

ANNUAL SURVIVAL OF ADULT AMERICAN REDSTARTS AND OVENBIRDS IN THE SOUTHERN BOREAL FOREST

ERIN M. BAYNE^{1,3} AND KEITH A. HOBSON²

ABSTRACT.—Using constant effort (1993–1996) and playback mist netting with color banding (1996–1999), we estimated annual survival rates of Ovenbirds (*Seiurus aurocapillus*) and American Redstarts (*Setophaga ruticilla*) at four sites in the boreal forest of central Saskatchewan. For both species, the model that best described our data included a residency index that differentiated individuals caught more than once within the breeding season of initial capture (residents) from individuals caught only once (transients). Transients had considerably lower recapture rates than residents. The residency index was a more effective means of addressing violations of the homogeneity of capture assumption inherent in Cormack-Jolly-Seber models than a two-stage or age-structured model. We detected no significant differences in survival or recapture rate of male Ovenbirds between constant effort and playback mist netting techniques, although our estimate of annual survival for male Ovenbirds captured using playback (0.62 ± 0.06 SE) was higher than when we used constant effort netting (0.44 ± 0.13 SE). We observed no significant differences in survival between male ($n = 99$) and female ($n = 113$) American Redstarts or between second-year ($n = 50$) and after-second-year ($n = 49$) American Redstart males (overall survival = 0.55 ± 0.09 SE). For Ovenbirds, the model that best fit the data incorporated sex specific differences in survival with females ($n = 76$) having lower survival (0.21 ± 0.09 SE) than males ($n = 197$, 0.60 ± 0.12 SE). Without accounting for the presence of transient birds in our models, our estimates of survival would have been unrealistically low. Residency indices based on the number of times an individual was captured within a season seem to provide an effective means to account for transients. Received 27 November 2001, accepted 15 July 2002.

An apparent decline of some North American passerine populations has stimulated considerable research into the factors influencing songbird populations (Holmes et al. 1996, Porneluzi and Faaborg 1999). Most research has focused on how habitat or landscape features are related to population density and nesting success (e.g., Donovan et al. 1995, Robinson et al. 1995). Less is known about adult and juvenile survival, although precise estimates of these life history parameters are key in creating realistic demographic models for use in conservation and management.

Constant effort netting is a common method used to capture passerines and estimate survival (DeSante and Burton 1994). Constant effort netting is limited by the problem that previously banded individuals are not always recaptured even though they are alive (Chase et al. 1997). Imperfect recapture histories can be caused by permanent dispersal from sites, which cannot be distinguished from mortality, or temporary dispersal from sites whereby individuals are alive but not captured each year

they are alive. To account for temporary dispersal, methods such as Cormack-Jolly-Seber (CJS) models have been used to correct survival estimates based on recapture rate.

The main assumption of CJS models is that marked individuals in the population have an equal probability of being recaptured (Lebreton et al. 1992). Constant effort netting can result in the capture of transient individuals who after initial capture are never seen again (i.e., migratory or individuals that are not territorial), violating the homogeneity of capture assumption (Chase et al. 1997, Bertram et al. 2000, Sandercock and Jamerilo 2002). To analyze data for which the homogeneity of capture assumptions were not met, some studies have used a residency index, whereby individuals captured at least twice within the same breeding season are treated as residents and individuals captured only once within a breeding season are assumed to be transients (Chase et al. 1997). A potential difficulty with this approach is the possibility that residents are captured only once and thus are incorrectly classified (Nur et al. 1999). Other studies allow for heterogeneous recapture rates among marked individuals by structuring CJS models into two stages such that survival and recapture in the year after marking differ from sur-

¹ Dept. of Biological Sciences, Univ. of Alberta, Edmonton, AB T6G 2E9, Canada.

² Canadian Wildlife Service, 115 Perimeter Rd., Saskatoon, SK S7N 0X4, Canada.

³ Corresponding author; E-mail: bayne@ualberta.ca

vival estimated over subsequent time periods (Pradel et al. 1997, Bertram et al. 2000). The main assumption of the two-stage approach is that individuals captured multiple times in future years are likely to be residents while individuals never seen again are more likely to be transients. This approach accommodates the possibility that some individuals captured only once within a season actually are residents. A final alternative has been to color mark individuals and utilize the capture history of only those individuals known to breed on the study area (Nur and Geupel 1993). Although all these techniques have been widely used, the relative effectiveness of these modeling strategies as a means of assessing survival of passerines rarely has been tested (Nur et al. 1999).

Here we report survival and recapture rates from four years of banding adult American Redstarts (*Setophaga ruticilla*) and Ovenbirds (*Seiurus aurocapillus*) from sites in the boreal forest of central Saskatchewan. Little is known about the demography of forest birds in this northern region. Given the vast size, the high diversity of birds, and the rapid pace of anthropogenic change in the boreal forest, studies are needed that document basic demographic parameters for birds in this area. Our objectives were to (1) generate estimates of survival in the presence of transient birds and determine if residency indices, two-stage models, or a combination of both methods were more parsimonious explanations for our data; (2) compare survival and recapture rates from Ovenbirds captured by constant effort mist netting versus a detailed population study using playback netting and color banding; and (3) determine if we could detect differences in survival or recapture rates among different sex and ages classes of both species.

METHODS

Study area.—We conducted field work on four study sites in Prince Albert National Park (53° 50' N, 105° 50' W), located in northcentral Saskatchewan (Bouman et al. 1996). Prince Albert National Park is a 387,500-ha protected area surrounded by agricultural land to the south and commercial forests with active forest harvesting on the other three sides. We sampled two sites from 1993–1996. Site 1 was a mature (70 years) trembling aspen (*Populus tremuloides*) forest with a 20- to 25-m canopy and a 2- to 3-m shrub layer of beaked hazelnut (*Corylus cornuta*). Site 2 was an

old (100 years) mixed wood forest with 40% white spruce (*Picea glauca*) and 60% trembling aspen in the canopy (25–30 m high). The understory at this site was relatively diverse with a variety of shrubs, including balsam fir (*Abies balsamifera*), white spruce, green alder (*Alnus crispa*), and beaked hazelnut. We sampled two other sites from 1996–1999. Site 3 was an old aspen forest, with a shrub layer dominated by green alder. Site 4 was an old mixed wood forest with 30% white spruce and 70% trembling aspen. Sites were ≥ 10 km apart, ≥ 1 km from the edge of the park boundary, and were surrounded on all sides by forest of a similar type.

Capture methods.—We conducted constant effort mist netting at sites 1 and 2 from June 1 through July 31, 1993–1996. Net lanes were placed along permanently established 2- to 4-m wide trails. Each lane consisted of 10 nets (12 m $\times$ 2 m, 36-mm mesh) spaced 10 m apart and alternated on opposite sides of a trail. We opened nets at 06:00 CST and monitored them for 6 h daily for two days per sampling period at each site. On the second day, we moved the lane so that the first net of the second day was 10 m farther along the trail than the last net of the first day. The number of monitoring periods ranged from 2–4 times per month with each monitoring period separated by a mean of 10 days. All recapture histories from constant effort mist netting were derived from physical captures, as none of these birds were color banded.

At sites 3 and 4, we placed two nets in a V shape and used playback to lure male Ovenbirds into nets. After capturing a bird, we moved the nets to the next territory until all males were captured or visually sighted to determine their banding status. We banded during June and early July, 1996–1999. We searched each 25-ha site (flagged cells, 50 m $\times$ 50 m) ≥ 3 times per year for marked birds (Bayne and Hobson 2002).

All birds captured at sites 1 and 2 received a USFWS numbered aluminum band. At sites 3 and 4, we also used plastic color bands to give each individual a unique band combination. We banded only during the breeding period, so we were able to determine the sex of all adult birds based on the presence of a brood patch or cloacal protuberance (Pyle et al. 1987). We aged individuals as either hatch-year (HY) or after-hatch-year (AHY) based on skull ossification and plumage characteristics (Pyle et al. 1987). HY birds were excluded from analysis. We aged male American Redstarts as second-year (SY) or after-second-year (ASY) based on plumage characteristics (Pyle et al. 1987).

Survival estimation.—We estimated annual survival (ϕ) and recapture (p) rates using methods described in Lebreton et al. (1992). Using program MARK (White and Burnham 1999), we fit CJS models to the data and used them to create maximum likelihood estimates for survival and recapture rates. Model selection within each candidate model set was assessed for plausibility using Akaike's Information Criterion corrected for small sample size (AIC_c ; Burnham and Anderson 1998). The model from each model set with the lowest

AIC_c was considered the most parsimonious explanation for the data. Comparisons of models within the candidate model set were based on an index of relative plausibility using normalized Akaike weights and the difference in AIC_c scores between models (Burnham and Anderson 1998).

To determine if it was necessary to account for transients when modeling the data from constant effort mist netting, we compared the fit of four models. Model 1 included a residency index in both the survival and recapture terms, whereby individuals captured more than once during different sampling periods within the same breeding season were classified as residents and individuals captured only once within the breeding season were considered transients (*sensu* Chase et al. 1997). In model 2, we used a two-stage structure to allow for differential survival and recapture between the year after marking and all subsequent periods (Pradel et al. 1997). This model is structurally analogous to models that account for age differences in survival between the first and second year of banding (Lebreton et al. 1992). The third model was a combination of model 1 and 2. We assumed the survival and recapture of transients was different than that of residents, but only in the year after initial capture. We assumed that "transients" that returned ≥ 2 years after initial capture had survival and recapture rates similar to those of residents (i.e., these birds likely held territories near the net lane but only happened to be captured once in the year of initial capture; Nott and DeSante 2002). We compared these models to a null model, where we assumed that all individuals had the same survival and recapture rate. We created each model set separately for each species. All individuals regardless of sex and age were pooled in these analyses.

To assess whether our estimates of survival and recapture rate of male Ovenbirds differed based on method of capture, we compared the fit of four other models. In model 1, we assumed the survival and recapture rates of male Ovenbirds differed based only on how they were captured (constant effort or playback). In model 2, we compared the survival and recapture rates of male Ovenbirds estimated from the different capture methodologies while accounting for transients. The transient model used in this model set included the residency index only (see results). In model 3, we assumed the survival and recapture rates of male Ovenbirds did not differ between techniques but that it was important to account for transient individuals. We compared these models to a null model that assumed that there were no differences between capture methods and that accounting for transients was unnecessary.

Finally, we determined whether or not we could detect differences in the survival or recapture rates of different sex and age classes while accounting for the presence of transients using the residency index (see results). For American Redstarts, we began with a model that included male age (SY or ASY), sex, and the residency index. As we did not have *a priori* hy-

potheses about how age and sex might interact with the residency index, we chose to use an all possible subsets approach to model these data (Kleinbaum et al. 1988). Using the approach outlined in Lebreton et al. (1992), we generated eight models that varied the different combinations of age, sex, and residency status for recapture rate. After generating the most parsimonious model in terms of recapture rate, we generated eight more models that varied these terms for survival. We used a similar approach for Ovenbirds, except that we did not include age of males in our models. We decided *a priori* not to include site or year in any of our analyses because of limited sample sizes within years and because the actual years Ovenbirds were monitored differed among capture methodologies. In addition, most (98%) American Redstarts were captured at site 1. Previous analyses indicated no detectable difference between sites 3 or 4 or between years at these sites in the survival or recapture rates of male Ovenbirds (Bayne and Hobson 2002).

To assess the generality of our results relative to previous studies, we generated a data set of published return rates and survival estimates for American Redstarts and Ovenbirds from various wintering and breeding locations. We selected studies from a search of the Biological Abstracts data base, 1980–2002, using the search terms "return" or "survival" and "redstart" or "ovenbird." We also used those studies listed in the literature cited of those papers. We classified each study based on the method of estimation (corrected survival estimate or simple return rate), method of capture and recapture (constant effort or color banding), and sex-age class (all sex-age class combined, SY male, ASY male, AHY male, and AHY female). No estimates of juvenile survival were included in this analysis. We entered these factors as main effects in a generalized linear model that assumed a Gaussian distribution. We assessed the significance of the main effects using a Wald test. Several studies reported survival-return estimates from different sex, age, and habitat classes. To account for potential nonindependence of the survival-return rate estimates from the same study, we used a robust cluster technique in the program STATA (StataCorp 2001). This approach reduces the effective sample size to the level of the cluster, resulting in inflated standard errors that provide valid statistical inference if samples within the cluster are not independent. We assumed return rate and survival estimates generated from different study areas within the same paper were independent (i.e., Jamaica and New Hampshire; Holmes and Sherry 1992).

RESULTS

Accounting for transients.—Between 1993 and 1995, we captured and released 212 adult American Redstarts (99 males and 113 females), and 37 returned at least once in a subsequent year (Table 1). Of the total sample, 43 were recaptured within the same breeding season and were classified as residents (25 males

TABLE 1. Reduced array for American Redstarts and Ovenbirds showing the number of marked and recaptured birds occurring in Prince Albert National Park, Saskatchewan, Canada. Numbers are pooled among banding sites. Constant effort mist netting was used from 1993 to 1996 while playback netting was used from 1996 to 1999. R_i is the number of marked individuals released in year i , including newly marked and previously marked individuals (i.e., in year 2, 75 American Redstarts were released with 59 individuals newly marked in that year along with 16 birds that were recaptured from year 1). Annual values are the number of individuals from a given release cohort that were first recaptured in that year.

Species	Year	R_i	Year 2	Year 3	Year 4	r_i^a
American Redstart (constant effort)	1	111	16	4	2	22
	2	75		15	1	16
	3	61			7	7
	m_j^b		16	19	10	
Ovenbird (constant effort)	1	57	8	2	0	10
	2	45		5	1	6
	3	49			5	5
	m_j^b		8	7	6	
Ovenbird (playback)	1	52	20	4	2	26
	2	79		27	7	34
	3	57			23	23
	m_j^b		20	31	32	

^a The total number of individuals from a release cohort captured at least once.

^b The total number of recaptures in a given year.

and 18 females). The model with the residency index was a far more likely explanation of the data than the null ($\Delta AIC_c = 29.5$), two-stage ($\Delta AIC_c = 32.5$), or combined model ($\Delta AIC_c = 6.2$). Based on the null model, the survival rate was 0.40 ± 0.07 SE while the recapture rate was 0.37 ± 0.10 SE. The model containing the residency index generated similar survival estimates for residents (0.55 ± 0.08 SE) and transients (0.44 ± 0.15 SE), but very different recapture rates (0.68 ± 0.13 SE and 0.16 ± 0.08 SE, respectively).

Using data from constant effort netting only, we captured 136 Ovenbirds (60 males and 76 females) between 1993 and 1995, and 19 returned to the same site in at least one year (Table 1). Twenty Ovenbirds (11 males and 9 females) met our criteria for classification as residents. The combined model was the most parsimonious explanation of the data and was far better than the null ($\Delta AIC_c = 7.9$) or two-stage model ($\Delta AIC_c = 10.9$). However, the combined model was no better than the model that included the residency index ($\Delta AIC_c = 0.2$; Table 2). Based on the null model, the survival rate was 0.32 ± 0.11 SE and recapture rate was 0.38 ± 0.16 SE. The parameter estimates derived from the model with the residency index indicated residents and transients had similar survival rates (0.33 ± 0.09 SE and 0.43 ± 0.19 SE, respec-

tively) but different recapture probabilities (1 and 0.18 ± 0.11 SE, respectively).

Constant effort versus playback.—Using playback, we captured 137 male Ovenbirds from 1996 to 1998 and 61 returned in at least one year (Table 1). Of these individuals, we believe four were transients that left their initial capture location during the breeding season. Male Ovenbirds captured by playback netting had a survival rate of 0.62 ± 0.06 SE and a recapture rate of 0.59 ± 0.08 SE. Males captured by constant effort mist netting had a survival rate of 0.44 ± 0.13 SE and recapture rate of 0.43 ± 0.17 SE. However, the model that provided the best fit to these data suggested no significant difference in survival or recapture rates for Ovenbirds caught using different capture techniques if transients were accounted for in the model (Table 2). Assuming no differences caused by capture method, we found that the recapture rate of transient male Ovenbirds (0.20 ± 0.13 SE) was considerably lower than that of residents (0.62 ± 0.07 SE), but that survival rates were not significantly different (0.55 ± 0.24 SE and 0.61 ± 0.05 SE, respectively).

Sex and age differences.—The model with the best fit to the American Redstart data incorporated constant survival (ϕ) for all sex-age-residency groups, with differences in the recapture rate (p) for resident and transient

TABLE 2. Summary of models comparing fit of different age and sex parameters as factors influencing survival and recapture rate of American Redstarts and Ovenbirds in Prince Albert National Park, Saskatchewan, Canada. Models are sorted by their AIC_c value, with the most parsimonious model listed first. The symbol ϕ indicates the survival rate while p is the recapture rate. Subscripts on model terms refer to different factors incorporated in the model (s = sex, r = residency status, a = age, and ‘.’ = constant).

Model	AIC _c	ΔAIC _c	Akaike weight	Number of parameters	Deviance
American Redstart					
$\phi.p_{sr}$	244.4	0.0	0.35	5	38.2
$\phi.p_{sr}$	245.7	1.3	0.19	6	37.3
$\phi.p_{sr}$	246.0	1.6	0.16	6	37.6
$\phi.p_{sr}$	246.5	2.1	0.13	6	38.1
$\phi_{sa}p_{sr}$	247.8	3.4	0.07	7	37.3
$\phi_{ra}p_{sr}$	248.6	4.2	0.04	8	36.0
$\phi_{sr}p_{sr}$	248.8	4.4	0.04	8	36.2
$\phi_{sra}p_{sr}$	251.5	7.1	0.01	10	34.6
$\phi_{sra}p_s$	252.4	8.0	0.00	8	39.8
$\phi_{sra}p_{sra}$	254.5	10.1	0.00	12	33.1
$\phi_{sra}p_{sa}$	254.5	10.1	0.00	9	39.8
$\phi_{sra}p_r$	256.6	12.2	0.00	8	44.0
$\phi_{sra}p_{ar}$	257.7	13.3	0.00	10	40.8
$\phi_{sra}p_{\cdot}$	261.5	17.1	0.00	7	51.0
$\phi_{sra}p_a$	261.7	17.3	0.00	8	49.1
Ovenbird					
$\phi.p_r$	457.2	0.0	0.77	4	23.9
$\phi_{sr}p_r$	461.0	3.8	0.12	6	23.5
$\phi_{sr}p_{\cdot}$	462.8	5.5	0.05	5	27.4
$\phi_{sr}p_{sr}$	464.1	6.8	0.03	8	22.4
$\phi_{sr}p_s$	464.5	7.3	0.02	6	27.1
$\phi.p_r$	465.2	7.9	0.01	3	33.9
$\phi.p_r$	466.7	9.4	0.00	4	33.4

birds and between the sexes ($\phi.p_{sr}$; Table 2). Overall, annual survival of American Redstarts was 0.55 ± 0.09 SE. The recapture rate was lowest for transient American Redstart females (0.09 ± 0.05 SE), followed by transient males (0.16 ± 0.06 SE), resident females (0.34 ± 0.14 SE), and resident males (0.90 ± 0.10 SE). This model ($\phi.p_{sr}$) was 1.9 times more likely than the model that included sex specific differences in annual survival ($\phi.p_{sr}$) and 2.2 times more likely than the model that included survival differences among resident and transient individuals ($\phi.p_{sr}$; Table 2). Assuming sex specific differences in survival ($\phi.p_{sr}$), our parameter estimates for female survival (0.72 ± 0.23 SE) were higher than that of males (0.52 ± 0.08 SE). Two females ini-

tially captured in 1993 that were not recaptured again until 1996 drove these results. When we removed these females from our analysis, female survival dropped to 0.39 ± 0.16 SE. However, the model selected as having the best fit was the same regardless of whether these two females were included in the data set or not. SY and ASY American Redstart males had identical survival values based on the model $\phi_{sa}p_{sr}$ (0.52 ± 0.15 SE and 0.52 ± 0.08 SE, respectively). The model providing the best fit to the Ovenbird data included sex specific differences in survival and differences in the recapture rate of resident and transient individuals ($\phi.p_r$; Table 2). Annual survival of male Ovenbirds was 0.60 ± 0.05 SE and that of female Ovenbirds was 0.21 ± 0.09 SE. The recapture rate of resident birds was 0.62 ± 0.07 SE, which was much higher than for transient individuals (0.19 ± 0.06 SE). The model $\phi.p_r$ was 6.4 times more likely than the model that incorporated the residency index in the estimation of survival rate ($\phi_{sr}p_r$).

Comparisons among studies.—We found 28 papers that reported return rates and/or survival estimates for Ovenbirds and American Redstarts (Table 3). Return rates of Ovenbirds ranged from 0.02–0.54, while return rates of American Redstarts ranged from 0.03–0.75. Few survival estimates based on robust methods such as Cormack-Jolly-Seber models were available with a range from 0.21–0.60 for Ovenbirds and 0.55–0.67 for American Redstarts. We detected no significant difference in the adjusted means for survival-return rate between Ovenbird (0.31) and American Redstarts (0.41; $\chi^2 = 3.2$, $df = 1$, $P = 0.076$). Robust estimates such as those provided by CJS models resulted in adjusted mean estimates of “survival” that were higher than those derived by simple return rate (0.61 and 0.28, respectively; $\chi^2 = 27.0$, $df = 1$, $P < 0.001$). Color banding also resulted in significantly higher estimates of “survival” than constant effort netting (0.48 and 0.27, respectively; $\chi^2 = 9.7$, $df = 1$, $P = 0.002$). Once we controlled for the other variables in the model, we could not detect any significant differences among the combined age-sex class (0.47), SY males (0.44), ASY males (0.49), AHY females (0.40), and AHY males (0.33; $\chi^2 = 2.6$, $df = 4$, $P = 0.63$).

DISCUSSION

To derive accurate estimates of survival required that we differentiate resident from transient individuals because transient individuals had a much lower probability of being recaptured than resident individuals. Resident individuals captured with constant effort netting, particularly males, had high recapture probabilities, suggesting that these individuals were returning to the same territory used during previous years. Similar results have been observed for Wilson's Warblers (*Wilsonia pusilla*), Song Sparrows (*Melospiza melodia*), Sedge Warblers (*Acrocephalus schoenobaenus*), and Winter Wrens (*Troglodytes troglodytes*; Chase et al. 1997). Although our residency index was crude, it was a more effective means of addressing violations of the assumption of homogeneity of capture than structuring the model to account for differential survival between the year after marking and subsequent periods. For both species, the two-stage model fit the data poorly, while combining the two-stage model with the residency index did not result in much improvement relative to the model with the residency index.

Previous studies have shown that unpaired territorial males and nonterritorial floaters are common in many Ovenbird and American Redstart populations (Sherry and Holmes 1989, Villard et al. 1993, Van Horn et al. 1995, Ortega and Capen 1999, Bayne and Hobson 2001). These results suggest that Ovenbird and American Redstart populations are male biased, possibly because survival of females is lower than that of males. Our data support this suggestion for Ovenbirds, as females had lower survival than that of males. Although this may reflect a true difference in survival between the sexes, our survival estimate for female Ovenbirds was unrealistically low and had a large error term associated with it. The extremely low survival rate of female Ovenbirds suggests that they had low site fidelity and were permanently dispersing from our sites. Alternatively, female Ovenbirds may have been more difficult to recapture than males, possibly because they were spending more time on the ground and moving around less.

In contrast to Ovenbirds, we detected no

significant difference in survival of male and female American Redstarts, but we did detect a large difference in recapture rate. In fact, our estimates of survival for female American Redstarts were higher than those for males. The markedly different parameter estimates derived for female American Redstarts, depending on the inclusion of two birds, highlights the need to search for outliers when using CJS models. Regardless, these results suggest that female redstarts have lower territory fidelity than males. By moving just a few territories between years, female redstarts may greatly reduce the likelihood they will be recaptured. In contrast, resident male redstarts had an extremely high recapture rate, suggesting that they were returning to the same territory they used during previous years. Lemon et al. (1996) found that 59% ($n = 22$) of returning female and 76% ($n = 71$) of returning male American Redstarts returned to the same or adjacent territory. While we do not refute the premise that female survival is lower than that of males in passerine species (Greenwood and Harvey 1982), our results and the results of our literature review indicate that detecting such patterns can be difficult given the wide variety of other factors that influence estimates of survival.

Survival estimates for Ovenbirds and American Redstarts in the boreal forest were similar to those observed in other areas of their range. However, our estimates of survival, like all such estimates made on the breeding grounds, should be treated as minimum estimators of true survival. Our work in Saskatchewan (Bayne and Hobson 2002) and that of Porneluzi and Faaborg (1999) in Missouri, indicates male Ovenbirds that do not breed successfully are less likely to return to the same breeding territory in subsequent years than males that raise young. When Porneluzi and Faaborg (1999) excluded those individuals that did not raise young, their survival estimate for male Ovenbirds increased by 9%. If failed breeders captured on the breeding grounds are more likely to disperse in subsequent years, survival may be underestimated. This also appeared to be the case in one year for ASY American Redstart males investigated by Lemon et al. (1996). Given that previous breeding success may be a strong determinant of breeding site fidelity in warblers,

TABLE 3. Annual survival or return rate estimates ($\pm$ SE) for adult Ovenbirds and American Redstarts from different studies conducted across the range of each species.

Study	Location	Sex ^a	N ^b	Years ^c	Survival- return rate	Method ^d
Ovenbird						
Hann 1948	Michigan	MF	38	10	0.54 $\pm$ 0.06	CB-R
Loftin et al. 1966	Panama	MF	143	2	0.02	CE-R
Anderson and Maxfield 1967	Massachusetts	MF	207	7	0.09	CE-R
Roberts 1971	Massachusetts	MF	27 ^e	6	0.85 $\pm$ 0.07	CE-S ^e
Diamond and Smith 1973	Jamaica	MF	118	5	0.08	CE-R
Savidge and Davis 1974	Pennsylvania	MF	38 ^e	6	0.54	CE-S ^e
Ely et al. 1977	Mexico	MF	79	7	0.16	CE-R
Rogers et al. 1982	Guatemala	MF	16	2	0.19	CE-R
Wander 1985	New Jersey	M,F	14/5	3	0.39/0.17	CB-R
Kricher and Davis 1986	Belize	MF	22	2	0.09	CE-R
Blake and Loiselle 1992	Costa Rica	MF	61	4	0.21	CE-R
Gonzalez-Alonso et al. 1992	Cuba	MF	26	2	0.19	CE-R
Conway et al. 1995	Belize	MF	312	2	0.24	CE-S
Faaborg and Arendt 1996	Puerto Rico	MF	28	17	0.43 $\pm$ 0.13	CE-S
Porneluzi and Faaborg 1999	Mississippi	M	74	4	0.52 $\pm$ 0.07	CB-S
Burke and Nol 2001	Ontario	M	74	4	0.36	CB-R
Murphy et al. 2001	San Salvador	MF	22	4	0.05	CE-R
DeSante et al. 2001	US Midwest	MF	368	5	0.49 $\pm$ 0.07	CE-S
This study	Saskatchewan	M	197	4	0.60 $\pm$ 0.06	CECB-S
This study	Saskatchewan	F	76	4	0.21 $\pm$ 0.09	CE-S
American Redstart						
Anderson and Maxfield 1967	Massachusetts	MF	44	7	0.03	CE-R
Diamond and Smith 1973	Jamaica	MF	126	5	0.12	CE-R
Nichols et al. 1981	New Hampshire	MF	—	11	0.67	CB-S
McNeil 1982	Venezuela	MF	9	2	0.44	CE-R
Rogers et al. 1982	Guatemala	MF	13	2	0.15	CE-R
Holmes and Sherry 1992	Jamaica	M	69/42	4	0.75, 0.49 ^f	CB-R
Holmes and Sherry 1992	Jamaica	M	69/42	4	0.46	CB-R
Holmes and Sherry 1992	New Hampshire	M	83/51	6	0.16, 0.39 ^f	CB-R
Holmes and Sherry 1992	New Hampshire	F	48	6	0.19	CB-R
Lemon et al. 1996	New Brunswick	M	~300	~10	0.26, 0.44 ^f	CB-R
Lemon et al. 1996	New Brunswick	F	112	~10	0.21	CB-R
Wunderle and Latta 2000	Dominican Rep.	M	48/27	3	0.30, 0.41 ^f	CB-R
Wunderle and Latta 2000	Dominican Rep.	F	52	3	0.39	CB-R
Marra and Holmes 2001	Jamaica	M	86/106	5	0.61, 0.70	CB-R
Marra and Holmes 2001	Jamaica	F	78	5	0.62	CB-R
Marra and Holmes 2001	Jamaica	M	25/10	5	0.44, 0.40 ^f	CB-R
Marra and Holmes 2001	Jamaica	F	63	5	0.37	CB-R
Murphy et al. 2001	San Salvador	MF	21	4	0.24	CE-R
This study	Saskatchewan	MF	212	4	0.55 $\pm$ 0.09	CE-S

^a Composition of sample at time of marking in respect to sex. MF = combined males and females in estimate. M,F = male and female survival calculated separately.
^b Number of individuals released.
^c Number of years sampled.
^d Method used to capture birds and generate survival/return rate estimate (CB = color banding, CE = constant effort netting, r = return rate, S = survival corrected for recapture rate).
^e Survival estimates based on correcting return rate for presence of transients.
^f SY and ASY males, respectively.

and assuming it has little influence on winter site fidelity, the most accurate assessments of survival may be obtained on the wintering grounds (Holmes and Sherry 1992, Sandercock and Jamerilo 2002). However, consider-

able variation also exists in return rates to wintering areas (Murphy et al. 2001) suggesting that individual variation also may have a strong influence on fidelity to nonbreeding sites. Nevertheless, adult survival estimates

that are more easily obtained from breeding ground data would benefit from more long term banding studies using CJS models rather than simple return rates to estimate survival.

We were unable to detect a significant difference in survival of male Ovenbirds generated by constant effort and playback netting. However, our estimate from the pooled data was higher than when we used only constant effort netting to assess survival. While our inference regarding the importance of capture method is weak due to the fact that our comparison of methods is confounded by temporal and spatial variation in survival (Sillett et al. 2002), it suggests that playback netting may be a more effective way of establishing survival and return rates (but see Nur et al. 1999). This assertion is supported by our review of other studies that show a much higher return rate-survival estimate when color banding is used relative to constant effort netting. However, most of the constant effort netting examined in our review did not separate transients from residents. The intensive effort required by playback netting may make it a less useful alternative to assess passerine survival than constant effort schemes. Where it is desirable to capture females, constant effort netting also may be the only viable method to capture large numbers of individuals. A compromise that we suggest is to color band captured individuals and spot map a fixed area surrounding the net lane, which might provide a more accurate assessment of which individuals were residents, and thus improve the accuracy of survival estimates generated from constant effort netting.

This study is one of the first to report survival rates of American Redstarts and Ovenbirds at the northern edge of their range. Our results are similar to or higher than those generated in more southern locations, suggesting that site fidelity and survival of American Redstarts and Ovenbirds in boreal environments is similar to other biomes. However, more work on survival rates of boreal passerines is required, particularly as it relates to habitat and landscape change (Bayne and Hobson 2002). Our results illustrate the importance of identifying transient individuals when estimating recapture rates. In addition to identifying transients, future work should endeavor to identify individual and possibly

habitat specific characteristics that influence survival and recapture rate (i.e., breeding success). Regardless, the residency index used here seems to provide a more effective means of identifying transients than two-stage models and should be incorporated in models that attempt to estimate passerine survival.

ACKNOWLEDGMENTS

We thank the numerous field assistants who participated in this project, including M. Smith, H. den Haan, T. Loran, E. Cumming, L. Quinn-Abott, and W. Jess. Funding was provided by the Canadian Wildlife Service (CWS), Prince Albert National Park, Prince Albert Model Forest (Project 211), and a Canada-Saskatchewan agreement in Forestry (PAIF Project No. CS-5009). Personal support to EMB was provided by CWS, a Natural Sciences and Engineering Research Council of Canada scholarship, a graduate fellowship from the Univ. of Saskatchewan, and the Integrated Landscape Management group at the Univ. of Alberta. Prince Albert National Park kindly granted permission to use sites and provided logistical support. All birds were captured under permits from Environment Canada and the Univ. of Saskatchewan Animal Care Committee. We are grateful to P. Porneluzi and two anonymous reviewers for their excellent suggestions on a previous version of the paper.

LITERATURE CITED

- ANDERSON, K. S. AND H. K. MAXFIELD. 1967. Warbler returns from southeastern Massachusetts. *Bird-Banding* 38:218–233.
- BAYNE, E. M. AND K. A. HOBSON. 2001. Effects of habitat fragmentation on pairing success of Ovenbirds: the importance of male age and floater behavior. *Auk* 118:380–388.
- BAYNE, E. M. AND K. A. HOBSON. 2002. Apparent survival of male Ovenbirds in fragmented and forested boreal landscapes. *Ecology* 83:1307–1316.
- BERTRAM, D. F., I. L. JONES, E. G. COOCH, H. A. KNECHTEL, AND F. COOKE. 2000. Survival rates of Cassin's and Rhinoceros Auklets at Triangle Island, British Columbia. *Condor* 102:155–162.
- BLAKE, J. G. AND B. A. LOISELLE. 1992. Habitat use by Neotropical migrants at La Selva Biological Station and Bravilo Carillo National Park, Costa Rica. Pp. 257–272 in *Ecology and conservation of Neotropical migrant landbirds* (J. M. Hagan, III and D. W. Johnston, Eds.). Smithsonian Inst. Press, Washington, D.C.
- BOUMAN, O. T., G. LANGEN, AND C. E. BOUMAN. 1996. Sustainable use of the boreal Prince Albert Model Forest in Saskatchewan. *For. Chron.* 72:63–72.
- BURKE, D. AND E. NOL. 2001. Age ratios and return rates of adult male Ovenbirds in contiguous and fragmented forests. *J. Field Ornithol.* 72:433–438.
- BURNHAM, K. P. AND D. R. ANDERSON. 1998. Model

- selection and inference: a practical information-theoretic approach. Springer-Verlag, New York.
- CHASE, M. K., N. NUR, AND G. R. GEUPEL. 1997. Survival, productivity, and abundance in a Wilson's Warbler population. *Auk* 114:354–366.
- CONWAY, C. J., G. V. N. POWELL, AND J. D. NICHOLS. 1995. Overwinter survival of Neotropical migratory birds in early-successional and mature tropical forests. *Conserv. Biol.* 9:855–864.
- DESANTE, D. F. AND K. M. BURTON. 1994. The Monitoring Avian Productivity and Survivorship (MAPS) program third annual report (1992). *Bird Popul.* 2:62–89.
- DESANTE, D. F., P. M. NOTT, AND D. R. O'GRADY. 2001. Identifying the proximate demographic cause(s) of population change by modeling spatial variation in productivity, survivorship, and population trends. *Ardea* 89:185–208.
- DIAMOND, A. W. AND R. W. SMITH. 1973. Returns and survival of banded warblers wintering in Jamaica. *Bird-Banding* 44:221–224.
- DONOVAN, T. M., F. R. THOMPSON, III, J. FAABORG, AND J. R. PROBST. 1995. Reproductive success of migratory birds in habitat sources and sinks. *Conserv. Biol.* 9:1380–1395.
- ELY, C. A., P. J. LATAS, AND R. R. LOHOEFENER. 1977. Additional returns and recoveries of North American birds banded in southern Mexico. *Bird-Banding* 48:275–276.
- FAABORG, J. AND W. J. ARENDT. 1996. Survival rates of Puerto Rican birds: are islands really that different? *Auk* 112:503–507.
- GONZÁLEZ-ALONSO, H., M. K. MCNICHOLL, P. B. HAMMEL, M. ACOSTA, E. GODINEZ, J. HERNÁNDEZ, D. RODRÍGUEZ, J. A. JACKSON, C. M. GREGO, R. D. MCRAE, AND J. SIROIS. 1992. A cooperative bird-banding project in Peninsula de Zapata, Cuba, 1988–1989. Pp. 131–142 in *Ecology and conservation of Neotropical migrant landbirds* (J. M. Hagan, III and D. W. Johnston, Eds.). Smithsonian Inst. Press, Washington, D.C.
- GREENWOOD, P. J. AND P. H. HARVEY. 1982. The natal and breeding dispersal of birds. *Annu. Rev. Ecol. Syst.* 13:1–21.
- HANN, H. W. 1948. Longevity of the Oven-bird. *Bird-Banding* 19:5–12.
- HOLMES, R. T., P. P. MARRA, AND T. W. SHERRY. 1996. Habitat-specific demography of breeding Black-throated Blue Warblers (*Dendroica caerulescens*): implications for population dynamics. *J. Anim. Ecol.* 65:183–195.
- HOLMES, R. T. AND T. W. SHERRY. 1992. Site fidelity of migratory warblers in temperate breeding and Neotropical wintering areas: implications for population dynamics, habitat selection, and conservation. Pp. 563–578 in *Ecology and conservation of Neotropical migrant landbirds* (J. M. Hagan, III and D. W. Johnston, Eds.). Smithsonian Inst. Press, Washington, D.C.
- KLEINBAUM, D. G., L. L. KUPPER, AND K. E. MULLER. 1988. Applied regression analysis and other multivariate methods, 2nd ed. PWS-Kent Publishing, Chapel Hill, North Carolina.
- KRICHER, J. C. AND W. E. DAVIS, JR. 1986. Returns and winter-site fidelity of North American migrants banded in Belize, Central America. *J. Field Ornithol.* 57:48–52.
- LEBRETON, J.-D., K. P. BURNHAM, J. CLOBERT, AND D. R. ANDERSON. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.* 62:67–118.
- LEMON, R. E., S. PERREAULT, AND G. A. LOZANO. 1996. Breeding dispersions and site fidelity of American Redstarts (*Setophaga ruticilla*). *Can. J. Zool.* 74:2238–2247.
- LOFTIN, H., D. T. ROGERS, JR., AND D. L. HICKS. 1966. Repeats, returns, and recoveries of North American migrant birds banded in Panama. *Bird-Banding* 37:35–44.
- MARRA, P. P. AND R. T. HOLMES. 2001. Consequences of dominance-mediated habitat segregation in American Redstarts during the nonbreeding season. *Auk* 118:92–104.
- MCNEIL, R. 1982. Winter residents, repeats, and returns of austral and boreal migrant birds banded in Venezuela. *J. Field Ornithol.* 53:125–132.
- MURPHY, M. T., A. PIERCE, J. SHOEN, K. L. MURPHY, J. A. CAMPBELL, AND D. A. HAMILTON. 2001. Population structure and habitat use by overwintering Neotropical migrants on a remote oceanic island. *Biol. Conserv.* 102:333–345.
- NICHOLS, J. D., B. R. NOON, S. LYNNE-STOKES, AND J. E. HINES. 1981. Remarks on the use of mark-recapture methodology in estimating population size. *Stud. Avian Biol.* 6:121–136.
- NOTT, M. P. AND D. F. DESANTE. 2002. Demographic monitoring and the identification of transients in mark-recapture models. Pp. 727–736 in *Predicting species occurrence: issues of scale and accuracy* (J. M. Scott, P. J. Heglund, M. Morrison, M. Raphael, J. Haufler, and B. Wall, Eds.). Island Press, Covello, California.
- NUR, N. AND G. R. GEUPEL. 1993. Evaluation of mist-netting, nest-searching and other methods for monitoring demographic processes in land-bird populations. Pp. 237–244 in *Status and management of Neotropical migratory birds* (D. Finch and P. W. Stangel, Eds.). USDA Forest Service General Technical Report RM-229, Fort Collins, Colorado.
- NUR, N., G. R. GEUPEL, AND G. BALLARD. 1999. The use of constant-effort mist-netting to monitor demographic processes in passerine birds: annual variation in survival, productivity, and floaters. Pp. 1–21 in *Strategies for bird conservation: the Partners in Flight planning process* (R. Bonney, D. N. Pashley, R. J. Cooper, and L. Niles, Eds.). Cornell Lab. of Ornithology, Ithaca, New York (<http://birds.cornell.edu/pifcapemay/nur.htm>).
- ORTEGA, Y. K. AND D. E. CAPEN. 1999. Effects of forest

- roads on habitat quality for Ovenbirds in a forested landscape. *Auk* 116:937–946.
- PORNELUZI, P. A. AND J. FAABORG. 1999. Season-long fecundity, survival, and viability of Ovenbirds in fragmented and unfragmented landscapes. *Conserv. Biol.* 13:1151–1161.
- PRADEL, R., J. E. HINES, J.-D. LEBRETON, AND J. D. NICHOLS. 1997. Capture-recapture survival models taking account of transients. *Biometrics* 53:60–72.
- PYLE, P., S. N. G. HOWELL, R. P. YUNICK, AND D. F. DESANTE. 1987. Identification guide to North American passerines. Slate Creek Press, Bolinas, California.
- ROBERTS, J. O. L. 1971. Survival among some North American wood warblers. *Bird-Banding* 42:165–184.
- ROBINSON, S. K., F. R. THOMPSON, III, T. M. DONOVAN, D. R. WHITEHEAD, AND J. FAABORG. 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science* 267:1987–1990.
- ROGERS, D. T., JR., D. L. HICKS, E. W. WISCHUSER, AND J. R. PARRISH. 1982. Repeats, returns, and estimated flight ranges of some North American migrants in Guatemala. *J. Field Ornithol.* 53:133–138.
- SANDERCOCK, B. K. AND A. JARAMILLO. 2002. Annual survival rates of wintering sparrows: assessing demographic consequences of migration. *Auk* 119: 149–165.
- SAVIDGE, I. R. AND D. E. DAVIS. 1974. Survival of some common passerines in a Pennsylvania woodlot. *Bird-Banding* 45:152–155.
- SHERRY, T. W. AND R. T. HOLMES. 1989. Age-specific social dominance affects habitat use by breeding American Redstarts (*Setophaga ruticilla*): a removal experiment. *Behav. Ecol. Sociobiol.* 25: 327–333.
- SILLETT, T. S. AND R. T. HOLMES. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. *J. Anim. Ecol.* 71:296–308.
- STATACORP. 2001. STATA statistical software, ver. 7.0. Stata Corporation, College Station, Texas.
- VAN HORN, M. A., R. M. GENTRY, AND J. FAABORG. 1995. Patterns of Ovenbird (*Seiurus aurocapillus*) pairing success in Missouri forest tracts. *Auk* 112: 98–106.
- VILLARD, M.-A., P. R. MARTIN, AND C. G. DRUMMOND. 1993. Habitat fragmentation and pairing success in the Ovenbird (*Seiurus aurocapillus*). *Auk* 110: 759–768.
- WANDER, S. A. 1985. Comparative breeding biology of the Ovenbird in large vs. fragmented forests: implications for the conservation of Neotropical migrant birds. Ph.D. diss., Rutgers Univ., New Brunswick, New Jersey.
- WHITE, G. C. AND K. P. BURNHAM. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:120–138.
- WUNDERLE, J. M., JR. AND S. C. LATTA. 2000. Winter site fidelity of Nearctic migrants in shade coffee plantations of different sizes in the Dominican Republic. *Auk* 117:596–614.



Bayne, Erin M. and Hobson, Keith A. 2002. "Annual Survival of Adult American Redstarts and Ovenbirds in the Southern Boreal Forest." *The Wilson bulletin* 114(3), 358–367.

View This Item Online: <https://www.biodiversitylibrary.org/item/215181>

Permalink: <https://www.biodiversitylibrary.org/partpdf/210399>

Holding Institution

Harvard University, Museum of Comparative Zoology, Ernst Mayr Library

Sponsored by

IMLS LG-70-15-0138-15

Copyright & Reuse

Copyright Status: In copyright. Digitized with the permission of the rights holder.

Rights Holder: Wilson Ornithological Society

License: <http://creativecommons.org/licenses/by-nc-sa/4.0/>

Rights: <https://biodiversitylibrary.org/permissions>

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.