Author's Accepted Manuscript

www.elsevier.com/locate/jtherbio

Badger setts provide thermal refugia, buffering changeable surface weather conditions

Marie Tsunoda, Chris Newman, Christina D. Buesching, David W. Macdonald, Yayoi Kaneko

PII: S0306-4565(17)30529-6
DOI: https://doi.org/10.1016/j.jtherbio.2018.04.005
Reference: TB2095

To appear in: *Journal of Thermal Biology*

Received date: 23 December 2017
Revised date: 1 April 2018
Accepted date: 4 April 2018

Cite this article as: Marie Tsunoda, Chris Newman, Christina D. Buesching, David W. Macdonald and Yayoi Kaneko, Badger setts provide thermal refugia, buffering changeable surface weather conditions, *Journal of Thermal Biology,* https://doi.org/10.1016/j.jtherbio.2018.04.005

Badger setts provide thermal refugia, buffering changeable surface weather conditions

Marie Tsunoda[1], Chris Newman[2]*, Christina D. Buesching[2], David W. Macdonald[2], Yayoi Kaneko[1]

[1]*Carnivore Ecology and Conservation Research Group, Tokyo University of Agriculture and Technology, Saiwaicho 3-5-8, Fuchu City, Tokyo 183-8509, Japan.*

[2]*Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, The Recanati-Kaplan Centre, Tubney House, Abingdon Road, Tubney, Oxon OX13 5QL, UK.*

* Corresponding author.: chris.newman@zoo.ox.ac.uk

Abstract

Den use can be crucial in buffering environmental conditions and especially to provide an insulated environment for raising altricial young. Through Sept-Dec 2016 we monitored temperature and humidity at 11 badger setts (burrow systems), using thermal probes inserted over 4-13 sett entrances to a depth of ca. 2 m, supplemented by continuous daily logging at one entrance per sett. Setts were cooler than exterior conditions Sept-Oct, and warmer than exterior conditions Nov-Dec. Setts cooled down when badgers left them to forage by night, and warmed up when badgers occupied them by day. Soil type and aspect also influenced sett temperature. Sett temperature did not affect the weight or body-condition of either adults or maturing cubs in autumn. However, cubs born into setts that were relatively warmer through the preceding autumn-winter were heavier in the following spring than contemporaries born in cooler setts (badgers exhibit delayed implantation), and so warmer setts might benefit early cub growth. We posit that sett quality may be important in providing badgers with a stable thermal refuge from variable weather conditions. More broadly, den use may buffer climate change effects for many fossorial carnivore species.

Key words: weather condition; fossorial den; thermal refugia; microclimate; *Meles meles*; climate change.

1. Introduction

Mammals can occupy a range of bioclimatic zones due to homeothermy; however, regulating core temperature to stay within a narrow range (Crompton et al. 1978) requires potentially costly energy expenditure, particularly in cold or variable environments (Boyles et al. 2011, Lowell and Spiegelman 2000). These costs can be especially high for neonatal and developing juvenile mammals that are less able to regulate core temperature, often have sparse fur, and are more prone to heat loss than adults due to scale laws in relation to their small body size (McNab 1988; see Noonan et al. 2015b).

As a consequence, mammals supplement physiological thermoregulatory mechanisms with behavioural strategies (Terrien et al. 2011). One key strategy employed by many rodents and carnivores for mitigating inclement weather is the use of subterranean refugia, especially while nursing young (Noonan et al., 2015b). Underground dens and burrows tend to have stable (or more stable) microclimates, which buffer changes in surface conditions (Boutros et al., 2007; Johnson and Pelton, 1980; Magoun and Copeland, 1998). Furthermore, dens offer complete protection against rain and snow (Blix and Lentfer, 1979), and even forest fire (Thompson and Purcell, 2016). Nevertheless, fossorial animals must leave their dens to forage, and engage in other activities, resulting in a trade-off between the proportions of time individuals can spend underground versus other essential activities (Noonan et al., 2014). The insulating quality of burrows and the ability of species to reduce activity during inclement above-ground conditions (e.g. torpor, hibernation; Humphries et al. 2013) can thus be critically important. This may be especially important during cold winter, or unusually aberrant conditions (Smith et al., 2009; Smith, 2011), when food availability may be low, but foraging incurs substantial heat loss.

Since the mid- 20th century, anthropogenic greenhouse gas concentrations have contributed substantially to increasing global average temperatures and extreme weather events (IPCC, 2014a). This rapid climate warming can affect animal ecology in two ways; either indirectly, through impacts on food resources, reducing available energy inputs (Tuomainen and Candolin, 2010), or directly, by costing the animal more energy to thermoregulate (Beever et al., 2017; Huey and Tewksbury, 2009; Sih, 2013). A decline in population survival rate will, however, only become apparent once conditions exceed the thermal tolerance range of the species examined (Scheffers et al., 2014; Silva et al., 2017) and their ability to adapt their daily and seasonal routines (see Newman et al. 2017a). It is therefore important to better understand how animals actually respond and adapt to the range of weather conditions they experience in order to project how they may cope with changed climatic conditions in the future (Beever et al., 2017; Scheffers et al., 2014; Noonan et al., 2015a).

Here we establish the conditions in fossorial dens (termed ‘setts’) used by the European badger (*Meles meles*; henceforth ‘badger’) in relation to prevailing weather. In the UK, badgers live mainly in agricultural mosaic habitats, locating setts in wooded areas (Macdonald et al. 2015). They are nocturnal, resting underground for on average 12.3 ± 1.69 SD hours per diem (same study population; Noonan et al., 2015c). Badgers are widely distributed across Europe, and have been established to achieve their highest densities where earthworms provide a major proportion of their diet, such as in Britain (Johnson et al., 2002); with congeneric *Meles* spp. across Asia (Zhou et al., 2017). Because microclimate affects the availability of earthworms (Jiménez and Decaëns, 2000), badger population dynamics are governed strongly by weather conditions (see Macdonald et al., 2010; Macdonald and Newman, 2002; Newman et al., 2017b; Nouvellet et al., 2013).

At high density, badgers form social groups (Macdonald et al., 2015) with each group sharing a sett (Noonan et al., 2014; Roper, 1992). Over winter, when food resources are in short supply, badgers can conserve energy by staying within their setts (Noonan et al. 2014; 2015a) and use periods of light torpor to conserve metabolic expenditure (Fowler and Racey, 1998; see also Newman et al. 2011)—strategies used predominantly by fatter badgers that are less desperate to feed (Noonan et al., 2014). Notably, in Scotland (Silva et al., 2017) and Ireland (Byrne et al., 2015) badgers prefer warmer sites.

We focused here on the autumn period leading into winter, when variation in weather can have a significant effect on badger survival (Macdonald et al., 2010). Note: after delayed implantation, badger gestation commences around late-December / early January, and maternal condition is known to affect embryonic development, litter size and neonatal mortality rate (Woodroffe, 1995; Macdonald & Newman, 2002). Specifically we tested whether:

i) microclimatic conditions within setts differed from prevailing above-ground weather conditions, and investigated how stable temperatures were within setts.

ii) the soil type in which the sett was dug, or its aspect were associated with the sett's thermal properties.

iii) sett temperature changed through the 24 h cycle in relation to badger occupancy

iv) autumn-winter sett temperature influenced the contemporaneous body-condition and weight of sett residents (cubs/adults), and the weight and body-condition achieved among natal cubs and resident adults in the subsequent spring.

We conclude by evaluating how our findings on subterranean refugia conditions and usage may enhance the ability of fossorial species to cope with more extreme weather conditions, as predicted by climate change scenario IPCC AR5 (IPCC, 2014a).

2. Materials and Methods

2.1. Study site

Wytham Woods, located 5 km north-west of the City of Oxford, comprise 424 ha of semi-natural woodland with areas of open grassland (for details see: Savill et al., 2010). Taylor et al. (2010) give mean annual temperature as 10°C (1993 to 2007) with mean annual rainfall of 717 mm, recorded at the top of Wytham Hill at an elevation of 160 m by the Environmental Change Network. Due to unique ecological circumstances, Wytham Woods have the highest published density of badgers in the world, at >40/km^2 (Macdonald et al., 2015), divided into 23 social groups, some of which utilize several large setts. Sixty-nine sett sites had more than 5 holes and have been monitored consistently via a long-term trapping programme since 1987 (Macdonald et al., 2015).

2.2. Measuring sett temperature and humidity

A pre-survey was conducted from 21st September to 9th October 2016 to select suitable setts and to design a temperature and humidity monitoring protocol. We selected 11 setts in separate territories, spread across the study site stratified to include different elevations and different soil types (see Taylor et al., 2010) (Fig.1; Table S1). Thereafter we took spot measures of sett temperatures between 12:00 and 18:00 (following Kaneko et al., 2010), once a week from October 19th to December 29th 2016, amounting to 12-14 repeat measures per sett (Table 1). The probe was left in each hole until temperature equilibrated, which typically took 5 –10 minutes.

We measured sett temperature using a hydrothermograph sensor (AD-5682, A&D Company, Limited, Japan), attached to a 3 m flexible rod, inserted into badger sett entrances to a consistent tunnel penetration of ca. 2 m. From prior studies of sett architecture and use (Noonan et al 2014), this method was intended to give a measure of temperature in tunnels linking subterranean chambers to the surface, so as to not have our readings biased by body-heat radiating from badgers potentially huddled together within resting chambers. Chambers tend to be much further from entrances and/or involve sharp junctions off of tunnels that our rods could not turn. It was not feasible to drill into setts to insert probes because most were dug under a limestone rock stratum at this site (Coombes & Viles, 2015), and badger setts are protected from destructive interventions in the UK (Protection of Badgers Act, 1992).

We measured only at larger setts (>6 holes) attempting to exclude inferior small outlier setts (Kaneko et al. 2010), so that any differences in resident badger condition could be attributed reliably to sett thermal properties. The number of entrances sampled differed between setts due to restrictions of internal architecture affecting probe insertion (Roper, 1992; Roper and Kemenes, 1997); for instance, tree roots sometimes prevented sufficiently deep probe insertion into entrances, and such entrances were not used. Nevertheless, we measured at least four entrances at smaller setts (setts with < 15 entrances) and 10 or more entrances at larger setts (> 15 entrances) (Table 1).

As well as sett interior temperature, at each weekly visit we simultaneously measured exterior surface temperature at the middle of each sett (henceforth 'exterior sett temperature'). We noted sett elevation, slope inclination, aspect (to the nearest octile), and soil type, categorized according to a map of principal Wytham soil types (Taylor et al., 2010; see Macdonald et al., 2004).

Comparisons to exterior weather conditions over daily, weekly and monthly periods were made against local meteorological records (daily mean, maximum and minimum temperature (˚C), and daily total rainfall (mm)), obtained from the National Meteorological Library and Archive —Met Office, UK (https://www.metoffice.gov.uk/) (Henceforth 'Met Office').

In addition to weekly temperature monitoring at a number of holes, we also logged the daily interior temperature and humidity at 2 m penetration at one entrance per sett continuously at 5 min intervals (calculating hourly means), using data loggers (EL-USB-2, Lascar Electronics Inc. UK). This gave daily temperature across a 24 h period, whereas samples taken on weekly surveys reflected a day-time value. Data were collected from October 23th to December 28th 2016, with a short break between November 23rd and December 2nd when logger batteries were replaced across all probes (Table S1). Nine of the 11 sampled setts were used for this supplementary monitoring, limited by the number of loggers available, although one more logger was added from 1st December. Each sett logger was moved among 4-5 entrances per sett between weeks.

2.3. Trapping protocol

The Wytham badger population has been trapped and marked systematically in seasonal trapping sessions since 1987, with a current population of ca. 200 adults, and around 45 cubs born each year (for full trapping protocol see Macdonald et al., 2015; Sun et al. 2015). Badgers were trapped in steel mesh cage traps (850 × 370 × 380 mm) deployed at all of the active setts (including outliers) associated with each social group, using peanuts as bait. During this November 2016 trapping session, six to 12 traps (depending on sett size) were set between 15:00 and 18:00 over 3 days at each sett. Captured badgers were transferred to holding cages between 06:00 and 08:30 the following morning and transported to an on-site field station. Badgers were sedated by an intra-muscular injection of ketamine hydrochloride (0.2mL kg^{-1} body weight; McLaren et al., 2005), which enabled handling. On first capture, all badgers have been tattooed with a unique number on the left inguinal region, for permanent individual identification. Sex, age class (cub or adult), weight, and Body Condition Index (BCI: subcutaneous fat score scaled 1 (thin) – 5 (fat), after Speedy 1980), *inter alia*, were recorded per capture. After a 3 h recovery period, badgers were released at their capture site.

Per sett monitored, we used these trapping data to provide: weight and BCI of adults, and also of cubs born in spring 2016, resident at setts in Nov 2016; weight and BCI of adults, and also of cubs born in spring 2017; and head-body length of cubs born in spring 2017, resident in spring 2017.

2.4. Data analysis

We used Mann-Whitney U tests to examine if mean (per sett) weekly spot measures of interior versus exterior sett temperatures (Met Office) differed significantly over the entire period. This revealed a sett thermal property basis on which to divide the full period into two intervals (see Results) and conduct separate analyses: Interval-1, Sept-Oct; interval-2 Dec-Jan. Mann-Whitney U tests were also used to assess if mean daily, monthly and overall interior sett temperature ranges (from loggers) differed significantly from corresponding Met Office temperature ranges.

Kruskal-Wallis one-way analysis of variance was used to compare interior sett temperature among setts, and interior sett humidity among hourly intervals. We used Ordinary Least Squares (OLS) models to further test whether interior sett temperature corresponded with exterior sett temperature, precipitation (mm; Met Office) sett aspect and soil type, and to establish when interior sett temperature exhibited a relative decrease or increase within a daily cycle (hourly).

OLS was also used to detect whether mean sett temperature (weekly spot measure) between 3rd October to 2nd November influenced resident adult/cub badger weight and BCI recorded for sett-resident badgers caught November 7th-16th 2016, and whether sett temperature over the period from 11th November to 29th December influenced subsequent weight and BCI of adults and cubs caught in the following spring (22nd May-3rd June 2017). If a significant difference was found in weight but not in BCI, Pearson's product-moment correlation was used to test for a relationship between weight and head-body length.

All analyses were performed in the R studio software environment, version 3.3.2.

3. Results

3.1. Sett temperature and humidity compared to exterior conditions

Weekly spot measures of interior sett temperature (n= 924; taken by day, when badgers were in residence) averaged 10.64 ± 2.53˚C (range: 3.90-16.60˚C, median = 10.8˚C) over the study period, versus a contemporaneous exterior sett temperature average of 10.78 ± 4.06˚C (range: 2.60-24.00˚C, median = 10.3˚C). From OLS tests, interior sett temperature followed the same patterns of increase and decrease as exterior sett temperature ($t = 17.97$, $p<0.0001$), with a negative effect of date ($t = -9.49$ $p<0.0001$) (Table 2).

Although no overall significant difference was detected between weekly sett interior and exterior temperature over the full survey period ($U = 479000$, $p = 0.71$), through Sept-Oct interior sett temperature (mean ± SD = 12.87 ± 1.42˚C, median = 12.8˚C) was significantly cooler than exterior sett temperature (mean ± SD = 14.81 ± 2.68˚C, median = 14.7˚C; $U = 37697$, $p<0.0001$; Fig. 2), conditions we characterize as interval-1. In comparison, through Nov-Dec, interior sett temperature (mean ± SD = 9.26 ± 2.01˚C, median = 9.1˚C) was significantly warmer than exterior sett temperature (mean ± SD = 8.27 ± 2.40˚C, median = 8.6˚C; $U = 218660$, $p<0.0001$; Fig. 2), which we characterize as interval-2.

Mean daily, monthly and overall interior sett temperature variability ranged over 0.9˚C, 4.7˚C and 8.1˚C, respectively; which was significantly less than equivalent exterior Met Office temperature variability ranges of 6.2˚C, 16.9˚C and 19.3˚C (U test: $U = 5232$, $p<0.001$; $U = 10$, $p<0.001$; $U = 3$, $p<0.001$ respectively; Table 3). Also, from Met Office data, the amount of daily precipitation (mm) had a negative effect on weekly interior temperature ($t = -3.65$, $p = 0.0003$) (Table 2). Notably, mean interior sett humidity was effectively 100% throughout the study period at all setts monitored, and so humidity was not included in further.

Over the full study period, from logger data, Mean ± SD˚C daily interior sett temperature (taken over 24-hrs, thus cooler than weekly mean spot samples, above) was 8.75 ± 2.00˚C (median = 8.5˚C), which was significantly (U test: $U = 2512$, $p=0.01$) warmer than daily mean Met Office temperature 7.57 ± 3.17˚C (median = 7.2˚C). Daily interior sett temperature ranged from 1.5 - 20.0˚C, while Met Office exterior temperature ranged from -4.7 - 16.6˚C (Table 3). This maximum interior sett temperature (20.0˚C) was, however, recorded only once, on November 14th at sett BL; temperature increased from 9.5˚C at 05:00 to 20.0˚C at 05:25 and then fell back to 11.5˚C within 1 hour, from which we infer that a badger may have sat in the tunnel close to the logger temporarily. Excluding this data point gave a maximum interior sett temperature over the study period of 14.2˚C. Hourly mean interior sett temperature decreased between 03:00 and 09:00 (OLS: all $p<0.05$) when badgers are typically out of their setts foraging, and increased between 12:00 and 18:00 when badgers are typically present within their setts (OLS: all $p<0.05$) (Table 4).

3.2. Factors affecting interior sett temperature

Interior temperature differed among setts (Kruskal-Wallis one-way analysis of variance: $x^2 = 45.93$, $p <0.0001$). South facing setts (including setts facing south, southwest and southeast) were significantly warmer than north facing setts (including setts facing north, northwest and northeast) (OLS: $t = 3.20$, $p = 0.001$, Table 2). Also, setts in lithomorphic soils and pelosols soils were significantly cooler than in brown sands (OLS: t = -3.85, p = 0.0001 and t = -2.84, p = 0.005 respectively, Table 2); conversely date (t = -9.49, p<0.0001), and the amount of daily precipitation (mm; Met Office), had a negative effect (t = -3.65, p = 0.0003) (Table 3).

3.3. Effect of sett temperature on the weight and BCI of resident badgers

In Nov 2016 twenty badgers (8 cubs born in the preceding spring and 12 adults) were caught at the 11 monitored setts (Table S2; however, we detected no effect of sett temperature on either adult (OLS: adjusted R^2 = -0.09, $F_{(1, 10)}$ = 0.11, t = 0.33, p = 0.75) or 2016 (maturing) cub (adjusted R^2 = -0.05, $F_{(1, 6)}$ = 0.67, t = 0.82, p = 0.44) bodyweights, or BCI (adjusted R^2 = 0.15, $F_{(1, 10)}$ = 2.97, t = 1.72, p = 0.12, and adjusted R^2 = 0.05, $F_{(1, 6)}$ = 1.37, t = 1.17, p = 0.29, respectively) at this later stage of juvenile development (aged c. 9 months).

In May - June 2017 we captured 27 badgers (9 cubs and 18 adults) in the monitored setts (Table S2). Again sett temperature was not associated with adult bodyweights (adjusted R^2 = -0.005, $F_{(1, 16)}$ = 0.91, t = -0.96, p = 0.35), or BCI (adjusted R^2 = 0.05, $F_{(1, 15)}$ = 0.25, t = 0.51, p = 0.62). However, weights of cubs born in 2017 (aged c. 3.5 months) were affected positively by sett temperature; being heavier in warmer setts (adjusted R^2 = 0.42, $F_{(1, 7)}$ = 6.81, t = 2.54, p=0.04, Fig. 3), although this did not translate into any significant effect on cub BCI (adjusted R^2 = -0.17, $F_{(1, 6)}$<0.0001, t = 0.01, p = 0.99). This implied that when cubs were heavier, they were also longer; i.e., cubs that resided in warm setts were generally bigger; corroborated by a positive correlation between cub weight and head-body length in Spring 2017 (Pearson's product-moment correlation coefficient = 0.91, p = 0.0006, Fig. 4).

4. Discussion

With regard to our first study aim, from logging daily sett interior temperature in a single entrance, we found that setts were generally warmer than exterior conditions. However, from weekly spot measurements over multiple entrances, we found that daytime (afternoon) sett temperatures (i.e., while badger were present and benefitted from the sett's thermal properties) were in actuality cooler than exterior conditions in the autumn (Sept-Oct), and warmer than exterior conditions once ambient air temperature cooled with a lower sun into the early winter (Nov-Dec). When looking at thermal effects in climate ecology subtle variation within data can prove a more significant driver of effects than simple overall mean predictor values (Benedetti-Cecchi et al., 2006; Newman et al., 2017b). Non-linear effects of temperature are increasingly evident in mammalian climate ecology (e.g., Campbell et al., 2012) – notably so in badgers (Nouvellet et al., 2013), exemplifying that, to attribute predictors properly, analysis of responses among the animals involved must be paired carefully with concurrent microclimatic conditions.

In relation to our second aim, we found that soil type was significantly influential on sett temperature, along with a south facing aspect. This suggests that the insulative properties of soil (Oliver et al., 1987; Yun and Santamarina, 2008) combined with relative extents of solar insolation (Loutre et al. 2004) contribute to sett thermal efficiency and potentially to the latency of daily heat gain/loss rates – likely linked to subtle differences between weekly interior temperatures taken by day, versus logger data recording 24 hr thermal conditions within setts (Moore and Roper, 2003).

Because endothermic mammals dissipate heat into their environments (McCafferty et al., 2011), this can cause burrow systems to warm up due to occupancy (McNab, 1979). Indeed, in relation to our third aim, we detected that setts were coolest (03:00-06:00), when nocturnal badgers had been out of the sett foraging since dusk, and warmest (12:00-18:00) several hours after badgers had returned to rest by day (Lindsay and Macdonald, 1985). Moore and Roper (2003) reported that temperature within occupied badger chambers was, on average, 2.4°C higher than in unoccupied chambers; to control in part for this effect we aimed to measure temperature in tunnels, not in deeper resting chambers. Co-occupancy (co-denning) may thus provide a mechanism of fine-scale sett temperature regulation (see Noonan et al., 2014).

All of the setts we investigated were elevated on Wytham Hill, well above the River Thames floodplain (Table 1). This mainly sandy ground is well draining and setts were not prone to flooding. The near 100 % humidity we observed in all setts in all months, consistent with Moore and Roper (2003), may be attributable to evaporation from moist soils, and /or respiration by resident badgers. Similarly, we saw that precipitation cooled simultaneous measures of sett interior temperature, likely due to a combination of absorbed or infiltrated rain evaporating within sett tunnels, along with implicitly less solar insolation during cloudy conditions (see Milly, 1984). All of the setts we monitored were relatively large (>10 holes), where we aimed to compare cub development in similarly-sized burrow systems; noting that Kaneko et al. (2010) found an effect where cub survival rate was generally lower in small outliers, where interior temperature was more variable. All setts followed the same interval -1 vs -2 patterns mentioned. Aspect, soil substrate, depth / soil digability and occupancy may, however, eclipse any simple effect of sett size between regions, where sett size is not always related to number of occupants (see Macdonald et al. 1996).

With regard to effects of sett temperature on the bodyweight or BCI of resident badgers, our forth aim, we found no effect for adults, or maturing 2016 cubs; however, in terms of effects on cub development in the following year (2017), heavier cubs were caught in warmer setts. Reasons may be two-fold: firstly, mothers in better body-condition tend to have more successful pregnancies and produce more milk when lactating subsequently (Woodroffe 1995; Macdonald & Newman, 2002); secondly, altricial young can be especially vulnerable to heat loss and likely expend less energy in warmer setts (Noonan et al., 2015b). Here weight provides the most meaningful metric for growth (skeletal size and condition), where cubs growing longer more quickly tend to be slimmer (and thus have lower BCI). Notably, Macdonald et al. (2010) observed that seasonably cool and moist environmental conditions in the early autumn prove beneficial for badger survival, as well as fecundity, in the following spring. While these conditions also co-favour the environmental availability of earthworms (*lit. cit.*), Nouvellet et al (2013) reported a quadratic effect of rainfall on badger cub survival in this same population, where conditions that are too dry (lack of food) but also too wet are detrimental. This infers that small cubs can succumb to chilling and hyperthermia more easily than larger adults if they have to venture from their setts to feed, post-weaning, during inclement conditions. Nevertheless, we concede that our findings here are based on one year's data, and that more data on cub development would enhance statistical power, building on the indicative association we observed; although no indicative trends were observed in our limited adult response variable data set. Importantly, we emphasize that all of the setts we monitored lay within the same 426 ha, and generally experienced the same weather conditions, and related influences on badger food supply (earthworms). With these *'other things being equal'* (the principle of *ceteris paribus*; sensu Vos et al. 2000), we are reassured that the differences in cub size we observed between setts were therefore likely substantially contingent on differences in sett thermal properties (see also Kaneko et al. 2010). Inevitably, more invasive and intensive monitoring of burrow systems, especially contrasting tunnels with nesting chambers, would provide more precise results; however, thus must be weighed against disturbing the subject animals, although new miniaturized sensors continually advance the research tools available (Powell et al. 2017)

Overall, our findings suggest a trade-off in sett function: for adults, cooler conditions may facilitate more effective periods of torpor, allowing individuals to reduce core temperatures and basal metabolic rates (Fowler and Racey, 1988), enabling them to conserve energy over the winter (Newman et al. 2011); in contrast warmer conditions favour the development of young cubs, which are more prone to heat loss due to immature physiology and scale laws (McNab 1988). Rödel et al. (2008) noted this same type of thermal benefit for the development for fossorial rabbit pups, and warm natal burrows may prove even more vital for small burrowing carnivores, such as stoats (*Mustela erminea*; see Erlinge 1987).

Conclusion

Maintaining homeothermic regulation is crucial for mammals, but incurs considerable energetic costs (Weiner, 1989). For animals exposed to prevailing weather conditions, the more extreme the environmental temperature (and other contributors such as soaking by rain; Webb and King, 1984) departs from the normative range to which that species is adapted, the more energy an animal has to commit to maintaining its constant body temperature (Terrien et al. 2011). Consequently, den use can be crucial in buffering environmental conditions, where Noonan et al. (2015b) propose a particular benefit to natal dens providing an insulated environment for raising altricial young in the Carnivora.

Despite weather acting as a substantial driver of badger population dynamics (see Newman et al., 2017b), Newman and Macdonald (2015) predict that there is only a moderate likelihood (AR5: 33-66%: IPCC, 2014b) that badger numbers will change across the UK as a singular result of climate change. Sett use may well provide the buffer that disarticulates weather effects from population responses in badgers, by providing thermal refugia. Indeed, Noonan et al. (2014) report that only thinner badgers leave their setts to forage during inclement autumnal weather. Fatter badgers, presumably less desperate to find food, stay within their setts; such are the benefits setts offer against net energy loss. With badgers expanding their distribution over their north-western biogeographical range edge with warming conditions (Byrne et al., 2015, Silva et al., 2017), we posit that sett use could play a major role in allowing them to exploit a greater proportion of more optimal foraging nights while offering refuge during poor foraging nights. Even in Mediterranean areas, warmer than our UK study site, setts continue to be important for badgers (Revilla et al 2001; Rosalino et al. 2005).

Living in subterranean burrows is not without its disadvantages, such as poor ventilation, the build up of ectoparasites, and the energy needed to dig (Burda et al. 2007); nevertheless 113 of 145 Carnivora species investigated by Noonan et al. (2015b) made at least some use of subterranean space, reinforcing the need to investigate further how den use may contribute to resilience to climate change effects among fossorial species.

Acknowledgements

We are grateful to the badger trapping team, past and present. We thank Ms. Nadine Adrianna Sugianto, a DPhil student atWildCRU, for supporting the surveys, and Prof. Andrew Markham, of Oxford University's Department of Computer Science, for loaning us data loggers We also thank Dr. Masayuki U. Saito, of Yamagata University's Faculty of Agriculture, for statistical advice in R. We thank the National Meteorological Library and Archive － Met Office, UK for the provision of meteorological data. Environmental Change Network (ECN), Natural England Open Data, the Ordnance Survey and Rural Payments Agency, and public sector information licensed under the Open Government Licence v3.0. enabled us to produce the study site map (Fig. 1) by providing GIS data .

Conflict of interest

The authors declare no conflicts of interest.

Funding

This work was supported by Grant-in Aid for Scientific Research (JSPS KAKENHI Grant Number JP26257404).

Animal Ethics Statement

All work was evaluated by the University Oxford Animal Welfare and Ethical Review Board. Interventions at badger setts were performed under UK government Natural

England licence numbers 2016-18558-SCI-SCI and 2017-27589-SCI-SCI. All animal trapping and handling procedures were performed under UK Animals (Scientific Procedures) Act, 1986 licence PPL 30-3379.

References

Beever, E. A., Hall, L. E., Varner, J., Loosen, A. E., Dunham, J. B., Gahl, M. K., Lawler, J. J., 2017. Behavioral flexibility as a mechanism for coping with climate change. Front. Ecol. Environ. 15 (6), 299-308.

Burda, H., Šumbera, R., Begall, S., 2007. Microclimate in burrows of subterranean rodents—revisited, in: Begall, S., Burda, H., Schleich, C. E. (Eds.), Subterranean Rodents: news from underground. Springer Berlin Heidelberg, Germany, pp.21-33.

Benedetti-Cecchi, L., Bertocci, I., Vaselli, S., Maggi, E., 2006. Temporal variance reverses the impact of high mean intensity of stress in climate change experiments. Ecology 87 (10), 2489-2499.

Blix, A. S., Lentfer, J. W., 1979. Models of thermal protection in polar bear cubs-at birth and on emergence from the den. Am. J. Physiol. - Regul. Integr. Comp. Physiol. 236 (1), 67-74.

Boutros, D., Breitenmoser-Würsten, C., Zimmermann, F., Ryser, A., Molinari-Jobin, A., Capt, S., Güntert, M., Breitenmoser, U., 2007. Characterisation of Eurasian lynx *Lynx lynx* den sites and kitten survival. Wildl. Biol. 13 (4), 417-429.

Boyles, J .G., Seebacher, F., Smit, B., McKechnie, A. E., 2011. Adaptive thermoregulation in endotherms may alter responses to climate change. Integr. Comp. Biol. 51 (5), 676-690.

Byrne, A. W., Fogarty, U., O'Keeffe, J., Newman, C., 2015. In situ adaptive response to climate and habitat quality variation: spatial and temporal variation in European badger (*Meles meles*) body weight. Glob. Change Biol. 21 (9), 3336-3346.

Campbell, R. D., Nouvellet, P., Newman, C., Macdonald, D. W., Rosell, F., 2012. The influence of mean climate trends and climate variance on beaver survival and recruitment dynamics. Glob. Change Biol. 18 (9), 2730-2742.

Coombes, M. A., Viles, H. A., 2015. Population-level zoogeomorphology: the case of the Eurasian badger (*Meles meles* L.). Physical Geogr.y 36 (3), 215-238.

Crompton, A. W., Taylor, C. R., Jagger, J. A., 1978. Evolution of homeothermy in mammals. Nature 272 (5651), 333-336.

Erlinge, S., 1987. Why do European stoats Mustela erminea not follow Bergmann's Rule?. Ecography 10 (1), 33-39.

Fowler, P. A., Racey, P. A., 1988. Overwintering strategies of the badger, *Meles meles*, at 57 °N. J. Zool. 214 (4), 635-651.

Huey, R. B., Tewksbury, J. J., 2009. Can behaviour douse the fire of climate warming? Proc. Natl. Acad. Sci. U.S.A. 106 (10), 3647-3648.

Humphries, M. M., Thomas, D. W., Speakman, J. R., 2002. Climate-mediated energetic constraints on the distribution of hibernating mammals. Nature 418 (6895), 313-316.

IPCC, 2014a. Climate Change 2014: Synthesis Report, in: Core Writing Team, Pachauri, R. K., Meyer, L. (Eds.), Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmantal Panel on Climate Change. IPCC, Geneva, 151 pages.

IPCC, 2014b. Impacts, adaptation, and vulnerability. Part A: Global and sectoral aspects, in: Field, C. B., Barros, V. R., Dokken, D. J., Mach, K. J., Mastrandrea, M. D., Bilir, T. E., Chatterjee, M., Ebi, K. L., Estrada, Y. O., Genova, R. C., Girma, B., Kissel, E. S., Levy, A. N., MacCracken, S., Mastrandrea, P. R., White, L. L. (Eds.), Climate Change 2014 Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge university press, Cambridge, UK, and New York, 1132 pages.

Jiménez, J., Decaëns, T., 2000. Vertical distribution of earthworms in grassland soils of the Colombian Llanos. Biol. Fertil. Soils 32 (6), 463-473.

Johnson, D. D. P., Jets, W., Macdonald, D. W., 2002. Environmental correlates of badger social spacing across Europe. J. Biogeogr. 29 (3), 411-425.

Johnson, K. G., Pelton, M. R., 1980. Environmental relationships and the denning period of black bears in Tennessee. J. Mammal. 61 (4), 653-660.

Kaneko, Y., Newman, C., Buesching, C. D., Macdonald, D. W., 2010. Variations in badger (*Meles meles*) sett microclimate: Differential cub survival between main and subsidiary setts, with implications for artificial sett construction. Int. J. Ecol. 2010, 1-10.

Lindsay, I. M., Macdonald, D. W., 1985. The effects of disturbance on the emergence of Eurosialn badgers in winter. Biol. Conserv. 34 (4), 289-306.

Loutre, M. F., Paillard, D., Vimeux, F., Cortijo, E., 2004. Does mean annual insolation have the potential to change the climate?. Earth Planet. Sci. Lett. 221 (1-4), 1-14.

Lowell, B. B., Spiegelman, B. M., 2000. Towards a molecular understanding of adaptive thermogenesis. Nature 404 (6778), 652-660.

Macdonald, D. W., Mitchelmore, F., Bacon, P. J., 1996. Predicting badger sett numbers: evaluating methods in East Sussex. J. Biogeogr. 23 (5), 649-655.

Macdonald, D. W., Newman, C., 2002. Badgers *Meles meles* population dynamics in Oxfordshire, UK, numbers, density and cohort life histories, and a possible role of climate change in population growth. J. Zool. 256 (1), 121-138.

Macdonald, D. W., Newman, C., Buesching, C. D., 2015. Badgers in the rural landscape - conservation paragon or farmland pariah? Lessons from the Wytham Badger Project, in: Macdonald, D. W., Feber, R. E. (Eds.), Wildlife Conservation on Farmland. Volume 2: Conflict in the Countryside. Oxford University Press, Oxford, pp. 65-95.

Macdonald, D. W., Newman, C., Buesching, C. D., Nouvellet, P., 2010. Are badgers 'Under The Weather'? Direct and indirect impacts of climate variation on European badger (*Meles meles*) population dynamics. Glob. Change Biol. 16 (11), 2913–2922.

Macdonald, D. W., Newman, C., Dean, J., Buesching, C. D., Johnson, P. J., 2004. The distribution of Eurasian badger, *Meles meles*, setts in a high-density area: field observations contradict the sett dispersion hypothesis. Oikos 106 (2), 295–307.

Magoun, A. J., Copeland, J. P., 1998. Characteristics of wolverine reproductive den sites. J. Wildl. Manag. 62, 1313-1320.

McCafferty, D. J., Gilbert, C., Paterson, W., Pomeroy, P. P., Thompson, D., Currie, J. L., Ancel, A., 2011. Estimating metabolic heat loss in birds and mammals by combining infrared thermography with biophysical modelling. Comp. Biochem. Physiol. A. Mol. Integr. Physiol. 158 (3), 337-345.

McLaren, G. W., Thornton, P. D., Newman, C., Buesching, C. D., Baker, S. E., Mathews, F., Macdonald, D. W., 2005. The use and assessment of ketamine-medetomidine-butorphanol combinations for field anaesthesia in wild European badgers (*Meles meles*). Vet. Anaesth. Analg. 32, 367-372.

McNab, B. K., 1979. The influence of body size on the energetics and distribution of fossorial and burrowing mammals. Ecology 60 (5), 1010-1021.

McNab, B. K., 1988. Complications inherent in scaling the basal rate of metabolism in mammals. Q. Rev. Biol. 63 (1), 25-54.

Milly, P. C. D., 1984. A simulation analysis of thermal effects on evaporation from soil. Water Resour. Res. 20 (8), 1087-1098.

Moore, J. A. H., Roper, T. J., 2003. Temperature and humidity in badger *Meles meles* settts. Mammal Rev. 33 (3-4), 308-313.

Newman, C., Macdonald, D. W., 2015. The implications of climate change for terrestrial UK mammals. Terrestrial biodiversity climate change impacts report card technical paper. Living With Environmantal Change (LWEC) Partnership. <http://www.nerc.ac.uk/research/partnerships/ride/lwec/report-cards/>.

Newman, C., Buesching, C. D., Macdonald, D. W., 2017a. Meline Mastery of Meteorological Mayhem: The effects of climate changeability on European badger population dynamics, in: Macdonald, D.W., Newman, C., Harrington, L. (Eds.), The Biology and Conservation of Wild Musteloids. Oxford University Press, Oxford, pp. 420-433.

Newman, C., Buesching, C. D., Macdonald, D. W., 2017b. Meline Mastery of Meteorological Mayhem: The effects of climate changeability on European badger population dynamics, in: Macdonald, D.W., Newman, C., Harrington, L. (Eds.), The Biology and Conservation of Wild Musteloids. Oxford University Press, Oxford, pp. 450-465.

Noonan, M. J., Markham, A., Newman, C., Trigoni, N., Buesching, C. D., Ellwood, S. A., Macdonald, D. W., 2014. Climate and the individual: inter-annual variation in the autumnal activity of the European badger (*Meles meles*). PLOS ONE 9 (1), e83156.

Noonan, M. J., Rahman, M. A., Newman, C., Buesching, C. D., Macdonald, D. W., 2015a. Avoiding verisimilitude when modelling ecological responses to climate change: the influence of weather conditions on trapping efficiency in European badgers (*Meles meles*). Glob. Change Biol. 21 (10), 3575-3585.

Noonan, M. J., Newman, C., Buesching, C. D., Macdonald, D. W., 2015b. Evolution and function of fossoriality in the Carnivora: implications for group-living. Front. Ecol. Evol. 3, 116.

Noonan, M. J., Markham, A., Newman, C., Trigoni, N., Buesching, C. D., Ellwood, S. A., Macdonald, D. W., 2015c. A new Magneto-Inductive tracking technique to uncover subterranean activity: what do animals do underground? Methods Ecol. Evol. 6 (5), 510-520.

Nouvellet, P., Newman, C., Buesching, C. D., Macdonald, D. W., 2013. A multi-metric approach to investigate the effects of weather conditions on the demographic of a terrestrial mammal, the European badger (*Meles meles*). Plos One 8 (7), e68116.

Oliver, S. A., Oliver, H. R., Wallace, J. S., Roberts, A. M., 1987. Soil heat flux and temperature variation with vegetation, soil type and climate. Agric. For. Meteorol. 39 (2-3), 257–269.

Powell, R.A., Ellwood, S., Kays, R., Maran, T., 2017. Stink or swim: techniques to meet the challenges for the study and conservation of small critters that hide, swim, or climb, and may otherwise make themselves unpleasant, in: Macdonald, D. W., Newman, C., Harrington, L. A. (Eds.), Biology and Conservation of Musteloids. Oxford University Press, Oxford, pp 231 -254.

Revilla, E., Palomares, F., Fernández, N., 2001. Characteristics, location and selection of diurnal resting dens by Eurasian badgers (*Meles meles*) in a low density area. J. Zool. 255 (3), 291-29.

Rödel, H. G., Hudson, R., Von Holst, D., 2008. Optimal litter size for individual growth of European rabbit pups depends on their thermal environment. Oecologia 155 (4), 677-689.

Roper, T. J., 1992. Badger *Meles meles* setts - architecture, internal environment and function. Mammal Rev. 22 (1), 43-53.

Roper, T. J., Kemenes, I., 1997. Effect of blocking of entrances on the internal environment of badger *Meles meles* setts. J. Appl. Ecol. 34 (5), 1311-1319.

Rosalino, L. M., Macdonald, D. W., Santos-Reis, M., 2005. Activity rhythms, movements and patterns of sett use by badgers, Meles meles, in a Mediterranean woodland. Mammalia mamm 69 (3-4), 395-408.

Savill, P., Perrins, C., Kirby, K., Fisher, N., 2010. Wytham Woods: Oxford's Ecological Laboratory. Oxford University Press, Oxford, 288pages.

Scheffers, B. R., Edwards, D. P., Diesmos, A., Williams, S., Evans, T. A., 2014. Microhabitats reduce animal's exposure to climate change. Glob. Change Biol. 20 (2), 495-503.

Sih, A., 2013. Understanding variation in behavioural responses to human-induced rapid environmental change: a conceptual overview. Anim. Behav. 85 (5), 1077-1088.

Silva, A. P., Curveira-Santos, G., Kilshaw, K., Newman, C., Macdonald, D. W., Simões, L., Rosalino, L. M., 2017. Climate and anthropogenic factors determine site occupancy in Scotland's Northern-range badger population: implications of context-dependent responses under environmental change. Divers. Distributions 23 (6), 627-639.

Smith, J. B., Schneider, S. H., Oppenheimer, M., Yole, G. W., Hare, W., Mastrandrea, M. D., Patwardhan, A., Burton, I., Corfee-Morlot, J., Magadza, C. H. D., Füssel, H. M., Pittock, A. B., Rahman, A., Suarez, A., van Ypersele, J. P., 2009. Assessing dangerous climate change through an update of the Intergovernmental Panel on Climate Change (IPCC) "reasons for concern". Proc. Natl. Acad. Sci. U.S.A. 106 (11), 4133-4137.

Smith, M.D., 2011. An ecological perspective on extreme climate events: a synthetic definition and framework to guide future research. J. Ecol. 99 (3), 656-663.

Speedy, A. W. 1980. Sheep Production, Science into Practice. Longman, London, 195 pages.

Sun, Q., Stevens, C., Newman, C., Buesching, C. D., Macdonald, D. W., 2015. Cumulative experience, age-class, sex and season affect the behavioural responses of European badgers (*Meles meles*) to handling and sedation. Animal Welf. 24 (4), 373-385.

Taylor, M. E., Morecroft, M. D., Oliver, H. R., 2010. The physical environment, in: Savill, P., Perrins, C., Kirby, K., Fisher, N. (Eds.), Wytham Woods: Oxford's Ecological Laboratory. Oxford University Press, Oxford, pp. 21-28.

Terrien, J., Perret, M., Aujard, F., 2011. Behavioral thermoregulation in mammals: a review. Front Biosci, 16, 1428-1444.

Thompson, C. M., Purcell, K. L., 2016. Conditions inside fisher dens during prescribed fires; what is the risk posed by spring underburns? For. Ecol. Manag. 359, 156-161.

Tuomainen, U., Candolin, U., 2010. Behavioural responses to human-induced environmental change. Biol. Rev. 86 (3), 640-657.

Vos, P., Meelis, E., Ter Keurs, W. J., 2000. A framework for the design of ecological monitoring programs as a tool for environmental and nature management. Environ. Monit Assess. 61 (3), 317-344.

Webb, D. R., King, J. R., 1984. Effects of wetting of insulation of bird and mammal coats. J. Therm. Biol. 9 (3), 189-191.

Weiner, J., 1989. Metabolic constraints to mammalian energy budgets. Acta Theriol. 34 (1), 3-35.

Woodroffe, R. (1995). Body condition affects implantation date in the European badger, Meles meles. J. Zool. 236(2), 183-188.

Yun, T. S., Santamarina, J. C., 2008. Fundamental study of thermal conduction in dry soils. Granul. Matter 10 (3), 197-207.

Zhou, Y., Newman, C., Kaneko, Y., Buesching, C. D., Chen, W., Zhou, Z-M., Xie, Z., Macdonald, D. W., 2017. Asian badgers - the same, only different: How diversity among badger societies informs socio-ecological theory and chanllenges conservation, in: Macdonald, D. W., Newman, C., Harrington, L. (Eds.), The Biology and Conservation of Wild Musteloids. Oxford University Press, Oxford, pp. 327-350.

Table 1. Summary of weekly badger sett temperature survey conducted from September to December, 2016, in Wytham Woods, UK. Mean interior sett temperature ± SD (℃) was calculated from data recorded October to December 2016.

Sett ID	Elevation (m)	Slope inclination	Slope aspect	No. of surveyed entrances	Soil type	Mean interior sett temperature ± SD (℃)

BL	102	steep	northeast	4 – 7	gley soils	10.89 ± 1.67
CH	157	steep	northwest	4 – 7	lithomorphic soils	9.85 ± 1.76
GATES	114	convex	northeast	4 – 5	brown soils	10.11 ± 2.33
GO	154	steep	southwest	4 – 10	brown sands	11.00 ± 1.86
KH	151	steep	northwest	4 – 5	brown sands	9.68 ± 2.13
LS	138	gentle	southeast	9 – 10	lithomorphic soils	9.77 ± 1.76
MT	102	gentle	southeast	7 – 13	pelosols	10.05 ± 1.72
RC	155	steep	south	4 – 6	brown sands	10.01 ± 1.86
SH	147	steep	north	4	lithomorphic soils	9.68 ± 1.98
SW	148	flat	-	4	brown soils	9.74 ± 2.09
UF	125	gentle	southeast	5 – 11	brown soils	10.55 ± 2.15

Table 2. Summary of OLS analyses of weekly interior sett temperature (n=974) recorded in Wytham Woods from September to December 2016. Exterior sett temperature, date, sett aspect (north/south), soil type (brown sands, brown soils, lithomorphic soils, pelosols and gley soils), and total daily precipitation were included as explanatory variables.

Variable	Estimate	Standard error	t value	Pr(>|t|)
(Intercept)	14.89	1.008	14.78	< 0.0001
exterior sett temperature	0.35	0.019	17.97	< 0.0001

date	-0.01	0.001	-9.49	< 0.0001
south	0.36	0.112	3.20	0.0014
brown soils	-0.14	0.134	-1.05	0.2947
lithomorphic soils	-0.50	0.129	-3.85	0.0001
pelosols	-0.43	0.150	-2.84	0.0047
gley soils	0.27	0.199	1.36	0.1739
precipitation (mm)	-0.10	0.027	-3.65	0.0003
Adjusted R^2 = 0.70; $F_{(8, 917)}$ = 265.2				

Table 3. Badger sett interior temperature versus Met Office exterior temperature range for each month and mean ranges per day, month and over the full study period in Wytham Woods, UK between October and December 2016. Interior sett temperature data was collected using thermal probes and exterior temperature data was acquired from the National Meteorological Library and Archive —Met Office, UK (https://www.metoffice.gov.uk/).

		Interior	Met Office / exterior
Range (˚C)			
	October	8.5-13.0	3.7-16.6
	November	1.5-20.0	-4.7-14.4
	December	1.5-13.0	-4.0-14.6
	Overall	1.5-20.0	-4.7-16.6
Mean range (˚C)			
	Daily	0.9	6.2
	Monthly	4.7	16.9
	Overall	8.1	19.3

Table 4. Summary of OLS analyses of daily interior sett temperature recorded in Wytham Woods from October to December 2016. 5-min interval interior temperatures response variables were combined into hourly averages per sett, and each hour was used as an explanatory variable.

Variable	Estimate	Standard error	t value	Pr(>|t|)
(Intercept)	8.74	0.03	338.34	< 0.0001
1:00	-0.02	0.04	-0.60	0.5455
2:00	-0.05	0.04	-1.44	0.1509
3:00	-0.07	0.04	-2.04	0.0415
4:00	-0.09	0.04	-2.50	0.0124
5:00	-0.09	0.04	-2.54	0.0112
6:00	-0.11	0.04	-2.99	0.0028
7:00	-0.11	0.04	-3.11	0.0019
8:00	-0.11	0.04	-3.10	0.0019
9:00	-0.10	0.04	-2.62	0.0087
10:00	-0.04	0.04	-1.12	0.2648
11:00	0.03	0.04	0.80	0.4246
12:00	0.10	0.04	2.73	0.0063
13:00	0.17	0.04	4.61	< 0.0001
14:00	0.20	0.04	5.39	< 0.0001
15:00	0.19	0.04	5.24	< 0.0001
16:00	0.16	0.04	4.41	< 0.0001
17:00	0.13	0.04	3.49	0.0005
18:00	0.18	0.04	4.75	< 0.0001
19:00	0.07	0.04	1.81	0.0701
20:00	0.04	0.04	1.16	0.2480
21:00	0.02	0.04	0.46	0.6461
22:00	-0.05	0.04	-0.15	0.8827
23:00	-0.02	0.04	-0.50	0.6161
Adjusted R^2 = 0.003; F (23, 139787) = 16.87				

Fig.1. Locations of badger setts surveyed at Wytham Woods, Oxford, UK, showing the

main habitat types in the Woods. Contains public sector information licensed under the Open Government Licence v3.0. Contains, or is derived from, information supplied by the Ordnance Survey and Rural Payments Agency. © Crown copyright and database rights [2016]. Ordnance Survey 100022021. Contains data from Natural England Open Data (http://naturalengland-defra.opendata.arcgis.com/) and from the Environmental Change Network (www.ecn.ac.uk).

Fig. 2. Fig. 2. Comparison of mean interior badger sett temperature (from weekly spot measurements of multiple sett entrances at a depth of 2 m) with exterior temperature (Met Office data) ± SE in Wytham Woods, UK, in autumn-winter 2016.

Fig. 3. Scatter plots of mean interior sett temperature (weekly spot measurements) versus weights of badger adult/cub caught in autumn (November) 2016 (A) and spring (May-June) 2017 (B). The line depicting cubs in spring 2017(B) exhibits a significant trend (Ordinary least squares: y = 0.53x -2.17, adjusted R^2 = 0.42, $F_{(1, 7)}$ = 6.81, t = 2.54, p = 0.04).

Fig. 4. Scatter plot representing the relationship between the head-body lengths and weights of badger cubs caught in spring (May-June) 2017.

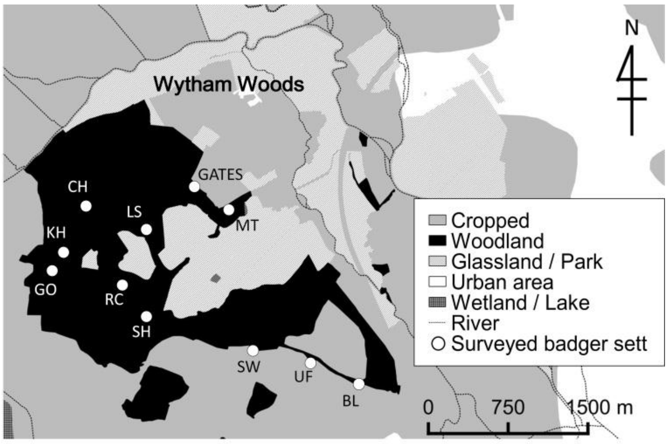
Wytham Woods
N
CH
GATES
LS
MT
KH
GO
RC
SH
SW
UF
BL
Cropped
Woodland
Glassland / Park
Urban area
Wetland / Lake
River
Surveyed badger sett
0
750
1500 m

Fig. 1

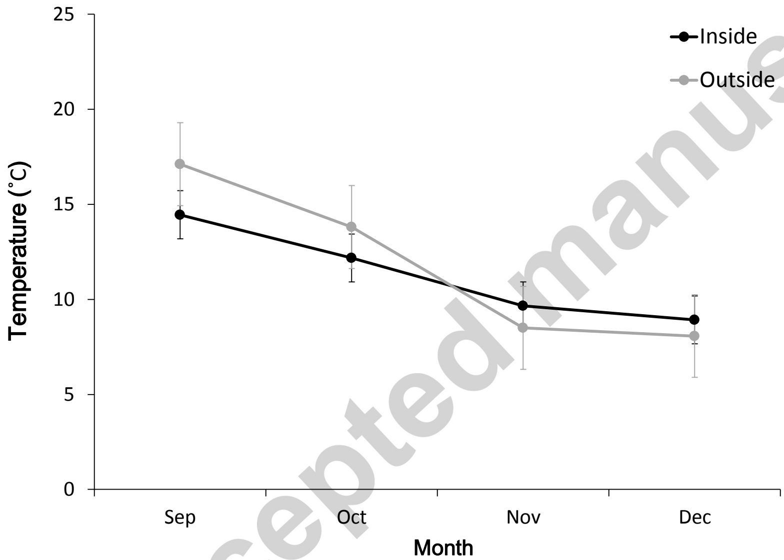
Inside
Outside
Temperature (˚C)
25
20
15
10
5
0
Sep
Oct
Nov
Dec
Month

Fig.2

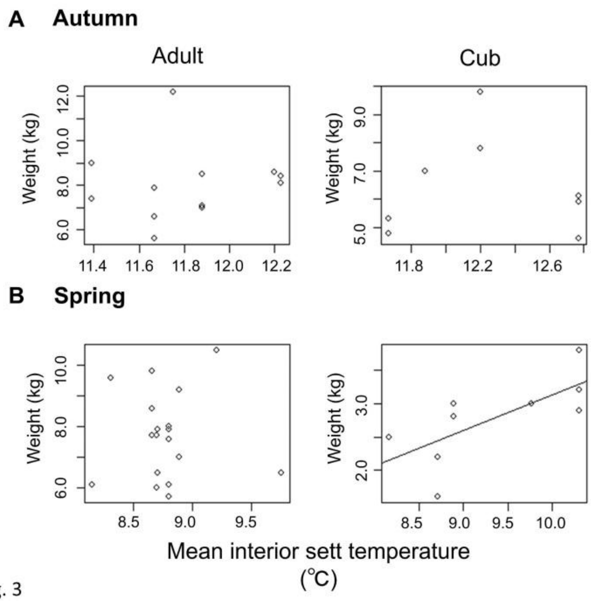

Fig. 3

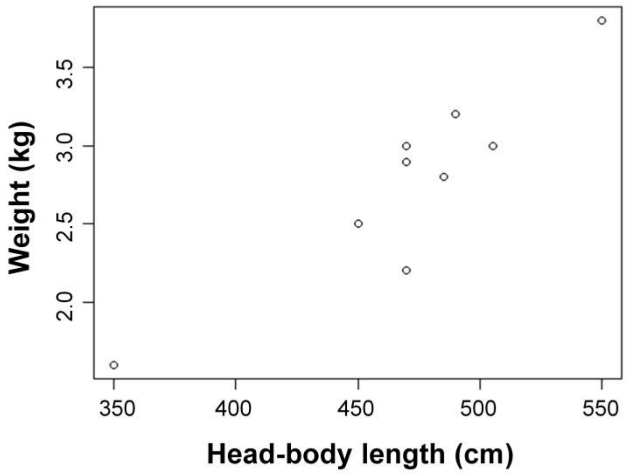

Fig. 4

Highlights

- We monitored microclimate in 11 European badger setts (dens) with a thermal probe
- Badger sett temperature was more stable than exterior conditions
- Soil type, aspect, and the presence of badgers all affected sett temperature

- Heavier cubs developed in warmer setts in the following spring
- Den use may buffer climate change effects for many fossorial carnivore species