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Research Article

Red Bat Fatality: Geographic Extents through Deuterium and Niche Models

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ABSTRACT Bat fatality at wind energy facilities is a conservation issue, but its effect on bat populations is difficult to estimate. We have little understanding of wind turbine effects on bat population persistence, in part because we have poor knowledge of bat migration pathways and hence the source populations for individual fatalities. We used deuterium ratio analysis combined with genetic algorithm for rule-set prediction and the web-based isoscapes modeling, analysis, and prediction in a geographic information system environment as a novel approach. Our objectives were to explore the utility of these methods together and map the geographic extents of eastern red bat (*Lasiurus borealis*) specimens salvaged in 2008–2010 from a single, 92-km^2 wind energy facility in Illinois, USA. Results indicate that combining these methods can be successful and support their use with species where ranges may be less well defined. Because of the migratory nature of this species and the range of deuterium values of pixels in our isotope model, we predicted that 18% and 82% of the specimens would have isotope results inside and outside of the wind facility's isocline respectively. We concluded that 71.4% of the specimens had isotope signatures placing them outside the wind facility's isocline. It could be argued that the wide distribution of bat fatalities dilutes the overall effect of those fatalities on the bat species; however, if other facilities show a similar pattern, each facility could have cumulative and far reaching population-level effects. © 2019 The Wildlife Society.

KEY WORDS eastern red bat, GARP, GIS, isotope, *Lasiurus borealis*, Midwest, wind.

Wind energy continues to expand in the United States. Throughout the United States, there are >54,000 turbines in operation across 41 states, Guam, and Puerto Rico (American Wind Energy Association 2018). Wind energy is an environmentally friendly alternative to fossil fuels, but negative effects on bats have become evident (Kunz et al. 2007, Arnett et al. 2008, Arnett and Baerwald 2013). For example, wind facilities in Midwestern agricultural fields can kill an estimated 4.45–7.14 bats/turbine/year (Jain et al. 2011), although other studies have produced higher averages (e.g., 15.7; Zimmerling and Francis 2016). It is difficult to estimate accurately all the bat fatalities across the continent because of differences in survey methods and a lack of representative sampling (Huso and Dalthorp 2014).

Multiple species are killed by wind turbines throughout North America, but across the contiguous United States, eastern red bats (*Lasiurus borealis*) comprised up to 60.9% of wind turbine bat fatalities (Arnett et al. 2008). Eastern red bats can migrate long distances between seasonal roosts (Racey and Entwistle 2003), and they experience the highest wind turbine fatality during their autumn migrations (Arnett et al. 2008). Another estimate predicts that this species, combined with hoary (*Lasiurus cinereus*) and silver-haired bats (*Lasionycteris noctivagans*) comprise 78.4% of bat fatalities (Arnett and Baerwald 2013).

There is evidence that the eastern red bat population is declining, for which wind turbine fatality is a potential contributing factor. In a paired netting survey of eastern red bats, Winhold et al. (2008) reported a 52–85% decline in netting captures/night from studies conducted from 1978 to 2006 and at least a 44% decline in the proportion of eastern red bats captured in Lower Michigan, USA. In addition to wind turbine fatality, habitat loss, fragmentation, and effects from pesticides are other possible factors contributing to this apparent population decline (Winhold et al. 2008). To discern the relative effects of these factors, it is important to understand all the components of a species' natural history. For migratory species, understanding migration pathways and patterns is critical.

Collecting the necessary data to determine these migratory patterns can be difficult, especially in nocturnal or cryptic species. Banding studies are not always an efficient way of tracking bat populations because of potentially low recapture rates (Cryan et al. 2014). Radio-transmitters have been successfully implemented in migratory bats and have given greater insight into bat migration movements

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(Castle et al. 2015, Weller et al. 2016). An alternative non-invasive method is to use deuterium ratio (δD) analysis to study migratory species that move between locations with different isotopic signatures (Bowen et al. 2005). This technique can be used to explore potential origins of untagged migratory species or even museum specimens and has been successfully employed in bats (Fraser et al. 2012, Sullivan et al. 2012, Cryan et al. 2014, Lehnert et al. 2014, Fraser et al. 2017). It involves analyzing a small sample of keratinized tissue from the animal such as hair, skin, or claws. Deuterium is deposited into growing tissues but is inert after the tissue formation. This allows the isotopic signature to remain for long periods of time after death. The δD of the keratin tissue (δD_k) is then related to the δD signature of precipitation (δD_p) to find probable origins. However, the δD_k does not reflect δD_p in a 1:1 ratio.

The discrepancy of δD_k and δD_p ratios is caused by multiple fractionation events where hydrogen and its isotopes are unevenly integrated into tissues causing a discrimination of these isotopes throughout the food web (Bowen et al. 2005). Several studies have developed equations that relate δD_k to δD_p (Cryan et al. 2004, Fraser et al. 2012, Ossa et al. 2012, Cryan et al. 2014, Plyant et al. 2014), and the resulting δD_p values can then be mapped onto a δD_p isoscape (a series of precipitation isoclines), which narrows possible geographic extents latitudinally (north to south). However, a δD_p isoscape does little to reduce the extent longitudinally (east to west). Using well-defined species ranges can help reduce these potential geographic extents further, but if the geographic range is unknown or not well defined for the time or season in question, niche modeling and other range modeling techniques may be an important tool. Niche modeling takes the data from geo-located specimens and models possible ranges using environmental data. The output from these models can help predict ranges of species that are difficult to study or are not common in reference collections.

Our first objective was to explore combining isotope and niche modeling methods to determine if this process would be useful for species whose ranges are less well known. Objective 2 was to investigate the potential geographic extents of bats killed at a single, large wind facility in central Illinois, USA. We used the δD_p of the wind energy facility to predict the number of potential local bats salvaged at the facility. Because eastern red bats are migratory (Cryan 2003), and we do not know their origin, we assumed even distribution of bats across their range. Based on the δD_p and this assumption, we predicted that 18% and 82% of the specimens would have deuterium ratios that would label them as potential local and non-local bats, respectively.

STUDY AREA

Specific timing of eastern red bat migration through the area is unknown, but we used samples salvaged July–October from 2008–2010 from a large wind energy facility located in central Illinois. The site is 237.7 m above sea level (https://www.isws.illinois.edu/statecli/newnormals/normals.USC00110764.txt, accessed 10 Dec 2018), and McLean County has an elevation ranging from 201 m to 301 m (https://www.anyplaceamerica.com/directory/il/mclean-county-17113/, accessed 4 Apr 2019). Data collected from 1981 to 2010 showed an average of 99.6 cm of precipitation and average normal temperatures ranging from −4.4°C to 23.8°C (https://www.isws.illinois.edu/statecli/newnormals/normals.USC00110764.txt, accessed 10 Dec 2018). The study site covered 92 km^2 of agricultural land, which was predominately corn and soybean production, with small pockets of grassland and deciduous forest. It contained 240 Vestas V82 1.65-MW wind turbines (Vestas, Aarhus, Denmark) with diameters of 82 m that sweep an area of 5,281 m^2 at the time of bat salvage (Direct Industry 2008, EDP Renewables, https://www.edprnorthamerica.com, accessed 15 Aug 2018).

METHODS

Sample Collection and Isotope Analysis

The wind energy company salvaged dead bats from around the wind turbines from July to October in 2008–2010 with salvage permits from the Illinois Department of Natural Resources and following salvage protocols described by the Institutional Animal Care and Use Committee (Illinois State University 2018). Specimens were frozen at −80°C for initial research by Rollins et al. (2012) using forensic pathology to determine whether traumatic injury or barotrauma was the main cause of bat fatality in wind energy facilities. Out of 267 bats salvaged, we collected hair samples that had grown during the summer prior to death for analysis from 35 adult eastern red bats (23 males and 12 females). The others were unusable because of decomposition or bodily damage. We cut hair samples from the rumps (Fraser et al. 2012) and, after cleaning (Popa-Lisseanu et al. 2012), packaged them into silver capsules with every third sample duplicated to ensure precision in the analysis. Technicians at the University of Wyoming Stable Isotope Laboratory then analyzed the samples on a temperature conversion elemental analyzer along with standards USGS42, USGS43, UWSIF33 (turkey), and UWSIF34 (chicken).

We chose deuterium for the isotopic analysis based on studies that focused on the correlation between δD_k and δD_p (Cryan et al. 2004, 2014; Fraser et al. 2012; Ossa et al. 2012; Plyant et al. 2014). Plyant et al. (2014) found differences in the relationship of δD_k and δD_p in male and female red bats such that female red bats have a higher variance, which could be due to some females in the sample rearing young during that season and having different metabolic demands. Although a single equation could be used for both sexes, we decided that the R^2 of the combined equation (0.37) was not a large enough increase from the female's R^2 of 0.29 to choose it when the male's R^2 was 0.69 (Plyant et al. 2014). Therefore, we converted the eastern red bat hair isotope values (δD_h) using 2 equations: for males, $\delta D_p = (\delta D_h + 13.95)/1.48$ and for females, $\delta D_p = (\delta D_h + 18.02)/1.75$ (Plyant et al. 2014; Data S1, available online in Supporting Information). We compared samples with their duplicates using an unpaired *t*-test ($\alpha = 0.05$) to examine potential differences in the isotopic signatures within the hair samples (R Version 3.3.1, www.r-project.org, accessed 20 Jan 2017).

We used Isomap.org, a web-based precipitation isotope modeling program, to develop a δD_p model using latitude and elevation as independent variables (Bowen et al. 2005). The program uses spatial interpolation to account for areas around the world where isotopic data are unavailable (The IsoMAP Project, www.isomap.org, accessed 21 Dec 2015). Our model used data collected from 423 stations throughout the Northern Hemisphere from May to August from 1960 to 2010 (U.S. National Geophysical Data Center 1998, Welker 2000; International Atomic Energy Agency, www.iaea.org/water, accessed 5 Feb 2014). We included more years than our bat sampling (2008–2010) to create the model to decrease potential bias created by short-term climate variation in those years (Bowen and Revenaugh 2003). We also included data from May to include precipitation nearer the beginning of the growing season. We then imported the resulting isoscape into ArcGIS 10.2© (Fig. S1, available online in Supporting Information; Environmental Systems Research Institute, Redlands, CA, USA). The IsoMAP model and statistics can be accessed through Isomap.org under the title 4DMay–Aug or key number 34229.

Modeling Summer Ranges

The genetic algorithm for rule-set prediction (GARP) program predicts the distributions of organisms and has been used to estimate ranges of various species (The University of Kansas Biodiversity Research Center, Lawrence, KS, USA; Peterson et al. 2002, McNyset 2005, Kostelnick et al. 2007, Sobek-Swant et al. 2012, Qin et al. 2015). The program uses species occurrence data in the form of geographic coordinates and environmental variables represented as raster datasets to predict areas of presence or absence for a species. We included seasonal precipitation and temperature because these factors are important components to the ecology of an area and are important variables in other studies (Sobek-Swant et al. 2012, Padalia et al. 2014, Qin et al. 2015). Studies of roost selection by tree bats found that a closed canopy is an important variable for eastern red bats (Menzel et al. 1998, Kalcounis-Rüppell et al. 2005), so we included percent tree cover as a variable. Throughout different studies, elevation is used as a variable in some GARP models (Peterson et al. 2002, McNyset 2005, Qin et al. 2015) but not by others (Kostelnick et al. 2007, Sobek-Swant et al. 2012, Padalia et al. 2014). These studies span a wide range of species and spatial scales that can affect whether to include elevation as a variable. Because the area modeled in this study covered a large latitudinal range where variables may be affected by latitude and elevation, we included it in the GARP model.

We decided to represent the environmental raster datasets at 1-km^2 spatial resolution because of the large mapping scale and data restrictions. When using GARP, each data layer needs to be in the same resolution before they are imported into the program. If they are not originally in the same resolution, then the data must be resampled so that their resolutions match. We imported June–August temperature and precipitation data into GARP as interpolated global climate data (Hijmans et al. 2005*a*, *b*), through WorldClim, a free climate data website for ecological modeling and GIS (www.worldclim.org, accessed Aug 2012). We obtained global map percent tree cover from moderate resolution imaging spectroradiometer (MODIS) images from the Terra satellite (Geospatial Information Authority of Japan and China University, www.globalmaps.github.io/ptc, accessed Aug 2012). The elevation dataset was a North American digital elevation model (DEM) provided by United States Geological Survey's Center for Earth Resources Observation and Science (U.S. National Geophysical Data Center 1998); we imported it through Data Basin (http://databasin.org/datasets/d2198be9d2264de19cb93fe6a380b69c, accessed Aug 2012).

We downloaded specimen data from the Mammal Networked Information System through Vertnet (http://portal.vertnet.org/search?q=class:Mammalia, accessed Aug 2012) to generate species occurrence points for training and testing the GARP models. We used only specimens from June–August ($n = 793$) and removed records where sex or coordinates were unknown. Using ArcGIS, we randomly assigned 80% of the coordinates as training points to create the GARP models ($n = 634$) and withheld the remaining 20% ($n = 159$) for an independent assessment of the final GARP model. The GARP program randomly split the training points again into 80% training ($n = 507$) and 20% ($n = 127$) for internal model testing in GARP during the iterations of the genetic modeling process. Following model convergence, GARP selects the 10 best models for visualization of a species' range, with each model specifying presence or absence for all pixels covering the geographic area of interest.

We imported the 10 best models back into the ArcGIS and summed the number of models predicting presence for each pixel (Fig. S2, available online in Supporting Information). The 10 models produced varying range options that extended northwards into Canada and south into Mexico. We assessed the accuracy of the range maps with the 20% testing points by extracting the raster value (ranging from 0–10 resulting from the 10 best models) from the pixel corresponding to each test point. We examined these models with a receiver operating characteristic (ROC) analysis for the area under the curve (AUC) to test the models' sensitivity and specificity using the testing points, following the methods described by McNyset (2005). Using the ROC analysis, we decided that areas where ≥7 of the 10 best models agreed as presence were representative of the bats' primary range from June through August.

Integrating Deuterium Ratios, Isoscape, and GARP Models

Because it cannot be assumed that all the bats migrated from the same location or are part of the same population, we mapped the δD_h of each specimen separately into the IsoMAP assignment tool (Bowen et al. 2014). The pixels in each resulting isotope raster represent the percent probability that the specimen originated from each individual pixel (Bowen et al. 2014).

We uploaded and reclassified these maps separately in ArcGIS to show pixels with the highest origin probability and then added them together by sex using the raster calculator (Fig. 1A). We clipped the resulting maps with the GARP range models to constrict the extents east to west so that the isotope prediction maps would be reduced to more probable and precise summer ranges (Fig. 1B). We calculated the ratios of the GARP range and the summed isotope rasters to determine the proportion of the summer range that could potentially be affected by a single wind facility. We also reclassified the isotope rasters by sex to investigate male: female extent overlap (1 = male or female, 2 = overlap; Fig. S3, available online in Supporting Information). We determined percent overlap by dividing the number of pixels where both sexes overlapped by the total number of pixels.

To predict the number of potential local bats, we extrapolated the wind facility's δD_{p} (−27.1‰). To incorporate a natural variation of ± 3‰ found in samples (Wassenaar and Hobson 2006), we expanded the δD_{p} range of the wind facility to include values −27‰ ± 3‰. Across the isoscape (Fig. S1), 18% of the pixels contained δD_{p} values of −27‰ ± 3‰. Because we did not know the specimens' origins prior to any analysis, we assumed an even distribution of bats across their range. Based on these factors and assumption, we estimated that 18% of the specimens would be potential local bats and the remaining 82% would be outside of that isotope range and non-local bats. In this study, we defined a bat as a potential local if it had a δD_{p} of −27‰ ± 3‰. This definition assumes that the main migratory movement of eastern red bats is north to south. We then used a chi-square goodness-of-fit test ($\alpha = 0.05$) to compare our expected and observed potential local bats (R version 3.3.1, www.r-project.org, accessed 20 Jan 2017).

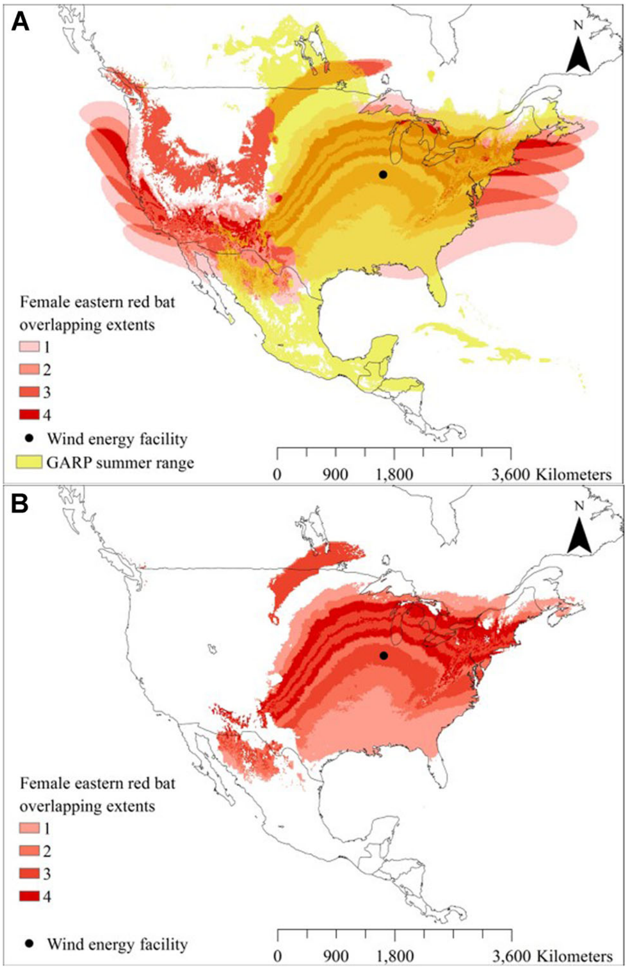

Figure 1. The genetic algorithm for rule-set prediction (GARP) summer range map (yellow) and the isotope extents (red) of female eastern red bat specimens (A) collected 2008–2010 at a central Illinois, USA, wind facility (black circle). Numbers 1–4 indicate the number of extents that overlap in an area (e.g., 2 = extents for 2 individuals overlap in that area). The extents originally cross the entire North American continent (A), but GARP restricts them on the east and west side (B).

RESULTS

We found a larger standard deviation of δD in the female samples ($\bar{x} = -45 \pm 14.41$‰ [SD]; range = −71‰ to −27‰) than the male samples ($\bar{x} = -28 \pm 12.77$‰; range = −44‰ to −17‰; Data S1). When we analyzed duplicates with their corresponding samples, they did not differ ($t_{24} = 0.24$, $P = 0.185$) and had an average difference of 1.0‰ (0.0–3.0‰). The AUC from the ROC analysis was 0.97 with an average omission error of 1.45%, indicating that the model overall generated good predictions. The GARP models accurately predicted the presence of the bat specimens 99.37% of the time with only 1 testing point falling outside the GARP prediction. This point occurred in a gap area surrounded by predicted range.

Assuming even distribution of bats across their range, we predicted that 18% or 6 out of the 35 specimens would have deuterium values of −27‰ ± 3‰ and be potential local bats by our definition. This was based on the δD_{p} of the wind facility's location (−27‰) and that 18% of the isoscape contained δD_{p} values of −27‰ ± 3‰. We observed 10 bats (28.6%) with this isotopic signature and 25 bats (71.4%) with signatures outside the wind facility's isotope value, but the chi-square goodness-of-fit test indicated there was no difference between the predicted and observed number of local bats ($\chi^2 = 0.265$, $P = 0.10$). There were areas of the map (Fig. 2A) where up to 4 of the 12 females overlapped north of the wind facility and their extents covered 71.5% of their range including Canada and areas south of the wind facility. For males, there were areas where up to 16–18 of the 23 specimens overlapped around the wind facility (Fig. 2B), covering 68.0% of their potential summer range. When we examined male:female overlap, their extents overlapped by 94.7%, but females showed a concentration of extent overlap farther north than the male bats.

DISCUSSION

The high AUC and low omission percentage of the GARP models demonstrates the success of ecological niche modeling for predicting the summer range of the eastern red bat across North America. However, like all models,

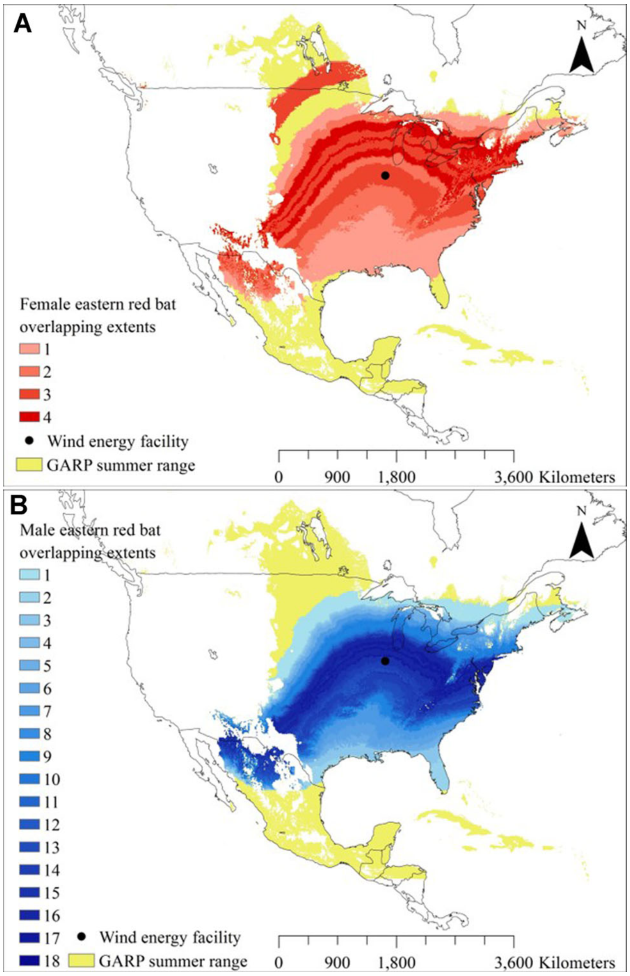

Figure 2. The deuterium isotope extents of eastern red bat specimens collected 2008–2010 from a central Illinois, USA, wind energy facility (black circle). Females ($n = 12$) are shown in red (A) and male bats ($n = 23$) are shown in blue (B). The genetic algorithm for rule-set prediction (GARP; in yellow) indicates the summer range prediction that was used to restrict the specimens' isotope ranges. Numbers and their corresponding shades of color indicate the number of specimen extents that overlap in an area (e.g., 2 = extents for 2 individuals overlap in that area). For females, there is a greater concentration of extents north of the wind facility with 2 specimens potentially coming from Canada. Males had a larger concentration of overlapping extents around the wind facility and throughout Iowa, Illinois, and Ohio, USA. Specimens from both sexes had extents with depleted deuterium signatures that placed them in an isocline that included northern Florida, USA, to southern Illinois.

GARP is subject to data restrictions. They are more prone to overestimate a range, but it is possible to get false negatives and fail to predict where species occur. Our GARP map had 1 testing point occur outside the predicted range. This data point occurred in a gap and was surrounded by GARP predicted range. The original and GARP-restricted isoscapes (Fig. 1A–B) provided excellent visualization of the application of these methods together.

Other models are used to predict species' ranges, and we would advocate a comparison of other ecological niche modeling packages (e.g., Maxent, BIOMOD) with the results generated here from GARP. Studies comparing species range maps generated by different ecological niche modeling approaches have reported mixed results regarding the best overall approach, and instead the optimal package may vary based on the specific application (Peterson et al. 2002). For example, Padalia et al. (2014) examined the use of GARP and Maxent and reported that Maxent had a greater predicting power than GARP. However, Qin et al. (2015) concluded the opposite; for large sample sizes ($n >$ 150) like ours, which used 634 GARP training points, Terribile and Diniz-Filho (2010) reported that Maxent and GARP were similar in their predicted areas. One of the commonly stated weaknesses of GARP is its potential to overestimate the geographic range and generate false positives (Elith and Graham 2009, Sobek-Swant et al. 2012). If these over predictions did occur, then our extent: summer range ratio is a more conservative estimate of the area affected, which we would argue is preferred for species protection initiatives. In future studies, other ecological niche range modeling packages and other isotopes (e.g., δ^{13}C, δ^{15}N) could also be used to predict or narrow origin estimations depending on the species in question (Hobson 1999).

The combination of GARP and isotope analysis showed that the bats' extents covered large portions of the summer range with many female overlapping extents north of the wind facility (Fig. 2A). The overlapping male extents were farther south and were closer to the wind facility's isocline (Fig. 2B), suggesting they may have originated closer to that area. When we examined the overlap of males and females (Fig. S3), their degree of overlap is consistent with the evidence that they occupy the same areas during the summer (Cryan 2003). When we analyzed the subsample of the specimens with their duplicates, they were not statistically different, and the maximum difference was within the range of variability expected within biological samples because of natural variability within growing tissues (Wassenaar and Hobson 2006). This supports the accuracy and precision of the hair sampling and laboratory analysis.

Using the wind energy facility's δD_p ratio, δD_p ratios of the isoscape, and the assumption of even distribution of bats across their range, we estimated that 18% of the bats could be within the local isotope range of $-27‰ \pm 3‰$. The non-significant chi-square goodness-of-fit test implied that we did not have more than expected local bats, and our prediction that a majority of the bats would be migrants from areas with a different isotope signature than the wind facility was supported. Eastern red bats are summer residents of Illinois (Hoffmeister 1989), but they are also long-distance migrators that are often killed during their fall migration (Arnett et al. 2008).

Bat fatality at wind energy facilities remains an ecological and economic issue. Bats are well established as important members of their ecosystems through controlling insect populations (Kalka et al. 2008, Williams-Guillén et al. 2008), and the positive effect of bats on agriculture via pest control is important (Boyles et al. 2011, Wanger et al. 2014, Maine and Boyles 2015). Other research has raised concerns about the conservation and economic implications from the negative effects of wind facilities on bat populations in combination with other pressures like white-nose syndrome

(Baerwald et al. 2014). Bat ranges and the effects of wind energy development on bat populations cross international boundaries, and comprehensive solutions will need to be just as expansive (Voigt et al. 2012, Lehnert et al. 2014).

Wind facilities currently offer a means of sampling specimens that cannot be easily duplicated. Such specimens can provide insight into many different aspects of bat biology, including age and sex class ratios, population genetic structure, diet, migratory timing and pathways, and seasonal ranges. This information is invaluable to their conservation, and although the desire is to reduce substantially any fatality, we encourage wind facility operators and permitting authorities to enable the collection of carcasses and museums to curate this material so that we do not waste the information opportunity from salvaged specimens.

MANAGEMENT IMPLICATIONS

Our results demonstrate that combining GARP with IsoMAP has significant predictive potential. This combination allows for estimation of species distributions that are not completely defined and are difficult to establish through field work alone. Through combining isotope analysis and GARP, we found that the bats killed came from large portions of their summer home range. Although it could be argued that such a wide range dilutes the overall effect of turbine-related fatalities on this population, these fatalities are likely to have a cumulative and far-reaching effect when other facilities are built within the same movement area.

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SUPPORTING INFORMATION

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