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Diffuse migratory connectivity in two species of shrubland birds: evidence from stable isotopes

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Abstract Connecting seasonal ranges of migratory birds is important for understanding the annual template of stressors that influence their populations. Brewer's sparrows (*Spizella breweri*) and sagebrush sparrows (*Artemisiospiza nevadensis*) share similar sagebrush (*Artemisia* spp.) habitats for breeding but have different population trends that might be related to winter location. To link breeding and winter ranges, we created isoscapes of deuterium [stable isotope ratio (δ) of deuterium; $\delta^2\text{H}$] and nitrogen ($\delta^{15}\text{N}$) for each species modeled from isotope ratios measured in feathers of 264 Brewer's and 82 sagebrush sparrows and environmental characteristics at capture

locations across their breeding range. We then used feather $\delta^2\text{H}_f$ and $\delta^{15}\text{N}_f$ measured in 1,029 Brewer's and 527 sagebrush sparrows captured on winter locations in southwestern United States to assign probable breeding ranges. Intraspecific population mixing from across the breeding range was strong for both Brewer's and sagebrush sparrows on winter ranges. Brewer's sparrows but not sagebrush sparrows were linked to more northerly breeding locations in the eastern part of their winter range. Winter location was not related to breeding population trends estimated from US Geological Survey Breeding Bird Survey routes for either Brewer's or sagebrush sparrows. Primary drivers of population dynamics are likely independent for each species; Brewer's and sagebrush sparrows captured at the same winter location did not share predicted breeding locations or population trends. The diffuse migratory connectivity displayed by Brewer's and sagebrush sparrows measured at the coarse spatial resolution in our analysis also suggests that local environments rather than broad regional characteristics are primary drivers of annual population trends.

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Introduction

Migratory birds spend portions of their annual cycle in locations separated not only by distance but often in significantly different environments. Although environmental phenomena may operate independently among seasonal ranges, their combined influence shapes the annual template experienced by birds (Fretwell 1972). Stressors during one period may be significant enough to override other

seasonal dynamics and drive annual population growth. The ability to link seasonal ranges can provide insights into the interactions of bird dynamics with habitat and geography that underlie a species' evolution. Understanding how migratory species respond to changes within their world also can help focus conservation efforts on critical locations (Sherry and Holmes 1995; Sillett and Holmes 2002; Webster et al. 2002; Norris and Marra 2007).

Brewer's (*Spizella breweri*) and sagebrush sparrows [*Artemisiospiza nevadensis* (formerly sage sparrow *Amphispiza belli*)] are sagebrush (*Artemisia* spp.)-obligate species that overlap extensively on their breeding ranges in the western United States. Both species are sensitive to spatial and temporal changes in sagebrush landscapes (Knick and Rotenberry 2002; Vander Haegen 2007) and are of conservation concern because of long-term trajectories of habitat loss (Rotenberry 1998; Knick et al. 2003; Dobkin and Sauder 2004). Although selected micro-environments may differ, Brewer's and sagebrush sparrows generally have similar habitat affinities (frequently with overlapping individual territories), comparable reproductive parameters, and experience the same coarse-scale environmental pressures during the breeding season. Yet, Brewer's and sagebrush sparrows have different range-wide and regional population trends. Range-wide trends estimated from annual counts on Breeding Bird Surveys (BBS) (Sauer et al. 2011) conducted from 1998 up to and including 2009 were -3.8% per year (-6.7 to -0.8 CI_{95}) for Brewer's sparrows and 0.1% per year (-3.3 to 3.0 CI_{95}) for sagebrush sparrows; state-wide trends were uncorrelated between species (Pearson's $r = -0.03$, $P = 0.98$). Given these similarities on the breeding grounds, differences in population trends may be caused by dynamics during migration or on winter grounds (Rotenberry and Wiens 1980).

Brewer's and sagebrush sparrows are short-distance migrants that winter in southwestern United States and central Mexico (Martin and Carlson 1998; Rotenberry et al. 1999); little is known about their migration pathways and wintering ecology (Knick et al. 2003). Therefore, our first objective was to locate winter areas used by Brewer's and sagebrush sparrows in the southwestern United States. Spatial overlap might indicate the extent to which these species experience similar environmental stressors during winter.

Our second objective was to assign probable breeding regions to wintering Brewer's and sagebrush sparrows using stable isotope signatures in feathers from captured birds. To do this, we created separate breeding range isoscapes for deuterium [stable isotope ratio (δ) of deuterium; δ^2H] and nitrogen ($\delta^{15}N$) derived from geographic and environmental relationships to isotopes measured in known-origin birds. Breeding regions were assigned to birds captured on winter grounds from the joint probability of occurrence on both isoscapes. We then connected

winter locations of captured birds to population trends estimated from the BBS conducted in breeding regions. The hypothesis that winter environment is an important driver might be supported if birds using the same winter locations were undergoing similar population trends on their breeding grounds. If migratory connectivity for Brewer's and sagebrush sparrows is strong (Webster et al. 2002) and populations segregate on both winter and breeding ranges, then local influences in each season could vary widely and remain relatively isolated. Conversely, if winter locations each contain a mixture of birds from multiple breeding regions, then environmental pressures during winter may drive population change across a large portion of a species' breeding range (Marra et al. 2006).

Materials and methods

Field surveys and bird captures

We conducted extensive surveys to locate winter (December up to and including early March) areas used by Brewer's and sagebrush sparrows across the southwestern United States from 2002 up to and including 2008. We first used maps from annual Christmas Bird Counts (Butcher 1990) but then expanded the surveys to most non-urban and unfor-ested regions of southern California, Arizona, Nevada, and New Mexico. Our study extent encompassed the approximate northern one-fourth of the wintering range of Brewer's sparrows (Rotenberry et al. 1999) and two-thirds of the sagebrush sparrow wintering range (Martin and Carlson 1998).

We captured Brewer's and sagebrush sparrows for isotope training data at breeding and post-breeding locations from April up to and including July in 2003–2007. We attempted to capture birds at sites representing spatial and environmental gradients across the breeding range (Fig. 1).

We captured birds in mist nets when detected on winter grounds at locations separated by a minimum of 15 km (Fig. 1). Actual capture sites varied within locations among years due to vagaries of flock movements. We revisited locations in multiple years, generally at the same time, but did not standardize length of time for netting because we frequently caught Brewer's sparrows in large flocks of >50 individuals. Therefore, we cannot infer relative abundance across years or locations.

We collected feathers from captured birds, which also were measured, weighed, banded with standard US Geological Survey (USGS) bands, aged according to variation in feather wear of primaries [HY and SY = juvenile, ASY and AHY = adult; Pyle (1997); M. Leu, unpublished data] and released at the site. Geographic coordinates for each capture location were recorded using a global positioning system (measurement error ≤ 10 m).

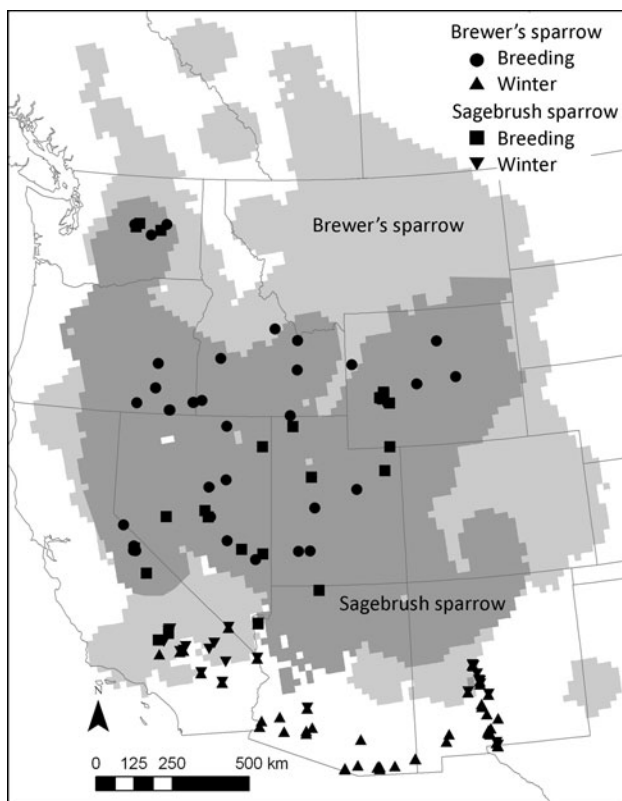


Fig. 1 Breeding and winter range capture locations for Brewer's and sagebrush sparrows. Shaded areas represent breeding ranges delineated from Breeding Bird Surveys

Isotopic signatures in feathers

Stable isotope ratios in feathers reflect abundances contained in foods eaten during the period of feather growth and also background variation across dominant geographic, topographic, and environmental gradients (Kelly 2000; Hobson 2005; Bowen 2010). Brewer's and sagebrush sparrows molt primary flight feathers proximally starting with the first primary (p1) during or immediately following the breeding season but prior to migration (Pyle 1997; M. Leu, unpublished data). We collected both p1 feathers from each captured bird on breeding and winter grounds because these feathers are grown first and likely contain an isotopic signature most closely correlated to their breeding location. One of 39 Brewer's sparrows captured in June was in primary flight feather molt compared to 24 of 80 captured in July. For sagebrush sparrows, one of four individuals captured in June was in primary flight feather molt compared to 14 of 17 in July (M. Leu, unpublished data). In central Nevada, six of seven sagebrush sparrows captured in September and all ten individuals captured in October within the breeding range had replaced all primaries. Therefore, most individuals in our study had initiated flight feather molt near breeding grounds.

The relationship between deuterium in feathers ($\delta^2\text{H}_f$) with published isoscapes of annual ($\delta^2\text{H}_p$) or growing season ($\delta^2\text{H}_{gs}$) deuterium in precipitation (Bowen et al. 2005) or when calibrated to latitude or geographic location has been important in assigning origins to birds captured elsewhere (Kelly et al. 2002; Wunder et al. 2005, 2010). However, efficacy of assignments for birds of unknown origin ultimately rests on the accuracy and resolution of the deuterium iscape (Farmer et al. 2008) and the assumption of a constant or defined scaling relationship between assimilated $\delta^2\text{H}_f$ and mapped values across the prediction range (Webster et al. 2002; Hobson 2005; Wunder et al. 2005; Wunder and Norris 2008). The potential for isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) also has been explored (Chamberlain et al. 1997; Hobson and Wassenaar 2001; Rubenstein et al. 2002; Bensch et al. 2006; Kelly et al. 2008; Franks et al. 2012) but these isotopes are not used as widely as $\delta^2\text{H}$ and regional or continental isoscapes have not been developed. All three isotopes discriminated among locations of known-origin individuals in preliminary analyses using linear discriminant functions. However, $\delta^{13}\text{C}$ had little explanatory power and we were unable to create a suitable iscape. Therefore, we modeled only $\delta^2\text{H}$ and $\delta^{15}\text{N}$, which created predictive surfaces along two isotopic gradients for probabilistic assignment of breeding range.

Laboratory analysis and accuracy

All isotope analyses and accuracy assessments were performed at the Northern Arizona University's Colorado Plateau Stable Isotope Laboratory. Deuterium values based on nonexchangeable hydrogen were expressed as the deviation (δ) in the ratio of $^2\text{H}/^1\text{H}$ relative to Vienna standard mean ocean water (VSMOW) (Wassenaar and Hobson 2003) and nitrogen ($\delta^{15}\text{N}/^{14}\text{N}$) relative to air normalized to International Atomic Energy Agency (IAEA)-N1 and IAEA-N2 standards measured in units/thousand (‰). Measurement accuracy was assessed with a standard double sample analyses conducted at random points within each of 39 runs. Intra-assays varied among runs with absolute differences between feather duplicates between 0.03–9.48 ‰ and average absolute differences between 1.61 and 4.79 ‰ (SD 0.69–2.45) among 36 runs (three runs had only one double sample); overall absolute difference across all runs averaged 2.74 ‰ (SD 1.71). Intra-assays for nitrogen varied among runs with absolute differences between feather duplicates between 0.00017 and 12.4 ‰ and average absolute differences between 0.08 and 3.12 ‰ (SD 0.07–4.31) among 29 runs (one run only had one duplicate); overall absolute difference across all runs averaged 0.75 ‰ (SD 1.46).

Spatial data

We modeled relationships between isotope content in feathers of known-origin birds sampled across the breeding range and environmental variables measured at the capture location. We selected variables based on known influence of elevation, precipitation, and vegetation characteristics on background isotope abundances (Kelly 2000; Hobson et al. 2003; Bowen 2010) and on availability of spatial data for predictive modeling of the isoscape surface. We averaged values within a 5-km radius surrounding the capture location to include a region sufficiently large to include post-breeding movements during which molt occurs, as well as surrounding environmental influences on isotope ratios. Sizes of breeding territories range from 0.1 to 2.4 ha for Brewer's sparrows (Rotenberry et al. 1999) and 0.7–7.1 ha for sagebrush sparrows (Martin and Carlson 1998). Little is known about post-breeding movements by Brewer's and sagebrush sparrows. Daily movements prior to migration by 35 radio-marked sagebrush sparrows were <1 km; median range size was 14 ha (range 1.3–1,436 ha) (Fesenmyer and Knick 2011).

We estimated elevation from USGS digital elevation models (Gesch et al. 2002). Vegetation greenness (normalized difference vegetation index; NDVI) was derived from 1-km Advanced Very High Resolution Radiometer satellite imagery (Eidenshink 1992). The NDVI is sensitive to green biomass, which is a function of the total amount of green plant cover and local precipitation (Tucker 1979). The approximate biweekly estimate is standardized to permit temporal comparisons over growing seasons and also spatially across regions. We selected NDVI period 16 (30 July–13 August) because it most strongly correlated to isotope ratios in feathers and also corresponded to the peak period of feather molt. We averaged NDVI estimates for 2002–2006 to provide a single measure because biweekly values were not available for all years. For the $\delta^2\text{H}$ model, we also included values derived from the deuterium isoscape for growing season ($\delta^2\text{H}_{\text{gs}}$) rather than annual precipitation ($\delta^2\text{H}_{\text{p}}$) (Bowen et al. 2005) because of stronger correlations with $\delta^2\text{H}_{\text{f}}$ (Brewer's sparrow: $r_{\delta^2\text{H}_{\text{gs}}} = 0.39$, $r_{\delta^2\text{H}_{\text{p}}} = 0.26$; sagebrush sparrow: $r_{\delta^2\text{H}_{\text{gs}}} = 0.67$; $r_{\delta^2\text{H}_{\text{p}}} = 0.50$).

Map resolution was coarsest for $\delta^2\text{H}_{\text{gs}}$ (20' \times 20' grid). Grid cell size of other coverages was 1 km for NDVI, and 180 m for elevation. We resampled all maps and the final predictive isoscapes to 1-km resolution using cubic convolution across neighboring cells to avoid sharp edges. Resampling did not change the original grain of the coarse-scale $\delta^2\text{H}_{\text{gs}}$ but permitted information contained in finer resolution data to be retained for elevation and NDVI, which can vary widely over short distances in our study region.

Model development

We used a generalized linear mixed-effects regression with a normal probability distribution (Nelder and Wedderburn 1972) to model relationships between feather isotope ratios and breeding season capture location (latitude, longitude, latitude \times longitude), elevation (m), NDVI, and $\delta^2\text{H}_{\text{gs}}$ (deuterium isoscape only). We treated capture location as a repeated measure because multiple individuals were sampled at locations (PROC MIXED; SAS Institute 2008). We evaluated model fit by individual and combined environmental variables using Akaike's information criteria adjusted for small sample size (AIC_c) (Burnham and Anderson 2002). Final parameter estimates were obtained by model-averaging the top candidate models having a cumulative sum of AIC_c weights = 0.95 (Burnham and Anderson 2002). The multivariate function then was applied to the breeding range to create a spatially explicit isoscape of predicted values of a feather's isotope based on geographic coordinates i, j and values of environmental characteristics within each grid cell.

We clipped breeding range isoscapes to boundaries of the BBS containing counts for Brewer's and sagebrush sparrows. The isoscape for sagebrush sparrows was restricted to the breeding range of its progenitor subspecies *Artemisiospiza belli* ssp. *nevadensis*, the only migratory subspecies of sage sparrow occurring outside of California (Martin and Carlson 1998). We included singing territorial sagebrush sparrows captured at three locations within California in the sample of breeding birds to expand the statistical inference space in our models.

Assignment to breeding range

We assigned breeding regions on each isoscape to wintering birds from the likelihood that feather and predicted map values were similar using a normal probability distribution. We estimated offset (bias in the predictive equation relative to known values) and variance around the predicted $\delta^2\hat{\text{H}}_{ij}$ and $\delta^{15}\hat{\text{N}}_{ij}$ by bootstrapping the residuals (5,000 replicates sampled with replacement) to estimate the statistical distribution. The final map of predicted breeding region for each wintering bird then was delineated from the joint probability surface for $\delta^2\hat{\text{H}}_{ij}$ and $\delta^{15}\hat{\text{N}}_{ij}$. The assumption of independence between isotopes was true for sagebrush sparrows ($r = 0.001$, $P = 0.98$) but not Brewer's sparrows ($r = 0.29$, $P < 0.01$).

We connected wintering birds to population trends on their predicted breeding range using estimates from the BBS, which were in ~ 22 -km grid cells (Sauer et al. 2011). Probability surfaces of predicted breeding region for each bird first were converted to binary presence/absence using a joint probability of assignments $P_{\delta^2\text{H}_{i,j}} \times P_{\delta^{15}\text{N}_{i,j}} > 0.7$

as a threshold prior to overlay with the BBS coverage. For birds with weakly overlapping assignment regions between individual isotopes, we used the upper 30 % of the joint probability distributions rescaled from the top value as the threshold. We then averaged BBS trend estimates across the assignment region for each bird. These thresholds represented a trade-off that was not overly restrictive (error of omission) and recognized the relative precision in isotope data, but not too general (error of commission) in assigning the area of predicted origin.

We tested for trends in latitude and population trend of predicted breeding areas relative to longitude of winter location and also between Brewer’s and sagebrush sparrows captured at the same locations. We used hierarchical mixed-effect models (PROC MIXED; SAS Statistical Institute 2008) to identify sources of variation treating capture location as a random effect.

Results

Isoscape models derived from breeding range birds

Brewer’s sparrows

We captured 264 Brewer’s sparrows at 54 locations on the breeding range (Table 1). Number of Brewer’s sparrows captured per location ranged from one to 39 birds; we captured a single bird at 24 locations and more than ten individuals at seven locations.

The predictive isoscape surface for deuterium (Fig. 2a) was created using model-averaged coefficients derived from nine candidate models (Table 2). Amount-weighted δ^2H_{gs} in

precipitation was included in all candidate models although the univariate model ($\Delta AIC_c = 33.7$) was not in the final set of candidate models. However, the relationship of feather δ^2H_f to δ^2H_{gs} is important for comparison in other studies to understand scaling relationships among species. For Brewer’s sparrows, the univariate function scaled as

$$\delta^2H_f = -49.0 (7.1SE) + 0.76 (0.11)\delta^2H_{gs}$$

across the breeding range. The final model had a strong geographic component: δ^2H_f decreased with increasing latitude and longitude and with their interaction (Table 3). Feather deuterium also was negatively related to vegetation greenness but increased with higher elevation.

Twelve candidate models (Table 2) were used to derive model-averaged coefficients for predicting $\delta^{15}N_f$. In the final equation (Table 3), ratios of $\delta^{15}N_f$ generally decreased from southwest to northeast. Finer spatial patterns in the $\delta^{15}N_{ij}$ surface (Fig. 2b) reflected a negative relationship between $\delta^{15}N_f$ and vegetation greenness and a positive relationship to elevation (Table 3).

Sagebrush sparrow

Feathers from 82 sagebrush sparrows were collected at 22 locations on the breeding range (Table 1). We captured from one to five birds at 20 sites, and 22 and 23 individuals each at one location.

We model-averaged the top 15 candidate models (Table 4) to derive the final predictive equation for deuterium (Table 3). Amount-weighted δ^2H_{gs} in precipitation was the primary variable in retained in all candidate models and also was the top candidate as a univariate model scaled to feather δ^2H_f as

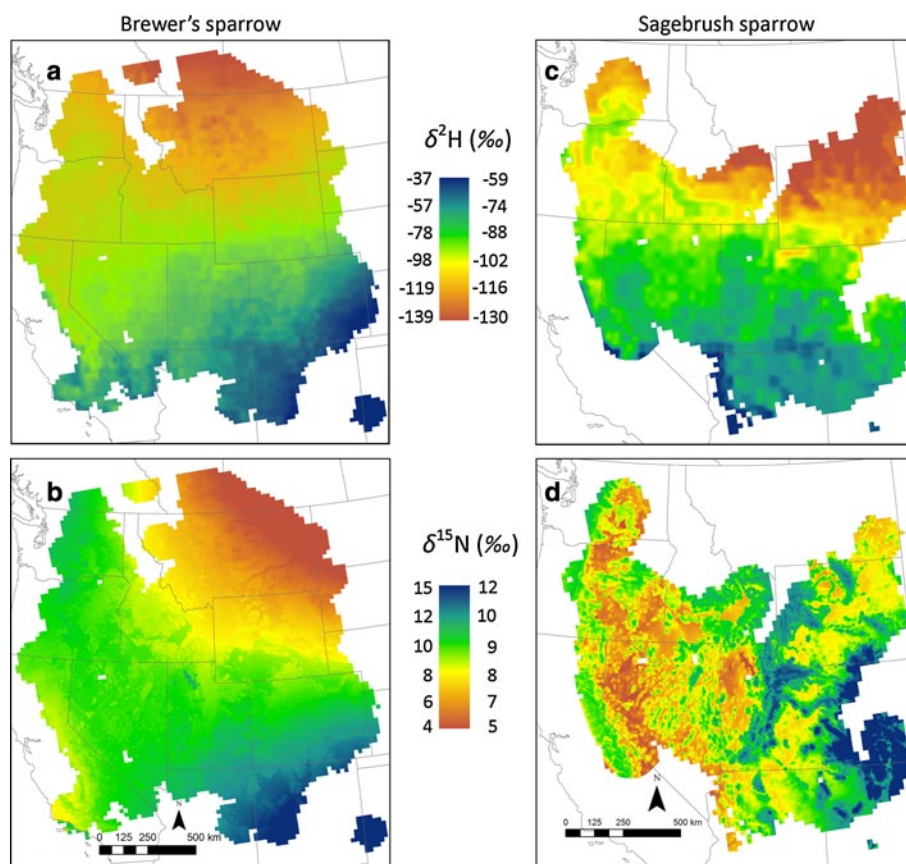
Table 1 Winter and breeding season captures of Brewer’s and sagebrush sparrows

Season	Period	Brewer’s sparrows		Sagebrush sparrows	
		No. captures	No. locations	No. captures	No. locations
Winter	January–February 2003	22	1	14	8
	January–February 2004	19	2	57	9
	December 2004–February 2005	100	5	66	14
	December 2005–February 2006	567	37	129	27
	December 2006–February 2007	209	21	181	22
	December 2007–February 2008	112	8	60	19
Total		1,029	49 ^a	507	53 ^b
Breeding	March–August 2003	23	10	19	10
	May–August 2004	19	14	2	2
	July–August 2005	3	2	2	2
	May–July 2006	200	24	59	9
	June–July 2007	15	3		
	July 2008	4	1		
Total		264	54	82	22

^a Includes 28 locations sampled in 1 year, 17 sampled in 2 years, and four sampled in 3 years

^b Includes 31 locations sampled in 1 year, 13 sampled in 2 years, five sampled in 3 years, three sampled in 4 years, and three sampled in 5 years

Fig. 2 Predictive $\delta^2\hat{H}_{ij}$ (*top*; where δ is stable isotope ratio) and $\delta^{15}\hat{N}_{ij}$ (*bottom*), isoscapes used for breeding range assignments for Brewer's sparrows and sagebrush sparrows. We assigned breeding origins of wintering Brewer's sparrows from the joint probability of occurrence using an offset and variance of a normal probability distribution for **a** deuterium ($\mu = -0.05$, $\sigma^2 = 126.7$) and **b** nitrogen ($\mu = 0.2$, $\sigma^2 = 5.7$) isoscapes. For sagebrush sparrows, we used an offset and variance for **c** deuterium ($\mu = 0.06$, $\sigma^2 = 108.8$) and **d** nitrogen ($\mu = 0.05$, $\sigma^2 = 5.1$) isoscapes



$$\delta^2H_f = -23.7 (8.7SE) + 1.11 (0.14)\delta^2H_{gs}$$

across the breeding range. Sagebrush sparrow δ^2H_f decreased with increasing latitude and also along a south-west to northeast gradient (Table 3). Feather deuterium also decreased with higher vegetation greenness and increasing elevation although these fine-scale influences were less dominant in the $\delta^2\hat{H}_{ij}$ isoscape (Fig. 2c).

We derived model-averaged coefficients for the $\delta^{15}\hat{N}_{ij}$ isoscape from 15 candidate models (Table 4). Broad-scale geographic gradients in the final predictive equation (Table 3) showed similar but less pronounced broad-scale geographic gradients and stronger fine-scale influences than for Brewer's sparrows. Feather $\delta^{15}N_f$ generally decreased along north and east gradients while small-scale positive relationships with vegetation greenness and elevation dominated the pattern in the $\delta^{15}\hat{N}_{ij}$ isoscape (Fig. 2d).

Winter range captures

We captured birds at 79 locations across the winter range in southwestern United States (Fig. 1). Birds were captured at 39 of these locations in one year, at 23 locations in 2 years, and at 17 locations in ≥ 3 years. Number of Brewer's

sparrows sampled per location in each year ranged from five or less ($n = 17$ locations) to 130 and number of sagebrush sparrows from five or less ($n = 27$) to 44. Brewer's and sagebrush sparrows were both captured at 23 locations. Of these, both species were captured in the same year at 20 sites and at four locations in 2 years.

Linking winter and breeding ranges

Individual winter locations were used by Brewer's or sagebrush sparrows that came from across a large part of their respective breeding ranges. Even within locations, raw isotope values for individual sparrows captured as a flock in a single flushing episode had widely different δ^2H_f and $\delta^{15}N_f$ without evident clustering (Fig. 3). Although some winter locations contained birds primarily from one region, predicted breeding locations of birds captured at any one winter location most often broadly overlapped those from any other winter location (Fig. 4).

Brewer's sparrows captured in the eastern part of their winter range had more northern breeding ranges than birds at western winter locations [breeding latitude = $60.5 (5.4 SE) + 0.2 (0.05)$ winter long; $F_{1,23,2} = 11.13$, $P = 0.0028$; Fig. 5a]. Although the larger trend with winter longitude was significant, a greater proportion of the variation

Table 2 Model fit (Akaike’s information criteria adjusted for small sample size; AIC_c), difference from top model (ΔAIC_c), and Akaike weight (w_i) for top models for feather stable isotope ratio (δ) of deuterium (δ^2H_f) and nitrogen ($\delta^{15}N_f$) of 264 Brewer’s sparrows captured on their breeding range

Isotope	Candidate model ^a	<i>K</i>	AIC_c	ΔAIC_c	w_i
δ^2H_f	$\delta^2H_{gs} + lat. + long. + lat. \times long.$	6	2,040.8	0.0	0.22
	$\delta^2H_{gs} + long.$	4	2,041.1	0.3	0.19
	$\delta^2H_{gs} + lat. + long. + lat. \times long. + DEM$	7	2,041.3	0.5	0.17
	$\delta^2H_{gs} + lat. + long. + lat. \times long. + DEM + NDVI$	8	2,042.6	1.8	0.09
	$\delta^2H_{gs} + lat. + long. + lat. \times long. + NDVI$	7	2,042.7	1.9	0.08
	$\delta^2H_{gs} + lat. + long.$	5	2,042.9	2.1	0.08
	$\delta^2H_{gs} + lat. + long. + DEM$	6	2,043.0	2.2	0.07
	$\delta^2H_{gs} + long. + NDVI$	5	2,043.1	2.3	0.07
	$\delta^2H_{gs} + lat. + long. + DEM + NDVI$	7	2,044.1	3.3	0.04
	$\delta^{15}N_f$	$lat. + long. + lat. \times long.$	5	1,185.6	0.0
$lat. + long. + lat. \times long. + NDVI$		6	1,185.7	0.1	0.29
$lat. + long. + lat. \times long. + DEM + NDVI$		7	1,187.3	1.7	0.13
$lat. + long. + lat. \times long. + DEM$		6	1,187.6	2.0	0.11
NDVI		3	1,189.6	4.0	0.04
$long. + NDVI$		4	1,189.6	4.0	0.04
$lat. + NDVI$		4	1,190.7	5.1	0.02
$lat. + long. + NDVI$		5	1,191.5	5.9	0.02
DEM + NDVI		4	1,191.7	6.1	0.01
$long. + DEM + NDVI$		5	1,191.9	6.1	0.01
$lat. + DEM$		4	1,192.0	6.3	0.01
$lat.$		3	1,194.1	6.4	0.01

Candidate models included latitude (*lat.*), longitude (*long.*), an index of vegetation greenness (normalized difference vegetation index; *NDVI*), and elevation (digital elevation model; *DEM*); models for δ^2H_f also included growing season deuterium (δ^2H_{gs}). Number of parameters (*K*) included the number of model variables plus the intercept and residual variance. AIC_c weights were rescaled to sum to 1 for model-averaging (Burnham and Anderson 2002)

^a Null model AIC_c was 2,119.6 for δ^2H_f and 1,191.7 for $\delta^{15}N_f$

Table 3 Model-averaged coefficients (SE) of predictive functions for $\delta^2\hat{H}_{ij}$ and $\delta^{15}\hat{N}_{ij}$ isoscapes used to assign breeding ranges to Brewer’s and sagebrush sparrows captured on winter ranges

	Isoscape surface model
Brewer’s sparrow	$\delta^2\hat{H}_{ij} = 912.2 (418.8) + 0.9 (0.2) \times \delta^2H_{gs} - 19.6 (10.2) \times lat + 8.2 (3.5) \times long - 0.2 (0.1) \times lat \times long - 1.0 (1.5) \times NDVI^a + 1.6 (1.2) \times DEM^b$ $\delta^{15}\hat{N}_{ij} = 232.8 (75.3) - 5.5 (1.8) \times lat + 1.9 (0.65) \times long - 4.7 (1.5) \times lat \times long^a - 9.4 (2.9) \times NDVI^b + 5.4 (1.0) \times DEM^c$
Sagebrush sparrow	$\delta^2\hat{H}_{ij} = -21.3 (63.2) + 1.1 (0.2) \times \delta^2H_{gs} - 0.2 (1.2) \times lat + 2.1 (4.3) \times long^a - 1.7 (0.8) \times lat \times long^a - 8.5 (2.4) \times NDVI^b - 1.7 (7.5) \times DEM^b$ $\delta^{15}\hat{N}_{ij} = 71.2 (37.5) - 1.4 (0.8) \times lat + 0.6 (0.3) \times long - 1.2 (0.7) \times lat \times long^a + 2.5 (1.4) \times NDVI^a + 4.0 (0.2) \times DEM^d$

Models included *lat.*, *long.*, an index of vegetation greenness (*NDVI*), and elevation (*DEM*) as predictor variables. Models for deuterium included δ^2H_{gs} (Bowen et al. 2005). For abbreviations, see Table 2

^a Coefficient multiplied by 10^{-2}

^b Coefficient multiplied by 10^{-3}

^c Coefficient multiplied by 10^{-5}

^d Coefficient multiplied by 10^{-4}

Table 4 Model fit (AIC_c), ΔAIC_c, and w_i for top models for δ²H_f and δ¹⁵N_f of 82 sagebrush sparrows captured on their breeding range

Isotope	Candidate model ^a	K	AIC _c	ΔAIC _c	w _i
δ ² H _f	δ ² H _{gs}	3	623.8	0.0	0.31
	δ ² H _{gs} + long.	4	625.8	2.0	0.11
	δ ² H _{gs} + lat.	4	626.0	2.2	0.10
	δ ² H _{gs} + DEM	4	626.0	2.2	0.10
	δ ² H _{gs} + NDVI	4	626.0	2.2	0.10
	δ ² H _{gs} + lat. + long.	5	628.0	4.2	0.04
	δ ² H _{gs} + long. + DEM	5	628.0	4.2	0.04
	δ ² H _{gs} + long. + NDVI	5	628.0	4.2	0.04
	δ ² H _{gs} + lat. + DEM	5	628.3	4.5	0.03
	δ ² H _{gs} + lat. + NDVI	5	628.3	4.5	0.03
	δ ² H _{gs} + DEM + NDVI	5	628.3	4.5	0.03
	δ ² H _{gs} + lat. + long. + lat. × long.	6	630.0	6.2	0.01
	δ ² H _{gs} + lat. + long. + DEM	6	630.3	6.5	0.01
	δ ² H _{gs} + lat. + long. + NDVI	6	630.3	6.5	0.01
	δ ² H _{gs} + long. + DEM + NDVI	6	630.3	6.5	0.01
δ ¹⁵ N _f	long. + NDVI	4	375.8	0.0	0.19
	NDVI	3	376.8	1.0	0.12
	DEM	3	377.0	1.2	0.11
	lat. + long. + lat. × long. + DEM	6	377.4	1.6	0.09
	long. + DEM	4	377.8	2.0	0.07
	long. + DEM + NDVI	5	377.8	2.0	0.07
	lat. + long. + NDVI	5	378.1	2.3	0.06
	lat. + DEM	4	378.2	2.4	0.06
	DEM + NDVI	4	378.4	2.6	0.05
	lat. + NDVI	4	379.0	3.2	0.04
	long.	3	379.2	3.4	0.04
	lat. + long. + DEM	5	379.5	3.7	0.03
	lat. + long. + lat. × long. + NDVI	6	379.5	3.7	0.03
	lat. + long. + lat. × long. + DEM + NDVI	7	379.5	3.7	0.03
	lat. + DEM + NDVI	5	380.0	4.2	0.02

Candidate models included lat., long., an index of vegetation greenness (NDVI), and elevation (DEM); models for δ²H_f also included growing season deuterium δ²H_{gs}. K included the number of model variables plus the intercept and residual variance. AIC_c weights were rescaled to sum to 1 for model-averaging (Burnham and Anderson 2002). For abbreviations, see Table 2

^a Null model AIC_c was 669.5 for δ²H_f and 377.9 for δ¹⁵N_f

was contained within locations ($\sigma^2 = 11.59$, $z = 22.29$, $P < 0.001$) than between capture sites ($\sigma^2 = 0.18$, $z = 1.03$, $P = 0.15$). Population trends at predicted breeding locations for Brewer's sparrows were not related to longitude of their winter capture location ($F_{1,1,026} = 1.63$, $P = 0.20$) (Fig. 5b). All variation in breeding population trend was

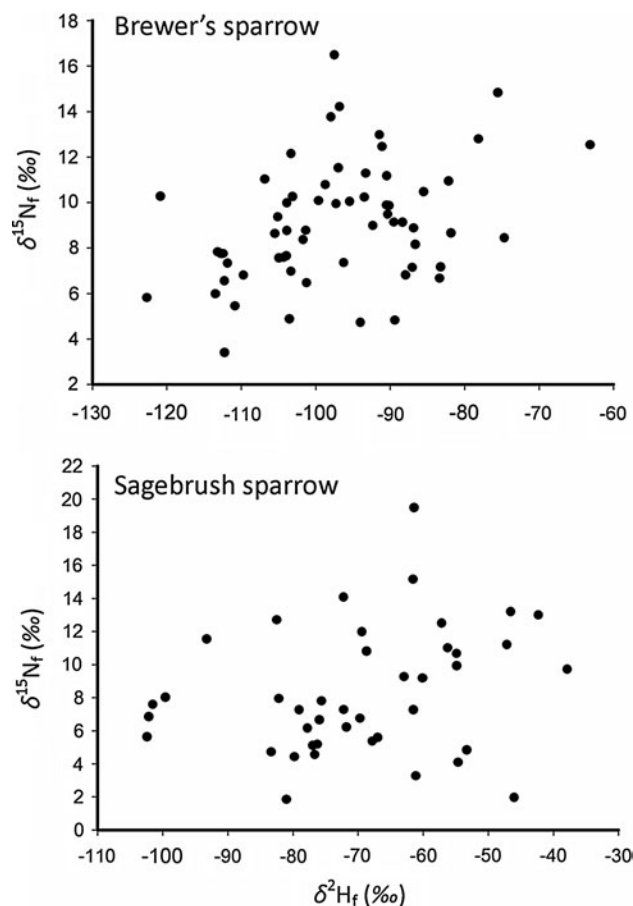


Fig. 3 Feather δ²H (δ²H_f) and δ¹⁵N_f measured in 61 adult Brewer's sparrows captured as a single flock on their winter range in western Arizona (top), and 42 adult sagebrush sparrows captured as a single flock on their winter range in southern California (bottom)

contained within capture locations; no variation was explained across capture locations.

Latitude of breeding range assignments for sagebrush sparrows was not related to longitude ($F_{1,482} = 0.05$, $P = 0.82$) of winter capture breeding locations (Fig. 5c). Variation contained within locations ($\sigma^2 = 8.78$, $z = 14.93$, $P < 0.0001$) was greater than between capture sites ($\sigma^2 = 2.42$, $z = 2.78$, $P = 0.002$). Longitude of winter locations also was not related to predicted breeding population trend ($F_{1,493} = 1.09$, $P = 0.30$) (Fig. 5d). Again, variation in predicted breeding trend across winter capture locations was small ($\sigma^2 = 1.03$, $z = 2.75$, $P = 0.003$) relative to that within contained within capture sites ($\sigma^2 = 4.94$, $z = 15.08$, $P < 0.001$).

Brewer's and sagebrush sparrows captured at the same winter location did not share the same breeding range (Fig. 6a). Predicted breeding ranges for Brewer's sparrows at winter locations averaged 3.4° higher latitude (range -1.7 to 7.7 latitude) compared to sagebrush

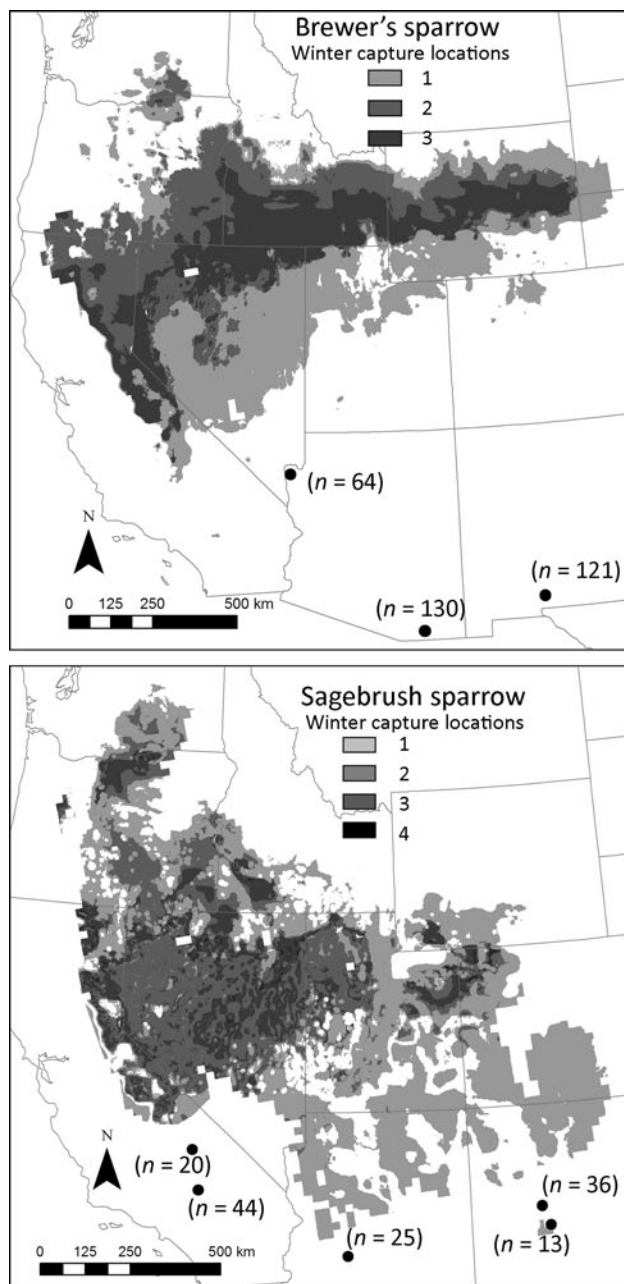


Fig. 4 Spatial overlap in predicted breeding ranges of individual Brewer's sparrows captured at three winter locations (*top*), and sagebrush sparrows captured at five winter locations in southwestern United States (*bottom*). Breeding range distributions represent the top 80 % of summed probabilities for all individuals captured at a winter location (n = location sample size)

sparrows, and likely reflected their overall more northerly breeding distribution. However, latitude at winter sites was not correlated between species ($r = 0.08$, $P = 0.76$) (Fig. 6b). Population trends of Brewer's sparrows on predicted breeding ranges averaged 3.8 %/year lower (range -1.4 to -7.2) than sagebrush sparrows captured at the same winter location. Population trends were

not correlated between species across winter locations ($r = 0.34$, $P = 0.22$) (Fig. 6c).

Discussion

Coarse-scale maps of winter ranges for Brewer's and sagebrush sparrows delineate broad-scale overlap (Martin and Carlson 1998; Rotenberry et al. 1999) that was not present at the finer scales of our study. Although we captured both species at some winter locations, there also was a clear separation of distributions and densities. Brewer's sparrows were not likely to occur at capture locations in southern California but instead were distributed across southern Arizona and New Mexico. In comparison, sagebrush sparrows were locally abundant in southern California and New Mexico but largely were absent from south-central and southeastern Arizona. Thus, broad-scale habitat differences across these ranges also may contribute to local differences in areas used by these species during winter.

Predictive isoscapes for breeding range assignments

We created species-specific isoscapes that delineated expected deuterium and nitrogen isotope ratios in feathers of Brewer's and sagebrush sparrows across their breeding range. Previous studies have used published isoscapes but few have attempted to derive study- or species-specific isoscapes modeled on relationships between known-origin individuals and the geographic and environmental variation across the breeding range (Hobson et al. 2012). Creating an isoscape required that we collected feathers in the location where the isotopic signature was assimilated. We sampled as broadly as possible and across the range of environmental variation likely to be found in the breeding range. We also were constrained to use predictor variables that were available as continuous spatial data across the breeding range and previously had been related to isotope ratios (Bowen et al. 2005, 2010).

The precision of origins assigned from individual isotopes is extremely coarse, even when probabilistic models are used (Wunder 2010). By using multiple isoscapes, the concordance of predicted locations increased the precision of breeding range origins assigned to individuals captured on their winter ranges. Multiple isotopes have been used for assigning origins of individuals to discrete locations using a classification and regression tree (CART) or discriminant methods (Caccamise et al. 2000; Hebert and Wassenaar 2005; Reichlin et al. 2010) or on kriged isotope surfaces (Wassenaar and Hobson 1998; Hobson et al. 1999). We created multiple isoscapes using spatially explicit models of geographic and environmental predictors for probabilistic assignment over a continuous surface. Ultimately,

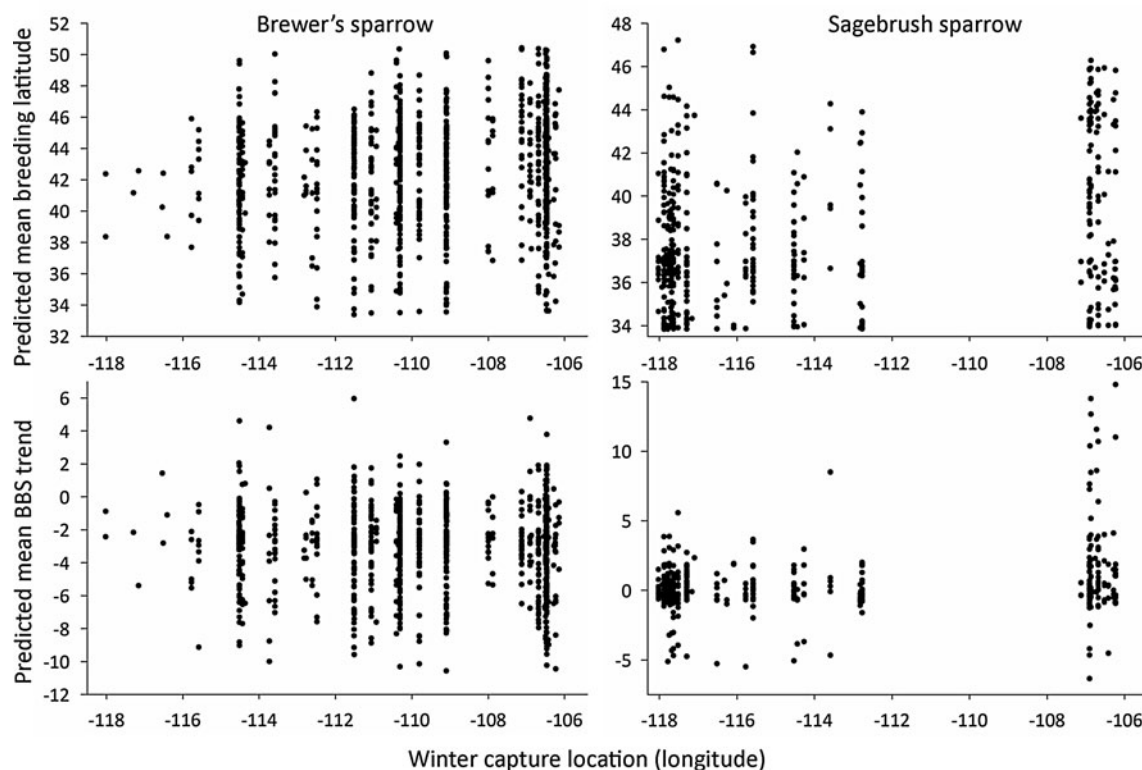


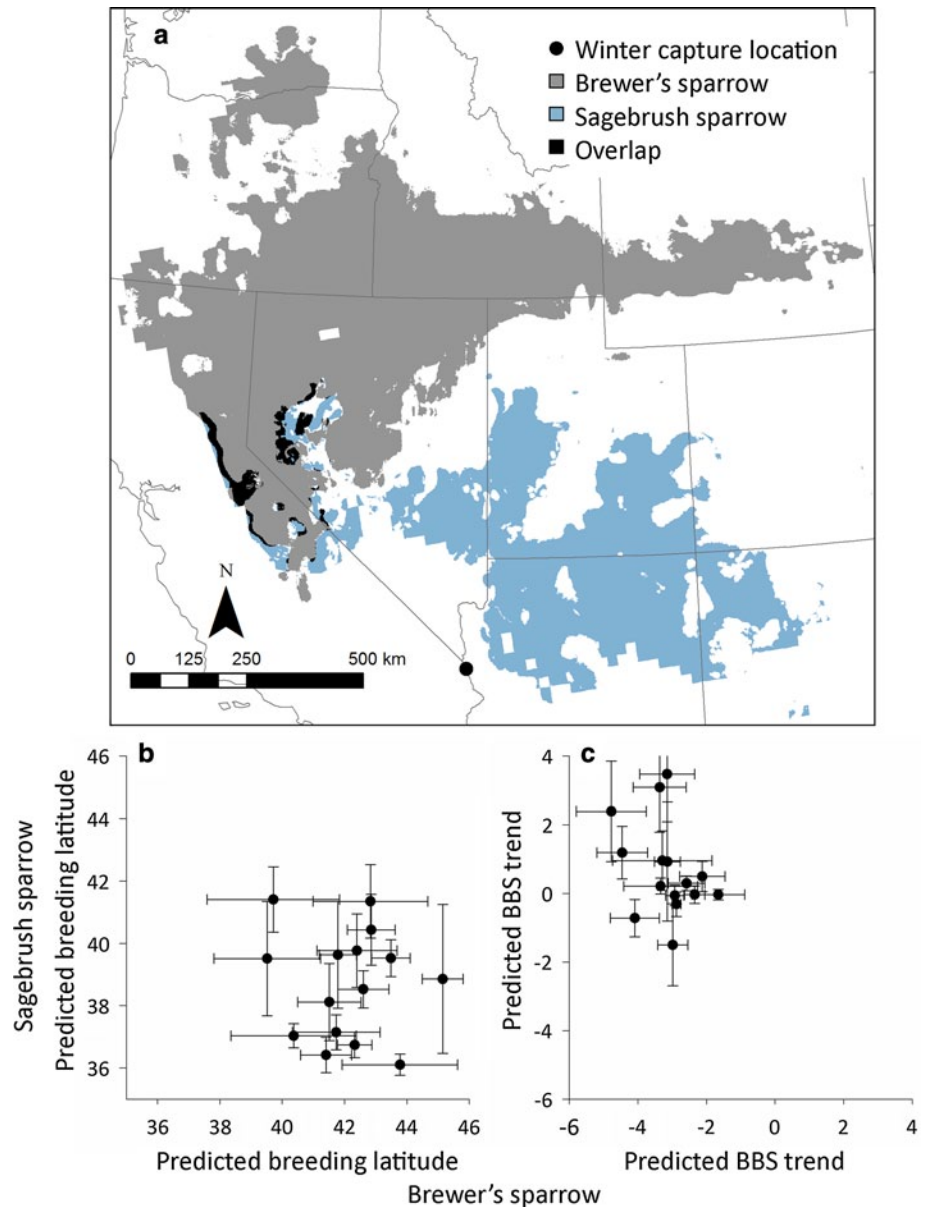
Fig. 5 Mean predicted breeding latitude (*top*) and population trend (*bottom*) estimated from Breeding Bird Surveys and capture longitude of winter locations of Brewer's and sagebrush sparrows across the southwestern United States

combining multiple signatures from isoscapes, trace elements, and genetic sources may be needed to develop the predictive resolution necessary to fully address local-scale linkages among environmental stressors and seasonal ranges (Kelly et al. 2005; Chabot et al. 2012). We used the joint probability of two isoscapes to assign breeding ranges assuming that predicted surfaces were independent (which was true for sagebrush sparrows but not Brewer's sparrows). Other functions, such as bivariate or multivariate normal distributions that account for correlation among variables might be more appropriate, particularly as an increasing number of predictive surfaces are used in the assignment.

Isoscapes, as derived for animals, are mapped representations of modeled relationships between isotope ratios in animal tissue, the physical and biotic factors that influence background abundances of the isotope, and the pathways by which the isotope is assimilated into an animal's tissue (Bowen 2010; Wunder 2010). Coefficients of predictor variables for latitude, longitude, and $\delta^2\text{H}_{\text{gs}}$ were consistent between Brewer's and sagebrush sparrows in direction (Table 3) but differed in direction of the relationship of $\delta^2\text{H}_{\text{f}}$ with elevation and NDVI in modeling $\delta^{15}\text{N}_{\text{f}}$. Thus, underlying relationships by which isotopes were assimilated into tissue generally were similar geographically but differed at finer scales and local environments.

The difference in scaling between feather and growing season deuterium estimated in the univariate model for Brewer's ($\delta^2\text{H}_{\text{f}} = 0.76 \pm 0.11 \delta^2\text{H}_{\text{gs}}$) and sagebrush ($\delta^2\text{H}_{\text{f}} = 1.11 \pm 0.14 \delta^2\text{H}_{\text{gs}}$) sparrows coupled with differences in magnitude of other coefficients also suggest that metabolic scaling, diet, or isotopic pathways may differ between species. Allometric relationships due to size differences between Brewer's [9–12 g; Rotenberry et al. (1999)] and sagebrush sparrows [15–22 g; Martin and Carlson (1998)] could influence physiological pathways. Diets of Brewer's and sagebrush sparrows consist primarily of arthropods during nesting and feather molt periods (Petersen and Best 1986; Martin and Carlson 1998; Rotenberry et al. 1999) and show little selection relative to arthropod abundance. Dietary differences between Brewer's and sagebrush sparrows, which often have overlapping territories during the breeding season, are unlikely to create these differences in modeled isotope assimilation in their feathers. However, habitat use and diet during molt may differ between species. Sagebrush sparrows, but not Brewer's sparrows, were located in low-elevation salt desert shrub communities during the post-breeding season (Fesenmyer and Knick 2011). Brewer's sparrows, but not sagebrush sparrows, were counted at higher elevation shrubsteppe (sagebrush) (Carlisle et al. 2004). The more

Fig. 6 **a** Predicted breeding ranges based on the top 80 % of the summed probabilities for 21 Brewer's and 25 sagebrush sparrows captured at one winter location in western Arizona. Predicted breeding **b** latitude and **c** population trend across winter sites where both Brewer's and sagebrush sparrows were captured



southern geographic difference for sagebrush sparrow distribution relative to the Brewer's sparrow breeding range also may have contributed to some of the observed patterns. Regardless of underlying mechanisms, our results reinforce the need to create species-specific isoscapes for assigning origins (Hobson et al. 2012; Chabot et al. 2012), even for species that share similar environments and diet.

Winter and breeding range relationships

Brewer's and sagebrush sparrows captured at any location on winter ranges in southwestern United States were predicted to come from any part of their respective breeding range. Brewer's sparrows captured on eastern winter locations generally had more northern breeding ranges, which

may be related to the more northern distribution of sagebrush in the eastern part of their breeding range. Otherwise, no discernible pattern emerged to describe the linkages between seasonal ranges; capture location had little power to explain the geographic location of the predicted breeding range.

The large amount of population mixing for Brewer's and sagebrush sparrows both within locations and within single flocks could subject broad areas of the breeding range to environmental threats when birds are concentrated on the winter range. Linking seasonal population trends in addition to locations is an important objective for understanding the annual dynamics of migratory birds (Fretwell 1972; Sherry and Holmes 1995; Marra et al. 2006). We connected population trends estimated from BBS for predicted

breeding locations to capture locations on winter grounds but were unable to estimate corresponding winter trends because of limited spatial coverage of estimates available from Christmas Bird Counts.

Winter location was not a significant factor in trends estimated for populations on breeding ranges for either Brewer's or sagebrush sparrows. Again, variation among capture locations explained little of the total variance contained in the predicted breeding range data. Lack of correlation for breeding population trends between Brewer's and sagebrush sparrows at sites where both wintered also suggests that winter location was not a consistent influence and reinforced our understanding that the population dynamics of each species are independent.

Winter stressors might still be important in the dynamics of Brewer's and sagebrush sparrows but not at the spatial scale of our study. We sampled only a portion of the winter range for Brewer's and sagebrush sparrows, which extends into central Mexico (Martin and Carlson 1998; Rotenberry et al. 1999). Individuals across the breeding range might similarly aggregate at more southern winter locations but experience different environments than in the southwestern United States. Large-scale conversion of native grassland habitat to agriculture is a significant environmental concern across part of the winter range in Mexico (Macías-Duarte et al. 2009). In addition to habitat loss, greater migration distances that potentially increase mortality (Silleet and Holmes 2002) also might have a stronger influence on birds that winter in Mexico.

Migratory connectivity

Brewer's and sagebrush sparrows exhibited a diffuse model of connectivity in that there was no discernible geographic pattern for birds from specific breeding regions to winter in distinct locations of the winter range in southwestern United States. Although regional patterns were not linked, migratory connectivity in these species may be expressed instead as a strong fidelity, once learned, by individuals or small groups to winter locations. We recaptured six individual Brewer's and ten sagebrush sparrows in successive years at their previous winter location (M. Leu, unpublished data). More interesting were two Brewer's and one sagebrush sparrow that were recaptured at the same winter location after 4 years (M. Leu, unpublished data). Winter foods (seeds) are highly variable in space both between and within years within the regions used by wintering sparrows due to seasonal differences in rainfall (Gordon 2000). We know little about winter movements of Brewer's and sagebrush sparrows; almost all observations in our study were based on a single capture event. Thus, the size of the region over which birds explore and their fluidity among different locations could obscure the effects of any specific location

on long-term annual population trends observed for the breeding range.

Conclusion

We have no evidence that dynamics on the winter range played a significant role in explaining differences in breeding population trends between Brewer's and sagebrush sparrows. Winter locality would not likely be associated with breeding trend for either species, particularly if winter locations consisted of birds from across the breeding range and birds exhibited breeding site philopatry. Winter stressors may be significant for each species individually, but we observed no correlation in breeding population trends between Brewer's and sagebrush sparrows at winter locations where both were captured. For both species, individuals at winter capture locations were predicted to have breeding ranges widely dispersed across the entire breeding distribution. Thus, the potential exists for environmental stressors on these aggregations of wintering birds to influence annual population dynamics for a broad part of the breeding range. Identifying specific locations or characteristics that drive winter dynamics remains challenging but ultimately may provide a critical component for the long-term conservation of these species.

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