

Spatial and temporal scale-dependence of the strength of migratory connectivity in a North American passerine

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Research Article

Keywords:

Posted Date: March 24th, 2022

DOI: <https://doi.org/10.21203/rs.3.rs-1483049/v1>

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Abstract

Background

Migratory connectivity describes the extent to which portions of a migratory population that are spatially associated during one stage of the annual cycle remain associated during other stages of the annual cycle. The strength of migratory connectivity may vary spatially across a species' range and temporally as individuals move through stages of their annual cycle. Few studies have quantified this spatial and temporal variation in the strength of migratory connectivity within a single species.

Methods

We investigated spatial and temporal variation in the strength of migratory connectivity in Painted Buntings (*Passerina ciris*), a small migratory bird that, uniquely among North American songbirds, breeds in disjunct eastern and western populations. Using tracking data from 113 individuals sampled at eleven breeding sites across the species' breeding distribution, we quantified the strength of connectivity at multiple spatial and temporal scales.

Results

We found strong breeding-to-winter connectivity at the range-wide scale, with interior and eastern Painted Buntings remaining separate throughout the annual cycle, but weak connectivity within populations, with individuals from different regions of both populations mixing extensively on the wintering ground. Despite weak breeding-to-winter connectivity within populations, the interior population displayed strong breeding-to-molting connectivity, with birds from different breeding sites showing distinct migratory strategies during the molting period.

Conclusion

These results demonstrate the extent to which the strength of migratory connectivity can vary across both space and time within a single species and underscore the importance of careful sampling design when quantifying this metric. Because inferences about the strength of connectivity can be sensitive to when and where sampling occurs, there is an urgent need for continued focus on study design regarding migratory connectivity.

Background

Populations of migratory species move annually between areas used during breeding, molting, and wintering [1]. Migratory connectivity (hereafter 'connectivity') describes the extent to which individuals remain together as they move between phases of the annual cycle [2]. 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) and is further strengthened if interpopulation mixing is low [3]. 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, where individuals from different breeding populations overlap on the wintering grounds, appears to be common for migratory songbirds [3].

Understanding the extent to which breeding populations are connected to specific non-breeding and stopover areas can be critical to the conservation of migratory species, which experience different conditions and risks as they move among breeding and non-breeding areas throughout their annual cycles [4, 5]. Quantifying the linkages among breeding and non-breeding regions can allow researchers to infer connections between demographic trends observed on the breeding ground and conditions on the non-breeding ground [6–9]. Despite its importance, migratory connectivity is rarely investigated and existing accounts are often derived from sampling that is limited in its spatial or temporal scale (but see [10–12]). For example, connectivity studies based on band recoveries are frequently based on only two locations per individual: a single location from the breeding ground and a single location from the non-breeding season [13, 14]. This approach precludes conclusions about connectivity at intermediate stages, such as stopover or molting. The logistical limitations of tracking technology (expense, difficulty of recovering archival devices) often constrain the spatial scale of many studies, such that the available data represent only a limited portion of the species-wide breeding range [15–17]. Detailed accounts of spatial and temporal variation in migratory connectivity are therefore missing for many species [18].

One such species is the Painted Bunting (*Passerina ciris*). Painted Buntings are small (~ 16g), short- to medium-distance migrants that are listed as a species of conservation concern by the US Fish and Wildlife Service [19]. They exist within two allopatric populations that are separated by a 500 km gap that stretches from eastern Mississippi to Georgia (but see [20]). 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 larger than that of the eastern population and is centered in Texas, extending east to Mississippi, north into Kansas, and southwest into northern Mexico [21]. Both populations have experienced population decline in the last fifty years, with the eastern population declining at a steeper rate [22]. In addition to their unique allopatric breeding populations, Painted Buntings show complex variation in molting and migration strategies across their breeding range. Like many migratory passerines, Painted Buntings in the eastern population molt on the breeding ground at the end of the breeding season (definitive prebasic molt) before initiating fall migration [23]. In contrast, some individuals from the interior population depart the breeding ground prior to molting (i.e. molt migration; [24]), 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 [25, 26]. The extent to which differences in molt-migration of Painted Buntings correlate with genetic differences is unclear. 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 [27–30]. 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 [28, 29, 31].

How the different migration strategies used by eastern and interior Painted Buntings influence the strength of migratory connectivity throughout the annual cycle is not well understood. There is limited information about breeding-to-winter connectivity for the eastern population [32] and, to date, published tracking data for the interior population comes from only a single breeding site [33]. As a result, it remains unclear how the complex breeding distribution and variation in molting behaviors influence the strength of connectivity in Painted Buntings. However, common sense leads us to the prediction that the geographic distance and open water (Gulf of Mexico) that separate the two disjunct populations should promote strong range-wide migratory connectivity.

Another unresolved question is whether population-level variation in molting strategy promotes strong migratory connectivity. Different molt strategies may lead to different migration distances or energetic demands, which in turn may affect selection of non-breeding locations. If this is the case, geographic variation in molt strategy should be associated with strong connectivity during the non-breeding period, with different breeding populations migrating to distinct non-breeding locations. Hence, we predict that geographic variation in molt strategy should promote strong connectivity to the molting grounds, with birds from different breeding regions remaining separate during the molting period. That said, variation in molt strategy may allow individuals that experience different conditions on the breeding ground to arrive at a common wintering location. In this case, weak breeding-to winter-connectivity should occur, as differences in molt strategy between breeding regions within a population would not necessarily be associated with differences in non-breeding location.

To test these hypotheses, we used tracking data from archival light-level geolocators to quantify spatial and temporal variation in the strength of migratory connectivity within and between the eastern and interior Painted Bunting populations. We estimated the strength of migratory connectivity across three scales: (1) range-wide breeding-to-winter connectivity, (2) breeding-to-molt connectivity within the interior population, and (3) breeding-to-winter connectivity within both the eastern and interior populations.

Methods

Geocator deployment and data analysis

We deployed light-level geolocators (hereafter ‘geolocators’) at eleven sites in the eastern and interior Painted Bunting populations. In the eastern population, geolocators were deployed at nine sites (see appendix for detailed site information) along a latitudinal gradient that spans the length of this population’s breeding range (Table 1; Fig. 1). During the summers of 2017, 2018, and 2019, we deployed 295 geolocators (stalked model P50Z11-7-DIP, Migrate Technology Ltd, Coton, Cambridge, UK) on eastern

Painted Buntings. In the first two years, we attempted to put tags only on after-second-year (ASY) males, which are easily identifiable by their characteristic colorful plumage [23]. In cases where we could not capture enough ASY males, the remaining tags were deployed on second-year (SY) males (n = 12). In 2019, we put approximately half (47/100) of the geolocators out on ASY females and the remainder on adult males. We used the Rappole method to attach geolocators [34]. Within the interior population, we deployed 135 geolocators in Oklahoma during the summers of 2010, 2011, and 2012 (Table 1; see [33] for field methods; [25]) and 14 geolocators in Arkansas during summer 2018.

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

Population	State	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)

Geocator Analysis

Geocator data consists of light levels recorded at predetermined intervals for the duration of the tag's battery life (eastern: range = 310-398 days, median = 364 days; interior: range = 45-324 days, median = 115 days). We used the R package SGAT [35] to generate location estimates from the raw light data (See appendix for details on geocator analysis). Twilights were identified using the function *preprocessLight*, which is part of the R package TwGeos [36]. We used different zenith angles for each individual and for each period of the annual cycle (i.e, breeding, molting, and winter; [5]). We used SGAT to determine appropriate zenith angles for each bird during the stationary breeding period when individuals are at known locations. For eastern birds, the breeding stationary period was defined as June 1st - August 1st. The non-breeding stationary period was defined as December 1st- February 1st. For interior birds, the stationary breeding period began when the geocator was deployed and ended when the individual 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 geocator on the breeding ground. We defined departure as the first significant (> 3 degrees) and persistent longitudinal or latitudinal movement away from a known stationary location. To determine appropriate zenith angles at times of the year when location is unknown (the nonbreeding season), we

used the Hill-Ekstrom calibration method [37,38], which works on the principle that the true zenith angle should result in the smallest variation in estimated latitudes. To decrease uncertainty in the generated locations, we incorporated a range mask as a prior to disallow locations over water or outside the known range of the Painted Bunting. We used one-way ANOVA to test for differences in wintering locations (latitude and longitude) among birds from different breeding sites. We took a weighted median of the location density estimate surface (generated using the *slice* function within *SGAT*) to generate a point-estimate location for each individual during the non-breeding stationary period(s). We used the straight-line distance between these estimated locations (breeding to molting to wintering) to generate conservative estimates of migration distance for each individual.

Estimating the Strength of Migratory Connectivity

We used the R package *MigConnectivity* [39] 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 fall between -1 and 1, although real-world scenarios typically result in an MC value that falls between 0 and 1 [39]. 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 0 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 level, so that the user must define discrete breeding and non-breeding regions. For this purpose, we binned the non-breeding grounds into five regions: Mexico, Central America, Florida, Cuba, and the Bahamas. To quantify breeding-to-molting ground connectivity within the interior population, we 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. We 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). To improve estimates of migratory connectivity, we accounted for differences in relative abundance between breeding sites in our estimate of MC [39]. Because relative abundance data was not available for our specific field sites, we divided the breeding range into polygons, with relative abundance within each polygon being assigned to any breeding site within that polygon. The eastern population was divided into three roughly equal-sized polygons. For Oklahoma and Arkansas breeding sites, relative abundance was extracted from a rectangle measuring one degree latitude by one degree longitude around each site. Estimates of relative abundance in each region were derived from data publicly available from eBird [40] using the R package *ebirdst* [41]. *EstMC* requires a single position (latitude and longitude) for each bird during the non-breeding season, for which we used the point-estimate generated during the core of the wintering period (December and January).

Results

We recovered 86 geolocators from the eastern population, of which 82 had viable data (Table 1). We 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 (Table 1). 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 (Fig. 1). We found no evidence that interior and eastern birds mix at any point during the annual cycle, resulting in strong range-wide connectivity (MC = 0.71 +/- 0.10; Table 2). In contrast, within both the eastern and interior Painted Bunting populations, we found low breeding-to-winter connectivity (eastern population MC = -0.05 +/- 0.04; interior population MC = 0.03 +/- 0.22; Table 2, Figs. 2 and 3). 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 an ANOVA test revealed no significant differences in wintering location (latitude and longitude) among the breeding sites ($p > 0.05$).

Table 2
Estimates of migratory connectivity. Connectivity can range from - 1 to 1, with connectivity of zero indicating random mixing.

Population	Connectivity Estimate	Standard Error
Range-wide (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

Despite weak breeding-to-winter connectivity within populations, breeding-to-molting connectivity within the interior population was high (connectivity = 0.81 +/- 0.16; Table 2), indicating that individuals from Arkansas and Oklahoma remained segregated during the post-breeding molting period. All Oklahoma breeders in our dataset 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

We show that the strength of migratory connectivity can vary dramatically within a single species, depending on the spatial scale of inference and the periods of the annual cycle during which migratory connectivity is measured. At the range-wide spatial scale, breeding-to-winter migratory connectivity was strong between the two populations, with no evidence of mixing at any point in the annual cycle. In contrast, breeding-to-winter connectivity within each population was weak, with individuals from different breeding sites within each population mixing extensively on the non-breeding ground. Despite weak breeding-to-winter connectivity, breeding-to-molting connectivity was strong in the interior population, demonstrating the importance of considering the strength of connectivity at stages intermediate to breeding and winter [42]. Our results suggest that differences in molting strategy may drive strong breeding-to-molting connectivity in molt-migrants like the Painted Bunting, but also that this strong connectivity does not necessarily persist forward to the stationary non-breeding (winter) season.

Our results underscore the importance of spatial scale in interpreting observed patterns of migratory connectivity. For Painted Buntings, sampling only within the eastern or interior populations would suggest that this species exhibits weak breeding-to-winter connectivity, despite the very strong breeding-to-winter connectivity at the range-wide spatial scale. As this example demonstrates, extrapolating patterns of migratory connectivity observed from limited spatial sampling to species-level metrics may produce misleading results and should be avoided where possible. At the very least, researchers should interpret results cautiously when based on only limited spatial sampling and should attempt to tailor sampling designs to the specific questions being asked. If range-wide connectivity is the quantity of interest, researchers should carefully consider how to collect representative samples from across the entire range. However, in some cases, range-wide connectivity may not be necessary if the focus is on a specific subunit of the population. Because the strength of migratory connectivity can differ significantly, both spatially and temporally, study design is critical when migratory connectivity is concerned.

Our results also highlight the need to consider how patterns of migratory connectivity change throughout the annual cycle. Despite weak breeding-to-winter connectivity within the interior population, individuals breeding in Oklahoma and Arkansas migrated to completely disjunct molting areas, resulting in very strong connectivity during the molting period. Oklahoma birds migrated westward to northwest Mexico during the molting period before continuing onto their final non-breeding ground, while Arkansas birds forwent any prolonged stopover at a distinct molting location when migrating to the non-breeding ground. These results offer evidence that birds from different regions of the interior population use different molting strategies. Oklahoma birds appear to be classic monsoon region stopover molt-migrants [24], while our limited results from Arkansas suggest that Arkansas birds may molt on the breeding grounds or on their ultimate non-breeding ground. This divergence of migratory behavior had 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 non-breeding period [28]. Despite this strong connectivity during the molting period, birds from Oklahoma and

Arkansas do not appear to occupy different regions of the non-breeding range. Why the Oklahoma birds migrate significant distances to reach their molting grounds, rather than moving to the much closer molting areas used by the Arkansas birds, is not fully understood. The *Passerina* clade likely radiated from the grasslands of central and western Mexico and the western-most breeding populations may be following ancestral routes that track historical range expansion [43, 44]. The western-most breeding populations also experience an increasingly arid landscape by midsummer, which likely exerts unique selection on molt and migration phenology relative to the more eastern breeding populations that breed in areas that remain green and productive later into the summer and fall. Being forced to depart the breeding grounds earlier, and prior to molt, may make the longer movements to the monsoonal regions of western Mexico adaptive. These hypotheses are not mutually exclusive and more work is needed to fully understand the complex variation in migration and molt strategies used by Painted Buntings.

These results have conservation implications for this declining songbird. Although birds from the interior populations spread out and mix on the non-breeding grounds, our results suggest that interior Painted Buntings diverge during the molting period, with large numbers of individuals funneling into a relatively small molting region in northwest Mexico. Conservation efforts in this critical region could have outsized benefit to interior Painted Buntings due to the high concentration of individuals relative to the breeding or non-breeding season. Conversely, habitat destruction and other negative factors that occur in this region (e.g. illegal trapping) could be particularly detrimental, and could be a potential culprit if interior bunting populations begin to decline more rapidly. Within the eastern population, weak breeding-to-winter migratory connectivity could be an important attribute if habitat loss continues or accelerates in the future. Weak connectivity can help to mediate the effect of winter habitat loss, as negative effects are spread across the entire breeding range such that no one region bears the brunt of the impact [3, 32]. This effect could be especially important to the eastern population, which exists in an area twenty-five times smaller than the interior population and may be declining faster than the interior population [22]. Much of the breeding/winter range of the eastern population is characterized by intense human development [45, 46], to which low connectivity should promote resilience. Strong range-wide connectivity in this species means that interior and eastern populations need to be managed separately, as we provide no evidence that individuals from either population mix at any point of the annual cycle. The lack of overlap 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.

Conclusion

The degree to which populations spread out and mix as they transition across different stages of the annual cycle defines migratory connectivity, and our results demonstrate the inherent spatial and temporal scale-dependence of this important metric. Although the allopatric breeding populations and high intraspecific variation in molting strategies observed in Painted Buntings may be somewhat unique among migratory songbirds, scale-dependence of migratory connectivity is likely to be a pervasive

phenomenon given the existence of population-specific migratory routes [9, 47] and well-known gradients in molt migration [26, 48]. At present, however, there is little evidence-based guidance on how to design tracking studies to accurately characterize migratory connectivity across relevant temporal and spatial scales. In the absence of such guidance, we encourage researchers to carefully match the scope of sampling to specific questions being addressed. For example, is the focus of the study on range-wide connectivity or connectivity of specific focal populations? Are there known bottlenecks (e.g., stopover sites, molting areas) that need to be connected to specific breeding or wintering populations? Although these types of questions can be useful for guiding the design of tracking studies, there is an urgent need for more formal guidance on study design, as has been done for other emerging technologies and methods (e.g., spatial capture-recapture - [49]; estimating abundance via camera traps - [50]). Going forward, such guidance will be critical to maximizing the potential of miniaturized tracking devices for uncovering migration patterns and informing conservation and management.

Declarations

Ethics approval and consent to participate: Not applicable.

Consent for publication: Not applicable.

Availability of data and materials: All data will be made publically available at Movebank.org pending acceptance of the manuscript.

Competing interests: No competing interests to declare.

Funding: Funding for this project was provided by The Disney Conservation Fund, Little St. Simons Island, Spring Island Land Trust, and USFWS NMBCA Grant #PN6759.

Authors' contributions: AS, CSR, VRG, and SS designed the study for the eastern population. ESB, JK, EB, JM, and AG designed the study for the western population. AS analyzed movement data and drafted the manuscript. All authors contributed to subsequent revisions of the manuscript.

Acknowledgements: AS was partially supported by funding from the Wildland Resources Department and Ecology Center at Utah State University. Additional financial support was provided by USFWS NMBCA Grant #PN6759, the Spring Island Land Trust, and Little St. Simons Island. We would like to thank the following groups for their assistance in obtaining movement data: Airlie Gardens, Audubon South Carolina, Bald Head Island Conservancy, Carolina Beach State Park, Kiawah Island, and Little Talbot Island State Park.

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Figures

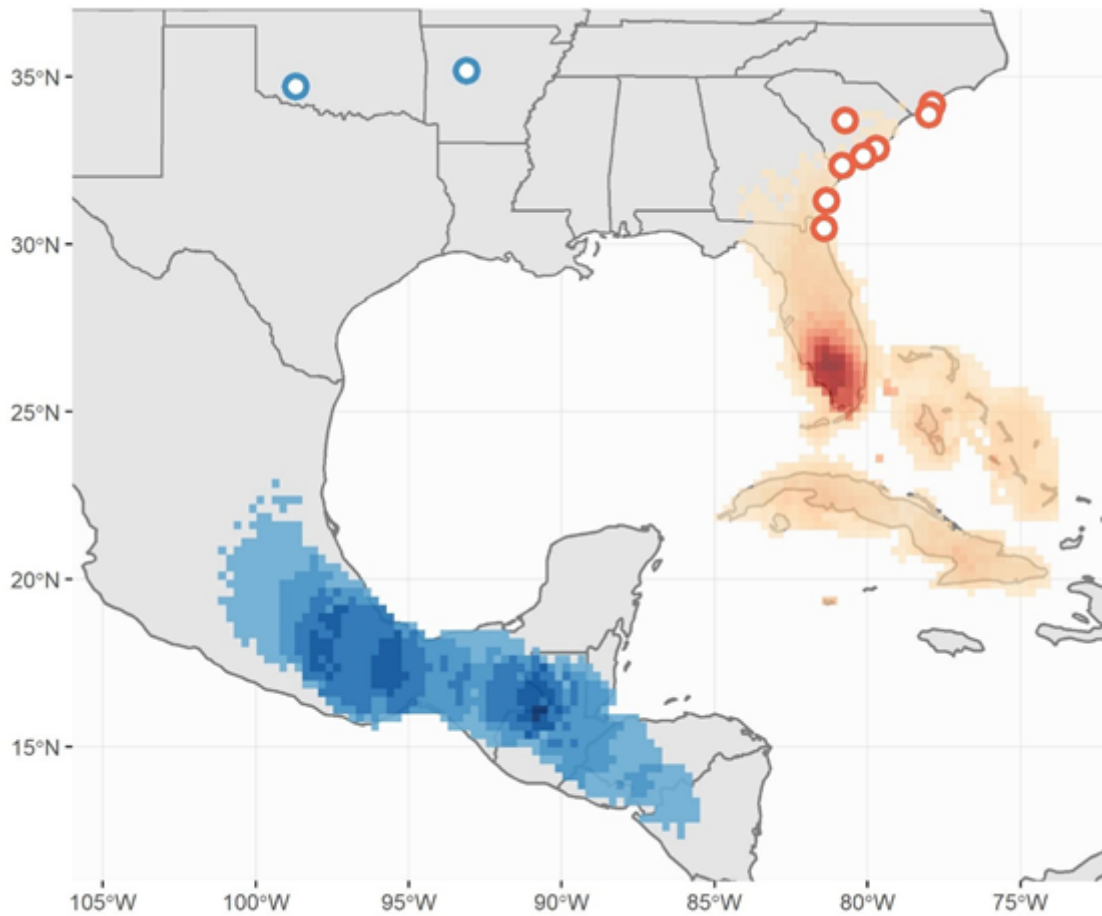


Figure 1

Deployment locations (circles) 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.

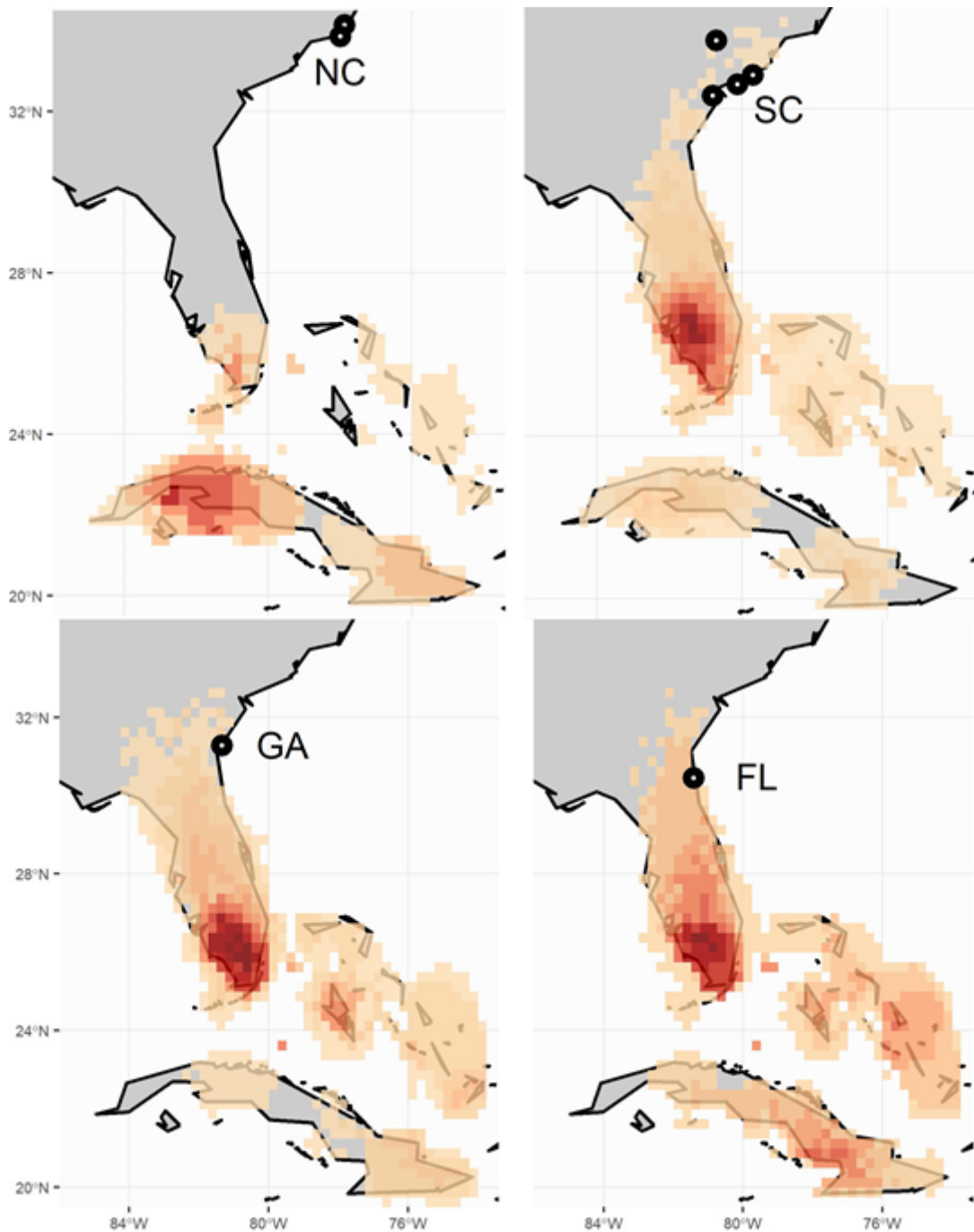


Figure 2

Estimated wintering locations for eastern Painted Buntings breeding in North Carolina ($n = 8$), South Carolina ($n = 32$), Florida ($n = 19$), and Georgia ($n = 23$). The intensity of the color ramp increases with the number of individuals with overlapping location estimates in that area.

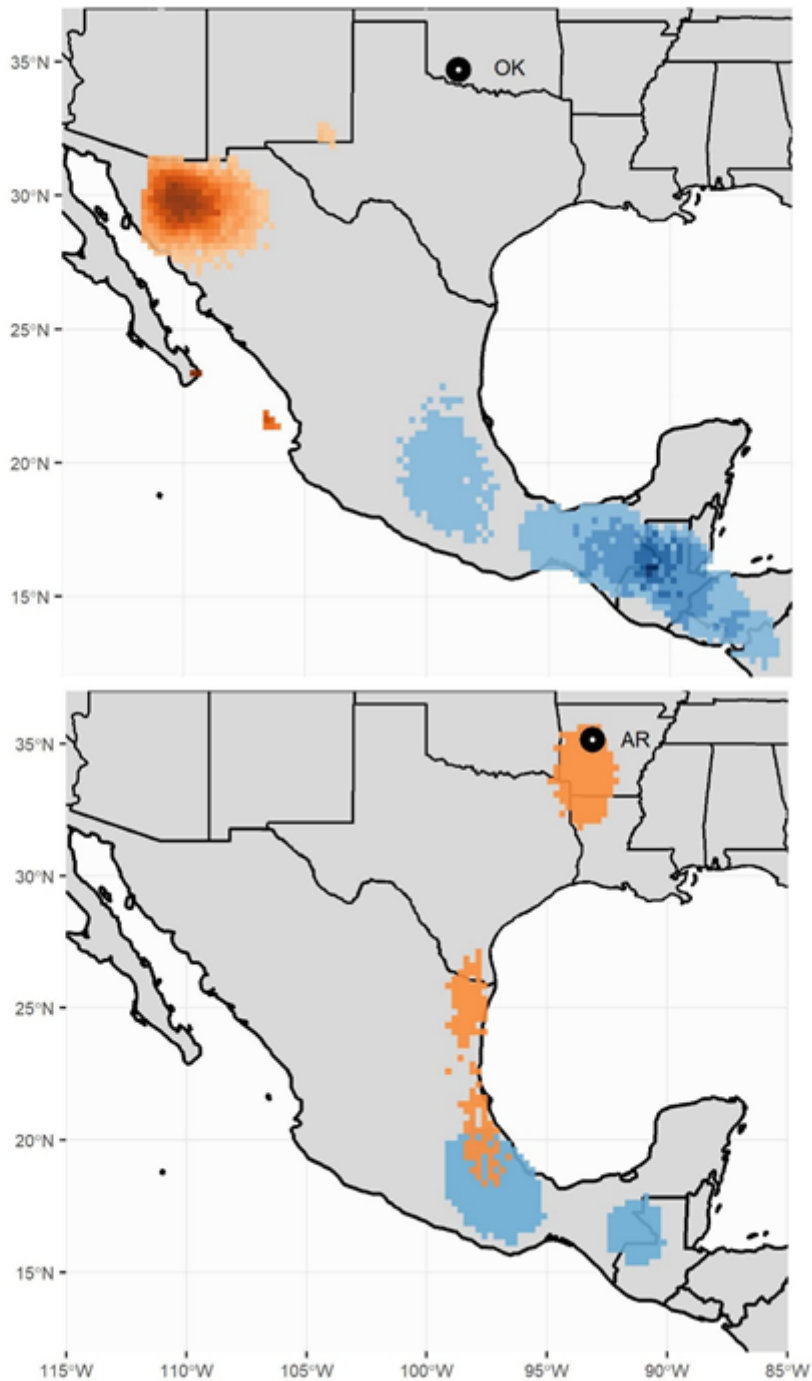


Figure 3

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.

Supplementary Files

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