REVIEW

The impact and implications of climate change for bats

Hayley A. SHERWIN *School of Biological Sciences, Queen's University, Belfast BT9 7BL, UK. E-mail: hsherwin01@qub.ac.uk*
W. Ian MONTGOMERY *School of Biological Sciences, Queen's University, Belfast BT9 7BL, UK. E-mail: I.montgomery@qub.ac.uk*
Mathieu G. LUNDY* *Centre of Irish Bat Research, School of Biological Sciences, Queen's University, Belfast BT9 7BL, UK. E-mail: m.lundy@qub.ac.uk*

ABSTRACT

1. Climate influences the biogeography of bats, their access to food, timing of hibernation, reproduction and development, frequency and duration of torpor and rate of energy expenditure.

2. Empirical data on the impact of climate change on bats are a cause for concern as current increases in global temperature are one fifth, or less, of those expected over the next century.

3. We review observed impacts of climate change on bats and identify risk factors allowing species-specific predictions.

4. The impact on species is reviewed in relation to six aspects, namely foraging, roosting, reproduction, biogeography, extreme weather events and indirect effects of climate change. For some aspects of species' ecology, there are insufficient data available to make accurate assessment of impacts.

5. We identify seven risk factors encompassing three broad aspects: biogeography – small range size, high latitude or high altitude range and a range occupying a geographic area likely to become water stressed; foraging niche – frugivory and species restricted to aerial hawking; dispersal ability – species with restricted dispersal behaviour.

6. We use the European and north-west African bats as a case study to assess the relative risk of climate change to individual species. Risk scores are compared with existing International Union for Conservation of Nature conservation assessments providing further insight into the conservation outlook for individual species.

7. We provide a base for Chiroptera to be incorporated into future frameworks of risk assessment and identify areas that require further research.

*Correspondence author.

INTRODUCTION AND METHODS

Although environmental change is a natural process, predicted rates of climate change are higher than rates which occurred over historical and geological time (Anonymous 2008). In combination with habitat destruction and other sources of environmental degradation, climate change poses a serious and increasing threat to biodiversity. During the last 30 years of the 20th century, evidence accumulated suggests that the phenology of organisms, species biogeography and the composition and dynamics of communities are changing in response to a changing climate (Walther et al. 2002). It is difficult to attribute change in the ecology or behaviour of any individual species or in any geographic region to a single cause. However, uncertainty in the role of climate change in any particular study does not preclude the development of an overall synthesis or model for the effects of climate change on particular taxa or communities (Parmesan & Yohe 2003).

   Within a community or population, species or other taxonomic group, the impact of global climate change may be highly variable as a result of an unequal magnitude of change across the globe and variation in responses of individuals, populations or species. To date, the impacts on arctic mammals have been most evident and pronounced (e.g. Hunter et al. 2010, Prost et al. 2010). Species that use climatic cues (e.g. ambient temperature or rainfall) to dictate the timing of foraging, breeding, hibernation, parturition or migration, rather than non-climatic factors (e.g. photoperiod), are expected to respond more immediately to climate change (Brook 2008).

   The Chiroptera constitute one of the most diverse and geographically dispersed groups of mammals (Yalden & Morris 1975); over 1100 species occur, in all regions except the Arctic, Antarctic and some isolated oceanic islands (Simmons 2005). Bats are small and slow-breeding with long life spans (Mello et al. 2009) and energetically expensive, sustained powered flight (Voigt & Lewanzik 2011). They provide important ecosystem services as pollinators in consuming large quantities of insects, suppressing insect populations and dispersing nutrients in landscapes (Pierson 1998, Boyles et al. 2011). In addition, bat guano is a rich food source for decomposers and scavengers (Yalden & Morris 1975). Bat populations are generally in decline due to their sensitivity to environmental stress and slow reproductive rates (Jones et al. 2009).

   Root et al. (2003) identified four potential responses of species to global climate change: changes in the density of species at given locations and shifts in the ranges of species either towards higher latitudes or upwards in elevation; changes in phenology of events such as migration or flowering; changes in morphology, such as body size and behaviour; shifts in genetic frequencies. Here, we review the effects of climate change on the Chiroptera, examining impacts on critical aspects of their ecology. This review was conducted using *Web of Science* to search for scientific literature based on keywords including 'bats' and 'climate', 'temperature', 'precipitation', 'reproduction' and 'global warming' over the years 1975 to 2011. We review the impacts of climate change, primarily in regard to the first three of the four potential responses, on aspects of bat ecology, namely foraging, roosting, reproduction and biogeography. We also review impacts of extreme weather and the indirect effects of climate change on bats. At present, the evolutionary (genetic) responses of many species groups remain poorly understood (Bradshaw & Holzapfel 2008); indeed, in slowly reproducing species such as bats, the evolutionary response to current climate change may take considerable time to become apparent.

Thomas et al. (2011) developed a framework for risk assessment of the impacts of climate change on species based on the International Union for Conservation of Nature (IUCN) red listing procedure and combining both impacts and benefits of climate change on species. Using this review of impacts of climate change on the global bat community, we identify risk factors of impacts of climate change, balancing the costs and benefits of a changing environment for individual species and specifically reviewing the ecological mechanisms underlying change. As an example, we apply this to the bat community of Europe and north-west Africa (47 species) by using data from the ecological review of Dietz et al. (2009). It is possible to identify factors that affect individual species, but quantitative assessment of the relative importance of discrete factors on individual species remains difficult. However, synthesis of existing literature permits assessment of the impact and proximate factors underpinning effects on individual bat species.

RESULTS AND DISCUSSION
Foraging
Bats occupy a diverse range of foraging niches, but most fall into two categories: insectivory, and consumption of fruit or nectar. Insectivorous bats depend on the availability of mainly ectothermic prey, whose activity is influenced by climatic conditions (Burles et al. 2009). Low ambient temperatures reduce the activity of volant insects and prolonged periods of low temperatures delay insect development (Anthony et al. 1981). Food abundance is a fundamental factor influencing the activity of bats (Wang et al. 2010). Dunbar and Tomasi (2006) confirmed that eastern red bats *Lasiurus borealis* exploit feeding opportunities on milder nights, and Park et al. (2000) reported an increase in activity duration of greater horseshoe bats *Rhinolphus ferrumequinum* with temperatures higher than 10 °C, relating this to a thermal threshold for insect activity.

There are conflicting views surrounding the effect of precipitation on insect activity. More rainfall has been predicted to lead to increases in the abundance of insects such as dipterans and lepidopterans (Frick et al. 2009), but may inhibit insect flight, thus decreasing the availability of insects to bats (Anthony et al. 1981). The Mexican free-tailed bat *Tadarida brasiliensis* has been identified as an indicator of climate change representative of tropical, cave-roosting bats, due to its reliance on high densities of insects (Newson et al. 2008). Scheel et al. (1996) suggested that some species of bats in the southern United States may be vulnerable to a developing mismatch in the roosting and foraging habitat under climate change scenarios. Changes in temperature and precipitation, which affect seasonal flowering and fruiting food plants, are correlated with foraging behaviour of the straw-coloured fruit bat *Eidolon hevlum*. These changes are predicted to alter colony structure, productivity and juvenile survival (Richter & Cumming 2008).

Temperature changes may have unequal effects on different bat species due to differences in foraging, habitat and reproductive requirements. Flight and hunting activity of Daubenton's bats *Myotis daubentonii* are not strongly affected by air temperature or insect abundance due to their flexible hunting strategy (Boonman et al. 1998, Ciechanowski et al. 2007). Aerial-hawking species are expected to be highly sensitive to climatic changes due to their dependence on a food supply that is highly variable both in time and space. In contrast, foragers at water surfaces,

such as Daubenton's bat, rely on stable and spatially concentrated food resources, and hence, climatic changes may not have a strong effect on their survival rates (Ciechanowski et al. 2007).

Due to their high surface area to volume ratios and large, naked flight membranes (Webb et al. 1995), the rate of evaporative water loss is higher in bats than in other mammals of similar size (Chruszcz & Barclay 2002). This may have detrimental effects on species that inhabit arid regions as they do not appear to have adaptations to a water-limited environment (e.g. urine-concentrating adaptations) and therefore depend on permanent water resources close to roosts (Adams & Hayes 2008). Travelling further to access food and water entails considerable energetic losses and may affect reproductive success. For example, growth and developmental rates of grey bat *Myotis grisescens* juveniles are relatively slow due to long travelling distances of lactating females, and as a consequence, the lactation period is significantly increased (Tuttle 1975). Lactating females, which typically produce milk composed of 76% water (Adams 2010), face the greatest dehydration threat. Adams and Hayes (2008) observed that lactating females visited a water source 13 times more often than non-reproductive females, regardless of the ambient conditions. It is thought that species that select roosts with high solar gain are likely to be most strongly affected, e.g. the fringed myotis *Myotis thysanodes* and the little brown bat *Myotis lucifugus* (Adams 2010).

Foraging risk factors
We conclude that two risk factors are directly related to foraging, namely: bats inhabiting regions likely to become more water-stressed and species reliant on temporally and spatially variable food sources (typically aerial hawking species) are at risk. Applying these risk factors to the European and north-west African bats reveals that a high proportion, 38 of 47 species, rely on an aerial hawking strategy and are therefore at risk. In total, 15 species occupy ranges likely to be subject to water stress (Table 1), i.e. are restricted to areas predicted to be under severe water stress by 2050 (Alcamo et al. 2007).

Roosting
Roosts are utilized for resting, raising young and, in heterothermic bats, for torpor and seasonal hibernation (Kunz & Fenton 2003, Dietz et al. 2009). Adopting a torpid state improves chances of survival during periods in which environmental conditions are unfavourable (Humphries et al. 2003). Torpor bouts can be short-term daily events or events that last a number of days. During the hibernation season, sequences of multi-day torpor bouts are often punctuated by periodic arousals involving metabolism of brown adipose tissue, which raises body temperature (Trayhurn 1993). Most mammals remain relatively quiescent during such arousals, but bats tend to be active both inside and outside the hibernaculum (Willis 1982, Lausen & Barclay 2006). Intermittent arousals in hibernating bats may occur to allow drinking (Speakman & Racey 1989, Thomas & Geiser 1997), mating (Berková & Zukal 2010) and urinating (Park et al. 2000). When bats select hibernacula, they must address the risk of death by freezing in less buffered roosts, starving in stable but warmer roosts due to the increased energetic demands, and roost switching in response to unsuitable conditions (Sendor & Simon 2003). The abundance of bats at underground

Table 1. Climate change risk factors identified for European and north-west African bat species, from species accounts in Dietz et al. (2009)

Species	Risk factors							Sum	IUCN classification
	Small range	Cave/tree roosting	Frugivore	Water stressed	Aerial hawking	Long-distance dispersal	Northern range/high altitude		
Rousettus aegyptiacus			•			•		2	LC
Rhinopoma hardwickei				•	•			2	LC
Nycteris thebaica				•	•			2	LC
Hipposideros caffer				•	•			2	LC
Asellia tridens		•		•	•			3	LC
Rhinolophus hipposideros					•	•		2	LC
R. ferrumequinum				•	•	•		3	LC
R. euryale	•	•			•			3	NT
R. mehelyi	•	•		•	•			4	VU
R. blasii		•			•	•		3	LC
Myotis daubentonii								0	LC
M. dasycneme	•						•	2	NT
M. capaccinii	•	•			•			3	VU
M. brandtii					•			1	LC
M. mystacinus					•			1	LC
M. aurascens					•			1	LC
M. nattereri					•			1	LC
M. emarginatus	•					•	•	3	LC
M. bechsteinii	•	•				•	•	4	NT
M. myotis	•							1	LC
M. blythii				•	•			2	LC
M. punicus				•	•	•		3	NT
Nyctalus noctula		•					•	2	LC
N. leisleri		•					•	2	LC
N. azoreum	•				•	•		3	EN

Table 1. (Continued)

Species	Risk factors							Sum	IUCN classification
	Small range	Cave/tree roosting	Frugivore	Water stressed	Aerial hawking	Long-distance dispersal	Northern range/high altitude		
Pipistrellus pipistrellus					•	•		2	LC
P. pygmaeus					•	•		2	LC
P. nathusii					•		•	2	LC
P. kuhlii					•	•		2	LC
P. maderensis	•			•	•	•		4	EN
P. rueppellii				•	•			2	LC
Hypsugo savii				•	•			2	LC
Vespertilio murinus					•		•	2	LC
Eptesicus serotinus					•	•		2	LC
E. nilssonii		•			•		•	3	LC
E. anatolicus	•			•	•			3	LC
Barbastella barbastellus	•	•		•	•			4	NT
Otonycteris hemprichii	•			•	•			3	LC
Plecotus auritus	•				•		•	3	LC
P. macrobullaris	•				•		•	3	LC
P. sardus	•	•			•			3	NT
P. austriacus	•				•	•		3	LC
P. kolombatovici	•				•	•		3	LC
P. teneriffae	•			•	•	•		4	EN
Nyctalus lasiopterus	•	•	•		•			4	NT
Miniopterus schreibersii	•	•			•	•		4	NT
Tadarida teniotis					•	•		2	LC
Frequency	19	11	1	15	39	18	10	Mean 2.49	

The IUCN classification of conservation status is given for each species: 'LC' least concern, 'NT' near threatened, 'VU' vulnerable and 'EN' endangered. IUCN, International Union for Conservation of Nature.

hibernating sites in Europe has been identified as an indicator of climate change, as temperature and humidity are important factors controlling hibernation (Newson et al. 2008).

Irrespective of their cause or function, arousals are energetically costly: 70–90% of winter energy expenditure can occur during these periods of activity (Kayser 1953). It is advantageous for bats, therefore, to maintain a torpid state throughout hibernation (Németh et al. 2009). The duration of torpor in free-living greater horseshoe bats is highly dependent on ambient temperature: the duration of bouts of torpor declines with temperature (Park et al. 2000). The same relationship occurs in captive eastern red bats (Dunbar & Tomasi 2006). The suggested reason for this relationship is that metabolic processes occur faster at higher temperature, and therefore, a critical metabolic imbalance is reached earlier (Park et al. 2000). In addition to metabolic increases, other complex interactions with environmental conditions may affect torpor bout duration, including water loss (Thomas & Geiser 1997).

Feeding is one of the most frequently documented reasons for arousal during hibernation (Willis 1982, Avery 1985, Humphries et al. 2003). In the subtropical nectar-eating blossom bat *Syconycteris australis*, daily torpor is deeper and longer in summer than in winter due to reduced nectar availability in the summer (Coburn & Geiser 1998). Bats must feed during spontaneous arousals or else risk loss of body mass, resulting in inadequate reserves for thermoregulation (Dunbar & Tomasi 2006). In the endemic New Zealand long-tailed bat *Chalinolobus tuberculatus*, overwinter survival declines in warmer years, probably as a result of decreased torpor bout duration, causing depletion of fat reserves, exacerbated by periods of low food availability (Pryde et al. 2005). Earlier springs, i.e. warmer temperatures earlier in the year, may shorten the hibernation season. If food is readily available during arousals and at the termination of hibernation, negative effects on population size may be limited. However, later periods of colder temperatures or lack of insect prey during arousals can cause significant mortality (Jones et al. 2009). The impact of climate change on patterns of hibernation and torpor are complex. Review of historic mammal extinction in relation to homeothermic and heterothermic life history suggests that in all mammal species, the opportunistic use of torpor allows species to avoid unfavourable conditions (Geiser & Turbill 2009, Liow et al. 2009). Five of eight bat species identified by Geiser and Turbill (2009) as having become extinct since the year 1500 are homeotherms.

The thermal properties of different roost types dictate that species restricted and adapted to these roosts are exposed to different aspects of a changing climate. Park et al. (2000) showed that arousal frequency in a cave-roosting bat species correlates with milder roost temperatures, but the relationship between roost and external temperature was relatively weak. Speakman and Racey (1989) reported a correlation between the internal temperature of a hibernaculum and the external ambient temperature, which allows bats to evaluate external temperatures while remaining inside the roosts. Tree-roosting bats arouse from torpor during short periods of mild weather and may forage if resources are available (Turbill & Geiser 2008). The frequency of El Niño Southern Oscillation winter conditions is expected to increase in south-eastern Australia due to climate change (Anonymous 2001). Clear, cool nights will be more frequent and warm, humid nights more infrequent, which may lead to reduced activity in tree-roosting bats. If species are exposed to extreme low temperatures, perhaps due to changing weather patterns, the impact

will be energetically very expensive: torpor bout duration will decrease and metabolic rate will increase to maintain body temperate (Geiser & Broome 1993). On milder winter nights, bats will experience higher energetic costs associated with necessary bouts of activity, suggesting that large-scale climatic shifts will directly influence the torpor of tree-roosting bats (Turbill 2008). However, Scheel et al. (1996) modelled the effects of climate change on bat species richness in Texas, USA, and suggested that the distribution of tree-roosting generalist species may shift in response to climate change and that cave-roosting species may be impacted as vegetation around caves changes. However, tree-roosting bats may also face a reduction in suitable roosts if the rate of climate change is too rapid to allow the development of equivalent areas of mature broadleaf forests in new 'climatically suitable areas' as their range extends northwards (Rebelo et al. 2010).

Roosting risk factors
It is difficult to attribute a definitive risk factor to homeothermic and heterothermic bat species given historic patterns of species extinction, but there is evidence of apparent impact on aspects of species' ecology due to changing climate conditions. We suggest that bats specialized in individual roost types, specifically cave and tree roosts, at distinct life history stages, are at great risk from changing vegetation and climatic conditions. Applying these risk factors to the European and north-west African bats reveals that 11 species are classified as restricted to roosting in trees or caves and are therefore at risk.

Reproduction
The timing of behaviours related to reproduction involves a suite of endogenous and exogenous factors (Mello et al. 2009). The latter factors include climate and the temporal availability of food (Crichton & Krutzsch 2000). The advancement of reproduction, leading to an earlier breeding season, is regarded as characteristic of climate change in biological systems (Peñuelas & Filella 2001). The effects are unlikely to be uniform in bats due to their different reproductive strategies. In the little brown bat, an aerial hawking species, reproductive success is higher during warmer years due to the increased availability of flying insects. In contrast, due to their foraging strategy of gleaning prey, reproductive success in Keen's myotis *Myotis keenii* is higher in cooler years as insects are still available for consumption despite a reduction in their activity. However, both species are more energetically stressed during cooler years, reflected by their lower body masses (Burles et al. 2009). For ground-foraging pallid bats *Antrozous pallidus*, lower spring temperatures are correlated with a higher percentage of non-reproductive females (Lewis 1993). Theoretically, warmer climates should increase the percentage of reproductive females, which could result in increased population sizes, and thus intensified competition for food and roosting sites. More data are required if we are to understand fully the relationships between climate, prey and reproduction in bat populations.

Temperate bat species are monoestrus (have one reproductive period and litter per year; Racey & Entwistle 2000). The majority of bat species mate in autumn or winter and delay fertilization, by storing spermatozoa in the female reproductive tract, until spring. It has been suggested that sperm storage is possible for torpid bats but that spermatozoa disappear quickly from reproductive tracts of active individuals (Racey 1979). Warming temperatures and an adequate supply of food in the second half of

the winter may result in arousal earlier than expected, followed by ovulation and pregnancy (Jones et al. 2009). Climate change can also influence the timing of parturition by altering food availability. For example, in greater horseshoe bats, an increase of 2 °C advances the birth rate by 18 days (Ransome & McOwat 1994). Torpor and gestation appear to be linked: prolonged torpor allows parturition to be delayed until favourable conditions occur (Willis et al. 2006). Food availability appears to be the prime factor determining when temperate insectivorous bats give birth, as parturition in lesser mouse-eared bats *Myotis blythii* is delayed in years when prey is scarce (Arlettaz et al. 2001). Precipitation has also been reported to cause delays in reproduction and later parturition in bats (Grindal et al. 1992).

Reproduction in insectivorous bats is dependent on insect availability: it is not delayed when there is a sufficient abundance of prey despite low temperatures and high precipitation levels (Racey 1973, Syme et al. 2001). Though the tropics are less seasonal than temperate regions, tropical bats are still affected by temperature changes. Ambient temperature affects the timing of reproduction in the frugivorous yellow-shouldered bat *Sturnira lilium* and exerts selection pressure on reproductive timing, independently of the effect of temperature, on food availability (Mello et al. 2009).

Warmer climates may benefit females by causing earlier parturition and weaning of young, allowing more time to mate and store fat reserves in preparation for hibernation. Similarly, earlier gestation and parturition may benefit juveniles by providing a longer growth period prior to the breeding season (Burles et al. 2009). Frick et al. (2009) supported this finding by showing that pups born early in the summer have higher survival and first-year breeding probabilities than those born later in the summer. In an extreme case of premature parturition, juvenile mouse-eared bats *Myotis myotis* were born 6 months early, suggesting that hibernation was abandoned due to warm and dry autumnal conditions (Ibáñez 1997). The development of juveniles is faster in warmer roosts: forearm length is greater in juvenile mouse-eared bats exposed to higher ambient temperatures (up to 24 °C; Zahn 1999).

Reproduction risk factors
It is difficult to make generalizations about the level of risk associated with changes in bat reproduction due to climate change. The impacts associated with changes in reproductive behaviour and performance require further research and assessment. None of the 47 north-west African and European species was scored as being at risk due to its reproduction.

Biogeography
Climate change has considerable impacts on the range limits of endotherms (Humphries et al. 2002). An increase in mean annual temperature of 3 °C corresponds to a shift in isotherms of 300–400km in latitude (in the temperate zone) or 500m in elevation (Hughes 2000). The effect of this may be the shifting of species' ranges to new, unoccupied areas (Rebelo et al. 2010), during which fragmentation and local extinctions may occur in currently occupied areas (Thomas et al. 2004). Species that have little or no overlap between current and future ranges, or with limited tolerance to environmental stress, are predicted to be most at risk (Rebelo et al. 2010). Although not identified in bat species, it is generally accepted that

species with small ranges are more vulnerable to environmental change as the entirety of their range is likely to be affected, leaving no refugia (Lawton et al. 1994, Johnson 1998, Colles et al. 2009).

Bats, uniquely among mammals, have powered flight, which facilitates relocation in response to climate change (Scheel et al. 1996). Thus, distributional changes of migrating bats capable of long-distance relocation may be indicators of climate change (Lundy et al. 2010). There is evidence of northwards movements of ranges among European bats. For example, the Mediterranean species Kuhl's pipistrelle *Pipistrellus kuhlii* has expanded its range northwards in the past 15 years in response to rising temperatures (Sachanowicz et al. 2006). The increase in average annual global temperature change is projected to be up to 6.4 °C (Anonymous 2008). Humphries et al. (2002) established a mechanistic link between temperature and biogeography using a bioenergetic model and predicted a northward range shift for the little brown bat. Bat species may decline or disappear from their current range to varying extents depending on their biogeographic groups (Rebelo et al. 2010). Species occupying northern latitudes are of particular concern: suitable climatic conditions could be eliminated as mean ambient temperatures rise regardless of the climate scenario modelled (Rebelo et al. 2010). Lundy et al. (2010) suggested that the migratory Nathusius' pipistrelle *Pipistrellus nathusii* has expanded its range in the UK in response to climate change and will continue to do so. This species has recently been recorded in Poland during the winter for the first time (Sachanowicz & Ciecha-nowski 2006).

The geographical range of the common vampire bat *Desmodus rotundus* is restricted in latitude and elevation, as it requires mean minimum temperatures of 10 °C (McNab 1973). It expanded its range into the Monteverde Cloud Forest in the Tileran Mountains of northern Costa Rica in response to a 2 °C temperature increase in the region (LaVal 2004). This temperature increase was suggested as a causative factor, leading 24 predominantly lowland bat species to be recorded at higher altitude (LaVal 2004). Similarly, the long-legged myotis *Myotis volans* moved to higher elevations when the summer temperatures at lower elevations exceeded its tolerance limits (Mollhagen & Bogan 1997). The grey-headed flying-fox *Pteropus poliocephalus* has established a colonial roost in the Royal Botanic Gardens, Mel-bourne (Parris & Hazell 2005), though bioclimatic analysis of long-term data shows that in the past, Melbourne's climate was unsuitable for this species. However, a warming trend and consequent reduction in frost days over the last five decades has placed Melbourne within the preferred climatic range of the grey-headed flying fox, and artificial watering in the park has allowed the roost to become established (Parris & Hazell 2005). As temperatures increase, movement to areas of higher altitude will allow lowland species to translocate to areas of suitable climate. This may not be possible for species currently occupying higher altitude areas, which will become increasingly dependent on a decreasing land area. Similarly, for species occupying higher latitudes, the area of suitable land within a favourable climate niche will become limited as all species' ranges move towards the poles.

Biogeography risk factors
Three risk factors are directly related to biogeography. Species with high latitude or altitude ranges, sedentary species with limited dispersal or seasonal movements and species that are restricted to a small range are at risk. For European and north-west

African bats, we identify as species with a northern range those that do not extend south of the geographical land border of the Iberian Peninsula. Ten species meet this criterion (Table 1). Species' range was considered in a global context, and 19 species were classified as being restricted to a small range (Table 1). Eighteen species with limited ranging behaviour were identified: those for which migratory movements have never been observed and those for which only small (<100km) movements have been recorded (Table 1). At present, it remains difficult to address how much individual or population motility is sufficient to counteract the impact of climate change in a given region. Future researchers should aim to identify the levels of species dispersal required to mitigate the impacts of environmental change.

Extreme weather
Current climate change models predict that the frequency, intensity and duration of heat waves will increase (Meehl & Tebaldi 2004). Hence, bats will be exposed more frequently to climatic extremes, e.g. extremes of temperature. Temperatures over 42 °C caused the mass mortality (>3500 individuals) of the tree-roosting Australian grey-headed flying fox and black flying fox *Pteropus alecto* (Welbergen et al. 2008). Over 30000 individuals of *Pteropus* spp. died during 19 episodes of extreme temperatures (Jones et al. 2009), mortality on a scale that could have negative, long-term impacts on the population and food plants. Weather data and climate models suggest that there may be an increase in year-to-year variability in Europe, which would increase the future incidence of droughts and heat waves (Schär et al. 2004). Henceforth, worldwide incidence of impacts of extreme temperatures on bats may be very significant. Sea levels are projected to rise by up to 80cm due to thermal expansion alone and by several meters by 2300 as a result of melting ice sheets (Anonymous 2008). This may restrict access to coastal cave roosts, particularly for island bat species (Goodwin 1970), and combined with tropical storms, could result in significant impacts on entire colonies. Indeed, if tropical storms increase in severity, frequency or distribution, vulnerable tropical tree-roosting bat species may be impacted greatly (Gannon & Willig 2009).

Extreme weather risk factors
Species occupying tropical and subtropical regions are most at risk from extreme weather in the form of tropical storms and extreme temperature events. European and north-west African bats that occupy higher latitudes or undertake seasonal migrations may have increased vulnerability to extreme weather events. However, given the difficulty of forecasting the occurrence of extreme weather events, extending these to concrete predictions about species-specific impacts is not possible, so no scores were allocated.

Indirect effects of climate change
The prevalence of fungal diseases in mammals is expected to rise due to changes in geographical ranges and selection for adaptive thermotolerance in potentially pathogenic species (Garcia-Solache & Casadevall 2010). Bats act as reservoirs for a number of infectious diseases and are killed by others (e.g. Jones et al. 2009), including White Nose Syndrome (WNS) caused by the fungal pathogen *Geomyces destructans*. The pathology and mode of spread of WNS among *Myotis* spp. in north-eastern America are not yet fully understood but may be exacerbated by

increased arousals and increased energetic stress, which enhance susceptibility to fungal infection (Jones et al. 2009, Boyles & Willis 2010).

Increasing renewable energy production is a way to reduce global carbon emissions in response to climate change. However, some wind energy facilities have been responsible for the death of large numbers of migratory bats (e.g. Johnson et al. 2003, Baerwald et al. 2008, Jana & Pogacnik 2008, Long et al. 2010, Rydell et al. 2010). Climate change may also indirectly alter prey–predator dynamics. In Eglinton Valley, New Zealand, for example, warmer-than-average temperatures led to increased production of beech *Fagus* mast, which provided an enhanced food supply for introduced mice *Mus musculus* and rats *Rattus rattus*. This, in turn, stimulated the prolific breeding of one of their predators, the stoat *Mustela erminea*, which also predates bats (Pryde et al. 2005). It remains unclear how the community dynamics of bats may be affected by such indirect effects of climate change. If human population growth continues, the pressure of hunting on fruit eating bats perceived as pests or as a food source (Epstein et al. 2009) could intensify beyond sustainable limits (Jenkins & Racey 2008). Habitat loss is recognized as a major threat to the world's biodiversity in the face of a changing climate. The growing human population and the consequent pressure on agricultural production may result in further habitat loss, degradation of natural habitats and further species declines. In addition, as some bat species utilize buildings as roosts (Marnell & Presetnik 2010), construction and redevelopment of buildings may have costs and benefits for bats which are difficult to predict.

Indirect effects risk factors
The indirect impacts of climate change are wide, varied and difficult to predict. The role of the environment in the proliferation of WNS remains unknown, but this disease is undoubtedly one of the greatest threats to the North American bat species. Although it is difficult to predict how, climate change and associated perturbations within communities may increase the risk of disease spread. Additionally, habitat loss and increased competition for dwindling resources will result in greater pressure on natural communities, dictating that those species commonly perceived as pests or a food source will be at greater risk as an indirect effect of climate change. Only one frugivore (*Rousettus aegyptiacus*) occurs in Europe and north-west Africa, and this is the only species classified here as likely to encounter high levels of persecution.

Summary of risk factors
The risk factors we have identified are not mutually exclusive, and species may be exposed to a range of impacts (Table 1). At present, quantifying the cumulative impacts of multiple risk factors on an individual species is difficult. We therefore sum individual risk factors but do not assess interactions between them. Summing the identified factors for the European and north-west African species provides a score ranging from 0–7. The mean score was 2.49 ($n = 47$, standard deviation $= 0.95$). A maximum score of four was given to seven species (Fig. 1): *Barbastella barbastellus*, *Miniopterus schreibersii*, *Myotis bechsteinii*, *Nyctalus lasiopterus, Pipistrellus maderensis, Plecotus teneriffae* and *Rhinolphus mehelyi*, which we consider to be most at risk from climate change in the test group.

The IUCN classifications of these species were scored as: 1, 'least concern'; 2, 'near threatened'; 3, 'vulnerable'; 4, 'endangered' and the scores were found to be strongly positively correlated with the cumulative risk score (Fig. 2, Spearman's rank
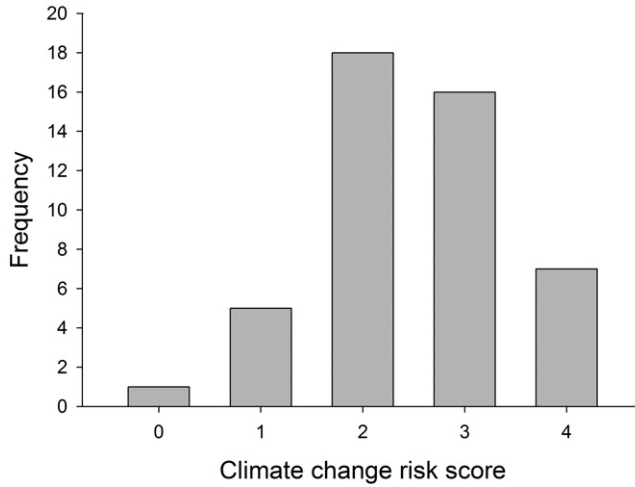
Fig. 1. Frequency distribution of summed climate change risk score (count of points given for: small range, cave/tree roosting, frugivore, water stressed, aerial hawking, long-distance dispersal, northern range/high altitude range) for 47 European and north-west African bat species.
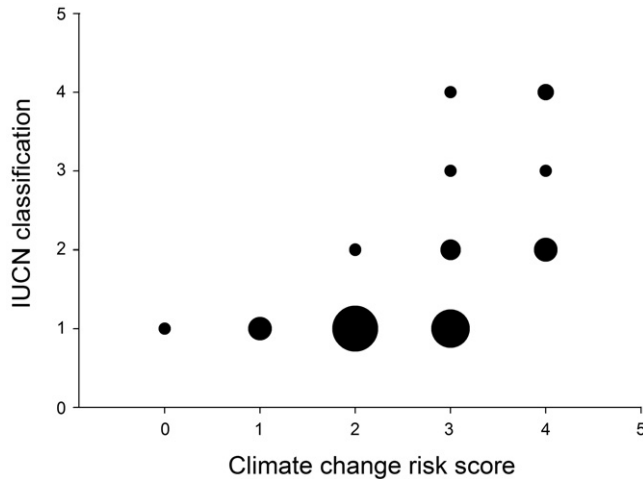

Fig. 2. Relationship between International Union for Conservation of Nature classification (1, 'least concern'; 2, 'near threatened'; 3, 'vulnerable'; 4, 'endangered') and summed climate change risk score (see Fig. 1) for 47 European and north-west African bat species. The size of points is scaled to the number of species.

correlation $R = 0.65$, $P < 0.01$). For all species, except those of least concern, where the ranks did not match, the assessed risk due to climate change was greater than the IUCN rank. This suggests that those risk factors identified may be species' traits that are associated with vulnerability to environmental change in general and that this vulnerability may be exacerbated by future change. However, all but one of the species identified as most at risk were not classed as 'endangered' by IUCN, suggesting either the overestimation of risk or a forecast of impacts yet to be observed in empirical data.

CONCLUSION

Bats have global distribution, diverse feeding and reproductive strategies and important ecological roles so are ideal indicators of environmental stress. Boyles et al. (2011) suggested that bats are among the most economically important non-domesticated animal groups in North America and that mitigating impacts on their populations is important for the integrity of ecosystems and international economies. Climate influences food availability, timing of hibernation, frequency and duration of torpor, rate of energy expenditure, reproduction and development rates of juveniles. Warming temperatures may benefit bats due to increased food availability, earlier parturition, faster development of juveniles and range expansion. However, disruption of hibernation, extreme weather events, reduced water availability in arid environments and the spread of disease may cause significant mortalities. If such changes are occurring in bats, which have excellent mobility, the impact on mammalian taxa that are less able to escape unfavourable conditions may be even more dramatic.

Although studies on the impact of climate change on bats are still at a preliminary stage, the changes reported to date have been alarming as current increases in temperature are only one fifth, or less, of those expected over the next century (Hughes 2000). Further research is required to extend these early studies, particularly on the effect of a warmer and drier climate on hibernation. Higher temperatures stimulate increased winter activity, which uses up vital energy reserves, unless food availability also increases. If seasonal events, such as hibernation and parturition, become out of synchrony with food supply, the risk of starvation will be heightened. Due to bats' important ecological roles as top predators and pollinators, lower trophic levels will also be impacted, e.g. insect pest abundance will increase and pollination of food plants will be reduced (Boyles et al. 2011).

Bat populations have responded to complex changes in their environment across geological time scales (Postawa 2004). Phylogenetic evidence of previous climate change is still present within many species (e.g. Flanders et al. 2009). It is difficult to predict how contemporary, more rapid climate change will affect the phylogenies of modern communities. However, if populations become fragmented, genetic diversity will be lost as smaller populations become isolated (Rossiter et al. 2000).

In identifying a set of risk factors, we do not aim to produce a definitive list of species-specific impacts but to create a base from which the impacts of climate change on the global bat community can be examined. Establishing interactions and cumulative effects, and indeed developing a hierarchy of impacts, will further our understanding of the threats to bats.

REFERENCES

Adams RA (2010) Bat reproduction declines when conditions mimic climate change projections for western North America. *Ecology* 91: 2437–2445.

Adams RA, Hayes MA (2008) Water availability and successful lactation by bats as related to climate change in arid regions of western North America. *Journal of Animal Ecology* 77: 1115–1121.

Alcamo O, Flöorke M, Märker M (2007) Future long-term changes in global water resources driven by socio-economic and climatic changes. *Hydrological Sciences Journal* 52: 247–275.

Anthony ELP, Stack MH, Kunz TH (1981) Night roosting and the nocturnal time budget of the little brown bat, *Myotis lucifugus*: effects of reproductive status, prey density, and environmental conditions. *Oecologia* 51: 151–156.

Arlettaz R, Christie P, Lugon A, Perrin N, Vogel P (2001) Food availability dictates the timing of parturition in insectivorous mouse-eared bats. *Oikos* 95: 105–111.

Anonymous (2008) *Fourth Assessment Report: Climate Change 2007*. Intergovernmental Panel on Climate Change Cambridge University Press, Cambridge, UK.

Anonymous (2001) Climate change projections for Australia. Climate impact group, CISRO atmospheric research group. Melbourne, Australia.

Avery MI (1985) Winter activity of pipistrelle bats. *Journal of Animal Ecology* 54: 721–738.

Baerwald EF, D'Amours GH, Klug BJ, Barclay RMR (2008) Barotrauma is a significant cause of bat fatalities at wind turbines. *Current Biology* 18: 695–696.

Berková H, Zukal J (2010) Cave visitation by temperate zone bats: effects of climatic factors. *Journal of Zoology* 280: 387–395.

Boonman AM, Boonman M, Bretschneider F, van de Grind WA (1998) Prey detection in trawling insectivorous bats: duckweed affects hunting behaviour in Daubenton's bat, *Myotis daubentoni*. *Behavioural Ecology and Sociobiology* 44: 99–107.

Boyles JG, Willis CKR (2010) Could localized warm areas in cold caves reduce mortality of hibernating bats affected by white-nose syndrome? *Frontiers in Ecology and the Environment* 8: 92–98.

Boyles JG, Cryan PM, McCracken GF, Kunz TH (2011) Economic importance of bats in agriculture. *Science* 332: 41–42.

Bradshaw WE, Holzapfel CM (2008) Genetic response to rapid climate change: it's seasonal timing that matters. *Molecular Ecology* 17: 157–166.

Brook BW (2008) In focus: global warming tugs at trophic interactions. *Journal of Animal Ecology* 78: 1–3.

Burles DW, Brigham RM, Ring RA, Reimchen TE (2009) Influence of weather on two insectivorous bats in a temperature Pacific Northwest rainforest. *Canadian Journal of Zoology* 87: 132–138.

Chruszcz BJ, Barclay RMR (2002) Thermoregulatory ecology of a solitary bat, *Myotis evotis*, roosting in rock crevices. *Functional Ecology* 16: 18–26.

Ciechanowski M, Zajac T, Bitas A, Dunajski R (2007) Spatiotemporal variation in activity of bat species differing in hunting tactics: effects of weather, moonlight, food abundance, and structural clutter. *Canadian Journal of Zoology/Revue Canadienne de Zoologie* 85: 1249–1263.

Coburn DK, Geiser F (1998) Seasonal changes in energetics and torpor patters in the subtropical blossom-bat *Syconycteris australis*. *Oecologia* 113: 467–473.

Colles A, Liow LH, Prinzing A (2009) Are specialists at risk under environmental change? neoecological, paleoecological and phylogenetic approaches. *Ecology Letters* 12: 849–863.

Crichton EG, Krutzsch PH (eds; 2000) *Reproductive Biology of Bats*. Academic Press, London, UK.

Dietz C, von Helversen O, Nill D (2009) *Bats of Britain, Europe and Northwest Africa*, 2nd ed. A&C Black, London.

Dunbar MB, Tomasi TE (2006) Arousal patterns, metabolic rate, and an energy budget of eastern red bats (*Lasiurus borealis*) in winter. *Journal of Mammalogy* 87: 1096–1102.

Epstein JH, Olival KJ, Pulliam JRC, Smith C, Westrum J, Hughes T et al. (2009) *Pteropus vampyrus*, a hunted migratory species with a multinational home-range and a need for regional management. *Journal of Applied Ecology* 46: 991–1002.

Flanders J, Jones G, Benda P, Dietz C, Zhang S, Li G, Sharifi M, Rossiter SJ (2009) Phylogeography of the greater horseshoe bat, *Rhinolophus ferrumequinum*: contrasting results from mitochondrial and microsatellite data. *Molecular Ecology* 18: 306–318.

Frick WF, Reynolds DS, Kunz TH (2009) Influence of climate and reproductive timing on demography of little brown myotis *Myotis lucifugus*. *Journal of Animal Ecology* 79: 128–136.

Gannon MR, Willig MR (2009) Islands in the storm: disturbance ecology of plant-visiting bats in the hurricane prone island of Puerto Rico. In: Fleming TH, Racey PA (eds) *Island bats*. 281–301. University of Chicago Press, Chicago IL.

Garcia-Solache MA, Casadevall A (2010) Global warming will bring new fungal diseases for mammals. *MBio* 1: e00061–e00010. doi:10.1128/mBio.00061-10.

Geiser F, Broome LS (1993) The effect of temperature on the pattern of torpor in a marsupial hibernator. *Journal of Comparative Physiology B, Biochemical, Systemic, and Environmental Physiology* 163: 133–137.

Geiser F, Turbill C (2009) Hibernation and daily torpor minimize mammalian extinctions. *Naturwissenschaften* 96: 1235–1240.

Goodwin RE (1970) The ecology of Jamaican bats. *Journal of Mammalogy* 51: 571–579.

Grindal SD, Collard TS, Brigham RM, Barclay RMR (1992) The influence of precipitation on reproduction by *Myotis* bats in British Columbia. *American Midland Naturalist* 128: 339–344.

Hughes L (2000) Biological consequences of global warming: is the signal already apparent? *Trends in Ecology and Evolution* 15: 56–61.

Humphries MM, Thomas DW, Speakman JR (2002) Climate-mediated energetic constraints on the distribution of hibernating mammals. *Nature* 418: 313–316.

Humphries MM, Kramer DL, Thomas DW (2003) The role of energy availability in mammalian hibernation: an experimental test in free-ranging eastern chipmunks. *Physiological and Biochemical Zoology* 76: 180–186.

Hunter CM, Caswell H, Runge MC, Regehr EV, Amstrup SC, Stirling I (2010) Climate change threatens polar bear populations: a stochastic demographic analysis. *Ecology* 91: 2883–2897.

Ibáñez C (1997) Winter reproduction in the greater mouse-eared bat (*Myotis myotis*) in South Iberia. *Journal of Zoology* 243: 836–840.

Jana S, Pogacnik M (2008) The impacts of wind farms on animal species. *Acta Veterinaria* 58: 615–632.

Jenkins RKB, Racey PA (2008) Bats as bushmeat in Madagascar. *Madagascar Conservation and Development* 3: 22–30.

Johnson C (1998) Species extinction and the relationship between distribution and abundance. *Nature*, 394: 272–274.

Johnson GD, Erickson WP, Strickland MD, Shepherd DA, Sarappo SA (2003) Mortality of bats at a large-scale wind power development at Buffalo Ridge, Minnesota. *American Midland Naturalist* 150: 332–342.

Jones G, Jacobs DS, Kunz TH, Willig MR, Racey PA (2009) Carpe noctem: the importance of bats as bioindicators. *Endangered Species Research* 8: 93–115.

Kayser C (1953) L'hibernation des mammiferes. *L' Annee Biologique* 29: 109–150.

Kunz T, Fenton MB (2003) *Bat Ecology*. University of Chicago Press, Chicago, Illinois, USA.

Lausen CL, Barclay RMR (2006) Winter bat activity in the Canadian prairies. *Canadian Journal of Zoology* 84: 1079–1086.

LaVal RK (2004) Impact of global warming and locally changing climate on tropical cloud forest bats. *Journal of Mammalogy* 85: 237–244.

Lawton J, Nee S, Letcher A, Harvey P, Edwards P, May R, Webb N (1994) Animal distributions: patterns and processes. In: Edwards PJ, May RM, Webb NR (eds) *Large-scale ecology and conservation biology*. 41–59. Blackwell Scientific Publications, London.

Lewis SE (1993) Effect of climatic variation on reproduction by pallid bats (*Antrozous pallidus*). *Canadian Journal of Zoology* 71: 1429–1433.

Liow LH, Fortelius M, Lintulaakso K, Mannila H, Stenseth CN (2009) Lower extinction in sleep-or-hide mammals. *American Naturalist* 173: 264–272.

Long CV, Flint JA, Lepper PA (2010) Wind turbines and bat mortality: Doppler shift profiles and ultrasonic bat-like pulse reflection from moving turbine blades. *Journal of the Acoustical Society of America* 128: 2238–2245.

Lundy M, Montgomery I, Russ J (2010) Climate change-linked range expansion of Nathusius' pipistrelle bat, *Pipistrellus nathusii* (Keyserling & Blasius, 1839). *Journal of Biogeography* 37: 2232–2242.

Marnell F, Presetnik P (2010) Protection of overground roosts for bats (particularly roosts in buildings of cultural heritage importance). EUROBATS Publication Series No. 4. UNEP/EUROBATS Secretariat, Bonn, Germany.

McNab BK (1973) Energetics and the distribution of vampires. *Journal of Mammalogy* 54: 131–144.

Meehl GA, Tebaldi C (2004) More intense, more frequent, and longer lasting heat waves in the 21st century. *Science* 305: 994–997.

Mello MAR, Kalko EKV, Silva WR (2009) Ambient temperature is more important than food availability in explaining reproductive timing of the bat *Sturnira lilium* (Mammalia: Chiroptera) in a montane Atlantic Forest. *Canadian Journal of Zoology* 87: 239–245.

Mollhagen TR, Bogan MA (1997) Bats of the Henry Mountains region of southeastern Utah. *Occasional Papers, The Museum, Texas Tech University* 170: 1–13.

Németh I, Nyitral V, Altbäcker V (2009) Ambient temperature and annual timing affect torpor bouts and euthermic phases of hibernating European ground squirrels (*Spermophilus citellus*). *Canadian Journal of Zoology* 87: 204–210.

Newson SE, Mendes S, Crick HQP, Dulvy NK, Houghton JDR, Hays GC, Hutson AM, Macleod CD, Pierce GJ, Robinson RA (2008) Indicators of the impact of climate change on migratory species. *Endangered Species Research* 7: 101–113.

Park KJ, Jones G, Ransome RD (2000) Torpor, arousal and activity of hibernating greater horseshoe bats (*Rhinolophus ferrumequinum*). *Functional Ecology* 14: 580–588.

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37–42.

Parris KM, Hazell DL (2005) Biotic effects of climate change in urban environments: the case of the grey-headed flying-fox (*Pteropus poliocephalus*) in Melbourne, Australia. *Biological Conservation* 124: 267–276.

Peñuelas J, Filella I (2001) Responses to a Warming World. *Science* 294: 793–795.

Pierson ED (1998) Tall trees, deep holes, and scarred landscapes: conservation biology of North American bats. In: Kunz TH, Racey PA (eds) *Bat Biology and Conservation*, 309–325. University of Chicago Press, Chicago, Illinois, USA.

Postawa T (2004) Changes in bat fauna during Middle and Late Holocene as exemplified by thanatocoenoses dated with ^{14}C AMS from Kraków-Czetochowa Upland caves, Poland. *Acta Chiropterologica* 6: 269–292.

Prost S, Smirnov N, Fedorov VB, Sommer RS, Stiller M, Nagel D, Knapp M, Hofreiter M (2010) Influence of climate warming on Arctic mammals? New insights from ancient DNA studies of the collared lemming *Dicrostonyx torquatus*. *PLoS One* 5: e10447.

Pryde MA, O'Donnell CFJ, Barker RJ (2005) Factors influencing survival and long-term population viability of New Zealand long-tailed bats (*Chalinolobus tuberculatus*): implications for conservation. *Biological Conservation* 126: 175–185.

Racey PA (1973) Environmental factors affecting the length of gestation in heterothermic bats. *Journal of Reproduction and Fertility Supplement* 19: 175–189.

Racey PA (1979) The prolonged storage and survival of spermatozoa in Chiroptera. *Journal of Reproduction and Fertility* 56: 391–402.

Racey PA, Entwistle AC (2000) Life history and reproductive strategies of bats. In: Crichton EG, Krutzsch PH (eds) *Reproductive biology of bats*. 363–414. Academic Press, London.

Ransome RD, McOwat TP (1994) Birth timing and population changes in greater horseshoe bat colonies (*Rhinolophus ferrumequinum*) are synchronized by climatic temperature. *Zoological Journal of the Linnean Society* 112: 337–351.

Rebelo H, Tarroso P, Jones G (2010) Predicted impact of climate change on European bats in relation to their biogeographic patterns. *Global Change Biology* 16: 561–576.

Richter HV, Cumming GS (2008) First application of satellite telemetry to track African straw-coloured fruit bat migration. *Journal of Zoology* 275: 172–176.

Root TL, Price JT, Hall RK, Schneider SH, Rosenzweig C, Pounds JA (2003) Fingerprints of global warming on wild animals and plants. *Nature* 421: 57–60.

Rossiter SJ, Jones G, Ransome RD, Barratt E (2000) Genetic variation and population structure in the endangered greater horseshoe bat *Rhinolophus ferrumequinum*. *Molecular Ecology* 9: 1131–1135.

Rydell J, Bach L, Dubourg-Savage MJ, Green M, Rodrigues L, Hedenström A (2010) Mortality of bats at wind turbines links to nocturnal insect migration? *European Journal of Wildlife Research* 56: 823–827.

Sachanowicz K, Ciechanowski M (2006) First winter record of the migratory bat *Pipistrellus nathusii* (Keyserling & Blasius 1839) (Chiroptera: Vespertilionidae) in Poland: yet more evidence of global warming? *Mammalia* 70: 168–169.

Sachanowicz K, Wower A, Bashta AT (2006) Further range extension of *Pipistrellus kuhlii* (Kuhl, 1817) in Central and Eastern Europe. *Acta Chiropterologica* 8: 543–548.

Schär C, Vidale PL, Lüthi D, Frei C, Häberli C, Liniger MA, Appenzeller C (2004) The role of increasing temperature variability in European summer heatwaves. *Nature* 427: 332–336.

Scheel D, Vincent TLS, Cameron GN (1996) Global warming and the species richness of bats in Texas. *Conservation Biology* 10: 452–464.

Sendor T, Simon M (2003) Population dynamics of the pipistrelle bat: effects of sex, age and winter weather on seasonal survival. *Journal of Animal Ecology* 72: 308–320.

Simmons NB (2005) Chiroptera. In: Wilson DE, Reeder DM (eds) *Mammal Species of the World: A Taxonomic and Geographic Reference*, 3rd ed. 312–529. John Hopkins University Press, Baltimore, Maryland, USA.

Speakman JR, Racey PA (1989) Hibernal ecology of the pipistrelle bat: energy expenditure, water requirements and mass loss, implications for survival and the function of winter emergence flights. *Journal of Animal Ecology* 58: 797–813.

Syme DM, Fenton MB, Zigouris J (2001) Roosts and food supplies ameliorate the impact of a bad summer on reproduction by the bat *Myotis lucifugus* LeConte (Chiroptera: Vespertilionidae). *Ecoscience* 8: 18–25.

Thomas DW, Geiser F (1997) Periodic arousals in hibernating mammals: is evaporative water loss involved? *Functional Ecology* 11: 585–591.

Thomas CD, Cameron A, Green RE, Bakkewes M, Beaumont LJ, Collingham YC et al. (2004) Extinction risk from climate change. *Nature* 427: 145–148.

Thomas CD, Hill JK, Anderson BJ, Bailey S, Beale CM, Bradury RB et al. (2011) A framework for assessing threats and benefits to species responding to climate change. *Methods in Ecology and Evolution* 2: 125–142.

Trayhurn P (1993) Brown adipose tissue – from thermal physiology to bioenergetics. *Journal of Biosciences* 18: 161–173.

Turbill C (2008) Winter activity of Australian tree-roosting bats: influence of temperature and climatic patterns. *Journal of Zoology* 276: 285–290.

Turbill C, Geiser F (2008) Hibernation by tree-roosting bats. *Journal of Comparative Physiology B, Biochemical, Systemic, and Environmental Physiology* 178: 597–605.

Tuttle MD (1975) Population ecology of the gray bat (*Myotis grisescens*): factors influencing early growth and development. Occasional Papers of the Museum of Natural History, The University of Kansas, Laurence, USA; 36: 102.

Voigt CC, Lewanzik D (2011) Trapped in the darkness of the night: thermal and energetic constraints of daylight flight in bats. *Proceedings of the Royal Society Series B, Biological Sciences* 278: 2311–2317.

Walther G-R, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin J-M, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. *Nature* 416: 389–395.

Wang J, Gao W, Wang L, Metzner W, Ma J, Feng J (2010) Seasonal variation in prey abundance influences habitat use by greater horseshoe bats (*Rhinolophus ferrumequinum*) in a temperate deciduous forest. *Canadian Journal of Zoology* 88: 315–323.

Webb PI, Speakman JR, Racey PA (1995) Evaporative water loss in two sympatric species of vespertilionids bat, *Plecotus auritus* and *Myotis daubentoni*: relation to foraging mode and implications for roost site selection. *Journal of Zoology* 235: 269–278.

Welbergen JA, Klose SM, Markus N, Eby P (2008) Climate change and the effects of temperature extremes on Australian flying-foxes. *Proceedings of the Royal Society Series B, Biological Sciences* 275: 419–425.

Willis JS (1982) The mystery of the periodic arousal. In: Lyman CP, Willis JS, Malan A, Wang LCH (eds) *Hibernation and Torpor in Mammals and Birds*, 92–103. Academic Press, New York, USA.

Willis CKR, Brigham M, Geiser F (2006) Deep, prolonged torpor by pregnant, free-ranging bats. *Naturwissenschaften* 93: 80–83.

Yalden DW, Morris PA (eds; 1975) *The Lives of Bats*. Douglas David & Charles Limited, West Vancouver, British Columbia, Canada.

Zahn A (1999) Reproductive success, colony size and roost temperature in attic-dwelling bat *Myotis myotis*. *Journal of Zoology* 247: 275–280.