

RESEARCH ARTICLE

Open Access



Hydrogen isotopes reveal evidence of migration of *Miniopterus schreibersii* in Europe

Patrick G. R. Wright¹, Jason Newton², Paolo Agnelli³, Ivana Budinski⁴, Ivy Di Salvo⁵, Carles Flaquer⁶, Antonio Fulco⁷, Panagiotis Georgiakakis⁸, Adriano Martinoli⁹, Maria Mas⁶, Mirna Mazija¹⁰, Mauro Mucedda¹¹, Eleni Papadatou¹², Boyan Petrov[^], Luisa Rodrigues¹³, Fiona Mathews^{14*}  and Danilo Russo¹⁵

Abstract

Background: The Schreiber's bat, *Miniopterus schreibersii*, is adapted to long-distance flight, yet long distance movements have only been recorded sporadically using capture-mark-recapture. In this study, we used the hydrogen isotopic composition of 208 wing and 335 fur specimens from across the species' European range to test the hypothesis that the species migrates over long distances.

Results: After obtaining the hydrogen isotopic composition ($\delta^2\text{H}$) of each sample, we performed geographic assignment tests by comparing the $\delta^2\text{H}$ of samples with the $\delta^2\text{H}$ of sampling sites. We found that 95 bats out of 325 showed evidence of long-distance movement, based on the analysis of either fur or wing samples. The eastern European part of the species range (Greece, Bulgaria and Serbia) had the highest numbers of bats that had moved. The assignment tests also helped identify possible migratory routes, such as movement between the Alps and the Balkans.

Conclusions: This is the first continental-scale study to provide evidence of migratory behaviour of *M. schreibersii* throughout its European range. The work highlights the need for further investigation of this behaviour to provide appropriate conservation strategies.

Keywords: Chiroptera, Long-distance migration, Stable isotope, Wildlife conservation, Schreiber's bat, Climate change, Movement ecology

Background

Long-distance migration occurs in several European bat species [1]. Yet the phenomenon is extremely difficult to study as most European bats are too small to carry GPS tags, and capture-mark-recapture approaches are suitable for gathering only incidental records. Understanding migratory patterns is fundamentally important to the assessment of conservation status, and also to the design of appropriate management strategies.

Miniopterus schreibersii is included as Near Threatened in the IUCN Red List, and is thought to be migratory at

least through some of its range [2]. The species is highly gregarious and philopatric, with both sexes always returning to the roosts in which they were born [1, 3]. Despite the scarce evidence for migration across Europe, in South Africa, the closely related *Miniopterus natalensis* covers up to 560 km to reach its hibernation sites in the north of the country, whereas the southern populations are more sedentary. These behavioural differences are also supported by a higher wing aspect ratio in the migratory individuals [4]. The high aspect ratio of *M. schreibersii* wings suggests that it is adapted to cover long distances [5]. Recorded movements between summer and wintering sites have been highly variable: short distances (e.g. 45 km for both males and females [6, 7]) are recorded, as well as long-distance movements (an individual has been recorded to move 833 km from southern

*Correspondence: F.Mathews@sussex.ac.uk

[^]Boyan Petrov—Deceased

¹⁴ University of Sussex, Brighton BN1 9RH, UK

Full list of author information is available at the end of the article



Spain to France (Oficina de Especies Migratorias D.G. de Conservación de la Naturaleza, unpublished data)).

Information to improve the conservation of *M. schreibersii* is urgently needed. Although the species is widely distributed and is common in southern Europe and Asia Minor, it has disappeared from much of the northern part of its range since the 1960s. Recently, unexplained mass mortality events have been observed in south-western Europe, with 40–60% fatality rates being reported in colonies of thousands of individuals [8].

In this study, we used stable hydrogen isotope ($\delta^2\text{H}$) analysis to improve our understanding of *M. schreibersii*'s migratory behaviour. We focused on collecting hair and wing samples (tissues likely to represent different isotopic signatures owing to timing differences in their growth—see “Methods” section) of both male and female bats in spring and autumn throughout the species' European range. We aimed to (a) identify seasonal, sex and tissue differences in the hydrogen isotopic composition of bats; and (b) infer the geographic origin of all fur and wing samples.

Results

Season and tissue were both predictors of $\delta^2\text{H}$ values (season: $X^2(1)=37.94$, $p<0.001$; tissue $X^2(1)=49.83$, $p<0.001$) whereas there was no evidence for an effect of sex ($X^2(1)=1.00$, $p=0.316$). There was also no evidence that the size of the differences in $\delta^2\text{H}$ values between tissues from the same individual differed

between either seasons or sexes (season: $X^2(1)=0.153$, $p=0.695$; sex: $X^2(1)=1.49$, $p=0.221$) (Table 1; Additional file 1: S4, S5 and S6).

By performing assignment tests for all fur and wing samples, we identified 23.5% (spring: 26.5%; autumn: 20.9%) of wing and 25.1% of fur samples (spring: 27.3%; autumn: 23.0%) as not originating from their sampling site. The combination of the different assignment tests performed resulted in the detection of 95 individual bats classified as ‘non-local’ out of 335.

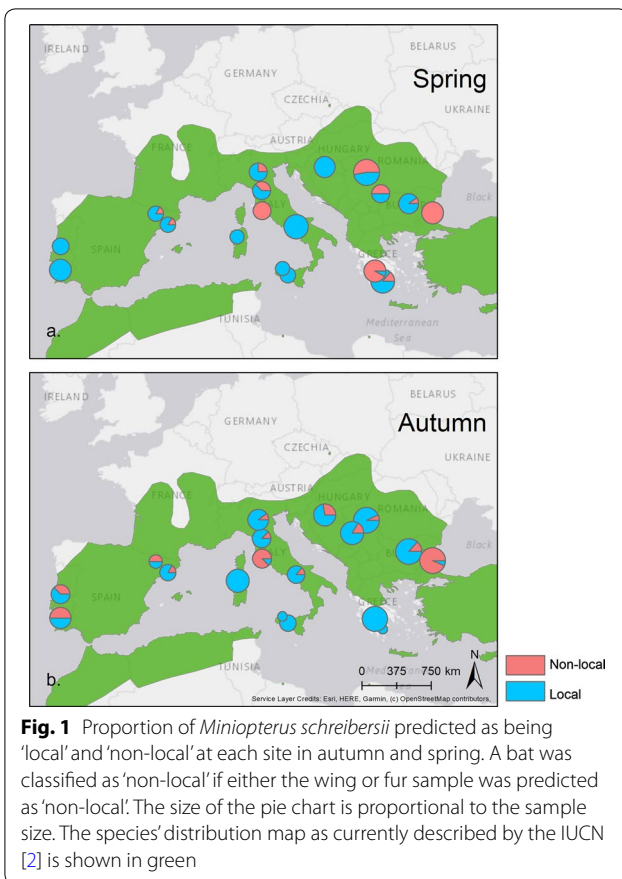
Most bats were predicted as originating from their sampling site throughout both seasons (72%). Only three sites in Tuscany, Greece and Bulgaria were found to have larger numbers of ‘non-local’ bats (Fig. 1). Most sites showed little seasonal variation in the number of ‘non-local’ bats with the exception of the Serbian and Greek sites in spring (a Greek site was not sampled in autumn) and the Portuguese sites in autumn which had a higher number of ‘non-local’ bats (Fig. 1).

Of the 49 bats identified as ‘non-local’ from the wing samples, very few individuals showed large differences in assignment predictions between fur and wing samples (such as those illustrated in Fig. 2c, d). Indeed, 35 bats out of 49 were also identified as ‘non-local’ when testing fur samples of the same individual (18 in autumn and 17 in spring).

The precise migratory routes for most bats were hard to predict from most sampled sites. However, movement from northern Africa and Portugal (Fig. 2) can be

Table 1 Mean $\delta^2\text{H}$ values of fur and wing tissue for all 208 *Miniopterus schreibersii* with standard deviations in brackets (see Additional file 1: S1 and S3 for location of sites)

Region	Site	Autumn			Spring		
		$\delta^2\text{H}_{\text{Fur}}$	$\delta^2\text{H}_{\text{Wing}}$	$\Delta\delta^2\text{H}$	$\delta^2\text{H}_{\text{Fur}}$	$\delta^2\text{H}_{\text{Wing}}$	$\Delta\delta^2\text{H}$
Portugal	1	− 20.37 (3.8)	− 25.04 (4.9)	6.39 (4.3)	− 22.17 (2.6)	− 28.93 (3.2)	6.76 (3.1)
Catalonia	2	− 25.19 (6.9)	− 27.76 (4.4)	4.46 (6.4)	− 24.71 (7.8)	− 25.47 (4.6)	6.97 (4.2)
Italy (Sardinia)	3	− 26.16 (4.6)	− 29.33 (2.3)	4.34 (3.8)	–	–	–
Italy	4	− 39.85 (2.3)	− 33.11 (3.2)	6.74 (2.3)	− 33.72 (2.8)	− 40.35 (6.2)	6.63 (7.1)
Italy	5	− 25.51 (4.3)	− 32.46 (2.9)	6.95 (5.1)	− 30.64 (6.3)	− 31.30 (4.8)	4.75 (4.0)
Italy	6	− 23.14 (1.8)	− 29.51 (5.1)	6.38 (4.2)	− 25.92 (6.3)	− 34.03 (2.1)	8.45 (6.2)
Italy (Sicily)	7	− 18.38 (4.6)	− 23.10 (3.7)	4.85 (5.7)	− 19.93 (5.3)	− 24.53 (4.2)	7.17 (6.0)
Italy	8	− 27.62 (2.5)	− 25.72 (4.7)	2.90 (2.5)	− 31.70 (2.6)	− 30.96 (3.7)	3.76 (2.1)
Croatia	9	− 32.28 (3.5)	− 37.67 (4.1)	5.39 (3.8)	− 43.13 (3.7)	− 43.55 (3.8)	2.61 (1.2)
Serbia	10	− 35.87 (4.8)	− 38.11 (4.2)	5.03 (4.3)	–	–	–
Serbia	11	− 36.07 (3.5)	− 42.25 (5.1)	6.18 (4.3)	− 40.46 (4.8)	− 46.25 (4.3)	7.75 (5.3)
Bulgaria	12	− 38.00 (2.8)	− 39.28 (3.4)	4.08 (2.3)	− 44.46 (3.7)	− 43.60 (4.5)	3.69 (2.5)
Bulgaria	13	− 40.32 (3.4)	− 43.29 (5.1)	5.33 (4.0)	− 41.58 (3.4)	− 43.32 (3.7)	3.03 (3.0)
Bulgaria	14	− 32.92 (4.2)	− 35.71 (3.8)	4.76 (3.7)	− 42.34 (5.9)	− 38.55 (4.7)	5.46 (3.7)
Greece	15	–	–	–	− 17.54 (4.5)	− 29.30 (3.4)	11.77 (5.3)
Greece	16	− 14.8	− 26.9	12.09	− 19.28 (4.7)	− 29.18 (4.5)	9.90 (4.3)

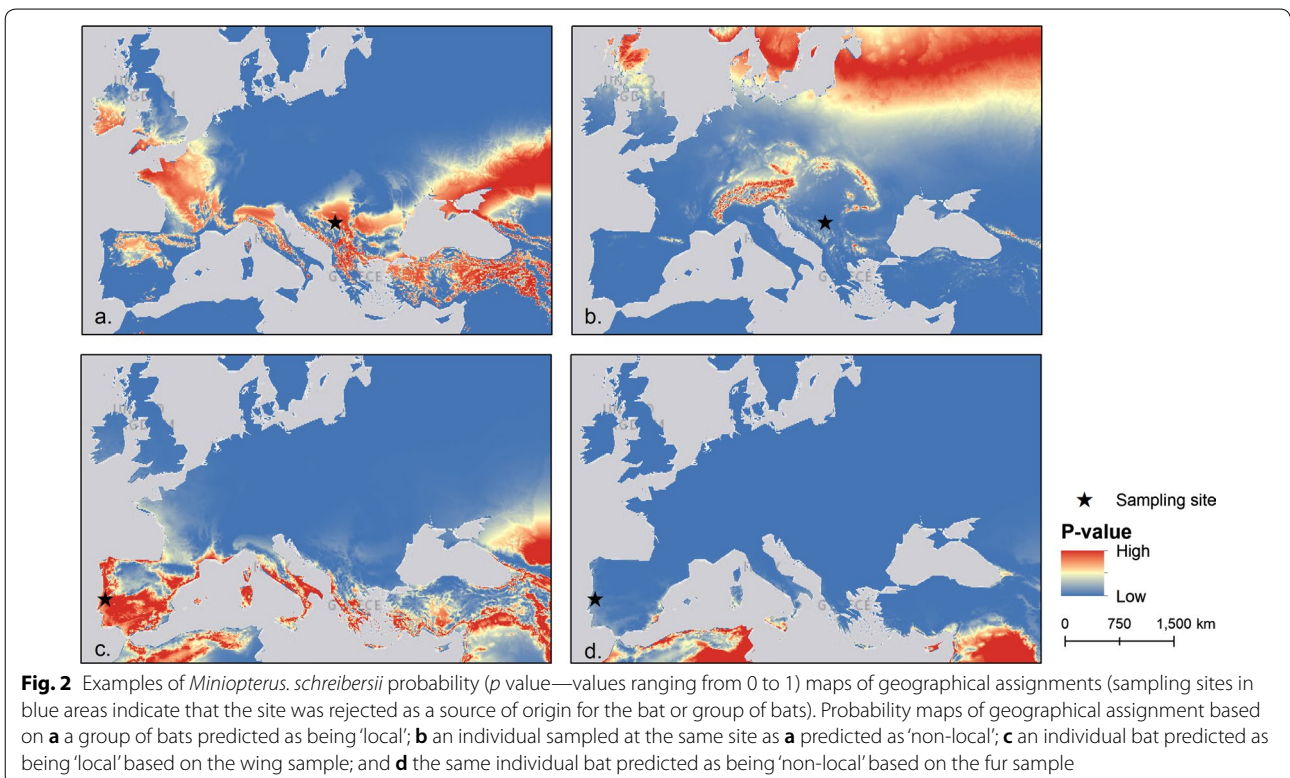


observed from the assignments. Movement from the European Alps was also predicted from multiple sites in eastern Europe and Italy (Fig. 2 and Additional file 1: S10).

Discussion

Based on the measurement of wing and fur stable hydrogen isotope (δ^2H), we confirmed that migratory behaviour occurs in the European population of *M. schreibersii*. This is the first continental-scale study performed on the species to provide evidence of long-distance movement throughout its European range. This behaviour appears site-specific—being predominantly found in eastern part of the species' European range—but does not appear to be sex-specific. Our results agree with previous anecdotal records of some bats travelling several hundreds of kilometres (> 800 km) (Oficina de Especies Migratorias D.G. de Conservación de la Naturaleza, unpublished data), but also with the majority of observations of bats undertaking short distance migration between summer and winter roosts (~ 50 km; [6]).

Most migratory European bats travel in a northeast-southwest direction [9]. Latitudinal migrations are better detected than longitudinal migrations when analysing stable hydrogen isotope data [10, 11]. Therefore, the assignment of a Mediterranean species showing east/west range, such as *M. schreibersii*, is often ambiguous.



For example, migratory routes in Greece were hard to characterise, as high probabilities of assignment were identified in Greece, but also in Portugal and northern Africa, providing multiple alternative routes (Additional file 1: S9). Nonetheless, our findings allow us to identify some possible migratory routes for *M. schreibersii*. Many of the migrant bats from Serbia and Bulgaria showed high probabilities of origin in northern Europe. The absence of the species from most of the latter region suggests that bats are likely to originate from the Alps, an area where *M. schreibersii* is known to be present. Movement from southern Spain to France (>800 km) has been confirmed for a single bat in the past by using banding data (Oficina de Especies Migratorias D.G. de Conservación de la Naturaleza, unpublished data). Our results suggest that this could be a migratory route as multiple bats from Catalonia were shown to be likely to originate from southern Portugal and northern Africa. Other long-distance migrations inferred from our results suggested possible movement from mainland Italy to Sardinia; and movement between southern Europe and northern Africa. The ability to detect movements from northern Africa may be particularly relevant when predicting future range-shifts of the species in response to climate change, and highlight the ability of these bats to cross the Mediterranean—something previously not possible to demonstrate owing to the very small number of banding studies being conducted.

The collection of samples from two tissue types with different turnover rates had the potential to reflect the isotopic signature of an individual at different points in time. While most individual bats showed little differences in fur and wing geographic assignments, these results could vary considerably at certain sites. For a small number of individuals, $\delta^2\text{H}_{\text{fur}}$ had a stronger tie with their sampling site than did $\delta^2\text{H}_{\text{wing}}$. The fact that wing samples are likely to reflect a more recent isotopic signature than fur samples (see “Methods” section) indicates that these individuals had recently returned to the sites where their fur had developed (likely to be June–August) after travelling significant distances. Such behaviour could be driven by the need to visit multiple sites for mating [12], to assess the condition of hibernacula, and/or transfer information to juveniles on the location of traditional roosting sites [13].

In comparison to birds, the migratory behaviour of most bat species remains largely unknown. However, differential migration, where populations migrate separately (sex-, age- or other subgroups), as opposed to random mixing, is thought to be the dominant pattern. Our results suggest regional differences but no obvious sex differences. Yet, *M. schreibersii* short-distance migration timing is known to vary according to sex and age [6]. In

Greece, where mostly migratory males were sampled, the absence of females may be a result of differing migration timings as the latter are also known to use these sites.

The creation of geographical assignments from stable isotopes has limitations in terms of geographical resolution of baseline isoscape data, poorly constrained transfer functions (i.e. the relationship between rainwater $\delta^2\text{H}$ and tissue $\delta^2\text{H}$), lack of information on the dietary intakes of different stable isotopes owing to evidence gaps for foraging behaviour of volant species [14], and the relative lack of variability in water isoscapes over large regions. Hence, only major advances with the miniaturisation of GPS-tag technologies and/or the creation of arrays of static receiver stations for VHS radio-tags will provide a better understanding of *M. schreibersii* migratory behaviour.

Roost temperature is a key driver explaining short-distance migration for *M. schreibersii* [6]. As climate change affects the distribution and survival of many bat species [15], more bats may undertake long-distance migration to find suitable roosts. The overall cost of long-distance migration—increased energy expenditure, greater exposure to anthropogenic threats [16, 17] and increased risk for the spread of diseases [18]—could substantially impact populations. Therefore, a better understanding of migratory routes and the drivers behind long-distance migration is essential.

Conclusions

Our results show that an important number of *M. schreibersii* bats undertake long-distance migration. This behaviour is observed through the species’ European range, but it also appears to be more common at some sites. This information is a first essential step towards better protecting this species, and demonstrates the utility of stable isotopes in informing landscape-scale conservation of bats more widely.

Methods

Sample collection

Bats were captured near roosts by mist nets or harp traps depending on roost characteristics, colony size and other local features. We collected 335 fur samples of *M. schreibersii* from 20 sites across southern Europe during spring and autumn 2015 (Additional file 1: S1). Wing biopsy punches were also taken from 212 of the 335 individuals sampled and stored in ethanol. All samples were collected under the appropriate licence of each country. After establishing sex, age class and taking other biometric measurements, bats were released at their capture location.

Stable isotope analysis

The same protocols were applied for wing and fur samples. Prior to analysis, we rinsed samples in 2:1 chloroform/methanol solution for 24 h, and repeated this a second time for 1 h. We then rinsed samples in ultra-pure water to remove all solvents and oils before letting them to dry at 44 °C (Additional file 1: S2). Samples were added to 5 × 3.5 mm silver capsules and were weighed to 0.15 mg (±0.05 mg) or less if insufficient material had been collected.

We loaded encapsulated samples and standards into a Eurovector UniPrep autosampler [19] and pumped at 60 °C for two 1-h periods separated by a 10-min break in a helium atmosphere. This ensures the removal of residual adsorbed moisture. Hydrogen in the samples was converted to H₂ gas in the reactor of a Thermo Fisher Scientific TC/EA—a high-temperature thermal conversion elemental analyser (HTC-EA). The reactor was filled with chromium powder and glassy carbon (following Gehre, Hoefling [20]), which prevents the formation of other hydrogenous gases such as hydrogen cyanide (HCN), a likely product of the thermal conversion of keratin. Then, δ²H was measured on the resulting H₂ on a Thermo Fisher Scientific Delta V Plus isotope ratio mass spectrometer.

Since a proportion of keratin contains H, which is exchangeable with ambient water vapour, we compared samples to matrix-equivalent reference materials which have known non-exchangeable δ²H to determine the non-exchangeable δ²H of the samples (no bat wing membrane standards were available for this study). The reference materials used were USGS42 and USGS43 hair (−72.2 ± 0.9 and −44.2 ± 1.0‰ respectively Soto, Koehler [21]). In addition, ground Maltese goat hair samples of unknown δ²H were added to each run as an independent assessment of quality control over the 4-week period of analysis. Repeated samples of the goat hair (n = 39) amongst the sample δ²H measurements gave a standard deviation of 1.65‰ (n = 39). All standards were analysed in triplicate in each run.

Statistical analysis and regional assignments

We undertook all statistical analyses in the R software (v. 3.4.3; [22]) and implemented them in R Studio (v. 3.5.1; [23]). We used lme4 [24] to perform a linear mixed effects analysis of the relationships between δ²H values and tissue type, season and sex (fixed effects) from individuals for which both tissue types were collected (n = 208). Site and individual ID were included as random effects. Then, we assessed the relationship between the difference in δ²H values between tissues from the same individual ($\Delta\delta^2\text{H} = |\delta^2\text{H}_{\text{wing}} - \delta^2\text{H}_{\text{fur}}|$)

with season and sex using site and individual ID as random effects. We obtained p-values by likelihood ratio tests of the full model against the models without the tested effects.

Isoscapes represent the spatial patterns of stable isotope ratios and helps with the interpretation and visualisation of data [25, 26]. Here, we made geographic assignments using the R package *IsoriX* which constructs isoscapes and assigns the origin of organisms based on their isotopic signature [27, 28]. Measurements of rainfall δ²H ranging from 2005 to 2017 during the months of June, July and August from the GNIP database (<https://websso.iaea.org/>) were used to create a spatial mixed model predicting isoscape. As bats in Europe and America tend to moult between June and August, origin assignments of fur samples should be representative of the preceding summer [29, 30]. Little is known about the timing and growth of wing membranes, but it is likely to be dependent on the bat's metabolism during the preceding months or weeks (i.e. hibernating, breeding period). However, as a fast healing tissue which regenerates in 2–3 weeks during the active season, they are likely to reflect a more recent isotopic signature than fur samples [31, 32].

We performed assignment tests for all fur and wing isotopic values, using comparisons against the summer isoscape (Additional file 1: S7 and S8). In the absence of data from a sedentary species that could be used for the calibration fit (transfer function—the relationship between sedentary bats δ²H against precipitation at those sites), we used data from individuals showing differences between wing and fur δ²H inferior to the standard deviation of the goat hair standard (< 1.65‰) as these were assumed to be sedentary animals. Then, we applied the transfer function ($\delta^2\text{H}_{\text{fur}} = 0.62 \delta^2\text{H}_{\text{isoscape}} - 14.66$; $\delta^2\text{H}_{\text{wing}} = 0.64 \delta^2\text{H}_{\text{isoscape}} - 14.64$, Additional file 1: S9) between the sample δ²H values and rainfall isoscape δ²H values obtained from the sedentary animals using the 'Calibfit' function to assign the origin of both fur and wing samples. Here, we classified a bat as 'non-local' if either the wing or fur sample was predicted as 'non-local'.

Supplementary information

Supplementary information accompanies this paper at <https://doi.org/10.1186/s12898-020-00321-7>.

Additional file 1. Summary of sampling sites and result outputs.

Acknowledgements

We would like to thank Martina Spada, Stefania Mazzaracca, Ambrogio Molinaru, Damiano Preatoni, Ermanno Pidinchedda, Luca Montanaro, Marta Ciaramella, Leonardo Ancillotto, Luca Cistrone, Giulia Console, Laura Ducci, Stefania Fei, Elena Frosali and Marco Zaccaroni for their help in the field. We dedicate

this paper to the memory of Boyan Petrov who tragically died on a climbing expedition during the period in which the manuscript was being prepared.

Authors' contributions

DR and FM designed the study, PW and JN analysed the samples, and PW wrote the manuscript and undertook the statistical analyses. DR, FM and JN commented on, and revised the manuscript. PA, IB, DS, CF, AF, PG, AM, MM, MarM, MiM, MauM, EP, BP, LR and DR helped with the collection of samples. PW, JN, PA, IB, IDS, CF, AF, PG, AM, MM, MarM, MirM, MauM, EP, BP, LR and DR authors gave approval for the final version of this manuscript. All authors read and approved the final manuscript.

Funding

This work was supported by the NERC Life Sciences Mass Spectrometry Facility funded the hydrogen isotope measurements (Grant Number EK296-19/17) and the Government of Catalonia for fieldwork in Catalonia. FM is supported by a NERC KE Fellowship NE/S006486/1 and the University of Sussex.

Availability of data and materials

All data are available on the Figshare digital repository (DOI: <https://doi.org/10.6084/m9.figshare.12369191.v1>).

Ethics approval and consent to participate

All samples were collected under the appropriate licence of each country.

Consent for publication

Not applicable.

Competing interests

None declared.

Author details

¹ Vincent Wildlife Trust, Ledbury HR8 1EP, UK. ² National Environmental Isotope Facility, Scottish Universities Environmental Research Centre, Glasgow, UK. ³ Sistema Museale dell'Università di Firenze, Museo di Storia Naturale, Sede di Zoologia "La Specola", via Romana 17, 50125 Firenze, Italy. ⁴ Department of Genetic Research, Institute for Biological Research "Siniša Stanković"-National Institute of Republic of Serbia, University of Belgrade, Bulevar despota Stefana 142, 11060 Belgrade, Serbia. ⁵ Ecomodel, Rome, Italy. ⁶ Museu de Ciències Naturals de Granollers, Barcelona, Spain. ⁷ Dipartimento di Scienze e Tecnologie Biologiche, Chimiche e Farmaceutiche, Laboratorio di Zoologia applicata, Università degli Studi di Palermo, via Archirafi 18, 90123 Palermo, Italy. ⁸ University of Crete-Voutes Campus, Natural History Museum of Crete, Heraklion, Greece. ⁹ Unità di Analisi e Gestione delle Risorse Ambientali, Guido Tosi Research Group, Dipartimento di Scienze Teoriche e Applicate, Università degli Studi dell'Insubria,, via J. H. Dunant, 3, 21100 Varese, Italy. ¹⁰ Samostalna djelatnost / Freelance Consultant, Koledinečka 3, 10 040 Zagreb, Croatia. ¹¹ Centro Pipistrelli Sardegna, Sassari, Italy. ¹² ARUP, 3 Piccadilly Place, Manchester, UK. ¹³ Divisão de Conservação da Biodiversidade, Instituto da Conservação da Natureza e das Florestas, Lisbon, PT, Portugal. ¹⁴ University of Sussex, Brighton BN1 9RH, UK. ¹⁵ Wildlife Research Unit, Dipartimento di Agraria, Università degli Studi di Napoli Federico II, via Università 100, 80055 Portici (Napoli), Italy.

Received: 24 June 2020 Accepted: 8 September 2020

Published online: 29 September 2020

References

- Hutterer R, Ivanova T, Meyer-Cords C, Rodrigues L. Bat migrations in Europe: a review of banding data and literature. Bonn: German Agency for Nature Conservation; 2005.
- Hutson AM, Aulagnier S, Benda P, Karataş A, Palmeirim J, Paunović M. *Miniopterus schreibersii*. The IUCN Red List of Threatened Species 2008: e.T13561A4160556. 2008. <http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T13561A4160556.en>.
- Palmeirim JM, Rodrigues L, editors. Dispersal and philopatry in colonial animals: the case of *Miniopterus schreibersii*. In: Symposia of the Zoological Society of London; 1995: London: The Society, 1960–1999.
- Miller-Butterworth CM, Jacobs DS, Harley EH. Strong population sub-structure is correlated with morphology and ecology in a migratory bat. *Nature*. 2003;424(6945):187.
- Norberg UM, Rayner JM. Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Phil Trans R Soc Lond B*. 1987;316(1179):335–427.
- Rodrigues L, Palmeirim J. Migratory behaviour of the Schreiber's bat: when, where and why do cave bats migrate in a Mediterranean region? *J Zool*. 2008;274(2):116–25.
- Serra-Cobo J, Sanz-Trullén V, Martínez-Rica JP. Migratory movements of *Miniopterus schreibersii* in the north-east of Spain. *Acta Theriol*. 1998;43(3):271–83.
- Roué S, Néméz M. Mortalité exceptionnelle du Minioptère de Schreiber en France lors de l'année 2002. Paris: Bilan national Société Française pour l'Etude et la Protection des Mammifères; 2002.
- Eurobats. Action Plan for the Conservation of All Bat Species in the European Union 2019–2024. 2018.
- Hobson KA, Doward K, Kardynal KJ, McNeil JN. Inferring origins of migrating insects using isoscapes: a case study using the true armyworm, *Mythimna unipuncta*, North America. *Ecol Entomol*. 2018;43(3):332–41.
- Van Wilgenburg SL, Hobson KA. Combining stable-isotope (δD) and band recovery data to improve probabilistic assignment of migratory birds to origin. *Ecol Appl*. 2011;21(4):1340–51.
- Rodrigues L, Pereira MJR, Rainho A, Palmeirim JM. Behavioural determinants of gene flow in the bat *Miniopterus schreibersii*. *Behav Ecol Sociobiol*. 2010;5(64):835–43.
- Fenton MB. Summer activity of *Myotis lucifugus* (Chiroptera: Vespertilionidae) at hibernacula in Ontario and Quebec Canadian. *J Zool*. 1969;47:597–602.
- Seifert N, Ambrosini R, Bontempo L, Camin F, Liechti F, Rubolini D, et al. Matching geographical assignment by stable isotopes with African non-breeding sites of barn swallows *Hirundo rustica* tracked by geolocation. *PLoS ONE*. 2018;13(9):e0202025.
- Rebello H, Tarroso P, Jones G. Predicted impact of climate change on European bats in relation to their biogeographic patterns. *Glob Change Biol*. 2010;16(2):561–76.
- Fleming TH, Eby P. Ecology of bat migration. In: Kunz TH, Fenton MB, editors. *Bat ecology*. Chicago: University of Chicago Press; 2003.
- Voigt CC, Popa-Lisseanu AG, Niermann I, Kramer-Schadt S. The catchment area of wind farms for European bats: a plea for international regulations. *Biol Cons*. 2012;153:80–6.
- Jourdain E, Gauthier-Clerc M, Bicoût D, Sabatier P. Bird migration routes and risk for pathogen dispersion into western Mediterranean wetlands. *Emerg Infect Dis*. 2007;13(3):365.
- Wassenaar LI, Hobson KA, Sisti L. An online temperature-controlled vacuum-equilibration preparation system for the measurement of $\delta 2H$ values of non-exchangeable-H and of $\delta 18O$ values in organic materials by isotope-ratio mass spectrometry. *Rapid Commun Mass Spectrom*. 2015;29(5):397–407.
- Gehre M, Hoefling R, Kowski P, Strauch G. Sample preparation device for quantitative hydrogen isotope analysis using chromium metal. *Anal Chem*. 1996;68(24):4414–7.
- Soto DX, Koehler G, Wassenaar LI, Hobson KA. Re-evaluation of the hydrogen stable isotopic composition of keratin calibration standards for wildlife and forensic science applications. *Rapid Commun Mass Spectrom*. 2017;31(14):1193–203.
- R Core Team. R: A Language and Environment for Statistical Computing. *Dim (ca533)*. 2018;1(1358):34.
- RStudio Team. RStudio: Integrated Development Environment for R Boston: RStudio, Inc.; 2015. 2018.
- Bates D, Maechler M, Bolker B, Walker S. lme4: linear mixed-effects models using Eigen and S4. R Package version. 2014;1(7):1–23.
- Bowen GJ. Isoscapes: spatial pattern in isotopic biogeochemistry. *Annu Rev Earth Planet Sci*. 2010;38(1):161–87.
- Sena-Souza JP, Costa FJV, Nardoto GB. Background and the use of isoscapes in the Brazilian context: essential tool for isotope data interpretation and natural resource management. *Revista Ambiente Água*. 2019;14:2.
- Courtiol A, Rousset F. Modelling isoscapes using mixed models. *bioRxiv*. 2017. p. 207662.

28. Courtiol A, Rousset F, Rohwäder M, Soto D, Lehnert L, Voigt C, et al. Isoscape computation and inference of spatial origins with mixed models using the R package IsoriX. In: Hobson KA, Wassenaar LI, editors. Tracking animal migration with stable isotopes. 2nd ed. London: Academic Press; 2018.
29. Fraser E, Longstaffe F, Fenton M. Moulting matters: the importance of understanding moulting cycles in bats when using fur for endogenous marker analysis. *Can J Zool*. 2013;91(8):533–44.
30. Pylant CL, Nelson DM, Fitzpatrick MC, Gates JE, Keller SR. Geographic origins and population genetics of bats killed at wind-energy facilities. *Ecol Appl*. 2016;26(5):1381–95.
31. Weaver KN, Alfano SE, Kronquist AR, Reeder DM. Healing rates of wing punch wounds in free-ranging little brown myotis (*Myotis lucifugus*). *Acta Chiropterologica*. 2009;11(1):220–3.
32. Voigt CC, Matt F, Michener R, Kunz TH. Low turnover rates of carbon isotopes in tissues of two nectar-feeding bat species. *J Exp Biol*. 2003;206(8):1419–27.

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Ready to submit your research? Choose BMC and benefit from:

- fast, convenient online submission
- thorough peer review by experienced researchers in your field
- rapid publication on acceptance
- support for research data, including large and complex data types
- gold Open Access which fosters wider collaboration and increased citations
- maximum visibility for your research: over 100M website views per year

At BMC, research is always in progress.

Learn more biomedcentral.com/submissions

