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## Estimates of breeding season location for 4 mesic prairie bird species wintering along the Gulf Coast

Christopher J. Butler,<sup>1\*</sup>† Auriel M.V. Fournier,<sup>2†</sup> and Jennifer K. Wilson<sup>3†</sup>

**ABSTRACT**—During the last 2 centuries, widespread declines have been observed in migratory species, and these declines have largely been linked to anthropogenic causes. Migrants move across multiple spatiotemporal scales with wide-ranging movements that can cross multiple jurisdictions. Consequently, conservation and management require the incorporation of these wide-ranging movements. However, for many nongame species, basic information on migration and wintering ecology is poorly known. Yellow Rails (*Coturnicops noveboracensis*), LeConte's Sparrows (*Ammospiza leconteii*), Nelson's Sparrows (*A. nelsoni*), and Sedge Wrens (*Cistothorus stellaris*) represent a diverse avian assemblage that breeds in prairie potholes, boreal forest, and coastal areas of northern and eastern Canada and winters in coastal prairies in the southern United States. We used a stable deuterium isotope ( $\delta^2\text{H}_f$ ) analysis to assign breeding season locations for individuals captured wintering in the southeastern US. We obtained deuterium values from secondary feathers of birds spending the nonbreeding season from Oklahoma and Texas east to Florida. We found substantial differences in the  $\delta^2\text{H}_f$  values of Yellow Rails and Nelson's Sparrows, with birds wintering in Oklahoma and the western Gulf of Mexico having  $\delta^2\text{H}_f$  values that were probabilistically assigned to the western half of their breeding range, while birds wintering in Florida were probabilistically assigned to the eastern portion of their breeding range. LeConte's Sparrow breeding season assignments for birds wintering in Texas and Oklahoma overlapped. Sedge Wrens did not exhibit spatial variation in isotope values. *Received 15 December 2019. Accepted 4 August 2021.*

**Key words:** LeConte's Sparrow, Nelson's Sparrow, Sedge Wren, species distribution models, stable hydrogen isotopes, Yellow Rail.

### Estimaciones de la localización de áreas reproductivas de 4 especies de aves de praderas mészicas que invernan a lo largo de la costa del Golfo

**RESUMEN** (Spanish)—Durante los 2 siglos recientes, se han observado amplios declines en especies migratorias que han estado en su mayoría ligados a causas antropogénicas. Los movimientos de especies migratorias se llevan a cabo en múltiples escalas espaciotemporales con movimientos amplios que pueden cruzar múltiples jurisdicciones. Consecuentemente, su conservación y manejo requieren la incorporación de información de estos movimientos. La polluela *Coturnicops noveboracensis*, los gorriónes *Ammospiza leconteii* y *A. nelsoni*, y la matraca *Cistothorus stellaris* representan un ensamble diverso que anida en pozas de praderas, bosques boreales y áreas costeras del norte y este de Canadá e invernan en las praderas costeras del sur de los Estados Unidos. Usamos análisis de isótopos estables de deuterio ( $\delta^2\text{H}_f$ ) para asignar localidades reproductivas de individuos capturados invernando en el sureste de los Estados Unidos. Obtuvimos valores de deuterio de plumas secundarias que pasaban la temporada no-reproductiva de Oklahoma y Texas al este hasta Florida. Encontramos diferencias sustanciales en los valores de  $\delta^2\text{H}_f$  en *C. noveboracensis* y *A. nelsoni*, donde las aves invernando en Oklahoma y el occidente del Golfo de México tuvieron valores de  $\delta^2\text{H}_f$  que fueron probabilísticamente asignados a la mitad occidental de su rango de distribución, mientras que las aves invernando en Florida fueron probabilísticamente asignados a la porción oriental del rango de distribución. Las asignaciones de localidades reproductivas de *A. leconteii* para individuos invernando en Texas y Oklahoma tenían traslapes. Los valores isotópicos de *C. stellaris* mostraron variación espacial.

**Palabras clave:** *Ammodramus nelsoni*, *Ammospiza leconteii*, *Cistothorus stellaris*, *Coturnicops noveboracensis*, isótopos estables de hidrógeno, modelos de distribución especial.

Widespread declines in migratory species have been noted during the last 2 centuries with most of the observed declines attributed to anthropogenic causes including habitat loss/degradation, overexploitation, and more recently, climate change (Brower and Malcolm 1991, Both et al. 2006,

Bolger et al. 2008, Wilcove and Wikelski 2008). However, despite the challenges facing migratory species, population-level conservation efforts have largely focused on sedentary species (Pressey et al. 2007, Runge et al. 2014). Migratory species, especially birds, may use wide geographic areas over the course of their annual cycle, which can expose them to a wide variety of threats, with different stressors occurring in different places (Sillert and Holmes 2002).

Understanding where individuals spend the breeding and nonbreeding seasons, and how these places are connected, is important for understanding which factors and threats might influence their

<sup>1</sup> Department of Biology, University of Central Oklahoma, Edmond, OK, USA

<sup>2</sup> Forbes Biological Station–Bellrose Waterfowl Research Center, Illinois Natural History Survey, Prairie Research Institute, University of Illinois at Urbana-Champaign, Havana, IL, USA

<sup>3</sup> Texas Mid-Coast NWR Complex, Brazoria, TX, USA

\* Corresponding author: cbutler11@uco.edu

† These authors contributed equally to this work

survival or reproductive productivity (Stanley et al. 2015). Despite this, how individuals move across the landscape during their annual cycle is poorly understood for many species (Van Wilgenburg and Hobson 2011).

Ornithologists have long used bird banding to study migration. However, re-encounter rates for species that are not widely hunted are approximately 1.2% annually (Brown and Miller 2016). For some larger species, it is possible to track movements using satellite transmitters (Clausen et al. 2003), but their weight currently limits them from use on smaller species (Webster et al. 2002). Light-level geolocators can be used to track migratory movements (Stutchbury et al. 2009), but these devices require recapturing individuals the next year, which can be challenging for species with low levels of site fidelity.

In contrast, stable hydrogen isotopes from a bird's feathers and other tissues can allow for study of a bird's migration on any size of bird, with only 1 capture event (Hobson 2005). Stable hydrogen isotope ratios vary in a predictable fashion across the landscape (Bowen et al. 2005) and the isotope ratios of an organism's metabolically inert tissues (e.g., feathers) reflect isotopic values of the environment where the tissue was grown (Webster et al. 2002). Consequently, if the bird molts at 1 location but is encountered at another location, it is possible to collect a feather and determine the approximate geographic location where the individual feather was grown (Hobson 2005). For example, if a species molts its flight feathers on the breeding grounds, the individual can be captured outside the breeding grounds, and through the inert isotopic values from a feather sample, we can estimate the individual's breeding location (Hobson 2005). The level of resolution from stable isotope markers is coarse, although resolution can be improved if another kind of marker or approach is included such as the incorporation of genetics, or a species distribution model (Rundel et al. 2013; Fournier et al. 2017a, 2017b). For these reasons, stable isotope study is an appropriate approach for determining movements of small bird species with low site fidelity.

Our objective was to examine the migratory movements of 4 species of conservation concern: Yellow Rail (*Coturnicops noveboracensis*), LeConte's Sparrow (*Ammodramus leconteii*), Nel-

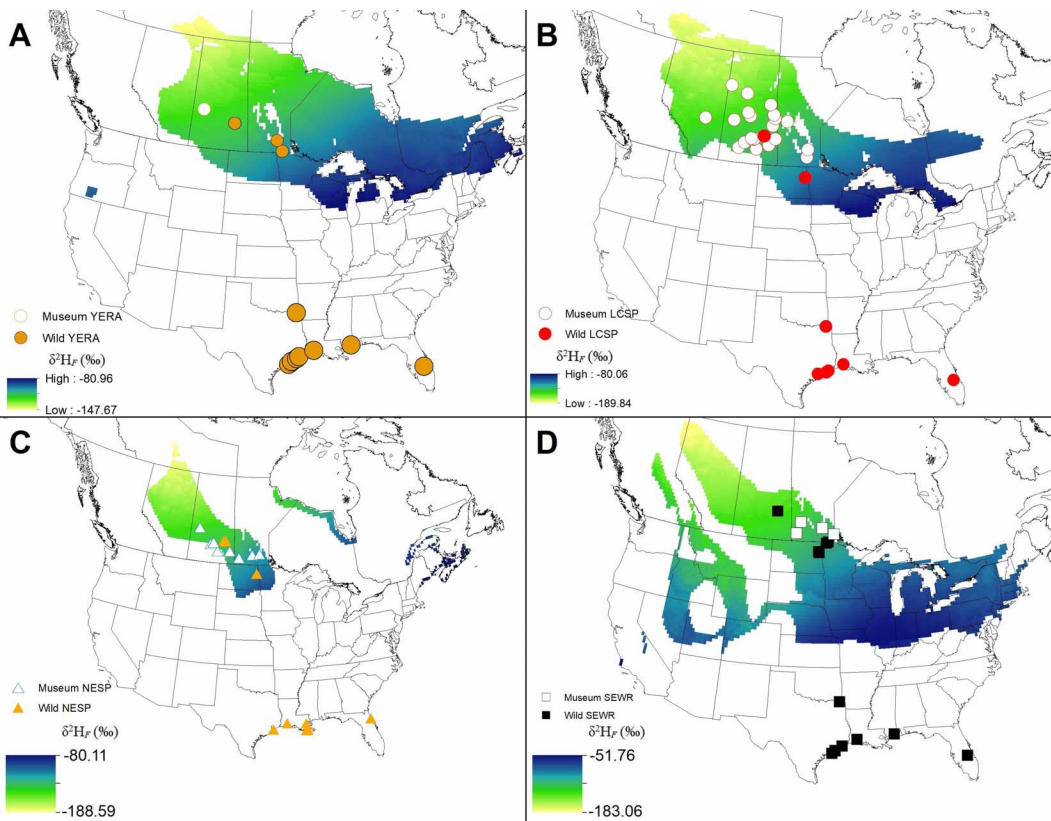
son's Sparrow (*A. nelsoni*), and Sedge Wren (*Cistothorus stellaris*). Limited knowledge exists of movements throughout the annual cycle, which is made apparent by examining the encounters of previously banded individuals for each of the 4 species. In North America, between 1960 and 2019, the percentage of all banded individuals subsequently recaptured across all locations reporting data was <4% for these 4 species (0.1% for Yellow Rail, 0.22% for LeConte's Sparrow, 3.95% for Nelson's Sparrow, and 0.28% for Sedge Wren; USGS Bird Banding Laboratory 2021).

We used a probabilistic assignment of feather hydrogen isotopes to assess the breeding season location of birds at differing wintering locations. Understanding the amount of, or lack of, separation among the eastern and western parts of the populations of each species of conservation concern will allow managers to better understand the possible threats individuals face. We hypothesized that individuals of all 4 species wintering in Oklahoma and along the western Gulf of Mexico bred in the western half of their breeding range, while individuals wintering along the eastern Gulf of Mexico bred in the eastern half of their breeding range.

## Methods

### Study species

The 4 species selected for this project were Yellow Rail, LeConte's Sparrow, Nelson's Sparrow, and Sedge Wren, which represent 3 avian families that breed in prairie potholes as well as in boreal forest and coastal areas of northern and eastern Canada, and winter in coastal prairies (Herkert et al. 2020, Leston and Bookhout 2020, Lowther 2020, Shriver et al. 2020). As a group, they are poorly studied and many aspects of their basic biology remain unknown (Herkert et al. 2020, Leston and Bookhout 2020). The Yellow Rail is a Species of Special Concern in Canada and most of the states where breeding occurs list Yellow Rails as "Vulnerable" or a "Species of Special Concern" (Fish 2002, COSEWIC 2009). The Sedge Wren, LeConte's Sparrow, and Nelson's Sparrow are listed as species of conservation concern (Fish 2002).



**Figure 1.** Feather sample collection locations of 4 species of mesic prairie birds wintering along the Gulf Coast (A = Yellow Rail, B = Sedge Wren, C = Nelson's Sparrow, and D = LeConte's Sparrow) superimposed on a map of modeled  $\delta^2H_r$  from a model of mean annual growing season precipitation, cropped to the breeding range of each species. Samples from museums are shown using hollow symbols, while samples collected from the field are shown with solid symbols.

## Field methods

We captured birds on the wintering grounds with the goal of being able to assign each to the part of the breeding range they spent the previous breeding season, the time when they molted the feather we collected. We also captured birds on the breeding grounds at the locations where they spent the breeding season, to ground truth the isotopic values and improve our predictions. We captured birds from November through March during 2013–2014 and 2014–2015 in Florida, Mississippi, Louisiana, Texas, and Oklahoma. Finally, we also included feather samples from Yellow Rails and LeConte's Sparrows wintering in Oklahoma and Texas 2008–2013. We captured and obtained feather samples from birds on the breeding grounds in 2014 in Minnesota, North Dakota,

Montana, Manitoba, and Saskatchewan. We also obtained LeConte's Sparrow, Nelson's Sparrow, and Sedge Wren feathers from birds collected during the breeding season from the Manitoba Museum and from the Royal Saskatchewan Museum to increase sample sizes. Museum sample collection dates ranged from 1913 to 1982 (Fig. 1 shows the locations where feather samples were obtained for each species).

To capture Yellow Rails during the breeding season (mid-May to end of June), we used recordings to lure birds close enough to catch with handheld nets. To catch the other 3 species during the same timeframe, we set up mist nets on territories and used recordings to attract LeConte's Sparrows, Nelson's Sparrows, and Sedge Wrens into nets. We removed a single secondary (s5) from each bird. We chose secondary feathers

because they are molted shortly after breeding, while still on the breeding ground, in all 4 species, and the molting is completed on the breeding grounds (i.e., they do not engage in interrupted molt; Pyle 1997, 2008).

During the nonbreeding season, we captured Yellow Rails as well as incidental LeConte's Sparrows and Sedge Wrens by dragging a 12 m weighted rope dragline through each wetland at night and using handheld nets (Butler et al. 2010). Sampling began ~30 min after sunset and lasted for 3 h. To capture Sedge Wrens and both sparrow species we used mist netting at the edge of mesic grasslands and salt marshes aided by the use of a rope to flush sparrows and wrens into the mist nets during daylight hours.

### Laboratory analyses

Feathers were analyzed at the University of Oklahoma Stable Isotope Lab (prior to 2014) or the University of Arkansas Stable Isotope Lab (from 2014 onward). Both labs followed the same procedure (Kelly et al. 2008). Feathers were cleaned in a 2:1 chloroform:methanol solution (Paritte and Kelly 2009) and then dried in a fume hood for 48 h. For the  $\delta^2\text{H}_f$  analysis, ~0.15 mg of feather was removed and then wrapped in a  $3.5 \times 5$  mm silver capsule using  $\text{CCl}_4$  to avoid contamination by hydrogen. Samples were analyzed using a temperature conversion elemental analyzer (interfaced with an isotope ratio mass spectrometer) where they were then combusted at  $1,300^\circ\text{C}$  in a reducing environment. Samples were then loaded into a Costech Zero Blank Autosampler (Costech Analytical Technologies, Valencia, California, USA) attached to a Thermo/Finnigan thermochemical elemental analyzer (TC/EA; Thermo Fisher, Bremen, Germany) and analyzed in triplicate. Runs were standardized to the Vienna Standard Mean Ocean Water (VSMOW), as well as internal standards including polyethylene foil, TURK-1, CCHIX-1, and IAEA 6. We expressed isotope ratios in delta notation (e.g.,  $\delta^2\text{H}_f$ ) where  $\delta = (\text{isotope ratio}_{\text{sample}} / \text{isotope ratio}_{\text{standard}}) \times 1,000$ , and where the isotope ratio was the ratio between the abundances of deuterium and hydrogen. The resulting ratios are presented in permille (‰) deviations from VSMOW for hydrogen isotopes. Based on replicate within-run measure-

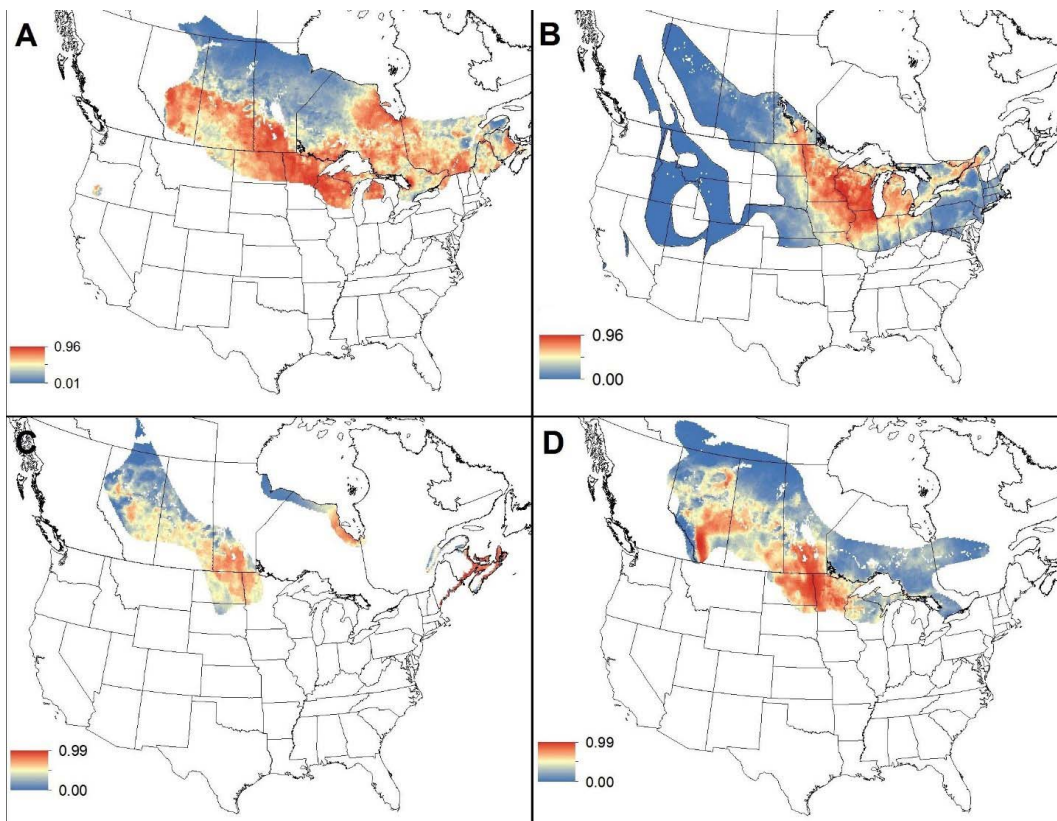
ments of standards, we estimate measurement error to be  $\pm 1.8\text{‰}$ .

### Statistical analyses

*Correcting isotopic values*—We corrected raw  $\delta^2\text{H}$  values by using the predicted values from a regression of raw  $\delta^2\text{H}$  values of feathers from known locations on the breeding grounds, and precipitation isotopic values  $\delta^2\text{H}_p$  from those same locations (Bowen et al. 2005). The precipitation isotopic values  $\delta^2\text{H}_p$  came from Isomap (Water-isotopes Database 2017). This calibration accounted for systematic differences between the  $\delta^2\text{H}_f$  of sampled feathers and  $\delta^2\text{H}_p$  in precipitation. We included data from other projects in our linear regression of  $\delta^2\text{H}_f$  of flight feathers to mean growing season  $\delta^2\text{H}$  across North America (Bowen et al. 2005) to increase our sample size and expand our geographic coverage. This known-origin dataset included 23 Yellow Rail feathers from Saskatchewan (Fournier et al. 2017a). In total we had 133 feathers from 14 different localities. We had sufficient Yellow Rail samples to regress those feathers separately ( $n = 45$ ) and so we regressed our data of known-origin feathers against  $\delta^2\text{H}_p$  precipitation to derive the calibration equation ( $\delta^2\text{H}_f = -45.56 + 0.74[\delta^2\text{H}_p]$ ,  $R^2 = 0.33$ ). For the other 3 species, we used a similar process, but grouped the data from all 3 species together, as there was not enough data to analyze them individually ( $\delta^2\text{H}_f = -19.10 + 1.20[\delta^2\text{H}_p]$ ,  $R^2 = 0.36$ ).

*Building species distribution models*—We created species distribution models, which we then used as our informative priors for Bayesian assignment of individuals (Fournier et al. 2017a). We used eBird and Vertnet data to create species distribution models in MaxEnt (Phillips et al. 2006, Phillips and Dudik 2008). We followed a similar procedure to Fournier et al. (2017b) except we used the *ENMeval* package in R 3.4.1 to fit our species distribution models (Muscarella et al. 2014). Our SDM input data were breeding season eBird presence records and data from museum records through VertNet (Sullivan et al. 2009, Constable et al. 2010). We used all Worldclim data layers as our predictors (Supplementary Table S1) since our goal was to create a model with the greatest predictive power, not one that would allow for inference about environmental drivers (Beau-





**Figure 2.** Species distribution models for each of the 4 species of mesic prairie birds wintering along the Gulf Coast (A = Yellow Rail, B = Sedge Wren, C = Nelson's Sparrow, and D = LeConte's Sparrow).

mont et al. 2005, Hijmans et al. 2005, Porfirio et al. 2014).

Randomly selected pseudo-absences generate the most reliable distribution models, so for each known point, we generated a random point in the breeding range (1:1 ratio of known to random points), obtained from BirdLife International and NatureServe (2015), and these random points served as our pseudo-absence points (Barbet-Massin et al. 2012). These random points were generated in R. This allowed us to use presence and pseudo-absence points in our MaxEnt model. MaxEnt minimizes the relative entropy between the biased presence and background points to determine environmental constraints (Dudík et al. 2005, Phillips et al. 2009). Our objective was to generate the SDM with the greatest predictive accuracy, as measured by the area under the receiver operating characteristic curve (AUC under

ROC; Hanley and McNeil 1982, Phillips et al. 2006, Fournier et al. 2017b). This distinction is important because our choice of settings is justified for estimating potential species distributions but should not be used to infer underlying environmental drivers (Merow et al. 2013). We developed a species distribution model for each species independently (Fig. 2).

*Predicting breeding season locations*—We used the methods and code of a previously published Bayesian framework to perform our spatially explicit isotopic assignments for each individual (Van Wilgenburg and Hobson 2011). Below is a summary of those methods. We used a likelihood-based assignment that incorporated estimates of parameter uncertainty (Royle and Rubenstein 2004).

For each feather we assessed the probability that any cell within the expected values of the  $\delta^2\text{H}_f$

**Table 1.** A summary of the number of each species captured during the nonbreeding and breeding seasons. Numbers in parentheses are the numbers from museum specimens and wild birds, respectively.

	Total sample size	Nonbreeding season sample size	Breeding season sample size	Nonbreeding season capture locations	Breeding season capture locations
Yellow Rail	142	120 (120 wild)	22 (1 museum   21 wild)	4 (0 museum   4 wild)	7 (1 museum   6 wild)
LeConte’s Sparrow	172	140 (140 wild)	32 (26 museum   6 wild)	5 (0 museum   5 wild)	23 (21 museum   2 wild)
Nelson’s Sparrow	43	24 (24 wild)	19 (15 museum   4 wild)	6 (0 museum   6 wild)	11 (8 museum   3 wild)
Sedge Wren	62	45 (45 wild)	17 (5 museum   12 wild)	8 (0 museum   8 wild)	9 (4 museum   5 wild)

isoscapes (geologic map of isotope distribution) was the origin of that individual using a normal probability density function as follows:

$$f(y^*|\mu_c\sigma_c) = \left(\frac{1}{\sqrt{2\pi}\sigma_c}\right)\exp\left[-\frac{1}{2\pi\sigma_c^2}(y^* - \mu_c)^2\right]$$

Where  $f(y^*|\mu_c\sigma_c)$  represents the probability that a given cell ( $c$ ) within the  $\delta^2H_f$  isoscape represents a potential origin for an individual of unknown origin ( $y^*$ ), given the expected mean  $\delta^2H_f$  for that cell ( $\mu_c$ ) from the calibrated  $\delta^2H_f$  isoscape and the expected standard deviation ( $\sigma_c$ ) of  $\delta^2H_f$  between individuals growing their feathers at the same locality.

To assign probable breeding areas to samples within a particular state, we summed the assignments from each feather sample in units of the number of birds with origins consistent with a given pixel and converted to proportions to enable comparisons with other states. For each individual we produced a surface of spatially explicit probability densities (i.e., 1 surface per bird in a sample). We then incorporated the prior probabilities from our SDM by applying Bayes’ Rule (Van Wilgenburg and Hobson 2011).

To depict these origins across the entire sample size we assigned each feather to the isoscape individually by determining the odds that any given assigned origin was correct relative to the odds it was incorrect. Based on 3:1 odds that a given bird had originated from within the pixel we recorded the set of raster cells that defined the upper 75% of estimated origins and coded them as 1, all others as 0. We choose 3:1 odds because this ratio provided a compromise between the possibility of being incorrect and the bird assignment geographic resolution (Van Wilgenburg and Hobson 2011).

The results of the individual assignments were then summed over all individuals by addition of

the surfaces to create a single species summed probability surface. We facilitated this step by rescaling the posterior probabilities ( $f_x$ ) relative to the maximum value within the posterior probability surface prior to applying the odds-ratio-based reclassification. We made assignments using functions within the R statistical computing environment (R Core Team 2019) using the *raster* package (Hijmans and van Etten 2012). All statistical tests used statistical program R 3.4.1 (Hijmans and van Etten 2012, R Core Team 2019).

Results

Yellow Rails

We sampled 142 Yellow Rails (Table 1). Feathers from Yellow Rails during the nonbreeding season ( $n = 120$ , Florida = 3, Texas/Louisiana = 63, Oklahoma = 54) had a median  $\delta^2H_f$  value of  $-121.3\text{‰}$  while feathers from breeding Yellow Rails ( $n = 22$ ) had a median  $\delta^2H_f$  value of  $-104.9\text{‰}$  (Table 2). We assigned Yellow Rails from Texas and Oklahoma primarily to the region from Alberta east to Ontario and south to Minnesota (Fig. 3). In contrast, the geographic assignment for birds captured in Florida included a breeding range that extended from North Dakota east to Newfoundland and south to Wisconsin and Michigan (Fig. 3).

LeConte’s Sparrows

We sampled a total of 172 LeConte’s Sparrows (Table 1). Feathers from nonbreeding season LeConte’s Sparrows ( $n = 140$ , Florida = 1, Texas = 14, Oklahoma = 125) had a median  $\delta^2H_f$  value of  $-102.3\text{‰}$  while feathers from breeding LeConte’s Sparrows ( $n = 32$ ) had a median  $\delta^2H_f$  value of  $-116.6\text{‰}$  (Table 2). Figure 4 shows that LeConte’s Sparrows from Oklahoma had  $\delta^2H_f$

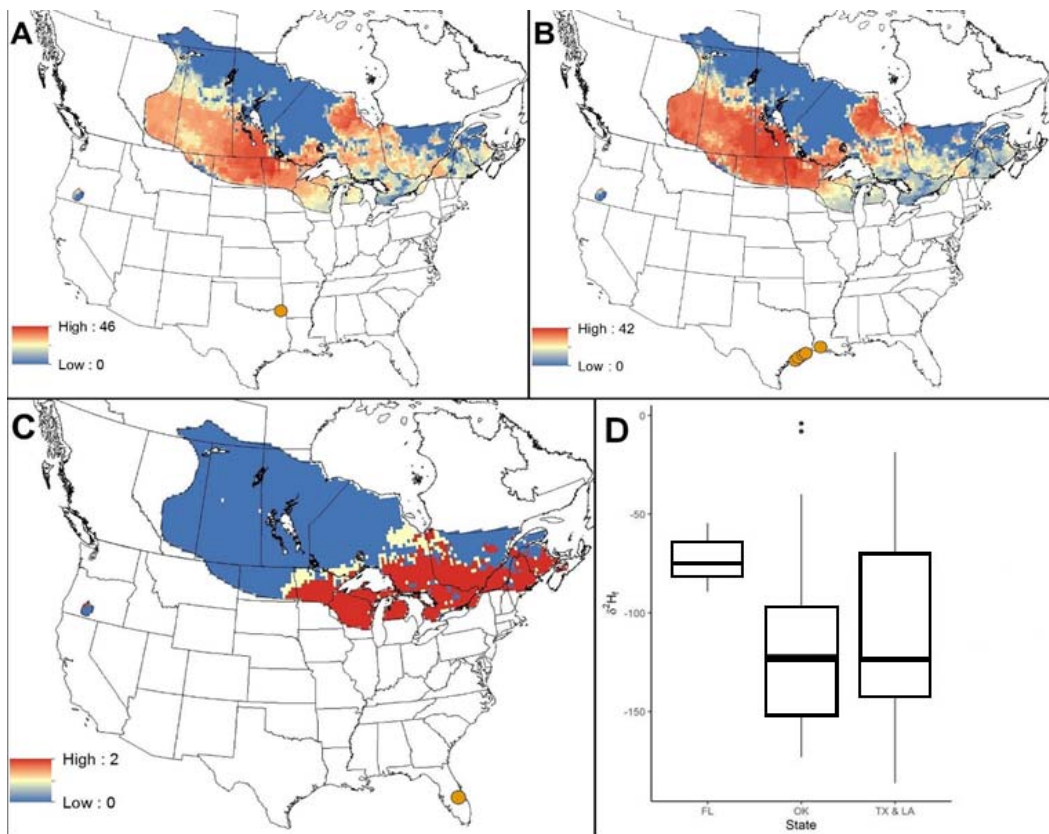
**Table 2.** A summary of the median  $\delta^2\text{H}_f$  ‰ values for each species sampled during the breeding and nonbreeding seasons.

	Season	Median $\delta^2\text{H}_f$ ‰	Lower 95% CI ‰	Upper 95% CI ‰
Yellow Rail	Breeding	-104.9	-113.2	-95.1
	Nonbreeding	-121.3	-131.1	-110.3
LeConte's Sparrow	Breeding	-116.6	-127.7	-107.8
	Nonbreeding	-102.3	-108.9	-97.7
Nelson's Sparrow	Breeding	-95.4	-112.7	-88.0
	Nonbreeding	-94.3	-111.5	-86.6
Sedge Wren	Breeding	-95.0	-110.2	-81.0
	Nonbreeding	-68.4	-71.7	-50.8

isotopic values consistent with the region from Alberta east to Minnesota. The geographic assignment for birds sampled in Texas overlapped broadly with Oklahoma birds, but with more birds showing isotopic values consistent with eastern North Dakota east to Ontario.

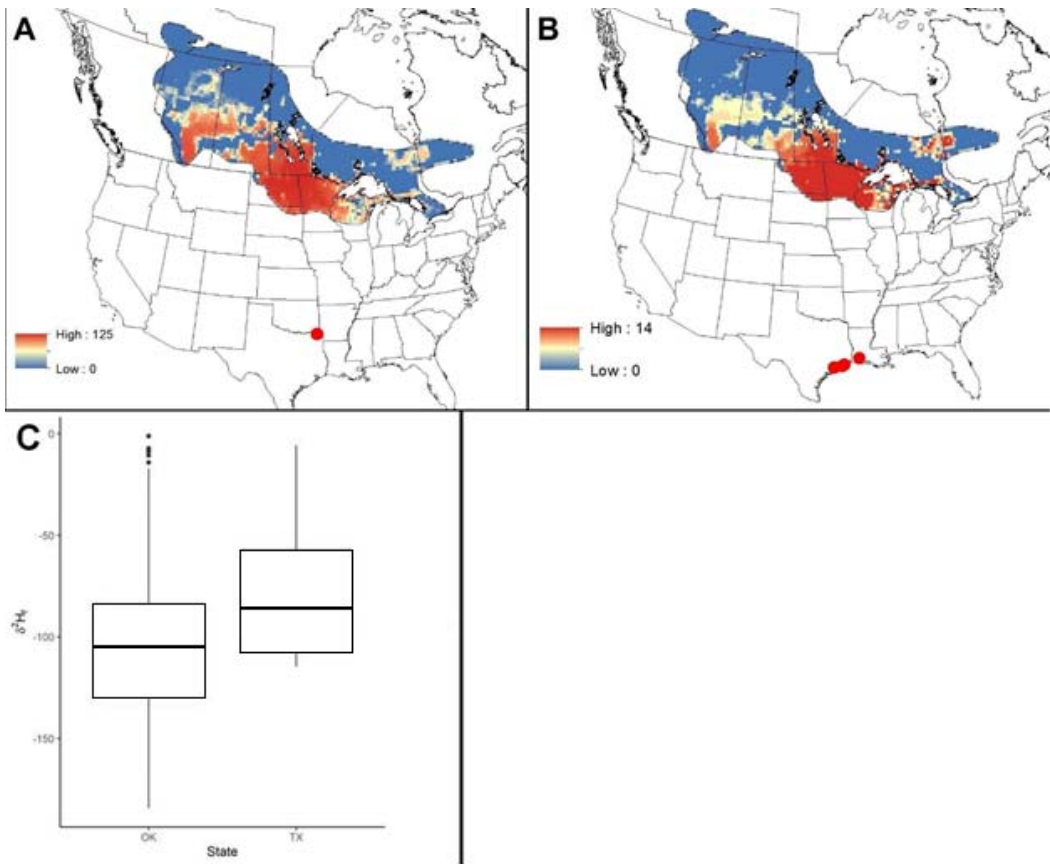
### Nelson's Sparrows

We sampled a total of 43 Nelson's Sparrows (Table 1). Feathers from Nelson's Sparrows during the nonbreeding season ( $n = 24$ , Florida = 3, Texas = 17, Louisiana = 4) had a median  $\delta^2\text{H}_f$  value of



**Figure 3.** The probabilistic origins of Yellow Rails based on  $\delta^2\text{H}_f$ . The scale reflects the number of birds potentially originating from a given pixel in the isoscape (A = birds sampled in Oklahoma, B = birds sampled in Texas and Louisiana, C = birds sampled in Florida, D = a boxplot of the  $\delta^2\text{H}_f$  values for each state where FL = Florida, OK = Oklahoma, TX = Texas, and LA = Louisiana). Sampling locations are shown with orange circles.





**Figure 4.** The probabilistic origins of LeConte's Sparrows based on  $\delta^2H_f$ . The scale reflects the number of birds potentially originating from a given pixel in the isoscape (A = birds sampled in Oklahoma, B = birds sampled in Texas, C = a boxplot of the  $\delta^2H_f$  values for each state where OK = Oklahoma and TX = Texas). Sampling locations are shown with red circles.

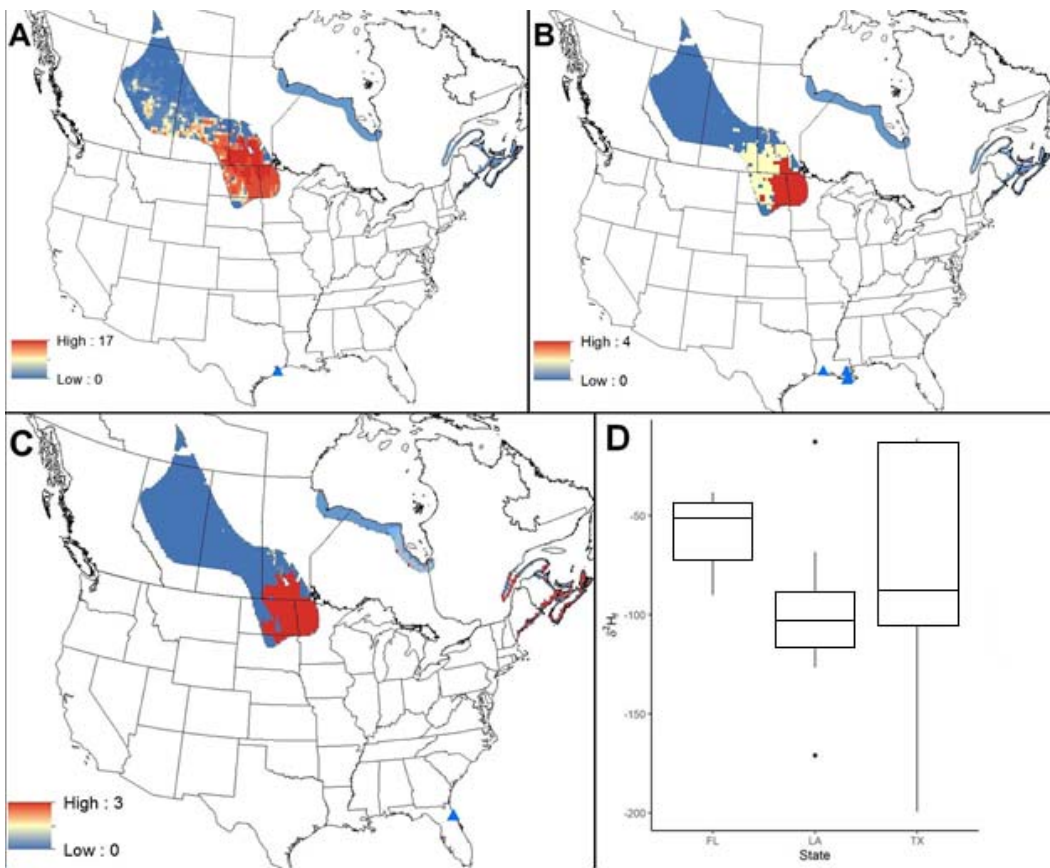
−94.3‰ while feathers from breeding Nelson's Sparrows ( $n = 19$ ) had a median  $\delta^2H_f$  value of −95.4‰ (Table 2). Birds from Texas were assigned to the prairie pothole region, predominantly extending from Alberta east to Minnesota (Fig. 5). In contrast, birds from Louisiana were assigned primarily to eastern North Dakota, southern Manitoba, and western Minnesota (Fig. 5).

There are 3 distinct subspecies of Nelson's Sparrows including *A. n. nelsoni*, *A. n. subvirgatus*, and *A. n. alter* (Shriver et al. 2010). The only location where we observed all 3 subspecies, based on morphometrics, was in northeastern Florida at Faver-Dykes State Park. Nelson's Sparrows captured in Louisiana and Texas were all *A. n. nelsoni*. Birds captured in Florida were assigned to 3 disjunct locations, including (1) eastern North Dakota, southern Manitoba, and western Minne-

sota (*A. n. nelsoni*); (2) southern James Bay; and (3) along the St. Lawrence River, coastal New Brunswick, Nova Scotia, and coastal Maine.

### Sedge Wrens

We sampled 62 Sedge Wrens (Table 1). Feathers from Sedge Wrens during the nonbreeding season ( $n = 45$ , Florida = 2, Texas = 37, Oklahoma = 6) had a median  $\delta^2H_f$  value of −68.4‰ while feathers from breeding Sedge Wrens ( $n = 17$ ) had a median  $\delta^2H$  value of −95.0‰ (Table 2). The geographic assignment for  $\delta^2H_f$  showed no differentiation among birds captured in Oklahoma, Texas, and Florida, and assigned Sedge Wrens captured over the course of the study to a region from Manitoba east to Ontario and south to Illinois and Indiana (Fig. 6).



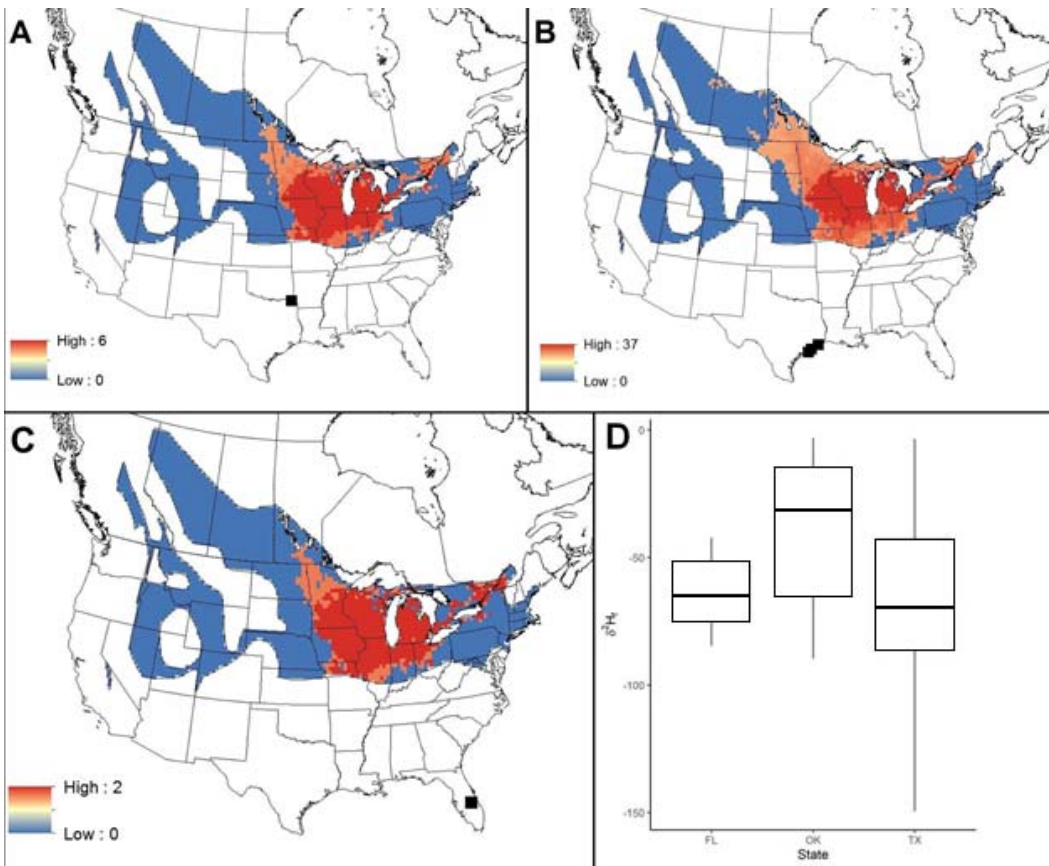
**Figure 5.** The probabilistic origins of Nelson's Sparrows based on  $\delta^2H_r$ . The scale reflects the number of birds potentially originating from a given pixel in the isoscape (A = birds sampled in Texas, B = birds sampled in Louisiana, C = birds sampled in Florida, and D = a boxplot of the  $\delta^2H_r$  values for each state where FL = Florida, LA = Louisiana, and TX = Texas). Sampling locations are shown with blue triangles.

## Discussion

Migratory birds with as wide a range as our 4 focal species may face different threats in different parts of their range and across their annual cycle. Here we see 2 examples of species where individuals in the western part of the wintering range are using different parts of the breeding range, which helps inform conservation efforts for each part of the population. For our 2 other focal species we did not find different breeding range usage from different parts of the wintering range, suggesting another strategy is being used by the birds, and will be needed from those who seek to conserve them.

Yellow Rails are thought to be most abundant in the prairie potholes of Canada and large numbers

also occur during the breeding season in the coastal marshes of James Bay, Ontario (Robert et al. 2004). Nonbreeding Yellow Rails in Texas and Oklahoma had  $\delta^2H_r$  values consistent with wide swaths of the breeding range, although more frequently in their western range. Yellow Rails captured in Missouri were found to have originated more in the central part of the breeding range, especially along Hudson Bay and the northern Great Lakes (Fournier et al. 2017a). The wintering location of birds captured during migration in Missouri is not known, but this difference in assignment could suggest that birds migrating through east of Texas and Oklahoma also breed slightly more east. The more easterly geographic range assigned for the Florida birds suggests that Yellow Rails overwintering in this state may also



**Figure 6.** The probabilistic origins of Sedge Wrens based on  $\delta^2H_r$ . The scale reflects the number of birds potentially originating from a given pixel in the isoscape (A = Oklahoma, B = Texas, C = Florida, and D = a boxplot of the  $\delta^2H_r$  values for each state where FL = Florida, OK = Oklahoma, and TX = Texas). The  $\delta^2H_r$  values for Sedge Wrens sampled in all 3 states exhibited similar probabilistic origins. Sampling locations are shown with black squares.

be breeding farther east than birds overwintering in Texas and Oklahoma. Wetland degradation and loss at breeding and nonbreeding season grounds may be the most significant factor affecting the population status of Yellow Rails (Taylor 1998, COSEWIC 2009, Leston and Bookhout 2020). The rate of wetland loss soared in the 20th century but has more recently stabilized (Dahl 2006). The largest known nonbreeding season population appears to be at the Texas Mid-Coast NWR Complex in Texas (Butler et al. 2014) and maintaining suitable habitat at this site should be a priority. However, the numbers of Yellow Rails spending the nonbreeding season across the Gulf Coast and in Oklahoma are not well understood, as most work in those areas has focused on occupancy and migratory origin (Butler et al.

2010, 2016; Morris et al. 2017, Soehren et al. 2018) and future efforts should be made to look for and manage this species in suitable habitat across this region.

Habitat loss and degradation are likewise the primary threats to populations of LeConte's Sparrows. LeConte's Sparrow has been noted as being common in the wet meadows of North Dakota historically (Lowther 2020), which no longer appears to be the case (Steward 1975, Lowther 2020). Dense stands of damp annual vegetation appear to be crucial habitat for this species, and practices such as burning, grazing, and mowing have decreased the amount of available habitat (Lowther 2020). Our results suggest that, although there is a possible broad overlap in breeding season assignment for birds

wintering in Oklahoma and Texas, LeConte's Sparrows wintering in Texas included individuals breeding farther south and east.

Our results suggest a west to east gradient of breeding origin for overwintering Nelson's Sparrows along the Gulf Coast, which is not otherwise known in the literature and is important for identifying conservation actions and threats. Habitat loss and degradation are the main threats to Nelson's Sparrows (Shriver et al. 2020). A large proportion of coastal wetlands has already been lost and the northeastern population (*A. n. subvirgatus*) in particular remains vulnerable (Shriver et al. 2020).

We did not find a difference among wintering locations in geographic assignment of breeding locations based on  $\delta^2\text{H}_f$  in Sedge Wrens. It has previously been noted that there is considerable variation in  $\delta^2\text{H}_f$  values in the tissues of Sedge Wrens, due to the unique breeding ecology and molt cycle of this species, where they may breed in multiple geographic locations during the same breeding season (Hobson and Robbins 2009). Early nesting in the northern breeding range (Wisconsin, Minnesota, North Dakota, and Saskatchewan) occurs from May to June (Herkert et al. 2020). Nesting in the southern portion of the Sedge Wren's breeding range (Arkansas, Kansas, Illinois, Nebraska, and Missouri) may not occur until July or August (Herkert et al. 2020). Sedge Wren nesting attempts late in the breeding season may represent reneesting attempts from individuals arriving from other areas within their breeding range (Herkert et al. 2020). Consequently, a more complete understanding of Sedge Wren migration may need to wait until active tracking systems are small enough to track this species, since stable isotope analysis alone is not able to resolve this uncertainty.

The resolution of the geographic assignment from stable isotopes alone is too coarse to definitively assign birds to specific geographic localities but can provide preliminary data to inform future work on their migratory ecology. Future work on LeConte's Sparrow, Nelson's Sparrow, and Sedge Wren would benefit from sample sizes large enough for species-specific correction equations. Geographic assignment can be improved with the incorporation of additional isotopes (such as strontium) or additional data, such as genetics (Rundel et al. 2013), breeding abundance (Rushing et al. 2017), or species

distribution models (Fournier et al. 2017a). Some future questions may require other methods, such as smaller tags, such as the VHF tags used in the Motus network (Taylor et al. 2017), or the use of satellite tags, which are quickly becoming options for passerine-sized birds, that allow for more precise geographic assignment.

All 4 species we examined appear to exhibit relatively low breeding season site fidelity, which may reflect a survival strategy in grassland environments where resources may fluctuate annually or across a large spatial extent due to disturbances such as fire, grazing, and variation in annual rainfall (Jones et al. 2007). It is reasonable that this same strategy may appear in overwintering passerines along the Gulf of Mexico, where marshes and grasslands are subject to the same disturbances. However, our study suggests that despite the low site fidelity displayed by our focal species, there appears to be some gradient of breeding ground origin that occurs among birds sampled from different overwintering sites. The scale at which this potentially nomadic survival strategy occurs is not well understood. Future studies should examine the interaction of site fidelity and migratory ecology to better inform management practices.

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