

OIKOS

Research article

The risk faced by the early bat: individual plasticity and mortality costs of the timing of spring departure after hibernation

Christine Reusch^{1,2}, Alexander Scheuerlein¹✉, Leo Grosche¹, Frauke Meier¹, Jutta Gampe³, Melanie Dammhahn⁴, Jaap van Schaik¹ and Gerald Kerth¹

¹Applied Zoology and Nature Conservation, Zoological Inst. and Museum, Univ. of Greifswald, Greifswald, Germany

²Dept of Evolutionary Ecology, Leibniz Inst. for Zoo and Wildlife Research, Berlin, Germany

³Laboratory of Statistical Demography, Max-Planck Inst. for Demographic Research, Rostock, Germany

⁴Behavioural Biology, Inst. for Neurobiology and Behavioural Biology, Univ. of Münster, Münster, Germany

Correspondence: Alexander Scheuerlein (alexander.scheuerlein@uni-greifswald.de)

Oikos

2023: e09654

doi: [10.1111/oik.09654](https://doi.org/10.1111/oik.09654)

Subject Editor: Allan Edelsparre

Editor-in-Chief: Dries Bonte

Accepted 15 November 2022



Hibernation is a widespread adaptation in animals to seasonally changing environmental conditions. In the face of global anthropogenic change, information about plastic adjustments to environmental conditions and associated mortality costs are urgently needed to assess population persistence of hibernating species. Here, we used a five-year data set of 1047 RFID-tagged individuals from two bat species, *Myotis nattereri* and *Myotis daubentonii* that were automatically recorded each time they entered or left a hibernaculum. Because the two species differ in foraging strategy and activity pattern during winter, we expected species-specific responses in the timing of hibernation relative to environmental conditions, as well as different mortality costs of early departure from the hibernaculum in spring. Applying mixed-effects modelling, we disentangled population-level and individual-level plasticity in the timing of departure. To estimate mortality costs of early departure, we used both a capture mark recapture analysis and a novel approach that takes into account individual exposure times to mortality outside the hibernaculum. We found that the timing of departure varied between species as well as among and within individuals, and was plastically adjusted to large-scale weather conditions as measured by the NAO (North Atlantic Oscillation) index. Individuals of *M. nattereri*, which can exploit milder temperatures for foraging during winter, tuned departure more closely to the NAO index than individuals of *M. daubentonii*, which do not hunt during winter. Both analytical approaches used to estimate mortality costs showed that early departing individuals were less likely to survive until the subsequent hibernation period than individuals that departed later. Overall, our study demonstrates that individuals of long-lived hibernating bat species have the potential to plastically adjust to changing climatic conditions, although the potential for adjustment differs between species.

Keywords: behavioural plasticity, environmental change, mortality costs, NAO, survival analysis



www.oikosjournal.org

© 2022 The Authors. Oikos published by John Wiley & Sons Ltd on behalf of Nordic Society Oikos.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

Introduction

Hibernation is a widespread adaptation in endothermic animals to survive periods with low food or water availability, especially during winter (Geiser 2013, 2021). Successful hibernation requires balancing the physiological costs and the energetic savings of torpor bouts (Humphries et al. 2003). To minimize costs, hibernation phenology must be carefully timed to synchronize with seasonal food peaks and to improve survival and reproductive success (Risch et al. 2007). A recent topic of high importance for conservation is the ability of hibernating species to respond to environmental changes, especially with regard to the expected increase in weather fluctuations with global climate change (Canale and Henry 2010, Williams et al. 2015, Wells et al. 2022).

Behavioural plasticity is the change in behaviour of an individual in response to different environments (Dingemans and Wolf 2013). It allows animals – in particular long-lived species, which cannot quickly respond by genetic adaptation – to cope with changing environments. Individuals with high behavioural and/or other forms of phenotypic plasticity have the potential to rapidly respond to changing environments (West-Eberhard 1989, van Buskirk 2012). Yet, behavioural plasticity may consistently vary between species, across populations or among individuals (Dingemans and Wolf 2013). Despite several decades of research on hibernation in mammals, there are only few studies linking individual timing of emergence from the hibernaculum with mortality costs in free-ranging populations (Ozgul et al. 2010, Lane et al. 2012, Wells et al. 2022). To predict population persistence of long-lived obligate hibernators, data on individual variation of emergence timing from hibernation and associated mortality costs are urgently required.

The few available studies (reviewed by Wells et al. 2022) showed that global climate change can affect mortality risk in hibernating species in either a positive (Ozgul et al. 2010) or a negative way (Williams et al. 2015, Rézouki et al. 2016). The latter is problematic since hibernating species tend to be situated at the slow end of the slow–fast life history continuum making their populations very vulnerable to high mortality rates (Turbill et al. 2011). There is growing evidence that hibernation phenology is associated with heritable traits such as body condition and body size, that interact with climatic conditions at the hibernation site (Vuarin et al. 2013, Williams et al. 2014). For example, in female Columbian ground squirrels *Urocitellus columbianus* the date of emergence from hibernation is heritable, yet it also showed plasticity as it was delayed in years with lower spring temperatures and late snowmelt (Lane et al. 2011, 2012).

Changing environmental conditions can have an immediate impact on population dynamics of long-lived hibernators. For example, in yellow-bellied marmots *Marmota flaviventris* earlier emergence from hibernation due to higher spring temperatures, and the associated earlier weaning of offspring ultimately resulted in faster population growth rates (Ozgul et al. 2010). In contrast, in alpine marmots *Marmota marmota* juvenile survival was reduced by warmer winter

temperatures because of reduced snowpack and less insulation (Rézouki et al. 2016). Finally, in hibernating bats, energy consumption increased with temperature in the hibernaculum (Williams et al. 2015).

Bats are exceptionally long-lived compared to other mammals of similar body size (Munshi-South and Wilkinson 2010), with low annual reproductive output (Fleischer et al. 2017) and long generation times (Mundinger et al. 2022). As a result, genetic adaptation to changing conditions is expected to happen at a slow rate (Reed et al. 2011). Therefore, plasticity of individual hibernation behaviour should be key to predict whether bats of the temperate zone are able to cope with climate change. Here, we test whether bats adjust their departure from the hibernaculum in spring to large-scale weather conditions at the population and individual level, and quantify bats' mortality costs associated with an early departure.

We compared two similar-sized, insectivorous European bat species, Natterer's bats *Myotis nattereri* and Daubenton's bats *Myotis daubentonii*. Both depend on hibernation to survive the period of low arthropod availability during winter (Dietz et al. 2016). However, the two species differ with respect to their foraging and hibernation behaviour (Meier et al. 2022). Daubenton's bats mostly hunt above water and their trawling foraging strategy is restricted to warmer temperatures, when insects emerge from, or drop into water bodies (Salvarina et al. 2017). As a consequence, Daubenton's bats are not able to feed efficiently during the hibernation period (Kokurewicz 2004). In contrast, Natterer's bats feed by gleaning arthropods from the vegetation or from the walls of stables of domestic animals, where prey can also be found at low ambient temperatures (Siemers and Schnitzler 2000). Indeed, there is evidence that Natterer's bats can forage during the hibernation period during mild nights (Hope et al. 2014).

Here, we test the hypothesis that the plasticity and the survival costs of phenological responses to weather conditions depend on the foraging mode in the two bat species studied. We used the winter index (December through March) of the North Atlantic Oscillation (NAO) as a proxy for large-scale winter weather patterns over Europe (Hurrell 1995, Post et al. 1997). As both of our study species are long-lived (Dietz et al. 2016), and individuals typically return to the same hibernaculum year after year (Hutterer et al. 2005, Steffens et al. 2007), we were able to track individual plasticity in the timing of departure from the hibernaculum in spring over several years.

With respect to the timing of departure we predicted that due to their dependency on flying insects, Daubenton's bats should depart later in spring than Natterer's bats. At the same time, because of their higher winter activity, Natterer's bats should have been able to track environmental parameters more closely and, therefore, depart earlier in milder winters with a high NAO (Hurrell 1995). We expected that Natterer's bats show higher individual plasticity with respect to the timing of departure than Daubenton's bats (Meier et al. 2022).

In both species, we expected age- and sex-specific differences in departure timing due to particular sex- and

age-specific energetic needs (Kohyt et al. 2016, Czenze et al. 2017, Meier et al. 2022). For example, young of the year should leave the hibernaculum earlier than adults due to their typically lower body weights at the start of hibernation thus exacerbating the need to start foraging again in spring before their first reproduction (Kokurewicz 2004, Trappmann 2005, Meier et al. 2022).

Finally, we also expected consistent inter-individual differences in departure timing. Our expectation is based on potential individual variation in traits such as body condition or metabolism, that we were not able to measure, but that presumably influenced individual departure (Norquay and Willis 2014, Czenze and Willis 2015, Boyles et al. 2020, Wells et al. 2022).

With respect to survival, we predicted that departing from the hibernaculum early, when food availability was likely to still be low, was associated with higher mortality. Because of the above-mentioned idiosyncrasies in foraging behaviour, we expected that the risk associated with early departure in spring was higher in Daubenton's bats than in Natterer's bats.

Material and methods

Bat capture and data logging

We studied arrival (first recorded activity per hibernation period) and timing of departure from the hibernaculum (last recorded activity per hibernation period) of individually marked Natterer's bats (*Myotis nattereri*: $n=540$) and Daubenton's bats (*Myotis daubentonii*: $n=507$) at a hibernaculum in North-Rhine Westphalia (Supporting information) (Stumpf et al. 2017, Meier et al. 2022). We caught bats using harp traps at the entrance of the hibernaculum, sexed them and distinguished two age classes, young of the year (1st hibernation) and adults (> 1 hibernation; for details see Reusch et al. 2019). At this site, bats have been marked with individual RFID-tags (ID 100, Trovan) since 2002 for Natterer's bats and since 2008 for Daubenton's bats. Here, we focused on the years 2011–2015, for which we had continuous monitoring of bats entering and exiting the hibernaculum. All capture and marking were conducted under the permits (50.0835.2.1, 84-02.04.2015.A508, 70.2-2012/0254, 70.2-0228/10, 70.2-0197/08 and 70.2.2.27), issued by the relevant authorities.

The studied hibernaculum has two small entrances (8×5 cm), which were monitored by RFID-logger-antenna systems (LID-650, EURO I.D.). These systems continuously recorded the ID and a timestamp for all tagged individuals without interfering with the bats' behaviour (Reusch et al. 2019, Meier et al. 2022). As only one antenna was employed per entrance, we could not directly assess whether a tagged bat entered or left the hibernaculum when detected by the RFID-logger. Therefore, we defined an arrival period (1 Aug–31 Dec) and a departure period (1 Jan–30 Apr) for each hibernation (H_t) based on activity patterns known from direct observations in the field, light barrier recordings (that

count the number of bats entering and emerging) and RFID recordings (as in Meier et al. 2022).

For each individual and year, we determined the date of the last recording during the departure period (departure date of H_t) and the date of the first recording during the subsequent arrival period (arrival date of H_{t+1}). An individual was considered dead if it was not recorded in the subsequent hibernation period (H_{t+1} , Aug–Apr). We confirmed this assumption based on the available data: In our 5-year study period of continuous monitoring at the hibernaculum only one out of 1047 tagged individuals re-occurred after not being recorded during a complete hibernation period. Moreover, in 13 years of bat surveillance only 24 out of 1111 bats (2.2%) assigned dead according to the abovementioned criteria re-appeared at another RFID-monitored hibernaculum in close proximity to the study site (< 500 m distance) for at least one more year (Grosche and Meier unpubl.).

To make sure that recorded individuals have indeed used the hibernaculum for hibernation, we excluded those individuals that had not been recorded during both, the arrival and the following departure period of a given hibernation period (Aug–Apr.; *M. nattereri*: 18 out of 540 individuals (3.3%); *M. daubentonii*: 32 out of 507 individuals (6.3%)).

Mixed-effect modelling

We compared average departure dates between species, using a Wilcoxon rank sum test with continuity correction, as data are not normally distributed but the variance was homogeneous (Bartlett test; Supporting information).

Plasticity analyses

To assess differences in departure date between sexes and age classes for each species separately, we applied restricted maximum likelihood linear mixed-effects models (REML LMMs) with normal errors (Zuur et al. 2009). Sex, age class and their interactions entered as fixed effects. Individuals were repeatedly sampled (*M. nattereri*: 59 individuals with at least two consecutive departure dates (maximum one individual with four consecutive departure dates); *M. daubentonii*: 121 individuals with at least two consecutive departure dates (maximum one individual with five consecutive departure dates)) and individual ID was entered as random effect, specified as random intercept, to estimate among-individual differences in average departure date across years.

In another set of models that include both random intercept and random slope, we included a proxy for the large-scale winter weather patterns over Europe (Hurrell 1995, Post et al. 1997), the widely used winter station-based index of NAO for 1 December to 31 March (Hurrell 1995). Positive values are associated with wetter/milder weather, while negative values are associated with dryer/colder weather over western Europe during winter (Hurrell 1995). NAO index data were provided by the Climate Analysis Section, NCAR, Boulder, USA, Hurrell (1995; accessed 30 September 2017, Supporting information). To investigate the plasticity of departure behaviour with respect to the NAO, we followed

an approach of within-individual centring (suggested by van de Pol and Wright 2009) and included two NAO terms as fixed effects. The first term was the mean NAO (NAOm) experienced by each individual over the years the individual was present (i.e. the between-subject variation component), which estimates whether individuals that (on average) experienced milder winters also departed earlier in general. The second term was the mean-centred NAO (NAOmc), which is the deviation of the NAO for all observations of an individual from its experienced mean NAO conditions (i.e. the within-subject variation component). The NAOmc allows to estimate – at the population level – whether each individual departs earlier in milder winters (i.e. phenotypic plasticity at the population level). We included the slopes of NAOmc as a random factor to test for individual variance in behavioural plasticity in departure date with winter weather conditions. Finally, we tested for sex-specific effects on departure date plasticity by adding an interaction between NAOmc and sex.

We compared models based on AICc and selected simpler models whenever $dAICc_i < 2$, for $dAICc_i = AICc_i - AICc_{\min}$ (Burnham et al. 2011). First, we established random effect structure by comparing models with and without random effects using the global model. Subsequently, we selected interactions and fixed main effects. All models were fitted using R, ver. 3.4.0 (package 'nlme', function *lme*) (www.r-project.org). Furthermore, we calculated adjusted repeatability (R), using the R-package 'rptR' as the proportion of variance explained by the between-individual differences of the random intercept adjusting for the fixed effects (Nakagawa and Schielzeth 2010, Stoffel et al. 2017), and estimated 95% confidence intervals of R based on 1000 bootstrapping runs and 1000 permutations.

Survival analysis

To assess whether animals that depart earlier from the hibernaculum differed in survival rates to those that depart later we employed two approaches: a traditional capture–mark–recapture (CMR) approach, and a novel approach (which we termed 'modelling individual exposure risk' = MIER) that takes individual-specific exposure times to mortality outside the hibernaculum into account. Using the traditional CMR approach, we took spring and autumn as discrete recording events. Bats recorded at least once in the months January until March in a given year were considered alive in spring, whereas bats recorded at least once in the months August through December were considered alive in autumn. Only individuals that had a departure day in spring entered the analysis. Goodness of fit tests (Gimenez et al. 2018) indicated slight overdispersion which was controlled for as recommended by adjusting the dispersal parameter in the final estimates. The time of departure (last registration in spring) was calculated as mentioned above. Analyses were performed using a Cormack–Jolly–Seber model with the hierarchical likelihood construction described by Pledger et al. (2003) as implemented in the package 'marked' in R (Laake and Johnson 2019). Estimated survival and recapture rates were in agreement with

Culina et al. (2017), who studied ringed populations of *M. nattereri* and *M. daubentonii* in Great Britain.

Our novel MIER approach intends to overcome the bias introduced by using passive continuous recording methods, which yield data that cannot be readily divided into a discrete sampling scheme as required by traditional CMR approaches (Barbour et al. 2013, van Harten et al. 2022). When individuals are exposed to a certain level of mortality, that is, to a certain risk of death per unit of time, then those individuals that are exposed to this mortality for longer will show a lower proportion of survivors at the end of the summer – not because their death rates were higher but solely because their exposure-to-risk was longer. For example, in our dataset if one individual departs 20 days earlier than another, the second individual is known to be alive during those 20 days (as it is recorded when it departs), while the first had a non-zero chance of having died during this period. As a result, even if the daily risk of dying were the same for all animals, using the departure date as a covariate for survival would produce a beneficial effect of later departure, which simply would reflect a shorter exposure time, although the death rates were identical. The length of exposure time is particularly relevant for hibernators, where individuals are typically safer while staying in the hibernaculum compared to the active phase outside (Wells et al. 2022). This is reflected in the comparatively high winter survival rates of our two study species (Reusch et al. 2019). Hence, a naïve approach that ignores exposure time would not be able to identify higher death rates of early-departing animals.

Our novel MIER approach required the following steps: We needed to estimate the average daily death rate for animals that do not depart early. This was done by standard survival analysis (Kleinbaum and Klein 2005). Second, we calculated the expected number of individuals surviving to the end of the summer among those bats that departed early under the assumption that these early-departing bats were exposed to the same daily mortality as the other group (later departing bats) taking the longer exposure-to-risk of the former group into account. If the observed number of survivors was markedly lower (or higher) than the expected number under the 'equal-mortality-hypothesis', we could conclude that early-departing bats suffered from higher (or lower) death rates, since the longer exposure times had already been accounted for. A proper test statistic was developed for this assessment. The formal details of the approach are deferred to the Supporting information.

To define which individuals were considered to have departed 'early', we used species- and year-specific cumulative departure curves (Supporting information, Fig. 1). We defined early departure as all individuals departing before the date when the daily increase of the relative cumulative departure curve exceeded 1.5 percent of the year-specific total number of departing individuals. To avoid the problem that a single day with relatively many departures surrounded by days of low activity triggers this criterion, the cumulative departure curve was smoothed by a 10-day moving average. We consider this a more sensitive method as opposed to using the inflection point of the cumulative departure curve.

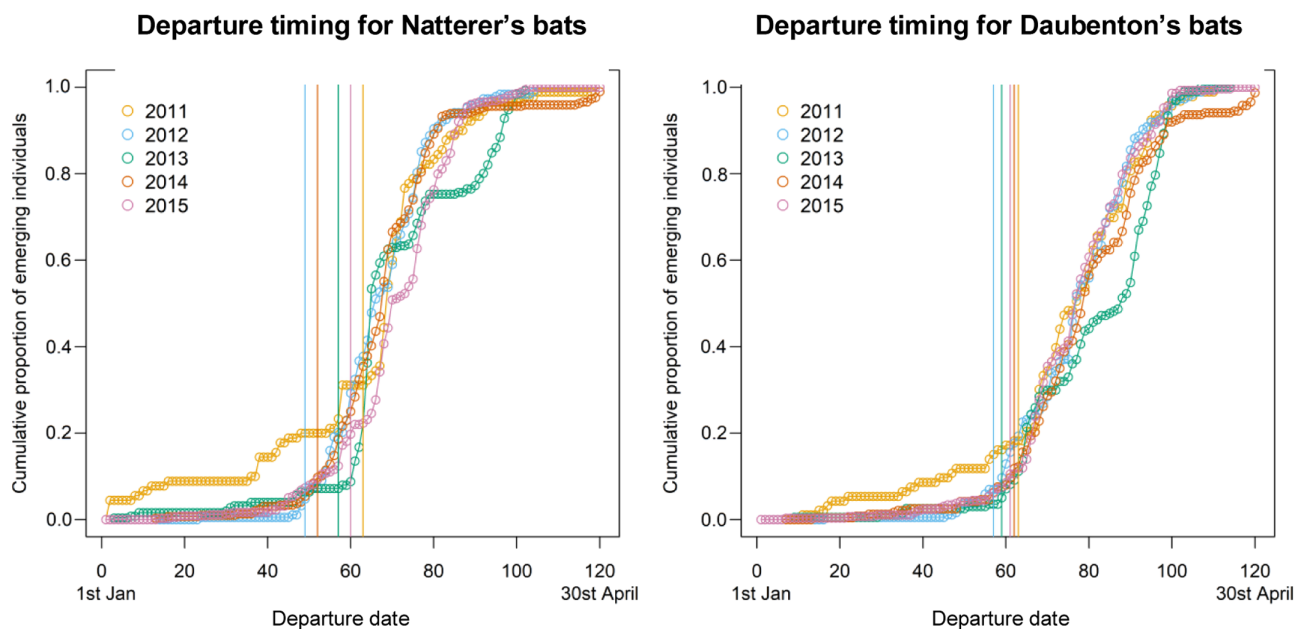


Figure 1. Curve showing the cumulative proportion of individuals that left the hibernaculum for the season with regard to date. Natterer's bat *Myotis nattereri* is plotted on the left side, Daubenton's bat *Myotis daubentonii* on the right side. These cumulative departure curves share the characteristic that their trajectory is flat in the beginning, followed by a steep increase during the period when the majority of bats leave the hibernaculum, concluded by another flat stretch towards the end of the departure season. The vertical lines characterize the year-specific threshold (colour coded according to the legend) to identify early bats, individuals that left the hibernaculum earlier or equal to the given threshold.

Results

General pattern

Overall, 1047 RFID-tagged individuals were recorded > 23 500 times, yielding 3945 individual arrival and departure dates over five years. The median of recordings of each individual per departure period was 1.5 times for Natterer's bats and 1.0 times for Daubenton's bats. The cumulative curves of departure date for the five years showed similar sigmoid patterns but they were shifted between the species (Fig. 1). In all years, Daubenton's bats departed from the hibernaculum later than Natterer's bats, on average between 7.5 to 12.6 days (Supporting information).

Species-specific patterns

The final REML-LMMs included both the mean NAO and the mean-centered NAO, as well as sex and age class, and were similar for both species. However, we did not find sufficient support for an interaction between sex and age class in Daubenton's bats where the timing of departure did not differ between the sexes in the first year (Supporting information, Fig. 2).

In Natterer's bats, individuals that experienced higher NAO conditions (warmer and wetter) left the hibernaculum 0.9 days later per NAO unit and young of the year left the hibernaculum 4 days earlier than adults. In this species, plastic adjustment of departure date to NAO was sex- and age-class specific. Male Natterer's bats departed from hibernation later when they experienced warmer years with higher NAO

(0.7 days per increase of the NAOmc by 1), while females left earlier with increasing NAO (on average -1.1 days per increase of the NAOmc by 1) (Fig. 2). Moreover, female young of the year left on average even 2.1 days earlier than male young of the year.

In Daubenton's bats departure date varied between age classes, with young of the year leaving the hibernaculum substantially earlier than adults (on average 8.0 days), but we did not find support for a between-individual effect (NAOm) on departure date. As in Natterer's bats, plastic adjustment of departure date to currently experienced NAO conditions (NAOmc) was sex-specific. Females departed from hibernation significantly earlier with higher NAOmc (on average -1.0 days per increase of the NAOmc by 1) but males did not change departure date with NAO.

Individual plasticity in departure dates

In both species, individuals consistently differed from each other in departure dates (standard deviation of the random intercept; *M. nattereri*: 10.9 days, *M. daubentonii*: 8.3 days), and remaining random variation in both species was high (standard deviation residual; *M. nattereri*: 11.4 days, *M. daubentonii*: 13.7 days). In Natterer's bats, individual plasticity of departure date to NAOmc (i.e. random slopes) differed among individuals (by 1.0 day on the population level), with a high negative correlation with the random intercept (Table 1). Thus, the later an individual departed on average over all study years, the more it advanced its departure in response to increasing NAO (Fig. 2). In Daubenton's bats, individuals did not differ in plasticity of departure to NAO conditions.

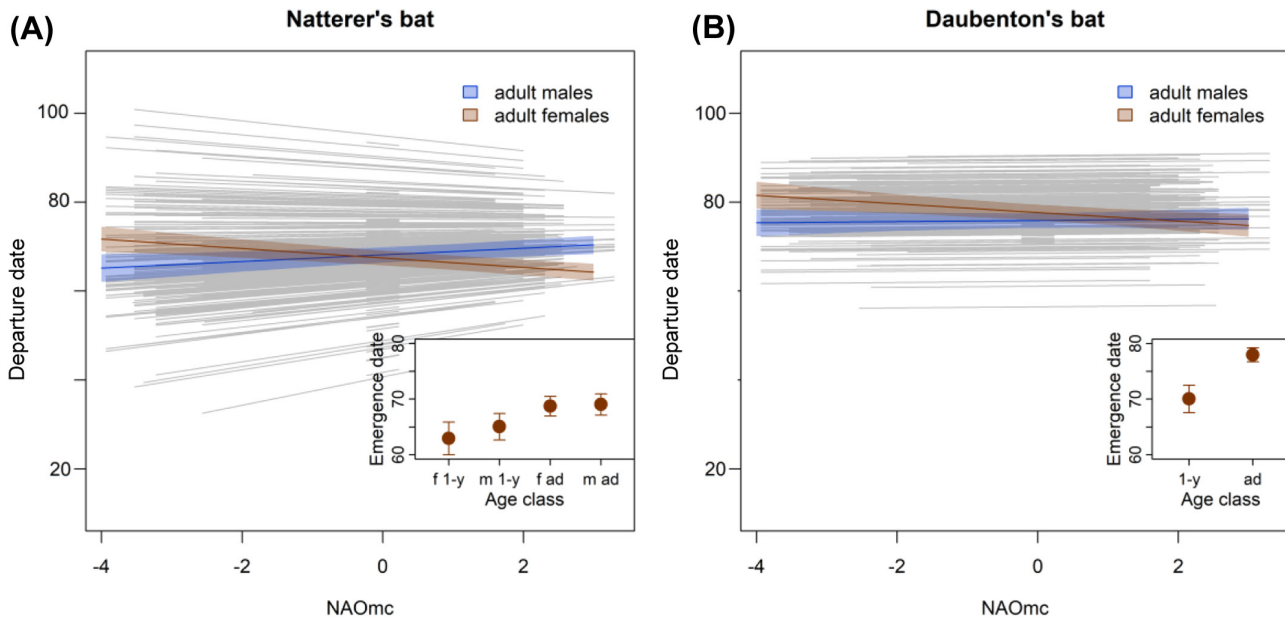


Figure 2. Estimated plastic adjustment of departure date to experienced large-scale weather conditions (NAO) for Natterer's bats, *Myotis nattereri* (A), and for Daubenton's bats, *Myotis daubentonii* (B), – shown are within-individual responses of departure date (1 = 1 January) to the mean-centred NAO (NAOmc) based on the estimated random intercepts for the species-specific linear mixed-effects models. Random slopes, i.e. individual differences in plastic adjustments, were supported for Natterer's bats but not for Daubenton's bats. The colour-coded lines and their confidence intervals show the differing interactions between NAOmc and sex (m – male, f – female), while the additional subplot shows the differences between sexes and/or age classes (1-y – young of the year, ad – adult).

Departure date and survival

In both species, there was no relationship between individual departure date and individual arrival date, neither at the beginning of the subsequent hibernation period (next fall; Supporting information) nor during the same hibernation period. Therefore, surviving individuals that left the

hibernaculum earlier in spring arrived at the hibernaculum concurrent with those individuals that departed later.

Both, the CMR approach, and our novel MIER approach yielded similar results. Over all five years, fewer bats that departed early survived until the following fall than expected based from exposure time (CMR: Supporting information, novel approach: Table 2). This holds true for both species,

Table 1. REML estimates of species-specific LMMs with departure dates as response (1 = 1 January) for Daubenton's bats and Natterer's bats. A random intercept controls for repeated observations of the same individual across years. The number of observations ($N_{\text{observations}}$) and the number of individuals (N_{ind}) that were included in the model are given. In brackets 95% confidence interval of each estimate is given. Reference levels for fixed effects are 'male' for sex and 'adult' for age class.

| Fixed effects | Estimate (95% CI) | Additional model information | Estimate (95% CI) |
|---|-------------------|--|-------------------|
| Natterer's bats | | | |
| Intercept | 67.3 (64.9;69.8) | Random intercept standard deviation | 10.9 (9.8;12.2) |
| NAOm | 0.9 (0.2;1.7) | Random slope standard deviation | 1.0 (0.9;1.2) |
| NAOmc | 0.7 (0.2;1.3) | Correlation between random slope and intercept | -0.9 (-1.0;0.0) |
| Sex | -0.3 (-2.9;2.3) | Residual standard deviation | 11.4 (10.8;12.0) |
| Age class | -4.0 (-6.5;-1.5) | | |
| Interaction age class × sex | -1.8 (-5.8;2.2) | $N_{\text{observations}}$ | 1179 |
| Interaction individually mean-centred NAO × sex | -1.8 (-2.5;-1.1) | N_{ind} | 522 |
| Daubenton's bats | | | |
| Intercept | 77.0 (74.5;79.3) | Random intercept standard deviation | 8.3 (6.9;10.0) |
| Individual mean NAO | 0.1 (-0.7;0.9) | Residual standard deviation | 13.7 (12.9;14.6) |
| Individually mean-centred NAO | 0.1 (-0.5;0.8) | | |
| Sex | 1.8 (-0.6;4.2) | $N_{\text{observations}}$ | 1006 |
| Age status | -8.0 (-10.6;-5.3) | N_{ind} | 475 |
| Interaction individually mean-centred NAO – sex | -1.1 (-2.0;-0.2) | | |

but the effect is stronger in Daubenton's bats when we performed the analyses for each year separately. In Daubenton's bats, in the years 2014 and 2015 early departing individuals had a significantly reduced survival, and there was a trend in the same direction in 2013 ($p=0.088$). In Natterer's bats, the effect seen in the general analysis was based on a significantly lower number of surviving early individuals in 2011 (Table 2, Supporting information). In all the remaining years with a higher number of early departing bats, early Natterer's bats did not show lower survival than expected. Due to low sample sizes, we were not able to control for age class effects in the survival analysis. However, the distribution of age classes among the early bats was comparable or showed a lower number of young of the year than adults (Supporting information).

Discussion

We found that emergence (departure from hibernation) date varied within individuals, among individuals and between two species of insectivorous bats. Individuals of Natterer's bats departed earlier, had higher within-individual plasticity of departure timing related to winter conditions (NAO), and early departing individuals typically suffered lower mortality costs than Daubenton's bats.

Species-specific differences in departure timing

Hibernating species should tune their emergence/departure from the hibernaculum to food availability (Wells et al. 2022). As predicted from their respective foraging mode, Daubenton's bats departed on average later from the hibernaculum than Natterer's bats in each year. This finding is in line with results of Meier et al. (2022) on species-specific difference in the length of the longest individual hibernation periods. Since Natterer's bats glean arthropods from surfaces (Siemers and Schnitzler 2000, Hope et al. 2014), their foraging strategy is less constrained by low ambient temperatures in early spring than the trawling of active insects above water preyed upon by Daubenton's bats (Salvarina et al. 2017).

In both bat species, young of the year departed on average earlier than adults. It has been described in many mammal species that young of the year enter hibernation with lower

body condition than adults (Kokurewicz 2004, Ozgul et al. 2010, Wells et al. 2022). Thus, young of the year may have been forced to depart from the hibernaculum earlier to replenish depleted fat reserves, as has been found in juvenile edible dormice (Bieber and Ruf 2004).

Females of both species departed later in colder winters and earlier in warmer winters, which is in line with findings from other hibernating species where female condition in spring affects reproductive effort in the coming breeding season (Czenze et al. 2017, Wells et al. 2022). In contrast, male Natterer's bats showed an opposite pattern, and departed later in milder winters and earlier in colder winters, whereas male Daubenton's bats did not adjust departure to winter conditions. This sex-specific departure pattern might be due to an interaction between sex-specific requirements and the specific climatic condition in the different years. In male bats, spermatogenesis occurs in later summer, followed by large energetic investments into mating-related activity at hibernacula during the autumn swarming phase. As a result, males must replenish their fat reserves just before the start of hibernation (Kohyt et al. 2016). In Daubenton's bats peak swarming activity occurs nearly a month before that of Natterer's bats (van Schaik et al. 2015). Thus, in cooler winters, when it was difficult to gain fat reserves in November and December, male Natterer's bats might have had to leave earlier once their fat reserves had been depleted. In contrast, females of both species strongly benefit from early departure in warm winters, as this would have ensured early arrival in the breeding habitat and a longer time to gather resources before fertilization and pregnancy. For comparison, Norquay and Willis (2014) reported an earlier departure of females compared to males in little brown bats *Myotis lucifugus*, which they explained with reproductive advantages (earlier birth of offspring and consequently a longer growing season).

Between-individual variation in departure timing

Our individual-based data from five consecutive years allowed us for the first time in bats to analyse variation in the average departure date among individuals. For Natterer's bats, we found significant inter-individual variation and a moderate correlation between repeated

Table 2. Results of the MIER survival analysis for Natterer's bats *Myotis nattereri* and Daubenton's bats *Myotis daubentonii*. The columns contain the number of early-departing animals (No. ind), the observed number of survivors (Survivor_{obs}) and the expected number of survivors under the hypothesis that early bats suffer the same risk of death as the rest of the population (Survivor_{exp}), and the resulting p-value. Significant values are given in bold font, and significance level is indicated by stars (* < 0.05, ** < 0.01, *** < 0.001). A tendency is characterized by italic letters and is indicated by a point (· < 0.1).

| Year | Natterer's bats | | | | Daubenton's bats | | | |
|-------------|-----------------|-------------------------|-------------------------|----------------|------------------|-------------------------|-------------------------|-----------------------------------|
| | No. ind | Survivor _{obs} | Survivor _{exp} | p value | No. ind | Survivor _{obs} | Survivor _{exp} | p value |
| All | 171 | 132 | 141.3 | 0.029* | 104 | 59 | 79.7 | 5.13 × 10⁻⁰⁷*** |
| 2011 | 29 | 18 | 24.8 | 0.002** | 17 | 10 | 12.5 | 0.143 |
| 2012 | 14 | 12 | 12.1 | 0.589 | 13 | 7 | 9.1 | 0.168 |
| 2013 | 20 | 13 | 14.0 | 0.384 | <i>14</i> | 6 | 8.9 | <i>0.088</i> |
| 2014 | 30 | 27 | 26.2 | 0.756 | 29 | 17 | 25.6 | 5.54 × 10⁻⁰⁵*** |
| 2015 | 78 | 62 | 64.2 | 0.299 | 31 | 19 | 23.6 | 0.045* |

observations of individuals over the years. Thus, individuals that had departed earlier than the population average in one year tended to be early also in other years. For comparison, [Dammhahn et al. \(2017\)](#) showed that the use of heterothermy, i.e. how deep an individual was in torpor during hibernation, was highly repeatable and, thus an individual-specific trait in eastern chipmunks *Tamias striatus* ([Dammhahn et al. 2017](#)).

Also, for Daubenton's bats we found support for inter-individual differences in departure timing, albeit repeatability was lower than in Natterer's bats. Due to their specific foraging technique ([Siemers et al. 2001](#)) the optimal time for departure seemed to be later and less weather dependent for Daubenton's bats. The ability of Natterer's bats to find food at lower temperatures might have led to a larger individual flexibility in activity patterns. This would explain the observed higher variation between individuals. However, in both species the observed moderate repeatability indicated a potential heritability of individual departure timing similar to the range shown for Columbian ground squirrels *Urocyon columbianus* (females: $h^2 = 0.22 \pm 0.05$, males: $h^2 = 0.34 \pm 0.14$) ([Lane et al. 2011](#)).

Individual variation in plasticity of departure date

In line with our hypothesis only Natterer's bat individuals differed in plasticity with respect to winter condition as reflected by the NAO. However, variation due to among-individual differences was much larger than variation due to plasticity. Overall, our results thus suggest that the two study-species differ in individual behavioural plasticity and their response towards weather conditions. This suggests that in bats the potential to behaviourally adjust to environmental change differs among individuals ([Dingemanse and Wolf 2013](#)) and species.

Mortality costs of early departure

Early departure from the hibernaculum incurred high mortality costs in both species. Early departure may have been triggered by depleted fat reserves and required immediate foraging even though insect abundance might still be low. Thus, this behaviour may correspond to 'making the best of a bad job'. For comparison, in a study based on activity data at a hibernaculum in Wisconsin, little brown bats *M. lucifugus* typically departed before insect abundance peaks ([Meyer et al. 2016](#)) which could also have been caused by depleted fat reserves. A forced early departure due to depleted fat reserves may be more problematic for Daubenton's bats as the emergence of their aquatic prey is far more synchronized and later than terrestrial insects ([Salvarina 2017](#)). Natterer's bats that are able to hunt during milder winters might have been able to easier compensate early departure from the hibernaculum. As a consequence, the timing of departure in Daubenton's bats carries a higher mortality load, and is more subject to the force of selection than the timing of the more plastic Natterer's bats.

Conclusions

Our results strongly suggest that hibernating bat species differ both in their capacity to buffer environmental variation (plasticity), and their evolutionary potential for adaptations to climate change. This should inform the assessment of species vulnerable to climate change, and at the same time guide conservation practices for the species in question.

Acknowledgements – We are grateful to the landowner, the nature and animal conservation departments and the Naturschutzzentrum Coesfeld for support and to our colleagues and friends, trainees and volunteers for help in the field. We are thankful to Carsten Trappmann and Björn Siemers for helping us starting our research project as well as to Sébastien Puechmaille for fruitful discussions concerning data preparation data exploration, and the conception of the project. Open Access funding enabled and organized by Projekt DEAL.

Funding – Christine Reusch was supported by the financial assistance of the German Research Foundation (DFG Research training Group 'Biological Responses to Novel and Changing Environments' (RTG 2010)). Alexander Scheuerlein was supported by grant no. 3520820300 from the German Federal Agency for Nature Conservation (BfN) with funds from the German Federal Ministry for the Environment, Nature Conservation, Nuclear Safety and Consumer Protection.

Ethics statement – All applicable institutional and/or national guidelines for the care and use of animals were followed. All bat captures, handling, marking and installations of monitoring systems were carried out under license of the respective authorities (permit no. 50.0835.2.1, 84-02.04.2015.A508, 70.2.2.27, 70.2-0197/08, 70.2-0228/10, 70.2-2012/0254, 70.2-2016/0023).

Author contributions

Christine Reusch and **Alexander Scheuerlein** contributed equally to this publication. **Christine Reusch:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Methodology (equal); Validation (equal); Visualization (equal); Writing – original draft (equal). **Alexander Scheuerlein:** Conceptualization (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Project administration (equal); Supervision (equal); Validation (lead); Writing – review and editing (equal). **Leo Grosche:** Data curation (equal); Resources (equal). **Frauke Meier:** Conceptualization (equal); Data curation (equal); Resources (equal). **Jutta Gampe:** Formal analysis (lead); Investigation (equal); Methodology (equal); Validation (equal); Writing – original draft (supporting). **Melanie Dammhahn:** Formal analysis (equal); Methodology (supporting); Validation (equal); Writing – original draft (supporting); Writing – review and editing (supporting). **Jaap van Schaik:** Methodology (equal); Writing – review and editing (equal). **Gerald Kerth:** Conceptualization (lead); Funding acquisition (lead); Project administration (lead); Resources (equal); Supervision (lead); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.sn02v6x7r> (Reusch et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

References

- Barbour, A. B., Ponciano, J. M. and Lorenzen, K. 2013. Apparent survival estimation from continuous mark–recapture/resighting data. – *Methods Ecol. Evol.* 4: 846–853.
- Bieber, C. and Ruf, T. 2004. Seasonal timing of reproduction and hibernation in the edible dormouse *Glis glis*. – In: Barnes, B. M. and Carey, H. V. (eds), *Life in the cold: evolution, mechanism, adaptation and application*. Inst. of Arctic Biology, Univ. of Alaska, pp. 113–125.
- Boyles, J. G., Johnson, J. S., Blomberg, A. and Lilley, T. M. 2020. Optimal hibernation theory. – *Mammal Rev.* 50: 91–100.
- Burnham, K. P., Anderson, D. R. and Huyvaert, K. P. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations and comparisons. – *Behav. Ecol. Sociobiol.* 65: 23–35.
- Canale, C. I. and Henry, P.-Y. 2010. Adaptive phenotypic plasticity and resilience of vertebrates to increasing climatic unpredictability. – *Clim. Res.* 43: 135–147.
- Culina, A., Linton, D. M. and Macdonald, D. W. 2017. Age, sex and climate factors show different effects on survival of three different bat species in a woodland bat community. – *Global Ecol. Conserv.* 12: 263–271.
- Czenze, Z. J. and Willis, C. K. R. 2015. Warming up and shipping out: arousal and emergence timing in hibernating little brown bats *Myotis lucifugus*. – *J. Comp. Physiol. B* 185: 575–586.
- Czenze, Z. J., Jonasson, K. A. and Willis, C. K. R. 2017. Thrifty females, frisky males: winter energetics of hibernating bats from a cold climate. – *Physiol. Biochem. Zool.* 90: 502–511.
- Dammhahn, M., Landry-Cuerrier, M., Réale, D., Garant, D. and Humphries, M. M. 2017. Individual variation in energy-saving heterothermy affects survival and reproductive success. – *Funct. Ecol.* 31: 866–875.
- Dietz, C., Nill, D. and von Helversen, O. 2016. *Handbuch Fledermäuse Europas*. – Kosmos.
- Dingemanse, N. J. and Wolf, M. 2013. Between-individual differences in behavioural plasticity within populations: causes and consequences. – *Anim. Behav.* 85: 1031–1039.
- Fleischer, T., Gampe, J., Scheuerlein, A. and Kerth, G. 2017. Rare catastrophic events drive population dynamics in a bat species with negligible senescence. – *Sci. Rep.* 7: 7370.
- Geiser, F. 2013. Hibernation. – *Curr. Biol.* 23: R188–R193.
- Geiser, F. 2021. *Ecological physiology of daily torpor and hibernation*. – Springer.
- Gimenez, O., Lebreton, J.-D., Choquet, R. and Pradel, R. 2018. R2ucare: an R package to perform goodness-of-fit tests for capture–recapture models. – *Methods Ecol. Evol.* 9: 1749–1754.
- Hope, P. R., Bohmann, K., Gilbert, M. T. P., Zepeda-Mendoza, M. L., Razgour, O. and Jones, G. 2014. Second generation sequencing and morphological faecal analysis reveal unexpected foraging behaviour by *Myotis nattereri* (Chiroptera, Vespertilionidae) in winter. – *Front. Zool.* 11: 39.
- Humphries, M. M., Thomas, D. W. and Kramer, D. L. 2003. The role of energy availability in mammalian hibernation: a cost–benefit approach. – *Physiol. Biochem. Zool.* 76: 165–179.
- Hurrell, J. W. 1995. Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. – *Science* 269: 676–679.
- Hutterer, R., Ivanonva, T., Meyer-Cords, C. H. and Rodrigues, L. 2005. *Bat migrations in Europe: a review of banding data and literature*. – Federal Agency for Nature Conservation.
- Kleinbaum, D. G. and Klein, M. 2005. *Survival analysis: a self-learning text*. – Springer Science and Business Media, LLC.
- Kohyt, J., Rozik, A., Kozakiewicz, K., Pereswiet-Soltan, A. and Gubala, W. J. 2016. Activity pattern and fat accumulation strategy of the Natterer's bat (Vespertilionidae, Chiroptera) swarming population indicate the exact time of male mating effort. – *Mammal Res.* 61: 383–389.
- Kokurewicz, T. 2004. Sex and age related habitat selection and mass dynamics of Daubenton's bats *Myotis daubentonii* (Kuhl, 1817) hibernating in natural conditions. – *Acta Chiropterol.* 6: 1508–1109.
- Laake, J. and Johnson, D. 2019. Package 'marked' in R. Ver. 1.2.6, <https://cran.r-project.org/web/packages/marked/index.html>.
- Lane, J. E., Kruuk, L. E. B., Charmantier, A., Murie, J. O., Colman, D. W., Buoro, M., Raveh, S. and Dobson, F. S. 2011. A quantitative genetic analysis of hibernation emergence date in a wild population of Columbian ground squirrels. – *J. Evol. Biol.* 24: 1949–1959.
- Lane, J. E., Kruuk, L. E. B., Charmantier, A., Murie, J. O. and Dobson, F. S. 2012. Delayed phenology and reduced fitness associated with climate change in a wild hibernator. – *Nature* 489: 554–557.
- Meier, F., Grosche, L., Reusch, C., Runkel, V., van Schaik, J. and Kerth, G. 2022. Long-term individualized monitoring of sympatric bat species reveals distinct species- and demographic differences in hibernation phenology. – *BMC Ecol. Evol.* 22: 7.
- Meyer, G. A., Senulis, J. A. and Reinartz, J. A. 2016. Effects of temperature and availability of insect prey on bat emergence from hibernation in spring. – *J. Mammal.* 96: 1623–1633.
- Mundinger, C., Fleischer, T., Scheuerlein, A. and Kerth, G. 2022. Global warming leads to larger bats with a faster life history pace in the long-lived Bechstein's bat *Myotis bechsteini*. – *Commun. Biol.* 5: 682.
- Munshi-South, J. and Wilkinson, G. S. 2010. Bats and birds: exceptional longevity despite high metabolic rates. – *Ageing Res. Rev.* 9: 12–19.
- Nakagawa, S. and Schielzeth, H. 2010. Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. – *Biol. Rev.* 85: 935–956.
- Norquay, K. J. O. and Willis, C. K. R. 2014. Hibernation phenology of *Myotis lucifugus*. – *J. Zool.* 294: 85–92.
- Ozgul, A., Childs, D. Z., Oli, M. K., Armitage, K. B., Blumstein, D. T., Olson, L. E., Tuljapurkar, S. and Coulson, T. 2010. Coupled dynamics of body mass and population growth in response to environmental change. – *Nature* 466: 482–485.
- Pledger, S., Pollock, K. H. and Norris, J. L. 2003. Open capture–recapture models with heterogeneity. I. Cormack–Jolly–Seber model. – *Biometrics* 59: 786–794.
- Post, E., Stenseth, N. C., Langvatn, R. and Fromentin, J.-M. 1997. Global climate change and phenotypic variation among red deer cohorts. – *Proc. R. Soc. B* 264: 1317–1324.

- Reed, T. E., Schindler, D. E. and Waples, R. S. 2011. Interacting effects of phenotypic plasticity and evolution on population persistence in a changing climate. – *Conserv. Biol.* 25: 56–63.
- Reusch, C., Gampe, J., Scheuerlein, A., Meier, F., Grosche, L. and Kerth, G. 2019. Differences in seasonal survival suggest species-specific reactions to climate change in two sympatric bat species. – *Ecol. Evol.* 9: 7957–7965.
- Reusch, C., Scheuerlein, A., Grosche, L., Meier, F., Gampe, J., Dammhahn, M., van Schaik, J. and Kerth, G. 2022. Data from: The risk faced by the early bat: individual plasticity and mortality costs of the timing of spring departure after hibernation. – Dryad Digital Repository, <https://doi.org/10.5061/dryad.sn02v6x7r>.
- Rézouki, C., Tafani, M., Cohas, A., Loison, A., Gaillard, J.-M., Allainé, D. and Bonenfant, C. 2016. Socially mediated effects of climate change decrease survival of hibernating Alpine marmots. – *J. Anim. Ecol.* 85: 761–773.
- Risch, T. S., Michener, G. R. and Dobson, F. S. 2007. Variation in litter size: a test of hypotheses in Richardson's ground squirrels. – *Ecology* 88: 306–314.
- Salvarina, I., Gravier, D. and Rothhaupt, K. O. 2017. Seasonal insect emergence from three different temperate lakes. – *Limnologia* 62: 47–56.
- Siemers, B. M. and Schnitzler, H.-U. 2000. Natterer's bat (*Myotis nattereri* Kuhl, 1818) hawks for prey close to vegetation using echolocation signals of very broad bandwidth. – *Behav. Ecol. Sociobiol.* 47: 400–412.
- Siemers, B. M., Dietz, C., Nill, D. and Schnitzler, H.-U. 2001. *Myotis daubentonii* is able to catch small fish. – *Acta Chiropterol.* 3: 71–75.
- Steffens, R., Zöphel, U. and Brockmann, D. 2007. 40th anniversary Bat Marking Centre Dresden – evaluation of methods and overview of results. – *Sächsisches Landesamt für Umwelt, Landwirtschaft und Geologie*.
- Stoffel, M. A., Nakagawa, S. and Schielzeth, H. 2017. rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. – *Methods Ecol. Evol.* 8: 1639–1644.
- Stumpf, M., Meier, F., Grosche, L., Halczok, T. K., van Schaik, J. and Kerth, G. 2017. How do young bats find suitable swarming and hibernation sites? Assessing the plausibility of the maternal guidance hypothesis using genetic maternity assignment for two European bat species. – *Acta Chiropterol.* 19: 319–327.
- Trappmann, C. 2005. Die Fransenfledermaus in der Westfälischen Bucht (Ökologie der Säugetiere). – Laurenti-Verlag.
- Turbill, C., Bieber, C. and Ruf, T. 2011. Hibernation is associated with increased survival and the evolution of slow life histories among mammals. – *Proc. R. Soc. B* 278: 3355–3363.
- van Buskirk, J. 2012. Behavioural plasticity and environmental change. – In: Candolin, U. and Wong, B.B.M. (eds), *Behavioural responses to a changing world*. Oxford Univ. Press, pp. 145–158.
- van de Pol, M. and Wright, J. 2009. A simple method for distinguishing within- versus between-subject effects using mixed models. – *Anim. Behav.* 77: 753–758.
- van Harten, E., Lawrence, R., Lumsden, L. F., Reardon, T. and Prowse, T. A. A. 2022. Novel passive detection approach reveals low breeding season survival and apparent lactation cost in a critically endangered cave bat. – *Sci. Rep.* 12: 7390.
- van Schaik, J., Jannssen, R., Bosch, T., Haarsma, A.-J., Dekker, J. J. A. and Kranstauber, B. 2015. Bats swarm where they hibernate: compositional similarity between autumn swarming and winter hibernation assemblages at five underground sites. – *PLoS One* 10: e0130850.
- Vuarin, P., Dammhahn, M. and Henry, P.-Y. 2013. Individual flexibility in energy saving: body size and condition constrain torpor use. – *Funct. Ecol.* 27: 793–799.
- Wells, C. P., Barbier, R., Nelson, S., Kanaziz, R. and Aubry, L. M. 2022. Life history consequences of climate change in hibernating mammals: a review. – *Ecography* 2022: e06056.
- West-Eberhard, M. J. 1989. Phenotypic plasticity and the origins of diversity. – *Annu. Rev. Ecol. Syst.* 20: 249–278.
- Williams, C. M., Henry, H. A. L. and Sinclair, B. J. 2015. Cold truths: how winter drives responses of terrestrial organisms to climate change. – *Biol. Rev.* 90: 214–235.
- Williams, C. T., Barnes, B. M., Kenagy, G. J. and Buck, C. L. 2014. Phenology of hibernation and reproduction in ground squirrels: integration of environmental cues with endogenous programming. – *J. Zool.* 292: 112–124.
- Zuur, A. F., Ieno, E. N., Walker, N., Saveliev, A. A. and Smith, G. M. 2009. *Mixed effects models and extensions in ecology with R*. – Springer.