

Origins and migratory patterns of bats killed by wind turbines in southern Alberta: evidence from stable isotopes

E. F. BAERWALD,^{1,†} W. P. PATTERSON,² AND R. M. R. BARCLAY¹

¹Department of Biological Sciences, University of Calgary, Calgary, Alberta T2N 1N4 Canada

²Saskatchewan Isotope Laboratory, Department of Geological Sciences, University of Saskatchewan, Saskatoon, Saskatchewan S7N 5E2 Canada

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Abstract. Large numbers of migratory bats are killed every autumn at wind energy facilities in North America. While this may be troubling from a population perspective, these fatalities provide an opportunity to learn more about bat migration and the origins and summer distributions of migratory bats by using endogenous markers. Such markers include stable isotope values, which have been used to answer questions about ecological systems, such as trophic levels and food webs, and the origins and migratory routes of animals. To estimate the origins of migratory bats, we determined nitrogen ($\delta^{15}\text{N}$), carbon ($\delta^{13}\text{C}$), and hydrogen ($\delta^2\text{H}$) stable isotope values of fur ($\delta^{15}\text{N}_f$, $\delta^{13}\text{C}_f$, $\delta^2\text{H}_f$, respectively) from hoary bats (*Lasiurus cinereus*) and silver-haired bats (*Lasionycteris noctivagans*) killed at a wind energy facility in southern Alberta, Canada. We determined that mean isotope values varied among species, year, sex, and age class. $\delta^{13}\text{C}_f$ and $\delta^2\text{H}_f$ values indicated that silver-haired bats likely originated in the boreal forest, farther north and/or at higher elevations than the aspen parkland-like habitat suggested by the isotope values of hoary bats. IsoMAP analysis indicated that bat fatalities may have originated from a large catchment area potentially hundreds of kilometers away. Our data provide further evidence for a migration route along the eastern slopes of the Rocky Mountains that is used by bats from across Alberta and beyond, and suggest that fatalities at a single wind energy site have the potential to have far-reaching ecological and population consequences.

Key words: Alberta; bat fatalities; catchment area; hoary bat; *Lasionycteris noctivagans*; *Lasiurus cinereus*; migration; silver-haired bat; stable isotopes; wind energy.

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† **E-mail:** erin.baerwald@ucalgary.ca

INTRODUCTION

Given the challenges of studying small, aerial, nocturnal migrants, the migration biology of bats is poorly understood (Fleming and Eby 2003, Cryan and Diehl 2009). Determining the origins and migratory patterns of bats has important conservation implications. Around the globe, large numbers of bats are being killed at wind

energy facilities (Kunz et al. 2007, Rydell et al. 2010, Arnett and Baerwald 2013). Most fatalities are of migratory bats during autumn migration and, although little is known regarding the use of migratory routes by bats, fatalities thus appear to occur along potential migration routes (Baerwald and Barclay 2009, Rydell et al. 2010, Arnett and Baerwald 2013). In North America, approximately 80% of fatalities are of migratory tree-roosting

bats: hoary bats (*Lasiurus cinereus*), eastern red bats (*L. borealis*), and silver-haired bats (*Lasionycteris noctivagans*) (Arnett and Baerwald 2013). In southern Alberta, the estimated fatality rate of bats ranges from 1.3 to 31.4 bats/turbine/year depending on the site (Baerwald and Barclay 2009) resulting in thousands of hoary bat and silver-haired bat fatalities in Alberta annually. If bats are primarily killed along migration routes, as has been hypothesized (e.g., Baerwald and Barclay 2009), and multiple wind facilities are placed along a route, the cumulative impact of these fatalities may be quite large (Arnett and Baerwald 2013).

Not only is there scant knowledge regarding the migration biology of migratory bats, little is known about their distributions and ranges. For example, two biodiversity databases, the Global Biodiversity Information Facility (GBIF) and the Mammal Networked Information System (MaNIS), list few records if any, of hoary bats or silver-haired bats in Canada. Additionally, range maps of hoary or silver-haired bats differ markedly among sources (e.g., Bat Conservation International [<http://www.batcon.org/index.php/all-about-bats/species-profiles.html>], Encyclopedia of Life [<http://eol.org/>], The Redpath Museum [<http://canadianbiodiversity.mcgill.ca/english/index.htm>]). Without information as basic as the distribution and movements of affected species, it is difficult to determine the cumulative effects of turbine-related fatalities. This is especially concerning given that migratory bats have ecological traits that increase their risk of extinction. In general, animals that migrate tend to be more vulnerable to extinction than those that do not (Pimm et al. 1988). Unlike sedentary bats, migratory bats require appropriate habitat in several, spatially disjunct locations: breeding/summering sites, hibernation/overwintering sites, stopover sites, and migratory corridors that link them (Hutson et al. 2001, Fleming and Eby 2003). Even though fatalities of bats may be a concern from a population perspective, especially given the slow life-history of bats (Barclay and Harder 2003), their carcasses provide the opportunity and impetus to study the migration of these species, and inform future conservation initiatives.

Migration has traditionally been studied by using exogenous markers, such as bands and

transmitters, and although these methods have been used to study various aspects of migratory-bat biology (e.g., Hutterer et al. 2005, Klug et al. 2012), they have been of limited use in tracking long-distance movements of tree-roosting bats in North America (Cryan and Diehl 2009). However, predictable relationships between an endogenous marker, the stable isotope values of animal tissue, and the environment, have enabled investigation of the origins and migratory behaviors of various animals (reviewed in Hobson 1999b, Rubenstein and Hobson 2004, Hobson and Wassenaar 2008). $\delta^2\text{H}$ decreases with increasing latitude and elevation (Poage and Chamberlain 2001, Bowen and Revenaugh 2003, Sellick et al. 2009). $\delta^{13}\text{C}$ values may also decrease with increasing latitude and elevation as vegetation shifts from predominantly C_4 to C_3 plants (Körner et al. 1988, Hobson et al. 2003, Suits et al. 2005). Likewise, $\delta^{15}\text{N}$ decreases with increasing latitude and the associated cooler, drier conditions (Handley et al. 1999, Hobson 1999a, Amundson et al. 2003). Animals incorporate the chemical composition (e.g., stable isotope values) of their diet into their tissues. Animal keratins, such as fur, are metabolically inert once grown and the stable isotope values of these tissues therefore reflect the environmental conditions (i.e., isoscape) where they were grown. Thus, the chemical composition of fur can be used to link an animal to the place where the fur was produced. The confidence in this estimate is greatly increased if we know the dietary ecology of an animal and the diet-to-tissue discrimination factor.

Fortunately, we know the dietary ecology of hoary bats and silver-haired bats summering in Canada (Barclay 1985, Reimer et al. 2010) and that diet-to-tissue discrimination in bats is similar to that for other vertebrates (Voigt et al. 2003, Voigt and Matt 2004, Mirón et al. 2006, Popa-Lisseanu et al. 2007). Stable-isotope analysis of bat tissue has been used in numerous dietary studies (Fleming et al. 1993, Voigt and Kelm 2006, Popa-Lisseanu et al. 2007, Painter et al. 2009, Cryan et al. 2012), and also to investigate the origins and migratory movements of bats. For example, $\delta^2\text{H}$ values of hoary bat fur ($\delta^2\text{H}_f$) accurately reflects $\delta^2\text{H}$ values of the precipitation ($\delta^2\text{H}_p$) at the latitude at which it was grown (Cryan et al. 2004, Cryan et al. 2014). Combining

this relationship with capture and museum records demonstrated that some hoary bats migrate long-distances (>2000 km; Cryan et al. 2004). Further studies have attempted to evaluate the use of stable-isotope analysis to assign origins to individuals of various bat species across Europe (Popa-Lisseanu et al. 2012), the eastern United States (Britzke et al. 2009, Sullivan et al. 2012), and Canada (Fraser et al. 2012). All of these studies found that, for numerous species, bat fur accurately reflects $\delta^2\text{H}_p$ where the fur was grown, and in some, that $\delta^{13}\text{C}_f$ values are correlated with $\delta^2\text{H}$ values in both hair and precipitation, and with latitude. Not all results have been consistent across species or age/sex classes, and thus analyzing each group separately is important (Britzke et al. 2009). Given the difficulty in studying bat migration, the ability to use endogenous markers, such as stable isotopes, offers a feasible alternative to more traditional but inefficient methods (i.e., banding or radio-tracking).

To learn more about the basic biology of migratory bats, and to apply this information to the issue of bat fatalities at wind turbines, we used stable isotope analysis ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^2\text{H}$) of fur ($\delta^{15}\text{N}_f$, $\delta^{13}\text{C}_f$, $\delta^2\text{H}_f$) from turbine fatalities to test hypotheses regarding the distribution and migration of hoary and silver-haired bats. Given that hoary and silver-haired bats differ in size, morphology, and roosting and foraging behavior, and thus likely differ in their optimal migration strategies (Barclay 1985, Hedenstrom 2008, 2009, Baerwald and Barclay 2011), our underlying hypothesis was that these differences influence their distribution and migration, which would be reflected in the isotopic signature of their fur. We thus predicted that the stable isotope values present in the fur of hoary and silver-haired bats differ. Based on published range maps, inferred migratory behavior (Barclay 1984, Cryan 2003, Baerwald and Barclay 2009), and the seasonal timing of fatalities (Baerwald and Barclay 2011), we specifically hypothesized that (1) bats killed at turbines in southwestern Alberta are migrants (i.e., not local) and that (2) hoary bats originate from farther north and from a broader range than silver-haired bats do. If bat fatalities at turbines represent migrants, we predicted that both the variance and the mean isotope values of their fur are greater than the isotope values in the fur of

resident bats (i.e., fur collected from bats on their summering grounds) from the same latitude as the wind energy facilities. If hoary bats originate from farther north and from a broader area than silver-haired bats do, then the isotope values in hoary bat fur should be lower and have greater variance than the isotope values of silver-haired bat fur.

Bats commonly exhibit sexual segregation on their summering grounds as well as sex-biased migratory behavior, with females tending to migrate more often and over longer distances than males do (Cryan 2003, Fleming and Eby 2003, Ibanez et al. 2009). We hypothesized that migration of both hoary and silver-haired bats differs between the sexes, much like in other bat species. We thus predicted that the isotope values in the fur of adult females are lower than those of adult males, reflecting the longer, more northern migration made by females. Based on capture and fatality records (Baerwald and Barclay 2011), we further predicted that the degree of sexual segregation, thus the difference in isotope values between males and females, is greater in hoary bats. Finally, to explore the temporal patterns of bat migration, we examined the relationship between isotope values and date. A correlation may indicate a pattern in the migratory movements of bats (e.g., differential or leapfrog migration; Mazerolle and Hobson 2007, Paxton et al. 2007, Langin et al. 2009).

MATERIALS AND METHODS

Study species

Hoary bats occur throughout much of the Americas, from northern Canada to southern Argentina and Chile (Shump and Shump 1982, Cryan 2003) (Fig. 1). Although the movement patterns and seasonal distributions of hoary bats in North America are poorly understood, in summer they occur throughout the aspen parkland and boreal forest of Canada. In autumn, they leave and overwinter in Mexico and the southern United States (Findley and Jones 1964, Cryan 2003, Cryan et al. 2004) (Fig. 1). Hoary bats arrive in southern Canada in May to early June and autumn migration begins with males in late July and continues with females and juveniles from early August to mid-September (Barclay 1984, Baerwald and Barclay 2011). There



Fig. 1. North American range maps of the hoary bat (*Lasiurus cinereus*, top), and the silver-haired bat (*Lasiomycteris noctivagans*, bottom). We chose these range maps over other possibilities because they are used by the IUCN in its evaluation of a species' status. Maps from Bat Conservation International (<http://www.batcon.org/index.php/all-about-bats/species-profiles.html>).

appears to be some degree of sexual segregation during summer, with females potentially migrating greater distances than males (Findley and Jones 1964, Cryan 2003, Cryan et al. 2004). Although their distribution is unknown, the relatively high proportion of adult male hoary bat fatalities at wind energy installations in Alberta (Baerwald and Barclay 2011) suggests that more adult males move into the province than previously suspected. In Alberta, 54% of bat fatalities at wind energy installations are hoary bats (E. F. Baerwald, *unpublished data*).

Silver-haired bats range from southeastern Alaska through southern Canada, south to central California and northern Mexico, and east to Georgia (Yates et al. 1976, Hall 1981) (Fig. 1). Wintering grounds seem to be in the Pacific Northwest, southwestern states, and middle latitudes of the eastern United States (Izor 1979, Cryan 2003). In spring, silver-haired bats from the east migrate north and east, while silver-haired bats in the west migrate northward (Cryan 2003). In summer, silver-haired bats are common in aspen parkland, but are also found throughout the southern three-quarters of Canada's boreal forest (Fig. 1). Silver-haired bats arrive in southern Canada in May to early June and autumn migration is from early August until mid to late September (Barclay 1984, Baerwald and Barclay 2011). As in hoary bats, there appears to be some degree of sexual segregation during summer, with females potentially migrating farther than males (Cryan 2003), although capture records indicate the presence of adult males in northern Alberta (Grindal et al. 2011) and fatalities at wind energy facilities suggest a relatively even sex ratio in southern Alberta during autumn migration (Baerwald and Barclay 2011). In Alberta, 37% of bat fatalities at wind energy installations are silver-haired bats (E. F. Baerwald, *unpublished data*).

Although no formal studies have been conducted on the molting patterns of either hoary or silver-haired bats (but see review by Fraser et al. 2013), observational and isotopic data suggest that both species molt on their summering grounds just prior to migration, thus between late June and early August (Cryan et al. 2004; E. F. Baerwald and B. J. Klug, *personal observation*). This timing of molt is similar to that observed in other bat species (Cryan et al. 2012, Fraser et al.

2012, Fraser et al. 2013). Thus, fur collected along the migratory route is fur grown on the summering grounds during the current year's molt.

Sampling

We collected hair samples from bat carcasses found under wind turbines in southwestern Alberta, Canada (49°35'04" N, 113°47'48" W), from 15 July to 30 September 2006 and 2007. For each carcass, we recorded species, age (Anthony 1988) and sex (when possible), and the degree of decomposition. We collected hair from between the scapulae of bats killed the previous night. We placed samples into plastic micro-centrifuge tubes and stored them in a freezer until analysis.

The fur of resident silver-haired bats was collected by E. Fraser from the Cypress Hills, SK (approx. 49°37' N, 109°58' W) between 20 July and 5 August 2008 and 2009. We collected hair from resident hoary bats captured at a maternity site, Delta Marsh, Manitoba, Canada (50°11'02.44" N, 98°22'55.15" W) in July 1991 and from 8 June to 3 August 2010. Bats tend to be highly philopatric (Perry 2011) and reproductive female hoary bats return annually to Delta Marsh (Koehler and Barclay 2000). We thus assumed that any hair collected pre-molt was hair grown at the same site the previous year. All methods were approved by the University of Calgary Life and Environmental Sciences Animal Care Committee, and all field captures were conducted under Manitoba Conservation Wildlife Scientific permit WB09615.

Stable carbon and nitrogen isotope analysis

We conducted stable carbon and nitrogen analyses at the Saskatchewan Isotope Laboratory (SIL) in the Department of Geological Sciences, University of Saskatchewan, Saskatoon, Saskatchewan, Canada. After washing hair samples with a mixture of chloroform:methanol (2:1) for 2 h, rinsing with distilled water, and oven drying overnight at 60°C, we weighed them in tin capsules and loaded them into the sample carousel. We determined stable isotope values by combustion using a Thermo Finnigan Flash 1112 Elemental Analyzer via a ConFlo III coupled to a Thermo Finnigan Delta Plus XL mass spectrometer. We pyrolyzed samples under helium in an oxidation furnace packed with chromium (VI) oxide and silvered cobaltic/cobaltous

oxide (to remove any halogens) at 1000°C. The resulting gas was passed through a reduction furnace packed with elemental copper at 680°C to reduce all nitrogen-bearing compounds to pure gaseous nitrogen. We passed the resulting gases through a water trap to eliminate moisture. A GC column at 50°C separated the carbon dioxide and nitrogen gases for analysis in the mass spectrometer. We blank-corrected the data, and then corrected carbon isotope values for ^{17}O contribution using the Craig correction (Craig 1957). Carbon isotope ratios are reported in per mil (‰) notation relative to the VPDB scale. Nitrogen isotope ratios are reported in per mil notation relative to AIR. We calibrated carbon data against the international standards L-SVEC ($\delta^{13}\text{C} = -46.6\text{‰}$ VPDB) and IAEA-CH6 ($\delta^{13}\text{C} = -10.4\text{‰}$ VPDB). IAEA-CH7, an intermediate international standard, gave the following result during calibration of the in-house standards: $\delta^{13}\text{C} = -32.1 \pm 0.04\text{‰}$ VPDB ($n = 11$). The accepted value of $\delta^{13}\text{C}$ is $-32.1 \pm 0.10\text{‰}$ VPDB. Nitrogen was calibrated against the international standards USGS-25 ($\delta^{15}\text{N} = -30.4\text{‰}$ AIR) and IAEA-305A ($\delta^{15}\text{N} = 39.8\text{‰}$ AIR). IAEA-NO3, an intermediate international standard, gave the following result during calibration of the in-house standards: $\delta^{15}\text{N} = 4.0 \pm 0.08\text{‰}$ AIR ($n = 8$). The accepted value of $\delta^{15}\text{N}$ is $4.7 \pm 0.2\text{‰}$ AIR. Accuracy of data was monitored via routine analyses of in-house standards that are calibrated against the IAEA standards above. The accuracy of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measurements are 0.1‰ and 0.2‰, respectively ($n = 18$, 2s).

Stable hydrogen isotope analysis

We conducted deuterium analyses at the SIL. We washed hair samples in a mixture of chloroform:methanol (2:1) for 2 h, rinsed them with distilled water, and oven dried them overnight at 60°C. To avoid mass linearity correction, we matched mass of the samples to the mass of the standards to get comparable signal intensity. We weighed fur samples and standards in silver capsules then equilibrated weighed samples at room temperature for at least 96 h prior to $\delta^2\text{H}$ determination (based on Bowen et al.'s [2005] finding that complete replacement of the exchangeable fraction of H in hair can occur in as little as 3–4 days). We analyzed samples using a Thermo Finnigan TC/

EA coupled to a Conflo III and a Delta-Plus XL mass spectrometer. We dropped samples into a glassy carbon furnace and pyrolyzed them at 1350°C to form hydrogen and/or carbon monoxide gases. These gases were carried in a helium stream to a GC column held at 100°C to separate the gases before being diluted in the Conflo III and passed to the mass spectrometer for analysis. We blank corrected isotope ratios and normalized them against Kudu Horn Standard (Africa) (KHS) and Caribou Hoof Standard (North America) (CBS) provided by the National Hydrology Institute, Saskatoon, Saskatchewan. Values are $\delta^2\text{H} = -197 \pm 1.8$ for CBS and -54.4 ± 0.6 ($n = 10$) for KHS. Results are reported as per mil (‰) notation relative to VSMOW, VSLAP scale. A third standard, Spectrum Keratin (source unknown), was used as a check standard for drift correction with an accepted value of -121.6 ± 2 for $\delta^2\text{H}$. The standard deviation for $\delta^2\text{H}$ was 1.8‰.

Data analysis

Based on potential inherent differences in isotopic ratios by age and sex (Britzke et al. 2009, Cryan et al. 2012), we divided fur samples from turbine fatalities into one of four categories; adult male, adult female, sub-adult male, and sub-adult female. To explore the relationships among the three isotopes found in the fur, we used a correlation matrix. We analyzed variation in carbon, nitrogen, and deuterium isotope values among species, age, and sex classes using ANOVA tests. Due to the potential for year-to-year variation in the isotope values present in fur (Haché et al. 2012), we included year in all models. We included all interactions, and used backward stepwise model selection to remove non-significant terms. We used Tukey's post-hoc tests to evaluate differences among groups.

To test our hypothesis that the majority of bats killed were migrants (i.e., not local), we compared the variance in isotope values from turbine-killed bats to the variance in values from the fur of resident silver-haired bats from the Cypress Hills, SK, and resident hoary bats from Delta Marsh, MB (Cypress Hills data from Fraser 2011). We used F-tests and either standard t-tests or unequal variance t-tests, whichever was appropriate based on the variance.

To investigate the summer distribution and

Table 1. Sample sizes of turbine-killed hoary bats (*Lasiurus cinereus*) and silver-haired bats (*Lasionycteris noctivagans*) used for fur samples.

Age/sex	2006		2007	
	Hoary bat	Silver-haired bat	Hoary bat	Silver-haired bat
Adult male	37	19	26	7
Adult female	25	25	9	13
Sub-adult male	17	9	26	15
Sub-adult female	16	13	20	18

catchment area of bats killed at turbines, we used published relationships between $\delta^2\text{H}_f$ and $\delta^2\text{H}_p$ and an online GIS-based mapping tool, IsoMAP (Bowen et al. 2012, Bowen et al. 2014). IsoMAP is a likelihood-based assignment method based on the isoscape of $\delta^2\text{H}_p$. It incorporates both the analytical error surrounding $\delta^2\text{H}_f$ and the errors inherent in the $\delta^2\text{H}_p$ isoscape. We created a precipitation model (see Baerwald 2013) similar to the Bowen et al. (2005) model used by Cryan et al. (2014) to assign a likelihood of geographic origin. To geographically assign individuals using IsoMAP, $\delta^2\text{H}_f$ values must first be converted to their predicted $\delta^2\text{H}_p$ using previously published relationships between the two variables. For hoary bats, we used the relationship published by Cryan et al. (2014). However, there is no published relationship for silver-haired bats, so we examined both the Cryan et al. (2014) relationship and the relationship published by Popa-Lisseanu et al. (2012). The latter relationship is based on multiple species of European bats, presumably making it more universal than other, more species-specific equations (e.g., Britzke et al. 2009, Fraser et al. 2012). Even though this equation is based on European species of bats, the general relationship between latitude and $\delta^2\text{H}_p$ is global, albeit with differences among continents. Additionally, there is no reason to think that bat species in Europe incorporate deuterium into their keratin differently than bats in North America do. We transposed the data so that the $\delta^2\text{H}_p$ was the response variable rather than the explanatory variable and then used the resulting regression equation to determine the predicted $\delta^2\text{H}_p$ (now y) given our $\delta^2\text{H}_f$ values (now x). The Cryan et al. (2014) data resulted in the regression equation $y = 0.7469x + 2.635$, and the Popa-Lisseanu et al. (2012) data resulted in $y = 0.6722x - 2.6195$. We used a two-sample t -test to compare the mean

predicted $\delta^2\text{H}_p$ values derived by the two different regression equations. Then, to determine the accuracy of these regression equations for silver-haired bats and the IsoMAP models in general, we used isotope values in fur from silver-haired bats of known geographical origins (Cypress Hills, SK), and compared the results of both the geostatistical (likekrig) and regression (likereg) models. For further analysis, we chose the regression equation (i.e., Cryan et al. 2014 or Popa-Lisseanu et al. 2012) and IsoMAP model that most accurately predicted geographic origin.

To better understand migration patterns of bats, we examined the relationship between isotope ratios and arrival date (i.e., night of death) via linear regressions between each isotope ($\delta^{13}\text{C}_f$, $\delta^{15}\text{N}_f$, or $\delta^2\text{H}_f$) and date. Based on the results of earlier analyses, we analyzed each species and year separately.

We used Shapiro-Wilk W tests to test for normality. We considered variables to be non-normal if $P < 0.05$, but if the W statistic was sufficiently close to one (i.e., ≥ 0.90), then we considered the data near-normal and did not transform them (Sen and Srivastava 1990) because ANOVAs with large sample sizes are robust in dealing with violations of normality (Zar 1999). We conducted statistical analyses with JMP 10.0.0 (SAS Institute, Cary, North Carolina) and present means \pm standard deviation (SD).

RESULTS

We analyzed fur from 295 bats killed at turbines in southwestern Alberta (Table 1). None of the isotope values from turbine fatalities were normally distributed, but all three had W statistic values close to one ($\delta^{13}\text{C}_f$, $W = 0.98$, $P = 0.001$; $\delta^{15}\text{N}_f$, $W = 0.98$, $P < 0.001$; $\delta^2\text{H}_f$, $W = 0.97$, $P < 0.0001$), and we thus considered them near-

Table 2. Results of the ANOVA used to test the variation of $\delta^{13}\text{C}$ values in fur collected from hoary bats (*Lasiurus cinereus*) and silver-haired bats (*Lasionycteris noctivagans*) killed at wind turbines in southwestern Alberta from 15 July to 30 September 2006 and 2007. Categories with different superscript letters are significantly different (Tukey's post-hoc test)

Categories	LSmeans	SD	df	Type III sum of squares	F	P
Year			1	1.9	1.79	0.18
2006	-24.5	1.0				
2007	-24.6	1.0				
Species			1	51.5	48.34	<0.0001
Silver-haired bat	-25.0	1.0				
Hoary bat	-24.1	1.1				
Age/sex class			3	10.2	3.18	0.02
Adult female ^{A,B}	-24.4	1.1				
Adult male ^A	-24.3	1.0				
Sub-adult female ^{A,B}	-24.7	1.1				
Sub-adult male ^B	-24.8	1.1				
Species \times age/sex			3	27.9	8.72	<0.0001

normal.

$\delta^{13}\text{C}_f$ and $\delta^2\text{H}_f$ values were positively correlated (Pearson's $r = 0.47$, $P < 0.001$), but $\delta^{15}\text{N}_f$ values were not correlated with either $\delta^{13}\text{C}_f$ or $\delta^2\text{H}_f$ values ($\delta^{13}\text{C}_f$ Pearson's $r = 0.06$, $P = 0.30$; $\delta^2\text{H}_f$ Pearson's $r = -0.07$, $P = 0.23$). In the ANOVA that assessed the variation in $\delta^{13}\text{C}_f$ values among species, years, and age/sex classes, the model explained a significant proportion of the variation (ANOVA, $F_{8,286} = 14.90$, $P < 0.001$; Table 2). $\delta^{13}\text{C}_f$ values differed among species and age/sex class, but not between years (Table 2). The significant interaction between species and age/

sex class indicates that $\delta^{13}\text{C}_f$ values are influenced by species, but that this relationship was influenced by the age and sex class (Table 2). Adult male and female hoary bats had similar values of $\delta^{13}\text{C}_f$, but these were higher than both sexes of sub-adult hoary bats and all classes of silver-haired bats (Fig. 2).

In the ANOVA that assessed the variation in $\delta^{15}\text{N}_f$ values among species, years, and age/sex classes, the model explained a significant proportion of the variation (ANOVA, $F_{8,286} = 3.91$, $P < 0.001$; Table 3). There was no significant difference between years, but there was a

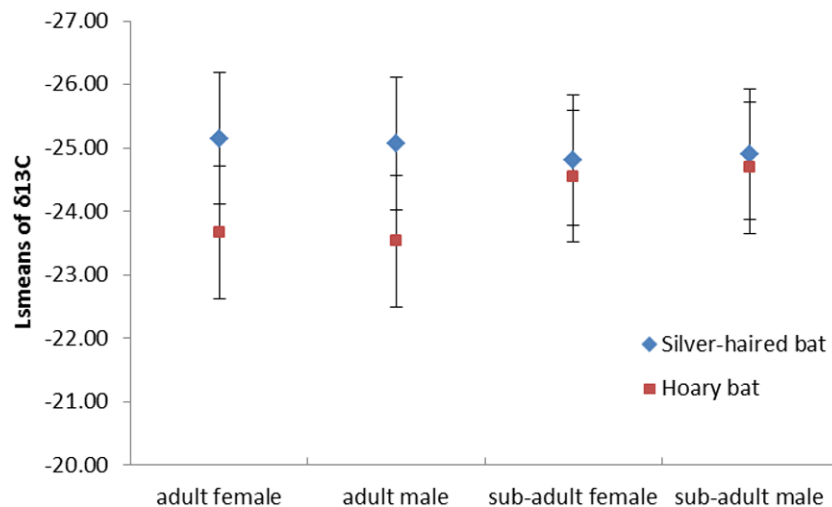


Fig. 2. LSmeans plot (\pm SD) of the interaction between age and sex category and species from the ANOVA that assessed the variation in $\delta^{13}\text{C}$ values among species, years and age/sex classes. The interaction was significant (ANOVA, $F_{3,286} = 8.72$, $P < 0.0001$).

Table 3. Results of the ANOVA testing variation of $\delta^{15}\text{N}$ values in fur collected from hoary bats (*Lasiurus cinereus*) and silver-haired bats (*Lasionycteris noctivagans*) killed at wind turbines in southwestern Alberta from 15 July to 30 September 2006 and 2007. Categories with different superscript letters are significantly different (Tukey's post-hoc test).

Categories	LSmeans	SD	df	Type III sum of squares	F	P
Year			1	0.48	0.31	0.58
2006	8.5	1.3				
2007	8.5	1.4				
Species			1	4.5	2.91	0.09
Silver-haired bat	8.6	1.3				
Hoary bat	8.4	1.3				
Age/sex class			3	25.86	5.58	0.001
Adult female ^{A,B}	8.6	1.3				
Adult male ^B	8.1	1.3				
Sub-adult female ^A	8.9	1.3				
Sub-adult male ^{A,B}	8.4	1.3				
Species \times age/sex			3	18.56	4.01	0.008

significant interaction between species and age/sex class, indicating that $\delta^{15}\text{N}_f$ values are influenced by species, and that this relationship was influenced by the age and sex class (Table 3; Fig. 3).

In the ANOVA that assessed the variation in $\delta^2\text{H}_f$ values among species, years, and age/sex classes, the model explained a significant proportion of the variation (ANOVA, $F_{8,286} = 9.26$, $P < 0.0001$). The mean $\delta^2\text{H}_f$ value of silver-haired bats was lower than that of hoary bats (Table 4). The significant interaction between year and age/sex class indicates that $\delta^2\text{H}_f$ differed by age and

sex class, but that this difference was influenced by year (Table 4; Fig. 4).

With the exception of $\delta^{13}\text{C}$, isotope values of fur from bats killed at wind turbines (putative migrants) were more variable than values in the fur of bats captured in the Cypress Hills or at Delta Marsh (residents; Table 5). In addition, mean isotope values differed significantly between putative migrants and residents. With the exception of $\delta^{13}\text{C}_f$ in hoary bats, putative migrants had lower $\delta^{13}\text{C}_f$, $\delta^{15}\text{N}_f$ and $\delta^2\text{H}_f$ values than residents (Table 5).

There was no difference in the mean $\delta^2\text{H}_p$

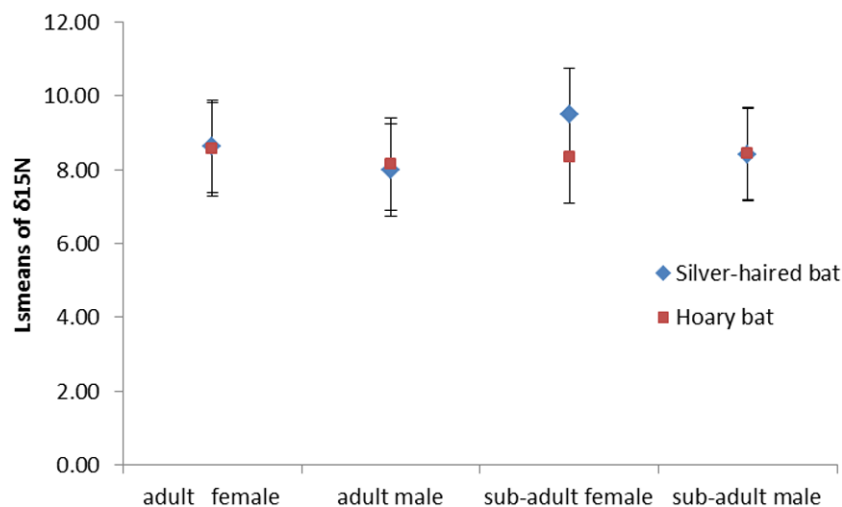


Fig. 3. LSmeans plot (\pm SD) of the interaction between age and sex category and species from the ANOVA that assessed the variation in $\delta^{15}\text{N}$ values among species, years and age/sex classes. The interaction was significant (ANOVA, $F_{3,286} = 18.56$, $P = 0.008$).

Table 4. Results of the ANOVA used to test the variation of $\delta^2\text{H}$ values in fur collected from hoary bats (*Lasiurus cinereus*) and silver-haired bats (*Lasionycteris noctivagans*) killed at wind turbines in southwestern Alberta from 15 July to 30 September 2006 and 2007.

Categories	LSmeans	SD	df	Type III sum of squares	F	P
Year			1	8191.55	12.69	<0.001
2006	-118.9	27				
2007	-129.9	26.4				
Species			1	24043.29	37.55	<0.0001
Silver-haired bat	-133.8	26.1				
Hoary bat	-115.0	26.5				
Age/sex class			3	4677.04	3.72	0.07
Adult female	-121.3	27.6				
Adult male	-119.5	27.1				
Sub-adult female	-128.5	25.6				
Sub-adult male	-128.3	26.4				
Year \times age/sex			3	5862.73	4.25	0.03

predicted by the equations derived from the Cryan et al. (2014) data and the Popa-Lisseanu et al. (2012) data (Cryan et al. [2014] mean = -92.92% Popa-Lisseanu et al. [2012] mean = -88.61% , $t = 1.97$, $P = 0.06$). The IsoMAP regression model, in conjunction with either equation, accurately predicted the origins of silver-haired bats resident in the Cypress Hills, SK (Fig. 5). Thus, for simplicity, we used the equation derived from the Cryan et al. (2014) data and the regression model (likereg) in IsoMAP to predict the origins of all turbine-killed bats. The IsoMAP analysis indicated that bats killed at wind turbines in southwestern

Alberta potentially came from a large catchment area and that silver-haired bats originated from farther north or from higher elevations than hoary bats (Figs. 6 and 7).

There was a negative correlation between $\delta^{15}\text{N}_f$ and fatality date for silver-haired bats in both 2006 and 2007 (2006, $r^2 = 0.43$, $P < 0.0001$; 2007, $r^2 = 0.18$, $P = 0.002$), and with the date of hoary bat fatality in 2007 ($r^2 = 0.08$, $P = 0.01$). There was a weak but significant negative correlation between $\delta^{13}\text{C}_f$ values and fatality date for silver-haired bats in 2006 ($r^2 = 0.07$, $P = 0.04$), but no other significant correlations between $\delta^{13}\text{C}_f$ or $\delta^2\text{H}_f$ values and date.

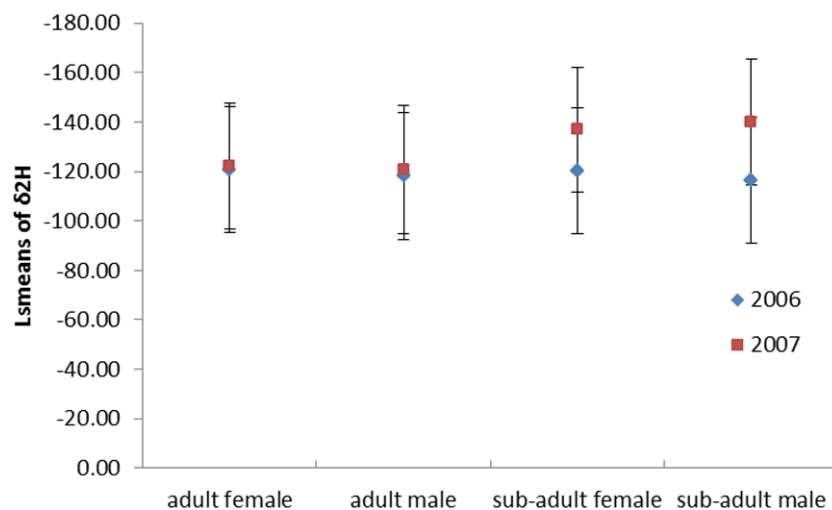


Fig. 4. LSmeans plot (\pm SD) of the interaction between year and sex category and species from the ANOVA that assessed the variation in $\delta^2\text{H}$ values among species, years and age/sex classes. The interaction was significant (ANOVA, $F_{3,286} = 5862.73$, $P = 0.03$).

Table 5. Comparison of isotope values (mean \pm SD) between putative migrants killed at turbines and resident silver-haired bats (*Lasionycteris noctivagans*) captured in the Cypress Hills, SK or resident hoary bats (*Lasiurus cinereus*) captured in Delta Marsh, MB. *F*, *t*, and *P* values correspond to the species at both sites.

Site by species	Isotope value	<i>F</i>	<i>F</i> -test <i>P</i>	<i>t</i> -stat	<i>t</i> -test <i>P</i>
Silver-haired bat		1.80	0.09	6.11	<0.001
Cypress Hills	$\delta^{13}\text{C}_f = -23.8 \pm 0.7$				
Wind turbines	$\delta^{13}\text{C}_f = -25.0 \pm 1.0$				
Hoary bat		1.32	0.41	3.89	<0.001
Delta Marsh	$\delta^{13}\text{C}_f = -25.0 \pm 1.1$				
Wind turbines	$\delta^{13}\text{C}_f = -24.0 \pm 1.2$				
Silver-haired bat		7.55	<0.001	5.91	<0.001
Cypress Hills	$\delta^{15}\text{N}_f = 9.7 \pm 0.6$				
Wind turbines	$\delta^{15}\text{N}_f = 8.7 \pm 1.5$				
Hoary bat		1.97	0.04	5.95	<0.001
Delta Marsh	$\delta^{15}\text{N}_f = 9.3 \pm 0.8$				
Wind turbines	$\delta^{15}\text{N}_f = 8.3 \pm 1.1$				
Silver-haired bat		4.09	<0.001	9.7	<0.001
Cypress Hills	$\delta^2\text{H}_f = -101 \pm 13.1$				
Wind turbines	$\delta^2\text{H}_f = -134 \pm 26.5$				
Hoary bat		8.22	<0.001	3.28	0.001
Delta Marsh	$\delta^2\text{H}_f = -107 \pm 9.3$				
Wind turbines	$\delta^2\text{H}_f = -115 \pm 26.5$				

DISCUSSION

Based on published range maps and inferred migratory behavior (Cryan 2003, Baerwald and Barclay 2009), we hypothesized that bats killed in southwestern Alberta were migrants and that hoary bats originated from farther north and

from a broader area than silver-haired bats. The differences in isotope values between putative migrants and residents, the lower mean $\delta^{13}\text{C}_f$ and $\delta^2\text{H}_f$ values, and the greater variances in isotope values in turbine fatalities relative to resident bats, are consistent with the hypothesis that the bats killed were migrants.

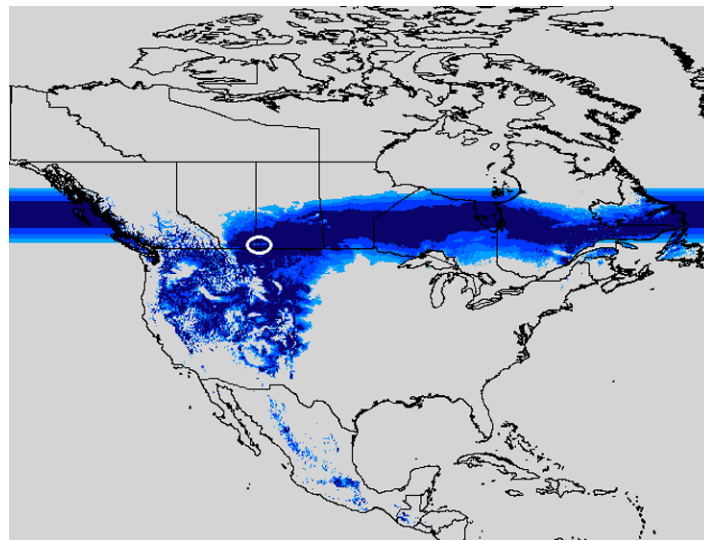


Fig. 5. The results of the IsoMAP assignment of fur collected from silver-haired bats (*Lasionycteris noctivagans*) that were putative residents of Cypress Hills, SK (approximate location indicated by the white circle). Shading darkens with increasing likelihood of origin. Analysis was based on the precipitation model by Baerwald (2013). Full interactive maps can be viewed online at <http://isomap.rcac.purdue.edu:8080/gridsphere/gridsphere?cid=DisplayAssignPortlet> (job id 29121).

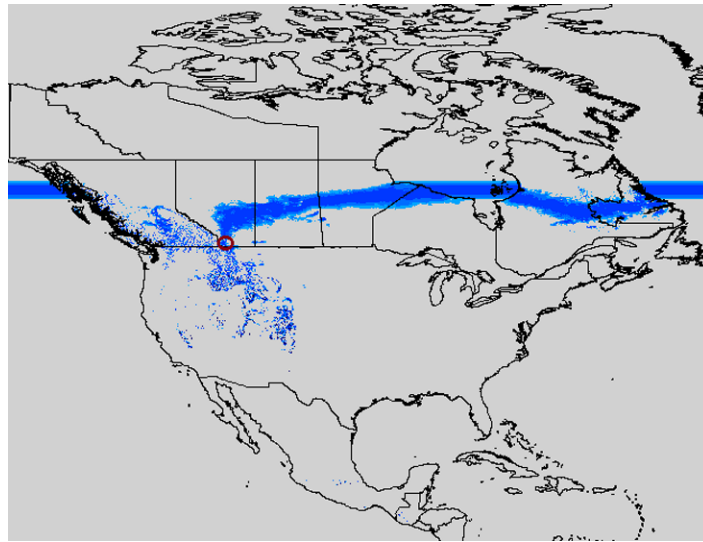


Fig. 6. IsoMAP analysis of the geographic origins of hoary bats (*Lasiurus cinereus*) killed at wind turbines in southwestern Alberta, Canada (approximate location indicated by the red circle). This likelihood-based assignment method is based on $\delta^2\text{H}$ values in precipitation. Shading darkens with increasing likelihood of origin. Analysis was based on the precipitation model by Baerwald (2013). Full interactive maps can be viewed online at <http://isomap.rcac.purdue.edu:8080/gridsphere/gridsphere?cid=DisplayAssignPortlet> (job id 29120).

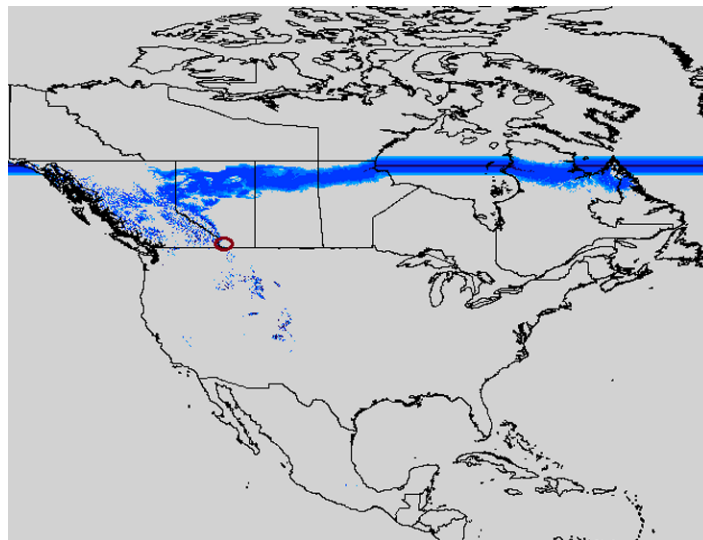


Fig. 7. IsoMAP analysis of the geographic origins of silver-haired bats (*Lasionycteris noctivagans*) killed at wind turbines in southwestern Alberta, Canada (approximate location indicated by the red circle). This likelihood-based assignment method is based on $\delta^2\text{H}$ values in precipitation. Shading darkens with increasing likelihood of origin. Analysis was based on the precipitation model by Baerwald (2013). Full interactive maps can be viewed online at <http://isomap.rcac.purdue.edu:8080/gridsphere/gridsphere?cid=DisplayAssignPortlet> (job id 29126).

As we also predicted, the isotope values in the fur of silver-haired bats and hoary bats killed at wind turbines differed, although not uniformly across all isotopes, years, or age/sex classes. Contrary to our prediction, however, silver-haired bats had lower $\delta^{13}\text{C}_f$ and $\delta^2\text{H}_f$ values than hoary bats. These differences could result from differences in diet (Barclay 1985, Reimer et al. 2010) or foraging habitat (i.e., different association with standing water and aquatic foodwebs; Britzke et al. 2009, Sellick et al. 2009) or the combination of the two. The diets of hoary bats and silver-haired bats on the summering grounds are slightly different, as are the diets of sub-adult hoary bats (at least for the first two weeks post-volancy; Rolseth et al. 1994). Although both species are opportunistic aerial-hawkers that eat similar types of insects, silver-haired bats and sub-adult hoary bats tend to eat smaller prey items than adult hoary bats (Barclay 1985, Rolseth et al. 1994). However, the stomach-content analysis of 54 of the bats used in this study revealed few dietary differences among species, age and sex classes (Reimer et al. 2010). Although this type of dietary analysis only represents the diet of an individual over a single night during migration, it suggests that the dietary differences among age/sex classes are unlikely to cause the different patterns present in the stable isotope signatures. In addition, the correlation we found between $\delta^{13}\text{C}_f$ and $\delta^2\text{H}_f$ values suggests that the inter-specific differences in these isotopes also reflect differences in the latitude of origin of individuals.

On average, silver-haired bats killed in southwestern Alberta had lower stable isotope values than hoary bats and thus appear to have originated from higher elevations and/or farther north, and from more boreal-like ecosystems than hoary bats, that appear to have originated from more aspen parkland-like ecosystems. This interpretation is reinforced by the IsoMAP analysis. That the observed ranges were different than the expected ranges suggests that the published range maps are inaccurate and/or that hoary bats originating from farther north or higher elevations use a different migration route and thus are not killed at the wind energy site in southwestern Alberta.

Care should be taken in the interpretation of the IsoMAP analysis. We are not suggesting that

stable isotope analysis be used to redefine species ranges or that bats originate from every possible location, as this method is based on global patterns and not constrained by the biology of the animal, although it can be (e.g., Sullivan et al. 2012). For example, our IsoMAP analysis shows that, based on stable isotopes, silver-haired bats killed in southern Alberta could have originated from eastern Canada. This is highly unlikely given what we know about the species' biology and bat migration in general. It is more likely that the silver-haired bats killed in Alberta originated from locations nearer to the wind facility, perhaps from the boreal regions of Alberta, the Northwest Territories, and Saskatchewan or from the higher elevations of the Rocky Mountains. Regardless, the data show that migratory bats killed in southwestern Alberta have the potential to come from large catchment areas, as recently found for bat species in Germany (Voigt et al. 2012).

We hypothesized that migratory bats exhibit sexual segregation during the summer and predicted that the isotope values of adult males would differ (likely by being higher) from adult females (i.e., females reside farther north). We further predicted that the degree of sexual segregation would be greater in hoary bats than in silver-haired bats. The lack of significant differences in mean isotope values between males and females of either species does not support our predictions. The lack of evidence for sexual segregation is surprising, especially for hoary bats. Sexual segregation and differential migratory behavior in bats is common (Cryan 2003, Fleming and Eby 2003, Ibanez et al. 2009), as evidenced by the fact that male hoary bats arrive at our wind-energy study site before females do (Baerwald and Barclay 2011) and by the limited number (or complete lack) of male hoary bats at maternity sites such as the Cypress Hills or Delta Marsh during the summer (Barclay 1984; C. Willis and J. Poissant, *personal communication*). It may be that males and females are segregated in such a way that the isotope values in their fur do not reflect the difference (e.g., elevationally and/or longitudinally). Indeed, given our site's proximity to the Rocky Mountains and that males are often found at higher elevations than females (Cryan et al. 2000, Cryan 2003), it seems likely that sexual segregation may

be occurring by elevation.

We examined the correlations between isotope value and date for evidence of differential migration (e.g., Mazerolle and Hobson 2007, Paxton et al. 2007, Langin et al. 2009). The weak or non-existent correlations between $\delta^{13}\text{C}_f$ or $\delta^2\text{H}_f$ and fatality date (i.e., arrival date) do not provide conclusive evidence for differential migration (see also Cryan et al. 2014). However, $\delta^{15}\text{N}_f$ was negatively correlated with fatality date of silver-haired bats in both years and hoary bats in 2007. Given the lack of correlation between $\delta^{15}\text{N}_f$ and $\delta^{13}\text{C}_f$ or $\delta^2\text{H}_f$, it is unlikely that the relationship between $\delta^{15}\text{N}$ and date indicates a latitudinal pattern of migratory movement, but rather, indicates dietary differences. $\delta^{15}\text{N}$ values increase by $\sim 3\text{‰}$ with each trophic level or by variable amounts in animals that are water or nutritionally stressed (Hobson et al. 1993, Kelly 2000, Voigt and Matt 2004, Smith et al. 2010). Thus, it may be that bats arriving earlier in the season were either foraging at a higher trophic level, or were more water or nutritionally stressed at the time their fur was grown, than bats arriving later in the season. The relationship between $\delta^{15}\text{N}_f$ values and date suggests differences in habitat quality or body condition that influence the timing of migration either at an individual or landscape level. For example, early migrants could be individuals in relatively poor condition (from high or low quality habitat) or bats from a region of relatively low quality habitat.

Our data show that migratory bats killed in southwestern Alberta may come from forests hundreds of kilometers away and potentially from large catchment areas, as was recently reported in the European study by Voigt et al. (2012) and a North American study by Cryan et al. (2014). Thus, the impacts of these fatalities may have broad-reaching ecological consequences. Although some wind energy facilities have successfully reduced the number of bat fatalities (Baerwald et al. 2009, Arnett et al. 2011), fatalities of bats remain a conservation issue, especially given the important ecosystem services provided by bats. The combined losses of bats from white-nose syndrome (Frick et al. 2010) and wind energy development could cost the North American agricultural sector billions of dollars/year (Boyles et al. 2011). However, the ecological

ramifications of bat fatalities extend beyond agriculture. Bats limit insects and their herbivory (Kalka et al. 2008, Williams-Guillén et al. 2008, Böhm et al. 2011), which is especially important when dealing with forest pests such as western spruce budworm (Wilson and Barclay 2006). Thus, the loss of migratory bats that summer throughout the boreal forest and aspen parkland, and then migrate through agricultural areas, has the potential to impact a wide variety of ecosystems over a large geographical range.

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SUPPLEMENTAL MATERIAL

SUPPLEMENT

Raw stable isotope values ($\delta^{13}C$, $\delta^{15}N$, and δ^2H) in bat fur collected from fatalities found at a wind farm in southwestern Alberta, Canada ([Ecological Archives C005-010-S1](#)).