

# Variation in survivorship of a migratory songbird throughout its annual cycle

T. SCOTT SILLETT\*† and RICHARD T. HOLMES\*

\*Department of Biological Sciences, Dartmouth College, Hanover, NH 03755, USA; and †Patuxent Wildlife Research Center, US Geological Survey, 11510 American Holly Drive, Laurel, MD 20708, USA

## Summary

1. Demographic data from both breeding and non-breeding periods are needed to manage populations of migratory birds, many of which are declining in abundance and are of conservation concern. Although habitat associations, and to a lesser extent, reproductive biology, are known for many migratory species, few studies have measured survival rates of these birds at different parts of their annual cycle.

2. Cormack–Jolly–Seber models and Akaike's information criterion model selection were used to investigate seasonal variation in survival of a Nearctic–Neotropical migrant songbird, the black-throated blue warbler, *Dendroica caerulescens*. Seasonal and annual survival were estimated from resightings of colour-ringed individuals on breeding grounds in New Hampshire, USA from 1986 to 2000 and on winter quarters in Jamaica, West Indies from 1986 to 1999. Warblers were studied each year during the May–August breeding period in New Hampshire and during the October–March overwinter period in Jamaica.

3. In New Hampshire, males had higher annual survival ( $0.51 \pm 0.03$ ) and recapture probabilities ( $0.93 \pm 0.03$ ) than did females (survival:  $0.40 \pm 0.04$ ; recapture:  $0.87 \pm 0.06$ ). In Jamaica, annual survival ( $0.43 \pm 0.03$ ) and recapture ( $0.95 \pm 0.04$ ) probabilities did not differ between sexes. Annual survival and recapture probabilities of young birds (i.e. yearlings in New Hampshire and hatch-year birds in Jamaica) did not differ from adults, indicating that from the time hatch-year individuals acquire territories on winter quarters in mid-October, they survive as well as adults within the same habitat.

4. Monthly survival probabilities during the summer (May–August) and winter (October–March) stationary periods were high: 1.0 for males in New Hampshire, and  $0.99 \pm 0.01$  for males in Jamaica and for females in both locations.

5. These annual and seasonal survival estimates were used to calculate warbler survival for the migratory periods. Monthly survival probability during migration ranged from 0.77 to  $0.81 \pm 0.02$ . Thus, apparent mortality rates were at least 15 times higher during migration compared to that in the stationary periods, and more than 85% of apparent annual mortality of *D. caerulescens* occurred during migration.

6. Additional data from multiple species, especially measures of habitat-specific demography and dispersal, will improve our understanding of the relative impacts of the breeding, migratory, and winter periods on population dynamics of migratory birds and thus enhance future conservation efforts.

**Key-words:** avian demography, capture–recapture models, *Dendroica caerulescens*, Nearctic–Neotropical migrant birds, population ecology, seasonal and annual survival.

*Journal of Animal Ecology* (2002) **71**, 296–308

## Introduction

One of the most studied and publicized avian conservation issues is the decline of migratory songbirds,

particularly those species that migrate between north-temperate breeding grounds and tropical winter quarters (Robbins *et al.* 1989; Terborgh 1989; Askins, Lynch, & Greenberg 1990; Baillie & Peach 1992; Peterjohn, Sauer, & Robbins 1995; Peach, Baillie, & Balmer 1998). The majority of published research on these species has focused on habitat-specific abundance and reproductive biology (e.g. papers in Keast &

Present address and correspondence: Dr Scott Sillett, Smithsonian Migratory Bird Center, National Zoological Park, Washington DC 20008, USA (Tel. 202-673-4908. E-mail: silletts@nnp.si.edu)

Morton 1980; Hagan & Johnston 1992; Martin & Finch 1995). We know considerably less about annual and seasonal survival rates of migratory passerines. Estimating survivorship can be more difficult than estimating abundance or fecundity due to the uncertainty about fates of marked birds that disappear from study populations (Clobert & Lebreton 1991; Lebreton *et al.* 1992). Furthermore, reliable estimates of survival typically require capture–recapture modelling and several years of data because all surviving marked individuals may not be detected each year or season (Pollock *et al.* 1990; Lebreton *et al.* 1992; Martin, Clobert, & Anderson 1995). Robust survival estimates are needed to elucidate the processes that determine distribution and abundance, to model population dynamics, and to develop management plans for species conservation (Lebreton *et al.* 1992).

Temperate–tropical migratory birds travel through a diversity of habitats on different continents, and their survival could thus be influenced by a multitude of processes operating at various times and locations during the year. Nevertheless, nearly all data on songbird survival come from populations studied during the 2–4-month-long temperate breeding season (e.g. Nichols *et al.* 1981; Chase, Nur, & Geupel 1997; DeSante *et al.* 1998; Siriwardena, Baillie, & Wilson 1998; Porneluzi & Faaborg 1999; Rosenberg *et al.* 1999). Events in the breeding season, such as habitat alteration and nest parasitism, have significant effects on migratory songbird populations (Robinson *et al.* 1995; Siriwardena *et al.* 1998), and reproductive effort can impact adult survival rates in some songbird species (Nur 1988; McCleery *et al.* 1996; Cichon, Olejniczak, & Gustafsson 1998). However, evidence indicates that the abundance of temperate–tropical migrants is also limited by factors affecting survival and physical condition during the non-breeding season (Rappole & McDonald 1994; Sherry & Holmes 1995; Latta & Baltz 1997; Marra, Hobson, & Holmes 1998). Despite the well-documented importance of the non-breeding period, estimates of annual or overwinter survival in the tropics, where many species spend more than half of each year, are rare (e.g. Conway, Powell, & Nichols 1995; Marra & Holmes 2001). Furthermore, as far as we can determine, no one has estimated survival during the migratory period or compared mortality rates among the breeding, overwinter, and migratory phases of the annual cycle for any migratory passerine. This lack of knowledge severely limits our understanding of how seasonal events interact to determine songbird distribution and abundance (DeSante 1995; Sherry & Holmes 1996; Marra & Holmes 2001).

In this study, we collected and analysed long-term, adult survivorship data from black-throated blue warblers, *Dendroica caerulescens* (nomenclature of North American birds follows American Ornithologists' Union 1998) on breeding grounds in New Hampshire, USA and on winter quarters in Jamaica, West Indies. We used this unique data set on survivorship at

breeding and wintering locations within the species range to estimate sex- and age-specific annual survival probabilities, as well as survival probabilities during the 6-month winter and 3-month summer stationary periods. From these data, we could then estimate survivorship for the 3-month migratory period. This paper thus provides the first analysis of how adult survival rates of a migratory songbird vary throughout all phases of its annual cycle, including the first survival estimates for a passerine during migration.

## Methods

### STUDY SYSTEM AND FIELD METHODS

We studied *D. caerulescens* at two times and locations during the annual cycle: (i) from October 1986 to March 1999 during the overwinter period at Cope Mountain, near Bethel Town in north-western Jamaica, West Indies (Holmes, Sherry, & Reitsma 1989); and (ii) from 1986 to 2000 during the breeding season in Hubbard Brook Experimental Forest near West Thornton, New Hampshire, USA (Holmes *et al.* 1992). The Jamaica site was visited twice annually, first at the beginning of the overwinter season in autumn, and again at the end of winter, prior to the start of spring migration, in the following calendar year. We worked on a 7-ha plot at 450 m elevation within a 40-ha remnant patch of primary, wet limestone forest on Cope Mountain. The New Hampshire site was studied each year during the breeding season. Research was conducted on a 64-ha plot at 600 m elevation within the 3100 ha experimental forest, which was contiguous with the much larger White Mountain National Forest. The forest at both study sites was high-quality habitat for *D. caerulescens* (Holmes *et al.* 1989; Holmes *et al.* 1992; Holmes 1994; Holmes, Marra, & Sherry 1996) and was relatively undisturbed by human activity.

*Dendroica caerulescens* is territorial and has strong fidelity to both breeding and winter territory sites (Holmes & Sherry 1992; Holmes 1994), although breeding populations mix extensively during the non-breeding season (Chamberlain *et al.* 1997). This species breeds in forested regions in eastern North America and overwinters primarily in the Greater Antilles (Holmes 1994). Individually marked warblers breeding at our New Hampshire site have never been resighted on winter quarters, nor have those ringed at our Jamaica site been resighted on breeding grounds. However, analyses of stable and radiogenic isotope ratios in feathers indicate that warblers overwintering in Jamaica breed in the northern half of the species breeding range (Chamberlain *et al.* 1997), and birds breeding at our New Hampshire site appear to overwinter mostly in Cuba and Jamaica (Rubenstein *et al.* 2002). Despite the lack of shared individuals between our study sites, recruitment of juvenile *D. caerulescens* in Jamaica each year was positively correlated with

warbler fecundity in New Hampshire the preceding summer (Sillett, Holmes, & Sherry 2000). Thus, we considered the individuals studied in New Hampshire and Jamaica to be different, local samples from a larger, regional breeding population.

Survival estimates were based on resightings of colour-ringed individuals on gridded study plots in New Hampshire and Jamaica. Surrounding areas were also searched, although with less intensity. Birds were resighted with binoculars, and returning birds were rarely missed in our surveys (see Results). Unringed birds were captured individually using a single mist-net, a warbler decoy, and song playbacks (Holmes *et al.* 1989), and marked with a unique combination of two colour rings and one aluminium US Fish and Wildlife Service ring. Most breeding females were caught in mist-nets near nests, usually during the last few days of incubation. Warbler age and sex were determined using plumage characters (Pyle *et al.* 1987). The New Hampshire data set was composed of capture histories of 336 marked individuals, averaging  $3.4 \pm 0.2$  (mean  $\pm 1$  SE) birds per 5 ha per year. The Jamaica data set consisted of 151 marked birds, with  $16.0 \pm 3.8$  birds per 5 ha annually overwintering at the site. Annual sex- and age-ratios differed slightly between the two sites. The Copse Mountain population tended to be more male-biased ( $0.66 \pm 0.13$ ) and to have a greater proportion of young (i.e. hatch-year) birds ( $0.45 \pm 0.20$ ) than the population at Hubbard Brook ( $0.54 \pm 0.11$  males,  $0.39 \pm 0.12$  yearlings). Population sizes at both locations were fairly stable and not undergoing any directional change (Holmes & Sherry 2001; R. T. Holmes, unpublished data).

#### DATA ANALYSIS

Warbler survival ( $\phi$ ) and recapture ( $p$ ) probabilities were estimated over both annual and seasonal time intervals with Cormack–Jolly–Seber (CJS) models (Pollock *et al.* 1990; Lebreton *et al.* 1992) using the MARK computer program (White & Burnham 1999). The complement of  $\phi$  in CJS models represents the probability of death or permanent emigration; the complement of  $p$  in these models denotes the probability of nondetection of an individual present in the study area and also incorporates temporary emigration (see Kendall, Nichols, & Hines 1997). Except where noted,  $\hat{\phi}$  and  $\hat{p}$  are likely to be accurate estimates of *D. caerulescens*' true survival and detection probabilities, respectively, due to the strong territory site fidelity of this species on both breeding grounds and winter quarters.

Survival and recapture were first modelled annually and then seasonally. Because we knew *a priori* that survival rates were high over the 6-month overwinter period (see Results) and that warblers had strong fidelity to breeding and overwinter territories, any birds resighted in March that were missed in the preceding October were included in annual analyses for Jamaica.

To estimate seasonal survival rates, we used resighting data from two sampling periods per year in each location. Sampling in Jamaica occurred during 3–5-day periods in mid-October–early November, and during 2–5-day periods in mid-March. This allowed survival to be estimated overwinter from October to March, and from March to October, encompassing migration and breeding. In New Hampshire, warblers were systematically resighted every 1–7 days from mid-May to mid-August, 1990–2000 ( $n = 262$  individuals). We considered two seasonal sampling periods in New Hampshire: mid-May to early June, and late July to mid-August. Survival was then estimated for the May–August breeding season, and from August to May, encompassing the migration and overwinter periods.

Sets of candidate models were chosen prior to data analysis, based on our knowledge of *D. caerulescens* biology (Burnham & Anderson 1998). The general, or global, model for each model set included all time and group variables hypothesized to affect  $\phi$  and  $p$ . Fit of global models was verified with the program RELEASE goodness-of-fit procedure (Burnham *et al.* 1987) implemented in program MARK. Time and group variables used in candidate models are described below. Model notation follows Lebreton *et al.* (1992).

#### Time variables

In annual analyses,  $\phi$  was modelled as either constant over time or as a function of year. Annual recapture probability was not modelled as a function of year because of high resighting rates and thus low inter-annual variation in  $p$ , given our sample sizes (see above). In seasonal analyses,  $\phi$  was modelled as either constant over time or as a function of season (e.g. different  $\phi_{\text{season}}$  for the October–March overwinter period compared to the March–October migration and breeding period). We did not model interannual variation in  $\phi_{\text{season}}$  because annual analyses provided little statistical support for yearly variation in survivorship (see Results). Both monthly and seasonal (i.e. survival for 6 months from October to March, and survival for 3 months from May to August) estimates of  $\phi_{\text{season}}$  were generated in program MARK. Monthly estimates allowed  $\phi$  to be directly compared between the summer and winter stationary periods. Seasonal estimates of  $\phi$  were used to estimate survival during the 3-month migratory period (see below).

Recapture probabilities were also modelled as a function of season because warblers were less conspicuous in late summer at Hubbard Brook and in late winter at Copse Mountain. In addition, personnel available and time spent resighting birds at the end of the stationary periods varied annually. Therefore,  $p$  was always modelled as a function of season, constant among years in May and October, but as a function of year in August and March.

*Sex and age variables*

We modelled  $\phi$  and  $p$  as a function of sex in both annual and seasonal analyses. Annual  $\phi$  was also modelled as a function of two age classes: young birds and adults. Young birds were defined as individuals in either their first breeding season in New Hampshire (second-year individuals, i.e. 11–12 months old) or in their first overwinter season in Jamaica (hatch-year juveniles, i.e. 3–4 months old). Adults were all individuals in at least their second breeding or second overwinter season. Age-based models were parameterized to contain separate structures for young and adult survival (e.g. Pollock 1981; Prevot-Julliard, Lebreton, & Pradel 1998). Seasonal  $\phi$  was not modelled as a function of age because annual analyses provided low statistical support for differences in survival between young and adult birds (see Results).

*Model selection and parameter estimation*

Model selection methods based on Akaike's information criterion, or AIC (Akaike 1973; Lebreton *et al.* 1992; Burnham & Anderson 1998) were used to: (i) provide the best estimates of annual and seasonal  $\phi$  for *D. caerulescens*; and (ii) assess the statistical evidence for time- and group-related differences in  $\phi$ . Models in each candidate set were first ranked by second-order AIC ( $AIC_c$ ) differences ( $\Delta_i$ ; Burnham & Anderson 1998). Relative likelihood of each model in a candidate set was then estimated with  $AIC_c$  Weights ( $w_i$ ; Burnham & Anderson 1998). The  $w_i$  values for all models in a candidate set sum to 1.

Program MARK's model averaging procedure was used to compute the average estimates for parameters of interest (e.g.  $\phi$  for females from October to March) from all models in a candidate set. Model averaging is based on  $w_i$  values for each model and thus includes model selection uncertainty in the estimate of each parameter and its associated variance (Burnham & Anderson 1998). Model-averaged estimators typically have better precision and reduced bias relative to the estimator of a given parameter from only the AIC-selected best model (Anderson, Burnham, & Thompson 2000). Statistical support for time- and group-related differences in  $\phi$  and  $p$  was assessed by summing the  $w_i$  for all models in which a parameter of interest occurred. This method of multimodel inference enables one to use the entire set of candidate models to judge the importance of a parameter to  $\phi$  or  $p$ , rather than basing conclusions on a single best-fit model, i.e. the model with  $\Delta_i = 0$  (Burnham & Anderson 1998; Anderson *et al.* 2000).

*Estimating survival during migration*

Annual survival probability is the product of survival probabilities during the stationary and migratory periods of the annual cycle, i.e.  $\phi_{\text{annual}} = \phi_{\text{overwinter}} * \phi_{\text{breeding}} * \phi_{\text{migration}}$ . Using seasonal estimates of  $\phi$  from New Hampshire

and Jamaica, this expression can be decomposed in two ways to estimate  $\phi_{\text{migration}}$ :

$$\phi_{\text{migration}} = \frac{(\phi_{\text{migration \& breeding}})}{(\phi_{\text{breeding}})} \text{ or } \frac{(\phi_{\text{migration \& overwinter}})}{(\phi_{\text{overwinter}})},$$

where  $\phi_{\text{migration \& breeding}}$  is survival from March to October as measured in Jamaica,  $\phi_{\text{breeding}}$  is survival from May to August in New Hampshire,  $\phi_{\text{migration \& overwinter}}$  is survival from August to May as measured in New Hampshire, and  $\phi_{\text{overwinter}}$  is survival from October to March in Jamaica. The associated variance in  $\hat{\phi}_{\text{migration}}$  can then be estimated with the delta method (Seber 1982), e.g.

$$\hat{\phi}_{\text{migration}}^2 \left[ \frac{\text{var}(\hat{\phi}_{\text{migration \& breeding}})}{(\hat{\phi}_{\text{migration \& breeding}})^2} + \frac{\text{var}(\hat{\phi}_{\text{breeding}})}{(\hat{\phi}_{\text{breeding}})^2} \right],$$

and a 95% confidence interval around  $\hat{\phi}_{\text{migration}}$  can be approximated as

$$\hat{\phi}_{\text{migration}} \pm 1.96 \sqrt{\text{var} \hat{\phi}_{\text{migration}}}.$$

Because  $\hat{\phi}_{\text{annual}}$  differed between May–May and October–October analyses (see Results),  $\phi_{\text{migration}}$ , its associated variance, and 95% confidence interval was estimated from two ratios:  $\hat{\phi}_{\text{migration \& breeding}}/\hat{\phi}_{\text{breeding}}$  and  $\hat{\phi}_{\text{migration \& overwinter}}/\hat{\phi}_{\text{overwinter}}$ . These two estimates of  $\phi_{\text{migration}}$  include any mortality that occurred immediately prior to the start of migration because March and August surveys were conducted at the end of the stationary periods.

Our data did not allow for robust, year-specific estimates of  $\phi_{\text{season}}$ , and we therefore did not compute survival probabilities separately for autumn and spring migration. To enable a direct comparison of apparent survivorship between the stationary and migratory periods, monthly survival probability during the three-month migratory period was estimated as the cube-root of  $\hat{\phi}_{\text{migration}}$ . Variance in monthly survival during migration was then estimated from  $\text{var} \hat{\phi}_{\text{migration}}$  using the delta method (Seber 1982).

**Results****ANNUAL MODELS**

Model selection (Table 1) and estimates of annual survival and recapture probabilities (Table 2) differed for the New Hampshire and Jamaica data sets. Males had higher annual survival and recapture probabilities than females in New Hampshire. In contrast, model-averaged estimates indicated that survival probabilities were similar between sexes in Jamaica (Table 2), as did sex-specific survival estimates from models [ $\phi_{\text{sex}}, p$ ] and [ $\phi_{\text{sex}}, p_{\text{sex}}$ ] (females,  $0.44 \pm 0.05$ ; males,  $0.42 \pm 0.04$ ). New Hampshire males had higher survival compared to males in Jamaica, but female survival was similar between locations. Recapture probabilities were higher in Jamaica for both sexes. Sex-specific estimates of

**Table 1.** Models of annual survival ( $\phi$ ) and recapture ( $p$ ) probabilities for *D. caerulescens*, number of estimable parameters ( $K$ ), second-order Akaike's information criterion values ( $AIC_c$ ),  $AIC_c$  differences ( $\Delta_i$ ), and  $AIC_c$  Weights ( $w_i$ ). Subscripts give parameterization for  $\phi$  and  $p$ : no subscript = constant over group and time variables; 'age' = two age classes; 'sex' = female and male; 'year' = annual variation. Subscripts joined by an '\*' indicate a factorial model. Statistics for best-fit models are in bold. The global model ( $\phi_{\text{age} \times \text{sex} \times \text{year}}, p_{\text{year}}$ ) fit the data well for both New Hampshire ( $\chi^2_{34} = 25.85$ ,  $P > 0.99$ ) and Jamaica ( $\chi^2_{26} = 10.97$ ,  $P > 0.99$ ) data sets

	Model	New Hampshire <sup>a</sup>				Jamaica <sup>b</sup>			
		$K$	$AIC_c$	$\Delta_i$	$w_i$	$K$	$AIC_c$	$\Delta_i$	$w_i$
(1)	$\phi, p$	2	775.45	6.62	0.01	<b>2</b>	<b>340.81</b>	<b>0</b>	<b>0.40</b>
(2)	$\phi, p_{\text{sex}}$	3	772.46	3.62	0.07	3	342.83	2.02	0.15
(3)	$\phi_{\text{age}}, p$	3	777.46	8.62	0.01	3	342.70	1.89	0.16
(4)	$\phi_{\text{age}}, p_{\text{sex}}$	4	774.49	5.65	0.02	4	344.74	3.93	0.06
(5)	$\phi_{\text{sex}}, p$	3	769.02	0.19	0.37	3	342.76	1.95	0.15
(6)	$\phi_{\text{sex}}, p_{\text{sex}}$	<b>4</b>	<b>768.84</b>	<b>0</b>	<b>0.41</b>	4	344.76	3.95	0.06
(7)	$\phi_{\text{age} \times \text{sex}}, p$	5	772.82	3.98	0.06	5	346.61	5.80	0.02
(8)	$\phi_{\text{age} \times \text{sex}}, p_{\text{sex}}$	6	772.81	3.97	0.06	6	348.67	7.86	0.01
(9)	$\phi_{\text{year}}, p$	15	789.85	21.01	0.00	13	350.51	9.70	0.00
(10)	$\phi_{\text{year}}, p_{\text{sex}}$	16	786.94	18.10	0.00	14	352.73	11.92	0.00
(11)	$\phi_{\text{age} \times \text{year}}, p$	29	803.70	34.86	0.00	25	370.39	29.58	0.00
(12)	$\phi_{\text{age} \times \text{year}}, p_{\text{sex}}$	30	800.70	31.87	0.00	26	372.89	32.08	0.00
(13)	$\phi_{\text{sex} \times \text{year}}, p$	29	805.51	36.68	0.00	25	369.19	28.38	0.00
(14)	$\phi_{\text{sex} \times \text{year}}, p_{\text{sex}}$	30	805.40	36.56	0.00	26	371.64	30.83	0.00
(15)	$\phi_{\text{age} \times \text{sex} \times \text{year}}, p_{\text{year}}$	58	835.07	66.24	0.00	50	404.00	63.19	0.00

<sup>a</sup>1986–2000.

<sup>b</sup>1986–98.

**Table 2.** Model averaged estimates of annual survival ( $\phi$ ) and recapture ( $p$ ) probabilities, unconditional standard errors, and profile likelihood 95% confidence intervals for *D. caerulescens* from Hubbard Brook Experimental Forest, New Hampshire, USA (1986–2000) and Copse Mountain, Jamaica, West Indies (1986–98)

Location	$\phi \pm 1 \text{ SE}$ (95% CI)		$p \pm 1 \text{ SE}$ (95% CI)
New Hampshire	Adult <sup>a</sup>	Yearling <sup>b</sup>	
Male	0.512 ± 0.034 (0.445–0.578)	0.514 ± 0.036 (0.443–0.584)	0.926 ± 0.034 (0.830–0.969)
Female	0.407 ± 0.040 (0.332–0.486)	0.404 ± 0.042 (0.326–0.488)	0.869 ± 0.061 (0.700–0.950)
Jamaica	Adult <sup>a</sup>	Hatch-year <sup>c</sup>	
Male	0.428 ± 0.038 (0.355–0.505)	0.422 ± 0.040 (0.346–0.503)	0.951 ± 0.037 (0.804–0.989)
Female	0.434 ± 0.041 (0.355–0.516)	0.427 ± 0.044 (0.344–0.514)	0.947 ± 0.041 (0.786–0.989)

<sup>a</sup>Individuals in at least their second breeding or second overwinter season.

<sup>b</sup>Individuals in their first breeding season in May.

<sup>c</sup>Individuals in their first overwinter season in October.

survival and recapture were nearly identical between adults and yearlings in New Hampshire and between adults and juveniles in Jamaica (Table 2). Based on  $\Sigma w_i$  from the New Hampshire model set, sex-specific survival (Table 1, models 5–8, 13–15) was 6.3 times more likely to provide the best fit to our data than age-specific survival (models 3–4, 7–8, 11–12, 15) and 10.9 times more likely than constant survival among sexes (models 1–2). In Jamaica, constant survival was only 2.3 times more likely to be the best fit to our data than either sex-specific or age-specific survival. Sex-specific models of recapture probability (Table 1: even-number models and model 15) were 1.2 and 2.7 times more

likely to fit our data than models of constant recapture probability among sexes (odd-numbered models, 1–13) in New Hampshire and Jamaica, respectively. Comparisons of  $\Sigma w_i$  for time-constant (Table 1: models 1–8) and year-specific (models 9–15) models of survival probability indicated strong statistical support for time-constant annual survival of *D. caerulescens*, given our data.

#### SEASONAL MODELS

$AIC_c$  ranking of seasonal CJS models differed between the New Hampshire and Jamaica data sets (Table 3).

**Table 3.** Models of seasonal survival ( $\phi$ ) and recapture ( $p$ ) probabilities for *D. caerulescens*, number of estimable parameters ( $K$ ), second-order Akaike's information criterion values ( $AIC_c$ ),  $AIC_c$  differences ( $\Delta_i$ ), and  $AIC_c$  Weights ( $w_i$ ). Subscripts give parameterization for  $\phi$  and  $p$ : no subscript = constant over group and time variables; 'sex' = female and male; 'season' = two seasons (see Methods); 's & yr' = two seasons, no variation among years for the breeding or overwinter intervals, but with annual variation for August–May or March–October intervals. Subscripts joined by an '\*' indicate a factorial model. Statistics for best-fit models are in bold. The global model ( $\phi_{\text{sex} \times \text{season}} p_{\text{sex} \times \text{s} \times \text{year}}$ ) fit the data well for both New Hampshire ( $\chi^2_{39} = 41.03$ ,  $P = 0.96$ ) and Jamaica ( $\chi^2_{30} = 14.71$ ,  $P > 0.99$ ) data sets

	Model	New Hampshire <sup>a</sup>				Jamaica <sup>b</sup>			
		$K$	$AIC_c$	$\Delta_i$	$w_i$	$K$	$AIC_c$	$\Delta_i$	$w_i$
(1)	$\phi_{\text{season}} p_{\text{s} \times \text{year}}$	14	1105.35	1.63	0.15	<b>16</b>	<b>656.97</b>	<b>0</b>	<b>0.81</b>
(2)	$\phi_{\text{season}} p_{\text{sex} \times \text{s} \times \text{year}}$	26	1103.94	0.22	0.31	30	677.45	20.47	0.00
(3)	$\phi_{\text{sex} \times \text{season}} p_{\text{s} \times \text{year}}$	<b>16</b>	<b>1103.72</b>	<b>0</b>	<b>0.34</b>	18	659.87	2.90	0.19
(4)	$\phi_{\text{sex} \times \text{season}} p_{\text{sex} \times \text{s} \times \text{year}}$	28	1104.76	1.05	0.20	32	682.16	25.18	0.00
(5)	$\phi, p_{\text{s} \times \text{year}}$	13	1126.42	22.70	0.00	15	701.59	44.61	0.00
(6)	$\phi, p_{\text{sex} \times \text{s} \times \text{year}}$	25	1125.49	21.77	0.00	29	719.60	62.63	0.00
(7)	$\phi_{\text{sex}} p_{\text{s} \times \text{year}}$	14	1122.93	19.21	0.00	16	703.71	46.73	0.00
(8)	$\phi_{\text{sex}} p_{\text{sex} \times \text{s} \times \text{year}}$	26	1124.11	20.39	0.00	30	721.95	64.98	0.00

<sup>a</sup>May 1990–August 2000.

<sup>b</sup>October 1986–March 1999.

**Table 4.** Model averaged estimates of monthly survival ( $\phi$ ) and recapture ( $p$ ) probabilities, unconditional standard errors, and profile likelihood 95% confidence intervals for four seasonal intervals for *D. caerulescens* at Hubbard Brook Experimental Forest, New Hampshire, USA (May 1990–August 2000) and Copse Mountain, Jamaica, West Indies (October 1986–March 1999)

Location	$\phi \pm 1 \text{ SE}$ (95% CI)		$p \pm 1 \text{ SE}$ (95% CI)	
New Hampshire	May–August <sup>a</sup>	August–May <sup>b</sup>	May	August <sup>c</sup>
Male	0.999 $\pm$ 0.001 (0.999–1.000)	0.929 $\pm$ 0.007 (0.913–0.943)	0.939 $\pm$ 0.028 (0.854–0.976)	0.807 $\pm$ 0.056 (0.697–0.917)
Female	0.991 $\pm$ 0.015 (0.800–0.999)	0.920 $\pm$ 0.008 (0.902–0.935)	0.890 $\pm$ 0.045 (0.765–0.953)	0.632 $\pm$ 0.064 (0.507–0.757)
Jamaica	October–March <sup>a</sup>	March–October <sup>b</sup>	October	March <sup>d</sup>
Male	0.990 $\pm$ 0.009 (0.943–0.998)	0.874 $\pm$ 0.014 (0.845–0.899)	0.882 $\pm$ 0.037 (0.790–0.937)	0.809 $\pm$ 0.068 (0.678–0.942)
Female	0.987 $\pm$ 0.009 (0.943–0.997)	0.877 $\pm$ 0.015 (0.845–0.903)	0.882 $\pm$ 0.037 (0.790–0.937)	0.779 $\pm$ 0.062 (0.657–0.901)

<sup>a</sup>Stationary period.

<sup>b</sup>Interval includes migration.

<sup>c</sup>Estimates = mean, SE, 95% CI of annual  $p$  from model [ $\phi_{\text{sex} \times \text{season}} p_{\text{sex} \times \text{s} \times \text{year}}$ ]; see Table 3.

<sup>d</sup>Estimates = mean, SE, 95% CI of annual  $p$  from model [ $\phi_{\text{season}} p_{\text{sex} \times \text{s} \times \text{year}}$ ]; see Table 3.

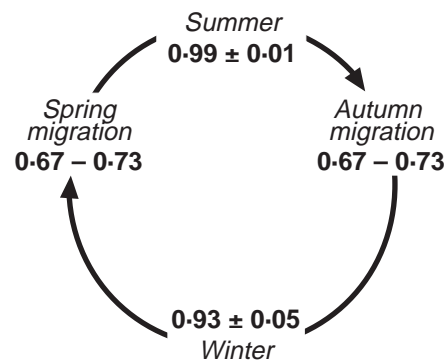
Both analyses, however, clearly indicated that monthly survival was higher during the May–August and October–March stationary periods of *D. caerulescens* annual cycle than during the opposite periods (i.e. August–May and March–October) that included migration (Tables 3 and 4). Monthly survival probabilities during the stationary periods were nearly identical in Jamaica and in New Hampshire, being  $\geq 0.99$  for males and females in both locations. Males had higher estimated survivorship than females from August–May in New Hampshire (Table 4). Based on  $\Sigma w_i$ , sex-specific survival (Table 3: models 3, 4, 7, 8) during this interval was 5.2 times more likely to be the best fit to our data than constant survival (Table 3: models 1, 2, 5, 6). Estimated survivorship did not differ appreciably between males and females in Jamaica from March–October (Table 4), and  $\Sigma w_i$  indicated that sex-specific

survival on winter quarters was only 1.8 times more likely than constant survival (Table 3).

Recapture probabilities were higher at the beginning of the stationary periods (May and October) than at the end (August and March), although differences between October and March were small (Table 4). Females tended to have lower recapture probabilities than males in New Hampshire, particularly at the end of the breeding season. Differences in seasonal recapture probabilities were negligible between sexes in Jamaica (Table 4).

#### SURVIVAL DURING MIGRATION

Monthly survival probability during migration was  $0.766 \pm 0.023$  (95% CI: 0.721–0.810) based on the  $\hat{\phi}_{\text{migration \& breeding}}/\hat{\phi}_{\text{breeding}}$  ratio, and  $0.813 \pm 0.024$  (95% CI:



**Fig. 1.** Survival probabilities for four seasonal intervals in the annual cycle of *D. caerulescens*. 'Summer' = breeding season survival May–August, 'Winter' = overwinter survival October–March, and the two migration intervals represent survival during the 6-weeks spring and autumn migration periods. Summer and winter survival estimates  $\pm 1$  SE are from model [ $\phi_{\text{season}}, p_s \& \text{yr}$ ] in Table 3; only male estimates were used for New Hampshire. Survival estimates during the migratory periods are monthly survival estimates (see Results) raised to the 1.5 power.

0.766–0.859) based on  $\hat{\phi}_{\text{migration}} \& \text{overwinter} / \hat{\phi}_{\text{overwinter}}$  and  $\hat{\phi}_{\text{migration}} \& \text{overwinter}$  where  $\hat{\phi}_{\text{migration}} \& \text{overwinter}$  came from New Hampshire males. Thus, estimated monthly survival rates during migration were dramatically lower than monthly survival rates during the summer and winter stationary periods (see Table 4). This comparison of seasonal survival estimates, summarized graphically in Fig. 1, corroborates model results from seasonal CJS analyses.

## Discussion

### METHODOLOGICAL CONSIDERATIONS

Annual survival probabilities for *D. caerulescens* in this study (0.40–0.51) are similar to CJS estimates for other shrub-nesting Parulidae (0.34–0.63, Nichols *et al.* 1981; DeSante *et al.* 1998). However, most published survivorship data for these and other wood warbler species are derived from *ad hoc* return rates and other methods (e.g. Farner 1955) that do not control for recapture probability. This failure to account for probability of detection can result in negatively biased survival estimates (Pollock *et al.* 1990; Lebreton *et al.* 1992; Martin *et al.* 1995). While methods that do not consider detection probability may provide data suitable for interspecific comparisons of life history (Sæther 1988; Martin 1995; Ricklefs 1997), survival probabilities estimated by these approaches should not be used in demographic and conservation studies unless recapture rates are close to 1.0.

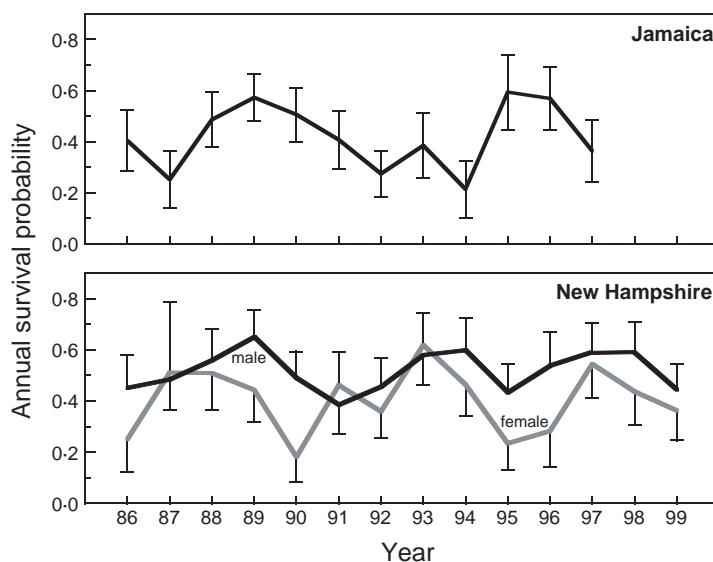
Our survivorship data were based on the resighting of colour-ringed individuals, whereas most of the existing mark–recapture data for migratory songbirds (e.g. Conway *et al.* 1995; Chase *et al.* 1997; DeSante *et al.* 1998; Rosenberg *et al.* 1999) comes from mist-net studies. Mist-nets are probably the only option for

collecting these data for cryptic understorey species (e.g. Kentucky warbler, *Oporornis formosus*; ovenbird, *Seiurus aurocapillus*) during the non-breeding season. However, recapture probabilities of marked individuals in mist-nets tend to be lower than the recapture probabilities typical of resighting studies (Sandercock *et al.* 2000). While this does not lead to biased CJS estimates of  $\phi$  (Nichols, Hines, & Pollock 1984), low recapture probabilities can reduce the precision of estimates and could thus reduce power to detect survival differences among sex- and age-classes and among sampling periods (Lebreton *et al.* 1992; Sandercock *et al.* 2000).

Mist-net data may also include floaters or transients because most passerines that hit nets are captured, regardless of their territorial behaviour or social status. Incorporating non-territorial individuals in analyses can underestimate survival if models are not parameterized to account for these groups (Peach 1993; Chase *et al.* 1997; Pradel *et al.* 1997). Resighting studies, like ours, usually examine only territorial birds or breeders, segments of the population that are more easily resighted and tend to have higher estimates of survival (Nichols *et al.* 1994; Cam *et al.* 1998; Sandercock *et al.* 2000). Resighting studies might therefore overestimate survival because they could fail to detect non-territorial individuals. We have no data on the presence of floater and transient *D. caerulescens* in Jamaica, although the small number of territories vacated in early winter are often reoccupied by unringed or neighbouring ringed conspecifics (Holmes *et al.* 1989). At our New Hampshire site, all females and approximately 90% of males each year are mated (Holmes *et al.* 1992; R. T. Holmes and T. S. Sillett, unpublished data) and floaters are rare (Marra & Holmes 1997). In general, floaters are considered to be poor-quality or younger individuals that either do not reproduce, or have low reproductive success if they acquire a breeding territory (reviewed by Newton 1998). Thus, the contribution of floaters to population growth rates, and hence relevance of floaters' survivorship to population studies remains unclear.

### ANNUAL SURVIVAL PATTERNS

Male *D. caerulescens* had higher annual survival than females on New Hampshire breeding grounds, while sexes had effectively equal annual survival on winter quarters in Jamaica (Table 2). However, our estimates of annual survivorship for breeding females could be negatively biased if females had a higher probability than males of permanent emigration from our Hubbard Brook study plot. Two lines of evidence support this possibility. First, *D. caerulescens* appear to have lower site fidelity and to move greater distances between years on breeding grounds compared to winter quarters (Holmes & Sherry 1992). Second, when both members of a divorced pair return to breed at Hubbard Brook, males typically remain on their original territories,



**Fig. 2.** Comparison of annual survival probabilities for *D. caerulescens* overwintering at Copse Mountain in Jamaica, West Indies, 1986–98 (top panel), and breeding at Hubbard Brook Experimental Forest in New Hampshire, USA, 1986–2000 (bottom panel). Jamaica data taken from model  $[\phi_{\text{year}}, p]$  in Table 1; New Hampshire data from model  $[\phi_{\text{sex} \times \text{year}}, p_{\text{sex}}]$  in Table 1. Error bars represent 1 SE. Estimates of annual survival probability in this figure supersede those in Fig. 2 of Sillett *et al.* (2000).

whereas females often disperse several hundred metres to a new territory site (P. P. Marra & R. T. Holmes, unpublished data). Divorce and dispersal by females was usually associated with low breeding success in the previous year. Increased dispersal distances would result in proportionally more females permanently emigrating from our 64 ha study plot, and thus in a lower CJS estimate of  $\phi$ . Female-biased breeding dispersal has been documented for many avian taxa (Greenwood 1980; Payne & Payne 1993; Clarke, Sæther, & Roskaft 1997; Blondel, Perret, & Galan 2000; Schjorring, Gregersen, & Bregnballe 2000).

The lower estimate of annual survival for warblers in Jamaica relative to New Hampshire males was probably due to the differential impact of climatic variation on birds at the two locations. Annual survivorship in Jamaica, but not in New Hampshire, varied with phase of the El Niño Southern Oscillation, or ENSO (Sillett *et al.* 2000). Estimated survival probability was low ( $0.318 \pm 0.045$ ) during El Niño years, high ( $0.545 \pm 0.060$ ) during La Niña years, and in between these values ( $0.493 \pm 0.071$ ) in normal years. From 1986 to 1998, El Niño years (1987, 1991–94, 1997) were more frequent than either La Niña years (1988–89, 1996) or normal years (1986, 1990, 1995, 1998; Sillett *et al.* 2000). Survivorship of Jamaica birds in normal years was similar to May–May survivorship of New Hampshire males (Table 2).

Survival probabilities for *D. caerulescens* in both New Hampshire and Jamaica exhibited considerable interannual variation (Fig. 2), although time-specific models of annual survivorship were not supported by AIC<sub>c</sub> model selection (Table 1). The standard errors shown in Fig. 2, however, as well as those produced by model averaging (Tables 2 and 4), only estimate sampling variation. Process variance, an estimate of the

variation in  $\phi$  that can be attributed to environmental stochasticity (see Lande 1993), is the appropriate estimate of  $\sigma^2$  to use in parameterizing population simulation models (White 2000). To estimate process variance in  $\phi$  for *D. caerulescens*, we calculated variance components in program MARK, using model  $[\phi_{\text{sex} \times \text{year}}, p_{\text{sex}}]$  for New Hampshire and model  $[\phi_{\text{year}}, p]$  for Jamaica. For males in New Hampshire, estimated process variance in  $\phi$  was negligible ( $\hat{\sigma} = 0.000$ ; 95% CI: 0.000–0.061), indicating that variation in annual survival estimates of these males was primarily due to sampling error. Estimated process variance in  $\phi$  was  $> 0$  for New Hampshire females ( $\hat{\sigma} = 0.044$ ; 95% CI: 0.000–0.166) and for both sexes in Jamaica ( $\hat{\sigma} = 0.068$ ; 95% CI: 0.000–0.188). Thus, some variation in  $\phi$  for these groups can be attributed to a biologically relevant factor, such as ENSO or annual variation in reproductive success.

For most bird species, survival is thought to be higher in males than in females, with this difference being responsible in part for male-biased sex ratios (reviewed by Breitwisch 1989). If female and male *D. caerulescens* have similar survival rates, as we contend, what could account for the apparent male-biased sex ratio in this species (Holmes *et al.* 1992; Holmes *et al.* 1996; Marra & Holmes 1997)? One explanation is higher mortality of female nestlings or fledglings. We cannot address this possibility with our data. A second explanation is differential mortality of females on winter quarters due to sexual habitat segregation (Gauthreaux 1978; Marra 2000). Females can be disproportionately relegated to suboptimal habitats in winter by behavioural dominance of male conspecifics (Marra 2000). Regardless of sex, birds in these habitats are in poorer physical condition by the end of winter (Marra & Holberton 1998; Marra *et al.* 1998) and have



lower survival rates from March–October than individuals in high-quality, male-dominated sites (Marra & Holmes 2001). Wunderle (1995) documented sexual habitat segregation in *D. caerulescens* wintering in Puerto Rico, and found that persistence rates of birds in female-dominated sites were lower than in male-dominated sites. Both our New Hampshire and Jamaica sites represented high-quality habitat for *D. caerulescens*. A full explanation for male-biased sex ratios in this and other migratory songbird species will require survival estimates from a broad range of winter habitats.

Hatch-year and yearling warblers had nearly identical annual survival rates as adults (Table 2). This implies that by the time hatch-year individuals acquire territories on winter quarters in mid-October, they can forage and survive as well as adults in the same habitat. Similarly, hatch-year American redstarts, *Setophaga ruticilla*, survive as well as adults in both high- and low-quality habitats (Marra & Holmes 2001). These patterns support the conclusions reached by others (Dhondt 1979; Krementz, Nichols, & Hines 1989; Sullivan 1989; Anders *et al.* 1997; Thomson, Baillie, & Peach 1999) that the time of greatest mortality for juvenile passerines occurs in the first several weeks after fledging. However, hatch-year birds, like females, can also be disproportionately forced into suboptimal habitats on winter quarters (Marra 2000), where survival rates are lower (Marra & Holmes 2001). If the majority of hatch-year individuals overwinter in poor-quality habitat, overall survival of birds in their first year should be lower than adult survival.

#### SURVIVAL DURING THE WINTER AND SUMMER STATIONARY PERIODS

*Dendroica caerulescens* had high survival rates during the winter stationary period, with less than 1% apparent mortality per month. To our knowledge, only two other published studies have used capture–recapture models to examine survivorship of temperate–tropical migratory songbirds during the overwinter period. Conway *et al.* (1995) estimated monthly survival and recapture probabilities for four species overwintering in mature forest in Belize: wood thrush, *Hylocichla mustelina*; hooded warbler, *Wilsonia citrina*; *O. formosus*; and *S. aurocapillus*. Monthly survival estimates for these species (0.89–0.93) were substantially less than our estimate 0.99 for *D. caerulescens*, although Conway *et al.* included all birds captured, regardless of territorial behaviour, in their analyses. Marra & Holmes (2001) analysed resighting data for territory-holding *S. ruticilla* wintering along the south-western coast of Jamaica. They found overwinter survival rates similar to ours in both high-quality and suboptimal habitat. Additional data from multiple species and localities are needed for a complete understanding of overwinter survival patterns in migratory songbirds.

Data on survival rates of adult passerines during the north temperate breeding season are scarce. Powell

*et al.* (2000) estimated that *H. mustelina* breeding in Georgia had oversummer survival rates of 1.0 for males and 0.82 for females. In a study of willow tits, *Parus montanus* L. in Finland, Lahti *et al.* (1998) estimated that the oversummer survival rate of adults was approximately 0.96. Smith (1995) reported low oversummer survival of subordinate yearling black-capped chickadees, *Poecile atricapillus*, in Massachusetts, but her sample sizes were small and survival estimates were based solely on *ad hoc* persistence rates. These data suggest that small passerines, with the possible exception of subordinate individuals, have high adult survival rates during the north-temperate breeding period. Although little direct evidence exists regarding the fates of adult songbirds that disappear from study populations, predators are probably the primary source of breeding season mortality (Newton 1998). For example, the high mortality rate of female *H. mustelina* documented by Powell *et al.* (2000) was due to avian and mammalian predation during the nesting period. Similarly, six of the seven *D. caerulescens* that vanished from our Hubbard Brook study population after the mid-May–early June sampling period had active nests. We suspect that these birds were killed by predators, probably sharp-shinned hawks, *Accipiter striatus* (R. T. Holmes, unpublished data).

#### COMPARING SURVIVAL BETWEEN THE MIGRATORY AND STATIONARY PERIODS

We found no published estimates of survival rates during migration for any passerine. This is not surprising, given the extreme difficulty in resighting individuals on both their breeding and winter grounds (Sherry & Holmes 1995). The only data that exist for birds are from studies of migratory waterfowl (e.g. Owen & Black 1991; Ward *et al.* 1997), and survival of some of these populations can be impacted by hunting. Despite the lack of data for passerines, it is highly probable that their survival rates during the migratory period are low compared to the stationary periods. Migration involves major physiological changes and expenses of energy (Gill 1990), and many migratory species must cross hundreds of kilometres of inhospitable habitat, such as oceans or deserts, separating breeding and wintering areas.

Our results suggest that monthly mortality rates of *D. caerulescens* are at least 15 times higher during migration compared to the stationary periods. The implications of this result are twofold. First, the majority of apparent adult mortality occurs during the migratory period or immediately prior to the start of autumn or spring migration. For example, start with 100 warblers counted on a May pre-breeding census. Given the seasonal survival estimates in Fig. 1, approximately 51–59 of these birds would be expected to die by the following May. Of these, 44–53, or 87–89%, would probably perish during spring or autumn migration. Second, our data indicate that during the stationary

periods, *D. caerulescens*, and possibly temperate–tropical migratory songbirds in general, have survival rates similar to those of nonmigratory, tropical passerines (Ricklefs 1997; Sandercock *et al.* 2000; and references therein). Lower adult survival rates in temperate-breeding passerines compared to tropical residents have been proposed as an explanation for the latitudinal gradient in clutch size and annual fecundity (Martin 1996; Martin *et al.* 2000). Increased mortality as a result of long-distance migration between temperate latitudes and the tropics could be one origin of these life-history differences.

## Conclusions

The distribution and abundance of migratory songbirds are limited by processes occurring throughout their annual cycle (Sherry & Holmes 1995; Latta & Baltz 1997; Newton 1998), and events during one stage of the cycle influence populations in subsequent stages (Baillie & Peach 1992; Marra *et al.* 1998; Sillett *et al.* 2000). To manage these species, we need to understand the relative impacts of the breeding, overwinter, and migratory periods on population dynamics (DeSante 1995; Sherry & Holmes 1995; Marra & Holmes 2001), yet basic demographic data are sorely lacking for most species. Our results indicated that survival rates of *D. caerulescens* were equal during the summer and winter stationary periods for individuals holding territories in high-quality habitat, regardless of age or sex. However, the availability of high-quality habitats for this species, especially on its winter grounds, is unknown, and we have no robust survivorship estimates from low-quality sites. Furthermore, we lack information on survival of juvenile *D. caerulescens* during the critical interval between fledging and territory establishment on winter quarters. Developing conservation plans for migratory songbirds and effective management of their populations will require three general types of data: (i) estimates of habitat-specific demography for both adults and juveniles; (ii) measures of habitat availability on north-temperate breeding grounds, at migratory stopover sites, and on tropical winter quarters; and (iii) predictions of how habitat distributions could change in the future. Until we have these data for multiple species, concluding that migrant populations are limited predominantly by events in either winter (e.g. Rappole & McDonald 1994), summer, or during migration is premature.

Little is known about the ecology of songbirds during migration, and the importance of the migratory period has frequently been ignored when developing conservation strategies (Moore *et al.* 1995; Hutto 2000). Mortality of adult *D. caerulescens* appears to be concentrated in the migratory period, but survival of migrating songbirds is probably determined by many factors. Events during the stationary periods, such as overwintering in suboptimal habitats or in drought-affected areas, can have adverse effects on birds'

physical condition (Marra & Holberton 1998; Katti & Price 1999; Strong & Sherry 2000). However, available data for Nearctic–Neotropical migrants (see above) imply that these species have high survival rates in the stationary periods, even those individuals holding territories in low-quality sites (Marra & Holmes 2001) or in areas negatively effected by climatic phenomena, such as ENSO (T. S. Sillett & R. T. Holmes, unpublished data). Thus, the influence of both breeding and overwinter seasons on adult survival might not be manifested until the migratory period. Survival of migrating passerines is certainly affected by events during passage as well, including storms (Butler 2000), collisions with communications towers (Avery, Springer, & Cassel 1976; Shire, Brown, & Winegrad 2000), and a lack of suitable stopover sites (Moore *et al.* 1995; Petit 2000). Consequently, migrant populations could be especially susceptible to processes that further reduce survival of individuals during migration, such as destruction of high-quality winter habitats and stopover sites, and increases in the number of communications towers along migration routes. Management plans for migratory songbirds should therefore consider not only the habitat requirements of these species throughout their annual cycle, but the potential risks imposed on migrating birds by human development.

## Acknowledgements

This research was funded by the US National Science Foundation through grants awarded to R.T. Holmes (Dartmouth College) and T.W. Sherry (Tulane University). We are grateful to the many people who helped with field work over the 15 years of this study, especially J.J. Barg, H.C. Chuang, P.D. Hunt, M.D. Johnson, P.P. Marra, L.R. Nagy, K.E. Petit, L.R. Reitsma, N.L. Rodenhouse, T.W. Sherry, A.M. Strong, and M.S. Webster. Our work in Jamaica would not have been possible without the support and hospitality of the Sutton and Williams families. This paper benefited from the advice and comments of M.P. Ayres, S.R. Baillie, D.A. Bolger, A.A. Dhondt, P.J. Doran, J.E. Hines, P.P. Marra, M.A. McPeck, S.A. Morrison, L.R. Nagy, J.D. Nichols, B.K. Sandercock, T.W. Sherry, and A.M. Strong. We thank the Jamaica Natural Resources Conservation Authority and the Hubbard Brook Experimental Forest of the US Department of Agriculture North-eastern Research Station for their cooperation.

## References

- Akaike, H. (1973) Information theory as an extension of the maximum likelihood principle. *Second International Symposium on Information Theory* (eds B.N. Petrov & F. Csaki), pp. 267–281. Akademiai Kiado, Budapest.
- American Ornithologists' Union (1998) *Check-List of North American Birds*, 7th edn. American Ornithologists' Union, Washington, DC.
- Anders, A.D., Dearborn, D.C., Faaborg, J. & Thompson,

- F.R. (1997) Juvenile survival in a population of Neotropical migrant birds. *Conservation Biology*, **11**, 698–707.
- Anderson, D.R., Burnham, K.P. & Thompson, W.L. (2000) Null hypothesis testing: problems, prevalence, and an alternative. *Journal of Wildlife Management*, **64**, 912–923.
- Askins, R.A., Lynch, J.F. & Greenberg, R. (1990) Population declines in migratory birds in eastern North America. *Current Ornithology*, **7**, 1–57.
- Avery, M.L., Springer, P.F. & Cassel, J.F. (1976) Effects of a tall tower on nocturnal bird migration: portable ceilometer study. *Auk*, **93**, 281–291.
- Baillie, S.R. & Peach, W.J. (1992) Population limitation in Palearctic–African migrant passerines. *Ibis*, **134**, 120–132.
- Blondel, J., Perret, P. & Galan, M.J. (2000) High divorce rates in Corsican blue tits: how to choose a better option in a harsh environment. *Oikos*, **89**, 451–460.
- Breitwisch, R. (1989) Mortality patterns, sex ratios, and parental investment in monogamous birds. *Current Ornithology*, **6**, 1–50.
- Burnham, K.P. & Anderson, D.R. (1998) *Model Selection and Inference: a Practical Information-Theoretic Approach*. Springer, New York.
- Burnham, K.P., Anderson, D.R., White, G.C., Brownie, C. & Pollock, K.H. (1987) *Design and Analysis Methods for Fish Survival Experiments Based on Release–Recapture*. American Fisheries Society Monograph, **5**.
- Butler, R.W. (2000) Stormy seas for some North American songbirds: are declines related to severe storms during migration? *Auk*, **117**, 518–522.
- Cam, E., Hines, J.E., Monnat, J.Y., Nichols, J.D. & Danchin, E. (1998) Are adult nonbreeders prudent parents? The kittiwake model. *Ecology*, **79**, 2917–2930.
- Chamberlain, C.P., Blum, J.D., Holmes, R.T., Feng, X.H., Sherry, T.W. & Graves, G.R. (1997) The use of isotope tracers for identifying populations of migratory birds. *Oecologia*, **109**, 132–141.
- Chase, M.K., Nur, N. & Geupel, G.R. (1997) Survival, productivity, and abundance in a Wilson's warbler population. *Auk*, **114**, 354–366.
- Cichon, M., Olejniczak, P. & Gustafsson, L. (1998) The effect of body condition on the cost of reproduction in female collared flycatchers *Ficedula albicollis*. *Ibis*, **140**, 128–130.
- Clarke, A.L., Sæther, B.-E. & Roskaft, E. (1997) Sex biases in avian dispersal: a reappraisal. *Oikos*, **79**, 429–438.
- Clobert, J. & Lebreton, J.-D. (1991) Estimation of demographic parameters in bird population dynamics. *Bird Population Studies: Their Relevance to Conservation and Management* (eds C.M. Perrins, J.-D. Lebreton & G.J.M. Hiron), pp. 75–104. Oxford University Press, Oxford.
- Conway, C.J., Powell, G.V.N. & Nichols, J.D. (1995) Overwinter survival of Neotropical migratory birds in early-successional and mature tropical forests. *Conservation Biology*, **9**, 855–864.
- DeSante, D.F. (1995) Suggestions for future directions for studies of marked migratory landbirds from the perspective of a practitioner in population management and conservation. *Journal of Applied Statistics*, **22**, 949–965.
- DeSante, D.F., O'Grady, D.R., Burton, K.M., Velez, P., Froelich, D., Feuss, E.E., Smith, H. & Ruhlén, E.D. (1998) The Monitoring Avian Productivity and Survivorship (MAPS) Program sixth and seventh annual report (1995 and 1996). *Bird Populations*, **4**, 69–122.
- Dhondt, A.A. (1979) Summer dispersal and survival of juvenile great tits in southern Sweden. *Oecologia*, **42**, 139–157.
- Farner, D.S. (1955) Bird banding in the study of population dynamics. *Recent Studies in Avian Biology* (ed. A. Wolfson), pp. 397–449. University of Illinois Press, Urbana, Illinois.
- Gauthreaux, S.A. Jr (1978) The ecological significance of behavioral dominance. *Perspectives in Ethology*, **3**, 17–54.
- Gill, F.B. (1990) *Ornithology*. W.H. Freeman, New York.
- Greenwood, P.J. (1980) Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour*, **28**, 1140–1162.
- Hagan, J.M. & Johnston, D.W. (1992) *Ecology and Conservation of Neotropical Migrant Landbirds*. Smithsonian Institution Press, Washington.
- Holmes, R.T. (1994) Black-throated blue warbler (*Dendroica caerulescens*). *The Birds of North America* (eds A. Poole & F. Gill), no. 87, pp. 1–24. Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, DC.
- Holmes, R.T., Marra, P.P. & Sherry, T.W. (1996) Habitat-specific demography of breeding black-throated blue warblers (*Dendroica caerulescens*): implications for population dynamics. *Journal of Animal Ecology*, **65**, 183–195.
- Holmes, R.T. & Sherry, T.W. (1992) Site fidelity of migratory warblers in temperate breeding and neotropical wintering areas: implications for population dynamics, habitat selection, and conservation. *Ecology and Conservation of Neotropical Migrant Landbirds* (eds J.M. Hagan & D.W. Johnston), pp. 563–575. Smithsonian Institution Press, Washington, DC.
- Holmes, R.T. & Sherry, T.W. (2001) Thirty-year bird population trends in an unfragmented temperate deciduous forest: importance of habitat change. *Auk*, **118**, 589–610.
- Holmes, R.T., Sherry, T.W., Marra, P.P. & Petit, K.E. (1992) Multiple brooding and productivity of a Neotropical migrant, the black-throated blue warbler (*Dendroica caerulescens*), in an unfragmented temperate forest. *Auk*, **109**, 321–333.
- Holmes, R.T., Sherry, T.W. & Reitsma, L. (1989) Population structure, territoriality and overwinter survival of two migrant warbler species in Jamaica. *Condor*, **91**, 545–561.
- Hutto, R.L. (2000) On the importance of *en route* periods to the conservation of migratory landbirds. *Studies in Avian Biology*, **20**, 109–114.
- Katti, M. & Price, T. (1999) Annual variation in fat storage by a migrant warbler overwintering in the Indian tropics. *Journal of Animal Ecology*, **68**, 815–823.
- Keast, A. & Morton, E.S. (1980) *Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation*. Smithsonian Institution Press, Washington, DC.
- Kendall, W.L., Nichols, J.D. & Hines, J.E. (1997) Estimating temporary emigration using capture-recapture data with Pollock's robust design. *Ecology*, **78**, 563–578.
- Krementz, D.G., Nichols, J.D. & Hines, J.E. (1989) Postfledging survival of European starlings. *Ecology*, **70**, 646–655.
- Lahti, K., Orell, M., Rytönen, S. & Koivula, K. (1998) Time and food dependence in willow tit winter survival. *Ecology*, **79**, 2904–2916.
- Lande, R. (1993) Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist*, **142**, 911–927.
- Latta, S.C. & Baltz, M.E. (1997) Population limitation in Neotropical migratory birds: comments. *Auk*, **114**, 754–762.
- Lebreton, J.-D., Burnham, K.P., Clobert, J. & Anderson, D.R. (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case-studies. *Ecological Monographs*, **62**, 67–118.
- Marra, P.P. (2000) The role of behavioral dominance in structuring patterns of habitat occupancy in a migrant bird during the non-breeding season. *Behavioral Ecology*, **11**, 299–308.
- Marra, P.P., Hobson, K.A. & Holmes, R.T. (1998) Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science*, **282**, 1884–1886.
- Marra, P.P. & Holberton, R.L. (1998) Corticosterone levels as indicators of habitat quality: effects of habitat segregation in a migratory bird during the non-breeding season. *Oecologia*, **116**, 284–292.

- Marra, P.P. & Holmes, R.T. (1997) Avian removal experiments: do they test for habitat saturation or female availability? *Ecology*, **78**, 947–952.
- Marra, P.P. & Holmes, R.T. (2001) Consequences of dominance-mediated habitat segregation in American Redstarts during the nonbreeding season. *Auk*, **107**, 96–106.
- Martin, T.E. (1995) Avian life-history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs*, **65**, 101–127.
- Martin, T.E. (1996) Life history evolution in tropical and south temperate birds: what do we really know? *Journal of Avian Biology*, **27**, 263–272.
- Martin, T.E., Clobert, J. & Anderson, D.R. (1995) Return rates in studies of life history evolution: are biases large? *Journal of Applied Statistics*, **22**, 863–875.
- Martin, T.E. & Finch, D.M. (1995) *Ecology and Management of Neotropical Migratory Birds: a Synthesis and Review of Critical Issues*. Oxford University Press, New York.
- Martin, T.E., Martin, P.R., Olson, C.R., Heidinger, B.J. & Fontaine, J.J. (2000) Parental care and clutch sizes in North and South American birds. *Science*, **287**, 1482–1485.
- McCleery, R.H., Clobert, J., Julliard, R. & Perrins, C.M. (1996) Nest predation and delayed cost of reproduction in the great tit. *Journal of Animal Ecology*, **65**, 96–104.
- Moore, F.R., Gauthreaux, S.A., Kerlinger, P. & Simons, T.R. (1995) Habitat requirements during migration: important link in conservation. *Ecology and Management of Neotropical Migratory Birds: a Synthesis and Review of Critical Issues* (eds T.E. Martin & D.M. Finch), pp. 121–144. Oxford University Press, New York.
- Newton, I. (1998) *Population Limitation in Birds*. Academic Press, London.
- Nichols, J.D., Hines, J.E. & Pollock, K.H. (1984) Effects of permanent trap response in capture probability on Jolly–Seber capture–recapture model estimates. *Journal of Wildlife Management*, **48**, 289–294.
- Nichols, J.D., Hines, J.E., Pollock, K.H., Hinz, R.L. & Link, W.A. (1994) Estimating breeding proportions and testing hypotheses about costs of reproduction with capture–recapture data. *Ecology*, **75**, 2052–2065.
- Nichols, J.D., Noon, B.R., Stokes, S.L. & Hines, J.E. (1981) Remarks on the use of mark–recapture methodology in estimating avian population size. *Studies in Avian Biology*, **6**, 121–126.
- Nur, N. (1988) The cost of reproduction in birds: an examination of the evidence. *Ardea*, **76**, 155–168.
- Owen, M. & Black, J.M. (1991) A note on migration mortality and its significance in goose populations dynamics. *Ardea*, **79**, 195–196.
- Payne, R.B. & Payne, L.L. (1993) Breeding dispersal in indigo buntings: circumstances and consequences for breeding success and population-structure. *Condor*, **95**, 1–24.
- Peach, W.J. (1993) Combining mark–recapture datasets for small passerines. *Marked Individuals in the Study of Bird Populations* (eds J.-D. Lebreton & P.M. North), pp. 107–122. Birkhauser-Verlag, Basel.
- Peach, W.J., Baillie, S.R. & Balmer, D.E. (1998) Long-term changes in the abundance of passerines in Britain and Ireland as measured by constant effort mist-netting. *Bird Study*, **45**, 257–275.
- Peterjohn, B.G., Sauer, J.S. & Robbins, C.S. (1995) Population trends from the North American Breeding Bird Survey. *Ecology and Management of Neotropical Migratory Birds: A Synthesis and Review of Critical Issues* (eds T.E. Martin & D.M. Finch), pp. 3–39. Oxford University Press, New York.
- Petit, D.R. (2000) Habitat use by landbirds along Nearctic–Neotropical migration routes: implications for conservation of stopover habitats. *Studies in Avian Biology*, **20**, 15–33.
- Pollock, K.H. (1981) Capture–recapture models: a review of current methods, assumptions, and experimental design. *Studies in Avian Biology*, **6**, 426–435.
- Pollock, K.H., Nichols, J.D., Brownie, C. & Hines, J.E. (1990) Statistical inference for capture–recapture experiments. *Wildlife Monographs*, **107**, 1–97.
- Porneluzi, P.A. & Faaborg, J. (1999) Season-long fecundity, survival, and viability of ovenbirds in fragmented and unfragmented landscapes. *Conservation Biology*, **13**, 1151–1161.
- Powell, L.A., Lang, J.D., Conroy, M.J. & Kremenetz, D.G. (2000) Effects of forest management on density, survival, and population growth of wood thrushes. *Journal of Wildlife Management*, **64**, 11–23.
- Pradel, R., Hines, J.E., Lebreton, J.-D. & Nichols, J.D. (1997) Capture–recapture survival models taking account of transients. *Biometrics*, **53**, 60–72.
- Prevot-Julliard, A.C., Lebreton, J.-D. & Pradel, R. (1998) Re-evaluation of adult survival of black-headed gulls (*Larus ridibundus*) in presence of recapture heterogeneity. *Auk*, **115**, 85–95.
- Pyle, P., Howell, S.N.G., Yunk, R.P. & DeSante, D.F. (1987) *Identification Guide to North American Passerines*, 1st edn. Slate Creek Press, Bolinas, CA.
- Rappole, J.H. & McDonald, M.V. (1994) Cause and effect in population declines of migratory birds. *Auk*, **111**, 652–660.
- Ricklefs, R.E. (1997) Comparative demography of new world populations of thrushes (*Turdus* spp.). *Ecological Monographs*, **67**, 23–43.
- Robbins, C.S., Sauer, J.R., Greenberg, R.S. & Droege, S. (1989) Population declines in North American birds that migrate to the Neotropics. *Proceedings of the National Academy of Sciences of the United States of America*, **86**, 7658–7662.
- Robinson, S.K., Thompson, F.R., Donovan, T.M., Whitehead, D.R. & Faaborg, J. (1995) Regional forest fragmentation and the nesting success of migratory birds. *Science*, **267**, 1987–1990.
- Rosenberg, D.K., DeSante, D.F., McKelvey, K.S. & Hines, J.E. (1999) Monitoring survival rates of Swainson's thrush *Catharus ustulatus* at multiple spatial scales. *Bird Study*, **46**, 198–208.
- Rubenstein, D.R., Chamberlain, C.P., Holmes, R.T., Ayres, M.P., Waldbauer, J.R., Graves, G.R. & Turoso, N.C. (2002) Linking breeding and wintering ranges of a migratory songbird using stable isotopes. *Science*, **295**, 591–593.
- Sæther, B.-E. (1988) Patterns of covariation between life-history traits of European birds. *Nature*, **331**, 616–617.
- Sandercok, B.K., Beissinger, S.R., Stoleson, S.H., Melland, R.R. & Hughes, C.R. (2000) Survival rates of a Neotropical parrot: implications for latitudinal comparisons of avian demography. *Ecology*, **81**, 1351–1370.
- Schjorring, S., Gregersen, J. & Bregnballe, T. (2000) Sex difference in criteria determining fidelity towards breeding sites in the great cormorant. *Journal of Animal Ecology*, **69**, 214–223.
- Seber, G.A.F. (1982) *The Estimation of Animal Abundance and Related Parameters*, 2nd edn. Charles Griffin & Company Ltd, London.
- Sherry, T.W. & Holmes, R.T. (1995) Summer versus winter limitation of populations: what are the issues and what is the evidence. *Ecology and Management of Neotropical Migratory Birds: a Synthesis and Review of Critical Issues* (eds T.E. Martin & D.M. Finch), pp. 85–120. Oxford University Press, New York.
- Sherry, T.W. & Holmes, R.T. (1996) Winter habitat quality, population limitation, and conservation of Neotropical–Nearctic migrant birds. *Ecology*, **77**, 36–48.
- Shire, G.G., Brown, K. & Winegrad, G. (2000) *Communication Towers: A Deadly Hazard to Birds*. American Bird Conservancy, Washington, DC.
- Sillett, T.S., Holmes, R.T. & Sherry, T.W. (2000) Impacts of a global climate cycle on population dynamics of a migratory songbird. *Science*, **288**, 2040–2042.

- Siriwardena, G.M., Baillie, S.R., Buckland, S.T., Fewster, R.M., Marchant, J.H. & Wilson, J.D. (1998) Trends in the abundance of farmland birds: a quantitative comparison of smoothed Common Birds Census indices. *Journal of Applied Ecology*, **35**, 24–43.
- Siriwardena, G.M., Baillie, S.R. & Wilson, J.D. (1998) Variation in the survival rates of some British passerines with respect to their population trends on farmland. *Bird Study*, **45**, 276–292.
- Smith, S.M. (1995) Age-specific survival in breeding black-capped chickadees (*Parus atricapillus*). *Auk*, **112**, 840–846.
- Strong, A.M. & Sherry, T.W. (2000) Habitat-specific effects of food abundance on the condition of ovenbirds wintering in Jamaica. *Journal of Animal Ecology*, **69**, 883–895.
- Sullivan, K.A. (1989) Predation and starvation: age-specific mortality in juvenile juncos (*Junco phaeotus*). *Journal of Animal Ecology*, **58**, 275–286.
- Terborgh, J. (1989) *Where Have All the Birds Gone?* Princeton University Press, Princeton, New Jersey.
- Thomson, D.L., Baillie, S.R. & Peach, W.J. (1999) A method for studying post-fledging survival rates using data from ringing recoveries. *Bird Study*, **46**, S104–S111.
- Ward, D.H., Rexstad, E.A., Sedinger, J.S., Lindberg, M.S. & Dawe, N.K. (1997) Seasonal and annual survival of adult Pacific brant. *Journal of Wildlife Management*, **61**, 773–781.
- White, G.C. (2000) Population viability analysis: data requirements and essential analyses. *Research Techniques in Animal Ecology: Controversies and Consequences* (eds L. Boitani & T.K. Fuller), pp. 288–331. Columbia University Press, New York.
- White, G.C. & Burnham, K.P. (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study*, **46**, 120–139.
- Wunderle, J.M. (1995) Population characteristics of black-throated blue warblers wintering in three sites on Puerto Rico. *Auk*, **112**, 931–946.

*Received 11 May 2001; revision received 15 November 2001*