

Assessing dispersal in threatened migratory birds using stable hydrogen isotope (δD) analysis of feathers

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ABSTRACT: Management decisions involving species at risk are typically made in the face of substantial biological uncertainty. Incorporating uncertainty into decision-making allows managers to perform risk/benefit analysis. Stable hydrogen isotope ratios (δD) provide a tool for studying large-scale movements of migratory organisms and can contribute to the management of migratory species at risk. However, this analytical approach is based on predicted precipitation amount-weighted average deuterium (δD_p) values, and individual years of interest can involve substantial departures from long-term averages. Local growing-season δD_p at locations within the Great Plains of North America deviates from that described by GIS-based models of δD_p derived from long-term estimates based on the Global Network of Isotopes in Precipitation (GNIP). We augmented the GNIP dataset with information from the US Network for Isotopes in Precipitation database for sites in the Great Plains, refining a previously published isoscape for inferring origins of migratory wildlife. Accounting for longitude and the coefficient of variation within precipitation in a single year at specific locations allowed us to determine year- and site-specific estimates of δD_p and estimated rates of long-distance dispersal for 3 species of grassland songbirds based upon δD values of feathers (δD_f). Using a likelihood-based approach to classify individuals as 'local' or 'immigrant,' we incorporated uncertainty in making these designations. This approach provides a convenient tool to effectively communicate research results to policy makers, who must make decisions at the level of risk which they are willing to assume when determining management strategies.

KEY WORDS: Species at risk · Stable isotopes · Global Network of Isotopes in Precipitation · Isoscape

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INTRODUCTION

Species at risk represent a particularly daunting challenge for conservationists and managers, particularly in the face of mounting anthropogenic pressures (Hoffmann et al. 2010). Necessarily, many management decisions regarding species at risk are made despite substantial biological uncertainty (i.e. habitat selection, feeding ecology, and migratory habits), and managers are often forced to undertake conservation actions without conclusive scientific evidence (Gregory & Long 2009). Failure to acknowledge and

account for such uncertainty can lead to poor decision making (Regan et al. 2005). Incorporating scientific uncertainty in the decision-making process can therefore allow managers to employ management approaches that incorporate risk assessment (Harwood 2000, Kriebel et al. 2001) and thus strike a balance between competing objectives.

Recognizing the importance of source-sink population dynamics in the effective conservation of species or populations has grown over the past 2 decades (Pulliam 1988, Watkinson & Sutherland 1995, Dias 1996, Tittler et al. 2006). Knowing which habi-

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tats or regions produce individuals ultimately recruited into breeding populations and which act as ecological traps or sinks clearly is fundamental to any species' recovery plan (Van Houtan et al. 2010). With limited fiscal resources for conservation, it is key that resources be directed to maintaining source populations (self-sustaining populations with a finite rate of increase >1) and their habitats, or to assisting sink populations (populations maintained only via immigration) in such a way to render them demographic sources. Furthermore, efforts directed towards translocations of endangered populations may be destined to fail without a firm understanding of dispersal dynamics (Van Houtan et al. 2010). However, such knowledge on movements of individuals within breeding populations among years (e.g. breeding and natal dispersal) is typically extremely difficult to acquire.

As migratory birds have the capacity for large-scale movements, techniques to infer their origins are necessary to address key biological uncertainties about the linkages of different populations via dispersal. The use of stable hydrogen isotope ratios (δD) in animal tissues is now recognized as an important tool for estimating the origins of migratory birds at continental scales (Wassenaar & Hobson 2000, Paxton et al. 2007, Hobson & Wassenaar 2008, Inger & Bearhop 2008), and has also been applied in studies of long-distance dispersal (Hobson et al. 2004, Hobson 2005). This approach takes advantage of the isotopic (δD , $\delta^{18}O$) composition of precipitation resulting from large-scale geographically predictable patterns associated with climate, latitude, and altitude (Dansgaard 1964). Stable isotope ratios in precipitation, averaged over time, are ultimately transferred to local foodwebs and subsequently reflected in tissues of organisms feeding within those foodwebs (Hobson 1999, Webster et al. 2002). Numerous studies have shown that the isotopic composition of a particular animal tissue reflects those in local dietary inputs, with some level of discrimination among trophic levels (see citations in Hobson & Wassenaar 2008). As organisms move between isotopically distinct foodwebs, they carry with them information on the previous feeding location (Hobson et al. 2010). In the case of migratory songbirds in North America, most species grow their flight feathers on or near the breeding grounds (Pyle 1997), and since such keratinous materials are metabolically inert following synthesis, the δD analysis of flight feathers allows the approximate location of the breeding grounds to be determined once the relationship between precipitation δD (δD_p) and feather δD (δD_f) is established (Hobson 2008).

In order for δD_f analyses to be an effective tool for studying the structure of bird populations, it is important that the technique reliably assign individuals to the correct region of feather growth. This, in turn, is based on a general knowledge of the spatial patterns of isotopes in precipitation or isoscapes (Vachon et al. 2010, West et al. 2010). The accuracy of geographically assigning molt origins based on δD_f is complicated by several factors, including sampling and analytical error, inter-individual variation in physiology, and uncertainty associated with the isoscapes to which samples are being assigned (Wunder & Norris 2008).

Typically, birds of unknown provenance are assigned to geographic origins by calibrating a δD_f isoscape from spatially explicit models of δD_p using feather samples of known origin (Hobson et al. 2009, Wunder 2010). Briefly, this process involves establishing δD_p values for locations with monthly δD_p sampling stations such as the Global Network of Isotopes in Precipitation (GNIP). The δD_p values derived for locations between sampling stations are predicted using spatially explicit techniques (regression, kriging, or some combination), creating a surface of predicted δD_p . These surfaces can subsequently be converted to δD_f isoscapes based upon regression of δD_f from samples where feather molt origin is known, against the isoscape-predicted δD_p value. Ideally, species-specific isoscapes will be calibrated using known-origin tissues collected from across the full extent of the geographic range and during the same years as the samples of interest (Wunder & Norris 2008). However, in most cases, these data are unavailable. The next best approach is to use published isoscapes and regression coefficients that most closely correspond to the species and geographic range of interest.

The δD_p isoscape developed by Bowen et al. (2005) has been successfully applied to assigning migratory species to origin globally. Bowen et al. (2005) constructed both mean annual and growing-season precipitation isoscapes using precipitation isotope data primarily from the GNIP database. Bowen et al. (2005) created isoscapes of monthly mean deuterium (δD_p) and weighted the monthly δD_p surfaces with interpolated long-term monthly precipitation average to derive a weighted growing-season (defined as all months with an average temperature $>0^\circ C$) δD_p surface.

There are several important limitations to the use of isoscapes derived largely from the GNIP database. First, the spatial distribution of sampling locations is variable and there are large areas of the North American continent with limited or no sampling (Welker 2000). Secondly, the GNIP database represents a

compilation of data collected over almost 50 yr, but data are not available for all years at all sampling locations for all months, and in many localities data are no longer collected. Importantly, because such isoscapes have been derived using long-term (e.g. many decades) averages of monthly δD_p , they do not account for short- or medium-term deviations in δD_p . Isoscapes of growing-season δD_p are typically generated by weighting monthly measurements of δD_p by the long-term average amount of precipitation falling in the months contributing to the growing season (Hobson & Wassenaar 1997, Bowen et al. 2005, Lott & Smith 2006) and therefore do not accurately capture the amount of inter-annual variation possible in some localities. Recent work (Farmer et al. 2008) suggests that inter-annual variance in δD_p is an important factor limiting the geographic precision to which migratory animals can be assigned to their origins. While this is undoubtedly true, Farmer et al. (2008) did not use precipitation-averaged GNIP data and chose some months outside the growing season. Therefore, their analysis does not directly reflect the isotopic variance important in the assignment of birds to their molt origins and so it is not yet clear what the fundamental limits are to the accuracy and precision of δD -based assignment of spatial origins. Currently, this limits a risk assessment approach to applying the isotope technique to key species at risk management objectives related to animal movements.

Despite limitations, the application of δD isoscapes has shown great promise in assigning migratory birds to their origin (Hobson et al. 2006, 2007, 2009, Lott & Smith 2006, Paxton et al. 2007). However, there is clearly considerable room for improvement (Hobson 2008, Smith et al. 2009a,b, Wunder et al. 2009). In particular, accurate year-specific deuterium-based isoscapes would reduce the uncertainty in assigning samples to their origins, particularly for regions with high inter-annual variance in δD_p . Here, we augmented the GNIP δD_p data with other, previously unpublished, δD_p data and modeled inter-annual variation in order to derive an improved δD_p isoscape using year- and site-specific data within the North American Great Plains. Our objective was to examine inter-annual variation in δD_p in the Northern Great Plains and determine whether it is possible to reduce uncertainty associated with using isoscapes in assessing dispersal in grassland birds, including species at risk. Secondly, we applied a framework for classifying birds as 'immigrants' versus 'local' using δD_i to account for uncertainties in the assignment process. Our motivation was to refine the isotope method for assessing the degree to which

breeding populations of grassland songbirds were sources or sinks and thus provide an important advance in the way isotope analyses can be used to assist in species conservation and management.

MATERIALS AND METHODS

Feather sampling and analysis

As part of a larger study by Brewster (2009), we conducted field work at Last Mountain Lake (LML), Saskatchewan, Canada (51° 20' N, 105° 15' W) from 1 May 2004 to 31 July 2006. This area is a mosaic of native grassland, planted grassland (hay fields and pasture), and cropland. The surrounding area is primarily used for agriculture, such as annual cropping, haying, and ranching.

We examined breeding philopatry and dispersal of Sprague's pipit *Anthus spragueii*, Baird's sparrow *Ammodramus bairdii*, and savannah sparrow *Passerculus sandwichensis* using δD analysis of feathers to determine the likelihood that breeding after-hatch-year males returned to our study area from the previous year. Both Sprague's pipit and Baird's sparrow are ground-nesting passerines that are endemic to the northern mixed-grass prairie (Mengel 1970) and exhibit restricted breeding ranges (Robbins & Dale 1999, Green et al. 2002). Although both are of conservation concern, only Sprague's pipit is currently listed as a species at risk ('threatened'; Environment Canada 2008). In contrast, the savannah sparrow is commonly found in both native and non-native grassland habitats (Davis & Duncan 1999, McMaster & Davis 2001) and is considered a grassland habitat generalist (Wheelwright & Rising 1993). The savannah sparrow's breeding range extends widely across North America, allowing us to contrast derived movement patterns of Baird's sparrow and Sprague's pipit with restricted ranges to a species with a much broader range of possible origins and consequent isotopic scope of variation.

All individuals were captured using digital playback of territorial male song and a decoy to lure males into mist nets. Once captured, birds were marked, sex and age (second-year versus after-second-year) were determined, morphological measurements were taken, feather samples were collected (see below), and birds were banded with a federal (US Fish and Wildlife Service) aluminum band. Primaries and/or rectrices were sampled, as these feathers are replaced on the previous year's breeding grounds (Pyle 1997). Feathers were typi-

cally pulled, rather than clipped, to initiate re-growth. Each feather was placed in a labeled paper envelope and stored at room temperature. Feather samples were cleaned of surface oils in a 2:1 chloroform:methanol solution overnight, drained, and air dried under a fume hood. The middle portion of the feather vane was cut out (average weight: to 0.35 ± 0.02 mg), and placed into 4.0×3.2 mm silver capsules for online hydrogen isotope analysis by continuous-flow isotope-ratio mass spectrometry. Stable hydrogen isotope analytical measurements (δD) followed the 'comparative equilibration' technique described by Wassenaar & Hobson (2003) to correct for uncontrolled isotopic exchange between samples and ambient water vapor (Wassenaar & Hobson 2003, 2006, Hobson et al. 2004). The reported values are thus equivalent to nonexchangeable feather hydrogen. Isotopic values were expressed in delta notation in parts per thousand (‰) normalized on the Vienna Standard Mean Ocean Water-Standard Light Antarctic Precipitation standard scale. Analysis of a control keratin reference material across 6 mo of autoruns suggests repeatability of $\pm 3.3\%$ ($n = 76$). Feather samples were analyzed at the Environment Canada stable-isotope facility of the National Hydrology Research Centre in Saskatoon, Canada.

Examining inter-annual variation in δD_p

We acquired δD_p data for 8 sites within the North American Great Plains from the GNIP and US Network for Isotopes in Precipitation (USNIP) datasets (Liu et al. 2010). The USNIP dataset constitutes an effort to provide $\delta^{18}O$ and δD isotopic values for ~80 sites across the US using National Atmospheric Deposition Program sampling stations (Welker 2000). The 8 sites we analyzed were Saskatoon ($52^\circ 08' N$, $106^\circ 37' W$; 2002–2005), Wynyard ($51^\circ 46' N$, $104^\circ 12' W$; 1977–1979 and 1981), Edmonton ($53^\circ 34' N$, $113^\circ 31' W$; 1962–1965), Calgary ($51^\circ 01' N$, $114^\circ 01' W$; 1992–1998, 2000, and 2001), Esther ($51^\circ 40' N$, $110^\circ 12' W$; 1997, 2000, and 2001), Cottonwood ($44^\circ 06' N$, $102^\circ 05' W$; 1989–1995), Glacier National Park –Fire Weather Station ($48^\circ 30' N$, $113^\circ 59' W$; 1989, 1992, and 1994), and Little Bighorn Battlefield National Monument ($45^\circ 42' N$, $107^\circ 35' W$; 1989, 1991, 1992, and 1994; Fig. 1). For these sites, we also acquired monthly precipitation and temperature data from the Canadian Climate Centre (Environment Canada 2005) and the Western Regional Climate Center (2008).

Using these precipitation and temperature data, we calculated year-specific local weighted growing-

season δD_p values (hereafter δD_{p-gs}) for each site. We compared year-specific δD_{p-gs} to the δD_{p-gs} predicted by the Bowen et al. (2005) isoscape (hereafter δD_{Bowen}), to determine how δD_{p-gs} deviates from the long-term Bowen et al. (2005) isoscape in any given year. Precipitation and temperature variables were assessed because latitude, altitude, and seasonal air-mass trajectories result in predictable patterns of precipitation and temperature (Bowen et al. 2005). We calculated the following year-specific explanatory variables: the year-specific growing-season percent deviance in precipitation amount from the long-term average growing-season precipitation, total growing-season precipitation, mean growing-season precipitation, and the coefficient of variation (CV) in precipitation during the growing season. The CV in precipitation was included as a proxy, as it may reflect differences among years in convectively generated versus frontal system generated precipitation, since intense rainout from convective storms can cause depletion in precipitation isotopes (Bowen 2008), while evaporation tends to enrich residual surface waters (Bowen & West (2008)). All precipitation values are based on growing-season precipitation because grasslands respond more readily to short-term rainfall events (Sala & Lauenroth 1982). Mean growing-season temperature was also included as a possible explanatory variable. We predicted that these variables may all have some effect on how the year-specific δD_{p-gs} deviates from the values predicted by the isoscape of Bowen et al. (2005). Longitude was included because we hypothesized that rain-shadow effects of the Rocky Mountains may influence δD_{p-gs} . Growing season was site-specific and was defined as all months at that site with an average temperature $>0^\circ C$.

Statistical analysis

We defined a set of *a priori* candidate models (excluding all correlated variables) to explain variation in δD_{p-gs} . These models included a null model including only an intercept, longitude (Long), mean growing-season temperature (Mean GS Temp), and the CV within precipitation (CVprecip) as main effects models, as well as all subsets of additive models including 2 variables. To avoid over-parameterization given the low sample size, more complex models were not considered. Competing models were analyzed using linear models with the deviance of the year- and site-specific δD_{p-gs} from the δD_{Bowen} treated as the dependent variable. We used Akaike's

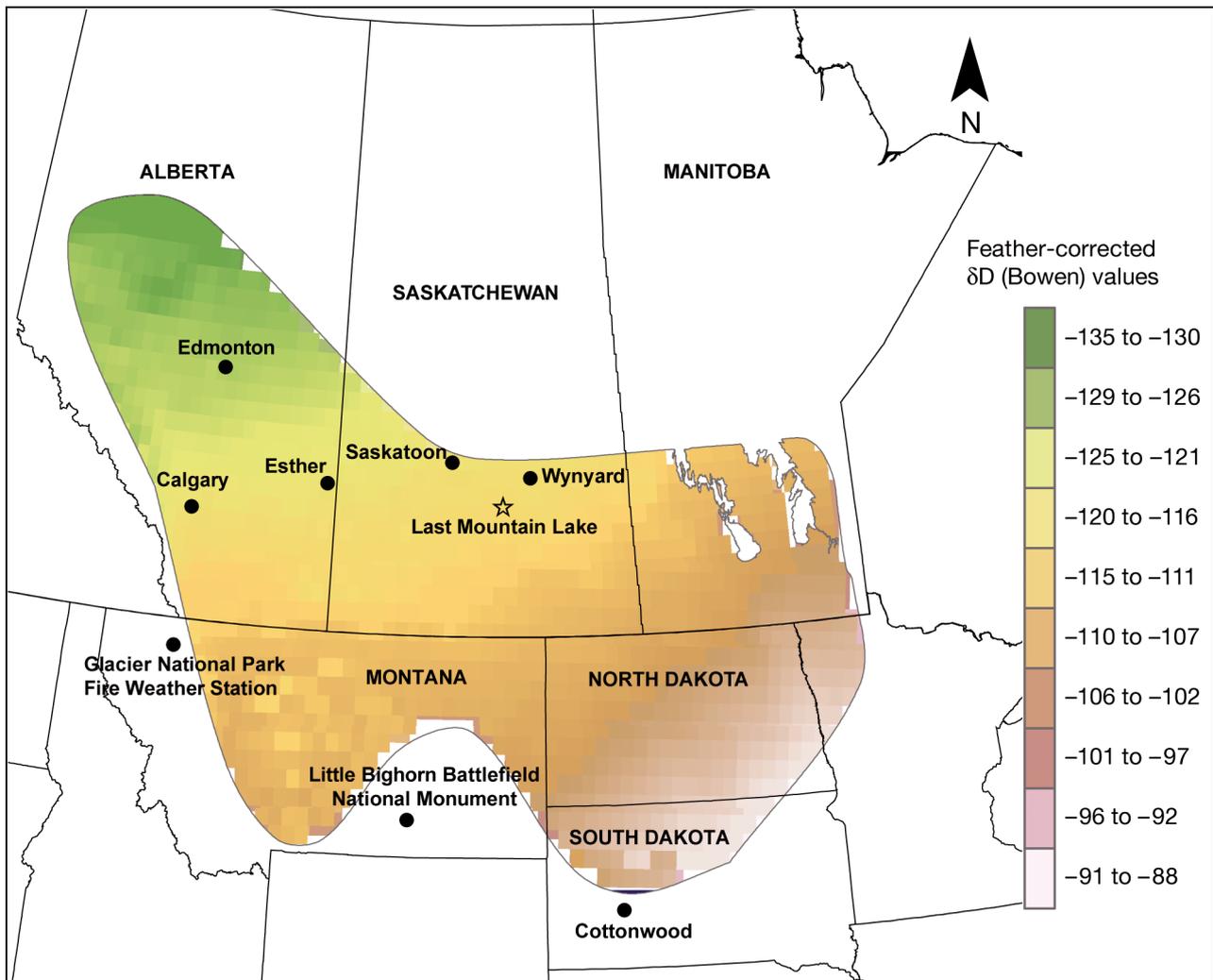


Fig. 1. Global Network of Isotopes in Precipitation and US Network for Isotopes in Precipitation station locations (●) within the Great Plains of North America. Feather-corrected growing-season precipitation δD (δD_{p-gs}) predicted by the Bowen et al. (2005) isoscape (δD_{Bowen}) values are indicated and constrained by the Sprague's pipit *Anthus spragueii* breeding range. Last Mountain Lake, Saskatchewan, Canada, is indicated with a star

Information Criterion (adjusted for small sample size, AIC_c ; Burnham & Anderson 2002) to select among 7 candidate models. The most parsimonious model was considered to be that with the lowest AIC_c value. All models with a ΔAIC_c value < 2 were considered to be supported by the data (Burnham & Anderson 2002). Akaike model weights were calculated to determine the weight of the evidence that a given model was the best model of those considered (Burnham & Anderson 2002).

Monthly growing-season precipitation data for sites within the Canadian Great Plains were acquired for 2002 through 2006 (Environment Canada 2005, Western Regional Climate Center 2008). Using these data, coupled with the algorithm derived from our selected top model (see above), we calculated year-

and site-specific δD_{p-gs} values from locations across the Canadian Great Plains. From these, we created year-specific isoscapes depicting the amount of deviation in δD_{p-gs} from δD_{Bowen} in the Great Plains using ArcMap9.3 (ESRI). These year-specific isoscapes were subsequently used to assign individuals as 'local' or 'immigrant' birds.

Although a direct comparison of predicted δD_f values to actual δD_f values is useful, limitations still exist in how precisely feathers can be assigned to molt origin and to the number of recaptured individuals available with which to test these methods. Given the importance of incorporating risk management into conservation efforts resulting from studies of philopatry, it is important to be able to assess the probability of correctly (or incorrectly) assigning

individuals to molt origin. In order to address uncertainty in our assignment of individuals as 'local' and 'immigrant,' we examined the likelihood that the observed δD_f for a given sample could have been generated by the bird having grown the feather within the local foodweb in a specific year. This was accomplished by assuming that variation in the stable isotope ratios of feathers grown at the same locality follows a normal distribution. Thus, we used a normal probability density function (see Van Wilgenburg & Hobson 2011) to estimate the likely distribution of potential δD_f values for feathers grown at the same site in the same year. Probability densities were estimated by employing our year-specific isoscape predictions as the mean for the distribution, and we assumed a standard deviation equivalent to the standard deviation of the residuals of the δD_f versus δD_p calibration equation ($SD = 12.6\%$). For comparison, we also assessed probability densities using the long-term mean predictions of the Bowen et al. (2005) isoscape (calibrated as per above). We then classified samples as 'immigrant' versus 'local' depending on whether they fell within the area under the curve associated with particular odds of correctly classifying an individual as a local bird.

RESULTS

Inter-annual variation

Extensive inter-annual variation in δD_{p-gs} was evident at locations within the North American Great Plains (Fig. 2). At Cottonwood, Edmonton, and Saskatoon, δD_{p-gs} ranged from -89 to -48% , -124 to -108% , and -121 to -87% , respectively, over 4 consecutive years. Years with greater variation in precipitation experienced more enriched values than was predicted by Bowen et al. (2005), while years with less variation experienced more depleted values. In either case, δD_{Bowen} provides a good estimate of mean values, but does not reflect inter-annual variation.

Year-specific deviations in δD_{p-gs} from the Bowen et al. (2005) isoscape were strongly influenced by longitude and variation in precipitation (Table 1). The most parsimonious model of those considered included longitude and the CV of precipitation and received $\sim 87\%$ of the support. This model explained approximately 43% of the variance in the data; other models received insufficient support to warrant further consideration (Table 1). Based on this model, the algorithm to estimate departures from δD_{Bowen} at specific sites and years is as follows:

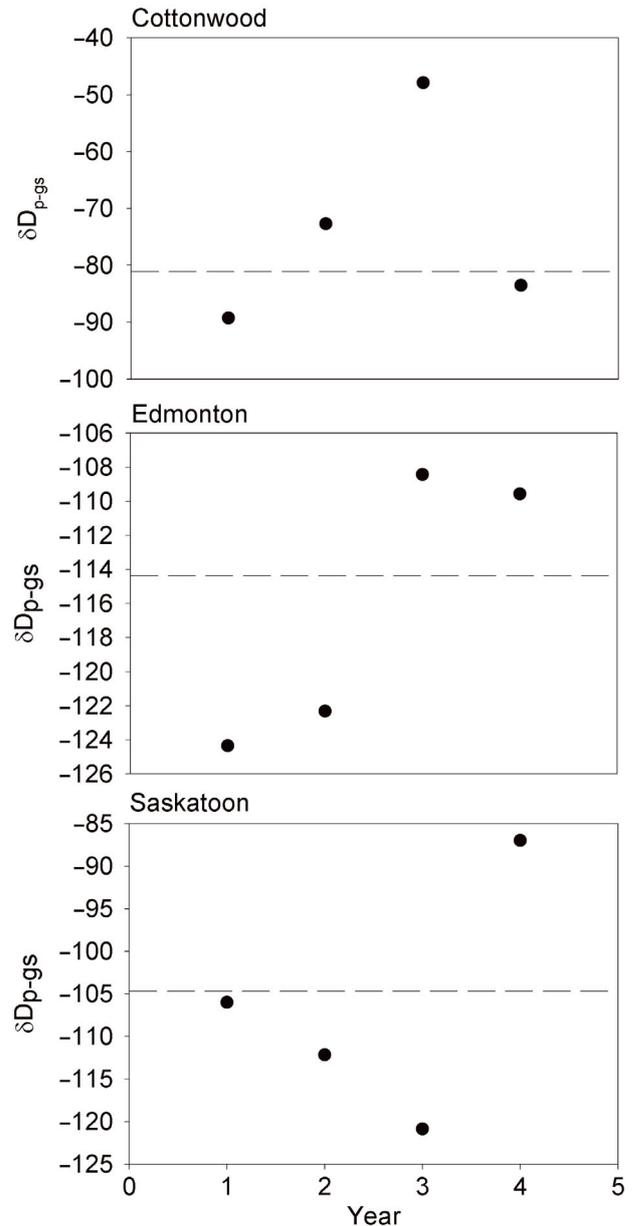


Fig. 2. Inter-annual variance in growing-season precipitation δD (δD_{p-gs} , ‰) over 4 consecutive years at 3 locations within the North American Great Plains. Dashed lines indicate long-term predicted precipitation δD (δD_p) from the isoscape of Bowen et al. (2005)

Deviance from $\delta D_{Bowen} =$

$$124.43 + 1.34(\text{Long}) + 22.05(\text{CVprecip}) \quad (1)$$

We used this algorithm to calculate the year- and site-specific deviance in δD_{p-gs} from the δD_{Bowen} predicted by the Bowen et al. (2005) isoscape. We then created year-specific interpolated maps (ArcMap 9.3, ESRI) of deviances in δD_{p-gs} from δD_{Bowen} . From these, we acquired year-specific corrections for the Bowen

Table 1. Summary of models developed to explain variables that cause year-specific deviances in the weighted growing-season precipitation δD (δD_{p-gs}) from the δD_{p-gs} predicted by the isoscape of Bowen et al. (2005). All models are shown. Data are from the Great Plains of North America ($n = 39$). K : number of parameters; AIC_c : Akaike’s Information Criterion adjusted for small sample size; ΔAIC_c : difference in AICc units between respective model and best model; w_i : Akaike weight; Long: longitude; Mean GS Temp: mean growing-season temperature; CVprecip: coefficient of variation within precipitation

Model	K	AIC_c	ΔAIC_c	w_i
Long, CVprecip	4	299.5	0.0	0.87
Long	3	305.2	5.6	0.05
Long, Mean GS Temp	4	305.7	6.2	0.04
CVprecip	3	307.1	7.6	0.02
CVprecip, Mean GS Temp	4	307.7	8.1	0.01
Mean GS Temp	3	313.3	13.8	0.00
Null (intercept only)	2	315.8	16.3	0.00

Table 2. Year-specific weighted growing-season precipitation δD (δD_{p-gs}) and feather δD (δD_f) values (‰) for Last Mountain Lake, Saskatchewan, Canada. For all years, the values based on Bowen et al. (2005) were -102 for δD_{p-gs} and -116 for δD_f

Year	Year-specific δD_{p-gs}	Year-specific δD_f
2002	-93	-108
2003	-107	-120
2004	-101	-115
2005	-99	-113
2006	-106	-119
2007	-105	-118
2008	-101	-115

et al. (2005) isoscape, specifically for LML (Table 2), thereby deriving corrected δD_{p-gs} values for this location. δD_{p-gs} values were converted to δD_f based upon regression of data from known-source feathers against δD_{p-gs} (Clark et al. 2006). Thus, we estimated δD_f as $-26.08 + 0.88(\delta D_{p-gs})$, providing the best approximation of the expected δD_f of a feather grown at these locations in these years and used this to compare to all captured individuals’ δD_f values to determine whether the individual was a returning (i.e. ‘local’) or non-returning (i.e. ‘immigrant’) breeder.

Application of year-specific isoscapes

We applied our technique of deriving year- and site-specific δD_f isoscapes for assigning migratory birds to molt origin

to Sprague’s pipits. By comparing predicted δD_f values to known-source Sprague’s pipit δD_f values, we qualitatively examined the ability of our algorithm to better predict the expected δD_f of a feather grown at a specific location. Three individuals (A, B, and C) were recaptured between 2004 and 2006 (Table 3). Although 3 of the 4 observed δD_f values were better predicted by the year-specific δD_f value, the difference between the year-specific δD_f value and that predicted by the δD_{Bowen} value fell within our measurement error, and therefore, little can be conclusively inferred from these data. More known-source individuals are necessary to further test our approach.

Assessing philopatry and immigration

Using our framework, it is possible to make probabilistic statements about the likelihood that a bird is a local bird or an immigrant. For example, $\sim 67\%$ of the distribution for birds growing their feathers at LML in 2006 fell between ca. -125 and -100% , corresponding to 2:1 odds of correct classification if δD_f for a sample fell within those bounds (Fig. 3). Similarly, $\sim 80\%$ of the distribution fell between ca. -129 and -97% , corresponding to 4:1 odds of correct classification if δD_f for a sample fell within those bounds (Fig. 3). Thus, a hypothetical bird with $\delta D_f = -97\%$ would be classified as a local bird based upon 4:1 odds (i.e. falls inside the bounds defining 80% of the highest likelihoods expected for a bird growing a feather at that locality), but would be considered an immigrant based upon 2:1 odds (Fig. 3). Using odds ratios allows us to set the risk we are willing to assume, which may be dependent on a variety of factors (e.g. the status of the species of interest). To demonstrate the differences these choices can make, we examined a dataset of grassland passerines cap-

Table 3. *Anthus spragueii*. Known-source Sprague’s pipits (SPPI) captured at Last Mountain Lake, Saskatchewan, Canada between 2004 and 2006. Feather δD (δD_f) values (‰) derived from Bowen et al. (2005) and calculated year-specific δD_f values (‰) for Last Mountain Lake are presented alongside the actual δD_f values (‰) for each individual. R4 denotes fourth rectrix; P6 corresponds to the sixth primary feather

Individual	1st capture	2nd capture	Feather	δD_f	Bowen et al. (2005) δD_f	Year-specific δD_f
SPPI A	2004	2005	R4	-112	-116	-115
SPPI B	2004	2005	P6	-112	-116	-115
SPPI B	2004	2005	R4	-118	-116	-115
SPPI C	2005	2006	R4	-111	-116	-113

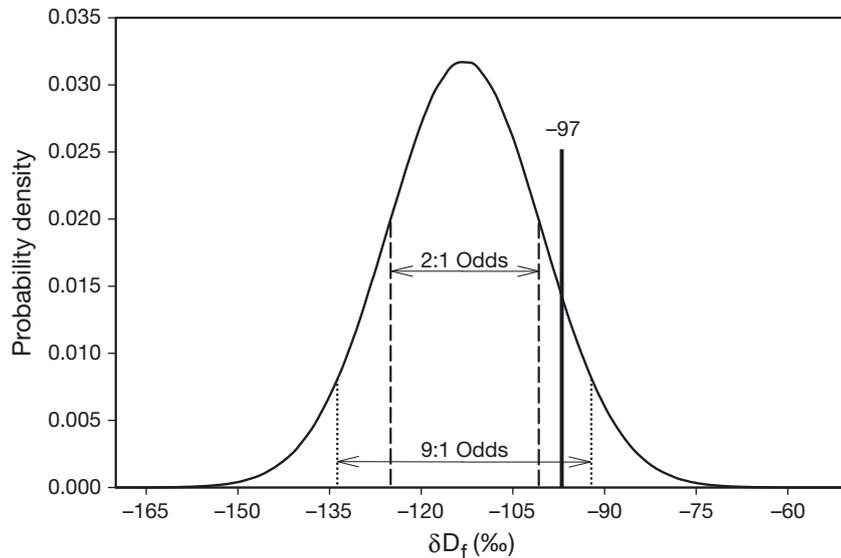


Fig. 3. Normal probability density function (mean = -113 , SD = 12.6) and example odds ratios for assigning individuals as 'local' or 'immigrant' birds to Last Mountain Lake, Saskatchewan, Canada in 2006. The solid line shows where a hypothetical bird ($\delta D_i = -97$) falls within the distribution

tured in 2006 at LML (see 'Feather sampling and analysis') and determined the number of individuals assigned as local birds given different degrees of risk (Table 4). For example, across all 222 birds sampled, the proportion of immigrants ranged from $\sim 39\%$ ($86/222$) at 2:1 odds to $\sim 14\%$ assuming 19:1 odds (Table 4). Baird's sparrow had a significant proportion of the individuals classified as immigrants into the LML population, ranging from $\sim 67\%$ at 2:1 odds ($33/49$), to a minimum of $\sim 39\%$ ($19/49$ birds) at 19:1 odds (Table 4). In comparison, the relatively common savannah sparrows appear to be largely local birds, with far fewer immigrants. We estimated that $\sim 23\%$ ($25/111$) of the sampled savannah sparrows were

immigrants at 2:1 odds, compared to only $\sim 2\%$ ($2/111$) immigrants assuming 19:1 odds (Table 4). In contrast, a relatively high proportion of Sprague's pipits were apparent immigrants into the LML population; at 2:1 odds, $\sim 45\%$ ($28/62$) of Sprague's pipits were considered immigrants, compared to $\sim 15\%$ ($9/62$) at 19:1 odds (Table 4).

Assessing philopatry and immigration using long-term mean predictions (based on a calibration of the Bowen et al. 2005 surface) provided different results (Table 5) from those provided by year-specific predictions (Table 4). Across all species, and depending upon choice of odds ratio, there was a 0 to 5% difference in the number of birds classified as local versus immigrants between the assessments made using long-term predictions versus those made using the year-specific prediction for 2006. The number of birds classified as local versus immigrants using each approach differed by 0 to 8% for Baird's sparrow, 1 to 9% for savannah sparrow, and 2 to 11% for Sprague's pipit.

DISCUSSION

Inter-annual variation in δD_{p-gs}

δD_{p-gs} shows substantial inter-annual variation (Wunder et al. 2005), particularly in the Great Plains of North America, which experience highly variable precipitation and temperature (Borchert 1950, Bryson

Table 4. Number of individuals classified as local or immigrant birds captured at Last Mountain Lake, Saskatchewan, Canada in 2006 given various levels of acceptable risk comparing feather δD (δD_i) against predicted δD_i via year-specific adjustments to calibration of the Bowen et al. (2005) surface (see 'Materials and methods'). The odds of correctly assigning a bird as a local breeder are 67% (2:1), 75% (3:1), 80% (4:1), 90% (9:1), and 95% (19:1). Numbers in parentheses represent proportions (%) of individuals classified as local or immigrant birds. BAIS: Baird's sparrow, SAVS: savannah sparrow, SPPI: Sprague's pipit

Species	Classification	Odds ratio				
		2:1	3:1	4:1	9:1	19:1
All species (n = 222)	Local	136 (61)	161 (73)	167 (75)	181 (82)	192 (86)
	Immigrant	86 (39)	61 (27)	55 (25)	41 (18)	30 (14)
BAIS (n = 49)	Local	16 (33)	22 (45)	23 (47)	27 (55)	30 (61)
	Immigrant	33 (67)	27 (55)	26 (53)	22 (45)	19 (39)
SAVS (n = 111)	Local	86 (77)	97 (87)	101 (91)	104 (94)	109 (98)
	Immigrant	25 (23)	14 (13)	10 (9)	7 (6)	2 (2)
SPPI (n = 62)	Local	34 (55)	42 (68)	43 (69)	50 (81)	53 (85)
	Immigrant	28 (45)	20 (32)	19 (31)	12 (19)	9 (15)

Table 5. Number of individuals classified as local or immigrant birds captured at Last Mountain Lake, Saskatchewan, in 2006 given various levels of acceptable risk when comparing feather δD (δD_f) against predicted δD_f via calibration of the Bowen et al. (2005) surface (see 'Materials and methods'). The odds of correctly assigning a bird as a local breeder are 67% (2:1), 75% (3:1), 80% (4:1), 90% (9:1) and 95% (19:1). Numbers in parentheses represent the proportion (%) of individuals classified as local or immigrant. BAIS: Baird's sparrow, SAVS: savannah sparrow, SPPI: Sprague's pipit

Species	Classification	Odds ratio				
		2:1	3:1	4:1	9:1	19:1
All species (n = 222)	Local	147 (66)	158 (71)	164 (74)	181 (82)	189 (85)
	Immigrant	86 (349)	61 (29)	55 (26)	41 (18)	30 (15)
BAIS (n = 49)	Local	20 (41)	22 (45)	23 (47)	24 (49)	27 (55)
	Immigrant	29 (59)	27 (55)	26 (53)	25 (51)	22 (45)
SAVS (n = 111)	Local	96 (86)	101 (91)	104 (94)	109 (98)	110 (99)
	Immigrant	15 (14)	10 (9)	7 (6)	2 (2)	1 (1)
SPPI (n = 62)	Local	31 (50)	35 (56)	37 (60)	48 (77)	52 (84)
	Immigrant	31 (50)	27 (44)	25 (40)	14 (23)	10 (16)

& Hare 1974). Our efforts suggest that there is meaningful variation in δD_{p-gs} that might be successfully exploited to create year-specific estimates of δD_{p-gs} . The top model for deviations from the long-term predictions of the Bowen et al. (2005) isoscape included the CV in precipitation which was included as a variable on the assumption that it may act as a surrogate variable for years in which convective-driven precipitation versus large system-driven precipitation may dominate. Convectively generated precipitation events are driven by evaporation (Bowen & West 2008), causing an overall enrichment of foodweb δD values, which ultimately drives δD_f . For example, a low CV in δD_{p-gs} could be experienced by either consistently hot, dry conditions or consistently cool, wet conditions. However, it seems that in the Great Plains, a low CV in δD_{p-gs} was accompanied by lower (compared to the long-term average) δD_{p-gs} values, and therefore we postulate that when precipitation amount is fairly consistent through the growing season (low CV), the area experienced consistently cool, wet conditions. Given this substantial inter-annual variation, large variations in δD_f between years are likely as well, though perhaps not as drastic as in precipitation due to attenuation of isotopic variance at higher trophic levels (Bump et al. 2007). While the isoscape of Bowen et al. (2005) provides accurate estimates of long-term average δD_{p-gs} at continental scales, accounting for the variance in δD_{p-gs} between years may prove extremely useful. Year-to-year variance in δD_{p-gs} can be substantial (Fig. 2), and an individual could be incorrectly assigned due to discrepancy between years if this variation is not considered.

By refining our best estimate of δD_{p-gs} by both site and year using the methods we have presented here, we are one step closer to determining a more accurate estimate of δD_{p-gs} . An accurate estimate of δD_{p-gs} ,

coupled with a precise, locally derived, regression equation with which to convert δD_{p-gs} values to δD_f values, will allow more reliable estimates of the origin of an unknown-source individual given δD_f . In short, accounting for the year should improve the ability to assign individuals to a location of origin. This may require additional isotopic datasets such as those provided by USNIP, historic literature, or individual scientists; however, practitioners will benefit from a soon to be released on-line isoscape calculator (IsoMap) recently developed by Bowen and colleagues. While we currently lack a sufficient sample of feathers from known-origin grassland birds from across the Great Plains with which to fully test our model, within this region, our analysis suggests that deriving year-specific estimates of δD_{p-gs} for sites of interest may prove useful, and warrants further consideration. Greater effort should now be given to acquiring more known-origin feathers and samples of growing-season precipitation to test our model and/or determine whether other models more accurately predict year-specific isoscapes for δD_f and δD_{p-gs} .

Philopatry, immigration, and uncertainty in assignments

Using our derived estimates of δD_{p-gs} , we assessed the likelihood that grassland birds sampled at LML were immigrants versus locally produced birds showing philopatry to LML. Our approach suggests that depending on the species and odds ratio assumed, as few as 2% of savannah sparrows and as many as 67% of Baird's sparrows may have been immigrants into the local population. The estimated rates of immigration seem high, although they are consistent with work by Jones et al. (2007) that suggested low annual

return rates based on mark–recapture (savannah sparrow 5.4%, Baird's sparrow 5.1%, Sprague's pipit 2.1%). These low annual rates of return may be related to migratory nomadism which may have evolved to deal with habitat instability within the highly variable prairie environment (Jones et al. 2007).

In addition to reducing the uncertainty in assigning individuals to location of origin by accounting for year-specific variation in δD_{p-gs} , some uncertainty in assignment using isoscapes will always remain. Thus, careful consideration of the risk we are willing to accept in our assignment of individuals to origin should be made. In many cases, accepting 2:1 odds of correctly assigning a bird as a 'local' individual would be appropriate (e.g. Hobson et al. 2009). However, in the case of managing species at risk, a more precautionary approach may be necessary and the choice of more conservative odds of correctly assigning an individual to origin, or at least to 'local' or 'immigrant' categories, may be needed. A manager might be more interested in reducing the risk of failing to categorize an individual as an immigrant when it truly was an immigrant, and thus more liberal (e.g. 2:1) odds than conservative (19:1) odds might be preferred. This is analogous to balancing Type I versus Type II statistical errors, and conservation biologists and policy makers should pay careful attention to which risks they must minimize, particularly when attempting to conserve endangered species for which statistical inference is notoriously difficult and the consequences can be far more pressing and immediate (Schultz 2008, Brosi & Biber 2009). Given the expense of endangered species management and recovery efforts and the profound influence dispersal can have on population persistence (Van Houtan et al. 2010), careful assessment of assignment uncertainty is necessary. All things being equal, sites with a high percentage of immigrants will more likely be sink habitats than those with a low percentage. Given that expensive restoration of sink habitats may be a viable option for species recovery, managers may wish to use a more conservative odds ratio when deciding whether a site should be considered a sink. In addition, high rates of dispersal might preclude certain management options such as translocations (Van Houtan et al. 2010). Thus, we feel that the odds ratio approach we have demonstrated here provides a convenient tool allowing the effective communication of research results to policy makers, who must make decisions at the level of risk which they are willing to assume. A similar approach could also be taken in presenting the results of population viability analyses (PVA; i.e. assessing the odds that a population will

become locally extirpated or go extinct), thus requiring managers to explicitly clarify the specified level of risk they assume. How the choice of odds ratios in classifying birds as 'local' versus 'immigrants' influences the results of PVA targeted at source–sink populations warrants further study and will likely be specific to individual species/populations.

Comparison of the classifications to local versus immigrant resulting from using long-term versus year-specific predictions of δD_f resulted in 0 to 11% differences in the number of birds considered immigrants into the local population(s). This result occurred despite the year-specific prediction (for 2006) being only 3% off the long-term mean prediction. Given that the observed and model-predicted inter-annual variation in δD_{p-gs} can be as much as 20% off the long-term mean, larger differences in classifications would have resulted had our test sample been collected in a different year. Furthermore, an 11% difference in the classifications for Sprague's pipit is likely large enough to be biologically relevant for a threatened species. Thus, while our model for year-specific departures from the long-term mean δD_{p-gs} , the model still requires further validation, we suggest that assessing philopatry and immigration against both year-specific and long-term predictions are now needed. We recommend that until year-specific isoscapes are routinely available, attempts should be made to examine sensitivity in local versus immigrant classifications resulting from employing long-term versus year-specific isoscape predictions. Sensitivity analyses could be employed either by modeling efforts such as that applied here, or via the use of multiple samples of known-origin feathers collected over multiple years.

Consistent with the low annual return rates reported by Jones et al. (2007), our results suggest very high rates of dispersal in grassland birds in the northern Great Plains. If these results hold as a generality, they suggest that grassland bird populations are likely dominated by meta-population dynamics via dispersal. The continued loss of native grassland habitats (Stephens et al. 2008), and recent work suggesting that planted grasslands may represent population sinks for some species relative to native grasslands (Fisher & Davis 2011), both suggest that conserving native grasslands should be given priority. However, high rates of dispersal suggest that management should be considered at broad spatial scales, and maintaining high quality grassland habitat across the entire species range may be more crucial to maintaining grassland bird populations than attempts at managing local populations.

CONCLUSION

Assessing uncertainty and applying risk management are important steps in avian conservation, particularly for rare species. We have presented spatially explicit tools and concepts that should decrease uncertainties in assignment of individuals to origin due to inter-annual variation in the δD_{p-gs} . These concepts provide an improvement over relying solely on long-term δD_{p-gs} averages such as the isoscape of Bowen et al. (2005). Future research involving the assignment of individuals to origins based on their δD_f values should consider applying year-specific corrections of the Bowen et al. (2005) isoscape or customized generation of year-specific isoscapes using tools such as IsoMap to provide improved assignments to origin. In addition, when applying this technique to species at risk, care should be taken in choosing an acceptable level of risk associated with the assignment of individuals to origin, and any subsequent management actions should be made acknowledging this uncertainty.

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