla*	45	3.8 (3)	4	1	0.06 (0)	7	-3	na	na	I	M
Prairie Warbler *Dendroica discolor*	14	1.2 (1)	5	7	0.4 (0)	3	+2	60.5	0.07	I	D
Cape May Warbler *Dendroica tigrina*	12	1.0 (1)	6	0	0	13.5	-7.5	na	na	I	M
Worm-eating Warbler *Helmitheros vermivorus*	10	0.8 (1)	7	0	0	13.5	-6.5	na	na	I	M
Hooded Warbler *Wilsonia citrina*	7	0.6 (0)	8	9	0.5 (0)	2	+6	92.5	0.67	I	M
Common Yellowthroat *Geothlypis trichas*	6	0.5 (0.5)	9	0	0	13.5	-4.5	na	na	I	M[f]
Blackpoll Warbler *Dendroica striata*	5	0.4 (0)	10	0	0	13.5	-3.5	na	na	I	D
Blue-winged Warbler *Vermivora pinus*	4	0.3 (0)	11.5	0	0	13.5	-2	na	na	I	M
Ovenbird *Seiurus aurocapillus*	4	0.3 (0)	11.5	0	0	13.5	-2	na	na	I	M
Magnolia Warbler *Dendroica magnolia*	2	0.3 (0)	13.5	0	0	13.5	0	na	na	I	M
Yellow-throated Vireo *Vireo flavifrons*	2	0.2 (0)	13.5	0	0	13.5	0	na	na	I	M
Yellow-rumped Warbler *Dendroiica coronata*	1	0.1 (0)	15.5	0	0	13.5	+2	na	na	I	D
Yellow-billed Cuckoo *Coccyzus americanus*	1	0.1 (0)	15.5	0	0	13.5	+2	na	na	I	D
Prothonotary Warbler *Protonotaria citrea*	0	0	17.5	1	0.06 (0)	7	+10.5	na	na	I	M
Yellow-bellied Sapsucker *Sphyrapicus varius*	0	0	17.5	1	0.06 (0)	7	+10.5	na	na	I	M[g]
RESIDENT LANDBIRDS											
Yellow Warbler *Dendroica petechia*	186	15.5 (12)	1	166	9.8 (9)	1	0	77	0.27	I	D[h]
Bananaquit *Coereba flaveola*	123	10.3 (9)	2	153	9.0 (9)	2	0	87	0.51	N	D
Pearly-eyed Thrasher *Allenia fusca*	92	7.7 (8)	3	42	2.5 (2)	6	-3	2.5	<0.001	O (F)[d]	M
Scaly-naped Pigeon *Patagioenas squamosa*	72	6.0 (6)	4	28	1.6 (2)	8	-4	23	<0.001	F	M
Black-faced Grassquit *Tiaris bicolor*	61	5.1 (5.5)	5	9	0.5 (0)	14	-9	24	<0.001	S-F	D
Gray Kingbird *Tyrannus dominicensis*	46	3.8 (4)	6	105	6.2 (5)	3	+3	71	0.17	I	D
Caribbean Elaenia *Elaenia martinica*	45	3.8 (4)	7	99	5.8 (6)	4	+3	42	0.008	F(I)[e]	D
Zenaida Dove *Zenaida aurita*	42	3.5 (4)	8	44	2.6 (1)	5	+3	60.5	0.07	S-F	D
Antillean Crested Hummingbird *Orthorhyncus cristatus*	23	1.9 (2)	9	13	0.8 (0)	13	-4	46	0.01	N	D
Black-whiskered Vireo *Vireo altiloquus*	15	1.3 (1)	10	23	1.4 (1)	11	-1	101.5	0.98	I	M[i]
Green-throated Carib *Eulampis holosericeus*	13	1.1 (1)	11	17	1.0 (1)	12	-1	99	0.89	N	D
White-crowned Pigeon *Patagioenas leucocephala*	12	1.0 (0)	12	24	1.4 (1)	10	+2	65.5	0.11	F	D

Table 2 continued.

Mangrove Cuckoo *Coccyzus minor*	9	0.8 (0.5)	13	34	2.0 (2)	7	+6	51	<0.001	I	D
Common Ground-Dove *Columbina passerina*	4	0.3 (0)	14	26	1.5 (2)	9	+5	56	<0.001	S-F	D
Northern Mockingbird *Mimus polyglottos*	1	0.1 (0)	15	3	0.2 (0)	15	0	na	<0.001	F	D
Red-tailed Hawk *Buteo jamaicensis*	0	0	16.5	1	0.06 (2)	16.5	0	na	na	R	M
Lesser Antillean Bullfinch *Loxigilla noctis*	0	0	16.5	1	0.06 (0)	16.5	0	na	na	F-S	D
WATERBIRDS											
Green Heron *Butorides virescens*	13	1.1 (1)	1	58	3.4 (3)	3	-2	23.5	na		
Spotted Sandpiper *Actitis macularia*	6	0.5 (0)	2	42	2.5 (2)	5.5	-3.5	19.5	na		
Belted Kingfisher *Ceryle alcyon*	4	0.3 (0)	3	28	1.6 (2)	8.5	-5.5	20	na		
Least Sandpiper *Calidris minutilla*	2	0.2 (0)	4	29	1.7 (0)	7	-3	na	na		
Little Blue Heron *Egretta caerulea*	0	0	12	104	6.1 (6)	1	+11	na	na		
Great Egret *Ardea alba*	0	0	12	83	4.9 (4)	2	+10	na	na		
Snowy Egret *Egretta thula*	0	0	12	51	3.0 (2)	4	+8	na	na		
Lesser Yellowlegs *Tringa flavipes*	0	0	12	42	2.5 (1)	5.5	+6.5	na	na		
Greater Yellowlegs *Tringa melanoleuca*	0	0	12	28	1.6 (1)	8.5	+3.5	na	na		
White-cheeked Pintail *Anas bahamensis*	0	0	12	15	0.9 (1)	10	+2	na	na		
Tricolored Heron *Egretta tricolor*	0	0	12	12	0.7 (1)	11	+1	na	na		
Great Blue Heron *Ardea herodias*	0	0	12	11	0.6 (1)	12	0	na	na		
Osprey *Pandion haliaetus*	0	0	12	9	0.5 (1)	13	-1	na	na		
Yellow-crowned Night-Heron *Nyctanassa violacea*	0	0	12	6	0.4 (0)	14	-2	na	na		
Semipalmated Plover *Charadrius semipalmatus*	0	0	12	4	0.2 (0)	15.5	-3.5	na	na		
Short-billed Dowitcher *Limnodromus scolopaceus*	0	0	12	4	0.2 (0)	15.5	-3.5	na	na		
Wilson's Snipe *Gallinago delicata*	0	0	12	3	0.2 (0)	17	-5	na	na		
Brown Pelican *Pelecanus occidentalis*	0	0	12	1	0.06 (0)	18.5	-6.5	na	na		
Cattle Egret *Bubulcus ibis*	0	0	12	1	0.06 (0)	18.5	-6.5	na	na		

[a]Rank is based on the mean (not median) number per visit, but Mann-Whitney *U* tests are based on comparisons of median counts (see text).

[b]Preferred diet categories are: F = fruit, I = insects, N = nectar, O = omnivorous, R = raptor, S = seeds (from Faaborg and Terborgh 1980, Askins and Ewert 1991, Wauer and Wunderle 1992).

[c]Preferred habitat categories for landbirds (none listed for waterbirds) are: D = dry forest and scrub, M = moist forest, including mangrove forest (from Robertson 1962, Askins and Ewert 1991, Arendt *et al*. 1992, Askins *et al*. 1992, Wunderle and Waide 1993, 1994, Steadman *et al*. in press, McNair pers. obs.).

[d]Pearly-eyed Thrasher is classified as a frugivore by Faaborg *et al*. (2000).

[e]Caribbean Elaenia regularly eats insects as well as fruits. Classified as an insectivore by Faaborg *et al*. (2000), which may be more appropriate in mangrove wetlands where fruits are generally scarce.

[f]Common Yellowthroat is usually more abundant in mangrove wetlands (though not in mature forest) than in other habitats in the Greater Antilles (Wunderle and Waide 1993), although this species is an infrequent winter resident in the U. S. Virgin Islands (Pashley 1988) where on St. Croix most occurrences have been at freshwater wetlands (McNair *et al*. 2006).

[g]Yellow-bellied Sapsucker in the Greater Antilles and the Bahamas occurs most frequently in mangrove forest (Wunderle and Waide 1993, 1994, McNair *et al*. 2006).

[h]Yellow Warbler is most numerous in mangrove wetlands, though otherwise also numerous in scrub but scarce in moist forest.

[i]Black-whiskered Vireo is an intra-tropical migrant primarily restricted to mangrove forest during the winter, when it is generally scarce on St. Croix.

a rather heterogeneous assemblage although the Black-faced Grassquit, the fifth ranked species before Hugo, decreased nine ranks after Hugo, comparable to its tenfold decrease in abundance. Including all species, the average number of 62 (744/12) residents per survey before Hugo was 25% greater than the 46.4 (788/17) birds after Hugo.

WATERBIRDS

All four waterbirds detected before Hugo (Green Heron, Spotted Sandpiper, Belted Kingfisher, and Least Sandpiper) were among the top nine ranked species after Hugo. Including the Green Heron, which tripled in abundance, three new ardeiids including the top-ranked Little Blue Heron as well as the Great and Snowy egrets were the most numerous species after Hugo (Table 2). The other three pre-Hugo species also increased in abundance, but decreased in rank. Two new sandpiper species, Lesser Yellowlegs and Greater Yellowlegs, were also among the top nine ranked species after Hugo. The remaining 10 waterbirds after Hugo represent five orders of birds, including three new orders. The average number of 31.2 (531/17) waterbirds per survey after Hugo was 15 times greater than the average of 2.1 (25/12) birds before Hugo.

DISCUSSION

Hurricane effects on waterbirds other than seabirds, especially in the Caribbean, have been less well documented than effects on landbirds (Wiley and Wunderle 1993). In spite of sampling differences between pre- and post-Hugo surveys at Sugar Bay, which included the number of surveys, area size, and inclusion of the small salt pond, these sampling differences were not important because of strong responses in the composition and abundance of waterbirds relative to habitat change 13 yr after Hurricane Hugo. Waterbird abundance and species richness was overestimated, but one magnitude of difference in abundance and a four-fold increase in species richness is too great a difference to be explained by a modest increase in area size, inclusion of a small salt pond, and an increase in detectability. Three species (White-cheeked Pintail, Brown Pelican, and Semipalmated Plover) on post-Hugo surveys were confined to the small salt pond, but many individuals of the other 16 waterbirds foraged or roosted within the original survey area of Wauer and Sladen (1992), including formerly closed forest now an open devastated area replanted with red mangroves where ardeiids and shorebirds were particularly numerous. None of the waterbirds are in danger of local extirpation because they occur at many other sites on St. Croix.

In contrast, differences in detectability of small landbirds in a formerly intact mature mangrove forest and in a largely semi-open swamp where most of the trees have been knocked down would favor a larger proportion of detections after Hurricane Hugo. Regardless, this study is the first to document long-term post-hurricane changes (decline) in species abundance and composition on the order of one magnitude for Nearctic-Neotropical migrants. Nearctic-Neotropical migrants such as the Northern Parula, Black-and-white Warbler, and American Redstart have barely begun their subsequent long-term recovery to pre-Hurricane Hugo population levels at Sugar Bay, even though they are still numerous in moist forest at nearby St. John (Steadman *et al*. in press). Even the Northern Waterthrush, a highly specialized warbler that is primarily restricted to mangrove wetlands (Wunderle and Waide 1993), was considerably less numerous after the hurricane. The direction and magnitude of changes in species composition and abundance post-Hugo in the mangrove forest at Sugar Bay were generally consistent with long-term expectations based on habitat preferences described in Wunderle and Waide (1993). The greater amount of taller, bare woody substrates for foraging and roosting immediately following Hurricane Hugo, before their later collapse from long-term decay, suggest that long-term population changes have been more pronounced than short-term changes following the later simplification of habitat structure and presumed decrease in the food base. Furthermore, even though insectivores are less likely to decline from short-term effects of severe hurricanes than nectarivores or frugivores and seedeaters (Wauer and Wunderle 1992), migrant insectivores (and a few residents) had similar long-term declines because of the devastated habitat. Hurricane Hugo at Sugar Bay not only reduced mangrove forest height, but also fragmented and reduced the length of fringing mangroves.

Resident landbirds were also less abundant after Hurricane Hugo, so differences in detectability did not significantly bias the results at Sugar Bay. However, most resident landbirds are generalist foragers across a broad range of microhabitats, so their decline was modest and a few species even increased (cf., Tejeda-Cruz and Sutherland 2005). The only anomalous result was the pronounced decrease post-Hugo of the Black-faced Grassquit, which prefers dry early successional habitats and forest edge, and would have been expected to increase (see Askins and Ewert 1991). The Smooth-billed Ani is the only resident landbird that regularly occurs in mangrove wetlands, in both the northern Virgin Islands (Robertson 1962) and on St. Croix (McNair pers. obs.), that did not occur at Sugar Bay either pre- or post-Hugo, even though the setback to an earlier successional stage could have favored its occurrence post-Hugo.

Wunderle *et al*. (1992) assessed short-term population changes of resident landbirds or migrants in Jamaica following Hurricane Gilbert, but I was unable to do so at Sugar Bay. An influx of birds, foraging at ground level by canopy dwellers, and increased detectability before departure of birds from mangrove forests contributed to short-term population increases in Jamaica (Wunderle *et al.* 1992). Thus, severe hurricanes may have short- and long-term effects on local avifauna in mangrove forests, exacerbated by slow recovery of habitats and anthropogenic habitat destruction and degradation. Since a severe hurricane may pass over an island approximately once every 70 yr (Neumann *et al*. 1993; also see Wiley and Wunderle 1993), these large-scale disturbances may affect local avian biodiversity in Caribbean mangrove forests.

The impact of loss of mature mangrove forest at Sugar Bay through natural causes such as severe hurricanes, from which they recover slowly, is magnified by anthropogenic loss of mangrove wetlands on St. Croix. Sugar Bay was the only tall mangrove forest on St. Croix since the destruction of Krause Lagoon for industrial development in 1962. These losses include Krause Lagoon, formerly the largest mature mangrove site in the U. S. Virgin Islands and one of the largest in the eastern Caribbean, more than half of Southgate Pond (replaced by a marina in the 1970s), and habitat degradation at many other sites, mainly from the 1950s through the 1970s (Scott and Carbonell 1986, Knowles 1997). Thus, the pronounced change in species composition and decline in abundance of migrants (and a few residents) at Sugar Bay 13 yr post-Hugo suggests that their diversity and abundance have declined in mangrove wetlands throughout St. Croix. I have no information on long-term inter-habitat movements because of loss of birds in mangrove forests, although the number of migrants is generally low in other forest habitats on St. Croix (pers. obs.), unlike recovering intact moist forests on St. John (Askins and Ewert 1991, Askins *et al*. 1992, Steadman *et al*. in press). Rather few migrants currently overwinter on St. Croix because of indirect effects from a severe storm, slow recovery of mangrove forests, and anthropogenic habitat destruction and degradation. Hurricanes have rarely struck the few other mature mangrove forests in the eastern Caribbean that have long-term baseline population data on migrant and wintering landbirds such as at Graeme Hall Swamp, Barbados (E. Massiah and M. Frost unpubl. data), where the last hurricane occurred in 1955. Moreover, the Nearctic-Neotropical migrant fauna is depauperate in the Lesser Antilles compared to their status in the Greater Antilles (Terborgh and Faaborg 1980). Nonetheless, my assessment of the significance of the extent of long-term habitat changes on an avian community in tall forest at only one site from the effects of a severe hurricane probably can be extended to avian communities at many other mangrove sites throughout the eastern Caribbean.

Acknowledgments

I thank R. A. Askins, D. N. Ewert, and J. Faaborg for reviewing a penultimate draft of this manuscript, and O. Komar and J. M. Wunderle, Jr. for reviewing the submitted manuscript. I also thank F. W. Sladen for supplying information on his study site at Sugar Bay, C. Cramer-Burke of the St. Croix Environmental Association for supplying information on mangrove restoration at Sugar Bay, the United States Fish and Wildlife Service for partial financial support (Federal Aid Program, Wetlands Conservation and Restoration Project W-15), and Carlos Diaz and Christine Willis for their support. Copies of unpublished manuscripts listed below are available from the author.

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