Research Papers

Contrasting Seasonal Survivorship of Two Migratory Songbirds Wintering in Threatened Mangrove Forests

Différence de survie saisonnière chez deux passereaux migrateurs hivernant dans des mangroves menacées

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ABSTRACT. Long-distance migrants wintering in tropical regions face a number of critical conservation threats throughout their lives, but seasonal estimates of key demographic parameters such as winter survival are rare. Using mist-netting-based mark-recapture data collected in coastal Costa Rica over a six-year period, we examined variation in within- and between-winter survivorship of the Prothonotary Warbler (*Protonotaria citrea;* 753 young and 376 adults banded), a declining neotropical habitat specialist that depends on threatened mangrove forests during the nonbreeding season. We derived parallel seasonal survivorship estimates for the Northern Waterthrush (*Seiurus noveboracensis;* 564 young and 93 adults banded), a cohabitant mangrove specialist that has not shown the same population decline in North America, to assess whether contrasting survivorship might contribute to the observed differences in the species' population trajectories. Although average annual survival probability was relatively similar between the two species for both young and adult birds, monthly estimates indicated that relative to Northern Waterthrush, Prothonotary Warblers exhibited: greater interannual variation in survivorship, especially within winters; greater variation in survivorship among the three study sites; lower average between-winter survivorship, particularly among females, and; a sharp decline in between-winter survivorship from 2003 to 2009 for both age groups and both sexes. Rather than identifying one seasonal vital rate as a causal factor of Prothonotary Warbler population declines, our species comparison suggests that the combination of variable within-winter survival with decreasing between-winter survival demands a multi-seasonal approach to the conservation of this and other tropical-wintering migrants.

RÉSUMÉ. Les migrateurs de longue distance qui hivernent dans les régions tropicales font face à d'importantes menaces tout au long de leur vie, et les estimations saisonnières de paramètres démographiques clés, comme la survie hivernale, sont rares. À partir de données de capture-recapture récoltées avec des filets japonais pendant 6 ans au Costa Rica, nous avons examiné la variation de la survie intra- et inter-hivernale de la Paruline orangée (*Protonotaria citrea*; 753 jeunes et 376 adultes bagués), migrateur néotropical en déclin qui dépend des mangroves menacées en dehors de la saison de reproduction. De la même façon, nous avons estimé la survie saisonnière de la Paruline des ruisseaux (*Seiurus noveboracensis*; 564 jeunes et 93 adultes bagués), espèce spécialiste de la mangrove qui cohabite avec la précédente, mais dont les populations n'ont pas montré le même déclin en Amérique du Nord. Ces données ont été utilisées afin d'évaluer si les taux de survie différents des deux espèces peuvent expliquer en partie les différences observées dans leurs trajectoires démographiques. Quoique la probabilité de survie annuelle moyenne était relativement semblable chez les deux espèces, tant pour les jeunes que pour les adultes, les estimations mensuelles ont indiqué que, comparativement à la Paruline des ruisseaux, la Paruline orangée montrait des variations interannuelles plus grandes de son taux de survie (particulièrement durant un même hiver), une plus grande variation de son taux de survie entre les trois sites d'étude, un taux de survie interhivernal moyen plus faible (particulièrement

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chez les femelles) et un déclin prononcé de son taux de survie interhivernal de 2003 à 2009 pour les deux groupes d'âges et les deux sexes. Étant donné les résultats différents obtenus pour nos deux espèces cibles et la variabilité du taux de survie intrahivernal combinée à la diminution du taux de survie interhivernal observées chez la Paruline orangée, nous croyons que la conservation de cette espèce et celle d'autres migrateurs néotropicaux doivent être abordées selon une approche multi-saisonnière.

Key Words: *conservation; demography; endangered; mark-recapture; neotropical migrant; northern waterthrush; passerine; prothonotary warbler; survival*

INTRODUCTION

Long-distance migrants are vulnerable to changes occurring in any of their seasonal habitats, yet their broad geographic distributions often hinder the identification of specific threats to population persistence. In addition to loss and degradation of habitat on their breeding grounds, population declines of neotropical migrants in North America (e.g., Keast and Morton 1980, Terborgh 1989, Stutchbury 2007, North American Bird Conservation Initiative 2009) have been variably attributed to breeding-season mortality (Bohning-Gaese et al. 1993), extreme seasonal weather conditions (Sauer et al. 1996, Butler 2000, Dionne et al. 2008), and destruction of tropical wintering habitats (Robbins et al. 1989, Rappole and McDonald 1994, Sherry and Holmes 1996). Temporal variation in population trends (Hussell et al. 1992) and emerging hazards throughout the migratory cycle (e.g., Stutchbury 2007, Calvert et al. 2009) suggest that songbird declines cannot be uniformly linked to one factor. As such, seasonal drivers of demography, i.e., productivity and survivorship, may need to be examined at the scale of individual populations.

The Prothonotary Warbler (*Protonotaria citrea,* hereafter warbler) is a neotropical migrant of particular conservation concern given its decline in abundance across most of its breeding range (COSEWIC 2007, Sauer et al. 2008) and its dependence on specialized habitats for both breeding (secondary cavities in forested wetlands) and wintering (tropical coastal mangroves; Petit 1999). Results from the North American Breeding Bird Survey showed a statistically significant decline averaging 1.1% annually during the period of 1966–2007, or close to 40% decline overall (Sauer et al. 2008). The warbler has been placed on the continental Partners In Flight's "watch list" for landbirds in North America (Rich et al. 2004) and is designated an endangered species under Canada's *Species at Risk Act* (COSEWIC 2007) because of documented declines and threats. Ongoing degradation of wetland forest breeding habitats throughout its range (e.g., Heltzel and Leberg 2006) has motivated the initiation of artificial nest-box conservation programs to increase the number of available nesting cavities, but predation, parasitism by brown-headed cowbird (*Molothus ater*), and interspecific competition for boxes with species such as house wren (*Troglodytes aedon*) appear to be impeding its recovery (COSEWIC 2007).

In addition to changes in the quantity and quality of breeding habitat, nonbreeding habitat change may also be limiting the recovery of this species (COSEWIC 2007). Wintering prothonotary warblers are primarily concentrated within a relatively small area of coastal mangrove forest in Central America and northern South America. Mangrove forest is a highly threatened habitat that faces increasing destruction stemming from tourism development, shrimp farming, salt extraction, and other intensive human disturbance (Terborgh 1989, McCracken 1998, Petit 1999, FAO 2007). A strong association with this restricted wintering habitat coupled with high winter site fidelity may make prothonotary warblers particularly sensitive to tropical habitat alteration (Warkentin and Hernandez 1996). However, another warbler species highly reliant on these mangrove wintering habitats, the Northern Waterthrush (*Seiurus noveboracensis,* hereafter waterthrush; Eaton 1995), has shown relatively stable trends in abundance over the same time period (Sauer et al. 2008), suggesting that the two species may respond differently to habitat change or that other factors may be implicated in prothonotary warbler declines.

The shared dependence on mangrove forests by both of these winter-habitat specialists presents a

valuable opportunity to quantify how seasonal demographics may differ between similar species. From 2003 to 2009, standardized mist-netting at three sites on the Pacific coast of Costa Rica allowed for the mark and recapture of wintering warblers and waterthrush on a monthly basis from November through March. Here, we use these data to estimate within-winter survivorship (S_{ww}) and between-winter survivorship (S_{bw}) for warblers (PROW) and waterthrush (NOWA), as well as to examine variation in survivorship by age and sex and over time for these two species that share a specialized wintering habitat.

METHODS

Study sites and data collection

From November to March each year, beginning in November 2003 and ending in March 2009, mist-netting and banding of wintering migrants was conducted in the province of Guanacaste on the north Pacific coast of Costa Rica. Study sites in Estero Iguanita (ESIG; 10°37'47" N, 85°37'42" W), Estero Naranjo (ESNA; 10°46'56" N, 85°39'52" W) and Estero Tamarindo (ESTA; 10°19'49" N, 85°50'24.5" W) were located in mangrove swamps (Southern Pacific Coast Mangroves; WWF 2009) dominated by Black Mangrove (*Avicennia germinans*), in transition zones adjacent to dry coastal forest. A study site at Playa Grande (PLGR; 10°19'40" N, 85°50'39" W and 1 km from ESTA) was located in a dry coastal mixed forest (Central American dry forest; WWF 2009). Given the frequent observations of daily bird movements between neighboring ESTA and PLGR (J. Woodcock, *personal observation*), these two sites were pooled for the purposes of survival estimation (denoted ESTA-PLGR). Banded birds were not recorded moving among the other sites. Straight-line distances among sites were as follows: ESIG was 17.4 km south of ESNA, and ESTA-PLGR was 40.5 km southwest of ESIG and 50.3 km south-southwest of ESNA.

The capture protocol followed the *Monitoreo de Sobrevivencia Invernal* (MOSI) program standards (see DeSante et al. 2004). Sixteen mist-nets (12 m × 2 m × 30 mm mesh) were used at fixed locations at each site. Nets were opened 30 min before sunrise and typically kept open until sunset, although strong wind conditions resulted in frequent midday net closures at ESNA and PLGR. All birds captured were fitted with individually numbered U.S. Fish and Wildlife Service metal leg bands. Birds were identified to by sex (for warblers only) and age, with age estimated as hatching year to second-year birds (≤ 12 mo old, hereafter young) or older birds (> 12 mo old, hereafter adult) following the observations of Pyle (1997). All within- and between-winter recaptures of banded birds were recorded.

Mist-netting was conducted for three consecutive days once a month at each site; sites were not sampled simultaneously because of logistical constraints, but the interval between sampling occasions at a given site was fairly consistent. Thus, for this analysis, we pooled data across days within each monthly sampling period and assumed that intervals among winter sampling periods (November through March) were all 1 mo in length and, therefore, that the interval between March and the following November was 8 mo in length. No sampling of any sites occurred in November 2003, but all other periods included sampling of at least one site, resulting in a total of 29 sampling periods between December 2003 and March 2009. ESIG was not sampled during 2003–2004, and ESNA was only sampled four times in most years. The total sampling effort ranged between 1001 and 2924 net-h site^{-1} yr^{-1}.

A total of 657 waterthrush (93 adult, 564 young) and 1129 warblers (254 adult male, 122 adult female, 391 young male, 362 young female) were banded over the course of six winters. For both species, the most birds were banded at ESTA-PLGR (648 warblers and 437 waterthrush) and the fewest at ESIG (80 warblers and 63 waterthrush). For survival estimation, banded birds were divided into groups based on species, age (young or adult), sex (warblers only), and site (ESIG, ESNA, ESTA-PLGR). The mark-recapture input derived from these data took the form of a binary encounter history (captured = 1, not observed = 0) over the 29 sampling periods for each of the 1786 individual birds banded.

Model structure

Traditional mark-recapture models use time-series of encounters of individually marked animals to estimate survivorship while accounting for the probability of observation (Cormack 1964, Jolly 1965, Seber 1965, Lebreton et al. 1992). However, the survivorship parameter estimated through these models represents local survival, i.e., the combined probability that an animal survives and returns to

the study site. Demographic survivorship is thus underestimated if individuals emigrate beyond the study site following capture, a bias that may be particularly strong in studies of weakly territorial or "floating" migrants during nonbreeding seasons (e.g., Lefebvre et al. 1994, Lefebvre and Poulin 1996, Warkentin and Hernandez 1996). In our data on banded warblers and waterthrush, there were indeed multiple instances in which individuals captured in the immediate study area during a sampling period in November were not recaptured during the subsequent few months (J. Woodcock, *unpublished data*). However, some of these birds were captured again in March, presumably on their return migration northward after having wintered outside the study area, precluding the use of models applied in other studies that classify and exclude as transients all birds that are captured only once (e.g., Cilimburg et al. 2002, Gardali et al. 2003, Brown and Long 2007).

Multi-state models, allowing estimation of changes in state (with probability ψ) in addition to state-specific survival (S) and recapture probabilities (p), specifically address this bias in local survival estimates by differentiating movement in and out of sampled sites from demographic survivorship (e.g., Arnason 1973, Schwarz 1993). Thus, to account for emigration from and subsequent re-immigration into the study population each November and March, respectively, we designed a multi-state model in which the two states distinguish the group of sampled study sites (state 1) from unobservable nonsampled sites elsewhere (state 2). The proportion of transient migrants, i.e., those present in the study sites in November and March only but wintering elsewhere from December to February, was thus estimated as the probability of changing from state 1 to 2 (ψ_{12}) in the November–December interval. By definition, all transient birds that survived the winter (i.e., from November to March, with probability S_2) were assumed to pass through the study sites again in March ($\psi_{12} = 1$ for the February–March interval) and to have the same probability of capture in March as birds that had remained on the study site. Movement between the two states was defined as impossible ($\psi_{12} = \psi_{21} = 0$) for all other time intervals (i.e., December–January, January–February, and March–November), as was capture of individuals elsewhere (i.e., beyond the study sites; $p_2 = 0$).

This model structure allowed the estimation of five main parameter types: capture probability p_1 for each sampling period; transient probability ψ_{12} (November–December interval only); within-winter survival of birds wintering outside the study sites S_2 (November–March interval); within-winter survival of birds wintering within the study sites S_{ww} (monthly intervals between November and March); and between-winter survival S_{bw} (March–November). All survival probabilities were estimated as monthly values to facilitate comparison among time periods of different lengths; i.e., the varying time intervals of either one, four, or eight months were incorporated into the model structure.

Candidate models and inference

We began with a general model, with parameter variation structured as follows. Recapture probability p_1 was allowed to vary fully by time (i.e., across all 28 recapture periods), species, and site, but was assumed invariant among age and sex groups and was fixed at zero in periods where no sampling occurred (5 of 28 periods at ESIG, 4 of 28 periods at ESNA). This fixing of $p = 0$ applied to all models regardless of constraints imposed, such that only periods with nets open were modeled as a function of other variables (e.g., species, sampling effort). November–December transient probability ψ_{12} was allowed to vary by species, site, age, and sex, but was assumed constant across years; it was not estimated for ESNA (i.e., fixed at zero) because that site was sampled in both November and March in one year only. Within-winter survival of birds wintering elsewhere, S_2, was allowed to vary by year, species, site, age, and sex. Within-winter survival of birds at the sampled sites, S_{ww}, could also vary by year, species, site, age, and sex, but was assumed equal among months within a given year. Finally, between-winter survival S_{bw} was allowed to vary among years, or with species, site, age, or sex. This general model (Table 1, model 53) was denoted as

$$\{p_{[t*sp*site]} \ \psi_{12[age*sex*sp*site]} \ S_{2[t*age*sex*sp*site]} \ S_{bw} S_{ww[t*age*sex*sp*site]}\}.$$

We next built a series of candidate alternative models that were simplifications of the general model to verify whether the data supported variation in parameters by species, age, sex, site, or time, or any interactions among these factors. Additionally, as alternatives to full time-variance across periods, we built models allowing p_1 to vary with sampling effort (total net-hours/period for each site) and survivorship to vary linearly among months within years (for S_{ww} only) or across years (for S_2, S_{bw}, and

Table 1. The five best-fit models of the candidate set, as well as the most general model (in bold) and other models referred to in the text, describing mark-recapture data of wintering prothonotary warblers (PROW) and northern waterthrush (NOWA) in Costa Rica from 2003 to 2009. Each model is shown with its relative rank in the candidate set; its absolute and relative sample-size-corrected Akaike Information Criterion (AIC$_c$ and ΔAIC$_c$) and weight of evidence relative to other models (ωAIC$_c$); its number of parameters K; and the model deviance. Parameters in these models were recapture probability p_1; transient probability ψ_{12}; over-winter survival of transient birds S_2; and within- and between-winter survival of birds at the study sites S_{ww} and S_{bw}, respectively; see text for further details on model characteristics and selection. Parameters could vary additively (+) or interactively (*) by age, species (sp), sex, year (t), site, sampling effort (Effort), or linearly over years (Lin); S_{ww} and S_{bw} are described together when variation was structured the same way for both parameters, but S_{ww} and S_{bw} were never set to be equal.

Rank	Model name	AICc	ΔAICc	ωAICc	K	Deviance
1	$p_{1[t*sp+site]}$ $\psi_{12[age*sex*sp]}$ $S_{2[age*sp]}$ $S_{bw}S_{ww-NOWA[t+age+site]}$ $S_{bw-PROW[age+sex+Lin+site]}$ $S_{ww-PROW[age+sex+t*site]}$	7275.62	0.00	0.9961	76	3813.72
2	$p_{1[t*sp+site]}$ $\psi_{12[age*sex*sp]}$ $S_{2[age*sp]}$ $S_{bw}S_{ww-NOWA[t+age+site]}$ $S_{bw-PROW[sex+age*t+site]}$ $S_{ww-PROW[age+sex+t*site]}$	7287.93	12.31	0.0021	89	3800.04
3	$p_{1[t*sp+site]}$ $\psi_{12[age*sex*sp]}$ $S_{2[age*sp]}$ $S_{bw}S_{ww-NOWA[t+age+site]}$ $S_{bw-PROW[age+sex+t+site]}$ $S_{ww-PROW[age+sex+t*site]}$	7288.97	13.35	0.0013	84	3811.07
4	$p_{1[t*sp+site]}$ $\psi_{12[age*sex*sp]}$ $S_{2[age*sp]}$ $S_{bw}S_{ww-NOWA[t+age+site]}$ $S_{bw-PROW[age+sex+t+site]}$ $S_{ww-PROW[sex+age*t+site]}$	7292.23	16.61	0.0003	89	3804.33
5	$p_{1[t*sp+site]}$ $\psi_{12[age*sex*sp]}$ $S_{2[age*sp]}$ $S_{bw}S_{ww-NOWA[t+age+site]}$ $S_{bw}S_{ww-PROW[sex+age*t+site]}$	7293.88	18.26	0.0001	94	3795.98
7	$p_{1[t*sp+site]}$ $\psi_{12[age*sex*sp]}$ $S_{2[age*sp]}$ $S_{bw}S_{ww-NOWA[t+age+site]}$ $S_{bw}S_{ww-PROW[age*t+site]}$	7295.75	20.13	0.0000	92	3801.86
24	$p_{1[t*sp+site]}$ $\psi_{12[age*sex*sp]}$ $S_{2[age*sp]}$ $S_{bw}S_{ww-NOWA[age]}$ $S_{bw}S_{ww-PROW[age+sex]}$	7333.71	58.09	0.0000	52	3919.82
25	$p_{1[t*sp+site]}$ $\psi_{12[age*sex*sp]}$ $S_{2[age*sp]}$ $S_{bw}S_{ww-NOWA[Lin+age+site]}$ $S_{bw-PROW[age+sex+t+site]}$ $S_{ww-PROW[age+sex+Lin*site]}$	7337.03	61.41	0.0000	96	3835.13
27	$p_{1[t*sp+site]}$ $\psi_{12[age*sex*sp]}$ $S_{2[age*sp]}$ $S_{bw}S_{ww[age*sp]}$	7341.37	65.75	0.0000	50	3931.47
28	$p_{1[t*sp+site]}$ $\psi_{12[age*sex*sp]}$ $S_{2[age*sp]}$ $S_{bw}S_{ww-NOWA[t+age]}$ $S_{bw}S_{ww-PROW[age+sex+t]}$	7342.04	66.41	0.0000	70	3892.14
53	$p_{1[t*sp*site]}$ $\psi_{12[age*sex*sp*site]}$ $S_{2[t*age*sex*sp*site]}$ $S_{bw}S_{ww[t*age*sex*sp*site]}$	**7718.09**	**442.46**	**0.0000**	**468**	**3472.19**
56	$p_{1[Effort^2*sp]}$ $\psi_{12[age*sex*sp]}$ $S_{2[age*sp]}$ $S_{bw}S_{ww[t*age*sex*sp*site]}$	7790.47	514.85	0.0000	326	3828.57
57	$p_{1[Effort*sp]}$ $\psi_{12[age*sex*sp]}$ $S_{2[age*sp]}$ $S_{bw}S_{ww[t*age*sex*sp*site]}$	7807.90	532.28	0.0000	326	3846.00
58	$p_{1[sp+site]}$ $\psi_{12[age*sex*sp]}$ $S_{2[age*sp]}$ $S_{bw}S_{ww[t*age*sex*sp*site]}$	7830.85	555.23	0.0000	310	3900.95

S_{ww}). Given the complexity of the general model and the consequent numerous possible combinations of parameter structures, we built these candidate models in stages, whereby informative parameter structures from one stage were retained for the next stage of model building. In the order in which they were built, these stages examined variation in p_1, ψ_{12}, S_2, S_{bw}, and S_{ww}. Finally, we also built a series of additional parameter-average models, regardless of their fit to the data, to estimate mean values of parameters under simplified model structures (e.g., a model with time-invariant recapture probability, even when time variance was strongly favored during the process of model building).

Inferences regarding parameter variation and model structure were based largely on the Akaike Information Criterion (AIC), a metric representing the inherent trade-off between model complexity and bias (Akaike 1973). We first tested the fit of our general model to the data using a bootstrap goodness-of-fit re-sampling procedure in the program MARK (White and Burnham 1999) and found no evidence of overdispersion (i.e., variation in the data unaccounted for by the general model). Consequently, we had no need for a variance-inflation-factor correction ($\hat{c}$; Lebreton et al. 1992), and proceeded to compare our candidate models based on relative differences in the value of sample-size-corrected AIC_c (ΔAIC_c), where a smaller AIC_c represents greater parsimony (Burnham and Anderson 2002). In cases in which two models differed by $\Delta AIC_c < 2$, we retained the simpler model. Parameters were estimated by maximum likelihood methods using a logit-link in MARK (White and Burnham 1999), and the importance of specific factors was further evaluated based on effect-size confidence intervals.

RESULTS

Recapture probability

Recapture probability p_1 varied with species and time interactively (i.e., temporal patterns differed between waterthrush and warblers) and showed additive differences between sampling sites $\{p_{1[t*sp \; + \; site]}\}$. The recapture probability of waterthrush was higher than that of warblers, and was highest in ESIG and lower but similar at ESNA and ESTA-PLGR for both species. As estimated from the final best-fit model (Table 1, model 1), p_1 varied between a maximum of 0.538 (standard error [SE] =

0.076) for waterthrush at ESIG in January of 2004–2005 and a minimum of 0.023 (SE = 0.013) for warblers in ESTA-PLGR in March of 2003–2004. Neither linear $\{p_{1[Effort*sp]}\}$ nor quadratic $\{p_{1[Effort^2*sp]}\}$ sampling-effort models were supported by the data ($\Delta AIC_c > 70$ relative to an equivalent time-variant model; Table 1, models 56 and 57). Nor was there support for equal p_1 across periods within a winter, or for parallel monthly p_1 variation between winters ($\Delta AIC_c > 30$ compared to the fully time-variant model). Based on a model in which p_1 was equal across all periods (Table 1, model 58), mean recapture probabilities (SEs) at ESIG, ESNA, and ESTA-PLGR, respectively, were 0.331 (0.030), 0.241 (0.022), and 0.210 (0.014) for waterthrush, and 0.219 (0.021), 0.153 (0.013), and 0.131 (0.009) for warblers.

Transient probability

Species, age, and sex, interactively, were the best descriptors of variation in transient probability ψ_{12} $\{\psi_{12[age*sex*sp]}\}$; intersite variation in ψ_{12} was not supported. In the more general models, ψ_{12} was estimated as close to zero for all groups, but in later stages of model selection (i.e., with constraints on other parameters), nonzero estimates of ψ_{12} were obtained for some groups of both species, though always with a high degree of uncertainty. For instance, ψ_{12} was estimated as 0.149 (SE = 0.085) for adult waterthrush in the overall best-fit model (Table 1, model 1); 0.207 (0.079) and 0.084 (0.103) for adult and young waterthrush, respectively, under the best time- and site-invariant model (Table 1, model 24); and 0.181 (0.085) and 0.212 (0.137) for adult female and young male warblers, respectively, under a model without sex-differences in survival (Table 1, model 7). In each of these models, however, ψ_{12} for all other groups was estimated at the zero boundary.

Between- and within-winter survival

Variation in within-winter survival of transient birds S_2 was best described by interactive species and age differences $\{S_{2[age*sp]}\}$. However, the best-fit models all provided boundary estimates of S_2 (i.e., equal to zero or one), suggesting that the data had little power to indicate variation in this parameter, likely because of the few transient individuals and near-zero estimates of ψ_{12}.

Temporal variation in survivorship of birds wintering at the study sites both within winters (S_{ww}) and between winters (S_{bw}) was best described by additive effects of year, age, and site, as well as additive effects of sex for warblers and nonparallel temporal trends among sites for

$S_{ww-PROW}$ ({$S_{bw}S_{ww-NOWA[t + age + site]}$
$S_{bw-PROW[age + sex + t + site]}$ $S_{ww-PROW[age + sex + t*site]}$});

Table 1, model 3). Using this model, we estimated S_{ww}(Fig. 1) and S_{bw} (Fig. 2). Broadly, this model supported the following: parallel interannual variation between age groups for each species, much stronger sex differences in $S_{bw-PROW}$ than in $S_{ww-PROW}$, greater temporal variation in survival of warblers than waterthrush during both seasons, a decline in $S_{ww-PROW}$ over time, and low estimates of S_{bw} for both species in the final year of the study. A modified version of this model without the site differences in survival (Table 1, model 28) further demonstrated the greater variability in survival of warblers than waterthrush, as well as the decrease in within-winter survival of both species during 2008–2009 (Fig. 3).

Constrained versions of the best time-variant model (Table 1, model 3) were used to examine interannual trends in seasonal survivorship. The data did not support linear changes over time (i.e., across years) in within-winter survivorship S_{ww} for either species (Table 1, model 25; $\Delta AIC_c = 48$, which was larger than that for the best time-variant model, with effect size confidence intervals encompassing zero). However, as implied by estimates from the time-variant model (Fig. 2), there was strong evidence for a linear decline in between-winter survivorship S_{bw} for warblers (Table 1, model 1; $\Delta AIC_c > 13$, which was smaller than that for the equivalent time-variant model; logit-transformed mean effect size = –0.365/year, SE = 0.084). This latter model was the best-fitting model among all the candidate models.

Finally, mean monthly survival estimates within and between winters were estimated from a further reduced version of this model without site or year variation in survivorship

({$S_{bw}S_{ww-NOWA[age]}$ $S_{bw}S_{ww-PROW[age + sex]}$}); Table 1, model 24).

These revealed strong seasonal differences in average monthly survival of female warblers (Fig. 4A). Total average survivorship over winter, between winters, and annually were calculated using these monthly

survival estimates for each species-age-sex group as $(S_{ww})^4$, $(S_{bw})^8$, and $(S_{ww}^4 \times S_{bw}^8)$, respectively, and suggested substantial overlap in mean values between the two species (Fig. 4B,C). Moreover, a model of average age-specific survival for each species (i.e., without sex differences in warblers; {$S_{bw}S_{ww[age*sp]}$}; Table 1, model 27) showed largely overlapping confidence limits on estimates between the species for equivalent age groups. Means (SEs, 95% confidence intervals) from this model were:

$S_{ww-NOWA-Adult} = 0.947$ (0.022, 0.884–0.977),
$S_{ww-PROW-Adult} = 0.944$ (0.024, 0.873–0.977),
$S_{ww-NOWA-Young} = 0.906$ (0.036, 0.808–0.956),
$S_{ww-PROW-Young} = 0.929$ (0.031, 0.839–0.971),
$S_{bw-NOWA-Adult} = 0.935$ (0.012, 0.908–0.955),
$S_{bw-PROW-Adult} = 0.922$ (0.012, 0.895–0.943),
$S_{bw-NOWA-Young} = 0.885$ (0.016, 0.850–0.913),
$S_{bw-PROW-Young} = 0.902$ (0.015, 0.868–0.927).

DISCUSSION

Effective identification of conservation priorities demands the quantification of seasonal demographic parameters (Calvert et al. 2009). However, these are often most difficult to assess for the species of greatest concern, as well as those that depend on specialized or threatened habitat, with the result that vital rate estimates for species of conservation priority are highly valuable (e.g., Bakermans et al. 2009). Our estimates of average within- and between-winter survivorship (S_{ww} and S_{bw}, respectively) over a six-year period were similar between co-habitant warblers and waterthrush, suggesting that factors other than survivorship may be driving observed differences in population trends between these two species or that demographic rates measured at the study sites are not representative of population-level dynamics. However, a detailed examination of temporal variability, site differences, and age/sex-variation in survival provides further insight into the current dynamics of these species and the demographic features that may be restricting the population growth of prothonotary warblers.

Temporal variation and site differences

Average annual survivorship by age, sex, and season suggest little broad-scale differences between these two species based on captures at their shared wintering grounds. Nonetheless, our

Fig. 1. Monthly within-winter survivorship (mean ± SE) for adult and young northern waterthrush (NOWA), and adult and young male and female prothonotary warblers (PROW) from 2003 to 2009, captured at three sites in western Costa Rica [ESIG (yellow), ESNA (green), ESTA-PLGR (brown)], as estimated from the model $S_{bw}S_{ww\text{-}NOWA[t + age + site]} S_{bw\text{-}PROW[age + sex + t + site]} S_{ww\text{-}PROW[age + sex + t * site]}$. Note that boundary estimates ($S_{ww} = 1$) are included, but without associated error bars.
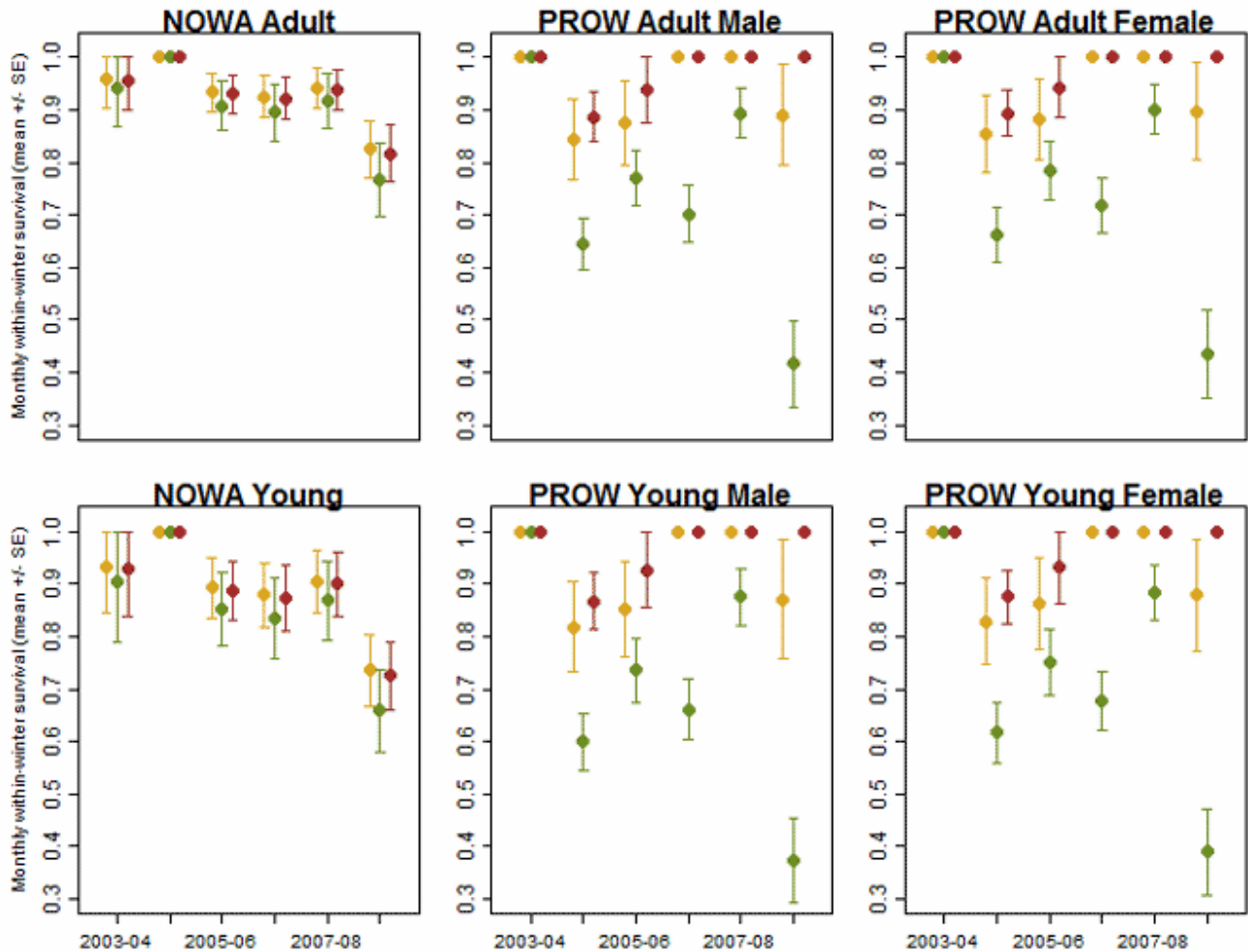

estimates of total annual warbler survival (adult male: mean = 0.436, SE = 0.071; adult female: mean = 0.372, SE = 0.071) are lower than the only published historical estimates (adult male: mean = 0.53, standard deviation [SD] = 0.07; adult female: mean = 0.47, SD = 0.09; Petit 1999). A separate analysis of some of our data suggests that prothonotary warbler winter survival was the lowest of all warblers wintering in the area ($S_{ww\text{-}PROW}$ = 0.813 for 2002–2007; Saracco et al. 2008). In our and these other studies, these values reflect local survival estimated through mark-recapture methods. However, given the evidence for high site-fidelity of wintering waterthrush and warblers (Warkentin and Hernandez 1996, Petit 1999), bias caused by emigration is likely low, and thus, these low recent estimates suggest the possibility of a decline in true survival over the past decade. Beyond the overall averages, warblers also exhibited much greater interannual variability in monthly survival than did

Fig. 2. Monthly between-winter survivorship (mean ± SE) for adult and young northern waterthrush (NOWA), and adult and young male and female prothonotary warblers (PROW) from 2004 to 2008, captured at three sites in western Costa Rica [ESIG (yellow), ESNA (green), ESTA-PLGR (brown)], as estimated from the model $S_{bw}S_{ww-NOWA[t + age + site]}$, $S_{bw-PROW[age + sex + t + site]}$, $S_{ww-PROW[age + sex + t * site]}$. Note that boundary estimates ($S_{bw} = 1$) are included, but without associated error bars.
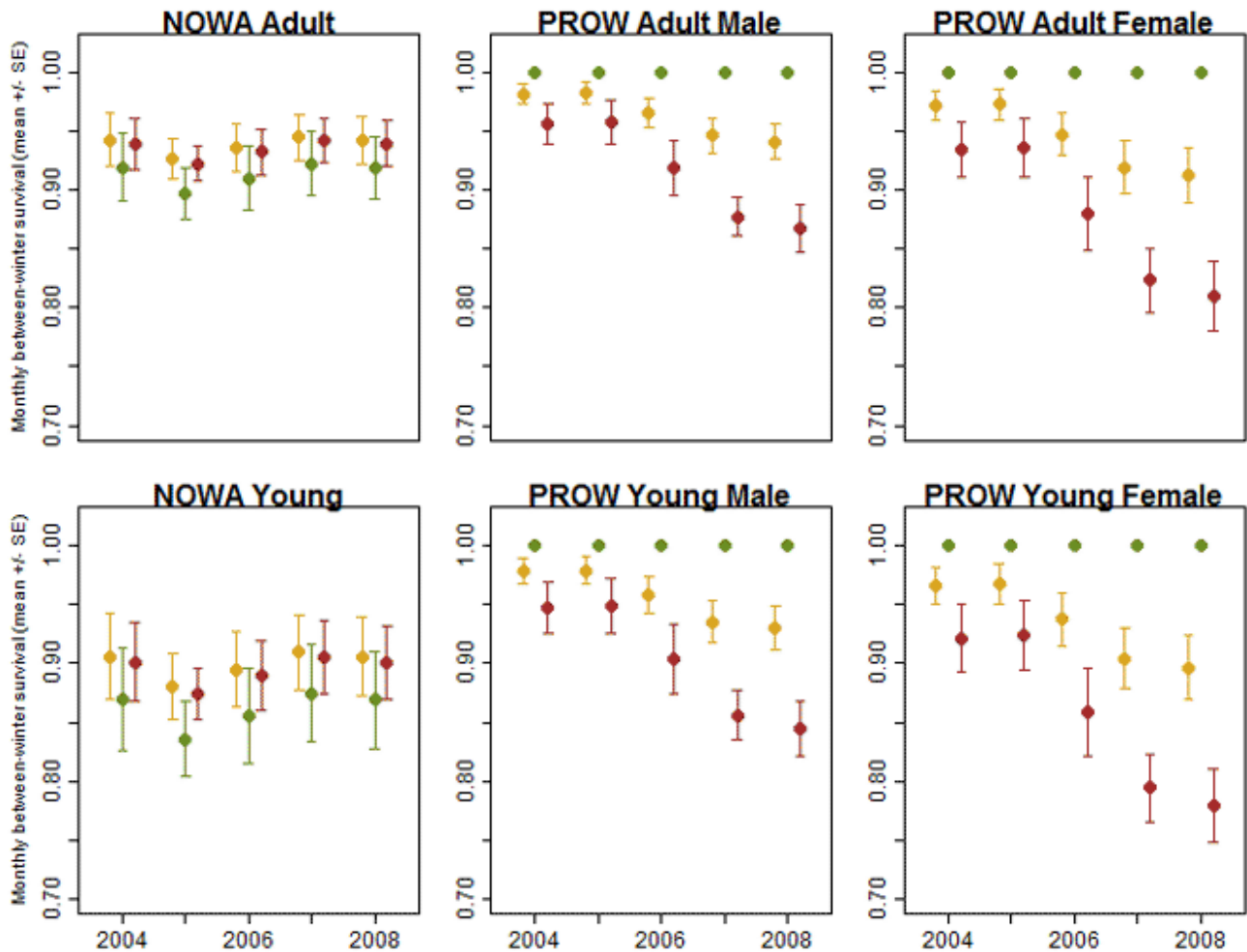
waterthrush, particularly within winters, as well as a larger survival disparity among sites (although variable sample sizes resulted in poor estimates of some site-specific values, i.e., $S = 1$). When monthly survival probabilities are compounded across a whole season, this temporal variability becomes even more pronounced, and the parallel estimation methods and larger sample sizes for warblers suggest that observation error alone does not likely account for this variation. Because variable survivorship can limit

population growth more than constant survivorship (with the same mean) in otherwise identical populations (Caswell 2001), this interannual variation in survival during both seasons could depress warbler recovery.

Mean survivorship values, therefore, do not fully represent the population dynamics of these two species. For instance, there was evidence for a sharp decline in S_{bw} for warblers, but not for waterthrush,

Fig. 3. Monthly within-winter (blue diamonds) and between-winter (orange triangles) survivorship (mean $\pm$ SE) for adult and young northern waterthrush (NOWA), and adult and young male and female prothonotary warblers (PROW), captured in western Costa Rica from 2003 to 2009, as estimated from the site-invariant model $p_{1[t*sp+site]} \; \psi_{12[age*sex*sp]} \; S_{2[age*sp]} \; S_{bw}S_{ww-NOWA[t+age]} \; S_{bw}S_{ww-PROW[age+sex+t]}$. Boundary estimates ($S_{ww} = 1$ or $S_{bw} = 1$) are included, but without associated error bars.
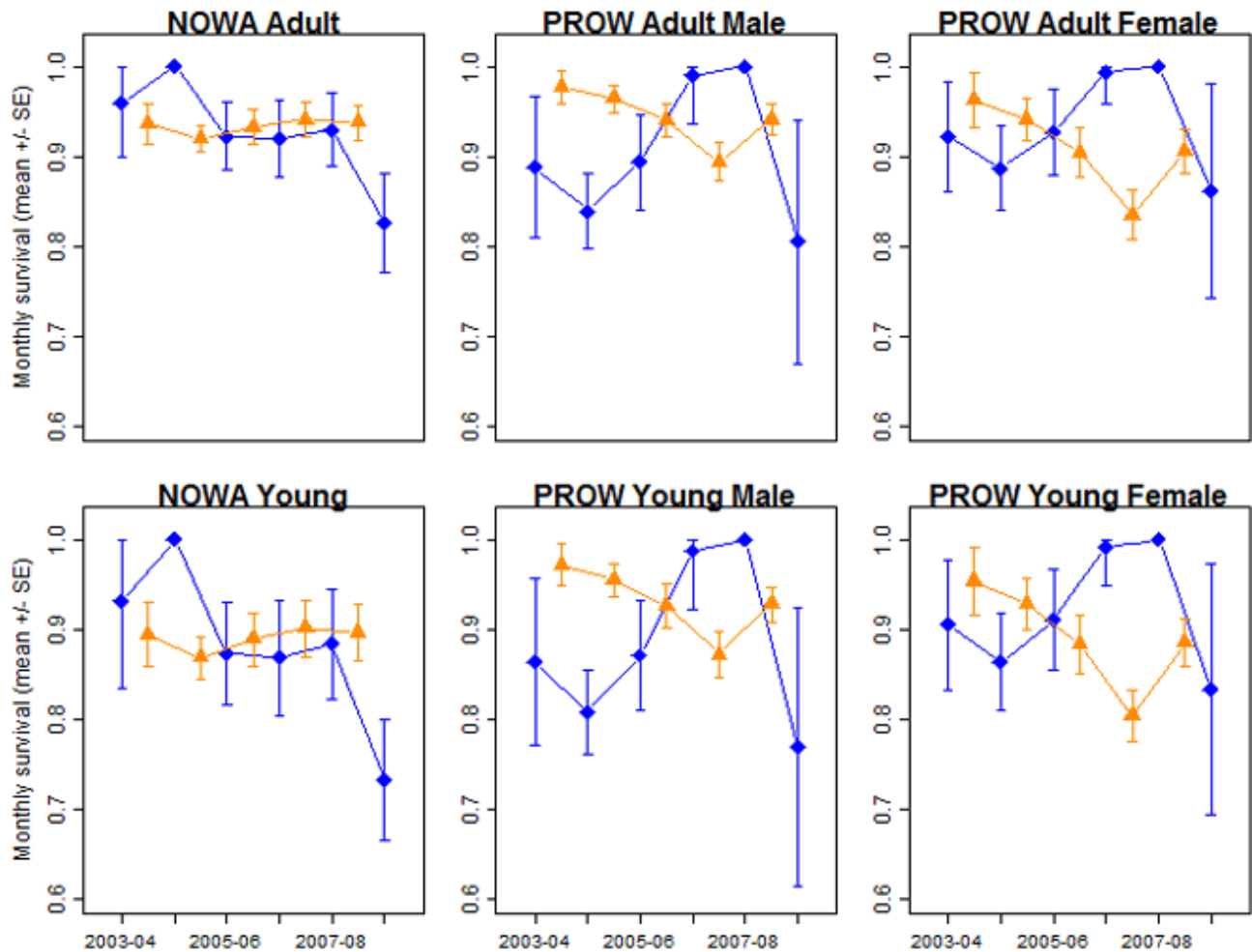
over the course of the study, and neither species showed a consistent tendency in S_{ww}. Temporal stability in S_{ww}, as well as its general similarity between waterthrush and warblers, imply that direct mortality on the wintering sites cannot fully explain the divergent population trends observed between the two species. In contrast, declines in $S_{bw-PROW}$ were very evident, even in fully time-dependent models, and were most pronounced at the site currently experiencing the greatest human disturbance in the

form of tourism development (ESTA-PLGR), where surrounding lands are being cleared of ground vegetation, shrubs, and vines to facilitate construction (J. Woodcock, *personal observation*). Between-winter survivorship is driven by mortality at the breeding ground and during migration, both of which may be particularly high in migrant songbirds (Bohning-Gaese et al. 1993, Sillett and Holmes 2002), as well as by wintering-site philopatry; thus, the potential causes of the decline

Fig. 4. Survival probabilities (mean ± SE) for northern waterthrush (NOWA, by age) and prothonotary warblers (PROW, by age and sex) captured in western Costa Rica from 2003 to 2009, as estimated from the time- and site-invariant model $p_{1[t*sp+site]}$ $\psi_{12[age*sex*sp]}$ $S_{2[age*sp]}$ $S_{bw}S_{ww-NOWA[age]}$ $S_{bw}S_{ww-PROW[age+sex]}$. (A) Monthly basis (direct model estimates): S_{ww}, blue diamonds; S_{bw} orange triangles. (B) Seasonal basis: within-winter survival (S_{ww}^4), blue diamonds; between-winter survival (S_{bw}^8), orange triangles. (C) Annual basis: annual survival ($S_{ww}^4 S_{bw}^8$).
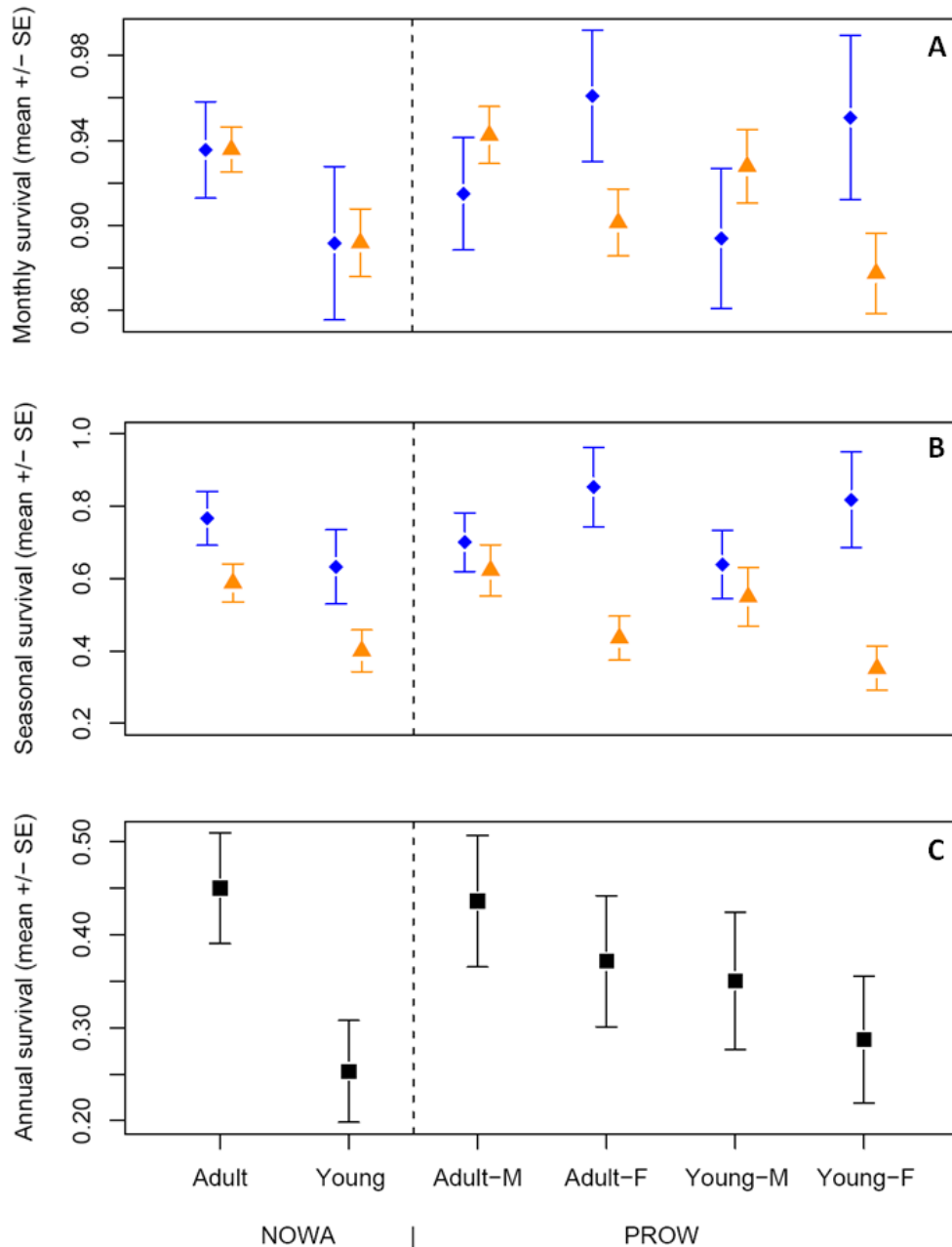
in $S_{bw\text{-}PROW}$ are numerous. Given that reduced access to high-quality winter habitat can affect later survival and reproduction negatively (Bearhop et al. 2004, Norris et al. 2004), habitat-driven reductions in local survival of warblers, whether reflecting changes in true breeding and migration survivorship or in wintering location, could have important population-level consequences.

Age- and sex-specific survivorship

Age and sex were generally good predictors of survivorship, but the magnitude of differences between adult and young birds or between males and females (warblers only) varied with the scale of measurement. Averaged across all years, age differences in monthly waterthrush survival were stronger for S_{bw} than for S_{ww} and, cumulatively, resulted in divergent estimates of total annual survivorship (see Fig. 4C). These mean estimates (0.450 and 0.253 for waterthrush adults and young, respectively) correspond fairly well to the general rule of thumb that approximates juvenile survival as half that of adults (discussed in Gardali et al. 2003 and references therein). Among warblers, age differences on a monthly basis were relatively small. Cumulatively over the year, mean adult survival was higher than that of juveniles, but by a smaller margin than for waterthrush; this is more consistent with other studies supporting similar survivorship among young and adult birds during the nonbreeding season (Marra and Holmes 2001) or annually (Sillett and Holmes 2002).

Perhaps more importantly, sex differences in warbler survival (which could not be examined in waterthrush) were highly seasonal and varied little with age. Female monthly S_{bw} was substantially lower than monthly S_{ww}, whereas male survival was similar between the seasons. This gap was even more apparent when accumulated across a whole season (i. e., S_{ww}^{4} and S_{bw}^{8}; see Fig. 4B), highlighting particularly low survival of females between consecutive winters. The observed male bias in total warbler captures throughout the banding study (Woodcock and Woodcock 2007) might thus reflect higher mortality of females during the migration and breeding seasons (e.g., from predation at the nest; Petit 1999). Sex-biased site fidelity might also be affecting these survival estimates because true demographic mortality cannot be separated entirely from emigration, even with models that account for transient behavior. Indeed, when resources are

declining, subordinate warblers, including females, may be forced into poorer quality habitat by dominant birds (Marra and Holmes 2001, Saracco et al. 2008), such that low values of S_{bw} might partially represent females' inability to return to the best winter sites.

Sex differences within warblers were particularly evident in estimates of temporal changes in S_{bw}. The sharp decline in S_{bw} at ESTA-PLGR, for instance, included a drop in estimated mean monthly survival from 0.921 to 0.779 for young female warblers and from 0.934 to 0.810 for adult females (see Fig. 2). Compounded across the eight months between winters, this implies a drop in total between-winter (March–November) local survival between 2003 and 2009 from 0.519 to 0.136 and from 0.579 to 0.185 for young and adult females, respectively. Moreover, differences in seasonal survivorship between waterthrush and warblers were greatest for between-winter female survivorship, supporting our second prediction, for females only. Even if some of this decline reflects increased movement to other wintering sites rather than higher mortality, the links between winter habitat and subsequent fitness (e.g., Bearhop et al. 2004, Norris et al. 2004) thus imply that this low and declining S_{bw} of females, even after accounting for transient behavior (see below), could have the potential to recover warbler populations.

Transient birds and recapture probability

We observed unusual transient behavior in this study system: the potential presence in November and March, but not in other months, of birds wintering outside of the study area. Even though we included it in our analysis, the proportion of transient birds and their overwinter survival were not well captured with the multi-state model. Both parameters were often estimated at the boundaries of zero or one, suggesting that small sample sizes (i.e., few transient birds) did not allow enough statistical power to distinguish these parameters from the others in the model. We assumed that all birds wintering elsewhere would pass through the study sites again in March, as well as equal capture probability in March among birds wintering at the study sites vs. elsewhere. Both assumptions were necessary for estimating all model parameters but were not tested empirically. Future modeling of winter capture data for these study sites might use a more traditional approach for dealing with

transient birds (e.g., Pradel et al. 1997, Cilimburg et al. 2002, Brown and Long 2007), although perhaps with little effect: modification of our model so that all $\psi_{12} = 0$ (data not shown) gave similar survivorship and transience estimates, but the model was not as well supported by the data. Moreover, interpretation of the survivorship and transience values must consider that even these multi-state models likely underestimate true demographic survivorship because mortality is still confounded with permanent emigration beyond the monitored wintering sites.

Nevertheless, some models did provide estimates of transience for groups of one or both species and may provide some insight into seasonal movements of wintering warblers in this area. Nonzero transient estimates for both adult and young waterthrush in many of the best-fit models suggest that these study sites may be a stopover, rather than final wintering destination, for a segment of this population. The somewhat weaker support for transient warblers among only adult females and young males might reflect their subordinance relative to adult males (e.g., Marra and Holmes 2001) and consequent emigration, although the $\psi_{12} = 0$ estimates for warblers in the best-ranked models suggest that this is not a consistent phenomenon.

The strong temporal variability in recapture probability p_1 among sampling periods could also be related to birds' movements in and out of the study sites. Behavioral observations of wintering warblers have demonstrated small-scale movements among neighboring habitats (Lefebvre et al. 1994, Brown and Long 2007), including for the warblers we studied (J. Woodcock, *unpublished data*). If the frequency and timing of these movements varied among sampling periods, then p_1 would indeed fluctuate in accordance with the presence or absence of birds still alive, but not always within the sampled area. Nevertheless, because both of these species exhibit fairly high winter site fidelity (Lefebvre et al. 1994, Warkentin and Hernandez 1996), most of these movements do not likely reflect permanent emigration from the sampling study area. By accounting for variation in *p,* survival estimates should thus be relatively unbiased.

Implications for conservation of neotropical migrants

Changes to high-quality wintering habitat have been implicated in population declines of songbirds (Robbins et al. 1989, Rappole and McDonald 1994, Sherry and Holmes 1996). However, breeding habitat destruction is also affecting prothonotary warblers (Heltzel and Leberg 2006, COSEWIC 2007). We therefore aimed to use winter mark-recapture data to link seasonal demographics with population change. A cursory assessment of average survival probability among years, under the assumption that these estimates represent population-level survivorship, suggests that factors apart from survival are likely driving the differences in warblers and waterthrush population trends: e.g., contrasting habitat changes between the more northerly waterthrush breeding grounds vs. the more southerly warbler breeding grounds. Upon closer examination, however, we find that between-winter survival was lower in warblers than in waterthrush and was particularly low among female warblers. Greater temporal variability in within-winter survival among warblers, despite mean values similar to those of waterthrush, could also negatively affect population growth. Additionally, the sharp decline in between-winter survivorship of birds banded at ESTA-PLGR supports the need for enhanced protection of varied wintering habitats. Only the mangrove swamps at ESTA, which are used for roosting, are protected; the surrounding dry forests at PLGR, which are used for feeding, have experienced major changes over the last decade (J. Woodcock, *unpublished data*). This use of multiple habitats on a daily basis also occurs in waterthrush and other wintering neotropical migrants (e.g., Warkentin and Hernandez 1996, Burson et al. 2005). Thus, protection of surrounding habitats may be as equally important as conservation of the mangroves. Although we cannot quantify the contribution of breeding parameters to population change or infer whether the measured seasonal survivorship is representative of the populations as a whole, our study highlights some particular aspects of survivorship that may be involved in recent declines. Survival of prothonotary warblers was low between winters for females, declined between winters across all age and sex groups, and was highly variable among years during both seasonal intervals; these are all characteristics that could depress population growth and recovery.

Isolation and resolution of the particular causal factors in the decline of prothonotary warblers and other threatened migrants will likely require additional information. Isotope studies (e.g., Mazerolle et al. 2005), for instance, could identify specific wintering grounds of conservation

importance such as those used by the diminutive Canadian breeding prothonotary warbler population. Matrix-based elasticity estimates could identify parameters most critical to population growth (e.g., Caswell 2001). Banding of individuals at other wintering sites could be valuable in determining whether the vital rates that we measured are representative of population-level dynamics. Tracking devices (radio-telemetry) also could be used to measure more accurately transient behavior between wintering sites. Studies of habitat change in Costa Rican mangrove swamps and other areas facing destruction could directly measure the effects of human disturbance on survival and site fidelity in critical wintering habitats. The examination of changes in body condition over the course of a winter might provide additional insight into site-differences in habitat quality (e.g., Bakermans et al. 2009). Our estimates of both within- and between-winter survivorship thus suggest that prothonotary warblers still face important obstacles to recovery and that a cautious approach to the conservation of habitat-specialist neotropical migrants should explicitly address the protection of both breeding and nonbreeding areas.

Responses to this article can be read online at:
http://www.ace-eco.org/vol5/iss1/art2/responses/

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