# Migratory bats and global climate change:
## climate-driven changes in migratory behaviour and distribution of the common noctule bat (*Nyctalus noctula*)

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**Kseniia Kravchenko**

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1. **Kravchenko KA**[**1,2**], Lehnert LS[1,2], Vlaschenko AS[3,4], Voigt CC[1,2]. Multiple isotope tracers in fur keratin discriminate between mothers and offspring. Rapid Communications in Mass Spectrometry. 2019 May 30;33(10):907-13.

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3. **Kravchenko KA**[**1,2**], Voigt CC[1,2], Lange S[6], Currie S[1]* Courtiol A*[5]. Hibernation energetics drive the range shift of a temperate zone bat in response to climate change. (In preparation)

[1] Leibniz Institute for Zoo and Wildlife Research, Department Evolutionary Ecology, Alfred-Kowalke-Strasse 17, 10315 Berlin, Germany

[2] Freie Universität Berlin, Department Animal Behaviour, Takustr. 3, 14195 Berlin, Germany

[3] Bat Rehabilitation Center of Feldman Ecopark, 62340 Lisne, Kharkiv Region, Ukraine

[4] Ukrainian Independent Ecology Institute, 61001 Kharkiv, Ukraine

[5] Leibniz Institute for Zoo and Wildlife Research, Department of Evolutionary Genetics, Alfred-Kowalke-Strasse 17, 10315 Berlin, Germany

[6] Potsdam Institute for Climate Impact Research (PIK), Department of Transformation Pathways, P.O. Box 60 12 03, 14412 Potsdam, Germany

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# 1. SUMMARY

Anthropocene is characterised by significant, and in many ways outcompeting natural processes, the impact of human activities on natural ecosystems. The excessive emission of greenhouse gases caused by global-scale use of fossil fuels, anthropogenic land-use change, and drastic decrease in pristine areas, have all contributed to global climate change. Although the Earth's climate has historically fluctuated, the current situation is novel as climatic change is occurring at an unprecedented rate and has mainly been driven by human behaviour.

The rapid pace of environmental change forces living organisms to respond fast in order to survive and reproduce. The magnitude of such responses might be especially prominent in migratory species due to their diverse and dispersed habitat requirements. Migratory species connect habitats across the globe, coupling biodiversity and ecosystem services. By travelling long distances, migratory species move biomass between habitats; transporting energy, nutrients, and other organisms. Also, migratory species alter the dynamics of resident communities that they connect on their journeys by foraging and becoming prey in numerous habitats during their annual cycle. Therefore environmental alteration leading to disruption of long-distance migratory behaviour will have far-reaching consequences which may drastically affect synchrony and unity in natural ecosystems.

The aim of this dissertation was to reveal climate-driven changes to populations of migratory bats, from a historical overview through to future perspectives. To understand the magnitude of ongoing changes in populations of bats, we require adequate reference points from the past. Here, I had a unique opportunity to study recent changes in migratory behaviour and distribution of common European migratory bat species, *Nyctalus noctula,* based on long term dataset. In the presented work, I combined different approaches such as stable hydrogen isotopes to reveal migratory destinations; analysis of demographic data to evaluate sex and age population dynamics; respirometry measurements to establish physiological parameters and environmental modelling to predict suitable for hibernation areas under three climate change scenarios. This variety of applied technics allowed for complex investigation of animal responses to climate change. The obtained results are reported in two peer-reviewed publications and one manuscript, which is in preparation for submission. The research outcome aims to bridge the most demanding gaps in knowledge related to climate-driven changes in populations of migratory animals. The **first chapter** contributed to the improvement of the method for studying migratory animals by using stable isotopes. The **second chapter** was dedicated to climate change responses, particularly to an

investigation of the mechanism of climate-driven range changes in populations of migratory bats. The **third chapter** described and evaluated the novel mechanistic approach in environmental modelling of species distribution under the impact of climate change.

In **chapter one,** I have contributed to the validation of the assumptions for stable hydrogen analysis. Stable isotopes are broadly applied for the identification of the geographical origin of bats via transfer function, which is consists of the isotope signature of animals of know origin. However, there was no age validation performed before for stable isotope signatures in bat tissues. The stable isotopes approach was planned as the main method for the assignment of migratory bats in a long-term dataset. Therefore, in **chapter one,** I presented a validation approach for age differences in stable isotope signatures to better understand variation around the transfer function and increase the precision in the prediction of the geographic origin.

In **chapter two** using a transfer function, which included individuals of both age classes, I investigated migratory behaviour and demographic structure of *N. noctula* under the distribution shift. The common noctule bats increased their winter range by more than 500 km during several decades. Apart from the observed biogeographic pattern little was known regarding the mechanism relevant for the range change. I hypothesized that the generation shift is the mechanism relevant to the range change in migratory bats. To test the hypothesis, I looked at the long-term data set regarding the demographic structure of winter colonies in the recently occupied winter range and I used stable hydrogen analysis to establish the geographic origin of bats. My finding supported the hypothesis regarding the generational shift in migratory behaviour of bats which resulted in winter range change. Obtained results, for the first time, demonstrated the relevance of generation shift in the regulation of species distribution in mammals.

**Chapter three** was dedicated to the elaboration of a mechanistic physiologically-based model for the evaluation and forecasting of suitable hibernation areas in migratory bats. Climate change is expected to affect the cost of hibernation in a given area and might ultimately modify species winter distribution. With a novel approach, I aimed to combine fine-scale thermoregulation data of noctule bats with environmental variables from their past and present winter ranges to model species occurrence dynamics. Firstly, this joint approach improved our understanding of species physiological requirements to external conditions. Secondly, it enabled us to refine the modelling of future species distribution under different climate change scenarios.

The presented work had revealed climate-driven changes in migratory behaviour and distribution of common noctule bats. By incorporation various technics and methodological

approaches, I could tackle the magnitude of responses to climate change on different levels of ecological organisation: from an organismal physiological response to environmental conditions; to change in migratory behaviour on a population level and change in geographic distribution on a species level. The main findings elaborate on physiological and behavioural mechanisms underlying climate-driven range change and provide evidence for migratory bats being able to respond fast to the rapid pace of climate change. However, the consistency of responses is conditioned by species-specific traits such as physiological flexibility, high mobility and dispersion rate, short generation life, and diversity of migratory strategies; and climate velocity, as a metric of speed, and direction of climate displacement.

## 2. ZUSAMMENFASSUNG

Das Anthropozän ist gekennzeichnet durch signifikante und in vielerlei Hinsicht natürliche Prozesse überlagernde Auswirkungen menschlicher Aktivitäten auf natürliche Ökosysteme. Der übermäßige Ausstoß von Treibhausgasen durch die weltweite Nutzung fossiler Brennstoffe, die anthropogene Landnutzungsänderung und die drastische Abnahme unberührter Gebiete haben alle zum globalen Klimawandel beigetragen. Obwohl das Klima der Erde historisch gesehen schwankte, ist die gegenwärtige Situation neuartig, da der Klimawandel in einem noch nie dagewesenen Tempo stattfindet und hauptsächlich durch menschliches Handeln angetrieben wurde.

Das rasante Tempo der Umweltveränderungen zwingt lebende Organismen schnell zu reagieren, um zu überleben und sich fortpflanzen zu können. Das Ausmaß solcher Reaktionen könnte bei wandernden Arten aufgrund ihrer vielfältigen und verstreuten Lebensraumanforderungen besonders ausgeprägt sein. Wandernde Arten verbinden Lebensräume auf der ganzen Welt miteinander und verbinden so Biodiversität und Ökosystemleistungen. Indem sie weite Strecken zurücklegen, bewegen wandernde Arten Biomasse zwischen Lebensräumen und transportieren Energie, Nährstoffe und andere Organismen. Außerdem verändern wandernde Arten die Dynamik der ansässigen Lebensgemeinschaften, die sie auf ihren Reisen verbinden, indem sie während ihres jährlichen Zyklus in zahlreichen Lebensräumen auf Nahrungssuche gehen und zur Beute werden. Daher haben Umweltveränderungen, die zu einer Unterbrechung des Fernwanderverhaltens führen, weitreichende Konsequenzen, die die Synchronität und Einheitlichkeit natürlicher Ökosysteme drastisch beeinträchtigen können.

Das Ziel dieser Dissertation war es, klimabedingte Veränderungen in Populationen wandernder Fledermäuse aufzuzeigen, von einem historischen Überblick bis hin zu Zukunftsperspektiven. Um das Ausmaß aktueller Veränderungen in Fledermauspopulationen zu verstehen, benötigen wir geeignete Bezugspunkte aus der Vergangenheit. Hier hatte ich die einmalige Gelegenheit, die jüngsten Veränderungen im Zugverhalten und in der Verbreitung der häufigen europäischen ziehenden Fledermausart *Nyctalus noctula* anhand von Langzeitdaten zu untersuchen. In der vorgestellten Arbeit kombinierte ich verschiedene Ansätze wie stabile Wasserstoffisotope, um Wanderungsziele zu ermitteln; die Analyse demographischer Daten, um die Populationsdynamik nach Geschlecht und Alter zu bewerten; Respirometrie-Messungen, um physiologische Parameter zu bestimmen und Umweltmodellierung, um geeignete Überwinterungsgebiete unter drei Szenarien des Klimawandels vorherzusagen. Diese Vielfalt an angewandter Technik ermöglichte eine komplexe Untersuchung der Reaktionen der Tiere auf den

Klimawandel. Die erzielten Ergebnisse werden in zwei begutachteten Publikationen und einem Manuskript, das zur Einreichung vorbereitet wird, berichtet. Das Forschungsergebnis zielt darauf ab, die anspruchsvollsten Wissenslücken in Bezug auf klimabedingte Veränderungen in Populationen wandernder Tiere zu schließen. Das **erste Kapitel** trug zur Verbesserung der Methode zur Untersuchung wandernder Tiere durch die Verwendung stabiler Isotope bei. Das **zweite Kapitel** war den Reaktionen auf den Klimawandel gewidmet, insbesondere der Untersuchung des Mechanismus der klimabedingten Arealveränderungen in Populationen wandernder Fledermäuse. Das **dritte Kapitel** beschrieb und bewertete den neuartigen mechanistischen Ansatz in der Umweltmodellierung der Artenverteilung unter dem Einfluss des Klimawandels.

Im **ersten Kapitel** habe ich zur Validierung der Annahmen für die Analyse von stabilem Wasserstoff beigetragen. Stabile Isotope werden allgemein zur Identifizierung der geographischen Herkunft von Fledermäusen über die Transferfunktion verwendet, die aus der Isotopensignatur von Tieren bekannter Herkunft besteht. Es wurde jedoch bisher keine Altersvalidierung für stabile Isotopensignaturen in Fledermausgeweben durchgeführt. Der Ansatz der stabilen Isotope war als Hauptmethode für die Zuordnungen von wandernden Fledermäusen in einem Langzeitdatensatz geplant. Daher habe ich in Kapitel eins einen Validierungsansatz für Altersunterschiede in stabilen Isotopensignaturen vorgestellt, um die Variation um die Transferfunktion besser zu verstehen und die Genauigkeit bei der Vorhersage der geographischen Herkunft zu erhöhen.

In **Kapitel zwei** untersuchten wir unter Verwendung einer Transferfunktion, die Individuen beider Altersklassen einschloss, das Wanderverhalten und die demographische Struktur von *N. noctula* unter der Verteilungsverschiebung. Die Abendsegler haben ihr Winterquartier über mehrere Jahrzehnte um mehr als 500 km erweitert. Abgesehen von dem beobachteten biogeographischen Muster war wenig über den für die Verbreitungsveränderung relevanten Mechanismus bekannt. Ich stellte die Hypothese auf, dass die Generationsverschiebung der relevante Mechanismus für die Arealveränderung bei wandernden Fledermäusen ist. Um die Hypothese zu testen, untersuchte ich den Langzeitdatensatz bezüglich der demographischen Struktur der Winterkolonien im kürzlich besetzten Winterquartier, und ich verwendete die Analyse des stabilen Wasserstoffs, um die geographische Herkunft der Fledermäuse zu bestimmen. Meine Ergebnisse unterstützten die Hypothese bezüglich einer Generationsverschiebung im Wanderverhalten der Fledermäuse, die zu einem Wechsel des Winterquartiers führte. Die erzielten Ergebnisse zeigten zum ersten Mal die Relevanz von Generationsverschiebungen bei der Regulierung der Artenverteilung bei Säugetieren.

**Kapitel drei** widmete sich der Ausarbeitung eines mechanistisch-physiologisch basierten Modells zur Bewertung und Vorhersage von geeigneten Überwinterungsgebieten bei wandernden Fledermäusen. Es wird erwartet, dass sich der Klimawandel auf die Kosten der Überwinterung in einem bestimmten Gebiet auswirkt und letztlich die Winterverbreitung der Arten verändern könnte. Mit einem neuartigen Ansatz habe ich versucht, feinräumige Thermoregulationsdaten von Fransenfledermäusen mit Umweltvariablen aus ihren vergangenen und aktuellen Wintergebieten zu kombinieren, um die Dynamik des Vorkommens der Art zu modellieren. Erstens verbesserte dieser gemeinsame Ansatz unser Verständnis der physiologischen Anforderungen der Arten an die äußeren Bedingungen. Zweitens ermöglichte es uns, die Modellierung der zukünftigen Verbreitung der Arten unter verschiedenen Szenarien des Klimawandels zu verfeinern.

Die vorgestellte Arbeit hat klimabedingte Veränderungen im Wanderverhalten und in der Verbreitung von Abendsegler aufgezeigt. Durch die Einbeziehung verschiedener Techniken und methodischer Ansätze konnte ich das Ausmaß der Reaktionen auf den Klimawandel auf verschiedenen Ebenen der ökologischen Organisation angehen: von der physiologischen Reaktion eines Organismus auf die Umweltbedingungen über die Veränderung des Wanderverhaltens auf Populationsebene bis hin zur Veränderung der geographischen Verbreitung auf Artniveau. Die wichtigsten Ergebnisse erläutern die physiologischen und verhaltensbezogenen Mechanismen, die der klimabedingten Veränderung des Verbreitungsgebiets zugrunde liegen, und liefern Beweise dafür, dass wandernde Fledermäuse in der Lage sind, schnell auf den rasanten Klimawandel zu reagieren. Die Beständigkeit der Reaktionen wird jedoch durch artspezifische Merkmale wie physiologische Flexibilität, hohe Mobilität und Dispersionsrate, kurze Generationsdauer und Vielfalt der Migrationsstrategien sowie die Klimageschwindigkeit als Maß für die Geschwindigkeit und Richtung der Klimaverschiebung bedingt.

# 3. GENERAL INTRODUCTION

## 3.1. Natural ecosystems under the impact of global climate change

Over the course of the 20th century, human activities have grown to become significant geological forces and initiated a new geologic epoch called Anthropocene (Crutzen 2006). Anthropocene is characterised by significant, and in many ways outcompeting natural processes, the impact of human activities on natural ecosystems (Waters et al. 2016). The excessive emission of greenhouse gases caused by global-scale use of fossil fuels, anthropogenic land-use change, and drastic decrease in pristine areas, have contributed to global climate change (Brovkin et al. 2004; Höök and Tang 2013). Climate change is categorised by the rise of annual temperatures, a shift in seasonality, and an increase in the frequency of extreme weather events such as heatwaves, floods, and droughts (Jentsch and Beierkuhnlein 2008; Alexander 2016). While the Earth's climate has historically fluctuated (Burke et al. 2018), the current situation is novel as climatic change is occurring at an unprecedented rate and has mainly been driven by human behaviour (Fig 1.).

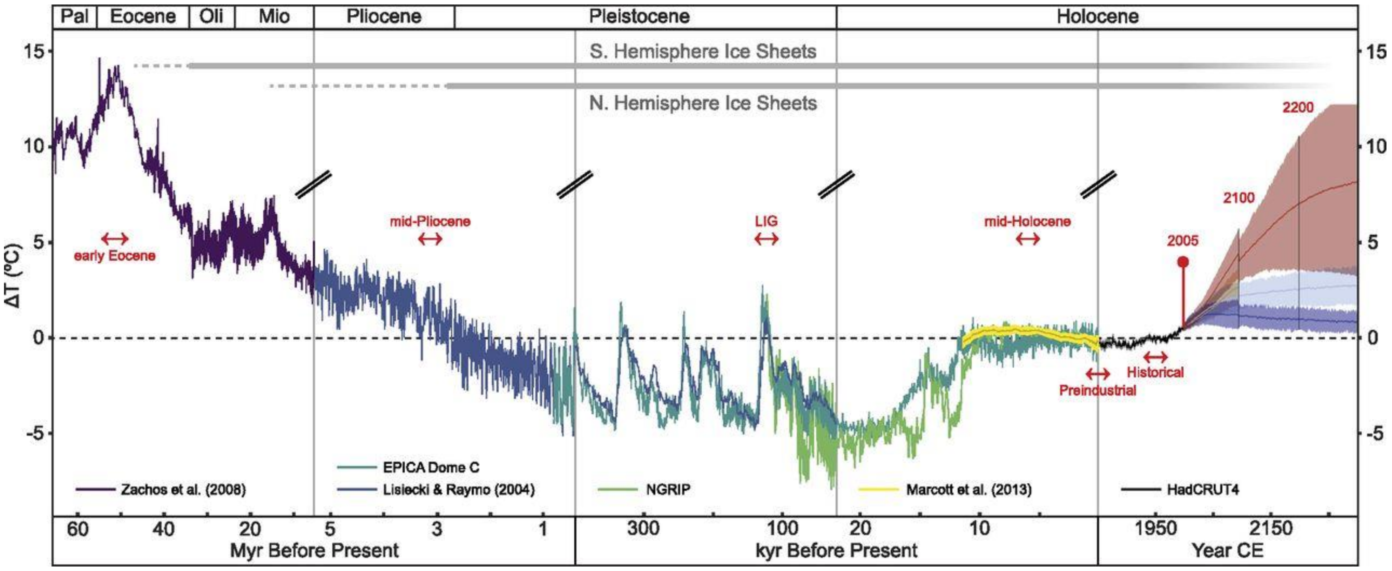

Fig. 1. Temperature trends on Earth for the past 65 million years (adapted from Burke et al. 2018).

The rate of ecological change, driven by climate, is often quantified through the magnitude of species responses (Nunez et al. 2019) and can be classified as ‘fast’, ‘slow’, and ‘abrupt’ (Williams, Ordonez, and Svenning 2021). ‘Fast’ ecological change is observed when the rate of species response follows the rate of climate change. Under ‘slow’ ecological change, the rate of species response lags behind climate change. While ‘abrupt’ ecological change is characterized by stark and potentially inconsistent responses, which can occur as a single event or as a cascade of successive events. Fast ecologic responses are considered as most adaptive as species try to mitigate fitness loss under changing environmental conditions (Hoffmann and Sgró 2011). However, given the pace and magnitude of current global change, even fast responses might be insufficient and threaten the persistence of many species (Radchuk et al. 2019; Diffenbaugh and Giorgi 2012). We need to, therefore, continuously improve our understanding of climate change impacts on natural ecosystems, and regularly evaluate and implement climate-adaptive conservation strategies (Williams, Ordonez, and Svenning 2021).

### 3.2 Impact of climate change on migratory animals

Dynamic conservation strategies that provide suitable habitats, when and where it is most needed, can be critically important for the persistence of species; especially for those with diverse and dispersed habitat requirements, such as migratory species. Migratory species connect habitats across the globe, coupling biodiversity and ecosystem services worldwide (Bauer and Hoye 2014; Semmens et al. 2011). By travelling long distances, migratory species move biomass between habitats; transporting energy, nutrients, and other organisms (Bauer and Hoye 2014). Furthermore, migratory species may alter the dynamics of resident communities that they encounter on their journeys by foraging and becoming prey in numerous habitats during their annual cycle (Bauer and Hoye 2014; Robinson et al. 2009). The magnitude of these transport and trophic roles is shaped by at least three features: first, the characteristics of migratory movements such as the timing, predictability, and frequency of migration; second, the extent to which they are integrated into trophic cascades within each habitat, such as primary pollinators or top-order predators; third, the spatial scale over which migratory animals connect communities and ecosystems (Bauer and Hoye 2014). Furthermore, it is important to consider the effects of climate change on migratory species through the environmental impact on the aforementioned features.

The timing of migration is synchronised with resource availability at migratory destinations, as it is highly relevant for survival and reproduction success (Bauer, McNamara, and Barta 2020; Thorup et al. 2017). Usually, migrants arrive at breeding grounds early in the season to synchronise the peak of food availability with the time of hatching or parturition (Arzel et al. 2009; Bauer, McNamara, and Barta 2020). However, due to increased global temperatures, many phenological events have advanced temporally (Parmesan and Yohe 2003). This is especially evident at high latitudes (Zhang et al. 2004; Post, Steinman, and Mann 2018), where the magnitude of the warming temperatures has been generally greater than at lower latitudes (Solomon et al. 2007). Advancement of the plant-growth season at breeding grounds causes mismatches between food supply and reproductive timing in many migratory species (Durant et al. 2007; Van der Jeugd et al. 2009; Both et al. 2009), amplifying seasonal fitness declines in later breeders and thus potentially contributing to a decrease in those populations (Verhulst, van Balen, and Tinbergen 1995; Visser et al. 2009; Both et al. 2010). From a long-term perspective, climate-driven phenological mismatches could negatively affect the extent of migratory behaviour as the costs of migration will likely outweigh the benefits.

The frequency and predictability of migration are important for resident communities as the presence of migratory species moderates interspecific interactions. Migratory species are known to support many weak trophic interactions in ecosystems, which act as a stabilising factor in complex food webs (Rooney and McCann 2012; Bauer and Hoye 2014). This means that the ephemeral presence of migratory species leads to seasonal resource switching among resident species (Bauer and Hoye 2014). For example, migratory herds of wildebeests and zebras indirectly affect the calf survival of giraffes in African savannahs, because the presence of migratory ungulates reduces lion predation on giraffes calves (Lee et al. 2016). However, adverse conditions at stopover sites and migratory destinations might introduce stochasticity into migratory behaviour, resulting in migratory species disappearing from their destination habitats in the capacity they once did (Xu et al. 2019; Robinson et al. 2005). Thus, less predictable or infrequent arrivals of migratory species could break weak trophic interactions. This could lead to greater dependence of interspecific interaction within residential communities, altering ecosystem functioning and affecting ecosystem resilience to environmental change.

Another essential ecological role of migratory species, which is also highly impacted by climate change, is to provide ecological connectivity of distant habitats (Bauer and Hoye 2014; Bowlin et al. 2010). Being present only seasonally and often in very large numbers, migratory species represent so-called ‘resource pulses’ for resident communities. ‘Resource pulses’ are defined as occasional, intense, and brief episodes of increased resource availability that can profoundly alter the abundance of interacting species (Bauer and Hoye 2014). The importance of these pulses increases with latitude as the number of species playing a similar ecological role and occupying related niches decreases. However, due to the spatiotemporal heterogeneity of environmental alterations, there is a greater chance that distant habitats will undergo different rates of climatic change (Ashcroft, Chisholm, and French 2009). Long-distance migrants, which are interacting with remote habitats, might not be able to anticipate heterogeneous changes, which may lead to a disruption of long-distant seasonal journeys. The decreases in migratory distances and abundance of individuals performing seasonal journeys may shorten the spatial magnitude of ecological impact between migrants and associated with them resident communities (Visser et al. 2009) and interrupt the flow of ecosystem services (Mooney et al. 2009). Thus disruption of long-distance migratory behaviour will have far-reaching consequences which may drastically affect synchrony and unity in natural ecosystems.

### 3.3. Responses of migratory animals to climate change

We have already begun to see that some migratory species are exhibiting ecological responses to climate change (Møller, Rubolini, and Lehikoinen 2008). The most commonly documented ecological responses are changes in the timing of seasonal activities in response to phenology shifts (Cohen, Lajeunesse, and Rohr 2018); changes in winter and/or summer ranges in response to alterations of habitat quality (Hitch and Leberg 2007); and decreases in migratory behaviour due to changes in seasonal ecosystem productivity at migratory destinations (Pulido and Berthold 2010). However, there are also environmental disturbances to which migratory species might not be capable to respond adequately. Predominantly, the highly stochastic temporospatial events that are increasing in frequency with climate change, such as heatwaves, floods, droughts, and invasive pathogens or competitors.

Changes in the timing of life-history events are the most well-documented types of ecological responses. The most noted examples of this are advances in the dates of spring migration, arrival at breeding grounds, and the start of reproduction (Rubolini et al. 2007). By adjusting the timing of these life-history events, individuals attempt to mitigate the effect of early spring phenology at their breeding grounds, and this is especially evident at high latitudes (Clausen and Clausen 2013). This type of response is most prominent in short-distance migrants and sedentary species, rather than long-distance migrants (Both et al. 2010). This occurs, in part, because the onset of spring migration in long-distance migrants, while controlled endogenously, is also moderated by environmental cues at non-breeding and stopover sites (Haest, Hüppop, and Bairlein 2020). Due to spatial heterogeneity of climate change, historic cues for spring migration may therefore no longer match appropriate timing at breeding sites (Cotton 2003). Yet some long-distance migrants can mitigate the phenological mismatch by moderating the pace of migration en route (Lameris et al. 2017; Both, Bijlsma, and Visser 2005) or by regulating the timing of reproduction (Ahola et al. 2004). In comparison to this notable advancement of life-history events in spring, the timing of seasonal events in autumn seems to be more ambiguous (Jenni and Kéry 2003). For example, for animals, with shorter migratory distances and high variation in arrival dates, the extension of plant-growing season supports the reproductive success of late breeders (Camacho 2013) and allows for more batches of young in multi-brooding species (Jenni and Kéry 2003). Whereas long-distant migrants and species with a single brood have demonstrated advances in the onset of autumn migration (Gallinat, Primack, and Wagner 2015). Thus, phenology shifts impose complex and sometimes opposing responses in the timing of life-history events, depending on the ecology and life history of a species.

Another climate-driven response exhibited by migratory species is a change in summer and/or winter ranges. Often, changes in geographic distribution are determined by species-specific physiological thresholds of temperature and precipitation tolerance (Hoffmann and Parsons 1997). Examination of the fossil records suggests that, in the Pleistocene, adaptations to climatic change occurred mostly through range shifts rather than direct adaptive evolution (Parmesan, Root, and Willig 2000; Parmesan 2006). Given the current rapid pace of climate change, it can therefore be assumed that species are more prone to shift their ranges to track favourable climatic conditions, rather than to remain in place and evolve new forms (Maggini et al. 2011). Change in species ranges can occur in all directions of their distribution. For clarity, these patterns of range change have been simplified and defined as such: leading-edge expansion, trailing edge retraction, range expansion, optimum shift, expansion, retraction, and shift (Maggini et al. 2011). The most commonly observed biogeographic trends are shifts and expansions of ranges poleward and with increasing elevation (Parmesan and Yohe 2003; Parmesan 2006). For migratory species, moving within the northern hemisphere, a range change may result in an overlap between seasonal distributions as conditions at breeding grounds may become favourable for overwintering (Austin and Rehfisch 2005). However, climate change may also lead to the loss of habitats at the southern border of the species range due to high temperatures and droughts (Norris et al. 2004; Studds and Marra 2005). For long distant trans-Saharan migrants poleward shifts of wintering areas increase the distance individuals must travel to reach their breeding sites in the northern hemisphere (Doswald et al. 2009). Individuals can only move alongside their optimal abiotic climate characteristics to the extent that geography, dispersal capacity and resource availability allow them.

For example, boundaries imposed by geographic barriers may include untraversable mountain ranges or gullies (Burrows et al. 2014) or anthropogenic habitat fragmentation (Caplat et al. 2016). Limited biotic factors include interspecific competition and the presence of unfamiliar parasites (Marion and Bergerot 2018; Bozick and Real 2015) as well as the pace of corresponding range shifts of required food resources (Van der Jeugd et al. 2009). Apart from possible geographic patterns based on environmental optima, little is known about the consecutive processes by which a species changes its geographic distribution (Gill, Alves, and Gunnarsson 2019b). Understanding the mechanisms of colonisation of new adjacent territories may help to build reliable mechanistic models of range change and estimate the possible rate of population adjustment in relation to the pace of climate change. Conservation assistance for species newly establishing outside of their historic range may be key for their persistence and an important approach in environmental management.

Climate change also imposes a decrease in migratory distances. It was shown that species with greater diversity in migration behaviour have a greater capacity to adjust to climate change (Gilroy et al. 2016). For example, species with large non-breeding ranges and species with partial migratory strategies have been less likely to suffer population declines than species with restricted seasonal habitats and uniform migratory behaviour (Gilroy et al. 2016). In addition, species that decrease migratory distances by overwintering within their breeding ranges have even demonstrated population increases (Bókony, Barta, and Végvári 2019). Some studies suggest that spatial extension of the non-breeding range is likely to be an indication of adaptations to past climate variation and may act as a guide for the capacity of these species to respond to future climate change (Patchett, Finch, and Cresswell 2018).

The rate of such responses depends on whether migratory behaviour is socially transmitted or has a genetic component (Pulido 2007). Cultural transmission of migration may facilitate very rapid changes in migratory behaviour (Sutherland 1998), although the adaptive response in such species is not necessarily faster than in organisms in which migration is controlled primarily by a genotype (van Noordwijk et al. 2006). Probably, species responses, which are expressed through the change in migratory strategy are moderated to a different extent by both genetic and social components. The genetic component represents the diversity of genes, influencing species traits, that predispose migratory behaviour on a different level from physiology and morphology, including personality and magnitude of exploratory behaviour (van Noordwijk et al. 2006). The social component implies the cultural transmission of fitness (Heyer, Sibert, and Austerlitz 2005), which is the non-genetic transmission of migratory behaviour that affects reproductive success. The interplay of these components is still poorly studied in migratory species (Liedvogel, Åkesson, and Bensch 2011). Further experimental and observational data is needed to reveal the impact of endogenous and exogenous factors on migratory strategies. However, what is known is that migratory behaviour may rapidly evolve multiple times in the lifetime of one species (Berthold 1991; Berthold et al. 1992). Some studies suggest that the current dynamic of environmental change leads to the evolution of residency in migratory species (Pulido and Berthold 2010), and the reduction of migratory activity is probably an important evolutionary process in the adaptation of migratory animals to climate change.

### 3.4. Methods to study climate-driven changes in migratory animals

Long-term and regular observations of migratory animals are challenging mainly due to the high mobility of the majority of migratory populations and little knowledge regarding migratory connectivity. However, several approaches provide reliable information regarding the migratory behaviour of species and have allowed us to track climate-driven ecological responses over relatively long periods.

One of the oldest methods that is still in use is long-term population censuses at summer and winter grounds. Numerous studies have demonstrated that those regular censuses at summer or winter grounds allow us to estimate population abundance and distribution, as well as phenology of migration behaviour. However, this method is highly dependent on observer experience and does not provide information regarding the connectivity of summer and winter grounds. Individual abundance at census sites often fluctuates greatly from year to year (Hostetler, Sillett, and Marra 2015). These fluctuations are influenced by several environmental factors and anthropogenic threats affecting individual survival along the migratory route and at seasonal destinations (Calvert et al. 2009). Unfortunately, seasonal census data alone does not provide information regarding the processes influencing the observed abundance and distribution of migratory populations.

Alternatively, mark and recapture methods provide details on migratory directions, destinations, and estimation of connectivity between seasonal habitats (Hutterer et al. 2005). Thus, regular observations of marked individuals allow us to estimate fidelity to seasonal habitats (Martinoli et al. 2006), and individual longevity (Lok et al. 2017). Yet mark-recapture studies are limited by the efficiency of recapturing the majority of marked individuals (Schorr, Ellison, and Lukacs 2014), and an inability to distinguish between death and dispersion (Neil Arnason 1972). This method also does not provide details of individual migratory pathways.

With recent technical advances in biologging techniques, radio telemetry (VHF), GPS and geolocator loggers have come into broad use. Such tracking systems allow for the direct measurement of individual trajectories, activity and rest patterns, and the calculation of home ranges (McKinnon and Love 2018). However, devices of high accuracy are still expensive, and the majority of tags have short battery life (from several days to several weeks). In addition, some devices (e.g., GPS) are still too heavy to be attached to small migratory birds and bat species. Furthermore, GPS tags and geolocator loggers with high resolution and additional information, such as acceleration and barometric pressure, require recapture of individuals to retrieve the data (McKinnon and Love 2018). Therefore, such tagging methods rely on the probability of recapture of tagged individuals, which limits their application by choosing species with high fidelity to seasonal roosts and destinations. Unless individuals are large enough to attach the current satellite telemetry tags with GPS components that allowed for remote data transmission.

A novel method for studying population migration without the need for animal handling is the use of radar observations. Information extracted from networks of radars can provide large-scale patterns of migratory movements and their long-term trends. Radars survey the airspace over large regions (e.g., entire continents) and allow comprehensive assessment and quantification of the biomass transport across, into and out, of large geographic regions (Bauer et al. 2019). However, due to much coarser taxonomic resolution, the scientific value of radar methods has often been questioned. Yet, the installation of new sensors and, more importantly, the compilation of data across entire networks of radars have increased radar application within migration ecology (Bauer et al. 2019).

Stable isotope analysis is another powerful approach in migratory ecology. Stable hydrogen isotopes are particularly useful for revealing animal movements over large spatial scales (Hobson 1999). This approach is based on the reflection of a latitudinal gradient of stable hydrogen ratio values from the environment in animal tissues (Cryan et al. 2004; Lott, Meehan, and Heath 2003). Organisms living in a particular area incorporate local hydrogen signatures via the food and water they consume (Hobson, Atwell, and Wassenaar 1999). Therefore, by knowing the timing of seasonal tissue turnover and using a specific transfer function (obtained from individuals of known origin) one can assign a geographic origin to sampled individuals. This approach is especially applicable for the investigation of small migratory animals (<50g), as the analysis requires only a small amount (~0.35 mg) of tissue (fur, fathers, cloves, or skin), which can be obtained by the minimally invasive sampling (Voigt and Lehnert 2019). Additionally, relatively low costs per sample make the analysis of a large number of individuals feasible, which when applied combined with other isotopes (carbon, nitrogen, strontium) reveals spatial connectivity between seasonal habitats (Popa-Lisseanu et al. 2012; Kruszynski et al. 2021). Moreover, stable isotope values can be obtained from carcass tissues and museum samples. The possibility of geographic assignment of such samples is very useful in the forensic studies of animal trafficking (Aggarwal, Habicht-Mauche, and Juarez 2008) and evaluation of the catchment area for infrastructures that cause fatalities to migratory species, for example, wind turbines (Voigt et al. 2012). Besides many applications of stable isotope analysis, unexplained variation in isotopic values in animal tissues remains large. Therefore, further studies, which aim to validate implicit assumptions, are required for better prediction of spatial assignments using this method.

### 3.5. Migratory bats as a model for climate change research

Bats are considered bioindicators groups of animals, meaning that they can respond fast to environmental alterations (Jones et al. 2009). Several ecological traits precondition fast environmental responsiveness in bats. The most relevant traits that make bats bioindicators are their high trophic position, significant energy demands, slow reproductive rate, requirements for different seasonal habitats and roosts, broad-scale spatial mobility (Sherwin, Montgomery, and Lundy 2013). However, bats represent a paradox in terms of the assessment risk of climate change. On one hand, their high vagility provides the ability to follow the preferred climatic conditions across seasonal habitats. On the other hand, the active flight is energy demanding and therefore makes bats sensitive to spatial predictability of food resources (Egert-Berg et al. 2018). That makes bats dependent on the availability of suitable habitats and roosts in multiple locations.

Bats, living in highly seasonal habitats, at the time of low food availability (winter) undergo prolonged torpor, namely hibernation (Körtner and Geiser 2000; Ruf and Geiser 2015). Before hibernation, bats move from their summer grounds to suitable winter roosts. Winter roosting ecology is one of the main traits which discriminate between long-distance migratory species and regionally commuting bats (Cryan and Veilleux 2007). Regional bats usually hibernate in underground cavities such as caves, basements, bunkers, and burrows (Boyles, Dunbar, and Whitaker 2006). Those roosts usually have stable microclimate conditions and ambient temperature above freezing (Webb, Speakman, and Racey 1996). The majority of migratory bats are above-ground hibernators, roosting in poorly insulated cavities such as tree hollows, crevices in cliffs, bat boxes, and human-made structures (Boyles, Dunbar, and Whitaker 2006). Therefore such species perform long-distance migration in search of hibernation sites in milder climates

(Cryan and Veilleux 2007). Due to the spatial heterogeneity of climate change, there is a high probability that distant habitats may undergo different rates of environmental alterations (Robinson et al. 2009). Thus, changing qualities of seasonal habitats may influence species distributions and the magnitude of migratory behaviour.

The common noctule bat (*Nyctalus nocula*) is a migratory species with a broad distribution range in Europe. Recently this species has received increasing attention from scientists and conservationists due to their high mortality at wind turbines (Lehnert et al. 2014; Măntoiu et al. 2020). Interestingly, the majority of fatalities under wind turbines were reported during migration (Măntoiu et al. 2020; Rydell et al. 2010), and have thus stimulated much-needed research into the species migratory behaviour. Stable hydrogen analysis reveals that common noctule bats have partial and differential migration (Lehnert et al. 2018). Partial migration implies that, within the same population, individuals with different migratory strategies are present: from long-distant travellers that cover more than 1600 km, to regionally commuting bats that travel no further than a couple of hundred km. Differential migration in noctule bats is sex-biased with females travelling longer distances than males (Lehnert et al. 2018). Additionally, it was reported that in response to milder climates at high latitudes, common noctule bats exhibit northward expansion of their winter range (Godlevska 2015). However, little is known regarding the mechanisms behind the observed biogeographical pattern. Additionally, noctule bats are one of the most abundant species in Europe, therefore they play a significant role in transport and trophic functions in ecosystems. Therefore, changes in migratory behaviour and seasonal distribution of common noctule bats may influence community structure in numerous habitats across Europe. Considering their sensitivity to environmental alterations, broad distribution ranges, variation in migratory behaviour and high risk from anthropogenic threats, common noctule bats represent an interesting model for climate change research.

### 3.6. Aim and thesis outline

The aim of this dissertation is to reveal climate-driven changes to populations of migratory bats, from a historical overview through to future perspectives. To understand the magnitude of ongoing changes in populations of bats, we require adequate reference points from the past. Here, I had a unique opportunity to study recent changes in migratory behaviour and distribution of common European migratory bat species, *Nyctalus noctula*, based on long term dataset. In the presented work, I combined different approaches such as stable hydrogen isotopes to reveal migratory destinations; analysis of demographic data to evaluate sex and age population dynamics;

respirometry measurements to establish physiological parameters and environmental modelling to predict suitable for hibernation areas under three climate change scenarios. This variety of applied technics allowed for complex investigation of animal responses to climate change. The obtained results are reported in two peer-reviewed publications and one manuscript, which is in preparation for submission. The research outcome contributed to fill the most demanding gaps in knowledge related to climate-driven changes in populations of migratory animals. The **first chapter** contributed to the improvement of the method for studying migratory animals by using stable isotopes. The **second chapter** was dedicated to climate change responses, particularly to an investigation of the mechanism of climate-driven range changes in populations of migratory bats. The **third chapter** described and evaluated the novel mechanistic approach in environmental modelling of species distribution under the impact of climate change.

In **chapter one,** I have contributed to the validation of the assumptions for stable hydrogen analysis. Stable isotopes are broadly applied for the identification of the geographical origin of bats via transfer function, which is consists of the isotope signature of animals of know origin. However, there was no age validation performed before for stable isotope signatures in bat tissues. The stable isotopes approach was planned as the main method for the assignments of migratory bats in a long-term dataset. Therefore, in **chapter one,** I presented a validation approach for age differences in stable isotope signatures to better understand variation around the transfer function and increase the precision in the prediction of the geographic origin. We sampled fur from adult females and their offspring and analysed their ratios for three isotopes: stable hydrogen, carbon, and nitrogen. We found significant age-related differences in signatures for all three isotopes in bat fur. Our results suggested that distinct isotope signatures between ages are due to differences in diets during the fur growth period. The young bats grow their fur when they are nursed by their mothers, which implies isotope flux during milk secretion. Thus, we could confirm that heavy water isotopes get depleted with an increase in trophic levels, which is reflected by stable hydrogen values in the fur of young bats. Therefore, depending on the research question, we recommended two possibilities for the age implementation into the transfer function. The first option was to use an age-specific transfer function to achieve high precision in age discriminating geographic assignments. The second option was to use samples from both age groups (adults and juveniles) to include age-related variation in geographic assignments, which allowed then for reliable assignment even of the individuals with unknown age. The latter could be especially useful for the identification of geographic origin for carcasses found under the wind turbines.

In **chapter two** using a transfer function, which included individuals of both age classes, we investigated migratory behaviour and demographic structure of *N. noctula* under the distribution shift. The common noctule bats increased their winter range by more than 500 km during several decades. Apart from the observed biogeographic pattern little was known regarding the mechanism relevant for the range change. In 2019, Gill and colleagues described two mechanisms responsible for range change in migratory animals (Gill, Alves, and Gunnarsson 2019a). The first mechanism was based on individual plasticity when individuals can change migratory distances based on environmental and/or social cues. Therefore, they can choose multiple seasonal destinations during their lifetime. The second mechanism implied a change in migratory destinations between generations. The young individuals could establish in new areas due to their dispersal capacity, whereas adult individuals remained consistent with their migratory strategy. A previous study showed that noctule bats are very consistent with their migratory strategy (Lehnert et al. 2018), therefore, we hypothesized that generation shift is the mechanism relevant to the range change in migratory bats. To test our hypothesis, we looked at the long-term data set regarding the demographic structure of winter colonies in the recently occupied winter range and we used stable hydrogen analysis to establish the geographic origin of bats. Our finding supported our hypothesis regarding the generational shift in migratory behaviour of bats which resulted in winter range change. Our results, for the first time, demonstrated the relevance of generation shift in the regulation of species distribution in mammals.

**Chapter three** was dedicated to the elaboration of a mechanistic physiologically-based model for the evaluation and forecasting of suitable hibernation areas in migratory bats. Climate change is expected to affect the cost of hibernation at a given area and might ultimately modify species winter distribution. Indeed, shorter and warmer winters might decrease the winter energy budget and enable individuals to hibernate at higher latitudes. With a novel approach, we aimed to combine fine-scale thermoregulation data of noctule bats with environmental variables from their past and present winter ranges to model species occurrence dynamics. Firstly, this joint approach improved our understanding of species physiological requirements to external conditions. Secondly, it enabled us to refine the modelling of future species distribution under different climate change scenarios. This project enabled us to stand one step ahead by developing effective conservation policies based on robust predictions of species distribution.

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# Chapter 1

## Stable isotope in studies of animal migration:

## Multiple isotope tracers in fur keratin discriminate between mothers and offspring

**https://doi.org/10.1002/rcm.8417**

(page 42-50)

# Chapter 2

## Generational shift in the migratory common noctule bat: first-year males lead the way to hibernacula at higher latitudes

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**Author for correspondence:**
K. A. Kravchenko
e-mail: kravchenko@izw-berlin.de

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**Population ecology**

# Generational shift in the migratory common noctule bat: first-year males lead the way to hibernacula at higher latitudes

K. A. Kravchenko[1,2], A. S. Vlaschenko[3,4], L. S. Lehnert[1,2], A. Courtiol[1] and C.C. Voigt[1,2]

[1]Leibniz Institute for Zoo and Wildlife Research, Alfred-Kowalke- Str. 17, 10315 Berlin, Germany
[2]Institute for Biology, Freie Universität Berlin, Königin-Luise-Str. 1-3, 14195 Berlin, Germany
[3]Bat Rehabilitation Center of Feldman Ecopark, 62340 Lesnoye, Kharkiv Region, Ukraine
[4]Ukrainian Independent Ecology Institute, Plekhanov St., 40 61001 Kharkiv, Ukraine

KAK, 0000-0003-2235-3117; ASV, 0000-0003-0616-8050; LSL, 0000-0003-1282-8334; AC, 0000-0003-0637-2959; CCV, 0000-0002-0706-3974

Many migratory species have shifted their geographic distribution in response to climate change, yet the underlying mechanisms are poorly understood, particularly for mammals. We hypothesized that generational shifts are underlying the observed colonization of hibernation sites further north in a migratory bat, the common noctule (*Nyctalus noctula*). To evaluate our hypothesis, we collected long-term data on the migratory status and demography of common noctules in a recently colonized hibernation area. Based on isotopic data of 413 individuals, we observed a significant decline in the proportion of long-distance migrants from 2004 to 2015 for both sexes and across all age groups. Demographic data collected between 2007 and 2016 from 3394 individuals demonstrated that subadult males were more abundant during the early colonization stage, followed by a gradual shift to a more balanced age and sex composition. Our results suggest that the colonization of hibernacula at higher latitudes is promoted by generational shifts, involving mostly first-year males. Generational shifts seem to be a likely mechanism for distribution changes in other bats and potentially also in other mammals.

## 1. Introduction

The current geological epoch of the Anthropocene is characterized by unprecedented rates of human-driven environmental changes [1]. These rapid changes force animals to respond adequately to survive and reproduce [2]. Migratory species are uniquely vulnerable to anthropogenic threats such as climate change [3,4]. The most commonly observed response of migratory species to climate change is an altered departure and arrival phenology. Yet, migratory animals may also change the geographic distribution of their wintering and summering areas. Such changes present key conservation challenges because altered phenology may cause mismatches between migratory events and resource availability. Also, newly established areas may be poorly protected [5]. Besides understanding these specific changes, it is equally important to investigate the underlying mechanisms, preferably based on long-term data that are sensitive to the dynamics of climate change. This might improve our ability to predict how responsive migratory species are to climate change.

Recently, Gill *et al.* [6] evaluated two possible mechanisms driving changes in the phenology and geographic distribution of black-tailed godwits. The first postulated mechanism was based on individual plasticity, i.e. individuals decide on destinations using environmental or social cues and thus migratory strategies may vary throughout their lifetimes. The second mechanism is based on migratory strategies changing from generation to generation, assuming that juveniles are key in colonizing new areas because of their dispersal capacity, whereas adults may not be able to respond adequately because they lack the flexibility in migration strategies. This mechanism may lead to a shift in the geographic distribution over several generations when individuals with successful migration strategies survive and reproduce. For black-tailed godwits, the authors confirmed the importance of a generational shift [6]. Yet, it is unknown if this mechanism is also relevant for other migratory taxa, such as mammals.

Bats are a diverse mammal taxon, with many species known to migrate over long distances [7]. Bats are particularly sensitive to adverse environmental conditions because the powered flight is energetically demanding [8], forcing individuals to feed almost constantly when airborne [9]. Accordingly, insectivorous bats strongly depend on the availability of insects throughout their active season. During winter, temperate-zone bats enter hibernation, a prolonged state of rest with lowered body temperature and metabolic rates. Bat survival during hibernation depends on an appropriate balance of fat stores, an adequate timing of hibernation and suitable hibernacula. Hence, many temperate-zone bats migrate to hibernate, particularly tree-dwelling species such as common noctules (*Nyctalus noctula*).

In common noctules, females migrate to hibernacula over longer distances than males [10,11], because in summer, females reach higher latitudes to give birth to their young. Males remain at lower latitudes where they mate with females in autumn close to hibernacula [10]. After weaning, young males are more likely to disperse than young females, and males do so in random directions [12]. Yet, most young males from northern breeding grounds seem to establish in areas south of their natal region [13], where they also occupy hibernacula at the northern border of the wintering range [14]. Survival of bats in these hibernacula depends on local temperatures and the length of the winter period [15], making the survival in these hibernacula highly dependent on climate change.

Shifts in hibernation latitude have already been documented for common noctules [16]. Over the last three decades, this species has colonized new wintering sites further north by around 4° latitude compared to previous wintering sites in Eastern Europe. The recent change in the distribution has led to a partial overlap of hibernation and breeding areas [14,17] (electronic supplementary material, S1), resulting in populations consisting of both migrating and non-migratory individuals [18]. Presumably, these changes in migratory behaviour may be driven by milder winters and longer plant growth periods [16,19,20]. However, the exact mechanisms mediating the observed changes in wintering sites remain unknown for bats. A mechanism based on behavioural plasticity would enable bats to respond quickly to new environmental conditions, whereas a generational shift may require more time since it depends on the recruitment of subadults with appropriate migration strategies. Our previous work demonstrated an individual consistency of migratory strategies in common noctules [11]. This argues against the individual plasticity hypothesis. Therefore, we hypothesized that changes in the northern limit of winter distribution of common noctules bats may be mediated by generational shifts.

Here, we used long-term observation data of common noctules in a region with newly occupied hibernacula in Eastern Europe to evaluate how migratory strategies changed within local wintering populations over time. Specifically, we used hydrogen stable isotope ratios in fur keratin to identify the summer origin of bats observed during 12 years in a newly colonized hibernation area. In the remainder of our paper, we refer to regional bats as those that remained within the range of similar isotopic composition, so-called isoclines, which encompasses usually 300–500 km in Europe, whereas long-distance migrants move beyond one or several isoclines [11]. Additionally, we document the age (subadults/adults) and sex composition in hibernacula of common noctules throughout this period. In line with the generational shift hypothesis and the male-biased dispersal documented for this species, we predict young males to be more present during the early colonization than other individuals. Due to climate change, young males may survive better at higher latitudes than before, which may account for the observed shift further north in the species' winter distribution, even when young males disperse in random directions [12,21].

## 2. Material and methods

### (a) Study site

We conducted our fieldwork between 2004 and 2017 in the Kharkiv region (49.9935°N, 36.2304°E; Ukraine), where the local climate is strongly seasonal, with mostly dry-cold winters (−7.1°C in January) and hot summers (+20.5°C in July). Although common noctules are known to breed there since the onset of monitoring in the early twentieth century, the first hibernating common noctule was documented in 1986 [22].

### (b) Collection of fur samples and demographic parameters

Fur samples were obtained from carcasses ($n = 137$) in the repository of the Bat Rehabilitation Center (BRC) of Feldman Ecopark and from individuals ($n = 276$) that were encountered in hibernacula in the Kharkiv area (https://datadryad.org/stash/share/mV6qK-JyQwbj4StU3h1On0Z6Ip3Ph38ULw45A8bes0w). Fur samples were taken with scissors from the interscapular region (electronic supplementary material, S4, for a more detailed description of moulting in common noctules). Between 2007 and 2016, we conducted surveys of 10 hibernacula and noted the sex and age (subadult (sad), i.e. individuals younger than 1 year, adult (ad)) of bats based on tooth wear and reproductive organs [23] (electronic supplementary material, S4).

### (c) Stable isotope analysis

Stable hydrogen isotope ratios of bat fur were analysed at the Leibniz Institute for Zoo and Wildlife Research (IZW) in Berlin as described before [24]. Samples were dried in silver capsules over several days in a drying oven and then transferred to an autosampler. We report stable isotope ratios of non-exchangeable hydrogen in fur keratin in the delta notation ($\delta$) as parts per thousand (‰) deviations from Vienna Standard Mean Ocean Water (V-SMOW). The precision of measurements was always better than 3‰ (one standard deviation) for repeated measurements of internal keratin standards.

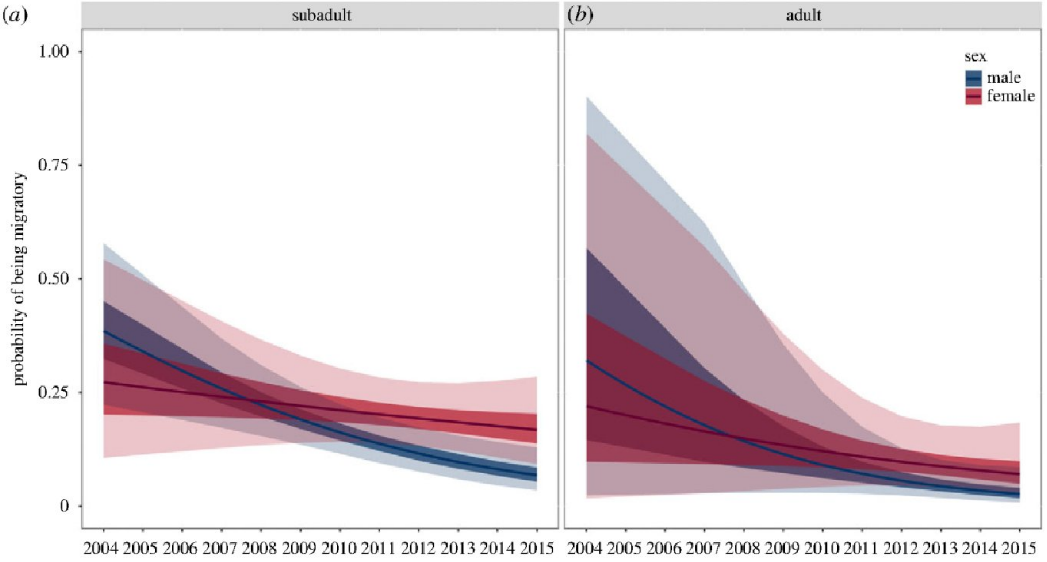

**Figure 1.** Probability for hibernating common noctule bats (*Nyctalus noctula*) of getting assigned as a long-distance migrant over the 12-year study period in the Kharkiv area.

### (d) Statistics

We performed statistical analyses in the R 3.6.0 environment [25]. First, we used the 'prepsource' function from the 'IsoriX' package [26] to aggregate data from the Global Network of Isotopes in Precipitation (GNIP) for years (from 1960 to present time) (electronic supplementary material, S2) [27]. Next, we used the 'IsoriX' package to assign the geographic origin of bats. We classified all bats to either regional or long-distant migrants based on a published transfer function [11]. We categorized bats as regional if $\delta^2H_f$ values were inside of the 95% confidence interval (CI) of the expected $\delta^2H_f$ values for the specific site and as long-distance migrants if individual $\delta^2H_f$ values fell outside the 95% CI. To estimate the probability of being a long-distance migrant, we used binomial generalized linear model (GLM) via the 'glm' function from R, with the binary migratory category (regional versus long-distance migrant) as a response variable and year, sex, age and interaction of year with sex and age as explanatory variables. To trace changes in demographic structure, we used a multinomial model from the package 'nnet' [28] function 'multinom' with year factor as the explanatory variable and the sex-age category (subadult male, subadult female, adult male or adult female) as a response. To test if migratory status was influenced by the proportion of subadult males, we used the 'glm' function with migratory category as a response variable and subadult male versus all other sex-age categories as a binary explanatory variable.

## 3. Results

### (a) Temporal changes in the geographic origin of hibernating bats

For hibernating common noctules of our study area, we did not observe an effect of the interaction of sex or age with time on the inferred migratory status, which suggests that both sexes and all age groups responded over time in a similar way (table 1). The probability of hibernating common noctules to be categorized as long-distance migrants decreased throughout the 12-year period, irrespective of sex and age (figure 1). Additionally, we observed an effect of sex on the probability of assignment as a long-distance migrant, with females being 2.8 times more likely to be long-distance migrants than males.

**Table 1.** Odds ratio, 95% confidence interval (CI) and *p*-values for the binomial GLM fit of the migratory status data. Significant effects are highlighted in italics.

| | migratory status | | |
|---|---|---|---|
| **predictors** | **odds ratios** | **CI** | ***p*** |
| (intercept, male sad) | 0.07 | 0.04–0.15 | *<0.001* |
| year | 0.82 | 0.73–0.92 | *0.001* |
| female | 2.78 | 1.09–7.08 | *0.032* |
| ad | 0.37 | 0.11–1.22 | 0.104 |
| year : female | 1.15 | 0.96–1.38 | 0.126 |
| year : ad | 0.94 | 0.68–1.30 | 0.703 |
| observations | 413 | | |
| AIC | 328.406 | | |

### (b) Temporal changes in the demography of hibernating bats

Between 2007 and 2016, our hibernacula surveys comprised 3,394 individuals (https://datadryad.org/stash/share/XmsW1SVv9mebDMjjQOW_tLOAnuZ-Yfbm1qsy1hlm5Zc). We observed a decrease in the proportion of subadult males from 60% to 23% and an increase in the proportion of adult males from 7% to 35% and adult females from 12% to 25% in the winter population (figure 2; table 2). The probability of being a subadult male did not reliably predict the probability of being migratory (electronic supplementary material, S3). Thus, changes in the proportions of demographic groups alone did not explain the decrease in long-distance migrants.

## 4. Discussion

We studied the mechanism underlying the colonization of a new wintering area in common noctule bats. We observed that regional bats dominated the hibernacula while the proportion of migrants decreased over time. Furthermore, first-year males

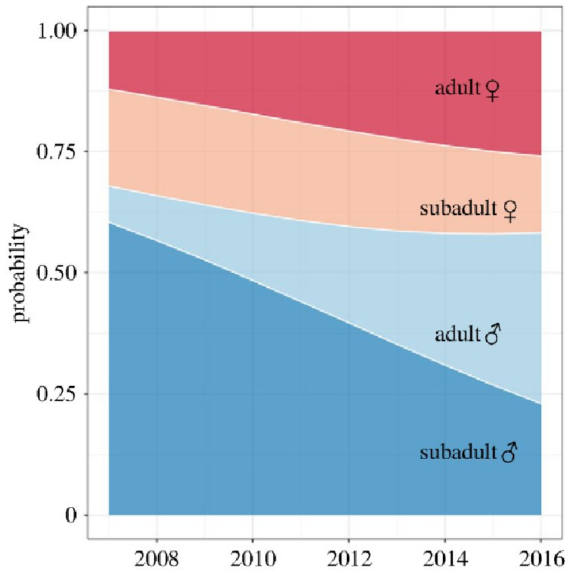

**Figure 2.** Probability for hibernating common noctules (*Nyctalus noctula*) of being in one out of four sex-age categories during the 10-year study period.

were more abundant during the early colonization and likely also the first to colonize the new wintering area. Our findings are consistent with a generational shift mechanism for the colonization of the new wintering area at higher latitude [6]. This is the first study showing the relevance of generational shifts underlying a changing geographic distribution of a mammal, most likely driven by climate change.

We showed that winter aggregations of common noctules in the recently occupied sites were predominantly formed by regional individuals. During our study period, we noted fewer long-distance migrants with a northern summer origin and thus a lower variability in migratory behaviour, yet females tended to migrate over longer distances than males [11]. The decrease in the proportion of long-distance migrants in the hibernacula might be explained by two, not mutually exclusive, processes. On the one hand, the absolute number of long-distance migrants may have decreased over time as a result of a change in migration behaviour. On the other hand, the number of non-migratory individuals may have increased over time as a result of an increasing local population. Since we lack data on the sizes of source populations, we can only speculate about these scenarios but both seem likely for our study area. Indeed, long-distance migrants may become less abundant in the study region as northern areas become more suitable for wintering. This would be consistent with the occurrence of milder winter allowing for shorter hibernation periods [16]. The disappearance of long-distance migrants from the wintering population might simultaneously be driven by old long-distance migrants not being replaced by conspecifics with a similar migration strategy. Notably, common noctule bats are relatively short-lived (2–3 year lifespan [29,30]), which could explain the fast demographic changes observed in our study. Since reproductive rates of common noctules are relatively high for a bat [31], it is likely that favourable climatic conditions could cause rapid growth of the local populations, when breeding and hibernating individuals benefit from an extended plant growth period.

We observed higher recruitment of subadult males than of subadult females in the newly colonized wintering area.

**Table 2.** Odds ratio, 95% confidence interval (CI) and *p*-values and categorical response for the multinomial model fit of the sex and age classes during the 12-year study period. Significant effects are highlighted in italics.

| | Sex-age group | | | |
|---|---|---|---|---|
| predictors | odds ratios | CI | *p* | response |
| (intercept) | 0.09 | 0.07–0.13 | *<0.001* | male ad |
| year | 1.32 | 1.26–1.38 | *<0.001* | male ad |
| (intercept) | 0.31 | 0.23–0.41 | *<0.001* | female sad |
| year | 1.08 | 1.04–1.13 | *<0.001* | female sad |
| (intercept) | 0.17 | 0.12–0.23 | *<0.001* | female ad |
| year | 1.21 | 1.16–1.26 | *<0.001* | female ad |
| observations | 3394 | | | |
| AIC | 8997.969 | | | |

This pattern contrasts with those observed in black-tailed godwits where juveniles of both sexes mediate the change in distribution [6,32]. For common noctules, we expected this sex-difference because young males are more likely to disperse than young females [12,21]. Despite males being known to disperse randomly, we observed that young males from northern breeding grounds dispersed most likely to the south where they established in an area close to the wintering site. By doing so, some young males may establish successfully at higher latitudes than previous generations because climate change may have turned wintering conditions suitable. This could move the northern border of the wintering area to high latitudes over time. We consider it likely that the summer range in common noctules is also undergoing a similar northward shift like the one documented for the wintering range, yet we acknowledge that we lack data on this. Male-biased dispersal is commonly observed in other mammals as well [33], including other bats [34,35]. Therefore, sex differences in the early establishment of wintering areas may occur more broadly across migratory bats and other mammals.

The relevance of generational shifts for mediating changes in the geographic distribution of animals implies that populations may respond slowly to global climate change. The capacity to respond adequately on the population level may be defined by the level of intra-specific variation in migratory strategies, the reproductive rate and the rate at which young individuals are able to settle at new, suitable wintering areas, which is largely defined by the dispersal capacity in case of bats. We envisage that common noctule bats may respond relatively quickly to changing climatic conditions, owing to their relatively short lifespan, high reproductive rate and high dispersal capacity. We anticipate that species with a lower intra-specific variation of migration strategies, lower reproductive rates and a lower dispersal capacity may require more time to adjust to a changing climate. In the extreme, these species may not be able to respond adequately to a rapidly changing climate. The conservation of mammal species may require the development of suitable measures that take into account the susceptibility of a species to climate change which seems to be largely defined by how species-specific traits influence the speed at which generational shifts can compensate the effect of a changing climate.

**Ethics.** Fieldwork was carried out under license numbers Kh_KU_1006 8212 260. The Bat Rehabilitation Center works under the permission of Kharkiv Oblast Authority of Ecology and Natural Resources, and Ethical Commission of V.N. Karazin Kharkiv National University.

**Data accessibility.** Data from the study have been deposit in the electronic supplementary materials (table S3 and table S4) and is available from the Dryad Digital Repository Table S3: https://datadryad.org/stash/share/mV6qK-JyQwbj4StU3h1On0Z6Ip3Ph38ULw45A8bes0w Table S4: https://datadryad.org/stash/share/XmsW1SVv9mebDMjjQOW_tLOAnuZ-Yfbm1qsy1hlm5Zc.

**Authors' contributions.** K.A.K., A.V. and C.C.V. designed the study; C.C.V. and A.C. advised the students; K.A.K. and A.V. carried out the fieldwork; K.A.K., A.C. and L.S.L. performed the analyses. K.A.K., C.C.V. and A.C. wrote the manuscript. All authors offered comments, agreed to be held accountable for the content herein and approved the final version of the manuscript.

**Competing interests.** We declare we have no competing interests.

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# Chapter 3

## Hibernation energetics drive the range shift of a temperate zone bat in response to climate change

# Hibernation energetics drive the range shift of a temperate zone bat in response to climate change

(Manuscript is in preparation for submission)

Kravchenko KK[1,2], Voigt CC[1,2], Lange S[3], Currie S[1]*, Courtiol A[1]*

[1]Leibniz Institute for Zoo and Wildlife Research, Alfred-Kowalke- Str. 17, 10315 Berlin, Germany

[2]Institute for Biology, Freie Universität Berlin, Königin-Luise-Str. 1-3, 14195 Berlin, Germany

[3] Potsdam Institute for Climate Impact Research (PIK), Department of Transformation Pathways, P.O. Box 60 12 03, 14412 Potsdam, Germany

*Authors with equal contributions

## Abstract

Many temperate zone species shift their geographical distribution in response to a warming climate, yet for most cases, we lack models to assess how rapid and how severe these shifts are. This is particularly true for heterothermic mammals that depend on optimal temperatures for hibernation. Here, we quantified the energetic requirements of hibernating common noctule bats (*Nyctalus noctula*), a widespread migratory bat from Europe, to explain its past and present distribution, and to predict its future range shift in response to a warming climate.

We measured the metabolic rate of captive common noctules across a range of temperatures typical for hibernacula. We, then, estimated the required energy budget of past (since 1850), and future (until 2100) hibernation periods using the historic climate record and the predicted ambient temperatures during winter based on three climate change scenarios varying in severity (mild, moderate and severe).

Respirometric measurements underlined a strong correlation between ambient temperature and metabolic rates of hibernating common noctule bats. We inferred from these measurements that shorter and warmer hibernation periods will cause hibernating bats to use less fat stores at northern latitudes. Our spatial model predicted that hibernation will become feasible at higher latitudes for common noctule bats, which will ultimately lead to a 200 km northward shift of the suitable hibernation region by the year 2100 even under mild climate change scenarios, and to a 300 km northward shift for both moderate and severe climate change scenarios by the year 2100.

The predicted northward shift of common noctule bats will alter the composition of local bat assemblage. Further, the predicted range shift will change the spatial and temporal patterns of migration of this species, thus requiring flexible management of populations which integrates over the current state and the future range shift.

**Keywords:** climate change, ecophysiology, migratory bats, shared socioeconomic pathways, winter budget, range shift

## Introduction

The current anthropogenic impact on global ecosystems affects the lives of animals worldwide, forcing individuals to respond quickly to environmental challenges such as climate change in order to survive (Scheffers et al. 2016; Radchuk et al. 2019). For many species, the speed of these environmental changes is too swift to allow evolution by natural selection. This will ultimately lead to the extirpation of populations or species (Etterson 2001). Previous work on the biological consequences of climate change has focussed by large on phenotypic plasticity, which likely supports changes in spatial distribution (Parmesan 2006; Nunez et al. 2019). Little is known, however, about the relevance of physiological plasticity for predicting changes in the spatial distribution of animals in response to a warming climate (Seebacher, White, and Franklin 2015). As the capacity for species to sustain particular temperatures is directly constrained by their thermoregulatory ability, it appears particularly important to better understand how global warming may influence organisms from different thermoregulatory strategies (Boyles et al. 2011). We here focus on heterothermic endotherms, which are particularly susceptible to changing ambient temperatures and which are arguably the least studied group with respect to the question of how climate change affects their survival and geographical distribution (Levesque, Nowack, and Stawski 2016).

Heterothermic endotherms are widespread among mammals, comprising about 40% of modern mammalian species and more than half of the orders (Geiser and Turbill 2009). As for all endotherms, heterothermic endotherms have the ability to use metabolic heat for maintaining a stable body temperature; a strategy which broadens their activity range at the cost of increased energetic expenditure at low temperatures (Grigg, Beard, and Augee 2004). Heterothermic endotherms, can sustain a high metabolic rate and maintain a stable body temperature when food is abundant, but unlike other endotherms they also have the capacity to survive periods of food shortage by reducing their metabolic rate followed by a corresponding drop in body temperature -- a physiological state known as torpor (Lovegrove 2012).

We hypothesise that heterotherms may be in a much better position than other mammals to cope with ongoing and future climate change due to their ability to enter torpor. Historical and pre-historical data support this view. For example, heterothermic species account for only 6.5% of mammalian extinctions that occurred during the last 500 years (Geiser and Turbill 2009). More speculatively, heterothermy is thought to account for the survival of mammals during the Cretaceous–Paleogene extinction marked by long episodes of scarce food availability and cold (Geiser and Turbill 2009; Liow et al. 2009; Nowack, Stawski, and Geiser 2017).

To assess more specifically the capacity of a particular heterothermic endotherm to respond to ongoing and future climate change, one needs to look precisely at periods of critical resource availability and at energy expenditure during this period (Kronfeld-Schor and Dayan 2013). When the limitation in food resources is both intense and long lasting, many heterothermic species enter prolonged torpor - a behaviour that can last from several weeks to an entire year (Geiser 2007); a thermoregulatory strategy called hibernation (Boyles et al. 2013; Geiser and Ruf 1995). At the physiological level, hibernation consists of torpor bouts that can last for weeks, intermittently dispersed with arousals where body temperature returns to a stable, normothermic level. Such arousals appear necessary for the excretion of metabolic by-products and homeostatic maintenance (Geiser 2004).

Climate change, through its influence on temperature, is expected to affect the energetic budget required for a successful hibernation at any given location. First, except within a very small range of ambient temperatures where metabolic rate is minimal (i.e. the thermoneutral zone; (Geiser 2004)), the metabolic rate of heterothermic organisms is strongly dependent on the ambient temperature during both torpor and normothermy. Second, the probability that, at a given time, an individual is either in torpor or normothermy depends also on the ambient temperature as individuals adjust their behaviour to balance between energy preserving torpor and energetically expensive normothermy. Therefore, studying how ambient temperatures impact the energetic cost of hibernation helps to evaluate how climate change shapes the area where a given heterothermic species may be able to live or not, and how the geographical distribution of such a species will change in the future. Combining this information with data on the capacity of animals to colonise new environments at the required pace may then help to assess the extinction risk of heterothermic endotherms in the future.

In the present study, we developed and applied an eco-physiological framework to assess the influence of climate change on the thermal niche of a heterothermic mammal: the European bat species *Nyctalus noctula*. Bats are a good model to study the interplay between climate change and heterothermy because they expend a large amount of energy when active because of powered flight. Accordingly, they depend on sufficient food supplies, yet they are constrained at the same time in the ability to store energy because of elevated flight costs when body mass increases (Stawski, Willis, and Geiser 2014; C. C. Voigt 2000). Accordingly, bat species of the temperate zone rely heavily on torpor to survive periods with limited food supply. Here, we quantified the relationship between metabolic rate and ambient temperature in torpid and normothermic individuals. Additionally, we measured the relationship between ambient temperature and the probability to be in either physiological state. We then fitted thermoregulatory curves to physiological state probability data using a model of energetic expenditure tailored to heterotherms, which generates information on how the thermal niche of our model species varies in space and time under different global climate scenarios. We conducted our analysis for three well-established climate change scenarios (SSP126, SSP370 & SSP585) to forecast the ability for our species to persist under different predicted climates. The general principles we deployed were i) to model the daily energy budget as a function of the ambient temperature, and ii) to deduce the total energy required to survive the entire hibernation period. We hypothesised that milder winters in northern latitudes enabled a northward shift in the species' range, due to the reduced energy requirements to survive shorter and warmer winters. Following this, we predict a progressing northward shift in the distribution of thermally suitable hibernation areas as these regions continue to experience milder winters with climate change. We selected common noctule bats (*Nyctalus noctula* ) as our models since this species is widespread in Central Europe and since it has already demonstrated a northward shift of its wintering range in the last 30 years (Kravchenko et al. 2020). Lastly, historical data on the geographical distribution of this species offers the unique opportunity to perform model hindcasting, which ultimately validates our approach.

## 2. Results and Discussion

Via a novel approach to physiological niche modelling for heterothermic species, we were able to track past and future changes in areas suitable for hibernation for a model bat species. This approach relied on our determination of a reliable proxy of required energy by means of accurate metabolic measurements taken at a wide range of temperatures. Alongside this, our classification of the probability of an individual to be in different physiological states ensured realistic budget calculations. We use the latest predictions for ambient temperature provided at the highest temporal resolution (daily averages) by validated models of climate change scenarios to estimate the energy budget for each day of the hibernation period across 250 years, at any location in Europe.

### 2.1 Ambient temperature, physiological state and energetics

By exposing 12 common noctule bats to a wide range of ambient temperatures, we were able to record changes in metabolic rates (Fig. 1). The relationship between metabolic rate of common noctule bats and ambient temperature followed the typical pattern documented for other heterothermic endotherms; with a linear increase in metabolism as compensation for heat loss during normothermy at low temperatures and a curvilinear relationship between ambient temperature and metabolic rate during torpor (McNab 2002). We assigned the metabolic rate to different physiological states such as torpor and normothermy in a standardised way using the "torpor" package, which circumvents debatable issues of arbitrary definitions/thresholds for classification (Fasel, Vullioud, and Genoud 2019). Below 33.2 °C, resting metabolic rate increased linearly as the ambient temperature fell. During torpor, metabolic rate was at its minimum ~5 °C when the body temperature of the bats approximated ambient temperature. At this specific temperature, the energy expenditure in torpor was only 1% of the energy expenditure in normothermy, and around 6% of the basal metabolic rate of bats within the thermoneutral zone (33.2-35°C). Such a significant reduction of the metabolic rate in torpor characterises common noctule bats as a truly hibernating species (Geiser 2004). Below this thermoconforming minima, metabolic rate increased linearly with decreasing temperature as individuals thermoregulated to maintain body temperature around 5°C. Yet despite these increased costs, metabolic rate during torpor down to 0°C was still substantially lower than if bats were normothermic.

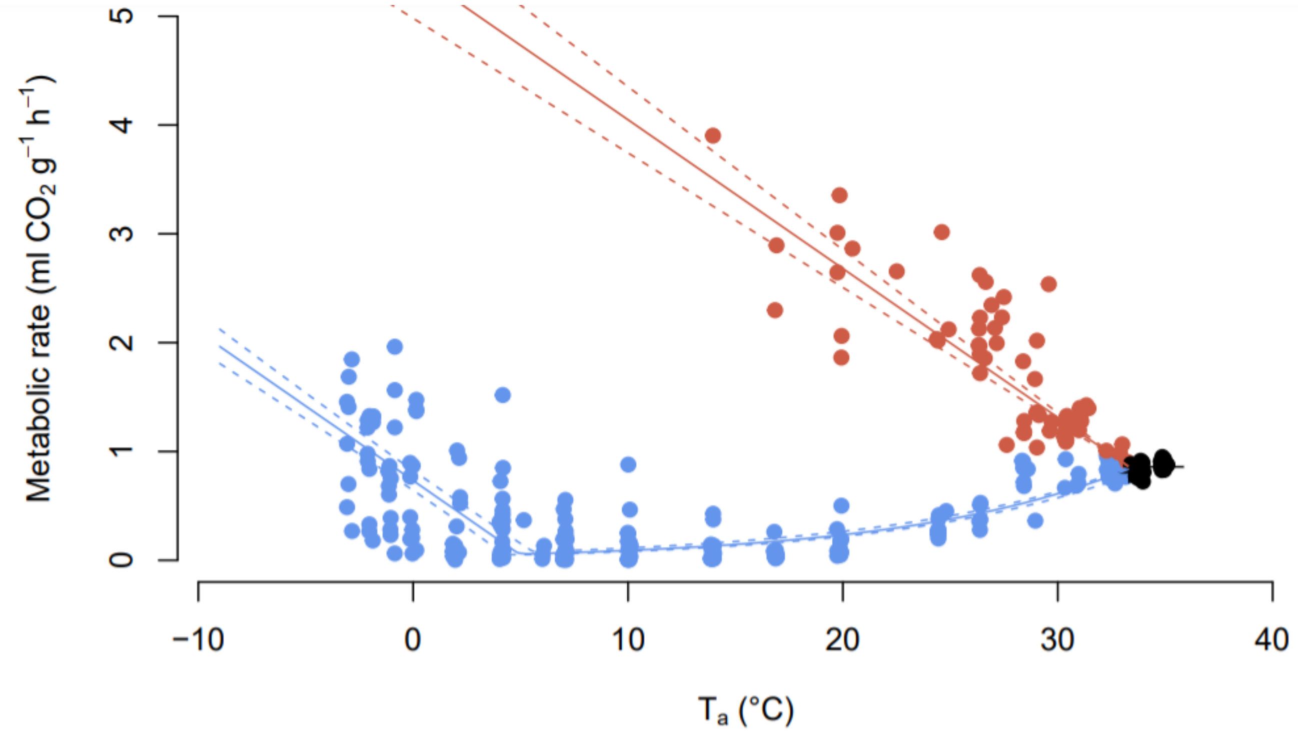

**Fig. 1.** Thermoregulatory curve of common noctule bats. Metabolic rate is expressed in standardised units representing ml of $CO_2$ production per gram of body during one hour. Metabolic rate values corresponding to basal metabolic are marked by black, metabolic values representing metabolic costs in eutermia, below the thermoneutral zone, are marked by red, and in blue are the metabolic costs in torpor.

The probability of arousal and the corresponding length of torpor bouts at a given temperature is an important variable that allows for the realistic prediction of energy expenditure throughout the entire hibernation period. To calculate this for our model species, we exposed 24 bats to a fixed ambient temperature (2, 7, or 12°C) for four weeks and quantified the frequency of arousals and duration of torpor bouts during this period (SI 3). We observed that the probability of arousal decreased as ambient temperature fell, as has been reported for other heterotherms (Geiser and Kenagy 1988). However, this is only true above a critical temperature corresponding to the minimal metabolic rate in torpor. Below this, further decreases in temperature lead to an increase in the probability of arousals as increased energy expenditure decreases torpor doubt duration (Geiser 2013; Humphries, Thomas, and Speakman 2002). For noctule bats, we detected that the lowest probability of arousal and maximum length of torpor bouts (ca two weeks) occurred at 2 °C. Below this, we assumed the probability curve to be a mirror image of the pattern we recorded for ambient temperature higher than this threshold as shown for other hibernators (Barnes and Buck 2000) (SI 3).

### 2.2. Costs of hibernation in relation to climatic characteristics

Since our model for estimating the overall energy expenditure during the hibernation season is based on daily temperatures, it was not *a priori* clear if any general climatic characteristics of the hibernation season would strongly correlate with such an integrative cost. We observed nonetheless that simple metrics were actually sufficient. In particular, the mean temperature and duration of the hibernation season turned out to be very accurate predictors of the overall energy budget required for hibernation (Table 1). Such a budget decreased with the mean temperature and increased the duration of the hibernation period (Fig. 2). These results suggest that one could rely on these two climatic characteristics to obtain qualitative predictions of how the hibernation energy budget may change in a given location as the climate is changing, without the need for physiological measurements. Here, we suggest that the increase in milder winters, predicted at northern latitudes, will require bats to expend less energy in order to persist during the hibernation period (Fig. 3). Consequently, global warming may allow heterothermic animals with a limited capacity of fat storage to hibernate at increasingly higher latitudes.

Our models are as yet limited in our ability to reliably predict the situation for the Southern limit of our species' distribution. While our predictions show that the energetic cost of hibernation should drop, warming winters in cold temperate climates may also impose additional costs on heterothermic endotherms which we did not consider. This is because higher temperatures make torpor less efficient energetically, but overall conditions may still be too unfavourable for heterotherms to avoid torpor altogether (Boyles et al. 2011). Under global warming, heterothermic species that shift their range poleward would thus be more likely to maintain a positive energy balance during the hibernation season more easily. However, at higher ambient temperatures, despite the increased costs of hibernation, the probability to replenish fat sources may also increase, as potential food sources become available earlier in the season or even throughout winter (Turbill and Geiser 2008b, 2008a). Further investigations regarding the effect of climate velocity on the phenology of producers and consumers in natural ecosystems are required to identify possible phenological mismatches in organismal energy consumption and expenditure (Bailey et al 2020).

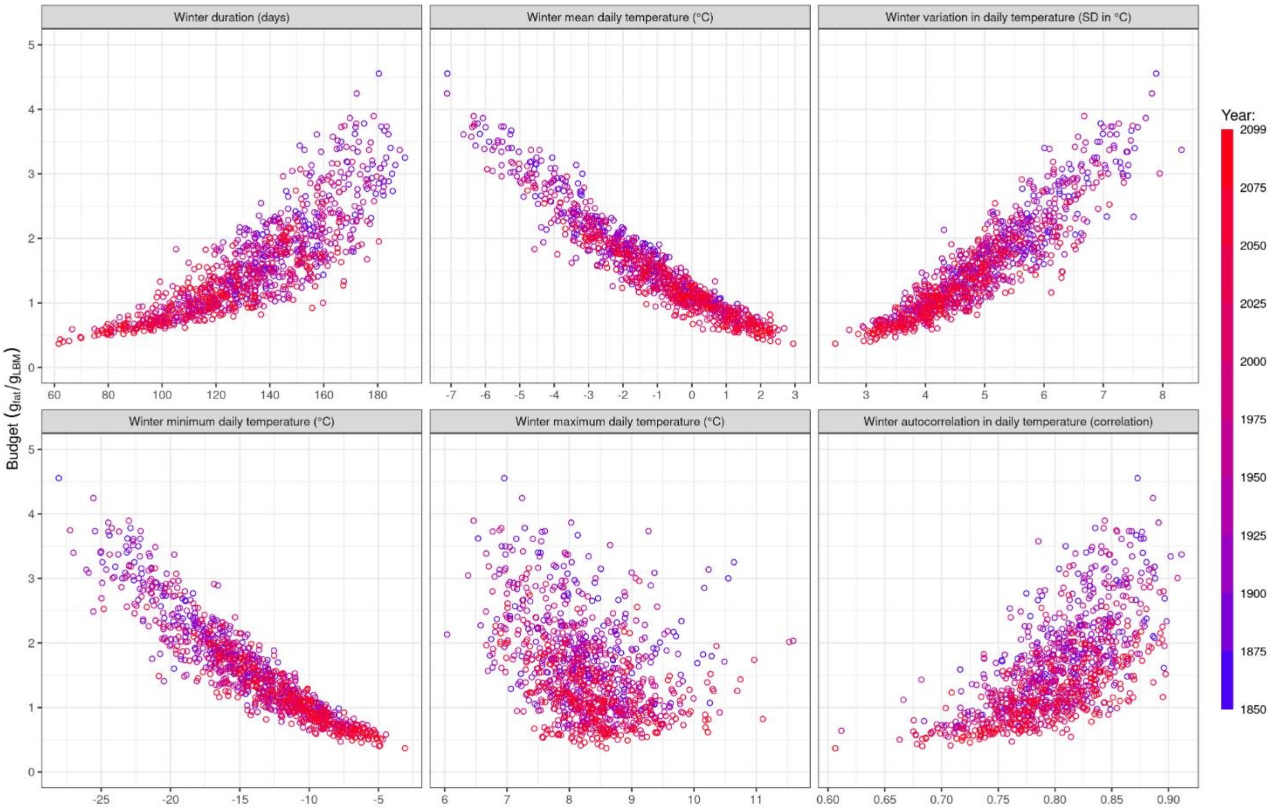

Fig 2. Relation between the hibernation budget (estimated in grams of fat fuel per gram of Lean Body Mass) and climatic variables during the hibernation period.

Table 1. Correlation coefficients for all climate characteristics vs hibernation budget

| Climat variable | correlation coefficient |
|---|---|
| Winter duration (days) | 0.872 |
| Winter mean daily temperature (°C) | -0.960 |
| Winter variation in daily temperature (SD in °C) | 0.917 |
| Winter minimum daily temperature (°C) | -0.940 |
| Winter maximum daily temperature (°C) | -0.401 |
| Winter autocorrelation in daily temperature (correlation) | 0.681 |

### 2.3. Latitudinal shift in thermally suitable hibernation areas under the different climate change scenarios

Performing physiological measurements provided us with the ability to go beyond qualitative predictions and make quantitative predictions. In our case, we delineated thermally suitable hibernation areas as the set of locations associated with an amount of fat fuel required for survival of hibernation period, set at a threshold of lower than 2 grams per gram of lean body mass (see Methods **3.5.3** for justification). Based on the estimations from our mechanistic model, we predict the mean latitude of the thermally suitable hibernation areas to move on average by at least 200 km by the end of the century. The exact magnitude of the predicted shift depends on the climate change scenario considered. Out of the three SSPs we considered (mild (SSP126), moderate (SSP370) and severe (SSP585)), the most severe scenario best tracks recent climate change, unless drastic climate change mitigations start to be put into effect. Without these mitigations, the common noctule bat will thus likely see an expansion or northward shift of their hibernation areas of 300 km by 2100. Importantly, the spatial distribution of the suitable areas we predict for recent years falls within the species range documented by IUCN, which validates our approach.

Whether a particular shift in areas suitable for hibernation has a critical impact on species survival or not depends on the ability of populations to track environmental change. Our model species is widespread and highly mobile and has been observed to be capable of range shifts in a few decades only (Kravchenko et al. 2020). These characteristics are likely to provide common noctules with the ability to track their preferred thermal conditions with little time lag. However, the high velocity at which suitable areas are shifting suggests that heterothermic endotherms with limited dispersion capabilities and small latitudinal ranges may not be able to keep pace with global warming. Therefore, future studies should attempt to estimate both the geographical shift in physiologically suitable hibernation areas provided by our approach and the capacity of species to follow them. Such comparisons, once performed in varied species, should provide us with essential information regarding the resilience of heterothermic endotherms to the ongoing global warming.

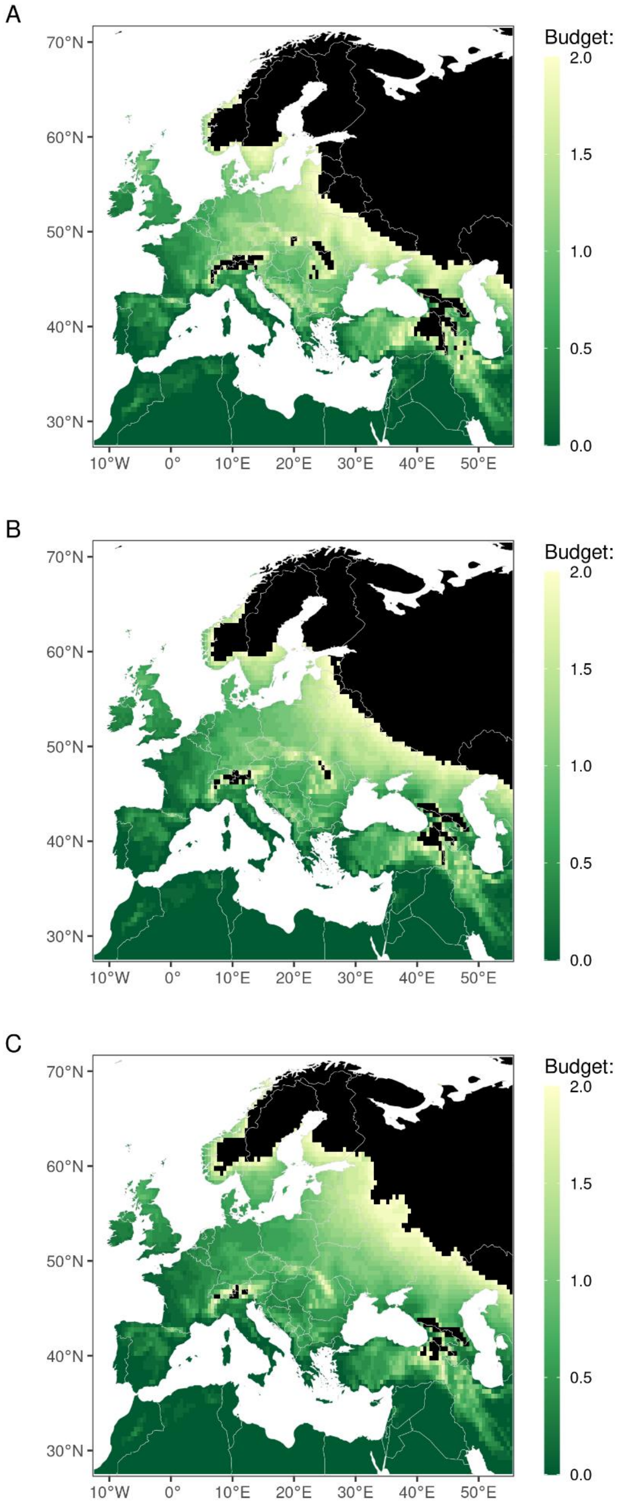

Fig. 3 Energy budget value per location based on 30 years' averages: A - 1850-1870; B - 1993-2013; C - 2069-2099. Areas in black represent locations where budget value is higher than the upper threshold for fat accumulation in 2 gram per gram of lean body mass.

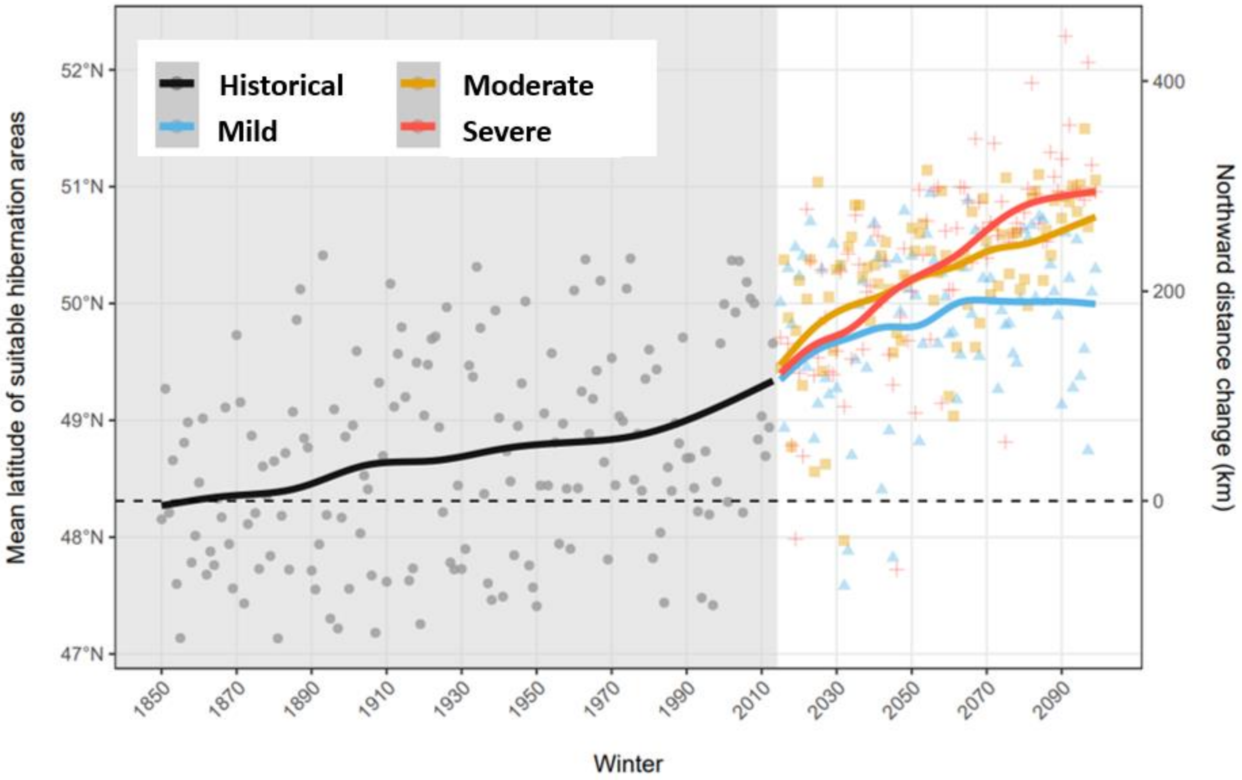

Fig 4. Northward shift of suitable hibernation areas under different shared socio-economic pathways (SSPs). The lines show smoothed trends in the mean latitude (left y-axis) and in the corresponding distance (right y-axis) from the mean latitude in 1850 (dashed horizontal line) for the suitable hibernation areas as predicted by a mechanistic model of the energetics of overwintering in a bat. The black line corresponds to historical temperature data while coloured lines correspond to predictions from three SSPs associated with varying intensity of global warming. Data represent year-by-year predictions.

## Conclusion

Our results are the first attempt to apply a mechanistic thermal niche modelling for heterothermic endotherms undergoing a period of vital resource bottleneck, which defines survival. The parametrization of a thermal niche model for heterotherms boils down to the estimation of two key variables across the range of ambient temperatures: (i) probability of animal to be either in an energy-saving state (torpor) or in an energy-expensive state (normothermy); (ii) actual energy expenditure at each of the physiological states described by the thermoregulatory curve. Such data is already available for hundreds of heterothermic species and thus our approach can readily be implemented across diverse mammalian taxa. However, on a broader scale, data regarding energy expenditure and metabolic rate is available only for around 10% of mammalian species. While this does not limit the implementation of our modelling approach provided that the necessary physiological measurements are performed, it emphasizes the urgent need to fill gaps in ecophysiological research across numerous taxa. Endangered species are significantly underrepresented in empirical physiological studies, however, information regarding their thermal physiological limits might be crucial in predicting species survival in times of climate change.

## 3. Methods

### 3.1. Animal collection, care and treatment

All husbandry and experimental procedures were approved by the German Committee of Animal Welfare in Research (permit no. 2347-26-2018) and the corresponding conservation authorities (permit no. 4743/128+17#222800/2018). Twenty-four male common noctule bats (*Nyctalus noctula*) were collected from hibernacula in Brandenburg in November 2018. After health and physical condition control by approved veterinarians, animals were housed at the field station of the Leibniz Institute for Zoo and Wildlife Research in Niederfinow, Germany. Animals were kept in polyvinyl chloride boxes (36× 25 × 23 cm) with holes in the lid and walls (for air circulation) with soft mesh from organic material glued to the walls (for animals to roost against and for comfort). Roost boxes were kept in a room with a temperature range of 14-18 C and a natural light cycle. Bats were taught to feed independently and food (larval *Tenebrio molitor*) and water were available ad libitum. We did daily observations of animal condition and body mass measurements and supplemented the food with a vitamin and mineral mixture (Korvimin, WDT, Germany). After the completion of all experiments, individuals were inspected by veterinarians and released back into the wild.

### 3.2. Metabolic measurements

To generate a complete thermoregulatory curve for *N. noctula* we measured CO2 production as a proxy for metabolic rate using open-flow respirometry at a range of ambient temperatures from +35 C to -3 C. For a more detailed description of our protocol of metabolic rate measurements and the thermoregulatory curve please see **Supplementary material 1**.

CO2 production was recorded at 5-min and 3-min intervals, over a period of 24h and animals were exposed to each temperature for at least 2h to ensure they were in a steady-state condition. Using these data, we calculated the mean amount of CO2 produced per hour and identified the minimum average value (taken from 1-h means) per temperature and individual. Metabolic rates were calculated following equation (4.25) from Lighton 2009:

$$Ms\,CO2 = [FR(F'\,e\,CO2 - F'\,i\,CO2) - F'\,i\,CO2\,(Ms\,O2)]/(1 - F'\,i\,CO2)$$

We converted total torpid and normothermic metabolic values first into kilocalories (0.004825 kcal/$CO_2$ ml) and then ultimately into fat mass (9.4 kcal/g) to estimate the amount of fuel mass in grams (9.4 kcal/g).

### 3.3 Determining the torpor bout duration and the probability of normothermy

We monitored torpor bout durations by dividing bats into three groups and exposing them to 3 experimental temperatures (12°C, 7°C, 2°C) for 4 weeks. Each animal had a temperature logger attached (type iButton DS1922L-F5#, Maxim/Dallas Semiconductor Corp., USA) to their back which was programmed to record skin temperature every 20 minutes. The number of arousals from torpor was calculated based on the increase in body temperature. Further analysis was performed in R 4.0.5 programming environment (R Core Team 2021). The probability of being normothermic across a range of temperatures was estimated using a generalised linear mixed-effect model (“glmer” function from lme4 R package). The state of the animal was converted to a binary response variable (0 - Torpor and 1 - Normothermy) and Ta was an explanatory variable, with individual as a random effect. Model structure and coefficients are presented in **Supplementary material 2**. We mirrored the Ta effect curve obtained from empirical data for the temperatures range below the lower critical temperature (Tlc) for thermoregulation in torpor. This assumption was based on Barnes and Buck 2000 studies on ground squirrels which showed that the lowest probability of arousals and longest torpor bout duration occur at Ta around Tlc when MR is at its lowest. Below the Tlc, the probability of arousal increases in the same fashion as above Tlc as metabolic rate during torpor increases with thermoregulation. The probability curve is presented in **Supplementary material 3**.

### 3.4 Estimation of hibernation energy budget

Based on our generated thermoregulatory curve and arousal probability function we predicted an energetic budget, expressed in grams of fat fuel per day as a function of ambient temperature at each degree from - 65 to +44 °C. This range of temperatures was chosen based on the range in our environmental data. We used daily averaged environmental data, with daily temperature resolution (described in 3.5.1). To estimate the overall winter budget at any location we sum up energy costs for all days during the defined winter period at the corresponding location. The table of metabolic costs per half an hour at each degree ºC is presented in ESM4.

## 3.5 Geospatial modelling

### 3.5.1. Temperature data set

We used the Inter-Sectoral Impact Model Intercomparison Project (ISIMIP3b) (https://www.isimip.org/) based on the output of phase 6 of the Coupled Model Intercomparison Project (CMIP6; (Eyring et al. 2016)). Within CMIP6 we used the global climate model MPI-ESM-HR (Germany) assembly member r1i1p1. The data on global surface temperatures is available for the period 1850-2100 at spatial resolution 0.5 x 0.5 degree (~55.5 km) and daily temporal resolution. Data from 2015-2100 included three climate change scenarios: mild SSP126, moderate SSP370 and severe SSP585.

### 3.5.2Winter definition

We define winter temperatures for each couple of calendar years. We consider 14 days as minimal winter duration which would require prolonged torpor. The start of the winter period was defined as the first day of two weeks period when Ta falls constantly below 7°C. The end of the winter was defined consequently as the last day of the period when Ta falls constantly below 7°C. We chose 7°C as a threshold for insect activity (Zahn and Kriner 2016).

### 3.5.3 Calculate suitable for hibernation areas

For each cell of the temperature raster, we calculated the total winter budget depends on the duration of winter within each cell. Next, we plotted energy budget values across Europe and marked territories, where the budget is not exceeding 2 grams of fat fuel per gram of lean body mass, as thermally suitable areas. 2 grams of fat fuel were estimated as the maximum possible fat load for an airborne animal of noctule size / estimated based on maximum known body mass obtained from free-ranging animals minus the weight of the lean body mass. This way we estimated thermally suitable areas for each year from 1850 to 2100.

### 3.5.4 Estimation of the shift in suitable wintering areas

For each thermally suitable area, we estimated mean latitude. Next, we calculated the difference between mean latitude for each pair of consecutive winters and expressed it in degrees of latitudes and additionally in kilometers. It allowed us to estimate the northward shift of suitable wintering areas with time and according to three climate change scenarios. Next, we plot the values of mean latitude against the time and according to 3 climate change scenarios based on shared socio-economic pathways. Plotting the smoothed average, we estimated the average shift in latitudes and kilometers over 250 years.

### 3.5.5. Data and code availability

We performed statistical analyses in the R 4.1.0 environment (R-Core Team 2021). The data and complete code needed to replicate the results of this paper are available on Zenodo & GitHub (https://github.com/courtiol/winteR). Additionally, temperature dataset ISIMIP is available at https://www.isimip.org/gettingstarted/data-access/ .

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# 7. GENERAL DISCUSSION

## 7.1 Prospects for migratory bats in a warming world

The increasing pace of climate change is affecting an ever-growing number of ecosystems worldwide. The survival of species within these ecosystems depends on the consistency of their responses to the pace of environmental change (Scheffers et al. 2016). Migratory species depend on a variety of remote habitats at different stages of their life cycle, and many of these habitats are undergoing environmental change at different paces (Robinson et al. 2009). In this regard, predicting how climate change impacts entire migratory systems is extremely complex. The overarching work of this thesis focussed on revealing climate-driven changes in the migratory behaviour and distribution of common noctule bats in Europe. By validating (Chapter 1) and incorporating (Chapter 2 and Chapter 3) various techniques and methodological approaches, I could tackle the magnitude of responses to climate change on different levels of the ecological organisation; from a physiological response to environmental conditions at the organismal level, to alterations in migratory behaviour on a population level, and changes in geographic distribution at the species level. My main findings elaborated on physiological and behavioural mechanisms underlying climate-driven range shifts and provided evidence that migratory bats were able to respond quickly to the rapid pace of climate change. Yet, the consistency of responses is conditioned by species-specific traits and climate velocity, as a metric of speed, and direction of climate displacement.

The ability of species to track the magnitude of environmental change is crucial for their persistence (Schloss, Nunez, and Lawler 2012). My results suggest that common noctule bats are able to follow the predicted northward shift of suitable hibernation areas, as they have already begun doing so (Chapter 2; Kravchenko et al 2020). However, the even greater northward shift of wintering range which we predict (up to 300km by 2100; Chapter 3), may result in significant changes in species migratory behaviour, as recently colonised wintering areas overlap with known breeding grounds (Kravchenko et al. 2020). This overlap means that there are now areas where individuals will reside permanently, year round. Even though common noctule bats are known to be partial migrants; my results (Chapter 2) provide new information about an increase in the proportion of permanent residents in populations in the north of their range. We observe the facilitation of a partial cessation of migratory behaviour in these bats. A shortening of migratory distances, and cessation of migration entirely, is not unique to bats and was previously described for migratory birds, insects, and fish in response to climate change (Flack et al. 2016; Moore et al. 1998; Jepsen et al. 2015; Wikelski et al. 2007; Gresh, Lichatowich, and Schoonmaker 2000).

Nevertheless, it is predicted to have significant ecological implications due to the resultant decrease in trophic and transport functions provided by migratory species worldwide (Wilcove and Wikelski 2008).

The establishment of resident populations in migratory species is promoted by changes in resource availability during the year, especially in habitats with pronounced seasonality (Robinson et al. 2009). In particular, the increase in productivity of boreal habitats in the Northern Hemisphere as the climate warms may provide sufficient food resources for potential migrants to survive the winter at high latitudes (Kong et al. 2017). Food availability, or more precisely food shortages during the winter, is the crucial factor driving southward migration in many bird species (Bruderer and Salewski 2008). In contrast, due to the fact that bats and are heterothermic endotherms and use torpor as an energy-saving mechanism, many are capable of using only internal fat stores to survive such food shortages (Ruf and Geiser 2015). Therefore, migration and prolonged torpor (hibernation) are generally considered two alternative strategies to escape resource bottlenecks during the year (Winger et al. 2019). Yet, migratory bats are unique in this sense as they use both strategies and migrate southward for hibernation. The need to combine both strategies is most probably conditioned by the roosting ecology of bats (Boyles, Dunbar, and Whitaker 2006), as migratory bat species use poorly insulated roosts and therefore require milder climates to persist through the winter. However, it is still unclear to which extent the abiotic factors such as winter temperatures, and biotic ones, such as food source availability, interplay in migratory decisions among bats.

My results (Chapter 3) showed that with shorter and warmer winters at higher latitudes bats require less energy, stored as fat, to survive the hibernation season. However, while it seems that milder climates might provide immediate benefits for individual survival, it is difficult to predict long-term consequences. It was shown that at least temporary, boreal zones will undergo an increase in productivity, mainly due to elongation of the plant-growing season (Piao et al. 2011). This extension may also facilitate insect activity during the season and thus provide bats with required food sources for pre-hibernation fat accumulation (Fernández-Tizón et al. 2020; Ekholm et al. 2019). Yet some studies highlight that soil conditions may be a limiting factor to support an extension of the plant-growing season (Laamrani et al. 2020). Moreover, due to climate warming, vegetation structure also may undergo significant structural changes. It was shown that broad-leaf forests in the US are shifting their distribution northward, being substituted by more heat and drought-resistant plants from the equatorial zone (Scheel, Vincent, and Cameron 1996).

Consequently, there was an increase in local extinctions of bat species who depend on deciduous forests as a source of food and roosts (Scheel, Vincent, and Cameron 1996).

Yet another limiting factor for residential bat persistence at high latitudes could be the ongoing massive insect extinction, caused by numerous human activities. This includes the use of pesticides in agricultural areas, a drastic decrease in natural grasslands, and numerous sources of disturbances, such as noise and light pollution, which negatively affect insect abundance and diversity (Goulson 2019). Thus, by becoming progressively more residential, common noctule bats increase their vulnerability to local habitat productivity. Moreover, it was shown that the evolution of residential sedentary behaviour is happening much faster than the development of novel long-distance migration behaviour (Gómez-Bahamón et al., 2020). Yet it is not clear to what extent migratory behaviour could be 'recovered' in newly residential populations should it once again become essential for species survival.

## 7.2 Conservation strategies for migratory bats

The development of effective conservation strategies for migratory species is a complex task. Migratory animals depend on a sequence of habitats across a broad geographical range (Robinson et al. 2009). Rapid environmental change results in highly fluctuating habitat quality and productivity throughout these ranges. Therefore, to provide adaptive conservation management, extensive development of protected areas is needed. For example, it was shown that only 9% of migratory bird species are adequately covered by protected areas across all stages of their annual cycle (Runge et al. 2015). However, for migratory bats, such estimations were never made due to the still-scarce knowledge regarding migratory routes and stopovers. Considering the high proportion of land cover worldwide already occupied to serve human needs, a significant increase in the proportion of strictly protected areas is impossible without agreement between numerous stakeholders. Nevertheless, to serve conservation needs for migratory species in times of rapid environmental change and prominent human population growth, the 'dynamic conservation strategy' was put forward (Reynolds et al. 2017).

The dynamic conservation strategy relies on the rent of suitable seasonal habitats from responsible stakeholders. Such a strategy provides spatial and temporal flexibility in the organisation of habitat protection. The advantages of such a strategy include the ability to adjust the timing, extent, and location of provisioned habitat to better match species' needs across their entire life-cycle (for example, breeding, migration, stopover), and to adapt to climate change, droughts, habitat conversion, and other threats (Reynolds et al. 2017). Moreover, many landowners rather prefer temporary loans of their properties for conservation needs rather than a one-time sale. The application of this dynamic conservation strategy is also raising human ethical awareness regarding shared rights with other species for environmental utilisation.

While the dynamic conservation strategy presents a suitable framework to provide habitat for species' seasonal needs, the initial identification of these suitable habitats is another quite complex task. Here, I have shown that the mechanistic modelling of a species' thermal niche based on their physiological limits is an important tool for the identification of suitable environments in space and time. We need to have a precise look at species physiological requirements, because rely only on species occurrence data may not necessarily provide us with information regarding species optimal environmental conditions. Animals are constrained by habitat fragmentation and various sources of environmental pollution (light, noise, chemical) to move along/between environmental gradients to find suitable environmental conditions. Therefore, using species-specific measured physiological capacity, we are better able to predict the ability of the animal to survive within an area, and we can more effectively manage these landscapes for conservation.

## 7.3 Conclusion

The traits of a species, which help them to respond quickly to environmental challenges, occur at different levels of organisation: individual plasticity in physiology and behaviour, demographic and social interactions acting on a population level, and flexibility in interspecific interactions, which affects the community. Change in distribution is one of the most immediate responses to rapid climate change which in general delimit species boundaries. Migratory bat species are of specific concern in terms of distribution change because they depend on the sequence of different habitats during their life cycle, many of which are significantly affected by climate change. In my research, I have been investigating the magnitude of migratory behaviour, mechanism of range shift, and physiological limits in species distribution under the impact of climate change. I analysed past and future climate change scenarios and determined the rate of species responses, and whether it was consistent with the pace of environmental change. In summary, my results provided important novel insights which help us understand how complex migratory systems respond to heterogeneous environmental change. These findings contribute to the improved conservation of migratory bats. By better understanding the environmental forces and mechanisms of species biogeographical patterns, we can adjust our action plans to preserve necessary habitats with species-specific requirements. We, humans, transform ecosystems so fast and unfortunately recognize it too late, only at the stage when the exhaustion of natural resources is negatively affecting our well-being. To achieve sustainable development during the Anthropocene, we must first to be accountable and conscious in the calculations of our civilization's impact on natural ecosystems. The ignorance of the laws, including the Laws of Nature, excuses no one.

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# 9. APPENDICES

## Chapter Two

### Generational shift in the migratory common noctule bat: first-year males lead the way to hibernacula at higher latitudes.

Kravchenko K. A.[1,2], Vlaschenko A. S.[3,4], Lehnert L. S. [1,2], Courtiol A. [1], Voigt C.C[1,2].

[1]Leibniz Institute for Zoo and Wildlife Research, Alfred-Kowalke- Str. 17, 10315 Berlin, Germany

[2]Institute for Biology, Freie Universität Berlin, Königin-Luise-Str. 1-3, 14195 Berlin, Germany

[3]Bat Rehabilitation Center of Feldman Ecopark, 62340 Lesnoye, Kharkiv Region, Ukraine

[4] Ukrainian Independent Ecology Institute, Plekhanov st., 40 61001 Kharkiv, Ukraine

## Supplementary material 1: Change of winter range in common noctule bats

**KHARKIV:** Sampling site
Period = 12 years (2004-2016)
N bats for $\delta^2H$ fur= 413
N bats sex/structure = 3394

**<u>Supplementary Table 2.</u>** Probability of being subadult male did not reliably predict the probability of being migratory

| | Migratory Status | | |
|---|---|---|---|
| *Predictors* | *Odds Ratios* | *CI* | *p* |
| (Intercept) | 0.10 | 0.06 – 0.18 | **<0.001** |
| Year3 | 0.87 | 0.77 – 0.99 | **0.028** |
| young_maleTRUE | 0.75 | 0.30 – 1.91 | 0.552 |
| Year3:young_maleTRUE | 0.96 | 0.80 – 1.14 | 0.606 |
| Observations | 413 | | |
| AIC | 332.272 | | |

**Supplementary material 3** and **Supplementary material 4** which contain raw data are available in Dryad depository:

https://doi.org/10.6084/m9.figshare.c.5124453

## Supplementary material 5: Moulting pattern in common noctule and age determination

### Moulting of common noctule bats

As it is standard for all our isotopic studies in bats, we collected a small tuft of fur from the interscapular region (between the shoulder blades). This region is known to molt first in adult individuals when they are still present at the breeding grounds (Ilyin 1990). Adult males molt in late June and adult females in early July. In case of juveniles, the fur indeed refers to the geographic place of birth since juveniles do not moult before migration. For example, Kleiman (1969) reported that common noctules are born naked and develop a complete pelage after 17 days. The studies published by Kleimann (1969) and Ilyin (1990) show that in young individuals (subadult) fur grows in the area where they were born and remain unchanged until the next summer when these bats will molt for the first time. In an earlier paper, we established that the isotopic composition of fur in juveniles matches with the location of the breeding area (Kravchenko et al. 2019). Further, we have observed a high consistency for the individual migratory strategy (Lehnert et al 2018), i.e. we have no evidence so far for a change in molting strategy and large-scale changes in the location of wintering ad breeding grounds within a life span. Therefore we are confident in categorizing subadult or adult individual as long-distance migrant or coming from more local populations.

### Age determination of bats

We used a combination of parameters to determine the age of bats, specifically tooth wear and the specific morphology of primary and secondary reproductive organs.

1) Tooth wear: By visual inspection of the teeth (specifically the canine teeth), we assessed the colour (Kozhurina and Morozov, 1994) and wear (Gazaryan and Kazakov, 2002) as proxies for a bat’s age. Individuals younger than one year have sharp teeth with transparent tips, particularly the tips of the canines. After the age of one year, adults have milk-white teeth, yet teeth are not yet worn down. The signs of tooth wear range from mildly rounded at the tip of the canines to a massive reduction by 20-40% of the initial length of the canine teeth in older individuals. As individuals of this species consume mostly hard-bodied large Coleoptera and Lepidoptera (Vaughan, 1997), signs of tooth wear become already apparent at an early age. Considering the short life-span of this species (2-3 years), it is relatively easy to assign bats to a specific age or age group.

2) Primary and secondary reproductive organs: Males with big testes (from 7×4 mm or more), and distended filled epididymis were categorized as adults (Kozhurina and Morozov, 1994). Males with small testes and undescended epididymis were categorized as subadult individuals, i.e. being born during the year of capture (Kozhurina and Morozov, 1994). In case of females, individuals with protuberant (1 mm or more in diameter) and brownish nipples were categorized as adults. Females with flat and pink nipples were categorized as subadult individuals.

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## Chapter Three

# Energy use predicts climate-driven changes in the distribution of common noctule bats.

(Manuscript is in preparation for submission)

Kravchenko KK[1,2], Voigt CC[1,2], Lange S, Courtiol A[1]*, Currie S[1]*

[1]Leibniz Institute for Zoo and Wildlife Research, Alfred-Kowalke- Str. 17, 10315 Berlin, Germany

[2]Institute for Biology, Freie Universität Berlin, Königin-Luise-Str. 1-3, 14195 Berlin, Germany

[3] Potsdam Institute for Climate Impact Research (PIK), Department of Transformation Pathways, P.O. Box 60 12 03, 14412 Potsdam, Germany

**Supplementary materials 1: Protocol of the metabolic rate mesurements**

We used open-flow respirometry to record the metabolic rate of bats measured as the rate of CO2 production. Measurements were conducted in a temperature-controlled cabinet. Each bat’s body mass was recorded immediately before and after the recording trial and we assumed a linear decrease in mass during recording for calculations of mass-specific metabolic rates. Bats were placed in airtight 537.6 ml transparent plastic metabolic chambers, lined with plastic mesh for roosting. Chambers were small to minimise washout time and allow for accurate measurement of V O_ 2 at low levels during torpor but still allowed space for bats to hang freely and move around inside the chambers. The outside air was pumped into the chamber at a rate of 300 ml/min during normothermia measurements and 180 ml/min during torpor. This flow rate was high enough to maintain O2 concentration in the excurrent air stream during normothermia and low enough to allow for accurate measurement of a differential between incurrent and excurrent O2 concentration at low metabolic rate during torpor. Incurrent air was not dried to provide close to natural humidity for animals and flow rate was measured with mass flowmeters. Excurrent air was also dried with silica gel and percentage carbon dioxide was then measured with an $CO_2$ analyser (FoxBox, Sable Systems International Inc., Las Vegas USA). To ensure long-term stable readings, we maintained the analyser in a constant temperature room. Four or five channels (3 or 4 animals and 1 outside-air reference) were scanned sequentially with flow multiplexer (RM-8 Respirometry Flow Multiplexer, Sable Systems International Inc., Las Vegas USA) for 5 or 3 min each (depending on number of channels - four or five respectively) (i.e., the metabolic rate of each animal and the reference were scanned once in every 20 and 15 min respectively). Outputs from the flowmeters were transferred to the computer via a digital serial connection. All equipment was calibrated prior to use. Measurements were taken over approximately 24 h to ensure that we recorded the entire daily thermal cycle (Geiser and Brigham 2000). All measurements of metabolic rate represent the minimum 1 hour average obtained during a period when the metabolic rate was stable at a constant ambient temperature for at least 1 h. We used two temperature protocols to measure the resting metabolic rate, the torpid metabolic rate and the basal metabolic rate of bats over a range of temperatures. In the first protocol, bats were placed in the chambers in the evening (17:00–18:00), with the ambient temperature held constant overnight, and measurements of the torpid metabolic rate were obtained the following day. This allowed for entry into torpor in the early morning hours, when other Vespertilionidae species use torpor in the wild (Turbill et al. 2003a, 2003b; McGuire et al. 2014), and ensured that the torpid metabolic rate and the body temperature reached steady state minima before the torpid metabolic rate values were recorded (Geiser and Brigham 2000). If their normothermic state, the rate of $CO_2$ production remained stable for at least an hour during these dusk arousals, we also recorded a resting metabolic rate measurement at that ambient temperature.

In the second protocol, we performed basal metabolic rate measurements for an ambient temperature progressively increasing from 25C to 35C. Specifically, we placed animals into the chamber in the morning between 7.00 and 8.00. After the recorded production of $CO_2$ and the ambient temperature in the chamber were stable for at least 1 h, we began recording and after a fourth hour at the initial ambient temperature, we slowly increased the temperature of the chamber in approximately 2C increments. We ensured that the ambient temperature and the metabolic rate were stable at each increment for at least an hour before recording the minimum average MR for that hour.

We used the “torpor” (Fasel et al. 2021) R package to estimate the lower critical temperature of the thermoneutral zone and determine physiological state membership using a mixture model.

**Supplementary material 2:** **Model for probability estimation of the physiological state**

Generalize d linear mixed model fit by maximum likelihood (Laplace Approximation) ['glmerMod']

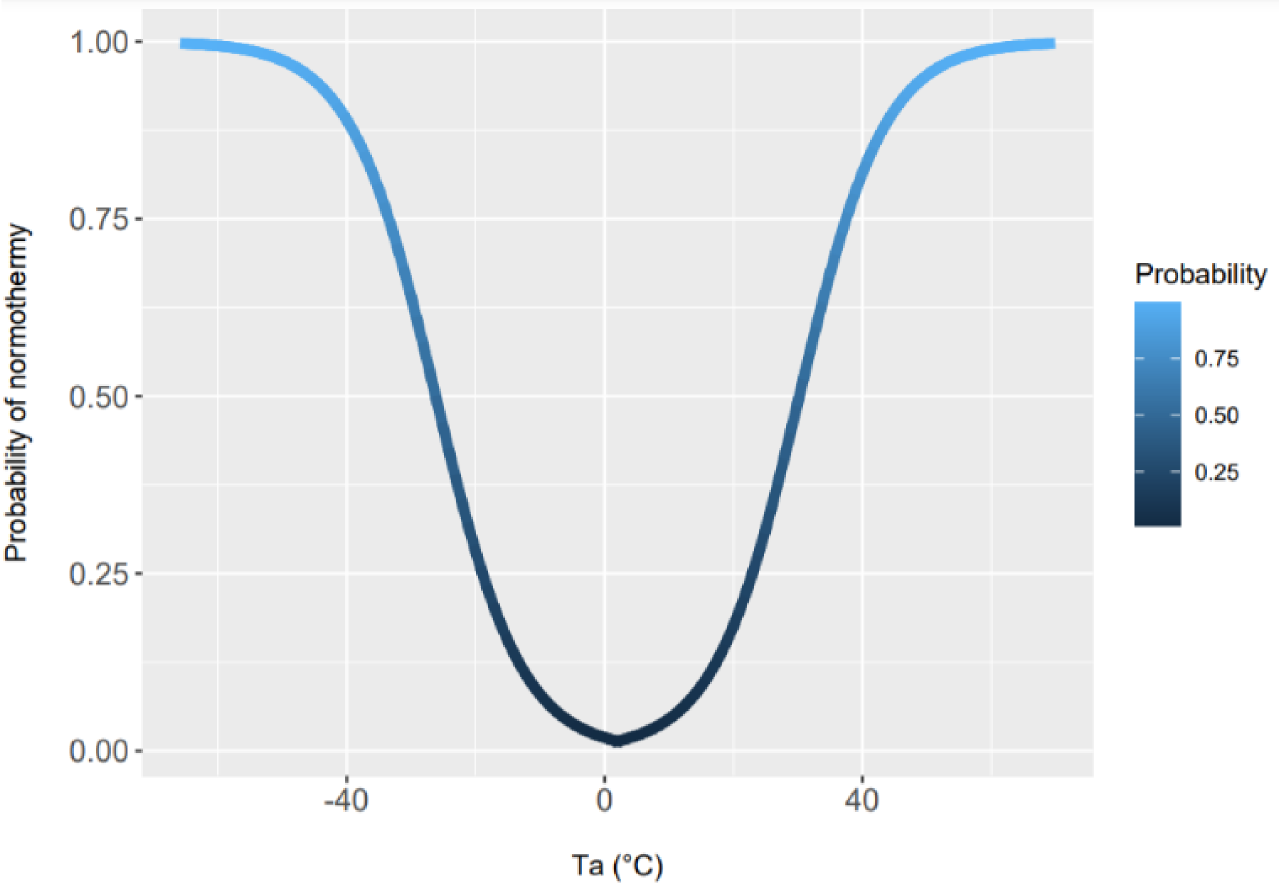
Family: binomial ( logit )

Formula: state ~ Ta + (1 | ID)

| | **State** | | |
|---|---|---|---|
| *Predictors* | *Odds Ratios* | *CI* | *p* |
| (Intercept) | 0.01 | 0.01 – 0.01 | **<0.001** |
| Ta | 1.16 | 1.11 – 1.22 | **<0.001** |
| **Random Effects** | | | |
| $\sigma^2$ | 3.29 | | |
| $\tau_{00\ \mathrm{ID}}$ | 0.09 | | |
| ICC | 0.03 | | |
| $N_{\mathrm{ID}}$ | 17 | | |
| Observations | 19134 | | |
| Marginal $R^2$ / Conditional $R^2$ | 0.088 / 0.112 | | |

## Supplementary material 3:

### Probability of being normothermic at a range of temperatures



## Supplementary material 4: Table of metabolic costs per hour and half an hour at each degree ºC.

| Ta [°C] | Euthermia_30m [CO2 ml h−1 g−1] | Torpor_30m [CO2 ml h−1 g−1] | Probability | VCO2_g_day | g_fat_g |
|---|---|---|---|---|---|
| **-65** | 7.192 | 4.835 | 0.997 | 344.901 | 0.253 |
| **-64** | 7.123 | 4.766 | 0.997 | 341.544 | 0.250 |
| **-63** | 7.055 | 4.697 | 0.996 | 338.187 | 0.248 |
| **-62** | 6.986 | 4.629 | 0.996 | 334.818 | 0.246 |
| **-61** | 6.917 | 4.560 | 0.995 | 331.427 | 0.243 |
| **-60** | 6.848 | 4.491 | 0.994 | 328.036 | 0.241 |
| **-59** | 6.779 | 4.422 | 0.993 | 324.622 | 0.238 |
| **-58** | 6.711 | 4.353 | 0.992 | 321.197 | 0.236 |
| **-57** | 6.642 | 4.284 | 0.991 | 317.750 | 0.233 |
| **-56** | 6.573 | 4.215 | 0.989 | 314.279 | 0.230 |
| **-55** | 6.504 | 4.147 | 0.987 | 310.775 | 0.228 |
| **-54** | 6.436 | 4.078 | 0.985 | 307.249 | 0.225 |
| **-53** | 6.367 | 4.009 | 0.983 | 303.676 | 0.223 |
| **-52** | 6.298 | 3.941 | 0.980 | 300.070 | 0.220 |
| **-51** | 6.229 | 3.872 | 0.977 | 296.408 | 0.217 |
| **-50** | 6.161 | 3.803 | 0.973 | 292.700 | 0.215 |
| **-49** | 6.092 | 3.735 | 0.969 | 288.925 | 0.212 |
| **-48** | 6.023 | 3.666 | 0.964 | 285.070 | 0.209 |
| **-47** | 5.954 | 3.597 | 0.959 | 281.135 | 0.206 |
| **-46** | 5.886 | 3.529 | 0.952 | 277.111 | 0.203 |
| **-45** | 5.817 | 3.460 | 0.945 | 272.974 | 0.200 |
| **-44** | 5.748 | 3.391 | 0.937 | 268.723 | 0.197 |
| **-43** | 5.679 | 3.323 | 0.927 | 264.337 | 0.194 |
| **-42** | 5.611 | 3.254 | 0.916 | 259.804 | 0.191 |
| **-41** | 5.542 | 3.185 | 0.904 | 255.101 | 0.187 |
| **-40** | 5.473 | 3.116 | 0.890 | 250.217 | 0.183 |
| **-39** | 5.404 | 3.048 | 0.874 | 245.140 | 0.180 |

| | | | | | |
|---|---|---|---|---|---|
| **-38** | 5.336 | 2.979 | 0.856 | 239.848 | 0.176 |
| **-37** | 5.267 | 2.910 | 0.837 | 234.318 | 0.172 |
| **-36** | 5.198 | 2.841 | 0.815 | 228.563 | 0.168 |
| **-35** | 5.129 | 2.772 | 0.791 | 222.558 | 0.163 |
| **-34** | 5.060 | 2.703 | 0.765 | 216.304 | 0.159 |
| **-33** | 4.992 | 2.635 | 0.737 | 209.814 | 0.154 |
| **-32** | 4.923 | 2.566 | 0.706 | 203.077 | 0.149 |
| **-31** | 4.854 | 2.498 | 0.674 | 196.124 | 0.144 |
| **-30** | 4.785 | 2.429 | 0.640 | 188.966 | 0.139 |
| **-29** | 4.717 | 2.360 | 0.604 | 181.648 | 0.133 |
| **-28** | 4.648 | 2.291 | 0.568 | 174.205 | 0.128 |
| **-27** | 4.579 | 2.222 | 0.530 | 166.659 | 0.122 |
| **-26** | 4.510 | 2.154 | 0.493 | 159.097 | 0.117 |
| **-25** | 4.442 | 2.085 | 0.455 | 151.531 | 0.111 |
| **-24** | 4.373 | 2.016 | 0.418 | 144.034 | 0.106 |
| **-23** | 4.304 | 1.947 | 0.382 | 136.628 | 0.100 |
| **-22** | 4.235 | 1.879 | 0.347 | 129.372 | 0.095 |
| **-21** | 4.167 | 1.810 | 0.313 | 122.295 | 0.090 |
| **-20** | 4.098 | 1.741 | 0.282 | 115.440 | 0.085 |
| **-19** | 4.029 | 1.673 | 0.252 | 108.795 | 0.080 |
| **-18** | 3.960 | 1.604 | 0.225 | 102.380 | 0.075 |
| **-17** | 3.892 | 1.535 | 0.199 | 96.236 | 0.071 |
| **-16** | 3.823 | 1.466 | 0.176 | 90.325 | 0.066 |
| **-15** | 3.754 | 1.397 | 0.155 | 84.648 | 0.062 |
| **-14** | 3.685 | 1.329 | 0.137 | 79.238 | 0.058 |
| **-13** | 3.616 | 1.260 | 0.120 | 74.032 | 0.054 |
| **-12** | 3.548 | 1.192 | 0.105 | 69.043 | 0.051 |
| **-11** | 3.479 | 1.123 | 0.091 | 64.220 | 0.047 |
| **-10** | 3.410 | 1.054 | 0.080 | 59.591 | 0.044 |
| **-9** | 3.341 | 0.985 | 0.069 | 55.119 | 0.040 |
| **-8** | 3.273 | 0.917 | 0.060 | 50.802 | 0.037 |
| **-7** | 3.204 | 0.848 | 0.052 | 46.600 | 0.034 |

| | | | | | |
|---|---|---|---|---|---|
| **-6** | **3.135** | **0.780** | **0.045** | **42.524** | **0.031** |
| **-5** | 3.066 | 0.711 | 0.039 | 38.536 | 0.028 |
| **-4** | 2.998 | 0.642 | 0.034 | 34.624 | 0.025 |
| **-3** | 2.929 | 0.573 | 0.029 | 30.786 | 0.023 |
| **-2** | 2.860 | 0.504 | 0.025 | 27.026 | 0.020 |
| **-1** | 2.791 | 0.435 | 0.022 | 23.329 | 0.017 |
| **0** | 2.723 | 0.366 | 0.019 | 19.697 | 0.014 |
| **1** | 2.654 | 0.297 | 0.016 | 16.095 | 0.012 |
| **2** | 2.585 | 0.229 | 0.014 | 12.547 | 0.009 |
| **3** | 2.516 | 0.160 | 0.016 | 9.489 | 0.007 |
| **4** | 2.448 | 0.091 | 0.019 | 6.480 | 0.005 |
| **5** | 2.379 | 0.032 | 0.022 | 3.980 | 0.003 |
| **6** | 2.310 | 0.031 | 0.025 | 4.236 | 0.003 |
| **7** | 2.241 | 0.034 | 0.029 | 4.722 | 0.003 |
| **8** | 2.173 | 0.038 | 0.034 | 5.257 | 0.004 |
| **9** | 2.104 | 0.041 | 0.039 | 5.845 | 0.004 |
| **10** | 2.035 | 0.045 | 0.045 | 6.490 | 0.005 |
| **11** | 1.966 | 0.050 | 0.052 | 7.184 | 0.005 |
| **12** | 1.897 | 0.055 | 0.060 | 7.948 | 0.006 |
| **13** | 1.829 | 0.061 | 0.069 | 8.779 | 0.006 |
| **14** | 1.760 | 0.067 | 0.080 | 9.659 | 0.007 |
| **15** | 1.691 | 0.073 | 0.091 | 10.609 | 0.008 |
| **16** | 1.622 | 0.081 | 0.105 | 11.620 | 0.009 |
| **17** | 1.554 | 0.089 | 0.120 | 12.677 | 0.009 |
| **18** | 1.485 | 0.098 | 0.137 | 13.782 | 0.010 |
| **19** | 1.416 | 0.107 | 0.155 | 14.918 | 0.011 |
| **20** | 1.347 | 0.118 | 0.176 | 16.074 | 0.012 |
| **21** | 1.279 | 0.130 | 0.199 | 17.233 | 0.013 |
| **22** | 1.210 | 0.143 | 0.225 | 18.367 | 0.013 |
| **23** | 1.141 | 0.157 | 0.252 | 19.453 | 0.014 |
| **24** | 1.072 | 0.173 | 0.282 | 20.465 | 0.015 |
| **25** | 1.004 | 0.191 | 0.313 | 21.366 | 0.016 |

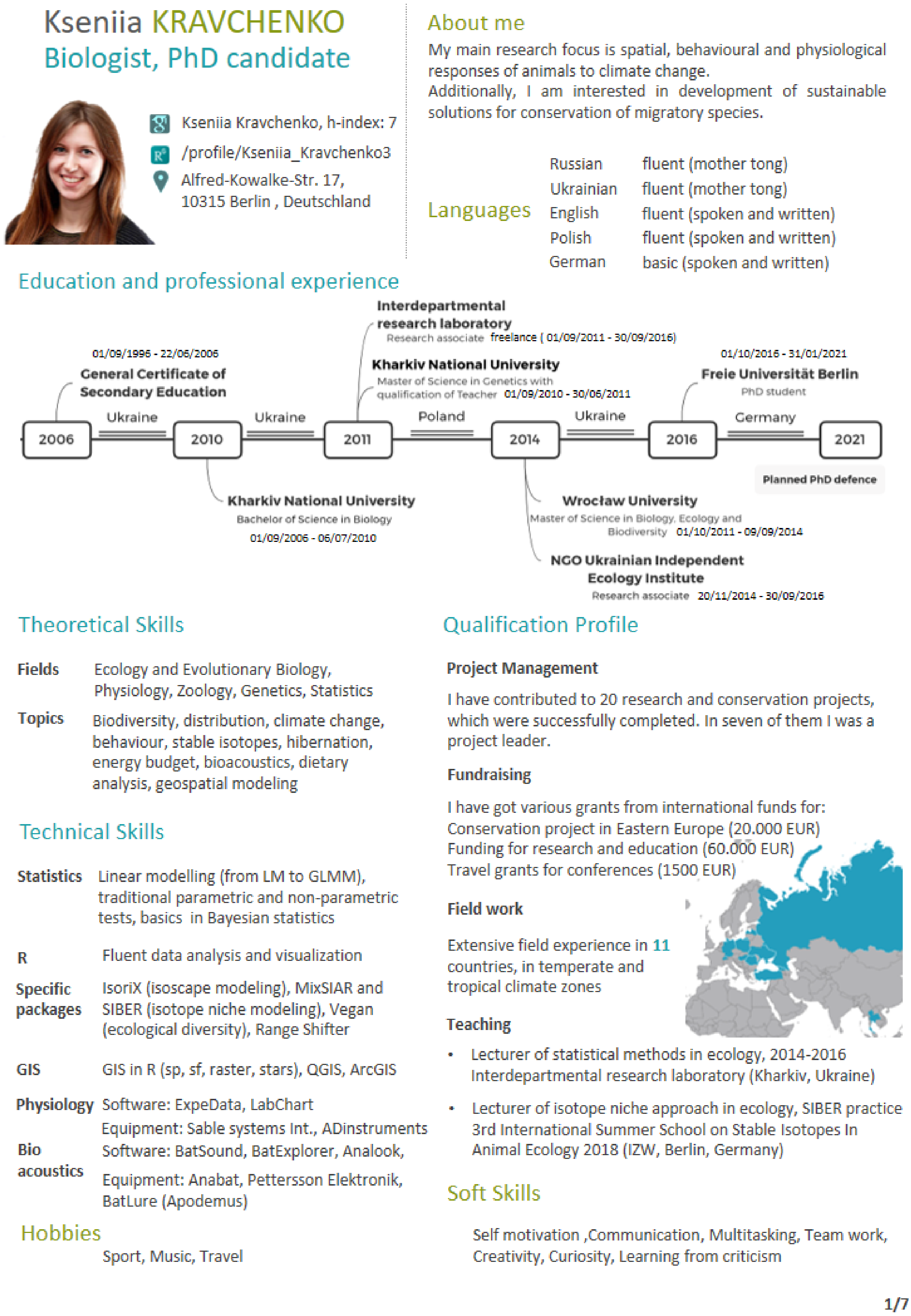
| | | | | | |
|---|---|---|---|---|---|
| **26** | **0.935** | **0.210** | **0.347** | **22.126** | **0.016** |
| **27** | 0.866 | 0.231 | 0.382 | 22.710 | 0.017 |
| **28** | 0.797 | 0.254 | 0.418 | 23.087 | 0.017 |
| **29** | 0.729 | 0.280 | 0.455 | 23.221 | 0.017 |
| **30** | 0.660 | 0.308 | 0.493 | 23.097 | 0.017 |
| **31** | 0.591 | 0.339 | 0.530 | 22.684 | 0.017 |
| **32** | 0.522 | 0.373 | 0.568 | 21.971 | 0.016 |
| **33** | 0.454 | 0.410 | 1.000 | 21.769 | 0.016 |
| **34** | 0.431 | 0.431 | 1.000 | 20.667 | 0.015 |
| **35** | 0.431 | 0.431 | 1.000 | 20.667 | 0.015 |
| **36** | 0.431 | 0.431 | 1.000 | 20.667 | 0.015 |
| **37** | 0.431 | 0.431 | 1.000 | 20.667 | 0.015 |
| **38** | 0.431 | 0.431 | 1.000 | 20.667 | 0.015 |
| **39** | 0.431 | 0.431 | 1.000 | 20.667 | 0.015 |
| **40** | 0.431 | 0.431 | 1.000 | 20.667 | 0.015 |
| **41** | 0.431 | 0.431 | 1.000 | 20.667 | 0.015 |
| **42** | 0.431 | 0.431 | 1.000 | 20.667 | 0.015 |
| **43** | 0.431 | 0.431 | 1.000 | 20.667 | 0.015 |
| **44** | 0.431 | 0.431 | 1.000 | 20.667 | 0.015 |

## 10. DECLARATION OF AUTHORSHIP

I hereby declare that I prepared this thesis independently under the guidance of my supervisor. All direct or indirect sources used are given as references. All contributions of co-authors are acknowledged.

Berlin, 30.06.2021 Kseniia Kravchenko

# 11. CURRICULUM VITAE



## Kseniia KRAVCHENKO
### Biologist, PhD candidate

Kseniia Kravchenko, h-index: 7
/profile/Kseniia_Kravchenko3
Alfred-Kowalke-Str. 17,
10315 Berlin , Deutschland

## About me

My main research focus is spatial, behavioural and physiological responses of animals to climate change.
Additionally, I am interested in development of sustainable solutions for conservation of migratory species.

## Languages

| | |
|---|---|
| Russian | fluent (mother tong) |
| Ukrainian | fluent (mother tong) |
| English | fluent (spoken and written) |
| Polish | fluent (spoken and written) |
| German | basic (spoken and written) |

## Education and professional experience

2006 — Ukraine — 2010 — Ukraine — 2011 — Poland — 2014 — Ukraine — 2016 — Germany — 2021

01/09/1996 - 22/06/2006
**General Certificate of Secondary Education**

**Kharkiv National University**
Bachelor of Science in Biology
01/09/2006 - 06/07/2010

**Interdepartmental research laboratory**
Research associate freelance ( 01/09/2011 - 30/09/2016)

**Kharkiv National University**
Master of Science in Genetics with qualification of Teacher 01/09/2010 - 30/06/2011

**Wrocław University**
Master of Science in Biology, Ecology and Biodiversity 01/10/2011 - 09/09/2014

**NGO Ukrainian Independent Ecology Institute**
Research associate 20/11/2014 - 30/09/2016

01/10/2016 - 31/01/2021
**Freie Universität Berlin**
PhD student

**Planned PhD defence**

## Theoretical Skills

| | |
|---|---|
| **Fields** | Ecology and Evolutionary Biology, Physiology, Zoology, Genetics, Statistics |
| **Topics** | Biodiversity, distribution, climate change, behaviour, stable isotopes, hibernation, energy budget, bioacoustics, dietary analysis, geospatial modeling |

## Technical Skills

| | |
|---|---|
| **Statistics** | Linear modelling (from LM to GLMM), traditional parametric and non-parametric tests, basics in Bayesian statistics |
| **R** | Fluent data analysis and visualization |
| **Specific packages** | IsoriX (isoscape modeling), MixSIAR and SIBER (isotope niche modeling), Vegan (ecological diversity), Range Shifter |
| **GIS** | GIS in R (sp, sf, raster, stars), QGIS, ArcGIS |
| **Physiology** | Software: ExpeData, LabChart<br>Equipment: Sable systems Int., ADinstruments |
| **Bio acoustics** | Software: BatSound, BatExplorer, Analook,<br>Equipment: Anabat, Pettersson Elektronik, BatLure (Apodemus) |

## Hobbies

Sport, Music, Travel

## Qualification Profile

**Project Management**

I have contributed to 20 research and conservation projects, which were successfully completed. In seven of them I was a project leader.

**Fundraising**

I have got various grants from international funds for:
Conservation project in Eastern Europe (20.000 EUR)
Funding for research and education (60.000 EUR)
Travel grants for conferences (1500 EUR)

**Field work**

Extensive field experience in 11 countries, in temperate and tropical climate zones

**Teaching**

- Lecturer of statistical methods in ecology, 2014-2016 Interdepartmental research laboratory (Kharkiv, Ukraine)
- Lecturer of isotope niche approach in ecology, SIBER practice 3rd International Summer School on Stable Isotopes In Animal Ecology 2018 (IZW, Berlin, Germany)

## Soft Skills

Self motivation ,Communication, Multitasking, Team work, Creativity, Curiosity, Learning from criticism

## Grants

- 2018 **DAAD grant**
  *participation in Falling Walls Berlin 2018 conference and lab*
- 2016 **British Ecological Society (BES) grant**
  *"Nocturnal noshing – become fat and happy: pre hibernation foraging activity of Nyctalus noctula bat in a new hibernation region."*
- 2014 **EUROBATS Projects Initiative grant**
  *"Trans-border collaboration in bat migration research in Eastern Europe and the Black Sea region. The pilot project."*
- 2013 **The Youth Activity Fund of the Explorers Club grant**
  *"Reach Another Bank of the Black Sea, Far Expedition following Bat Migration."*
- 2012 **The Youth Activity Fund of the Explorers Club grant**
  *"Migration of bats in Crimea peninsula (Ukraine): international student expedition as action on international expansion of Wind Energy Companies."*
- 2012 **Bat Conservation International (Student Research Scholarship Program) grant**
  *"Bat Migration and Development of Wind Energy in Ukraine".*
- 2010 **The Youth Activity Fund of the Explorers Club grant**
  *"Bats and Fungi in the Eastern Europe: the first step for search of White Nose Syndrome signs."*

## Awards

- 2021 **3rd Best Oral Presentation** at 6th International Berlin Bat Meeting (Berlin, Germany)
- 2019 **Best Poster Award** at $N^2$ Event from research to application (Berlin, Germany)
- 2015 **Green Talent Award** from the German Ministry for education and research (BMBF)
- 2015 **Best Oral Presentation** at 36th Conference of Young zoologists (Kyiv, Ukraine)

## Scholarships

- 2016 **DAAD scholarship for full Doctoral studies (**Germany at Freie Universität Berlin)
- 2015 **Green Talent scholarship** for 3-month research stay (IZW, Berlin, Germany)
- 2012 **ERASMUS scholarship** for research internship in stable isotope ecology (IZW, Berlin, Germany)
- 2011 Competitive full-tuition scholarship for Master studies from non-commercial urban project No.1 in Poland **"Teraz Wrocław"** (Wroclaw University, Poland)
- 2006 Competitive full-tuition scholarship from the Ukrainian government (Kharkiv Natinal University, top University in Ukraine)

## Memberships

- 2016 – present member of the British Ecological Society (BES)
- 2015 – present member of NGO Ukrainian Independent Ecological Institute (UIEI)
- 2011 – 2013 member of Students Scientific Society of Mammalogists of Wrocław University
- 2009 – 2012 member All-Ukrainian youth NGO "Foundation of Regional Initiatives" (FRI)
- 2009 – 2011 member of Nature Conservation Team of Kharkiv National University
- 2007 – 2011 member of Student Scientific Society of Cytology and Genetics of Kharkiv National University

## Conferences

**Presented research results during 25 international conferences and symposiums.**
**In 8 of them I was a member of organizing committee:**

- 2007-2009 International conference "Biology: from a molecule up to the biosphere" , Kharkiv, Ukraine
- 2013, 2017, 2021 International Berlin Bat meeting, Berlin, Germany
- 2017 The 4th Leibniz PhD Student symposium, Berlin, Germany
- 2019 International Kharkiv Bat Meeting, Kharkiv, Ukraine

## Projects participation:

- 2016 "Searching for birth-place: determination of connection between summer and winter locations of threatened bat populations" supported by The Youth Activity of the Explorers Club.

- 2013-2016 "Bat Rehabilitation Center" Kharkiv, Ukraine supported by Olexander Feldman Foundation.

- 2013-2014 "Kharkiv bat education program" Kharkiv, Ukraine supported by EUROBATS Projects Initiative.

- 2013 "*Nyctalus lasiopterus* in the Eastern Europe: inventory of current status, proposals to revise the species status in IUCN Red List and conservation" supported by Rufford Small Grants for Nature Conservation (UK) and EUROBATS Projects Initiative (EU).

- 2012-2013 practical training in stable isotope ecology, Leibniz Institute for Zoo and Wildlife Research, Berlin, Germany.

- 2011-2012 "The International Year of Forests in the North eastern Ukraine: Establishing of Long-Term Program on Forest Biodiversity Conservation" supported by Rufford Small Grants for Nature Conservation (UK). http://www.ruffordsmallgrants.org/rsg/projects/stanislav_viter

- 2011 took part in the "Night of explorers" student volunteer science pop program "Projektor" supported by American-Polish Freedom Foundation (Pl/USA).

- 2010 – 2013 "Fauna of bats as an indicator of the most valuable natural complexes in Chernobyl Exclusion Zone worthy of legislative protection" supported by Rufford Small Grants for Nature Conservation (UK). http://www.ruffordsmallgrants.org/rsg/projects/sergey_gashchak

- 2010-2011 iBats Ukraine (Indicator Bat Programme) supported by The Darwin Initiative (UK).

- 2010-2011 "Estimation of Impact of Wind Energy Turbines on Migratory Bats in the South of Ukraine, the Pilot Project" supported by Global Grassroots Bat Conservation Fund of Bat Conservation International (USA).

- 2010-2011 "*Nyctalus lasiopterus* in Ukraine: inventory of current status, proposals to revise the species status in IUCN Red List and conservation" supported by Rufford Small Grants for Nature Conservation (UK).

- 2009-2010 "Development of new system of summer bat population monitoring on the territory of nature reserves in Ukraine and Russia" supported by The Bat Conservation International, Scholarship program and Sigma Xi (USA).

- 2009 "Community for conservation of nature protected areas" in Kanevskij Zapovednik, supported by The Global Environment Fund (GEF).

## Other activities

Supervision of 6 undergraduate and 2 master students.

Author of 5 popular broadcasts about bat ecology and wildlife conservation on TV.

## List of publications:

**Peer reviewed**

Vlaschenko, Anton, Yehor Yatsiuk, Vitalii Hukov, Alona Prylutska, Tanja M. Straka, **Kseniia Kravchenko (2021)** Urban forest preserves local bat species diversity, but not forest dweller specialists—renewed study 65 years later (Kharkiv city, Ukraine). *Mammal Research*, 1-12.

**Kravchenko K**, Vlaschenko A, Lehnert LS, Courtiol A, Voigt CC **(2020)** Generational shift in the migratory common noctule bat: First-year males lead the way to hibernacula at higher latitudes. *Biology Letters*, *16*(9), p.20200351.

Măntoiu DŞ, **Kravchenko K,** Lehnert LS, Vlaschenko A, Moldovan OT, Mirea IC, ... & Voigt CC **(2020)** Wildlife and infrastructure: impact of wind turbines on bats in the Black Sea coast region. *European Journal of Wildlife Research*, *66*, 44.

Lindecke O, Currie S, Fasel NJ, Fritze M, **Kravchenko K**, Kruzsynski de Assis C, Lehnert L, Roeleke M, Voigt-Heucke S, Voigt CC. (2020) Common noctule (*Nyctalus noctula*). Handbook of Mammals (eds. Hackländer, K., Zachos, F.E.). SpringerNature

Vlaschenko A, Prylutska A, **Kravchenko K**, Rodenko O, Hukov V, Timofieieva O, Holovchenko O, Moiseienko M, Kovalov V **(2020)** Regional recaptures of bats (Chiroptera, Vespertilionidae) ringed in eastern Ukraine. *Zoodiversity*, 54(1):53–66

Voigt C, **Kravchenko K**, Liechti F, Bumrungsri S **(2019)** Skyrocketing flights as a previously unrecognized behaviour of open-space foraging bats. Acta Chiropterologica. *Acta Chiropterologica*, *21*(2), 331–339.

**Kravchenko K**, Lehnert LS, Vlaschenko A, Voigt CC **(2019)** Multiple isotope tracers in fur keratin discriminate between mothers and offspring. *Rapid Communications in Mass Spectrometry*, *33*(10), 907-913.

Vlaschenko A, Kovalov V, Hukov´V, **Kravchenko K**, Rodenko O **(2019)** An example of ecological traps for bats in the urban environment.*European journal of wildlife research*, *65*(2), 20.

Lehnert LS, Kramer-Schadt S, Teige T, Hoffmeister U, Popa-Lisseanu A, Bontadina F, Ciechanowski M, Dechmann D, **Kravchenko K**, Presetnik P, Starrach M, Straube M, Zoephel U, Voigt CC **(2018)** Plasticity and repeatability of noctule bat migration in Central Europe: evidence for partial and differential migration. *Proceedings of the Royal Society B*, *285*(1893), 20182174.

Szentiványi T, Kravchenko K, Vlaschenko A, Estók P **(2018)** First record of Laboulbeniales (Fungi: Ascomycota) infection on bat flies (Diptera: Nycteribiidae) from the Caucasus region. *Folia entomologica hungarica*, *79*, 195-201.

Kemenesi G, Zana B, Kurucz K, Foldes F, Urban P, Vlaschenko A, **Kravchenko K**, et al., Jakab F **(2017)** High diversity of replication-associates protein encoding circular DNA viruses in guano samples of European bats. *Archives of Virology*, 163 (3): 671-678. DOI: 10.1007/s00705-017-3678-5

**Kravchenko K**, Vlaschenko A, Prylutska A, Rodenko O, Gukov V, Shuvaev V **(2017)** Year-round monitoring of bat records in big city area: Kharkiv city (NE Ukraine), 2013 year as a case study . *Turkish Journal of Zoology*, *41*(3), 530-548.

Vlaschenko A, Gukov V, Naglov A, Prylutska A, **Kravchenko K**, Rodenko O. **(2016)** New underground hibernaculum of brandt's bat (myotis brandtii) in ukraine, and comparison of summer and winter bat populations. *Vestnik zoologii*, *50*(3), 231-240.

Vlaschenko A, **Kravchenko K**, Prylutska A, Ivancheva E, Sitnikova E, Mishin A **(2016)** Structure of summer bat assemblages of forests in European Russia. *Turkish Journal of Zoology*, *40*(6), 876-893.

**Kravchenko K**, Vlaschenko A,Prylutsky O, Prylutska A **(2015)** A search of Geomyces destructans , adangerous pathogen of bats in caves of Eastern Europe. *Russian Journal of Ecology*, *46*(5), 490.

Gashchak S, Vlaschenko A, Estok P, **Kravchenko K (2015)** New long-distance recapture of a noctule (*Nyctalus noctula*) from eastern europe . *Hystrix, the Italian Journal of Mammalogy*, *26*(1), 59-60.

Rodenko E, **Kravchenko K**, Vlaschenko A, Chepiznaja A, Suvorova A, Prylutska A **(2014)** The record of *Nyctalus noctula* in winter time in Poltava city (Ukraine). *Plecotus et al*, *17*, 43-51.

### Peer reviewed

Gashchak S, Vlaschenko A, Naglov A, **Kravchenko K**, Prylutska A **(2013)** Bats fauna of the exclusion zone in concern of assessment of environmental value of its areas. Problems of Chernobyl exclusion zone. *Problems of Chernobyl exclusion zone*, *11*, 56-78.

**Kravchenko K (2013)** The technique for visualization of hyphal interaction zones of *Botrytis cinerea* isolates. *Annales UMCS, Biologia*, *67*(2), 35-43.

Vlaschenko A, Godlevska L, **Kravchenko K**, Tyshchenko V, Gukasova A, Sudakova M **(2012)** Contribution to bat fauna of Holosiyivsky National Nature Park. *Nature Reserves in Ukraine*, *18*, 51-58.

Gukasova A, Vlaschenko A, Kosenkov G, **Kravchenko K. (2011)** Bat fauna and structure of bat (Chiroptera) assemblage of the National Park "Smolensk Lakeland", Western Russia. *Acta Zoologica Lituanica*, *21*(2), 173-180.

Buchko V, Vlaschenko A, **Kravchenko K**, Sudakova M, Gukasova A, Kusnezh A **(2011)** Contribution to bat fauna (Chiroptera) of Galytskiy National Nature Park (Ivano-Frankivsk region). *Visnyk of Lviv University. Biology ser*, *55*, 146-159.

### Conference proceedings

**Kravchenko K,** Voigt C, Courtiol A, Currie S **(2021)** Energy use predicts climate-driven changes in the distribution of common noctule bats. Abstract of 15th European Bat Research Symposium, 4-7 May, Turku, Finland.

**Kravchenko K,** Vlaschenko A, Lehnert L, Courtiol A, Voigt C **(2021)** Migratory behaviour and demographic structure of bats under distribution shift. Part 2. Abstract of 6th International Berlin Bat Meeting: "The human perspective on bats", 22-24 February, Berlin, Germany.

**Kravchenko K,** Vlaschenko A, Lehnert L, Courtiol A, Voigt C **(2019)** Migratory behaviour and demographic structure of bats under distribution shift. Part 1. Wildlife Research and Conservation 2019 (WRC2019), 30th September - 2nd October 2019, Berlin, Germany.

**Kravchenko K ,** Butschkau S **(2019)** Diet analysis of *Nyctalus noctula* following a new hibernacula range. 5th IZW PhD symposium, 26-27 September, Berlin, Germany.

**Kravchenko K,** Kovalov V, Timofieieva O, Rodenko O, Vlaschenko A **(2018)** Places of pre-hibernation foraging activity of *Nyctalus noctula* (Vespertilionidae, Chiroptera) in Eastern Ukraine. The Tenth International Zoological Congress of "Grigore Antipa" Museum (CZGA 2018), 21-24 November 2018, Bucharest, Romania.

Vlaschenko A, Kovalov V, Tovstukha I, **Kravchenko K**, Domanskaya A, Holovchenko O, Hukov V, Timofieieva O, Rodenko O, Muzyka D, Prylutska A **(2018)** Bats as natural reservoir and potential vector of zoonotic pathogens in modern urban environment. Abstract of 3rd Annual BTRP Ukraine Regional One Health Research Symposium, 16-20 April 2018, Kyiv, Ukraine: 347.

Tovstukha I, Vlaschenko A, Kovalov V, **Kravchenko K**, Orlenko A, Orlenko E **(2018)** White blood cells as an indicator of immunological status of bats. Deutsches Treffen für Fledermausforschung 2018, 12-14 January 2018, Heidesee, Germany.

Holovchenko O, **Kravchenko K**, Vlaschenko A. Whose females are larger? Sex dimorphism in skull parameters of two air-hawking Vespertilionidae bats **(2017)** The Ninth International Zoological Congress of "Grigore Antipa" Museum (CZGA 2017), 22-25 November, Bucharest, Romania.

Prylutska A., Vlaschenko A., **Kravchenko K.**, Rodenko O., Holovchenko O., Kovalov V., Hukov V., Domanska A **(2017)** Results of Bat Rehabilitation Center work during 2012-2017, Kharkiv, Ukraine. Abstract of XXVI Ogólnopolska Konferencja Chiropterologiczna,17-19 November 2017, Wiezyca, Poland: 30.

**Kravchenko K,** Vlaschenko A, Rodenko O, Hukov V, Belovetskaya S **(2017)** The results of all-winter rehabilitation of *Nyctalus noctula*: a case study (Kharkiv, NE Ukraine). Abstract of 5 th International Berlin Bat Meeting: "Are bats special?", 24-26 February, Berlin, Germany: 102.

Vlaschenko A, **Kravchenko K**, Hukov V, Prylutska A, Rodenko O **(2017)** Contribution to bat longevity studies in Ukraine. Abstract of 5 th International Berlin Bat Meeting: "Are bats special?", 24-26 February 2017, Berlin, Germany: 58.

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**Kravchenko K**, Furmankiewicz A **(2015)** Winter activity of Common Noctule (*Nyctalus noctula*) in Wroclaw city (Lower Silesia, Poland). Abstr. of the 36th Conference of Young zoologists, 18-19 of November 2015, Kyiv, Ukraine.

Gukov V, Vlaschenko A, **Kravchenko K**, Shuvaev V, Rodenko O. **(2015)** An example of ecological trap for bats in city area (on example of "Derzhprom" building, Kharkiv city). Abstr. of the 36th Conference of Young zoologists, 18-19 November 2015 ,Kyiv, Ukraine.

Vlaschenko A, K. **Kravchenko K**, A. Prylutska, O. Rodenko, V. Gukov, V. Shuvaev. Year round monitoring of bat assemblage in Kharkiv city, results of 2013 year **(2015)** Abstr. of the 36th Conference of Young zoologists, 18-19 of November 2015, Kyiv, Ukraine.

Suvorova A, Shuvaev V, Vlaschenko A, **Kravchenko K**, Prylutska A, Rodenko O, Gukov V **(2015)** Acoustic monitoring of bats by Batsi program in Kharkiv region. Abstr. of the 36th Conference of Young zoologists, 18-19 of November 2015, Kyiv, Ukraine.

Rodenko O, Gukov V, Vlaschenko A, **Kravchenko K**, Prylutska A, Suvorova A, Shuvaev V **(2015)** Bat assemblage of the center area of Kharkiv city in warm season of year (2014-2015). Abstr. of the 36th Conference of Young zoologists, 18-19 of November 2015, Kyiv, Ukraine.

Rodenko O, Gukov V, Vlaschenko A, Shuvaev V, Suvorova A, Prylutska A, **Kravchenko K (2015)** Bat assemblage in Kharkov city during breeding and migration time. Abstr. of the 3th Student Teriological Conference, 24-25 of May 2015, Wroclaw, Poland. P. 11-12.

Vlaschenko A, **Kravchenko K**, Prylutska A, Gukov V, Suvorova A, Rodenko E **(2015)** Seasonal movement of bats in big city area (Kharkiv, NE Ukraine). Abstr. of 4rd International Berlin Bat Meeting: Movement Ecology of Bats, 13st – 15rd of March 2015, Berlin,Germany. P. 140.

Vlaschenko A, Gukov V, **Kravchenko K**, Naglov A, Rodenko O, Suvorova A **(2014)** Microclimate and biological studies in mines of Kharkov region. "Exploration of undergrounds of Kharkiv region": Proceedings of V research and practice conference, November 2014, Kharkiv , Ukraine. P.47-50.

**Kravchenko K**, Vlaschenko A, Voigt CC **(2014)** Stable hydrogene isotope analysis in study of changes in migration status of *Nyctalus noctula* in Eastern Europe. Abstr. of the XXIII Polish Chiropterological Conference, 28-30 of March 2014, Poznan, Poland. P. 25 (in Polish)

Prylutska A, Vlaschenko A.S., **Kravchenko K**, Rodenko E **(2014)** Bat rehabilitation during winter in Kharkiv, Ukraine. Abstr. of the XXIII Polish Chiropterological Conference, 28-30 of March 2014, Poznan, Poland. P. 35 (in Polish)

**Kravchenko K**, Vlaschenko S, Klochko A, Gukasova A **(2013)** Seasonal changes of bat assemblage in primeval beech forest of Crimea. International Conference Primeval Beech Forests "Reference System of the Management and Conservation of Biodiversity, Forest Resources and Ecosystem Services", 2-9 June 2013, Lviv, Ukraine. P. 109.

**Kravchenko K**, Vlaschenko A, Gukasova A **(2013)** Bats in Kharkov city – urban residence is not for all. Abstr. of the 1th Student Teriological Conference, 25-26 of May 2013, Wroclaw, Poland. P. 21-22.

**Kravchenko K**, Gukasova A, Vlaschenko A **(2013)** The method of inventory and monitoring of summer bat populations by using of ultra-thin mistnets. Abstr. of the Polish Chiropterological Conference, 22-24 of March 2013, Krynica Zdroj, Poland. P. 26-27 (in Polish)

**Kravchenko K**, Vlaschenko A, Voigt CC **(2013)** Bat migration in the South of Ukraine – an area of intensive development of wind power facilities. Abstr. of 3rd International Berlin Bat Meeting: Bats in the Anthropocene, 1st – 3rd of March 2013, Berlin, Germany. P. 151.

### Conference proceedings

Vlaschenko A, **Kravchenko K**, Gukasova A **(2013**) New winter aggregation of *Nyctalus noctula* in cities of NE Ukraine: evolution step in anthropocene or ecological trap? Abstr. of 3rd International Berlin Bat Meeting: Bats in the Anthropocene, 1st – 3rd of March 2013, Berlin, Germany. P. 86.

Vlaschenko, **Kravchenko K**, Gukasova A **(2013)** Prediction of the future fatalities: Bats and wind energy in Ukraine. Abstr. of the Conference on Wind Power and Environmental Impacts, 5-7 February 2013, Stockholm, Sweden. P. 109.