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GREATER MASS INCREASES ANNUAL SURVIVAL OF PROTHONOTARY WARBLERS WINTERING IN NORTHEASTERN COSTA RICA

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Abstract. Estimates of survival of nearctic–neotropic migrants have broadened our understanding of life-history variation across taxa and latitudes. Despite the importance of assessing migrants' survival through all phases of their life-cycle, data from their tropical winter ranges are few. In this study we used 14 years of data on captured birds to quantify the influence of mass on the annual survival of the Prothonotary Warbler (*Protonotaria citrea*) in northeastern Costa Rica and compared our results to survival estimates generated from the breeding grounds. Furthermore, from estimates of population growth (λ) based on marked individuals, we projected the Prothonotary Warbler's demographic trajectory at our study site. Our results suggest that heavier individuals had higher rates of annual survival. Population growth at our study sites was stable, punctuated by swings in growth and decline. We believe the benefits of weight gain (preparation for migration and intraspecific competition for territories) outweigh inherent costs (greater susceptibility to predation).

Key words: *Costa Rica, migrant, survival, population growth, mass, over-winter.*

Una Masa Mayor Aumenta la Supervivencia Anual de los Individuos de *Protonotaria citrea* que Invernan en el Noreste de Costa Rica

Resumen. Las estimaciones de supervivencia de los migrantes neárticos–neotropicales han ampliado nuestro entendimiento de las variaciones en la historia de vida a través de los taxones y las latitudes. A pesar de la importancia de evaluar la supervivencia de los migrantes en todas las fases de sus ciclos de vida, son pocos los datos provenientes de sus rangos de invernada tropicales. En este estudio empleamos 14 años de datos de aves capturadas para cuantificar la influencia de la masa en la supervivencia anual de *Protonotaria citrea* en el noreste de Costa Rica y comparamos nuestros resultados con las estimaciones de supervivencia generadas desde los territorios de reproducción. Más aún, a partir de las estimaciones de crecimiento poblacional (λ) basadas en individuos marcados, proyectamos la trayectoria demográfica de *P. citrea* en nuestro sitio de estudio. Nuestros resultados sugieren que los individuos más pesados tuvieron tasas de supervivencia anual más altas. El crecimiento poblacional en nuestro sitio de estudio fue estable, puntuado por vaivenes en crecimiento y disminución. Creemos que los beneficios del aumento de peso (preparación para la migración y competencia intraespecífica por los territorios) superan los costos inherentes (mayor susceptibilidad a la depredación).

INTRODUCTION

Demographic estimates of nearctic–neotropic migrant landbirds ("migrants") have informed life-history variation across taxa and conservation efforts across latitudes (e.g., Rappole et al. 1989, Karr et al. 1990, Conway et al. 1995, Saracco et al. 2009a). Despite broad interest in measuring migrants' demography through their entire life cycle, the majority of monitoring efforts remain in temperate regions (DeSante and Saracco 2009, Saracco et al. 2009b). The relatively few studies addressing wintering migrants have examined factors limiting population growth (Sillett and Holmes 2002), associations between condition and arrival on the breeding grounds (Marra et al. 1998), how conditions migrants experience on their winter grounds affect summer breeding (e.g., carry-over effects; Norris 2005), climatic influences on survival (Sillett et al. 2000), and physiological condition (Wolfe and Ralph 2009). In this vein, the Tortuguero Integrated Bird Monitoring Project was initiated in 1994 in northeastern Costa Rica to broaden our collective knowledge of tropical and migrant birds (Ralph et al. 2005). Although smaller in geographic scale than similar efforts such as the Institute for Bird Population's

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Monitoreo de Sobrevivencia Invernal (DeSante et al. 2005), the temporal breadth of bird-capture data from Tortuguero is unparalleled in Costa Rica and can provide novel insights into migrants' natural history.

For example, Wolfe and Ralph (2009) found that migrants' body mass is correlated with weather and habitat quality, dry weather associated with El Niño possibly suppressing fruit eruptions, resulting in leaner frugivorous migrants. Similar findings have been reported in Jamaica, where wintering American Redstarts (*Setophaga ruticilla*) lost mass in poorer-quality habitat and heavier individuals returned to the breeding grounds earlier, clearly indicating that body mass in winter was positively correlated with habitat quality (Sherry and Holmes 1996, Marra et al. 1998). Strong and Sherry (2000) reported corresponding results in wintering Ovenbirds (*Seiurus aurocapilla*): through the winter, individuals lost more mass in poorer-quality habitats. Conversely, in the southeastern United States, heavier wintering Henslow's Sparrows (*Ammodramus henslowii*) were associated with poorer-quality habitat, suggesting that extra mass may mitigate unpredictable resources in low-quality habitats (Strong and Sherry 2000, Johnson et al. 2011). Winker et al (1990) found a similar pattern with the Wood Thrushes (*Hylocichla mustelina*) wintering in Mexico, transient individuals being significantly heavier than their resident counterparts. Contradictory interpretations from populations of wintering birds, pertaining to the acquisition of mass and habitat quality, obscures broad relationships between winter mass and migrants' fitness.

In this study we used 14 years of bird-capture data from Tortuguero, Costa Rica, to explore relationships between survival and mass of an overwintering population of the Prothonotary Warbler (*Protonotaria citrea)*. We also used bird-capture data to examine population growth to determine the demographic trajectory of Prothonotary Warblers wintering at Tortuguero.

STUDY SITE

Monitoring stations were located near the village of Tortuguero on the northeast coast of Costa Rica, in Limón Province (83° 31′ W, 10° 33′ N). The study area is dominated by lowland, wet broadleaf tropical forest (Holdridge 1987) that is dissected by canals and rivers that flow east into the Caribbean Sea. The area receives an average rainfall of more than 5 m per year (Janzen 1983), making it one of the wettest regions in the country. Tortuguero's wet season begins from mid to late April and continues through January. The wet season is interrupted by a short dry season during September. A long dry season tends to occur through February and March, but precipitation is common even during this period (Janzen 1983). Forests surrounding the village are protected by the 170 000-ha Tortuguero National Park and Barra del Colorado National Wildlife Refuge (Ralph et al. 2005).

METHODS

Since 1995, up to seven capture stations located near the village of Tortuguero have operated 10–15 mist nets for most of the year. For this study, we selected the four stations that routinely capture Prothonotary Warblers and have been continuously operated annually from mid-January to November since 1995. One "central" station was run at least 3 times every 10 days, and the other "satellite" stations were run at least once every 10 days. Protocols for capturing and processing birds were described in Ralph et al. (1993). We used records of wintering Prothonotary Warblers captured from 1995 through 2008, for the months December, January, and February. Although each winter encompasses two calendar years, for simplicity's sake, we identify each winter by December's calendar year (e.g., the winter of 1996 is defined as December 1996 through February 1997).

We used condition indices to represent a bird's mass, where condition index = mass × 100/wing chord (Winker 1995). Some studies have generated condition indices on the basis of residuals from an ordinary least-squares linear regression of body mass against a linear measure of size (i.e., wing chord; Green 2001). We considered residuals unsatisfactory for the present study because of frequently unsatisfied assumptions associated with analyses by ordinary least squares of residuals as they pertain to condition indices (see Green 2001).

We estimated apparent survival of Prothonotary Warblers by formulating and ranking candidate Cormack–Jolly–Seber models by their associated corrected Akaike information criterion (AIC_c) in program MARK (White and Burnham 1999). In addition to varying modeled probability of survival (ϕ) and recapture (p) by time, we included time-since-marking models with ϕ, where survival in the first interval (ϕ_1) differed from survival during the second (ϕ_2) and subsequent capture intervals (Blake and Loiselle 2008, Cooch and White 2012). Time-since-marking models can account for deflation of apparent survival due to the effects of transients moving through the study area (Johnston et al. 1997, Pradel et al. 1997).

In the models we also included bird-condition indices as individual covariates to examine the influence of winter mass on annual survival and probability of recapture. In total, we formulated 15 candidate models representing every possible variation of time and time-since-marking dependency with condition covariates (Table 1). We calculated the overdispersion factor ($\hat{c}$) for each species by dividing the deviance of each species' global model by the deviance estimated via a boot-strapping goodness-of-fit routine (1000 iterations; Cooch and White 2012). The resulting $\hat{c}$ value was 2.36, indicating relatively good model fit. To examine net shyness, we used program RELEASE; its results were uniformly not significant ($P > 0.05$), further supporting adequate model fit. To produce

TABLE 1. Candidate Cormack–Jolly–Seber (CJS) models for the Prothonotary Warbler. Model parameters include annual survival (ϕ) and recapture probability (p), varying by time (t), constant time (.), time-since-marking transiency (2./.), and standardized mass (condition). Data associated with each model include differences in AIC_c values between the candidate model and top model (ΔAIC_c), AIC_c weights (w_i) and number of parameters (K). Results are based on Prothonotary Warblers captured in northeastern Costa Rica from December through February, 1995–2008.

Model	ΔAIC_c	w_i	K
ϕ(condition) p(condition)[a]	0.00	0.25	4
ϕ(2./. – condition) p(condition)	0.63	0.18	5
ϕ(2./.) p(.)	1.29	0.13	3
ϕ(2./.) p(condition)	1.31	0.13	4
ϕ(.) p(.)	1.86	0.10	2
ϕ(.) p(condition)	2.25	0.08	3
ϕ(2./. – condition) p(.)	3.10	0.05	4
ϕ(condition) p(.)	3.66	0.04	3
ϕ(2./. – condition) $p(t)$	5.18	0.02	14
ϕ(2./.) $p(t)$	7.77	0.01	15
ϕ(condition) $p(t)$	7.96	0.00	14
ϕ(.) $p(t)$	8.28	0.00	14
$\phi(t)$ p(condition)	10.23	0.00	14
$\phi(t)$ p(.)	12.64	0.00	14
$\phi(t)$ $p(t)$	22.15	0.00	25

[a]AIC_c of the top model was 359.94.

more general estimates of annual survival, we averaged all candidate models encompassing 0.95 of the total AIC_c weight.

Finally, to examine demographic trajectory, we employed Pradel models in program Mark to generate estimates of annual population growth (λ). All candidate models varied λ, ϕ, and p by time for a total of eight candidate models, and, as in the Cormack–Jolly–Seber analysis, we averaged all Pradel models encompassing 0.95 of the total AIC_c weight to produce general estimates of λ (Table 2).

RESULTS

During winters between 1995 and 2008, we captured Prothonotary Warblers 354 times, of which 192 were recaptures of previously banded birds (many individuals were recaptured multiple times), representing a total of 212 individuals. The birds' mass and wing length varied (Fig. 1). The Cormack–Jolly–Seber routine of model selection yielded a top model with condition-index covariates associated with ϕ (β = 0.43, 95% CI = 0.01, 0.84) and p (β = –0.73, 95% CI = –1.20, –0.26), suggesting that heavier wintering birds had increased annual survival and were recaptured less often. Eight models encompassed 0.95 of the total AIC_c weight and were subsequently averaged, yielding an estimate of annual survival (ϕ) of 0.55 (SE = 0.06) and an estimate of annual recapture probability (P) of 0.42 (SE = 0.08).

The Pradel model-selection routine yielded four models that encompassed 0.95 of the total AIC_c weight and were subsequently averaged, yielding estimates of λ for 1995 through 2008; however, the estimate of λ for 1996 failed to statistically converge and we excluded it from the results. To explore trends of population growth in the Prothonotary Warbler, we ran a linear regression in program R (R Development Core Team 2011), regressing estimates of λ with year and found no significant trend ($P > 0.05$, adjusted $r^2 = 0.04$; Fig. 1).

TABLE 2. Candidate Pradel models. Model parameters include annual survival (ϕ), probability of recapture (p), and population growth (λ), which varied by time (t) and constant time (.). Data associated with each model include difference in AIC_c values between the candidate model and top model (ΔAIC_c), AIC_c weights (w_i) and number of parameters (K). Results are based on Prothonotary Warblers captured in northeastern Costa Rica from December through February, 1995–2008.

Model	ΔAIC_c	w_i	K
$\phi(t)$ p(t) $\lambda(t)$[a]	0.00	0.45	27
ϕ(.) $p(t)$ λ(.)	0.49	0.35	16
ϕ(.) $p(t)$ $\lambda(t)$	2.67	0.12	23
ϕ(.) p(.) $\lambda(t)$	3.36	0.08	15
$\phi(t)$ p(.) $\lambda(t)$	16.92	0.00	27
$\phi(t)$ p(t) λ(.)	17.70	0.00	28
ϕ(.) p(.) λ(.)	34.80	0.00	3
$\phi(t)$ p(.) λ(.)	46.20	0.00	15

[a]AIC_c of the top model was 1345.03.

DISCUSSION

At our study site, we found that the annual survival of heavier wintering Prothonotary Warblers was greater than that of their leaner counterparts. Although, to our knowledge, our study is the first to include body-condition indices within survival models for a wintering population of a migratory bird, our results are similar to those of other studies that have correlated increased migrants' body mass with increased fitness in tropical latitudes (Sherry and Holmes 1996, Marra et al. 1998,

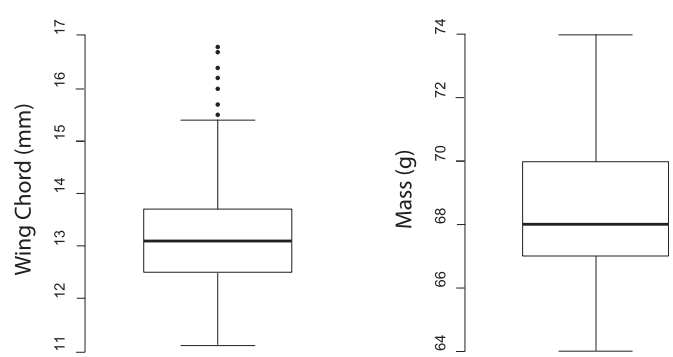

FIGURE 1. Tukey boxplots (showing median, quartiles, and outliers) of wing chord (mm) and mass (g) of Prothonotary Warblers captured in northeastern Costa Rica from December through February, 1995–2008.

Norris et al. 2003). Conversely, several studies have demonstrated the opposite effect, that is, heavier individuals wintering in poorer habitat (Winker et al. 1990, Johnson et al. 2011). We believe the rigors of long-distance migration may influence migrants' mass gain so that wintering birds may deposit muscle and fat well before migration to facilitate their successful return to the breeding grounds. Furthermore, our results suggest that wintering Prothonotary Warblers select high-quality habitats that provide the food resources necessary to accumulate fat. Increased mass may increase vulnerability to predators (Lima 1986, Rogers 1987), but, if migration limits populations (Sillett and Holmes 2002), wintering migratory birds may be under strong selective pressure to ensure the successful completion of migration by increasing mass despite the risk of predation. Alternatively, acquiring a winter territory in the tropics may be more daunting because of less habitat available in Central America than in North America (Cox 1985), resulting in more competition for territory. Presumably, competition may be manifested in more fit winter birds gaining mass. Preparation for migration and intraspecific competition are not mutually exclusive and could act synergistically to produce the association we found between Prothonotary Warbler survival and mass. We believe future studies should consider endocrinological methods to correlate differences in migrants' stress hormones with their condition (Marra and Holberton 1998).

In general, our estimate of the Prothonotary Warbler's annual survival in northeastern Costa Rica ($\phi = 0.55$, SE = 0.06) is higher than estimates from North America, for example, those of the Monitoring Avian Productivity and Survival program (MAPS; DeSante et al. 2004) from the south-central ($\phi = 0.48$, SE = 0.05) and southeastern ($\phi = 0.46$, SE = 0.05) United States (DeSante and Kaschube 2009). In addition to interesting patterns of survival, we also found annual to biennial fluctuations in the population of the Prothonotary Warbler we marked in northeastern Costa Rica (Fig. 2).

Although all standard error bars overlapped greatly, our estimates of Prothonotary Warbler population growth oscillated around a value of one, indicating a stable population (Fig. 1). The cyclical nature of Prothonotary Warbler population growth may reflect a Lotka–Volterra model, in which bird communities exhaust food resources at regular intervals or, conversely, predators or disease diminish the population at regular intervals, leading to predictable oscillations of declines followed by increases. We recommend similar studies with resident birds and other species of migrants in northeastern Costa Rica to determine if demographic oscillations reflect statistical vagaries associated with a single species or a broad demographic response to ecologically meaningful phenomena.

Here, we have demonstrated that at our study site in northeastern Costa Rica estimates of the Prothonotary Warbler's annual survival are higher than those based on birds captured on the breeding grounds and that wintering birds' mass is positively associated with annual survival. Additionally, we believe Prothonotary Warblers in northeastern Costa Rica represent a stable population potentially subject to predictable demographic peaks and troughs. We hope our study promotes a continued effort to study migrants' demography on their tropical wintering grounds.

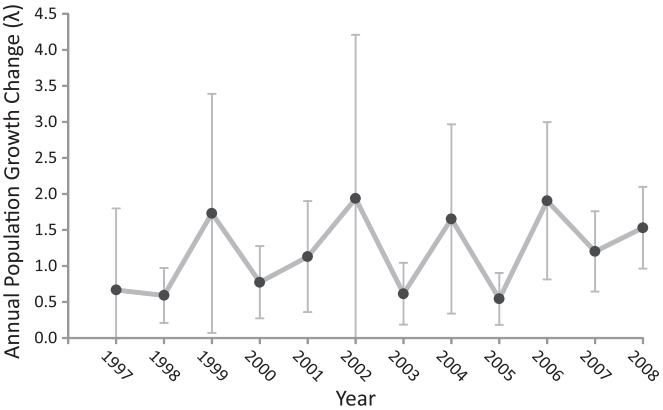

FIGURE 2. Population growth (λ) and associated standard error bars for Prothonotary Warblers captured in northeastern Costa Rica from December through February, 1995–2008.

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