

SURVIVAL AND LONGEVITY OF THE PUERTO RICAN VIREO

BETHANY L. WOODWORTH,^{1,2,5} JOHN FAABORG,³ AND WAYNE J. ARENDT⁴

ABSTRACT.—The Puerto Rican Vireo (*Vireo latimeri*), a Puerto Rican endemic, is declining in at least one forest reserve as the result of pressures from introduced nest predators and an introduced brood parasite. We collected data on adult survival, adult longevity, and juvenile survival from a long-term mist netting study (1973–1999) and a demographic study of color-marked birds (1990–1993) in Guánica Forest, Puerto Rico. Of the adult birds banded in the first three years of the demographic study, 24 of 32 males (75%) and 6 of 7 females (86%) were known to survive until June of the year following their banding. Model-based estimates of adult survival rate from capture/resighting of 65 color-marked birds was 0.74 (± 0.05 SE); for 51 adult males analyzed separately, survival rate was 0.74 (± 0.06 ; data were insufficient to estimate survival rate of females). We recorded a new longevity record for the Puerto Rican Vireo of 13 years, 2 months. Juvenile survival was estimated by enumeration to be 0.40 (± 0.15). Juveniles spent prolonged periods on their natal territory, which might increase their probability of surviving to first breeding. Puerto Rican Vireos have relatively high survival rates despite the presence of numerous introduced predators in their habitat, a highly seasonal environment, and the stress of reneating as many as 6 times in a season. Received 19 Oct. 1998, accepted 25 Feb. 1999.

Survival rate is an important component of life history models, and it is a central parameter examined in comparative demographic studies (e.g., Ricklefs 1982, Martin 1995). From a conservation perspective, precise estimation of adult and juvenile survival rates is critical because population dynamics often show great sensitivity to variation in these parameters (e.g., Lande 1988, Ryan et al. 1993). Despite their importance, relatively few data are available regarding the survival rates and longevity of tropical birds in general, and insular species in particular (but see Karr et al. 1990, Faaborg and Arendt 1995, Johnston et al. 1997).

The Puerto Rican Vireo (*Vireo latimeri*), is a small (11–12 g) passerine restricted to the island of Puerto Rico (Wetmore 1916). The population of vireos in Guánica Forest, Puerto Rico's largest dry forest reserve, has declined steadily over the past 20 years as a result of parasitism by an exotic avian brood parasite, the Shiny Cowbird (*Molothrus bonariensis*), and nest predation by introduced mammals

[rats (*Rattus* spp.), mongoose (*Herpestes auro-punctatus*), and feral cats (*Felis catus*); Faaborg et al. 1997; Woodworth 1997, 1999]. A population dynamics analysis indicated that estimates of the Puerto Rican Vireo's population growth rate were very sensitive to adult survival rate; consequently precise estimates of this parameter are crucial for useful population modeling (Woodworth 1999). In this paper we present data on adult and juvenile recoveries, from which we estimate survival rates and longevity of the Puerto Rican Vireo, compare them to temperate mainland congeners, and comment on their implications for persistence of this single-island endemic.

METHODS

We studied the Puerto Rican Vireo population in Guánica Forest Reserve (17° 58' N, 66° 52' W) along the southwestern coast of Puerto Rico. The reserve comprises 4,015 ha of mature dry subtropical forest over shallow limestone soils. Rainfall averages 860 mm annually, almost all of which falls between April and November (Murphy and Lugo 1986), and Puerto Rican Vireos generally breed from April through July (Woodworth 1997). Guánica is the site of a long-term constant effort mist netting study of wintering and resident landbirds (see Faaborg and Arendt 1989a), during which 135 Puerto Rican Vireos were marked with aluminum bands from 1973–1996.

From 1990–1993, B.L.W. conducted a demographic study of color-marked vireos in four 50-ha study areas (Woodworth 1997). Resident vireos were captured by playing recorded vireo songs to lure territorial males or pairs into mist nets. Because males were more aggressive than females toward intruders, most known sex birds we captured were males (78%, $n = 65$; 1 bird was of unknown sex). Individuals were resighted by revisiting all territories within the study areas and

¹ Dept. of Ecology, Evolution and Behavior, Univ. of Minnesota, 1987 Upper Buford Circle, St. Paul, MN 55108.

² Present address: Pacific Island Ecosystems Research Center, Biological Resources Division, U.S.G.S., Kilauea Field Station, P.O. Box 44, Hawaii National Park, HI 96718.

³ Division of Biological Sciences, Univ. of Missouri, Columbia, MO 65211.

⁴ USDA Forest Service, International Institute of Tropical Forestry, Sabana Field Research Station, P.O. Box 490, Palmer, PR 00721.

⁵ Corresponding author;

E-mail: Bethany.Woodworth@usgs.gov

areas within 300 m (about two territory widths) of their borders, and by broadcasting Puerto Rican Vireo song. Color-marked birds were relocated every few days (range: 1–9) throughout the breeding season as part of a study of their seasonal reproductive success (Woodworth 1997). In order to approximate the general assumption of capture-recapture models that all sampling is instantaneous, “capture periods” were defined so as to be short in relation to interval length (breeding season; Smith and Anderson 1987). Thus we defined two sample (capture) periods each breeding season (1990, 1991, and 1993), one consisting of the first two weeks after arrival on the study area, and the second including the two weeks immediately preceding the end of the field season. Birds banded at other times were included only if they were resighted during one of these sampling periods and were treated as if they were originally banded during that sampling period. The June 1992 and January 1993 capture periods consisted of 15 and 11 day visits to the study area, respectively.

We estimated adult survival rate from capture/resighting data on 66 color-marked, territorial adults over 4 years and 7 capture intervals [average interval length = 0.45 ± 0.31 (SE) years]. Five of the birds used in this analysis were originally banded by J.F. and W.J.A. prior to 1990, and so were included in a survival analysis by Faaborg and Arendt (1995), but time periods of the two survival datasets did not overlap. We used the program JOLLY (Pollock et al. 1990) to produce estimates of survival rate under five different capture-recapture models which vary in their assumptions about capture and survival probabilities. These models and their assumptions have been presented in detail elsewhere (Pollock et al. 1990 and references therein). In general, the capture/resighting field methods used here and the more widely used constant effort mist netting methods meet (or not) the assumptions of the Jolly-Seber models to similar degrees, with a few exceptions: (1) although fixed placement of nets in relation to territory boundaries may result in heterogeneous capture probabilities in mistnetting studies (Pollock et al. 1990), we were able to search entire territories for marked individuals; (2) trap response (net shyness) was not a concern in this study because we did not need to catch a bird in a net in order to resight it; (3) we were able to exclude transients from the study (the presence of transients in a sample may bias survival rate estimates if special models are not employed; Pradel et al. 1997); (4) we were able to rule out temporary emigration. Because the capture probability in this study was very high (0.92), we expect the model-based estimators to provide reasonably unbiased estimates of survival rate despite the relatively short time span of the study and moderate sample size (Gilbert 1973).

The program JOLLY provides goodness-of-fit tests to assess the fit of a model to a given data set. Where several models fit the data, likelihood ratio tests were used to test among models, with the simplest adequate model preferred. For statistical comparisons among survival rates we used the χ^2 statistic proposed by Sauer and Williams (1989).

Model-based estimators account for the possibility that a bird is alive and in the study area, but is not resighted in a particular sample period. To facilitate comparison with other studies, we also present survival rate as the number of birds banded in the first three years of the study that were known to be alive in the June following their banding (i.e., enumeration).

Because of the small sample size of fledglings, we could not use model-based estimators of juvenile survival. Thus, juvenile survival was calculated as the proportion of birds originally banded as fledglings that were recaptured or resighted in any subsequent year, and variance was estimated assuming binomial sampling.

As is true in all capture-recapture studies of open populations, dispersal outside of the study area could not be distinguished from mortality. However, typical dispersal rates and distances for the Puerto Rican Vireo are small (Woodworth et al. 1998) so the effect should be relatively minor in this study.

During the demographic study, B.L.W. recaptured 7 birds that had been originally banded prior to 1990. Estimated maximum longevity of the recaptured birds was calculated as the time from initial banding to the last recapture, plus the time from initial banding to the previous June 1, assuming that all birds were hatched on that date (following Klimkiewicz et al. 1983).

RESULTS

We color-banded 51 males, 14 females, 13 fledglings, and 10 birds of unknown sex (winter captures). Of the adult birds banded in the first three years of the study, 24 of 32 males (75%) and 6 of 7 females (86%) were known to survive (i.e., were alive and present on the study area) until the June of the year following their banding (Table 1). Over the four years, there were 59 opportunities for males to survive between breeding seasons, and the males survived in at least 43 of these cases (73%). Females were documented to survive in 11 of 13 opportunities (85%).

Territorial adult Puerto Rican Vireos during this study had an estimated annual survival rate of $0.74 (\pm 0.05)$. JOLLY model D, which is based on constant survival and capture probabilities throughout the study, provided the best fit to the data (overall $\chi^2 = 9.7$, $df = 8$, $P = 0.29$). Our capture/resighting methodology resulted in a very high annual capture probability (0.92 ± 0.03). Male annual survival rate estimated for 51 males was $0.74 (\pm 0.06)$; Model D, capture probability = 0.95 ± 0.02 . Data for 14 females were insufficient to fit a model describing female survival because most were banded in the last year of the study. Juvenile

TABLE 1. Bandings and resightings of male Puerto Rican Vireos known to be at least one year old when banded (demographic study only). The 8 sample periods, each 2 weeks long, took place in April 1990, July 1990, March 1991, August 1991, June 1992, January 1993, March 1993, and August 1993, resulting in 7 intervals. No new birds were banded during sample periods in July 1990, June 1992, or August 1993.

Sample period when banded	Number banded	Returns in sample period following banding						
		One	Two	Three	Four	Five	Six	Seven
Apr 1990	10	8	7	7	4	2	1	1
Mar 1991	7	5	6	5	6	6	—	—
Aug 1991	13	10	11	8	6	—	—	—
Jan 1993	3	3	2	—	—	—	—	—
Mar 1993	18	17	—	—	—	—	—	—
Total	51	43	26	20	16	8	1	1

survival rate from fledging to first breeding was estimated at 0.40 (± 0.15 ; $n = 10$).

The oldest Puerto Rican Vireo we recaptured was at least 13 years, 2 months (13-02) old, exceeding the previous longevity record for the Puerto Rican Vireo by nearly 4 years (09-04; Faaborg and Arendt 1989b). Three other birds that nearly matched the previous record were also recaptured (09-01, 09-02, and 09-02). All were color-banded territorial males that we observed over 1–2 complete breeding seasons before they disappeared or the study ended. None had dispersed more than 500 m in the decade since they were originally banded (see Woodworth et al. 1998 for details of dispersal behavior).

DISCUSSION

Faaborg and Arendt (1995) estimated an adult annual survival rate of 0.68 (± 0.08) for the Puerto Rican Vireo population in Guánica, based on their long-term mist netting study (Jolly-Seber model D, 19 individuals over 18 years and 15 capture intervals). Although their mean survival value is slightly less than that presented here (probably because of the inclusion of a higher proportion of female birds, along with non-territorial individuals), the two estimates are not significantly different ($\chi^2 = 0.40$, $df = 1$, $P > 0.05$).

Our Puerto Rican Vireo survival rate estimate is high relative to survival and recovery rates reported for temperate vireos. Recovery percentages of White-eyed Vireos (*Vireo griseus*) studied over 9 years on their breeding grounds were 48% for males, and 50% for females (Hopp et al. 1999). Return rates of adult male Black-capped Vireos (*V. atricapillus*) to breeding territories in central Texas

were 55–75% (Grzybowski 1991). The survival rate of Red-eyed Vireos (*V. olivaceus*) based on returns to breeding grounds in Maryland, was estimated at 59% (Jolly-Seber model A; Nichols et al. 1981). Return rates of adult Gray Vireos (*V. vicinior*) to wintering territories in Mexico were 46–71% (Bates 1992), and for Bell's Vireo (*V. bellii*) returning to breeding territories in California, 47% (Salata 1983). Interestingly, compared to survival rate estimates for other tropical island passerines studied to date, the survival rate of the Puerto Rican Vireo is not unusually high [e.g., average 68% (51–79%) for 7 Puerto Rican species, Faaborg and Arendt 1995; 65.3% (45–85%) for 17 Trinidadian species, Johnston et al. 1997; and 76% (55–88%) for 5 Hawaiian species, van Riper 1987, Lepson and Freed 1995, Ralph and Fancy 1995, Woodworth et al. in press].

Likewise, the longevity record for the Puerto Rican Vireo of 13 years, 2 months is long relative to most of its temperate congeners. Records for six other temperate *Vireo* species range from 6 years, 1 month to 10 years (Davis 1995, Kennard 1975, Klimkiewicz et al. 1983, Rodewald and James 1996). The record for the Warbling Vireo (*Vireo gilvus*), a neotropical migrant, is very similar (13-01, Klimkiewicz et al. 1983) to the Puerto Rican Vireo. Such records are complicated by many factors (Krementz et al. 1989). Although it is surprising that such a seemingly long longevity record from a nonmigratory species would be equaled by a long distance migrant, it is worth noting that over 15,000 Warbling Vireos have been banded (Klimkiewicz et al. 1983), but only a few hundred

Puerto Rican Vireos have been banded and many of these have been long lived.

The relatively high survival and longevity of this insular species is remarkable in light of the presence of numerous introduced predators in its habitat, high rates of nest failure causing females to renest up to 6 times in a season (Woodworth 1997), and the stresses of a highly seasonal environment (almost no rain falls from December to March, and Guánica loses up to 50% of its leaf area in winter; Murphy and Lugo 1986). Puerto Rican Vireos have a small clutch size relative to temperate vireos (Woodworth 1995), which, when coupled with the generally observed trade-off between fecundity and survival (Martin 1995), might allow birds to survive through more breeding seasons (Cody 1966). In addition, a non-migratory insular species might outlive its migratory counterparts because it does not pay the price of annual migration.

Juvenile survival rates of passerines are poorly known, especially for tropical birds. Return rates of juvenile Bell's Vireos and Black-capped Vireos were measured as 24%, although actual survival rate is likely to be higher (Salata 1983, Grzybowski 1991; respectively). Survival of juvenile Wood Thrush (*Hylocichla mustelina*) in their first 12 weeks is only 0.42 (Anders et al. 1997). Juvenile survival may be enhanced if young are allowed to remain in their natal territory for an extended period (discussed in Karr et al. 1990) as Puerto Rican Vireo fledglings have been observed to do (at least 80–98 days post-fledging; Woodworth 1995).

A population dynamics model of this population showed that, as is common in many population models, the vireo's predicted population growth rate was greatly dependent upon the value of adult survivorship used in the model (Woodworth 1999). Therefore, a precise and accurate estimate of adult survivorship is critical to evaluating the long-term prospects for survival of this population. The close agreement between two independent estimates (Faaborg and Arendt 1995 and this study) of adult survival rate for this population improves confidence in the predictions of a model using these estimates, although additional data on female and juvenile survivorship is needed.

The relatively high adult and juvenile survival rates we documented would seem to bode

well for the persistence of Puerto Rican Vireos in Guánica Forest. However, other work on this population has shown that the vireos suffer extremely high nest losses to native and introduced predators, and to parasitism by the exotic Shiny Cowbird (Woodworth 1997). Despite as many as 6 nest attempts in a single season, females succeed in fledging young from only 0.41–0.67 nests per year (Woodworth 1997). These factors result in an overall negative population growth rate for the vireo over the range of "reasonable" survival rate values (the 95% confidence limits of the estimates; Woodworth 1999). Thus, the declines observed over the previous decade (Faaborg et al. 1997) are likely to continue unless active management is undertaken to reduce predation and/or brood parasitism in the forest.

ACKNOWLEDGMENTS

J. Colón kindly provided information on two birds he originally banded. We thank the dozens of volunteers who have participated in these projects over the years. The Puerto Rico Departamento de Recursos Naturales Ambiente and M. Canals kindly gave permission to work in Guánica. B.L.W. was supported by the International Council for Bird Preservation-U.S. Section; Frank M. Chapman Fund of the American Museum of Natural History; Sigma Xi Grant-in-Aid of Research; Dayton Natural History Fund and Wilkie Fund for Natural History Research, Bell Museum of Natural History; Eastern Bird Banding Association; Paul A. Stewart Award of the Wilson Ornithological Society; fellowships and assistantships from the Department of Ecology, Evolution and Behavior, University of Minnesota; and Grants for Research Abroad and a Doctoral Dissertation Fellowship from the Graduate School of the University of Minnesota. Support for J.E. and W.J.A. was provided by the Frank M. Chapman Fund of the American Museum of Natural History, National Sciences Foundation Doctoral Dissertation Improvement Fund, University of Missouri-Columbia (Research Council of the Graduate School), USDA Forest Service (International Institute of Tropical Forestry), Biological Resources Division of the U.S. Geological Survey, and the U.S. Fish and Wildlife Service. K. Dugger, S. Hopp, J. Bates, and two anonymous reviewers provided helpful comments on earlier drafts of this manuscript.

LITERATURE CITED

- ANDERS, A. D., D. C. DEARBORN, J. FAABORG, AND F. R. THOMPSON, III. 1997. Juvenile survival in a population of Neotropical migrant birds. *Conserv. Biol.* 11:698–707.
- BATES, J. M. 1992. Winter territorial behavior of Gray Vireos. *Wilson Bull.* 104:425–433.

- CODY, M. L. 1966. A general theory of clutch-size. *Evolution* 20:174–184.
- DAVIS, J. N. 1995. Hutton's Vireo (*Vireo huttoni*). In *The birds of North America*, no. 189 (A. Poole and F. Gill, Eds.). The Academy of Natural Sciences, Philadelphia, Pennsylvania; The American Ornithologists' Union, Washington, D.C.
- FAABORG, J. AND W. J. ARENDT. 1989a. Long-term declines in winter resident warblers in a Puerto Rican dry forest. *Am. Birds* 43:1226–1230.
- FAABORG, J. AND W. J. ARENDT. 1989b. Longevity estimates of Puerto Rican birds. *N. Am. Bird Bander* 14:11–13.
- FAABORG, J. AND W. J. ARENDT. 1995. Survival rates of Puerto Rican birds: are islands really that different? *Auk* 112:503–507.
- FAABORG, J., K. M. DUGGER, W. J. ARENDT, B. L. WOODWORTH, AND M. E. BALTZ. 1997. Population declines of the Puerto Rican Vireo (*Vireo latimeri*) in Guánica Forest. *Wilson Bull.* 109:195–202.
- GILBERT, R. O. 1973. Approximations of the bias in the Jolly-Seber capture-recapture model. *Biometrics* 29:501–526.
- GRZYBOWSKI, J. A. 1991. Survivorship, dispersal and population structure of Black-capped Vireos at the Kerr Wildlife Management Area, Texas. *Resour. Protection Div., Texas Parks Wildl. Dept., Austin*.
- HOPP, S. L., A. KIRBY, AND C. A. BOONE. 1999. Banding returns, arrival pattern, and site-fidelity of White-eyed Vireos. *Wilson Bull.* 111:46–55.
- JOHNSTON, J. P., W. J. PEACH, R. D. GREGORY, AND S. A. WHITE. 1997. Survival rates of tropical and temperate passerines: a Trinidadian perspective. *Am. Nat.* 150:771–789.
- KARR, J. R., J. D. NICHOLS, M. K. KLIMKIEWICZ, AND J. D. BRAWN. 1990. Survival rates of birds of tropical and temperate forests: will the dogma survive? *Am. Nat.* 136:277–291.
- KENNARD, J. H. 1975. Longevity records of North American birds. *Bird-Banding* 46:55–57.
- KLIMKIEWICZ, M. K., R. B. CLAPP, AND A. G. FUTCHER. 1983. Longevity records of North American birds: Remizidae through Parulinae. *J. Field Ornithol.* 54:287–294.
- KREMENTZ, D. G., J. R. SAUER, AND J. D. NICHOLS. 1989. Model-based estimates of annual survival rate are preferable to observed maximum lifespan statistics for use in comparative life-history studies. *Oikos* 56:203–208.
- LANDE, R. 1988. Demographic models of the Northern Spotted Owl (*Strix occidentalis caurina*). *Oecologia* (Berlin) 75:601–607.
- LEPSON, J. K. AND L. A. FREED. 1995. Variation in male plumage and behavior of the Hawaii Akepa. *Auk* 112:402–414.
- MARTIN, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecol. Monogr.* 65:101–127.
- MURPHY, P. G. AND A. E. LUGO. 1986. Structure and biomass of a subtropical dry forest in Puerto Rico. *Biotropica* 18:89–96.
- NICHOLS, J. D., B. R. NOON, S. L. STOKES, AND J. E. HINES. 1981. Remarks on the use of mark-recapture methodology in estimating avian population size. *Stud. Avian Biol.* 6:121–136.
- POLLOCK, K. H., J. D. NICHOLS, C. BROWNIE, AND J. E. HINES. 1990. Statistical inference for capture-recapture experiments. *Wildl. Monogr.* 107:1–97.
- PRADEL, R., J. E. HINES, J. D. LEBRETON, AND J. D. NICHOLS. 1997. Capture-recapture survival models taking account of transients. *Biometrics* 53:60–72.
- RALPH, C. J. AND S. G. FANCY. 1995. Demography and movements of 'Apapane and 'I'iwi in Hawai'i. *Condor* 97:729–742.
- RICKLEFS, R. E. 1982. Comparative avian demography. *Curr. Ornithol.* 1:1–32.
- RODEWALD, P. G. AND R. D. JAMES. 1996. Yellow-throated Vireo (*Vireo flavifrons*). In *The birds of North America*, no. 247 (A. Poole and F. Gill, Eds.). The Academy of Natural Sciences, Philadelphia, Pennsylvania; The American Ornithologists' Union, Washington, D.C.
- RYAN, M. R., B. G. ROOT, AND P. M. MAYER. 1993. Status of Piping Plovers in the Great Plains of North America: a demographic simulation model. *Conserv. Biol.* 7:581–585.
- SALATA, L. R. 1983. Status of the Least Bell's Vireo on Camp Pendleton, California: research done in 1983. *U.S. Fish and Wildl. Serv., Laguna Niguel, California*.
- SAUER, J. R. AND B. K. WILLIAMS. 1989. Generalized procedures for testing hypotheses about survival or recovery rates. *J. Wildl. Manage.* 53:137–142.
- SMITH, D. R. AND D. R. ANDERSON. 1987. Effects of lengthy ringing periods on estimates of annual survival. *Acta Ornithol.* 23:69–76.
- VAN RIPER, C., III. 1987. Breeding ecology of the Hawaii Common Amakihi. *Condor* 89:85–102.
- WETMORE, A. 1916. Birds of Porto Rico. *U.S. Dept. Agric. Bull.* 326:1–140.
- WOODWORTH, B. L. 1995. Ecology of the Puerto Rican Vireo and the Shiny Cowbird in Guánica Forest, Puerto Rico. *Ph.D. diss., Univ. of Minnesota, St. Paul*.
- WOODWORTH, B. L. 1997. Brood parasitism, nest predation, and season-long reproductive success of a tropical island endemic. *Condor* 99:605–612.
- WOODWORTH, B. L. 1999. Modeling the population dynamics of a songbird exposed to parasitism and predation and evaluating management options. *Conserv. Biol.* 13:67–76.
- WOODWORTH, B. L., J. FAABORG, AND W. J. ARENDT. 1998. Breeding and natal dispersal in the Puerto Rican Vireo. *J. Field Ornithol.* 69:1–7.
- WOODWORTH, B. L., J. T. NELSON, E. J. TWEED, S. G. FANCY, M. P. MOORE, E. B. COHEN, AND M. S. COLLINS. In press. Breeding productivity and survival of the endangered Hawai'i Creeper in a wet forest refuge on Mauna Kea, Hawai'i. In *The status, ecology, and conservation of the Hawaiian avifauna* (J. M. Scott, S. Conant, and L. A. Freed, Eds.). *Stud. Avian Biol.*