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RANGE-WIDE MIGRATORY CONNECTIVITY OF PAINTED BUNTINGS

by

Andrew J. Sharp

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Ecology

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2021

ABSTRACT

Range-wide Migratory Connectivity of Painted Buntings

by

Andrew Sharp, Master of Science

Utah State University, 2021

Major Professor: Dr. Clark S. Rushing
Department: Wildland Resources

The Painted Bunting (*Passerina ciris*) is a small (~16g), short/medium-distance migrant passerine that is listed as a species of conservation concern by the US Fish and Wildlife Service. Painted Buntings breed in two distinct populations, one eastern population and one interior population, separated by a 500 km gap that stretches from Mississippi to Georgia. I analyzed tracking data from 112 Painted Buntings from 11 different breeding sites to explore how migratory connectivity (chapter 2), migratory phenology (chapter 3), and differential migration (chapter 4) vary across the breeding range. My results reveal strong range-wide migratory connectivity in this species, with eastern and interior Painted Buntings remaining separate throughout the annual cycle. Within each population, migratory connectivity was weak, with individuals from different regions of each population mixing extensively on the non-breeding ground. Migratory phenology was drastically different between the two populations, with interior Painted Buntings departing the breeding ground two months prior to birds from the eastern population. In eastern Painted Buntings, some variation in fall departure was

correlated with differences in vegetation greenness and temperature, suggesting that eastern birds may adjust their fall departure from year to year in accordance with yearly variation in environmental conditions. Fall departure was not closely linked to environmental conditions in the interior population. I found that eastern Painted Buntings arrive on the breeding ground at approximately the same time each year, suggesting strong endogenous influence on spring migration phenology. In eastern Painted Buntings, males arrived on the breeding ground before females, but I found no differences in fall departure between the sexes. In the eastern population, females wintered slightly farther north on average than males. This work demonstrates the considerable differences in migratory behavior that are possible within a single species.

(85 Pages)

PUBLIC ABSTRACT

Range-wide Migratory Connectivity of Painted Buntings

Andrew Sharp, Master of Science

The Painted Bunting (*Passerina ciris*) is a small (~16g), short/medium-distance migratory songbird that is listed as a species of conservation concern by the US Fish and Wildlife Service. Painted Buntings breed in two distinct populations, one eastern population and one interior population, separated by a 500 km gap that stretches from Mississippi to Georgia. I analyzed tracking data from 112 Painted Buntings from 11 different breeding sites to explore how individuals from different breeding sites differ in wintering location (chapter 2) and migratory timing (chapter 3). Additionally, I examined differences in migratory behavior between male and females in the eastern population (chapter 4). My results reveal that eastern and interior Painted Buntings remain separate throughout the annual cycle. Within each population, individuals from different regions of each population mix extensively on the non-breeding ground. Migratory timing was drastically different between the two populations, with interior Painted Buntings departing the breeding ground two months prior to birds from the eastern population. In eastern Painted Buntings, some variation in fall departure could be attributed to differences in vegetation greenness and temperature, suggesting that eastern birds may adjust their fall departure from year to year in accordance with yearly variation in environmental conditions. Fall departure was not closely linked to environmental conditions in the interior population. I found that eastern Painted Buntings arrive on the breeding ground at approximately the same time each year, suggesting that spring arrival

timing may have a strong instinctual component. In eastern Painted Buntings, males arrived on the breeding ground before females, but I found no differences in fall departure timing between the sexes. In the eastern population, females wintered slightly farther north on average than males. This work demonstrates the considerable differences in migratory behavior that are possible within a single species.

DEDICATION

This thesis is dedicated to Charles “Zig” Ziegenfus, whose willingness to educate and mentor has made such a difference to so many.

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Andrew Sharp

CONTENTS

	Page
ABSTRACT	ii
PUBLIC ABSTRACT	iv
DEDICATION	vi
ACKNOWLEDGMENTS	vii
LIST OF TABLES	xi
LIST OF FIGURES	xii
CHAPTER I: INTRODUCTION	1
Species Account	1
Field Methods	2
Geocator Analysis	5
Literature Cited	10
CHAPTER II: RANGE-WIDE MIGRATORY CONNECTIVITY	14
Introduction	14
Methods	18
Results	20
Discussion	24
Literature Cited	27
CHAPTER III: MIGRATORY PHENOLOGY OF PAINTED BUNTINGS	34
Introduction	34
Methods	39
Results	44
Discussion	46
Literature Cited	50
CHAPTER IV: DIFFERENTIAL MIGRATION OF PAINTED BUNTINGS	57
Introduction	57
Methods	59
Results	61
Discussion	64

Literature Cited	68
CHAPTER V: SUMMARY.....	72
Summary	72

LIST OF TABLES

	Page
Table 1. Geolocator deployment/recovery statistics	3
Table 2. Geolocator deployment sites.....	5
Table 3. Estimates of migratory connectivity generated using the R package MigConnectivity	21
Table 4. Sample sizes of estimated dates of spring arrival and fall departure for each state	40
Table 5. List of environmental covariates with descriptions	42
Table 6. Top spring arrival models ($\Delta < 2$) for eastern Painted Buntings.....	45
Table 7. Top fall departure models ($\Delta < 2$) for eastern Painted Buntings.....	46
Table 8. Top fall departure models ($\Delta < 2$) for interior Painted Buntings	46
Table 9. Hypotheses for differential migration.....	59
Table 10. Recovered geolocators for male and female eastern Painted Buntings	60
Table 11. Predictions for each hypothesis for differential migration	61
Table 12. Mean winter location, migration distance, and phenology, with associated p values for male and female Painted Buntings.....	63

LIST OF FIGURES

	Page
Figure 1. Painted bunting distribution and geolocator deployment sites.....	4
Figure 2. Deployment locations and probability of winter residence for eastern and interior Painted Buntings	18
Figure 3. Estimated wintering locations for eastern Painted Buntings, broken up by origin state.....	22
Figure 4. Estimated molting and wintering locations for Oklahoma and Arkansas Painted Buntings	23
Figure 5. Vegetation greenness over the course of the year for the interior and eastern population	38
Figure 6. Estimated phenology for male Painted Buntings from five states	44
Figure 7. 75% and 25% utilization kernels for male and female eastern Painted Buntings on the non-breeding ground.....	62
Figure 8. Migration distance and timing data from male and female Painted Buntings ...	64

CHAPTER I

INTRODUCTION

SPECIES ACCOUNT

The Painted Bunting is a small (~16g), short- to medium-distance migrant that is listed as a species of conservation concern by the US Fish and Wildlife Service (USFWS, 2008). It exists within two allopatric populations that are separated by a 500 km gap that stretches from Mississippi to Georgia (but see Gilbert et al., 2019; Figure 1). Male Painted Buntings are instantly recognizable by their brilliant red, blue, and green plumage. The green plumage of the female is more subtle but still fairly unique among birds breeding in the United States. Painted Buntings show delayed plumage maturation, meaning males resemble females until the autumn after their first breeding season (Thompson, 1991a). Like many passerines, Painted Buntings are socially monogamous, although polygyny may occur. Painted Buntings feed their chicks arthropods but subsist mainly on seeds as adults. Like most members of their genus, Painted Buntings visit bird feeders zealously and covet white millet. This habit makes Painted Buntings an easy target for capture, making them a prime candidate for research. They are commonly targeted in the pet trade throughout their winter range, an activity which is generally only actively prohibited in the United States (Sykes, 2006). For eastern Painted Buntings especially, access to supplemental food is nearly ubiquitous year-round. It is unknown how this unlimited food source affects breeding or site fidelity, migration distance, phenology, or lifespan (average = 2-3 years, record = 12 years). The long-term effects of backyard bird feeding are not well understood (Robb et al., 2008). If nothing else, the ubiquity of bird feeders within the eastern breeding range means that all eastern

individuals tracked in this study had equal access to supplemental food, and any effect thereof should be constant across the population.

The eastern population of Painted Buntings stretches from southern North Carolina south to northern Florida, and is restricted mostly to the coast except for in parts of South Carolina and Georgia. Frequently-used breeding habitat includes coastal scrub, maritime hammock, and early successional habitat. The interior population is much larger, both in land area and number of birds. Centered in Texas, it stretches north to Kansas, southeast to Louisiana, and south just into Mexico. Birds from the interior population breed in scrubby edge habitat, including fallow fields. Interior Painted Buntings are slightly larger than eastern birds on average, though this difference is only apparent with careful measurement. Although individuals from the two populations are indistinguishable to the human eye, there are more life-history differences within this species than within many genera (Thompson, 1991b). Much of this thesis revolves around using these differences to explore ecological concepts such as connectivity and phenology.

FIELD METHODS

In the eastern population, geolocators were deployed on Painted Buntings in the summers of 2017, 2018, and 2019 (Table 1 and 2). Geolocators were deployed at nine eastern sites, but not all sites were used in all years. Birds were trapped at feeders using a wire walk-in trap or flushed into a V-shaped mist net array. All trapped birds were banded with a federally-issued aluminum band with a unique serial number inscribed. Birds were aged, sexed, and morphometric measurements were taken. Geolocators were applied in the manner of Rappole and Tipton, 1991 using flexible jewelry cord (Pepperell

Braiding Company, 1917). In the first two years, I attempted to put tags on only after-second-year (ASY) males, which are easily identifiable by their characteristic colorful plumage. In cases where I could not capture enough ASY males, the remaining tags were deployed on second-year (SY) males ($n = 12$). In 2019, I put approximately half of the allotted geolocators out on ASY females (47/100). Raw geocator data from the two interior sites (Oklahoma and Arkansas) was generously shared with me by Dr. Andrea Contina. A subset of this raw data was used in an analysis published in 2013 (Contina et al., 2013). See Contina et al., 2013 for geocator deployment methods for interior birds.

Table 1. Geocator deployment/recovery statistics. Geolocators were excluded from analysis if they failed to record viable data.

Population	Origin	Deployed	Recovered (<i>viable data</i>)
Eastern	North Carolina	47	9 (8)
Eastern	South Carolina	116	34 (32)
Eastern	Georgia	67	23 (23)
Eastern	Florida	65	20 (19)
Interior	Oklahoma	215	53 (28)
Interior	Arkansas	14	2 (2)
Total		525	141 (112)

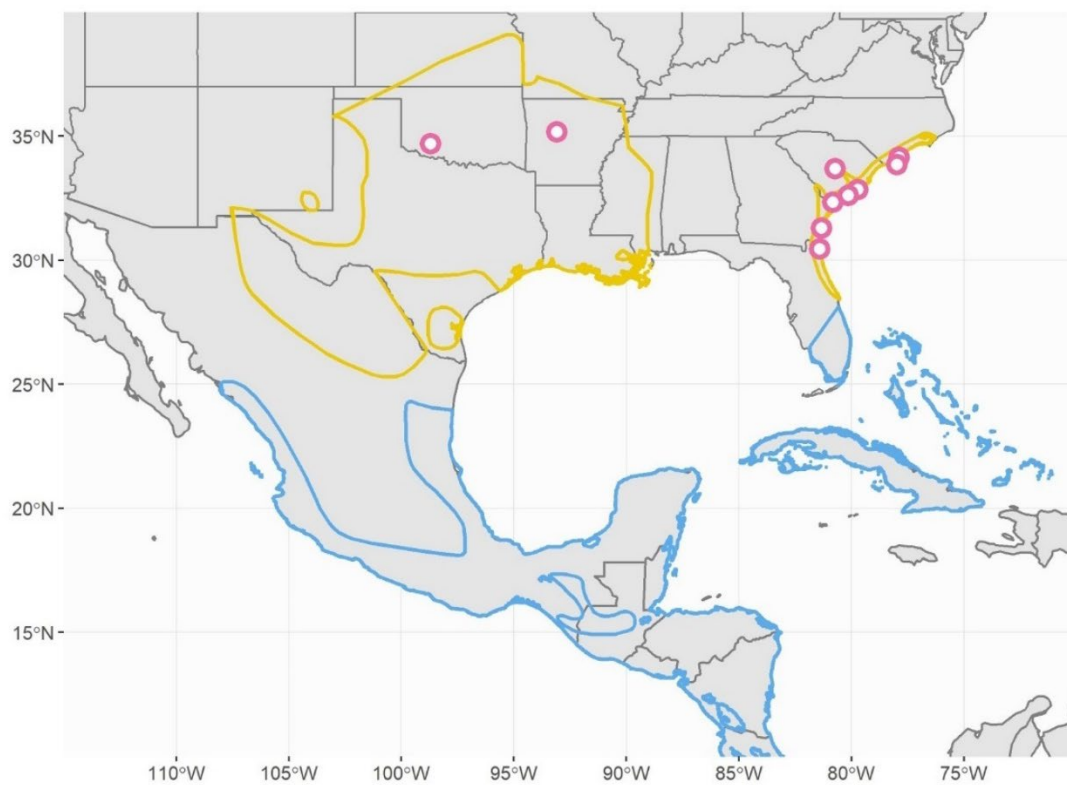


FIGURE 1. Painted bunting distribution and geolocator deployment sites. Outline of breeding range (yellow) and non-breeding range (blue) of Painted Buntings (shapefile from Birdlife Intl). Pink circles mark the breeding sites where geolocators were deployed.

Table 2. Geolocator deployment sites. Year indicates years in which geolocators were deployed at that breeding site.

Site	State	Lat	Lon	Years
Airlie Gardens	North Carolina	34.22	-77.83	2017
Carolina Beach State Park	North Carolina	34.05	-77.92	2017
Bald Head Island	North Carolina	33.86	-77.98	2019
Kiawah Island	South Carolina	32.61	-80.02	2017, 2018, 2019
Spring Island	South Carolina	32.35	-80.84	2018, 2019
Deweese Island	South Carolina	32.84	-79.72	2018
St. Matthews	South Carolina	33.69	-80.73	2018
Little Saint Simons Island	Georgia	31.26	-81.30	2017, 2018, 2019
Little Talbot Island State Park	Florida	30.46	-81.41	2017, 2018, 2019
Wichita Mountains NWR	Oklahoma	34.7	-98.7	2011, 2012
Holla Bend NWR	Arkansas	35.16	-93.1	2018

GEOLOCATOR ANALYSIS

The development of miniaturized light-level geolocators has been transformative to the study of migratory birds (Stutchbury et al., 2009; McKinnon et al., 2013; McKinnon and Love, 2018). Birds as small as 7 grams (about the weight of 3¢) can now

be tracked throughout their annual migration with a reasonable degree of accuracy. However, the process of analyzing and interpreting geolocator data is complex and should be done thoughtfully and transparently, especially as it concerns latitudinal movement (Lisovski et al., 2018). The following analysis draws heavily from Lisovski et al., 2020 and the accompanying online manual.

Raw geolocator (Eastern population: stalked model P50Z11-7-DIP, Migrate Technology Ltd, Coton, Cambridge, UK; Interior population: See Contina et al., 2013) data consist of light levels recorded at predetermined intervals for the duration of the tag's battery life. Geolocator analysis relies on accurate estimates of twilights (sunrise/sunset). Twilights were identified using the function *preprocessLight*, which is part of the R package TwGeos (Wotherspoon, Sumner, and Lisovski, 2016). Twilight editing/filtering was done only by automation, with the following parameters: If an identified twilight was more than 45 minutes different from the 2 twilights on either side, and those 2 twilights were within 25 minutes of each other, the outlier twilight was replaced with the median value of the 2 twilights on either side. If the 2 twilights on either side of the outlier were not within 25 minutes of each other, the outlier twilight was deleted. This method of geolocator analysis requires the user to define light-level thresholds that define transitions between day and night. Light-levels above the threshold indicate daytime, light levels below the threshold indicate nighttime. I kept the light threshold consistent for all birds within each population unless extraordinary shading required threshold adjustment. Adjusting the threshold does not strongly affect location estimates unless zenith (sun angle) estimates are not reevaluated using the new threshold.

Analysis of light-level data requires calibration to account for inaccuracies in twilight estimation. These inaccuracies can be related to the sensor's inability to perfectly detect light-levels or by shading effects caused by vegetation, topography, or even the feathers adjacent to the sensor. The calibration period(s) refers to time periods where the location of the individual is known. In this case, calibration starts when the tag is deployed and ends before the individual has left the breeding ground. For eastern birds, the calibration period terminated on August 1st, as it is extremely unlikely for eastern Buntings to depart the breeding ground prior to this date. For interior birds, the stationary breeding period began when the geolocator was deployed and ended when the bird departed the breeding ground. This flexible time frame was necessary because some interior birds had already reached the molting ground and stopped recording locations before others had even received their geolocator on the breeding ground. For individuals whose geolocators lasted long enough to record the return to the breeding ground the following spring, I used two calibration periods. The second calibration period started as soon as the bird was assured to have returned to the breeding ground and ended when the geolocator stopped recording locations. The *thresholdCalibration* function in R package SGAT creates the threshold model by fitting a gamma distribution to the twilight error (minutes) during the calibration period (Wotherspoon, Sumner, and Lisovski, 2013). The parameters from this model help to inform the model that optimizes location estimates later on. The zenith angle that is associated with the median twilight error during the calibration period is taken to be the best zenith estimate for the calibration period, as that is the zenith angle that results in the average amount of error. One of the most difficult steps of geolocator analysis is determining an appropriate zenith angle for time periods

when the bird is at an unknown location (away from the breeding ground, in this case). Adjusting zenith angles will drastically change estimates of latitude. There is some precedent for using a constant zenith angle for the duration of the track, but I (and others) found that using a zenith calibrated for the breeding ground did not result in realistic location estimates on the non-breeding ground (Cooper et al., 2017). To determine appropriate zenith angles at times of the year when location is unknown (e.g., the nonbreeding season), I used the Hill-Ekstrom calibration method (HEC) (Lisovski et al 2012, Lisovski et al, 2020), which works on the principle that the true zenith angle should result in the smallest variation in estimated latitudes. I attempted to be as methodical as possible in how I implemented this method by using the same window (December 1st-March 15th) for each bird. Even so, this method occasionally returned spurious zenith estimates.

I specified a gamma-distributed movement model with parameters that assume most movements are near-zero distance (stationary periods) but that allow for long-distance movements (migration). I specified a location mask to constrain location estimates to the known range of the Painted Bunting (Hallworth et al., 2015). The built-in MCMC sampler in SGAT uses the initial crude locations generated from recorded light-levels, the land mask, and the prior distributions from the threshold model and the movement model to simulate thousands of tracks (Sumner et al., 2009). For each time point, the mean location estimate from all iterations is taken to be the best location estimate. For visualization of non-breeding locations, I created a location density layer from the posterior distribution from each individual using the *slices* function within SGAT.

Estimates of latitude from light-level tags will have considerable uncertainty and error even under the best conditions. During the equinox periods, which can last up to 30 days on either side of the fall and spring equinox, estimates of latitude are unreliable due to the lack of latitudinal variation in day length during this period. Unfortunately, this often coincides with migration, such that only longitudinal movements can be inferred. Naturally, this can make determining dates of arrival/departure using geolocator data difficult. I defined departure as a significant (>2 degrees) longitudinal movement away from a known stationary location. To determine arrival, I looked for longitude to stabilize during a stationary period, and then tracked backwards until longitude moved significantly (>2 degrees) away. I only assigned arrival/ departure dates for individuals whose movements allowed confident determination of arrival/departure. Some individuals had such little longitudinal movement or migrated such short distances that assigning arrival or departure dates was not feasible or appropriate.

Accurate time keeping is critical to geolocator analysis. If the clock onboard the geolocator speeds up or slows down, estimates of longitude will become increasingly biased as the clock drift accumulates. Clock drift is apparent if longitudinal estimates of known locations (breeding ground) are accurate when the geolocator is deployed, but have shifted east or west by the time the bird returns the following spring. Most of our geolocators showed no sign of clock drift. For the handful of tags that showed evidence of clock drift, I used the following method to correct the bias:

I. Determine total amount of clock drift (ΔT)

a. $\Delta T = (\text{Fall Breeding Longitude} - \text{Spring Breeding Longitude}) * 60 * 5$

- II. For each recorded date time at time step i , add (or subtract, depending on direction of clock drift) a portion of ΔT proportional to how far along that time step is in the data set
- a. Corrected Time $_i$ = Biased Time $_i$ + ($\Delta T * (i / \text{total number of time steps})$)
 - b. The result of this method is that I add very little correction to date-times early on in the dataset, because very little clock drift has accumulated. By the final time step, I add 100% of the total clock drift.

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CHAPTER II

RANGE-WIDE MIGRATORY CONNECTIVITY

INTRODUCTION

Populations of migratory species move annually between areas used during breeding, molting, and wintering. Migratory connectivity (hereafter ‘connectivity’) describes the extent to which individuals remain together as they move between phases of the annual cycle (Webster et al., 2002). Connectivity is considered “strong” when individuals that are spatially associated during one period of the annual cycle (e.g., breeding) remain close together during other periods of the annual cycle (e.g., non-breeding). Connectivity is further strengthened if interpopulation mixing is low (Finch et al., 2017). In contrast, connectivity is weakened when sympatric individuals in one stationary period of the annual cycle are allopatric in another stationary period and/or mix with individuals from other regions when transitioning from one stationary period to the next. Weak migratory connectivity appears to be common for migratory songbirds, with individuals from different breeding populations overlapping on the wintering grounds (Finch et al., 2017).

Quantifying the strength of connectivity is important for understanding the ecology of migratory species and for conservation. Migratory species present a unique conservation challenge because they experience different conditions and risks as they move between breeding and non-breeding areas throughout their annual cycles and, as a result, information about connectivity is critical to understanding and reversing declines (Marra et al., 2015). The strength of connectivity affects gene flow, speciation rate, and the ability for populations to adapt to changing conditions (Webster and Marra, 2005).

Species that exhibit weak connectivity may be more resilient to habitat loss and other detrimental factors on the non-breeding ground, as no single region of the breeding range is composed entirely of individuals from a single non-breeding region (Gilroy et al., 2016). Understanding how different regions within the breeding range are connected to non-breeding regions can allow researchers to infer connections between demographic trends observed on the breeding ground and conditions on the non-breeding ground (Faaborg et al., 2010; Marra et al., 2011, Hewson et al., 2016; Rushing et al., 2016). Connecting breeding populations to specific non-breeding and stopover areas can be critical to the conservation of sensitive species (Cooper et al., 2017). Protecting declining migratory bird populations is therefore highly challenging without knowing the specific linkages between breeding and non-breeding populations. Despite this importance, detailed accounts of migratory connectivity are missing for many species (McKinnon and Love, 2018).

Painted Buntings (*Passerina ciris*) are small (~16g), short- to medium-distance migrants that are listed as a species of conservation concern by the US Fish and Wildlife Service (USFWS, 2008). They exist within two allopatric populations that are separated by a 500 km gap that stretches from Mississippi to Georgia (but see Gilbert et al., 2019). Much of the eastern population exists within 10 miles of the Atlantic Ocean from southern North Carolina to northern Florida, with the only significant inland intrusion occurring in central South Carolina and Georgia. The interior population occupies an area approximately twenty-five times the size of the eastern population and is centered in Texas, extending east to Mississippi, north into Kansas, and southwest into northern Mexico (Sykes and Holzman, 2005). Both populations have experienced population

decline in the last fifty years, with the eastern population declining at a steeper rate (Sauer et al., 2013). In addition to geographic variation in population trends, Painted Buntings show complex variation in migration strategies across their breeding range. Like many migratory passerines, Painted Buntings in the eastern population undergo a primary molt on the breeding ground at the end of the breeding season before initiating fall migration (Thompson, 1991). In contrast, some individuals from the interior population depart the breeding ground prior to molting (i.e. molt migration; Rohwer et al., 2005), though it is not known whether all interior Painted Buntings are molt-migrants or if this strategy is only undertaken by individuals that breed in the most arid regions of the breeding range. It is unclear how the complex distribution and variation in molting behaviors influence the strength of connectivity in Painted Buntings.

The extent to which differences in molt-migration of Painted Buntings correlate with morphological or genetic differences is unclear. Historically, two subspecies have been recognized on the basis of clinal morphological differences, with the eastern population and the eastern portion of the interior population being of the nominate race *ciris*, and the western portion of the interior population belonging to subspecies *pallidior*. Studies have shown that wing length increases from east to west across the Painted Bunting's range (Storer, 1951). More recent research has provided evidence of three genotypes, with the interior population being composed of two genetic clusters and the eastern population forming a distinct third genotype (Herr et al. 2011, Battey et al., 2018, Contina et al., 2019a, Contina et al., 2019b). The extent to which the more eastern of the two interior genotypes extends north and west out of Louisiana into Arkansas and Texas is not well resolved, and it remains unclear whether individuals from these three

genotypes remain separate on the non-breeding grounds (Sykes et al., 2007, Battey et al., 2018, Contina et al., 2019a).

I used tracking data from archival light-level geolocators to investigate the migratory connectivity of the Painted Bunting across its breeding range. I estimated the strength of migratory connectivity across multiple spatial and temporal scales: (1) range-wide breeding- to- winter connectivity, (2) breeding- to- molt connectivity in the interior population, and (3) breeding- to- winter connectivity within the eastern and interior populations. I predicted strong range-wide connectivity, as there is limited evidence that eastern and interior populations mix during the non-breeding season. Additionally, I predicted weak connectivity within the eastern population, given the small wintering range. Finally, I predicted that both breeding-winter and breeding-molt connectivity in the interior will be strong, with birds from different breeding regions within the interior population migrating to separate molting and wintering areas.

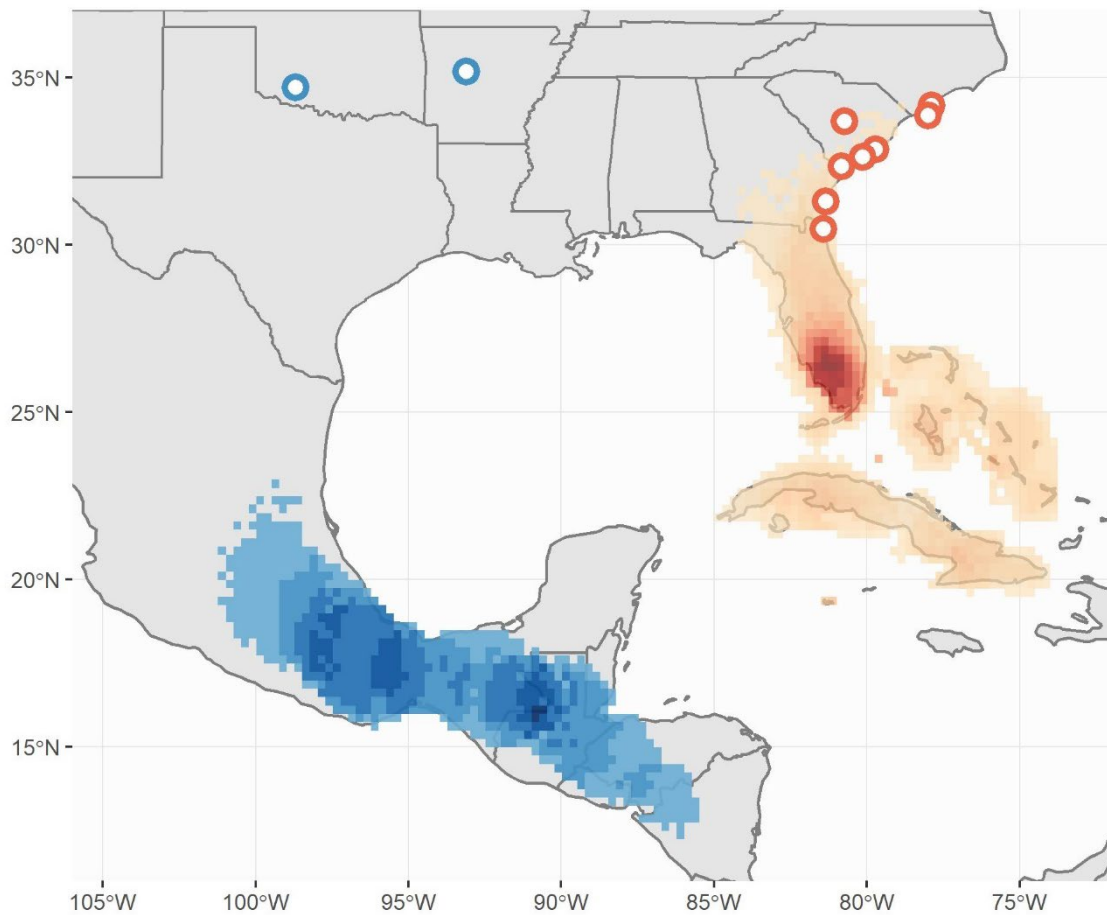


FIGURE 2. Deployment locations and probability of winter residence for eastern (red, $n = 82$) and interior (blue, $n = 10$) Painted Buntings. The intensity of the color ramp increases with the number of individuals with overlapping locations in that area. Points are breeding sites.

METHODS

Estimating the Strength of Migratory Connectivity

I used the R package MigConnectivity (Cohen et al. 2018) to quantify the strength of migratory connectivity between stationary periods: breeding, molting (interior only), and winter. The *estMC* function estimates the strength of connectivity (MC) from geolocator data while taking into account uncertainty in the estimated locations. Values

of MC between -1 and 1, although real-world scenarios typically result in an MC value that falls between zero and one (Cohen et al., 2018). Negative values indicate a propensity for birds from one region to spread out away from each other as they transition from one stationary period to the next. Values close to zero indicate that birds from all breeding regions mix uniformly on the non-breeding ground. Values close to 1 indicate that birds from individual breeding regions remain clustered together from one stationary period to the next, and remain segregated from birds from other breeding regions. *MigConnectivity* defines connectivity at the population, not individual, level, so that the user must define discrete “origin” and “target” regions. For this purpose, the non-breeding ground was binned into 5 discrete regions: Mexico, Central America, Florida, Cuba, and The Bahamas. For quantifying breeding to molting ground connectivity within the interior population, I designated two molting regions: northwest Mexico, and a more eastern region that encompasses the area between the interior breeding sites and the Gulf of Mexico. I examined range-wide (inter-population) breeding to winter connectivity, breeding to molting connectivity within the interior population, and breeding to winter connectivity within each population (intra-population). Ignoring differences in abundance between breeding regions can bias estimates of migratory connectivity when sampling efforts are not proportional to relative abundance (Cohen et al., 2018). *EstMC* allows the user to input estimates of relative abundance to account for this. Estimates of relative abundance in each region were derived from data publicly available from eBird (Fink et al., 2020) using the R package *ebirdst* (Auer et al., 2020). For each individual, I used the point-estimate generated during the core of the wintering period (December and January) as the best estimate of the wintering location.

RESULTS

I recovered 86 geolocators from the eastern population, of which 82 had viable data. I recovered 28 viable geolocators from the interior population, of which 22 collected data through the autumn molting period but stopped recording data before the bird reached the final winter destination. Eight Oklahoma tags and two Arkansas tags recorded data long enough to reveal the wintering location.

Data from light-level geolocators revealed a strong migratory divide between the eastern and interior Painted Bunting populations (Figure 2). I found no evidence that interior and eastern birds mix at any point during the annual cycle, equating to strong range-wide connectivity (Table 3). In contrast, both eastern and interior Painted Buntings exhibited low breeding-to-winter connectivity within populations (Table 3, Figure 3 and 4). In the eastern population, no portion of the wintering range was dominated by individuals from any one breeding site and all breeding sites were represented throughout most of the wintering range. Individuals from the northernmost breeding site (North Carolina, n=8) tended to migrate to the southern portion of the wintering ground, but ANOVA revealed no significant ($p < 0.05$) differences in wintering location among the breeding sites. Although sample size was limited, birds from the two interior breeding sites appeared to mix during the stationary winter period, resulting in low breeding-to-winter connectivity (Table 3).

Table 3. Estimates of migratory connectivity generated using the R package MigConnectivity. Connectivity can range from -1 to 1, with connectivity of zero indicating random mixing.

Population	Connectivity Estimate	Standard Error
Eastern vs. Interior (breeding to winter)	0.71	0.10
Eastern sites (breeding to winter)	-0.05	0.04
Interior sites (breeding to winter)	0.03	0.22
Interior sites (breeding to molting)	0.80	0.16

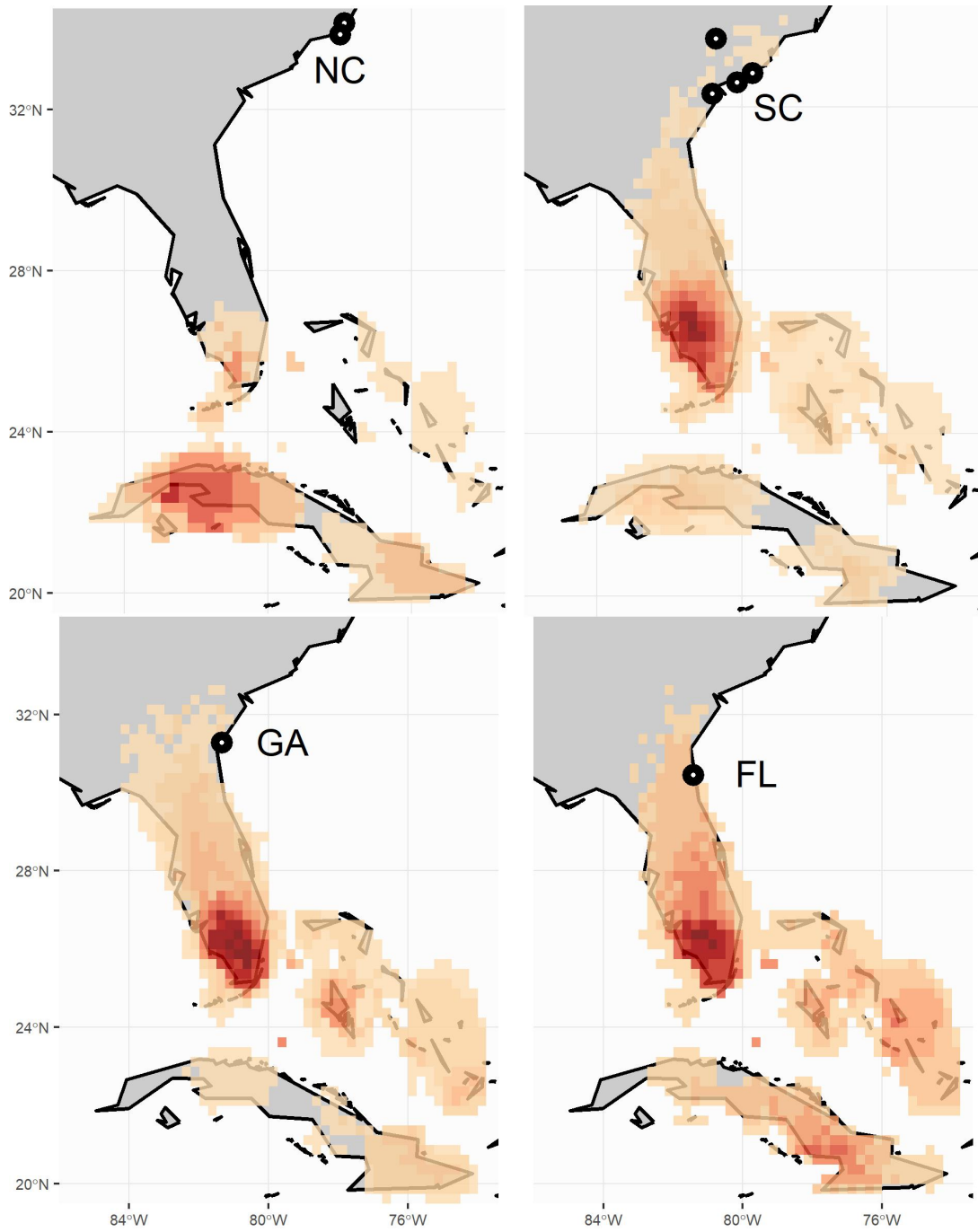


FIGURE 3. Estimated wintering locations for eastern Painted Buntings, broken up by origin state. Clockwise from top left: North Carolina, South Carolina, Florida, Georgia. The intensity of the color ramp increases with the number of individuals with overlapping locations in that area.

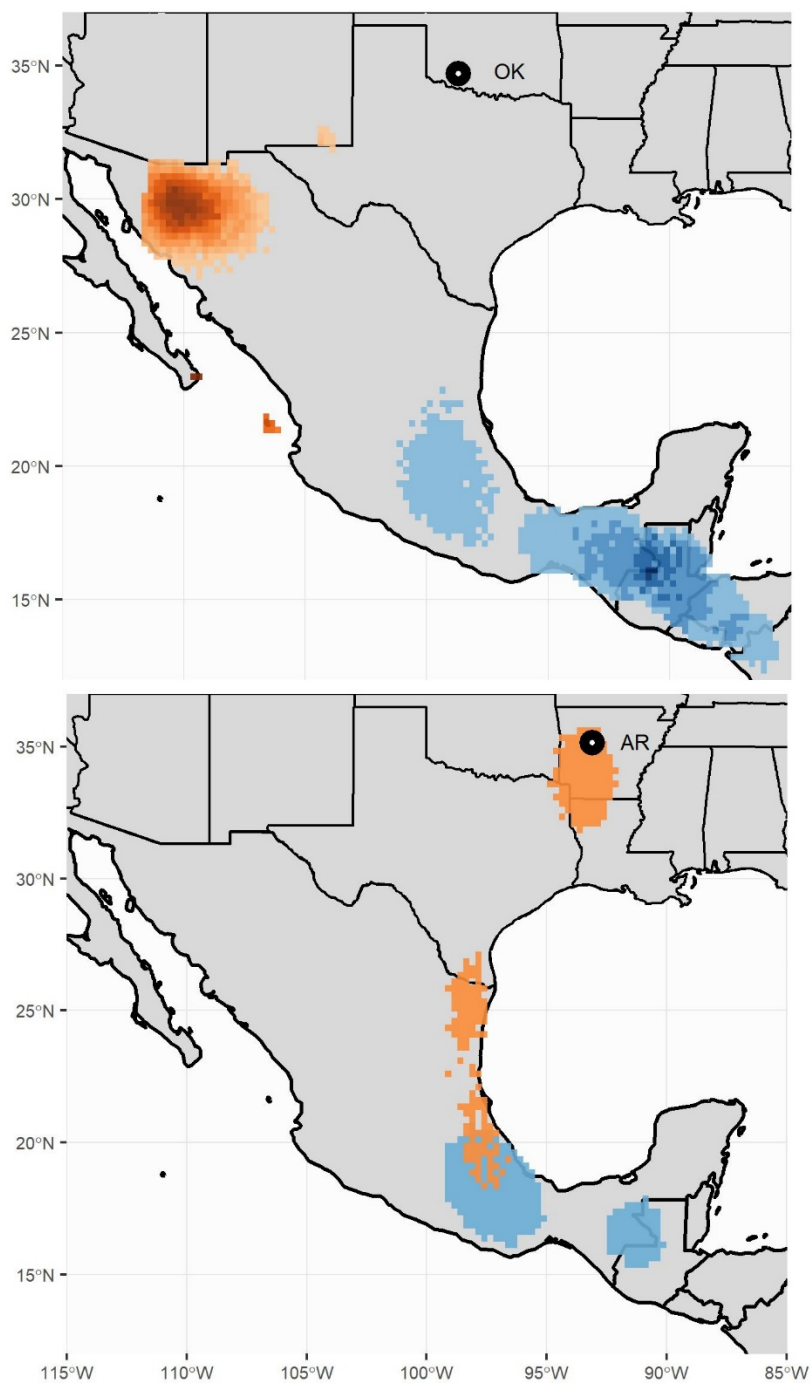


FIGURE 4. Estimated molting (orange) and wintering (blue) locations for Oklahoma (top panel, molting $n = 28$, winter $n = 8$) and Arkansas (bottom panel, $n = 2$) Painted Buntings. The intensity of the color ramp increases with the number of individuals with overlapping locations in that area.

Despite weak breeding-to-winter connectivity, breeding-to-molting connectivity within the interior population was high (connectivity = 0.81 +/- 0.16; Table 3), indicating that individuals from Arkansas and Oklahoma remain segregated during the post-breeding molting period. All Oklahoma breeders migrated to northwestern Mexico to molt. On average, individuals from Oklahoma (n=6) travelled nearly 1,500 km farther than Arkansas birds (n=2) to reach the wintering ground, and more than 2,500 km farther than birds from the eastern population. Of the two Arkansas birds, one stayed within the breeding region during the molting period before migrating around the Gulf of Mexico en route to its wintering ground in southern Mexico/ northern Central America. The second Arkansas bird forewent any prolonged stopover during the post-breeding period; it moved directly from the breeding ground to its wintering ground in southern Mexico, making its way south in short hops along the Gulf coast.

DISCUSSION

Migration strategy and migratory connectivity can differ drastically within and between populations of a single species. At the range-wide scale, eastern and interior Painted Buntings exhibited strong migratory connectivity, with no evidence of mixing at any point in the annual cycle. This result is contrary to some predictions that birds from the eastern population might winter in Mexico/Central America (Sykes et al., 2007), but supports the findings of more recent work, which has found little evidence of mixing between eastern and interior birds (Battey et al. 2018, Contina et al. 2019a).

Interior birds exhibited strong connectivity during the molting period. Painted Buntings breeding in Arkansas and Oklahoma remained entirely separated during the molting period, indicating the presence of a molting divide between the two adjacent

breeding populations. In addition to the spatial divide, I observed evidence of different molting period strategies within the interior population. All Oklahoma birds travelled to northwestern Mexico and remained there for nearly 2 months during the molting period. Both Arkansas birds departed the breeding ground, stopped over for about three weeks (eastern/ southeastern TX), and then continued on to the wintering ground. One Arkansas bird left the breeding ground around August first and made its way south to the wintering area without any prolonged stopovers, indicating that it likely completed molt on the wintering ground. The second Arkansas bird stayed within the breeding region until late September, which suggests the possibility that it may have molted on the breeding ground. Overall, these results indicate that a large portion of the interior population may funnel into the Sonora/Sinaloa monsoon region to molt, but also that alternate strategies exist. Further work is needed to understand how pervasive each strategy is and the demographic and genetic consequences of these movements.

Despite strong range-wide connectivity, intra-population breeding-to-winter connectivity was weak. During the nonbreeding season, individuals from all eastern breeding sites co-occurred throughout the winter range, though individuals breeding in North Carolina were less likely to winter in Florida than individuals from other breeding sites. Although based on only 8 geolocator recoveries, Painted Buntings from the northern edge of the eastern breeding range appear to migrate primarily to the southernmost portion of the eastern winter range. This "leapfrog" migration pattern (Alerstam and Hogstedt 1980) is common in songbirds (Clegg et al., 2003; Stanley et al., 2015) and could result in northern populations of eastern Painted Buntings being more at risk of threats specific to Cuba (Rushing et al. 2020). Breeding-to-winter connectivity

within the interior population was similarly weak. My results indicate that birds from Arkansas and Oklahoma do not occupy unique portions of the wintering range, though larger sample sizes are needed to determine the full extent to which this mixing occurs.

My results demonstrate the impressive range of migratory behavior that is possible within a single species. Particularly within the interior population, my results demonstrate striking variation in migratory and molting strategies. This variation supports the hypothesis that molt migration in the west is a flexible process that is driven by decisions made by individual birds and not defined at the population or species level (Pyle et al, 2009). My results from Arkansas suggest that some Painted Buntings from less arid regions of the interior breeding range may remain on the breeding ground during the molting period like their eastern counterparts or may migrate directly to the wintering ground without interrupting migration to molt (continuous molt-migration: Tonra and Reudink, 2018). This divergence of migratory behavior has profound implications on migratory distance. On average, individuals from Oklahoma that molted in northwest Mexico travelled nearly 1,500 km farther than Arkansas birds to reach the wintering ground, and more than 2,500 km farther than birds from the eastern population. This sizable difference in migratory distance provides support for the theory that morphological differences observed in Painted Buntings (increasing wing length moving from east to west) are selected for and maintained by a migratory divide during the molting period (Battey et al., 2018). It should be noted that the low spatial resolution of geolocator data does not allow for the detection of the very short-range molt-migration movements that may be more common than previously believed (Pyle et al., 2018).

My results also underscore the scale-dependence of migratory connectivity, with strong range-wide connectivity and weak regional connectivity. Weak migratory connectivity within the eastern population could be an important attribute if habitat loss continues or accelerates in the future. Low connectivity can help to mediate the effect of winter habitat loss, as negative effects are spread across the entire breeding range (Finch et al., 2017). This effect could be especially important to the eastern population, which exists in an area 25 times smaller than the interior population and may be declining faster (Sauer et al., 2013). Much of the breeding/winter range of the eastern population is characterized by intense human development (Jones et al., 2013; Napton et al., 2010), to which low connectivity should promote resilience. On the other hand, the lack of immigration between the two populations could have conservation implications in the future as the eastern population continues to be threatened with habitat destruction and other threats on the wintering grounds. Without immigration from the much larger interior population, eastern Painted Buntings are completely reliant on this increasingly fragmented coastal habitat.

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CHAPTER III

MIGRATORY PHENOLOGY OF PAINTED BUNTINGS

INTRODUCTION

Thousands of bird species around the world make predictable annual movements as they transition between spatially disjunct periods of their annual cycle. These movements are often motivated by seasonality and have evolved to capture the fitness benefits of breeding site fidelity while avoiding unfavorable conditions caused by resource senescence (Winger et al., 2019). The timing of these movements has been extensively studied and discussed, but the highly nuanced or even contradictory conclusions about what motivates migratory phenology suggest that the relative importance of different selective forces may vary by species or even by population (Knudsen et al., 2011; Miller-Rushing et al., 2008; Jenni and Kery, 2003; Richardson, 1990). In particular, the degree to which arrival and departure phenology are driven by environmental conditions (flexible migration phenology) vs. genetic programs (scheduled migration phenology) remains unresolved (Vardanis et al., 2011; Pedersen et al., 2018).

The ability to adjust migration timing in accordance with environmental conditions allows individuals to maximize their exposure to resources in seasonal habitats in which the timing and magnitude of resource escalation and senescence can vary significantly from year to year (Melaas et al., 2013; La Sorte et al., 2015; Rickbeil et al., 2019). When migrating to the breeding grounds, arrival timing is generally thought to be a trade-off between arriving early to secure limited breeding habitat and mates versus avoiding the danger of inclement conditions in early spring (Aebischer et al., 1996; Newton, 2007). Some species may track environmental conditions en route to the

breeding ground to optimize their arrival on the breeding ground within the context of this trade-off (Balbontin et al., 2009). Flexible phenology can also help individuals optimize their departure. For migratory birds that are not territorial in the non-breeding season, the timing of that departure is driven not as much by competition to get to the non-breeding ground first, but by the decline in suitability of environmental conditions on the breeding ground (Newton, 2010; Xu and Si, 2019). Flexibility in migration phenology can also be a result of unpredictable resource availability, not just an adaptation to take advantage of it. Research has shown that birds wintering in the Caribbean arrive at the breeding ground later when conditions on the wintering ground are less productive, suggesting that individuals are forced to adjust their migration based on food availability or other environmental conditions (McKeller et al., 2013).

Flexible departure behavior may be disadvantageous if selective forces other than breeding ground condition affect annual survival or fitness. For example, delaying fall departure to take advantage of favorable late-season conditions on the breeding ground could have fitness carryover effects for birds that are territorial on the non-breeding ground. Individuals that arrive late to the wintering ground may be relegated to a poor-quality territory, which can delay spring arrival on the breeding ground, which is associated with reduced fitness (Marra et al., 1998; Studds and Marra, 2005). Under these conditions, when the “pull” of the destination location is disconnected from the “push” of the origin location, scheduled migration may be advantageous.

Scheduled migration phenology may be favored when birds are not able to accurately sense the condition of their target destination (Both and Visser, 2001). Long-distance migrants departing from the tropics may have no mechanism for judging the

progression of spring at their breeding ground and must rely on photoperiod to cue migration (Gwinner, 1990). One potentially disadvantageous aspect to scheduled phenology is that it may not allow individuals to maximize exposure to resources in non-average years. Endogenous control of migration may put individuals at risk in years when scheduled arrival is too early relative to the onset of favorable conditions (Newton, 2007). Additionally, scheduled migration can restrict a species' ability to quickly adapt to climate change and can lead to phenological mismatch (Doiron et al., 2015).

Selection for flexible versus scheduled migration phenology can be affected by the relative strength of factors that push individuals away from one stationary period (decreasing food availability, dropping temperatures, etc.) and pull individuals to the next stationary period (a flush of resources, warmer temperatures, etc.). Patterns of migration can be shaped by the speed at which resources become available and for how long they remain available (Aikens et al., 2020). It is unclear how differences in the magnitude or timing of breeding ground productivity may influence selection for scheduled versus flexible phenology. Flexible migration may be selected for in birds that rely on resources that increase and decrease gradually, as the fitness costs of arriving a few weeks early or late are relatively low. For birds migrating to a location where resources are ephemeral, the narrow window of time that birds must arrive in order to effectively take advantage of resources may favor strict, repeatable timing. By this logic, territoriality may also encourage scheduled migration, as late arrival to a territorial stationary period can have significant fitness consequences. Life history traits can affect selection for migration strategy. For example, the ability to double-brood and differences in migration length have been shown to affect how birds are able to adjust their phenology to match

environmental conditions (Jenni and Kery, 2003). Climate change is pushing back the average fall departure date for double-brooded species more than single-brooded species, because double-brooded species are increasingly extending the breeding season to take advantage of longer summers. It is unclear how molt strategy affects selection for arrival/departure strategy. Flexible migration may be favored in molt-migrants, giving them the ability to depart for the molting ground early if they finish reproduction early due to nest failure (Bridge et al., 2011).

Painted Buntings (*Passerina ciris*) provide a unique system to examine the drivers behind migratory phenology. This species has two distinct breeding populations with contrasting life history strategies. Eastern birds molt on the breeding ground before migrating to the non-breeding ground, where they are not territorial. At least some interior birds are molt-migrants, migrating to northwest Mexico to molt before continuing on to the wintering ground. Reports of extreme aggression between interior Painted Buntings on the molting ground suggest that there may be strong selection to arrive at the molting area quickly to compete for resources (Rohwer et al., 2020). In general, the interior range experiences a flush of productivity in early spring but becomes increasingly arid as the summer progresses. In contrast, the eastern population has a gradual green-up that peaks midsummer before slowly declining in the fall (Figure 5).

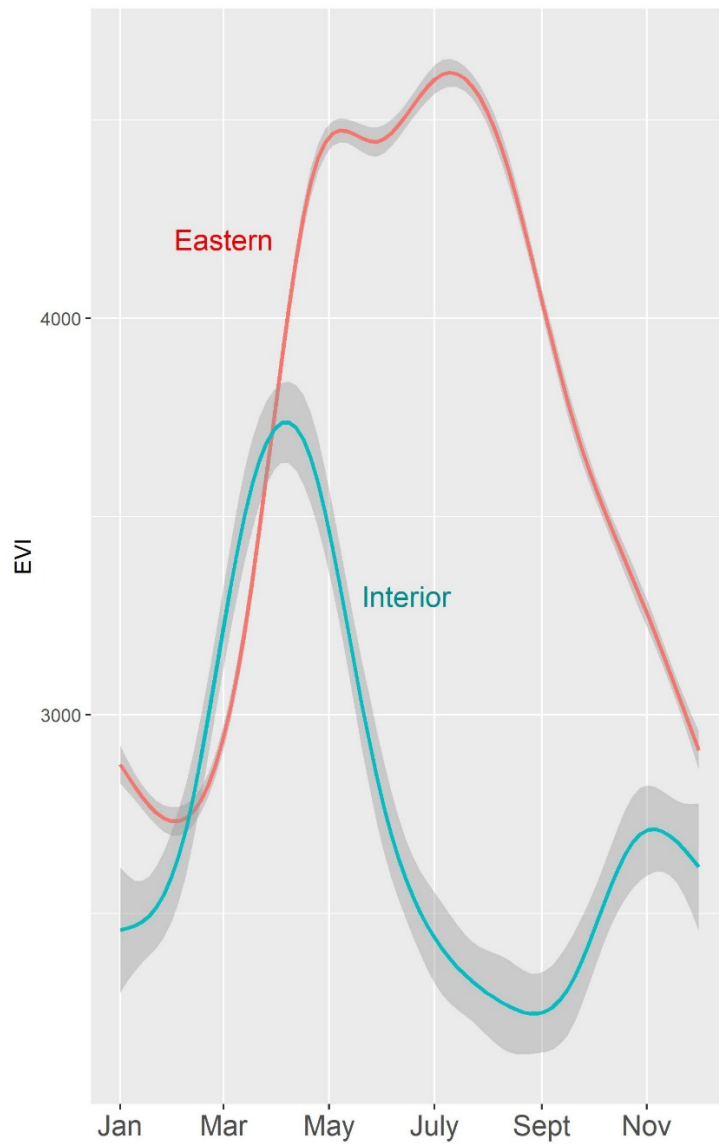


FIGURE 5. Vegetation greenness over the course of the year for the interior (blue) and eastern (red) population.

I used light-level geolocator data from 113 Painted Buntings from 10 different breeding sites to examine differences in migratory phenology across the species-wide breeding range and evaluate likely predictors for arrival and departure timing.

If Painted Bunting phenology is flexible, I predict that birds will adjust their phenology from year to year in accordance with conditions on the breeding ground. In

years with early springs, I would expect birds to arrive on the breeding ground earlier than in years with colder spring temperature and later leaf-out dates. Likewise, in years when the progression from summer to autumn occurs earlier or faster, I would expect birds to depart the breeding ground earlier than in years when the onset of cold weather is delayed. If migration in this species has a significant endogenous component, birds should arrive and depart the breeding ground at roughly the same time every year, regardless of inter-annual variation in breeding ground conditions. I would expect interior birds to be flexible in their fall departure if departure is largely dictated by completion of reproduction. However, it may be that fall departure is repeatable from year to year in order to time arrival on the molting ground with the annual monsoon-driven bloom in resources. I would expect Painted Buntings to show evidence of scheduled spring arrival due to competition for territories and mates upon arrival to the breeding ground. Likewise, I would expect eastern birds to be flexible in their fall departure, as there is no ephemeral resource on the wintering ground imposing strict selection on fall departure, and Painted Buntings are not known to be territorial on the non-breeding ground.

METHODS

Estimating Arrival/ Departure Dates

Estimating dates of arrival/departure from light-level geolocator data is complex and should be done with care (Lisovski et al., 2018). I defined departure as a significant (>2 degrees) longitudinal movement away from a known stationary location. To determine arrival, I looked for longitude to stabilize during a stationary period, and then tracked backwards until longitude moved significantly (>2 degrees) away. I only assigned

arrival/ departure dates for individuals whose movements allowed confident determination of arrival/departure. Some individuals had such little longitudinal movement or migrated such short distances that assigning arrival or departure dates was not feasible or appropriate. I excluded females from this analysis because sex-related differences in phenology are well-established and breeding sites had different male: female ratios. Additionally, I did not include spring arrival for Oklahoma birds in this analysis because sample size was limited (Table 4).

Table 4. Sample sizes of estimated dates of spring arrival and fall departure for each state.

	Oklahoma	North Carolina	South Carolina	Georgia	Florida
Spring Arrival	2	5	22	14	12
Fall Departure	28	6	20	12	11

Extracting Environmental Covariates

I extracted environmental covariates from Google Earth Engine databases using the R package *rgee* (Aybar et al., 2020; Didan, 2015; Copernicus Climate Change Service, 2017). I used enhanced vegetation index (EVI) to quantify primary productivity. EVI is similar to normalized difference vegetation index (NDVI), but does not saturate as quickly and is less affected by shadows, air moisture, or variations in the soil (Huete et al., 2002). These properties help ensure accurate comparisons of vegetation greenness across dissimilar landscapes and atmospheric conditions. Measurements of vegetation greenness have been shown to be a useful proxy for insect abundance, which is a required resource for successful reproduction (Fernandez-Tizon et al., 2020). For each Painted Bunting included in the analysis, I extracted environmental variables from an area +/- 0.5

degrees longitudinally and latitudinally surrounding the known breeding location. The full list of predictive variables included EVI, delta EVI, minimum daily temperature, year, origin latitude, and breeding to winter migration distance (Table 5). EVI data was only available for download at the bimonthly timescale. Delta EVI is a measure of the rate of change of vegetation greenness. This metric, also known as the instantaneous rate of green-up, has been shown to drive green wave surfing in herbivores (Van der Graaf et al., 2006). Because rapidly growing vegetation is more nutritious, herbivores benefit from staying as close to the leading edge of spring green-up as possible. Many insects prefer or require young plant growth, so here I extend this concept of green wave surfing to insectivorous birds (Cizek, 2005; La Sorte et al., 2014). Additionally, sharp declines in vegetation greenness may be a stronger cue for departure than gentle declines, even if overall greenness is higher. If minimum daily temperature is a significant predictor, it would signal that birds cue in on temperature to schedule their arrival/ departure (Tottrup et al., 2010). Lastly, I included breeding to winter migration distance as a predictor. Migration distance as a significant predictor of arrival/ departure could signal that birds are constrained/ motivated by migration distance.

Table 5. List of environmental covariates with descriptions.

Variable Name	Description	Ecological Interpretation	Prediction
EVI	Index of vegetation greenness	The magnitude of vegetation greenness is an important cue to birds	Birds will time their arrival/ departure to coincide with a certain threshold level of vegetation greenness
Delta EVI	$EVI - EVI_{t-1}$	Birds cue in on how quickly vegetation is greening up or senescing, not just the magnitude	Birds will time their arrival/ departure to coincide with a certain rate of EVI increase/ decline
Minimum daily temperature	Minimum Temperature	Constraints on thermoregulation may motivate arrival/ departure	Birds will depart the breeding ground when the temperature drops below a certain threshold
Migration Distance	Breeding to winter migration distance (km)	Birds with longer migrations may be more constrained in their arrival/ departure	Birds with longer migration will arrive later on the breeding ground

Model Selection and Validation

I first used 2-sample t-tests to test for differences in phenology between the eastern and interior population. Additionally, I used ANOVA to test for significant differences in phenology among years in each population. Then, for each population, I constructed a linear model of fall departure date using the predictors listed in Table 5 to test which factors are associated with Painted Bunting departure phenology. I followed the same procedure for modeling spring arrival date within the eastern population. To ensure that the phenology models did not include highly-correlated predictor variables, I used the Pearson correlation method to test for pair-wise correlation among all predictors. Within the interior population, EVI and delta EVI were highly correlated (correlation coefficient > 0.8). To reduce redundancy, I chose to exclude delta EVI because it had lower explanatory power on its own than EVI. Additionally, latitude was excluded from the interior model because there was only one breeding site sampled within that population. For each population, I generated all possible subsets of the global model (Equations 1 and 2) and then ranked these models using AICc. Models within two AIC units were considered of equivalent value. I used leave-one-out cross validation (LOOCV) to validate top-ranked models.

Equation 1.

Global Model: Eastern Population

$$\text{Fall Departure / Spring Arrival} \sim \text{Year} + \text{EVI} + \text{Delta EVI} + \text{Temperature} + \text{Latitude} + \text{Migratory Distance}$$

Equation 2.

Global Model: Interior Population

$$\text{Fall Departure} \sim \text{Year} + \text{EVI} + \text{Temperature} + \text{Migratory Distance}$$

RESULTS

Interior Buntings arrived later in the spring than eastern Buntings, though this effect was not found to be significant (likely due to sample size $n=2$ for interior birds). I found that interior birds departed the breeding ground 75 days earlier on average than eastern birds (Figure 6).

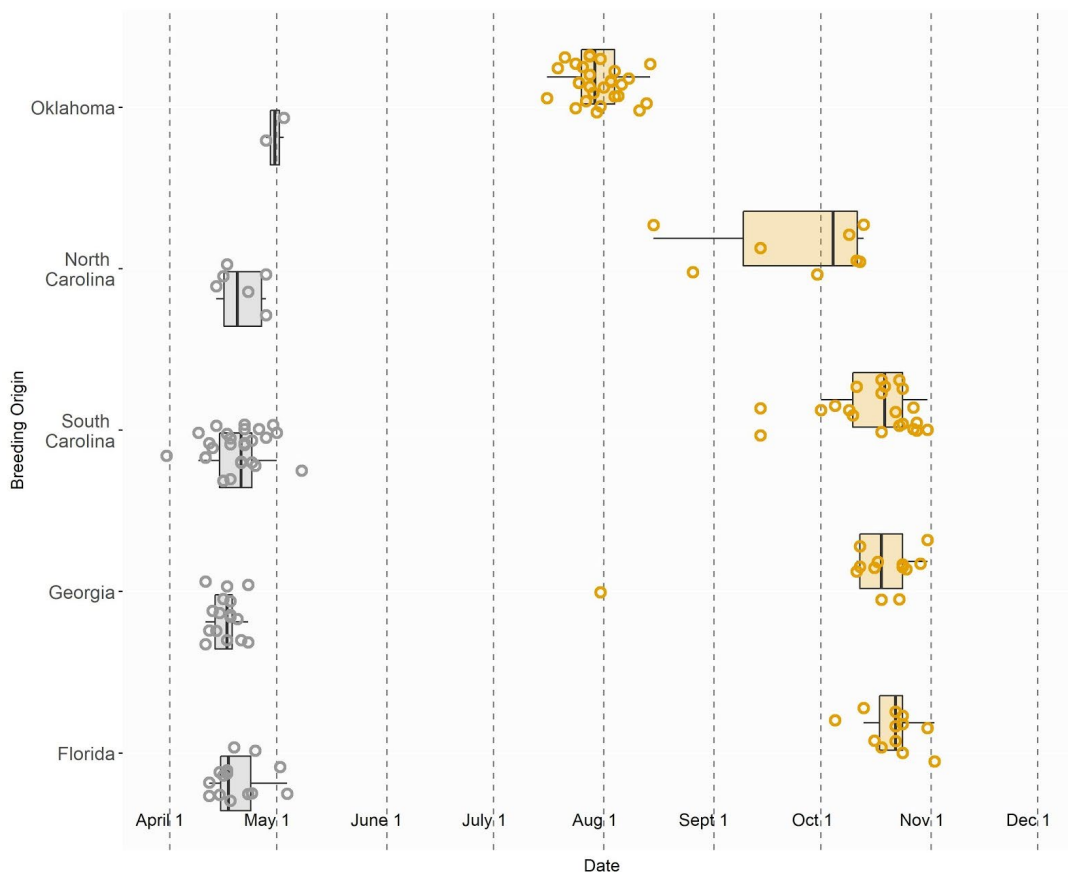


FIGURE 6. Estimated phenology for male Painted Buntings from five states. Grey circles spring arrival dates for individuals, yellow circles are fall departure dates for individuals.

There were two equivalent top models for spring arrival in the eastern population (Table 6). Both models included year, EVI, delta EVI, and temperature. The second model also included migratory distance and performed slightly better when cross-validated (0.13 vs. 0.10). The three top models for fall departure in the eastern population all included breeding latitude, EVI, and migratory distance (Table 7). Cross-validation revealed that these models were able to account for a large amount of variation in fall departure date ($R^2 = 0.86 - 0.87$). There were four equivalent top models for fall departure in the interior population, but the most parsimonious was the null model (Table 8). Cross-validation indicated poor performance in the three less parsimonious models, with R^2 values falling between 0.01 and 0.03.

Table 6. Top spring arrival models ($\Delta < 2$) for eastern Painted Buntings. Check marks indicate included predictors. AICc is a relative model performance score that allows model comparison. The last two columns are outputs of cross-validation and measure predictive performance. Mean absolute error (MAE) describes the average absolute difference between observed and expected outcomes, while R^2 describes the correlation between predicted and observed values.

Model Number	Year	EVI	Delta EVI	Minimum Daily Temperature	Lat	Migratory Distance	AICc	Δ AICc	R^2	MAE
1	✓	✓	✓	✓	✗	✗	328.4	0	0.10	4.13
2	✓	✓	✓	✓	✗	✓	328.4	0.01	0.13	4.01

Table 7. Top fall departure models ($\Delta < 2$) for eastern Painted Buntings. Check marks indicate included predictors. AICc is a relative model performance score that allows model comparison. The last two columns are outputs of cross-validation and measure predictive performance. Mean absolute error (MAE) describes the average absolute difference between observed and expected outcomes, while R^2 describes the correlation between predicted and observed values.

Model Number	Year	EVI	Delta EVI	Minimum Daily Temperature	Lat	Migratory Distance	AICc	Δ AICc	R^2	MAE
1	✗	✓	✓	✗	✓	✓	320.2	0	0.87	4.95
2	✗	✓	✓	✓	✓	✓	321.1	0.94	0.86	5.03
3	✗	✓	✗	✓	✓	✓	321.1	0.95	0.86	5.00

Table 8. Top fall departure models ($\Delta < 2$) for interior Painted Buntings. Check marks indicate included predictors. AICc is a relative model performance score that allows model comparison. The last two columns are outputs of cross-validation and measure predictive performance. Mean absolute error (MAE) describes the average absolute difference between observed and expected outcomes, while R^2 describes the correlation between predicted and observed values.

Model Number	Year	EVI	Minimum Daily Temperature	Migratory Distance	AICc	Δ AICc	R^2	MAE
1	✗	✗	✓	✗	191.2	0.00	0.03	5.82
2	✗	✓	✓	✗	192.8	1.57	0.01	5.83
3	✓	✗	✓	✗	192.9	1.69	0.01	5.79
4	✗	✗	✗	✗	193.0	1.73		

DISCUSSION

The drivers of migration phenology are easiest to intuit at the very fine-scale and the very broad-scale. For example, we know that birds are less likely to initiate migration when there is a headwind because it is less efficient to fly into the wind (Liechti, 2006).

Similarly, we understand that boreal breeders that arrive on the breeding ground in February would almost certainly starve or succumb to the elements before breeding commences. Studies that seek to identify potential drivers of phenology at an intermediate scale often have diverse results because the composition and relative strength of the factors considered (local climate, thermotolerance, reproductive strategy, foraging guild, carryover effects, geography, etc.) likely differ for every population (Beaumont et al., 2006; Moussus et al., 2011; Vaitkuvienė et al., 2015). For example, in response to warming climate and longer summers, some species are leaving earlier, some leaving later, and some have shown no change at all (Haest et al., 2019). This variation in response suggests that even well-supported hypotheses regarding migration phenology may not be universally applicable and should be tested at the population level by tracking individual organisms in both spring and fall.

The progression of spring did not occur uniformly in all three years that I tracked eastern painted buntings. In the first year, spring was colder and later than the next two years. Spring green-up lagged about a month behind and peak summer greenness occurred approximately two weeks later in the first year compared to the next two years. The top-ranked linear model for spring arrival in the eastern population included three different environmental variables (EVI, delta EVI, and temperature) in addition to migratory distance and year (Table 6). However, the model performed poorly in cross validation and was only able to explain 13% of the variation in spring arrival. Despite these findings, I found no significant differences in spring arrival date between any of the three years ($p = 0.97$). These results suggest that, although the spring arrival is fairly

consistent from year to year, individuals may tweak their arrival in accordance with environmental conditions.

For the first two years of data, there was no significant difference in breeding ground departure timing from year to year in the eastern population ($p = 0.77$). In the third year, fall departure occurred slightly earlier than the first two years ($p = 0.03$), but sample size was very small for that year (only 5 individuals, each from a different breeding site). Unlike in spring, there was little annual variation in autumn EVI or temperature during the study period. Without variation in environmental conditions, it is difficult to say whether consistent migration timing is the result of endogenous timing or simply birds reacting to the same conditions every year. However, all of the top models for fall departure in the eastern population included environmental covariates (EVI + delta EVI or temperature or both) in addition to latitude and migratory distance (Table 7). This hints that eastern Painted Buntings may adjust their fall departure in accordance with temperature and vegetation greenness.

Interannual variation in environmental conditions during the departure period did occur in the interior population. In year one, spring green-up and fall decline both occurred approximately a month earlier than in year two. Interior birds left at the same time both years, despite a considerable difference in EVI between the two years. Of the four top-ranked models, the most parsimonious was the null model (Table 8). The three other equivalent models had low explanatory power ($R^2 = 0.01- 0.03$). Similar to spring arrival in the eastern population, my results do not show evidence that interior birds adjust their departure phenology in accordance with variation in environmental conditions.

This difference in fall departure between eastern and interior painted buntings likely has to do with the considerable differences in both migration strategy and the environments in which the two populations exist. Eastern Painted Buntings experience a greener breeding ground than interior Painted Buntings from arrival to departure. The highest EVI experienced by Painted Buntings at the interior site was still lower than the lowest EVI experienced by eastern birds. Interior birds arrive on the breeding ground near peak greenness, and the breeding ground becomes progressively drier as the breeding season moves forward. Because of this aridity, interior Painted Buntings have evolved to be molt-migrants, meaning they leave the breeding ground to molt at the end of the breeding season. As the breeding ground is drying, the molting ground is greening up, so interior Painted Buntings are likely under pressure to depart the breeding ground as soon as reproduction is complete. The molting ground rapidly flushes with productivity due to monsoon rains, but begins to dry again as fall progresses. This selection to take full advantage of an ephemeral resource likely overpowers any selection for remaining on the breeding ground just because EVI may be higher in that year. In contrast, eastern birds arrive about two months before peak greenness and have plenty of time to complete reproduction on a wet, productive landscape. Eastern birds molt on the breeding ground, so there is no selection for expeditious departure following reproduction.

These results provide support for the idea that migration phenology may not be as simple as endogenous control versus flexible individual choices. Eastern Painted Buntings may be less constrained in their fall departure, which allows for flexibility. Eastern buntings breed on a mild landscape, migrate short distances, and many have access to supplemental food year-round. Interior buntings breed on a much drier

landscape with a shorter window for reproduction. Additionally, these molt-migrants have an extra step in their migration and winter much farther from their breeding ground than eastern birds do. These constraints likely limit the benefit of staying on the breeding ground after reproduction is completed. The notable differences in phenology within this single species speak to the extent to which a bird's migration is shaped by the environments in which it exists.

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CHAPTER IV

DIFFERENTIAL MIGRATION OF PAINTED BUNTINGS

INTRODUCTION

Differential migration describes the phenomenon wherein certain cohorts within a migratory population differ in migratory behavior, including timing, route, or destination (Ketterson and Nolan, 1983). Sex-related differential migration appears to be common in migratory birds. In many passerines, males and females show consistent differences in phenology and migration distance (Otahal, 1995; Stouffer and Dwyer, 2003; Palacin et al., 2009). For example, female dark-eyed juncos (*Junco hyemalis*) winter farther south on average than males (Ketterson and Nolan, 1976) and in many species, males arrive on the breeding ground earlier than females, known as protandry (Francis and Cooke, 1986; Morbey and Ydenberg, 2001).

Numerous hypotheses have been proposed to explain observed patterns of differential migration related to migration distance and timing (Ketterson and Nolan, 1976), with most hypotheses focusing on asymmetric costs or benefits of different migration strategies (Table 9). The rank-advantage hypothesis states that intra-sex competition for territories selects for early arrival. Individuals that arrive later are relegated to poorer quality territories and have reduced fitness. Because intra-sex competition occurs in both sexes, simultaneous male-female arrival on the breeding ground would support the rank-advantage hypothesis. The susceptibility hypothesis suggests that differential migration occurs because one sex is more susceptible to adverse environmental conditions (Ketterson and Nolan, 1983). For example, the smaller sex may arrive later to the breeding ground because it is more susceptible to cold early spring

temperatures. Additionally, the larger sex may have increased cold tolerance that allows it to spend the winter farther north. Decreasing body size has been connected to climate warming, indicating that body size correlates with thermal tolerance (Buskirk et al., 2010). If differential migration is driven by differences in susceptibility between males and females, I would expect protandry to increase with latitude. Because daily minimum temperatures decrease with latitude, constraints due to cold weather should also increase with latitude. In addition, I would expect it to be warmer on average when females arrive than when males arrive. The constraint hypothesis suggests that differences in phenology occur because one sex is constrained (by migration distance, for example) more than the other in how early it can reach the breeding ground. If the constraints drive differential migration in this system, I would expect differential migration (e.g., females arrive later than males) to be accompanied by a constraining mechanism (e.g., females winter farther away than males). Additionally, I would not expect to see protandry/ protogyny in fall departure, as males and females occupy the same habitats during the breeding season, so there is no mechanism of restraint. The mate-opportunity hypothesis states that males arrive before females because males maximize their mating opportunities by arriving early relative to females. Well-defined protandry in the spring regardless of differences in wintering location would lend support to the mate-opportunity hypothesis. Additionally, I would not expect a differential fall departure, as there is no sexual selection for arrival timing going into the non-breeding season. Indirect support for the mate-opportunity hypothesis is provided by studies that show a lack of spring protandry in sexually monogamous species (Hedh and Hedenstrom, 2020).

I used light-level geolocator data from male and female eastern Painted Buntings to test for sex-related differences in migration distance and timing and evaluate the likely influence of four different hypotheses that can result in differential migration.

Table 9. Hypotheses for differential migration.

Hypothesis	Mechanism	Outcome
Rank-advantage	Intra-sex competition for limited territories and mates	Both sexes arrive as early as possible
Susceptibility	Stronger selection for more susceptible (smaller) sex to avoid exposure to adverse early spring conditions on the breeding ground	Smaller sex arrives later on breeding ground
Constraint	One sex is constrained by migration distance/ non-breeding territory quality/ physical attributes in its ability to reach the breeding ground as early as the other sex	Constrained sex arrives later on the breeding ground
Mate-opportunity	Males (or females, in polyandrous species) optimize mating opportunities by arriving early relative to females	Males (or females, in polyandrous species) arrive first

METHODS

Geolocator Deployment

During the summer of 2019, I deployed 47 geolocators on ASY females and 53 geolocators on ASY males. The following summer I recovered 11 female geolocators and 9 male geolocators. In addition, I had tracking data from 62 males from previous years, for a total of 71 males and 11 females (Table 10).

Table 10. Recovered geolocators for male and female eastern Painted Buntings.

	Female	Male	Total
North Carolina	2	6	8
South Carolina	5	27	32
Georgia	2	21	23
Florida	2	17	19
Total	11	71	82

Testing for Differential Migration

I used 2-sample t-tests to test for differences in migration timing and non-breeding location between males and females. I tested for differences in winter latitude, winter longitude, breeding to winter distance, fall departure date, and spring arrival date (Table 11). I built three linear models to test for an effect of latitude and migration distance on differential arrival to the breeding ground, one with sex as the sole predictor, one with an interaction between sex and breeding latitude, and one with an interaction between sex and migration distance. I compared these three models using a likelihood ratio test.

Table 11. Predictions for each hypothesis for differential migration. Check marks indicate differences that must be detected for that hypothesis to be supported. X's indicate differences that should not be present for that hypothesis to be supported.

Hypothesis	Differences in migration distance	Differences in temperature at arrival	Protandry - Spring Arrival	Spring protandry increase with latitude	Protandry - Fall Departure	Protogyny - Fall Departure
Rank-advantage			✗	✗	✗	✗
Susceptibility		✓	✓	✓	✗	✓
Constraint	✓		✓		✗	✗
Mate-opportunity			✓		✗	✗

RESULTS

Spring arrival was earlier for males than females (Table 12, $p < 0.01$). I found no significant difference in breeding to winter migration distance between males and females ($p = 0.19$), although males wintered farther south and east than females (Figure 7, Table 12, $p = 0.02, 0.03$). Although the mean fall departure date for females was ten days earlier than males, the median departure dates were only one day apart and the difference was not significant ($p = 0.44$). I found no significant difference in breeding ground temperature at arrival between males and females ($p = 0.34$). Including interactions between sex and latitude or sex and migration distance in a linear model of spring arrival did not improve model fit over the sex-only model ($p = 0.73, 0.43$), indicating that neither breeding latitude or migration distance are useful predictors of protandry. See Figure 8 for distribution of data points with boxplots.

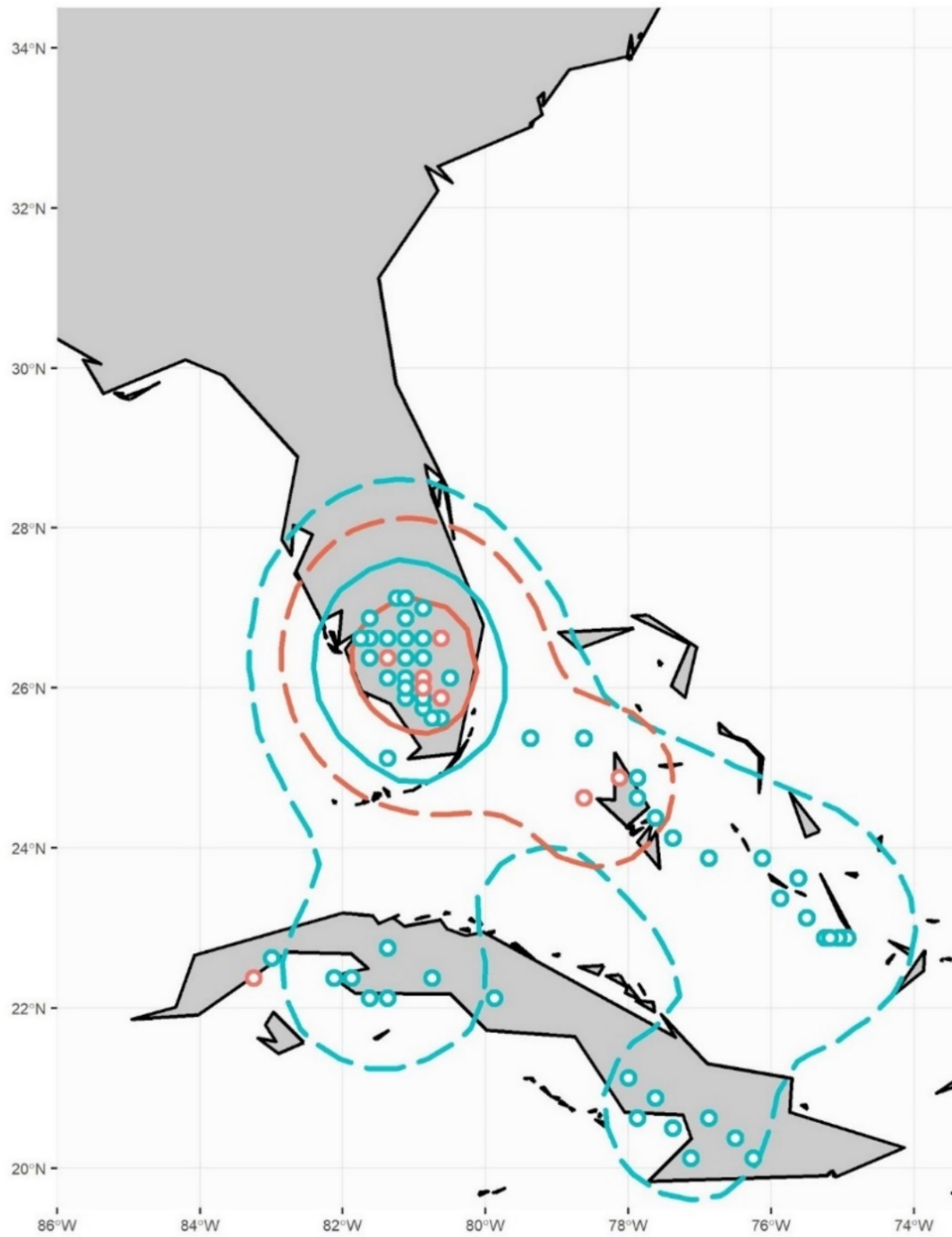


FIGURE 7. 75% and 25% utilization kernels for male (blue) and female (red) eastern Painted Buntings on the non-breeding ground. Points represent weighted median winter (Dec-Jan) locations for each individual. Kernels were calculated using R package *adehabitat* (Calenge, 2006).

Table 12. Mean winter location, migration distance, and phenology, with associated p values ($p < 0.05 = \text{bold text}$) for male and female Painted Buntings.

	Female	Male	p
Winter Latitude	25.66	24.43	0.02
Winter Longitude	-80.73	-79.54	0.03
Breeding to Winter (km)	745	859	0.19
Fall Departure Date	276	287	0.44
Spring Arrival Date	118	107	<0.01

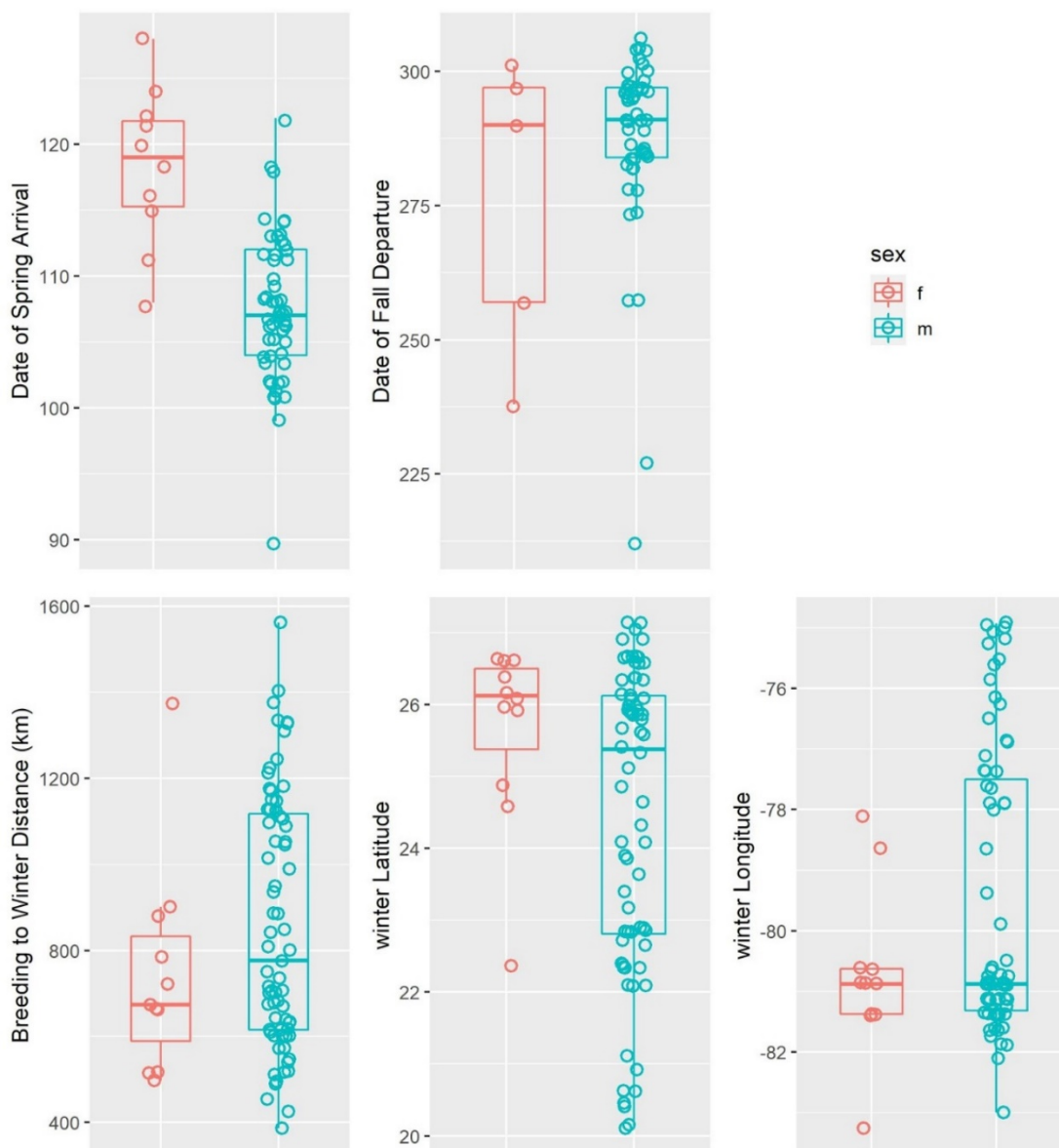


FIGURE 8. Migration distance and timing data (Julian date) from male and female Painted Buntings.

DISCUSSION

The eastern population of Painted Buntings provides a unique lens through which to view differential migration because the breeding and wintering ranges are so geographically constrained. The breeding range stretches only 500 km from north to

south and, on average, individuals travel only 850 km to reach their wintering ground. To put that in context, many of the species in which differential migration has been documented migrate several thousand kilometers to reach their non-breeding area (Rubolini et al., 2004; Tottrup and Thorup, 2008). Additionally, the breeding ground stays fairly mild throughout the winter, so high mortality risk due to returning to the breeding ground early is unlikely. Eastern Painted Buntings have a short migration, face little risk of encountering snow/ freezing temperatures by returning to the breeding ground early, and many have access to supplemental food year-round. Logically, these birds are likely to be less constrained in the timing of their migration than the majority of species in which differential migration has been studied.

My results are consistent with predictions of protandry driven by the mate-opportunity hypothesis. Arriving after females costs males mating opportunities. Arriving after males does not cost females mating opportunities, and arriving before them is not advantageous because females do not claim territories and would just have to wait around for males to arrive (i.e. the waiting-cost hypothesis; Morbey and Ydenberg, 2001). My results are consistent with the mate-opportunity in a second way: I did not find evidence that males depart the breeding ground earlier than females. The mate-opportunity hypothesis is driven by sexual selection for maximizing mating opportunities, of which there is none going into the non-breeding season.

My results do not support the susceptibility hypothesis. Although I found clear evidence for protandry in spring arrival, I found no evidence of higher minimum daily temperature when females arrive. Additionally, I did not see that protandry was more pronounced at higher latitudes, which would likely be the case if higher susceptibility to

cold temperature was constraining females from arriving as early as males. The largest difference between average male and female arrival occurred in Florida at the southern edge of the breeding range, where early spring temperatures should be the least repressive.

The constraint hypothesis was similarly unsupported by my results. I found no evidence for a constraining mechanism for the observed protandry. In some species, the fact that females winter farther from the breeding ground has been proposed as a mechanism for protandry. My results can exclude this explanation as, on average, males actually wintered farther away from the breeding ground than females. Although the effect was weak, I found that males are more likely than females to winter in the southern and eastern portions of the non-breeding range. This is an unexpected result because it contradicts the pattern documented in many species of males remaining closer to the breeding ground than females during the non-breeding season (Adriaensen and Dhondt, 1990; Ketterson and Nolan, 1976; Bai and Schmidt, 2012; Moreno-Opo et al., 2015; Woodworth et al., 2016). Additionally, the southern portion of the non-breeding range (Cuba) is thought to be a region where adult male Buntings face lower survival than females due to high illegal trapping pressure. One would expect that, over time, selection against males wintering in Cuba would occur. Additionally, if males are trapped in Cuba more than females, apparent connectivity for males would skew north, as fewer tracked males that go to Cuba would return. Female sample size was small in this study, however, and additional tracking data from females is needed to substantiate the validity of this observed pattern. In some migratory birds, females are forced into lower-quality habitat by competitively-dominant males, which can delay an individual's departure from the

wintering ground. Painted Buntings are not territorial on the wintering ground, so this is unlikely to be the case in this species. These results strongly suggest that there is little reason to believe that females are constrained in their ability to arrive on the breeding ground as early as males. An alternative hypothesis is that protandry is the result of intra-sex competition.

The rank-advantage hypothesis should only result in protandry if intra-sex competition is more intense for males. As has been pointed out, females and males both face intra-sex competition in the spring (Kokko et al., 2006). Females that arrive late on the breeding ground compared to other females lose out just as males that arrive late compared to other males do. Females may actually be under more intense intra-sex competition. Males that occupy a poor-quality territory may be able to compensate by attempting to gain extra-pair copulations. Because there is no evidence of egg dumping in this species, female reproductive success is tied completely to the quality of her mate and her territory. Given this, my result of pronounced protandry does not support the rank-advantage hypothesis.

I found no significant difference in mean fall departure date between males and females. Some taxa have well-documented differential fall departure between males and females (Rousseau et al. 2020), but conflicting results from multiple studies suggest that sex-related differences in fall migration timing are lacking in many species, or at least less pronounced than during spring migration (Ketterson and Nolan, 1985; Morris and Glasgow, 2001; Carlisle et al., 2005; Mills, 2005). One explanation for this phenomenon is that, unlike spring migration, there is no direct selection for one sex to arrive at its destination before or after the other. This general lack of pronounced protandry in the fall

provides indirect support for the idea that sexual selection directly motivates differential spring migration. My results suggest that, without selection for maximizing mating opportunities, males and females generally migrate at the same time.

Differential migration (and migration in general) is likely shaped by competing forces, which can mask each other or work synergistically. For example, birds that breed at high latitudes may have reduced protandry because the sexual selection for males to arrive before females is masked by the narrow window both sexes have to arrive on the breeding ground early enough to have time to reproduce. The eastern population of Painted Buntings is an interesting system for examining the selection behind differential migration because it allows us to discount several selective forces that rely on environmental and physical constraints. The fact that males on average arrived eleven days earlier than females in the spring but showed no difference in fall departure speaks to the power of selection in determining migration phenology.

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CHAPTER V

SUMMARY

SUMMARY

Painted Buntings have a unique breeding distribution among songbirds in North America, with two disjunct breeding populations that differ significantly in migratory habits. This project used light-level geolocators to examine migratory connectivity, migratory phenology, and differential migration within and between these two populations.

First, I examined the strength of migratory connectivity between and within the two breeding populations. I found no evidence that eastern and interior Buntings co-occur at any point of the annual cycle. This result suggests that the two populations are isolated from each other and that conservation action needs to be population-specific. I found evidence for weak migratory connectivity on the non-breeding ground in both populations. I show no evidence that birds from different regions of either population occupy a unique portion of their respective non-breeding range, although individuals from the most northern portion of the eastern range are more likely to migrate to Cuba than birds from farther south. This indicates that attempts to manage Painted Bunting non-breeding habitat will have diffuse effects across the breeding range. Weak connectivity also implies that conditions on the non-breeding ground are unlikely to be the source of any variation in population growth rate between different breeding regions within each population. A more thorough sampling of the interior population is needed to increase the confidence of this assumption as it applies to the interior population. I found that Painted Buntings that breed in Oklahoma migrate to northwest Mexico en masse

during the molting period, likely existing in higher density than anywhere else at any point of the annual cycle. Degradation of this critical molting region would likely negatively affect population growth for a large swath of the interior population, although more data is needed to understand just how prevalent this migration strategy is.

Next, I examined the differences in migratory timing between the eastern and interior population. I found that birds from the interior breeding site depart the breeding ground nearly two months earlier than eastern Painted Buntings and that environmental conditions were not useful predictors of fall departure in this population. In contrast, fall departure in the eastern population was correlated with decreasing vegetation greenness and temperature. The top model for spring arrival in the eastern population also included environmental covariates, but its poor explanatory power suggests that birds do not adjust their spring arrival considerably to match interannual variation in environmental conditions.

Finally, I examined sex-related differences in migratory behavior within the eastern population. I found that males arrived on the breeding ground earlier than females but found no differences in average fall departure date between the sexes. The best-supported explanation for protandry in this system is sexual selection by males to maximize mating opportunities. On average, males wintered farther south and farther east than females. Although female sample size was small, males were more likely than females to winter in Cuba. This is a pattern that should be monitored and explored further, as the prevalence of illegal trapping in Cuba could result in males facing a decreased survival rate relative to females.