ESTIMATING PROBABILITIES OF SURVIVAL OF MALE BACHMAN’S SPARROWS FROM PLOT-BASED, MARK–RESIGHTING, OFF-ПLOT SURVEYS AND MULTI-STRATA MODELS

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Abstract. Bachman’s Sparrow (Peucaea aestivalis) is listed as a species of conservation concern throughout its range and therefore an important candidate for demographic studies. We estimated probabilities of males’ annual survival by monitoring a large color-marked population for 4 years by using a combination of (1) mark–resighting within a primary study area and (2) surveys outside the primary area to document emigration. We used multi-strata models to assess probabilities of survival, detection, and movement between the primary study area and the surrounding landscape. In the top models included in our confidence set, probabilities of annual survival were ≥0.68. Probabilities of detection and dispersal varied among the top models but averaged 0.86 and ≤0.14, respectively, for individuals in the primary study area. We used a survival probability of 0.68 in combination with published information on the species’ productivity to construct a two-stage Leslie matrix. Survival of adult males had the greatest proportional influence on population projections (elasticity = 0.52), while survival of juveniles and annual productivity had equal influence (elasticities = 0.24). Our results suggest that off-plot surveys and multi-strata models provide an efficient method for estimating probabilities of survival of Bachman’s Sparrow.

Key words: Peucaea aestivalis, Bachman’s Sparrow, detection, elasticity, emigration, multi-strata model, survival.

INTRODUCTION

Probabilities of survival of small (≤20 g) passerines typically are estimated by recapturing or resighting marked individuals at one or more study areas (Cilimburg et al. 2002, Marshall et al. 2004). Estimates based on these methods are invariably low because observations are made within an area small relative to the total area individuals are capable of utilizing (Koenig et al. 2000, Cilimburg et al. 2002, Marshall et al. 2004). Individuals that move outside the areas surveyed are not monitored, so estimates of survival become the product of true survival and the confounded probabilities of emigration and detection (Lebreton et al. 1992).

The bias created by emigration has been evaluated for several migratory passerines (Bayne and Hobson 2002, Cilimburg et al. 2002, Marshall et al. 2004) that regularly move...
widely (Paradis et al. 1998). For resident, nonmigratory species the bias has been evaluated less frequently (Loery et al. 1987, Peach et al. 2008) even though some nonmigratory species often move great distances in search of suitable habitat (Koenig et al. 2000). In particular, movements undertaken by resident species that use ephemeral habitats created by disturbance may be extensive because habitat suitability can be influenced by the extent, frequency, timing, and nature of disturbances as well as the speed with which habitat suitability recovers following disturbance (Brawn et al. 2002).

Bachman’s Sparrow (*Pruela aestivalis*) is a disturbance-dependent species associated with mature pine forests and ruderal lands in the southeastern U.S. (Dunning 1993). Habitat conditions for Bachman’s Sparrow are ephemeral and closely linked to disturbance in the form of prescribed fire (Dunning 1993, Tucker et al. 2006). Prescribed fires open ground-level vegetation where the sparrows nest and forage (Jones 2008) and also reduce the density of hardwood shrubs (Dunning 1993). Bachman’s Sparrows hold territories over multiple seasons and years (Cox and Jones 2007) but also move as a result of (1) abandoning a site when prescribed fires temporarily remove ground-cover vegetation (Seaman and Kremenzt 2000, Cox and Jones 2007), (2) colonizing a site once vegetation recovers after a prescribed fire (typically ≤ 2 months; Cox and Jones 2007), and (3) abandoning a site as post-fire plant succession reduces habitat suitability (sometimes ≤ 18 months following a fire; Jones 2008).

Although female Bachman’s Sparrows are difficult both to mark and to resight (Jones 2008), males can be marked and resighted with broadcast of conspecific vocalizations and a system of nets and poles deployed quickly in open pinelands (Jones and Cox 2007). We established and monitored a large system of nets and poles deployed quickly in open pinelands (Jones and Cox 2007). We followed procedures used by Pulliam et al. (1992), Liu (1993), and Perkins et al. (2003) in which parameter estimates derived from field observations were used in conjunction with published estimates for other parameters. We then used the Leslie matrix to estimate the influence productivity and survival might exert on the population’s growth rates (i.e., elasticities; Caswell 1989), generation length, and the efficiency of the new field methods in monitoring males’ survivorship (Fletcher et al. 2002).

**METHODS**

**STUDY AREA**

Our study centered on the Wade Tract (Thomas County, Georgia; 30° 46′ N, 84° 00′ W), an 80-ha old-growth forest dominated by longleaf pine (*Pinus palustris*) and surrounded by >8000 ha of mature pine forests (Engstrom et al. 2001). No living pine trees have been cut on the Wade Tract, ground-cover disturbance has been rare (Engstrom et al. 2001), and fire-return intervals within the Wade Tract and throughout surrounding forests have been <2 years for decades (Tail Timbers Research Station, unpubl. data). Accordingly, Bachman’s Sparrows are abundant (>0.4 singing males per ha; Jones 2008).

Forests surrounding the Wade Tract consisted of mature (>90-year-old) longleaf pine and a ground-cover community dominated by native forbs and grasses (Ambrose 2001). Habitat suitable for the sparrow represented approximately 77% of the total area within 1 km of the Wade Tract, while other dominant habitats included hardwood forests (13% of total area), dense stands of young pines (6%), and fallow fields and open pastures (4%). Approximately 50% of the Wade Tract was burned each year, and the extent of prescribed burns (which affected habitat both within and outside the Wade Tract) averaged 60–80 ha each day a fire was set (J. Cox, unpublished data). Surrounding forests supported sparrow densities similar to those found on the Wade Tract (J. Cox, unpubl. data) as well as a dense population (1 territory 40 ha−1; Cox et al. 2001) of the Red-cockaded Woodpecker (*Picoidea borealis*), which is widely regarded as an indicator of mature, well-managed pine forests (Jackson 1994).

**MARKING AND RESIGHTING**

Netting of Bachman’s Sparrows began in 2002 and has continued annually within the Wade Tract and a 200-m buffer outside the tract. The Wade Tract and its buffer represented
the primary area (164 ha) for this study (as well as our previous study; Cox and Jones 2007). Within this area, using recorded songs, we lured males into mist nets from March to June (Jones and Cox 2007). We sexed the birds by the presence or absence of a brood patch or cloacal protuberance and behavior. Banded birds were fitted with one U.S. Geological Survey band and three color bands (two bands per leg) under federal permit 24466 and state permit 29-WMB-02-143. In these analyses we used only marked males (n = 132) observed or netted 2005–2008. One year of study (2007) coincided with a severe drought (Fuchs 2008).

From 2006 to 2008, to resight marked males within the primary study area, we made ≥70 morning surveys each year from March to July. Surveys typically took ≥4 hr and covered approximately 25% of the primary area. We determined color-band combinations through spotting scopes and during each visit recorded locations of all singing males (both marked and unmarked) with a hand-held global positioning system (GPS) with ≤5 m accuracy (Trimble Explorer III). Locations of unmarked singing males were recorded strictly for estimation of the proportion of marked and unmarked individuals observed during each survey.

Additional surveys (off-plot surveys; n = 26) took place within 1 km area of the primary study area along transects of 500–1000 m spaced 150–200 m apart and traversing suitable habitat. The length and direction of transects varied with the available habitat, and we played recorded vocalizations of Bachman’s Sparrow intermittently to improve detection of males. Up to six transects were surveyed on ≥8 mornings each year, and locations of marked and unmarked males were recorded by GPS. Locations were processed for analysis in a geographic information system (GIS) using a Universal Transverse Mercator projection (zone 16, North American datum 1983). GIS data were analyzed with ArcView.

SURVIVAL AND MULTI-STRATA ANALYSIS
We used the multi-strata model (Brownie et al. 1993) in the program MARK (White and Burnham 1999) to estimate probabilities of annual survival, detection, and movement between strata. Males were assigned to one of two strata each year on the basis of whether they were observed within the primary study area (stratum 1) or during off-plot surveys (stratum 2). Most males were easily classified, but a few individuals moved between strata in some years. We assigned these individuals (n = 8) to a stratum on the basis of observations at the end of the sampling period (July). These procedures follow the assumption of multi-strata models that transitions take place before follow-up encounters but also may reduce the precision of parameter estimates as a result of misclassification of the stratum occupied (Kendall 2004).

We used the program U-CARE (Choquet et al. 2001) to assess the goodness of fit of our data and multi-strata models. Tests for transients (test 3G, \( P = 0.947 \)), equivalence among resighted individuals (test M, \( P = 0.908 \)), and the sum of these components (test JMV; \( P = 0.989 \)) indicated no significant deviations from the model’s assumptions. We developed six a priori candidate models to describe the probabilities of survival (\( \Phi \)), detection (\( p \)), and movement between strata (\( \phi \)): (1) survival may be time dependent (\( \Phi_{t} p_{t} \phi_{t} \); descriptions of models follow White and Burnham (1999)) as a result of drought or other annual variations; (2) detection probabilities may be time dependent as a result of annual variation in observers, weather, or other factors (\( \Phi_{t} p_{t} \phi_{t} \)); (3) survival and detection might covary as a result of the preceding considerations (\( \Phi_{t} p_{t} \phi_{t} \)); (4) movement between strata could be influenced by fires, weather, and other factors varying from year to year (\( \Phi_{t} p_{t} \phi_{t} \)); (5) probabilities of survival, detection, and movement may be constant (\( \Phi_{t} p_{t} \phi_{t} \)); and (6) all parameters may be time dependent as a result of higher-level interactions (\( \Phi_{t} p_{t} \phi_{t} \)). We evaluated models with Akaike’s information criterion (AIC) and considered all models with \( \Delta \text{AIC} \leq 2 \) of the top-ranked model part of our confidence set (Anderson and Burnham 2002).

We constructed a two-stage Leslie matrix model (Caswell 1989) for male Bachman’s Sparrows from survival probabilities provided by models in our confidence set. Following Pulliam et al. (1992), Liu (1993), and Perkins et al. (2003), we used 1.5 juvenile males per adult male as an estimate of annual productivity. This approach allowed us to compare directly the effects our survival estimates might have on results provided elsewhere (Pulliam et al. 1992, Perkins et al. 2003). Rates of survival of juvenile Bachman’s Sparrows are difficult to estimate (Pulliam et al. 1992), so we again followed Pulliam et al. (1992) and Perkins et al. (2003) and assumed juvenile survival produced a stable population (i.e., \( \lambda = 1.0 \)). We then used the two-stage matrix to calculate the relative contributions of survival and fecundity to the population’s growth rates (i.e., elasticities) and generation length (Caswell 1989). Values reported are means (± SD) except where indicated.

RESULTS
We analyzed 3768 records of locations of marked males, and 92% of the observations were made within the primary study area. The total observations recorded annually for marked birds averaged 16.4 (±8.7) per individual. Sightings of color-marked birds within the primary study area averaged 76% (±24) of the observations recorded during daily surveys (i.e., 24% of individuals observed were unmarked males), while color-marked birds averaged 7% (±6) of the observations recorded during off-plot surveys (unmarked birds made up 93% of the observations). We recorded a total of 26 males outside the primary study area (20% of all marked birds).

The top model emerging from program MARK held annual survival, annual detection probabilities, and movement
next model, in which movement between strata varied over

**Table 1.** Candidate survival models used to estimate probabilities of annual survival of male Bachman’s Sparrows (2005–2008). Models are described in the format of White and Burnham (1999) and were ranked by Akaike’s information criterion (AIC). For each model, the number of parameters (K), differences in QAIC scores relative to the top-ranked model (Δi), QDeviance (QDev), and weight (wi) are listed. Candidate models included (1) time-dependent survival (Φp, Ψ1, Ψ2, Table 1), (2) time-dependent detection probabilities (Φp, Ψ1, Ψ2, Table 1), (3) time-dependent survival and detection probabilities (Φp, Ψ1, Ψ2, Table 1), (4) time-dependent transitions between strata (Φp, Ψ1, Ψ2, Table 1), (5) constant survival, detection, and movement probabilities (Φp, Ψ1, Ψ2, Table 1), and (6) parameters all time-dependent as a result of higher-level interactions (Φp, Ψ1, Ψ2, Table 1).

<table>
<thead>
<tr>
<th>Survival model</th>
<th>K</th>
<th>Δi</th>
<th>wi</th>
<th>QDev</th>
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<tbody>
<tr>
<td>(5) Φp, Ψ1, Ψ2, Ψ3</td>
<td>6</td>
<td>0.00</td>
<td>0.49</td>
<td>27.83</td>
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<td>(4) Φp, Ψ1, Ψ2, Ψ3</td>
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<td>0.94</td>
<td>0.31</td>
<td>22.11</td>
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<td>(1) Φp, Ψ1, Ψ2, Table 1</td>
<td>2</td>
<td>2.92</td>
<td>0.11</td>
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<td>(6) Φp, Ψ1, Ψ2, Table 1</td>
<td>13</td>
<td>4.50</td>
<td>0.05</td>
<td>16.36</td>
</tr>
<tr>
<td>(3) Φp, Ψ1, Ψ2, Table 1</td>
<td>12</td>
<td>6.24</td>
<td>0.02</td>
<td>20.48</td>
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<tr>
<td>(2) Φp, Ψ1, Ψ2, Table 1</td>
<td>10</td>
<td>6.57</td>
<td>0.02</td>
<td>25.46</td>
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</tbody>
</table>

*QAIC of top-ranked model = 324.3.

between strata constant for all parameters (Φp, Ψ1, Ψ2, Table 1). This model was 1.6 times more likely to be the best model for estimating annual survival probabilities than the next model, in which movement between strata varied over time while the probabilities of survival and detection were constant (Φp, Ψ1, Ψ2, Table 1). The remaining models had ΔQAIC > 2.0 and were not part of our confidence set (Table 1).

In both models included in our confidence set, estimated annual survival of males within the primary study area was ≥0.68 (Table 2), while probabilities of detection within the primary study were ≥0.85 (Table 2). Estimated survival of males observed outside the primary study area also exceeded 0.68 (Table 2) under our top models, but these estimates lacked precision (SE ≥ 0.17). In our top models, the probability of males emigrating from the primary study area was ≤0.14, while the probability of movement back into the primary study area averaged 0.07–0.45 for various intervals (Table 2).

When we set the probability of male survival at 0.68 and the annual productivity per adult male at 1.5 male offspring, the rate of survival of juveniles needed to sustain the population (i.e., λ = 1.0) was 0.21. The estimated generation time for a population with these characteristics was 4.1 years, while elasticities for matrix elements were 0.24 for both annual productivity and juveniles’ survival and 0.52 for adult males’ survival.

**Discussion**

The combination of plot-based mark–resighting, off-plot surveys, and multi-strata modeling appears to be a useful approach for estimating probabilities of survival of male Bachman’s Sparrows. Our previous estimate (Cox and Jones 2007)

<table>
<thead>
<tr>
<th>Survival model</th>
<th>Parameter</th>
<th>Parameter estimate</th>
<th>SE</th>
<th>Lower 95%</th>
<th>Upper 95%</th>
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<td>(5) Φp, Ψ1, Ψ2, Ψ3</td>
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<td></td>
<td>p1</td>
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<tr>
<td></td>
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<td></td>
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<td></td>
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<td>0.00</td>
<td>0.45</td>
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<td>0.06</td>
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<td></td>
<td>Ψ2-5</td>
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<td>0.08</td>
<td>0.01</td>
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*Model names follow White and Burnham (1999).*
of annual survival (0.59 ± 0.09) was 15% lower and also more variable (Table 2). The previous estimate likely was biased by emigration, which in this study we found to average ~14% annually (Table 2), similar to the emigration rate Cilimburb et al. (2002) estimated for the migratory Yellow Warbler (Dendroica petechia).

One model included in our confidence set incorporated variation in probabilities of movement between strata over time. This result was likely related to the small number of marked individuals observed annually in off-plot surveys as well as growth in the number of marked individuals over time (which included survivors and newly marked individuals). The unusual transition probabilities observed for one interval ($\Psi_{2,1}$, Table 2) stemmed from two individuals marked in 2004 but first observed in this study outside the primary area. One of these individuals moved into the plot the following year, while the other was never seen again. Estimates of movement into the primary area lacked precision, but, if we had not recorded and evaluated individuals’ movements with multi-strata models, estimated survival would have been approximately 15% lower (≈0.6) and indistinguishable from our previous estimate. Variation in probabilities of detection also would have increased, further decreasing precision.

No other estimates of annual survival based on mark–resighting procedures exist for this species, but two studies provide data from which monthly survival rates can be estimated. On the basis of passive mist netting Kremenetz and Christie (1999) reported a monthly survival probability of ~0.97 (4-month survival probability 0.88), while Stober and Kremenetz (2004), monitoring radio-tagged individuals, estimated a monthly survival rate of ~0.95 (3-month survival probability 0.89). If survival of adult males is constant through the year, our survival estimate corresponds to a monthly survival probability of ~0.97 and is similar to these estimates. Variation in probabilities of detection also <0.10% also is comparable to the variation observed for other nonmigratory sparrows (e.g., Lockwood et al. 2001, Morrison et al. 2004).

The absence of robust survival estimates has led to use of generic values in efforts to assess probabilities of extinction (Liu 1993), lifetime opportunities to breed (Seaman and Kremenetz 2000), and population source–sink dynamics (Perkins et al. 2003, Pulliam et al. 1992) of Bachman’s Sparrow. The maximum survival probabilities used in all of these studies were ≤0.6, a value toward the lower range of our 95% CI (0.58–0.78). The low values obviously might influence results. For example, Perkins et al. (2003) suggested habitat patches used by Bachman’s Sparrows in central Florida represented demographic “sinks” (Pulliam 1998) because annual productivity did not offset losses to mortality (with survival ≤0.6). Substituting our estimate for average survival (0.68) changed the status of almost all “sinks” to “sources” (i.e., productivity offset losses to mortality). Survival probabilities likely vary from site to site, but the influence that generic values may have on results needs to be evaluated carefully (Cilimburb et al. 2002, Marshall et al. 2004).

In our proposed two-stage Leslie matrix model, survival of adult males had the largest proportional influence on population growth rates (>50%), while the influences of productivity and juvenile males’ survival were equal (0.24). Better estimates for juvenile males’ survival and productivity may change the influence that these parameters have on population growth rates, but juveniles’ survival and productivity need to reach levels much higher than published estimates (Haggerty 1988, Perkins et al. 2003) before they will influence population growth in a manner comparable to survival of adult males. Estimating juveniles’ survival is considered a research priority but also is one of the most difficult parameters to estimate for wild populations (Kershner et al. 2004). For Bachman’s Sparrow, adult males’ survival and annual productivity collectively account for approximately 75% of the proportional influence on population growth rates. Adults’ survival and annual productivity are easier to monitor than juveniles’ survival (Pulliam et al. 1992, Haggerty 1988, Cox and Jones 2007), so a focus on these two vital rates likely represents the most efficient method for monitoring variation in rates of this species’ population growth.

Marshall et al. (2004) evaluated methods for assessing the effects of emigration on survival estimates and recommended off-plot surveys similar to ours. The area covered by off-plot surveys is an important consideration because chances of detecting dispersed individuals decrease geometrically as larger areas are covered and may lead to inefficiencies. Fletcher et al. (2002) proposed using survival elasticities to estimate the added precision that off-plot surveys might provide in terms of estimating population projections. With their procedures and our estimate of elasticity for males’ survival, emigration rates need to be double the rate observed (~14%) before the bias on population projections becomes significant (i.e., ≥0.05). Observations of marked birds during off-plot surveys were also uncommon, while detection probabilities consistently were ~0.85. For these reasons, we believe the 1-km search radius we used provides a balanced and efficient approach to monitoring survival of Bachman’s Sparrow in this setting.

Our study was conducted in a large area of contiguous, high-quality habitat and likely serves as a good reference point. Although in this setting off-plot surveys within 1 km appeared to monitor emigration, Bachman’s Sparrows may move more broadly in areas where the extent and timing of prescribed burns differ. For example, Haggerty (1988) reported lower annual return rates in an area burned less frequently. The generation length (4.1 years) estimated for Bachman’s Sparrow exceeds the time that habitat conditions typically remain suitable after a fire (Tuckner et al. 2006, Jones 2008), so Bachman’s Sparrows in most settings must move if they are to find and use ephemeral habitats created by fire. Additional studies are needed where the fire-return intervals...
are longer, the extent and season of fires differ, or logging creates widely distributed habitat patches (Dunning et al. 1995). The landscape in which Bachman’s Sparrows now occur has been altered substantially, and characteristics of survival of populations associated with more complex landscapes may provide important insights into the ecology of this disturbance-dependent species.

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LITERATURE CITED


