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BREEDING AND NATAL DISPERSAL IN THE PUERTO RICAN VIREO

BETHANY L. WOODWORTH[1]
Department of Ecology, Evolution and Behavior
University of Minnesota
St. Paul, Minnesota 55108 USA

JOHN FAABORG
Division of Biological Sciences
University of Missouri
Columbia, Missouri 65211 USA

WAYNE J. ARENDT
International Institute of Tropical Forestry
P.O. Box B
Palmer, Puerto Rico 00721 USA

Abstract.—Information on dispersal is critical for understanding the population dynamics of birds. We estimated breeding and natal dispersal in two studies of a population of the Puerto Rican Vireo (*Vireo latimeri*) that is in danger of local extirpation due to low reproductive success. From 7.1–29% of adult males and 12.5–25% of adult females changed territories between breeding seasons. The median breeding dispersal distance of 12 birds (7 males, 2 females, and 3 of unknown sex) was 370 m (range 110–560 m). Four fledglings dispersed a median distance of 490 m from their natal nests to breeding territories (range 300–2030 m). The implications of these data for population trends of the vireo in Guánica Forest are discussed.

DISPERSIÓN REPRODUCTIVA Y NATAL EN *VIREO LATIMERI*

Sinopsis.—La información sobre el patrón de dispersión de un ave es crítica para entender la dinámica poblacional de la especie. Estimamos la dispersión reproductiva y natal del Bienteveo (*Vireo latimeri*) en dos estudios poblaciónales que se llevaron a cabo en el Bosque de Guánica, Puerto Rico. Esta población está en peligro de extinción debido al bajo éxito reproductivo de la misma. El 7.1–29% de los machos adultos y el 12.5–25% de las hembras adultas cambiaron de territorio entre épocas de reproducción. La dispersión reproductiva promedio de 12 individuos (7 machos, 2 hembras y 3 de sexo desconocido) fue de 370 m (alcance 110–560 m). Cuatro volantones tuvieron una dispersión promedio, del lugar en donde nacieron, de 490 m (alcance 300–2030 m). Se discute en el trabajo las implicaciones de estos resultados.

[1] *Current address: Pacific Island Ecosystems Research Center, Biological Resources Div., U.S.G.S., P.O. Box 44, Hawaii National Park, Hawaii 96718 USA.*

The Puerto Rican Vireo (*Vireo latimeri*) is a small (11–12 g) foliage-gleaning insectivore (Cruz and Delannoy 1984, Wetmore 1916) endemic to the island of Puerto Rico (Bond 1956). Long-term monitoring in Guánica Forest, Puerto Rico's largest dry forest reserve, has shown a gradual decline in numbers during 1973–1989, with a more precipitous decline during 1989 to the present (Faaborg et al. 1997). Additionally, reproductive success of this vireo in Guánica in recent years has been low, due to high rates of brood parasitism by the introduced Shiny Cowbird (*Molothrus bonariensis*) and high rates of nest predation (Woodworth 1997). A population dynamics model for the species indicates that, as a result of cowbird parasitism, the vireo population in Guánica Forest has become a "sink" population (Pulliam 1988, Woodworth, in press). The prospects for continued existence of this population depend in part on the ability of the Puerto Rican Vireo to disperse long distances from areas of greater reproductive success ("source" populations). The coupling of two studies, one a long-term mist-net study (1973–present) and the other a demographic study of color-marked individuals (1990–93), provides the first published information available on the frequency and distances of natal and breeding dispersal in the Puerto Rican Vireo.

METHODS

Guánica Commonwealth Forest Reserve (17°55'N, 67°05'W) is a 4015-ha dry subtropical forest on the southwestern coast of Puerto Rico. In the eastern tract where these studies took place, the upland forest includes scrub, deciduous, and semi-evergreen associations. A detailed description of the vegetation and bird communities can be found in Terborgh and Faaborg (1973) and Woodworth (1995). Rainfall is variable, with an average of 860 mm falling annually in a bimodal pattern: a short rainy season April–May, and heavy rains from August–November, with almost no rainfall from December–February (Murphy and Lugo 1986). Puerto Rican Vireos generally breed from April–July, depending upon rainfall (Woodworth 1997).

We collected data during a long-term mist-net study and a 4-yr demographic study of color-marked individuals. The long-term mist-net study (Faaborg and Arendt 1995) has been conducted continuously since 1973, except in 1977 and 1979. One net line was operated from 1973 to present, with 7–8 additional net lines in operation since 1989. At each site, 16 mist nets (36-mm mesh, 12-mm long, and 2.6-m high) were placed along trails end-to-end. The length of each line was approximately the same as the average Puerto Rican Vireo territory (200 m; B. L. Woodworth, unpubl. data). The net in which each bird was captured was recorded so that each bird's capture site was known to within 12 m. Net lines were operated from dawn to dusk for three consecutive days in January or February each year.

The demographic study (Woodworth 1997) was conducted from 1990–1993 on four 50-ha study areas. Study areas encompassed the locations of four of the long-term net lines, and were within 500 m of four of the

other lines. Birds were captured and color-banded by luring territorial males or pairs into nets using recorded vireo song. Territorial boundaries were determined by recording all sightings of color-marked birds, nests, song perches, boundary disputes, and territorial response to playback on 1:2500-scale maps. Observations of color-marked birds outside of their defended area, or in areas known to be defended by other birds, were excluded. From 10–42 vireo territories were under observation each year. Twice each season we surveyed all habitat within 300 m of the study area boundaries using playback, to search for dispersed birds.

We defined breeding dispersal as movement of individuals between successive breeding sites (Greenwood and Harvey 1982). Because Puerto Rican Vireos build several nests in a single season within a single territory, we considered the breeding site to be the territory (Class A territories, Nice 1941). Because no case of within-season breeding dispersal was recorded during the demographic study, we consider only between-season breeding dispersal here. We counted the number of opportunities for a bird to disperse as the number of years elapsing between capture and recapture. If a bird was present on the study area for two consecutive years, it was considered to have had one opportunity to disperse. If present on the study area for three years, it was judged to have had two opportunities, and so on.

Using data from the two studies, we estimated breeding dispersal in three ways:

Mist-netting study.—Capture-recapture data from the mist-net study were examined for evidence of movement. A bird recaptured in the net line in which it was originally banded was assumed to have remained on its original territory, and if captured in a different net line was assumed to have moved. Dispersal distances were measured as the distance between capture and recapture sites. Dispersing birds are unlikely to be recaptured in the net lines, and so this estimate is expected to underestimate dispersal.

Mist-netting and relocation on territory.—We examined movements of birds originally captured in the mist-net study and recaptured on territory during the demographic study. For this analysis, we considered a bird to have remained on its original territory if its territory boundaries at the time of relocation included the site where it was originally banded. Dispersal distances were measured as the distance between the original banding site and the geometric center of its new territory. In this analysis, birds originally captured during extra-territorial forays will have been wrongly judged as dispersing, and so this sample will tend to overestimate breeding dispersal.

Demographic study.—We examined territorial boundaries of color-banded birds present on the study area for two or more breeding seasons. We considered a male to have remained on his previous territory if his territory of one year overlapped his territory of the previous breeding season by at least 80% (following Nolan 1978). Because males are more active in territory maintenance than are females (B. L. Woodworth, unpubl.

data), a female's territory was considered to coincide with that of her mate. In the demographic study, dispersal distances were measured as the distance between the centers of the territories.

We defined natal dispersal as the movement from birth site to first breeding or potential breeding site (Greenwood and Harvey 1982). Natal dispersal is usually measured as the distance between the natal nest and the first breeding nest. We relocated birds marked as nestlings and, because the location of a bird's first breeding nest was often not known, measured the distance from the natal nest to the center of the bird's first breeding (or potential breeding) territory. Because of the extremely low rate of reproductive success in this population, data were available on only four birds marked as fledglings.

In studies covering a finite study area, bias exists in the distribution of recorded dispersal distances because birds dispersing long distances are less likely to be detected by the investigator (Barrowclough 1978). It is possible to correct for this bias, but sample size was too low to do so in this study.

RESULTS

From 1973–1996, 135 AHY Puerto Rican Vireos were banded as part of the mist-net study, and 42 (31%) were recaptured at least once in a later year. We also studied two birds banded in a separate study in the early 1980s (J. Colon, pers. comm.). Twenty-five of these vireos were recaptured on their territories during the demographic study. Finally, from 1990–1993, 78 vireos were color-banded as part of the demographic study, and 25 were followed in two or more breeding seasons.

Between-year breeding dispersal of males ranged from 10–29% (5–11% of between-year opportunities) and of females ranged from 13–25% (9–10% of between-year opportunities) (Table 1). Median breeding dispersal distance of 12 birds (7 males, 2 females, and 3 of unknown sex) was 370 m (range 110–560 m). Four males recaptured 8–12 yr after initial banding were still resident within 500 m of their original banding sites.

In the demographic study, none of 5 males present in the study area for 2 yr changed territories; 2 of 15 birds present for 3 yr changed territories; and 1 bird remained on territory for 4 yr. In both instances of dispersal, males moved to an adjacent territory upon death or disappearance of a neighbor, and so dispersal distances were small (Table 1). Of four females color-banded in 1990–1991, one was resident on her territory for 3 yr, and two remained for 4 yr. One female moved to an adjacent territory after her first breeding season. On four occasions, a marked female's mate disappeared; in each case, the female remained and subsequently paired with the new territory owner. In no case did a male with a mated female move, so we could not examine the relative importance of mate versus site fidelity in females.

Ten vireos were color-banded as fledglings during the demographic study. Of these, four were relocated in the breeding season following their

TABLE 1. Breeding dispersal frequency and distance of Puerto Rican Vireos in Guánica Forest, Puerto Rico, as determined from three sampling techniques. Sampling techniques are described in detail in the text.

	Sampling technique and sex				
	Mist-netting study[a]	Mist-netting and recapture on territory[b]		Demographic study[c]	
Parameter	Both	Males	Females	Males	Females
No. birds recaptured	42	17	8	21	4
Median time to recap (yr)	1.0	1.6	0.6	0.75	0.75
No. opportunities to disperse	71	44	11	38	10
No. birds dispersed	3	5	1	2	1
Percent dispersal (per bird)	7.1	29	12.5	9.5	25
Percent dispersal (per opportunity)	4.2	11	9.1	5.3	10
Median distance (m)	380	460	240	120	340
(Range)	(360–480)	(130–560)		(110–130)	

[a] Birds were captured and recaptured in the long-term mist-net study.
[b] Birds were originally captured in the long-term mist-net study, recaptured on their territories using playback, and their territories mapped.
[c] Territories of color-banded birds were spot-mapped.

birth. Their median natal dispersal distance was 490 m (300 m and 2040 m for two females; 410 m and 490 m for two males).

DISCUSSION

Adult Puerto Rican Vireos in Guánica Forest exhibited a relatively low frequency of between-season breeding dispersal. Vireos that did disperse typically remained within two territory widths of their original banding site. Puerto Rican Vireo pairs are resident on, and defensive of, their territories throughout the year (B. L. Woodworth, unpubl. data). Tropical birds that are resident year-round on their breeding territory may be expected to exhibit higher site-fidelity than breeding migrants, because permanent residents do not have to re-establish territorial boundaries each spring. In the migrant Prairie Warbler (*Dendroica discolor*), Nolan (1978) found that 22% of returning males, and 90% of returning females, changed territories between breeding seasons. Likewise, 60% of male Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*, Beletsky and Orians 1994) and 94% of male Great Reed Warblers (*Acrocephalus arundinaceus*, Bensch and Hasselquist 1991) dispersed between breeding seasons. However, some migrants exhibit low rates of breeding dispersal (e.g., 4% of male Eastern Kingbirds, *Tyrannus tyrannus*, Murphy 1996; 5% of ASY male Indigo Buntings, *Passerina cyanea*, Payne and Payne 1993).

A high proportion of banded nestlings was relocated on the study area in subsequent years, reflecting high natal philopatry or high juvenile survival. Resident passerines generally show high natal philopatry as com-

pared to migratory ones (reviewed in Weatherhead and Forbes 1994). Of 11 studies of resident populations, only the isolated population of song sparrows on Mandarte Island had natal philopatry approaching that observed in this study (39.7%, n = 463; Arcese 1989, Smith 1988). In passerines, natal dispersal distance is frequently female-biased, and natal dispersal distances are usually greater than breeding dispersal distances (Greenwood and Harvey 1982). The longest dispersal distance recorded in this study was for a female, banded as a nestling, who was relocated in her second year over 2 km from her natal nest site. However, most young in this study settled within one to three territory widths of their natal nest.

We caution that our estimates of dispersal frequency and dispersal distances were underestimates of the true values. This was because it was impossible to exhaustively search all suitable habitat in Guánica Forest for marked birds, and dispersal outside of the searched areas could not be distinguished from mortality. This limitation is present with all studies of open populations (Pollock et. al 1990). However, adult mortality rates recorded for the Puerto Rican Vireo in Guánica Forest have historically been low (32%, Faaborg and Arendt 1995; 26%, Woodworth 1995), and this suggests that few dispersing birds were missed.

The data suggest that this non-migratory bird does not routinely disperse over long distances, at least within Guánica Forest. This may reflect the fact that a declining population creates available territories in high quality breeding habitat close to current breeding territories or natal sites. In a more saturated population, dispersal distances might be larger. However, if dispersal frequency and distances for Puerto Rican Vireos are typically small, this behavior may accentuate the isolation of the Guánica Forest vireo population. The eastern tract of Guánica Forest is bordered on two sides by ocean, with agricultural fields and residential areas separating it from other possible vireo habitat to the north and east. If the Guánica population is isolated, it will survive only by reproducing enough to replace mortality, which in recent years has not occurred (Woodworth, in press). The data presented here suggest that immigration from distant source populations is not likely to sustain the population in Guánica Forest. The location and extent of potential "source" habitats, and the species' dispersal frequency and distance in saturated habitats, should be priorities for further research.

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