Demographic rates of two southeastern populations of Painted Bunting, 2007–2015

Authors: Yirka, Liani M., Collazo, Jaime A., O'Shea, Brian J., Gerwin, John A., Rotenberg, James A., et al.

Source: The Condor, 120(2) : 319-329

Published By: American Ornithological Society

URL: https://doi.org/10.1650/CONDOR-17-74.1

THE CONDOR
Ornithological Applications
AmericanOrnithology.org

Volume 120, 2018, pp. 319–329
DOI: 10.1650/CONDOR-17-74.1

RESEARCH ARTICLE

Demographic rates of two southeastern populations of Painted Bunting, 2007–2015

Liani M. Yirka,[1,2] Jaime A. Collazo,[2]* Brian J. O'Shea,[3] John A. Gerwin,[3] James A. Rotenberg,[4] and David T. Cobb[5]

[1] North Carolina Museum of Natural Sciences, Raleigh, North Carolina, USA
[2] U.S. Geological Survey, North Carolina Cooperative Fish and Wildlife Research Unit, Department of Applied Ecology, North Carolina State University, Raleigh, North Carolina, USA
[3] North Carolina Museum of Natural Sciences, Raleigh, North Carolina, USA
[4] Department of Environmental Studies, University of North Carolina Wilmington, Wilmington, North Carolina, USA
[5] North Carolina Wildlife Resources Commission, Raleigh, North Carolina, USA
* Corresponding author: jcollazo@ncsu.edu

Submitted April 10, 2017; Accepted December 30, 2017; Published March 21, 2018

ABSTRACT

Painted Buntings (*Passerina ciris*) have been declining in the southeastern United States since the 1970s. A recent demographic assessment highlighted the importance of estimating demographic parameters, which have received little attention to date. The dearth of information is troublesome because attempts to reverse declining trends require a better understanding of the relationship between habitat quality and age- and sex-specific survival and recruitment rates. We used capture–mark–recapture data collected from 2007 to 2015 on Bald Head Island (BHI) and at Hammocks Beach State Park (HBSP) in North Carolina, USA, to estimate local age- and sex-specific annual survival rates and local population size and recruitment rates using programs MARK and LOLASURVIV. Juveniles had lower local survival rates than adults (HBSP: 0.28 ± 0.14 vs. 0.67 ± 0.06; BHI: 0.28 ± 0.04 vs. 0.57 ± 0.02). Local annual survival rates for males on BHI (0.50 ± 0.03) were lower than those for females (0.57 ± 0.02). Age-specific differences were consistent with known differential age-dependent survival skills, and sex-specific differences were consistent with the potential influence of sexual dichromism. Conservative estimates of population size on BHI averaged 101 juveniles and 263 adults annually. Annual in situ reproductive recruitment averaged 28 individuals plus an additional 120 new immigrants, indicating successful reproduction and connectivity with neighboring coastal populations. Local adult survival estimates from our 2 North Carolinian study populations were similar to high-end estimates from across the eastern and western range of the species (~0.60). Finite observed population growth rate estimates between the BHI population ($\lambda = 1.10$) and a South Carolinian population ($\lambda = 0.87$) underscore the potential role of differential habitat quality and the importance of information from multiple sites, including nonbreeding grounds, for proper inferences about the status of the species. Reported vital rates provide a stronger foundation on which to base habitat quality as assessed with demographic parameters and to guide Painted Bunting conservation regionally.

Keywords: local survival, North Carolina, *Passerina ciris,* local population size, local recruitment, southeastern United States

Tasas demográficas de dos poblaciones del sureste de *Passerina ciris*, 2007–2015

RESUMEN

La especie *Passerina ciris* ha estado disminuyendo desde los años 1970's en el sudeste de Estados Unidos. Una evaluación demográfica reciente señala la importancia de estimar los parámetros demográficos, los cuales han recibido poca atención hasta la fecha. La escasez de información es problemática debido a que los intentos de revertir las tendencias decrecientes requieren de un mejor entendimiento de la relación entre la calidad del hábitat y la supervivencia específica por edad y sexo, y las tasas de reclutamiento. Usamos datos de captura-recaptura colectados desde 2007 hasta 2015 en la Isla Bald Head (IBH) y en el Parque Estatal Hammocks Beach (PEHB), Carolina del Norte, para estimar las tasas locales de supervivencia anual específicas por edad y sexo, el tamaño poblacional local y las tasas locales de reclutamiento usando los programas MARK y LOLASURVIV. Los juveniles presentaron tasas locales de supervivencia más bajas que los adultos (PEHB: 0.28 ± 0.14 vs. 0.67 ± 0.06; IBH: 0.28 ± 0.04 vs. 0.57 ± 0.02; respectivamente). La supervivencia local anual para los machos en IBH fue más baja (0.50 ± 0.03) que para las hembras (0.57 ± 0.02). Las diferencias específicas por edad fueron consistentes con las habilidades diferenciales conocidas de supervivencia por edad y las diferencias específicas por sexo fueron consistentes con la influencia potencial del dicromismo sexual. Las estimaciones conservadoras del tamaño poblacional en IBH promediaron 101 juveniles y 263 adultos anualmente. El reclutamiento reproductivo anual *in-situ* promedió 28 individuos más un

adicional de 120 nuevos inmigrantes, indicando el éxito de la reproducción y la conectividad con las poblaciones costeras vecinas. Aunque los hallazgos vienen de dos poblaciones de Carolina del Norte, las estimaciones de supervivencia local de los adultos fueron similares con las estimaciones más altas a lo largo del rango este y oeste de la especie (∼0.60). Las tasas de crecimiento finito observadas en IBH (λ =1.10) y las estimadas a partir de una población de Carolina del Sur ($\lambda = 0.87$) subrayan el rol potencial de la calidad del hábitat diferencial y la importancia de la información proveniente de múltiples sitios, incluyendo los sitios no reproductivos, para realizar inferencias apropiadas sobre el estatus de la especie. Las tasas vitales reportadas brindan una base más sólida para indexar la calidad del hábitat según los parámetros demográficos y guían la conservación de *P. ciris* a nivel regional.

Palabras clave: Carolina del Norte, este de Estados Unidos, *Passerina ciris*, reclutamiento local, supervivencia local, tamaño poblacional local

INTRODUCTION

Painted Buntings (*Passerina ciris*) are small Neotropical migrants that breed across the southern United States (Shipley et al. 2013). Their range is characterized by populations that breed within 2 disjunct geographic extents (Thompson 1991a, Shipley et al. 2013). The eastern range of the species extends from northern Florida into Georgia, South Carolina, and North Carolina, and the western range from portions of Kansas into Texas, Oklahoma, Arkansas, and Louisiana (Schulenberg 2009, Herr et al. 2011). These ranges are separated by a 500-km gap, with no evidence of gene flow between populations (Herr et al. 2011).

Numbers of Painted Buntings have declined consistently since the 1970s in the eastern range of the species (–1.63% per year, 95% CI = –3.86% to –0.24%; Meyers 2011, Sauer et al. 2017), prompting studies aimed at understanding their habitat requirements, with a few papers reporting estimates of abundance (e.g., Hobbs and Meyers 1999, Springborn and Meyers 2005, Sykes and Holzman 2005, Meyers 2011, Delany et al. 2013, Lowther et al. 2015). Surprisingly, information on demographic rates is scant. Available information consists mostly of annual return rates (23–65%; Lowther et al. 2015), that is, the proportion of individuals marked and released on some occasion that were encountered on a subsequent occasion (Cooch and White 2015). Recently, DeSante et al. (2015) reported demographic estimates obtained from data collected between 1992 and 2006 at the Dill Observatory, South Carolina, after accounting for capture–recapture probabilities. The local annual adult survival rate was 0.61 ± 0.05 SE, with the population exhibiting a negative annual finite growth rate ($\lambda = 0.87$). Over the same period, western populations exhibited local adult survival rates ranging from 0.45 to 0.65 and growth rates of slightly decreasing to increasing populations ($\lambda = 0.99$–1.05). DeSante et al. (2015) stressed the need to determine whether the decline in eastern populations was primarily caused by conditions on the nonbreeding grounds or low recruitment of surviving young on the breeding grounds. Moreover, they suggested directing efforts toward understanding the relationship between habitat quality and survival rates, as well as patterns of connectivity, as a means of promoting targeted habitat actions to help reverse the declining trend of eastern region populations.

North Carolina is at the northern extreme of the eastern range of Painted Buntings (Sykes et al. 2007). Populations in this portion of the range are of conservation concern for 2 reasons. First, there are no estimates of age- or sex-specific survival or recruitment rates, information that is needed to assess their status (DeSante et al. 2015). Second, North Carolina's populations are restricted to a narrow band of coastal habitats (1,547 km^2), compared with the much wider habitat band in South Carolina and Georgia (8,125 km^2; Hobbs and Meyers 1999, Meyers 2011). Prime habitat, such as maritime forests, occurs along this coastal band (Hamel 1992), and is being lost at high rates; 36% has been lost in North Carolina in the last 23 yr (Jones et al. 2013). This trend underscores the vulnerability of Painted Buntings to land use changes (Sykes and Holzman 2005).

The predicaments faced by Painted Buntings highlight several challenges that are also applicable to other Neotropical migratory species. First, there is a dearth of information on juvenile survival rates (McKim-Louder et al. 2013). This has been a long-standing challenge, which has prompted theoretical work that suggests that juvenile survival for Neotropical migrants needs to be at least 50% of adult rates for population maintenance (Ricklefs 1973, Donovan et al. 1995, Faaborg et al. 2010). Second, lack of information on age-specific survival rates of Painted Buntings impinges on our ability to understand how habitat conditions influence demographic parameters and to estimate recruitment rates (Nichols and Pollock 1990). Indeed, reliable estimates of local annual adult survival are only available for a population in South Carolina (DeSante et al. 2015).

In this study, we used capture–mark–recapture data for Painted Buntings collected from 2007 to 2015 on Bald Head Island and at Hammocks Beach State Park, North Carolina, to test whether local survival differed between age classes. We expected survival to be higher for adults because juveniles lack experience in foraging, predator avoidance, and migration (Gardali et al. 2003, Maness and Anderson 2013, Cox et al. 2014). We also tested whether local annual survival rates from Bald Head Island and

Hammocks Beach State Park differed, given that both sites are within proximity of each other and provide high-quality habitat for Painted Buntings. We note that, throughout this work, local and apparent survival rates are synonymous, meaning that our estimates are lower than true survival rates unless study area fidelity equals one (Schaub and Royle 2013). In addition, strong sexual dichromatism in the Painted Bunting, a striking feature of the species, presented an opportunity to ask whether there was evidence for sex-biased mortality rates. Thus, we examined whether local survival differed between the sexes on Bald Head Island. The expectation is that females have lower survival due to risks induced by parental care; however, Promislow et al. (1992) and Liker and Székely (2005) advanced hypotheses and evidence suggesting that survival costs incurred by males during mate selection could be higher. We discuss the conservation implications of our findings for eastern Painted Buntings and ecological insights applicable to other passerine Neotropical migrants.

METHODS

Study Sites

We trapped, marked, and released Painted Buntings on Bald Head Island and at Hammocks Beach State Park (Figure 1). Bald Head Island is located at the extreme southeastern coastal point of North Carolina, at the mouth of the Cape Fear River (33.8617°N, 77.9942°W). Approximately 620 ha of the island is upland habitat, with various successional stages of maritime forest–shrub, dune–grassland, tidal marsh, and residential development (Oosting 1954, Bourdeau and Oosting 1959, Lopazanski et al. 1988). A 77-ha reserve, Bald Head Woods, is located in the center of the island as part of the Smith Island Complex. The reserve consists of a canopy of old growth live oak (*Quercus virginiana*) and laurel oak (*Quercus laurifolia*) and a mixture of understory shrubs such as American holly (*Ilex opaca*) and yaupon (*Ilex vomitoria*; http://www.nccoastalreserve.net/web/crp/bald-head-woods). We captured Painted Buntings in the extreme southeastern portion of the island, between Middle and Bald Head Islands (~840 ha).

Hammocks Beach State Park (34.6709°N, 77.1396°W; Figure 1) is located between Camp Lejeune (administered by the U.S. Marine Corps, Jacksonville, North Carolina, USA) and Croatan National Forest (administered by the USDA Forest Service, Asheville, North Carolina, USA). The park encompasses more than 400 ha and is composed of a 13-ha gateway area accessible from the mainland, 2 islands designated as nature preserves and with no public access (Huggins and Jones islands), and Bear Island. We captured Painted Buntings between the mainland gateway area and Bear Island, covering an area of ~200 ha. The vegetation in this region is composed of shrub–scrub thickets and maritime forest in addition to large swaths of salt marsh in between the mainland and Bear Island. Bear Island is predominantly covered with large sand dunes and beach habitat that has overtaken much of the maritime forest on the island in recent decades (https://www.ncparks.gov/hammocks-beach-state-park/ecology). In shrub and maritime forest thickets, the primary vegetation consists of wax myrtle (*Myrica cerifera*), eastern redcedar (*Juniperus virginiana*), yaupon, and live oak, among others, bordered by salt marsh habitat dominated by 2 species of cordgrass (*Spartina alterniflora* and *Spartina patens*; Dickerson 1978).

Field Methods

We collected capture–mark–recapture data between May 15 and August 30 from 2007 to 2015. There were 3–4 trapping occasions per year, lasting ~3–5 days each. Trapping occasions were in late May–mid-June, mid-July, and mid-August, with occasions separated by a minimum of 14 days. Painted Buntings were captured at 4–7 trapping stations on Bald Head Island and at 2 trapping stations at Hammocks Beach State Park. Trapping was conducted for 4.5 hr from sunrise in the morning and for an equal amount of time before sunset in the afternoon, coincident with peak Painted Bunting activity. We alternated morning and afternoon trapping sessions to avoid systematic errors (e.g., recapture probability).

Painted Buntings were trapped using 2 wire cages with feeders containing a tube feeder filled with white millet seed (Sykes 2006). Each bird was aged and sexed following Pyle (1997) and Froehlich (2003), and marked and released within 15–20 min. Captured individuals were uniquely marked with 3 colored plastic bands (either Darvic or Acetal) and 1 U.S. Geological Survey aluminum band obtained from the Bird Banding Laboratory (Patuxent Wildlife Research Center, Laurel, Maryland, USA). We believe that juvenile birds, still accompanied by their parents, were captured 2–4 days postfledging. At the completion of each 4.5-hr trapping session, trap feeders were removed and replaced with regular feeders. All trapping efforts were carried out by a minimum of 2 people (an experienced bander and a data recorder).

Data Analysis

We treated Bald Head Island and Hammocks Beach State Park as our primary experimental units; thus, data from all trapping stations within each location were pooled for analysis. We captured 1,155 individuals on Bald Head Island and 174 at Hammocks Beach State Park over the 9-yr study period. We excluded records of individuals that could not be tracked after capture (e.g., escaped before banding). This process yielded 1,139 and 173 encounter histories for Bald Head Island and Hammocks Beach State

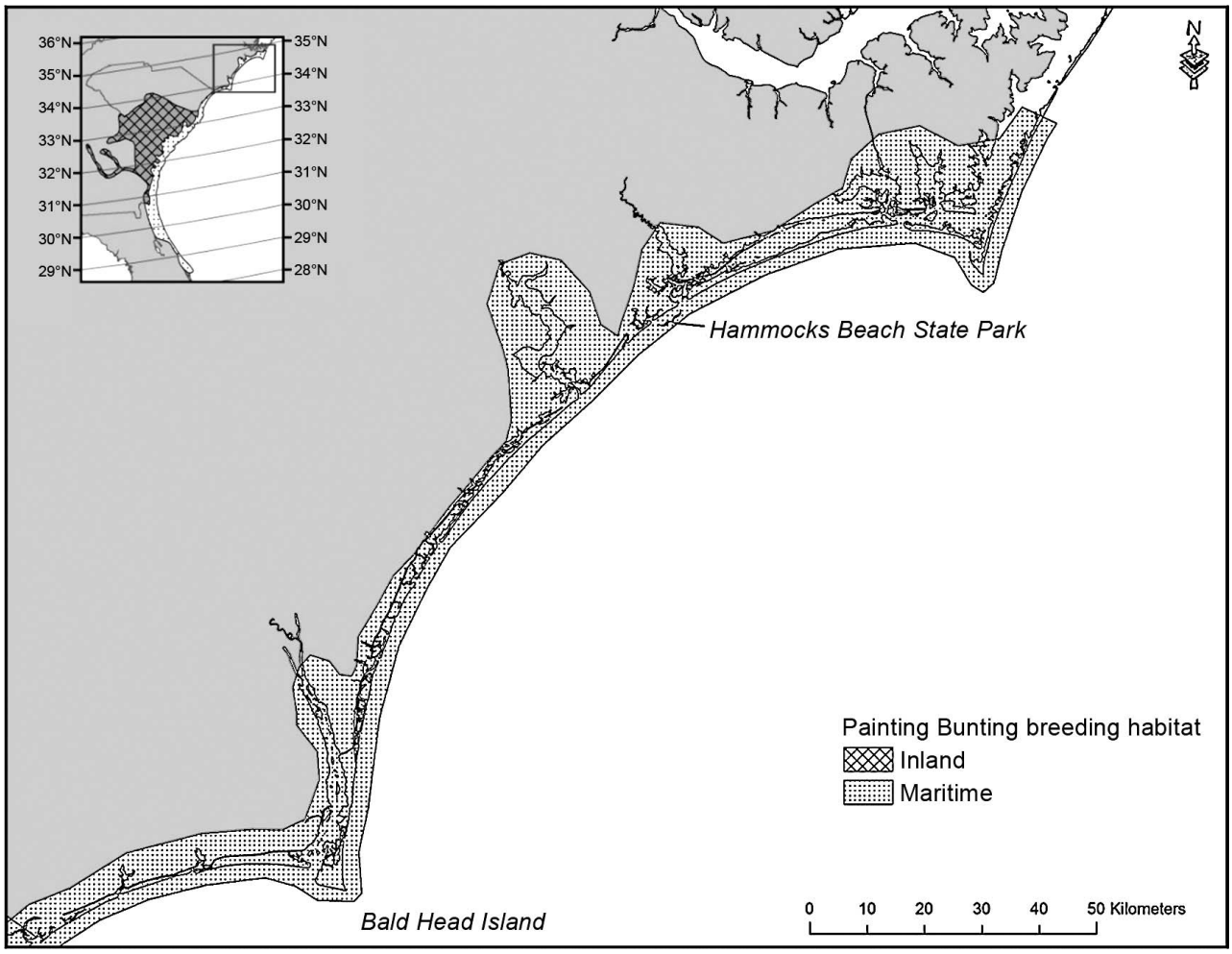

FIGURE 1. Map of coastal North Carolina, USA, depicting the location of Hammocks Beach State Park and Bald Head Island. The inset depicts the southeastern United States and the range of Painted Buntings along the coast of Florida and North Carolina, and along the coast and inland in South Carolina and Georgia.

Park, respectively. Captures from both locations were classified as juvenile (HY or hatch-year) or adult (AHY or after-hatch-year). Birds from Bald Head Island were also classified as male (M), female (F), or unknown sex (U). The latter designation accounted for instances in which there was uncertainty in the sex designation, either due to age (i.e. HY) or because the individual escaped or was released without having been sexed.

We used Cormack-Jolly-Seber (CJS) models to determine whether local annual survival rates were age-specific for the Hammocks Beach State Park population using program MARK (White and Burnham 1999). CJS models yield estimates of local (apparent) survival (S) and capture probability (p). We note that resulting estimates of survival reflect appropriate parameterization within MARK to account for the transition in survival probability from juvenile to age $\geq$2 yr. CJS models make the following assumptions: (1) that every marked animal present in the population in year i has the same probability of recapture (p); (2) that every marked animal in the population immediately after year i has the same probability of surviving to year $i + 1$; (3) that marks are not lost or missed; and (4) that all samples are instantaneous, relative to the interval between occasion i and occasion $i + 1$. Our sampling design led us to believe that assumptions 1 and 4 were met, and that tag loss (assumption 3) was negligible. From our best sample (Bald Head Island), we recorded 1 band loss from >1,100 individuals. There was the possibility that assumption 2 was violated, and thus we conducted permanent trap tests on the Bald Head Island dataset. The test is detailed below.

We analyzed data from Bald Head Island using a robust design modeling framework to examine whether survival rates, as well as population size and recruitment rates, were influenced by age, which was not possible using the CJS approach (Pollock 1982, Kendall et al. 1995, 1997). For

this analysis, years were designated as primary sampling periods, a time interval when the population was open or subject to change (through immigration, emigration, deaths, and births). Within-year trapping periods were designated as secondary sampling occasions, time intervals within which population closure was assumed (Pollock 1982, Kendall et al. 1995). Secondary sampling occasions were late May–mid-June, mid-July, and mid-August.

We tested for evidence of temporary emigration using 2 competing models that could be parameterized for adults and juveniles: Markovian temporary emigration and no movement models. In the Markovian temporary emigration model, the probability of transitioning between the available and unavailable states between primary periods depends on the availability of the bird in the previous primary period. This model has 2 different parameters: gamma prime (γ') and gamma double-prime (γ''). The γ' parameter represents the probability of a bird remaining unavailable during sampling period i, given that the bird was not available during the previous sampling period $i-1$ and that it survived to period i. The γ'' parameter represents the probability of a bird being unavailable for capture during sampling period i, given that the bird was available for capture during the previous sampling period $i-1$ and that it survived to period i (Kendall et al. 1997). The second parameterization, the no movement model, assumes that unavailable birds remain unavailable and available birds remain available across all sampling periods. To parameterize the Markovian temporary emigration model, we modeled γ' and γ'' separately, and for the no movement model, we set $\gamma' = 0$ and $\gamma'' = 1$.

We also tested for temporary emigration using a random or classic temporary movement model, but with an adjustment. In this model, the probability of transitioning between the available and unavailable states between primary periods does not depend on the availability of a bird in the previous period. Gamma parameters are typically set as $\gamma' = \gamma''$. In our case, however, there was no γ' parameter for juveniles (i.e. the probability of a juvenile returning from temporary emigration). This is because juveniles become adults as soon as they temporarily emigrate. To have a random movement model for juveniles, one would need several primary periods in which birds remain juveniles (i.e. within-season primary periods), a data structure outside the scope of this work. Therefore, we parameterized a model that assessed random movement for adults but Markovian movement for juveniles. Assumptions for robust design models are the same as for CJS models. We note that our sampling period occurred within known seasonal bounds, that is between arrival at the site (late May) and molt completion (mid-August; Thompson 1991b), for appropriate robust design inferences.

We modeled survival and capture probabilities as constant (.), year-specific (Yr), and age-specific (Age) for the Hammocks Beach State Park population. The interaction between age and year overparameterized models and thus was not included in the candidate model set. For the Bald Head Island population, we assessed 8 models using the robust design with the Huggins closed captures data type option in program MARK (Cooch and White 2015). We started with Markovian and no movement models that featured age-specific but time-invariant survival, age-specific but time-invariant gamma, and constant capture–recapture probability. We then assessed no movement and Markovian models with year-specific and age-specific survival (Age*Yr), age-specific but time-invariant gammas (prime and double-prime), and constant capture–recapture probability. We modified these models to parameterize gamma as random movements for adults and Markovian movements for juveniles as noted above. Finally, the best-supported model up to this point (i.e. the best-supported of the aforementioned models) was parameterized in 3 additional ways to further explore sources of variation for all parameters. First, we created a model that featured age-specific survival, year-specific and age-specific gammas (prime and double-prime), and constant capture–recapture probability. Second, we created a model that featured time-invariant age-specific survival, age-specific gammas (prime and double-prime), and year-specific capture–recapture probability. Lastly, we created a model that featured the same parameterization as the previous model, but with year-specific and age-specific survival. A global (saturated) Markovian model was not included because it was overparameterized.

Recruitment rates for Bald Head Island were estimated following Nichols and Pollock (1990). The number of in situ reproductive recruits was estimated as surviving juveniles, calculated as:

$$\hat{B}_i^{(1)\prime} = \hat{N}_i^{(0)} \hat{\phi}_i^{(0)}.$$

The number of new immigrants was obtained by subtracting surviving adults and juveniles from abundance and was calculated as:

$$\hat{B}_i^{(1)''} = \hat{N}_{i+1}^{(1)} - \hat{N}_i^{(1)} \hat{\phi}_i^{(1)} - \hat{N}_i^{(0)} \hat{\phi}_i^{(0)}.$$

In these equations, juveniles = age 0 and adults = age 1; $\hat{N}_i^{(a)}$ = the abundance of age a in period i; $\hat{\phi}_i^{(a)}$ = the survival rate (i to $i+1$) for age a; $\hat{B}_i^{(1)'}$ = new recruits via in situ reproduction entering the adult population between i and $i+1$ and present at $i+1$; and $\hat{B}_i^{(1)''}$ = new recruits via immigration entering the adult population between i and $i+1$ and present at $i+1$. We calculated the 95% confidence

intervals (CI) for recruitment rates by directly substituting the 95% confidence limits (upper and lower) of age-specific survival and population size into the above recruitment equations. We used annual estimates of the number of adults to obtain an average estimate of population exponential growth (r_{obs}) to assess the status of the species (stable, increasing, or decreasing). The estimate of r_{obs} ($\pm$ SE) was obtained by regressing log-transformed population estimates on years, expressed as the finite population growth (λ; Caughley 1977).

We tested whether local annual survival rates of the Bald Head Island population were sex-specific using an extension of Cormack-Jolly-Seber models for open populations, but with multiple groups (Nichols et al. 2004). Groups were "known males (M)," "known females (F)," and "unknown sex (U)." For Painted Buntings, most uncertainty in sex designation is resolved on an annual time step, and no attempt (or need) was made to determine the sex of a bunting following the initial designation (sampling situation B; Nichols et al. 2004). Model parameters in these models were: S_i = the probability of local survival from year i to year $i + 1$ for individuals of sex s, where $s \in \{M, F\}$, p_i = the probability of capture in year i for individuals of sex s, where $s \in \{M, F\}$, delta_i = the probability that sex was ascertained in year i for individuals of sex s that were captured in year i, where $s \in \{M, F\}$, and pi_i = the probability that the first individual captured in year i was male. We assessed 126 competing models, but report only models with a difference from the top model of Akaike's information criterion corrected for small sample size (ΔAIC_c) ≤ 10 (Burnham and Anderson 2002). Model names indicate how parameters were modeled. For example, S(Sex) means that survival was different for the 2 sexes, S(Yr) means that survival varied by time, S(Sex*Yr) means that survival was affected by the interaction between sex and time, and S(Sex + Yr) means that survival varied by sex with an additive effect of time. Analyses were conducted using program LOLASURVIV (Hines 1994).

Finally, we tested for permanent trap responses to help us interpret model results because capture–recapture data were obtained using baited traps. Nichols et al. (1984) showed that trap responses do not induce biases in survival estimates, but that they can induce biases in estimates of population size. To conduct tests, we used closed population models and a 2-group approach in program MARK (Cooch and White 2015). Painted Buntings were grouped for each year into those never caught in a previous year and those caught in a previous year. Our prediction for no trap response was that capture (p) > recapture (c) for those individuals never caught in a previous year and $p = c$ for individuals previously trapped.

We used Akaike's information criterion (AIC) to select the most parsimonious model. Models were ranked by AIC corrected for small sample size (AIC_c), where the model with the lowest AIC_c value was the model with the most support from the data. The difference in AIC_c value between the best-supported model and any other model (ΔAIC_c) was used to calculate the Akaike model weight (w_i), which indicates the relative likelihood of the model given the data (Burnham and Anderson 2002). Models with $\Delta AIC_c \leq 2$ were considered to have the highest support. We report parameter estimates $\pm$ SE.

TABLE 1. Model selection results for Cormack-Jolly-Seber models used to test whether local annual survival of Painted Buntings was age-specific at Hammock Beach State Park, North Carolina, USA, 2007–2015. Models were ranked by the difference from the top model in Akaike's information criterion corrected for small sample size (ΔAIC_c). Model parameters also include the Akaike weight (w_i), deviance, and number of parameters (K). Local survival rates (S) were modeled as constant (.) or age-dependent (Age). Capture rates (p) were modeled as either constant (.) or variable with respect to year (Yr).

Model	ΔAIC_c	w_i	K	Deviance
{S(Age), p(Yr)}	0.00 [a]	0.990	11	72.22
{S(Age), p(.)}	10.51	0.006	3	100.20
{S(.), p(.)}	11.04	0.004	2	102.81

[a] The AIC_c of the top model = 291.93.

RESULTS

Variation in local annual survival rates of Painted Buntings at Hammocks Beach State Park was best explained by a model that featured age (HY, AHY) and year-specific capture probability (w_i = 0.99; Table 1). Local annual survival was 0.28 $\pm$ 0.14 for juveniles and 0.67 $\pm$ 0.06 for adults. Year-specific capture probabilities ranged from 0.09 $\pm$ 0.06 to 0.46 $\pm$ 0.13. Variation in local annual survival on Bald Head Island was best explained by a model that featured age, age-specific gammas (no movement), and year-specific capture and recapture probabilities (w_i = 0.99; Table 2). Estimates of local survival rates were 0.28 $\pm$ 0.04 for juveniles and 0.57 $\pm$ 0.02 for adults. Year-specific capture probabilities ranged from 0.01 $\pm$ 0.01 to 0.37 $\pm$ 0.04, whereas recapture probabilities ranged from 0.08 $\pm$ 0.05 to 0.51 $\pm$ 0.06.

The top CJS model indicated that variation in annual survival rates of Painted Buntings on Bald Head Island was sex-specific, that capture probability varied by year, and that the probability of ascertaining sex designation varied with the interaction of sex and year (w_i = 0.30; Table 3). The annual survival rate for females was 0.57 $\pm$ 0.02, whereas for males it was 0.50 $\pm$ 0.03. The capture probability for both males and females ranged between 0.16 $\pm$ 0.04 and 0.63 $\pm$ 0.06. The probability of classifying sex in any given year ranged from 0.60 $\pm$ 0.08 to 0.84 $\pm$ 0.06 for males and from 0.63 $\pm$ 0.05 to 0.91 $\pm$ 0.05 for

TABLE 2. Model selection results for robust design models used to determine whether local annual survival of Painted Buntings was age-specific on Bald Head Island, North Carolina, USA, 2007–2015. Secondary sampling occasions ($n = 3$) occurred in late May–mid-June, mid-July, and mid-August. Models were ranked by the difference from the top model in Akaike's information criterion corrected for small sample size (ΔAIC_c). Model parameters also include the Akaike weight (w_i), deviance, and number of parameters (K). Local survival rates (S) and gammas (γ'' and γ') were modeled as constant (.), age dependent (Age), and age dependent variable with respect to year (Age*Yr). Age is defined as HY = juvenile and AHY = adult. Gammas were used to test for random, no movement, and Markovian temporary migration. Capture (p) and recapture probabilities (c) were modeled as either constant or variable with respect to year (Yr).

Model	ΔAIC_c	w_i	K	Deviance
{S(Age), γ''=0(Age), γ'=1(Age), p(Yr), c(Yr)}no movement	0.00 [a]	0.996	45	8,013.19
{S(Age*Yr), γ''=0(Age), γ'=1(Age), p(Yr), c(Yr)}no movement	11.31	0.003	57	7,998.99
{S(Age), γ''=0(Age*Yr), γ'=1(Age*Yr), p(.), c(.)}no movement	306.43	0.000	20	8,371.59
{S(Age), γ''(Age), γ'(Age), p(.), c(.)}Markovian	312.54	0.000	23	8,371.54
{S(Age*Yr), γ"=0(Age), γ'=1(Age), p(.), c(.)}no movement	315.22	0.000	34	8,351.46
{S(Age*Yr), γ''(Age), γ'(Age), p(.), c(.)}random AHY, Markovian HY	320.26	0.000	37	8,350.24
{S(Age*Yr), γ''(Age), γ'(Age), p(.), c(.)}Markovian	321.87	0.000	38	8,349.76
{S(Age), γ''(Age*Yr), γ'(Age*Yr), p(.), c(.)}Markovian	354.34	0.000	50	8,348.76

[a] The AIC_c of the top model = 6,670.35.

females. Three other models were considered to be competitive ($\Delta AIC_c \leq 2$; Table 3), 2 of which featured constant (equal for both sexes) survival rates. The estimate from models with a constant survival rate was 0.54 ± 0.20.

Population size estimates for Bald Head Island varied across years, and averaged 101 juveniles and 263 adults annually (Figure 2). Annual estimates of the number of adults indicated that the population was growing ($r_{obs} = 0.10 \pm 0.03$ or $\lambda = 1.10$, 95% CI = 1.04–1.16; $F_{1,7} = 9.17$, $P = 0.02$). On average, 28 individuals were recruited annually through in situ reproduction (range: 8–52) and an additional 120 individuals were recruited as new immigrants (range: 0–222; Figures 3A and 3B). This yielded an average per capita recruitment rate of 0.56 (148/263) individuals. Trap response tests indicated that there was a strong positive response by Painted Buntings on Bald Head Island over the years (Table 4).

TABLE 3. Model selection results for modified Cormack-Jolly-Seber models used to examine whether local annual survival of Painted Buntings was sex-specific on Bald Head Island, North Carolina, USA, 2007–2015. Models were ranked by the difference from the top model in Akaike's information criterion corrected for small sample size (ΔAIC_c). Model parameters also include the Akaike weight (w_i), deviance, and number of parameters (K). We report models that had support of $\Delta AIC_c \leq 10$. Local survival (S), capture (p), and sex classification (dlta) rates, and the probability that the first individual captured in a year was male (pi), were modeled as constant (.), variable by year (Yr), and variable by sex (Sex). We also included additive and interactive effects of sex and year (Sex + Yr and Sex*Yr). Competitive models ($\Delta AIC_c \leq 2$) are indicated with an asterisk.

Model	ΔAIC_c	w_i	K	Deviance
*S(Sex), p(Yr), pi(Yr), dlta(Sex*Yr)	0.00 [a]	0.295	37	−2,287.13
*S(.), p(Sex + Yr), pi(Yr), dlta(Sex*Yr)	0.59	0.219	37	−2,278.42
*S(.), p(Yr), pi(Yr), dlta(Sex*Yr)	0.63	0.215	36	−2,279.51
*S(Sex), p(Sex + Yr), pi(Yr), dlta(Sex*Yr)	1.53	0.137	38	−2,277.82
S(Sex), p(Yr), pi(Yr), dlta(Sex + Yr)	4.17	0.037	29	−2,288.69
S(Sex), p(Sex + Yr), pi(Yr), dlta(Sex + Yr)	5.20	0.022	30	−2,288.15
S(.), p(Sex + Yr), pi(Yr), dlta(Sex + Yr)	6.54	0.011	29	−2,289.87
S(Sex + Yr), p(Yr), pi(Yr), dlta(Sex*Yr)	6.85	0.010	44	−2,274.03
S(Sex), p(Yr), pi(Yr), dlta(Yr)	7.08	0.009	28	−2,291.20
S(.) p(Yr), pi(Yr), dlta(Yr)	7.37	0.007	27	−2,292.39
S(Yr), p(Sex + Yr), pi(Yr), dlta(Sex*Yr)	7.38	0.007	44	−2,274.30
S(Sex + Yr), p(Sex + Yr), pi(Yr), dlta(Sex*Yr)	8.17	0.005	45	−2,273.61
S(.), p(Sex + Yr), pi(Yr), dlta(Yr)	8.18	0.005	28	−2,291.75
S(Yr), p(Yr), pi(Yr), dlta(Sex*Yr)	8.35	0.005	43	−2,275.87
S(.), p(Yr), pi(Yr), dlta(Sex + Yr)	8.79	0.004	28	−2,292.05
S(Sex), p(Sex + Yr), pi(Yr), dlta(Yr)	9.10	0.003	29	−2,291.16
S(.), p(Sex*Yr), pi(Yr), dlta (Sex*Yr)	9.44	0.003	44	−2,275.33
S(Sex), p(Sex*Yr), pi(Yr), dlta(Sex*Yr)	9.65	0.002	45	−2,274.35

[a] The AIC_c of the top model = 4,632.67.

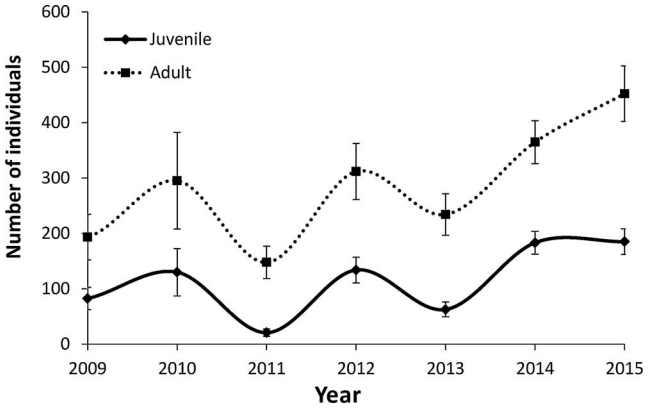

FIGURE 2. Estimates (± SE) of age-specific population size of Painted Buntings from 2007 to 2015 on Bald Head Island, North Carolina, USA. Estimates were derived from the robust design model with the highest support (Table 2).

DISCUSSION

We report the first estimates of local juvenile survival rates for Painted Buntings across their eastern range, which also represent the first available estimates for western population demographic assessments. Juvenile survival estimates are valuable because they are scant or nonexistent for many Neotropical migrant species (McKim-Louder et al. 2013). Estimates were similar to or slightly less than 50% of adult survival rates, lending support to previous work suggesting that juvenile survival needs to be at such levels to achieve population maintenance (Ricklefs 1973, Donovan et al. 1995). Knowledge of local juvenile survival is valuable for rating habitat quality, a priority underscored by DeSante et al. (2015), but also aids in the assessment of tradeoffs among alternative strategies that promote local population growth, such as the production of multiple broods per season (Farnsworth and Simons 2001, Podolsky et al. 2007). Lastly, estimates help to assess the sensitivity of juvenile survival to postbreeding factors (e.g., connectivity, and habitat quality during migration and on the wintering grounds; Ricklefs 1973, Sillett and Holmes 2002, Norris and Marra 2007, Faaborg et al. 2010, McKim-Louder et al. 2013).

TABLE 4. Permanent trap response test results for the years 2007–2014 for Painted Buntings captured (*p*) and recaptured (*c*) on Bald Head Island, North Carolina, USA, 2007–2015. Estimates ± SE are reported. Tests were conducted with closed population models, using a 2-group approach in which buntings for each year were grouped as those never caught in a previous year and those caught in a previous year. No trap response would be indicated by $p > c$ for buntings never caught (new individuals) and by $p = c$ for those caught previously (old individuals).

Year	*p* new	*c* new	*p* old	*c* old
2007	0.00 ± 0.00	0.06 ± 0.03	0.00 ± 0.00	0.22 ± 0.08
2008	0.00 ± 0.00	0.04 ± 0.03	0.00 ± 0.00	0.30 ± 0.09
2009	0.05 ± 0.15	0.10 ± 0.04	0.66 ± 0.14	0.09 ± 0.06
2010	0.00 ± 0.00	0.00 ± 0.00	0.19 ± 0.18	0.25 ± 0.07
2011	0.00 ± 0.00	0.18 ± 0.03	0.13 ± 0.19	0.20 ± 0.07
2012	0.00 ± 0.00	0.15 ± 0.05	0.41 ± 0.11	0.23 ± 0.05
2013	0.00 ± 0.00	0.26 ± 0.02	0.00 ± 0.00	0.56 ± 0.07
2014	0.00 ± 0.00	0.14 ± 0.02	0.24 ± 0.09	0.15 ± 0.03

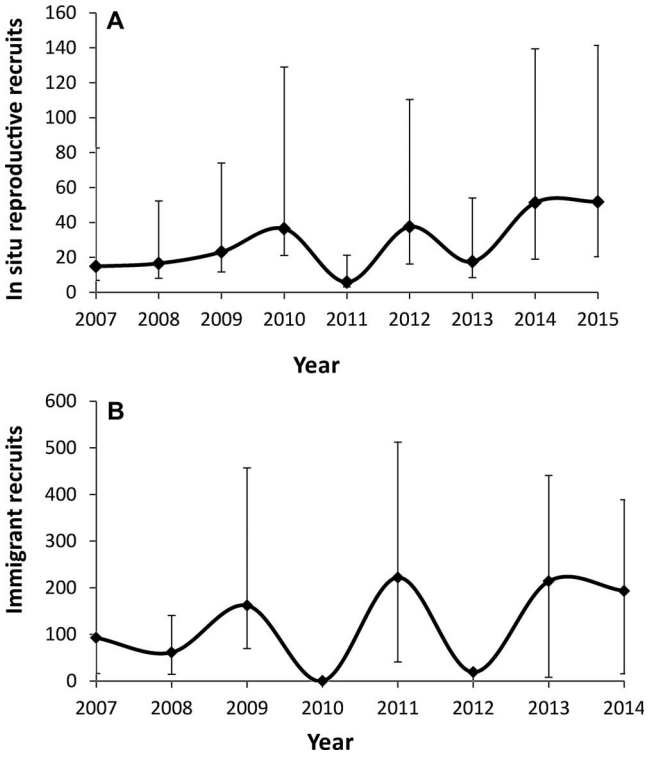

FIGURE 3. Estimates (± 95% CI) of (**A**) in situ reproductive recruitment and (**B**) new immigrant recruitment of Painted Buntings from 2007 to 2015 on Bald Head Island, North Carolina, USA. Estimates were derived from the robust design model with the highest support (Table 2). New immigrant recruitment was not estimable for 2015 because data from 2016 ($t + 1$) were required.

As expected, adults had higher estimated survival than juveniles, both on Bald Head Island and at Hammocks Beach State Park. Lower juvenile survival in avian species is attributed to lack of experience in behaviors such as foraging and predator avoidance (Gardali et al. 2003, Maness and Anderson 2013, Cox et al. 2014), and to mortality risks during first-year migration (Klaassen et al. 2014). Estimates of age-specific survival rates between Bald Head Island and Hammocks Beach State Park were similar (95% CIs overlapped). Numerous factors may have contributed to these similarities (e.g., shared nonbreeding habitat, predation, migration routes), but we highlight the potential contribution of spatially correlated habitat conditions, given that the 2 locations were just 116 km apart. Examples of habitat similarities include the presence of maritime forest (13% at Hammocks Beach State Park;

55% on Bald Head Island), considered optimal habitat for Painted Buntings (Hamel et al. 1982, Hamel 1992, Yirka 2016), and access to tidal marshes, important foraging grounds for the species (Sykes and Holzman 2005).

Sex-specific estimates indicated that males had lower local survival rates than females. This outcome supports predictions made by Primislow et al. (1992) and Liker and Székely (2005). We included this test because Painted Buntings are strongly dichromatic, invoking potential limits and costs regarding how distinct sexes can be while still gaining advantages from sexual dimorphism (Primislow et al. 1992, Huhta et al. 2003). When examining sex-specific survival, we minimized any biases related to uncertainty associated with the sex designation of captured Painted Buntings (Nichols et al. 2004). Admitedly, estimates from 2 competing models suggested that survival rates were similar between the sexes, indicating that additional studies will be required before more definitive statements can be made about mortality costs due to sexual dichromatism or the potential role of other factors (e.g., nonbreeding habitat). The topic of sex-specific mortality costs is one of continued interest in avian ecology due to its implications for life history strategies, and we argue that Painted Buntings could be one of the species used to test outstanding hypotheses. For example, Painted Buntings exhibit polygynous breeding in portions of their range (Lowther et al. 2015). As such, these populations may provide an opportunity to contrast mortality costs with monogamous populations, testing whether avian polygynous males incur higher mortality costs, as has been observed for polygynous males in mammalian species (Liker and Székely 2005). From a conservation perspective, estimating sex-specific survival rates is justified because males are selectively trapped for the pet trade (Sykes 2006, Sykes et al. 2007), and such removals might be an additive source of mortality. This is the case for the Lazuli Bunting (*Passerina amoena*; Johnson et al. 2012), a case study that highlights management actions that may apply to Painted Buntings if the linkage between trapping and male survival is established.

We found strong evidence that Painted Buntings exhibited permanent trap responses on Bald Head Island. In and of itself, a positive trap response does not bias point estimates of survival and estimates are still precise (Nichols et al. 1984). The reader must bear in mind, however, that our estimates of local (apparent) survival are underestimates of true survival, not because of a trap response, but because of the possibility that some Painted Buntings may permanently emigrate from Bald Head Island (Schaub and Royle 2014). Positive trap responses, however, will induce estimates of local population size that are biased low (Nichols et al. 1984). Nevertheless, we report estimates of population size and recruitment rates because (1) we modeled various sources of individual heterogeneity using a robust design, (2) inferences err on the side of being conservative, and (3) these estimates provide important insights into key demographic processes (e.g., in situ reproduction, immigration). Our results indicated that the average population size on Bald Head Island was 364 individuals (HY + AHY), and the observed average finite annual growth rate between 2007 and 2015 was positive, with the population increasing 10% per year (95% CI: 4–16%). The annual average recruitment rate of 0.56 is also noteworthy, an estimate similar to the highest reported for western populations (0.41–0.55; DeSante et al. 2015). Both of these findings are encouraging because western populations have exhibited population growth in recent years (DeSante et al. 2015, Sauer et al. 2017). On average, 28 in situ recruits were added annually to the population, providing evidence of successful reproduction. The local population also benefited from an average of 120 immigrant recruits annually, evidence that Painted Buntings on Bald Head Island are not isolated. Identifying interconnected populations was a research priority identified by DeSante et al. (2015), but outside the scope of the present study. On the basis of proximity to Bald Head Island, Fort Fisher (14 km to the north) and Sunset Beach (49 km to the south) are likely sources of potential recruits, but we do not exclude the possibility that immigrants may come from other, yet undiscovered, neighboring populations.

The vital rates reported in this study come from just 2 populations in North Carolina. Nonetheless, they advance eastern Painted Bunting conservation in several important ways. First, the estimates provide additional evidence that local adult annual survival in coastal habitats is ~0.60 (DeSante et al. 2015, Lowther et al. 2015). We also note that our local adult survival estimates (0.57 and 0.67) are in the upper range of estimates available for western populations (0.45–0.65). Second, these age- and sex-specific local survival estimates, some reported for the first time for eastern populations, should lead to more robust inferences about Painted Bunting status through expanded parameterization of demographic models (Noon and Sauer 1992). Third, the sharp contrast between finite growth rates from Bald Head Island ($\lambda = 1.10$) and Dill Conservatory, South Carolina ($\lambda = 0.87$; DeSante et al. 2015), although derived from different sampling periods, emphasizes the potential role that differences in habitat quality may play in regional population dynamics. The latter underscores the importance of broadening geographic sampling efforts, and of including inland and nonbreeding habitats, to conduct a comprehensive, quantitative assessment of the status of eastern Painted Buntings. In this vein, we also stress the importance of identifying habitat features associated with successful reproduction and local survival (Martin 1992, Sykes and Holzman 2005, DeSante et al. 2015, Lowther et al. 2015), and the value of threat–risk assessments to guide habitat conservation prioritization (Araújo and Williams 2000, Yirka 2016). Our reported local (apparent) demographic

rates are conservative, but expand our knowledge base to better understand the population dynamics of eastern Painted Buntings. Future studies should be designed to report true estimates of demographic rates for stronger inference (Gilroy et al. 2012, Schaub and Royle 2014).

ACKNOWLEDGMENTS

We thank S. Jolly, J. Jacobs, S. Bohr, M. Fisk, D. Huston, G. Deason, T. Michels, E. Landi, S. McGrath, and B. Williams for their field assistance. We are also grateful to J. E. Hines and J. D. Nichols for their advice and assistance with statistical analyses, and to S. Dinsmore, N. Haddad, K. Pacifici, J. Saracco, and 3 anonymous reviewers for suggestions on earlier versions of the manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Funding statement: We thank the North Carolina Wildlife Resources Commission for providing the financial support to conduct the analyses of long-term data collected by the North Carolina Museum of Natural Sciences (project WM-0294). We also thank the Cape Fear Audubon Society, Bald Head Island Conservancy, and the Giacci, Grantmyer, Quanstrom, Coryell, Prak, and Douglas families for their support. No funders had input into the content of the manuscript, and no funders required their approval of the manuscript before submission or publication.

Ethics statement: Data were collected by trained and experienced North Carolina Museum of Natural Sciences personnel, always safeguarding the well-being of birds during trapping sessions. This research was conducted in compliance with the *Guidelines to the Use of Wild Birds in Research*.

Author contributions: J.A.G., J.A.R., and B.J.O. conceptualized the study; L.M.Y., J.A.G., and D.T.C. collected the data and supervised research; J.A.C., D.T.C., and L.M.Y. formulated questions and analyzed data; and L.M.Y. and J.A.C. wrote the paper.

Data deposits: Our data is deposited with the North Carolina Museum of Natural Sciences.

LITERATURE CITED

Araújo, M. B., and P. H. Williams (2000). Selecting areas for species persistence using occurrence data. Biological Conservation 96:331–345.

Bourdeau, P. F., and H. J. Oosting (1959). The maritime live oak forest in North Carolina. Ecology 40:148–152.

Burnham, K. P., and D. R. Anderson (2002). Model Selection and Multimodel Inference: A Practical Information–Theoretic Approach, second edition. Springer-Verlag, New York, NY, USA.

Caughley, G. (1977). Analysis of Vertebrate Populations. John Wiley & Sons, New York, NY, USA.

Cooch, E. G., and G. C. White (Editors) (2015). Program MARK: A Gentle Introduction, fourteenth edition. http://www.phidot.org/software/mark/docs/book/

Cox, W. A., F. R. Thompson, III, A. S. Cox, and J. Faaborg (2014). Post-fledging survival in passerine birds and the value of post-fledging studies to conservation. The Journal of Wildlife Management 78:183–193.

Delany, M. F., B. Pranty, and R. A. Kiltie (2013). Painted Bunting abundance and habitat use in Florida. Southeastern Naturalist 12:61–72.

DeSante, D. F., D. R. Kaschube, and J. F. Saracco (2015). Vital Rates of North American Landbirds. The Institute for Bird Populations, Point Reyes Station, California, USA. www.vitalratesofnorthamericanlandbirds.org

Dickerson, T. J. (1978). Floristic survey and plant community descriptions of Bear Island (Hammocks Beach State Park), Onslow County, North Carolina. M.S. thesis, North Carolina State University, Raleigh, NC, USA.

Donovan, T. M., F. R. Thompson, III, J. Faaborg, and J. R. Probst (1995). Reproductive success of migratory birds in habitat sources and sinks. Conservation Biology 9:1380–1395.

Faaborg, J., R. T. Holmes, A. D. Anders, K. L. Bildstein, K. M. Dugger, S. A. Gauthreaux, Jr., P. Heglund, K. A. Hobson, A. E. Jahn, D. H. Johnson, S. C. Latta, et al. (2010). Recent advances in understanding migration systems of New World land birds. Ecological Monographs 80:3–48.

Farnsworth, G. L., and T. R. Simons (2001). How many baskets? Clutch sizes that maximize annual fecundity of multiple-brooded birds. The Auk 118:973–982.

Froehlich, D. (2003). Ageing North American Landbirds by Molt Limits and Plumage Criteria: A Photographic Companion to the Identification Guide to North American Birds, Part I. Slate Creek Press, Bolinas, CA, USA.

Gardali, T., D. C. Barton, J. D. White, and G. R. Geupel (2003). Juvenile and adult survival of Swainson's Thrush (*Catharus ustulatus*) in Coastal Californinia: Annual estimates using capture–recapture analyses. The Auk 120:1188–1194.

Gilroy, J. J., T. Virzi, R. L. Boulton, and J. L. Lockwood (2012). A new approach to the "apparent survival" problem: Estimating true survival rates from mark–recapture studies. Ecology 93: 1509–1516.

Hamel, P. B. (1992). The Land Manager's Guide to the Birds of the South. The Nature Conservancy, Chapel Hill, NC, USA, and U.S. Forest Service, Southern Region, Atlanta, GA, USA.

Hamel, P. B., H. E. LeGrand, Jr., M. R. Lennartz, and S.A. Gauthreaux, Jr. (1982). Bird habitat relationships on southeastern forest lands. USDA Forest Service General Technical Report SE-22.

Herr, C. A., P. W. Sykes, Jr., and J. Klicka (2011). Phylogeography of a vanishing North American songbird: The Painted Bunting (*Passerina ciris*). Conservation Genetics 12:1395–1410.

Hines, J. E. (1994). LOLASURVIV (ver 1.0) User's Manual. National Biological Service, Patuxent Wildlife Research Center, Laurel, MD, USA.

Hobbs, M., and J. M. Meyers (1999). A bird without equal—Will it survive? Yes! We can make a difference. U.S. Fish and Wildlife Service, Brunswick, GA, USA. www.fws.gov/athens/pdf/painted_bunting_brochure_for_public.pdf

Huhta, E., S. Rytkönen, and T. Solonen (2003). Plumage brightness of prey increases predation risk: An among-species comparison. Ecology 84:1793–1799.

Johnson, F. A., M. A. H. Walters, and G. S. Boomer (2012). Allowable levels of take for the trade in Nearctic songbirds. Ecological Applications 22:1114–1130.

Jones, G., A. Snider, and S. Luo (2013). Changes in the extent of North Carolina barrier island maritime forests 1988–2011: An

assessment of past efforts at protection. Journal of Forestry 111:186–193.
Kendall, W. L., J. D. Nichols, and J. E. Hines (1997). Estimating temporary emigration using capture–recapture data with Pollock's robust design. Ecology 78:563–578.
Kendall, W. L., K. H. Pollock, and C. Brownie (1995). A likelihood-based approach to capture–recapture estimation of demographic parameters under the robust design. Biometrics 51: 293–308.
Klaassen, R. H. G., M. Hake, R. Strandberg, B. J. Koks, C. Trierweiler, K.-M. Exo, F. Bairlein, and T. Alerstam (2014). When and where does mortality occur in migratory birds? Direct evidence from long-term satellite tracking of raptors. Journal of Animal Ecology 83:176–184.
Liker, A., and T. Székely (2005). Mortality costs of sexual selection and parental care in natural populations of birds. Evolution 59:890–897.
Lopazanski, M. J., J. P. Evans, and R. E. Shaw (1988). An Assessment of Maritime Forest Resources on the North Carolina Coast. Final report submitted to the North Carolina Department of Natural Resources and Community Development, Division of Coastal Management, Raleigh, NC, USA. irmafiles.nps.gov/reference/holding/463405?accessType=DOWNLOAD
Lowther, P. E., S. M. Lanyon, and C. W. Thompson (2015). Painted Bunting (*Passerina ciris*), version 2.0. In The Birds of North America (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bna.398
Maness, T. J., and D. J. Anderson (2013). Predictors of juvenile survival in birds. Ornithological Monographs, No. 78.
Martin, T. E. (1992). Breeding productivity considerations: What are the appropriate habitat features for management? In Ecology and Conservation of Neotropical Migrant Landbirds (J. M. Hagan, III, and D. W. Johnston, Editors). Smithsonian Institution Press, Washington, DC, USA. pp. 455–473.
McKim-Louder, M. I., J. P. Hoover, T. J. Benson, and W. M. Schelsky (2013). Juvenile survival in a Neotropical migratory songbird is lower than expected. PLOS One 8:e56059.
Meyers, J. M. (2011). Population densities of Painted Buntings in the southeastern United States. Southeastern Naturalist 10: 345–356.
Nichols, J. D., and K. H. Pollock (1990). Estimation of recruitment from immigration versus in situ reproduction using Pollock's robust design. Ecology 71:21–26.
Nichols, J. D., J. E. Hines, and K. H. Pollock (1984). Effects of permanent trap response in capture probability on Jolly-Seber capture–recapture model estimates. The Journal of Wildlife Management 48:289–294.
Nichols, J. D., W. L. Kendall, J. E. Hines, and J. A. Spendelow (2004). Estimation of sex-specific survival from capture–recapture data when sex is not always known. Ecology 85: 3192–3201.
Noon, B. R., and J. R. Sauer (1992). Population models for passerine birds: Structure, parameterization, and analysis. In Wildlife 2001: Populations (D. R. McCullough and R. H. Barrett, Editors). Elsevier Applied Science, London, UK, and New York, NY, USA. pp. 441–464.
Norris, D. R., and P. P. Marra (2007). Seasonal interactions, habitat quality, and population dynamics in migratory birds. The Condor 109:535–547.
Oosting, H. J. (1954). Ecological processes and vegetation of the maritime strand in the southeastern United States. The Botanical Review 20:226–262.
Podolsky, A. L., T. R. Simons, and J. A. Collazo (2007). Modeling population growth of the Ovenbird (*Seiurus aurocapilla*) in the southern Appalachians. The Auk 124:1359–1372.
Pollock, K. H. (1982). A capture–recapture design robust to unequal probability of capture. The Journal of Wildlife Management 46:752–757.
Promislow, D. E. L., R. Montgomerie, and T. E. Martin (1992). Mortality costs of sexual dimorphism in birds. Proceedings of the Royal Society of London, Series B 250:143–150.
Pyle, P. (1997). Identification Guide to North American Birds, Part I: Columbidae to Ploceidae. Slate Creek Press, Bolinas, CA, USA.
Ricklefs, R. E. (1973). Fecundity, mortality, and avian demography. In Breeding Biology of Birds (D. S. Farner, Editor). National Academy of Sciences, Washington, DC, USA. pp. 366–435.
Sauer, J. R., D. K. Niven, J. E. Hines, D. J. Ziolkowski, Jr., K. L. Pardieck, J. E. Fallon, and W. A. Link (2017). The North American Breeding Bird Survey, Results and Analysis 1966–2015. Version 2.07.2017. USGS Patuxent Wildlife Research Center, Laurel, MD, USA.
Schaub, M., and J. A. Royle (2014). Estimating true instead of apparent survival using spatial Cormack-Jolly-Seber models. Methods in Ecology and Evolution 5:1316–1326.
Schulenberg, T. S. (2009). Painted Bunting (*Passerina ciris*), version 1.0. In Neotropical Birds Online (T. S. Schulenberg, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/nb.paibun.01
Shipley, J. R., A. Contina, N. Batbayar, E. S. Bridge, A. T. Peterson, and J. F. Kelly (2013). Niche conservatism and disjunct populations: A case study with Painted Buntings (*Passerina ciris*). The Auk 130:476–486.
Sillett, T. S., and R. T. Holmes (2002). Variation in survivorship of a migratory songbird throughout its annual cycle. Journal of Animal Ecology 71:296–308.
Springborn, E. G., and J. M. Meyers (2005). Home range and survival of breeding Painted Buntings on Sapelo Island, Georgia. Wildlife Society Bulletin 33:1432–1439.
Sykes, P. W., Jr. (2006). An efficient method of capturing Painted Buntings and other small granivorous passerines. North American Bird Bander 31:110–114.
Sykes, P. W., Jr., and S. Holzman (2005). Current range of the eastern population of Painted Bunting (*Passerina ciris*). Part 1: Breeding. North American Birds 59:4–17.
Sykes, P. W., Jr., S. Holzman, and E. E. Iñigo-Elias (2007). Current range of the eastern population of Painted Bunting (*Passerina ciris*)—Part II: Winter range. North American Birds 61:378–406.
Thompson, C. W. (1991a). Is the Painted Bunting actually two species? Problems determining species limits between allopatric populations. The Condor 93:987–1000.
Thompson, C. W. (1991b). The sequence of molts and plumages in Painted Buntings and implications for theories of delayed plumage maturation. The Condor 93:209–235.
White, G. C., and K. P. Burnham (1999). Program MARK: Survival estimation from populations of marked animals. Bird Study 46 (Supplement):S120–S139.
Yirka, L. M. (2016). Demographic rates and prioritization of habitat for conservation for Painted Buntings in North Carolina. M.S. thesis, North Carolina State University, Raleigh, NC, USA.