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Potential costs, benefits and constraints of responses to  
recent climate change in bats

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Christine Reusch

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Dekan: Prof. Dr. rer. nat. Werner Weitschies

1. Gutachter : Prof. Dr. Gerald Kerth

2. Gutachter: Prof. Dr. Oliver Krüger

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## 1. GLOSSARY

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Daily torpor	<b>Daily torpor</b> is a hypometabolic state with a reduced body temperature (on average down to 17-22 °C) that lasts less than 24 h and is accompanied by continued food intake during normothermic periods. During torpor the metabolic rate is on average reduced down to 35 % of the basal metabolic rate during normothermy (Ruf and Geiser 2015). Torpor is a strategy to overcome short-term periods of unfavourable conditions.
Dispersal	<b>Dispersal</b> is defined as a movement by an organism from one breeding patch to another (Chaine and Clobert 2012).
Genetic adaptation	<b>Genetic adaptation</b> describes the change of one or multiple heritable traits between generations with changing environmental conditions as a result of natural selection.
Heritability	<b>Heritability</b> is a statistical estimate that describes the degree of variation within a trait in a population that can be explained by genetic variation between individuals in the population (Wray and Visscher 2008).
Hibernation	<b>Hibernation</b> is a strategy to overcome times of food or water shortage by means of a reduction of body temperature (on average down to 4 °C), metabolic rate (down to 6 % of the basal metabolic rate) and, thus, energy consumption (Geiser and Ruf 1995, Geiser 2013, Ruf and Geiser 2015). It is described by multiday torpor bouts interrupted by energy-costly periodic arousals (<24 h) to normal body temperature

	<p>(Ruf and Geiser 2015, Czenze and Willis 2015). Torpor bout length and depth are species-specific. Successful hibernation is suggested to be based on an interplay of a circannual clock, as well as climatic parameters (Hut et al. 2014).</p>
Migration	<p><b>Migration</b> describes the seasonal movement, e.g. from summer to winter grounds, to deal with unfavourable seasonal changes. It is a well-known strategy, especially in birds, that allows sustaining a high metabolism by temporary changing to a habitat with favourable conditions (Gienapp 2012).</p>
Phenotypic plasticity	<p><b>Phenotypic plasticity</b> describes the ability of a single genotype to express different phenotypes in different environmental conditions. It is often characterized by a reaction norm of the phenotypic trait to an environmental condition (Canale and Henry 2010).</p>
Behavioural plasticity	<p><b>Behavioural plasticity</b>, also known as behavioural flexibility (Piersma and Drent 2003), is described as a reversible change in behaviour of an individual in response to different environments (Dingemanse and Wolf 2013). Thus, it is a more specific form of phenotypic plasticity.</p>
RFID-tag	<p>Radio frequency identification (<b>RFID</b>) uses a signal transmission between an electronic device (e.g. PIT-tags) and a reading device. In animals, passive integrated transponder (PIT-tags) are often used. A PIT-tag is an electronic microchip with a size of 10-14 mm that is encased in biocompatible glass and, thus, can be transplanted under the skin of individuals. Passive RFID-tags are inductively charged by</p>

the reader and do not need a battery to transmit the unique transponder code. Therefore, they can remain operational for decades. This approach allows to automatically follow individuals through their unique ID without disturbing them again after initially marking them once (Gibbons and Andrews 2004).

## Seasonality

**Seasonality** describes a regularly and often predictable changing environment within an annual cycle. In the field of biology it is also often used to describe the responses of organisms to those regularly changing environments (Battey 2000). Potential responses to seasonality are for example migration and hibernation.

## 2. SUMMARY

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In times of recent climate change, mechanisms to deal with different environments (e.g. via dispersal to other habitats, or via in-situ responses such as genetic adaptation or phenotypic plasticity) are essential. In regions showing seasonality, organisms are already adapted to regular and, thus, often predictable environmental changes. One well-known strategy to survive periods of food shortage, especially during the winter, is hibernation. Although hibernation is already an adaptation to overcome unfavourable conditions, the optimal timing of hibernation to match for example food abundance peaks is likely to be influenced by changing climatic conditions, as expected during human-induced global change. Thus, the ability to respond to changes in optimal timing of hibernation can be crucial for organisms. All hibernators are positioned at the slow end of the slow-fast life history continuum. Longevity combined with a low annual reproductive output can result in slow recovery from population crashes and is expected to be associated with slow genetic adaptation. Therefore, it is assumed that phenotypic plasticity, a rather rapid and sometimes reversible process, is a crucial mechanism in long-lived organisms to adapt to changing environments. However, how differences in individual hibernation behaviour influence mortality and whether individuals are plastic with respect to their hibernation behaviour are largely unknown.

Recent studies suggest that climatic change can influence hibernation behaviour in various species differently, in a positive or negative way. Female Columbian ground squirrels (*Urocitellus columbianus*) delayed their emergence from hibernation with later snow melt and lower spring temperatures. Next to the environmental impact, emergence date showed a moderate heritability in female Columbian ground squirrels. Yellow-bellied marmots (*Marmota flaviventris*) emerged earlier from hibernation with warmer spring temperatures which resulted in a longer growing period for their offspring and, therefore, higher survival rates. In contrast, in alpine marmots (*Marmota marmota*) lower snow cover due to higher temperatures and, thus, less isolation led to lower juvenile survival. Negative effects, such as reduced juvenile survival, would be of high concern, especially for long-lived species with a low reproductive output.

Bats are exceptionally long-lived compared to other mammals of the same size and often show a low reproductive output with one offspring per year. This is especially true in the temperate zone where bats, furthermore, are characterized by

seasonality and depend on hibernation during winter period to survive food and water shortage. Because bats are of high conservation concern it is of prime importance to understand their ability to respond to different climatic conditions and associated mortality costs.

The basis of this study was a five-year data set of 1047 RFID-tagged individuals from two bat species, Natterer's bats (*Myotis nattereri*) and Daubenton's bats (*Myotis daubentonii*), that were automatically tracked when entering or leaving the joint hibernaculum, "Brunnen Meyer", located in north-western Germany. The two species are similar sized, share demographical traits and often occupy the same areas. Nevertheless, they differ in their foraging strategy and activity pattern during hibernation period. Natterer's bats are able to glean insects from surfaces, even at low temperatures. Daubenton's bats depend on flying arthropods and, thus, warmer temperatures. And indeed there is evidence that Natterer's bats are able to hunt during hibernation period, while in Daubenton's bats a lack of feeding during the hibernation period is suggested. Furthermore, Natterer's bats are characterized by a higher activity at the hibernaculum throughout the hibernation period, while Daubenton's bats on average arrive earlier, stay inactive through the winter and leave later in spring.

In both species, the aim was to investigate the impact of their individual hibernation behaviour, precisely the timing of departure in late winter and early spring, on mortality, their adjustment of departure timing to the North Atlantic Oscillation Index (NAO), as well as differences within and between the two species from 2011 until 2015.

To later on estimate the potential mortality costs of departure timing, gaining knowledge about the seasonal survival pattern (winter vs. summer) in the two species was a first necessity. In birds, particularly small species were described as winter-regulated populations with a higher mortality during winter. In contrast, in hibernating mammal species, such as bats, a relatively lower or similar winter survival compared to summer survival was shown. In this study, the analysed data demonstrated that the winter 2010/2011 was exceptionally catastrophic in Natterer's bats and did not impact Daubenton's bats. When excluding this catastrophic winter in Natterer's bats, our results revealed a stable winter-summer-survival difference (higher winter and lower summer survival) in adult Natterer's and Daubenton's bats, with inter-annual variation in the level of survival which indicates a potential

environmental impact on survival. This winter-summer survival pattern is in line with the survival pattern shown for other hibernators. Juveniles always had a lower survival rate than adult bats in both species. Nevertheless, the extent to which the species differ between seasons and age classes was stronger in Daubenton's bats. They always showed a slightly higher winter survival and a lower summer survival than Natterer's bats. Together with the catastrophic winter 2010/2011 in Natterer's bats, this indicates a species-specific sensitivity to the timing of specific weather events which is in line with their foraging strategies and activity pattern during hibernation period.

With respect to emergence behaviour from the hibernaculum, the results of this study suggest considerable differences among individuals within as well as between bat species. In comparison to Daubenton's bats, Natterer's bats tuned their emergence more closely to weather conditions, specifically the NAO, a large scale weather index related to winter severity, and showed individual variation in behavioural plasticity. In Daubenton's bats only the females responded to changing conditions and left earlier in individually-experienced warmer and milder winters, comparable to Natterer's bats females. A potential reason might be reproductive advantages for the females resulting in a longer growing period for their offspring. The shown higher winter survival in adult bats of both species indicated already higher energy expenditure outside the hibernaculum. Thus, leaving early, being active and staying outside longer by itself bore a risk (exposure risk effect). Under consideration of longer exposure times, early departing individuals had on top of that an increased risk to die. This was not given in each year, but a species- and year-specific pattern was revealed. Natterer's bats were only significantly affected by early departure in 2011, while the remaining years show no significant additional risk of leaving early. In Daubenton's bats, the years 2014 and 2015 were associated with a significantly higher mortality of leaving early. This is in line with the hypothesis that Daubenton's bats might not be able to hunt for insects leaving too early and do so as a best out of a bad job. Nevertheless, the year-specific pattern suggests that early bats might profit from advantageous weather conditions during early spring.

An additional hint for an environmental impact on early bat survival in at least Daubenton's bats is that the median proportion of night hours above 3 °C within five days after departure was included in the model with the lowest AIC. However, the

effect was not strong enough to be selected as the best model and, therefore, further analyses are needed to investigate this first hint.

In conclusion, the reduced winter survival of juveniles compared to adults highlights the importance of considering age class effects in studies that investigate seasonal survival patterns. The stable species-specific winter-summer-survival difference with a higher winter survival compared to summer survival, as well as the one catastrophic winter in Natterer's bats underline the importance of including seasonal survival patterns in assessing potential fitness costs of changed behaviour. Furthermore, our results suggest that long-lived hibernating bat species have the potential to plastically adjust to changing climatic conditions, but this potential differs between species. Among-individual differences in emergence together with species-specific mortality costs of early emergence suggest the potential for natural selection to shape hibernation phenology. In summary, our findings suggest species-, population- and group-specific differences in the ability to respond to changing environments and, therefore, underline the necessity to further investigate local responses in various organisms to estimate consequences of recent climate change on a wider range.

### 3. INTRODUCTION

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Global climate change is a recent topic of high concern that is almost omnipresent in the public media as well as in scientific reports and research studies. The fifth Intergovernmental Panel on Climate Change (IPCC) report for example predicts an increase in surface temperature of at least 1.5 °C for the end of the 21st century, rising sea levels, shrinking ice cover and increasing contrasts between wet and dry regions, as well as between seasons within a region (IPCC 2013). As these effects are predicted to continue beyond 2100, it is of high importance to understand possible responses of species to the resulting environmental changes and to gain knowledge about costs, benefits and constraints of those responses (Both et al. 2006, Møller et al. 2008, Frick et al. 2010, Sheridan and Bickford 2011). Due to differences in species ecology and in their ability to respond to recent climate change, it is crucial to study various habitats, populations and species.

Several recent studies investigated the consequences of global climate change for various taxa and drew general, as well as, contrasting conclusions (Both et al. 2006, Møller et al. 2008, Frick et al. 2010, Sheridan and Bickford 2011, Sherwin

et al. 2013). For example, Sheridan and co-authors (2011) reviewed the influence of temperature on body size and described the phenomenon “global shrinking”. They stated that in several species a positive correlation between rising temperatures and decreasing body size exists, which is suggested to lead to decreasing fertility (Sheridan and Bickford 2011). The decreasing size effect is supported by a study of Post and co-authors (1997) analysing the impact of winter variation on red deer cohorts. The winter variation was assessed by the North Atlantic Oscillation index (NAO), the difference of the standardized air pressure anomalies between the Azores and Iceland, which drives fluctuations between temperatures and precipitation during winter (Post *et al.* 1997). They stated that calves born after warm winters were smaller than those born after cold winters (Post *et al.* 1997). Nevertheless, in some exceptional cases body size increased with rising temperatures, which may be a result of required warm temperatures during growth (Sheridan and Bickford 2011).

Furthermore, Chen and co-authors (2011) summarized in their review on range shifts that latitudinal and elevational shifts were significantly greater in studies with higher level of warmings which implies range expansion initiated by warmer temperatures in terrestrial organisms. They expect that species-specific range shifts differ between regions (Chen *et al.* 2011). Both and co-authors (2006), as well as Møller and co-authors (2008), mentioned a mismatch of arrival date, the period of rearing offspring and highest food abundance in migratory birds due to climatic changes at the summer habitat and an insufficient response to it by the migrating birds (Both *et al.* 2006, Møller *et al.* 2008). The authors suggest that in areas with earliest food peaks the relatively fixed spring migration programme in long-distance migrants does not allow an adaptation that is fast enough to match the earlier food abundance (Both *et al.* 2006). Another potential reason could be that long-distance migrants are not only less influenced by environmental conditions than short-distance migrants (Møller *et al.* 2008), but adapt to a cue given in their winter habitat that does not fit conditions in the summer habitat (Taylor *et al.* 2016). As a result, the populations of the respective species are in decline (Both *et al.* 2006, Møller *et al.* 2008). In contrast, Lane and co-authors (2012) describe a delayed emergence from hibernation in female ground squirrels associated with decreasing spring temperature and delayed snowmelt due to an increasing occurrence of late-season snowstorms (Lane *et al.* 2012).

In general, the available studies further underline the different mechanisms (e.g. phenotypic plasticity, genetic adaptation, as well as, dispersal (Glossary)), that might enable individuals to respond to different conditions, and highlight the importance of investigating various taxa instead of only a few selected model organisms. Nevertheless, despite the high interest in the topic, studies investigating adaptation to environmental conditions and associated benefits or costs are still rare and face numerous difficulties (e.g. lack of data, confounding factors in the wild) in various taxa.

Especially in long-lived species assessing responses to climate change in free-ranging populations is strongly depending on individual-based long-term data. Although all of the abovementioned mechanisms to respond to different environments are associated with certain benefits and costs, phenotypic plasticity is expected to play a key role in long-lived organisms to cope with changing environments. Behavioural plasticity (Dingemans and Wolf 2013) (Glossary) also known as behavioural flexibility (Piersma and Drent 2003) is described as a reversible change in behaviour of an individual in response to different environments. Particularly in cases, where genetic adaptation is assumed to be slow and recovery from population crashes might take several years, such as in bats (Fleischer et al. 2017), behavioural plasticity should enable individuals to adapt to changing environments. Individuals with high behavioural 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 even among individuals (Dingemans and Wolf 2013). This might be, especially, the case in environments where the benefit of a fast response does not necessarily exceed the costs of being plastic (e.g. maintenance costs, information acquisition costs or genetic costs) (DeWitt 1998, DeWitt et al. 1998). In some situations phenotypic plasticity in general can even be maladaptive if individuals respond to a cue that is not representative for the current environment (DeWitt 1998). Thus, it is essential to further investigate behavioural plasticity as a response to changing environments and its consequences, especially in long-lived organisms.

One mechanism that might be impacted by changing climatic conditions is hibernation (Glossary), a widespread strategy as a response to seasonality (Glossary) in endothermic animals to survive periods with low food or water availability, especially during the winter (Geiser 2013). This strategy is defined as a

multiday torpor (Glossary) which results in a reduction in body temperature, water loss and energy expenditure (Geiser 2013). Successful hibernation requires the intricate interplay of physiological processes such as maintenance of essential body functions in a low temperature state with behaviours such as the optimal timing of emergence from hibernation (Hut et al. 2014, Czenze and Willis 2015). 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 during global climate change (Canale and Henry 2010, Williams et al. 2015).

Despite several decades of research on hibernation in mammals, there are only few studies about how the individual timing of departure from the hibernaculum translates into mortality costs in free-ranging populations (Ozgul et al. 2010, Lane et al. 2012). To predict population persistence of long-lived obligate hibernators, data on individual variation of departure timing from hibernation and the mortality costs associated with different departure times are urgently required.

The few available studies clearly show that global climate change can affect mortality risk in hibernating species in either a positive (Ozgul et al. 2010) or negative way (Williams et al. 2015, Rézouki et al. 2016). The latter might be particularly problematic since all hibernating species are on the slow end of the slow-fast life history continuum (Turbill et al. 2011). Studies of this kind suggest that emergence time from hibernation, as well as torpor characteristics in general are affected by both body condition and variation in factors such as metabolic rate, that might even be heritable and interact with micro-climatic conditions at the hibernation site (Vuarin et al. 2013, Williams et al. 2014).

Environmental conditions outside the hibernaculum are then often responsible for fine-tuning emergence (Williams et al. 2014). For example, in female Columbian ground squirrels (*Urocitellus columbianus*) hibernation emergence was characterized by a moderate heritability (Lane et al. 2011), but emergence date was delayed in years with lower spring temperatures and late snowmelt (Lane et al. 2012). 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) due to a longer growing season, an increase in body mass before hibernation, and a reduction in adult mortality. 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 (e.g. Indiana bat (*Myotis sodalis*) (Day and Tomasi 2014); little brown bat (*Myotis lucifugus*) (Humphries and Speakman 2002)) energy consumption increased with warmer ambient temperature in the hibernaculum (Williams et al. 2015). Thus, changing environmental conditions can have a crucial impact on long-lived hibernators.

Bats form the widely distributed, species-rich order Chiroptera which occurs on almost all continents (except Antarctica) and most of the islands (Kunz 1982). They are mostly nocturnal and cover various foraging niches and ecological functions (e.g. seed distribution, flower pollination) which highlights their importance for different ecosystems and the necessity to study their responses to different environments. Especially their unique ability to actively fly sets them apart from other mammals. Despite their high metabolic rate, similar to the one of birds (Munshi-South and Wilkinson 2010), bats are exceptionally long-lived compared to other mammals of a similar body size (Wilkinson and Munshi-South 2002, Munshi-South and Wilkinson 2010). The oldest captured bat in the wild was a 41-year old Brandt's bat (*Myotis brandtii*) (Podlutzky et al. 2005). Additionally, bats show a low annual reproductive output (Fleischer et al. 2017). As a result of the longevity in combination with the low reproductive output, genetic adaptation to changing conditions is expected to be slow (Reed et al. 2011). Therefore, as already mentioned above, phenotypic plasticity, in particular behavioural plasticity, should be a key mechanism for bats to cope with changing weather conditions during climate change.

The aim of the study was to investigate whether bats of two temperate species, Natterer's bats (*Myotis nattereri*, further on also referred to as mn) and Daubenton's bats (*Myotis daubentonii*, further on also referred to as md) plastically adjust their behaviour to weather conditions at the population and individual level, show a potential heritability (Glossary) of departure timing and bear associated mortality costs. To investigate whether the species also differ in the impact of environment on departure behaviour, the winter station-based index (December through March) of the North Atlantic Oscillation (NAO) as a proxy for the large-scale winter weather patterns over Europe (Hurrell 1995, Post et al. 1997) was used. Positive values indicate wetter/milder weather, while negative values indicate dryer/colder weather over western Europe during winter (Hurrell 1995).

In order to measure fitness consequences, more specifically potential mortality costs, of responses to changing environments in individual phenology or behaviour (Møller et al. 2008, Lane et al. 2012, Sherwin et al. 2013, Williams et al. 2015), the first step is to identify critical periods for population growth in the annual cycle of populations. Further on it is essential to understand which groups (e.g. sexes, age classes) are particularly affected by those critical time periods. However, suitable data are also in this case rare for long-lived animals since individuals must be followed over years without interfering with their natural behaviour, which is a challenging task in most taxa.

Seasonal survival is comparatively well-studied in birds, due to the availability of long-term studies of marked populations, high-quality long-term ringing data, and sophisticated statistical methods for survival analysis (Leyrer et al. 2013, Klaassen et al. 2014, Rockwell et al. 2017). In this field of research, the concept of summer- and winter-regulated populations has been introduced some time ago (Newton 1998, Blumstein and Fernández-Juricic 2010). This concept states that in smaller species, populations are often regulated by a high mortality in winter, while particularly in larger species, higher summer mortality or a lacking ability to reproduce regulates the population dynamics (Newton 1998, Blumstein and Fernández-Juricic 2010). This pattern, however, breaks down when hibernating mammals are considered.

So far only few studies were able to quantify seasonal variation in individual-based mortality in long-lived mammals, due to a paucity of suitable long-term data sets (Turbill et al. 2011, Marra et al. 2015, Fleischer et al. 2017). The available studies suggest that in hibernating animals, winter mortality does not exceed or is even lower than mortality during summer/breeding season (Turbill et al. 2011).

With their low annual reproductive output, bats' population dynamics have been suggested to be driven mainly by adult mortality (Fleischer et al. 2017). The few existing studies that tried to quantify mortality during hibernation in bats, suggested a low winter mortality or at least one that is comparable to mortality during summer (Sendor and Simon 2003, Culina et al. 2017, Fleischer et al. 2017, Fritze and Puechmaille 2018). However, the existing studies used very different sampling schemes and different methods, and their data are not easily comparable. Fritze and Puechmaille (2018) for example described very low baseline mortality during hibernation based on dead bat counts in hibernacula. The authors explain the low number of dead bats found in hibernacula either due to a high rate of survival during

hibernation or that sampling once per year might not be suitable to discover the real mortality rate (Fritze and Puechmaille 2018). In a different approach, Culina and co-authors (2017) used multi-state capture-mark-recapture models based on ringing data of three different bat species at their summer roosts, covering seven years to show the effect of individual traits and selected weather parameters on survival. The authors found differences in survival across species, and generally lower winter survival of juveniles (Culina et al. 2017). In again a different approach, Fleischer and co-authors (2017) used a large individualised data set spanning 19 years. This data set was based on summer records of Bechstein's bats (*Myotis bechsteini*) that had been marked with individual RFID-tags (Glossary), in early and in late summer. This study revealed that both summer and winter mortality is equally low in most years ( $\leq 10\%$ ) but that extreme mortality ( $> 50\%$ ) occurred during one winter (Fleischer et al. 2017).

Natterer's bats and Daubenton's bats are of similar size (about 10 g) and show the typical annual cycle of temperate zone bats (Dietz et al. 2016). During summer females form maternity roosts and raise generally one offspring per year without the help of the males. There is less known about the summer roosts of males – the sex that disperses from their natal colony - but they seem to stay solitary or form bachelor groups depending on the species. In autumn both sexes leave their summer roosts for their hibernaculum and depending on the species a more or less extensive swarming period and mating takes place. Afterwards, the individual bats hibernate for several months over winter (e.g. in caves, buildings, bunkers or tree-roosts). Both species depend on hibernation to overcome the food (arthropod) shortage over winter (Dietz et al. 2016) and show a high site fidelity to their hibernaculum (Steffens et al. 2004). In spring bats leave again for their summer roosts to which specifically the females return year after year and form closed societies. Moreover, the two species are both long-lived. The oldest Natterer's bat observed in the wild was 20 years old and the oldest Daubenton's bat was observed with an age of 28 years in the field (Wilkinson and Munshi-South 2002).

While Natterer's bats and Daubenton's bats are comparable in their demography, they differ in their foraging strategies (Dietz et al. 2016). In various insectivorous bats (e.g. common noctule (*Nyctalus noctula*), common pipistrelle (*Pipistrellus pipistrellus*) and parti-coloured bat (*Vespertilio murinus*)), Zahn and co-authors showed a lack of hunting activity below 3 °C, which occurs regularly during

European winters (Zahn and Kriner 2016). Both study species depend on insects. However, Daubenton's bats mostly hunt above water (Flavin et al. 2001, Siemers et al. 2001). This trawling foraging strategy is restricted to warmer temperatures when insects emerge from, or fall into water. Consequently, Daubenton's bats do not seem to feed during the hibernation period (Kokurewicz 2004). In contrast, Natterer's bats are gleaners that collect arthropods from the vegetation or from the walls of stables of domestic animals, where prey can also be found at lower ambient temperatures (Siemers and Schnitzler 2000, Siemers et al. 2012, Andreas et al. 2012). Indeed, there is evidence that Natterer's bats can forage during the hibernation period (Hope and Jones 2012). As a result, Natterer's bats are characterized by a higher activity throughout hibernation period and, therefore, might be able to track ambient environmental conditions, but might also be exposed to potential disadvantageous winter conditions. In contrast, Daubenton's bats seem to stay inactive throughout hibernation period and remain in their hibernaculum.

In summary, this study aimed to answer the above outlined questions in two chapters based on the data set about the two species at "Brunnen Meyer". The chapters 5.1. and 6.1. particularly dealt with seasonal survival and tested the following hypotheses:

1. Juveniles are characterized by a lower winter survival compared to adults in both species.
2. Males and females might differ in seasonal survival due to sex-specific behavioural patterns and differing reproductive investments.
3. Seasonal sensitivity to the timing of adverse weather conditions differs between the two species due to distinctive activity and foraging patterns. Thus, adult Natterer's bats show a lower winter survival and a higher summer survival compared to adult Daubenton's bats.
4. Winter-to-summer difference in adult survival is a stable and species-specific pattern that might show inter-annual variation in its level reflecting environmental fluctuations.

The chapters 5.2. and 6.2. focussed on departure behaviour from hibernation and addressed hypotheses regarding timing, potential plasticity and costs associated with departure timing:

5. Because their foraging behaviour aims on capturing active insects, Daubenton's bats depart later from the hibernaculum than Natterer's bats.

6. Because of their higher winter activity, Natterer's bats should track environmental parameters more closely and, therefore, depart earlier with increasing NAO and should also exhibit higher individual plasticity than Daubenton's bats.
7. In Daubenton's bats endogenous cues are expected to play a more important role and departure timing should be less dependent on the NAO. Thus, individual plasticity towards the NAO was assumed to be low.
8. In both species, between-individual differences in departure timing were expected due to potential variation in physiological traits, e.g. metabolism, or morphological traits, such as body condition, between individuals.
9. Females depart earlier to gain reproductive advantages, especially in years with a positive NAO.
10. Yearlings leave earlier than adults due to potentially lower fat reserves at the beginning of the hibernation period.
11. Due to the fact that, in contrast to males, female bats can already reproduce in their first year, the average departure date might differ between sexes in their first year.
12. Emerging from the hibernaculum early, when food availability was likely to still be low, was associated with a higher mortality risk. Because of their species-specific foraging behaviour, it was suspected that this risk was higher in Daubenton's bats than in Natterer's bats.
13. With a decreasing median proportion of night hours above 3 °C within five days after individual departure from hibernation the survival in early bats should be decreased. This effect was expected to be species-specific and should mainly be present in Daubenton's bats due to their foraging strategy with a strong dependency on flying arthropods. In contrast, Natterer's bats might be even unaffected by local weather conditions because of their ability to collect arthropods from surfaces.

## 4. MATERIAL AND METHODS

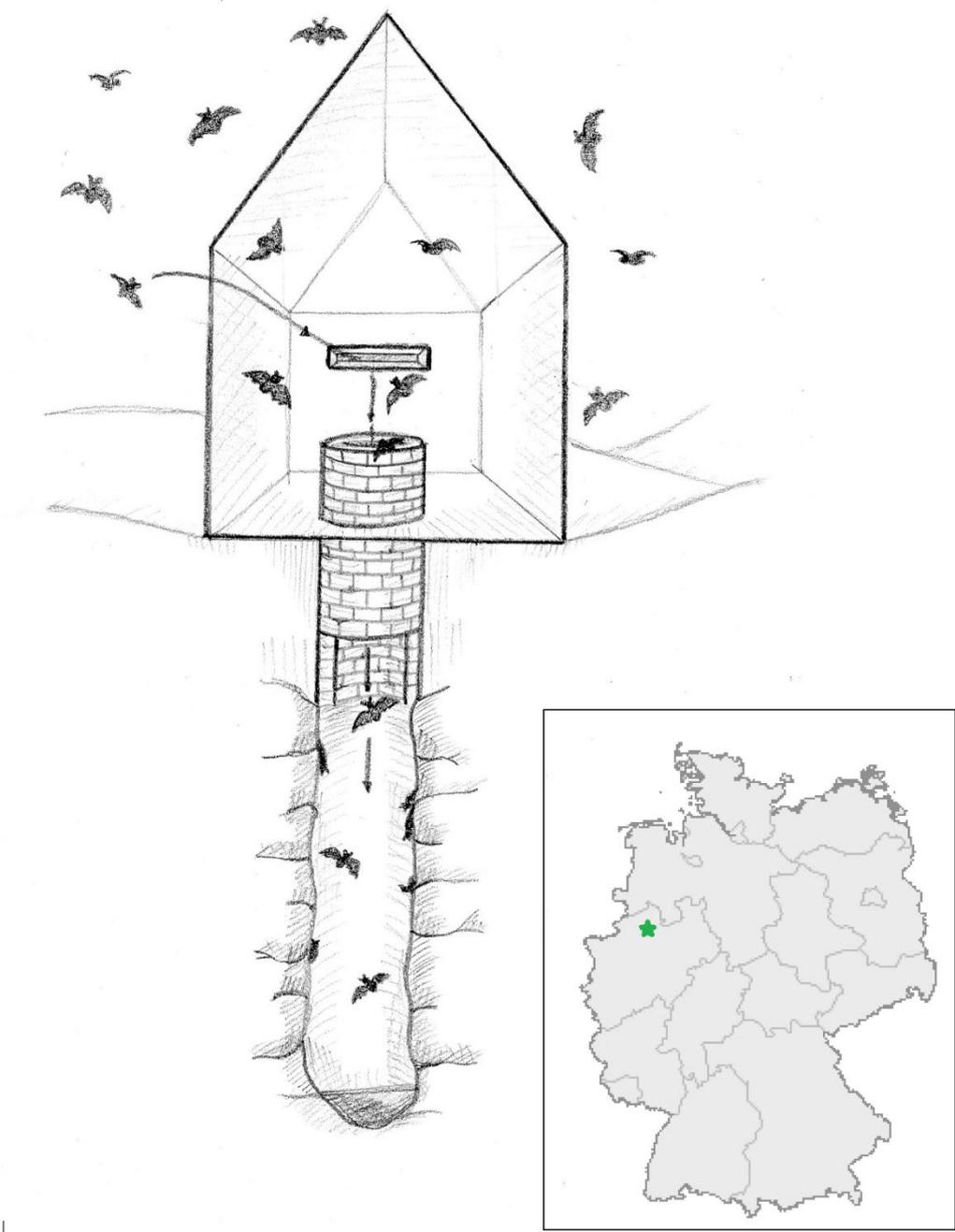
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### 4.1. STUDY SITE, BAT CAPTURE AND DATA LOGGING

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The study focussed on seasonal survival, arrival and departure of individually marked Natterer's bats and Daubenton's bats at the hibernaculum "Brunnen Meyer" in North Rhine-Westphalia (Figure 1) (Trappmann 2005, Stumpf et al. 2017). The

“Brunnen Meyer” is a deep-well which was still used in the 1970s due to the water shortage given in that area. It is surrounded by a small well house located within a 300 m wide strip of woodland (Trappmann 2005). The well itself is about 60 m deep, has a diameter of 2 m and is covered by a wooden lit with two small entrances. The hibernaculum is already known since the end of the 19<sup>th</sup> century and first research started in 1992 with net capturing individual bats (Trappmann 2005). While the temperature in the well directly beneath the lit was following the ambient temperature more closely, temperature measurements in the year 2002/2003 revealed a stable temperature regime between 2-6 °C in 8 m depth (Trappmann 2005). Currently, more than 6,000 individuals of ten species are hibernating at this site. Thus, the “Brunnen Meyer” is one of the biggest hibernacula in Germany and is, therefore, of national importance. The main occupants of the hibernaculum are Natterer’s bats (Figure 2) and Daubenton’s bats (Figure 3) (Trappmann 2005).



**Figure 1** Structure of the study site, the “Brunnen Meyer”, a hibernaculum in North Rhine-Westphalia, and its location in Germany (green star) (modified after Stumpf et al. 2017)



#### **Natterer's bat (*Myotis nattereri*)**

- **Family:** Vespertilionidae
- **Protection status:** Read list of Threatened Species: least concern; under protection of the Habitats Directive
- **Appearance:** Brown fur, tending to greyish-white on its underside; 4-5 cm length; weight: ~ 7-12 g, long and slender ears; fringe of stiff bristles along the trailing edge of the tail membrane
- **Maximal age so far:** 20 years (detected in the wild)
- **Distribution:** across most of Europe, parts of the Near East and South Africa
- **Diet and foraging strategy:** insectivorous; feeds on insects which they catch in flight or collect from surfaces; change in diet composition over winter
- **Behaviour:** nocturnal; typical annual cycle of temperate zone bats (maternity roosts during summer, mating in autumn, hibernation over winter); seasonal migration up to 120 km
- **Annual reproductive output:** 1 offspring
- **Habitat:** deciduous and coniferous forest; summer roosts: tree cavities, buildings or bat boxes; winter hibernacula: caves, tunnels, mines or cellars (often hiding in crevices)

**Figure 2** Summary of characteristics describing Natterer's bats (*Myotis nattereri*)

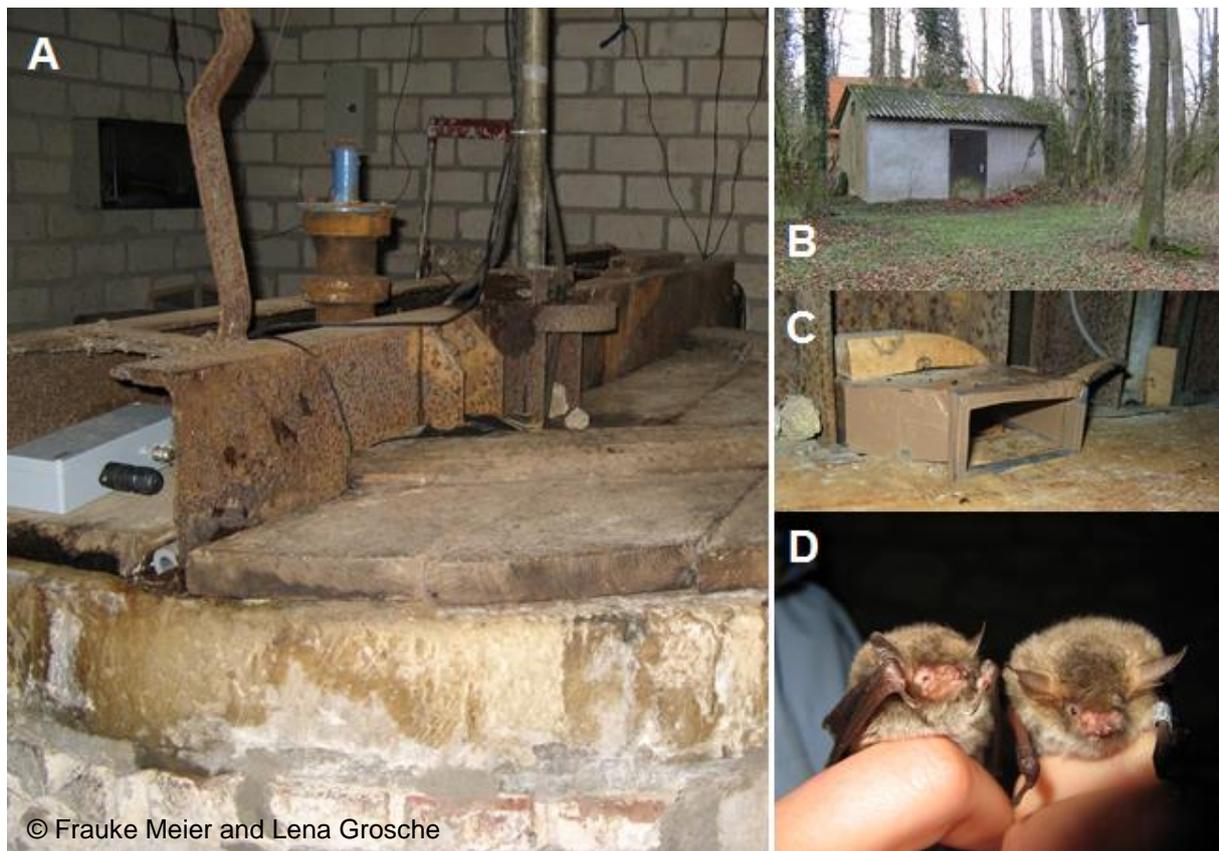


### Daubenton's bat (*Myotis daubentonii*)

- **Family:** Vespertilionidae
- **Protection status:** Read list of Threatened Species: least concern; under protection of the Habitats Directive
- **Appearance:** brownish-grey fur, tending to silver-grey on its underside; short ears; 4.5-5.5 cm length; weight: ~ 7-15 g
- **Maximal age so far:** 28 years (detected in the wild)
- **Distribution:** across Europe, as far as Japan and Korea
- **Diet and foraging strategy:** insectivorous; feeds on flying insects which they catch in flight above water
- **Behaviour:** nocturnal; typical annual cycle of temperate zone bats (maternity roosts during summer, mating in autumn, hibernation during winter); seasonal migration mostly within 100-150 km
- **Annual reproductive output:** 1 offspring
- **Habitat:** mostly in woodlands close to water grounds; roosts during summer and winter e.g. in caves, tunnels, mines or cellars

**Figure 3** Summary of characteristics describing Daubenton's bats (*Myotis daubentonii*)

Bats were caught using harp traps at the sole entrance of the well house (Figure 4B). At first capture, individuals were sexed and marked with unique RFID-tags (ID 100, Trovan) (Figure 4D). Two age classes, juveniles (young of the year that were captured in autumn, 1<sup>st</sup> hibernation) and adults (>1 hibernation), were separated based on colouration of chin spots, epiphyseal closure, level of dental plaque and tooth abrasion, as well as the lack of signs of reproduction (Brunet-Rossini and Wilkinson 2009). Bats had already been marked at this site with individual RFID-tags since 2002 for Natterer's bats and since 2008 for Daubenton's bats. However, in this study the focus was on the years 2010/2011 to 2014/2015. All capture and marking was conducted under the permits for species protection (70.2.2.27, 70.2-0197/08, 70.2-0228/10 and 70.2-2012/0254), issued by the nature conservation authority of the district Coesfeld (Germany).



**Figure 4** Pictures of the „Brunnen Meyer“: A) Installed RFID-logger-antenna systems (LID-650, EURO I.D.); B) the well house; C) one of the two small entrances into the well that has to be passed by each individual bat; D) captured individuals of the main occupants of the hibernaculum, Daubenton's bats (*Myotis daubentonii*) and Natterer's bats (*Myotis nattereri*).

As abovementioned, the hibernaculum has two small entrances (8 cm x 5 cm), which offered the unique possibility to place RFID-logger-antenna systems (LID-650,

EURO I.D.) in each of the entrances (Figure 4A and 4C). These systems continuously recorded ID and passage time for all tagged individuals without interfering with the bats' behaviour (Gibbons and Andrews 2004, Kerth et al. 2011). As only one antenna was employed per entrance, direct assessment whether a bat entered or left the hibernaculum was not possible. Therefore, an arrival period (Aug-Dec) and a departure period (Jan-Apr) for each hibernation ( $H_t$ ) was defined based on activity patterns known from direct observations in the field, light barrier recordings and the available RFID recordings [Grosche and Meier, unpublished data].

For each individual and year, the date of its last recording during the departure period (departure date of  $H_t$ ) and the date of its first recording during the subsequent arrival period (arrival date of  $H_{t+1}$ ) was determined. An individual was considered as dead if it was not recorded in the entire subsequent hibernation period ( $H_{t+1}$ , Aug-Apr) because bats have high site fidelity (Steffens et al. 2004). In 13 years of bat surveillance only 24 out of 1111 bats assigned dead re-appeared at another RFID-monitored hibernaculum in close proximity to the study site for at least one more year [Grosche and Meier, unpublished data], and only one out of 1047 tagged individuals in our 5-year study period re-occurred at the hibernaculum „Brunnen Meyer“ after being not recorded for a complete hibernation period.

## 4.2. STATISTICAL ANALYSES

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The research questions were addressed by applying mixed-effect logistic regression models (assessing seasonal survival), logistic regression model (investigating the impact of local weather on early bat survival) and restricted maximum likelihood linear mixed-effects models (LMMs) with normal errors (estimating departure timing). The criteria for model selection were the same in each of the approaches. Simpler models were selected over more complex models with a lower AIC/AICc whenever the difference in the AIC/AICc-values were smaller than 2 (Burnham et al. 2011, Culina et al. 2017). All models were fitted using R, version 3.4.0 (library nlme, function lme (Pinheiro et al. 2018) or library lme4, function glmer (Bates et al. 2015)) (R Development Core Team 2015).

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#### 4.2.1 SEASONAL SURVIVAL

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To investigate seasonal survival and the factors influencing it, data obtained during the continuous monitoring of 820 RFID-tagged Natterer's bats and 625 RFID-tagged Daubenton's bats at the hibernaculum "Brunnen Meyer" from 2010/2011 until 2014/2015 were used. Survival was coded as 0 if the individual died and as 1 if it survived. Nevertheless, to assure that individuals have indeed used the hibernaculum, those individuals from the analyses that had not been recorded either during the arrival or the departure period, but reappeared later (mn: 62 out of 820 individuals (7.5 %); md: 24 out of 625 individuals (3.8 %)) were excluded.

Individuals, for whom the last recording was during an arrival period (but not again thereafter), consequently had survived the preceding summer but were assumed to have died in the following winter. Similarly, those bats that were recorded for the last time during a departure period had survived the preceding winter but were assumed to have died during the following summer period. In this study "winter" includes, depending on the species and sex, a more or less intensive autumn swarming at the hibernaculum and the hibernation itself. The "summer" includes the transfer flights from and to the hibernaculum, as well as the time in their summer habitat.

As a first step, the proportions of survivors in the two species were compared in each of the 10 periods (two seasons – summer and winter – in five years, from winter 2010/11 to summer 2015). The hypothesis of equal survival in the two species was tested (two-sided alternative, chi-square test statistic with  $df=1$ , Yates' continuity correction) using the function `prop.test` in R (R Development Core Team 2015).

Regression models were used to study the effects of the individual characteristics sex and age-class (juveniles vs. adults), as well as of changing environment on survival. The binary response – survival or death – was modelled by logistic regression with an individual-specific random intercept to account for repeated observations per individual and potential inter-individual variation in survival which remained unexplained by the covariates. As Culina and co-authors (2017) reported differences between sexes and age classes as well as differences in the effect of environmental parameters on survival within three bat species (Culina et al. 2017), the model was set up separately for each species. Sex and age class (juvenile or adult) were included as binary covariates with fixed effects. As the animals are observed at the hibernaculum it should be noted that juvenile survival (as compared

to adults) can be estimated only for the first winter in the life of the respective individual; thereafter the animals enter the adult age class (Table 1).

**Table 1** Number of individuals per time period and species, Natterer's bats (*Myotis nattereri*) and Daubenton's bats (*Myotis daubentonii*) assigned according to sex and age class (juv – juveniles; ad - adults). Winter periods are characterized by “w” and the two partly encompassed years and summer periods are specified with “s” and the specific year. Due to our sampling location at a hibernaculum it was only possible to assign juveniles in winter.

Time Period	Natterer's bats				Daubenton's bats			
	Male		Female		Male		Female	
	Juv	Ad	Juv	Ad	Juv	Ad	Juv	Ad
w 2010/11	72	55	41	53	35	17	27	50
s 2011	/	35	/	46	/	32	/	64
w 2011/12	58	53	33	67	32	71	29	90
s 2012	/	85	/	88	/	91	/	100
w 2012/13	45	93	34	99	17	104	15	88
s 2013	/	112	/	120	/	106	/	98
w 2013/14	60	107	24	128	32	124	16	97
s 2014	/	144	/	136	/	139	/	109
w 2014/15	31	146	38	160	29	165	21	115
s 2015	/	159	/	175	/	176	/	131

To capture the impact of changing environmental conditions over the study period models of increasing complexity were estimated. The simplest model included the binary covariate season (summer vs. winter), postulating a stable seasonal pattern in survival, but no inter-annual variation. The next more complex model allowed that each year could have its own level of mortality (categorical covariate with one level for each year) combined with an additive effect of season. This model describes a consistent summer-to-winter difference (on the logit scale) in survival, but on possibly different levels across years. The most flexible (and least parsimonious) model includes a covariate that permits a different level of survival in each of the periods and forces no constant summer-to-winter relation. Note that this final model is formally equivalent to the model including a year-by-season interaction, but estimates are easier to interpret when coded as a single variable with a level for each period.

Models were compared based on the values of the AICc (Hurvich and Tsai 1991, Burnham et al. 2011), which converges in AIC for large samples. Furthermore, the intra-class correlation coefficient (ICC) was calculated on the scale of the linear

predictor from the variance of the individual-specific random intercept (Rodríguez and Elo 2003).

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#### 4.2.2. DEPARTURE BEHAVIOUR FROM HIBERNATION

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In a similar approach as used for seasonal survival, those individuals from the analyses that had not been recorded either during the arrival or the departure period, but re-appeared later were again excluded to assure that individuals have indeed used the hibernaculum. The number of excluded individuals (mn: 18 out of 540 individuals (3.3 %); md: 32 out of 507 individuals (6.3 %)) differed slightly due to using another data subset focussing on departure from hibernation without the winter 2010/2011. In this case, survival was also coded as 0 if the individual died after disappearing from the hibernaculum, i.e. was not recorded again after departure, and as 1 if it survived at least to the beginning of  $H_{t+1}$ .

Average departure dates between species were compared, using a Wilcoxon rank sum test with continuity correction, after a Bartlett test revealed variance homogeneity for the not normally distributed data.

Restricted maximum likelihood linear mixed-effects models (LMMs) with normal errors (Zuur et al. 2009) were applied to assess differences in departure date between sexes and age classes for each species separately. Further, the winter station-based index of NAO (North Atlantic Oscillation) for 1<sup>st</sup> December to 31<sup>st</sup> March, which is based on the difference of normalized sea level pressure between Lisbon, Portugal and Reykjavik, Iceland (Hurrell 1995) was taken into account. The NAO is a widely used proxy for the large-scale winter weather patterns over Europe (Hurrell 1995, Post et al. 1997). 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 (2003, updated regularly; accessed 30th September 2017). During our study period the NAO values ranged from -1.97 to 3.56 in comparison to -4.89 - 5.08 between 1864 and 2015. Since not all of the individuals have been present in the same years and, therefore, differ in their experienced environment over the years, it is important to take that into account. To investigate potential individual variation in plasticity of departure behaviour with NAO under consideration of individually experienced environments over the years, the approach of within-individual centring which was introduced into the field of

behavioural ecology by van de Pol and Wright (2009), and included two NAO terms as fixed effects, was chosen. First, the mean NAO experienced by each individual over the years the individual was present (NAOm), and second the mean-centred NAO (NAOmc; deviation of the NAO for all individual observations from the experienced mean NAO) (van de Pol and Wright 2009) were used. Additionally, the effect of sex-specific age class was tested for by adding an interaction between sex and age class, and for sex-specific effects on departure date by adding an interaction between NAOmc and sex. Sex, age, and their interactions were entered as fixed effects. Individuals were repeatedly sampled (median: 2 years in both species) and individual ID was entered as random effect, specified as random intercept, to estimate among-individual differences in average departure date across years. Furthermore, to test for individual variance in behavioural plasticity in departure date with winter weather conditions, random slopes of NAOmc were also included.

Model selection followed the criteria mentioned in the beginning. However, in contrast to the seasonal survival analyses, the significance of the random effects was tested first by comparing models with and without random effects using the full fixed structure. Thus, the simplest candidate model included individual ID as a random intercept and, thus, allowed for individual variation in average departure date. The next more complex model included, additionally to individual ID as random intercept, NAOmc as random slopes to allow for individual variation in the response towards the NAOmc. The third and most complex candidate model contained the two already mentioned random effects and a correlation between random intercept and slope. So, in the random effect structure average departure date and the response towards the NAOmc would not be independent from each other. Individuals that left the hibernaculum on average late would respond differently to a changing NAOmc than those leaving on average earlier. After identifying the best fitted random effect structure, interactions and fixed main effects were selected. Finally, the intra-class correlation coefficient (ICC) was calculated again as the proportion of variance explained by the between-individual differences of the random intercept (Nakagawa and Schielzeth 2010).

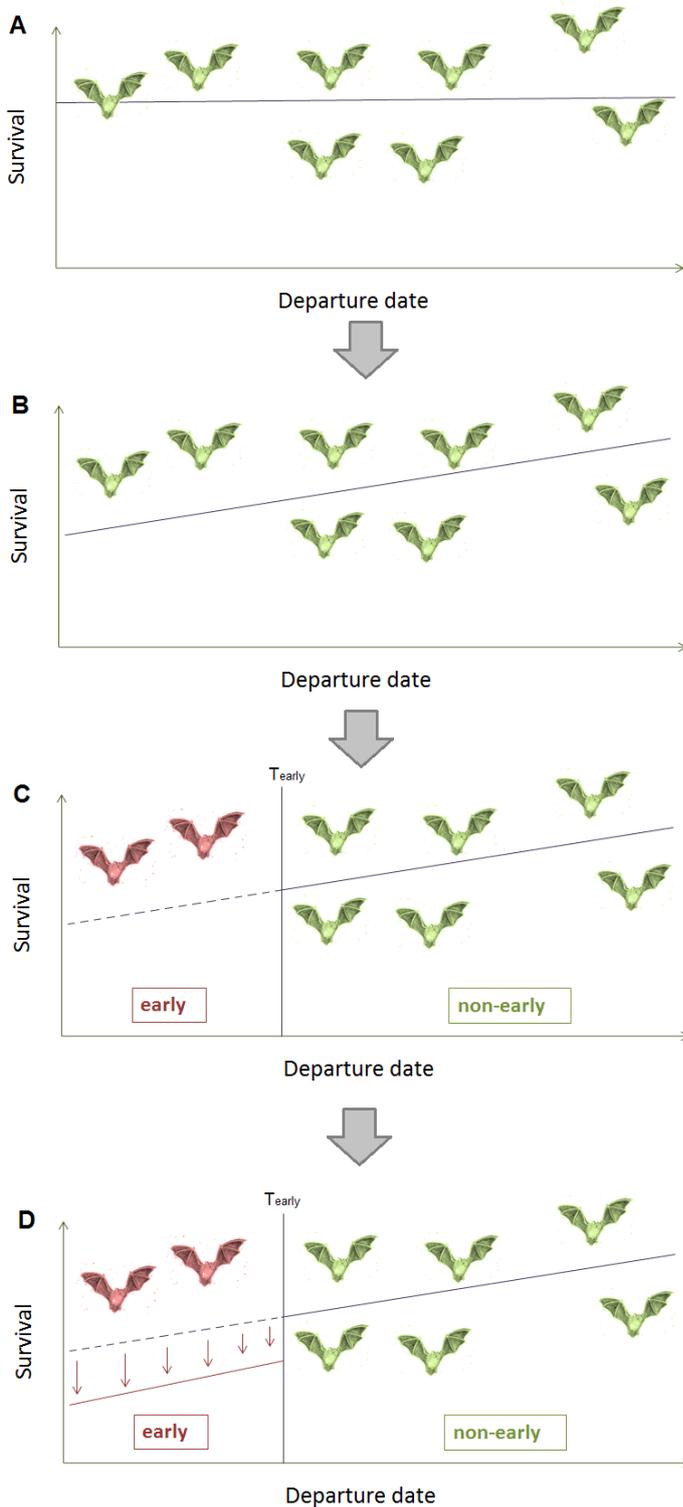
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#### 4.2.3. SURVIVAL OF THE EARLY BATS

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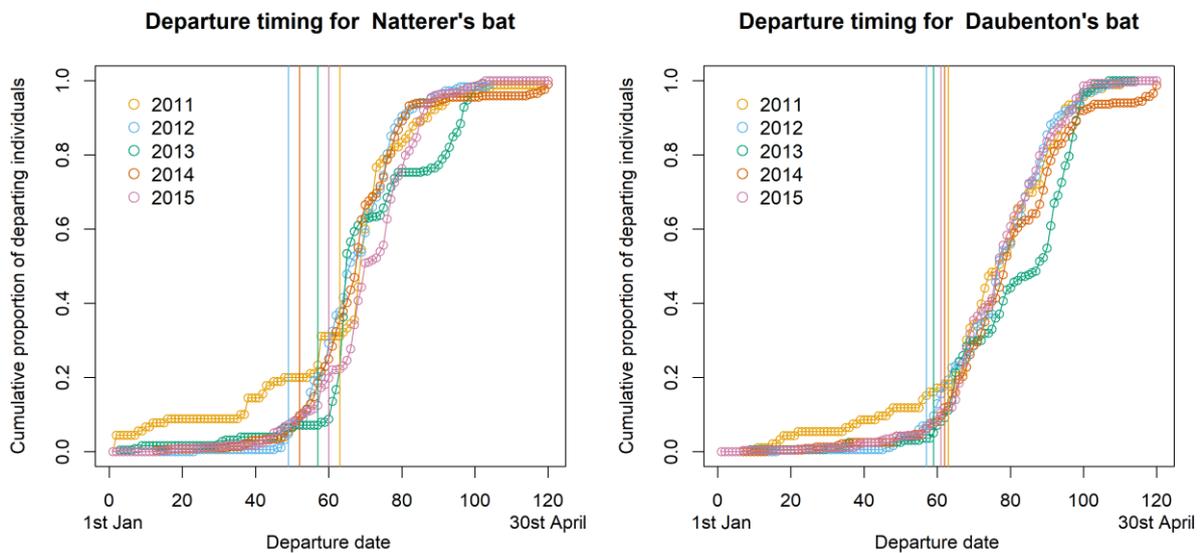
A challenge in assessing whether leaving the hibernaculum early is associated with mortality costs due to disadvantageous conditions at this time point was the

choice of a suitable method to distinguish between different types of risk in leaving early. Bats that left the hibernaculum early simultaneously faced two types of risks affecting their survival: 1) lower survival probability due to an increased death risk that results solely from being outside the hibernaculum for a longer time period (exposure effect) and 2) lower survival probability because they left the hibernaculum at times when food was typically still scarce (ecological effect). The direct discrimination between both types of mortality risk, as the exact time of death was unknown, was not possible. Traditional capture-mark-recapture models, as well as, commonly used logistic regression models do not account for different individual risk exposure times and, thus, assume an equal risk of death independent from departure timing as null hypothesis when testing whether timing of departure date has a significant impact on survival (Figure 5A). However, to try to distinguish the exposure effect and a potential ecological effect, the exposure effect has to be taken under consideration and, thus, the null hypothesis needs to be newly defined (Figure 5B). To determine the new baseline, it is necessary to separate the departing bats into early and non-early individuals and use the non-early ones to determine the expected survival probabilities for the early ones with regard to a pure exposure effect (Figure 5C).



**Figure 5** Schematic illustration of reasons for method choice to disentangle exposure and ecological risk effect on survival of early bats. A) Null hypothesis in traditional methods: equal survival probabilities independent of departure date. B) Necessity to newly define null hypothesis to take exposure risk effect into account: Due to higher energy expenditure purely caused by longer exposure times to environment outside of the hibernaculum, decreased survival probability with decreasing departure date. C) Necessity to separate bats in early and non-early individuals to assess a daily mortality risk based on the assumed exposure effect in the non-early individuals as a newly defined null hypothesis. D) Assessing whether observed survival of early bats was below the one expected under a pure exposure effect as a strong indication for an ecological risk effect of leaving early.

Following the outlined approach to test whether early emerging individuals had a higher mortality risk due to an ecological effect, first individuals were classified as those that left the hibernaculum ‘early’ based on the analysis of the cumulative number of departing animals, separated by species and year (Table 2, Figure 6). The separation of early from non-early departure was defined as the point in time when the sigmoid-shaped cumulative departure curve changed from flat to steep increase (i.e. when the majority of individuals started to depart). This was operationalised as 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 low activity at both sides triggers the above criterion, the cumulative departure curve was smoothed by a 10-day moving average. All individuals that left before this so identified date were labelled ‘early’. This method is considered to be more sensitive as opposed to using the inflection point of the cumulative departure curve.



**Figure 6** 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.

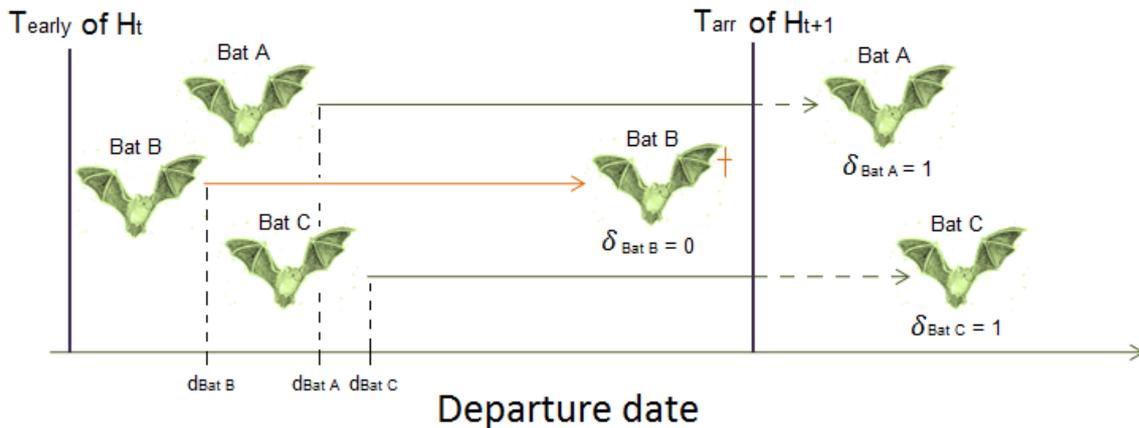
**Table 2** Year specific parameters to determine if early bats show a lower survival probability than expected for Natterer's bat (*Myotis nattereri*) and Daubenton's bat (*Myotis daubentonii*). Year contains the study years.  $T_{\text{early}}$  is the year- and species-specific threshold to identify early bats (individuals with an earlier or equal departure date compared to  $T_{\text{early}}$ ).  $T_{\text{arr}}$  is the species and year specific time point that determined survivors from dead individuals. Individuals that have been recorded afterwards count as survivors. Lambda is the constant mortality rate per day calculated on the remaining bat individuals (early bats excluded).

Species	Year	$T_{\text{early}}$	$T_{\text{arr}}$	Lambda
<b>Natterer's bat</b>	2011	63	212	0.000889
	2012	49	224	0.000826
	2013	57	212	0.002005
	2014	52	217	0.000786
	2015	60	213	0.001199
<b>Daubenton's bat</b>	2011	63	213	0.001793
	2012	57	214	0.002166
	2013	59	215	0.002667
	2014	62	212	0.000782
	2015	61	212	0.001668

Next, it was indirectly assessed whether early departing individuals had higher mortality due to an ecological effect. Therefore, a comparison of the observed number of survivors to the expected number of surviving 'early' bats - under the assumption that all bats in this study population suffer the same species- and year-specific daily risk of death outside the hibernaculum - was done (Figure 5C). The actual year-specific arrival period started when the first animal was recorded back at the hibernaculum between August and December. This arrival date, again specific for each species and year, is denoted as  $T_{\text{arr}}$ . From all animals that had not left early the average daily death rate for the summer season was estimated by standard survival analysis (Kleinbaum and Klein 2005). Animals that re-entered the hibernaculum in the arrival period of  $H_{t+1}$  were included in the analysis as right-censored (they had survived from their departure date of  $H_t$  to at least  $T_{\text{arr}}$ ; e.g. Bat A and C in Figure 7), while animals that were not recorded again at the site during the arrival period of  $H_{t+1}$  were considered as having died between their departure date and  $T_{\text{arr}}$ .

Under the assumption that this estimated death rate also applies to the early-departing animals, the survival probability to  $T_{\text{arr}}$  was calculated for each of these individuals, taking the longer time at risk of death (due to the earlier departure) into account. Therefrom the expected number of survivors to  $T_{\text{arr}}$  among the early

departing animals was determined and the corresponding p-values were calculated. Thus, a lower survival for early bats was already assumed and in this step it was tested whether the number of surviving early bats was even below the one that was expected (Figure 5D). If that is the case, it would be a strong indication for a mortality risk beyond the exposure effect.



**Figure 7** Schematic illustration of the survival method. The individual bats are described by a bat ID based on letters. The individual departure date is highlighted by vertical dashed lines and the letter “d” specified by the individual bat ID. The time point separating early from non-early bats is  $T_{early}$  of the current hibernation period  $H_t$ . The beginning of the actual arrival period in the subsequent hibernation period  $H_{t+1}$  is  $T_{arr}$ . The individual survival indicator  $\delta$  is set to 0 if the individual did not survive to  $T_{arr}$  and to 1 if it survived at least until  $T_{arr}$ . Those bats that survived beyond  $T_{arr}$  are treated as right-censored (horizontal dashed line).

In more detail (Figure 7), if animal  $i$  departs on day  $d_i$  and survives at least to  $T_{arr}$  then its survival time is equal or larger than  $l_i = T_{arr} - d_i$ . Its contribution to the likelihood function is  $e^{-\lambda l_i}$ , where  $\lambda$  denotes the daily death rate. If the animal is not recorded during the arrival season then its survival time is shorter than  $l_i$ , and its contribution to the likelihood is  $1 - e^{-\lambda l_i}$ . The survival indicator  $\delta_i$  was defined, with  $\delta_i = 1$ , if the animal survived to  $T_{arr}$  (Figure 7 Bat A and Bat C), and  $\delta_i = 0$  otherwise (Figure 7 Bat B). (By assuming that their death happened before  $T_{arr}$  the death rate was eventually overestimated, should the death actually have occurred after  $T_{arr}$  during the arrival period. In view of the intended analysis, see below, this is a conservative assumption). To estimate  $\lambda$ , the log-likelihood  $\ell(\lambda) = \sum_i [\delta_i \ln e^{-\lambda l_i} + (1 - \delta_i) \ln(1 - e^{-\lambda l_i})]$  is maximized. The death rate is estimated for the animals that did not depart early from the hibernaculum, the estimate is denoted by  $\hat{\lambda}$ .

Now, under the assumption that the estimated death rate  $\hat{\lambda}$  also applies to early-departing animals, for an individual that leaves the hibernaculum on day  $e_i$  the probability to survive to  $T_{arr}$  is  $p_i = e^{-\hat{\lambda}(T_{arr} - e_i)}$ . For  $n$  early-departing individuals, each with its own survival probability  $p_i$ , the expected numbers of survivors to  $T_{arr}$  is  $S_{exp} = \sum_{i=1}^n p_i$ . To gauge the observed number of survivors  $s_{obs}$ , the distribution of the number of survivors  $S$  under the null hypothesis (early-departing animals suffer from same risk of death as other animals) has to be determined. It is the sum of  $n$  Bernoulli variables with different success probabilities  $p_i$  and the distribution is derived via convolution (Feller 1959). Here this convolution was calculated using the R-package `distr` (Ruckdeschel et al. 2006, Ruckdeschel and Kohl 2014). If the number of individuals  $n$  is large enough, a Normal approximation to the distribution of the statistic  $S$  is also possible. The left-tail probability  $p = P(S \leq s_{obs})$  then gives the (one-sided) p-value. The obtained p-values allow us to decide whether there were significantly fewer survivors observed among the early-departing animals than expected, if they would have experienced the same daily risk of death as the rest of the population. Hence, small p-values indicate that the mere risk of a longer time spent outside the hibernaculum is unlikely to explain the observed (low) number of survivors and early departure did involve additional mortality costs. The hypothesis of no extra mortality cost was rejected, if the p-value was below 0.05.

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#### 4.2.4. IMPACT OF LOCAL WEATHER ON SURVIVAL OF EARLY BATS

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After the assessment of potential ecological risk effects of leaving early independent from the longer exposure time, the question was whether local environmental conditions directly after departure that have an impact on survival of early bats can be identified. Thus, concentrating on the early bats, a window of five days after individuals' departure was defined and the median proportion of night hours (sunset to sunrise) above 3 °C was determined. The hourly weather data from the weather station Havixbeck-Tilbeck in an approximately 6 km distance to the study site were provided by the Meteogroup (Meteomedia GmbH, Bochum, Germany). Since a general impact of departure date was assumed due to the associated longer exposure time and, thus, probably higher energy expenditure, departure date was controlled for by including it as a fixed effect in the species-specific models. To assure an absence of correlation between departure date and median proportion of

night hours above 3 °C, a Spearman's rank correlation test was performed. Further on, it was tested whether age class or the median proportion of night hours above 3 °C had an impact on survival of the early bats on top of departure date by including those as fixed effect into the logistic regression model. Model selection followed the abovementioned approach. The years were analysed together in one model since the effect of temperatures below 3 °C should not differ between years. The number of individuals with repeated measurements was comparably small (mn: 27 out of 135; md: 5 out of 99), therefore, individual ID was not included as random effect.

## 5. RESULTS

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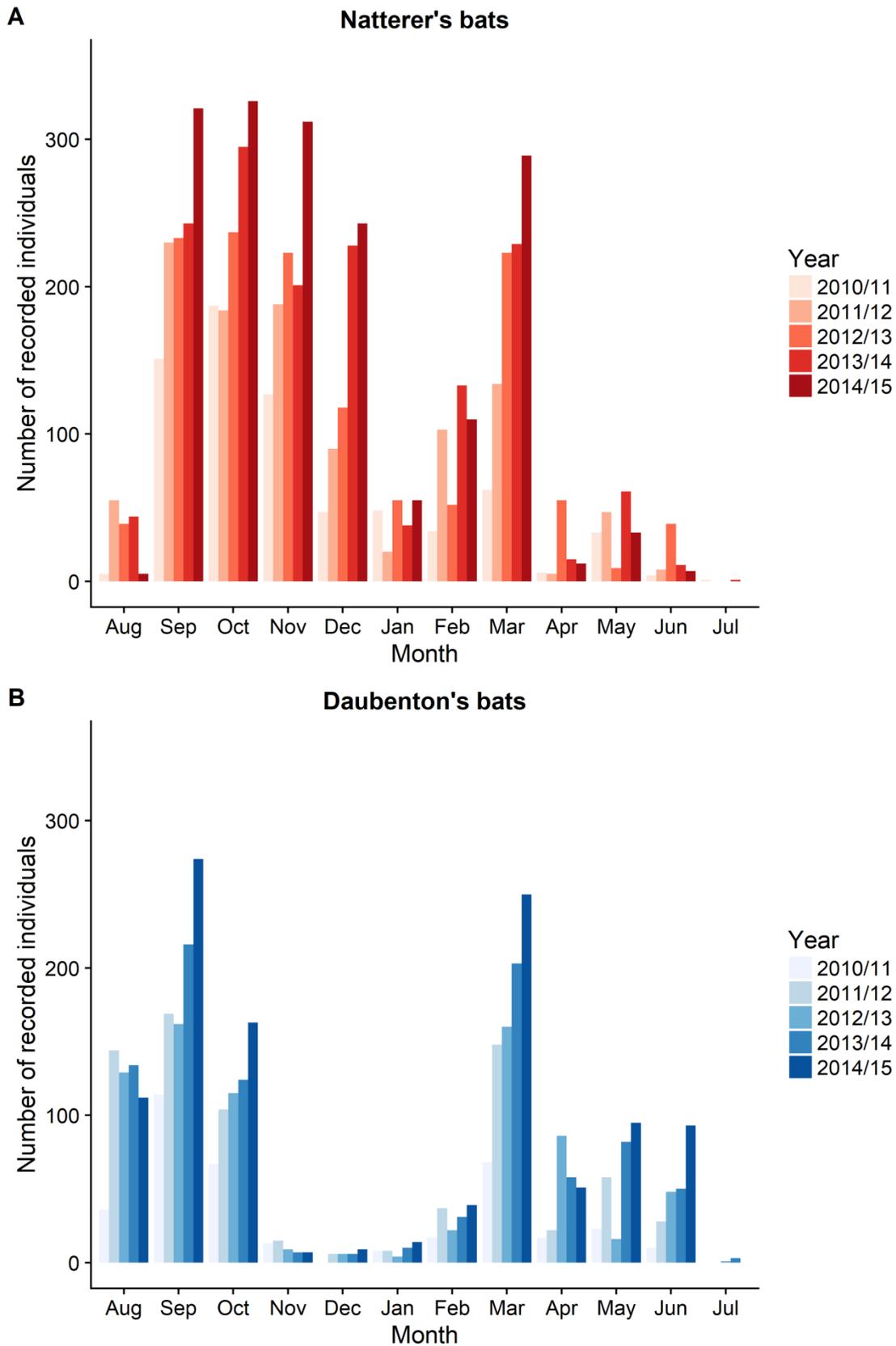
### 5.1. SEASONAL SURVIVAL

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#### 5.1.1. ACTIVITY PATTERN AT THE "BRUNNEN MEYER"

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To confirm the described activity pattern of Natterer's bats and Daubenton's bats at the hibernaculum "Brunnen Meyer", the number of recorded RFID-tagged individuals per month and species for each study year separately has been determined. The resulting activity pattern supported the species-specific activity patterns described by other studies (Kunz 1982, Trappmann 2005, Dietz et al. 2016) (Figure 8A and 8B). Natterer's bats started to arrive mainly in September and the number of active individuals stayed high until December, decreased strongly in January and started to rise again in February with its peak of recorded individuals in March (Figure 8A). In both species clearly two activity peaks are recognizable, arrival/swarming and departure. In contrast to Natterer's bats, Daubenton's bats started to arrive in August, had their peak in September and only a relatively small part of individuals was recorded in November until throughout January. In March, the majority of individual Daubenton's bats was active and likely departed from the hibernaculum (Figure 8B). Furthermore, it showed that the hibernaculum is used almost continuously with a, nevertheless, clear seasonal pattern. In July there is almost no activity in both species and, thus, the separation into hibernation periods (Aug-Apr) seems to be justified (Figure 8A and 8B). The same seemed to be valid for the arrival period (Aug-Dec) and the departure period (Jan-Apr). Although the actual individual numbers change between years, which is partly due to marking more individuals with each additional year, the activity pattern was quite stable over the five study years (Figure 8A and 8B).



**Figure 8** Activity pattern at the hibernaculum “Brunnen Meyer” showing the number of RFID-tagged individuals recorded per month over the five hibernation periods (2010/11 – 2014/15) for the two species, Natterer’s bats (*Myotis nattereri*, A, red) and Daubenton’s bats (*Myotis daubentonii*, B, blue).

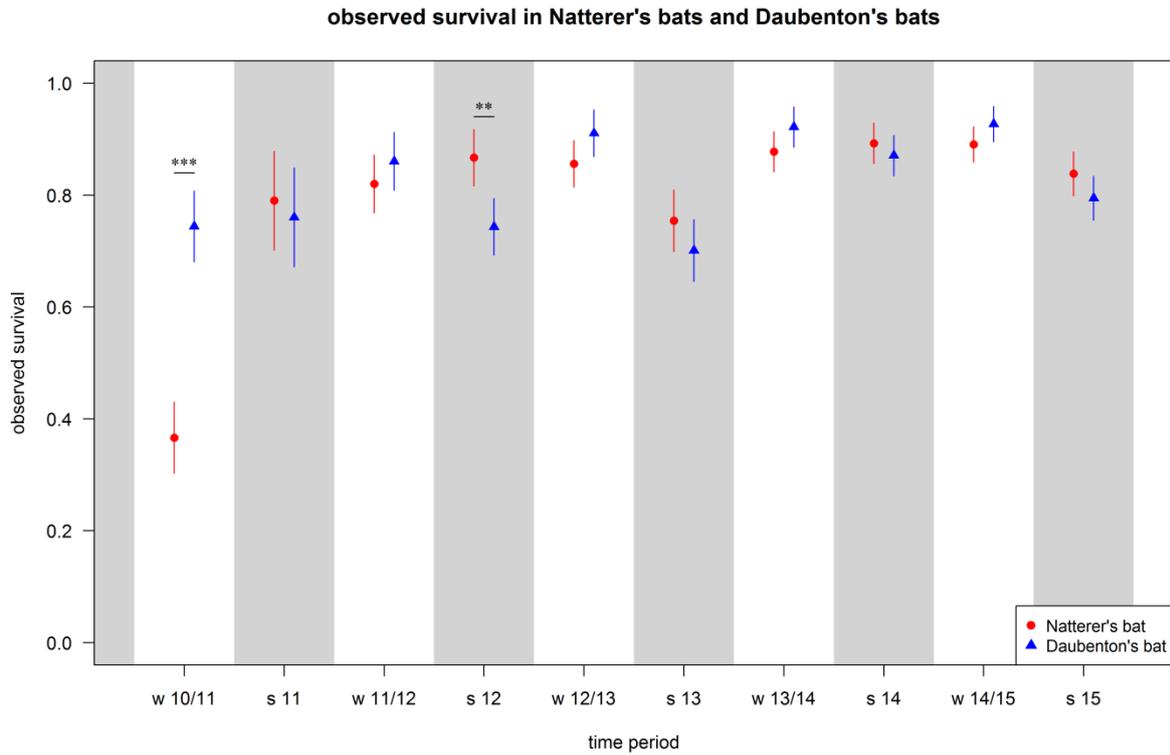
### 5.1.2. DIFFERENCES IN SURVIVAL BETWEEN THE TWO BAT SPECIES ACROSS PERIODS

Significant differences in survival between the two species were only found in two periods: winter 2010/2011 and summer 2012 (Table 3; Figure 9). While in winter 2010/2011 Natterer's bats showed a much lower survival than Daubenton's bats, in summer 2012 a contrasting pattern was detected. Otherwise both species showed similar survival. Furthermore, a comparatively low survival in summer 2013 was similarly observed for both species. The observed differences in survival between species in the abovementioned periods highlighted a potentially species-specific importance of certain periods.

**Table 3** Estimated survival probabilities of Natterer's bats (*Myotis nattereri*, mn) and Daubenton's bats (*Myotis daubentonii*, md). Winter periods are denoted by "w" and the respective years, while summer periods are labelled as "s" combined with the respective year. "Dead" and "Survived" contain the number of individuals that have been assigned dead or survived the respective period. The following column gives the proportion of survivors (in %). In each period, it was tested whether the survival proportions were the same in the two species (two-sided alternative, chi-squared test with  $df=1$ , yate's continuity correction). The final two columns give the value of the test statistic and the resulting  $p$ -value. Significant results are printed in bold letters 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 ( $\cdot < 0.1$ ).

Period	Species	Dead	Survived	% survived	$X^2$	$p$ -value
<b>w 10/11</b>	<b>mn</b>	<b>140</b>	<b>81</b>	<b>36.7</b>	<b>44.980</b>	<b>1.99x10<sup>-11</sup> ***</b>
	<b>md</b>	<b>33</b>	<b>96</b>	<b>74.4</b>		
s 11	mn	17	64	79.5	0.084	0.772
	md	23	73	76.0		
w 11/12	mn	38	173	82.3	1.037	0.309
	md	31	191	86.0		
<b>s 12</b>	<b>mn</b>	<b>23</b>	<b>150</b>	<b>87.3</b>	<b>7.978</b>	<b>0.005 **</b>
	<b>md</b>	<b>49</b>	<b>142</b>	<b>74.3</b>		
w 12/13	<i>mn</i>	39	232	86.0	2.985	0.084 $\cdot$
	<i>md</i>	20	204	91.1		
s 13	mn	57	175	75.0	1.306	0.253
	md	61	143	70.1		
w 13/14	mn	39	280	88.0	2.647	0.104
	md	21	248	92.2		
s 14	mn	30	250	89.1	0.415	0.519
	md	32	216	87.1		
w 14/15	mn	41	334	89.2	2.390	0.122
	md	24	306	92.7		

s 15	mn	54	280	83.4	1.751	0.186
	md	63	244	79.5		



**Figure 9** Comparison of observed survival between species (Natterer's bats (*Myotis nattereri*, red points); Daubenton's bats (*Myotis daubentonii*, blue triangles) in each period. Vertical lines indicate 95% confidence intervals for the estimated survival probabilities. Periods that describe summer survival are indicated by a light grey background. The stars in winter 2010/11 and summer 2012 indicate significant differences in observed survival between species, see Table 1.

### 5.1.3. THE ROGUE WINTER 2010/11

Winter 2010/11 evidently was an extraordinary period for Natterer's bats (Figure 9) and including this winter in the regression model inevitably would have forced the choice of the least parsimonious model. Therefore, the regression model for this species was built from summer 2011 to summer 2015, excluding the extraordinary winter 2010/11.

### 5.1.4. IMPORTANCE OF INDIVIDUAL CHARACTERISTICS

When testing the influence of fixed effects on survival, the best fitted species-specific models (Table 4-6; Figure 10) showed that a moderate portion of the variance could be explained by between-individual differences (random intercept of 0.19). Nevertheless, age turned out to be a major determinant of survival in both

species with consistent effects in all years. Survival of juveniles that were in the first winter of life was on average reduced by 30 percentage points in Daubenton's bats, and much less, by 20 percentage points in Natterer's bats.(Table 4; Figure 10). Both species-specific models did not support a general sex difference in survival (Table 4-5).

**Table 4** Model selection to choose the best fitted fixed effect structure for Natterer's bats (*Myotis nattereri*). In each case individual entered the model as random intercept. Model selection was based on the lowest AICc and a difference in AICc (delta AICc (dAICc)) of at least 2 was chosen to select a model with more parameter over a simpler one. The best fitted model is given in bold letters.

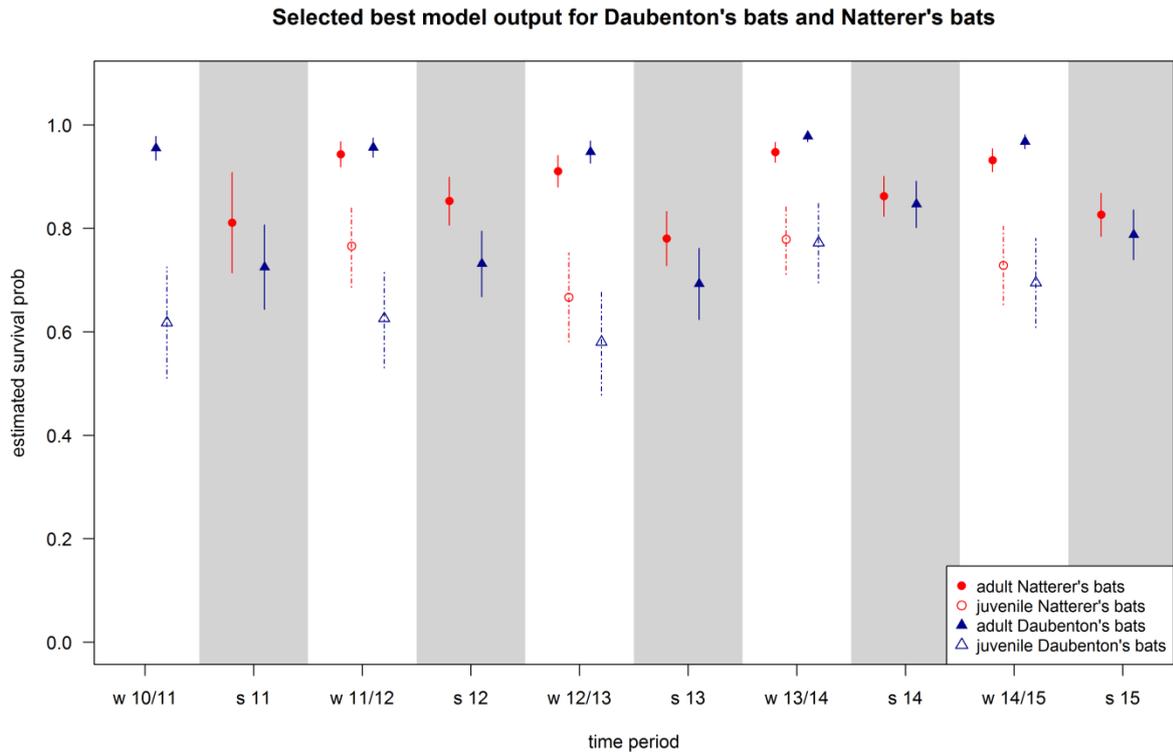
Model	K	AICc	dAICc
age	3	1852.96	48.15
age + sex	4	1854.33	49.52
age + season	4	1809.06	4.26
<b>age + season + year</b>	<b>8</b>	<b>1806.74</b>	<b>1.94</b>
age + period	11	1804.80	0.00
age + sex + period	12	1806.21	1.41

**Table 5** Model selection to choose the best fitted fixed effect structure for Daubenton's bats (*Myotis daubentonii*). In each case individual entered the model as random intercept. Model selection was based on the lowest AICc and a difference in AICc (delta AICc (dAICc)) of at least 2 was chosen to select a model with more parameter over a simpler one. The best fitted model is given in bold letters.

Model	K	AICc	dAICc
age	3	1886.23	171.13
age + sex	4	1888.21	173.11
age + season	4	1727.57	12.47
<b>age + season + year</b>	<b>8</b>	<b>1715.10</b>	<b>0.00</b>
age + period	12	1717.65	2.56
age + sex + period	13	1719.64	4.54

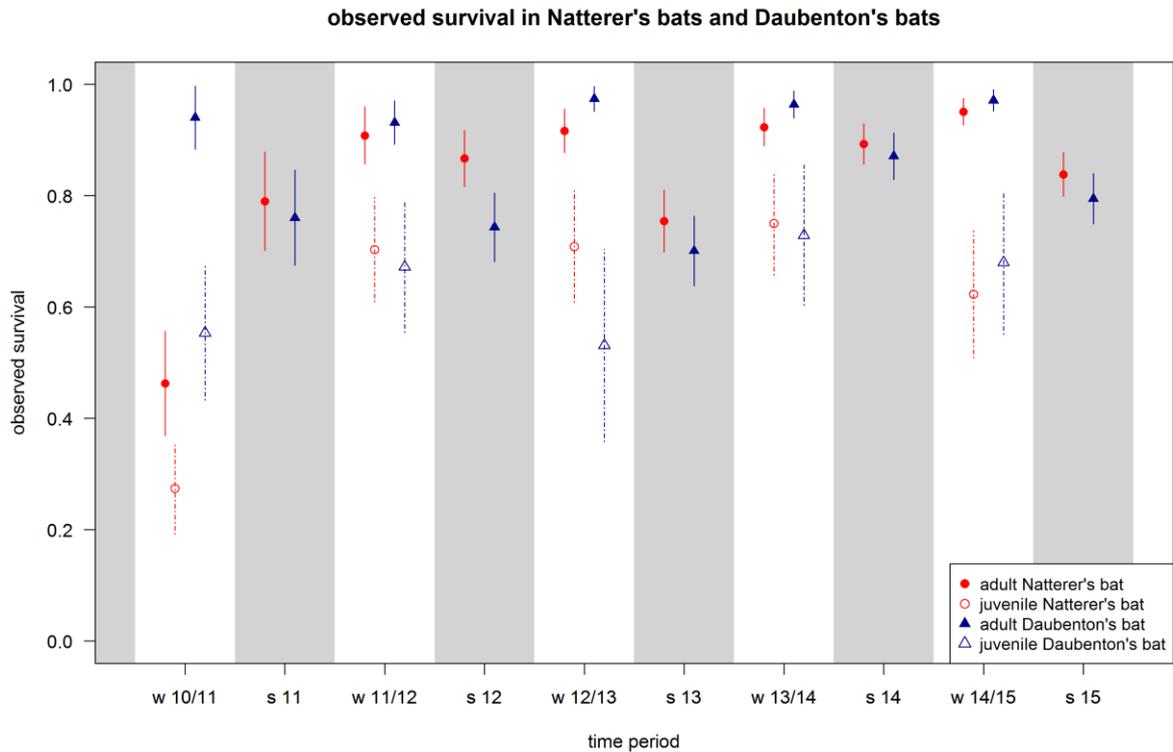
**Table 6** Estimates for the binomial generalized linear mixed-effects model with survival as response for Daubenton's bat (*Myotis daubentonii*, md) and Natterer's bat (*Myotis nattereri*, mn; excluding winter 2010/11). Winter periods are denoted by "w" and the respective years, while summer periods are labelled as "s" combined with the respective year. 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 ( $N_{\text{groups}}$ ) that were included in the model are given. Estimates are given in logit scale. In parentheses, 95% confidence interval of each estimate is given. For the fixed effects, the reference levels (Ref) are mentioned in parentheses. The resulting intra-individual correlation is  $ICC = (0.9^2) / ((0.9^2) + (\pi^2/3)) = 0.19$  for mn and md.

Fixed effects	Estimates (95% CI)	Additional model information	Estimates (95% CI)
<b>Natterer's bats (surv ~ age class + season + year + (1 ID))</b>			
Intercept	1.6 (1.4;1.8)	Random intercept standard deviation	0.9 (0.5;1.3)
Age status "juvenile" (Ref="adult")	-1.6 (-2.0;-1.2)		
Season "winter" (Ref="summer")	1.1 (0.7;1.4)	Data subset	w2010/11 – s2015
Year "2010_2011" (Ref="mean")	-0.1 (-0.6;0.4)		
Year "2011_2012" (Ref="mean")	0.2 (-0.1;0.5)		
Year "2012_2013" (Ref="mean")	-0.3 (-0.6;0.0)		
Year "2013_2014" (Ref="mean")	0.3 (0.0;0.5)	$N_{\text{observations}}$	2276
Year "2014_2015" (Ref="mean")	0.0 (-0.3;0.2)	$N_{\text{groups}}$	618
<b>Daubenton' bats (surv ~ age class + season + year + (1 ID))</b>			
Intercept	1.2 (1.0;1.3)	Random intercept standard deviation	0.9 (0.5;1.2)
Age status "juvenile" (Ref="adult")	-2.6 (-3.0;-2.1)		
Season "winter" (Ref="summer")	2.1 (1.7;2.5)	Data subset	s2011 – s2015
Year "2010_2011" (Ref="mean")	-0.2 (-0.5;0.1)		
Year "2011_2012" (Ref="mean")	-0.2 (-0.4;0.1)		
Year "2012_2013" (Ref="mean")	-0.3 (-0.6;-0.1)		
Year "2013_2014" (Ref="mean")	0.5 (0.3;0.8)	$N_{\text{observations}}$	2220
Year "2014_2015" (Ref="mean")	0.2 (-0.1;0.4)	$N_{\text{groups}}$	601



**Figure 10** Estimated survival probabilities based on the selected logistic regression mixed-effect models for both species. In both species-specific models individual was included as random intercept. The model for Natterer's bats (*Myotis nattereri*, red circles/points) was built excluding the extraordinary winter 2010/2011. The results of the best model for Daubenton's bats (*Myotis daubentonii*, blue triangles) and of the one for Natterer's bats – in both cases including season, age class and year as fixed effects - are shown. Due to sampling at a hibernaculum, it was only possible to estimate juvenile survival over winter. Juveniles are characterized by open symbols, while adults are defined by filled symbols.

Under consideration, of a strong age effect the observed data were repeatedly investigated (Figure 11). Separating age classes supported the results of the species-specific models. The consequences just concerned winter survival which was increased for adults by treating them separately. The yearly pattern for adult bats stayed the same and underlined the differences between species just in particular time periods, winter 2010/2011 and summer 2012. However, in both species a stable pattern of higher winter survival and lower summer survival in adult bats, excluding 2010/2011 in Natterer's bats, was then more strongly accentuated.



**Figure 11** Comparison of observed survival between species (Natterer's bats (*Myotis nattereri*, red points); Daubenton's bats (*Myotis daubentonii*, blue triangles)) in each period under consideration of age classes. Vertical lines indicate 95% confidence intervals for the estimated survival probabilities. Periods that describe summer survival are indicated by a light grey background. The stars in winter 2010/11 and summer 2012 indicate significant differences in observed survival between species, see Table 1. Due to sampling at a hibernaculum, it was only possible to observe juvenile survival over winter. Juveniles are characterized by open symbols, while adults are defined by filled symbols.

#### 5.1.5. THE EFFECTS OF SEASON AND YEAR

The factor "season" was not sufficient to explain variation in survival in both species and "year" had to be added for better survival estimation (Table 4-5). Even though the model with the lowest AICc included the specific periods in Natterer's bats, the difference in AICc did not exceed 2. Thus, in both species adult survival showed a consistent pattern between seasons (summer vs winter) that varied in its level across years. In comparison to the mean over the years, particularly the year 2012/2013 demonstrated lower adult survival while the year 2013/2014 was associated with a higher adult survival in both species (Table 6; Figure 10).

Visual inspection of the data suggested that Daubenton's bats had higher adult survival in winter than Natterer's bats, while the reverse was true in summer (Figure 9). This was confirmed in our species-specific models. While both species showed significantly higher winter adult survival compared to summer survival, the

difference in adult survival between seasons was higher in Daubenton's bats (Table 5; Figure 10). Nevertheless, juvenile survival over winter was even lower than summer survival in both species (Table 5; Figure 10).

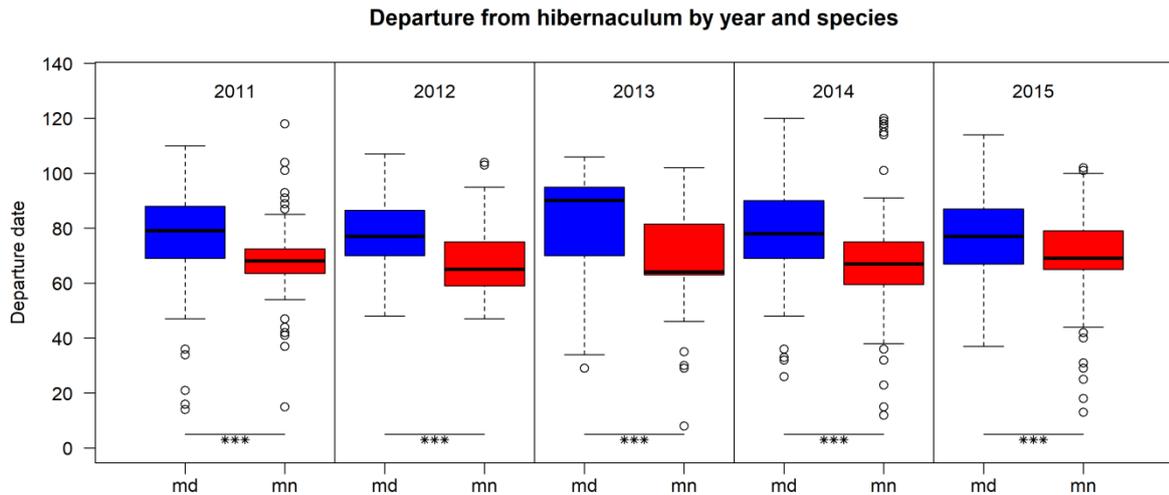
## 5.2. DEPARTURE BEHAVIOUR FROM HIBERNATION

### 5.2.1. GENERAL PATTERN

Overall 1,047 RFID-tagged individuals were recorded > 23,500 times, yielding 3,945 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. For both species the cumulative curves of departure date for the five years showed similar sigmoid patterns but they were shifted between the species; with 2011 and 2013 being slightly different from the other years (Figure 6). In all years, Daubenton's bats departed from the hibernaculum later than Natterer's bats, on average 7.5 – 12.6 days (Table 7; Figure 12).

**Table 7** Results of the Bartlett test and Wilcoxon rank sum test to compare average departure date of the surviving individuals between species. A lack of significance in the Bartlett test confirmed variance homogeneity, a requirement for comparing departure timing between both species with the Wilcoxon rank sum test with continuity correction. Significant results are printed in bold letters.

Year	Bartlett test	Wilcoxon rank sum test
2011	$K^2 = 1.4984$ , $df = 1$ , $p\text{-value} = 0.2209$	<b><math>W = 3448.5</math>, <math>p\text{-value} = 1.506 \times 10^{-4}</math></b>
2012	$K^2 = 0.1496$ , $df = 1$ , $p\text{-value} = 0.699$	<b><math>W = 16569</math>, <math>p\text{-value} = 1.067 \times 10^{-12}</math></b>
2013	$K^2 = 0.6333$ , $df = 1$ , $p\text{-value} = 0.4262$	<b><math>W = 17832</math>, <math>p\text{-value} = 4.892 \times 10^{-10}</math></b>
2014	$K^2 = 0.3576$ , $df = 1$ , $p\text{-value} = 0.5498$	<b><math>W = 40454</math>, <math>p\text{-value} = &lt; 2.2 \times 10^{-16}</math></b>
2015	$K^2 = 0.3998$ , $df = 1$ , $p\text{-value} = 0.5272$	<b><math>W = 43806</math>, <math>p\text{-value} = 8.638 \times 10^{-9}</math></b>



**Figure 12** Variation in departure dates between species (Daubenton's bats (*Myotis daubentonii*, md) and Natterer's bats (*Myotis nattereri*, mn)) and across years. The stars indicate significance level of species comparison resulting out of the Wilcoxon rank sum test per year.

### 5.2.2. SPECIES-SPECIFIC PATTERNS

The final LMMs were similar for both species, except that there was no sufficient support for an interaction between sex and age class in Daubenton's bats (Table 8-11, Figure 13). Although for both species the interaction between sex and age class was included in the LMM with the lowest AIC, the difference in AIC between the LMM with the lowest AIC and the simpler one without the interaction was below two in Daubenton's bats and, therefore, the simpler LMM was selected. Thus, the sexes did not seem to strongly differ in their first year in Daubenton's bats. Despite the similarity in factors influencing survival in the two species, the relative impact of effects varied between species.

In Natterer's bats, average departure date differed among age classes. Yearlings left the hibernaculum on average 4.0 days earlier than adults. Nevertheless, considering the significant interaction between age class and sex in Natterer's bats, this difference between age classes seems to be sex-specific with female yearlings leaving on average even 2.1 days earlier than male yearlings. Additionally, with respect to the NAO differences in average departure date between sexes, across individuals (NAOm, ranging from -1.97 to 3.56) as well as within individuals (NAOmc, ranging from -3.94 to 3.29) were found in Natterer's bats. Natterer's bats that experienced on average higher NAOs within our study period left

slightly later: 0.9 days per an increase of the experienced NAOm by 1. Thus, those individuals that experienced on average wetter/milder winters over the years departed on average later from the hibernaculum. While there was no consistent sex-difference in average departure date over all five years, the sexes showed contrasting patterns with regard to the NAOmc. The within-individual component showed that male individuals emerged from hibernation later in study years with higher NAOs (wetter/milder winters) compared to what they experienced over the years (0.7 days per increase of the NAOmc by 1). Females left earlier in years with higher NAOs (wetter/milder winters) under consideration of their experiences over the years (on average -1.1 days per increase of the NAOmc by 1) (Figure 13).

In contrast, in Daubenton's bats, only age class and the interaction between sex and the within-individual component of the NAO (NAOmc, ranging from -3.94 to 3.29) significantly influenced the average departure date, while no consistent significant impact of the NAO components (NAOm, ranging from -1.97 to 3.56, and NAOmc) or sex by itself existed although they improved the model fit. Yearlings consistently left the hibernaculum on average 8.0 days earlier than adults in Daubenton's bats. Additionally, the results showed that females were significantly affected by the NAOmc and emerged from hibernation earlier in years with higher NAOmc (on average -1.0 days per increase of the NAOmc by 1). Thus, while in Daubenton's bats males did not show a clear response in average departure date over the years, females departed from hibernation earlier in wetter/milder winters compared to their individual experience over the study years.

Average individual departure dates in both species were moderately repeatable among years (ICC: mn:  $r = 0.48$ ; md:  $r = 0.27$ ).

**Table 8** Model selection to choose the best fitted random structure based on our full model for Natterer's bats (*Myotis nattereri*). In each case the same fixed effects were entered: individual mean NAO (NAOm), individually mean-centred NAO (NAOmc), sex, age class, the interaction between these two variables and the interaction between sex and the NAOmc. Model selection was based on the lowest AIC and a difference in AIC (dAIC) of at least 2 was chosen to decide between a model with more parameter compared to a simpler one.

Random effects	K	AIC	dAIC
<b>Random intercept, random slope and a correlation between both</b>	<b>11</b>	<b>9653.24</b>	<b>0.00</b>
Random intercept	9	9667.49	14.25
Random intercept and random slope	10	9669.52	16.28

**Table 9** Model selection to choose the best fitted fixed effect structure based on our selected random structure for Natterer's bats (*Myotis nattereri*). In each case the same random effects were entered: individual as random intercept, individual random slope towards mean-centred NAO (NAOmc), a correlation between these two variables. Model selection was based on the lowest AIC and a difference in AIC (dAIC) of at least 2 was chosen to decide between a model with more parameter compared to a simpler one.

Model	K	AIC	dAIC
<b>mean NAO (NAOm) + mean-centred NAO (NAOmc) + sex + age class + interaction sex - age class + interaction sex - NAOmc</b>	<b>11</b>	<b>9653.24</b>	<b>0.00</b>
NAOm + NAOmc + sex + age class + interaction sex - NAOmc	10	9655.42	2.18
NAOm + NAOmc + sex + age class + interaction sex - age class	10	9675.11	21.87
NAOm + NAOmc + sex + age class	9	9676.37	23.13
NAOm + age class	7	9678.65	25.41
sex + age class	7	9679.19	25.95
NAOm + NAOmc + age class	8	9679.35	26.11
age class	6	9682.91	29.67
NAOmc + age class	7	9683.34	30.10
NAOm + sex	7	9696.69	43.45
NAOm	6	9698.16	44.92
NAOm + NAOmc + sex	8	9699.57	46.33
sex	6	9699.72	46.48
NAOm + NAOmc	7	9701.06	47.82
NAOmc + sex	7	9702.53	49.29
NAOmc	6	9704.47	51.23

**Table 10** Model selection to choose the best fitted random structure based on our full model for Daubenton's bats (*Myotis daubentonii*). In each case the same fixed effects were entered: individual mean NAO (NAOm), individually mean-centred NAO (NAOmc), sex, age class, the interaction between these two variables and the interaction between sex and the NAOmc. Model selection was based on the lowest AIC and a difference in AIC (dAIC) of at least 2 was chosen to decide between a model with more parameter compared to a simpler one.

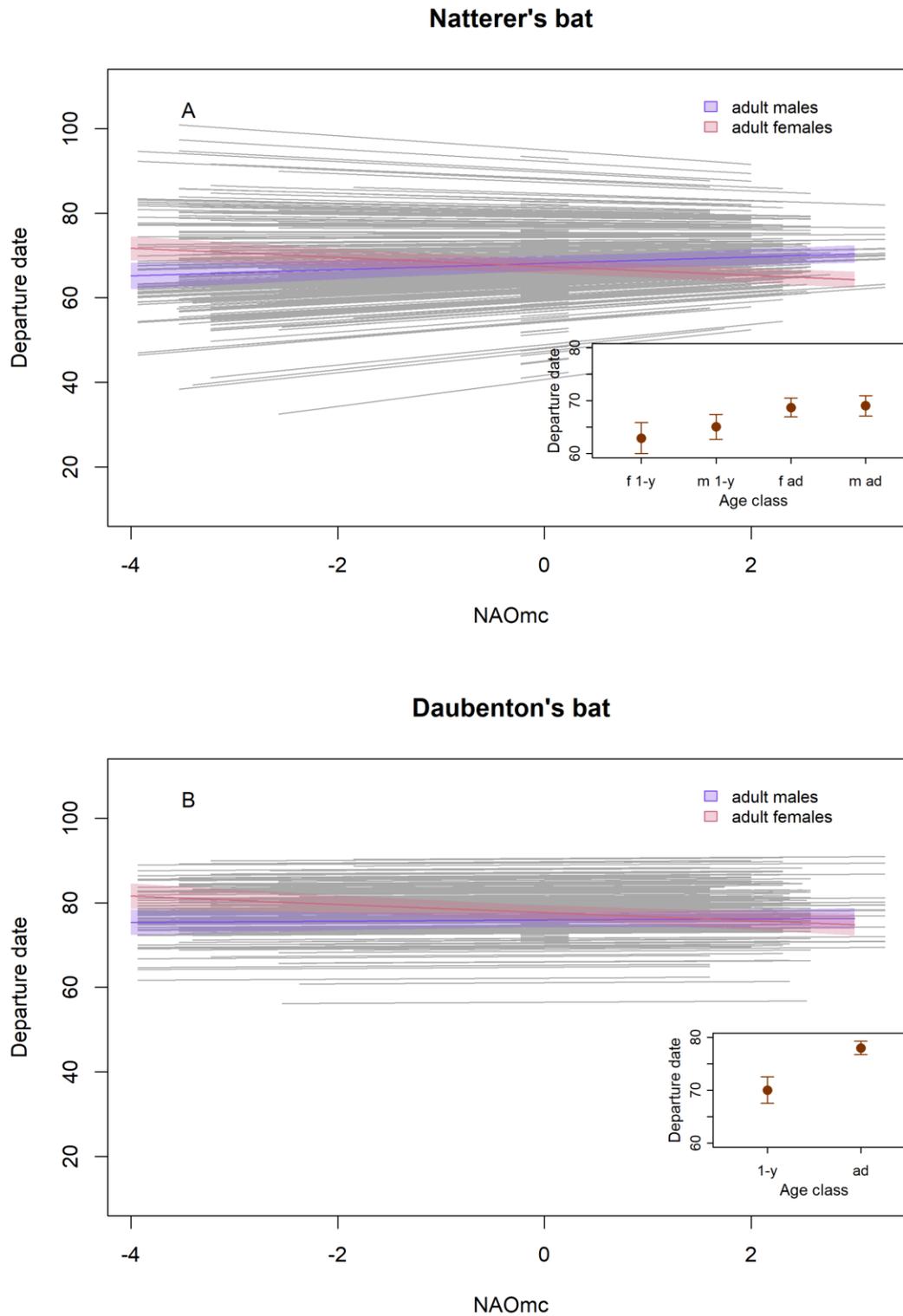
Random effects	K	AIC	dAIC
<b>Random intercept</b>	<b>9</b>	<b>8385.61</b>	<b>0.00</b>
Random intercept and random slope	10	8387.61	2.00
Random intercept, random slope and a correlation between both	11	8389.61	4.00

**Table 11** Model selection to choose the best fitted fixed effect structure based on our selected random structure for Daubenton's bats (*Myotis daubentonii*). In each case the same random effects were entered: individual as random intercept. Model selection was based on the lowest AIC and a difference in AIC (dAIC) of at least 2 was chosen to decide between a model with more parameter compared to a simpler one.

Fixed effects	K	AIC	dAIC
mean NAO (NAOm) + mean-centred NAO (NAOmc) + sex + age class + interaction sex - age class + interaction sex - NAOmc	9	8385.61	0.00
<b>NAOm + NAOmc + sex + age class + interaction sex - NAOmc</b>	<b>8</b>	<b>8387.49</b>	<b>1.88</b>
NAOm + NAOmc + sex + age class + interaction sex - age class	8	8389.81	4.21
sex + age class	5	8390.36	4.76
NAOm + NAOmc + sex + age class	7	8391.67	6.07
NAOmc + age class	5	8392.12	6.51
age class	4	8392.71	7.10
NAOm + NAOmc + age class	6	8394.11	8.50
NAOm + age class	5	8394.69	9.09
sex	4	8423.60	38.00
NAOmc + sex	5	8423.88	38.28
NAOm + sex	5	8425.46	39.86
NAOm + NAOmc + sex	6	8425.74	40.13
NAOmc	4	8426.17	40.57
NAOm	4	8427.85	42.25
NAOm + NAOmc	5	8428.12	42.52

**Table 12** Estimates for the linear species-specific mixed-effects models with departure dates as response (1= January, 1st) for Daubenton's bat (*Myotis daubentonii*, md) and Natterer's bat (*Myotis nattereri*, mn). 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 ( $N_{\text{groups}}$ ) that were included in the model are given. Estimates were obtained by REML. In brackets 95% confidence interval of each estimate is given. For the fixed effects the reference levels (Ref) are mentioned in parentheses. The resulting intra-individual correlation is  $r=8.32/(8.32+13.72)=0.27$  for md and  $r=10.92/(10.92+1.02+11.42)=0.48$  for mn. Furthermore, for mn the proportion of variance explained by the random slope was  $r = 1.02/(10.92+1.02+11.42)=0.004$ .

Fixed effects	Estimate (95% CI)	Additional model information	Estimate (95% CI)
<b>Natterer's bats (Departure date ~ NAOm + NAOmc * sex + age class + sex : age class + (1+NAOmc ID))</b>			
Intercept	67.3 (64.9;69.8)	Random intercept standard deviation	10.9 (9.8;12.2)
Individual mean NAO (Ref=0)	0.9 (0.2;1.7)	Random slope standard deviation	1.0 (0.9;1.2)
Individually mean-centred NAO (Ref=0)	0.7 (0.2;1.3)	Correlation between random slope and intercept	-0.9 (-1.0;0.0)
Sex "female" (Ref="male")	-0.3 (-2.9;2.3)	Residual standard deviation	11.4 (10.8;12.0)
Age class "yearling" (Ref="adult")	-4.0 (-6.5;-1.5)		
Interaction age class – sex "yearling- female"	-1.8 (-5.8;2.2)	$N_{\text{observations}}$	1179
Interaction individually mean-centred NAO – sex "NAO – female"	-1.8 (-2.5;-1.1)	$N_{\text{groups}}$	522
<b>Daubenton's bats (Departure date ~ NAOm + NAOmc * sex + age class + (1 ID))</b>			
Intercept	77.0 (74.5;79.3)	Random intercept standard deviation	8.3 (6.9;10.0)
Individual mean NAO (Ref=0)	0.1 (-0.7;0.9)	Residual standard deviation	13.7 (12.9;14.6)
Individually mean-centred NAO (Ref=0)	0.1 (-0.5;0.8)		
Sex "female" (Ref="male")	1.8 (-0.6;4.2)	$N_{\text{observations}}$	1006
Age status "yearling" (Ref="adult")	-8.0 (-10.6;-5.3)	$N_{\text{groups}}$	475
Interaction individually mean-centred NAO – sex "NAO – female"	-1.1 (-2.0;0.2)		



**Figure 13** Estimated within-individual responses of departure date (1=January 1<sup>st</sup>) to the mean-centred NAO (NAOmc) based on the estimated random intercepts for the species-specific linear mixed-effects models. In the case of Natterer's bats (*Myotis nattereri*) random slopes had to be integrated in the model selected by AIC. 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 effect of age class (1-y – yearling, ad – adult) on departure date, which was consistent with regard to NAOmc. A) Estimated within-individual responses to NAOmc for Natterer's bats. B) Estimated within-individual responses to NAOmc for Daubenton's bats (*Myotis daubentonii*).

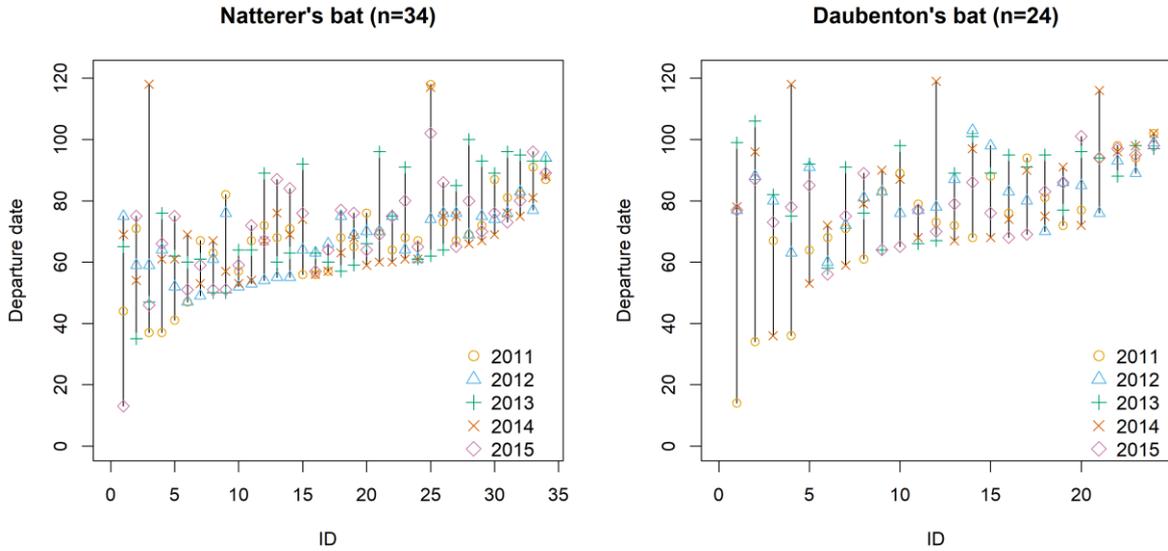
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### 5.2.3. INDIVIDUAL PLASTICITY IN DEPARTURE DATES

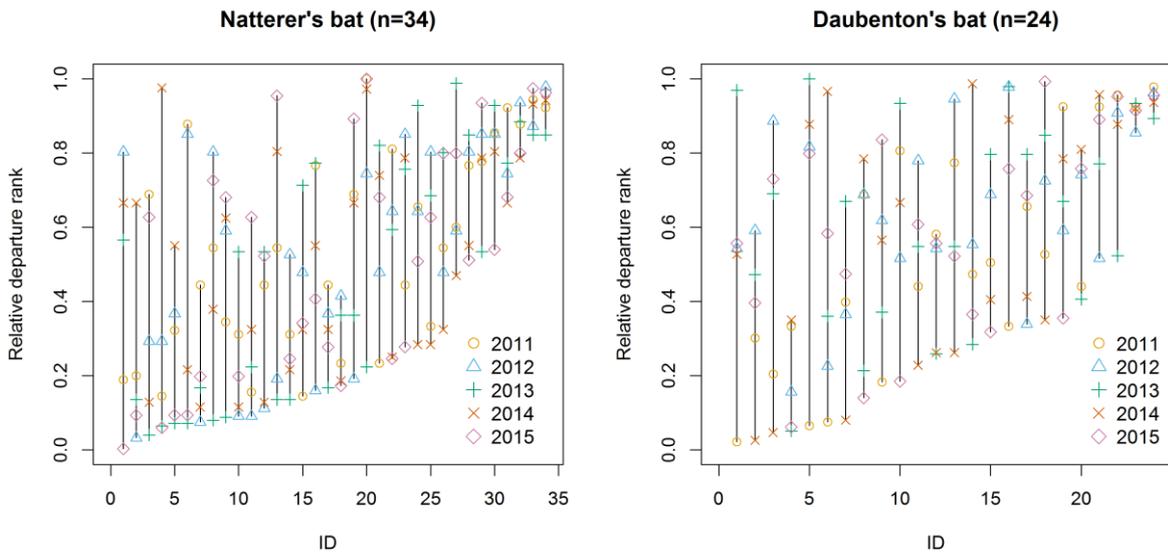
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In both species, individuals differed with respect to departure dates (standard deviation of the random intercept; mn: 10.9 days, md: 8.3 days), and remaining random variation in both species was high (standard deviation residual; mn: 11.4 days, md: 13.7 days). Individual plasticity of departure date with respect to NAOmc (i.e. random slopes) differed only among individuals of Natterer's bats (1.0 day on the population level), with a high negative correlation with the random intercept (Table 12). Thus, individuals that emerged on average later over all study years departed earlier with increasing NAOmc, while those with lower average departure dates departed later with increasing NAOmc (Figure 13). In Daubenton's bats no variation in individual random slopes over NAOmc was supported.

The variation of individual departure behaviour was illustrated further by looking at individuals that were present in all five study years and, thus, experienced the same environmental conditions. Some bats left the hibernaculum each year at very similar dates, while others showed a high plasticity in their departure dates, which differed widely among years (Figure 14). The same pattern was observed when looking at the relative departure rank (Figure 15). Some bats always left the hibernaculum late, while others showed a broader range and switched their relative departure rank. Interestingly, no individuals consistently left early with regard to the definition of early bats in the survival analyses (Figure 14-15).



**Figure 14** Variation between individuals concerning the range covered by departure date over the years for individuals that survived all five years. Each line represents one individual and the year specific departure date is characterized by different symbols for the years. On the left side Natterer's bat (*Myotis nattereri*, n = 34) are shown, on the right side Daubenton's bat (*Myotis daubentonii*, n = 24).



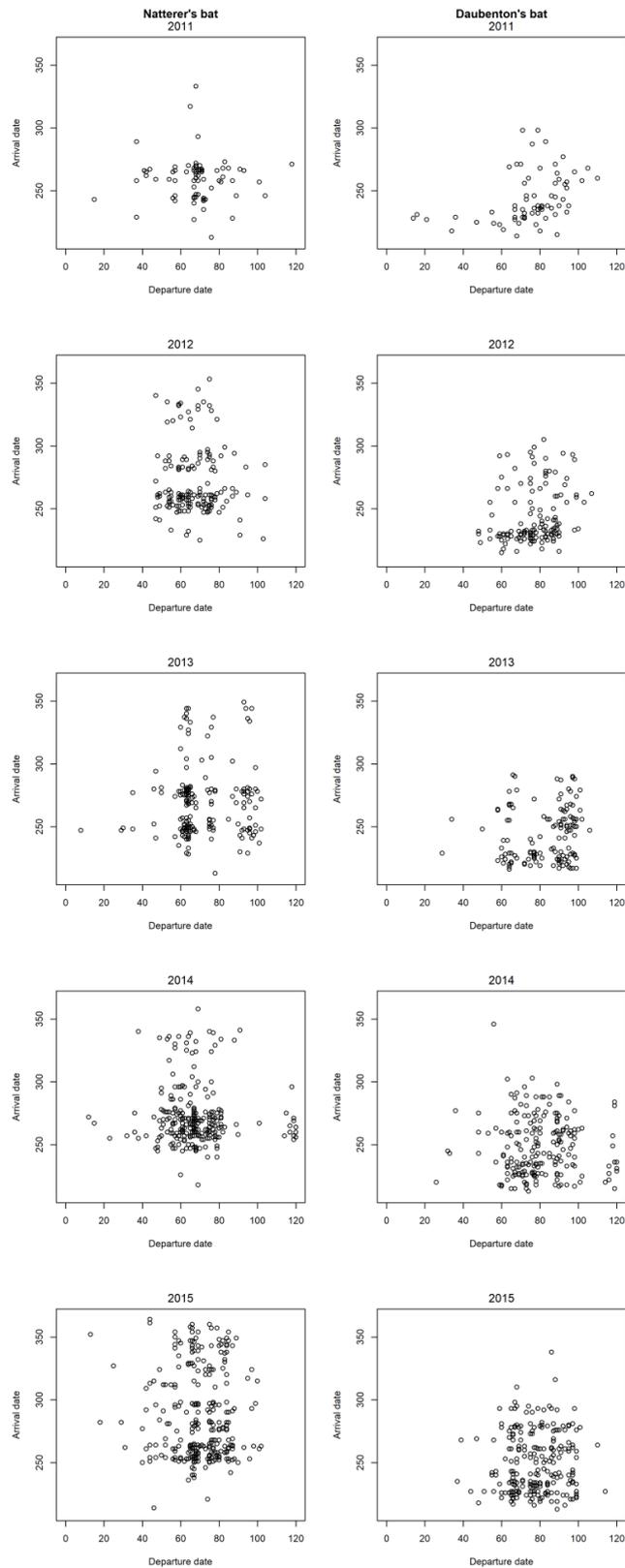
**Figure 15** Variation between individuals concerning the range covered by relative departure positioning over the years for individuals that survived all five years. A relative departure rank of 0 means that the individual left the hibernaculum as the first or at least one of the first bats. A value of 1 indicates that the individuals departed from the hibernaculum as the last or rather together with the last bats present. Each line represents one individual and the year specific relative departure rank is characterized by different symbols for the years. On the left side Natterer's bats (*Myotis nattereri*, n = 34) are shown, on the right side Daubenton's bats (*Myotis daubentonii*, n = 24).

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#### 5.2.4. DEPARTURE DATE AND SURVIVAL IN EARLY BATS

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## Results



**Figure 16** Scatterplot describing the relationship of arrival date related to departure date. Years are plotted separately with departure date on the x axis and arrival date on the y axis. On the left side the plots for Natterer's bat (*Myotis nattereri*) are shown, on the right side plots for Daubenton's bat (*Myotis daubentonii*).

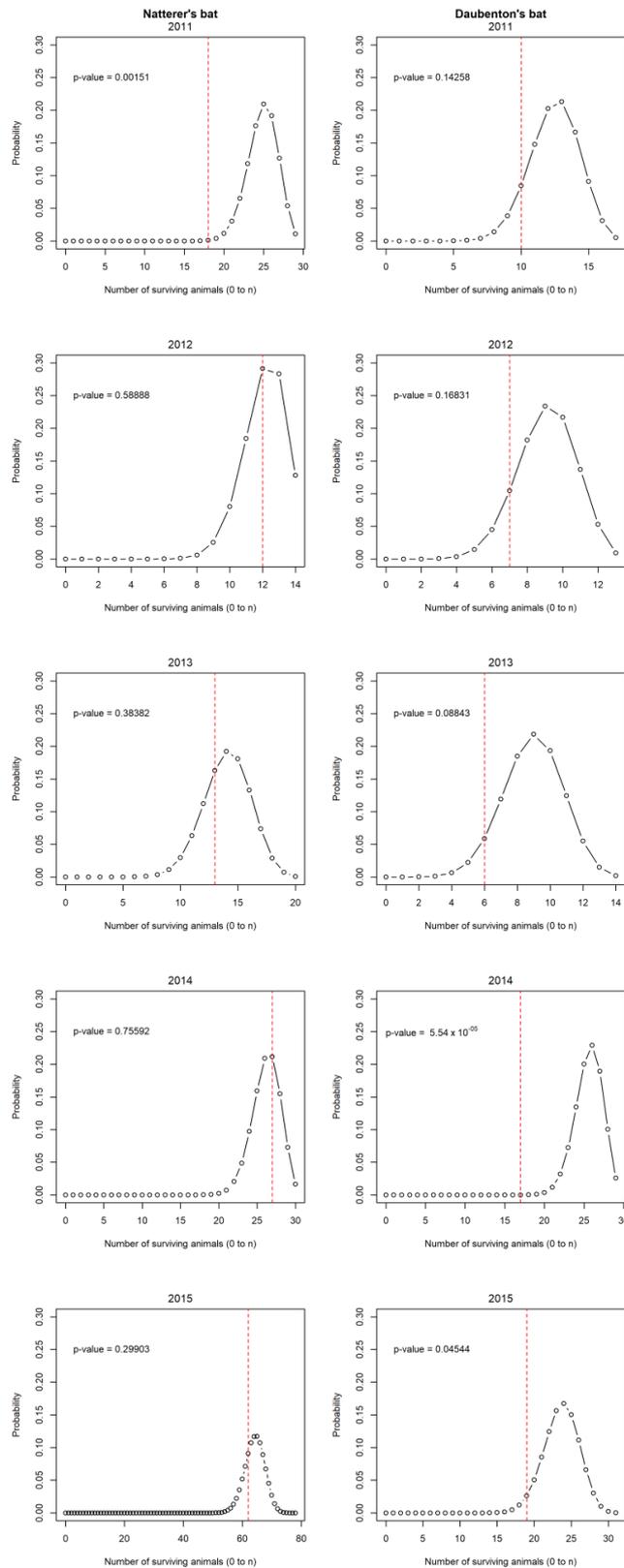
In both species there was no relationship between individual departure date and individual arrival date at the beginning of the subsequent hibernation period (Figure 16). Therefore, surviving individuals that left the hibernaculum earlier in spring had a similar arrival date in the following autumn to those individuals departing later. This resulted in longer exposure times to the environment outside of the hibernaculum and, thus, likely higher energy expenditure for earlier leaving individuals compared to later ones.

Under consideration of this likely higher energy expenditure, the numbers of survivors among the early departing animals were significantly lower than expected over all years (Table 14). This holds for both species, but the effect is stronger in Daubenton's bats. When the analyses were performed for each year separately the low numbers of early departing animals reduced the power of the individual tests.

**Table 13** Results of the survival analysis for both species (Natterer's bats and Daubenton's bats). The columns contain the number of early-departing animals (No. ind), the observed number of survivors (Surv), and the expected number of survivors under the hypothesis that early bats suffer the same risk of death as the rest of the population (Exp. surv), and the resulting p-value. Significant values are given in bold letters, 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	Surv	Exp. surv	p value	No. ind	Surv	Exp. surv	p value
<b>all</b>	<b>171</b>	<b>132</b>	<b>141.3</b>	<b>0.029 *</b>	<b>104</b>	<b>59</b>	<b>79.7</b>	<b>5.13x10<sup>-07</sup> ***</b>
<b>2011</b>	<b>29</b>	<b>18</b>	<b>24.8</b>	<b>0.002 **</b>	17	10	12.5	0.143
2012	14	12	12.1	0.589	13	7	9.1	0.168
<i>2013</i>	20	13	14.0	0.384	<i>14</i>	6	8.9	<i>0.088 ·</i>
<b>2014</b>	30	27	26.2	0.756	<b>29</b>	<b>17</b>	<b>25.6</b>	<b>5.54x10<sup>-05</sup> ***</b>
<b>2015</b>	78	62	64.2	0.299	<b>31</b>	<b>19</b>	<b>23.6</b>	<b>0.045 *</b>

## Results



**Figure 17** Probability distribution of the number of surviving individuals under the assumption that early-departing animals are exposed to the same daily risk of death as the rest of the population (same species (Natterer's bats (*Myotis nattereri*; left), Daubenton's bats (*Myotis daubentonii*; right)), same year) for each year. The p-value is the cumulative probability to the left up to the observed number of survivors, indicated by the vertical red dashed line.

In Daubenton's bats, in the years 2014 and 2015 early departing individuals had a significantly reduced survival, while there was a trend 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 13, Figure 17). In all the remaining years early Natterer's bats did not show lower survival than expected. This result is not likely due to the reduced power, since the number of early Natterer's bats for the specific years is sufficient. It was not possible to control for age class effects in this survival analysis since that would further reduce our sample size and power. However, the distribution of age classes among the early bats was comparable or showed a lower number of yearlings (Table 14).

**Table 14** Distribution of age classes (yearlings and adults) under the early bats (individuals with an earlier or equal departure date compared to  $T_{\text{early}}$ ) separately for each year and species (Natterer's bat (*Myotis nattereri*) and Daubenton's bat (*Myotis daubentonii*)). Yearlings states the number of early bats assigned to yearlings and adults shows the number of early bats characterized as adults.

Species	Year	Yearlings	Adults
Natterer's bat	2011	13	16
	2012	5	9
	2013	4	16
	2014	13	17
	2015	16	62
Daubenton's bat	2011	13	4
	2012	6	7
	2013	2	12
	2014	6	23
	2015	9	22

#### 5.2.5. IMPACT OF LOCAL WEATHER ON SURVIVAL OF THE EARLY BAT

In both species, departure date and median proportion of night hours below 3°C were not correlated (Spearman's rank correlation test; mn:  $\rho = 0.163$ ,  $S = 697220$ ; md:  $\rho = -0.044$ ,  $S = 195890$ ). The species-specific logistic regression models revealed that while in Natterer's bats "departure date" was the only parameter included in the model with the lowest AICc to estimate survival of the early bats, in Daubenton's bats, the model with the lowest AICc included additionally to "departure date" the median proportion of night hours (sunset to sunrise) below 3°C

within five days after individual departure (Tables 15-17). However, the difference in AICc was below two and, thus, also for Daubenton's bats early bat survival was primarily determined by "departure date" (Table 16). Nevertheless, the order of the models hints towards a potential ecological effect with regard to temperatures below 3 °C. Although it was not possible to test the age class effect in the survival analyses directly, focussing on the early bats, age class did not show an impact on survival in both species. In both species, the model including departure date and age class was characterized by the highest AICc and, thus, did perform slightly worse compared to the others (Table 15 and 16). Even though the parameter in the finally selected models to estimate early bat survival was the same in both species, the strength of the impact of departure date differed between species. Natterer's bats showed a higher increase in estimated survival probability with increasing departure date compared to Daubenton's bats (Table 17, Figure 18).

**Table 15** Model selection to choose the best fitted fixed effect structure for estimating survival of early bats in Natterer's bats (*Myotis nattereri*). Model selection was based on the lowest AICc and a difference in AICc (delta AICc (dAICc)) of at least 2 was chosen to select a model with more parameter over a simpler one. The best fitted model is given in bold letters.

<b>Fixed effects</b>	<b>K</b>	<b>AIC</b>	<b>dAIC</b>
<b>Departure date</b>	<b>3</b>	<b>172.82</b>	<b>0.00</b>
Departure date + age class	4	174.89	2.07
Departure date + median proportion night hours $\geq$ 3 °C	4	174.86	2.04

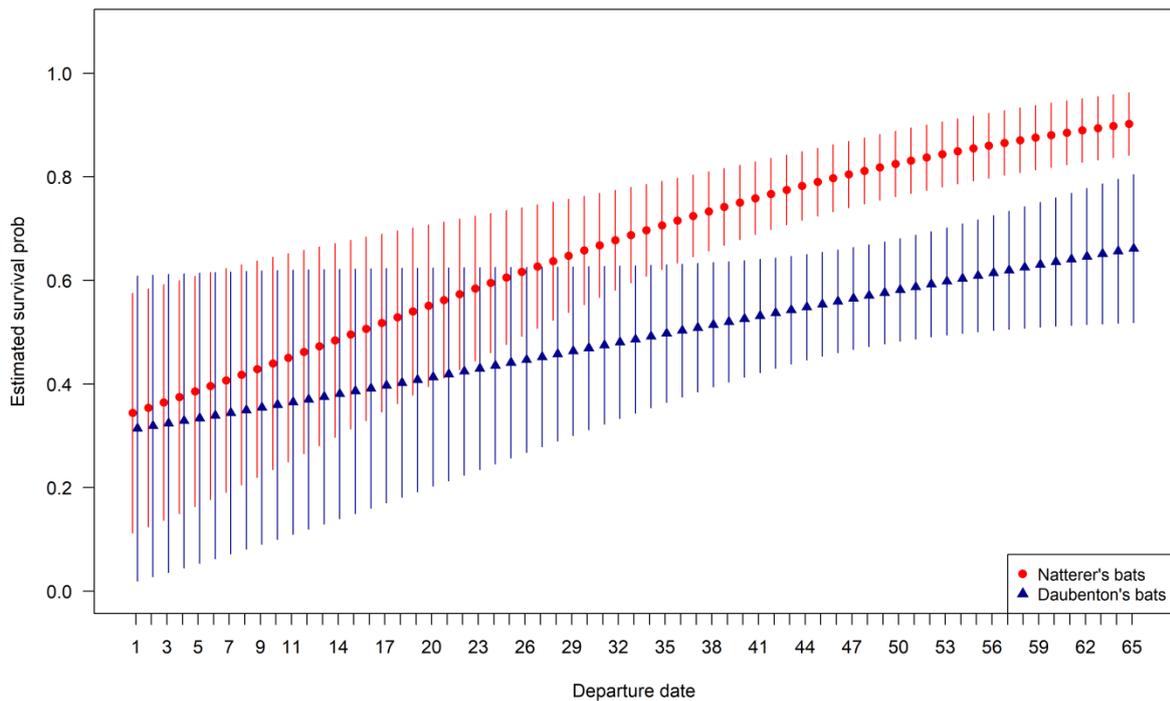
**Table 16** Model selection to choose the best fitted fixed effect structure for estimating survival of early bats in Daubenton's bats (*Myotis daubentonii*). Model selection was based on the lowest AICc and a difference in AICc (delta AICc (dAICc)) of at least 2 was chosen to select a model with more parameter over a simpler one. The best fitted model is given in bold letters.

<b>Fixed effects</b>	<b>K</b>	<b>AICc</b>	<b>dAICc</b>
<b>Departure date</b>	<b>3</b>	<b>143.74</b>	<b>1.94</b>
Departure date + age class	4	145.66	3.86
Departure date + median proportion night hours $\geq$ 3 °C	4	141.80	0.00

**Table 17** Estimates for the mixed-effect logistic regression model with survival as response for Daubenton’s bat (*Myotis daubentonii*, md) and Natterer’s bat (*Myotis nattereri*, mn). The species-specific models were exclusively based on the early bats which left the hibernaculum before the majority of bats (see definition  $T_{early}$ ). The number of observations ( $N_{observations}$ ) that were included in the model are given. Estimates are given in logit scale. In parentheses, we give 95% confidence interval of each estimate. For the fixed effects, the reference levels (Ref) are mentioned in parentheses.

Fixed effects	Estimate (95% CI)		Additional model information	Values	
	mn	md		mn	md
Intercept	-0.69 (-1.75;0.33)	-0.80 (-2.23;0.54)	<b>AICc</b>	172.82	143.74
Departure date (Ref=0)	0.04 (0.02;0.07)	0.02 (-0.00;0.05)	<b>dAICc</b>	0.00	1.94
			<b>Deviance</b>	178.75	139.62
			<b><math>N_{observations}</math></b>	171	104

Selected best model output for Daubenton's bats and Natterer's bats



**Figure 18** Estimated survival probabilities with 95% confidence intervals based on the selected logistic regression models for both species. The results of the best model for Daubenton’s bats (*Myotis daubentonii*, blue triangles) and of the one for Natterer’s bats (*Myotis nattereri*, red points) – in both cases including departure date as fixed effects - are shown. Both models were built exclusively taking early bats (see definition  $T_{early}$ ) into account.

## 6. DISCUSSION

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### 6.1. SPECIES-SPECIFIC SEASONAL SURVIVAL PATTERNS

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#### 6.1.1. INDIVIDUAL CHARACTERISTICS AFFECT SEASONAL SURVIVAL PATTERN

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In line with the hypothesis 1, age class was an important factor influencing survival with juveniles showing a lower survival than adults in both species. This was consistent with results of other studies investigating age class-specific survival in bats (Sendor and Simon 2003, Culina et al. 2017). With regard to the low annual reproductive output, the higher juvenile mortality underlines the importance of adult survival in long-lived species, including bats, for population stability (Gaillard and Yoccoz 2003, Péron et al. 2016, Fleischer et al. 2017). Furthermore, the high difference in survival between age classes highlighted the necessity to distinguish between juvenile and adult survival. Although the different survival pattern between the age classes does not necessarily affect population dynamics, particularly in declining populations, knowledge about which age class is affected by decreased survival can be essential for well-directed conservation management, such as suggested in reef manta ray (*Manta alfredi*) (Smallegange et al. 2016).

Culina and co-authors (2017) suggested differences in fat reserves as a potential reason for the reduced juvenile survival in three bat species. In an experiment, in garden dormice (*Eliomys quercinus*) late-born juveniles were not able to gain the same amount of fat reserves before hibernation as early-born individuals (Stumpfel et al. 2017). In line with this, timing of parturition had an important effect on juvenile survival in little brown bats, with early-born juveniles showing higher survival than the ones born later (Frick et al. 2010). Frick and co-authors also suggested the time to build fat reserves as a potential reason (Frick et al. 2010). In this study, juvenile Daubenton's bats suffered the lowest survival compared to that of adult Daubenton's bats. Since this species is strongly dependent on flying insects above water, time to build fat reserves might be more restricted for juveniles in Daubenton's bats.

Compared to other studies, however, the reduction in survival in juvenile Daubenton's bats at the "Brunnen Meyer" was moderate. Culina and co-authors (2017) demonstrate a juvenile survival probability over winter of about 0.4 in Daubenton's bats (Culina et al. 2017), whereas in this study it was estimated to be

about 0.66. Potential explanations for this high difference in juvenile winter survival in the two studies might be either population-specific effects on juvenile survival or differences in the methods of analyses. Culina and co-authors (2017) analysed winter survival based on summer roosts and this study tested seasonal survival at a hibernaculum. The estimated juvenile winter survival at “Brunnen Meyer” might be higher than that in the study of Culina and co-authors (2017) because only those juveniles that arrive at the hibernaculum were included. Thus, juveniles that left the summer habitat but did not arrive at the hibernaculum were not considered in the resulting estimates in this study. To distinguish between potential methodological or population-specific causes, individual-based long-term data sets picturing the complete annual cycle and, thus, monitoring individual bats over their life time at their summer roosts and hibernaculum are required.

In both species, sexes did not consistently differ in survival. Thus, hypothesis 2 had to be rejected which was in contrast to other studies (Monticelli et al. 2014, Culina et al. 2017). For comparison, Culina and co-authors (2017) reported a generally higher survival of females in Natterer’s bats. Culina and co-authors (2017) suggested that the polygamous mating system was associated with higher costs for male Natterer’s bats due to a higher intensity on sexual selection for males (Culina et al. 2017). If this is the case, it cannot be confirmed in these study populations. Sendor and Simon (2003) also found no difference in seasonal survival between sexes for pipistrelle bats (*Pipistrellus pipistrellus*) (Sendor and Simon 2003).

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#### 6.1.2. DIFFERENCES IN SEASONAL SURVIVAL BETWEEN THE TWO BAT SPECIES ACROSS YEARS

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In line with the similarly high life span in both species (Dietz et al. 2016), no consistent difference in observed survival between Natterer’s bats (range in the different periods: 0.37-0.89) and Daubenton’s bats (0.70-0.93) was found. However, in specific periods, in detail winter 2010/2011 and summer 2012, the two species showed a significant difference in survival. In the winter 2010/2011 both species had lower survival, but only Natterer’s bats experienced a population crash during this winter with a reduction in survival down to only 0.37 compared to 0.75-0.89 in the other periods. Interestingly, in a different study site in southern Germany, Fleischer and co-authors (2017) found that Bechstein’s bats populations also crashed in the winter 2010/2011. Population dynamics in their 19-year data set were driven by this

particular winter and the authors concluded that rare catastrophic events have a major influence on population dynamics (Fleischer et al. 2017). This may also be the case for other bat species as suggested by our results. Nevertheless, Daubenton's bats have been much less impacted by the winter 2010/2011, even though they used the same hibernaculum as the Natterer's bats. Thus, the species-specific pattern is still elusive.

A species-specific sensitivity to the timing of weather conditions, such as assumed in hypothesis 3 might be a potential cause for these differences in the importance of specific periods for survival. The distinctive foraging strategies and activity patterns (Siemers and Schnitzler 2000, Siemers et al. 2001, 2012, Dietz et al. 2016, Culina et al. 2017) may lead to a different effect of weather conditions on species depending on the timing of unfavourable conditions and consequently low arthropod availability. In a comparative study on birds, a positive correlation between survival and the North Atlantic Oscillation index (NAO, Dec-Mar) was found in seven out of ten bird species with strong positive effects in four species (Robinson et al. 2007). The NAO is described as a large-scaled weather parameter for winter severity with negative values indicating cold and dry winters (Hurrell 1995, Post et al. 1997). Interestingly, the winter 2010/2011 with an extraordinary low survival in Natterer's bats was one of the two winters in our study period that had negative NAO values (winter 2010/2011: -1.57; winter 2012/2013: -1.97; data were provided by the Climate Analysis Section, NCAR, Boulder, USA, Hurrell (2003, updated regularly; accessed 19th March 2018)).

Looking at it in more detail, the monthly NAO indicated that in winter 2010/2011 the December was particularly harsh. According to the logger data, a lot of activity at the hibernaculum indicated that Natterer's bats are typically still active at this time of the year. Particularly males try to accumulate their fat reserves very late in Natterer's bats (Kohyt et al. 2016). Since Daubenton's bats start to hibernate much earlier, they should not have been affected by the cold conditions during that month. Even though the NAO value in winter 2012/2013 was lower than in winter 2010/2011, the timing of the harshest conditions differed. Unlike in the winter 2010/2011 in winter 2012/2013, the lowest NAO value was in March, the month when individuals of both species depart from the hibernaculum. Refilling energies consumed during hibernation might not have been possible under those conditions. Thus, individuals emerged from hibernation but may not find the necessary conditions to survive the

subsequent summer. If bats die during that period of emergence, in these analyses, a low survival for the summer 2013 would have been found. This is the case with the lowest estimated summer survival in summer 2013 in adults of both species (mn: 0.78 (se  $\pm$  0.03); md: 0.69 (se  $\pm$  0.01)). In conclusion, adverse weather conditions at different time points might result in species-specific responses, depending on their respective phenology. This is in line with a study by Jan and co-authors (2017), which outlined the importance of weather conditions during crucial but short-termed periods and, thus, fine-scaled temporal resolution for population dynamics (Jan et al. 2017).

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### 6.1.3. STABLE SEASONAL SURVIVAL PATTERN WITH INTER-ANNUAL SHIFTS

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After excluding the extraordinary winter 2010/2011 in Natterer's bats, the data revealed a stable seasonal survival pattern that shifts in its level across years for adult bats in both species, which is in line with hypothesis 4. In birds, small species have often been characterized as winter-regulated populations with a higher mortality during winter than during summer (Newton 1998, Blumstein and Fernández-Juricic 2010). In contrast to this concept of summer- and winter-regulated bird populations (Newton 1998, Blumstein and Fernández-Juricic 2010), winter survival was significantly higher than summer survival in the two bat species despite their equally small size ( $\leq 10$  g). Nevertheless, it is in line with the seasonal survival pattern that has been described for mammalian hibernators (Turbill et al. 2011). The stable seasonal survival pattern with inter-annual level shifts highlighted that under average conditions, the hibernation strategies of both species with regard to activity and foraging pattern reveal high survival probabilities over winter in adults.

However, the difference in seasonal survival in adult Natterer's bats (estimated summer survival: 0.78-0.86; estimated winter survival: 0.91-0.95) was smaller than the respective difference in adult Daubenton's bats (estimated summer survival: 0.69-0.84; estimated winter survival: 0.95-0.98). As a result, adult Daubenton's bats showed an at least slightly lower survival in summer and a higher one in winter compared to adult Natterer's bats in each year, which supported hypothesis 4. Thus, the consistently switching seasonal survival pattern when comparing both species at "Brunnen Meyer" might indicate a differing season-specific sensibility of the two species to unfavourable conditions. The described pattern confirms the expectations based on their different foraging strategies and activity patterns during the

hibernation period. The finding that the population crash of Natterer's bats occurred in a winter (2010/2011) and the lowest survival probabilities in Daubenton's bats occurred during two summers (2012 and 2013) is in line with a difference in the season-specific mortality risk between the two species.

## 6.2. DEPARTURE TIMING FROM HIBERNATION

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### 6.2.1. SPECIES-SPECIFIC DIFFERENCES IN DEPARTURE TIMING

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The optimal timing of emergence from hibernation should be tuned to the availability of their main food resource of the species. Comparing two insectivorous bat species with different foraging strategies, consistent differences in departure timing between species were found. As predicted in hypothesis 5, Daubenton's bats departed on average later from the hibernaculum than Natterer's bats in each year. Since Natterer's bats are gleaners and have the ability to collect arthropods from vegetation or other structures (Siemers and Schnitzler 2000, Siemers et al. 2012, Andreas et al. 2012), their foraging strategy is less constrained by ambient temperatures than in Daubenton's bats. Daubenton's bats are trawlers and are highly dependent on active insects above water.

Additionally, in both species a significant effect of age class on departure timing was given with yearlings emerging on average earlier than adults as expected in hypothesis 10. In Daubenton's bats, individuals experiencing their first hibernation left on average 8.0 days earlier than adults in each year. Several studies demonstrated that in many species yearlings enter hibernation with lower body condition than adults (Kokurewicz 2004, Vuarin et al. 2013). The importance of fat reserves for hibernating species and the influence of reduced time to build those fat reserves in juveniles were for example highlighted in little brown bats (Frick et al. 2010) and garden dormice (Stumpfel et al. 2017). Thus, yearlings may have been forced to emerge earlier to replenish depleted fat reserves, as has been found in juvenile edible dormice (Bieber and Ruf 2004). Because of the automated data collection in this study, which allowed to minimize physical interference with the study animals but did not allow for the collection of individual body mass data, directly analysing the effect of juvenile body condition was not possible.

In Natterer's bats yearlings left the hibernaculum earlier than adults, but there was a slight difference in departure behaviour of yearlings between sexes. While

male yearlings left the hibernaculum on average 4.0 days earlier than adults, female yearlings emerged from hibernation by a difference of 2.1 days even slightly earlier than male yearlings. In bats females can already reproduce during their first year, although the proportion of successfully reproducing females is lower during the first year compared to the following years and has been shown to depend on spring conditions (Linton and Macdonald 2018). Therefore, the earlier departure in female yearlings could be caused by pregnant yearlings either due to higher energy expenditure during hibernation or the necessity to replenish fat reserves early on to allow for foetal growth. However, the difference in average departure date between sexes in yearlings was low and Daubenton's bats did not show sufficient support for such an interaction between age class and sex, although female Daubenton's bats are also able to reproduce in their first year (Linton and Macdonald 2018).

Weather effects on hibernation phenology are still not well understood, but Berková and Zukal (2010) observed for unidentified bats that average temperature and mean barometric pressure were positively correlated with nightly activity during the departure period, whereas previous day rainfall resulted in a decline of nightly activity (Berková and Zukal 2010). The unique setting at the study site allowed a direct comparison of variation in departure from the hibernaculum between two sympatric species and the individual-based results underline evidence for species-specific weather effects on departure timing.

In general, individuals that experienced on average milder winters departed later than those experiencing colder winters (NAOm) in Natterer's bats, while there was not such an impact of NAOm on average departure date in Daubenton's bats. In contrast to Daubenton's bats, Natterer's bats are known to be regularly active and forage during the hibernation period (Hope and Jones 2012). This seems to enable them to track environmental conditions during the hibernation period and fine-tune their departure timing to coincide with favourable ecological conditions. Similarly, Columbian ground squirrels have been shown to delay emergence when snow melt is late and spring temperatures are low (Lane et al. 2012).

Nevertheless, adults of both species showed differences between sexes in the response to the NAOmc. In Natterer's bats males and females respond to changes in winter severity (NAOmc), which is in line with hypothesis 6. In accordance with hypothesis 9 in case of positive NAOmc values, females of Natterer's bats adjusted their emergence more closely to overall weather conditions and left later than males

in colder winters and earlier in warmer winters. The same was the case in Daubenton's bats, which seems to reject hypothesis 7 expecting a lack of clear responses in departure date towards the NAO. While male Natterer's bats showed a contrasting pattern, and departed later in milder winters and earlier in colder winters, male Daubenton's bats did not show a clear adjustment towards winter conditions. In contrast to the pattern estimated in females, male behaviour contradicts our hypothesis 6 in Natterer's bats and supports hypothesis 7 in Daubenton's bats. This variation in emergence date between sexes of both species in response to environmental parameters might be due to changing sex-specific requirements over the years.

For males the necessity to accumulate fat just before start of hibernation might be critical in Natterer's bats (Kohyt et al. 2016). Thus, males in general might have departed from hibernation as late as possible, whereas in cooler winters male Natterer's bats might have had to leave earlier once their fat reserves have been depleted. In contrast, females of both species may have benefitted from early departure in warm winter, as this would have ensured early arrival in the breeding habitat and likely advanced time of parturition. Norquay and Willis (2014) reported an earlier emergence of females in little brown bats compared to males, which they explained with reproductive advantages (earlier birth of offspring and consequently a longer growing season) (Norquay and Willis 2014). Because Norquay and Willis (2014) collected data on only one hibernation period and individual recordings could not be performed continuously during the entire hibernation period, variation between years due to environmental cues could not been investigated in their study.

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#### 6.2.2. BETWEEN-INDIVIDUAL VARIATION IN DEPARTURE TIMING

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For the first time in bats, analysing variation in the average departure among individuals was possible due to the availability of continuous, individualised long-term data. For Natterer's bats, significant between-individual variation in average departure timing (random intercept) and a moderate correlation between repeated observations of individuals over the years (repeatability) were found. Thus, individuals that had emerged earlier than the population average in one year tended to be early also in other years. For comparison, Dammhahn and co-authors (2017) showed that the use of heterothermy, i.e. how deep an individual was in torpor, during hibernation was a repeatable – albeit at a much higher degree than in our

study species - and an individual-specific trait that varied among individual Eastern chipmunks (Dammhahn et al. 2017). Even though repeatability of departure date was lower in Daubenton's bats than in Natterer's bats, between-individual differences in departure timing were supported in them, too. Therefore, the results from both species confirmed hypothesis 8. Due to their specific foraging technique (Flavin et al. 2001, Siemers et al. 2001) the optimal time frame for departure seemed to be later and less weather dependant for Daubenton's bats. The ability of Natterer's bats to find food at lower temperatures (Siemers and Schnitzler 2000, Siemers et al. 2012), might have led to a larger flexibility in activity patterns based on individual traits. This would explain the observed higher variation between individuals. However, a potential heritability of individual departure timing was given in both species indicated by the relatively moderate repeatability similar to the range shown for actual heritability in Columbian ground squirrels (females:  $0.22 \pm 0.05$ , males:  $0.34 \pm 0.14$ ) (Lane et al. 2011). To investigate the actual heritability of departure dates in Natterer's bats and Daubenton's bats further studies are required. Heritability of departure dates could allow microevolution in response to climate change. Therefore, further investigations concerning the genetic basis of responses to recent climate change would be of high importance for conservation.

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### 6.2.3. SPECIES-SPECIFIC INDIVIDUAL PLASTICITY IN DEPARTURE TIMING WITH WEATHER CONDITIONS

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Variation between individuals in the response to changing environmental conditions and, thus, potential differences in plasticity between individuals has been suggested especially in the field of behavioural research lately, but the investigation requires long-term individualised data sets and studies are still rare (Dingemanse et al. 2010, Rodriguez-Prieto et al. 2010, Dingemanse and Wolf 2013). In line with hypotheses 6 and 7, only in Natterer's bats individuals differed in their behavioural plasticity to NAOmc, although variance explained by variation in behavioural plasticity was quite small. Nevertheless, despite both species hibernating at the same site, our results suggest that they differ in individual behavioural plasticity and their response towards the NAO.

This novel finding of differing behavioural plasticity in annual departure time between individuals of two sympatric species was complemented when we descriptively analysed only those individuals that survived all five study years. In

Natterer's as well as Daubenton's bats, some individuals exhibited a relatively low plasticity (narrow range) in their annual departure dates while most individuals were characterized by large plasticity. As all bats contributing to this analysis were present during the complete study period and, thus, are expected to be exposed to the same environmental conditions at the hibernaculum, the observed differences in individual behavioural plasticity are unlikely to be induced by different environmental conditions. This suggests that to a certain degree among-individual plasticity of departure date might be a heritable trait, as shown for emergence date in Columbian ground squirrels (Lane et al. 2012) and indicated in the use of heterothermy in eastern chipmunks (Dammhahn et al. 2017).

Focussing on the few individual bats with a narrow departure range, all of them departed from hibernation relatively late and no individual consistently departed early with regard to the definition of an 'early' bat. This supports hypothesis 12 indicating towards an additional cost of leaving early that would result in lower survival probabilities of an individual being 'early' as a strategy in at least some years. Hence a 'low plasticity' strategy of always leaving 'early' should have been counter-selected in long-lived bats.

These results suggest that the potential to behaviourally respond to environmental change differs between individuals (Dingemanse and Wolf 2013) and species.

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#### 6.2.4. MORTALITY COSTS OF EARLY DEPARTURE

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The method employed in this study to disentangle potential exposure and ecological effects in 'early' bat survival represents an analytical solution to the problem that the exact time and cause of death of the study animals was unknown. In field studies of highly mobile and/or elusive species, a lack of knowledge about the exact time of death and the reasons behind it is a regularly encountered problem. In those cases, the described methodological approach should be useful for investigating mortality costs of behaviour in free-ranging animal populations.

In the two study species, over all five analysed years, departing from the hibernaculum 'early' was associated to mortality costs likely due to an ecological risk effect in both species, as expected in hypothesis 12. In more detail, in Natterer's bats, 'early' departing individuals had a significantly lower number of survivors exclusively in 2011. The remaining years did not show a lower survival of 'early' bats

than expected. In contrast, ‘early’ departing Daubenton’s bats fared worse in most years, particularly in the years 2014 and 2015. An opposite effect has been observed in yellow-bellied marmots, with individuals entering hibernation with large body mass emerging early and surviving better (Ozgul et al. 2010).

Identifying potential weather parameters characterising unfavourable conditions related to survival was one crucial step to potentially understand possible ecological effects on ‘early’ departure. A promising candidate is low temperature and consequently low arthropod availability in late winter and early spring. Zahn and co-authors described a lack of foraging activities during winter at temperatures below 3°C in various bat species (Zahn and Kriner 2016). Therefore, low temperatures, particularly below 3 °C, would make it more difficult for the early departing bats to find food and fill-up depleted energy reserves. Especially since a study based on activity data at a hibernaculum in Wisconsin revealed that little brown bats generally emerge before insect abundance peaks (Meyer et al. 2016). Thus, ‘early’ bats might experience a particularly big challenge to find food immediately or shortly after departure, specifically in Daubenton’s bats. The assumption is that the few Daubenton’s bats that left the hibernaculum ‘early’, did so as a ‘best of a bad job’, because depleted fat reserves prevented them from hibernating longer. In contrast, Natterer’s bats are able to also hunt during milder winters (Siemers and Schnitzler 2000, Siemers et al. 2012) and, therefore, might have been able to compensate those early departures more often. In line with this, Culina and co-authors (2017) estimated based on capture-mark-recapture models with ringed bats that hibernation survival in Daubenton’s bats is positively associated with average breeding-season temperature, although the variation in survival between years was described as not substantial. In Natterer’s bats none of the tested weather variables influenced survival (Culina et al. 2017).

However, the results of my study showed that departure date itself already is a good estimator for survival probability in Natterer’s and Daubenton’s bats, as expected due to an “exposure effect”. Especially in Natterer’s bats there was no hint for an effect of the proportion of night hours above 3°C within five days after departure on survival of ‘early’ bats. In comparison, in Daubenton’s bats the model with the lowest AICc contained departure date and on top of that the median proportion of night hours above 3°C. Although the difference in AICc was not high enough to support this relationship, it might be a hint for an environmental climatic

impact on 'early' bat survival in Daubenton's bats. This would fit to the different foraging strategies of the two species. Especially since the strong dependency of Daubenton's bats on flying insects, the absence of winter foraging in this species (Kokurewicz 2004) and the found low survival probabilities in 'early' bats suggest that climatic conditions outside of the hibernaculum should have an impact on the ability of 'early' Daubenton's bats to hunt for food. Nevertheless, the results do not clearly support that reasoning so far and, thus, were not in line with hypothesis 13 for Daubenton's bats, but confirmed the expectation of no strong environmental impact on early bat survival for Natterer's bats.

### 6.3. CONCLUSIONS

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With exception of the extraordinary winter 2010/2011 in Natterer's bats, our data revealed a stable seasonal difference in adult survival which varied in its level across years in both species. The stable pattern and, particularly, the high winter survival highlighted the role of hibernation as an adaptation to seasonality and a mechanism to cope with unfavourable conditions in bats. Nevertheless, our data emphasize the importance of specific periods as potential driver for population dynamics and suggest that at least in bats responses to global climate change might be species-, population- and even age class-specific.

Optimal timing of hibernation has been discussed to be an interplay of a circannual clock and environmental cues (Hut et al. 2014, Czenze and Willis 2015), whereas the contribution of the two influences can differ between species. Especially, since environmental conditions that are advantageous for one species, population or age class might be detrimental to others. The indicated differing season-specific sensibility of the two species to the timing of adverse weather events might play an important role for understanding consequences of changing climatic conditions. Thus, this aspect needs to be further investigated in future studies in order to better understand population responses to global climate change. Clearly, this will also be a prerequisite for conservation.

Studying the phenology and the mortality consequences of departure timing in two species of bats, the results revealed that departure date varied within individuals, among individuals, and between species, with Natterer's bats emerging earlier. Individuals of Natterer's bats also had higher within-individual plasticity of departure timing towards the NAO, and early emerging individuals suffered less mortality costs,

except for the year 2011, than Daubenton's bats. This can lead to the prediction that Natterer's bats will be better able to adapt their departure date to different environmental conditions matching food abundance peaks or gaining reproductive advantages and, therefore, will be better able to cope with recent climate change through behavioural plasticity. However, the population crash in Natterer's bats during the winter 2010/2011 might also be a first indication of limits in adaptation to unfavourable conditions.

So far, potential costs of phenotypic plasticity in general are rarely investigated compared to potential benefits and seem to be difficult to demonstrate (DeWitt et al. 1998). Potential costs can be, for example, the collection of information to assess the environmental state and maintenance costs (DeWitt 1998, DeWitt et al. 1998). By identifying mortality costs of early departure, this study did a first step towards assessing limitations in adaptation of a behaviourally plastic trait with a potential for heritability. Although the exact identification of an ecological effect of mortality in early departing bats was not successful, further studies investigating fine-scale local conditions are recommendable. Additionally, comparing survival in plastic individuals versus non-plastic individuals within populations will be a crucial step for assessing consequences of responses through behavioural plasticity to recent climate change.

Finally, the combination of the results presented here and those of other studies strongly suggest that species differ in their capacity to buffer the negative effects of environmental variation. This has severe consequences in the face of global climate change, which is expected to result in warmer and more variable temperatures during the hibernation period.

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## 8. LIST OF ABBREVIATIONS

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>	larger than
<	smaller than
·	trend (significance level smaller than 0.1)
*	significance level smaller than 0.05
**	significance level smaller than 0.01
***	significance level smaller than 0.001
°C	degrees Celsius
AIC	Akaike information criterion
AICc	Akaike information criterion corrected for small sample sizes
e.g.	for example
h	hours
H <sub>t</sub>	current hibernation period
H <sub>t+1</sub>	subsequent hibernation period
km	kilometres
mn	Natterer's bats ( <i>M. nattereri</i> )
<i>M. nattereri</i>	<i>Myotis nattereri</i>
md	Daubenton's bats ( <i>M. Daubentonii</i> )
<i>M. daubentonii</i>	<i>Myotis daubentonii</i>
NAO	North Atlantic Oscillation index
NAOm	mean of the NAO experienced by each individual separately
NAOmc	mean-centered NAO (following a procedure highlighted by Van de Pol and Wright (2009))
T <sub>arr</sub>	year and species specific date when the first animal was recorded back at the hibernaculum between August and December; start of the actual arrival period
T <sub>early</sub>	year and species specific threshold to identify early bats (individuals with an earlier or equal departure date compared to T <sub>early</sub> )
vs.	versus

## 9. TABLE OF FIGURES

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