Ecological Applications, 26(3), 2016, pp. 771–783

Habitat use of migratory bats killed during autumn at wind turbines

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Abstract. The killing of large numbers of migratory bats at wind turbines is a pressing conservation problem. Even though avoidance and mitigation measures could benefit from a better knowledge of the species' migratory habits, we lack basic information about what habitats and corridors bats use during migration. We studied the isotopic niche dimensions of three bat species that are frequently killed at wind turbines in Germany: non-migratory *Pipistrellus pipistrellus*, mid-distance migratory *Nyctalus noctula*, and long-distance migratory *Pipistrellus nathusii*. We measured stable carbon and nitrogen isotope ratios ($\delta^{13}C$, $\delta^{15}N$) in five tissues that differed in isotopic retention time (fur, wing membrane tissue, muscle, liver, blood) to shed light on the species-specific habitat use during the autumn migration period using standard ellipse areas (SEA_c). Further, we used stable isotope ratios of non-exchangeable hydrogen (δ^2H_K) in fur keratin to assess the breeding origin of bats. We inferred from isotopic composition ($\delta^{13}C$, $\delta^{15}N$) of fur keratin that isotopic niche dimensions of *P. nathusii* was distinct from that of *N. noctula* and *P. pipistrellus*, probably because *P. nathusii* was using more aquatic habitats than the other two species. Isoscape origin models supported that traveled distances before dying at wind turbines was largest for *P. nathusii*, intermediate for *N. noctula*, and shortest for *P. pipistrellus*. Isotopic niche dimensions calculated for each sample type separately reflected the species' migratory behavior. *Pipistrellus pipistrellus* and *N. noctula* showed similar isotopic niche breadth across all tissue types, whereas SEA_c values of *P. nathusii* increased in tissues with slow turnaround time. Isotopic data suggested that *P. nathusii* consistently used aquatic habitats throughout the autumn period, whereas *N. noctula* showed a stronger association with terrestrial habitats during autumn compared to the pre-migration period.

Key words: aquatic habitats; bat fatalities; connectivity; conservation; migration; molt; policy management; terrestrial habitats.

Introduction

Over the past decades, energy production from renewable sources, such as wind and solar power, has gained an increasing momentum (DoE 2008, EU 2009, Geißler 2013), particularly in Central Europe where Denmark and Germany have the highest densities of on-shore wind turbines worldwide (Berkhout et al. 2014). However, recent studies have highlighted that wind energy production is associated with large numbers of bat fatalities (Rydell et al. 2010, Hayes 2013, Korner-Nievergelt et al. 2013, Lehnert et al. 2014, Voigt et al. 2015*a*). In central Europe, this conservation problem is exacerbated because major migratory routes of bats pass this area when moving seasonally between their north-eastern breeding areas (i.e., Fennoscandinavia, the Baltic countries, Belarus, and Russia) and their hibernation sites in southwestern Europe (i.e., Italy, Switzerland, France, and Spain; Pētersons 2004, Steffens et al. 2004, Hutterer et al. 2005). Thus, the current promotion of wind energy bears large potential for conflicts between environmental and conservation goals, the latter being defined by international legislation (EU Habitat Directive 92/32/CEE: Annexes II and IV) and conventions (UN convention for the protection of migratory species of wild animals dated Bonn 1979 and London 1991). Even though mitigation measures such as curtailment speeds are available (Baerwald et al. 2009, Arnett et al. 2011, Brinkmann et al. 2011), it is often unknown how effective they are because post-construction surveys are usually not commissioned (Voigt et al. 2015*a*). In addition, avoidance measures such as the banning of wind turbine constructions from sensitive places are rarely practiced in Europe (Voigt et al. 2015*a*). Here, we explored the breeding origin and isotopic ecology of bats killed during autumn at wind turbines in Germany to shed light on the distance traveled between summer habitats and sites of mortality and the foraging habitats used before and during migration. In our study, we use the term habitat in a relatively broad sense by

Manuscript received 15 April 2015; revised 6 August 2015; accepted 17 August 2015; final version received 16 September 2015. Corresponding Editor: D. Brunton.

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distinguishing only between two categories: habitats of terrestrial and limnic ecosystems. A detailed knowledge about habitats used during migration are highly relevant for defining areas in which wind turbine developments should be either avoided or carried out with particular caution.

We focused on three open-space foraging bat species that constitute more than 70% of the recorded carcasses found below German wind turbines (Rydell et al. 2010) and which vary in their migratory behavior: Local or short-distance migratory *Pipistrellus pipistrellus*, regional or mid-distance migratory *Nyctalus noctula*, and long-distance migratory *P. nathusii* (Pētersons 2004, Steffens et al. 2004, Hutterer et al. 2005). We inferred the location of summer residency of focal bats by analyzing the stable hydrogen isotope ratios of fur keratin (δ^2H_K). This so-called isoscape origin approach is possible because of large-scale gradients of δ^2H values in precipitation water (δ^2H_P) across continents (Hobson 1999, 2008, Bowen et al. 2005) and because stable isotopes from a bat's diet are assimilated into keratin when they molt at the place of summer residency (Cryan et al. 2004, Voigt et al. 2012*a,* 2014). Consequently, δ^2H_K values of keratin correlates positively with annual means of δ^2H_P for precipitation at the site of fur growth (Britzke et al. 2009, Popa-Lisseanu et al. 2012, Sullivan et al. 2012, Voigt et al. 2012*a,b,* Voigt et al. 2014, Baerwald et al. 2014). Since fur keratin is metabolically inert, δ^2H_K values do not change when bats start to migrate to their wintering sites. The isoscape origin method is especially suitable to delineate large-scale, i.e., continent-wide, migratory behavior (e.g., Bowen et al. 2005), yet only when a clear relationship between the animal's isotope ratio and that of precipitation water can be established. The isotopic map for precipitation water has a resolution of about 100 km^2 (20″ arcseconds), subsuming local differences in precipitation. Standard deviations of 5–10‰ are usually observed for mean δ^2H_K values of local non-migratory bats (Voigt et al. 2012*a,* 2014). Thus, differences in origins will only be detected beyond that level of uncertainty. The limitations to this approach are twofold in respect to mismatches on both axes. Firstly, precipitation values might be imprecise due to spatial interpolation of deuterium values in poorly sampled regions of the world, and secondly, unknown isotope effects within the species' food webs might lead to weak relationships between δ^2H values of precipitation and δ^2H_K values of animals (Bowen 2009, Britzke et al. 2009, Voigt et al. 2013, 2015*b*).

We refined our isotope approach by analyzing stable isotope ratios of three elements ($\delta^{13}C$, $\delta^{15}N$, δ^2H_K) and by studying several tissues within individuals. Our multiple-tissue approach takes advantage of the fact that migratory bats feed on insects while migrating (Voigt et al. 2012*b*). Therefore, migratory bats have an isotopic record of habitats in which they foraged. This isotopic record varies according to the tissue-specific isotopic retention time (Sponheimer et al. 2006, Martinez del Rio and Carleton 2012), i.e., stable isotope ratios of blood integrate over a bat's diet of past days and weeks, liver and muscle over that of several weeks, and wing membrane tissue over that of weeks or even months (Voigt et al. 2003, Míron et al. 2006). Lastly, fur keratin integrates over the period of molt (Cryan et al. 2004), which is most often finished in mid-summer in bats of the Northern hemisphere (Fraser et al. 2013). In *N. noctula* and *P. nathusii*, fur changes between late June/early July and mid-August (Heise 1982, Schmidt 1984, Ilyin 1990, Gebhard and Bogdanowicz 2004, Spitzenberger 2007), which suggests that these two species have new fur when migrating to their wintering sites in autumn. In order to test this for central European populations, we monitored the renewal of dorsal fur in a population of *P. nathusii* in Germany. We then tested several hypotheses with respect to habitats used by *P. pipistrellus*, *N. noctula*, and *P. nathusii* before and during migration. Firstly, we hypothesized that isotopic niches, as defined by the isospace of consumers in the corresponding isoscape of their environment (Martinez del Rio et al. 2009), should be typical for aquatic ecosystems in *P. nathusii* and typical for terrestrial ecosystems in *N. noctula* and *P. pipistrellus*, since previous studies suggested a relatively strong association of *P. nathusii* with ponds, lakes, bogs, swamps, and rivers (Heise 1982, Hackethal and Oldenburg 1984, Schmidt 1984, Vaughan 1997, Mackie and Racey 2007, Flaquer et al. 2009, Furmankiewicz and Kucharska 2009, Krüger et al. 2013), and of *N. noctula* and *P. pipistrellus* with agricultural land, parks, and woodlands (Racey and Swift 1985, Vaughan 1997, Verboom and Huitema 1997, Nicholls and Racey 2006, but see Furmankiewicz and Kucharska 2009). Accordingly, we predicted that isotopic niches of the pre-migration period should overlap between *N. noctula* and *P. pipistrellus*, but those of *P. nathusii* should be largely exclusive from the others (Voigt et al. 2015*b*). Secondly, we hypothesized that δ^2H_K values should match with the distance traveled by bats. Specifically, we predicted that δ^2H_K values of *P. pipistrellus* should be similar to those of local bats, δ^2H_K values of *N. noctula* and *P. nathusii* should be lower than those of *P. pipistrellus* owing to the longer distances traveled by these species. Thirdly, we hypothesized that the two migratory bat species use aquatic habitats such as rivers and lakes for navigation during migration as suggested by Furmankiewicz and Kucharska (2009), whereas non-migratory bats should use about the same habitats as during the breeding season. We made use of the fact that species-specific isotopic niches calculated for each tissue should vary according to the assumed isotopic retention time and thus provide information about the habitats used before and during migration. We formulated three predictions to test this hypothesis: (1) Isotopic niche dimensions remain similar across all studied tissues for *P. pipistrellus* but not for *N. noctula* and *P. nathusii*. This prediction is based on the expectation that mid- to long-distance migrants, such as *N. noctula* and *P. nathusii*, respectively, come from a larger geographical area, and thus isotopically more heterogeneous areas, than regional

P. pipistrellus (Voigt et al. 2012*a,b*). (2) $\delta^{15}N$ values of blood samples should be higher than corresponding values of fur keratin in *N. noctula* and *P. nathusii* if these species use more aquatic habitats during migration than during the pre-migration period. This prediction is based on the observation that $\delta^{15}N$ values of consumers in aquatic food webs are usually higher than those of terrestrial food webs, if aquatic food webs are affected by agricultural fertilizers (Voigt et al. 2015*b*). Lastly, (3) $\delta^{2}H_{K}$ values of individual bats should correlate negatively with $\delta^{15}N$ values of tissue with relatively fast turnaround time, e.g., blood, but not with those of slow turnaround time, e.g., wing membrane tissue, or fur keratin, if migratory bats use more aquatic ecosystems during than before the migration period.

Material and Methods

Evaluation of the molting period in a European migratory bat

During the breeding, post-breeding, and migration period, we first assessed the onset and end of the molting period in a European migratory bat by surveying a population of banded *P. nathusii* in about 200 artificial bat boxes that were set up in a pine forest in eastern Germany (Saxony-Anhalt). We defined the breeding period as the period when females reproduced and when individuals remained in the area where fur grew during the previous year. We use the term breeding period for the reason of simplicity, yet we acknowledge that not all bats were breeding. At the end of the breeding period, we collected small tufts of fur from the interscapular region of *P. nathusii*. Sample collection was performed between 29 June and 19 September 2012, covering the end of breeding in late June and the end of migration in late September. We revisited these bat boxes repeatedly in 2-week intervals and monitored the area from which fur was removed in case banded bats were encountered again. If the area from which we collected fur remained bare, we defined the period elapsed between fur collection and survey as belonging to the non-molting period. At the onset of spring migration (Meineke 2012), we checked for the presence of banded bats of the previous year (4 May, 10 May, 11 May 2013). This allowed us to evaluate if molting occurred early in the annual cycle, i.e., after hibernation and spring migration but before lactation.

Collection of fur from bats found dead below wind turbines

We collected tissue and fur samples from carcasses belonging to three species of bats, i.e., *P. pipistrellus*, *N. noctula*, and *P. nathusii*. Carcasses were found below wind turbines during commissioned carcass searches and deposited at authorized collections, namely at the "Vogelschutzwarte Buckow" of the federal ministry of environment of Brandenburg, the Natural Science Collections of the University Halle-Wittenberg, and the Natural History Museum of Braunschweig. Carcasses were found between 2008 and 2012 during the autumn period at sites indicated in Appendix S1: Fig. S1. We did not collect samples from any severely or mildly decomposed carcasses, since we assumed that the degeneration of organic tissue would alter isotopic ratios. We identified the sex of each carcass, but failed to recognize the age in most individuals. Thus, we did not distinguish between juvenile and adult bats in our analysis. From each carcass, we cut a tuft of fur from the back, we took two biopsy punches from the wing membrane tissue, we cut a small piece of the pectoral muscle, and we collected a piece of liver and some coagulated blood from the heart caverns. All samples were transferred into plastic vials, immediately transported to the Leibniz Institute for Zoo and Wildlife Research to avoid further decomposition and dried to constant mass in a drying oven at 50°C.

Stable isotope analyses

All fur samples were analyzed for stable carbon, nitrogen, and hydrogen isotopes, whereas organic tissues were only analyzed for $\delta^{13}C$ and $\delta^{15}N$. Analysis of stable isotope ratios followed the protocol according to Popa-Lisseanu et al. (2012) and Voigt et al. (2012*a,b*). Details are provided in Appendix S1.

Statistical comparison of isotopic values across species

All statistical analyses were performed with R 3.0.1 (R Core Team 2013) if not stated otherwise, using a level of significance of 0.05. All parameters are presented as mean ± 1 standard deviation. For isotopic data obtained from bat carcasses at wind turbines, we tested if stable isotope ratios differ between species and sex, using a two-way crossed analysis of similarity with factors species and sex (ANOSIM; Primer 6, version 6-1-15, Primer-E, Ivybridge, UK). In case of significant differences among factor categories, we tested for differences among dyads. We then calculated and plotted isotopic standard ellipse areas (SEA measured in $‰^2$) for $\delta^{13}C$ and $\delta^{15}N$ values of fur keratin using the SIBER routine (Jackson et al. 2011, Parnell and Jackson 2011) as part of the SIAR and CAR package in R (version 3.0.1; R Core Team 2013). SEA values were corrected for small sample size (SEA_c measured in $‰^2$) using "Stable Isotope Bayesian Ellipses in R" (SIBER; Jackson et al. 2011) from the "SIAR package, version 4.2, in R (R Core Team 2013). We defined the 95% confidence intervals of these niches as the boundaries of species' isotopic niches at our study site (see Jackson et al. 2012). We then used 1000 parametric bootstraps to create Bayesian estimates of SEA_c (SEA.B), which allowed calculations of diet niche overlaps by comparing 95% confidence intervals. We defined the 95% confidence intervals of the Bayesian standard ellipses as the boundaries of species' isotopic niches (Jackson et al. 2012). Then, we estimated the

overlap of SEA.B dimensions across species by looking at the extent at which ellipses overlapped. The percentage overlap of SEA.B ranged from 0 to 100% for each species, with values closer to 100% suggesting complete isotopic overlap and implying that species occupied an identical isotopic niche.

Isoscape origin model

To predict the breeding origin of *N. noctula*, we followed the approach as outlined in Voigt et al. (2012*a*, 2014*)*. Briefly, we used δ^2H_K values of non-migratory species (n = 178 individuals of various species as reported in Voigt et al. [2012*a,b*] for bats of the genus *Pipistrellus* and n = 217 individuals for bats of the genus *Nyctalus* as reported in Voigt et al. [2014]) captured in Europe and mapped δ^2H_P values of mean annual precipitation (Bowen et al. 2005) using a reduced major axis regression to account for errors in both measures (SMA in package "lmodel2"; Legendre 2008). For one of the two species with a predominant diet of terrestrial insects, i.e., *N. noctula*, we used the reduced major axis (RMA) regression equation from Voigt et al. (2014), $\delta^2H_P = 4.03 + 0.73 \times \delta^2H_K$, and for the other species, *P. pipistrellus* and *P. nathusii*, we used Voigt et al. (2012*a*), $\delta^2H_P = 5.8 + 0.79 \times \delta^2H_K$. Associated uncertainty within the same sampling locations stemming from analytical error, intra-population differences between non-migratory individuals, and error of the δ^2H_P values of precipitation of the isoscape was modeled by using the δ^2H_K values of fur standard deviations (σ_i) of the known origin bat populations used in the regression model as error estimate, with samples at location $i \geq 3$. According to Voigt et al. (2012*a*, 2014), we fitted a gamma distribution Γ to σ_i using maximum likelihood (package MASS; Venables and Ripley 2002). For *P. pipistrellus*, and *P. nathusii* the shape of this function was k = 5.85 and the scale was θ = 1.07, leading to a standard deviation of around ±5.2 (maximum of density function; Voigt et al. 2012*a,b*). For *N. noctula* the shape of this function was k = 3.93 and the scale was h = 1.97, leading to a standard deviations of around ±5.7 (Voigt et al. 2014).

Statistical evaluation of the differential use of habitats before and during migration

We calculated isotopic ellipses for $\delta^{13}C$ and $\delta^{15}N$ values for each tissue and species separately as described before. We compared SEA_B among tissues of each species as described before. To test if bats would use more terrestrial or aquatic ecosystems during autumn, we compared $\delta^{15}N$ values of blood, representing the most

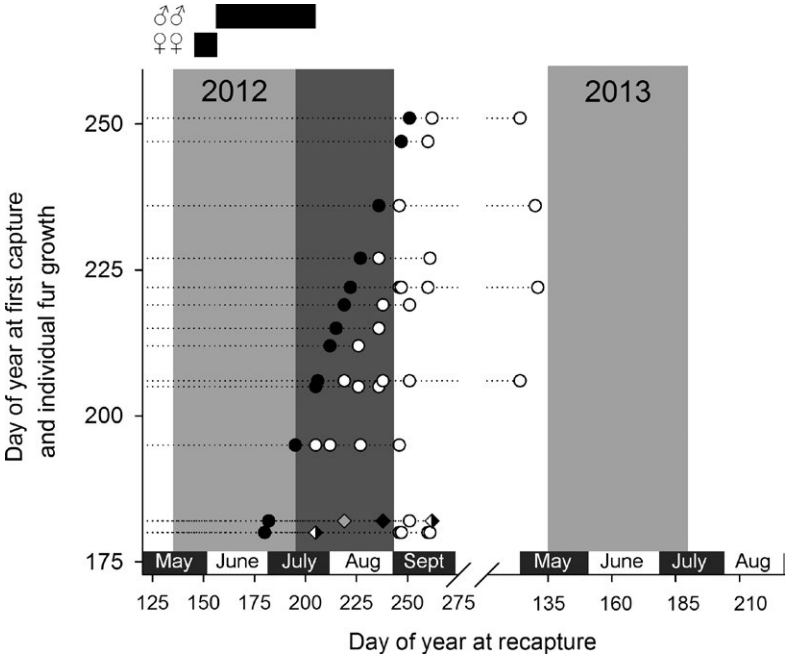

FIG. 1. Day of year at first capture (solid circles) of *Pipistrellus nathusii* at two German sites monitored between 29 June (day 179) and 19 September 2012 (day 261) and between 4 and 11 May 2013 (day 123 and day 130) in relation to day of year at recapture (no regrown fur, open circles). Fur growth may occur after 1 July in some (n = 2, male) individuals (fur growth progressing, gray diamond; fully regrown hair, black diamond). Semi-filled diamonds represent days of recapture when a proportion of individuals showed complete fur renewal, whereas others did not show any fur growth. Dotted lines indicate data for individuals with the same day of first capture. The two male individuals which continued fur growth (gray diamonds) finished molting mid-August. The light gray area indicates the pre-molting or molting period and the dark gray area the post-molting period. Black bars on top of the graph illustrate the assumed sex-specific time of fur growth onset based on own observations and Ilyin (1990).

immediate time before the mortality event, and $\delta^{15}N$ values of fur keratin, representing the isotopic composition of the summer habitat, using paired Student's *t* tests. Further, to test for gradual changes in isotopic compositions among tissues of varying isotopic retention time, we calculated spearman rank indices for correlations between $\delta^{2}H_{K}$ and tissue-specific values of $\delta^{13}C$ and $\delta^{15}N$ for each species separately.

Results

Evaluation of the molting period in P. nathusii

In total, we removed the fur from the interscapular region of 31 *P. nathusii* (27 males, four females). One male from which fur was removed from the interscapular region at the end of June (29 June 2012) showed fully regrown hair less than 25 d later (24 July 2012). Fur growth of three more males sampled around the same date (29 June and 1 July) reached 80–90% of hair length compared to surrounding dorsal fur on 7 August, but had completed fur growth during the secnd half of the month (26 August). These examples indicate that molting may occur after 1 July in some males (Fig. 1). However, two bats from which we collected fur on the 29 June 2012 showed no signs of fur renewal, indicating that the onset and end of molting period may vary among individuals. None of the bats from which fur was removed after the 13 July 2012 showed signs of fur growth several weeks later, suggesting that molt was completed before this date (Fig. 1). In May 2013 (4 May, 10 May, 11 May), we recaptured four individuals from which we removed fur between 25 July and 8 September 2012. None of these individuals showed signs of regrown fur in the interscapular region, suggesting that fur renewal ended in mid-July and that molting period has not yet started in early May of the following year.

Comparison of isotopic niches among species

We collected samples from 11 *Pipistrellus pipistrellus* (four males/seven females), 38 *Nyctalus noctula* (17/21), and 19 *P. nathusii* (6/13). Raw isotopic data is presented in Appendix S1: Table S1). A comparison of $\delta^{13}C$ and $\delta^{15}N$ values based on a two-way crossed ANOSIM revealed that the isotopic composition did not differ between the sexes ($r = -0.049$, $P = 0.893$), but among species (global $r = 0.262$, $P < 0.001$). We found significant differences between *P. nathusii* and *N. noctula* ($r = 0.406$, $P < 0.001$), but not between *P. pipistrellus* and the other two species, *N. noctula* ($r = 0.021$, $P = 0.362$) and *P. nathusii* ($r = 0.115$, $P = 0.114$). During the pre-migration period, SEA_c of *N. noctula* was larger than that of *P. pipistrellus* ($P = 0.018$), but smaller than that of *P. nathusii* ($P = 0.021$; Fig. 2). SEA.B of *P. pipistrellus*

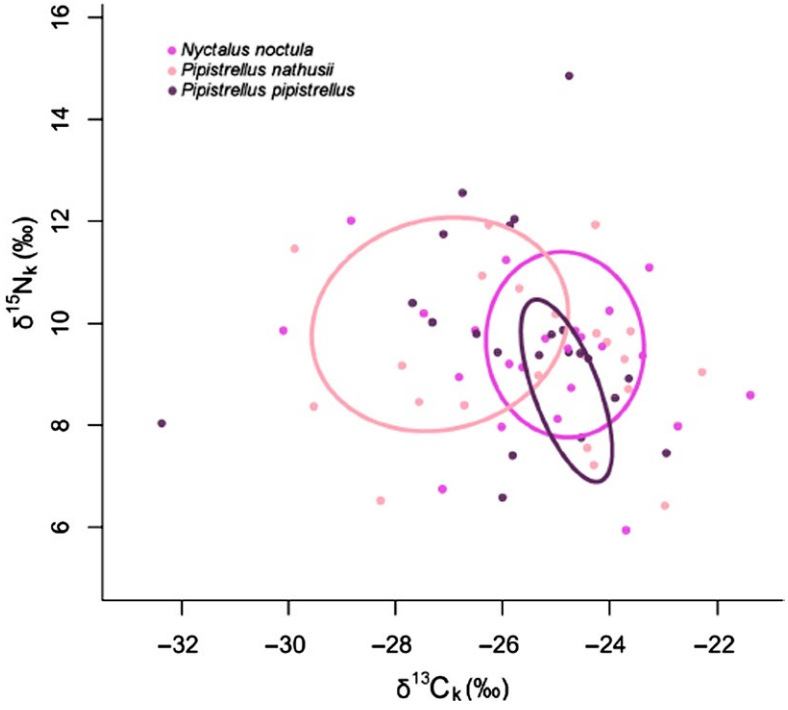

Fig. 2. $\delta^{15}N_{K}$ (‰) in relation to $\delta^{13}C_{K}$ values (‰) of fur keratin for individuals of the three study species (circles represent individual values colored according to the legend): Non-migratory *P. pipistrellus*, mid-distance migrating *N. noctula* (about 200–1600 km one-way; Steffens et al. 2004, Hutterer et al. 2005, Lehnert et al. 2013), and long-distance migrating *P. nathusii* (about 500–1900 km; Steffens et al. 2004, Hutterer et al. 2005) Standard ellipses were calculated as a proxy for the isotopic niches of bats before migration.

TABLE 1. Species-specific standard ellipse areas (SEA, SEA_c, and SEA.B; ‰^{2}) and dyadic comparisons of percentaged ellipse overlaps.

Species	Isotopic niche sizes			Overlap of isotopic niches (%)		
	SEA	SEA_c	SEA.B	*N. noctula*	*P. nathusii*	*P. pipistrellus*
P. pipistrellus	3.26	3.63	4.02	33.9	6.5	…
N. noctula	8.21	8.44	8.18	…	20.3	79.0
P. nathusii	14.83	15.70	14.41	37.7	…	28.0

Notes: As an example of dyadic comparisons of percentaged ellipse overlaps, 79.0% of SEA_c of *Pipistrellus pipistrellus* overlaps with that of *Nyctalus noctula*, yet only 33.9% of SEA_c of *N. noctula* overlaps with that of *P. pipistrellus*.

was also smaller than that of *P. nathusii* ($P < 0.001$). Also, SEA.B of *P. pipistrellus* and *N. noctula* were largely overlapping (Table 1). We observed the least percentage overlap of SEA.B between *P. nathusii* and the other two species (Table 1, Fig. 2).

Estimated geographical location of summer habitats

δ^2H_K values varied among species (one-way ANOVA, $F_{64,2} = 14.9$, $P < 0.001$). A post-hoc Tukey–Kramer test revealed that δ^2H_K values differed between *N. noctula* and *P. pipistrellus* by −17.9‰ ($q = 17.9$, $P < 0.001$) and between *P. nathusii* and *P. pipistrellus* by −25.7‰ ($q = 10.1$, $P < 0.001$). However, δ^2H_K values did not differ between *N. noctula* and *P. nathusii* ($q = 7.85$, $P < 0.05$). δ^2H_K values averaged −82.9 ± 18.0‰ for *P. pipistrellus*, −100.8 ± 10.5‰ for *N. noctula*, and −108.7 ± 12.6 ‰ for *P. nathusii*. Isoscape origin models suggested that the locations of summer residency were mostly in Germany for *P. pipistrellus* (Fig. 3A), in southern Sweden, northern Poland, Lithuania, Latvia, and Belarus for *N. noctula* (Fig. 3B), and in Fennoscandinavia, the Baltic countries, Belarus, and Russia for *P. nathusii* (Fig. 3C).

Differential use of habitats before and during migration

In *P. pipistrellus*, we found significant differences in SEA_c between liver, a tissue with relatively fast isotopic turnaround, and fur, representing the isotopic niche of the bats' summer residency (Fig. 4A, Table 2). We also observed a non-significant trend for differences in SEA_c between blood and fur keratin, and also between liver and wing membrane tissue. In *N. noctula*, we did not observe any differences in SEA_c among tissues (Fig. 4B, Table 2), whereas in *P. nathusii*, we detected larger SEA_c in fur compared to liver and muscle tissue, which have fast and medium isotopic turnaround times, respectively (Fig. 4C, Table 2). Also, we observed a trend for significant differences in SEA_c between fur and blood and between liver and wing membrane tissue in *P. nathusii*.

We observed no difference in $\delta^{15}N$ values between blood and fur samples in *P. pipistrellus* (paired *t* test, $t_{10} = 0.2$, $P = 0.879$; Fig. 5A), and *P. nathusii* (paired *t* test, $t_{18} = 0.9$, $P = 0.385$; Fig. 5C), but significantly lower $\delta^{15}N$ values in blood compared with fur samples in *N. noctula* (paired *t* test, $t_{37} = 9.1$, $P < 0.001$; Fig. 5B). When using δ^2H_K values as a proxy for the distance traveled between the summer habitat, i.e., the site of fur growth and the site of fatality, we observed no correlations between δ^2H_K values and $\delta^{13}C$ and $\delta^{15}N$ values in *P. pipistrellus* (Table 3), but two positive correlations in *N. noctula* ($\delta^2H_K/\delta^{13}C$ values of muscle and fur) and six correlations, four positive ($\delta^2H_K/\delta^{13}C$ values of blood, liver, wing membrane tissue, and fur) and two negative ($\delta^2H_K/\delta^{15}N$ values of wing membrane tissue and fur) in *P. nathusii* (Table 3).

DISCUSSION

We studied the isotopic ecology of bats that were killed during autumn by wind turbines in Germany to shed light on the habitats used by these bats before they died. Specifically, we tested for differences in isotopic niche dimensions in relation to their movement ecology and feeding habits in three focal species: local or short-migratory *Pipistrellus pipistrellus*, mid-distance migratory *N. noctula*, and long-distance migratory *P. nathusii*. We expected to find differences in δ^2H_K values according to the expected distance that bat species traveled between their places of summer residency where they molted and the sites of mortality. Finally, we expected to find differences in isotopic compositions of tissues with fast and slow isotopic turnaround times that could inform about the relative association of bats with aquatic or terrestrial habitats along their migratory route (Voigt et al. 2015*b*).

Evaluation of the molting period and regression model for P. nathusii

It was important for our isoscape origin model that δ^2H_F values accurately reflect the variation in δ^2H_P values of the breeding locations. Therefore, we studied the molting period of *P. nathusii*. Our monitoring confirmed earlier observations from German and Russian populations that showed an end of the molting period between mid-July and early August (Heise 1982, Hackethal and Oldenburg 1984, Schmidt 1984, Ilyin 1990). Our data also suggest that molting does not start before mid-May in *P. nathusii* in German populations;

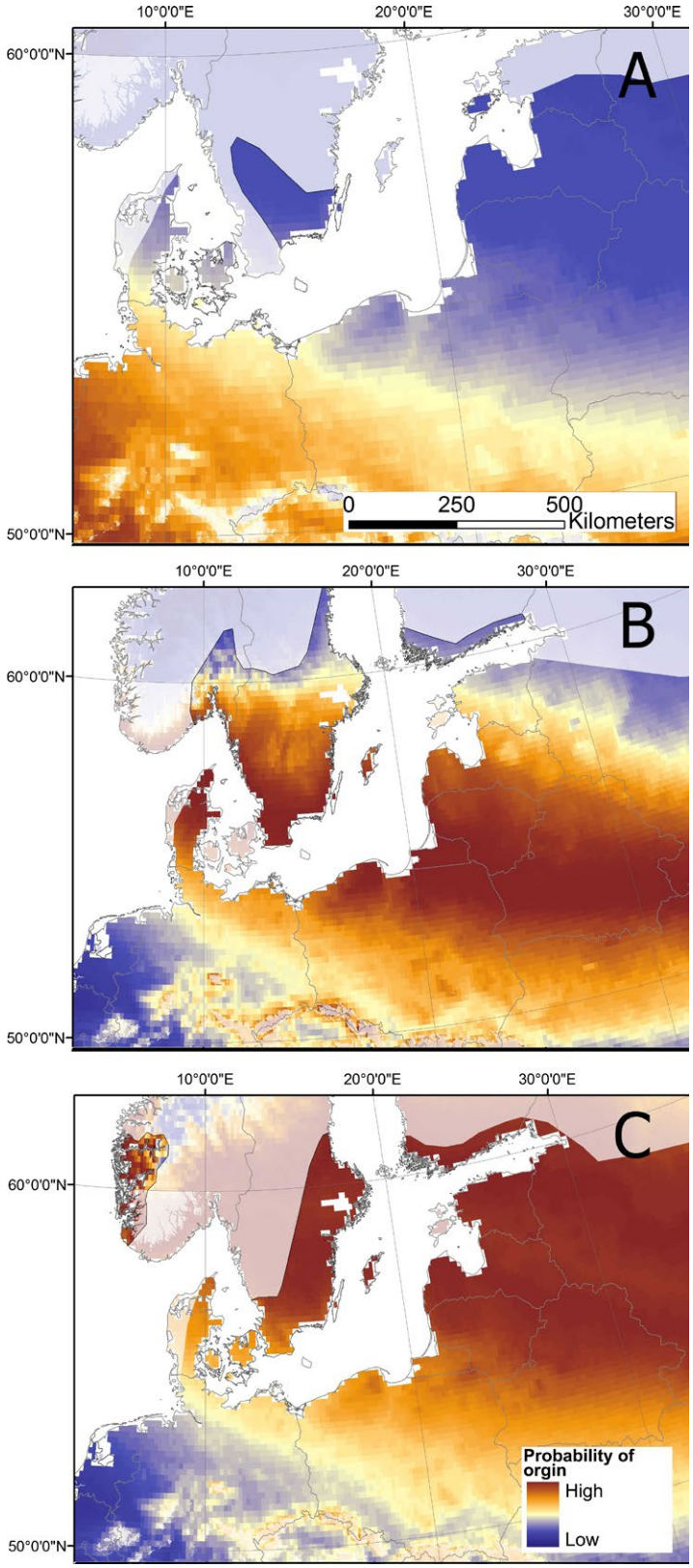

FIG. 3. Probability maps for the summer origin of all studied (A) *Pipistrellus pipistrellus*, (B) *Nyctalus noctula*, and (C) *Pipistrellus nathusii*. Areas outside the distribution range (IUCN) as well as elevation >500 m a.s.l. are shaded.

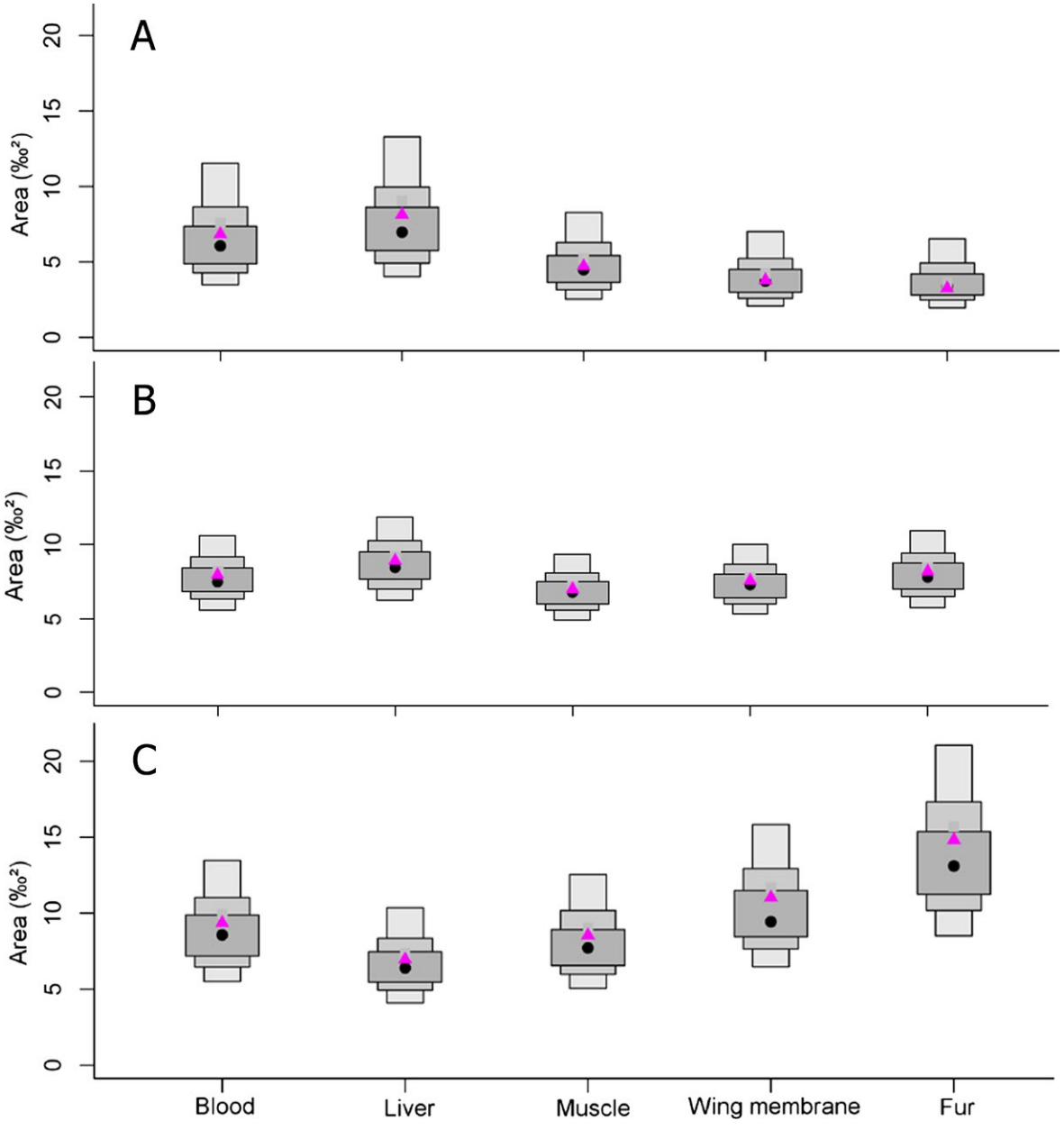

FIG. 4. Standard ellipse areas (SEA; ‰^{2}) for (A) *Pipistrellus pipistrellus*, (B) *Nyctalus noculta*, and (C) *Pipistrellus nathusii* calculated for $\delta^{13}C$ and $\delta^{15}N$ values of five sample types separately (sorted according to decreasing turnaround time). Gray boxes indicate the 50%, 75%, and 95% credibility intervals (dark to light gray) of SEA.B; black dots represent the mode and pink triangles SEA_c.

yet we could not define the exact onset of molting for bats of our German study site, probably because the onset of molting varies largely among individuals. Further, due to animal welfare considerations, we had to refrain from a tight monitoring during the period of late gestation and lactation in May and June. Based on our findings and those reported in the literature, we extrapolated the assumed time of fur growth onset in *P. nathusii* for the non-migratory period in 2012. Since females require about 50–55 d to complete molt (Ilyin 1990), individuals captured by 13 July 2012 most likely started fur renewal before 25 May. Our own observations indicate a higher degree of variability in male molting duration (25–50 d). Due to this difference, assumed time of male fur growth onset spans over a longer period, but it may start later than in females. Thus, we inferred that molting started during the second half of May (later than 10 May), which is consistent with the data from recaptures in 2013. We defined the end of the non-migratory period as approximately 15 July. Banding data from

TABLE 2. Pair-wise comparison of SEA_c across tissues for each of the three study species.

Tissue	*P. pipistrellus*				*N. noctula*				*P. nathusii*			
	Liver	Muscle	Wing	Fur	Liver	Muscle	Wing	Fur	Liver	Muscle	Wing	Fur
Blood	0.361	0.774	0.885	0.089	0.317	0.711	0.581	0.457	0.813	0.609	0.313	0.081
Liver	…	0.127	0.063	**0.040**	…	0.849	0.761	0.637	…	0.269	0.085	**0.012**
Muscle	…	…	0.670	0.725	…	…	0.364	0.246	…	…	0.222	**0.048**
Wing	…	…	–	0.563	…	…	–	0.365	…	…	…	0.184

Notes: Numbers depict P values and $P < 0.05$ are highlighted in bold.

several sites across Europe suggested that *P. nathusii* starts to migrate after this date (Heise 1982, Schmidt 1984).

Comparison of isotopic niches among species

Across all tissues measured, isotopic niches of *P. nathusii* and *N. noctula* were different in breadth, but the isotopic niche of *P. pipistrellus* were not different from those of the other two species, probably because the isotopic niche of *P. pipistrellus* was intermediate between the other two based on the isotopic composition of all tissues. We refined our isotopic niche approach by focusing on the stable isotope ratios in fur keratin, which informs about habitats used during the molting period in summer, and by calculating standard ellipse areas (SEA_c) for all three species. For the time of summer residency, isotopic niches of *P. pipistrellus* and *N. noctula* were largely overlapping, yet that of *P. nathusii* was separate from those of the other two species. Lower $\delta^{13}C$ values in fur keratin of *P. nathusii* suggested that this species is generally more associated with aquatic ecosystems during the period of summer residency than *P. pipistrellus* and *N. noctula*, because aquatic ecosystems are known for their lower enrichment in ^{13}C compared with terrestrial ecosystems (Farquhar et al. 1989). Yet, such a difference was not apparent for $\delta^{15}N$ values, although a previous studies suggested higher $\delta^{15}N$ values but not $\delta^{13}C$ values for bats with a diet of insects with an aquatic larval stages compared with species with a purely terrestrial diet (Voigt et al. 2015*b*). However, the isotopic evidence of a relatively strong association of *P. nathusii* with aquatic ecosystems matches with findings from earlier studies on the foraging behavior and diet of this species (Heise 1982, Hackethal and Oldenburg 1984, Schmidt 1984, Flaquer et al. 2009, Krüger et al. 2013). The observed isotopic niches of *N. noctula* and *P. pipistrellus* are largely consistent with previous studies that indicated a primary association of these two species with terrestrial habitats (Racey and Swift 1985, Vaughan 1997, Verboom and Huitema 1997, Davidson-Watts and Jones 2006, Nicholls and Racey 2006). Isotopic niches of *N. noctula* and *P. pipistrellus* were also largely overlapping suggesting that these two species forage in overlapping habitats or habitats that are isotopically similar. This notion is supported by Kelm et al. (2014) who showed for our study area that both species shared, at least partially, the same habitat, yet *Pipistrellus pipistrellus* was more associated with forest edges than *N. noctula*.

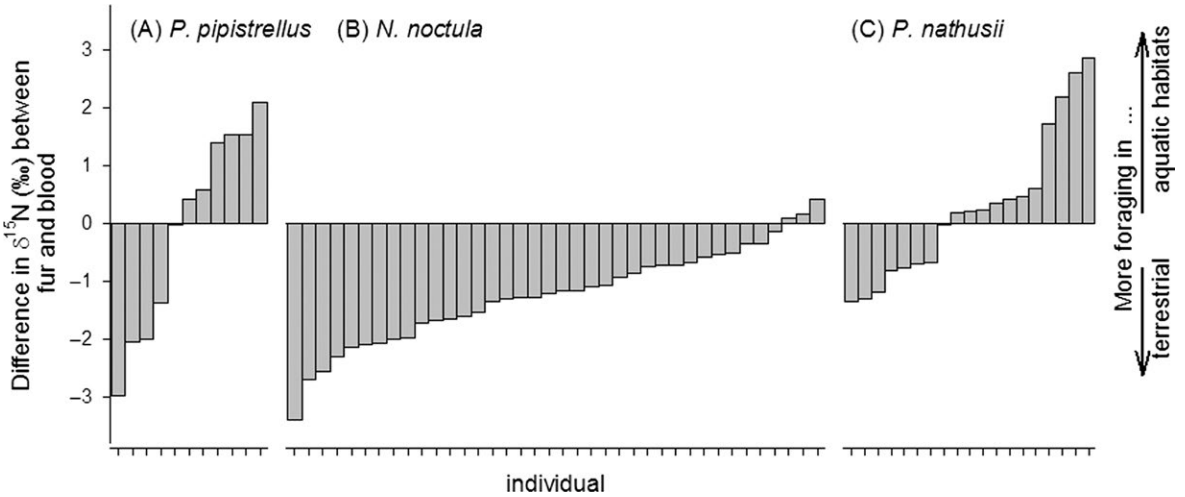

FIG. 5. Difference in $\delta^{15}N$ values (‰) between blood and fur keratin in individual bats of the three study species, sorted according to increasing enrichment in ^{15}N in blood in relation to fur keratin.

TABLE 3. Spearman rank index (r_s) for the correlation between δ^2H values and tissue-specific $\delta^{13}C$ and $\delta^{15}N$ values for each of the three study species.

	$\delta^{13}C$					$\delta^{15}N$				
Species	Blood	Liver	Muscle	Wing	Fur	Blood	Liver	Muscle	Wing	Fur
P. pip.	$r_s = 0.346$,	$r_s = 0.353$,	$r_s = 0.178$,	$r_s = 0.182$,	$r_s = 0.168$,	$r_s = -0.172$,	$r_s = -0.238$,	$r_s = -0.146$,	$r_s = -0.102$,	$r_s = -0.070$,
$n = 11$	$t = 1.105$,	$t = 1.133$,	$T = 0.542$,	$T = 0.555$,	$T = 0.513$,	$T = -0.523$,	$T = -0.734$,	$T = -0.444$,	$T = -0.307$,	$T = -0.211$,
	$P = 0.298$	$P = 0.286$	$P = 0.601$	$P = 0.592$	$P = 0.620$	$P = 0.614$	$P = 0.481$	$P = 0.668$	$P = 0.766$	$P = 0.838$
N. noct.	$r_s = 0.331$,	$r_s = 0.294$,	$r_s = \mathbf{0.36}$,	$r_s = 0.31$,	$r_s = \mathbf{0.40}$,	$r_s = -0.23$,	$r_s = -0.18$,	$r_s = -0.18$,	$r_s = -0.13$,	$r_s = -0.13$,
$n = 38$	$t = 1.9$,	$t = 1.8$,	$T = \mathbf{2.31}$	$T = 1.95$,	$T = \mathbf{2.57}$,	$T = -1.37$,	$T = -1.06$,	$T = -1.08$,	$T = -0.78$,	$T = -0.75$,
	$P = 0.066$	$P = 0.077$	$P = \mathbf{0.027}$	$P = 0.059$	$P = \mathbf{0.015}$	$P = 0.181$	$P = 0.297$	$P = 0.287$	$P = 0.441$	$P = 0.461$
P. nath.	$r_s = \mathbf{0.58}$,	$r_s = \mathbf{0.684}$	$r_s = 0.440$,	$r_s = \mathbf{0.613}$,	$r_s = \mathbf{0.533}$,	$r_s = -0.363$	$r_s = -0.286$,	$r_s = -0.374$,	$r_s = \mathbf{-0.521}$,	$r_s = \mathbf{-0.537}$,
$n = 19$	$t = \mathbf{2.936}$,	$t = \mathbf{3.869}$,	$T = 2.021$,	$T = \mathbf{3.202}$	$t = \mathbf{2.594}$,	$T = -1.604$,	$T = -1.230$,	$T = -1.661$,	$T = \mathbf{-2.516}$,	$T = \mathbf{-2.623}$,
	$P = \mathbf{0.009}$	$P = \mathbf{0.001}$	$P = 0.059$	$P = \mathbf{0.005}$	$P = \mathbf{0.019}$	$P = 0.127$	$P = 0.235$	$P = 0.115$	$P = \mathbf{0.022}$	$P = \mathbf{0.018}$

Note: Significant values are highlighed in bold.

Estimated geographical location of summer habitats

We estimated the location of summer residency of bats killed at wind turbines using an isoscape origin model as outlined by Voigt et al. (2012*a,* 2014). Estimated places where bats stayed before the onset of migration, i.e., during the time of molt, differed between the three species. The inferred distances that bats travelled between the sites of origin and the places of mortality were consistent with those of banding studies (Pētersons 2004, Steffens et al. 2004, Hutterer et al. 2005). *Pipistrellus pipistrellus* were of local origin, probably from populations adjacent to the wind turbines where bats were killed and from more western populations, *N. noctula* originated from a relatively large catchment area that included southern Sweden, northern Poland, Lithuania, and Belarus, and *P. nathusii* came from places as far as Fennoscandinavia, the Baltic countries, Belarus, and Russia. However, since δ^2H_K values might be lower in *P. nathusii* foraging in aquatic habitats than in other species that forage predominantly or exclusively in a terrestrial diet, our spatial modeling has to be treated with caution (Voigt et al. 2015*b*). Relatively lower δ^2H_K values in *P. nathusii* might lead to an overestimation of the traveled distances, i.e., bats might come from breeding areas further to the South than predicted by our model. Overall, the estimated place of summer residency of *P. nathusii* was consistent with previous studies using the same methodological approach (Voigt et al. 2012*a,* 2014, Lehnert et al. 2014) and also consistent with independent banding studies (Pētersons 2004, Steffens et al. 2004, Hutterer et al. 2005). Our current data confirms that the catchment area of bats dying at German wind turbines is covering large areas of northeastern Europe.

Differential use of habitats before and during migration

We estimated isotopic niche dimensions for each tissue and species by calculating tissue-specific SEA_c, assuming that SEA_c would differ between tissues with different isotopic turnaround times if bats move between isotopically distinct habitats during autumn, e.g., along their migratory route from the summer habitats to the sites of mortality in case of migratory bats. In contrast to our expectation, we found smaller SEA_c in liver compared with those of fur in *P. pipistrellus*. Liver tissue is assumed to have a relatively fast isotopic turnaround time, whereas fur keratin integrates over the period of molt. Possibly this pattern is associated with large home ranges of pipistrelle bats when maternity colonies dissolve after reproduction and when both sexes engage in swarming behavior and mating during autumn (Parsons et al. 2003). In *N. noctula*, none of the pair-wise comparisons of SEA_c proved to be significant, suggesting that the isotopic niche dimensions of *N. noctula* remain constant, albeit variable between the molting time in late summer and the autumn period. In *P. nathusii*, isotopic niches estimated based on the isotopic composition of fur

material were significantly larger compared to those derived from liver and muscle. This pattern is consistent with the observation of relatively large geographical catchment areas of *P. nathusii* that die at wind turbines in Germany (Voigt et al. 2012*a*). Accordingly, *P. nathusii* found dead below wind turbines in Germany may originate from areas that are isotopically heterogenous and this may translate into a larger variation of isotopic values in fur keratin compared with that of liver and muscular tissue, two tissues that likely incorporate isotopes from areas closer to the site of mortality. Based on the same argument, we would have also expected a difference between isotopic niches between blood and fur, yet we could not find such a difference. Thus, the observed patterns of tissue-specific SEA_c values are partly but not completely consistent with our expectation.

Further, we found no differences in $\delta^{15}N$ values between blood and fur values in the two *Pipistrellus* species, which suggests that *P. pipistrellus* and *P. nathusii* did not change their relative association with terrestrial and aquatic habitats when having moved during autumn from the sites where they molted to the sites of mortality. Thus, *P. nathusii* used aquatic habitats as often during migration as before migration, which confirms observations by Furmankiewicz and Kucharska (2009) who recorded a high density of *P. nathusii* along a large river during the autumn migration period. Thus, rivers, ponds, and lakes appear to be important for this species when migrating. In *N. noctula*, we observed a stronger association with terrestrial habitats during the migration period compared to the time of molt in late summer. Indeed, our isotopic data suggest that *N. noctula* may have migrated independently of aquatic landscape structures such as rivers and lakes, which contrasts with the findings of Furmankiewicz and Kucharska (2009). However, the study by Furmankiewicz and Kucharska (2009) only monitored bat activity at a riparian habitat without any control sites at non-aquatic habitats.

Our approach may have been hampered by general differences in trophic discrimination between fur and blood. Yet, we assume that such differences should be similar among the studied species and therefore should not be responsible for the observed differences between the two *Pipistrellus* species and *N. noctula*. Lastly, in *P. nathusii* we observed negative correlations between $\delta^{2}H_K$ values of bats and $\delta^{15}N$ values of blood and liver, i.e., *Nathusius* bats that originated further from the north showed higher $\delta^{15}N$ values. Since there is no indication of a gradient of $\delta^{15}N$ values across ecosystems of the European continent (Pardo and Nadelhoffer 2010), we speculate that this negative correlation may be explained by northern populations of *P. nathusii* foraging in more eutrophicated aquatic habitats than southern populations. By doing so, northern populations would benefit form a higher productivity in eutrophicated aquatic habitats in a colder environment. We also observed significant positive correlation between $\delta^{2}H_K$ values of bats and $\delta^{13}C$ values in *N. noctula* (blood, liver, wing membrane tissue, and fur) and *P. nathusii* (liver and fur), which might be explained by gradients of $\delta^{13}C$ values across ecosystems of the European continent (Still and Powell 2010, Popa-Lisseanu et al. 2012).

Conclusions

Isotopic data collected from bats killed at German wind turbines suggested that during the pre-migration period *P. nathusii* was more associated with aquatic habitats than the other two species. The relatively strong association of *P. nathusii* with aquatic habitats remains constant throughout the migration period, suggesting that this species depends largely on aquatic habitats such as rivers and lakes when migrating. Migratory *N. noctula* were more associated with terrestrial habitats, which lends support to the notion that this species migrates independent of landscape structures such as rivers and lakes. Isoscape origin models based on stable isotopes confirmed data on the species' specific movement ecology obtained by previous banding campaigns. Our findings show that aquatic habitats are particularly relevant for *P. nathusii* but not necessarily for *N. noctula* during migration.

Acknowledgments

We thank Mateusz Ciechanowski and Aliksai Shpak for providing fur samples, and Yvonne Klaar, Karin Sörgel, and Anja Luckner for analyzing the samples. Doris Fichte helped preparing samples. We thank Kerstin Kraemer and Peter Busse for support of fieldwork in Germany. The Bat Marking Centre Dresden kindly provided rings for individual monitoring of animals. This study was funded by the Leibniz Institute for Zoo and Wildlife Research. The study of molting patterns in *P. nathusii* was supported by the Gesellschaft für Wildtier- und Jagdforschung e.V.

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