

UNDERSTANDING SURVIVAL AND ABUNDANCE OF OVERWINTERING WARBLERS: DOES RAINFALL MATTER?

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Abstract. We investigated relationships between warbler abundance and survival rates measured on a Puerto Rican wintering site and rainfall patterns measured on the wintering site and in regions where these warblers breed, as estimated using stable-isotope analysis (δD) of feathers collected from wintering birds. We banded birds using constant-effort mist netting from January 1989–2003 in the Gunica Forest of southwestern Puerto Rico. Black-and-white Warblers (*Mniotilta varia*), American Redstarts (*Setophaga ruticilla*), and Ovenbirds (*Seiurus aurocapilla*) dominated the Neotropical migrant capture totals each winter, with resulting sample sizes large enough to estimate survival rates. Estimates of capture probability from survival modeling allowed us to estimate abundance from mist-netting capture totals for Black-and-white Warblers and Ovenbirds. Stable-hydrogen isotopes showed that the three focal species came mostly from the eastern United States. Black-and-white Warbler abundance was related to rainfall total deviations from normal in Guánica Forest, and Ovenbird abundance was related to total annual rainfall in the United States. Survival models with rainfall covariates were weakly supported overall, but apparent survival of Black-and-white Warblers and American Redstarts was negatively related to rain during the first 6 months of the year at Guánica, and Ovenbird survival was related to rainfall during the spring in the southeastern U.S. Abundance and apparent survival exhibited similar, species-specific patterns of association with rainfall for Black-and-white Warblers and Ovenbirds. Winter rainfall was important to demographic parameters of Black-and-white Warblers, and breeding-season rain was important to Ovenbirds.

Key words: American Redstart, Black-and-white Warbler, Ovenbird, population size variation, Puerto Rico, stable isotopes, survival.

Entendiendo los Patrones de Supervivencia y Abundancia de Parúlidos Residentes de Invierno: ¿Es Importante la Precipitación?

Resumen. Investigamos las relaciones entre la abundancia y las tasas de supervivencia de parúlidos residentes de invierno en Puerto Rico y los patrones de precipitación de los sitios invernales y de las áreas de anidación, éstas últimas deducidas a partir del análisis de isótopos estables (δD) en plumas colectadas de las aves migratorias. Las aves fueron capturadas y anilladas utilizando redes de niebla en el Bosque de Guánica en el suroeste de Puerto Rico durante el mes de enero, desde 1989 hasta el 2003. Las especies de aves neotropicales con mayor número de capturas totales durante cada invierno fueron *Mniotilta varia*, *Setophaga ruticilla* y *Seiurus aurocapilla*, con un tamaño de muestra lo suficientemente grande como para estimar sus tasas de supervivencia. La estimación de las probabilidades de captura a partir de los modelos de supervivencia nos permitieron evaluar la abundancia utilizando datos de capturas totales para *Mniotilta varia* y *Seiurus aurocapilla*. Los isótopos de hidrógeno estable mostraron que las tres especies de aves focales provinieron principalmente de la región Este de Estados Unidos. La abundancia de *Mniotilta varia* estuvo relacionada a las variaciones totales de precipitación en el Bosque de Guánica y la abundancia de *Seiurus aurocapilla* estuvo relacionada a la precipitación anual total en los Estados Unidos. Los modelos de supervivencia con covariables de precipitación tuvieron muy poco respaldo. Sin embargo, la supervivencia aparente de *Mniotilta varia* y *Setophaga ruticilla* estuvo relacionada negativamente a la precipitación durante los primeros seis meses del año en Guánica y la supervivencia de *Seiurus aurocapilla* estuvo relacionada a la precipitación durante la estación de primavera en el sureste de Estados Unidos. La abundancia

y la supervivencia aparente mostraron patrones de asociación similares y específicos para cada especie con la precipitación para *Mniotilta varia* y *Seiurus aurocapilla*. La precipitación de invierno fue un factor importante para determinar los patrones demográficos de *Mniotilta varia* y la precipitación durante la temporada de anidación también fue un factor significativo para *Seiurus aurocapilla*.

INTRODUCTION

Understanding how populations of long-distance migratory birds are regulated is a difficult task, as it involves regulatory processes in at least two widely separated locations that are occupied for long periods (breeding and wintering sites) plus the effects of limiting factors while in transit between these sites. To date, we have little information linking breeding and wintering populations, so even detailed information from breeding and wintering locations for a species may be compromised by the possibility that one is measuring separate subpopulations. In addition, there are temporal as well as spatial considerations since any count of population size at a time or place along this annual cycle is a function of both survival within the population being measured and reproductive success during prior breeding seasons.

A density-dependent model developed by Sherry and Holmes (1995) presented potential limiting factors at work throughout a migrant bird's annual cycle. Under this model, individual survival is a component of all elements of the seasonal cycle, while reproductive success and postfledging survival are primarily components of the breeding season. Sherry and Holmes (1995) suggest that habitat quality is an important component for both breeding and nonbreeding season habitat selection, with survival and reproductive success increasing with habitat quality. Their model suggests that habitat quality, in both seasons when birds are stationary, is a function of food, predation, and weather, and they discuss the possibly strong relationship between weather conditions and food supply.

To date, most suggested effects of rainfall on migratory populations have been through severe drought, although Sillett et al. (2000) and Nott et al. (2002) have also noted the effects of severe rainfall. Rainfall was highly correlated with population declines in seven species of Palearctic–African migrants during severe drought in the Sahel region of sub-Saharan Africa (Baillie and Peach 1992) and for grassland birds breeding in the Great Plains of North America (George et al. 1992). Faaborg and Arendt (1992) suggested

that drought explained at least part of a long-term decline in winter-resident warbler populations documented in the Guánica Forest of southwestern Puerto Rico. Although they suggested that part of this decline was due to movement of two species into alternative habitats that had become available within the region, they thought that a sharp decline in populations of the three most regularly captured species during 1986–1988 was due to a severe widespread drought across the United States during that time, with strong corroborating evidence provided by Blake et al. (1992) for migrants in Minnesota and Wisconsin. Thus, populations of wintering warblers monitored on Puerto Rico study sites may have declined because of drought-induced reduction in nesting success or survival of adults on the breeding grounds. To investigate this hypothesis, we need to link migrants wintering in Guánica with their breeding grounds in North America.

In addition to breeding-ground effects, migrant populations measured on the wintering grounds could have declined because weather conditions in southwestern Puerto Rico reduced the quality of habitat in these sites, thereby either decreasing annual survival rates or increasing emigration from Guánica Forest to other wintering areas. We have evidence that local rainfall patterns affect both population size and survival rates of resident birds (Dugger et al. 2000), so it is not unexpected that winter residents might be similarly affected. This previous modeling effort with resident birds in Guánica Forest suggested that extreme rainfall can be as detrimental to annual survival as droughts (Dugger et al. 2000). Indeed, measures of rainfall that reflect the extent and severity of the dry season, the occurrence and timing of spring rains (which are important for resident bird breeding success), and the amount of rain during August–October (when the bulk of rainfall normally occurs) are important population and survival covariates for resident bird species over time (Dugger et al. 2000).

Here, we present our investigations into relationships between demography (population size

and annual apparent survival) and rainfall patterns from both the breeding and wintering grounds for birds that winter in Guánica Forest. Because we studied temperate-tropical migrants on their wintering grounds, we did not expect temperature to affect winter survival. Prolonged rainfall and large storms likely have thermodynamic consequences for small birds, but freezing temperatures do not occur; thus rainfall is likely the dominant component of weather for consideration on the wintering grounds. Temperatures on the breeding grounds, in early spring in particular, may influence the onset of breeding, and ultimately, productivity if the breeding season is shortened; however direct effects on survival are less likely. Thus, for this investigation we included only wintering and breeding season rainfall effects on annual apparent survival and population size of three warbler species that winter in Guánica Forest. To do this, we used stable-hydrogen isotope analysis (δD) to determine North American breeding-ground latitudes for the three most common winter-resident species, Black-and-white Warbler (*Mniotilta varia*), Ovenbird (*Seiurus aurocapilla*), and American Redstart (*Setophaga ruticilla*; see Hobson 1999). Our objectives were then to develop models to determine whether warbler population size variation and annual apparent survival rates were related to rainfall patterns on the breeding grounds, wintering grounds, or perhaps both areas.

METHODS

STUDY SITE

The 4015-ha Guánica Commonwealth Forest Reserve (17°55'N, 67°05'W) is located along the southwestern coast of Puerto Rico. This reserve is composed of mature dry subtropical forest over shallow limestone soils (Ewel and Whitmore 1973). Approximately half of the reserve is second growth, whereas the other half is relatively pristine. The vegetation is generally short (usually <10 m) and is partially evergreen with many arborescent cacti. A detailed description of the vegetation and bird communities with a photograph can be found in Terborgh and Faaborg (1973). In 1973 we began a long-term winter bird-banding study in Guánica Forest, which continues through the present (Faaborg et al. 2000).

RAINFALL MEASURES

Rainfall amounts at Guánica Forest were recorded daily at the refuge headquarters in the center of the forest reserve. Monthly totals were then compiled and were used to develop a variety of rainfall measures over time (Table 1). Variables reflecting deviations from normal are the absolute values of mean-centered parameters ($x_i - \bar{x}$), with long-term means for total and first-six-months rainfall calculated from 19 years (1984–2003) of rainfall data collected at Guánica Forest.

We investigated a variety of specific hypotheses related to the amount and timing of rainfall during winter, following our previous modeling efforts with resident bird species at this site (Dugger et al. 2000). Of primary interest were the total amount of annual rainfall (TOT) and the amount of rain that fell during the first six months of the year (January–June; FIR), ending the drought and triggering breeding of resident birds (Table 1). Although migrants leave Guánica Forest by February or March of each year, we believe this first-six-months rainfall is particularly important to overall habitat quality for the upcoming year and might be important to warbler survival or population size, particularly as it may underlie density-dependent effects of resident bird populations on winter residents. Rainfall totals during the second six months of the year (July–December) are highly correlated with total annual rain (Dugger et al. 2000), so we excluded this period and used annual and first-six-months rainfall totals in this analysis. We also included a rainfall total for October, November, and December (Table 1; OND) to directly reflect the period when migrants arrived in Guánica Forest.

Habitat quality as perceived by migrants might not be related to the current year's rainfall, so we also investigated hypothesized relationships between demographic parameters and time lags (PREV, F_{prev}), cumulative effects (SUM, F_{sum}), and deviations from normal (DFN, F_{dfn}) associated with Guánica rainfall (Table 1). We generally predicted positive relationships between rainfall parameters and warbler demographics; that is, more rain was expected to result in higher warbler populations or higher survival. The exception was for variables measuring deviations from normal, in which higher deviations (either much wetter, or much drier) were expected to decrease population size or survival.

TABLE 1. Description of rainfall variables used to model survival and for regression with annual warbler population estimates. Because netting occurred in January (year i), rainfall measures correlated with population estimates are from the prior calendar year ($i - 1$), and previous year's rainfall from 2 years earlier ($i - 2$). Because annual estimates of survival in January cover the prior year, rainfall measures for survival in year i are from year i , and previous year's rainfall from year $i - 1$.

| Variable | Description |
|---------------------------|--|
| Guánica Forest rainfall | |
| TOT | Total annual rainfall |
| FIR | Rainfall in first six months (January–June) |
| TDFN | Deviations from normal (DFN) for total rainfall |
| F.dfn | Deviations from normal for first six months |
| SUM | Sum of total rainfall of the current year and the previous year |
| F.sum | Sum of total rainfall in first six months of current and previous year |
| PREV | Total rainfall in previous year |
| F.prev | Total rainfall from first six months of previous year |
| OND | Rainfall totals for October, November, and December of current year |
| Continental U.S. rainfall | |
| US_tot | Mean annual rainfall for the entire U.S. |
| NE_Tot | Total annual rainfall for the Northeast Region ^a |
| NE_spr | Total spring (Mar–May) rainfall for the Northeast Region |
| NE_smr | Total summer (June–Aug) rainfall for the Northeast Region |
| SE_Tot | Total annual rainfall for the Southeast Region ^b |
| SE_spr | Total spring (Mar–May) rainfall for the Southeast Region |
| SE_smr | Total summer (June–Aug) rainfall for the Southeast Region |
| CE_tot | Total annual rainfall for the Central Region ^c |
| CE_spr | Total spring (Mar–May) rainfall for the Central Region |
| CE_smr | Total summer (June–Aug) rainfall for the Central Region |
| ENC_Tot | Total annual rainfall for the East North Central Region ^d |
| ENC_spr | Total spring (Mar–May) rainfall for the East North Central Region |
| ENC_smr | Total summer (June–Aug) rainfall for the East North Central Region |

^a Regions correspond to state groupings from National Climatic Data Center (2004). Northeast Region includes Maine, Vermont, New Hampshire, Massachusetts, Rhode Island, Connecticut, New Jersey, Delaware, Maryland, and Pennsylvania.

^b Virginia, North Carolina, South Carolina, Georgia, Florida, Alabama.

^c Missouri, Illinois, Indiana, Ohio, West Virginia, Kentucky, Tennessee.

^d Minnesota, Iowa, Wisconsin, Michigan.

In addition, during September 1998, Hurricane Georges extensively damaged the canopy of Guánica Forest, although relatively few trees were blown over. Populations of some resident species appeared to severely decline after this hurricane, so we hypothesized the hurricane or associated high rainfall might have also reduced survival of some warbler species. We added a “hurricane model” to our initial model set for survival, which tested for a different, decreased survival rate in 1998, compared to other years, because of direct mortality associated with the hurricane.

To investigate relationships between warbler populations and survival and rainfall on the breeding grounds, we used regional data from the National Climatic Data Center (NCDC 2004). These data are area-weighted averages computed by averaging the rainfall totals for sta-

tions within each of nine regions of the United States. We investigated patterns using mean total U.S. rainfall, and spring (March–May), and summer (June–August) rainfall totals from four regions in North America that correspond to warbler breeding areas (Table 1). We relied on stable-isotope data (see below) to develop hypotheses regarding which U.S. regional rainfall measures might be important for each species, using data from the following NCDC-defined regions: Northeast (Maine, Vermont, New Hampshire, Massachusetts, Rhode Island, Connecticut, New Jersey, Delaware, Maryland, Pennsylvania), Southeast (Virginia, North Carolina, South Carolina, Georgia, Florida, Alabama), Central (Missouri, Illinois, Indiana, Ohio, West Virginia, Kentucky, Tennessee), and East North Central (Minnesota, Iowa, Wisconsin, Michigan). In all cases we hypothesized that warbler survival and

population size would increase with spring or summer rains, as increased rainfall represented increased habitat quality on the breeding grounds.

We investigated the effects of a total of nine winter and 10 breeding-season rainfall parameters on survival and population size of three winter residents. We also included a hurricane model on survival for each species. Because of the large number of rainfall parameters we were investigating and because we were unsure how winter and breeding season rainfall patterns may work together, only single-factor rainfall models were part of our *a priori* model set. We wanted to minimize the possibility of finding spurious effects, so we only included variables that addressed current, specific hypotheses regarding spatial and temporal variation in rainfall effects.

POPULATION MONITORING AND BANDING

We monitored bird populations in the Guánica Forest using a form of constant-effort mist netting described by Terborgh and Faaborg (1973) and Faaborg et al. (2004). A line of sixteen 12-m-long mist nets with 30-mm mesh was placed end-to-end along a trail in as straight a line as possible during January or early February of each year. This line was operated from dawn to dark for three consecutive days. All birds were marked upon initial capture with U.S. Fish and Wildlife Service aluminum leg bands. Subsequent recaptures within and among years were carefully recorded. Species were aged and sexed when possible following Pyle (1997). Birds recaptured during the 3-day sampling period were counted only once for capture totals used in abundance estimates. Capture rates declined dramatically during this sample, obviating the need for a fourth day of netting; 92% of winter resident totals for the 3-day samples were captured during the first 2 days of sampling. We have been operating one of these net lines since 1973 (except 1977 and 1979), and most of our previous publications have reported results from this line only (Faaborg and Arendt 1995, Dugger et al. 2000). In this study, we report on our expanded study that includes data from additional net lines added beginning in 1989. The number of lines sampled was seven in 1989, eight in 1990, and nine from 1991 to the present. Dispersal between net lines was minimal, with <1% of banded birds recaptured (within or among

years) on a line other than the one where it was initially banded.

We captured 16 species of warblers over the 15 years of sampling (1989–2003), with species abundances varying twofold, from over 18 species per net line (165 individuals) to nine per net line (81 individuals). Only five species were caught every year. Of these five, the Northern Parula (*Parula americana*) had several years with only one or two captures and individuals were rarely recaptured. The Worm-eating Warbler (*Helmitheros vermivorus*) was captured annually and appeared to have high recapture rates, but with fewer than five birds per year, sample sizes were too small for modeling. In contrast, three species, Black-and-white Warbler, Ovenbird, and American Redstart, were captured annually in relatively high abundance and with many recaptures among years (6% to 33% of total annual captures). These three species made up, on average, about 77% of total warbler captures, and in years with low overall warbler populations, as much as 89% of total captures.

DETERMINING SOURCES OF WINTER RESIDENTS

Tail feathers were collected from all winter-resident warblers in 2003 for stable-isotope analysis. We assumed that the nonexchangeable deuterium isotopic composition (δD) of this feather would give us an idea of the latitude in North America where the feather was formed, which we also assumed was proximate to the breeding grounds of the individual (Hobson and Wassenaar 1997, Hobson 1999).

In the laboratory, feathers were washed with a 2:1 chloroform:methanol solvent to remove surface contaminants. Cleaned feather vanes were then subsampled for deuterium isotope analysis. Stable-hydrogen isotope analyses of feathers are more complicated than conventional measurements of ^{13}C and ^{15}N due to the problem of uncontrolled isotopic exchange between samples and ambient water vapor (Wassenaar and Hobson 2000). We used routine keratin standards to correct for this effect so that the values we report are equivalent to nonexchangeable feather hydrogen (details in Wassenaar and Hobson 2003). Briefly, this process involves the simultaneous measurement of unknowns with several replicates of three different keratin standards whose nonexchangeable D values are known and which span the range of expected

feather values. Algorithms generated from each run that relate δ values of unknowns to their expected nonexchangeable values are then used on a run-by-run basis.

Stable-hydrogen isotope measurements on feathers and keratin standards were performed on H_2 derived from high-temperature flash pyrolysis of feathers and continuous-flow isotope-ratio mass spectrometry (CF-IRMS). Pure H_2 was used as the sample analysis gas and the isotopic reference gas. A Eurovector 3000[®] (Euro Vector, Milan, Italy) high-temperature elemental analyzer with autosampler was used to automatically pyrolyze feather samples to a single pulse of H_2 gas. The resolved H_2 sample pulse was then introduced to the isotope-ratio mass spectrometer (Micromass Isoprime[®] with electrostatic analyser; GV Instruments, Manchester, UK) via an open split capillary. All δD results are expressed in the typical delta notation, in units of per mil (‰), and normalized on the Vienna Standard Mean Ocean Water-Standard Light Antarctic Precipitation (VSMOW-SLAP) scale. Repeated analyses of the hydrogen isotope intercomparison material IAEA-CH-7 (−100‰), routinely included as a check, yielded an external repeatability of better than $\pm 1.5\%$.

Feather δD values were assigned to approximate origins by comparing the feather δD values predicted in the contour map of Wassenaar and Hobson (2001) and the breeding range of the species considered. Values falling between isotopic contours were placed to approximate latitude of origin using linear interpolation between kriged δD contours. This approach enabled us to define to the species level the catchment areas of our wintering birds in Puerto Rico.

STATISTICAL ANALYSIS

SURVIVAL RATE MODELING

Capture-recapture methods and Cormack-Jolly-Seber models (Pollock et al. 1990, Lebreton et al. 1992) in Program MARK (White and Burnham 1999) were used to estimate apparent survival rates and model the effects of rainfall covariates on the survival of Black-and white Warblers, Ovenbirds, and American Redstarts. We used Program RELEASE (Burnham et al. 1987) to test for goodness-of-fit of our global model to the Cormack-Jolly-Seber model and to estimate overdispersion (\hat{c}). We used the combined χ^2 values and degrees of freedom (df) from Test 2

and Test 3 from Program RELEASE to estimate overdispersion ($\hat{c} = \chi^2/df$; Lebreton et al. 1992, White 2002). We used information-theoretic approaches as detailed in Burnham and Anderson (2002) to select our best models, including Akaike's Information Criterion corrected for small sample sizes (AIC_c) and small-sample-size corrected quasi- AIC_c ($QAIC_c$) when overdispersion was indicated. We generally selected the model with the lowest AIC_c or $QAIC_c$ value as our best model. We also used ΔAIC_c , AIC_c weights and the degree to which 95% confidence intervals for slope coefficients (β_i) overlapped zero to evaluate the strength of evidence for competing models ($\Delta AIC_c < 2$) and specific rainfall parameters.

We used a multistep process to model capture probability and apparent survival because we felt the potential model set was too large and would facilitate finding spurious effects (Anderson et al. 2001) if we modeled every combination of survival and capture probability covariates. Instead, we began by modeling capture probabilities, while maintaining a basic time structure on survival (ϕ). We investigated the effects of the winter rainfall parameters on capture probabilities, as we hypothesized there might be an effect of winter habitat quality on capture rates (i.e., during poor habitat years birds may choose not to winter in Guánica). We did not model breeding-season rainfall on capture probabilities as we did not believe this would affect a migrant's decision to winter in Guánica Forest. We also included the time-dependent and constant capture probability models in our initial model set to evaluate the effect of rainfall on capture probability, so we had 10 models in our *a priori* model set for Black-and-white Warblers and American Redstarts. The number of recaptured Ovenbirds appeared to decline dramatically in recent years, although the total number of Ovenbirds captured did not. Therefore, in addition to the 10 models above, we also included a linear time trend model on capture probabilities for Ovenbirds. Based on our field observations we hypothesized a declining trend in Ovenbird capture rates.

After the best capture probability model was chosen, we modeled warbler survival under a transient model framework using the best structure on capture probability from our first step. Transient models are important for modeling landbird survival (Chase et al. 1997, Bayne and

Hobson 2002, Hilton and Miller 2003) because they distinguish resident birds with some probability of recapture and survival from transient or nonterritorial birds that disappear after banding and are never recaptured in subsequent years. In this context, transient birds have essentially zero probability of recapture. When mixed in the data set with residents, these transients negatively bias survival estimates for residents (Pradel et al. 1997). This bias can be reduced by modeling survival the first year after capture differently from all years after that first year (Pradel et al. 1997). Previous work with resident birds in Guánica Forest did not warrant the use of transient models because these species showed high site fidelity and stable territories. However, little is known about territoriality or site fidelity of warblers wintering in Guánica (Faaborg and Arendt 1984). Furthermore, a significant number of capture histories for each species represented birds that were banded and then never recaptured, suggesting transient models might be appropriate for these species.

We did not have gender or age information for Ovenbirds, and nearly 90% of Black-and-white Warblers and American Redstarts captured in Guánica were adult females, so sample sizes were too small to include sex or age effects in our survival modeling for these species. Therefore, our global model included time-dependent survival the first year, time-dependent survival for all years after the first year, and the best capture probability model from the first step (ϕ^1 , ϕ^2 , p_{best}). We also included time-dependent survival (no transient effects), and constant survival models both with and without transient effects in this initial model set, to determine whether transient models were warranted for each species. There was no reason to assume that climate would affect nonterritorial migrants in Guánica Forest any differently than winter residents, so we modeled rainfall covariates similarly on both first-year survival and after-first-year survival if transient models were warranted.

MODELING ABUNDANCE ESTIMATES

We used annual capture totals from our net lines and time-specific model-averaged capture probability estimates from our mark-recapture survival analysis to estimate abundance for Black-and-white Warblers and Ovenbirds. Because the last survival rate and last capture rate are confounded in time-dependent models, model-av-

eraged estimates of capture probability were only available for 13 years (1990–2002). We used the following formula to estimate abundance (Williams et al. 2002:244):

$$\hat{N}_i = \frac{n_i}{\hat{p}_i}$$

where \hat{N}_i is abundance at time i , n_i is the total number of individuals caught at time i , (over all net lines), and \hat{p}_i is the estimated capture probability (probability that a member of N_i is caught at time i) from our survival analysis. Since only eight net lines were monitored in 1990, compared to nine lines from 1991–2002, we divided our 1990 estimates of \hat{N} by 0.89 (8/9) to adjust our estimate by the fraction of the total area monitored that year. Variances for annual abundance estimates were derived via the delta method as follows:

$$\text{Var}(\hat{N}_i) \approx \left[\frac{\text{var}(n_i)}{n_i^2} + \frac{\text{var}(\hat{p}_i)}{p_i^2} \right] N_i^2$$

Estimates of annual population size were regressed on rainfall parameters using Proc REG in SAS (SAS Institute 1997). Residual plots suggested errors were independent and normally distributed, so we did not use transformations. Since warblers were captured in January or February of each year, we regressed rainfall parameters from the previous calendar year with the current year's estimates of abundance (Table 1). We used AIC_c and associated model selection statistics (ΔAIC_c , AIC_c weights) to choose our best regression model for population size (Burnham and Anderson 2002). All values reported are means \pm SE unless otherwise indicated.

RESULTS

SOURCE OF WINTER RESIDENT WARBLERS

We obtained δD values from tail feathers of 15 Ovenbirds, 15 American Redstarts, and 21 Black-and-white Warblers in 2003. These isotope values were then placed relative to contour maps developed for feather δD isotope values for North America, where contours run generally east and west in the eastern United States but become more diagonal northeast to southwest in Canada. Stable-isotope values for each individual are shown as straight lines in Figure 1 that approximate the location of that isotope contour. We were not able to determine where each individual bird occurred on the line; lines

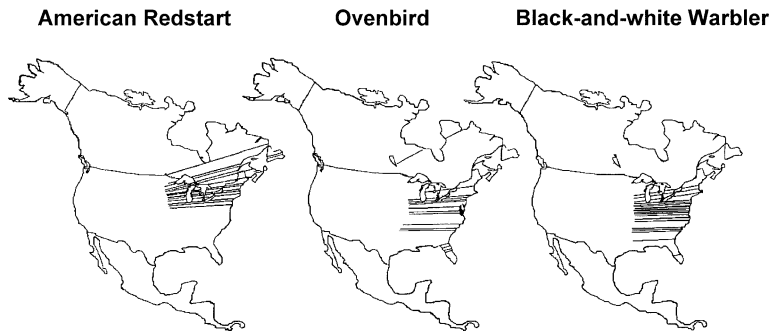


FIGURE 1. Potential breeding locations for individuals of three warbler species sampled in Guánica Forest, Puerto Rico, during 2003 and analyzed using stable-hydrogen isotope ratios. Each line delineates the approximate location of the deuterium contour corresponding to an individual's tail feather.

terminate in the Midwest at the approximate western limit of the breeding range for these species.

According to feather δD values nearly all of our birds came from the eastern or central United States, with a few birds from as far north as Canada (Fig. 1). Black-and-white Warblers (mean value -60‰) originated throughout the eastern United States, with only a few birds from as far north as the Maine—Ontario—Minnesota contour. Ovenbirds (mean value -63‰) had a similar range, but with fewer birds in the southeastern U.S. and only one bird from northern Canada. Several American Redstarts (mean value -86‰) occurred in southeastern Canada, and no birds were from farther south than the Delaware—Iowa contour. Based on these isotope maps, we investigated relevant breeding season rainfall from three regions in the U.S. For Black-and-white Warblers and Ovenbirds we modeled population size and survival with rainfall from the Northeast, Southeast and Central Regions, and for American Redstarts we used Northeast, Central and East North Central Region rainfall for all modeling (Table 1).

RAINFALL AND SURVIVAL RATE MODELS

Black-and-white Warbler. We captured 516 Black-and-white Warblers between 1989 and 2003. There was no indication of overdispersion or lack of fit for the general CJS model ($\phi_t p_t$; $\chi^2_{36} = 18.0$, $P = 1.00$; $\hat{c} < 1.0$). The capture probability model with the lowest AIC_c included first-six-months rainfall total (FIR) as a covariate; however, model weight was only 1.2 times better (0.21 vs. 0.18) than the second-best model with constant capture probability ($\Delta AIC_c =$

0.32). In addition, the slope coefficient for the FIR covariate had 95% confidence intervals that included zero ($\beta = -0.02$; 95% CI = -0.05 to $+0.01$), suggesting a weak effect. Therefore, we chose to use the constant capture probability model to continue with our survival modeling. Capture probability estimates for Black-and-white Warblers from the constant capture probability model with no time or covariate effects was 0.29 ± 0.04 (95% CI = 0.23 – 0.37).

Of the initial models, six were run without rainfall covariates to investigate a potential transient effect; the transient model with first-year survival different from after-first-year survival, with no time dependence, was the best model for Black-and-white Warbler survival (Table 2). Model weight for this best model was over seven times better than the second-best model, which included no time-dependence or transient effects on survival (Table 2). Therefore, we continued the covariate modeling using a transient framework.

After adding the covariate models to the Black-and-white Warbler model set, the survival model with the lowest AIC_c included first-six-months total rainfall (FIR) in Guánica Forest (Table 3). The slope parameter for FIR was negative, but the 95% confidence interval included zero ($\beta = -0.18$; 95% CI = -0.38 to $+0.02$). Two closely competing survival models included total annual (CE_{tot}) and spring (CE_{spr}) rainfall in the Central Region, but neither of these covariate models had slope coefficients with confidence intervals excluding zero (CE_{tot}: $\beta = 2.26$; 95% CI = -0.42 to $+4.93$; CE_{spr}: $\beta = 0.37$; 95% CI = -0.06 to $+0.81$),

TABLE 2. Model selection results for models developed to determine the effect of transients (nonterritorial winter residents) on apparent survival rates (ϕ) of Black-and-white Warblers, Ovenbirds, and American Redstarts. Models were ranked according to Akaike's Information Criterion adjusted for small sample size (AIC_c). The number of parameters (k), ΔAIC_c , and AIC_c weights are given for all models with $\Delta AIC_c < 10$ as well as the global model. Model effects indicated as follows: ϕ^1 = first-year survival, ϕ^2 = After-first-year survival, t = time dependence. Capture probability (p) structure for all survival models reflects the best capture probability model for each species as follows: Black-and-white Warbler: no time or rainfall effects (p); Ovenbird: linear time trend (p_T); American Redstart: time-dependent recapture rates with four years (1994, 1997, 2000, 2001) fixed to zero ($p_{t, 4fixed}$).

| Model | Deviance | k | ΔAIC_c | AIC_c weight |
|--------------------------------------|----------|-----|----------------|----------------|
| Black-and-white Warbler ^a | | | | |
| ϕ^1, ϕ^2 | 178.83 | 3 | 0.00 | 0.86 |
| ϕ | 184.79 | 2 | 3.94 | 0.12 |
| ϕ^1, ϕ^2_t | 162.29 | 15 | 8.20 | 0.01 |
| ϕ^1_t, ϕ^2_t (global) | 150.95 | 28 | 25.97 | 0.00 |
| Ovenbird ^b | | | | |
| ϕ^1, ϕ^2 | 138.24 | 4 | 0.00 | 0.80 |
| ϕ | 143.26 | 3 | 2.99 | 0.18 |
| ϕ^1_t, ϕ^2 | 117.88 | 17 | 6.98 | 0.02 |
| ϕ^1_t, ϕ^2_t (global) | 105.74 | 30 | 26.99 | 0.00 |
| American Redstart ^c | | | | |
| ϕ | 63.48 | 11 | 0.00 | 0.45 |
| ϕ^1, ϕ^2 | 61.36 | 12 | 0.08 | 0.43 |
| ϕ^1_t, ϕ^2 | 33.75 | 25 | 2.68 | 0.12 |
| ϕ_t | 41.98 | 24 | 8.47 | 0.01 |
| ϕ^1_t, ϕ^2_t (global) | 29.78 | 31 | 24.35 | 0.00 |

^a The lowest AIC_c value for this analysis was 910.05.
^b Model-selection criteria were adjusted for overdispersion ($\hat{c} = 1.19$). The lowest QAIC_c value was 547.62, and $\Delta QAIC_c$ and QAIC_c weights are reported in place of ΔAIC_c and AIC_c weights.
^c The lowest AIC_c value in this analysis was 274.71.

so support for these covariates was weak. The transient model with no time dependence ($\phi^1 \phi^2$) was within two AIC_c units of the top covariate models and the 95% confidence limits on the slope coefficient associated with the transient effect did not include zero ($\beta = -0.77$; 95% CI

$= -1.33$ to -0.22) suggesting that the difference in survival between transients and winter residents was the most important aspect of Black-and-white Warbler survival given our current model set. For the two Central Region rainfall parameters, the relationship with Black-and-

TABLE 3. Black-and-white Warbler model selection results for the top five survival (ϕ) models (treating capture probability, p , as constant) and the global model relating rainfall parameters on the wintering and breeding grounds with Black-and-white Warbler apparent survival. Models were ranked by Akaike's Information Criterion adjusted for small sample sizes (AIC_c). The number of parameters (k), ΔAIC_c , and AIC_c weights are given for each model. The global base model was the time-specific transient model with constant capture probability (ϕ^1_t, ϕ^2_t, p). Rainfall variable abbreviations are described in Table 1.

| Model | Deviance | k | ΔAIC_c^a | AIC_c weight |
|--|----------|-----|------------------|----------------|
| $\phi^1_{FIR}, \phi^2_{FIR}$ | 175.62 | 4 | 0.00 | 0.13 |
| $\phi^1_{CE_{tot}}, \phi^2_{CE_{tot}}$ | 175.87 | 4 | 0.26 | 0.11 |
| $\phi^1_{CE_{spr}}, \phi^2_{CE_{spr}}$ | 175.99 | 4 | 0.37 | 0.10 |
| ϕ^1, ϕ^2 | 178.83 | 3 | 1.19 | 0.07 |
| $\phi^1_{F_{sum}}, \phi^2_{F_{sum}}$ | 177.06 | 4 | 1.44 | 0.06 |
| ϕ^1_t, ϕ^2_t | 150.95 | 28 | 25.97 | 0.00 |

^a The lowest AIC_c score in the analysis was 908.86.

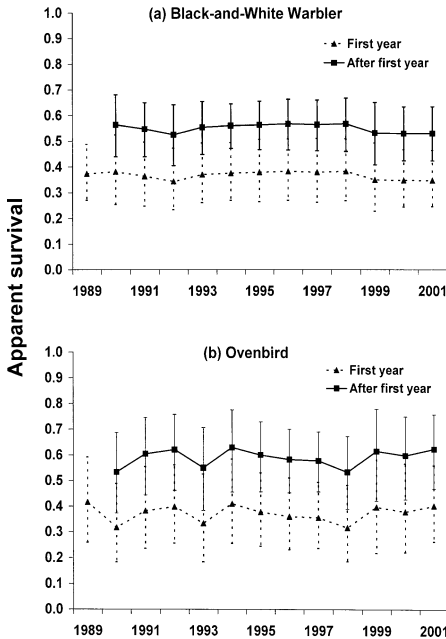


FIGURE 2. Model-averaged apparent survival estimates with 95% CI for (a) Black-and-white Warblers and (b) Ovenbirds wintering in Guánica Forest, Puerto Rico. Survival was estimated using a transient-model structure with first-year survival treated differently than after-first-year survival.

white Warbler apparent survival was as hypothesized, with higher rainfall amounts associated with higher Black-and-white Warbler survival; however, first-six-months rainfall was negatively related to survival, contrary to our hypothesis. Model-averaged estimates of apparent survival (Burnham and Anderson 2002) were not highly variable over time, but were substantially lower

overall for first-year survival (0.34–0.38) compared to after-first-year survival (0.52–0.57; Fig. 2).

Ovenbird. Ovenbirds constituted our second-largest winter-resident capture-recapture data set with 364 individuals. Although there was no indication of lack of fit for the general CJS model ($\phi_t p_t$; $\chi^2_{33} = 39.4$, $P = 0.21$), there was a small amount of overdispersion in the data ($\hat{c} = 1.19$), so we used QAIC_c (Burnham and Anderson 2002).

The capture probability model with the lowest QAIC_c included a time trend on capture rates and had >12 times more support based on model weights than the second-best model (0.88 vs. 0.07), which included the cumulative effect of total rainfall in Guánica during the previous two years (SUM). As hypothesized, the time trend was negative and the slope coefficient had 95% confidence intervals that did not include zero ($\beta = -0.18$; 95% CI = -0.28 to -0.08), suggesting this was a significant effect. We retained this time trend structure on capture probability (p_T) to continue our survival modeling.

Similar to Black-and-white Warblers, the transient model with first-year survival different from after-first-year survival with no time-dependence had almost 4.5 times as much support as the second-best model (Table 2), which included no time-dependence or transient effects on survival. So, we continued the covariate modeling using a transient framework.

QAIC_c model results suggested we had three competitive ($\Delta\text{QAIC}_c < 2.0$) survival models that included different rainfall covariates for Ovenbirds (Table 4). The model with the lowest

TABLE 4. Ovenbird model selection results for the top five survival (ϕ) models (with a linear trend on capture probability; p_T) and the global model relating rainfall parameters on the wintering and breeding grounds with Ovenbird apparent survival. Models were ranked by Akaike's Information Criterion adjusted for small sample sizes and overdispersion (QAIC_c · $\hat{c} = 1.19$). The number of parameters (k), ΔQAIC_c , and QAIC_c weight are given for each model. The global base model was the time-specific transient model with a time-trend on capture probability (ϕ^1_t , ϕ^2_t , p_T). Rainfall variable abbreviations are described in Table 1.

| Model | Deviance | k | ΔQAIC_c^a | QAIC _c weight |
|---|----------|-----|-------------------------|--------------------------|
| $\phi^1_{\text{SE.smr}}$, $\phi^2_{\text{SE.smr}}$ | 133.06 | 5 | 0.00 | 0.25 |
| $\phi^1_{\text{US.tot}}$, $\phi^2_{\text{US.tot}}$ | 133.98 | 5 | 0.91 | 0.16 |
| ϕ^1_{TDFN} , ϕ^2_{TDFN} | 135.03 | 5 | 1.97 | 0.09 |
| ϕ^1 , ϕ^2 | 138.24 | 4 | 3.13 | 0.05 |
| ϕ^1_{OND} , ϕ^2_{OND} | 136.45 | 5 | 3.38 | 0.05 |
| ϕ^1_t , ϕ^2_t | 105.74 | 30 | 26.99 | 0.00 |

^a The lowest QAIC_c score in the analysis was 544.49.

TABLE 5. American Redstart model selection results for the top five survival (ϕ) models (time-dependent capture probability with four years fixed to zero; $p_{t, 4\text{fixed}}$) and the global model relating rainfall parameters on the wintering and breeding grounds with apparent survival. Models were ranked by Akaike's Information Criterion adjusted for small sample sizes (AIC_c). The number of parameters (k), ΔAIC_c , and AIC_c weight are given for each model. The global base model was the time-specific transient model with a time-trend on capture probability ($\phi^1_t, \phi^2_t, p_t, p_{t, 4\text{fixed}}$). Rainfall variable abbreviations are described in Table 1.

| Model | Deviance | k | ΔAIC_c^a | AIC_c weight |
|--|----------|-----|------------------------|-----------------------|
| $\phi^1_{\text{FIR}}, \phi^2_{\text{FIR}}$ | 48.70 | 13 | 0.00 | 0.90 |
| $\phi^1_{\text{CE_spr}}, \phi^2_{\text{CE_spr}}$ | 55.77 | 13 | 7.07 | 0.03 |
| $\phi^1_{\text{F_dfn}}, \phi^2_{\text{F_dfn}}$ | 57.41 | 13 | 8.71 | 0.01 |
| $\phi^1_{\text{F_sum}}, \phi^2_{\text{F_sum}}$ | 58.03 | 13 | 9.33 | 0.01 |
| $\phi^1_{\text{TOT}}, \phi^2_{\text{TOT}}$ | 58.78 | 13 | 10.08 | 0.01 |
| ϕ^1_t, ϕ^2_t | 29.78 | 31 | 24.18 | 0.00 |

^a The lowest AIC_c score in the analysis was 264.34.

QAIC_c suggested a positive relationship between summer rainfall in the Southeast Region (SE_smr) and Ovenbird survival (Table 4). The two other competitive models included total U.S. rainfall (US_TOT), and deviations from normal for total rainfall on the wintering grounds (TDFN), both of which were negatively related to Ovenbird survival. Only the top model had confidence intervals for the rainfall coefficient that did not include zero ($\beta = 0.51$, 95% CI = 0.06–0.95). Model-averaged estimates of annual survival (Burnham and Anderson 2002) for Ovenbirds were more variable across time than for Black-and-white Warblers, ranging from 0.32 to 0.42 for first-year survival and from 0.53 to 0.63 for after-first-year survival (Fig. 2).

American Redstart. The American Redstart data set was the smallest of the winter-resident data sets we analyzed, containing 250 individuals. There was no indication of overdispersion or lack of fit for the general CJS model ($\phi_t p_t$; $\chi^2_{15} = 7.4$, $P = 0.95$; $\hat{c} < 1.0$). However, modeling capture probability for this species proved to be problematic, as we observed large fluctuations in the proportion of banded individuals that were captured each year. Our best capture probability model was time dependent with almost twice the AIC_c weight as the next best model containing the sum of total rainfall for the previous 2 years in Guánica (0.58 vs. 0.32). However, capture probability estimates for the years 1994, 1997, 2000, and 2001 were essentially zero in this time-dependent model, and precision was low. In order to increase precision of the other parameters and improve parsimony, we ran an *a posteriori*, time-dependent model in

which we fixed these four capture rates to zero ($p_{t, 4\text{fixed}}$). This improved, time-dependent model received strong support via model weight (AIC_c weight = 0.99) and precision of our capture probability estimates was improved, so we used this structure on capture probability to continue survival modeling.

The transient model on survival was much less strongly supported for American Redstarts than for Black-and-white Warblers or Ovenbirds and was not the model with the lowest AIC_c (Table 2), likely because of several years with recapture rate estimates equal to zero. However, the best transient model was highly competitive with the best model without transient or time-dependent effects ($\Delta\text{AIC}_c = 0.08$; Table 2). Given the importance of the transient model for the other warbler species, the large number of banded American Redstarts we never recaptured, and the highly competitive ranking of our best transient model, we decided to continue our covariate model using the transient model structure.

Similar to Black-and-white Warblers, our best rainfall-covariate survival model for American Redstarts included the first-six-months rainfall in Guánica Forest (FIR) and had 30 times more support than the second-best model (Table 5). Similar to Black-and-white Warblers, there was a negative relationship between FIR and American Redstart survival; however, confidence intervals on the slope of this parameter also included zero ($\beta = -1.41$; 95% CI = -3.16 to $+0.33$). The second-best model included spring rain in the Central Region, but this model was not competitive ($\Delta\text{AIC}_c > 7$) and confidence intervals on the slope coefficient also included zero ($\beta = 0.30$; 95% CI = -0.06 to $+0.66$).

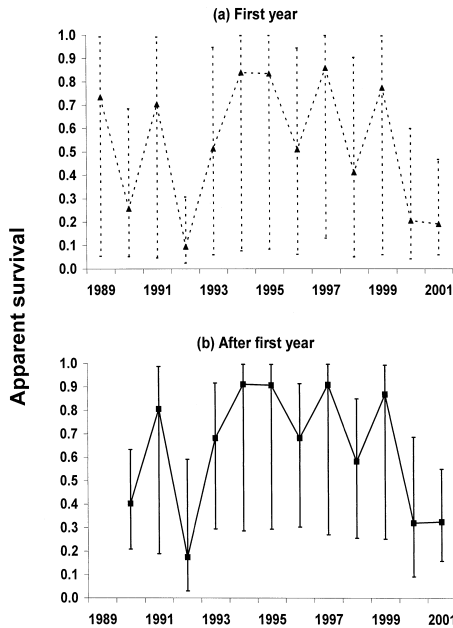


FIGURE 3. Model-averaged apparent survival estimates with 95% CI for American Redstarts wintering in Guánica Forest, Puerto Rico with (a) first-year survival modeled differently than (b) after-first-year survival (i.e., transient model structure).

Model-averaged estimates for first-year survival were very imprecise, but slightly better for after-first-year survival compared to first-year survival (Fig. 3). In general, survival rates for transients vs. residents were very similar, which supported the model selection results. Survival estimates were highly variable across time, ranging from lows of <20% to highs over 90%.

RAINFALL AND POPULATION SIZE ESTIMATES

Model-averaged estimates of annual capture probability from the initial model set used to model capture rates in the first step of our survival modeling were combined with capture totals to develop abundance estimates (Fig. 4). Because our capture probability estimates for American Redstarts were imprecise and we had 4 years of essentially zero estimates (Fig. 4), we could not use these capture probabilities to generate reliable estimates of American Redstart abundance. Therefore, we continued our modeling of abundance with rainfall covariates for Black-and-white Warblers and Ovenbirds only.

Population estimates for Black-and-white Warblers and Ovenbirds based on capture totals

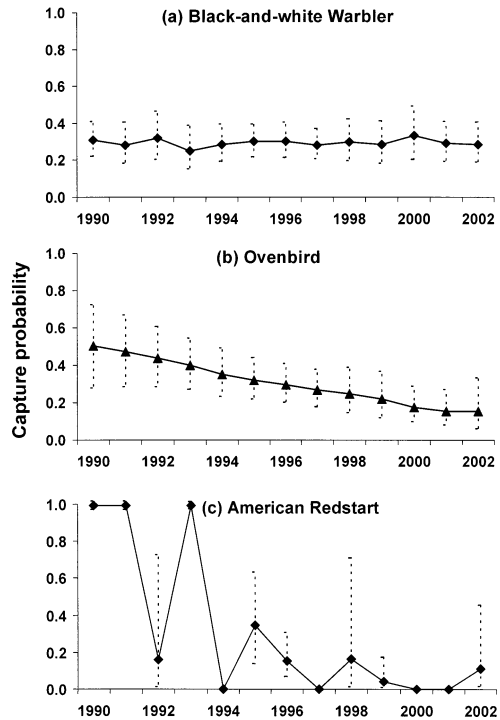


FIGURE 4. Model-averaged capture probabilities with 95% CI for Black-and-white Warblers, Ovenbirds, and American Redstarts wintering in Guánica Forest, Puerto Rico.

and estimates of capture probability from our survival modeling were fairly precise for both species, with better precision for Black-and-white Warblers, which had more consistent capture rates. Abundance of Black-and-white Warblers ranged from a low of 98 in 2002 to a high of 210 in 1991 and appeared to decline slightly over time (Fig. 5). Coefficients of variation for Black-and-white Warbler abundance estimates ranged from 16–25%. Estimates of abundance for Ovenbirds were more variable, and appeared to increase through time, ranging from a low of 46 in 1994 to a high of 257 in 2001 (Fig. 5). Coefficients of variation were generally 20–25%, but ranged from 26–44% in recent years.

Our univariate analysis of Black-and-white Warbler abundance estimates and rainfall parameters suggested that winter rainfall in Guánica, particularly the total deviations from normal each year ($TDFN$; $\Delta AIC_c = 0.00$, AIC_c weight = 0.47) were important predictors of population abundance for this species. This top model received 9.4 times more support than the next best

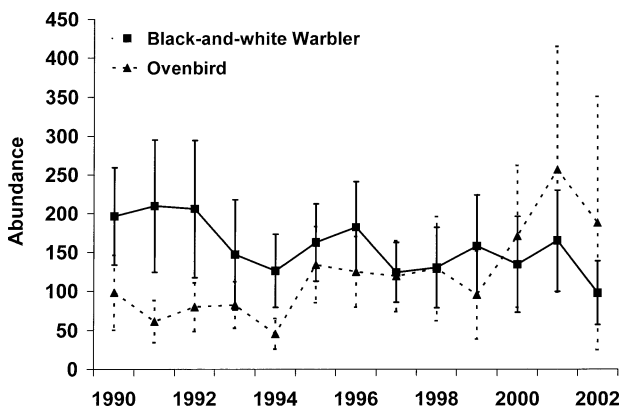


FIGURE 5. Population size estimates with 95% CI for Black-and-white warblers and Ovenbirds wintering in Guánica Forest from 1990–2002.

model (F_{sum}; $\Delta AIC_c = 4.38$, AIC_c weight = 0.05), and explained approximately 33% of the variation in Black-and-white Warbler abundance (adjusted $R^2 = 0.33$; Fig. 6). The best breeding-season rainfall parameter was more than four AIC_c units below the top model (CE_{spr}; ΔAIC_c

= 4.62, AIC_c weight = 0.05), so we did not attempt any *a posteriori* two-factor models with both a winter and a breeding season parameter. In contrast, the rainfall parameters that were the best two predictors of Ovenbird abundance were both breeding-season parameters: total annual rainfall in the U.S. (US_{TOT}; $\Delta AIC_c = 0.00$, AIC_c weight = 0.63), and total annual rainfall in the Central Region (CE_{TOT}; $\Delta AIC_c = 4.30$, AIC_c weight = 0.07). The US_{TOT} parameter had the most support, with nine times the model weight, and it explained 44% of the variation in Ovenbird abundance on the wintering grounds (adjusted $R^2 = 0.44$; Fig. 6).

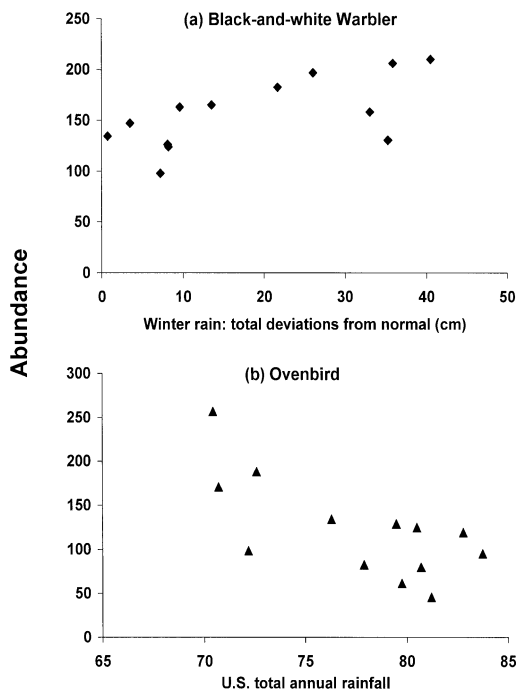


FIGURE 6. Relationship between estimates of (a) Black-and-white Warbler abundance and total deviations in annual rainfall (cm) in Guánica Forest, 1990–2002, and (b) Ovenbird abundance and U.S. total annual rainfall (cm), 1990–2002.

DISCUSSION

In general, the high capture rates and large sample sizes for Black-and-white Warblers and Ovenbirds enabled us to develop reasonably precise estimates of apparent survival for both species. Because we captured transient (nonterritorial) Black-and-white Warblers and Ovenbirds, the transient model framework allowed us to generate unbiased estimates of resident survival for both species. However, the rate of permanent emigration by resident birds, and the subsequent bias on apparent survival, is currently unknown for either species. Resident, adult female Black-and-white Warblers wintering in Guánica appeared to exhibit strong site fidelity to their wintering grounds and maintain consistent territories within winter with resulting stable capture rates and estimates of apparent survival from year to year. In addition, despite a lack of age or sex information for our marked Ovenbird popula-

tion, model fit and precision of estimates suggested that as with Black-and-white Warblers, we were working with a fairly homogeneous population in terms of survival and capture rate. Ovenbird recapture rates appear to be declining for reasons that are unclear, but the decline may simply be related to the increased number of Ovenbirds wintering in Guánica in recent years. More birds in the forest may force birds to shift territories such that they are less likely to be recaptured on our net lines.

Capture totals and capture rates for American Redstarts were highly variable among years, which resulted in some years with very small sample sizes, and capture rates equal to zero. Thus, apparent survival estimates for American Redstarts were imprecise and difficult to interpret. The effect of transients was difficult to distinguish for American Redstarts compared to Black-and-white Warblers and Ovenbirds, but poor recapture probabilities with some years equal to zero decreased our ability to detect transient effects. Our estimates suggested that both survival and recapture rates of adult, female American Redstarts were highly variable among years and, while rainfall covariates may help explain some of this variability, this is clearly a species that requires further study.

SURVIVAL AND RAINFALL

For Black-and-white Warblers and American Redstarts we observed the strongest relationship between apparent survival rates and first six months of rainfall (FIR) in Guánica Forest, whereas for Ovenbirds, summer rainfall in the Southeast Region (SE_{smr}) was the best covariate on survival. For both Black-and-white Warblers and American Redstarts, survival rates declined with increasing amounts of rainfall during the first six months of the prior year, contrary to what we predicted. Earlier work has shown significant patterns between winter-resident capture totals and this same rainfall parameter (Faaborg et al. 1984, Faaborg and Arendt 1992, Dugger et al. 2000), but we did not expect to see this relationship with survival. At least two possible explanations exist for this pattern. First, high rainfall during this period could reduce habitat suitability the following September or October (when migrants return). Consequently, new birds might not settle here and returning birds might either settle and die or permanently emigrate (reflected as mortality in capture-recapture mod-

els). However, this would be contrary to what we know about habitat conditions for the resident birds in response to first-six-months rains, and although high-quality habitat for migrants may be different than for residents, this possibility seems unlikely.

A more plausible alternative involves diffuse interspecific competition between winter residents and permanent residents. We have repeatedly found that high rainfall during January–June is highly correlated with high resident bird populations, as these birds require this rain to end the dry season and allow them to breed (Faaborg et al. 1984, Faaborg and Arendt 1992, Dugger et al. 2000). Thus, plentiful spring rains may mean more resident insectivores, which would increase competition and decrease habitat quality by greatly diminishing insect food resources, resulting in decreased survival or site fidelity and thus lower abundance of winter residents. This could be a particular problem for the American Redstart as it is the same size and has very similar foraging behavior to the very abundant resident Adelaide's Warbler (*Dendroica adelaidae*). Although the Black-and-white Warbler is a bark-foraging specialist, the resident insectivores are perhaps generalized enough in foraging to affect its resource base as well. In contrast to these species, the Ovenbird is a ground-foraging specialist that eats ants (Strong and Sherry 2000), so competition from other winter residents and permanent residents may be reduced. Of the nine resident species known to forage on the ground, only four are predominately ground-feeders, and all are granivores. This may be why Ovenbird survival was more strongly related to rainfall patterns on the breeding grounds.

Hurricane Georges. The hurricane model was nearly competitive for Black-and-white Warblers ($\Delta AIC_c = 2.34$) and the effect was as hypothesized, with survival estimates during the year of the hurricane lower than survival estimates for other years. Support for a hurricane effect was much weaker for Ovenbirds and American Redstarts, and the direction of the effect was only observed as hypothesized for American Redstarts. Hurricane Georges did considerable damage to the Guánica Forest, primarily by breaking tree limbs from their trunks. The forest canopy cover was reduced, but there was little change in the number of stems occurring at breast height (KMD, pers. obs.). The hurricane occurred in

late September, before most winter residents returned, although the great amount of rain associated with the hurricane likely influenced habitat quality in Guánica through the winter. The abundance of a few of the resident species appeared to be affected by the hurricane (JF, unpubl. data), but its effect on winter resident survival was not strong.

POPULATION SIZE VARIATION AND RAINFALL

Consistent with our survival models, the strongest rainfall effect on Black-and-white Warbler abundance was a winter-rainfall covariate, whereas for Ovenbirds, a breeding-season variable was most important. Total year's deviations from normal rainfall (TDFN) were positively correlated with Black-and-white Warbler abundance, which was contrary to initial predictions. However, this variable was an important covariate for survival in resident frugivores (Dugger et al. 2000), with a negative relationship such that increased deviations from normal (too wet or too dry) resulted in decreased survival rates. This relationship between Black-and-white Warblers and TDFN may reflect density-dependent effects of permanent-resident bird populations on the abundance of winter residents.

Ovenbird abundance at Guánica decreased in response to increased rainfall in the U.S., consistent with the relationship we observed between Ovenbird apparent survival and the same variable (second-best survival model), but contrary to what we predicted. However, of the rainfall variables we investigated, total U.S. rainfall was highly correlated with spring rain in the Southeast Region ($r = 0.69$), total rain in the East North Central Region ($r = 0.60$), and total and spring rain in the Central Region ($r = 0.59$, $r = 0.60$, respectively). Thus, total U.S. rainfall may reflect negative effects of high rainfall during the breeding season on overall productivity for a ground-nesting species such as the Ovenbird. High rainfall during certain periods of the breeding season, in some regions, may reduce nest success, by flooding nests or chilling chicks. We did not investigate fall rainfall patterns in this study, but rain in late summer and fall may decrease juvenile survival, perhaps lowering the number of young birds migrating to Guánica each year. Drought conditions have been prevalent in the Midwest since the late 1990s, which coincides with the increase in Ov-

enbird abundance we have observed in Guánica during this same time period. This is an interesting relationship that warrants more research.

WHICH AREA'S RAINFALL MATTERS?

The answer to this question is much less clear for winter-resident survival than it is for abundance, but our results suggest that the rainfall that matters depends on the species being considered. Although no rainfall effects were strongly supported for survival of either Black-and-white Warblers or American Redstarts, our best covariate models for these species included a negative relationship with the same covariate (first-six-months rainfall total), suggesting that despite weak model support in this analysis, these are not spurious results and rainfall on the wintering grounds may be important to both of these species. There was stronger support for the effect of breeding-season rain on Ovenbird survival, which increased during years when summer rains were higher in the Southeast Region.

In contrast, abundance of Black-and-white Warblers and Ovenbirds appeared clearly related to winter and breeding-season rain respectively, as these variables explained a substantial amount of variation in abundance estimates for each species. This is especially striking considering how many factors influence bird abundance, and the fact that we only looked at single-variable rainfall models in this analysis. It is also noteworthy that these general patterns for abundance (winter rain for Black-and-white Warblers and breeding-season rain for Ovenbirds) were consistent with our best survival models for these species.

Ultimately, we will probably find that all rainfall matters, depending on what subset of birds is being considered, but this initial modeling effort has brought us closer to understanding which parameters are important to Black-and-white Warblers, Ovenbirds, and American Redstarts. Furthermore, although we hypothesized direct relationships between rainfall, habitat quality, and winter resident demography, our modeling efforts with Black-and-white Warblers suggest these mechanisms can be much more complex and include the effects of other species. Both our survival and abundance models for Black-and-white Warblers suggested a density-dependent mechanism, linking the survival and abundance of this species to the abundance of permanent residents in Guánica. This is an interesting avenue of continued research, requiring

continued monitoring of wintering and permanent-resident populations, and an understanding of how those populations fluctuate together over time. In addition, our ongoing efforts to estimate survival, recapture rates, and abundance for resident species in Guánica Forest will allow us to test some of the density-dependent mechanisms hypothesized here. Finally, continued use of stable isotopes can increase our understanding of the specific, regional breeding areas used by the birds wintering in Guánica Forest.

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