



# The catchment area of wind farms for European bats: A plea for international regulations

Christian C. Voigt<sup>a,\*</sup>, Ana G. Popa-Lisseanu<sup>a</sup>, Ivo Niermann<sup>b</sup>, Stephanie Kramer-Schadt<sup>a</sup>

<sup>a</sup> Leibniz Institute for Zoo and Wildlife Research, Alfred-Kowalke-Str. 17, 10315 Berlin, Germany

<sup>b</sup> Leibniz Universität Hannover, Institute of Environmental Planning, Herrenhäuser Str. 2, 30419 Hannover, Germany

## ARTICLE INFO

### Article history:

Received 6 February 2012

Received in revised form 17 April 2012

Accepted 23 April 2012

Available online 29 June 2012

### Keywords:

Alternative energy

Chiroptera

Conservation

Migratory species

Wind energy facilities

Wind parks

## ABSTRACT

Wind turbines are increasingly established throughout Europe and North America with often fatal consequences for wildlife, most importantly bats and birds. Yet, it is often unknown over what geographical distances wind farms are affecting animal populations. Based on stable hydrogen isotopes in fur, we assessed the geographic provenance of bats killed in summer and autumn at German wind turbines. We found that killed *Pipistrellus nathusii* originated from Estonia or Russia, and *Pipistrellus pipistrellus* from more local populations. Noctule bats (*Nyctalus noctula*) and Leisler's bats (*Nyctalus leisleri*) were of Scandinavian or northeastern origin. Our isotopic geo-location reveals that wind turbines kill bats not only of sedentary local populations but also of distant populations, thus having potentially a negative impact beyond political borders; an observation that calls for international regulations for implementing mitigation measures to prevent large-scale detrimental effects on endangered bat populations.

© 2012 Elsevier Ltd. All rights reserved.

## 1. Introduction

During the last decade, wind turbines have been particularly promoted in many North American and European countries, although recent risk assessment studies have highlighted that wind farms may involve severe costs to biodiversity. For example, large raptors and some songbirds are frequently killed when colliding with wind turbines at daytime (e.g. Barrios and Rodriguez, 2004). At night, large numbers of bats are also killed at wind farms (Arnett et al., 2008; Rydell et al., 2010), which may cause significant declines in breeding populations due to the low capacity of bats for recovering from increased mortality rates (Jones et al., 2003; Kunz et al., 2007). A large portion of bats killed at turbines are considered to be migrants that travel in autumn from their breeding to their wintering grounds; an assumption that has not yet been documented or proven. If wind turbines do not only kill sedentary but also migratory bats, wind farm facilities may bear the potential of causing declines in bat populations on a large geographical scale. Therefore, we investigated the provenance of bats that were found dead next to five wind farm facilities in Germany. We focused on four bat species that comprise the major recorded fatalities at wind turbines in Germany: Noctule bats *Nyctalus noctula*, Leisler's bats *Nyctalus leisleri*, Common pipistrelles *Pipistrellus pipistrellus* and Nathusius' bats *Pipistrellus nathusii*. Since all four

species form breeding populations in the vicinity of most studied wind farm facilities as well (Dietz et al., 2009), we investigated whether killed bats originate from local or from more remote populations. We used an isotopic approach that is based on two observations: (1) Stable hydrogen isotope ratios of precipitation water vary across continents according to rainfall and temperature (Hobson, 1999; Bowen et al., 2005). This is because evaporated water is exposed to gradual cooling as it travels along latitudinal temperature gradients. As water vapor capacity decreases in the evaporated water mass – leading to condensation – it loses heavy isotopes to precipitation. Since the isotopic content of meteoric water depends on the isotopic content of the water vapor it condensed from, rainfall water and consequently also surface water varies in isotopic composition with latitude (Craig, 1961). (2) Body tissues or products, such as hair keratin, are made of dietary nutrients that animals assimilate at the places where they live. In particular, stable isotope ratios of fur keratin matches with that of surface water in the summer habitat, because migratory bats molt before the onset of migration (Cryan et al., 2004).

We hypothesized that wind turbines kill both sedentary and migratory bats, and we therefore expected stable hydrogen isotope ratios ( $\delta^2\text{H}$ ) to vary among species and migratory populations. We used spatial models to extrapolate the origin of breeding grounds of the four species. The results of our study are essential for policy as well as land use planning, since the construction of wind farms affect European bats species that are protected by the 'EU Habitats Directive 92/43/CEE (Annexes II and IV)', in particular migratory

\* Corresponding author.

E-mail address: [voigt@izw-berlin.de](mailto:voigt@izw-berlin.de) (C.C. Voigt).

species that are covered by the convention on the 'Conservation of Migratory Species of Wild Animals' (Bonn, 1979) through the EUROBATs agreement (London, 1991).

## 2. Materials and methods

### 2.1. Sample collection and isotope analysis

We collected 47 bat carcasses from wind farms between July 2008 and September 2009 from five natural regions in Germany. Three of these natural regions (Mecklenburg Lake Plateau Hinterland, Brandenburg Heath and Lake District, Upper Lusatia) are located in the Northeast German Plain, the fourth region in the Lüneburg Heath of Northwest Germany, and the last in the Saar-Nahe Hills, situated in the westernmost part of Germany. The dataset included 7–16 individuals from each of the four focal species (*N. noctula*, *N. leisleri*, *P. pipistrellus* and *P. nathusii*). From each carcass, we removed hair from the interscapular region, and shipped these samples in plastic vials to the stable isotope laboratory of the Leibniz Institute for Zoo and Wildlife Research (IZW) in Berlin. We cleaned the fur from surface oils and contaminants using a 2:1 chloroform–methanol solution and then dried them in a drying oven over 24 h at 50 °C. From each hair sample, we placed a subsample of 1 mg ( $\pm 0.1$  mg) in a silver foil capsule (IVA Analysetechnik e.K. Meerbusch, Germany). The methodological approach in analyzing stable hydrogen isotope ratios in the IZW laboratory has been described in detail in Erzberger et al. (2011) and Popa-Lisseanu et al. (2012). Briefly, fur samples were placed in the autosampler (Zero Blank autosampler; Costech Analytical Technologies Inc., Italy) of the elemental analyzer (HT Elementaranalysator HEKAtech GmbH, Wegberg, Germany). Before combustion, samples were flushed in the autosampler for at least 1 h with chemically pure helium (Linde, Leuna, Germany). We used a Delta V Advantage isotope ratio mass spectrometer (ThermoFischer Scientific, Bremen, Germany) that was connected via an interface (Finnigan Conflo III, ThermoFisher Scientific, Bremen, Germany) with the elemental analyzer. Analytical precision based on the repeated analyses of stable hydrogen ratios in laboratory keratin standards was always better than 0.74‰ (one standard deviation of mean ratios).

### 2.2. Modeling the origin of bats based on $\delta^2\text{H}$ of fur keratin

Since we lacked reference material of sedentary bat species for large areas of the potential breeding area in Northeastern Europe, we did not follow a triple isotope approach in assigning the breed-

ing origin of bats as described in Popa-Lisseanu et al. (2012). Instead, we used an extrapolation approach adapted from Hobson et al. (2009) to delineate the origins of the bat casualties in the  $\delta^2\text{H}_p$  isoscape of Europe. This procedure allows establishing a relationship between deuterium in bat hair and mean annual precipitation in Europe and accounts for potential geospatial assignment errors leading to robust conclusions about the origin of migrant bats. All statistical tests were performed using R (R Development Core Team, 2009). For every hair value, a range of possible mean annual precipitation values is estimated and used to map the probability of origin, i.e. each map value is assigned a certain probability to generate the observed deuterium value in bat hair (Hobson et al., 2009). To this end, we linked  $\delta^2\text{H}$  of sedentary bat hair ( $\delta^2\text{H}_h$ ,  $n = 178$ ) captured throughout Europe (Popa-Lisseanu et al., 2012) and mapped values of  $\delta^2\text{H}$  in mean annual precipitation ( $\delta^2\text{H}_p$ ; Bowen et al., 2005) using a reduced major axis regression to account for errors in both measures (SMA in package 'lmodel2'; Legendre, 2008). This regression equation read:  $\delta^2\text{H}_p = 5.81 + 0.79 * \delta^2\text{H}_h$  ( $p < 0.001$ ). We then used the regression parameters to convert  $\delta^2\text{H}_h$  values to  $\delta^2\text{H}_p$  values for the four different bat species. We first modeled the uncertainty associated with analytical error, intra-population differences between sedentary individuals and error of the  $\delta^2\text{H}_p$  isoscape: For this, we used the  $\delta^2\text{H}_h$  standard deviations ( $\sigma_i$ ) of the known-origin bat populations  $i$  used in the regression model as error estimate and fitted a gamma distribution  $\Gamma$  to  $\sigma_i$  using maximum likelihood. However, from our original 178 samples, only 137 did have overlapping locations with more than two individuals found at the same place (Popa-Lisseanu et al., 2012). Therefore, we focused on the 16 locations  $i$  where  $n \geq 3$  samples were collected ( $n_{\text{total}} = 137$ ), among which only seven locations  $i$  had  $n \geq 10$  samples from sedentary bat populations (Table 1). We therefore used an approach where we traded off the exact derivation of the Gamma function fitted to the number of the standard deviations  $\sigma_i$  calculated from the respective locations  $i$  versus the exact derivation of  $\sigma_i$  when using small sample sizes, i.e. we fitted  $\Gamma_j$  to 16, 11, 9, 7 and 4 numbers of  $\sigma_i$  when we had at least  $n = 3, 5, 7, 10$  or 13 samples per location  $i$  (Table 2), resulting in five different  $\Gamma$ .

For each of the five fitted  $\Gamma_j$ , we propagated errors by simulating 1000 possible values of  $\delta^2\text{H}_p$  for each  $\delta^2\text{H}_h$  of the four species depending on a normal distribution  $N(\mu^*, \sigma^*)$ , where the mean  $\mu^*$  of the simulations was the corresponding  $\delta^2\text{H}_p$  directly obtained from the reduced major axis regression model that links  $\delta^2\text{H}_h$  of known-origin bats and  $\delta^2\text{H}_p$ , and the standard deviation  $\sigma^*$  was randomly drawn from  $\Gamma_j$  previously calculated. We built five probability density maps for the four species groups by calculating

**Table 1**

Overview over the 16 sample locations  $i$  of sedentary bat individuals of known origin; number of samples ( $n > 2$ ), place of origin and mean  $\delta^2\text{H}_h$  ( $\pm 1$  SD) for each location  $i$ .

Location $i$	Country	$n$	Longitude	Latitude	$\delta^2\text{H}_h$
1	Spain	20	−5.977033	37.518606	−47.71 $\pm$ 5.93
2	Spain	13	−6.8452	37.597006	−48.98 $\pm$ 3.45
3	Spain	3	−2.680556	42.071389	−69.75 $\pm$ 3.47
4	Spain	13	−7.896256	43.452694	−56.44 $\pm$ 6.23
5	France	11	9.171672	41.749667	−46.65 $\pm$ 7.92
6	France	5	−1.28095	47.7887	−77.39 $\pm$ 8.45
7	France	3	6.80448	48.8238	−87.93 $\pm$ 3.80
8	France	4	4.655113	43.466376	−70.85 $\pm$ 2.65
9	France	7	3.45654	44.4806	−73.17 $\pm$ 7.55
10	United Kingdom	11	0.973548	51.203805	−62.60 $\pm$ 6.38
11	Slovakia	3	19.09652	48.582711	−88.29 $\pm$ 6.59
12	Hungary	10	18.704669	46.348678	−74.05 $\pm$ 5.55
13	Poland	19	18.958408	49.664775	−94.14 $\pm$ 12.00
14	Poland	7	17.565593	53.872355	−83.79 $\pm$ 4.82
15	Poland	5	18.726022	54.037661	−86.48 $\pm$ 4.03
16	Poland	3	18.646638	54.352025	−102.52 $\pm$ 11.58

**Table 2**

Parameters of the Gamma distribution  $\Gamma_j$  with shape  $k_j$  and scale  $\theta_j$  fitted to the standard deviations SD of  $\delta^2\text{H}_h$  (see Table 1 last column) by maximum likelihood, with  $j$  being a different realization of  $\Gamma$  depending on the number of locations  $i$  with calculated SD's used to fit the Gamma distribution  $\Gamma_j$  and  $n$  being the minimum number of samples per location  $i$  from which the SD's were calculated.  $\Gamma_j$  was then used to draw the standard deviations  $\sigma^*$  for error propagation.

	Number of locations with calculated SDs	Minimum number $n$ of samples per location $i$	$K$	$\theta$
1	16	3	5.85	1.07
2	11	5	8.99	0.73
3	9	7	9.42	0.71
4	7	10	8.32	0.82
5	4	13	5.22	1.32

probability density functions (PDFs) for each species group (library MASS), and thus the probability that a particular grid cell within the  $\delta^2\text{H}_p$  isoscape will be a potential origin. PDFs of each species group and  $\Gamma_j$  were standardized to range between 0 and 1. From the so obtained association of  $\delta^2\text{H}_p$  isoscape values with the standardized PDFs, we created five ASCII remap files for each of the four species to reclassify the  $\delta^2\text{H}_p$  isoscape values into probability values in 0.01 steps. The final map of the origins of each species

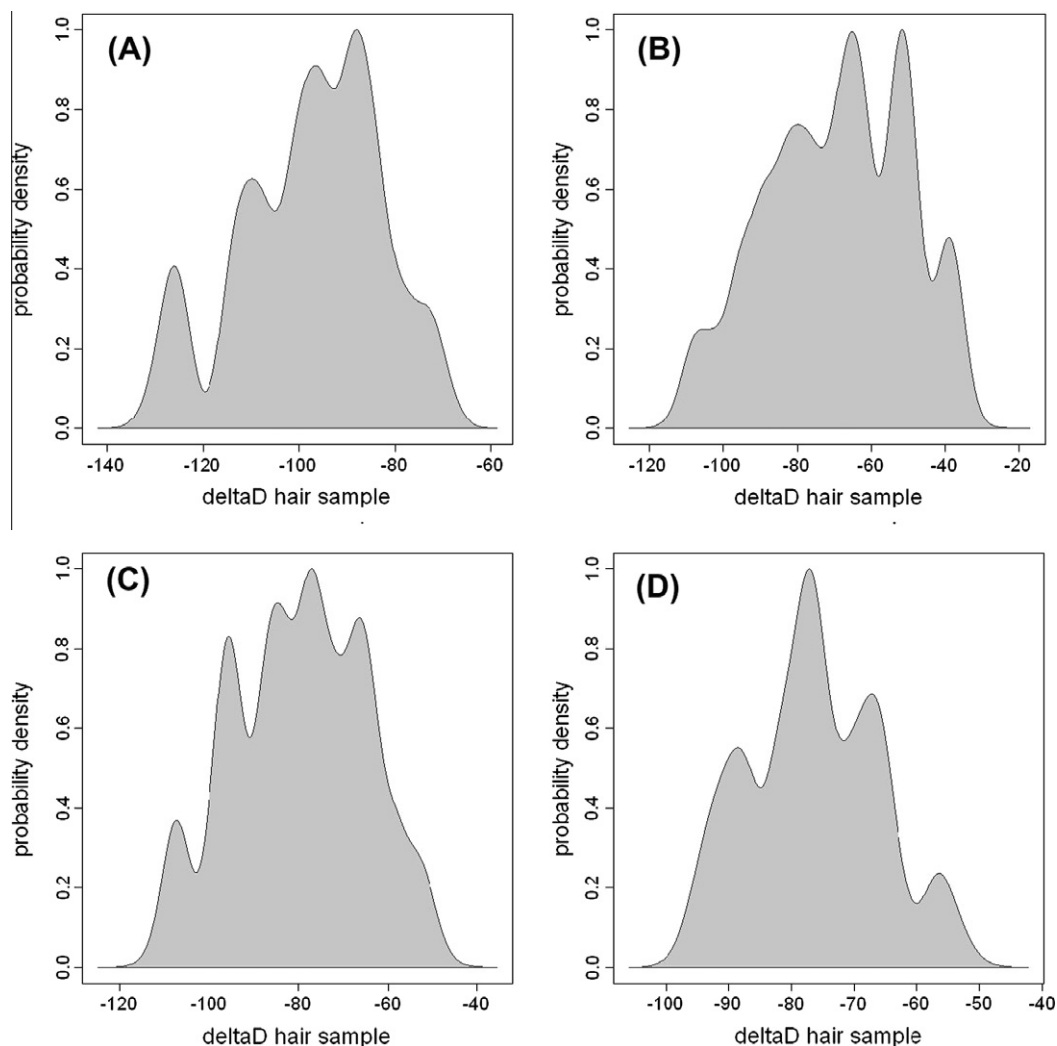
was obtained by multiplying the origin probability of the five maps fitted with different  $\Gamma_j$  with the product raised to the power of 0.2.

We used ArcGIS v. 9.3.1 to map the reclassified raster surface with a resolution of  $10' \times 10'$  (arc minutes). Elevations higher than 500 m above sea level were excluded because all included bat species form predominantly lowland populations, and distribution ranges were digitized from the IUCN Red List of Threatened Species ([www.iucnredlist.org](http://www.iucnredlist.org)).

### 3. Results

#### 3.1. Stable hydrogen isotope ratios of bat fur

The four bat species differed in  $\delta^2\text{H}_h$  (one-way ANOVA:  $F_{3,45} = 7.8$ ,  $p = 0.0003$ ). Post-hoc Tukey–Kramer tests revealed that fur keratin of *P. nathusii* (Mean  $\delta^2\text{H}_h \pm \text{SD}$ ;  $-130.3 \pm 17.2\text{‰}$ ;  $n = 10$  bat individuals) was more depleted in deuterium than all other bat species (*P. pipistrellus*:  $-94.6 \pm 22.8\text{‰}$ ;  $n = 16$ ;  $q = 6.81$ ,  $p < 0.001$ ; *N. leisleri*:  $-103.4 \pm 10.6\text{‰}$ ;  $n = 7$ ;  $q = 4.21$ ,  $p < 0.05$ ; *N. noctula*:  $-108.1 \pm 17.1\text{‰}$ ;  $n = 14$ ;  $q = 4.43$ ,  $p < 0.05$ ). All other pair-wise comparison proved not to be significant ( $p > 0.05$  in all other cases).



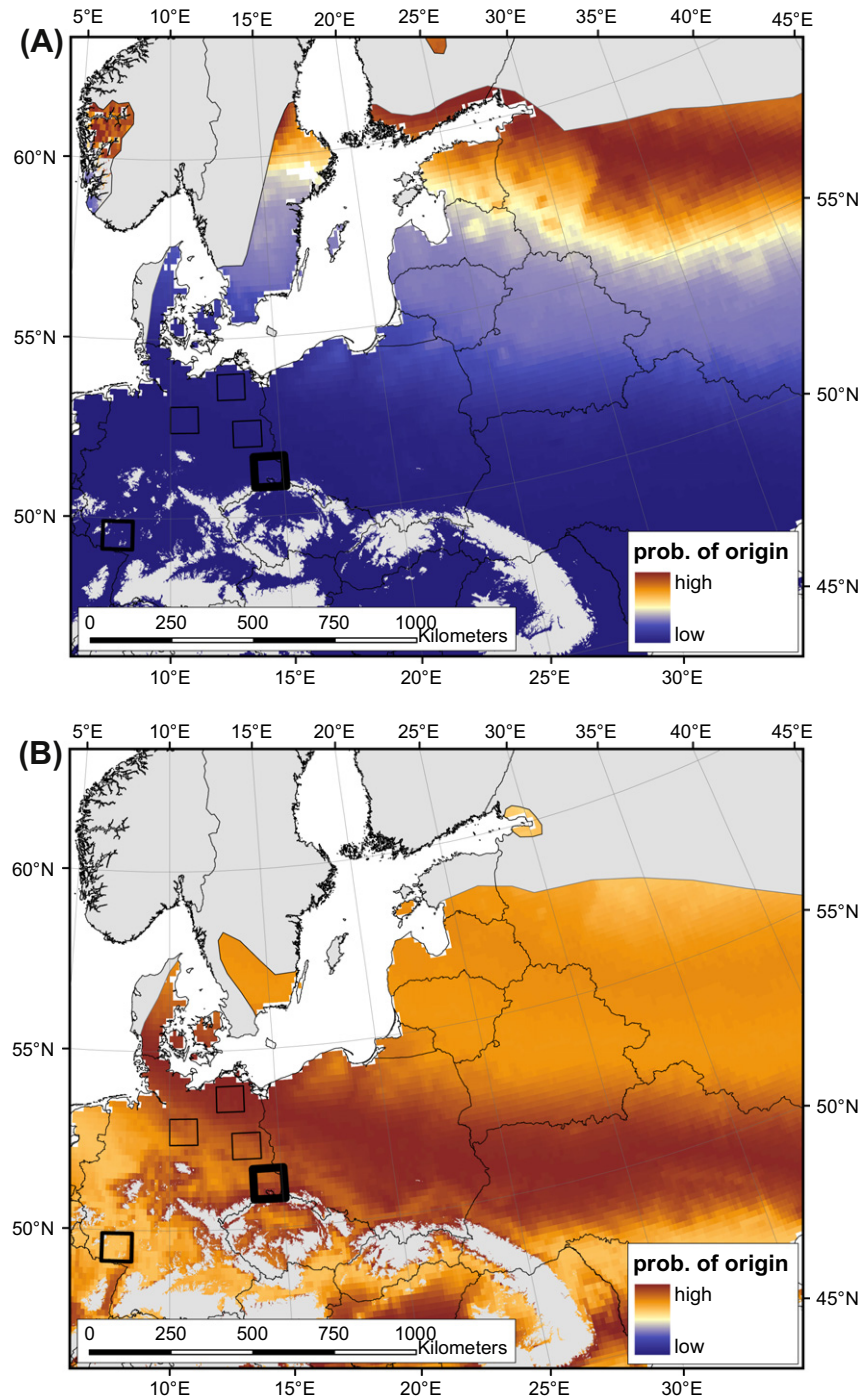
**Fig. 1.** Corresponding standardized probability density functions in relation to  $\delta^2\text{H}_h$  (deltaD hair sample) based on a Gamma distribution fitted for each species (A: *Pipistrellus nathusii*, B: *P. pipistrellus*, C: *Nyctalus noctula*, D: *N. leisleri*).

### 3.2. Modeling the origin of bats based on $\delta^2\text{H}$ of fur keratin

We obtained five gamma distributions for incorporating the error propagation in the spatial model that we used for geo-locating the four study species. Gamma distributions were of similar shape, trading-off low accuracy in standard deviation estimation ( $n \text{ samples} = 3, j = 1$ , Table 2) with high accuracy in gamma distribution estimation ( $n \text{ SD's} = 16, j = 1$ , Table 2). This yielded differences in prediction probability of about  $\pm 10\%$  compared with a gamma distribution fitted to a high accuracy in standard deviation estimation ( $n \text{ samples} = 10, j = 4$ , Table 2) but lower accuracy in gamma distri-

bution estimation ( $n \text{ SD's} = 7, j = 1$ , Table 2). This signals that the results are relatively robust. In all species, the standardized probability density showed several peaks (Fig. 1), suggesting that individuals of a given species may have originated from various locations. This is especially apparent for *P. pipistrellus* with two peaks reaching a standardized probability of 1.0.

Based on our spatial model, we found that individuals of *P. nathusii* originated from distant populations, probably from Estonia or Russia (Fig. 2A), whereas those of *P. pipistrellus* were probably of short and mid-distance origin (Fig. 2B). Noctule bats (*N. noctula*) most likely came from mid-distance populations (Poland, Scandina-



**Fig. 2.** Predicted geographical provenance of four European bat species within their range distribution (A: *Pipistrellus nathusii*, B: *P. pipistrellus*; C: *Nyctalus noctula*, D: *N. leisleri*) killed at wind energy facilities in Germany (approximate location indicated by squares with their line width adjusted in size according to sample size).



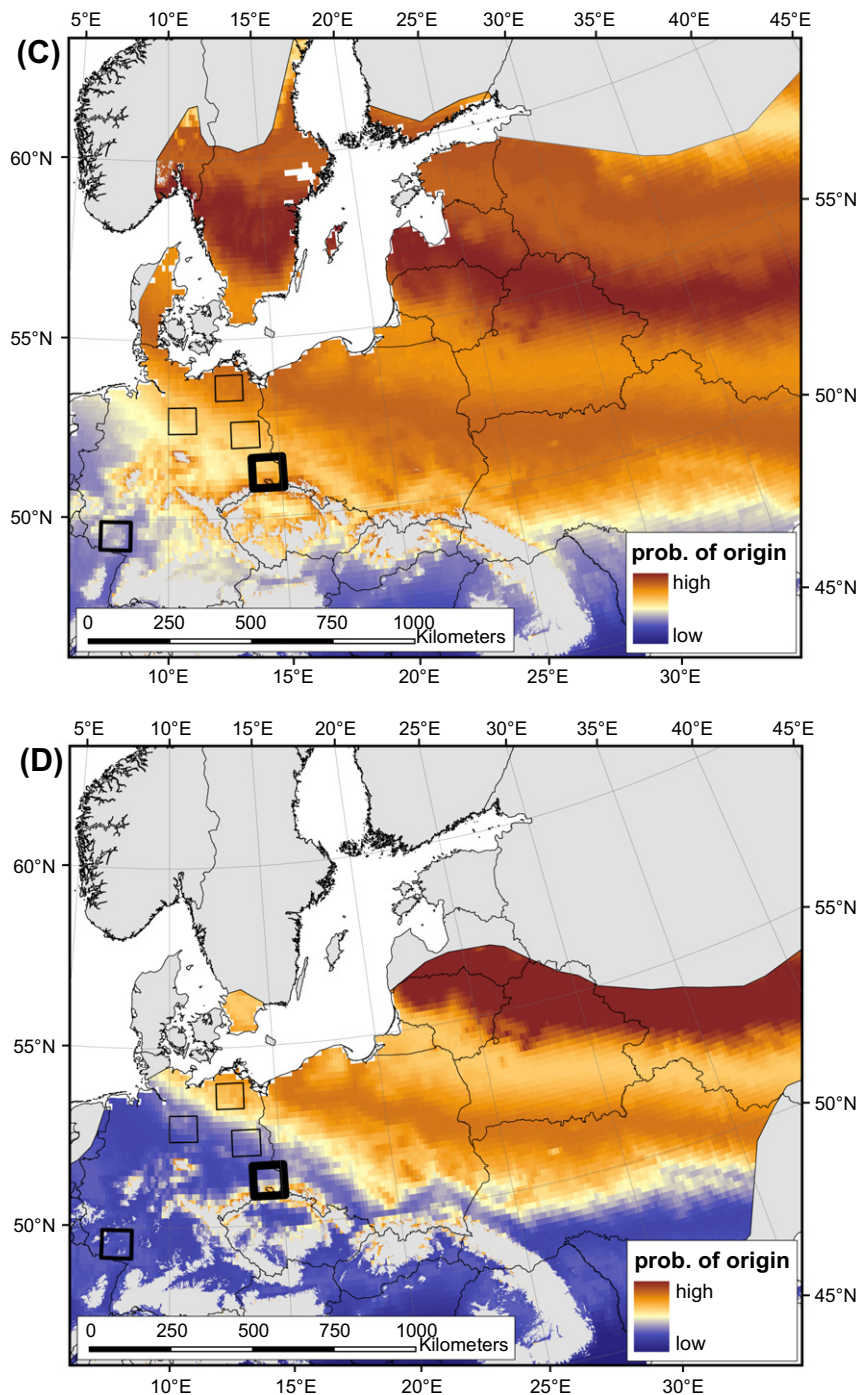


Fig. 2 (continued)

via, Baltic States or Belarus; Fig. 2C), and Leisler's bats (*N. leisleri*) most likely originated from the Baltic States or Belarus (Fig. 2D).

#### 4. Discussion

##### 4.1. Breeding provenance of bats killed by German windfarms

Recent studies have highlighted that significant numbers of bats are killed at North American and European wind farm facilities (Barclay et al., 2007; Kunz et al., 2007; Arnett et al., 2008; Rydell et al., 2010); a fact that already calls for immediate action accord-

ing to existing laws in many countries, for example those of the European Union (EU). Yet, the size and form of catchment areas from which killed bats originate from is completely unknown. This catchment area may be even larger than the scale for which legislation is effectual. Here, we used a stable isotope approach to assess the geographic provenance of bats killed by wind turbines in Germany. We found stable hydrogen isotope ratios of fur keratin ( $\delta^2H_h$ ) to vary largely among species, indicating that bats originated not only from local breeding populations but also from more distant populations. Fur keratin of *P. nathusii* exhibited the lowest enrichment in deuterium which suggests that these bats came from Northeastern Europe. Indeed, data from *P. nathusii* suggest

that killed bats originated from the northeastern border of their geographical distribution range, i.e. Estonia or Russia (Dietz et al., 2009). In contrast, individuals from the congeneric bat *P. pipistrellus* mostly originated from local populations in Germany. *N. leisleri* killed at German wind turbines also originated from northeastern populations, probably from Poland, Lithuania or Belarus. In both *Nyctalus* species,  $\delta^2\text{H}_h$  indicated a Northeastern core area as breeding provenance, yet the origin distribution of individuals was more even than in *P. nathusii*. In our wildlife forensic approach based on stable isotopes, we assumed that bats molted before migration; a pattern that has been confirmed for North American bats (Cryan et al., 2004). In the unlikely case that bats molted along the migratory route, our estimated breeding origins of bats would have been underestimated because  $\delta^2\text{H}_h$  would match with the stable isotope ratio of precipitation water from some place between breeding and hibernation site. Yet, the established data on migratory connectivity is consistent with the reported distances covered by the respective bat species during migration (Hutterer et al., 2005). Therefore, we feel confident that migratory bats carried the isotopic ratio of the breeding habitat where they molt before taking off for their migratory journey. In summary,  $\delta^2\text{H}_h$  of the studied species indicated that many bats killed at German wind farms may come from populations beyond the borders of Germany or even the EU. This calls for international regulations when wind farms are established throughout Eurasia, because for example populations of endangered migratory bats from outside the EU may suffer from the installation of wind farms in countries of the EU.

#### 4.2. Modeling the origin of bats based on $\delta^2\text{H}$ of fur keratin

Previously, studies on migratory bats were based either on capture–recapture of marked animals (e.g. Hutterer et al., 2005) or on genetic approaches (Petit and Mayer, 1999). Yet, finding a killed bat at a wind turbine that has been marked at some distant place with a forearm band is highly unlikely, given that banding efforts have been decreased over the last decades in most Northeastern countries from which bats could potentially originate from. Also, genetic studies revealed a lack of genetic structure in populations of migratory bats (e.g. *N. noctula*: Petit and Mayer, 1999; reviewed in Burland and Wilmer, 2001) and even in the studied sedentary species (*P. pipistrellus*: Bryja et al., 2009), rendering this approach as well impracticable for tracking the breeding provenance of the studied bats. The spatial stable isotope method is a relatively young and developing field (Hobson, 1999), and early applications have been replaced by approaches including more sophisticated error propagation models to overcome problems in the assignment of individuals to origins (Hobson et al., 2009). Since we were dealing with low sample sizes, we adapted the conservative approach by Hobson and colleagues (Hobson et al., 2009) by accounting for different error magnitudes associated with the estimation of population standard deviations. By this, we smoothed the probability surface that may otherwise have shown very distinct and sharp distribution edges, as indicated by the range of possible associations of bat hair values with the precipitation map. However, with a higher sample size, this method may even enable researchers to delineate origin hotspots for specific migratory routes, and may thus help in ameliorating our understanding of vertebrate migratory behavior. Including stable isotopes of more than one element (e.g. Popa-Lisseanu et al., 2012) may even help to delineate the geographic origin of migratory bats along an east–west axis and with a finer resolution. Also, we suggest collecting fur samples of sedentary bats in Northeastern Europe to optimize the predictive value of geospatial models. These approaches will provide crucial additional information that

may improve efforts in protecting endangered vertebrates with cryptic large-scale movements, such as bats.

#### 4.3. Conclusion

Our study demonstrates for the first time that wind turbines do not only kill bats from local populations but also from populations at far distance, i.e. not only bat populations in Germany are negatively affected by wind farms in Germany but also bat populations in Scandinavia, the Baltic countries, Belarus or Russia. Therefore, wind farms do not only influence populations in close-by areas, but also at distances of several hundreds of kilometers or even beyond one thousand kilometers. These results indicate the urgent need to develop and implement species and scale-specific conservation and monitoring approaches in countries of the EU; particularly also in countries adjacent to the EU that have not yet signed the Agreement on the Conservation of Populations of European Bats (EUROBATS). This agreement aims at the protection of bats over their entire migratory range. Since permits for the construction and operation of wind turbines are issued based on national regulations, it is timely to adopt these regulations to existing trans-boundary approaches (e.g. EU Habitats Directive 92/43/EEC of 21 May 1992) and also to recent findings about factors that may help in reducing mortality rates of bats at wind farms. For example, recent experiments point out that slightly altered cut-in speeds can significantly reduce bat-fatality rates at wind turbines while causing only little revenue losses (Baerwald et al., 2009).

#### Acknowledgments

Many thanks go to Karin Sörgel and Anja Luckner from the IZW Stable Isotope Laboratory for isotope analyses. We thank Jürgen Niedballa for digitizing the bat range maps and designing the figures and three anonymous reviewers for providing constructive comments.

#### References

- Arnett, E.B., Brown, K., Erickson, W.P., Fiedler, J.K., Hamilton, B.L., Henry, T.H., Jain, A., Johnson, G.D., Kerns, J., Koford, R.R., Nicholson, C.P., O'Connell, T.J., Piorkowski, M.D., Tankersley Jr., R.D., 2008. Patterns of fatality of bats at wind energy facilities in North America. *J. Wildlife Manage.* 72, 61–78.
- Baerwald, E.F., Edworthy, J., Holder, M., Barclay, R.M.R., 2009. A large-scale mitigation experiment to reduce bat fatalities at wind energy facilities. *J. Wildlife Manage.* 73, 1077–1081.
- Barclay, R.M.R., Baerwald, E.F., Gruver, J.C., 2007. Variation in bat and bird fatalities at wind energy facilities: assessing the effects of rotor size and tower height. *Can. J. Zool.* 85, 381–387.
- Barrios, L., Rodriguez, A., 2004. Behavioural and environmental correlates of soaring-bird mortality at an on-shore wind turbine. *J. Appl. Ecol.* 41, 72–81.
- Bowen, G.J., Wassenaar, L.I., Hobson, K.A., 2005. Global application of stable hydrogen and oxygen isotopes to wildlife forensics. *Oecologia* 143, 337–348.
- Bryja, K., Kanuch, P., Fornuskova, A., Bartonicka, T., Rehak, Z., 2009. Low population genetic structuring of two cryptic bat species suggest their migratory behaviour in continental Europe. *Biol. J. Linn. Soc.* 96, 103–114.
- Burland, T.M., Wilmer, J.W., 2001. Seeing in the dark: molecular approaches to the study of bat populations. *Biol. Rev.* 76, 389–409.
- Cryan, P.M., Bogan, M.A., Rye, R.O., Landis, G.P., Kester, C.L., 2004. Stable hydrogen isotope analysis of bat hair as evidence for seasonal molt and long-distance migration. *J. Mammal.* 85, 995–1001.
- Craig, H., 1961. Isotopic variations in meteoric waters. *Science* 133, 1702–1703.
- Dietz, C., von Helversen, O., Nill, D., 2009. Handbook of Bats of Europe and Northwest Africa. A & C Books.
- Erzberger, A., Popa-Lisseanu, A., Lehmann, G.U.C., Voigt, C.C., 2011. Potential and limits in detecting altitudinal movements of bats using stable hydrogen isotope ratios of fur keratin. *Acta Chiropterol.* 13, 431–438.
- Hobson, K.A., 1999. Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia* 120, 314–326.
- Hobson, K.A., Lormee, H., Van Wilgenburg, S.L., Wassenaar, L.I., Boutin, J.M., 2009. Stable isotopes ( $\delta\text{D}$ ) delineate the origins and migratory connectivity of harvested animals: the case of European woodpigeons. *J. Appl. Ecol.* 46, 572–581.

- Hutterer, R., Ivanova, T., Meyer-Cordes, C., Rodrigues, L., 2005. Bat migrations in Europe – a review of banding data and literature. *Naturschutz Biologie Vielfalt*, 28.
- Jones, K.E., Purvis, A., Gittleman, J.L., 2003. Biological correlates of extinction risk in bats. *Am. Nat.* 161, 601–614.
- Kunz, T.H., Arnett, E.B., Erickson, W.P., Hoar, A.R., Johson, G.D., Larkin, R.P., Strickland, M.D., Thresher, R.W., Tuttle, M.D., 2007. Ecological impacts of wind energy development on bats: questions, research needs, and hypotheses. *Front. Ecol. Environ.* 5, 315–324.
- Legendre, P., 2008. *lmodel2: Model II Regression*. R package version 1.6–3.
- Petit, E., Mayer, F., 1999. Male dispersal in the noctule bat (*Nyctalus noctula*): where are the limits? *Proc. Roy. Soc. Lond.: Biol. Sci.* 266, 1717–1722.
- Popa-Lisseanu, A.G., Soergel, K., Luckner, A., Wassenaar, L.I., Ibanez, C., Kramer-Schadt, S., Ciechanowski, M., Görföl, T., Niermann, I., Beuneux, G., Myslajek, R.W., Juste, J., Fonderflick, J., Kelm, D.H., Voigt, C.C., 2012. A triple isotope approach to predict breeding origins of European bats. *PLoS ONE* 7, e30388.
- R Development Core Team, 2009. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN: 3-900051-07-0. <<http://www.R-project.org>>.
- Rydell, J., Bach, L., Dubourg-Savage, M.-J., Green, M., Rodriguez, L., Hedenström, A., 2010. Bat mortality at wind turbines in northwestern Europe. *Acta Chiropterol.* 12, 261–274.