The Wilson Journal of Ornithology 120(3):460–466, 2008

REPRODUCTIVE SUCCESS OF THE PUERTO RICAN VIREO IN A MONTANE HABITAT

ADRIANNE G. TOSSAS[1,2]

ABSTRACT.—I studied the reproductive success of the Puerto Rican Vireo (*Vireo latimeri*) from 1998 to 2000 in Maricao State Forest, a montane reserve in the southwestern part of Puerto Rico. No parasitism by the Shiny Cowbird (*Molothrus bonariensis*) was found but 63% of 38 active nests were depredated with an overall daily nest survival of 0.932 ± 0.007 (± SE). Mean nest survival estimates following Hurricane Georges did not vary significantly before and after the hurricane. However, a return rate of only 39% was estimated for color-marked adults the year including the hurricane compared to 72% for the year without a hurricane. A 26% decline in density of territorial males was observed in the post-hurricane year. *Received 26 May 2007. Accepted 11 November 2007.*

The nesting success of a bird species can vary geographically as a result of differences in abundance of brood parasites, particularly if habitat characteristics favor the parasitic species (Ward and Smith 2000, Purcell 2006). These effects can be exacerbated if the host has not evolved nest defense strategies following recent colonization by the parasitic species (Rothstein 1990). This may be the case of the Puerto Rican Vireo (PRVI; *Vireo latimeri*), which has experienced sharp decreases in population size in Guánica State Forest (henceforth Guánica) on the dry coastal plain in southern Puerto Rico (Faaborg et al. 1997). However, the species is still commonly found throughout the island (Raffaele 1989). The population decline has been mainly associated with high rates (73–83%; Woodworth 1997) of brood parasitism by the Shiny Cowbird (*Molothrus bonariensis*), a species first reported in Guánica by 1969 (Kepler and Kepler 1970), while expanding its range into the Caribbean region from its native distribution in South America (Cruz et al. 1985). The PRVI population in Guánica from 1973 to 1996 showed an average annual decrease of 5% (Faaborg et al. 1997). Mean annual survival estimates for the PRVI in Guánica decreased from 0.68 in 1973–1990 (Faaborg and Arendt 1995) to 0.61 for a longer time period including data through 1996 (Faaborg et al. 1997).

Little is known about the reproductive success of the PRVI and the effects of cowbird parasitism in habitats other than Guánica. Parasitism rates may differ within the island, particularly since the Shiny Cowbird is rare or absent in some habitats. Cowbird parasitism of vireo nests has been found to be less intensive in highly forested montane habitats than in the more fragmented coastal habitats (Cruz et al. 1985, Pérez-Rivera 1986). Pérez-Rivera (1986) reported that 36% of PRVI nests and 35% of Black-whiskered Vireo (*Vireo altiloquus*) nests in the central mountain region were parasitized. In contrast, cowbirds parasitized 87% of the Black-whiskered Vireo nests in coastal forests (Cruz et al. 1985).

The objectives of my study were to examine if the Puerto Rican Vireo was affected by Shiny Cowbird parasitism in Maricao as has been reported in Guánica (Woodworth 1997, 1999; Woodworth et al. 1998, 1999), and to compare the breeding biology between the two populations. The incidental passage of Hurricane Georges through the Maricao study area in September 1998 provided an opportunity to evaluate how reproductive parameters were affected by the natural event. I hypothesized that higher nesting success should occur at Maricao due to the scarcity of cowbirds at this site, compared to Guánica, and that parameters related to the breeding biology of the Puerto Rican Vireo should differ in the years before and after the passage of the hurricane.

METHODS

Study Area.—Maricao (18° 09′ N, 66° 59′ W) is in the western part of the central mountain range of Puerto Rico, 16 km northwest of

[1] Department of Biology, University of Puerto Rico, Río Piedras, Puerto Rico 00931, USA.

[2] Current address: Villas del Río, 1100 Bambú, Mayagüez, Puerto Rico 00681, USA;
e-mail: agtossas@gmail.com

Guánica. It comprises 4,150 ha with elevations ranging from 150 to 875 m (Silander et al. 1986). Annual rainfall and temperature from 1961 to 1990 averaged 232.6 cm and 21.7° C, respectively. The area contains subtropical moist forest, subtropical wet forest, and lower montane wet forest (Ewel and Whitmore 1973). Dominant tree species include *Micropholis chrysophylloides*, *Terebraria resinosa*, *Linociera dominguensis*, *Homalium racemosum*, *Tabebuia schumanniana*, and *Eugenia stahlii* (Silander et al. 1986).

Maricao was struck by Hurricane Georges on 21–22 September 1998. This hurricane (category 3 on Saffir-Simpson scale of 5) damaged the forest structure with sustained winds of 184 kph and gusts of 240 kph (Bennett and Mojica 1998). The strong winds opened the canopy by severe defoliation, tree falls, and stem and branch breakage, all of which affected the resident avifauna (Tossas 2006).

Nest Searching and Monitoring.—Thirty-six adult PRVIs were color-banded from 1998 to 2000 to facilitate behavioral observations. Individuals were lured to mist nets by playing the male's song on a tape recorder near or within their territories. Gender, age, and breeding condition were assigned for captured vireos when possible. Twenty adult vireos were confidently separated by gender, 15 were males and five were females. All captured individuals were marked with a USGS aluminum band and a unique combination of two plastic color bands. At least one member of all pairs studied was color-banded.

Vireo pairs were monitored from March to July each year from 1998 to 2000 along three trails with similar floristic composition and vegetation structure. I followed singing males looking for behavioral cues that could lead to their nests, or pairs carrying nesting material up to ~50 m into the forest on each side of the trails surveyed. Nest contents were examined every 2–5 days for signs of predation, parasitism or nest abandonment. Nests were checked directly or with a mirror fixed to a 6-m pole. Nests were checked when possible from a distance of ~10 m to avoid disturbing breeding pairs, altering the nesting habitat, or increasing the risk of predation. I looked for Shiny Cowbird eggs or chicks in PRVI nests as signs of brood parasitism. Predation was assumed if eggs disappeared before their hatching date. Chicks were considered predated if they disappeared from the area around the nest before the expected fledging date. Incubation and nestling stages are 15 and 12 days, respectively (Woodworth 1997). The dates marking the initiation or end of each stage were assigned by direct observation or by back-dating or forward-dating from other observed events. Nest abandonment was recorded if adults or chicks were not seen in the nest or in the vicinity during three consecutive visits of 30 min each. I noted if abandoned nests included eggs or were empty.

Nest searching in 1999 was limited because of changes in forest structure related to Hurricane Georges and management practices that restricted access to trails. However, I monitored pairs throughout the breeding season and was able to ascertain their productivity even when I did not find the nest structures. Breeding season length was calculated for each study year from the day when the first pair started building a new nest until no active nests were found.

Nest Success.—Daily nest survival rates and standard errors were generated following Mayfield (1975) and Johnson (1979). Estimates were calculated for two nesting intervals separately, from egg laying to incubation, and for the nestling period. An overall estimate was calculated for both intervals combined.

Index of Annual Reproductive Success.—An estimate of annual reproductive success was calculated for all nests built by a pair monitored throughout the entire breeding season. However, only single nests were found for most pairs in 1998 (17/22) and 2000 (11/22), and only three nests were monitored in 1999. Thus, identifying whether a pair had successfully raised chicks was based on observations of juveniles attended by color-marked adults at the end of the breeding season. This method was possible because juvenile PRVIs remain within their natal territories and are fed by adults for as long as 2 months after fledging (pers. obs.).

Territories of color-marked individuals were visited every 2–5 days throughout the breeding season in search of nests, but searches for juveniles were more intensive from June to

July, the final weeks of the breeding season. I played the song of the PRVI in a tape recorder 1–2 times from the center of each territory for 5-min intervals and looked for both members of the pair during visits that lasted from 30 min to 1 hr. Adults usually approached the source of the intruder's song and responded with alarm calls, providing an opportunity to observe accompanying juveniles. Each territory was visited 10–15 times, and 20–22 pairs were monitored each year with at least one member of the pair being observed in every visit.

I calculated the proportion of juveniles attended by adults as an index of annual reproductive success by the end of the breeding season. The index was the mean number of young fledged/pair/year. This method may underestimate reproductive success if chicks were depredated after leaving the nest, if their presence was not detected by being concealed and quiet, or if the brood was split between the pair. However, even with these biases, the index allows comparisons among study years.

Shiny Cowbird Surveys.—I performed 60 point counts with playbacks of the Shiny Cowbird chatter call along the two trails where I did most nest searching. Counts were conducted in June 1998 ($n = 30$) and 1999 ($n = 30$) when PRVIs and most resident bird species were breeding. Fifteen point counts of unlimited radius, 100 m apart, were conducted in each trail. I played the call in the center of each plot for 5 min and waited 5 min for a cowbird aural or visual response. I also carefully looked for indications of cowbird presence during field visits throughout the project.

Return Rates and Territory Mapping.—Marked PRVIs were followed over time to obtain estimates of their return rates (finite survival rate described by Krebs 1989). The annual return rate was estimated as the number of marked adults present in their territories in year t that were recaptured or reobserved in their territories in year $t + 1$. The probability of relocating banded PRVIs using this method is high (Woodworth et al. 1999), although it does not account for individuals that may be alive but not in the sampling area. Thus, adults were assumed to have died or dispersed outside the search area if not observed the following year. The study included 26 adult vireos color-banded in 1998 ($n = 13$) and 1999 ($n = 13$). Males and females were pooled for analysis due to small sample size and inability to differentiate gender of all individuals. Return rates were calculated for two time periods, a year including the hurricane event (1998–1999) and a year without a hurricane (1999–2000). Confidence intervals for return rates were calculated assuming binomial sampling.

Spot maps were prepared for PRVIs along three transects to measure size and density of male territories. I assumed territorial boundaries occurred where males or pairs engaged in aggressive encounters with neighbors and intruders (Bibby et al. 2000). The location of singing males, nests, and movements of individuals also helped delineate territories. The mating status of males was assigned from observations during repeated visits to the territories throughout the breeding season. Unpaired males were excluded from the total density of territorial males (Wenny et al. 1993). All results are presented as mean ($\pm$ SD), except for nest survival rates ($\bar{x} \pm$ SE).

RESULTS

Nest Success.—I found 38 active PRVI nests in Maricao during the breeding seasons of 1998 to 2000. Most were found during nest building or early in the incubation period. All cases of nesting failure (24 of 38 nests) were attributed to predation, resulting in loss of the entire clutch or brood. Average clutch size was 2.03 ± 0.16 eggs (range = 2–3, $n = 38$). Mean nest height was 4.9 ± 1.29 m (range = 2.4–7.0 m, $n = 19$). Breeding seasons lasted 90, 107, and 88 days in 1998 (26 Apr to 24 Jul), 1999 (23 Mar to 15 Jul), and 2000 (14 Apr to 10 Jul), respectively. Nesting activity was not observed after 15 July of any year.

None of the PRVI nests was parasitized by the Shiny Cowbird. Cowbirds were not detected on any of the point counts in the forest interior with or without playbacks. I only had incidental observations of individual cowbirds outside of the study sites, along edges or in disturbed areas such as around the forest headquarters and near the communications antennae and vacation center. I observed single cowbirds on two occasions following Greater Antillean Orioles (*Icterus dominicensis*) at the forest edge and twice observed single cowbirds flying high over the forest canopy.

TABLE 1. Nest survival rates ($\bar{x} \pm$ SE) of the Puerto Rican Vireo in Maricao State Forest, Puerto Rico, 1998–2000.

Year	Nests	Observation days	Daily survival rates[a]		
			Egg laying and incubation	Nestling	Overall (egg laying through nestling)
1998	20	411	0.981 ± 0.008	0.953 ± 0.017	0.935 ± 0.029
1999	2	27	[b]		
2000	16	246	0.951 ± 0.017	0.976 ± 0.017	0.928 ± 0.013
Totals	38	684	0.968 ± 0.008	0.963 ± 0.012	0.932 ± 0.007

[a] Incubation and nestling stages consist of 15 and 12 days, respectively (Woodworth 1997).
[b] Analysis not possible due to small sample size, data added to total.

Fourteen nests were lost during 440 nest-days of incubation and nine nests were lost during 244 days of the nestling stage (Table 1). The probabilities ($\bar{x} \pm$ SE) that a nest would survive 15 days of incubation and 12 days of the nestling stage were 0.62 ± 0.008 and 0.64 ± 0.012, respectively. The probability of survival from incubation to fledging was 40%. Daily survival rates did not differ between the incubation and nestling periods ($\chi^2_1 = 4.08$, $P = 0.25$) or between study years ($\chi^2_3 = 0.05$, $P = 0.83$).

Annual Reproductive Success.—Puerto Rican Vireo pairs in Maricao renested as many as three times in a single season after losses to predation, but most pairs (17/22, based on 1998 data) had a single nest. The percent of successful pairs ranged from 36 in 1998 to 65 in 1999, and was 55% in 2000. None of the pairs had two successful clutches in one season. A total of 40 fledglings was produced by 33 successful pairs ($n = 64$ total pairs) during the 3 years. Successful pairs produced an average (± SD) of 1.21 ± 0.55 fledglings/year, ranging from 1.15 ± 0.55 fledglings/pair in 1999 to 1.25 ± 0.62 fledglings/pair in 2000.

I was able to follow 16 PRVI pairs for more than one breeding season. Most pairs (81%) were successful in at least 1 of the 3 years. Four of the nine pairs I observed during 1998-2000 were successful once, two were successful twice, and three pairs failed to produce fledglings in any year. None of the pairs was successful in all 3 years. Seven pairs were followed in two breeding seasons. Three successfully reared young in both years, while the rest were successful in 1 year. Fifty-one percent of all pairs ($n = 64$ pair years) produced offspring in at least 1 year.

Return Rates and Territory Size.—The return rate ($\bar{x} \pm$ SD) of territorial adults from 1998 to 1999 was 0.39 ± 0.14 ($n = 5/13$; 95% CI = 0.14–0.68). Thirteen individuals marked in 1999 were added to the sample group of five survivors from 1998. The return rate from 1999 to 2000 was 0.72 ± 0.11 ($n = 13/18$; 95% CI = 0.47–0.90). None of the individuals marked in 1998 and missing in the 1999 sampling period was reobserved in 2000.

Mean (± SD) territory size was 0.86 ± 0.20 ha and ranged from 0.56 to 1.08 ha ($n = 9$). I did not observe territory switching in marked individuals. Ninety-one percent of all territorial males (1998–2000) were paired ($n = 69$). This number ranged from 96% in 1998 ($n = 23$) to 87% in 1999 ($n = 23$) and 91% in 2000 ($n = 23$). Density of male territories was 0.57, 0.44, and 0.41/ha, in 1998, 1999, and 2000, respectively.

DISCUSSION

The main difference in nesting success between Maricao and Guánica PRVI populations was related to parasitism rates. Brood parasitism was absent in the montane population, but 73–83% of the nests in the lowland were parasitized by the Shiny Cowbird (Woodworth 1997). The dissimilarity is related to high cowbird abundance in the southern coastal plain where the species is favored by land uses such as agriculture and cattle ranching. Large pastures in the vicinity of the forest reserve in Guánica (S. Molina-Colón, pers. comm.) contrast to only 4% pastures in 19,382 ha surrounding Maricao (Tossas and Thomlinson 2007). The lower and more open structure of the dry forest in Guánica may also facilitate nest searching by cowbirds.

Differences in reproductive success between PRVIs in Maricao and Guánica may be

affecting the amount of effort invested by pairs in nest building and egg-laying. Pairs in Maricao built new nests after a nesting failure but not after a successful nest. However, pairs in Guánica renested as many as six times after previous failures and also had second broods (Woodworth 1997). This behavior may compensate for high rates of nest loss and low reproductive success. Weather condition may be the ultimate factor affecting the number of nesting attempts and population dynamics overall, as extremely dry conditions have been shown to have a direct relationship with bird population declines in Guánica (Faaborg et al. 1984). Woodworth (1997) found the arrival of rains early in 1991 facilitated rapid initiation of breeding behavior by the PRVI in Guánica with increased opportunities for laying second clutches. That year, six pairs that had fledged young by the beginning of June were able to initiate second broods 1–2 weeks later. In addition to higher chances of reproductive success, nests initiated early in the season were less likely to be parasitized (Woodworth 1997).

Maricao and Guánica can be considered the extremes of a gradient differing in elevation above sea level and habitat characteristics, but aspects of the biology of PRVI were similar in both populations. For example, breeding season lengths at Maricao were similar to those observed in Guánica (106 days in 1991, 69 days in 1993; Woodworth 1997). High levels of nest predation were responsible for nest losses at both sites with 63% of nests at Maricao (this study) and 70% of nests at Guánica (Woodworth 1997) lost to predation. These numbers are typical for open-cup understory nests in the Neotropics, as 67% of nests in wet forests in Costa Rica (Skutch 1985), and 62 and 68% of nests in lowland Panama, in 1996 and 1997, respectively (Robinson et al. 2000) were lost to predation.

The identity of predators could not be ascertained in most cases in the present study, but the lack of damage to the nests suggests birds or reptiles were responsible. Snakes (*Alsophis portoricensis*, *Epicrates inornatus*) that could predate bird eggs or young are uncommon in Maricao, but potential avian predators were frequently observed. The latter include the Puerto Rican Sharp-shinned Hawk (*Accipiter striatus venator*), Pearly-eyed Thrasher (*Margarops fuscatus*), Puerto Rican Lizard Cuckoo (*Coccyzus vieilloti*), and Red-legged Thrush (*Turdus plumbeus*). I cannot dismiss the possibility that nest losses were caused by rodents due to the difficulty of predator identification based on nest damage characteristics (Marini and Melo 1998).

Woodworth (1999) indicated that Guánica is a population sink for the PRVI due to high levels of nest parasitism and depredation. A computer simulation model of the PRVI population with the levels of reproductive success found at Maricao implies this population has a positive growth rate even when the productivity index used in the model is probably an underestimate of the real number of fledglings produced (Tossas 2002). The differences in nest success between the two populations contribute to the idea of a source-sink metapopulation structure, but the short dispersal distances reported for juvenile PRVIs (Woodworth et al. 1998) suggest that Maricao individuals may not migrate as far as Guánica. Alternatively, the surplus of individuals produced at Maricao may disperse to forest fragments surrounding this forest reserve (Tossas and Thomlinson 2007).

Hurricanes directly increase avian mortality rates due to collisions during the storm, or indirectly by destroying the resources on which they depend (Wiley and Wunderle 1993). A study of the impacts of Hurricane Georges in 1998 to the Maricao avian community showed that 16 of 21 species, including the PRVI, declined after the hurricane (Tossas 2006). The reasons for the decline of each species may vary since they have particular ecological requirements and evidence on how resources are affected is scant. Nesting success parameters of PRVI did not vary significantly before and after the hurricane, but a low return rate of color-banded adults was observed in 1999 suggesting that disappearance of individuals was related to the effects of the hurricane. This finding contrasts with the vireo's high return rate and territorial fidelity in a year without a hurricane. Thus, the 1999–2000 annual return rates of 72% was likely typical for the species, while the 39% return estimated from 1998 to 1999 was probably caused by either mortality or dispersal during or immediately after the hurricane. The estimated return in 1999–2000 is similar to the annual survival

probabilities (68–74%) of PRVIs at Guánica reported by Woodworth et al. (1999), Faaborg and Arendt (1995), and Faaborg et al. (1997). The decline in adult return rate resulted in 26% lower density of territorial males the year following the hurricane.

Nest parasitism was not found to threaten the PRVI in this study, but the Shiny Cowbird population may increase at Maricao if hurricanes facilitate their colonization by opening the canopy and altering microhabitat characteristics. Brood parasites and predators may become more abundant if the amount of dense forest in the area surrounding Maricao is affected by fragmentation and deforestation. Changes in land-use practices affecting habitat continuity include rural development by an increased human population and substitution of traditional shade-coffee plantations for sun-grown varieties or other crops with higher yields.

ACKNOWLEDGMENTS

This work was supported by the Department of Biology at the University of Puerto Rico, Río Piedras and grants from the National Science Foundation (Center for Research Excellence in Science and Technology, HRD-9353549; Alliance for Graduate Education and the Professoriate, HRD-9817642). The Puerto Rico Department of Natural and Environmental Resources provided permits to work in Maricao State Forest. Beatriz Hernández and L. A. Muñiz-Campos were helpful in the field. I am grateful to J. M. Wunderle Jr. and R. B. Waide for guidance during the development of the research project, and to B. L. Woodworth for thoughtful reviews of the manuscript. This paper also benefited from comments by J. D. Nichols, E. A. VanderWerf, and two anonymous reviewers.

LITERATURE CITED

BENNETT, S. P. AND R. MOJICA. 1998. Hurricane Georges preliminary storm report: from the tropical Atlantic to the United States Virgin Islands and Puerto Rico. National Weather Service, San Juan, Puerto Rico.

BIBBY, C. J., N. D. BURGESS, D. A. HILL, AND S. MUSTOE. 2000. Bird census techniques. Second Edition. Academic Press, London, United Kingdom.

CRUZ, A., T. MANOLIS, AND J. W. WILEY. 1985. The Shiny Cowbird: a brood parasite expanding its range in the Caribbean region. Ornithological Monographs 36:607–620.

EWEL, J. J. AND J. L. WHITMORE. 1973. The ecological life zones of Puerto Rico and the U.S. Virgin Islands. Research Paper ITF-18. USDA, Forest Service, Institute of Tropical Forestry, Río Piedras, Puerto Rico.

FAABORG, J. AND W. J. ARENDT. 1995. Survival rates of Puerto Rican birds: are islands really that different? Auk 112:503–507.

FAABORG, J., W. J. ARENDT, AND M. S. KAISER. 1984. Rainfall correlates of bird population fluctuations in a Puerto Rican dry forest: a nine year study. Wilson Bulletin 96:575–593.

FAABORG, J., K. M. DUGGER, W. J. ARENDT, B. L. WOODWORTH, AND M. E. BALTZ. 1997. Population declines of the Puerto Rican Vireo in Guánica Forest. Wilson Bulletin 109:195–202.

JOHNSON, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. Auk 96:651–661.

KEPLER, C. B. AND A. K. KEPLER. 1970. Preliminary comparison of bird species diversity and density in Luquillo and Guánica forests, Pages E183–191 *in* A tropical rain forest (H. T. Odum, Editor). U.S. Atomic Energy Commission, Oak Ridge, Tennessee, USA.

KREBS, C. J. 1989. Ecological methodology. Harper and Row, Publishers, New York, USA.

MARINI, M. Â. AND C. MELO. 1998. Predators of quail eggs, and the evidence of the remains: implications for nest predation studies. Condor 100:395–399.

MAYFIELD, H. F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456–466.

PÉREZ-RIVERA, R. A. 1986. Parasitism by the Shiny Cowbird in the interior parts of Puerto Rico. Journal of Field Ornithology 57:99–104.

PURCELL, K. L. 2006. Abundance and productivity of Warbling Vireos across an elevational gradient in the Sierra Nevada. Condor 108:315–325.

RAFFAELE, H. A. 1989. A guide to the birds of Puerto Rico and the Virgin Islands. Princeton University Press, Princeton, New Jersey, USA.

ROBINSON, W. D., T. R. ROBINSON, S. K. ROBINSON, AND J. D. BRAWN. 2000. Nesting success of understory forest birds in central Panama. Journal of Avian Biology 31:151–164.

ROTHSTEIN, S. I. 1990. A model system for coevolution: avian brood parasitism. Annual Review of Ecology and Systematics 21:481–508.

SILANDER, S., H. GIL DE RUBIO, M. MIRANDA, AND M. VÁZQUEZ. 1986. Los bosques de Puerto Rico. Pages 210–236 *in* Compendio enciclopédico de los recursos naturales de Puerto Rico. Volumen 10. (J. L.Vivaldi, Editor). Departamento de Recursos Naturales, San Juan, Puerto Rico.

SKUTCH, A. F. 1985. Clutch size, nesting success, and predation on nests of neotropical birds, reviewed. Ornithological Monographs 36:575–594.

TOSSAS, A. G. 2002. Puerto Rican Vireo demography in a montane habitat, with metapopulation implications. Dissertation. University of Puerto Rico, Río Piedras.

TOSSAS, A. G. 2006. Effects of Hurricane Georges on the resident avifauna of Maricao State Forest, southwestern Puerto Rico. Caribbean Journal of Science 42:81–87.

TOSSAS, A. G. AND J. THOMLINSON. 2007. Landscape characteristics of Puerto Rican Vireo (*Vireo latimeri*) nesting habitat, with source-sink implications. Ornitologia Neotropical 18:233–242.

WARD, D. AND J. N. M. SMITH. 2000. Brown-headed cowbird parasitism in a sink population in Warbling Vireos. Auk 117:337–344.

WENNY, D. G., R. L. CLAWSON, J. FAABORG, AND S. L. SHERIFF. 1993. Population density, habitat selection and minimum area requirements of three forest-interior warblers in central Missouri. Condor 95:968–979.

WILEY, J. W. AND J. M. WUNDERLE JR. 1993. The effects of hurricanes on birds, with special reference to Caribbean islands. Bird Conservation International 3:319–349.

WOODWORTH, B. L. 1997. Brood parasitism, nest predation, and season-long reproductive success of a tropical island endemic. Condor 99:605–621.

WOODWORTH, B. L. 1999. Modeling population dynamics of a songbird exposed to parasitism and predation and evaluating management options. Conservation Biology 13:67–76.

WOODWORTH, B. L., J. FAABORG, AND W. J. ARENDT. 1998. Breeding and natal dispersal in the Puerto Rican Vireo. Journal of Field Ornithology 69:1–7.

WOODWORTH, B. L., J. FAABORG, AND W. J. ARENDT. 1999. Survival and longevity of the Puerto Rican Vireo. Wilson Bulletin 111:376–380.