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Annual survival, site fidelity, and longevity in the eastern coastal population of the Painted Bunting (*Passerina ciris*)

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ABSTRACT—A long-term study of annual survival, longevity, and site fidelity in the eastern coastal population of the Painted Bunting (*Passerina ciris*) during the breeding season was conducted from 1999 through 2018 in the outer coastal plain of the Atlantic coast of the United States. Painted Buntings were uniquely color-banded from 1999 through 2003 at 40 study sites paired at 20 locations from southeastern NC south to northeastern FL. Survival analysis used capture histories through 2005 for 994 birds banded as hatch-year and 2,420 birds banded as post-hatch-year (adults). Annual estimates of apparent survival (1999–2004) averaged 0.71 and 0.66 for adult males and females, respectively, and 0.33 for hatch-year birds. We did not find evidence that survival differed in relation to latitude or extent of human development near study sites, although estimates for adult females were higher for birds banded on sheltered islands compared to the mainland. Expected time in the population, based on estimated survival, was 3.9 and 3.4 years for adult males and females, respectively. The oldest observed birds were a 14-year-old male observed in June 2016 at Harris Neck National Wildlife Refuge, GA, the site at which he had been banded in July 2003 as a second-year bird, and a 13-year-old male seen at Ft. George Island, FL, in June 2016, 2 km across a tidal estuary from the site where the bird was banded in August 2003 as hatch-year. The males were sighted at these 2 sites in 9 and 11 different years, respectively. Overall, 78% (males) and 81% (females) of resightings and recaptures of birds banded as adults occurred at the same study site where individuals were banded, compared to 59% (males) and 60% (females) of birds banded as hatch-year. Known mortalities of banded buntings included 9 birds trapped for the caged-bird trade. This study shows the potential for high survival and longevity in the eastern coastal population of the Painted Bunting, and given evidence of high site fidelity in the breeding range, the vulnerability of the population to human development along the southeastern US coast as well as to illegal trapping. *Received 29 December 2017. Accepted 6 October 2018.*

Key words: annual survival, longevity, mark/recapture, Painted Bunting, *Passerina ciris*, site fidelity.

Sobrevivencia annual, fidelidad a sitio y longevidad en la población costera del este del azulejo *Passerina ciris*

RESUMEN (Spanish)—Un estudio de largo plazo sobre la sobrevivencia anual, longevidad y fidelidad a sitio de la población costera del este del azulejo *Passerina ciris* durante la temporada reproductiva tuvo lugar de 1999 hasta 2018 en la planicie costera exterior del Atlántico en los Estados Unidos. Los azulejos fueron anillados con combinaciones únicas de colores de 1999 hasta 2003 en 40 sitios de estudio pareados en 20 localidades desde el sureste de North Carolina hacia el sur hasta el noreste de Florida. El análisis de sobrevivencia utilizó el historial de capturas hasta 2005 de 994 pájaros anillados como del año-de-eclosión y 2,420 pájaros anillados como pos-año-de-eclosión (adultos). Las estimaciones anuales de sobrevivencia aparente (1999–2004) promedian 0.71 y 0.66 para machos y hembras adultos, respectivamente, y 0.33 para pájaros del año-de-eclosión. No encontramos evidencia de que la sobrevivencia difiera en relación a la latitud o a la extensión de la ocupación humana cerca de los sitios de estudio, aunque las estimaciones para hembras adultas fueron más altas para los pájaros anillados en islas protegidas comparadas con aquellas de tierra firme. El tiempo esperado en la población, basado en sobrevivencia estimada, fue 3.9 y 3.4 años para machos y hembras adultos, respectivamente. Los pájaros más viejos observados fueron un macho de 14 años observado en junio de 2016 en el Harris Neck National Wildlife Refuge, Georgia, el mismo sitio en el cual había sido anillado en julio de 2003 como pájaro del segundo-año, y un macho de 13 años visto en Ft. George Island, Florida, en junio de 2016, 2 km frente al estuario intermareas en el que fue anillado en agosto de 2003 como pájaro del año-de-eclosión. Los machos fueron observados en estos dos sitios en 9 y 11 años diferentes, respectivamente. De todos ellos, las reobservaciones y recapturas de 78% (machos) y 81% (hembras) anillados como adultos fueron encontrados en el mismo sitio de estudio donde fueron anillados originalmente, comparado con el 59% (machos) y 60% (hembras) de los pájaros anillados en su año-de-eclosión. La mortandad conocida de azulejos anillados incluye nueve pájaros capturados para el comercio de pájaros de jaula. Este estudio muestra el potencial de alta sobrevivencia y longevidad en la población costera del este para *Passerina ciris* dada la evidencia de una alta fidelidad a sitio en su rango reproductivo, así como la vulnerabilidad de esta población a su captura ilegal y al desarrollo de actividades humanas a lo largo de la costa de sureste de los Estados Unidos. Recibido 29 diciembre 2017. Aceptado 6 octubre 2018.

Palabras clave: Azulejo, captura-recaptura, fidelidad a sitio, longevidad, *Passerina ciris* sobrevivencia anual.

The Painted Bunting (*Passerina ciris ciris*) is highly ranked as a species in need of management attention in a physiographic area of importance in the southeastern United States (Hunter et al. 1993, USFWS 2008). The Painted Bunting has eastern and western allopatric breeding populations whose ranges are separated by ~500 km (Thompson

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1991, Lowther et al. 1999, Herr et al. 2011). Although a few buntings occur within the gap, the status of these birds is uncertain and the population to which they belong is unresolved (Haggerty 2009). Unlike declining forest interior Neotropical migratory birds, the eastern population of the Painted Bunting depends on early successional habitat and is found breeding primarily in upland maritime shrub-scrub, natural openings of old-growth maritime forests, and other habitats with a shrub-scrub component of the South Atlantic Coastal Plain from southeastern NC to northeastern FL (Lowther et al. 1999, Sykes and Holzman 2005, Meyers 2011). Upland coastal habitat on barrier islands and the nearshore mainland is highly vulnerable to loss from development (Hunter et al. 1993). Habitat loss, however, may not be the aggregate cause of an annual population decline of ~1.1% since 1966 for the bunting (Sauer et al. 2017). Causes for decline are not fully known, but may include a combination of degradation or loss of breeding habitat, nest parasitism by the Brown-headed Cowbird (*Molothrus ater*), increased predation in the declining breeding habitat, trapping for the caged-bird trade, or mortality on the wintering grounds, in migration, or at stopover sites. The breeding range of the eastern population of the Painted Bunting is 4.0% of that of the western population (Sykes and Holzman 2005). The eastern birds are thus at higher risk of habitat loss and modification, and other anthropogenic impacts (i.e., trapping of buntings for the caged-bird trade) than that of the much larger western population.

Management and conservation of the eastern population of the Painted Bunting could benefit substantially from a better understanding of factors limiting population growth. Previous survival estimates for the eastern population of Painted Buntings are limited to 63 individuals tracked on 1 island during 2 breeding seasons (Springborn and Meyers 2005), and to 89 individuals banded at a single Monitoring Avian Productivity and Survivorship (MAPS) station (DeSante et al. 2015). A 2-year study (Lanyon and Thompson 1986) also provides evidence for high fidelity of Painted Bunting males to nesting territories on a coastal barrier island. Breeding Bird Survey (BBS) count data for eastern Painted Buntings are based on inland routes and may not reflect trends in coastal populations, where the greatest number of buntings occur (Lowther et al. 1999, Sykes and Holzman 2005), because coastal routes are limited by lack of roads of sufficient length. This limitation notwithstanding, analyses of BBS data provide evidence of a latitudinal gradient in population trends in the eastern Painted Bunting population, with long-term population decline in FL contrasting with population increase in NC (Sauer et al. 2017). Because managers need information that accounts for spatial as well as temporal variation in population dynamics, we have conducted this research to estimate annual survival, longevity, and an index of site fidelity, by age and sex, of Painted Buntings along the south Atlantic coast, where breeding birds occur in highest densities (PWS, pers. obs.).

Our objectives are to estimate annual apparent survival of adult and hatch-year Painted Buntings banded across the coastal breeding range of the eastern population. Our study sites span a latitudinal gradient, as well as variation in habitat corresponding to locations on the coastal mainland and islands. We thus evaluate evidence that survival varies in relation to latitude or landform, or with extent of nearby human land development. We also compare estimated expected time in the population of adult and hatch-year birds, based on survival estimates, to median and maximum observed longevity based on 18 years of observations of banded birds. Finally, we estimate an index of site fidelity during the breeding season by buntings to locations where individuals were initially banded, and report observed anthropogenic causes of mortality, including illegal capture for the caged-bird trade.

Methods

Study areas

The range of the eastern population of the Painted Bunting on the southeastern Atlantic coast extends from the vicinity of Cape Lookout and Morehead City, Carteret County, NC, southward on the immediate coast to Cape Canaveral, Brevard County, FL, and inland to Columbia, SC, and Augusta and Macon, GA (Lowther et al. 1999, Sykes and Holzman 2005). Our study areas are located in a narrow corridor, within 8 km of the Atlantic Ocean, along the coast from southeastern NC south to northeastern FL. This corridor includes barrier islands, sheltered islands (those islands in the estuarine systems between the mainland and the barrier islands), and the immediate upland communities on the mainland (Fig. 1, Appendix Table A1). Away from the coast, the distribution of Painted Buntings is patchy and density is reduced based upon BBS results and other sources (Post and Gauthreaux 1989, Robertson and Woolfenden 1992, Peterjohn et al. 1995, Beaton et al. 2003, Springborn and Meyers 2005, Meyers 2011, Sauer et al. 2017). The species occupies a range of upland habitats that typically contain a shrub-scrub component (Lowther et al. 1999, Springborn and Meyers 2005, Meyers 2011). Most (70%) of our study sites have adjacent tidal salt marsh, along with maritime shrub-scrub habitat (28% of sites). Study sites are located on private, state, and federal lands (Appendix Table A1).

We scouted for potential study areas in NC, SC, GA, and FL during the Painted Bunting breeding season (mid-Apr to mid-Sep) in 1998. Forty sites (10 per state) were selected that met the following criteria: (1) a high density of buntings, to maximize potential sample size; (2) good feasibility of capturing buntings (e.g., readily accessible, flat terrain); (3) a secure locality (away from vehicle traffic and not in localities used by the public, to avoid harm to the birds, vandalism, or theft of the feeders); (4) site availability for 6 or more years; and (5) local cooperator(s) (all volunteers) willing to tend the feeder (check once or twice per week, keep feeder filled with bird seed, and keep the feeder clean) for 3–6 months for the field season each year (Sykes 2006).

Field methods

Permanent study sites were systematically numbered and sampled each year during the breeding season in 1 of 2 periods, May–June or July–August. Odd-numbered sites were worked south to north, FL to NC, the first period, and even-numbered sites south to north during the second period. Starts with even- and odd-numbered sites were alternated from year to year, for a 7 year period (1999–2005), but always starting south and proceeding north.

We employed a technique developed to capture a large number of Painted Buntings for color marking with leg-bands (Sykes 2006). The birds were attracted to a focal point using bird feeders provisioned with untreated (no pesticides or herbicides) white-proso millet (*Panicum vergi*). With birds on the feeder, one person rushed the feeder clapping their hands to scare the birds into mist nets. Birds were immediately removed and banded. We generated unique 4-band combinations consisting of 3 color-bands (cellulite, size XF = 2.3 mm inside diameter, made by A. C. Hughes, Hampton Hill, Middlesex, England) and one US Geological Survey (USGS) numbered metal butt-end band (size 1C), and placed 2 bands on each leg (Supplemental Figs. S1 and S2).

We stopped deploying new bands after 2003, but we did re-trap and replace bands on buntings with missing or badly faded color bands (but retaining the USGS band). After 2000, we initiated a separate 5 h observation session starting at first good light in the morning. Thus, for 2001 through 2003 we had 2 sessions at the sites, with the observation session preceding the banding session on a different day. After 2003 and through 2018, we conducted observation sessions only. Field crews observed banded birds using 20–60× zoom spotting scopes at a distance of ~10 m from the feeders. The feeder was arranged so that 5 of the 6 feeding ports could be observed, with the sixth port out of view plugged. During the observation periods (2001 through 2018), crews double-, triple-, and quadruple-checked, when possible, each banded bunting to prevent errors in recording band combinations (Milligan et al. 2003).

At time of capture, we aged and sexed each bird using the protocol developed by Clapp et al. (1982, 1983) and adapted by the Bird Banding Lab, USGS Patuxent Wildlife Research Center, Laurel, MD. We used 4 age classes: HY (hatch year), SY (second year), AHY (after hatch year), and ASY (after second year) (Klimkiewicz and Futcher 1987, 1989; Lutmerding and Love 2014). Hatch-year birds were sexed by length of the wing chord (unflattened); less than 61 mm were female and 70 mm or greater were male (PWS, 1999–2003, unpubl. data). For the HY birds with wing chords between 61 and 69 mm in length, we sent a whole-blood sample from the brachial vein on the underside of a wing to Zoogen, Davis, CA, for gender determination using nuclear DNA analysis. We included blood samples for known-sex birds to determine the reliability of the DNA gender analysis. The blood samples were archived at the Georgia Museum of Natural History, University of Georgia, Athens.

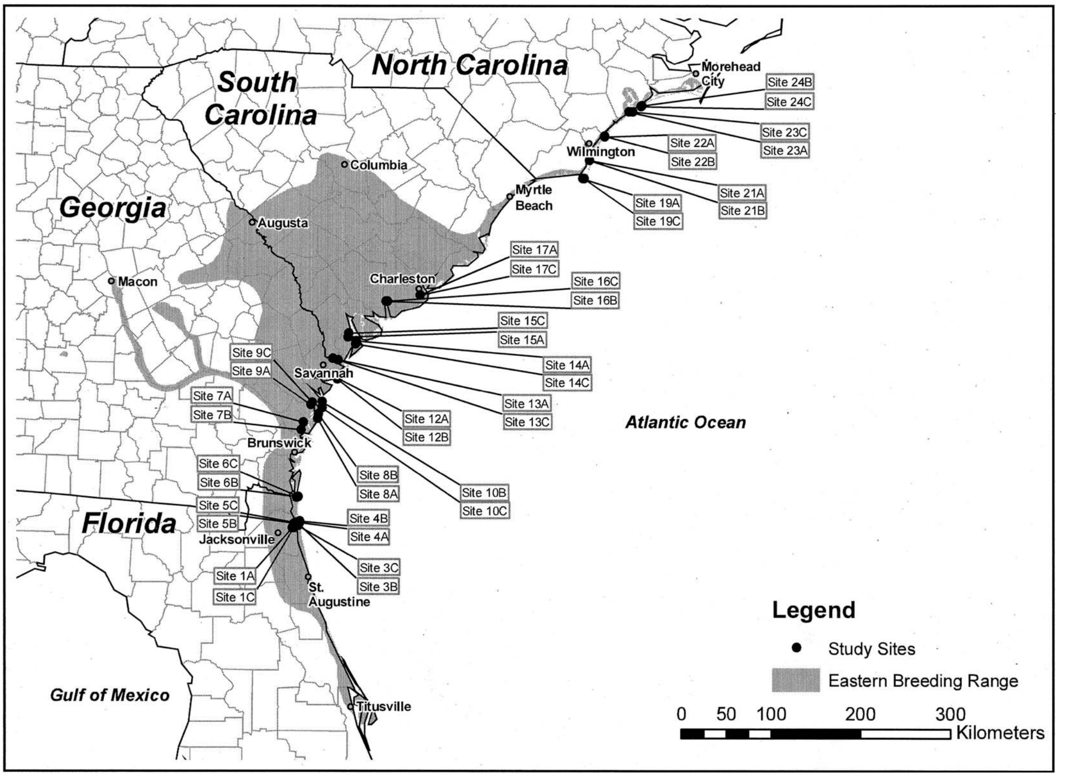

Figure 1. Distribution of the 40 study sites within the range of the eastern population of the Painted Bunting (*Passerina ciris*) in the southeastern United States (Thompson 1991, Sykes and Holzman 2005). Details for each study site are presented in the Appendix. After pilot year 1999, study areas 2, 11, 18, and 20 and one study site in each of the remaining study areas were eliminated. Thus, there are gaps in the alphanumeric system for the study sites. Map prepared by Steve Holzman, US Fish and Wildlife Service.

After 2004, the number of study sites was reduced to 10 (25% of the original) because of time, costs, and difficulty of accessing barrier islands. Sites that were retained were 3B and 4A in FL; 7B, 9A, 9C, and 10C in GA; 14A and 15C in SC; and 19C and 24B in NC. After 2005, site 7B was dropped when the house was sold. In 2011, sites 8A and 12A were reactivated as they were among the most productive sites originally, but difficult to reach as they were on barrier islands. The protocol for otherwise dropping a study site from the project was 2 consecutive years in which no marked Painted Buntings were observed at the given site.

Data analyses

We estimated annual apparent survival using encounter histories for 3,414 individuals banded at the 40 monitored feeders. Our survival analysis used recaptures and sightings of live banded buntings from 2000 through 2005 (the first year in which 10 or fewer of the feeders were monitored, explained above). Resightings were too sparse in subsequent years to extend survival estimation. We did not include encounter histories for 16 birds that were recovered dead or that were reported captured and caged in Cuba prior to 2005 because our survival model was based on live encounter data. We also excluded 25 sightings involving 21 banded individuals at locations other than one of the monitored feeders. Twelve of these birds were also recorded at a feeder in the same year when sighted away from feeders and thus excluding the latter sightings did not alter annual encounter histories for these birds. Survival and detection could not be separately estimated during the last year in the analysis (i.e., 2005; Williams et al. 2002), resulting in survival estimates for 5 annual periods (1999–2000, 2000–2001, 2001–2002, 2002–2003, and 2003–2004).

Our objectives were to estimate annual survival for males and females, and for hatch year (HY) and post-hatch year (comprising SY, AHY, ASY) birds, and to test for variation in survival related to feeder latitude, feeder location (coastal mainland, barrier island, or sheltered island), or proportion of land surrounding the feeder that was classified as developed. We anticipated that survival would be highest on barrier islands (which generally are larger than sheltered islands), higher at higher latitude (based on estimated long-term population increase in NC and decrease in FL based on counts for the entire eastern population; Sauer et al. 2017), and would decline in relation to human development near the feeder. To estimate human development, we summed the area classified as low, medium, or high intensity development in the National Land Cover Database for 2001 (Homer et al. 2007) and expressed this sum as a proportion of the land (i.e., excluding open water) around each feeder within a radius of 700 m (an upper range of measured foraging distance from the nest by Painted Buntings; Springborn and Meyers 2005) and 3,000 m (approximate distance we suspected Painted Buntings may travel, e.g., from the mainland to barrier island sites).

We applied a state-space formulation of the Cormack–Jolly–Seber (CJS) model to the encounter histories to jointly estimate probabilities of annual apparent survival and detection (Williams et al. 2002, Gimenez et al. 2007, Kéry and Schaub 2012). The state-space formulation of the CJS model provided flexibility for additionally accounting for unexplained heterogeneity in survival among birds banded at different feeders and among individuals in probability of detection. We expected a priori that survival differed between males and females, and would be lower for HY compared to post-HY birds, and that survival would vary among years. We thus allowed for time-varying survival in all models, and applied an age-specific extension of the CJS model in which birds banded as HY transitioned to post-HY the next year (Pollock 1981, Williams et al. 2002). We initially tested our a priori expectation of survival differences between males and females, and of lower survival in HY birds, by fitting a model with fixed, additive effects of sex and age on survival. We subsequently fit a less-constrained model that allowed survival to vary independently among years for adult (post-HY) males, adult females, and HY birds in a model without covariates, and in 3 additional models that tested for effects on survival of (1) latitude and landform (feeder location on a sheltered or a barrier island as opposed to on the mainland), (2) latitude and proportion of land developed within 700 m of the feeder, and (3) latitude and proportion of land developed within 3,000 m of the feeder. We did not test other variable combinations because of relatively strong correlation between land developed at the 2 distances ($r = 0.52$), and markedly lower development on sheltered islands (mean proportion developed at 700 m = 0.0007, compared to >0.03 on barrier islands and the mainland). Feeder latitude and developed land use values were scaled and centered for analyses.

In all models, we included a random effect for the feeder where an individual was banded to account for otherwise unmodeled spatial variation in survival. To estimate detection, we included 3 binary covariates that accounted for differences in lengths of observation periods among years and feeders. These covariates designated whether efforts comprised (1) only banding (all feeders in 2000 and one feeder in 2001), (2) 15 h of observation (4 feeders, 2002–2004) rather than the nominal 5 h, or (3) that a feeder was not monitored (30 feeders in 2005). Finally, we also included a random effect of individual on detection to account for expected heterogeneity among individuals in the time spent at feeders (including the potential effect of transient individuals in the banded population; Abadi et al. 2013).

We fitted CJS models to the encounter histories using a Bayesian analysis implemented with the Markov chain Monte Carlo (MCMC) software JAGS (Plummer 2003) through the R package rjags (Plummer 2014, R Core Team 2014). We used vague priors for parameter coefficients; for covariates estimated on a logit scale, we refit models using 3 levels of variance (2.7, 2.0, 1.3) in normally distributed priors as suggested by Northrup and Gerber (2018) in order to evaluate sensitivity of parameter estimates to choice of priors. Posteriors were derived from 3 chains run for 20,000–50,000 iterations and thinned by 3, with a burn-in of 5,000. Convergence was assessed using the Brooks–Gelman–Rubin statistic (R-hat; Brooks and Gelman 1998). To assess model fit, we computed a Bayesian p value based on the discrepancy (Freeman–Tukey statistic) between the observed and (model-based) expected number of annual detections for each banded individual, summed over all individuals, and the same statistic calculated for a replicate data set simulated using survival and detection estimates at each MCMC iteration (Kéry and Schaub 2012). The Bayesian p value was the proportion of summed discrepancy values for the simulated data that exceeded the same for the observed data, with an expected value of approximately 0.5 for models that adequately fit the data (Kéry and Schaub 2012). Model code is provided (Supplemental Appendix A).

We used survival estimates for birds banded as HY and adults to estimate longevity as the mean expected time that a bird remained in the study population. Specifically, we estimated mean expected time in the population for a bird entering the adult population as $1/–\log(\phi_{AD})$ (Cormack 1964), where ϕ_{AD} was the average of the 5 annual survival estimates for post-HY males or females. Mean expected lifespan of a SY bird would thus be $(1/–\log(\phi_{AD})) + 1$. This approach assumed continuous, exponential mortality (or emigration) from the study population at a rate equal to $–\log(\phi_{AD})$, and that our averaged survival estimate for post-HY birds was applicable to SY and all subsequent ages. To estimate the expected time in the population for HY birds, we equivalently estimated probability of surviving the first year using the averaged HY survival (ϕ_{HY}), and then for subsequent years using the averaged adult survival (ϕ_{AD}, separately for males and females), at a time-step of 0.0001 year (to approximate exponential mortality). Thus, we calculated the mean number of years an individual banded as HY was expected to remain in the population as:

$$\Sigma\Big(\Pr(HY\_loss\_at\_age\_i{*}i)) + \Sigma(\Pr\Big(AD\_loss\_at\_age\_j{*}(j+1)\Big),$$

Where $i = 0.0001$ to 1, by 0.0001,

$j = 0.0001$ to 30, by 0.0001,

$$\Pr(HY\_loss\_at\_age\_i) = ((\phi_{HY}\hat{\ }i) * (1 - \phi_{HY}\hat{\ }0.0001)),\ \text{and}$$

$$\Pr(HY\_loss\_at\_age\_i) = ((1 - \Sigma(\Pr(HY\_loss\_at\_age\_i))) * ((\phi_{AD}\hat{\ }j) * (1 - \phi_{AD}\hat{\ }0.0001)).$$

We obtained posterior distributions of estimated mean times in the population by including these calculations in the MCMC models for survival. For comparison to observed data, we also calculated the age or minimum age at last encounter based on encounter histories for 1,472 individuals that were sighted (or recaptured) at least once after banding, or that were recovered dead on a known date, using records through 2016. For each individual, we calculated the number of months between June in the year the individual was banded and the month and year for the last time the individual was sighted ("elapsed months"), including sightings and recoveries of dead birds away from study-site feeders. For individuals captured and caged in Cuba, we used the date reported caged to calculate age or minimum age. For birds banded as HY, elapsed months equaled age. We estimated ages for birds banded as SY by adding 12 to the elapsed months. We added 12 and 24 months, respectively, to the calculated elapsed months to estimate minimum ages for birds banded as AHY and ASY.

For this study, we defined an index of site fidelity as the probability a bird was only resighted at the feeder where it was initially captured and banded. We used logistic regression conditioned on all birds ever resighted (or recaptured) at one or more of the study feeders after banding, to estimate sex- and age- (banded as HY vs. post-HY) specific probabilities of being sighted only at the feeder where banded. We estimated 95% confidence intervals as the mean probabilities ± 2 SE (estimated using glm in R; R Core Team 2014).

Results

Captures

We banded 3,430 Painted Buntings at the 40 study sites from 1999 through 2003, with 4,174 total catches (including recaptures) in a total effort comprising 3,393 net hours. We used nuclear DNA analysis to determine sex for 487 HY and SY birds (375 males and 112 females) captured from 2000 through 2003 and having wing chords between 61 and 69 mm in length. A blind test of 21 whole-blood samples of known-sex birds (18 males and 3 females) submitted on 2 occasions (5 in 2001 and 16 in 2003) was returned with 100% correct identifications. Thus, we were satisfied the lab accurately sexed the birds.

Capture rates varied between sites and among years, but were generally highest at feeder locations on barrier islands and at sites in GA. The Blackbeard National Wildlife Refuge (NWR), GA, (8A) location had the highest capture numbers in a single day with 72 in 2000, 75 in 2001, and 80 in 2003. Daily captures also exceeded 50 individuals at feeders on St. Catherines Island, GA (10C; 2002 and 2003), and Wassaw Island, GA (12A; all years). Total number of captures decreased in relation to proportion of land classified as "developed" within a 3,000 m radius around the feeder location ($r = -0.43$, $P < 0.005$; Fig. 2); this relation was not as strong for developed land within a 700 m radius of the feeder ($r = -0.18$, $P > 0.05$). Across all feeders, developed land ranged from 0 to 17.5% and 0 to 36.2% within 700 and 3,000 m (Appendix Table A1), respectively, and was nearly uncorrelated with latitude ($r = 0.12$ and 0.06, respectively).

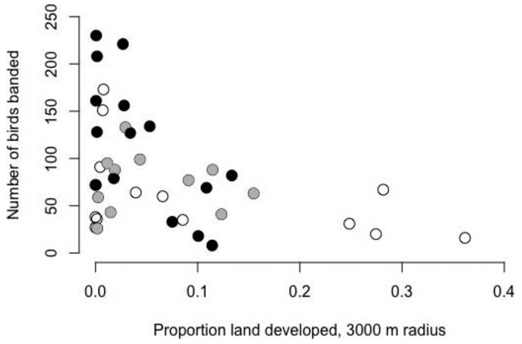

Figure 2. Total number of Painted Buntings banded, 1999–2003, at 40 coastal study sites located on the mainland (open circles), sheltered islands (gray circles), and barrier islands (black circles) plotted in relation to the proportion of land classified as "developed" (2001 National Land Cover Data, Homer et al. 2007) within 3,000 m of the feeder.

Annual apparent survival

The 3,414 birds used in the survival analysis comprised 994 individuals banded as HY (439 males, 520 females, and 35 birds with sex recorded as unknown that were treated as females) and 2,420 individuals banded as adults (SY and AHY; 1,216 males, 1,201 females, and 3 birds with sex recorded as unknown that were treated as females). All survival models provided adequate fits to the data (Bayesian p values = 0.49–0.51); posterior medians and credible intervals for parameter estimates were essentially the same across the range of priors we tested. Estimates for detection probability were nearly identical across models, increasing from a mean of 0.37 (0.30–0.45, 95% credible interval) when efforts comprised only banding (2000 and one feeder in 2001), to 0.60 (0.55–0.64) during 2001–2004 when we conducted 5 h observation sessions at a feeder. Increasing observation times to 15 h had no measurable effect on detection (which averaged 0.58, 0.48–0.60). Variance in detection among individuals was substantial (1.6, or SD = 1.26, about 320% greater than logit mean detection).

Results from all models showed higher apparent annual survival of males than females and of adults compared to HY birds. Male survival odds were an estimated 43% (95% credible interval, 26–64%) greater than females, and survival odds for HY birds were 80% (76–84%) lower than for post-HY birds, when sex and age were modeled as additive effects on time-varying survival. Similarly, modeling survival as varying independently across years for adult male, adult female, and HY birds ("interactive model") resulted in estimates for adult male survival exceeding that of females in 3 out of 5 annual estimates, and adult survival exceeding that of HY birds in all years (Fig. 3a). Estimates of annual apparent survival were similar between the 2 models (Fig. 3a, b), averaging 0.72 (0.69–0.75; additive model) or 0.71 (0.67–0.74; interactive model) for adult males, and 0.65 (0.62–0.68; additive model) or 0.66 (0.62–0.69; interactive model) for adult females, for the years 1999–2004. Estimates for HY birds for the same years averaged 0.36 (0.31–0.41) for males and 0.28 (0.24–0.33) for females (additive model), or 0.33 (0.28–0.38) when HY birds were modeled as single category in the interactive model.

Overall, the estimated random effect representing variance in survival among study sites was relatively low (about 0.055, or standard deviation = 0.230, about 35% of logit mean survival of females). Additionally, we found no evidence that survival of males, females, or HY birds varied in relation to latitude or to extent of developed land at either 700 m or 3,000 m from the feeder where a bird was banded (Table 1). However, when landform was included as a covariate, survival of females banded on sheltered islands (0.72, 0.66–0.77) appeared higher than survival of females

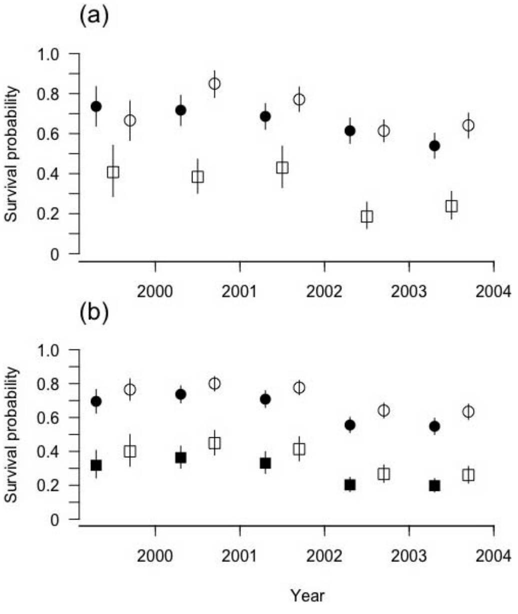

Figure 3. Estimated annual apparent survival of Painted Buntings banded and resighted at 40 study sites along the southeastern Atlantic Coast. Survival was estimated using time-varying, CJS models with (a) independent variation for male, female, and hatch-year birds or (b) with sex and age fit as additive effects on survival. Estimates are posterior means and 95% credible intervals; symbols represent adult males (open circles) and females (closed circles), and hatch-year birds (squares; open and closed for males and females, respectively, in the additive model).

banded at feeders on the mainland (0.63, 0.57–0.69); landform did not appear to influence survival of males or HY birds (Table 1).

We could determine the causes of death for 19 birds in our marked population of Painted Buntings. All causes of death determined in this study were of an anthropogenic nature and thus had a higher probability of detection of the dead birds than in the case of more "natural" deaths. We recognized 5 general categories for mortality: road kill ($n = 2$), free-roaming house cats ($n = 2$), collision with glass windows ($n = 5$), and in Cuba, shot ($n = 1$) and trapped for the caged-bird trade or for personal pets ($n = 9$).

Longevity

Estimated mean expected times in the population for birds that survive the first year of life, based on survival estimates for adults, were 3.9 years (95% credible interval, 3.5–4.3) for males and 3.4 years (3.1–3.7) for females (interactive model without site-specific covariates on survival). Adult females banded on sheltered islands had greater expected longevity, 4.1 years (3.4–4.8) compared to 3.2 years (2.8–3.7) if banded on the mainland. All estimated longevity estimates for adult females exceeded the mean ages at last resighting for birds banded as SY (and thus known-age; Table 2). Estimated and observed mean longevity were similar for known-age adult males (i.e., 3.9 and 3.6 years, Table 2). Hatch-year birds had lower expected times in the population, 1.6 years (1.3–1.8) for males and 1.4 years (1.2–1.6) for females. These values were less than observed mean ages for birds banded as HY (2.3 years for males, 1.8 years for females; Table 2). The oldest observed birds were males (Fig. 4, 5), with over 30% of resighted adult males surviving at least 5 years, compared to about 15% of adult females (Table 2).

On the morning of 9 June 2016, we observed a banded male (color combination BOOS with band no. 2020-67761) at Study Site 9C (Goose Pond, Harris Neck NWR, McIntosh County, GA). It was originally banded as an SY bird at this same site on 17 July 2003. This bird was 14 years old. In late afternoon of 9 June 2016, we saw another banded male (FYIS, band no. 2020-68204) at Study Site 3B (Kingsley Plantation, Ft. George Island, Jacksonville-Duval County, FL). He was originally banded as an HY bird at Study Site 4A (Little Talbot Island St. Pk., Jacksonville-Duval County, FL) on 20 August 2003, making him 13 years old. Both birds were studied through a zoom spotting scope under uniform conditions of light shade at ~10 m while the birds were at feeders and appeared to be in good physical condition.

Site fidelity index

Overall, 76% of 1,463 banded birds resighted (or recaptured) in the study areas were only seen or recaptured at the same study site where initially banded. This index of site fidelity was similar for males and females, but lower for birds banded as HY compared with those banded post-HY. Probabilities that birds banded as SY, ASY, or AHY were only sighted at the feeders where they were banded were similarly high for males (0.78, 95% CI = 0.75–0.81) and females (0.81, 0.77–0.84). In comparison, probabilities were reduced by 25% in

Table 1. Parameter estimates for covariates on survival of Painted Buntings that were banded and resighted at 40 feeder locations on the southeastern US Atlantic coast, 1999–2005. Covariates were included in CJS models that allowed adult male, adult female, and hatch-year survival to vary independently among years and in relation to latitude (included in all models) and one of 3 other covariates: proportion of land classified as developed within (1) 700 m or (2) 3,000 m of the feeder location, and (3) landform for the feeder location (barrier island or sheltered island, with mainstem as the baseline). Latitude and developed land proportions were continuous (centered and scaled) variables; landform was represented by 2 binary variables. Values are posterior means (and 95% credible intervals) on the logit scale. The positive effect of sheltered island-location on female survival is bolded for emphasis. A dash (–) indicates terms not included in a particular model.

	Model		
Covariate	Latitude, developed land within 700 m	Latitude, developed land within 3,000 m	Latitude, landform
Latitude			
Females	–0.02 (–0.16, 0.11)	–0.04 (–0.16, 0.09)	0.00 (–0.13, 0.14)
Males	0.06 (–0.07, 0.19)	0.06 (–0.08, 0.19)	0.05 (–0.08, 0.18)
Hatch-year	0.04 (–0.16, 0.24)	0.05 (–0.16, 0.25)	0.01 (–0.18, 0.22)
Developed land			
Females	–0.09 (–0.22, 0.04)	0.03 (–0.10, 0.15)	–
Males	0.01 (–0.12, 0.15)	–0.01 (–0.14, 0.12)	–
Hatch-year	–0.01 (–0.20, 0.19)	–0.09 (–0.30, 0.13)	–
Barrier Island			
Females	–	–	0.02 (–0.29, 0.34)
Males	–	–	–0.09 (–0.41, 0.24)
Hatch-year	–	–	0.17 (–0.38, 0.70)
Sheltered Island			
Females	–	–	**0.41 (0.05, 0.77)**
Males	–	–	–0.09 (–0.45, 0.27)
Hatch-year	–	–	–0.11 (–0.68, 0.43)

birds banded as HY (males: 0.59, 0.50–0.67; females: 0.60, 0.50–0.69). The oldest recorded Painted Bunting, banded as SY, was sighted in 9 different years and only at the same site (9C, Goose Pond) where it was banded. The second-oldest bird, banded as HY, moved approximately 2 km across a tidal estuary from Site 4A (Little Talbot Island SP) where it was banded to Site 3B (Kingsley Plantation), where it was subsequently sighted in 11 different years.

Discussion

Painted Buntings returning to feeders where they were banded at 40 locations along the Atlantic coast of the southeastern United States exhibited high apparent survival and correspondingly long potential lifespan of individuals that survive to age 1. Apparent annual survival estimates (averaged over 5 years) were higher for males (0.71) than females (0.66), possibly reflecting the greater stress to females of reproductive activities. The female Painted Bunting exclusively

Table 2. Observed age or minimum age at last encounter for Painted Buntings banded and resighted at least once from 1999 through 2016 at 40 feeder locations on the southeastern US Atlantic coast, and the number of individuals known to survive at least 5 years. Mean and maximum ages at last encounter are shown for males and females banded as hatch year (HY) or second year (SY) birds. Values for birds banded after second year (ASY) or after hatch year (AHY) are for the minimum age at last encounter.

	Males				Females			
Banded as:	*n*	# ≥5 years	Mean	Maximum	*n*	# ≥5 years	Mean	Maximum
HY	130	9	2 years, 3 months	13 years, 0 months	110	3	1 year, 10 months	7 years, 11 months
SY	299	48	3 years, 7 months	14 years, 0 months	82	7	2 years, 10 months	10 years, 0 months
ASY	369	116	4 years, 6 months	12 years, 0 months	18	6	4 years, 4 months	6 years, 2 months
AHY	1	–	1 year, 11 months	1 year, 11 months	463	65	3 years, 4 months	9 years, 0 months

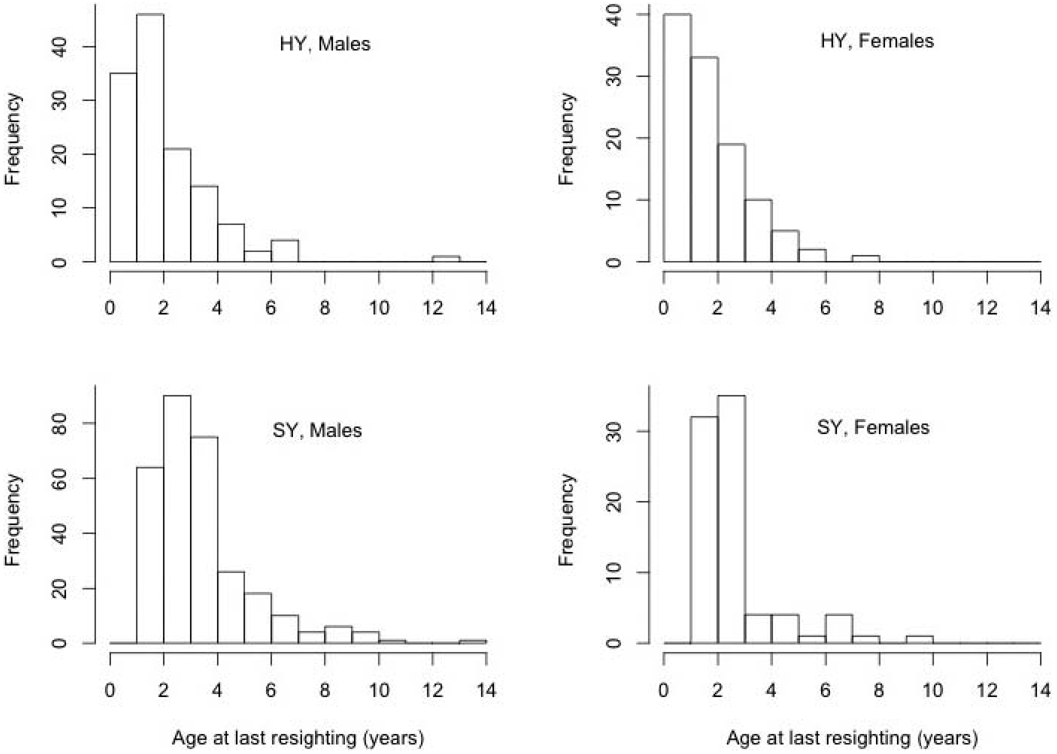

Figure 4. Frequency distributions of age at last resighting for Painted Buntings banded as hatch-year (HY) or second year (SY) birds.

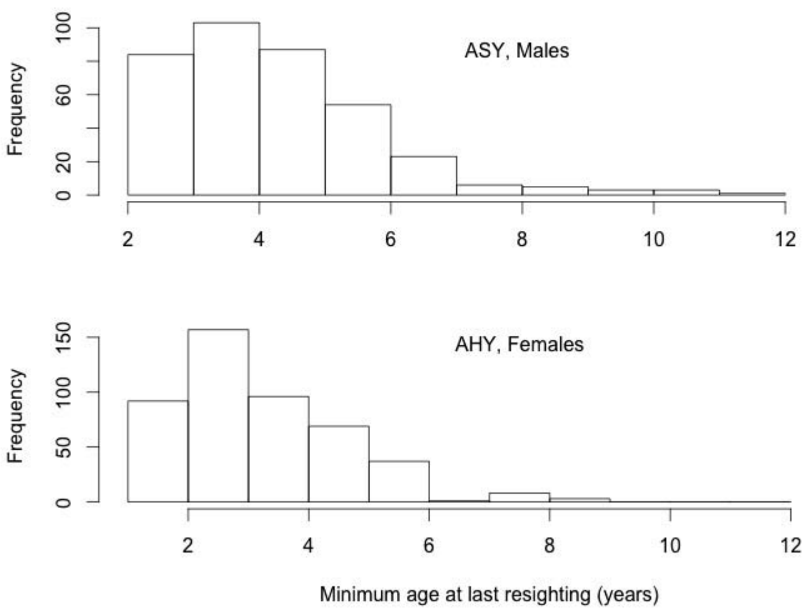

Figure 5. Frequency distributions of minimum age at last resighting for Painted Bunting males banded after their second year (ASY) and females banded after their hatch year (AHY).

incubates the eggs and broods the young (Lowther et al. 1999), and consequently may have greater exposure to predators while at the nest, particularly during darkness. Expected longevities (i.e., time in the sampled population) derived from our survival estimates, 3 and 4 years for females and males, respectively, were generally similar to our observed mean ages at last encounter for known-aged banded birds. However, by monitoring feeders with one or more returning banded birds for 19 years, we documented individuals with known-ages of 13 and 14 years. These observations extended the maximum recorded longevity for the Painted Bunting by 2 years; the oldest reported wild individual prior to this study was for a bird at least 12 years old at Ft. Lauderdale, FL (J. Fleugal in Fisk 1974). Adults also displayed high fidelity to locations where initially banded, although birds banded as hatch-year appeared less likely to return to the feeder where banded.

Survival and longevity of birds may be influenced by evolutionary history together with constraints related to behavior, physiology, and genetics, as well as the environment (Finch 1990, Holmes and Austad 1995, Wasser and Sherman 2010, Rowan et al. 2014). Closely related taxa might be expected to exhibit similar survival and longevity except for effects of extrinsic factors. However, our annual survival estimates for adults of the eastern coastal population of the Painted Bunting are substantially higher than estimates for this and other species of *Passerina* based on analyses of long-term capture-mark-recapture data developed in the MAPS program (DeSante et al. 2015; Table 3). The MAPS data for Painted Buntings are primarily from the western population; survival estimated for a single monitoring station on the Atlantic coast at Wassaw Island, GA (0.644, based on data for 89 banded birds), is higher than the overall MAPS estimate for the species, but lower than our estimates for males or for females banded on sheltered islands.

We estimated high annual survival in Painted Buntings breeding along the southeastern Atlantic Coastal Plain in spite of human development occurring throughout the region (Dame et al. 2000, NOAA 2010). We had hypothesized that survival would be higher for birds banded on islands, which are generally less developed than the coastal mainland, or that survival would decline in relation to extent of human development surrounding our banding locations. However, except for elevated female survival on sheltered islands compared to the mainland, we found little support for effects on apparent survival of latitude, landform, or nearby human development. Importantly, our study sites were not chosen to represent a gradient of coastal development, but rather as sites along the length of the southeastern coastal breeding range where it was possible to catch and band a large number of birds. Most of our sites were in areas that were relatively isolated from nearby development, and the majority of land classified as "developed" around our study sites was defined as low-intensity development such as single-family housing units (Homer et al. 2004). Nonetheless, we caught the greatest numbers of birds at the sites with the lowest proportions of developed land within 3,000 m. Our highest capture rates were mostly at lower latitudes, particularly in GA, possibly attributable to extent of high habitat quality in the form of undeveloped maritime shrub and forest habitat adjacent to salt marsh (Lanyon and Thompson 1986, Springborn and Meyers 2005) on barrier islands, sheltered islands, and the mainland within tidal reach. We hypothesize that access to salt marsh habitat, in particular, may lessen effects of human development on landscape productivity for foraging Painted Buntings, such that survival may remain high even at more developed sites where

Table 3. Estimated adult apparent survival for Painted Bunting and 5 other species of *Passerina*. Estimates from this study (*) are posterior means (and 95% credible intervals) of 5 annual estimates (1999–2004) for males and females modeled independently, in the eastern coastal population. Estimates from the Monitoring Avian Productivity and Survivorship program (MAPS; DeSante et al. 2015) are time-constant means for 1992–2006 (95% confidence intervals) for males and females combined, for all monitored regions.

Species	Adult apparent survival
Painted Bunting (*P. ciris*)*	
Males	0.708 (0.674–0.741)
Females	0.659 (0.625–0.693)
MAPS estimates:	
Painted Bunting (*P. ciris*)	0.576 (0.537–0.613)
Lazuli Bunting (*P. amoena*)	0.520 (0.465–0.575)
Indigo Bunting (*P. cyanea*)	0.493 (0.468–0.518)
Varied Bunting (*P. versicolor*)	0.499 (0.286–0.713)
Blue Grosbeak (*P. caerulea*)	0.622 (0.506–0.725)

local habitats may support fewer breeding territories.

Our observations suggest that the most serious threat to the coastal population of the Painted Bunting is the further loss of suitable habitats in the population's breeding range. Others have observed high site fidelity in the coastal population of Painted Buntings, with males returning to territories in maritime forest within foraging range of marsh habitat (Lanyon and Thompson 1986). Similarly, our observation of at least 75% of resightings of adult Painted Buntings at the feeders where birds were initially banded suggests that adults commonly return to previously occupied areas on the breeding grounds. In contrast, we expect that lower apparent survival of hatch-year birds in our study at least partly reflects lower probability that young birds return to reside in the area where they were hatched, as supported by our lower index of site fidelity for hatch-year birds compared to adults. DeSante et al. (2015) similarly suggest that given high adult survival, the Painted Bunting population on the Southeastern Coastal Plain (Bird Conservation Region 27) is likely limited either by hatch-year survival (on the nonbreeding grounds or in migration) or by subsequent recruitment of surviving hatch-year birds on the breeding grounds. Thus, residential development in coastal areas that replaces maritime forest and shrub-scrub adjacent to salt marsh with large areas of grass that is mowed on a regular basis (thus eliminating the seed component of the diet) and various types of structures and roads with wide rights-of-way may limit populations by reducing breeding territories available to either established or new birds.

Other threats to the eastern population of Painted Buntings include habitat modification in wintering and migration stopover sites, increasing frequency and intensity of severe storms, and spread of the illegal caged-bird trade. Painted Buntings that breed along the Atlantic coast migrate to southern FL, Cuba, and the Bahamas for winter (Sykes et al. 2007, Battey et al. 2018), where the birds occupy shrub-scrub habitats (Lowther et al. 1999, Sykes et al. 2007). Low-pressure systems with strong winds and heavy precipitation often occur while the buntings are in migration as well as when the birds have reached their wintering areas. Increases in the frequency of major (i.e., category 4 and 5) hurricanes in the western Atlantic associated with global warming and rising sea-surface temperatures (Bender et al. 2010, Knutson et al. 2013) threaten increased habitat loss and bird mortality due to associated storm surges, overwash of low-lying islands, and erosion of coastal habitats in wintering and breeding ranges (Morton 2003). Painted Buntings on the wintering grounds are also currently vulnerable to capture for the caged-bird trade in Cuba and southern FL (Sykes et al. 2006, 2007). Expansion of the caged-bird trade into the breeding range, where males defending territories could be baited using live ASY male decoys, could decimate local populations. Although our estimates indicate currently high annual survival for Painted Buntings breeding along the Atlantic coast, future research to monitor effects of changing habitat, weather patterns, and trapping activities on survival and recruitment will further aid conservation of the eastern population of the Painted Bunting.

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Literature cited

Abadi F, Botha A, Altwegg, R. 2013. Revisiting the effect of capture heterogeneity on survival estimates in capture-mark-recapture studies: does it matter? PLOS ONE 8(4):e62636.

Battey CJ, Linck EB, Epperly KL, French C, Slager DL, et al. 2018. A migratory divide in the Painted Bunting (*Passerina ciris*). American Naturalist 191:259–268.

Beaton G, Sykes PW Jr, Parrish JW Jr. 2003. Annotated checklist of Georgia Birds. 5th edition. Culloden (GA): Georgia Ornithological Society. Occasional Publications Number 14.

Bender MA, Knutson TR, Tuleya RE, Sirutis JJ, Vecchi GA, et al. 2010. Modeled impact of anthropogenic warming on the frequency of intense Atlantic hurricanes. Science 327:454–458.

Brooks SP, Gelman A. 1998. General methods for monitoring convergence of iterative simulations. Journal of Computational and Graphical Statistics 7:434–455.

Clapp RB, Klimkiewicz MK, Kennard JH. 1982. Longevity records of North American birds: Gaviidae through Alcidae. Journal of Field Ornithology 53:81–124.

Clapp RB, Klimkiewicz MK, Futcher AG. 1983. Longevity records of North American birds: Columbidae through Paridae. Journal of Field Ornithology 54:123–137.

Cormack RM. 1964. Estimates of survival from the sighting of marked animals. Biometrika 51:429–438.

Dame R, Alber M, Allen D, Mallin M, Montague C, et al. 2000. Estuaries of the South Atlantic Coast of North America: their geographical signatures. Estuaries 23:793–819.

DeSante DF, Kaschube DR, Saracco JF. 2015. Vital rates of North American landbirds. Point Reyes Station (CA): The Institute for Bird Populations. www.VitalRatesOfNorthAmericanLandbirds.org

Finch CE. 1990. Longevity, senescence and the genome. Chicago (IL): University of Chicago Press.

Fisk EJ. 1974. Wintering populations of Painted Buntings in southern Florida. Bird-Banding 45:353–359.

Gimenez O, Rossi V, Choquet R, Dehais C, Doris B, et al. 2007. State-space modelling of data on marked individuals. Ecological Modelling 206:431–438.

Haggerty TM, editor. 2009. Alabama breeding bird atlas 2000–2006. Tuscaloosa (AL): Alabama Ornithology Society [cited 22 Jan 2009]. www.una.edu/faculty/haggerty/BBA%20Homepage.htm

Herr CA, Sykes PW Jr, Klicka J. 2011. Phylogeography of a vanishing North American songbird: the Painted Bunting (*Passerina ciris*). Conservation Genetics 12:1395–1410.

Holmes DJ, Austad SN. 1995. The evolution of avian senescence patterns: implications for understanding primary aging processes. American Zoologist 35:307–317.

Homer C, Huang C, Yang L, Wylle B, Coan M. 2004. Development of a 2001 national land-cover database for the United States. Photogrammetric Engineering and Remote Sensing 70:829–840.

Homer C, Dewitz J, Fry J, Coan M, Hossain N, et al. 2007. Completion of the 2001 National Land Cover Database for the conterminous United States. Photogrammetric Engineering and Remote Sensing 73:337–341.

Hunter WC, Pashley DN, Escano REF, Rowald EF. 1993. Neotropical migratory landbird species and their habitats of special concern within the Southeast Region. In: Finch DM, Stangel PW, editors. Status and management of Neotropical migratory birds. Ft. Collins (CO): USDA, Forest Service, Rocky Mountain Forest and Range Experiment Station. General Technical Report RM-229.

Kéry M, Schaub M. 2012. Bayesian population analysis using WinBUGS: A hierarchical perspective. Waltham (MA): Academic Press.

Klimkiewicz MK, Futcher AG. 1987. Longevity records of North American birds: Coerebinae through Estrilidae. Journal of Field Ornithology 58:318–333.

Klimkiewicz MK, Futcher AG. 1989. Longevity records of North American birds: supplement I. Journal of Field Ornithology 60:469–494.

Knutson TR, Sirutis JJ, Vecchi GA, Garner S, Zhao M, et al. 2013. Dynamical downscaling projections of twenty-first-century Atlantic hurricane activity: CMIP3 and CMIP5 model-base scenarios. Journal of Climate 26:6591–6617.

Lanyon SM, Thompson CF. 1986. Site fidelity and habitat quality as determinants of settlement pattern in male Painted Buntings. Condor 88:206–210.

Lowther PE, Lanyon SM, Thompson CW. 1999. Painted Bunting (*Passerina ciris*). In: Poole A, editor. Birds of North America. Ithaca (NY): Cornell Lab of Ornithology. Number 398.

Lutmerding JA, Love AS. 2014. Longevity records of North American birds. Version 2014.1. Laurel (MD): USGS Patuxent Wildlife Research Center.

Meyers JM. 2011. Population densities of Painted Buntings in the southeastern United States. Southeastern Naturalist 10:345–356.

Milligan JL, Davis AK, Altizer SM. 2003. Errors associated with using colored leg bands to identify wild birds. Journal of Field Ornithology 74:111–118.

Morton RA. 2003. An overview of coastal land loss: With emphasis on the Southeastern United States. St. Petersburg (FL): USGS Center for Coastal and Watershed Studies. Open File Report 03-337.

[NOAA] National Oceanic and Atmospheric Administration. 2010. Southeast regional land cover change report 1996–2010. Washington (DC): NOAA, Office for Coastal Management, National Coastal Zone Management Program.

Northrup JM, Gerber BD. 2018. A comment on priors for Bayesian occupancy models. PLOS ONE 13:e0192819.

Peterjohn BG, Sauer JR, Robbins CS. 1995. Population trends for the North American Breeding Bird Survey. In: Martin TE, Finch DM, editors. Ecology and management of Neotropical migratory birds. New York (NY): Oxford University Press; p. 357–380.

Plummer M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. Proceedings of the Third International Workshop on Distributed Statistical Computing (DSC 2003), March 20–22, Vienna (Austria).

Plummer M. 2014. rjags: Bayesian graphical models using MCMC. R package version 3–14. http://CRAN.R-project.org/package=rjags

Pollock KH. 1981. Capture–recapture models for age-dependent survival and capture rates. Biometrics 37:521–529.

Post W, Gauthreaux SA Jr. 1989. Status and distribution of South Carolina birds. Charleston (SC): Contribution from the Charleston Museum, no. 18.

R Core Team. 2014. R: A language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing. http://www.R-project.org/

Robertson WB Jr, Woolfenden GE. 1992. Florida bird species: An annotated list. Gainesville (FL): Florida Ornithological Society, Special Publication Number 6.

Rowan E, Sigel RB, Kaschube DR, Tork S. 2014. North American longevity records for nine landbird species monitored at Yosemite National Park's MAPS stations. North American Bird Bander 39:153–159.

Sauer JR, Niven DK, Hines JE, Ziolkowski DJ Jr, Pardieck KL, et al. 2017. The North American Breeding Bird Survey, results and analysis 1966–2015. Version 2.07.2017. Laurel (MD): USGS Patuxent Wildlife Research Center. www.mbr-pwrc.usgs.gov/bbs/bbs.html

Springborn EG, Meyers JM. 2005. Home range and survival of breeding Painted Buntings on Sapelo Island, Georgia. Wildlife Society Bulletin 33:1432–1439.

Sykes PW Jr. 2006. An efficient method of capturing Painted Buntings and other small granivorous passerines. North American Bird Bander 31:110–115.

Sykes PW Jr, Holzman S. 2005. Current range of the eastern population of Painted Bunting (*Passerina ciris*). Part 1: Breeding. North American Birds 59:4–17.

Sykes PW Jr, Holzman S, Iñigo-Elias EE. 2007. Current range of the eastern population of Painted Bunting (*Passerina ciris*). Part II: Winter range. North American Birds 61:378–406.

Sykes PW Jr, Manfredi L, Padura M. 2006. A brief report on the illegal cage-bird trade in southern Florida: A potentially serious negative impact on the eastern population of Painted Bunting (*Passerina ciris*). North American Birds 60:310–313.

Thompson CW. 1991. Is the Painted Bunting actually two species? Problems determining species limits between allopatric populations. Condor 93:987–1000.

[USFWS] U.S. Fish and Wildlife Service. 2008. Birds of conservation concern 2008. Arlington (VA): US Department of Interior, Fish and Wildlife Service, Division of Migratory Bird Management. http://www.fws.gov/migratorybirds/

Wasser DE, Sherman PW. 2010. Avian longevities and their interpretation under evolutionary theories of senescence. Journal of Zoology 280:103–155.

Williams BK, Nichols JD, Conroy MJ. 2002. Analysis and management of animal populations. San Diego (CA): Academic Press.

Appendix Table A1. Locality, physiography, feeder status, and estimates of land development for 40 Painted Bunting study sites along the southeastern US Atlantic coast. The proportion of land developed is derived from the 2001 National Land Cover Database, and is the proportion of land (i.e., excluding open water) classified as low, medium, or high intensity developed (Homer et al. 2004) within 700 m and 3,000 m of the feeder.

				Proportion land developed within:	
Study site no.[a]	Study site name (state, county)	Physiography	Feeder status[b]	700 m	3,000 m
1A	Ft. Caroline, Jacksonville (FL, Duval)	Mainland	Temporary	0.175	0.362
1C	Rebault Monument, Jacksonville (FL, Duval)	Mainland	Temporary	0.054	0.274
3B	Kingsley Plantation, Staff Residence, Ft. George Is. (FL, Duval)	Sheltered island[c]	Permanent	0.001	0.019
3C	Dyal Residence, Ft. George Is. (FL, Duval)	Sheltered island	Permanent	0	0.155
4A	Staff Residence, Little Talbot Is. St. Pk. (FL, Duval)	Barrier island	Permanent	0.085	0.027
4B	Park Office, Little Talbot Is. St. Pk. (FL, Duval)	Barrier island	Temporary	0.021	0.018
5B	Bridge View, Cedar Point (FL, Duval)	Sheltered island	Temporary	0	0.002
5C	Carl's Point, Cedar Point (FL, Duval)	Sheltered island	Temporary	0	0.003
6B	Beach Camping Area, Ft. Clinch St. Pk. (FL, Nassau)	Barrier island	Temporary	0.016	0.109
6C	Staff Residence, Ft. Clinch St. Pk. (FL, Nassau)	Barrier island	Permanent	0.088	0.133
7A	Sheppard Residence, Meridian (GA, McIntosh)	Mainland	Permanent	0.002	0.005
7B	Marra Residence, Black Is. (GA, McIntosh)	Sheltered island	Permanent	0	0.029
8A	Turtle Cabin, Blackbeard NWR (GA, McIntosh)	Barrier island	Permanent	0.001	0.001
8B	Marsh Pond, Blackbeard NWR (GA, McIntosh)	Barrier island	Temporary	0	0
9A	Refuge Office, Harris Neck NWR (GA, McIntosh)	Mainland	Temporary	0	0.007
9C	Goose Pond, Harris Neck NWR (GA, McIntosh)	Mainland	Temporary	0.030	0.008
10B	King New Ground Field, St. Catherines Is. (GA, Libery)	Barrier island	Temporary	0	<0.001
10C	South Beach Road, St. Catherines Is. (GA, Libery)	Barrier island	Temporary	0.001	0.001
12A	Staff Residence, Wassaw Is. (GA, Chatham)	Barrier island	Permanent	0.004	0.001
12B	Boundary Fire Break, Wassaw Is. NWR (GA, Chatham)	Barrier island	Temporary	0.004	0.001
13A	Impoundment 13A, Savannah River Dredge-Spoil Site (SC, Jasper)	Mainland	Temporary	0.051	0.066
13C	Field's Cut, Savannah River Dredge-Spoil Site (SC, Jasper)	Mainland	Temporary	0	0.001
14A	Staff Residence, Pinckney NWR (SC, Beaufort)	Sheltered island	Permanent	0	0.044
14C	Bull Point, Pinckney NWR (SC, Beaufort)	Sheltered island	Temporary	0	0.091
15A	Schaller Residence, Spring Is. (SC, Beaufort)	Sheltered island	Permanent	0	0.015
15C	Masaschi Residence, Spring Is. (SC, Beaufort)	Sheltered island	Permanent	0	0.012
16B	Grove Unit 12, ACE Basin NWR (SC, Charleston)	Mainland	Temporary	0	<0.001
16C	Grove Unit 6, ACE Basin NWR (SC, Charleston)	Mainland	Temporary	0	0
17A	Stono Plantation House, James Is. (SC, Charleston)	Sheltered island	Permanent	0.007	0.123
17C	Battery Tynes, James Is. (SC, Charleston)	Sheltered island	Permanent	0	0.115
19A	Baxley Residence, Bald Head Is. (NC, Brunswick)	Barrier island	Temporary	0.113	0.075
19C	Frech Residence, Bald Head Is. (NC, Brunswick)	Barrier island	Permanent	0.002	0.053
21A	Sugarloaf Trail, Carolina Beach St. Pk. (NC, New Hanover)	Mainland	Temporary	0.024	0.249
21B	Marina, Snow's Cut, Carolina Beach St. Pk. (NC, New Hanover)	Mainland	Temporary	0.026	0.282
22A	Darby Residence, Figure Eight Is. (NC, New Hanover)	Barrier island	Permanent	0.071	0.114
22B	Community Utility, Figure Eight Is. (NC, New Hanover)	Barrier island	Temporary	0.076	0.101
23A	Grant Residence, Sneads Ferry (NC, Onslow)	Mainland	Permanent	0.015	0.039
23C	Cowgill Residence, Sneads Ferry (NC, Onslow)	Mainland	Temporary	0.038	0.085
24B	Middle Area, Onslow Is. (NC, Onslow)	Barrier island	Temporary	0.022	0.028
24C	Water Tower, Onslow Is. (NC, Onslow)	Barrier island	Temporary	0.116	0.034

[a] There are no study areas numbered 2, 11, 18, and 20 as these were the least productive areas (one from each of 4 states) and were dropped from the study after the first year. Originally there were 3 study sites per study area, but the least productive from each study area was dropped at end of first year; hence, one letter code is skipped within each study area.
[b] Permanently maintained at site (some existed prior to this study), as opposed to temporarily maintained for 3–6 months specifically for this study.
[c] Sheltered islands are surrounded by salt marsh in the estuarine system between barrier islands and the mainland.