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2. The Implications of climate change for terrestrial UK Mammals

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EXECUTIVE SUMMARY

Mammals face a variety of threats in the UK, where faunal diversity and distribution has already been impacted historically. Climate change, particularly unprecedented extremes and extents of weather variability, add substantially to these threats. Even where climate change is perhaps not the primary threat to, or stressor of, a species' population dynamics, climatic effects can nevertheless interact with other factors, such as habitat loss, disease, or competition with invasives, to exacerbate the pressures on wildlife.

We identify a range of climate-related risk-factors and highlight those climate-mediated mechanisms with the potential to affect terrestrial UK mammal species. We attempt to answer the 'what if' question, so that mammal responses against climate predictions can be assessed and interpreted in the context of conservation management; but do so in spite of a lack of primary data for most species.

Four interactive consequences of climate change stand out as the main areas of concern: changes to food availability; thermoregulatory compromise; altered disease exposure / susceptibility and habitat change.

Changes in primary productivity influence herbivores (deer, rabbits, hares and many rodents). These may be absolute changes in food availability, or phenological changes influencing food at critical times. Insectivores (shrews, hedgehogs, moles & bats) are similarly vulnerable to invertebrate availability. Many invertebrates are most abundant during wet weather, however persistent rainfall can cause flying insects to become 'washed-out' of the air (affecting bats), and flood conditions compromise the ability of cursorial insectivores to hunt effectively. Carnivore species are, in turn, vulnerable to changes in this herbivore prey base, and to inclement conditions compromising their ability to hunt effectively. Even versatile omnivorous Carnivores, such as badgers and foxes are influenced by food-availability fluctuations, benefitting when frost-free winter nights give them access to important earthworm prey, but suffering when spring-droughts curtail this food source at a crucial time for juvenile development.

Thermoregulatory stresses are most profound for small species, such as rodents and insectivores. Some of these, for example dormice, hedgehogs and bats, have evolved to obviate this risk in part through winter hibernation. This strategy, however, is being compromised by winters too warm to make it fully effective, where metabolic rates cannot remain sufficiently suppressed for efficiency. Warm winters benefit the fecundity and development of red deer, and are associated with better over-winter badger survival, while cold-damp spring conditions cause badger cub mortality and can retard population growth rates in rodents.

Both exposure to-, and response to-, pathogens can be exacerbated by climate change, and effects on both enzootic and epizootic disease dynamics can result. The spread of disease by mobile insect vectors (e.g., mosquitoes), as well as altered susceptibility to parasite infestation, are well-recognised features of climate change projections. Furthermore, the persistence of pathogens on 'fomites' (any object or substance capable of carrying infectious organisms) is a function of microclimatic conditions, where often sustained winter frost is necessary to sterilise the environment. Crucially, the extent of disease and morbidity experienced by the host, which may ultimately impact population mortality rates, is in part a function of immune resource allocation – in turn the product of evolved selective traits. Conditions of food stress or habitat stress, resulting from climate change, may 'tip the

balance', where under more usual conditions the same disease would cause less pathology.

Habitat changes are also a projected corollary of climate change, interacting with habitat management. Loss of northern coniferous forests reduces areas suitable for pine martens and red squirrels (where spreading deciduous forest favours greys). Wet conditions, creating more Scottish peat-bog areas, would further limit suitable wildcat habitat. In particular, changes in the stability of aquatic habitats are predicted, where riverine specialists, such as water shrews, water voles, re-introduced beavers, (invasive) mink and otters might experience difficulties along water courses in response to drought or flood, and indeed almost all mammals suffer when the land is inundated over large areas, especially small species unable to escape the deluge.

In addition, we discuss a variety of effects on key life history stages, where often young mammals are more vulnerable than are adults. We also highlight cascade effects, related to climate change, such as climate effecting hybridisation risks for Scottish wildcats, or warm winters tempting badgers to forage further and expose themselves to a higher risk of road traffic accidents.

For each Order of mammals, we examine data quality, and the confidence we have in the ways mammals will respond to climate change, using IPCC AR5 criteria; though often restricted by a lack of empirical data. We conclude from generally weak evidence that climate change presents a moderate risk, overall, for mammals in the UK – against a back-cloth of other pressing vulnerabilities.

INTRODUCTION

There is a pressing need to develop a thorough, evidence-based understanding of the mechanisms driving population trends for UK mammals (Macdonald *et al.* 2008; SoBM, 2011; 2014). This imperative is, however, limited by a lack of empirical studies, and thus robust information, on whether trends are occurring, and why (TMP, 2005; 2009). This is a particular issue with respect to the influence of climate change, where a precarious reliance upon supposition and conjecture often limits confidence in projections for populations, undermining capacity to plan conservation and management.

Climate, and the bio-climatic niche envelope this defines (see Berry *et al.* 2002), is one of the major regulatory factors affecting mammal ecology. Palaeo-climate has been highly influential in the evolution of mammalian faunas, where rapid climate change events stand out in the fossil record as being particularly significant in determining mammal species distribution and abundance (Fernández *et al.* 2005; Bhaghwat & Willis, 2008; Lister & Stuart, 2008).

Predicting the diverse effects of climate change on terrestrial mammals within different ecosystems presents a major challenge for conservationists and policy makers (e.g., Crick and Sparks 1999; Post and Stenseth 1999; Inouye *et al.* 2000; Walther *et al.* 2002; Hulme 2005; Harrison *et al.* 2006; Grosbois *et al.* 2008; Walther 2010; Macdonald *et al.* 2010; Dawson *et al.* 2011). Climate trends are composed by weather patterns –principally temperature and rainfall regimes (though wind conditions may also be influential), where variation from normative values can destabilise optimal life-history adaptations and survival dynamics. Adverse abiotic conditions fall into three main categories: unseasonable conditions - resulting in phenological asynchrony: (e.g., Charmantier *et al.* 2008; Post and Forchhammer 2008; Drever *et al.* 2012; see also Root *et al.* 2006); persistent weather extremes (e.g., drought - Macdonald & Newman, 2002; Macdonald *et al.* 2010 / flood -

Campbell *et al.* 2013); and atypical weather variability (e.g., Campbell *et al.* 2012; Nouvellet *et al.* 2013; Zhou et al. 2013).

While warming trends are well established (e.g., Smith 2011), the potential for changing variability and increased uncertainty in regional weather patterns (IPCC 2007; 2012) must also be considered in developing scenarios (CCRA, 2012). UKCP09 predicts that drier summers and wetter winters are likely, against a general warming trend with considerable regional variation – though other outcomes are also plausible.

Due to the complexity of patterns of climate change, where mean trends are set against a background of changes in frequency, amplitude and variation, it is important to understand how these various components that comprise climate, impact on species (e.g., Luterbacher *et al.* 2004).

To survive and reproduce, mammals must adapt life-history decisions to environmental changes (McNamara *et al.* 1995; Feró *et al.* 2009). Physiological adaptability and decision-making processes are honed by evolutionary selection pressures according to the probability distribution of the environmental conditions experienced by the organism's ancestors (McNamara *et al.* 2001). Changes in the patterns and extent of fluctuation in the environment can therefore generate changes in the selective pressure on life-histories (Boyce *et al.* 2006; Ruzzante *et al.* 2008; Campbell *et al.* 2012; Nouvellet *et al.* 2013) and interact with the allocation of physiological resources, such as ability to respond to disease (Lafferty 2009). Assessing future conditions accurately in regions where weather conditions are variable, such as the UK (UKCP09; CCRA 2012), has a higher potential for error compared with environments that are relatively predictable (Gaillard & Yoccoz 2003). As a consequence, the degree of stochasticity in the environment can have a major influence on the optimal phenotype (Tuljapurkar *et al.* 2009; Annavi *et al.* 2014). Mammalogists must therefore gather data on how mammal populations are likely to respond to, and thus be vulnerable to, a comprehensive range of plausible climate outcomes, as proposed by experts in climate prediction (Grosbois *et al.* 2008; Tuljapurkar 2010). That is, ecologists should be equipped to reply with maximum confidence on how species will respond, to the 'what if' question, based in future climate scenario prediction.

Here we focus on mammalian biotic responses to these stressors. These can be direct, such as compromised ability to secure sufficient food, compromised thermoregulation (Wunder 1975; Webb and King 1984) or range changes (e.g., Hersteinsson and Macdonald 1992; Parmesan *et al.* 1999; Beever *et al.* 2011); or indirect, resulting from habitat change, exposure to different risk factor regimes (e.g., road traffic accidents - Macdonald *et al.* 2010), or interaction with disease (Walther *et al.* 2002; Macdonald *et al.* 2010; Lafferty 2009; Newman *et al.* 2001); all operating synergistically (see Brook *et al.* 2008).

Tipping points and state-shifts, due to the compound action of climate-driven and disease-driven stresses on organisms, warrant particular consideration. There is a finite burden of physiological stress each individual can tolerate, where a fraction less foraging success could allow a formerly immune-regulated disease to gain in pathology, or a newly arrived disease could overcome host immune resilience through co-infection (e.g., Hoberg *et al.* 2008).

Changing exposure of native mammals to pathogens, due to climate change, is a particular concern; one well established in the livestock industry (e.g., Van Dijk *et al.* 2010; Gale *et al.* 2010). There is a lack of focused investigation on wild mammals,

although spill-over and spill-back between farm animals and wildlife is well-recognised (SoBM, 2014). Diseases concerned can involve direct transmission, such as bovine tuberculosis, infecting deer (Böhm *et al.* 2007) and badgers (Gotazar *et al.* 2006), or involve indirect vectors (reviewed by Mills *et al.* 2010) such a blue-tongue, communicated between wild and domestic ruminants by culicoide midges, favoured under warmer, wetter climatic conditions (Purse *et al.* 2005). Similarly, there is a risk that future climate change could exacerbate the incidence of tick-borne diseases (Randolph *et al.* 2004; Rogers and Randolph 2006), with a broad range of native mammals sustaining *Ixodes sp.* ticks, which are extending their distribution further northward with changing climate (Lindgren *et al.* 2000). With specific regard to Lyme disease, however, in a report on climate change driven impacts of vector-borne diseases on human health, Rogers et al. (2012) highlight that there is no simple correlation between temperature and incidence of Lyme disease in people in the UK. Furthermore, they state that I would almost be impossible to predict reliably any change in tick abundance with climate change, because this will be the outcome of two opposing forces: higher temperatures, especially over winter, will accelerate development and may eliminate diapause (a period of winter quiescence, when ticks do not feed), while drier summers will limit tick host-seeking activity and increase mortality directly. They do acknowledge, however, that if climate change leads to an increase in key wild vertebrate fauna, especially deer, this could present an important risk factor.

Noteworthy too is that the capability of bats to undertake extensive and rapid dispersal movements, combined with a general northern shift in suitable habitats (Rebelo *et al.* 2010), has lead to them vectoring the spread of zoonotic diseases in Asia (Field, 2009) – diseases which also cause bat mortality (Mühldorfer *et al.* 2011). Worryingly, these caronaviruses have been detected for the first time recently in Europe (Reusken *et al.* 2010) and the UK (August *et al.* 2012).

Crucially, we also highlight inherent age class effects, where often neonatal / juvenile and geriatric individuals are most susceptible to climate-related stress (e.g., Coulson *et al.* 2001; Jacobson *et al.* 2004 – ungulates; Macdonald *et al.* 2010 - badgers; Campbell *et al.* 2012 - beavers). Incorporating demographic heterogeneities into population models can therefore influence dynamic responses to climate change (Coulson *et al.* 2001). Similarly, the level of influence climatic variables have on population dynamics can vary substantially without necessarily resulting in any change in population numbers, due to opposing forces, interacting population drivers and adaptability. That is, a population dynamic effect of climate change does not implicitly result in a change in population numbers.

Similarly key life-history events may represent the most sensitive periods to climatic stressors, such as mating periods, pregnancy, weaning/independence, dispersal, hibernation etc (Humphries *et al.* 2004). Care should, however, be exercised not to focus on climate to the exclusion of other potentially pertinent variables when interpreting climate-centered studies (Krebs and Berteaux 2006). For example, reproductive success may be influenced by prior reproductive effort (Ruusila *et al.* 2000; Dugdale *et al.* 2011), or offspring number may trade-off against offspring quality (Smith and Fretwell 1974), while population density may influence both reproductive success and survival, and be complicated by such factors as Allee effects (Albon *et al.* 1987; Coulson *et al.* 2000; Courchamp & Macdonald, 2001; Macdonald *et al.* 2002). Extensive studies of large mammals indicate that climatic extremes appear to influence juvenile survival, primarily during winter, although not independently of population density (Milner *et al.* 1999; Post & Stenseth, 1999; Coulson *et al.* 2001; Zhou *et al.* 2013). Increasingly warm winters are known to influence the development and fecundity of red deer (*Cervus elaphus*; Post *et al.*

1997) and Soay sheep (*Ovis aries*; Forchhammer *et al.* 2001) in Norway and the UK. The impact of such life history responses on population dynamics can occur years later when cohorts have reached reproductive maturity (Post & Stenseth, 1999; Forchhammer *et al.* 2001) and may, as in the case of Soay sheep, occur only above certain population densities (Grenfell *et al.* 1999; Coulson *et al.* 2000). On Isle Royale, USA, climate directly influences temporal dynamics at producer, herbivore and carnivore trophic levels (Post & Forchhammer 2001), as well as indirectly through mediation of trophic interactions such as wolf predation and moose herbivory (Post *et al.* 1999; Vucitech & Peterson, 2004).

Importantly, at the population level, not all the affects of increased environmental variability appear to be negative (e.g., Macdonald & Newman, 2002; Drake 2005; Brown *et al.* 2012) and the effects of projected increases in weather variability remain poorly understood (Weltzin *et al.* 2003; Boyce *et al.* 2006).

In the UK, the issues of climate change present challenges linked broadly to weather variability (UKCP09), moderated by maritime conditions and gulf-stream influences (CCRA, 2012). Moreover the conservation and management of mammals in the UK must contend with the interaction between climate affects and habitat loss and fragmentation, wildlife diseases, introduced species, impoverished ecosystem functionality, and human-wildlife conflict (SoBM, 2011).

To understand the impacts of climate change on the UK's 35 species of terrestrial mammals it is essential to be able to rely upon sound, evidence-based, long-term monitoring data (Macdonald *et al.* 1998; Macdonald *et al.* 2000).

Despite a host of specialist interest groups the UK still lacks an all-encompassing national mammal monitoring network (through initiatives have been undertaken, such as the Tracking Mammals Partnership; TMP 2009) and therefore only around half of UK mammal species are monitored with sufficient detail and scale to assess national population changes (TMP, 2009; SoBM, 2011). As a consequence, UK Mammal conservation cannot match the precision with which birds are monitored (Risley *et al.* 2011), exposing the need for systematic assessment of the changing fortunes of British mammals, and how best to consider climate in Species, and Biodiversity, Action Plans (UK BAP).

In response to this need, here we present a comprehensive assessment of how UK mammal population dynamics interact with climate, based on an extensive review of available literature. From this information we evaluate how populations are likely to respond to projected future climate stresses, where our confidence is tentative in some instances, where existing data are sparse. Our emphasis in doing so is to draw attention to questions that it would be helpful to answer when considering future mammal conservation scenarios and simultaneously to draw attention to the paucity of existing data. Throughout we rely upon population distribution and abundance data collated by the Tracking Mammals Partnership (TMP, 2005) and their update reports on population trends (most recently TMP, 2009), supplemented, as appropriate, by data from the State of Britain's Mammals annual perspective reports (most recently SoBM, 2014); details that we do not duplicate here, for brevity.

In overview, data-deficiencies that hamper understanding of the fortunes of British mammals generally are exacerbated further when one limits consideration to potential impacts due to changes in temperature and precipitation (SoBM, 2011). Our approach therefore focuses on the unifying mechanisms through which climate-based vulnerabilities operate on each species, to identify where policy and management could be most beneficial (IPCC, 2014).

In many instances, climate change is not the major factor affecting population dynamics, but may operate in tandem with other constraints. For example, the capacity for range shifts in response to northward progression of optimal climate niches, as observed in other taxa, are limited for many mammals by habitat fragmentation and habitat loss (SoBM, 2011) in excess of their dispersal distances; with the notable exception of bats (Huston, 2005; Rebelo *et al.* 2010). We combine the quality of data (evidence) and our confidence in these data to provide an assessment of how likely it seems that future UK population numbers will be affected, using IPCC, AR5 criteria – making the distinction that the population dynamics of all species, through climate niche adaptation, is always a function linked tightly to climatic factors.

For the western hemisphere Schloss *et al.* (2012) predict that on average 9.2% of mammals at a given location will likely be unable to keep pace with climate change. In some places, up to 39% of mammals may be unable to track shifts in suitable climates. Eighty-seven percent of mammalian species are expected to experience reductions in range size and 20% of these range reductions will likely be due to limited dispersal abilities as opposed to reductions in the area of suitable climate.

Adaptability and Climate Variability

Ability to predict the consequences of climate change hinges on understanding how species may, or may not, adapt to changing environmental conditions over a range of temporal and spatial scales (Dormann *et al.* 2009).

While rare species occupy a central place in biodiversity concerns, because they are the most prone to extinction (Pimm *et al.* 1988; Gaston, 1994), species that encounter a broader array of climatic conditions across their range are expected to have broader tolerances to climate change than restricted species (Brown, 1995; Fisher-Reid *et al.* 2012). Slow-living, generalist and wide-ranging mammals (e.g., badgers, Nouvellet *et al.* 2013; and beavers Campbell *et al.* 2012; 2013; also foxes etc) would be predicted to exhibit resilience in vital rates to environmental variation (Johnson 1998; Boyles & Storm 2007; Tuljapurkar *et al.* 2009; Dalgleish 2010; Macdonald *et al.* 2010; Huey *et al.* 2012). Resilient responses (Folke 2006) manifest as an adaptive capacity to follow new trajectories (Smit and Wandel, 2006), evident as changes in survival or fecundity (Stenseth *et al.* 1999; Gaillard *et al.* 2000; Sæther, Sutherland and Engen 2004; Stenseth *et al.* 2003; Kausrud *et al.* 2008; Campbell *et al.* 2012), or as phenological adjustments (Visser *et al.* 1998; Visser and Holleman 2001; Macdonald *et al.* 2010), which result in altered synchronicity of time-sensitive events (Parmesan 2006; Feró *et al.* 2009; Macdonald *et al.* 2010).

The UK Climate Change Risk Assessment (CCRA, 2012) highlights that those species with the most specialised niche requirements are likely to be most vulnerable to climate change, and that although some could benefit, many more would be impacted negatively (Brown *et al.* 2012; IPCC 2014). Levinsky *et al.* (2007) predict that, for Europe's 120 native terrestrial non-volant European mammals, under an unlimited migration scenario 32-46% of species may be severely threatened, with 1% extinction. Under a no migration scenario, however, things are much worse, with 70-78% of species threatened and 5-9% extinction rate. They predict that under the no migration assumption endemic species would be strongly negatively affected by future climatic changes, while widely distributed species would be affected less.

The impacts of climate change in northern European regions are likely to be shaped by the appearance of new species at least as much as by the disappearance of current species (Humphries *et al*. 2004). In particular Levinsky *et al*. (2007) propose that mammalian species richness will be reduced most dramatically in the Mediterranean region, but may increase towards the northeast and for higher elevations.

INSECTIVORES

Order Eulipotyphla
Family Soricidae – *Shrews*

The UK's native shrews (Common shrew, *Sorex araneus*; Pygmy shrew, *Sorex minutus*) have a wide distribution and occur commonly (TMP, 2005) and are not considered a species of especial concern (UK BAP, 2007 – TMP, 2009 species status not listed). Habitat loss and degradation, and not climate change, appear to be the biggest threat to shrews in the short term.

The direct effects of climate on shrews are data deficient, however studies outside of the UK have investigated the mechanisms through which climate effects operate. Shrews have tight energy budgets, requiring near constant hunting for invertebrates. Russel & Grimm (1990) highlight how the availability of prey (especially beetles) is crucial to shrew success, posing the question on to how climate-change may influence invertebrate numbers and seasonal availability. Particularly, any increase the length of the productive (summer) season, would extend annual food availability.

An intrinsic component of energy budgets for small mammals is growth potential and heat-loss conservation (surface area : volume ratio). Recent increases in body size have been observed in the masked shrew *Sorex cinereus* in Alaska (Yom-Tov & Yom-Tov, 2005); a trend attributed indirectly to global warming, due apparently to the higher food availability in winter and autumn leading to greater prey availability, thus enabling shrews to utilise this extra available energy for growth (see also Millien *et al*. 2006). There is thus little evidence to support how climate change may affect UK shrew numbers with any certainty (AR5 likelihood <33%), where other ecological factors will be more influential on future population dynamics.

Water shrews (*Neomys fodiens*) are also locally common (TMP, 2005) and we speculate, in the absence of direct studies, that here again climate-mediated abundance and seasonality of their aquatic invertebrate prey-base may be key. Water shrews would also be vulnerable to reduced river flow during drought periods (transitory habitat loss), especially in headland streams – a risk scenario acknowledged in the CCRA (2012), along with greater abstraction pressures on the freshwater environment. Again low evidence affords low confidence in the likelihood of major future population abundance effects (AR5 33-66% ~ however, drought effects are likely to be influential).

Family Talpidae – *Moles*

The European mole, *Talpa europaea*, is common (TMP, 2005) but there is insufficient data to monitor its ongoing status in the UK (TMP, 2009; SoBM, 2011) – though slight increases are suggested (British Mole Catchers Registry reports). There is a deficiency of literature discussing climatic affects on moles (AR5: low evidence, thus little confidence).

Main risks to moles are not primarily climate related, and involve direct attempts at control by landowners suffering damage from mole-hills, or from clostridium contamination of silage (Atkinson, *et al.* 1994: SoBM, 2011).

As with the other insectivores, effects on food supply are likely the greatest climatic risk – see discussion on earthworms and climate in the Badger section, below. Localised flooding, from intensifying rainfall patterns, would also be a risk factor (CCRA, 2012). As a consequence, we rate the likelihood of climate change having a major affect on future UK population numbers as AR5: <33%. Other factors are expected to be far more influential.

Order Erinaceomorpha – *Hedgehog*

The Hedgehog (*Erinaceus europaeus*) is locally common (TMP, 2005), but is in sharp decline (-44% 25 year trend, -23% 10 year trend; TMP, 2009) and was made a BAP species in 2007. Numbers have declined from an estimated 30 million in the 1950s, the UK population shrank to about 1.5 million in 1995, and has almost certainly fallen further since then (Wembridge, 2011).

Risks to hedgehogs predominantly relate to habitat loss, road traffic accidents, molluscicide poisoning and predation by badgers (Doncaster, 1992; Wembridge, 2011). Climate related risks, ancillary to these, would implicitly be exacerbated by warmer winters (disrupting torpor) and drier springs (limiting earthworm prey) (SoBM, 2011). Localised temporary flooding of foraging grounds would also be detrimental (UKCP09; CCRA, 2012). Hedgehogs are also especially susceptible to tick infections, potentially carrying Lyme disease (Gem *et al.* 1997), where future climate change could be monitored to see how this might enhance the broader spread of tick-borne diseases (Rogers & Randolph 2006).

Despite climatic effects on winter hibernation being long-established (e.g., Morris, 1984; Turbill *et al.* 2011) empirical studies, especially relating to distribution and abundance patterns, are surprisingly lacking in the UK. Hibernators also have approximately 15 per cent higher annual survival than similar sized non-hibernating species, where small hibernating mammals generally have longer maximum life spans (50% greater for a 50 g species), reproduce at slower rates, mature at older ages and have longer generation times compared with similar-sized non-hibernators (Turbill *et al.* 2011).

In New Zealand, where the European hedgehog is introduced, Webb & Ellison (1998) have modelled that body fat stores would be depleted in <1 day and >100 days in non-hibernating vs. hibernating hedgehogs, respectively. Ideally hedgehogs hibernate just below freezing point, where atypically warm winter conditions, with temperatures of 8-10ºC, cause fat reserves to be used up more quickly, simply because metabolism proceeds faster at higher temperatures (see Carey *et al.* 2003).The lack of definitive knowledge on the fortunes of UK hedgehogs has led the British Hedgehog Preservation Society and People's Trust for Endangered Species, to review the state of British Hedgehogs (Wembridge, 2011 & PTES Annual Hedgehog Hibernation Survey Reports). They found that the emergence time of hedgehogs does seem linked to variation in proximate climatic conditions, but without any substantial evidence currently on climate change mediated trends. For example, in 2013 the mean day number for first sightings was 10 days earlier in the South West than in Scotland. In 2012, however, with the particularly cold and wet spring conditions in southern England the reverse was true with hedgehogs north of the Scottish border active earlier than those in the south; a finding corroborated by hedgehogs seen by BTO *Garden BirdWatch* volunteers.

With regard to Morris's observation in the 1960s, that Scottish hedgehogs became active later than those in southern England, the PTES compared data from 1966 with that of 2012, 2013 and 2014. They found no significant difference in emergence timings, suggesting that climate change is yet to be having a measurable impact on this aspect of hedgehog behaviour. The final PTES 2014 Report concludes that: "Phenological differences between regions do not appear to be clear, nor does the impact of climate change on patterns of emergence."

As with the shrews (above) insectivorous hedgehogs are also affected by climatic influences on their food supply, principally earthworm, *Lumbricus terrestris* (see Doncaster, 1994) – a phenomenon we discuss in more detail in the Badger section, below. With little evidence but moderate-high confidence in response mechanisms, we assess that hedgehogs are likely (AR5: >66%) to be vulnerable to population decline in the UK, in response mostly to altered hibernation and food supply dynamics, but against a back-cloth of more major population drivers.

Order Chiroptera – *Bats*

Bats exhibit traits that make good indicators of the status of habitat type and structure, food variety, and the availability of microhabitat niches (Medellin et al. 2000). Of the 11 of Britain's 17 bat species for which sufficient data are available, four are increasing (greater and lesser horseshoe bats, Natterer's bats and common pipistrelles), and seven are stable (whiskered bats, Brandt's bats, Daubenton's bats, serotines, noctules, soprano pipistrelles and brown long-eared bats).

Key pressures on bats (landscape change, agricultural intensification, development, habitat fragmentation) are also relevant to many other wildlife groups. Bats are sensitive to pollution and factors affecting their insect prey (e.g., pesticides, drainage, land management change). Climatic shifts are predicted to affect bat populations through changes in their yearly hibernation cycles, breeding success and food availability. Bat dispersal is not entirely unrestricted and it does require habitat corridors, notably hedgerows, to provide landscape connectivity. The ability of bats to disperse over extensive ranges also exposes populations to emergent diseases with ever more northerly distributions; an especial concern when these diseases are zoonotic, such as coronaviruses, lyassaviuses etc (Smith and Wang, 2013).

Bat life-history strategies are unique for their size; they are generally long-lived (*c.* 20–30 years) and typically have small litters of 1–2 pups per annum. Reduced litter size and lower mortality risks may be influenced by their ability to fly (Ransome & McOwat, 1994; Sherwin *et al.* 2012).

Although, again, scientific reports on the effects of climate change on bats in the UK are few, climate likely influences their survival and reproduction by controlling the productivity of insects, and thus food availability, during the energetically demanding period of reproduction (Ransome & McOwat, 1994). The timing of birth and growth rate of young pipistrelle, greater horseshoe and lesser horseshoe bats are demonstrably related to climate – higher temperatures cause earlier birth dates and faster growth rates (Ransome & McOwat, 1994)

Hibernation contributes to increased longevity in bats by enhancing over-winter survival rate and through long periods of inactivity slowing senescence (Wilkinson & South, 2002) – thus, as with hedgehogs, warm winter conditions can prove detrimental to metabolic conservatism. Sherwin *et al.* (2012) have reported recently that greater horseshoe bats in the UK spend less time in torpor when the outside

temperature warms. They also found that captive eastern red bats, and other species of wild tree-roosting bats, respond similarly.

Also, climate changes that would lead to changes in the internal temperatures of roosts that have been used by bats for decades will force bats to locate and use new, or different, roosts. Colder conditions to around −30˚C may trigger migration movements, as recorded in Eastern European countries (Tattersall & Macdonald, 2001).

Of note is that while *Pseudogymnoacsus destructans*, the causal agent of white-nose syndrome (WNS), has extended its range – linked to climate change (Mahler *et al.* 2012), and has been detected in the UK, UK bats seem more immune to disease than North American counterparts (SoBM, 2015). In North America the irritation caused by WNS can cause bats to awaken from hibernation, consequently exhausting energy reserves, leading to mortality (Foley et al. 2011).

Length of the productive season is also critical, where parturition in spring must provide sufficient time for young to learn to forage successfully and establish adequate fat reserves before winter; critical for over-winter survival for hibernating species (Ransome, 1989); Thomas *et al.* 1990). In addition, natural selection favours matching high energetic demands of lactation to coincide with greatest seasonal resource availability (Visser *et al.* 1998). If bats arouse before their food source is available in the spring, due to warming trends effecting the internal temperature of roosts, they could face starvation.

While detailed research on climate-bat interactions is limited in the UK, work in North America is informative and supports inference. Frick *et al.* (2010) provide a comprehensive assessment of the effects of climate on a population of little brown myotis *Myotis lucifugus,* in southern New Hampshire, USA – using 16 years (1993–2008) of mark–recapture data to test whether survival and breeding propensity is influenced by regional weather patterns and timing of reproduction.

Adult female survival was highest in wet years with high cumulative summer precipitation. First-year survival was considerably lower than adult survival and depended on pup date of birth, such that young born earlier in the summer (*c.* late May) had a significantly higher probability of surviving than young born later in the summer (*c.* mid-July). Similarly, the probability of young females returning to the maternity colony to breed in the summer following their birth year was higher for individuals born earlier in the summer. Sherwin *et al.* (2012) argue that in the UK warmer climates in the future may benefit females by allowing them to give birth and wean their young earlier, leaving more time for the mothers to store fat reserves in preparation for hibernation.

Although minimum temperature is most often associated with limiting volant insect availability and bat foraging activity Frick *et al* (2010) found that cumulative precipitation during the period of bat activity (April–October) was more strongly associated with annual survival. High precipitation is generally associated with greater insect abundance, including culicids (mosquitoes), dipterans (flies), and lepidopterans (moths), which are important components in diets of *M. lucifugus* in the north-eastern U.S. (Anthony *et al.* 1981). The link between moisture availability and insect abundance is the likely driver of the observed positive influence of summer precipitation on survival*.* Frick *et al.* (2010) further stress that bats can be affected negatively by summer drying patterns, associated with climate change and limiting insect prey. They found a lack of support for an influence of average minimum temperature on bat survival; however this could be due to low year-to-year variability

in temperature compared to that of seasonal precipitation. They also found that less rainfall in the spring and summer resulted in fewer insects (e.g., Culicidae), for bats to eat, due to a lack of standing water bodies for insects to breed in. Further recent commentary from Sherwin *et al.* (2012) adds that during dry conditions bats, particularly lactating females, may have to fly further to drink. Bats are more vulnerable to dehydration than other mammals of a similar size, especially in arid areas, as they lack specific adaptations to retain water and it evaporates at a high rate from the large surface area of their wings.

Linton (pers comm.), from an ongoing study of bats in Wytham Woods, Oxfordshire, however, has found that the protracted and heavy rain in the spring – early summer of 2012 has 'washed out' insects from the air in which bats forage, leading to a lack of feeding opportunities. Clearly, 'optimal' rainfall conditions vary with circumstances.Generally, bats are more mobile than other mammals of their size, and their movements are less conspicuous than those of larger mammals (Huston, 2005). In a review of bat species distributions across Europe, Rebelo *et al.* (2010) predict that bat species more associated with colder climates, hence northern latitudes, could be more severely affected by climate warming, with some extinctions predicted by the end of the century. The Mediterranean and Temperate groups seem to be more tolerant of temperature increases; however, their projections varied considerably under different climate change scenarios. Evidence for a major climatic affect on UK bat populations is thus mixed, supported by inferences from other regions. Confidence for a climate-related change in UK bat species distribution and abundance is however high, thus overall we assess that bats are very likely (AR5: >90%) to be affected by future climate change, interactive with habitat loss and fragmentation.

INSECTIVORE SUMMARY:

Climatic Vulnerabilities:
- *Limited capability to relocate (flooding) by small terrestrial species*
- *Sensitivity to invertebrate food supply, where climate change related reduction in insect availability would impact population dynamics negatively.*
- *Flooding – Mole tunnels / Water shrews & stream flow*
- *Hibernation – disruption to cycle & trait efficiency; hedgehogs & bats*

Importance of Climatic effects:
- *Most significant for hibernators – less important issue for other representatives*

Data quality & confidence:
- *Bats – very likely to be affected by climate change – negative effect on numbers for most species: high agreement, medium evidence – giving high confidence*
- *Hedgehogs – likely to be affected negatively, in terms of numbers: high agreement, limited evidence – medium confidence*
- *Others – Unlikely to be affected significantly: medium agreement, limited evidence – low confidence*

RODENTS

Order: Rodentia
Families Cricetidae – *voles;* **Muridae** *– mice & rats*

In the UK, the most abundant small mammals (e.g., Field vole, *Microtus agrestis*; Bankvole, *Clethrionomys / Myodes glareolus*; Woodmouse, *Apodemus sylvaticus*: see TMP, 2005 for estimated abundances) are vulnerable to a wide range of threats (TMP, 2005), however climate change is not chief amongst these. Nevertheless, given how responsive small mammal population densities are known to be to environmental fluctuations, it seems very likely that climate change will have significant impacts on rodent populations. Moreover, such changes will have cascade effects on their predators (see Lima *et al.* 2002).

Perhaps precisely because of this axiom, the effects of climate on small rodent species are not well represented in the literature and, somewhat surprisingly, these species are all data deficient, particularly in the UK (AR5: low evidence).

Blois *et al* (2010) report palaeo-climatic evidence for small diversity loss in response to late-Pleistocene climate change (favouring the versatile deer-mouse in North America, to the expense of other species), and therefore effects on these species definitely warrant concern (see also Lima *et al.* 2002).

Historically, as the hosts of the blood-feeding arthropod vectors, rodent species were associated with the spread of various zoontic diseases, such as plague, typhus, malaria, yellow fever, and dengue fever. Gubler *et al.* (2001) draw attention to how these diseases, still endemic to various rodent populations in North America, are at heightened risk of re-establishing, due to climate-driven mechanisms.

Food supply and variation in seasonal food supply, length of the productive season and inter-annual differences in food availability prove critical to small mammal population dynamics, where high natality or mortality rates can affect densities on short temporal scales (Flowerdew *et al.* 2004). Herbivorous voles and omnivorous mice are subject to different dietary regulation, however – where the invertebrate prey base, as discussed for shrews and bats (above) presents an extra variable for mice.

Most crucial in this food supply is the abundance of the autumn mast crops (Flowerdew *et al.* 2004). Selås *et al.*'s (2002) study of bank vole and wood mouse abundance in Norway revealed that the bilberry index of both the current and previous year, and within-year spruce seed index, contributed significantly to population growth indices of the bank vole; whereas the acorn index significantly influenced only the wood mouse, apparently through increased winter survival. In the UK, Flowerdew *et al.* (2004) demonstrated quantitatively the effects of mast crops and local food supplies on rodent dynamics, with evidence of population synchrony between sites for wood mice and voles. They propose that it may therefore be possible to extrapolate population changes from site-specific to national scenarios.

Vole population abundance also cycles inter-annually, however these cycles are less clear in the UK than they are in boreal populations (see Lambin *et al.* 2006). Where vole populations do cycle, climatic conditions are influential. For example, Kvrre *et al.* (2008) found that, under winter snow conditions in Fennoscandia, winter weather and snow conditions, together with density dependence in the net population growth rate, accounted for changes in lemming (*Lemus lemus*) population dynamics. Ars & Imms, 2002 found similar effects for Tundra voles (*Microtus oeconomus*), where mild weather that led to the formation of ice on the ground seemed to be detrimental for winter survival.

Increased temperature, especially during the winter, also enables rodents to divert energy from maintenance to growth. Furthermore, elevated temperature may

increase the length of the growing season, thus increasing primary production and consequently food availability. For instance, recent increases in body size have been observed in the Japanese large field mouse *Apodemus speciosus* (Yom-Tov & Yom Tov, 2004). Buesching (Pers Comm; see also notes on Squirrels, below, e.g., Koprowski. 1991), working in Nova Scotia, Canada, also reports that unpredictable spring weather can affect early population success at the start of the productive season. That is, unseasonably wet, or cold weather – typified by resurgent wintery conditions – causes loss of early litters and thermoregulatory stress-mortality.

It is also important to note that small mammals may play a role in mediating climatically driven vegetation change. In addition, predators and prey may be less able to detect one another during wet weather, with consequent impacts on the trade-offs between predator avoidance and energy budgets (e.g., Hilton *et al.* 1999).

One of the most detailed mechanistic studies of climate effects on a rodents species in the UK, by Marsh *et al.* (2001), is for the Yellow-necked Mouse *Apodemus flavicollis*; where the TMP (2005) highlight this rodents' greater sensitivity to climatic effects. Maximum summer temperature was the most significant variable explaining distribution, while mean rainfall and winter temperature parameters were not influential. Marsh *et al.* (2001) speculate that low summer temperature may limit Yellow-necked Mouse distribution through impacts on tree seed production and diversity; such that climatic change leading to a rise in summer temperature might encourage range expansion (see also Alcantara *et al.* 1991).

The harvest mouse (*Micromys minutus*) is another small rodent species where climate change is considered a major vulnerability (TMP, 2005). Harvest mice have a preference for dry conditions and may be limited under conditions of heavy summer rainfall, or through habitat effects, such as the flooding of reed-beds (Macdonald & Tattersall, 2001). Climatic effects, however, are probably secondary to the impact of changing agricultural practice (Macdonald *et al.* 1998)

The water vole, *Arvicola amphibius* (formerly *A. terrestris*), is a BAP species of concern, declining in numbers (TMP, 2005; 2009; SoBM, 2012). While habitat destruction and change with intensification of agriculture are probably the greatest threats to this species, population decline has been exacerbated greatly in the last 20–25 years by the spread of the introduced American mink (*Neovison vison*), a predator against which the water vole has little defense (Macdonald & Harrington, 2003). Water voles are also threatened by water pollution, increased cattle grazing, human disturbance and, to a more limited extent, climatic change (Macdonald & Tattersall, 2001). Moorhouse *et al.* (2008) demonstrate an association between forage availability, individual water vole growth rates and time to sexual maturity, suggesting that any climatic limitation on riparian growth would have an impact. Obviously, as an aquatic species, water voles will also be vulnerable to changing river flow rates (CCRA, 2012), particularly to riparian flooding. Studies addressing climatic affects on water vole populations specifically are lacking.

Pests: Rats & House mouse

The common rat (*Rattus norvegicus*) and House Mouse (*Mus musculus*) are considered as pests in the UK, due to conflict with people resulting in physical damage to buildings and machinery, infestation of food stores and the spread of

zoonotic diseases, such as toxoplasmosis, Q-fever, Hantaan fever, *Cryptosporidium*, *Salmonella, cryptosporidium* and *Leptospirosis* (Macdonald & Tattersall, 2001; SoBM, 2014). These are diseases that the IPCC is concerned may spread in response to climate change, if rodent populations expand, particularly during episodes of extreme precipitation (Githeko & Woodward, 2003).
Both species have broad climatic niches, and thus wide biogeographic distributions (Berry & Jakobson, 1975), aided by introductions (e.g., Chapuis *et al*. 1994. As a consequence, their numbers do not seem especially restricted by climate trends, though inter-annual variation in temperature regimes and effects of food supply are likely influential on annual population success. Increases in either species in the UK, however, would be undesirable. For example plagues of house mice have been associated with periods of prolonged dry weather in Australia (Saunders & Giles, 1977).

The Black rat (*Rattus rattus*), legally protected in the UK (TMP, 2005), is at the northern extremity of its range in the UK, and therefore restriction of their distribution may increase with climate warming (Macdonald *et al*. 1998).

In overview, evidence quality is mixed for these rodent species, but nevertheless we would place high confidence in the mechanisms involved. While it is thus a likely-very likely that milder winters, longer productive summers and better autumn mast crops will benefit small rodents, the importance of this population driver is unlikely to be of major significance in determining overall population abundance, versus more dominant population drivers.

Family: Scuiridae – *Squirrels*

Eurasian red squirrels (*Sciurus vulgaris*) are a BAP species in the UK, in rapid decline (SoBM, 2011), while introduced American grey squirrels (*S. carolinensis*) are assurgent (Gurnell *et al*. 2004). This is due in major part to loss and fragmentation of preferred red squirrel coniferous woodland habitat, due mainly to management – though with climatic interactions - and through transfer of squirrel parapoxvirus; a disease that is fatal in red squirrels but not in greys (Tompkins *et al*. 2002). As Eurasia warms, the climatic niche of red squirrels is retreating northwards (Bertolino *et al*. 2003), which is a particular issue in the British Isles, where reds are already reduced to strongholds in northern Scotland.

Despite the substantial vulnerability red squirrels have to climate change effects in the UK, evidence is lacking, leaving full evaluation data deficient. By way of illustrating climate effect mechanisms, Reale *et al*. (2003) report that in response to warmer spring temperatures and greater seasonal food supply in the Canadian Yukon, an American red squirrel population (*Tamiasciurus hudsonicus*) has advanced the timing of breeding by 18 days over the last 10 years (6 days per generation).

While grey squirrels may be succeeding and reds declining over most of the UK, Ozgul *et al*. (2010) reports that recent climate-linked extension of the productive season benefits yellow-bellied marmots (*Marmota flaviventris* – a ground squirrel studied in Colorado) could be curtailed if future climate change increases the severity of late-summer droughts. This highlights a plausible vulnerability that warrants further research for grey squirrels in the UK. In support of this, Koprowski (1991), working in Kansas, reported that juvenile (but not adult) grey squirrel over-winter survival was effected significantly by reduced mast crop in the previous autumn; seed production known to be tied to weather conditions (e.g., Silvertown *et al*. 1980). Similarly, the

timely availability of spring food was also important to the survival of squirrel litters (Koprowski, 1991).
In overview, future climate change seems unlikely to be a major driver of squirrel population success, however mixed evidence, in which we place medium confidence, leads us to acknowledge that there is a 33-66% (AR5) likelihood that squirrel populations may experience habitat related range changes or experience stress due to autumn drought.

Family: Gliridae – *dormice*

The hazel dormouse (*Muscardinus avellanarius)* is a UK BAP species, which despite concerted conservation efforts, is still in slight decline (SoBM, 2011). Habitat loss and fragmentation are recognised as the primary risks to hazel dormice, and they are better suited to Continental European climates, with warm dry summers and cold dry winters. Bright & Morris (1995; and the TMP, 2005) highlighted that the unpredictable British maritime climate results in very variable dormouse annual recruitment rates, increasing the vulnerability of small populations in fragmented habitats. Despite this recognition, empirical studies on climate effects in the UK are lacking. As with other hibernators (bats & hedgehogs, above), warmer winters are also likely to disrupt hibernation (TMP, 2005).

A detailed study of climatic effects on dormouse hibernation physiology and energy balance in Germany, by Pretzlaff & Dassmann (2012), found that *M. avellanarius* body temperature followed ambient temperature for most of the hibernation season (with skin temperature down to −2.9°C) and that they did not compensate for changes in ambient temperature. Dormice are thus more likely to deplete fat reserves before the end of hibernation with warmer temperatures. Arousals also occurred more frequently during warmer months, also after seasonal effects were eliminated, causing substantial additional energy expenditure.

Despite the scarcity of dormice in northern England, and their absence from Scotland, Bright & Morris (1995) attest that cold winters are not the issue, as this species lives in Eastern Europe and also further north in Sweden, areas where the winters are very much colder than in Britain. They propose that the problem lies in the summer weather, where hazel dormice survive best in warmer and drier parts of Britain. When the weather, or food supplies, are poor in the summer, dormice frequently enter facultative torpor. This can delay their breeding until August or later (the mean birth date in south-west England is 3rd August, 11 = 72 litters, Bright & Morris, 1995). Young born late in the season may not survive hibernation, especially if winter begins early. Thus total reproductive output can be affected.

According to Bright & Morris (1995), it is not only absolute temperature, nor amounts of rainfall, that limit dormice, but also the fact that the timing and duration of summer is much less certain in Britain than in Continental Europe. Summer (productive season) can commence or conclude by up to several weeks difference inter-annually. The date of first flowering (crucial to spring pollen feeding by dormice) may vary by up to 6 weeks (Hepper, 1975). Summers are therefore of unpredictable duration and have no fixed point in the calendar (see also Badger section; Macdonald *et al.* 2010). Breeding too early or too late can reduce dormouse numbers, yet successful timing is opportunistic, where small populations are particularly vulnerable to a succession of bad breeding years. Bright & Morris (1995) suggest that three bad years in a row may occur several times in less than 100 years, and even five bad years in succession is possible.

The edible (or 'fat') dormouse (*Glis glis*) is not native to England, having been introduced in 1902 (Burgess *et al.* 2003). This species has a conflicted status in the UK, being an introduced alien nationally, listed on Schedule 9 of the W&CA, while simultaneously listed in Appendix III of the European Bern Convention and Schedule 6 of the W&CA. While a very restricted UK distribution (TMP, 2005) limits assessment of climate change impacts, the fortunes of edible dormice are known to relate to reproductive failure due to paucity of autumn fruit (Bieber, 1998; Burgess *et al.* 2003), where any climatic factors exacerbating this effect would be detrimental to population success.

Habitat loss is likely to continue as the major concern for future dormouse population success, but moderate evidence with medium confidence leads us to predict that especially hazel dormice are likely (AR5: >66%) to benefit from warmer summers with a later onset of winter, however mild winters may disrupt hibernation efficiency.

Family: Castoridae – *Beavers*

While Eurasian Beavers (*Castor fiber*) were extinct from the UK until recently, re-introductions in Scotland (Knapdale) and England (Cotswolds) are proceeding well (SoBM, 2011: http://www.scottishbeavers.org.uk/). Despite this restricted UK distribution and abundance, beavers warrant consideration with respect to climate interactions because of the thoroughness with which their responses have been investigated by work in Norway. This is also broadly instructive for how climate can be influential on reintroduction schemes.

Campbell *et al.* (2012) examined ≥90 year trends in different components of climate in Telemark, southern Norway (precipitation mean and coefficient of variation; temperature mean, seasonal amplitude and residual variance), with respect to survival and recruitment rates for 242 beavers over a 13 year population study. They observed no long-term trends in precipitation, but did see trends in all components of temperature, with mean and residual variance increasing and seasonal amplitude decreasing over time. Beaver kit, juvenile and dominant (territory holder) adult survival all benefitted from lower coefficients of variability in precipitation, with further benefits to dominant adults of lower residual temperature variance; benefits to kit and juvenile survival was associated with lower mean annual precipitation. No significant effects were found on the survival of non-dominant adults, though the sample size for this category was low. Greater recruitment was linked (in order of influence) to higher seasonal amplitude of temperature, lower mean precipitation, lower residual variance in temperature and higher precipitation coefficients of variation.

This highlights that both climatic means and, especially, variance can influence beaver population dynamics significantly. In terms of direct mechanisms through which these effects operate, further work by Campbell *et al.* (in press) is revealing that weather conditions affect the quality, availability and the seasonal phenology of beaver forage. In accord with studies on other herbivores (see *note on herbivory*, below), juvenile body-weights tend to be lighter after colder winters, while warmer spring temperatures are associated with lighter adult body-weights, mediated by enhanced green-up phenology rates.

Counter-intuitively, Campbell *et al.* (in press) report a negative association between annual rainfall and body-weight in juveniles and adults, and also with reproductive success. They attribute this to effects on the growth of Alder (*Alnus incana*), the beavers' principal food tree in the study area. Alder exhibits a positive relationship with rainfall for trees growing at an elevation of >0.5m above the mean water level, but a negative relationship for trees growing <0.5m, such that trees near water level,

prone to water-logging, produce less forage in wetter years. This suggests that temperature influences beavers at the landscape scale via effects on spring green-up phenology and thermoregulation, while rainfall influences beavers at finer spatial scales, through topographical interactions with plant growth. Unlike most other herbivores, beavers are an obligate aquatic species and central place foragers utilising a restricted foraging range, limiting their ability to take advantage of better forage growth further from water during wetter years.

The effect of climate extremes must also be mentioned in this context. Buesching (pers comm) reports that in Nova Scotia Canada, the driest spring on record in Nova Scotia in 2012 (Environment Canada) has resulted in North American beaver (*C. Canadensis*) lodges being stranded far above the water-line along many lakes and rivers, leading beavers to abandon them – perhaps increasing their vulnerability to predators and road traffic accidents.
That environmental variation proves significant to this generalist, wide ranging species, at the slow end of the slow-fast continuum of life-histories, has broad implications for the susceptibility of populations and species to changes in climate.

The most significant factor for post-reintroduction beaver success in the UK over the next 20 years is going to be the rate and success with which recover their former range. While there is robust evidence that beavers population dynamics are controlled closely by climate variability, varied inter-annual responses lead us to assess that a concerted affect of climate on UK beaver numbers is marginal (AR5 likelihood: 33-66%)

RODENT SUMMARY:

Climatic Vulnerabilities:

- *Limited capability to relocate (flooding) by small terrestrial representatives (mice & voles)*
- *Linked climate-disease vulnerabilities in pestilential rodents species, with zoonotic implications*
- *Seasonal phenology, suitable spring weather, autumn mast crop (mice, voles, rats, squirrels ~ also beavers)*
- *Summer rainfall – wet conditions disadvantage esp. harvest mice and house mice*
- *Hibernation - disruption to cycle & trait efficiency; dormice*
- *Stream flow rate changes – Water voles (beavers)*
- *Longer-term influences on habitat change – red/grey squirrel distribution.*
- *Negative effect of climatic variability and unseasonable extremes – beavers,*

Importance of Climatic effects:

- *Most significant effects noted for dormice*
- *Food chain effects for Carnivores consuming rodents*

Data quality & confidence:

- *Generally – even though small rodent population dynamics are very responsive to climate, it seems unlikely that that climate change will be the primary driver of future UK population numbers or distribution, against a back-cloth of other factors: medium agreement, limited evidence – giving low confidence.*

- *Beavers – likely to be affected, but unlikely that this will be a major population driver: medium agreement & robust evidence – high confidence.*

RABBITS & HARES

Order: Lagomorpha: Family: Leporidae - *hares and rabbits*

Energy budgets increase during cold and wet conditions. These factors are particularly pertinent for small herbivores: internationally, greater over-winter survival of both the Brown hare *Lepus europaeus* and the European rabbit *Oryctolagus cuniculus* are associated with warmer winters (Marboutin and Hansen 1998; Rödel *et al.* 2004) while increased thermoregulatory costs, along with the flooding of burrows, are cited as the mechanism by which some populations of rabbit (and vole *Microtus* spp.) show a negative response to rainfall (Heikura 1977; Pinter 1988; Palomares 2003; Tablado *et al.* 2012).

Smith *et al.* (2005) report a decline in hares (*L. europaeus*) throughout Europe since the 1960s. Possible reasons include agricultural intensification and changes in climate and predator numbers, but no clear consensus has been reached as to the relative importance of each. Their study found that field size, temperature, precipitation and hunting had no effect on hare density across Europe, although fecundity was affected adversely by heavy summer rainfall.

Rodel & Dekker (2012), working in The Netherlands and Germany, found (from hunting bag surveys) that the number of hares shot was lower in years with higher amounts of precipitation during late summer/autumn, and the number of rabbits shot was lower in years with high precipitation in spring. They propose that rainy weather conditions could reduce the survival rate of young rabbits in spring and heighten the risk of disease outbreak, specifically in autumn. They also identified a time-delayed, interactive effect between precipitation in spring and winter weather for rabbit dynamics: rabbit numbers were limited by low temperatures during the prior winter season, but only when precipitation was high during spring of that previous year. They propose that lower body condition results from rainy spring weather, leading to a subsequent greater vulnerability to harsh winter conditions.

UK-specific studies of climate effects on lagomorphs are again limited. Rabbits are abundant in the UK and while climatic effects reducing their numbers may be desirable, the rabbit is an important prey species for mammalian and avian predators and is considered useful in preventing secondary succession in some calcareous grassland, dune and heathland habitats (TMP, 2005). By contrast the Brown hare, as well as the Mountain hare (*L. timidus*) are both UK BAP species (SoBM, 2011), where especially the latter is declining, and so further climatic stresses would be of concern, causing the mountain hares bio-climatic envelope to shift northwards (Anderson *et al.* 2009). Rabbit mortality, due to haemorrhagic disease, may also be exacerbated due to climate change-related stresses (Cooke, 2002); Real *et al.* (2009) linked this climate x disease decline in rabbits to effects on Iberian lynx predator populations in Spain.

The colour-change of mountain hares (*L. timidus scoticus*) is also linked to climatic conditions, changing white more rapidly under inter-annually colder autumn conditions and back to brown under warmer spring conditions (Watson, 1963; Flux, 1970).

Due to low evidence and low confidence it seems about as likely as not (AR5: 33-66%) that future climate change will be a major driver of lagomorphs population success, where the benefits of milder winters could be off-set if conditions become wetter.

LAGOMORPH SUMMARY:

Climatic Vulnerabilities:
- *Exposure and thermoregulatory stress: cold winters & wet summers have negative consequences*
- *Flooding of burrows – rabbit*

Importance of Climatic effects:
- *Minor (current) impact*

Data quality & confidence:
- *About as likely as not for UK populations to be affected by climate change in the future: Medium agreement, limited evidence – giving low confidence*

A note on Herbivory

Weather can influence vegetation growth, impacting herbivores indirectly through resource availability. Within limits, plant primary productivity increases with temperature and moisture (Rosenzweig 1968). Thus, for many ungulate herbivores (e.g., Sæther 1985; Owen-Smith 1990; Georgiadis *et al.* 2003), high rainfall is associated with greater body-weight, enhanced body-condition and increased population growth. Impacts on northern temperate ungulates, due to changes in total plant productivity resulting from changes in temperature regimes, have proven less evident (Steinheim *et al.* 2004). This is conceivably because of interactions between moisture and temperature (e.g., Xu *et al.* 2004) or due to the direct effects of heat-stress on vertebrate herbivores (e.g., Aublet *et al.* 2009).

Mechanistically, in seasonal environments, variation in climate can also influence the phenology of vegetation growth (Pettorelli *et al.* 2005a; Cleland *et al.* 2007). In temperate regions, warmer spring temperatures promote the rapid growth of plants, dormant over winter (Laycock and Price 1970). During this early growth phase plant tissue has higher concentrations of nutrients, and lower concentrations of tough structural and defensive compounds, than in the season (Mattson 1980; Veraart *et al.* 2006). Herbivores thus gain greater benefits, per unit foraging time, when feeding on this earlier growth (Demment and Van Soest 1985).

UNGULATES

Order: Artiodactyla - *deer, wild sheep & wild boar*

Climatic effects on particularly red deer (*Cervus elaphus*) are among the most thoroughly studied responses for UK mammals. Even here, however, it is the mechanisms of influence, rather than the direct distributional consequences, that are best known, and the majority of UK deer species are data deficient.

High densities of native deer can be responsible for extensive (commercial) woodland damage and habitat degradation and act as a reservoir for diseases, such as Bovine Tuberculosis (Fuller & Gill, 2001; TMP, 2005; 2009), while numbers of introduced deer species continue to give cause for concern (SoBM, 2011). Intuitively

introduced deer from lower latitude regions, such as muntjac deer (*Muntiacus reevsi*) and Chinese water deer (*Hydropotes inermis*), might be expected to thrive better under generally milder conditions, though surprisingly this does not appear to have been investigated formally in the literature.

There is also a spill-over / -back interaction between wild and domestic ruminant diseases (Böhm *et al.* 2007), the worsening of which has been linked to climate change by several livestock studies (e.g., Gale *et al.* 2009; Van Dijk *et al.* 2010). Notably, deer often carry ticks and thus spread, and are susceptible to, a range of tick-borne diseases (Gray *et al.* 2009), in-turn linked to climate change (Randolph, 2004). Deer also suffer from, and thus act as wildlife reservoirs for, a range of culicoid midge-vectored diseases (Wittmann & Byalis, 2000) including blue-tongue (Purse et al. 2005).

Post & Stenseth (1999) report that in Norway, individual red deer (*Cervus elaphus*) and reindeer *(Rangifer tanandus*) within mainland populations responded to warmer winter conditions with reduced body size and increased fecundity, whereas warmer winters in maritime regions led to increased body size but reduced fecundity. Across sex and age classes, between 43% and 70% of the observed range in body mass among years was attributable to the dynamics of climate. All but two populations of northern ungulate populations studied declined following warmer winters, in concert with direct density dependence limitations on populations. Forchhammer *et al.* (2001) report similar interactions between the population dynamics of Soay sheep (*Ovis aries)* and variation in winter temperature.

Red deer born following warm winters, counter-intuitively, tend to be smaller than those born after cold winters, which Post *et al.* (1997) attribute to phenotypic variation. In particular, they highlight that the recent trend toward increasingly warm winters in northern Europe and Scandinavia may lead to reduced body size and fecundity of red deer. A similar response has been noted for reindeer in Norway (Weladji & Holand, 2003; see also Clutton-Brock & Albon, 1983).

Red deer condition during summer is affected by weather effects on plant growth (Bowyer *et al.* 2002), although Mysterud *et al.* (2008) found no solid evidence of direct effects of snow depth on autumn body mass in Norway.

Studies outside of the UK suggest that colder winter conditions would have a negative impact on large herbivores, due to increased costs of movement, thermoregulation and reduced access to food when snow is deep (Mysterud *et al.* (2008). Snow cover depth is a greater issue for deer subject to natural predators, however (e.g., Telfer & Kelsall, 1984) – not an issue in the UK.

Importantly, the life history consequences to ungulate population dynamics can occur years later, when cohorts have reached reproductive maturity (Post & Stenseth, 1999; Forchhammer *et al.* 2001) and may, as in the case of Soay sheep, occur only above certain population densities (Grenfell *et al.* 1999).

Recent work by Moyes *et al.* (2011) highlights how climate change has resulted in phenological advancement of life-history traits in red deer on the Isle of Rum. Oestrus date and parturition date in females, and antler cast date, antler clean date, rut start date and rut end date in males all advanced by between 5 and 12 days across a 28-year study period. Local climate measures associated with plant growth in spring and summer (growing degree days) increased significantly over time and

explained a significant amount of variation in all six phenological traits, largely accounting for the temporal advances observed. Moyes *et al.* (2011) report no evidence for temporal changes in key female reproductive performance traits (offspring birth weight and offspring survival) in this population, despite significant relationships between these traits and female phenology. For males, average antler weights increased over time, presumably as a result of improved resource availability and physiological condition through spring and summer. They also report no evidence for any temporal change in average male annual breeding success, as might be expected if the timing of male rutting behaviour was failing to track advances in the timing of oestrus in females.

Coulson *et al.* (2001) provide an analysis of weather pattern interactions with population crashes in Soay sheep, in relation to age, sex and population density. They highlight that identical weather conditions can result in different population dynamic responses, even when populations are of equal size, due to the different way in which age classes and sexes respond. They also report the strength of density-dependent processes to be a function of the distribution of weather events.

There are also secondary climate-interactive corollaries of deer density that we will not elaborate on here, suffice it to note that Brodie *et al.* (2012) report that in the Rocky Mountains Elk (*C. elephus*) cause more extensive tree damage when there is less winter snow, while the Deer Commission for Scotland acknowledge that deer also contribute to greenhouse gas emissions.
Overall there is robust evidence providing high confidence that, through a variety of often subtle mechanisms, deer are very likely (AR5: >95%) to be susceptible to future climate change effects; most notably benefitting from milder winters.

Wild boar (*Sus Scrofa*) are only present in small (but growing) numbers in southern counties of England. Nevertheless, studies on how boar respond to climate change are available, which are informative toward broader ungulate projections.

Melis *et al.* (2006) report that winter harshness imposes density-independent mortality on wild boar populations at higher latitudes and that, in particular, mean January temperature and vegetation productivity are the most important factors explaining biogeographical variation in population densities. They predict that wild boar will respond to global warming through both an increase in local population densities and an expansion of their geographical range north and north-eastwards in Europe (see also Bieber & Ruff, 2005) – exposing a risk of spread in the UK; wild boar are considered a significant agricultural pest on the continent and also a potential reservoir of swine fever and other diseases (TMP, 2005).

Despite only low evidence of medium confidence it seems likely that warmer winter conditions would benefit UK wild boar populations and favour northward range expansion.

UNGULATE SUMMARY:

Climatic Vulnerabilities:
   • *Negative effect of cold winters (esp. snow cover)*
   • *Some climate-disease and deer-supported climate-vector interactions noted*
   • *Optimal conditions for summer plant growth favour population success*
Importance of Climatic effects:
   • *Currently, secondary to other issues*
   • *Noting greater risk of tick-borne disease spread if ungulate numbers increase*
Data quality & confidence:

- *Likely that populations will benefit from mild winters and decline due to harsh winters: High agreement, medium-high evidence (depending on species) – giving high-very high confidence*

A note on Carnivory

Wilmers *et al.* (2007) show that top predators can buffer some of the ecological effects of climate change within an ecosystem. Top predators can regulate the structure of entire communities and dampen their population variability; in their absence, prey populations are likely to fluctuate more substantially, owing to bottom-up factors. Given that UK ecosystems tend to be depauperate of large carnivores, this increases exposure to climatic risks. Restoring top predators to their natural environment could provide insurance against undesired effects of climate change on ecological communities (Sala, 2006).

CARNIVORES

Order: **Carnivora**
Family: Canidae – *red fox*

The red fox (*Vulpes vulpes*) is extremely versatile and successful and occurs over an extensive bio-climatic range (Macdonald & Reynolds, 2008), leading to them being listed by the IUCN as amongst the World's 100 worst invasive species (IUCN). As a consequence, they are relatively adaptable in the face of climate change. Nevertheless, Hersteinsson and Macdonald (1992) suggested that red fox distribution and regional abundance is limited by climate-driven primary productivity. Barton´ and Zalewski (2007) rather proposed that climate limits the northern geographical range extent of red foxes directly, through winter thermal stress increasing energetic (i.e., food) requirements and through duration of snow cover that impedes access to prey, leading to shorter reproductive period / lower reproductive output as well as lower survival rates. Gallant *et al.* (2012) have, however, recently rejected that climate warming has led to increasing dominance of red fox over arctic fox (*Alopex lagopus*) in North Yukon tundra; favouring that, as per Hersteinsson and Macdonald (1992), benefits to red foxes are primarily due to increasing prey availability through a bottom-up effect, starting with increased primary production.

In the UK, a substantial proportion of the fox's diet is typically comprised by earthworms (*Lumbricus terrestris*), the availability of which, to foragers, is influenced significantly by micro-climatic conditions (see Macdonald, 1980; discussed at length in the badger section – pertinent also to hedgehogs). Soulsbury *et al.* 2008 identified that a paucity of earthworms during the key cub developmental period of independent foraging can impact population dynamics, because juveniles cannot forage as competently as adults. Inter-annual variation in the volume of rainfall at nutritional independence was positively correlated to the proportion of earthworms in cub diet. Rainfall immediately following nutritional independence, combined with pre-independence cub mass, thus proved significant in determining full-grown mass, which is ultimately an important component of individual reproductive potential.

It would therefore seem that while climate change, per se, in the UK is unlikely to exceed the phenotypic plasticity of the red fox, drought scenarios for spring/early summer (CCRA, 2012) could affect juvenile growth and survival, with population effects. As small mammal predators, climatic effects on mice, voles and lagomorphs may also cascade onto fox numbers.

Other sources of climate stress, such as weather variability, have not been investigated formally for foxes, though we highlight here that they may share an extent of this vulnerability that we go on to discuss for badgers. Morgan *et al.* (2008) discusses how *Angiotrongylus vasorum* heartworm infection in foxes could be exacerbated by climate effects benefitting mollusc (snail) intermediate hosts. Similarly, sarcoptic mange mite infectivity is likely to be heightened during mild and wet conditions (Kołodziej-Sobocińska *et al.* 2014).

Overall, there is medium evidence and confidence that climate affects fox populations, through food supply. Due to their adaptability, however, foxes are capable of accommodating substantial climate change without evidencing a change in numbers or distribution; hence future affects seem unlikely (AR5: <33%).

Family: Felidae – *Wildcat*

The wildcat (*Felis silvestris*) is a critically endangered species in Britain (BAP – SoBM, 2011) native to Scotland (Macdonald *et al.*, 2004) – though once widespread. The main threats to populations are through hybridisation with domestic cats (and thus the shooting of nuisance domestic-looking cats by gamekeepers) and by disease (TMP, 2005). As a consequence of association, domestic cat diseases can also infect wildcat populations (Daniels *et al.* 1999).

While the wildcat is usually considered a cold-climate specialist, across the species it actually has an extensive biogeographic range. Levinsky *et al* (2007) propose that in continental Europe and Asia the wildcat may actually be quite resilient in the face of warmer, drier, conditions.

In the light of more pressing threats, concerns about climate change effects on wildcats and has not yet received formal attention in the literature, however ongoing research in the Cairngorms National Park (WildCRU: Kerry Kilshaw pers comm.) highlights some concern areas.

Snow levels: Wildcats have trouble moving around in deep snow and move to lower elevations (<600m), particularly under forest cover during periods of heavy snowfall. If climate change results in more substantial snow depth in elevated regions, wildcats may move to lower-lying farmland regions, possibly exposing them to greater risks of hybridisation with domestic cats.

Harsher winters: - Intuitively, prey availability (i.e., typically rodents and rabbits) is crucial to wildcat success (see Lozano *et al.* 2006), thus trophic cascade effects could be influential. The severe winters in the Cairngorms NP in 2009-10 and 2010-11 were noted to decimate regional rabbit numbers. Food shortages have two major consequences: wildcats move in toward farmland where they (i) predate on poultry, leading to human-wildlife conflict, and thus cats being shot; (ii) wildcats will encounter more domestic cats on farmland, with greater risks of hybridisation – risks exacerbated if the already very low wildcat numbers fall, reducing the number of pure-bred wildcat mates available.

Milder conditions: By extension, less snow may allow the wildcat to expand into areas previously inaccessible or avoided due to heavy snowfall, i.e., higher elevations, or to extend its population range northwards.

Wetter conditions: A large proportion of the wildcat's Scottish range is comprised of unsuitable peat bog. Wetter weather could therefore increase the amount of unsuitable habitat, and impact the success of prey populations (see above).

There is thus limited evidence that different facets of future climate change predictions could affect wildcat populations in opposing ways, which restricts our capacity to make predictions with confidence. We thus propose that they are about as likely as not (AR5: 33-66%) to exhibit changes in distribution and abundance in response to future climate change.

Family: Mustelidae – *Pine martens, Polecats, Stoats, Weasels, Otters, Mink & Badgers*

Mustelids are predominantly evolved to have long, slender bodies (Brown and Lasiewski 1972), most effective for subnivean, arboreal, aquatic and fossorial activity; although badgers are an exception, with a more rotund ecomorph, evolved to dig (Newman *et al.* 2011).

These fierce constraints toward slenderness and athleticism constrain the capacity for the weasel family to carry excess body-fat, and thus they have limited capacity to buffer food shortages, and have a thermally inefficient body shape (see Newman *et al.* 2011). As a consequence, any climatic perturbation limiting their food supply could affect populations significantly; the major mustelid climatic vulnerability.

Subfamily*: Martinae*

The pine marten (*Martes martes*) is locally common in parts of Scotland, but is BAP-listed and very rare in England and Wales (TMP, 2005; 2009). Predation on poultry and game-birds lead to conflict with gamekeepers and to massive declines in the 19th century (Langley & Yalden, 1977), with a continued threat from illegal trapping and poisoning (Tapper, 1992). There is evidence that intra-guild competition with foxes may limit pine marten numbers and therefore any (climate-induced, or otherwise) increase in fox numbers in the UK may be a hindrance to pine marten recovery (Macdonald & Tattersall, 2001).

The potential effects of climate change on martens is particularly data deficient in the literature, beyond self-evident inferences, such as factors reducing rodent prey, or autumn fruit, abundance – where very extreme winter cold would induce a significant thermoregulatory cost (e.g., Krohn *et al.* 1995). Zhou *et al.* (2013) report how extreme winter weather conditions (snow) impacted the diets and distribution patterns of yellow-throated martens, and other frugivorous meso-carnivores, in sub-tropical China.

Perhaps the greatest long-term threat to martens would result from climate-mediated habitat change, as they favour northern-type coniferous forest, which may be increasingly succeeded by southerly deciduous forest, under warming scenarios (e.g., Sykes & Prentice, 1996). Suffling & Scott (2002) make this point about forest-type effects on the Fisher (*Martes pennanti*) in Canadian National Parks, in response to climate change.

From low evidence, providing little confidence, we assess that pine martens are unlikely (AR5: <33%) to respond to climate change in any major way.

Subfamily Lutrinae: *Otters*

UK populations of European otters (*Luta lutra*) are internationally important, since otter populations have declined across much of their western European range (TMP,

2005). Again subject to historic persecution (Chanin & Jefferies 1978; Jefferies, 1989), numbers in the UK are recovering gradually (TMP, 2009).

Formal studies of climate change impacts on otters are limited to investigations of body-size changes in response to global warming (Yom-Tov *et al.* 2006), where elevated sea temperatures appear to benefit otters in coastal populations in Norway.

Intuitively (in the absence of direct data), as an obligate aquatic hunting species, otters would likely be affected by changing river flow rates (flood / drought; CCRA, 2012; see also Lake, 2003) and by any second-order climatic effects on riverine fish stocks (e.g., Xenopoulos *et al.* 2006). With a distributional range extending into the Arctic, more extreme winter conditions in the UK would be unlikely to present a singular risk factor (Macdonald & Mason, 1983).

Medium evidence and confidence leads us to assess that otters are likely (AR5 >66%) to be susceptible to changes in river flow rates, but unlikely to respond to climate change significantly in other ways (AR5: <33%).

Subfamily: *Mustelinae*

Polecats (*Mustela putorius*) share many similarities with the fortunes of martens, also having a restricted present day distribution in Britain due to heavy persecution associated with game preservation in the late 19th Century (Birks & Kitchener, 1999). With BAP status, numbers are recovering slowly (TMP, 2005, 2009; SoBM, 2011). Vulnerability to climate change is not amongst the main threats to polecats; noting again the fundamental mustelid predisposition toward carrying little body-fat in reserve for times of restricted food supply, and the ecomorphic tendency to conserve heat poorly (Newman *et al.* 2011).

In terms of foraging success for these obligate carnivores, climate-related changes in the abundance of small rodents and lagomorphs might be influential as a second-order effect.

No studies of climate effects on polecats appear to have been conducted – extreme data deficiency, limits confidence to an assessment that they are unlikely (AR5 <33%) to respond significantly to future climate change.

The American Mink (*Neovison vison*) is an extremely adaptable and successful small predator across North America, consuming a diverse diet of rodents, lagomorphs, fish, crustaceans and birds. Introduced to the UK late 1920s, for fur farming, it has spread extensively through the UK (Jefferies *et al.* 2003) and is implicated in the decline in water vole populations (Macdonald & Strachan, 1999) and impacts nesting birds on offshore islands, game birds and fish stocks (Macdonald & Tattersall, 2001; Macdonald & Harrington, 2003).

Climate has been found to influence mink in its native North American range. Schooley *et al.* (2012) demonstrate that suitable habitat occupancy dynamics of mink were related to variable water depths, which has implications for climate related flood / drought scenarios (CCRA, 2012). Such effects of climate change could be heightened in urbanised and intensively drained agricultural regions.

The climate-related effects Magnúsdóttir *et al* (2014) have observed recently in Iceland, where mink were also introduced in the 1930s, reveal that mink populations are declining due to competition for food with an increasing number of arctic foxes, where the foxes appear more successful at adapting to changes in prey availability.

The lack of any specific research on climate effects on mink in the UK leave us to make plausible inferences on possible effects – where as in North America, and as with otters, changing rainfall patterns and effects on hydrology are foremost (CCRA, 2012).

Medium evidence and confidence leads to our assessments that mink are likely (AR5 >66%) to be susceptible to changes in river flow rates, but unlikely to respond markedly to other climate change variables.

Stoats (*Mustela erminea*, aka 'ermine') and weasels (*Mustela nivalis*) are amongst the smallest of Carnivores, and thus have very tight energy budgets. Disruptions in their food supply or energy expenditure (heat loss or activity patterns) can therefore affect population dynamics. Nevertheless, both species have an extensive distribution through Europe, Asia and North America (with various introductions in other regions).

While Zub *et al.* (2011) tested the hypothesis that those larger male weasels, favoured by sexual selection in summer, might struggle more than smaller males to find sufficient winter food: they rejected this. Large(r) weasels proved more adaptable and were capable of exploiting larger prey species / prey individuals; illustrating adaptability.

As both species specialise in rodent and rabbit prey, climate-induced changes in prey abundance (positive or negative) would logically affect their population dynamics, however this has not been investigated formally. Similarly, stoats and weasels are susceptible to habitat loss (McDonald & Birks 2003); while climate may be influential in this regard concerns are principally connected to management, e.g., loss of linear features.

In Scotland and in parts of Northern England stoats change pelage colour to white in winter (King 1989), thus changes in snow cover regimes would interact with the effectiveness of this camouflage, which is under endocrinological control (Rust, 1966)

More study is required to establish any robust ecological effects of climate on these small mustelids.

Stoats and weasels are clearly very likely (AR5: >90%) to experience thermoregulatory stress, and would be vulnerable to climate-related habitat loss, however, there is little empiracal evidence, providing low confidence in this assessment

Subfamily: *Melinae*

Of all the mammal species in the UK, the mechanisms through which climate influences badger (*Meles meles*) population dynamics are the most thoroughly understood. Badger densities and survival rates tend to be highest under circumstances where mild, damp conditions increase the availability of earthworms (Kruuk 1978b; Kruuk and Parish 1982; Johnson *et al.* 2002). As facultative earthworm specialists in the UK, badgers are affected by microclimatic effects on the surfacing behavior of this prey (Fragoso and Lavelle 1992; Gerard 1967; Macdonald 1980, 1984). Consequently badger distribution and abundance are heavily dependent on weather patterns.

Working at Wytham woods, near Oxford, Macdonald *et al.* (2010) found that badger life history parameters (see Macdonald *et al.* 2009) interact in complicated ways with

annual variability in the seasonality of temperature and rainfall, both in absolute and in phenological terms. Summer rainfall is particularly effective, where drought conditions affect annual fecundity (Macdonald *et al.* 2010); dry and cool May conditions promote higher reproductive success, as apparent in the number of cubs recorded in June (per adult female). Virgos *et al.* (1999) report that, in more arid parts of the badgers range in central Spain, a sufficiency of rainfall is particularly important for predicting local badger population densities.

Spring rainfall is a particular population stressor – affecting annual cub survival rates significantly (Woodroffe and Macdonald 1995; Macdonald & Newman 2002). This is in part due to interactions with gut parasites (Newman *et al.* 2001; Macdonald *et al.* 2010) – where badgers are one of the few UK mammals where a clear interactive link is evident between the pathogenicity of disease and climatic factors. All badger cubs contract juvenile coccidiosis, caused by the protozoan parasite *Eimera melis*, prior to the full establishment of their cellular immune defences. This parasitosis causes the malabsorption of nutrients and fluid loss through diarrhoea. If cubs are also food stressed in years when drought limits the availability of their favoured earthworm prey, they can die of infection. In wetter years, with greater earthworm availability, they can tolerate the parasitic infection while still achieving adequate nutrition for somatic development, leading to higher survival rates (see Macdonald *et al.* in press). Annavi *et al.* (2014) also observed a genetic interaction where heterozygosity was only beneficial to cub survival and fitness in wetter years, when subtle genetic advantages could come into play. In dry years, drought-mediated food deprivation, compounded by coccidiois led to non-selective death across the entire cub cohort, irrespective of heterozygous advantages.

Badgers have evolved to cope with severe winter weather conditions across their range, and to do so have adaptations to alleviate thermoregulatory stress (e.g., living in an underground sett and winter lethargy, but without hibernation; see Newman *et al.* 2011). Amelioration in winter conditions in recent decades has broadly benefitted badger over-winter survival in the UK, with heavier winter weights being sustained – this has been associated with an increase in national population numbers (see Macdonald & Newman, 2002). Noonan *et al.* (2014) report an interaction between badger body-condition, weather and foraging activity. Thinner, more desperate badgers emerged from their setts to engage in autumnal foraging in sub-optimal conditions to a greater extent than did fatter badgers, which were less desperate to find food. This highlights how winter weather conditions interact with the badgers' physiological energy management. Milder winters in Finland are also associated with badgers colonising further north, beyond the arctic circle (Kauhala, 1995). Johnson *et al* (2002) also report a relationship between seasonal temperature range and badger densities across Europe

A surprising corollary of climate change, is that warmer conditions during the badgers' peak February breeding season are linked to higher rates of road traffic accidents (Macdonald *et al.* 2010), where warmer conditions tempt badgers to make more extensive exploratory movements. This underlines the intricate ways in which a changing climate might interact with anthropogenic agents to influence population processes.

Equinoctial conditions also produce significant population driver effects. That is, while summers will always be relatively warm compared with winters, spring and autumn weather can be more variable and functionally delimit the 'productive' vs. non-productive period of the year in terms of badger behavioural and physiological cycles (Macdonald *et al.* 2010). Early autumn - specifically September, conditions present a critical period for all aspects of badger population dynamics (Macdonald *et al.* 2010);

seasonably cool and moist conditions prove beneficial for both juvenile adult survival and fecundity in the following spring. That is, weather patterns that militate for damp soil conditions and thus provide suitable micro-climatic conditions for anecic earthworms to surface and present themselves to foraging badgers (Gerrard 1967, Bouché 1977) are advantageous, demonstrated by a positive benefit on badger-weight gain, both at the individual level and generally within population demographic data (Macdonald *et al.* 2010).

Nouvellet *et al.* (2013) decompose the effects of yearly temperature and rainfall into mean trends, yearly amplitude of change and residual variation, using daily records, and examine effects on annual mortality and recruitment rates for the life-histories of 1125 individual badgers from 1987-2008. Mean rainfall was by far the most influential predictor, however juvenile survival and recruitment rates were highest with '*intermediate*' levels of mean rainfall, whereas low adult survival rate was associated with only the driest, and not the wettest, years (a quadratic effect). Both juvenile and adult survival rates also exhibited a range of tolerance for residual standard deviation around daily predicted temperature values, beyond which survival rates declined. These findings identify a badger 'Goldilocks Zone' (see Nouvellet *et al.* 2013): life-history parameters, annual routines and the capacity to make effective behavioural responses that define the badgers' climatic niche are predicated upon a limited range of climatic stability, which result in optimal survival and recruitment dynamics.

Exploring how rainfall and temperature, and habitat suitability, influenced badger body-weights on a biogeographic scale across the Republic of Ireland, Byrne *et al.* (2015) found that badgers were heaviest in Counties in the east and south-east of the country and lighter in the west and north-west of the country. Mean body-weight was affected significantly and positively by temperature, and by all lag metrics of temperature. Interestingly, they also report a mean 1kg difference in winter body-weights observed between warm (standardised 2˚C > longer-term mean) and cold (standardised 2˚C < longer-term mean) years in this study.

They found less support for rainfall effects across all temporal scales; nevertheless, badgers did exhibit heavier weights when greater rainfall occurred one or two months prior to capture Possibly, therefore, badgers in this Irish study may already have adapted to highly variable rainfall patterns; a feature of temperate mid-latitude maritime climates (Köppen-Geiger climate classification; Cfb). Byrne *et al.* (2015) conclude that, with predicted increases in temperature, and rainfall, augmented by on-going agricultural land conversion in the ROI, individual badger body-weights will become heavier in the future; a phenomenon work by Nouvellet *et al.* (2013) implies is likely to enhance fecundity, recruitment and survival rates, due to improved food availability and energetic budgets.

That variability in weather conditions is influential, in combination with mean climatic trends, on the vital rates of a generalist, wide ranging and K-selected medium-sized carnivore, exposes how perturbation from typical, seasonally affective conditions in any trajectory can, *in extremis*, destabilise population dynamics.

Robust data of high confidence allow us to observe the intricate ways in which climate can be influential for badgers. Against a back-cloth of road traffic accidents, farming / habitat management and even regionally prescribed culling however badger numbers in the UK seem only about as likely as not (AR5: 33-66%) to change as a singular result of climate.

CARNIVORE SUMMARY:

Climatic Vulnerabilities:
- *Changes in prey abundance (to include micro-climatic effects on earthworm availability for badgers & foxes)*
- *Interaction between parasitic disease and weather-mediated food availability – Badgers*
- *Effects of weather on emergence from den / foraging behaviour – Badgers (though also plausible for other Carnivores)*
- *Negative consequences of weather variability and fluctuations from seasonal norms to which life-history traits are adapted – Badgers & foxes*
- *Stresses on energy budgets in elongate mustelids, susceptible to thermoregulatory costs*
- *Body size – exposure for stoats and weasels*
- *Winter severity: frost-badger; snow cover – wildcats*
- *Habitat changes (longer term): Forest composition – pine martens; peat bog development – wildcats*
- *Aquatic species – otter, mink; changes in flow rates and fish stocks*
- *Disrupted seasonal movement patterns: Badgers – winter RTA exposure; wildcats – moving down to farmland – hybridisation*

Importance of Climatic effects:
- *Minor, in the face of other more pressing threats*

Data quality & confidence:
- *Generally – Unlikely to be the major affecter of UK population numbers : Low agreement, limited evidence – giving low confidence*
- *Badgers – About as likely as not (in terms of change in UK numbers): medium agreement, robust evidence – giving high confidence*

CONCLUSIONS

The nature and projected consequences of global climate change are not yet fully resolved, and it remains unclear how animal populations will be affected by even the most widely accepted and robust components of projected affects (Humphries *et al*. 2004).

Although mammals have a broad thermal tolerance and have evolved highly specialised adaptations for dealing with seasonal temperature variation, like all animals, they remain fundamentally affected by temperature. Given that climate change is predicted to alter ambient temperature patterns in northern Europe substantially, as well as change many other components of the abiotic (e.g., precipitation, snow and ice cover) and biotic environment (e.g., abundance and distribution of resources and predators), the mammal fauna of the UK is likely to undergo substantial changes during the next century. Most striking is the deficiency of detailed studies examining both the demographic mechanisms involved and, particularly, the consequences for regional distributions.

Many of the 'self-evident truths' recited for mammalian responses to climate are not well supported by peer-reviewed literature, and often precisely because responses are considered too obvious to warrant investigation there is an unsatisfactory dearth of empirical research – which is not to doubt the plausibility of possible responses, simply to observe the lack of direct evidence.

In major part, the reliance upon inference, assumption and 'educated guesses' about plausible effects is born out of the short-term nature of many research projects, which do not persist through sufficient inter-annual weather variation to be able to fully

resolve population dynamic responses for longer-lived mammals. The best data quality available is therefore associated with those few studies that have the longest duration, e.g., red deer on Rum; beavers in Norway; badgers in Oxford.

Despite a strong national awareness about the risks associated with climate change in the UK (e.g., UKCIP, 2009; CCRA, 2012), and valiant attempts at systematic national mammal monitoring programmes (e.g., TMP 2005, 2009; SoBM, 2011; 2014; see also Macdonald *et al*. 1998; Tattersall & Macdonald 2002), especial attention to climate-related affects warrants further dedicated academic study. Throughout this assessment it has often been necessary to rely on inferences about focal species gleaned from studies in other regions, especially North America (e.g., Kerr & Packer, 1998). Nevertheless, these studies are broadly instructive as to where concerns lie.

Much UK mammal monitoring is undertaken by specialist interest groups and NGOs, which are not always well-placed to conduct detailed analyses. That climate change will have impacts is clear at an obvious level: if the food supply is altered, or the range of thermoregulatory tolerance for any mammal is (seasonally) exceeded, there will be consequences. However, policy-makers need more refined insights, and these are largely lacking.

Mammals have diverse niche requirements; regional populations may be exposed to different weather patterns; susceptibility to certain risk factors varies with an individual's age; and climate effects can interact with other variables synergistically. There is also an interaction relating to greater exposure to infectious diseases and disease vectors, due to climate change (Daszak *et al*. 2001), where morbidity can be exacerbated by weather-linked stresses on energy budgets. The adaptability of extant species is restricted by the physiological and behavioural repertoire inherited from their ancestors (McNamara *et al.* 2001), limiting future possibilities through genetic constraints (Nogués-Bravo, 2009) or precipitating evolutionary change (e.g., Pörtner 2004).

Notably, shorter-lived, r-selected (see Reznick *et al*. 2002) species are vulnerable to short-term weather effects within years, yet due to their rapid generational interval can be highly adaptive to longer-term environmental change, through natural selection. Longer-lived, K-selected species are also influenced by weather variability, but may additionally experience climate trend effects within their own lifetime; effects they may adapt to behaviourally (or not) but are less capable of evolving better fitting phenotypes, due to longer inter-generational times (Gotthard & Nylin, 1995).

Generalist species might also be assumed more adaptable than specialist ones, however, the work on badgers and beavers, described above, does highlight that even generalist species are not immune to shifting climate conditions, while specialist species may benefit from changes to the advantage of their specific requirements (Huey *et al*. 2012).

Because of the complexities of the impacts of climate on any given species, and because each species is part of an intricate community, we can expect cascades of effects. We must also be alert to unexpected consequences, such as aquatic beavers doing less well with more rain, or badgers prompted to greater winter foraging activity by mild conditions, exposing themselves to a greater risk of road traffic accidents.

In summary, additional data and better theory are needed to predict the direction and magnitude of climate change impacts on specific mammal species.

Acknowledgements

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