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SHORT-TERM EFFECTS OF HURRICANE GEORGES ON THE FORAGING BEHAVIOR OF THE PUERTO RICAN TODY *TODUS MEXICANUS*

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Abstract.— It is not fully understood why insectivore populations are not strongly affected after a hurricane compared to the dramatic declines of nectarivores and fruit and seed-eaters. This study documents the short-term effects of Hurricane Georges (which struck Puerto Rico on 21 September 1998) on the foraging behavior of the Puerto Rican Tody (*Todus mexicanus*), a common insectivore. A reduction in the foraging height of the bird was observed, with 87% of todies foraging below the mid-level of the canopy. Also, todies foraged in sites with significantly greater foliage cover than in nearby randomly selected sites. The principal foraging techniques used by the todies did not change from those previously reported during non-hurricane years, but the feeding rate did. By foraging in sites with adequate foliage density, todies were able to use their normal foraging behavior to obtain prey following hurricanes.

Resúmen.—Aún se desconoce las razones por las cuales las poblaciones de aves insectívoras no se encuentran gravemente afectadas luego del paso de un huracán, a diferencia de la dramática disminución observada en las poblaciones de nectarívoros, frugívoros y granívoros. Este estudio documenta el efecto a corto plazo del Huracán Georges (el cual azotó la Isla el 21 de septiembre de 1998) en el comportamiento de forrageo de un insectívoro común en Puerto Rico, el San Pedrito (*Todus mexicanus*). Se observó una reducción en la altura de forrageo del San Pedrito, con un 87% de los individuos forrageando en áreas con mayor densidad foliar en comparación con aquellas áreas analizadas al azar. Las principales técnicas de forrageo utilizadas por el ave luego del huracán fueron las mismas que las utilizadas en años sin huracanes, mientras que el número de intentos de forrageo fue mayor. El estudio demonstró que el San Pedrito no cambió su comportamiento de forrageo. Por lo tanto, el forragear en áreas con una densidad foliar adequada permitió al ave continuar con el mismo comportamiento de forrageo para obtener su presa luego del paso del huracán.

SEVERAL STUDIES HAVE REPORTED the adverse effects of hurricanes on birds (reviewed in Wiley and Wunderle 1993). One of the best-documented patterns after a hurricane has been the dramatic decline in populations of nectarivores, frugivores, and granivore species, caused by the loss of food supplies and foraging substrates. In contrast, insectivores are less likely to show population declines. It is not fully understood, however, why insectivores are not strongly affected, although the resiliency of insect populations to disturbance has been mentioned as a possible explanation (Wiley and Wunderle 1993). Some evidence suggests diet shifts in insectivores (Waide 1991), as well as changes in foraging behavior following storms (Wunderle 1995); but the evidence is not as strong for insectivores as for

frugivores (Pérez-Rivera 1991).

This study documents the short-term effects of Hurricane Georges (which struck the Puerto Rico on 21 September 1998) on the foraging behavior, including shifts in foraging sites, of the Puerto Rican Tody (*Todus mexicanus*), a common and widespread endemic bird in Puerto Rico (Raffaele *et al*. 1998). The tody is an insectivore, its diet consisting of small insects which it captures from different substrates. In the Luquillo Mountains the highest tody densities occur below 500 m of elevation in the tabonuco forest type (Kepler 1977).

STUDY SITE AND METHODS

This study was conducted from 6 November through 2 December 1998, six and a half weeks after Hurricane Georges, along the Big Tree Trail in the Luquillo Experimental Forest. The trail is within the tabonuco forest type (*Dacryodes excelsa*), at aproximately 400 m of elevation, and was one of the most heavily damaged sites. Despite the extensive forest canopy loss, trees of more than 20 m in height remained standing.

My sampling technique involved walking along the trail until a bird was encountered. If the bird was observed foraging, I recorded information on canopy height and the bird's foraging height, foraging techniques, and number of seconds between foray attempts in a two-minute sequence. The canopy and bird's foraging height were visually estimated. Foraging techniques were classified as leaf-feeding, air-feeding, or miscellaneous using all the foraging maneuvers made by a bird in a two-minute sequence. Feeding rate per minute (all feeding attempts made by the bird in a two-minute sequence) was described using a portable tape recorder. The information was later transcribed and an average was calculated for each sequence. For the microhabitat analysis, I used the site of the second foraging movement in the two-minute sequence. A spherical densiometer was used to determine canopy cover at each of the four cardinal directions at this site. Each foraging site was compared to a random site at a random distance and direction obtained from a table of random numbers. The random distances were less than 50 m from the foraging site. Distance was measured using a hip chain. I compared my results with those reported by Kepler (1977), using a paired *t*-test and a *G*-statistic (Ott 1993). The standard error was used to describe variation around the mean.

RESULTS

The average height at which Puerto Rican Todies foraged was 4.5 $\pm$ 0.82 m (median 3.0, $N = 23$). The average maximum canopy height at foraging sites was 14.4 $\pm$ 0.93 m. Some todies were observed foraging at great canopy heights in trees moderately damaged by the hurricane winds, but most were at 31.09 $\pm$ 0.05% of the tree height. Kepler (1977) reported an average foraging height of 4.7 m (N = 2187) during non-hurricane years. I observed no significant difference for the bird's foraging height after the hurricane, Kepler's value falls between two S.E. of the mean value I observed. Of 59 foraging maneuvers, 86.4% consisted of leaf-feeding, and 8.5% air-feeding. The remaining 5.1% consisted of miscellaneous foraging techniques, such as tree trunk snapping. The proportions of foraging techniques used after the hurricane did not significantly differ (G = 0.02, d.f.=1, P>0.05) from those found by Kepler (1977) in 698 observations, which included 86.8% leaf-feeding, 8.0% air-feeding and 5.2% miscellaneous. I observed an average post-hurricane feeding rate of 1.6 $\pm$ 0.23/min (N = 18), which was significantly higher than that reported by Kepler (1.0/min; N = 670; i. e., Kepler's value falls outside two S.E. of the mean value I observed). After the hurricane, todies foraged in sites with significantly greater foliage cover (43.4 $\pm$ 4.4%) than in nearby randomly selected sites (35.2 $\pm$ 3.5%; Paired t = 2.47, d.f. = 21, P = 0.02).

DISCUSSION

Previous studies have reported an increase in net capture rates of todies shortly after a hurricane (Waide 1991, Wunderle 1995). This general increase in capture rate is attributed to a post-hurricane reduction in foraging height that made birds more susceptible to capture in mist nets. My results showed a reduction in the foraging height of the Puerto Rican Tody after Hurricane Georges, with 87% of todies foraging below the mid-level of the canopy height. Because todies forage where there are leaves, regardless of height above ground, the reduction in its foraging height allowed the bird to forage more frequently near the ground where foraging substrate remained. This flexibility undoubtedly contributes to post-hurricane survival.

Foraging site shifts also involve limiting activities to less-damaged areas. For some species this could involve expanding their home range size to

forage over a greater area, as observed in Puerto Rican Parrots (*Amazona vittata*) after Hurricane Hugo (1989), whereas for others it could involve more foraging within the original home range (Wiley and Wunderle 1993). The microhabitat analysis demonstrated that Puerto Rican Todies used the less-damaged areas as foraging sites after the hurricane. The average canopy cover at the bird's foraging sites were significantly higher than in the randomly selected sites. It is likely that todies remained in their original territory after the hurricane. This could be because the post-hurricane distribution of insect prey may be more predictable, or at least less clumped, than flowers, fruits, and seeds. Despite the low density of vegetation remaining after the hurricane, the local movement to less-damaged strata allowed the todies to find and capture their food without changing their usual feeding methods.

The principal foraging techniques used by the todies are leaf-feeding and air-feeding (Kepler 1977), both of which I observed after Hurricane Georges. Leaf-feeding involves flying up to the leaf to capture insects from upper or lower surface, usually in a single movement. In the air-feeding technique the tody sallies up and out in the air to catch a flying insect. Kepler (1977) found seasonal differences in these two principal feeding techniques used by the todies in the Luquillo rainforest. She observed that todies air-feed mostly during the spring when insects density is greatest, whereas they only leaf-feed during summer and autumn. Despite the increase in flying insects documented after hurricanes (Wolcott 1932, Torres 1992), the todies were using the same feeding method as reported by Kepler (1977) for September: leaf-feeding. Because I did not obtain any specific dietary information, I do not know if todies were feeding on the Order Diptera, including those from the Family Simuliidae (Kepler 1977), which became common after the hurricane (Silverio Medina, pers. com.; pers. obs.). The abundance of some insects after the hurricane could also account for the increase in the Puerto Rican Tody's feeding rate.

This study demonstrated that the Puerto Rican Tody did not show major changes in its foraging behavior after the passage of Hurricane Georges. Thus, by foraging in sites with adequate foliage cover, todies may not need to shift foraging behavior to obtain adequate insect prey following hurricanes.

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