Macro-evolutionary trade-offs as the basis for the distribution of European bats

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Abstract

Bats have a high species diversity and show unique ecological traits. The distribution patterns of European bat species differ between species. In this paper we seek to explain which life history traits, or interrelations between traits, can best explain observed differences in the distribution patterns of bats. Traits are interrelated and sometimes involve trade-offs, implying that a change in one trait may have positive or negative consequences for other traits. We describe the main morphological, physiological and ecological adaptations of insectivorous European bat species. We make pair-wise relations between traits, indicating the interrelations between traits, in terms of possible trade-offs. We relate the consequences of these trade-offs to the distribution maps of the species, focusing on the traits relevant for southern and northern distribution limits. We found coarse patterns that might indicate the distribution of related species are a consequence of their physiological, morphological and ecological adaptations and the interrelations between these adaptations. Hence, we think life-history strategies can be used to explain differences in species distribution. The method presented in this paper might also be useful for other mammal groups with a high species diversity, such as Rodentia and Soricidae.

Keywords

Geographic range; habitat adaptations; hibernation strategy; morphological adaptations; reproductive tactics

Introduction

Geographical ranges of species continually shift (Brown et al., 1996). These changes are the result of two contrasting processes: establishment and local extinctions (e.g., Pearman et al., 2008). In addition, each species’ distribution is also

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affected by interactions with competing species, social organisation and their habitat requirements (Guo et al., 2012; Laiolo, 2013). The distribution limits of mammal species across Europe are well established (Mitchell-Jones et al., 1999). However, the underlying causes that limit the spread and occurrence of species remain poorly understood. The habitat template theory of Southwood (1988) posits that environmental conditions are matched by the biological traits of species. Each individual or species is specialised to minimise its energy costs. Although species are often specialised for a specific type of habitat, this theory is not always able to explain the northern and southern distribution limits of species distribution (e.g., Letcher et al., 1994; Pereswiet-Soltan, 2007). Other studies have linked the distribution limits with life history traits (e.g., Fenton & Bogdanowicz, 2002; Kaliontzopoulou et al., 2012). However, it is difficult to explain the distribution limits of a species by studying only a small number of life history traits. Living organisms have sets of co-adapted traits, termed tactics or strategies (Stearns, 1992), that help them face the ecological challenges they encounter. Some studies, e.g., Siepel, 1994 or Verberk et al., 2008, stress the importance of taking the interrelations between these co-adapted traits into account when linking distribution with life history traits.

Interrelations between traits, or trade-offs, predict that a change in one trait may have a negative or positive consequence for a second trait. For example, the common pipistrelle bat (*Pipistrellus pipistrellus*) cannot store large quantities of fat, because this will limit its agility or even ability to fly (Barclay & Harder, 2003). Hence, this bat species needs other traits (e.g., torpor) to survive a long period without food. Not all species are affected by the same constraints and are, therefore, able to adapt to ecological limitations in different ways (tactics; e.g., Southwood, 1988; Rochet, 2000). A tactic is, therefore, always context-dependent, related to both environmental conditions and physiological limitations. Some tactical responses exhibit plasticity (Nylin & Gotthard, 1998; Sæther & Bakke, 2000), for example the number of offspring, age of sexual maturity and duration of sexual reproduction. Tactics can vary within populations, or across age groups and distribution range (e.g., Sollick & Barclay, 2007). The plasticity of a tactic is limited either by the ability of a genotype to vary its response to the environment or by environmental conditions themselves.

Here we examine the relationship between life history traits and geographic distributions using European bats as a study group. Bats are a highly diverse group, with traits such as active flight, ability to enter torpor, relative high longevity (in comparison with other mammals of the same size) and slow reproduction rate. With approximately 18 recognised families, encompassing 202 genera and 1116 species worldwide (Simmons, 2005), bats constitute more than 20% of living mammal species. These numbers are only surpassed by the order Rodentia. Just three bat families have colonised the higher latitudes (above 38° north) of northern Europe: the Vespertilionidae (30 species), the Rhinolophidae (5 species) and the Miniopterae (1 species, in: Miller-Butterworth et al., 2007). A representative of a fourth family (the Molossidae), *Tadarida teniotis*, occurs in the southern parts of both Eu-
rope and Asia. We hypothesised that: 1) the life history traits of bats living in high latitudes differ from those of bats living in lower latitudes; 2) some set of traits, especially morphological traits and traits related to reproduction and physiology, are co-adapted; 3) these sets of co-adapted traits can be linked to distribution of species. In this paper we seek to explain which life history traits, or interrelations between traits, can best explain observed differences in the distribution patterns of bats. We use pair-wise relations to demonstrate interrelations between traits and show their consequences of these trade-offs for the distribution.

**Life history traits of European (north temperate zone) bats**

*Data compilation*

We have compiled a dataset of life history traits and distribution characteristics of 30 European bat species, based on a literature study of a total of 56 primary and secondary sources. In order to have reliable data on species ecology, only those species that have been recognised as a species for more than 15 years were taken into account (supplementary table S1). All European bats are predominantly insectivorous. Supplementary table S2 gives a complete description of the studied traits. These life history traits are grouped into morphological, physiological and ecological adaptations. Values for each trait are described, with one average value covering the entire population (supplementary table S3). In some cases values consist of aggregate measurements from different individual bats and from various sources. For some species, we could not find citations of values of one or several traits. We did not do complementary research, therefore, missing values were left blank. We used seven parameters to describe the distribution of the 30 bat species, these include the northern, western and eastern limit of range. The latitude is an important factor contributing to the seasons. Further from the equator the hours of darkness each day (i.e., hunting hours for bats) become less.

**Macro-evolutionary trade-offs among European bat species**

In this section, traits are compared in a pair-wise fashion. Statistical analysis were carried out using SPSS V17. Regression analyses was used to test the relation between ordinal dependent variables with a normal distribution. Generalized Linear Models with Poisson distribution (identity link function) were used for non-normal distributed variables. Missing values were excluded from analyses. We grouped the selected bat species with a northern distribution (above 55° latitude) and southern species (below 54° latitude). 55° latitude coincides with 7 hours of darkness during midsummer (21st June).

*The trade-off between the number of young and the weight of a litter*

The mass of a near-term litter influences the ability of a female to fly and forage (Racey & Entwistle, 2000). The extra load increases the flight cost, reduces agility
and manoeuvrability (Speakman & Racey, 1987) and may, therefore, impair the female’s foraging efficiency. Paradoxically, this constraint does not result in bats producing lighter litters than similar-sized terrestrial mammals (Barclay & Harder, 2003). Terrestrial mammals produce litters of many small young, with an overall mass that averages 25% that of the female (Carranza, 1996; Stockley & MacDonald, 1998). With a similar female to litter mass ratio, bats produce small litters of large young. Larger offspring exhibit a more developed neuromuscular and skeletal system than smaller ones (Kunz & Hood, 2000). Bats also raise their young to a larger mean relative size than terrestrial mammals (Kunz & Kurta, 1987; Hayssen & Kunz, 1996). Each of these longer development periods is needed because, in order to avoid damage, a young bat’s skeleton must be almost fully ossified by the time it first flies. The forearm length of fledgling bats is >90% of that of the adult (Kunz, 1987; Barclay, 1994; Kunz & Stern, 1995; Reiter, 2004). Birds face similar constraints, they fledge only when they approach or attain adult size (Ricklefs, 1973; Hedenström et al., 2009).

The 30 selected European bats show a geographic variation in average litter size (fig. 1). Bats can give birth to maximum 3 young per litter (Baagøe, 2004). The average litter size varies between 1 and 1.9 pups. Species living in higher latitudes tend to have larger average litters than the southern species (respectively an average litter size of 1.4 versus 1.2). Earlier studies found a similar relationship between average litter size and distribution (Lord, 1960; Gaisler, 1979; Jones et al., 2003; Barclay et al., 2004). Some species show flexibility in the number of young they produce per litter; in these species, individuals living in northern regions produce twins more often than individuals living in the southern regions (e.g., Ryberg, 1947; Tuttle & Stevenson, 1982; Gaisler et al., 1997; Krapp, 2011). For species at both

![Figure 1. Relation between average litter size and the most northerly distribution limit of the reproductive population for several European bat species. The marker shapes indicate the northern boundary of the species reproductive range: below 54° latitude (diamond markers) and above 55° (triangular markers). See table S1 for species abbreviations.](image)
the northern and the southern ends of their distribution range we found a pattern that might indicate a trade-off between the average relative weight of a single offspring and the average litter size (Wald $\chi^2 = 27.730$, $P < 0.0001$; abbreviations of excluded species: Mcap, Rmeh, Tien, Mem, Mbec, Bbar, Nlei; see also table S2). The relative weight of European neonates varies from between 15.3% and 37.7% of the body weight of the female (fig. 2). Species with relatively heavy neonates include *Myotis nattereri*, *M. mystacinus* and *Rhinolophus euryale*, usually give birth to single offspring (i.e., have a low average litter size). *Eptesicus nilssonii* also gives birth to heavy neonates, but does not reproduce each year and can, therefore, make a larger investment during reproductive years (Rydell, 1990). Twins are common among *Nyctalus noctula*, *P. nathusii*, *P. pipistrellus* and *Vespertilio murinus*, species in which the individual young have a relatively low body weight compared to the mother. In species which produce either one or two offspring, the twins are, on average, lighter than single offspring (Hayssen et al., 1993; Kunz & Hood, 2000; Krapp, 2011). We found a similar relation as in fig. 2 between the relative size of the neonate (i.e., forearm length) and the average litter size. As size of the neonate is related to weight, this relation is not shown.

The trade-off between number of weaning weeks and relative weight of litters

The time needed to rear a litter seems to depend on the body mass of the adult (fig. 3, Wald $\chi^2 = 4.566$, $P = 0.033$; all 30 species included). This suggest that larger bodied species need disproportional more time to wean their young than smaller species, such as *M. brandtii*, *M. capaccinii* and *E. nilssonii*. Probably the increased time to rear large offspring prevents the larger bodied species to produce large litters.
The maternal investment is the total energy that females transfer into their offspring during the gestation period (prenatal costs), the lactation period and postnatal care period (postnatal costs). All offspring must be independent by autumn, when food supplies start to become scarce. Females are able to optimise the growth speed of their offspring, in both the prenatal and the postnatal periods (e.g., Altringham, 1996). Although gestation may have a negative effect on foraging efficiency, the production of milk is generally considered to be the most energetically costly aspect of reproduction for a female bat (e.g., Speakman & Racey, 1987; Kurta et al., 1989; Speakman, 2008). Additional costs during the lactation period involve grooming the young, thermoregulatory behaviour and moving offspring between or within the roost(s) (Studier & O’Farrell, 1980; McLean & Speakman, 1997). Smaller pups are more susceptible to low temperatures (and need more attention in terms of thermoregulatory heating) than larger ones (Reiter, 2004).

We could not find enough data for all selected bat species to combine into two variables describing true prenatal and postnatal investment cost. Instead, we used relative weight of litters and number of weaning weeks as rough indication for, respectively, prenatal and postnatal cost. We found a negative correlation between the number of weaning weeks and the relative weight of litters that might indicate a trade-off between these traits (fig. 4, $R^2 = -0.267$, $P = 0.012$; abbreviations of excluded species: Nlei, Mcap, Mbec, Tfen, Mema, Bbar, Rmeh; see also table S2). An earlier study of Barclay & Harder (2003) found similar correlations between several traits associated with the energetic investment of bats (both tem-
Figure 4. The relation between the number of weaning weeks and relative weight of litters \( (R^2 = -0.267, P = 0.012) \). The marker shapes indicate the northern boundary of the species’ reproductive range: below 54° latitude (diamond markers) and above 55° (triangular markers). The difference between the two encircled groups is significant (paired samples \( T \)-test, both groups \( N = 15, t = -1.606, P = 0.004 \)). See table S1 for species abbreviations.

... perate and tropical) in their young. Species with a more northerly distribution, such as \( E. nilssonii \), \( M. myotis \), \( M. nattereri \), \( P. nathusii \) and \( M. daubentonii \) are likely to have a higher relative weight of litter to mother (above 55° latitude: average 36.5%, below 54° latitude: 29.9%), whereas species living in warmer regions, such as \( Miniopterus schreibersii \), \( N. lasiopterus \), \( R. ferrumequinum \) and \( V. murinus \) tend to spend more days weaning their young (above 55° latitude: average 34.6 days, below 54° latitude: 29.3 days). The difference between these two groups is significant (paired samples \( t \)-test, both groups \( N = 15, t = -1.606, P = 0.004 \)).

Trade-offs between reproduction, maturity and longevity

The goal of reproduction can be seen as maximising an individual’s genetic contribution to the next generation and this is best done by maximising lifetime reproductive output (e.g., Stearns, 1992). This contribution can vary due to a set of interrelated characteristics, such as timing and frequency of reproduction, age of sexual maturity and life span (Barclay & Harder, 2003). Each individual strives to contribute to the future generation, but reproduction has its costs: the energy and nutrient demands of reproducing are large. Furthermore, morphological changes are needed to better meet these demands (e.g., Cockburn, 1989; Lidgard et al., 2012). In each maternity roost only between 50-90% of females participate in reproduction, because some females need a recovery year after successful reproduction (Ransome, 1995; Barclay et al., 2004). Bats do not reproduce when their physical condition is low (Kunz & Stern, 1995). Bats are long-lived animals and postponing reproduction may have a positive effect on reproduction success over
their lifetime. We, therefore, assume a trade-off between longevity and reproduction rate.

The age of sexual maturation forms another possible trade-off with reproduction (Kunz & Hood, 2000; Jones & MacLarnon, 2001; Wilkinson & South, 2002; Barclay & Harder, 2003; Speakman, 2008). Researchers have found that females that breed later in life have higher survival rates than females that breed earlier (e.g., *R. ferrumequinum*, in: Ransome, 1995; *N. noctula*, in: Gaisler et al., 1997; *Plecotus auritus*, in: Speakman & Racey, 1986; Entwistle et al., 1998). Ransome (1995) found that although early breeding seemed to decrease lifespan, it had no effect on lifetime reproductive success. In accordance with the results of Ransome (1995) fig. 5 shows a pattern indicating a trade-off that can be seen between average litter size and the observed average age for 20 of the 30 European bat species (Wald $\chi^2 = 177.4$, $P < 0.0001$. Abbreviations of excluded species: *Mnat, Nlei, Vmur, Enil, Mcap, Mbec, Paus, Tien, Nlas, Hsav*; see also table S2).

The coarse pattern between observed average age and average litter size might be linked to distribution. In general, species with a southern distribution range are less likely to produce large litters. Furthermore, they achieve sexual maturity relatively late (i.e., in their second summer or later; on average 433 days, northern species reproduce on average after 350) and tend to have a higher observed average age (average 3.8 years, northern species have an average age of 3.9 years). Among the northern species *P. pipistrellus, P. nathusii* and *N. noctula* have the largest average litter size in combination with a low observed average age. Individuals of these three species are often found sexual mature before or during their first winter (at approximately 80 days old).
The trade-off between reproduction, migration and choice of hibernacula

From fertilisation in spring to weaning at the end of the summer, females devote a large proportion of their time and energy to their offspring (Neuweiler, 2000). Only after their offspring are fully weaned, can mothers prepare themselves for the oncoming winter, which includes accumulating a fat reserve and migrating to a hibernaculum (Hedenström, 2009). Foraging efficiency during migration is limited, bats are known to loose up to 25% of their fat during migration (Fleming & Eby, 2003). The greater the distance between the summer and winter roosts, the more energy is required for migration (Hedenström, 2009). Female bats and their offspring have a limited time to accumulate fat reserves and to migrate towards a hibernaculum. It may take two to three weeks to accumulate a fat reserve (e.g., Speakman & Rowland, 1999; Krapp, 2011) and it may take an equal period of time to reach a hibernaculum (e.g., Schmidt, 1989). The energy cost of migration (both time and distance) can, therefore, be indirectly considered as a trade-off with reproduction (in time and the amount of energy used). This assumption is supported by earlier researchers (Racey & Entwistle, 2000; Hedenström, 2009). We assume that this trade-off is more severe in northern latitudes, because of the more extreme conditions during a northern winter and the shorter summer season.

The trade-off between reproduction and migration distance is influenced by the need, and the ability, to migrate. Each bat species has characteristic thermal preferences during hibernation, ranging from very cold (below 0°C) to relatively warm (12°C) although this can vary greatly within a single species due to individual preferences (e.g., Webb et al., 1996; Speakman & Thomas, 2003; Siivonen & Wermundsen, 2008). Bats observed during hibernation are expected to survive the winter. The minimum temperature at which each species is observed, can be interpreted as the minimum temperature from which that species, although not necessarily all individuals, can revive. This minimum temperature is significantly linked to the distribution limits of a species ($R^2 = -0.569$, $P < 0.0001$, fig. 6; abbreviations of excluded species: Rmeh and Hsav). All species with a northern distribution (i.e., a northern reproductive range) are able to revive from temperatures of below zero degrees (above 55° latitude: average 3.3°, below 54° latitude: −4.9°). Of the species with a southern distribution only P. austriacus and P. kuhlii have been observed at such low temperatures. Species with deep hibernation abilities should have, at least in theory, less need to migrate.

Specialised adaptations in wing design and echolocation are among the morphological specialisations that have emerged among bat species to help them locate and grasp their prey (Findley et al., 1972; Norberg & Rayner, 1987). Species with a low aspect ratio, low wing loading and a echolocation type with a limited range such as R. hipposideros and P. auritus, have a limited migration abilities (Findley et al., 1972; Fleming & Eby, 2003; see also fig. 7; abbreviations of excluded species: Rmeh and Hsav). The distribution of species with limited migration abilities is, therefore, limited by the availability of suitable hibernacula, within the preferred temperature range of the species. They can be contrasted with species with stronger
Figure 6. The minimum temperature at which each species is observed hibernating within their reproductive range ($R^2 = -0.569$, $P < 0.0001$). The shape of the markers indicates the northernmost point at which each species has been found reproducing: below 54° latitude (triangular markers) and above 55° (diamond markers). See table S1 for species abbreviations.

migration abilities and the ability to hibernate in a wide range of winter roosts, such as *N. noctula* and *P. nathusii* (Muslin & Vischer, 1942; Nagel & Nagel, 1991). Such non-obligatory migratory species can, in the southern range of their distribution, choose not to migrate and as a consequence are able to spend more energy on reproduction.

Figure 7. The relation between wing aspect ratio and wing load. The shape of the markers indicates the main component of the echolocation type used by each bat species: CF (circular markers), FM (square markers), and QCF (cross markers). The font style indicates the northern boundary of each species' reproductive range (roman below 54° latitude and underlined above 55°). See table S1 for species abbreviations.
We found a coarse pattern between reproduction (expressed as weaning days) and migration that might indicate a trade-off between these two traits (fig. 8, abbreviations of excluded species: Hsav). The interaction between migration distance and migration need and ability was not taken into account. In southern species the trade-off between reproduction and migration is not significant ($R^2 = 0.207, P = 0.102$). The five non-obligatory migratory bat species *N. noctula*, *N. leisleri*, *V. murinus*, *P. nathusii* and *P. pipistrellus* form an outlier in the figure (the arrows). If we exclude these outliers from the analyses, we found a (non-significant) negative relation for species with a northern distribution ($R^2 = -0.331, P = 0.082$). Hence, northern species with specific hibernation needs, such as *M. brandtii* and *E. nilssoni*, are likely to spend less days weaning their young and more on migration between summer and winter roosts.

**Consequences for distribution of bat species**

We studied the link between latitude and several life history traits, with latitude as an important factor contributing to the seasons and the hunting hours each night. Above 67° latitude there is no night at all during mid-summer. Remarkably, this does not necessarily limit bat distribution ranges. Some species, such as *N. noctula*, *P. pipistrellus* and *M. daubentonii* have been observed foraging in daylight in northern regions (Ryberg, 1947; Nyholm, 1965; Baagøe, 1987; Michaelsen, 2007).
Pipistrellus pygmaeus (a European species closely related to *P. pipistrellus*) uses the topography of their habitat, steep mountains with early shade out the sun before sunset, to increase its hunting time (Michealsen et al., 2011).

The harshness of the winter, both in length and minimum temperature, has large consequences for the distribution of bat species. The risks during the winter can be large, especially for the northern species. The direct risks include: predation while in an inactive state (Kokurewicz, 2004; Estók et al., 2010), fungal infection (e.g., White Nose Syndrome, in: Gargas et al., 2009; Puechmaille et al., 2011) and freezing (Lemaire et al., 1994). The choice between (local) hibernacula and migration seems to be linked to the physiological and morphological characteristics of each species. Migration capacities depend on wing load, the aspect ratio of the wings and echolocation type (see also fig. 7). Species, such as *Rhinolophus* spp., which prefer warm hibernacula (fig. 6) and lack migration abilities, seem, therefore, restricted in their distribution. Their survival in local hibernation conditions may depend on their ability to store enough fat to remain warm enough during an energy-consuming winter. Thermophilic species, such as *M. emarginatus* and *M. schreibersii*, can live in relative northern regions in summer, as their wing morphology is suitable for long distance migration. Species with minimum torpor abilities such as *T. teniotis* and *M. capaccinii* seem to be restricted to regions where, after minimum migration effort, hibernation is not strictly necessary (Arlettaz et al., 2000; Levin et al., 2006).

The harshness of the winter also has indirect consequences on the distribution of bat species, due to possible trade-offs between the interrelated traits. In the short northern summer, females have limited time to wean their young, accumulate fat reserves needed for hibernation and migrate towards a hibernaculum. We assume to have found, at least for the northern species, a trade-off between the average migration distance and reproduction (fig. 8). Species with a long average distance between summer and winter roost tend to spend less time weaning their young. Exceptions are bats species, such as *N. noctula*, *P. nathussii*, *V. murinus* with both hibernation and migration abilities. If they live in the centre of their distribution range they can choose not to migrate and save energy, which can be used for reproduction. This is probably the reason why *N. noctula* and *P. nathusii* spend, on average, relative much time weaning their young (arrow in fig. 8).

During the reproductive season bats living in higher latitudes face other problems; a shorter night length, a shorter summer (compared to lower latitudes) and less predictable weather. Adaptation to northern latitudes involves larger litter size, short time required to rear offspring, low longevity and low age of first reproduction. In general, the time required to rear offspring is related to the relative body weight of the newborn (fig. 4). Most northern species (fig. 3) have relatively short weaning periods; *V. murinus* and *P. auritus* complete their weaning within six weeks, while *M. brandtii* and *E. nilssonii* manage to complete it within four weeks. As a consequence of the rapid growth of their offspring most northern species still have enough time remaining to migrate towards hibernacula.
We assume the overall lifetime reproductive output of females in southern and northern populations is equal, females from southern populations become sexually mature later, giving birth to one young with a relatively low body weight each year (fig. 2) and consequently have a longer life span. Females from northern populations become sexually mature in their first year, frequently give birth to twins with a relative high body weight and die younger. We expect females in northern regions to reproduce less frequently (not every year) than females in southern regions; they need a recovery year after successful reproduction or only reproduce in favourable years and climatic conditions (Racey & Entwistle, 2000).

Discussion

In this paper we focused on the consequences of interrelations between traits on the distribution of bat species. This approach differs from previous studies that have focused on the correlation between environmental characteristics and variations in species richness at large geographic scales. The vast majority of results have found significant associations (e.g., Humphries et al., 2002; Hawkins, 2004; Safi & Kerth, 2004; Davies et al., 2007; Ulrich et al., 2007; Tello & Stevens, 2010), but these associations did not lead to an explanation of the distribution limits of the species studied. Other researchers have tried to link morphological adaptations or specialisations to a specific habitat type to distribution patterns (e.g., Barcley, 1991; Kalcounis & Brigham, 1995; Ševčík, 2003; Swartz et al., 2003). Indeed, the feeding behaviour and subsequent morphological adaptations links bats to certain habitat structures; places with or without clutter, places where they can fly high or low, etc. Bat species, however, seem extremely variable in the habitat types they use, as long as there are enough insects to feed on (e.g., Baagøe, 1987; Barcley & Harder, 1994; Krusop, 2004; Haupt, 2005). The absence or presence of a specific habitat only affects the distribution of a reproductive population for a few extreme specialist species. For example, the distribution of *M. dasycneme* is related to large water bodies (Horacek & Hanak, 1989) and the species is absent in regions without such features. Hence, we think that the distribution patterns of European bats cannot be fully explained by linking morphological adaptations to distribution patterns.

We acknowledge the importance of phylogeny in ecological studies. We are aware that some of the correlations we report here could be due to phylogenetic constraints, i.e., closely-related species resembling each other. However within phylogenetic groups similarity sometimes is primarily found within one group of traits (i.e., morphological, physiological or ecological). As each species has a set of co-adapted traits which helps it face the ecological challenges it encounter, even within one phylogenetic group several combinations of traits are possible. Therefore, we decided not to use phylogenetic relations in this paper.
General conclusions

To live and reproduce in northern regions, bats need a combination of the following morphological and physiological adaptations: good migration abilities, ability to hibernate under extreme conditions, a short and flexible reproductive season and large and preferably fast growing offspring. In northern bats these traits, essential for their survival, override other traits that are not compatible with these (e.g., late sexual maturity, long weaning period). Furthermore, northern bats need the flexibility to take advantage of favourable years for reproduction. Often morphological characteristics are given as the main reason for these distribution differences. Here, we have shown the influence of a combination of traits and their trade-offs. These findings suggest that differences in the distribution of European bat species can be explained by morphological, physiological and ecological adaptations. In this paper several traits of a total of 30 species were compared. As a result of molecular techniques, new species have been recognised, leading to a total of 52 species in Europe (Anonymous, 2010). With additional data on the traits of these new species, maybe even more striking patterns can be found. The method presented in this paper might also be useful for other mammal groups with a high species diversity, such as Rodentia and Soricidae. Such findings have both an intrinsic value and are also valuable to applied ecological research, particularly in relation to climate change assessment and mammal protection programmes.

References


