The socio-ecological functions of fossoriality in a group-living carnivore, the European badger (*Meles meles*)

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Abstract

This thesis examines the role played by den use in socio-ecology, especially in leveraging group formation (i.e., the Fossorial Benefits Hypothesis; FBH), using badgers as a model species. In particular, I benefit from recent technological developments, facilitating detailed measurements of activity, energetic expenditure, ranging behaviour, and underground localisation, enabling the examination of hitherto intractable facets of badger socio-ecology, allowing a comprehensive investigation.

Group-living is theorised to evolve when the benefits of living with conspecifics outweigh the costs. While pack hunting, and allo-parenting play a specific role in fostering communal living, I demonstrate in Part I that continued cohabitation at natal dens can often acts as a precursive mechanism initiating cohabitation, that can persists into adulthood among small, omnivorous/insectivorous, den-using carnivores. In this context, I then consider the implications of delayed dispersal and reproductive suppression. This provides an evolutionary basis linking fossoriality and group-living in the Carnivora, where sociality is, in part, explained by burrow-dwelling.

Part II establishes that the energetic benefits of using fossorial dens as refugia from adverse weather provide a functional basis for persistent co-occupation of a common den by conspecifics. Badgers use setts strategically, with reference to their body-condition and their imperative to forage, to reduce energy expenditure and optimise their capacity for achieving minimal food security. This section also considers how badgers may compensate for ongoing rapid climate change.

Part III demonstrates that cohabitation at dens does not infer group collaboration or social structure; individuals may still act independently. Nevertheless, burrow use patterns were coordinated between badger group members, evidencing that dens act as social foci.

Collectively these lines of evidence support the FBH as a playing a causal role promoting spatial group formation and a complementary role driving persistent benefits of group-living in suitable resource-scapes; resulting in 'spatial' though not necessarily 'social' -groups.

Contents

Part I

The 'Grass Roots' of Denning

'...the world Cenozoic orogenies, which started differentially in the Paleogene across the Planet, but were reinforced in the Neogene, completed the global trend of increasing cold, drought, and seasonality. Archaic forms were replaced by modern forms exemplified in whales, the transition from prosimian to anthropoid primates, and the dramatic evolution of subterranean mammals.'

– Eviatar Nevo

Chapter 1

General introduction

In his seminal review, Eisenberg (1966) draws attention to three forms of mammalian socio-spatial organisation:

i) simple social systems with minimal cohesion and coordinated behaviour, often the result of temporary feeding aggregations;

ii) social systems arising from reproductive behaviour, ranging from brief copulatory associations, to prolonged periods of mate guarding; and

iii) long-term associations of multiple adults from both sexes, maintained throughout both reproductive, and non-reproductive life-cycle phases.

Although these three forms of social organisation are not mutually exclusive, the latter form is both the most derived, and least prevalent (Eisenberg, 1966; Bekoff et al., 1984; Johnson et al., 2000; Macdonald and Johnson, 2015). For these long-term associations to develop and persist, temporary aggregations resulting from either feeding ecology or reproductive behaviour must be maintained over time. Axiomatically, for these to be maintained, the individual level benefits of living with conspecifics must outweigh the costs (Alexander, 1974; Emlen, 1982; von Schantz, 1984; Bacon et al., 1991; Koenig et al., 1992).

It should be noted however, that there are two crucial caveats to these general classifications. First, that 'solitary' is not synonymous with 'asocial'. Indeed, the spatial organisation of solitary species is often the result of interactions with neighbouring conspecifics (Eisenberg, 1966; Sandell, 1989; Temeles, 1994; Pereira et al., 2003), and even the most solitary of species must meet, at least briefly, to reproduce. Second, that 'long-term associations' are not synonymous with 'cooperative societies'. As Hans Kruuk (1972) first observed, there are numerous group-living species that do not interact cooperatively, and forage alone. Indeed, Alexander (1974) stressed the distinction between factors that lead to i) the formation of 'social groups'; and ii) the subsequent evolution of 'social behaviours'. Thus, cooperation is not a prerequisite for the formation of social groups, and, crucially, not a subsequent necessity of group-living (Clutton-Brock, 2009; Smith et al., 2012; Macdonald and Johnson, 2015). As such, a distinction is made here between 'spatial groups', which have largely over-lapping home ranges, but with little evidence of cooperative behaviour (*sensu* Leyhausen, 1965), and 'social groups', which exhibit at least some extent of social behaviour. In this thesis, I focus primarily on the second of these two caveats, investigating ecological factors promoting the maintenance of socio-spatial aggregations in

non-cooperative societies. In the present chapter, I first provide consilient evidence, in a step-wise manner, demonstrating the basis of a novel hypothesis leveraging group formation: the Fossorial Benefits Hypothesis. In particular, I draw attention to the role of fossorial dens in maintaining an energetic balance. I then focus on a specific exemplar, the European badger (*Meles meles*), investigating the socio-ecological implications of their fossorial life-histories.

1.1 Evolution of spatial groups

The Order Carnivora presents a unique opportunity towards understanding the cost-benefit balance of living with conspecifics. With only 10-15% of carnivores exhibiting a propensity towards group-living (Bekoff et al., 1984; Gittleman, 1989; Johnson et al., 2000), the relative rarity of sociality is suggestive of high associated costs (Wrangham et al., 1993). Addressing these costs is, however, not straightforward, due in no small part to the extensive variability in carnivoran life-histories. Diets range from the wholly carnivorous felids (Sicuro and Oliviera, 2011), and extreme herbivorous specialist such as the giant panda (*Ailuropoda melanoleuca,* Chorn and Hoffmann, 1978), to less particular opportunistic omnivores such as the mephitids, procyonids, and ursids (Wilson et al., 2009). There is also a 1000-fold difference in body size within the Order, from the 100g least weasel (*Mustela nivalis*, Sheffield and King, 1994), to the 500+kg polar bear (*Ursus maritimus*, DeMaster and Stirling, 1981). Carnivores have adapted to nearly every habitat niche, from the predominantly aquatic pinnipeds (Wilson et al., 2009), to the scansorial viverrids (McClearn, 1992) and *Martes* spp. (Newman et al., 2011), and from the long legged cursorial canids (Andersson, 2004), to short, sturdy fossorial specialists (Hildebrand, 1985; Andersson, 2004). With the extensive range of life-histories across the Order, the variability in group-living propensities is unsurprising.

What is of further interest however, is the intraspecific variation in group-living propensities under differing ecological conditions (Cavallini, 1996; Blundell et al., 2002; Johnson et al., 2002*a*; Macdonald and Johnson, 2015). Given the variation in life-history modes, it is clear that no single mechanism is, or indeed can be, universal within this Order (Eisenberg, 1966). Nonetheless, several non-mutually exclusive hypotheses present a useful framework for addressing the formation of carnivoran spatial groups:

i) the predator avoidance hypothesis, first mentioned by Francis Galton in 1871, but formalised a century later by Hamilton (1971), states that aggregations serve to dilute the individual level predation threat (Hamilton, 1971), and increase collective vigilance (Lima, 1990). As early models made clear however (e.g., Hamilton, 1971; Treisman, 1975; Lima, 1990), the maintenance/size of these groups poses a significant challenge. Although the dilution effect increases ad infinitum favouring the largest possible group, this would inevitably lead to extreme competition. Rubenstein (1978) suggested a useful caveat to this theory, that the risk of predation was the most important force responsible for the formation and maintenance for groups of poor competitors (e.g., grazing ungulates competing for grass). Nonetheless, it is clear these assemblages cannot be supported unless local resources can support the energetic requirements of multiple adults. In this respect, a number of smaller, group-living carnivores benefit from cooperative anti-predator behaviour (e.g., mobbing of predators, collective vigilance, and protection of neonates in meerkats, *Suricata suricatta*, Doolan and Macdonald, 1997; Clutton-Brock, 2009), however as adults, many carnivores are at a trophic level with few predators, and the extent to which predator avoidance underlies carnivoran group-formation remains tentative.

ii) the Information Center Hypothesis (ICH; Ward and Zahavi, 1973), proposes that aggregations of solitary foragers provide individuals with information on the foraging activities of conspecifics. Although this mechanism has been met with mixed support in a number of species (e.g., supported in bank swallows, *Riparia riparia*, Emlen, 1971; cliff swallows, *Hirundo pyrrhonota*, Mobley and Schenker, 1981; and hooded crows, *Corvus corone cornix*, Sonerud et al., 2001; but refuted in prairie dogs, *Cynomys* spp. Hoogland, 1981; striped mice, *Rhabdomy pumilio*, Schradin, 2007; and Bechstein's bats, *Myotis bechsteinii*, Kerth et al., 2001), it remains largely untested in the Carnivora. It should be noted however, that ICH type benefits are unlikely to occur in a number small predatory carnivores, where small vertebrate prey tend to be localised and indivisible; conditions associated with competition (Macdonald et al., 2004*a*) and territorial defence (Waser, 1981);

iii) the Resource Dispersion Hypothesis (RDH; Macdonald, 1983*b*; Macdonald and Johnson, 2015) proposes that, should the dispersion and renewal rate of local resources result in a territory that can viably accommodate multiple individuals, groups can arise without any specific benefits where there are minimal costs to the primary 'territory holder'. This is a flexible process however, where many species

form temporary 'fission-fusion' societies under appropriate, but temporary RDH conditions (reviewed in Macdonald and Johnson, 2015). A crucial proviso to this hypothesis is that secondary conspecifics must have a physiology capable of tolerating secondary food security during periods of resource depletion (Newman et al., 2011). As a further caveat, similar to the ICH, RDH type benefits are less likely to occur in those species with a carnivorous diet. From an economic standpoint, these predators must be less numerous than prey items (Eisenberg, 1966), and tend to space themselves out as local resources can rarely support the requirements of multiple adults (Eisenberg, 1966; von Schantz, 1984). As such, this mode of group formation is most prevalent in omnivorous/insectivorous carnivores (Macdonald, 1983*b*; Macdonald and Johnson, 2015);

iv) that reproductive competition promotes the formation of stable, adult groups as a form of mate guarding (Alexander, 1974; Clutton-Brock, 1989; Lukas and Clutton-Brock, 2013). As with predatory defence however, the local environment must be able to support these groups outside of the mating period in order for them to be maintained. In this respect a number of carnivores form mating pairs that subsequently disipate outside of the breeding season (e.g. bush dogs, *Speothos venaticus*, Beisiegel and Zuercher, 2005; honey badgers, *Mellivora capensis*, Vanderhaar and Hwang, 2003; Corsac foxes, *Vulpes corsac*, Clark et al., 2009); where female spacing patterns are typically dictated by local resource abundance, and males by that of females (Powell, 1979; Lukas and Clutton-Brock, 2013). Furthermore, it is important to note that in groups experiencing elevated levels reproductive competition, reproductive suppression of subordinates poses a serious cost to the formation of stable groups (Creel and Creel, 1991; Creel and Macdonald, 1995); and

v) trade-offs between the costs and benefits of dispersal from natal territories promoting philopatric behaviour (Emlen, 1982; Lindström, 1986; Macdonald and Carr, 1989; Creel and Macdonald, 1995; Waser, 1996; Hatchwell and Komdeur, 2000; Kokko and Ekman, 2002; Isbell, 2004). Traditionally, models of philopatry have been based on cost-driven criteria, such as the greater mortality risk for dispersing individuals (Lucas et al., 1994), competition for breeding opportunities (Koenig et al., 1992; Kokko and Lundberg, 2001), and local habitat saturation (Emlen, 1982) – i.e. the Ecological Constraints Hypothesis (ECH). Other research has focused on a 'benefit-driven' basis for philopatry (i.e., the benefits of philopatry hypothesis; Brown and Brown, 1984; Pen and Weissing, 2000), where

natal territories act as a 'safe haven' (*sensu* Kokko and Ekman, 2002) increasing offspring survival (Ekman et al., 2000), and promoting delayed dispersal and inclusive fitness (Koenig et al., 1992). Nevertheless, it is evident that both the costs and benefits associated with dispersal/philopatry operate in congruence, where ultimately, the balance between these will determine dispersal patterns.

Although synergistic in nature, regardless of which of these hypotheses underlies a species' propensity for group-living, mechanistically, local ecological factors can tip the balance in favour of gregarious or solitary life-histories (*sensu* Macdonald, 1983*b*). Signs of nascent group formation for carnivore species on the margins of achieving a cost-benefit balance indicate that these mechanisms can be pivotal, where more marginal groups are prone to dissipate. Vangen et al. (2001) for example, report that juveniles and sub-adults wolverines (*Gulo gulo*) can remain with their natal territory in years with good prey availability, but disperse in low abundance years. Similarly, Sillero-Zubiri and Gottelli (1995) report that in Ethiopian wolf (*Canis simensis*) populations, prey availability in natal territories was a significant predictor of dispersal patterns and subsequent group size.

Furthermore, while these hypotheses have proven insightful for explaining the group-living propensity of many carnivores (reviewed in Macdonald and Johnson, 2015), there are also a number of species with life-histories, and trophic resource characteristics that, on the basis of these hypotheses, might have been expected to form spatial groups, but do not (e.g. slender mongooses, *Galerella sanguinea*, Taylor, 1975; ringtails, *Bassariscus astutus*, Harrison, 2012; ursids, *Ursus* spp., Pasitschniak-Arts, 1993; Larivière, 2001; and African civets, *Civettictis civetta*, Ray, 1995). This prompts consideration of the circumstances that militate for group formation in these apparently contrarian societies. Here, I note the previously overlooked commonality that among gregarious, yet non-cooperative carnivores, many tend to have a substantial reliance upon subterranean dens. If local environmental carrying capacity permits, then philopatry/delayed dispersal at natal dens may impose communal aggregation upon individuals, leading to (not necessarily cooperative) spatial groups. As such, I propose a further mechanism towards the origin and maintenance of group formation, which will be the central focus of this thesis: the Fossorial Benefits Hypothesis (FBH).

1.2 Fossoriality

Fossoriality – which I define here as the propensity for digging and life underground (from Medieval Latin *fossorius* used for digging, from Latin *fossor* digger) – is a trait exhibited by various mammal species, principally from the Orders Rodentia, Eulipotyphla, and Carnivora (Kinlaw, 1999; Nevo, 1999). Fossorial habits vary along a continuum from the totally subterranean naked mole rats (*Heterocephalus glaber*) to species only excavating dens for specific periods of their life-cycle, such as utilising winter hibernaculae or relying upon natal dens to raise altricial young. Thus, a distinction is made here between subterranean and fossorial species; subterranean animals spend the majority of their lives below ground, only emerging incidentally, and fossorial species in contrast use the underground space for shelter or reproduction, but forage above-ground (Nevo, 1999).

Although largely under-investigated, two main hypotheses relating fossoriality to group-living propensity have been suggested. The Territorial Defence Hypothesis (TDH; Nevo, 1979) proposes that the low productivity of the subterranean environment, and the defendable nature of burrow systems leads to strong resource competition, militating for solitary social systems. In contrast, the Expansible Burrow Hypothesis (EBH; Alexander et al., 1991) proposes that the benefits of subterranean, predator-free refugia militate for philopatry, cooperation, and thus sociality. Although local ecology may tip the balance of either of these modes of group formation in one direction or another (for example, the Aridity Food Distribution Hypothesis, AFDH, reviewed in Jarvis et al., 1994, highlights patchy and unpredictable resources as a driver of sociality in subterranean mole-rats), there exists substantial support for a relationship between the evolution of burrowing, and sociality in the Rodentia (Ebensperger and Blumstein, 2006; Sobrero et al., 2014; Smorkatcheva et al., 2014).

In the Rodentia, it has been proposed that fossoriality leverages group formation by reducing predation threat, thereby benefiting individual survival (*sensu* Kokko and Ekman, 2002), and encouraging philopatric behaviour. In this thesis, I propose an extension of this concept (i.e., the FBH). For iteroparous species, fitness can increase with age provided the individual; i) survives until the next reproductive season; ii) remains reproductively active; iii) is in sufficiently good condition to reproduce at this time; and iv) is at the front of the breeding 'queue' (Kirkwood and Rose, 1991; Clark, 1994; Kokko and Ekman, 2002). Mathematically, this relationship can be

represented as the summation of the probability of survival to age x (l_x), and age-specific reproduction (m_x; Pianka, 2000):

$$R_o = \sum l_x \; m_x \tag{1.1}$$

Mechanistically therefore, fitness (R_o) can accrue via direct investment in reproduction, maximising m_x (Gittleman and Thompson, 1988; Stearns, 1992), or indirectly through investment in survival maximising l_x (Charnov, 1991; Kirkwood and Rose, 1991; Vaupel et al., 2004). I posit therefore, that if the benefits provided by fossorial dens result in a situation where the survival probability associated with philopatry is greater than that associated with dispersal, the associated fitness benefits will favour natal philopatry and subsequent group-living (for further details see 8.1). Subterranean living is not without its challenges however, including the high energetic cost of burrowing (Vleck, 1979, 1981), hypoxia/hypercapnia, permanent darkness, and conditions of high pathogen infectivity, which can lead to the spread of parasites and disease (Nevo, 1999). Consequently, it should not be presumed that fossorial dens always provide a net-benefit to occupants. As such, any attempt to investigate the FBH must find support for two underlying assumptions: i) that dens provide a net-benefit to the survival probability of occupants; and ii) that den living plays a central role in determining the dispersal patterns and group-structure of the species. Conversely, should investigation of this hypothesis evidence clear survival benefits associated with philopatry at natal dens, but without any substantive influence on dispersal patterns and group size, this would result in the rejection of the FBH, and of the causative role of fossoriality in the evolution of group-living generally. Importantly however, understanding the factors that promote philopatry at fossorial dens requires not only quantifying the cost-benefit balance of den-living, but also consideration of interactions with extrinsic factors such as the local carrying capacity (Macdonald, 1983*b*; von Schantz, 1984), the specific capacity to tolerate secondary food security (Newman et al., 2011; Macdonald and Johnson, 2015), reproductive suppression (Creel and Macdonald, 1995; Kokko and Ekman, 2002), and/or constraints on dispersal (Koenig et al., 1992; Kokko and Lundberg, 2001).

Despite the socio-ecological importance of burrows militating for group-living in rodent societies, little is actually known about the involvement of fossoriality in carnivore social systems, or indeed of fossoriality in the Carnivora generally. For example, an understanding as to why the use of subterranean natal dens supports philopatric and social behaviour in certain species (benefits of philopatry hypothesis: Brown and

Brown, 1984), versus those that disperse into solitary territories, is entirely unresolved. Thus, an exact understanding as to the drivers of fossoriality, and how these relate to their socio-ecology remains unclear. Therefore, before focusing on a single species, Chapter Two provides a consilient overview of carnivoran fossoriality, investigating the potential link between fossorial life-histories and sociality. Specifically, I test the prediction that group formation will be more evident among those carnivores that extend the use of fossorial natal dens into adulthood, which serve as a 'central-place' facilitating philopatric behaviour and societal congregation (an extension of the EBH, and the benefits of philopatry hypothesis).

For any of the hypotheses promoting group-formation presented above to viably accommodate stable adult groups, individuals must be able to maintain a balanced energetic budget. Indeed, Eisenberg (1966) even defines a species' social organisation as "the sum of all adjustments to the local environment including habitat exploitation and energetic budgets". Subsequently, though there are clearly numerous factors that contribute to the extent of fossoriality (e.g., innate digging ability; Andersson, 2004; the need to protect altricial neonates; Case, 1978*a*; as well as the need for refugia from predators and/or harsh weather; Kinlaw, 1999; Nevo, 1999), this thesis will focus on the energetic foundations of carnivoran fossoriality and socio-ecology. Therefore, Part II of this thesis focuses on the extent to which burrows benefit individuals' capacity to balance energetic budgets by serving as thermal refugia to mitigate potential energetic losses.

1.3 Energetics and the grass roots of fossoriality

Environmental temperature exhibits a critical influence on animal energetics, and the capacity to maintain homeostasis (McNab, 2002). Animals lose heat to the environment according to the Fourier law equation:

$$\frac{\mathrm{d}E}{\mathrm{d}t} = k_1 A(\frac{\Delta T}{L}) \tag{1.2}$$

The difference in temperature between an animal's core and the environment (i.e., ΔT) will determine the directionality of heat transfer, and the conductance k_1, thickness (L), and area (A) of an animal's insulative layers (e.g., stored body fat, fur/feather thickness and density, etc) play key roles in determining the rate of heat transfer ($\mathrm{d}E/\mathrm{d}t$) (McNab, 1983; Ciancio et al., 2016), where convection (i.e., the flow

rate of the environment over the animal's surface) must also be considered (Mitchell, 1976). For homeothermic species, the value of $\mathrm{d}E/\mathrm{d}t$ proves crucial as maintaining homeostasis under circumstances that result in heat gain/loss has to be achieved by increased metabolic rate (Schmidt Nielsen, 1997). Any increase in metabolic rate however, must be accompanied by a correlated increase in consumption, which must be tenable in terms of both the availability, and rate at which food can be physically acquired (discussed in Ciancio et al., 2016). It should be noted however, that because muscular efficiency is on the order of ca. 25% (Gaesser and Brooks, 1975), 75% of muscular work is released as thermal, rather than kinetic energy. As such thermal substitution via muscular thermogenesis as opposed to metabolic thermogenesis may play an important role in maintaining homeostasis (e.g., Ciancio et al., 2016).

After a warm and relatively stable period in the 'Eocene Climatic Optimum', with mean annual temperatures in North America, ranging from 9-24 °C, and winter temperatures well above freezing (Greenwood and Wing, 1995), the earth entered a period of cooling and aridisation (38-33.5 Mabp; Prothero and Berggren, 2014). Cold ocean currents began to flow between the newly separated Antartica and Australia (Bijl et al., 2013; Prothero and Berggren, 2014), the polar ice caps expanded (Huber and Nof, 2006), and seasonality became increasingly pronounced (Prothero and Berggren, 2014). This shift to globally cooler (7-10 °C over the Paleogene; Savin, 1977) and increasingly variable (Katz et al., 2008) conditions in turn resulted in mass extinctions in pelagic, littoral, and terrestrial fauna at the end of the middle-late Eocene transition (Nevo, 1999).

The climatic stresses over the Eocene-Oligocene boundary did not only affect fauna directly, through stressing homoeothermic regulation, as this period also saw major changes in the floral composition of ecosystems. Conditions favoured plants using C4 photosynthesis only found in angiosperms, predominantly poaceae grasses (Vicentini et al., 2008), and forest ecosystems, abundant in the middle-Eocene gave way to late-Eocene dry woodland, then to early-Oligocene wooded grasslands, and finally to mid-Oligocene grasslands (Prothero and Berggren, 2014). Thus, carnivores were faced with two principal challenges during this hypothermal transition; the first being how to achieve an energetic balance under these colder climatic conditions (i.e., a new, and greater ΔT) and the second being how to adapt to the changing habitat and foraging conditions. Natural selection therefore favoured taxa more able to adapt to these challenges (i.e., minimising $\mathrm{d}E/\mathrm{d}t$) either via the adjustment of their

conductive properties (k_1, and L), or by occupying environments that minimised ΔT. Conditions in the subterranean environment proved considerably warmer, and more stable than those above-ground, triggering a pronounced radiation in burrowing behaviour amongst mammalian taxa during this cooling phase (Nevo, 1999). Indeed, 447 of 777 genera of extant terrestrial mammals include species that engage in burrowing behaviour (Kinlaw, 1999), and burrowing may well have been responsible for the success of many species within these phyla.

Energetics are thus at the root of this radiation, where maintaining energy intake versus more extreme losses to thermoregulation and often locomotion is essential. Though endothermy allows mammals to survive in increasingly frigid ranges, beyond the capabilities of ectotherms (Grigg et al., 2004), ultimately they reach a temperature threshold (Shelford, 1931; Pörtner, 2002). Endothermy thus places mammals in cold regions, where burrow use provides a means of mitigating the limitations of cold weather on range expansion (Fløjgaard et al., 2009). Indeed, of the vertebrates, the principal burrowers are the mammals (Kinlaw, 1999) where their dentition, claws and strong forelimbs, in tandem with a muscle mass large enough to exert the force required to dislodge soil, provide a further disposition for digging behaviour (Hildebrand, 1985; Kinlaw, 1999; Nevo, 1999).

In particular, shifting vulnerable life-cycle stages below ground (e.g., natal dens for altricial young, and/or hibernaculae for overwintering) permits a degree of independence from variable external conditions during critical periods (Kinlaw, 1999). In terms of foraging energetics, resting/hibernating in a thermally stable burrow mitigates thermal loses during the most stressful and food limited periods (Harlow, 1981; Barclay et al., 2011; Kowalczyk et al., 2003). A range of carnivores make use of this stability when over-wintering, where this enables some species to conserve nearly half of their fat reserves over these months (Harlow, 1981), benefitting their subsequent reproductive success (Woodroffe, 1995; Robbins et al., 2012; López-Alfaro et al., 2013). *Ursus* spp. for example, will excavate burrows in autumn, hibernating below ground for the extent of winter (Beecham et al., 1983; Elgmork and Unander, 1998; Immell et al., 2013), where in polar bears, although burrows tend to be subnivean, this allows them to conserve 86% of their body mass (Ramsay and Stirling, 1988). Similarily, in overwintering brown bears (*Ursus arctos*), males that remain in a single hibernaculum can conserve 84% of their body mass, yet if disturbed, and forced above-ground, this is reduced to 75% (Tietje and Ruff, 1980). American badgers (*Taxidea taxus*)

will enter a flexible extent of torpor, varying with the duration and severity of winter, remaining below ground for up to 70 days, where temperatures can be 20 °C warmer than above-ground (Harlow, 1981).

Important however, in terms of energetics and therefore fitness and selection, the costs of constructing burrows are non-trivial. For even a 150g pocket gopher (*Thomomys bottae*), burrowing a 1m tunnel may require up to 3,400 times more energy expenditure than traveling the same distance above-ground (Vleck, 1979). Furthermore, the energetic costs associated with burrow construction increases with body size (Vleck, 1981; White, 2005). Indeed, body size is the main factor accounting for most of the variation of energy expenditure in mammals, and an ultimate maximum body-size constraint is present for burrowing animals (McNab, 1979; Vleck, 1981). As a consequence, while there has been a wide variety of small (<1.0 kg) burrowing species(Nevo, 1999), large fossil burrows are rare (e.g., Voorhies and Toots, 1970), and the largest extant burrowers, aardvarks (*Orycteropus afer*), weigh >50 kg (McNab, 1979). In addition to body size, above-ground habitat will also have a strong role in influencing the cost of burrowing (Vleck, 1981), where loose, well drained soils, provide the optimal cost-benefit relationship and are excavated preferentially (Kinlaw, 1999; Revilla et al., 2001; Macdonald et al., 2004*b*). Further variables such as distance to resources (Gahr, 1992), habitat cover (Young, 1990), or the presence of sloped ground to reduce the chance of flooding (Zimmerman, 1990; Macdonald et al., 2004*b*) will also have a substantial impact on this decision.

1.4 The European badger as a model species

The European badger, (henceforth 'badger') is a prime representative of the fossorial carnivore guild, and is well suited to address the sociological implications of fossorial living. Badgers reside in elaborate burrow systems (termed 'setts'; Roper, 1992), and their behaviour, morphology and physiology are adapted to a semi-fossorial existence (Roper et al., 2001). Badgers have an extensive biogeographic distribution (Johnson et al., 2002*a*) and experience varying degrees of seasonality, trophic dispersion, predation threat, and consequential sett use (Kowalczyk et al., 2003) across their range. Furthermore, they exhibit varying degrees of sociality across their range, due primarily to local ecological factors (Kruuk, 1989; Revilla and Palomares, 2002; Johnson

et al., 2002*a*; Rosalino et al., 2005*b*; Do Linh San et al., 2007).

1.4.1 Badger diet and climatic vulnerability

Sensitive interactions between trophic ecology, climatic conditions, survival, and reproductive rates (see: Johnson et al., 2002*a*; Macdonald and Newman, 2002; Macdonald et al., 2010; Nouvellet et al., 2013) make badgers a particularly good model for studying the energetic implications of weather variability on fossorial living. Badgers occupy a biogeographical range that encompasses regions exhibiting a broad spectrum of seasonality (Griffiths and Thomas, 1993; Virgos and Casanovas, 1999; Kowalczyk et al., 2000; Johnson et al., 2002*a*). Over their evolutionary history, badgers have also been exposed to a wide range of climatic conditions, and are relatively resilient to climatic extremes (Sommer and Benecke, 2004). Nonetheless, a growing body of literature is evidencing that badger exhibit a substantial responsiveness to prevailing conditions, and weather plays a crucial role in determining badger survival, and population dynamics (Macdonald and Newman, 2002; Macdonald et al., 2010; Nouvellet et al., 2013; Byrne et al., 2015).

In regions with particularly harsh winters, they exhibit a range of adaptations to cope with winter months (e.g. life-history synchronicity, Yamaguchi et al., 2006; fat storage, Fowler and Racey, 1988; Macdonald and Newman, 2002; reduced metabolic rate, McClune et al., 2015; and winter torpor, Newman et al., 2011), and life histories are punctuated by a cycle of seasonal weight gain (Macdonald and Newman, 2002). Foremost among these adaptations however, is an increase in the amount of time spent below ground (Fowler and Racey, 1988; Butler and Roper, 1996; Broseth et al., 1997; Roper et al., 2001; Macdonald and Newman, 2002; Kowalczyk et al., 2003, 2004). In northern parts of Russia for example, the winter dormancy period can extend for upwards of 170 days, whereas badgers in Mediterranean regions forgo torpor altogether (Kowalczyk et al., 2003). Autumnal weight gain is crucial for extended periods of torpor however, and is dependent upon optimising individual activity regimes to achieve net-positive energetic returns. In temperate zones however, setts are used primarily as diurnal refuges and for the rearing of young, and badgers exhibit minimal seasonal life-cycle synchronicity (Revilla et al., 1999; Kowalczyk et al., 2003).

In addition to thermoregulatory challenges, badger diet and foraging strategies are the crux of much of their ecology/behaviour (Johnson et al., 2002*a*; Macdonald

and Newman, 2002; Kowalczyk et al., 2003; Macdonald et al., 2010; Nouvellet et al., 2013). Across much of their range, badgers are generalists (Roper, 1994), feeding opportunistically on berries, nuts, cereals, earthworms, carrion, and small mammals (Ciampalini and Lovari, 1985; Shepherdson et al., 1990; Roper, 1994; Roper and Mickevicius, 1995). In other regions, such as lowland Britain, they tend toward trophic specialisms, feeding extensively, though not exclusively, on one species of earthworm, *Lumbricus terrestris* (Kruuk and Parish, 1981; Hofer, 1988; Goszczyński et al., 2000). Earthworms are sensitive to microclimatic conditions (Jiménez and Decaëns, 2000; Curry, 2004), and their distribution, abundance, and availability to foragers is highly dependent on weather patterns (Macdonald, 1983*a*; Johnson et al., 2001; Kowalczyk et al., 2003). Summer droughts will limit earthworm availability (Kruuk, 1978; Macdonald, 1983*a*; Kowalczyk et al., 2003), and in regions with particularly harsh winters, ground frosts also render earthworms unavailable to badgers when temperatures drop below 2 °C (Holmstrup and Zachariassen, 1996; Holmstrup, 2001; Kowalczyk et al., 2003; Nuutinen and Butt, 2009). Under these conditions, badgers may attempt to compensate for poor foraging success by devoting over 2.5 hrs more to foraging per night (Kowalczyk et al., 2003).

As well as influencing variation in food supply, the climatic conditions that militate for earthworm abundance are not necessarily conditions that result in net-positive energetic returns. While cool, moist conditions will make earthworms more available to badgers (Macdonald, 1983*a*; Johnson et al., 2001; Kowalczyk et al., 2003), burrowing animals tend to have a higher thermal conductance in comparison to similar sized non-burrowing mammals (McNab, 1983) and are particularly prone to heat loss under cold, damp conditions. As such, a set of optimal weather conditions benefit badgers' capacity to improve/maintain body condition and ultimately survival rates (Kruuk and Parish, 1985; Macdonald and Newman, 2002; Macdonald et al., 2010; Nouvellet et al., 2013). Consequently, individuals must attempt to balance trade-offs between the energetic expenditure of their activity (both foraging and non-foraging), and that conserved by inactive periods within their thermally stable (Kaneko et al., 2010) setts, against potential foraging returns. In Part II therefore, I investigate the extent to which badgers modify their activity regimes, and risk-taking propensity against prevailing weather conditions, testing the hypothesis that setts are used as thermal refugia against thermoregulatory challenging conditions. In particular, I explore behavioural responses to weather patterns in the context of both thermoreg-

ulatory challenges and feeding ecology.

1.4.2 Badgers: social system variability

Over their range, badger densities vary extensively (from <1 badger/km^2 across much of Continental Europe to >36 badgers/km^2 in high density regions of the United Kingdom; Johnson et al., 2002*a*). Under these different densities, badger populations exhibit considerable variation in their propensity for group-living (Johnson et al., 2002*a*), ranging from little more than pair-living (Kruuk, 1989; Kowalczyk et al., 2000, 2004; Revilla and Palomares, 2002; Do Linh San et al., 2007) to large groups of 25+ animals (da Silva et al., 1993; Buesching et al., 2003; Macdonald et al., 2015). Trophic ecology, resource abundance, and dispersion play a major role in driving badgers' flexible sociality (Macdonald, 1983*b*; Macdonald and Johnson, 2015). Badger group-living correlates positively with the distribution and abundance of trophic resources, in particular that of earthworm prey (Johnson et al., 2002*a*). Research from low-density populations outside of the United Kingdom corroborates that when mixed omnivory contributes more towards primary food resources than does vermivory (e.g., Ciampalini and Lovari, 1985; Rosalino et al., 2005*b*), less gregarious social systems arise (reviewed in Roper, 1994, 2010). This flexible sociality, dictated by feeding ecology, is in line with predictions of the RDH, namely that groups may develop where resources are dispersed such that the smallest economically defensible territory for a pair can also sustain additional animals (Macdonald, 1983*b*). Under these circumstances, secondary animals can cohabit with the primary occupants at little or no trophic cost (Carr and Macdonald, 1986; Macdonald and Johnson, 2015), provided they can tolerate secondary food security (Newman et al., 2011).

Although RDH type criteria do appear to explain badger group-living propensities (Johnson et al., 2001, 2002*a*; Macdonald and Johnson, 2015), these assume no costs to the primary territory holder (Macdonald, 1983*b*). Group-living badgers however, suffer from severe ectoparasite infestation as a result of contact with one another (Johnson et al., 2004), in particular from nidiculous parasites within commonly used setts (Roper et al., 2001). These infestations are non-trivial as badger ectoparasites are vectors for other, potentially lethal pathogens (Macdonald et al., 1999; Newman et al., 2001; Lizundia et al., 2011). Although allo-grooming is a potent defence against ectoparasites, and badgers spend a considerable proportion of their time grooming one another (Stewart and Macdonald, 2003), this is typically directed to areas of the body

that are hard to reach alone (Johnson et al., 2004) with strict tit-for-tat reciprocity (Stewart and Macdonald, 2003). As well as severe ectoparasite loads, communal subterranean chambers, contaminated with helminths and coccidia (*Eimeria* spp.), are a major source of infection for badger neonates, significantly increasing mortality at this vulnerable life-stage (Newman et al., 2001).

Although living in groups may decrease the individual levels costs associated with defending territories (Kruuk, 1989), there is little evidence to suggest active territorial defence in badgers (Stewart et al., 2001; Christian, 1995; Tinnesand et al., 2015). In addition, although allo-parental care presents a significant advantage to group-living (Clutton-Brock, 2009), its occurrence among badgers remains tentative at best (Woodroffe and Macdonald, 1995*b*). Several litters of cubs can be raised in one sett at the same time and, from genetic and video-surveillance evidence, some females appear to occasionally suckle cubs that are not their own (Dugdale et al., 2011). Nevertheless, the availability of more potential helpers in larger groups, or in groups with more than one breeding female, does not increase cub survival rates. Indeed, these groups tend to have higher reproductive failure rate (da Silva et al., 1994), and long-term fitness costs (Dugdale et al., 2011). Current understanding of badger socio-ecology thus provides little evidence towards any particular benefits of group-living. As such, in Part III of this thesis, I investigate the role of fossorial benefits in leveraging badger group-formation under these otherwise marginal circumstances.

1.4.3 Badger denning behaviour

Badgers occupy extensive multi-purpose burrows, which they excavate where soil geology permits (Macdonald et al., 2004*b*; Remonti et al., 2006) There is preliminary evidence to suggest that the location, surrounding habitat characteristics, size and complexity of setts, has significant influence on the success of individuals therein. For example, previous work from the badger population in Wytham Woods, Oxford has identified that mean body weight was significantly higher for badgers occupying territories with setts in sandy soils, situated on NW-facing slopes, than in territories with less optimal sett characteristics (Macdonald et al., 2004*b*). Also, working on this same population, Kaneko et al. (2010) found that sett complexity and internal microclimate were influential on the survival of cubs born therein. With a unique opportunity to measure 19 excavated setts, Roper (1992) provides one of the most detailed descriptions of sett architecture, ranging from simple single-entrance burrows to

complex tunnel systems hundreds of meters long with multiple entrances and underground chambers. Roper reports that although main setts are larger than other setts in terms of area and volume, and contain more chambers, nests and latrines, setts of different sizes and types are built according to the same basic architectural principles.

While badgers use setts primarily to rear young (Newman et al., 2011; Roper, 1992) and escape harsh weather (Fowler and Racey, 1988; Kowalczyk et al., 2003), the granularity of this use is coarse (Butler and Roper, 1996; Broseth et al., 1997; Roper et al., 2001; Kowalczyk et al., 2004). As such, although it is quite evident that badgers use setts, how and why they do so has largely relied on inferential reasoning (*sensu* Popper, 2014). Furthermore, due to a lack of evidence, underground inactivity is often assumed, but without substantiation. Therefore, in Chapter Seven of this thesis, I apply a novel Magneto-Inductive (MI) tracking technology (Markham et al., 2010*b*, 2012) to test the assumption of underground inactivity, further exploring inter-individual patterns of sett use with fine-scale resolution, with particular emphasis on sociological implications.

1.5 Thesis structure and aims

This thesis examines the role of fossoriality in leveraging group formation (i.e., the Fossorial Benefits Hypothesis), using badgers as a model species. In particular, I examine how burrow use benefits energetic budgets, and how this may promote philopatric behaviour, delayed dispersal, and shared territories. Tinbergen's (1963), 'four questions' provide a comprehensive schema for the systematic examination of fossorial behaviour, in terms of phylogeny, ontogeny, mechanism (causation) and adaptation (function), with emphasis on ultimate and proximate processes, and this framework is applied throughout. The present section provides the framework for this thesis, where each chapter is structured as a stand-alone body of work, either published, or to be submitted for publication. As such, any variation, both in the style and structure of these chapters, as well as the inclusion of repetitive elements, are due to their independent nature, as well as specific journal requirements. While each chapter is designed to stand alone, together they provide convergent evidence towards the role of fossoriality in leveraging group formation in the Carnivora.

Part I (Chapters One, and Two) of this thesis utilises consilient evidence, and an evolutionary perspective to establish the potential role of fossoriality in leveraging group formation.

In **Chapter Two** I review data on the life-histories, ecology, and phylogeny of the Carnivora to investigate whether sociality may be intrinsically associated with the extent of fossoriality. I provide evidence for an evolutionary relationship between fossoriality, and sociality, demonstrating that among small, den-using carnivores, and especially for omnivorous/insectivorous species for which food resource dispersion is favourable, continued cohabitation at natal dens can promote cohabitation among adults; that is, philopatric benefits leading to (not necessarily cooperative) spatial groups.

In **Part II** (Chapters Three, Four, and Five) I establish the energetic function of burrows as a primary benefit of fossorial living. In particular, I explore the relationship between badger behaviour and climate, demonstrating the unique capability of underground space in balancing energetic budgets.

In **Chapter Three** I present the results of a pilot study, using prototype accelerometers to quantify badger activity regimes. I establish inter-individual and -annual variability in badger activity, where individuals modify their behaviour in relation to proximate weather conditions, and individual body condition, in order to maximise energetic returns.

In **Chapter Four**, based on the discovery of weather and body condition as modifiers of activity regimes, I use 19 years of capture-mark-recapture (CMR) data to further demonstrate that badgers vary their risk-taking behaviour in relation to both weather conditions, and body condition, as evidenced by their propensity to enter traps. This chapter also raises some more general considerations regarding the veracity of CMR studies (discussed therein).

In **Chapter Five** I solidify the extent to which weather conditions serve to influence badger behaviour, versus more general motivators (i.e., reproductive status, and body condition), and the extent to which setts provide thermal refugia from external conditions. I then demonstrate that the constraints imposed by weather conditions cascade in effect across the amount of time badgers spend above-ground

and active, and their propensity for inter-group movement. This chapter also addresses some more general considerations regarding badgers' capacity to respond to climate change events (discussed therein).

In **Part III** (Chapters Six, and Seven), with respect to the energetic benefits established in Part II, I investigate the role of burrow-dwelling in leveraging group-formation in badger societies.

Macdonald et al. (2008) demonstrated that while badgers defecate to mark inferred territory borders, they trespass beyond these when foraging, making temporary visits to one another's setts. In addition, they exhibit high rates of extra group paternity (47%; Annavi et al., 2014) with 84% of these being attributable to neighbouring males. Informed by theses observations, **Chapter Six** investigates: i) whether the spatial organisation of badger latrines demark discrete territories; ii) whether individual sett use follows a territorial framework; and iii) whether individuals are restricted to their own 'territory'.

In **Chapter Seven** I present a new magneto-inductive technology for monitoring animals underground. I elaborate on individual chamber use and the periodicity of movement between chambers, evidencing a potential thermoregulatory function of sett use. I further test for any synchronicity in the way individuals make use of underground space.

Part Four (Chapter Eight), consists of the general synthesis of these findings. I contextualise the findings of these chapters, returning to the question of "how fossoriality leverages group formation", and addressing how this advances understanding of the paradigm of socio-ecology generally.

Part Five (Appendix A) contains an appendix detailing further original work. This collaborative study is included as an appendix as I have made a substantial contribution, but am not the lead author.

Chapter 2

Evolution and function of fossoriality in the Carnivora: implications for group-living

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2.1 Abstract

The societies of group-living carnivores that neither hunt nor interact cooperatively may arise due to ecological drivers and/or constraints. In this study we evaluate whether group-living may be intrinsically associated with fossoriality; a link that is well supported in other taxa, but hitherto under-evaluated in the Carnivora. We make two over-arching predictions: (i) that fossoriality will be associated with carnivoran sociality; and (ii) that this association will be most evident in those species making extended use of subterranean dens. From a meta-analysis of key behavioral, ecological, ontogenetic, and trophic traits, we demonstrate that three quarters of carnivore species exhibit some reliance on underground dens. Congruence between life-history traits and metrics of fossoriality evidenced that: (1) there are phylogenetic, and morphological constraints on wholly fossorial life-histories; (2) fossoriality correlated positively with the extent of offspring altriciality, linked to the use of natal dens; (3) burrow use increased with latitude; and (4) insectivorous carnivores were more fossorial than predatory carnivores. Corroborating work in the Rodentia, fossorial traits associated strongly with carnivoran group-living tendencies, where species utilizing subterranean natal dens are 2.5 times more likely to form groups than those that do not. Furthermore, using comparative analyses, we evidence support for an evolutionary relationship between diet, fossoriality, and sociality. We propose that fossorial dens act as a safe haven, promoting fitness benefits, territorial inheritance and cooperative breeding. We conclude that, among smaller (<15kg) den-using carnivores, and especially for omnivorous/insectivorous species for which food resource dispersion is favourable, continued cohabitation at natal dens can promote cohabitation among adults; that is, philopatric benefits leading to (not necessarily cooperative) spatial groups.

2.2 Introduction

Understanding the factors that enable conspecifics to congregate, or establish co-operative societies is central to socio-ecology (Alexander, 1974; Smith et al., 2012; Macdonald and Johnson, 2015). Axiomatically, group-living is theorized to evolve when the fitness benefits of joining/remaining in a (natal) group outweigh the costs of sharing key resources (e.g. Alexander, 1974; Emlen, 1982; von Schantz, 1984; Bacon et al., 1991; Koenig et al., 1992), and/or when there are strong ecological constraints on reproducing independently of the group (Lindström, 1986; Hatchwell and Komdeur, 2000; Kokko and Ekman, 2002). Among many of the Carnivora, the benefits of group-living manifest through enhanced hunting ability, where packing power facilitates endurance hunting (e.g. grey wolves, *Canis lupus*: MacNulty et al., 2014), or strategic kills (e.g. lions, *Panthera leo*: Mosser and Packer, 2009). There are, however, numerous group-living carnivores that do not hunt, or interact co-operatively (reviewed in Gittleman, 1989; Creel and Macdonald, 1995; Macdonald et al., 2004*a*; Macdonald and Johnson, 2015).

We observe that among gregarious, yet broadly non-cooperative carnivore species, many tend to have a substantial reliance on subterranean dens. There are two provisos to this observation: i) these carnivores tend to be small; and ii) the inverse is not true (i.e. not all small, fossorial carnivores are group-living). Understanding how these factors relate to group-living requires deeper enquiry into carnivoran *fossoriality* (L. to dig) and associated life-history traits.

In this study we examine two over-arching predictions: i) that fossoriality will associate with carnivoran sociality; and ii) that this association will be most evident in those carnivores with extended use of subterranean dens. Our primary set of questions thus pertain to life-history traits associated with fossoriality; particularly how morphological and energetic traits influence both digging ability and/or reliance upon the subterranean ecotope. For example, burrow size, and the cost of burrowing scale allometrically, depending on substrate cohesion (McNab, 1979; Vleck, 1981; White, 2005), suggesting the action of body size constraints on carnivoran fossoriality. Furthermore, although interlinked with body-size, there is support for an evolutionary relationship between longevity and fossoriality across a wide range of taxa (Healy et al., 2014; Williams and Shattuck, 2015), a factor of potential influence in the Carnivora. In addition, carnivoran young are born along a continuum of altriciality to

precociality (Derrickson, 1992), altriciality requiring a secure environment for rearing neonates (Case, 1978*a*,*b*; Wolff, 1997). Although natal dens can be as simple as a hollow log (e.g. Carter et al., 2012), increased investment in natal den construction can enhance conditions of warmth and security for dependent, altricial young (Kinlaw, 1999; McClellan et al., 2008). This indicates that the extent of neonate altriciality, and parental investment are likely to influence fossorial tendencies. As an extension of this, the extended use of pre-excavated natal dens into adulthood can influence use of the subterranean ecotope, and make a substantial contribution to both group formation (Lindström, 1986; Koenig et al., 1992; Kokko and Ekman, 2002). Furthermore, in line with predictions of the Expansible Burrow Hypothesis (see below), those carnivores that experience a substantial predation threat into adulthood will tend to be more fossorial (Alexander et al., 1991; Ebensperger and Blumstein, 2006). There is also evidence for a link between climate and the extent of fossoriality (Nevo, 1999). While endothermy allows carnivores to exploit cold regions (Grigg et al., 2004), fossoriality can provide a means of alleviating untolerable temperature thresholds in colder environments (e.g. Fløjgaard et al., 2009).

These factors are likely to interact with species' evolutionary trajectories however, where carnivoran fossoriality evolved around the Eocene/Oligocene boundary (ca. 35 Mabp: Andersson, 2004) for the excavation, or lithe pursuit, of burrowing prey (Martin, 1989; Andersson, 2004). The most fossorial carnivores tend to exhibit morphological adaptations evolved to dislodge substrate (Hildebrand, 1985; Andersson, 2004); species we define here as primary excavators (Kinlaw, 1999). Notably, these fossorial exaptations ('pre-adaptations', *sensu* Gould and Vrba, 1982) permitted subsequent selection for further intrinsic (reproductive/physiological) benefits (Hypothesis of Phylogenetic Constraints, HPC: Burda et al., 2000; Šumbera et al., 2007).

The involement of life-history traits linked to fossoriality has received little attention in explaining carnivore social systems. This is especially apparent in contrast to the substantial support for a link between fossoriality and the evolution of rodent societies (e.g. hystricognath rodents: Ebensperger and Blumstein, 2006; Sobrero et al., 2014, and various marmot species: Barash, 1989; Hoogland, 1995). Smorkatcheva and Lukhtanov (2014) draw attention to three hypotheses, which resonate with pre-established models of carnivoran sociality: i) the Territorial Defence Hypothesis (TDH: Nevo, 1979) proposes that the low productivity of the subterranean ecotope leads to strong resource competition, militating for solitary social systems.

Similarly, the prey of small predatory carnivores tend to be localized and indivisible; conditions associated with competition (Macdonald et al., 2004*a*) and territorial defence (Waser, 1981); ii) the Aridity Food Distribution Hypothesis (AFDH: reviewed in Jarvis et al., 1994) highlights patchy and unpredictable resources as a driver of sociality in subterranean mole-rats (family Bathyergidae). This is consistent with the Resource Dispersion Hypothesis (RDH: Macdonald, 1983*b*; review in Macdonald and Johnson, 2015), which proposes that groups will arise independent of cooperative benefits where the dispersion, or renewal rate, of resources result in a territory that can viably accommodate additional individuals; and iii) the Expansible Burrow Hypothesis (EBH: Alexander et al., 1991) proposes that predator-free subterranean refuges militate for philopatry, cooperation, and thus sociality. Crucially, while small rodents are vulnerable to predation throughout their lives, for large(r), predatory carnivores, this is only a substantial (or greater) risk for their altricial young; hence the protective benefits of a secure natal den for carnivore neonates. Potentially, as with the EBH, some interaction between natal den use and philopatry may also explain components of carnivore sociality (e.g. Greenwood, 1980; Lindström, 1986; Blackwell and Bacon, 1993).

We also evaluate the role fossoriality may play in relation to promoting group formation from a socio-ecological perspective. This leads to our subsequent set of questions on behavioral, developmental, and trophic traits, relating to why some species can remain philopatric as they mature, leading to the formation of adult groups, versus those that disperse into solitary territories. We propose that group formation in non-co-operatively hunting carnivores will be more evident among omnivorous/insectivorous species, in a suitable RDH-scape, in those species that extend the use of fossorial natal dens into adulthood, which serve as a 'central-place' facilitating societal congregation. By way of 'exceptions that prove the rule' this framework yields two further postulates. First, that predatory fossorial carnivores, for which the dispersion of their food supply is not suitable, will not form stable adult groups; and second, that omnivorous/insectivorous species that do not use subterranean dens, will tend not to form stable adult groups.

Shifting vulnerable life-cycle stages below ground permits a degree of independence from variable external conditions during critical periods (Kinlaw, 1999; Ebensperger and Blumstein, 2006). This can benefit longevity (Healy et al., 2014; Williams and Shattuck, 2015), energy budgets (Noonan et al., 2014, 2015*b*), and facilitate extended

periods of hibernation (Davenport and Davenport, 1992), aiding the maximisation of fitness (Nevo, 1999). Depending on the relative importance of burrow construction, often substantial energetic investments are made in den construction/maintenance (Vleck, 1981). Furthermore, burrows are important for secondary heterospecific competitors, which comandeer burrows (referred to as 'kleptoclaustromy'; e.g. Mills, 1982; Kaneko et al., 1998; Kowalczyk et al., 2008). As such, pre-excavated/actively maintained burrows are valuable resources, often inherited by offspring (*sensu* Lindström, 1986).

This leads us to posit whether fossorial dens support a 'benefit-driven' basis for philopatry, as an extension of the EBH and the benefits of philopatry hypothesis (Brown and Brown, 1984; Pen and Weissing, 2000). Models of philopatry are typically based on cost-driven criteria, such as the greater mortality risk for dispersing individuals (Lucas et al., 1994), competition for breeding opportunities (Kokko and Lundberg, 2001), and habitat saturation (Emlen, 1982) – i.e. the Ecological Constraints Hypothesis (ECH: Pen and Weissing, 2000). In contrast, we examine whether dens promote inclusive fitness (Herre and Wcislo, 2011), territorial inheritance (Zack and Stutchbury, 1992) and cooperative breeding (Koenig et al., 1992) by acting as a 'safe haven' (*sensu* Kokko and Ekman, 2002). Conditions where there are strong ecological constraints on dispersal from natal territories, limiting independent breeding, favour the perpetuation of natal groups to form persistent (sub-)adult groups (Emlen, 1982; Macdonald and Carr, 1989; Creel and Macdonald, 1995; Waser, 1996; Isbell, 2004).

Nevertheless, in many predatory, fossorial carnivores, prey availability becomes a limiting factor as litters develop and begin to forage independently (von Schantz, 1984; Clutton-Brock and Lukas, 2012). Thus, while maternal-offspring groups may persist temporarily (e.g. Dahle and Swenson, 2003; Kaneko et al., 2014), these groups often dissolve as offspring mature. For omnivorous and/or insectivorous species, however, the dispersion of trophic resources is often such that they are not monopolized by primary territory holders and, provided secondary individuals can tolerate inconsistent food supply (Newman et al., 2011; Macdonald and Johnson, 2015), their nutritional needs may still be met as they mature – leading to persistent adult groups (Macdonald, 1983*b*).

We test these sets of questions linking life-history, socio-ecological, and evolutionary components of fossoriality to the propensity for group-living, by compiling a database of key ontogenetic, ecological, and trophic variables across the Carnivora. We then apply Bayesian modelling to conduct a comparative analysis.

2.3 Materials and Methods

We applied our analyses to the 281 extant species of Carnivora listed by Wilson et al. (2009); the 36 pinnipeds were excluded *a priori* due to their predominantly aquatic life-histories. Additionally, no, or too few, data were available for 100 less well-known species, where we could access only anecdotal records, or derive metrics from museum specimens. The resultant database thus comprized a mix of complete and partial data for 145 species (Table S1). Two families (Nandiniidae, and Prionodontidae) were excluded totally from our database because too few data were available for extant species – consequently analyses were conducted across eleven families (Ailuridae, Canidae, Eupleridae, Felidae, Herpestidae, Hyaenidae, Mephitidae, Mustelidae, Procyonidae, Ursidae, Viverridae). Reference sources for these data are listed in Table S1, and detailed in Appendix S1.

We define three response variables: group-living propensity, fossorial propensity and burrowing class.

2.3.1 Group-Living Propensity

Due to intra-specific variation in the level of social integration, we rejected a Boolean, solitary/group-living classification, instead classifying group-living typologies according to Johnson et al. (2000) as: i) solitary: species with predominantly solitary life-histories; ii) pair-living: species with predominantly pair-living life-histories; iii) facultative groups: species with both solitary and group-living life-histories, variable across populations; and iv) group-living: species exhibiting predominantly obligate groups.

2.3.2 Fossorial Propensity

In accord with Nevo (1999), we differentiate here between truly '*subterranean*' species, which spend the majority of their lives below ground, only emerging occasionally, and '*fossorial*' species, which use the underground space for distinct activities (e.g. shelter

or reproduction), but forage above ground. We therefore catagorize fossorial activities into the function of burrows as a:

1. natal den: during parturition and the rearing of young;
2. weather refugia: during hibernation and/or to avoid inclement weather;
3. refuge from predation: for predator avoidance;
4. food storage facility: used to store/cache food;
5. residence: resting and/or sleeping site.

Several species utilize dens according to one or more of the functions listed above, on an opportunistic basis, as an alternative to epigean options (e.g. hollow logs, rock crevices, man-made structures, etc). We therefore quantified subterranean den use for each of the categories listed above as: (0) little or none; (0.5) facultative; (1) predominant. The summation of these five uses yielded a measure of fossorial propensity, ranging on a scale from 0-5.

2.3.3 Burrowing Class

To account for the energetic investment each species makes in its burrow, we classified burrowers according to Kinlaw (1999) as:

1. primary excavators: strong burrowers, for which digging plays a major role in their life-history;
2. secondary modifiers: species that inhabit and modify burrows dug by primary excavators;
3. tertiary occupants: species that play no role in digging burrows, but take advantage of burrows dug by other species.

In certain instances, species overlap these burrowing categories (i.e. able to dig their own burrow, but also making use of existing burrows); these were treated as intermediate between categories. Consequently, we quantified burrowing class as: (0) no burrow use; (1) tertiary occupants; (2) secondary modifier; and (3) primary burrowers; with intermediate species categorized as the mean of their respective burrowing classes (i.e. 2.5 for primay/secondary burrowers, and 1.5 for secondary/tertiary). This yielded a measure of burrowing class on a scale from 0-3.

2.3.4 Predictive Traits; Life-History, Socio-Ecology and Phylogeny

We explored a diverse initial range of morphometric, ontogenetic, and ecological traits inferred to influence fossorial propensity and burrowing class (with units in parentheses): (1) length: mean adult head-body length, excluding tail (mm ± 0.1 mm); (2) height: mean adult shoulder height (mm ± 0.1 mm); (3) female mass: mean mass of adult females (kg ± 100 g); (4) male mass: mean mass of adult males (kg ± 100 g); (5) adult mass: mean combined mass of adult males and females (kg ± 100 g); (6) age eyes open: mean duration from birth, until the neonates' eyes open (days); (7) duration of lactation: mean length of time, from birth, until the neonate becomes nutritionally independent of lactation (days); (8) age of independence: mean duration, from birth, until the neonates typically disperse from the natal territory or, in philopatric group-living species, become independent of parental food provisioning (days); (9) gestation length: mean length of time between implantation and parturition (days); (10) litter size: mean number of offspring produced per parturition; (11) age of sexual maturity: mean age at which offspring becomes physiologically capable of conception, averaged across sexes (months); (12) absolute longevity: age of the oldest living individual recorded in the wild; longevity records of individuals living in captivity were disregarded (months); (13) home range: mean combined home range of adult males and females across their geographic range (km^2); (14) predators: number of known species that predate the adult life-stage; (15) latitude of biogeographical distribution: the northern-most distribution of the species (degrees north or south of the equator; source IUCN Red List species database) as a proxy for surface temperature, and seasonality therein (Fricke and O'Neil, 1999, although limited by local variation in altitude and continentality: Driscoll and Fong, 1999). Data and distributions concerning expatric, introduced populations were not included beyond their native range. Furthermore, as a categorical predictor we included: (16) diet: a species' main food source, defined as constituting at least 60% of the diet (Gittleman, 1985); classified as: carnivorous, insectivorous, omnivorous, frugivorous/herbivorous) as a proxy for trophic RDH compatibility (see Macdonald and Johnson, 2015).

Many of the traits we initially considered proved inter-correlated. To avoid the ineffectual inclusion of variables in our models, we applied a principal component analysis (PCA) across our continuous trait data to generate independent variables. Two significant correlates of adult mass (female mass; and male mass; Pearson's r >0.98, corresponding to a p-value of less than 0.001), were not included in the PCA.

Furthermore, height, and age of independence were excluded from the PCA, due to too few data. This procedure resulted in the retention of 3 principal components (PC) as predictive variables (determined using the *R* package *nFactors*; Raiche and Magis, 2010), which cumulatively summarized 76.1% of the variance in these ontogenetic/ecological data (Table 2.1). Factor loadings indicated that body size, and its correlates (home range; longevity; and age of sexual maturity) were the most influential parameters along the axis of PC 1. PC 2 was determined primarily by measures of altriciality, and northernmost latitude, and PC 3 by predation threat. For clarity, in subsequent analyses these components are refered to by descriptive names based on factor loadings (i.e., body mass PC, latitude/altriciality PC, and predation threat PC respectively).

Table 2.1: Summary of the first three components of a principal components analysis performed over carnivoran ontogenetic/ecological trait data.

Variable	**PC 1**	**PC 2**	**PC 3**
Eigenvalue	5.07	2.16	1.14
% of variance explained	46.05	19.68	10.34
Cumulative % of variance explained	46.05	65.73	76.06
Factor loadings			
Adult mass	0.40	0.15	0.03
Head-body length	0.38	-0.01	0.24
Home range	0.37	0.24	-0.04
Age of sexual maturity	0.37	-0.04	-0.13
Longevity	0.36	0.02	0.25
Gestation length	0.26	-0.45	0.14
Age eyes open	0.05	0.49	-0.59
Duration of lactation	0.37	0.11	0.01
Litter size	-0.16	0.37	0.05
Number of predators	-0.25	0.22	0.59
Northernmost latitude	0.05	0.53	0.38

2.3.5 Statistical Analyses

All statistical analyses were conducted in the *R* environment (version 3.0.3; R Core Team, 2014). Due to phylogenetic inertia (Hansen and Orzack, 2005), closely related species may exhibit similiarities in life-history traits from common descent rather than independent evolution, requiring controlled comparisons (Harvey and Pagel, 1991). Accordingly, we did not treat species data records as independent, but rather corrected for this inertia by fitting models using Bayesian phylogenetic mixed models

using the *R* package *MCMCglmm* (Hadfield, 2010). By including the phylogenetic relationships among species as a random variable, this approach incorporates phylogenetic information into species data, allowing independent evolutionary events to be identified. Phylogenetic relationships were taken from a recent consensus phylogeny of the carnivora Agnarsson et al. (2010). For the Canidae, however, we took relationships from Lindblad-Toh et al. (2005), chosen for its completeness. Phylogenetic data were not available for four species in our database (*Caracal caracal*; *Leptailurus serval*; *Martes martes*; and *Vulpes velox*), consequently we excluded these from our analyses.

To test our primary questions concerning the co-evolution of fossorial propensity, burrowing class, and ontogenetic/ecological traits, the following two models were fitted:

i) burrowing class = f(body mass PC + latitude/altriciality PC + predation threat PC + diet)

ii) fossorial propensity = f(body mass PC + latitude/altriciality PC + predation threat PC + diet)

To test our subsequent questions concerning the socio-ecological association between subterranean life-histories, resource dispersion, and sociality, the following model was fitted:

i) social class = f(fossorial propensity + burrowing class + diet)

Following Hadfield 2010, we used uninformative, inverse-gamma prior distributions. The number of iterations, thinning interval and the burn-in period were determined using diagnostic tests in the *R* package *coda* (Plummer et al., 2006). Convergence between model chains was verified using the Geweke diagnostic (Geweke, 1992).

2.4 Results

Of the 145 carnivore species for which we were able to source specific trait data, 113 made at least some use of subterranean space, and 85 of these for more than a singular purpose (Fig. 2.1). Underground burrows were used, in descending order, as natal

dens (74.5%, $n = 108$), residences (57.2%, $n = 83$), weather refugia (19.3%, $n = 28$), refuges from predation (19.3%, $n = 28$), and/or for food storage (10.6%, $n = 12$).

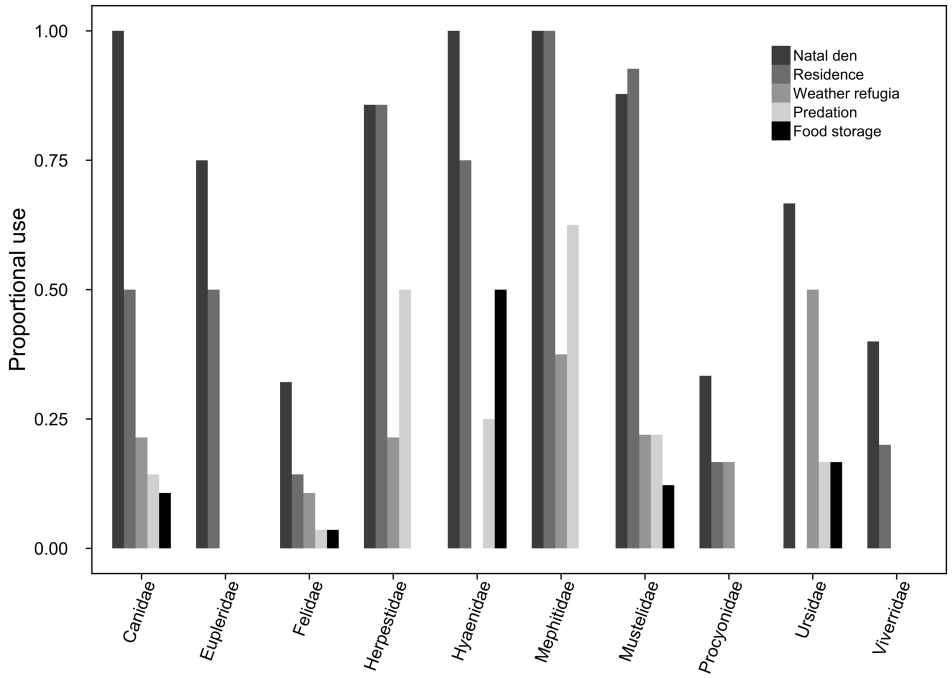

Figure 2.1: For each carnivore family, the proportion of species exhibiting at least facultative use of subterranean dens for each of the behavioral use categories (i.e. natal dens; residences; weather refugia; predation refugia; and food storage).

2.4.1 Life-history, Socio-ecology and Fossoriality

Bayesian modeling evidenced that a strong phylogenetic signal exists in carnivoran burrowing class (Table 2.2), and fossorial propensity (Table 3). Fossoriality was more prevalent in the Caniformia (Fig. 2.2) than in the Feliformia (Fig. 2.3); mephitids, mustelids and hyaenids being the most fossorial families. None of the felids, procyonids, or viverrids (for which we had data) proved to be primary excavators, and of these families, only two species of felids (*Felis margarita*; and *Felis nigripes*) were secondary modifiers, the rest being tertiary occupants. All other families included primary excavators, with the mephitids having the highest proportion (87.5%) of these.

We found support for an evolutionary relationship between fossorial life-histories and socio-ecological traits. Posterior coefficient estimates for the latitude/altriciality

Table 2.2: Relationship between burrowing class and life-history traits in the Carnivora. Coefficient estimates (β), and their 95% confidence intervals (CI) are presented. Asterisks denote variables that differed statistically from zero (based on 95% confidence intervals). Note: 3.2 x 10^6 iterations with 1.0 x 10^5 burn-in and thinning interval of 5.0 x 10^2.

	β	**lower CI**	**upper CI**
Fixed terms			
Intercept	2.03**	0.78	3.24
Body mass PC	0.04	-0.06	0.14
Latitude/altriciality PC	0.16*	0.03	0.31
Predation threat PC	-0.14	-0.30	0.02
Omnivorous diet	-0.57	-1.16	<0.01
Carnivorous diet	-0.50	-1.15	0.19
Herbivorous/frugivorous diet	-1.36*	-2.46	-0.28
Random terms			
Phylogenetic effect	0.94*	0.12	1.96
Residual variance	0.72**	0.52	0.95

** p >0.01, * p >0.05

PC, and the herbivorous/frugivorous dietary class indicated that these factors contributed significantly to our model predictive of burrowing class. Measures of body size and predation threat proved relatively unimportant in this model.

There was also evidence for an evolutionary relationship between fossorial propensity and diet, as well as PCs defined by body mass and latitude/altriciality. Generally, smaller carnivore species, producing large(r) litters, of altricial young were more likely to be fossorial than larger carnivore species producing smaller litters of well developed young. Indeed, no fossorial, primary excavator had an adult mass that exceeded 15 kg. Furthermore, insectivorous and omnivorous carnivores were generally more fossorial than carnivorous or frugivorous/herbivorous species.

2.4.2 Fossoriality and Group-Living

Modelling predictive of group-living evidenced that carnivores from different burrowing classes differed significantly in their propensity for group-living (Table 2.4). Primary excavators tended to form groups significantly more often than other burrowing classes; tertiary burrow users were least likely to form groups. There was also clear support for an evolutionary relationship between diet, fossoriality and social class.

Table 2.3: Relationship between fossorial propensity and life-history traits in the Carnivora. Coefficient estimates (β), and their 95% confidence intervals (CI) are presented. Asterisks denote variables that differed statistically from zero (based on 95% confidence intervals). Note: 3.2 x 10^6 iterations with 1.0 x 10^5 burn-in and thinning interval of 5.0 x 10^2.

	β	**lower CI**	**upper CI**
Fixed terms			
Intercept	2.28**	0.87	3.66
Body mass PC	-0.11*	-0.22	-0.01
Latitude/altriciality PC	0.31***	0.16	0.47
Predation threat PC	0.04	-0.13	0.21
Omnivorous diet	-1.05**	-1.67	-0.43
Carnivorous diet	-0.85*	-1.55	-0.12
Herbivorous/frugivorous diet	-1.28*	-2.48	-0.13
Random terms			
Phylogenetic effect	1.21*	<0.01	2.61
Residual variance	0.82**	0.57	1.10

*** p >0.001,** p >0.01, * p >0.05

Crucially, in tandem with burrowing class, diet proved highly significant, where carnivorous and frugivorous/herbivorous carnivores tended to form groups significantly less often than insectivorous or omnivorous carnivores.

2.5 Discussion

Of extant terrestrial mammals, 447 of 777 genera include species that engage in burrowing behavior (Kinlaw, 1999). These represent diverse mammalian species, from small rodents and soricomorphs (Nevo, 1999) to the largest extant burrowers, aardvarks (*Orycteropus afer*: Taylor and Skinner, 2003). Reflecting the extent of fossoriality observed across terrestrial mammals generally (Kinlaw, 1999), three quarters of carnivore species exhibited at least some level of reliance on the subterranean ecotope. Congruence between ecological/ontogenetic traits and metrics of fossoriality in the Carnivora accorded with four broad themes: 1) there were phylogenetic, and morphological constraints on wholly fossorial life-histories; 2) fossoriality correlated positively with the extent of offspring altriciality, linked to the use of natal dens; 3) burrow use increased with latitude; and 4) insectivorous carnivores were more fossorial than predatory carnivores. Furthermore, congruent with the strong support for a link between fossoriality and sociality in rodent societies (Barash, 1989; Hoog-

Table 2.4: Relationship between social class, fossoriality and diet in the Carnivora. Coefficient estimates (β), and their 95% confidence intervals (CI) are presented. Asterisks denote variables that differed statistically from zero (based on 95% confidence intervals). Note: 3.8 x 10^7 iterations with 2.0 x 10^6 burn-in and thinning interval of 1.0 x 10^3.

	β	**lower CI**	**upper CI**
Fixed terms			
Intercept	2.29***	0.52	1.96
Fossorial propensity	-0.08	-0.25	0.12
Burrowing class	0.32**	0.10	0.54
Omnivorous diet	-0.52	-1.21	0.18
Carnivorous diet	-1.05**	-1.71	-0.41
Herbivorous/frugivorous diet	-1.73**	-2.95	-0.54
Random terms			
Phylogenetic effect	0.56*	<0.01	1.24
Residual variance	0.55*	<0.01	1.23

*** p >0.001,** p >0.01, * p >0.05

land, 1995; Ebensperger and Blumstein, 2006; Sobrero et al., 2014), we evidenced a positive evolutionary relationship between the extent of fossoriality and the propensity for group-living. These fossorial traits have, functional, mechanistic, ontogenetic, and phylogenetic components (*sensu* Tinbergen, 1963), which, in turn, significantly influence species' socio-ecology.

2.5.1 Allometric constraints

We found an association between fossorial propensity and the PC defined by body size, highlighting allometric constraints on fossoriality (McNab, 1979; Vleck, 1981). Indeed, no fossorial, primary excavator had a mean adult mass greater than 15 kg. Although forelimb supination (see below) can support large body sizes (e.g. 300+ kg ursids: Andersson, 2004), as weight increases, cursoriality becomes more economical (Kram and Taylor, 1990). Consequently, with increasing body size, the opposing effects of relaxed running costs versus greater burrowing costs McNab (1979); Vleck (1981) can act as significant drivers for, or against, fossorial life-histories.

Although carnivores larger than 15 kg are still able to burrow, smaller species made greater use of underground space. In addition to the energetic cost of burrowing scaling allometrically (*sensu* Vleck, 1981), burrow size also scales allometrically

(White, 2005) and there is an upper limit on burrow size. Simply, even the most consolidated soil types cannot support the large and extensive excavations that would be needed to house, for example, a group of bears. Furthermore, although a wide variety of small (<1.0 kg) subterranean species appear in the paleontological record (Nevo, 1999), large fossil burrows are rare (e.g. Voorhies and Toots, 1970). Indeed, fossil evidence suggests that larger carnivorans were restricted to the use of cave formations, rather than subterranean burrows, as denning sites (e.g. cave bears, *Ursus spelaeus*: Stiner, 1999; and cave hyaenas, *Crocuta crocuta spelaea*: Diedrich and Žák, 2006).

2.5.2 Energetic Adaptations

Mammals exposed to cold winter conditions cope through two mechanisms; i) low thermal conductance to minimize heat loss (e.g. thick winter fur and/or insulating fat layer: Shield, 1972; McNab, 1983); or ii) by reducing their exposure to the cold, through the use of refugia (Noonan et al., 2014, 2015*b*), and/or entering a torpid state therein (Harlow, 1981; Lyman, 2013). Thus, while endothermy allows carnivores to exploit cold regions, and higher latitudes (Grigg et al., 2004), fossoriality provides a means of mitigating temperature thresholds (Shelford, 1931; Pörtner, 2002), permitting the species to live in colder environments (Fløjgaard et al., 2009). Also, small carnivores often utilize the subnivean ecotope directly for hunting (e.g. American martens, *Martes americana*: Raine, R Michael, 1987; least weasels, *Mustela nivalis*: Sheffield and King, 1994; black-footed ferrets, *Mustela nigripes*: Hillman and Clark, 1980; European polecats, *Mustela putorius*: Heptner and Sludskii, 2002). As a consequence, we found that the PC defined by latitude was influential in predicting the importance of fossoriality to species across all sizes (irrespective of Bergmann's rule, *sensu* Blackburn et al., 1999). Smaller predatory carnivores, however, are less suited to hibernation (for example no *Martes spp.* hibernate whereas the larger *Meles spp.* do: Newman et al., 2011), and tend not to form groups at high latitude.

High latitudes, and seasonality therein, also place particular ecological constraints (ECH: Pen and Weissing, 2000) on dispersing juveniles, leading to delayed dispersal (Ferreras et al., 2004), due to greater seasonal variation in food supply, shorter productive seasons and increased energetic requirements (Blank, 1992; Noonan et al., 2014). Futhermore, in those species large enough to undergo extended hibernation, group-living may be promoted by the thermoregulatory benefits of huddling in groups within subterranean burrows (e.g. Roper et al., 2001; Hwang et al., 2007; Kitao et al., 2009). These factors are likely influential in the integration of subsequent generations

into natal groups (Dahle and Swenson, 2003; Ferreras et al., 2004; Kaneko et al., 2014).

2.5.3 Ontogenetic Adaptations

Fossoriality and burrowing class were related to measures of altriciality. Among the Carnivora, while offspring are born along a continuum of altriciality to precociality (Derrickson, 1992), precocial young are incompatible with large litter sizes (reviewed in Martin and MacLarnon, 1985). This is especially so where pregnant females need to maintain hunting agility (Case, 1978*b*; Woodroffe and Ginsberg, 1997). Thus, altriciality is likely ancestral (Hopson, 1973; Case, 1978*b*). Altriciality however, requires a secure environment for rearing neonates (Case, 1978*a*,*b*; Wolff, 1997), and although natal dens can be as simple as a hollow log (e.g. Carter et al., 2012), subterranean burrows are more thermally stable (e.g. Buffenstein, 1984; Nevo, 1999; Moore and Roper, 2003; Kaneko et al., 2010). Thus, bespoke natal dens extend womb-like conditions of warmth and security, while altricial offspring are provisioned with milk (Kinlaw, 1999; McClellan et al., 2008). A similar scenario can be seen in the Leporidae where cursorial, precocious hares (*Lepus spp.*) are capable of following their mother soon after birth, while burrowing, altricial rabbits (*Oryctolagus spp.*) are born blind and hairless, remaining underground until they are 4 weeks old (Macdonald, 2006).

We found that species utilizing subterranean natal dens tend to form groups roughly 2.5 times more often than those that do not. Natal dens can effectively support philopatric and social behavior (benefits of philopatry hypothesis: Brown and Brown, 1984) – mirroring correlations found in birds where extended parental care leads to delayed offspring dispersal (Brown and Brown, 1984; Ekman and Rosander, 1992; Ekman et al., 1994). Even in the absence of any other benefits of sociality, if local environmental carrying capacity permits, then the continuing philopatric use of natal dens (Isbell, 2004), resulting from delayed dispersal (Kokko and Ekman, 2002), may impose communal aggregation upon individuals (an extension of the EBH).

It is important to note, however, that in group-living species where philopatry accrues fitness benefits through enhanced survival (Kokko and Ekman, 2002), inclusive fitness (Herre and Wcislo, 2011) and cooperative breeding (Koenig et al., 1992), reproductive suppression of subordinates often occurs (Creel and Creel, 1991; Creel and Macdonald, 1995). Indeed, even for those non-cooperative breeders in which offspring always disperse, reproductive opportunities may be just as limited as they are

for offspring that remain philopatric (Brown and Brown, 1984). Thus, albeit through different mechanisms, both strategies result in similar ecological constraints (ECH: Pen and Weissing, 2000).

2.5.4 Phylogenetic Exaptations

Paleo-ecological selection pressures favouring fossorial traits arose around the Eocene-Oligocene boundary, circa 35 Mabp (Nevo, 1999). During this transition, the earth underwent a shift to cooler (7-10 °C over the Paleogene; Savin, 1977), and increasingly variable conditions (Katz et al., 2008), causing aridisation and greater seasonality (Prothero and Berggren, 2014). As a result, forest ecosystems, abundant in the Eocene, gave way to Oligocene grasslands (Vicentini et al., 2008; Prothero and Berggren, 2014), impacting habitat availability and food chains. This drove selection for two adaptive herbivore strategies; i) plains herbivores (Stebbins, 1981), which grew large and migratory in developing prairies and savannahs; and ii) smaller rodent species, able to burrow for protection (Nevo, 1999). Prior to this transition, carnivore ancestors tended to be arboreal forest dwellers (Macdonald, 1992), however, in a typical 'Red Queen' response (Van Valen, 1973), carnivorans invading this new grassland ecotope underwent selection along four formats: i) cursorial pursuit predators able to chase fleet-footed ungulates, exemplified in the digitigrade canids (Martin, 1989; Andersson, 2004); ii) 'stalk and ambush' predators, with supinated limbs adapted for grappling, common among extant feliformia (Andersson, 2004); and strategists capable of pursuing prey underground, giving rise to ecomorphs undergoing selection for either; iii) digging power, represented today by the bear-badger type (with selection for specific forelimb anatomy for digging; see Andersson, 2004; Samuels et al., 2013); and iv) slender ecomorphs evolved to slip into burrows to capture prey, represented today by the polecat-mongoose type (Martin, 1989).

Ebensperger and Blumstein (2006) reported that evolutionary trajectories constrained fossoriality in the Rodentia significantly. Similarily, we found that use of the subterranean ecotope was not consistent across all carnivore families. Phylogenetic constraints were apparent, limiting which carnivores are able to dig; inertia consequent of ancestral specialisation for cursoriality, scansoriality, and for grasping claws. For example, felids, procyonids and viverids proved the least fossorial carnivore lineages. Indeed, ichnofossil evidence of burrowing behavior (as distinct from den use, per se) also reflects that ancestral felids, procyonids, and viverids evolved along

trajectories incompatible with digging (Macdonald, 1992; Andersson, 2004). The felids are the only wholly carnivorous Carnivora family (Macdonald, 1992; Sicuro and Oliviera, 2011), and possess hook-shaped, retractable claws, adapted for hunting prey (Bryant et al., 1996; Kitchener et al., 2010), which would be damaged by digging. Burrowing species, in contrast, typically have flattened claws adapted for dislodging soil (Hildebrand, 1985). Several epigean viverid species also have retractable claws (Bryant et al., 1996). Similarly, the substantially arboreal Procyonidae have forelimbs adapted to climbing (McClearn, 1992). Coatis (*Nasua spp.*), being predominantely terrestrial but with arboreal dens, provide an interesting contrast to other procyonids. While they dig holes proficiently to capture invertebrate prey, they do not excavate subterranean burrows, and are the least agile climbers in this family (McClearn, 1992).

Further in line with our findings here, a clear phylogenetic signal for digging ability is evident in the forelimb morphology of carnivores, where shared ancestry significantly constrains kinesiology (Andersson, 2004; Samuels et al., 2013). Forelimb supination is crucial for both scansorial and fossorial carnivores, but is maladaptive for cursorial pursuit predators (Andersson, 2004). Unlike scansoriality however, scratch digging requires elongated humeri and ulnae to provide stable elbow joints (Van Valkenburgh, 1987; Andersson, 2004; Samuels et al., 2013). Due to these phylogenetic constraints, those species that use burrows but are unable to excavate them themselves, rely on kleptoclaustromy, and so burrowing species are 'keystone' (Mills and Doak, 1993) to the subterranean ecotope (e.g. Whittington-Jones and Bernard, 2011).

2.5.5 Diet, Trophic Resource Dispersion and Sociality

Carnivores that evolved along phylogenetic trajectories adaptive for fossorial traits are often those that also exhibit the tendancy to form groups. Here diet proves important: among the 145 species examined, we found a 27.8% overlap (33 species) between the 62 species showing a significant extent of fossoriality and the 62 with omnivorous/insectivorous diets. Of these 33 species, only 3 were solitary; white-tailed mongooses (*Ichneumia albicauda*); American hog-nosed skunks, (*Conepatus leuconotus*); and Sechura foxes, (*Pseudalopex sechurae*).

This substantial interaction between fossoriality and omnivorous/insectivorous diets proves insightful. Although 75% of carnivores utilize fossorial natal dens, species consuming a carnivorous diet tend to disperse as they mature because the resources

available in their natal territory cannot support the requirements of multiple adults (von Schantz, 1984). For species that consume a diet where food resources have a dispersion able to support adult groups (typified by omnivory/insectivory; *sensu* Macdonald, 1983*b*), dispersal may be delayed or obviated. When these species are small enough to cohabit, fossorial dens act as foci leading to the formation of philopatric groups. By increasing the variety of trophic resources available, omnivory (to include insectivory) effectively reduces competition for resources (Gittleman, 1986). Furthermore, the dispersion and renewal characteristics of these alternative food types preclude sufficient resources being monopolized by a primary individual to prevent secondary conspecifics being tolerated in the same range (Macdonald et al., 2004*b*; Macdonald and Johnson, 2015), leading to range sharing. This is a flexible process; many omnivores form temporary 'fission fusion societies' under appropriate but temporary RDH conditions (e.g. raccoons, *Procyon lotor*; red foxes, *Vulpes vulpes*; arctic foxes, *Vulpes lagopus*; Blandford's foxes, *Vulpes cana*; and kinkajous, *Potos flavus*; reviewed in Macdonald and Johnson, 2015).

There are nevertheless likely limiations to a fossorial group formation process among the Carnivora. Omnivores/insectivores too big to cohabit will still be driven to disperse, although they may congregate temporarily in rich resources patches, (e.g. ursids at salmon runs: Reimchen, 2000). Furthermore, secondary conspecifics need to have a physiology capable of tolerating secondary food security (Newman et al., 2011; Macdonald and Johnson, 2015). Small, subnivean and/or agile scansorial predators for example, cannot carry sufficient body fat without compromising required hunting athleticism (King, 1989; Newman et al., 2011). Chinese ferret badgers (*Melogale moschata*) appear to be at the lower body-weight extreme for being able to form burrow-dwelling groups, benefitting from (sub-)tropical levels of productivity (Zhang et al., 2010). Consequently, fossoriality, even in a suitable trophic resource-scape, is unlikely to leverage group-living if these critera are not met.

2.5.6 Conclusions

We evidence that the extent of fossoriality in the Carnivora is an important driver of group-living behaviour, resonating with research in the Rodentia (e.g. Ebensperger and Blumstein, 2006; Sobrero et al., 2014; Smorkatcheva et al., 2014). This provides consilient support to an ecological basis to non-cooperative societies (*sensu* Macdonald, 1983*b*). According to the TDH (Nevo, 1979), under conditions leading to strong resource competition, fossoriality leads to solitary social systems (*sensu* Gittleman,

1989). Although the role of TDH in the evolution of rodent societies was rejected by Smorkatcheva et al. (2014), we observed that extant (semi-) fossorial predatory carnivores that compete for indivisible, small vertebrate prey, which do not simultaneously satisfy RDH sociality criteria (see Macdonald and Johnson, 2015), tend not to be gregarious (e.g. American badgers, *Taxidea taxus*: Long, 1973; least weasels: Sheffield and King, 1994; black-footed ferrets: Hillman and Clark, 1980; European polecats: Heptner and Sludskii, 2002; wolverines, *Gulo gulo*: Pasitschniak-Arts and Larivière, 1995; and sand cats, *Felis margarita*: Sunquist and Sunquist, 2002). Similarly, albeit satisfying dietary RDH criteria, certain epigean carnivores (e.g. tayras, *Eira barbara*: Presley, 2000; ringtails, *Bassariscus astutus*: Harrison, 2012; ursids, *Ursus spp.*: Pasitschniak-Arts, 1993; Larivière, 2001; and African civets, *Civettictis civetta*: Ray, 1995) proved less gregarious than otherwise ecologically similar fossorial species; that is, fossoriality leverages group formation under marginal circumstances.

Subterranean living is not without its challenges, including hypoxia/hypercapnia, permanent darkness, and conditions of high pathogen infectivity, which can lead to the spread of disease and parasites (Nevo, 1999). Indeed den sharing has been implicated in the spread of *Mycobacterium bovis* among several social burrowers (e.g. yellow-bellied marmots, *Marmota flaviventris*: Van Vuren, 1996; brushtail possums, *Trichosurus vulpecula*: Corner et al., 2003; European badgers, *Meles meles*: Rogers et al., 2003; wombats, *Vombatus ursinus*: Skerratt et al., 2004). For those carnivores where the benefits outweigh the costs, we evidence that the extent of fossoriality accords with the TDH, the EBH, and RDH criteria. In tandem with the benefits of philopatry (Brown and Brown, 1984), this can act as a significant precursor for group-living. This also explains why certain carnivores that satisfy the dietary critera of the RDH, but are not strongly fossorial, do not form (semi-) permanent groups. Cohabitation provides the initial step toward group-living. If conditions arise where omnivorous species, living in an environment with suitable resource dispersion (*sensu* Macdonald, 1983*b*), continue to remain associated with their fossorial natal dens, then a propitious scene is set for the formation of permanent social groups.

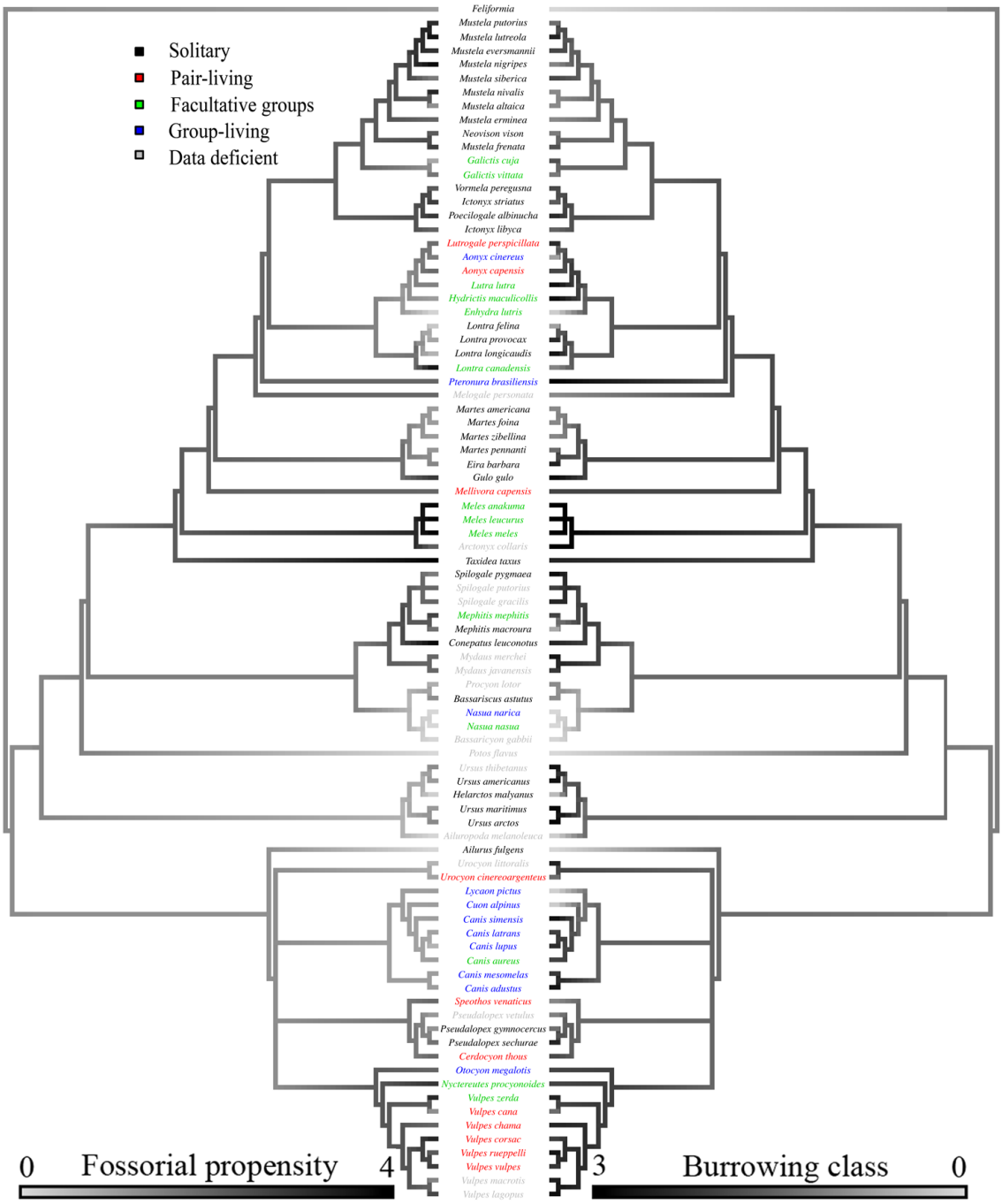

Figure 2.2: Consensus tree of the Caniformia based on phylogenetic relationships from Agnarsson *et al.* (2010). Relationships between the Canidae were taken from Lindblad-Toh *et al.* (2005). For clarity, the Feliformia are collapsed. Shading of the left hand branches depicts fossorial propensity scaled from wholly epigean, to wholly fossorial. Shading of the right hand branch depicts burrowing class scaled from no burrow use, to primary excavators. Coloration of species labels denotes group-living propensity, classified as: black) solitary: species with predominantly solitary life-histories; red) pair-living: predominantly pair-living species; green) facultative groups: species with both solitary and group-living life-histories, variable across populations; and blue) group-living: species exhibiting obligate groups. Data deficient species are listed in gray.

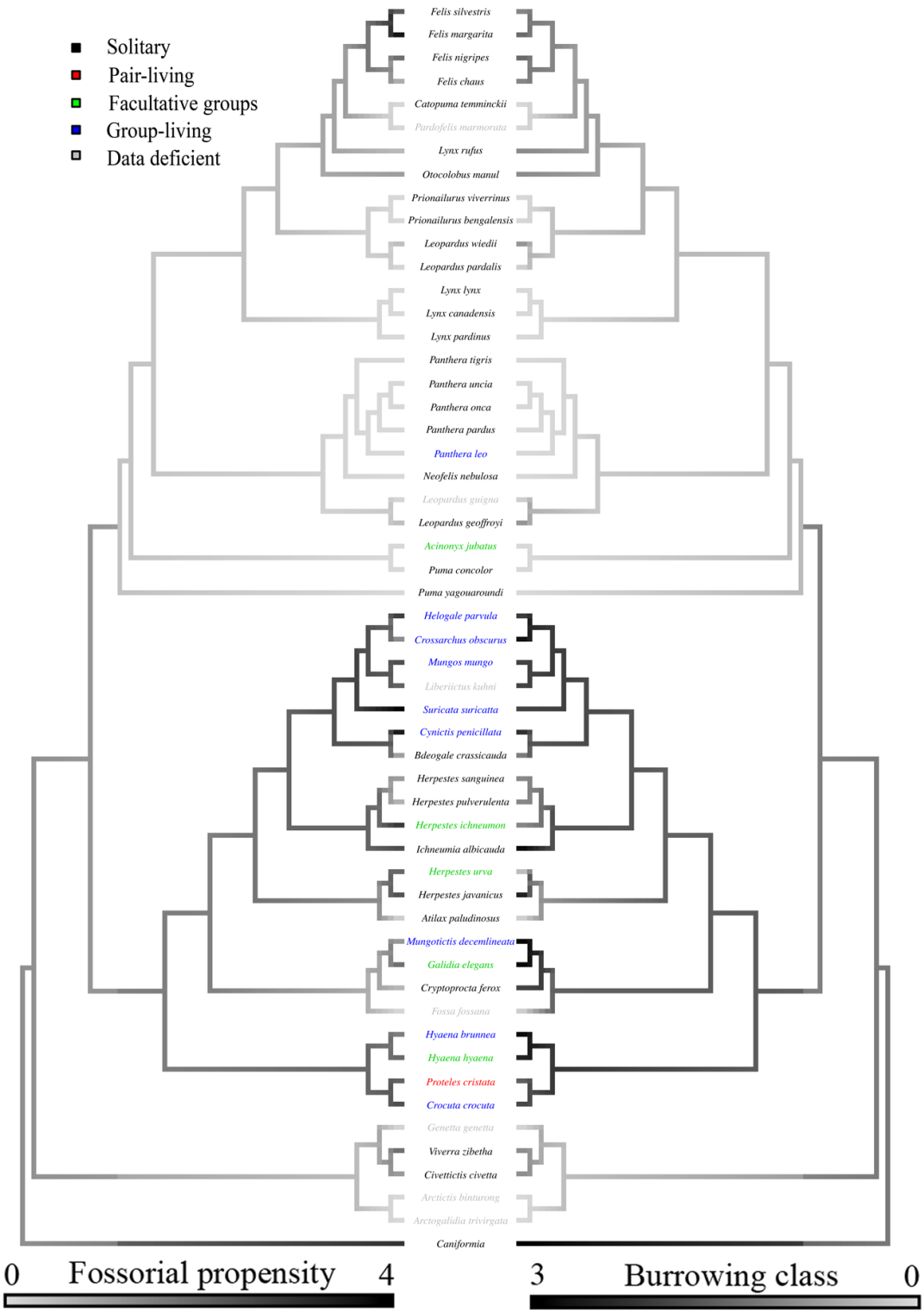

Figure 2.3: Consensus tree of the Feliformia based on phylogenetic relationships from Agnarsson *et al.* (2010). For clarity, the Caniformia are collapsed. Shading of the left hand branches depicts fossorial propensity scaled from wholly epigean, to wholly fossorial. Shading of the right hand branch depicts burrowing class scaled from no burrow use, to primary excavators. Coloration of species labels denotes group-living propensity (see Fig. 2.2). Data deficient species are listed in gray.

Part II

Ecological Constraints and Fossorial Living

'It was after tea-time; it was pouring with rain, and had been all day; his hood was dripping into his eyes, his cloak was full of water... "Bother burgling and everything to do with it! I wish I was at home in my nice hole by the fire, with the kettle just beginning to sing!'

– J.R.R. Tolkein

Chapter 3

Climate and the individual: Inter-Annual Variation in the Autumnal Activity of the European Badger (*Meles meles*)

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3.1 Abstract

We establish intra-individual and inter-annual variability in European badger (*Meles meles*) autumnal nightly activity in relation to fine-scale climatic variables, using tri-axial accelerometry. This contributes further to understanding of causality in the established interaction between weather conditions and population dynamics in this species. Modelling found that measures of daylight, rain/humidity, and soil temperature were the most supported predictors of ACTIVITY, in both years studied. In 2010, the drier year, the most supported model included the SOLAR*RH interaction, RAIN, and30cmTEMP ($w = 0.557$), while in 2012, a wetter year, the most supported model included the SOLAR*RH interaction, and the RAIN*10cmTEMP ($w = 0.999$). ACTIVITY also differed significantly between individuals. In the 2012 autumn study period, badgers with the longest *per noctem* activity subsequently exhibited higher Body Condition Indices (BCI) when recaptured. In contrast, under drier 2010 conditions, badgers in good BCI engaged in less *per noctem* activity, while badgers with poor BCI were the most active. When compared on the same calendar dates, to control for night length, duration of mean badger nightly activity was longer (9.5 hrs ± 63.3 SE) in 2010 than in 2012 (8.3 hrs ± 61.9 SE). In the wetter year, increasing nightly activity was associated with net-positive energetic gains (from BCI), likely due to better foraging conditions. In a drier year, with greater potential for net-negative energy returns, individual nutritional state proved crucial in modifying activity regimes; thus we emphasise how a '*one size fits all*' approach should not be applied to ecological responses.

3.2 Introduction

In seasonal ecosystems, biological and chemical processes (Gaedke and Straile, 1994; Catalan et al., 2002; Ishii et al., 2004), along with phenological responses (e.g., see: Campbell et al., 2013), generally respond to annual cyclicity in primary productivity (Nemani et al., 2003), weather patterns, and hydrological, nutrient, and carbon cycles (Barth and Veizer, 1999; Huxman et al., 2003; Greco and Baldocchi, 1996). A species' climatic niche, and range of tolerance around this niche, are thus defining elements in evolution (Caswell, 1982; Thuiller et al., 2005; Wolf et al., 2007). Considering that ecological responses are typically non-linear (May, 1986; Nouvellet et al., 2013), even minor changes in environmental conditions can have substantial effects across trophic levels (Post et al., 1999). For consumers, seasonal variation in food supply and associated thermal stresses while foraging create energetic demands (Blank, 1992; Owen et al., 1992; Tinkler et al., 2009), driving physiological and/or behavioural adaptations – for example, endocrinological changes (Boyce, 1979), fat deposition (Kunz et al., 1998; Macdonald and Newman, 2002; Giroud et al., 2012), winter hibernation/torpor (Harlow, 1981; Barclay et al., 2011), life-cycle synchronicity (Sandell, 1990; Yamaguchi et al., 2006), migration (Ferguson and Elkie, 2004), and food caching (Macdonald, 1976; Post et al., 2006). Matching species' mechanistic responses to fine-scale environmental variability, while imperative, proves challenging (e.g., Easterling et al., 2000; King, 2005; Tuljapurkar, 2010).

To these ends, recent advancements in accelerometery technology capable of measuring both animal orientation and the dynamics of movement, have considerably enhanced the capacity to achieve behavioural activity sampling on a fine-scale (Yoda et al., 1999; Ellwood et al., 2007; Shepard et al., 2008; Wilson et al., 2008). Accelerometry has elaborated a wide range of behaviours – such as diving (Hays et al., 2007; Ropert-Coudert et al., 2009), feeding (Okuyama et al., 2010; Viviant et al., 2009), and mating behaviour (Whitney et al., 2010) – which often cannot be recorded as systematically by other techniques in wild, cryptic animals (Markham et al., 2010*b*; Shamoun-Baranes et al., 2012). Important in this study, the activity data accelerometers generate can be utilised to provide an accurate proxy for energy expenditure (Gleiss et al., 2010).

Here, we apply accelerometry as a tool to investigate the interaction between proximate weather conditions and European badger (*Meles meles*) activity regimes

(Macdonald et al., 2010; Nouvellet et al., 2013); that is, this approach enables us to assess how activity is promoted or inhibited by micro-climatic conditions 'per individual'.

The European badger provides a particularly good model for studying the effects of weather, because of its sensitivity to climatic conditions (Johnson et al., 2002*a*; Macdonald and Newman, 2002; Nouvellet et al., 2013) and its trophic specialism, favouring earthworms, *Lumbricus terrestris*, in lowland Britain and Ireland (Kruuk and Parish 1981, Hofer 1988, da Silva et al. 1993, Muldowney et al. 2003).

Badgers undergo autumnal weight gain (Woodroffe, 1995; Macdonald and Newman, 2002)) in advance of a flexible extent of winter torpor (Newman et al., 2011), where they rest inside extensive dens, termed setts (Fowler and Racey, 1988; Thornton, 1988; Kaneko et al., 2010). This inactivity period is most evident in higher latitude regions of their range, where winter frosts restrict earthworm availability (Macdonald, 1983*a*; Holmstrup and Zachariassen, 1996; Kowalczyk et al., 2003; Nuutinen and Butt, 2009). Earthworms become less available under frosty conditions (Boyle and Whelan, 1990), and so in order to maintain or increasing their body-condition in the lead up to food supply restriction (i.e., over the autumn) badgers must attempt to balance trade-offs between the energetic expenditure of their activity (foraging and non-foraging), against energy conserved by inactive periods within their setts. As a consequence early autumn – specifically September – weather conditions present an important transition point in badger activity regimes influenced by variability in the change over from 'productive' to 'less/non-productive' conditions (Macdonald and Newman, 2002; Macdonald et al., 2010), where more activity has been observed under sub-optimal conditions, to attempt to compensate for lower foraging success (Revilla and Palomares, 2002; Kowalczyk et al., 2003; Do Linh San et al., 2007).

In addition to nutrition, there are also other individual-specific motivators of activity, such as territorial marking (Stewart et al., 2001; Kilshaw et al., 2009), scent communication (Buesching et al., 2003), and associated social contact networks (Dyo et al., 2010) potentially pertinent to reproductive success and thus fitness (Dugdale et al., 2008). Consequently, complex individual-specific differences in activity patterns are apparent (Kowalczyk et al., 2004; Palphramand and White, 2007; Byrne

et al., 2012).

Given that interactions between badger population dynamics and weather metrics have been established (Macdonald and Newman, 2002; Macdonald et al., 2010; Nouvellet et al., 2013), here we aim to advance understanding causality by examining how variation in autumnal weather conditions in two non-consecutive years influenced activity budgets. We use overall dynamic body acceleration (ODBA) from tri-axial accelerometers (Markham et al., 2010*b*, 2012), to expose real-time variation in badger activity levels through late summer/early autumn. We also postulate that variation in nutritional state will yield differing individual responses to environmental stressors, evidenced as differences in activity levels.

3.3 Methods

From trapping morphometrics data we used the ratio of body length to weight (L:W) to calculate Body condition indices (BCI) (log mass vs. log length), as a measure of an individual's nutritional state (Kruuk and Moorhouse, 1990; Macdonald et al., 2002). To monitor seasonal and individual-specific changes in BCI, we calculated the index for the summers in which animals were instrumented and, provided the animals were (re-)captured, the spring and autumn preceding/following these summers.

We instrumented four badgers in 2010 (3 males and 1 female) and four different individuals in 2012 (3 males and 1 female) with prototype tracking tags [39mm (l) x 22mm (w) x 12mm (h)] mounted on a leather collar, with a complete assembly weight of 105g (for detailed description of the collars and data collection system see: Markham et al., 2010*b*, 2012). Henceforth individual badgers were identified by their unique collar ID.

In 2010, data were collected from September 28 until batteries ran out on November 24, i.e., for a total of 58 days. All batteries lasted for the same duration except for those in one collar (N30), which ran out after only 45 days. In 2012, data were collected from September 1 until all batteries ran out on October 30, i.e., for a total of 60 days.

We converted these acceleration values for the three axes/channels to overall dynamic body acceleration (ODBA), using the method developed by Wilson et al.

(2006). That is, each channel was smoothed individually; using running means over 10 min time frames. The values for these smoothed data, for any particular time frame, were then subtracted from the corresponding unsmoothed data for that time frame. This gives a value for g resulting from dynamic acceleration that we converted into absolute positive units using the L1 norm, combining values from all three channels, to produce an ODBA metric. ODBA values were compared to a threshold, determining badger activity from inactivity for each data period (ACTIVITY). To satisfy assumptions of normality, hourly measures of activity were subjected to angular transformations for all statistical analyses.

Meteorological records were obtained from the UK Environmental Change Network (ECN)'s weather station in Wytham Woods (T08) and are availably freely. In order to separate the proximate effects of weather on badger ACTIVITY from inter-annual variation, we decomposed climatic data into 7 environmental variables, known to influence badger behaviour and physiology (Fowler and Racey, 1988; Johnson et al., 2002*a*; Kaneko et al., 2010; Macdonald et al., 2010): (1) solar radiation, providing a measure of photoperiod (SOLAR, in W/m^2) with the additional benefit of including cloud cover and thus more subtle influences on the timing of dusk emergence; (2) relative humidity (RH, in %); (3) mean air temperature (TEMP, in °C); (4) total rainfall (RAIN, in mm); (5) soil temperature at a depth of 10cm (10cmTEMP, in °C); (6) soil temperature at a depth of 30cm (30cmTEMP, in °C); (7) volumetric water content of the soil (WATER, m^3/m^3). We then modelled the effects of these climatic components on badger ACTIVITY both within each study period and between years. Given the importance of photoperiod on badger activity (Fowler and Racey, 1988), we utilised the terms '*per diem*' and '*per noctem*' to distinguish between daylight and night-time hours respectively, and avoid confusion associated with the dual meaning of the term 'per day'.

3.3.1 Statistical Analyses

We performed a preliminary analysis of daily measurements using analyses of variance (ANOVA) with analyses of covariance (ANCOVA), paired-sample t-tests, coefficients of variation (CV), and Levene's tests ($p = 0.05$). As ACTIVITY data were collected over two discrete windows within the two years, analyses relating climate to ACTIVITY were performed for each period separately and then compared.

We then applied an information theoretic approach (Burnham and Anderson, 2002; Burnham et al., 2011) to examine finer scale-hourly data, using Akaike's information criterion (AIC), in a mixed model approach. SOLAR was included in all multi-variate models to reflect the nocturnality of badgers, and to avoid superfluous testing; no model included more than one measure of temperature (i.e., TEMP, 10cmTEMP, or 30cmTEMP). In addition, because badgers differed individually in their activity regimes, we included individuality as a random effect variable. We acknowledge that although a degree of variation in activity regimes was likely due to inter-sexual variation, sample sizes here did not permit us to investigate this in detail. Given that seven climatic variables were derived for each year, we constructed 26 models without interaction and 33 models that included (an) interaction term(s). We therefore evaluated 59 models with climatic parameters as predictors of badger ACTIVITY. For each model, we derived the AIC, which we used to rank the support for each model (a lower value indicating greater support), as well as the delta AIC (Δi) in relation to the highest ranking model and the Akaike weight (w; Burnham and Anderson, 2002). As per Anderson (2008), Δi cut-off points were not used, though models with Δi values above 9-11 were considered to have relatively little support, and models with Δi values > 20 had no empirical support (Burnham et al., 2011).

Statistical analyses were conducted in the R environment (version 3.0.1; R Core Team, 2014). Although statistical analyses were performed on transformed data, for visual purposes, we used the un-transformed data in all figures.

3.4 Results

3.4.1 Autumnal climatic conditions

Between the autumn study periods in the two years, we found no difference in daily TEMP (ANOVA: $F_{[1,116]} = 1.69$, $p = 0.20$), (summarised in table 3.1), nor between TEMP variability (2010: CV 27.8%, $n = 58$; 2012: CV = 27.1%, $n = 60$; Levene's: $F_{[1,116]} = 0.66$, $p = 0.43$). Badgers are nocturnal however, and, controlling for night length, 2012 proved significantly colder (daily TEMP 4 °C cooler) than 2010 (paired sample t-test: $t_{32} = -8.35$, $p < 0.0005$) over matched calendar dates.

Decomposing temperature variables further, we found that in 2012 TEMP decreased steadily over the duration of the study period. In contrast, in 2010 there was a cold interlude of 16 days in early November (Nov. 7 – Nov. 22), where TEMP

Table 3.1: Climatic parameters and ACTIVITY. Mean values for climate parameters and ACTIVITY SD over the duration of the study periods in 2010 (58 days) and 2012 (60 days). Paired parameters represent means over the same calendar dates (Sep. 28 – Oct. 30)

	2010	2012
TEMP (°C)	11.75 ± 3.24	11.00 ± 2.96
TEMP paired (°C)	13.34 ± 2.11	9.41 ± 2.24
10cmTEMP (°C)	13.07 ± 2.62	12.78 ± 2.38
10cmTEMP paired (°C)	14.65 ± 1.44	11.11 ± 1.38
30cmTEMP (°C)	13.91 ± 1.79	13.90 ± 1.84
30cmTEMP paired (°C)	15.05 ± 0.86	12.47 ± 0.82
RH (%)	83.80 ± 7.43	87.84 ± 8.64
RH paired (%)	83.09 ± 8.48	91.67 ± 6.45
RAIN (mm)	1.82 ± 3.35	2.73 ± 5.75
RAIN paired (mm)	2.21 ± 3.81	2.98 ± 5.68
WATER (m^3/m^3)	0.306 ± 0.118	0.383 ± 0.053
WATER paired (m^3/m^3)	0.301 ± 0.117	0.42 ± 0.019
ACTIVITY (hrs)	9.48 ± 3.32	8.27 ± 1.86
ACTIVITY paired (hrs)	11.25 ± 1.02	9.22 ± 1.17

decreased rapidly, from 16 °C per day to 8.5 °C over 5 days, and averaged 7.2 °C ± 1.8 SD over the length of the interlude compared to 13.4 °C ± 1.8 SD over the first 40 days of the study period. TEMP variability over this interlude, through to the end of the study period, was also significantly more variable than the first month and a half of the study (CV = 29.5%, n = 18; CV = 14.9%, n = 40 respectively; Levene's: $F_{[1,56]} = 8.61$, $p = 0.005$) (Fig. 3.1).

As with TEMP, there was no evidence for a difference in daily 10cmTEMP (ANOVA: $F_{[1,116]} = 0.38$, $p = 0.54$), but 2012 was significantly colder than 2010 when compared directly on the same calendar dates (paired sample t-test: $t_{57} = 13.55$, $p < 0.0005$) with mean daily 10cmTEMP being 3.5 °C cooler. Similarly, there was no evidence for a difference in 30cmTEMP, (ANOVA: $F_{[1,116]} = 0.003$, $p = 0.99$), but 2012 was significantly colder than 2010 when compared on matched calendar dates (paired sample t-test: $t_{57} = 24.71$, $p < 0.0005$) with mean per day 30cmTEMP being 2.6 °C colder. Within years, 10cmTEMP was significantly more variable than 30cmTEMP (2010: CV = 49.4%, $n = 58$; CV = 20.2%, $n = 58$ respectively; Levene's: $F_{[1,114]} = 44.50$, $p < 0.0005$; 2012: CV = 18.8%, $n = 60$; CV = 13.4%, $n = 60$ respectively; Levene's: $F_{[1,118]} = 4.78$, $p = 0.031$). Between years, both 10cmTEMP and 30cmTEMP in 2010 were significantly more variable than in 2012 (Levene's: 10cmTEMP; $F_{[1,116]} =$

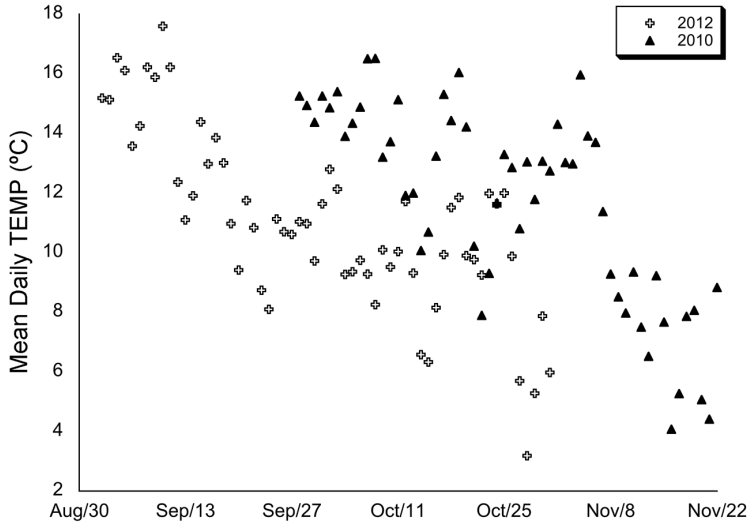

Figure 3.1: Mean daily TEMP over the study periods. Mean daily air temperature (TEMP) over the course of the study periods in 2010 and 2012. Between the two years, we found no difference in daily TEMP (ANOVA: $F_{[1,116]} = 1.69$, $p = 0.20$), nor between TEMP variability (2010: CV 27.8%, $n = 58$; 2012: CV = 27.1%, $n = 60$; Levene's: $F_{[1,116]} = 0.66$, $p = 0.43$) but 2012 proved significantly colder (daily TEMP 4 °C cooler) than 2010 (paired sample t-test: $t_{32} = -8.35$, $p < 0.0005$) over matched calendar dates.

51.12, $p < 0.0005$; 30cmTEMP: $F_{[1,116]} = 7.01$, $p = 0.009$). With respect to measures of humidity, although there was no evidence for a difference in RAIN between these years (ANOVA: $F_{[1,116]} = 1.09$, $p = 0.30$), the 2012 study period had significantly higher RH (ANOVA: $F_{[1,116]} = 7.29$, $p = 0.008$), and WATER (ANOVA: $F_{[1,116]} = 20.84$, $p < 0.0005$) than 2010.

3.4.2 Badger activity

Inter-annual differences in badger activity

From September through October in 2012 *per noctem* ACTIVITY increased with night length and thus correlated negatively with photoperiod (ANCOVA: $F_{[1,230]} = 74.31$, $p < 0.0005$). In 2010, however, ACTIVITY was monitored over a later period, from October through November, and *per noctem* ACTIVITY decreased with lengthening nights, resulting in a positive correlation with SOLAR (ANCOVA: $F_{[1,216]} = 16.96$, $p < 0.0005$). Over the study period in both years, there was no significant difference between individuals (ANCOVA 2010: $F_{[1,216]} = 3.30$, $p = 0.07$; 2012: $F_{[1,230]} = 3.58$, $p = 0.06$) This suggested that some other variable, such as weather, was counteracting night length. Badgers were significantly more active in 2010 than in

2012 (ANOVA: $F_{[1,1454]} = 13.51$, $p < 0.0005$; Table 3.1), when compared on the same calendar dates between years, to control for night length. As well as being more active, the duration *per noctem* ACTIVITY was significantly more variable in 2010 than it was in 2012 (CV = 35.3%, $n = 58$; CV = 22.7%, $n = 60$ respectively; Levene's: $F_{[1,116]} = 8.46$, $p = 0.004$) (Fig. 3.2).

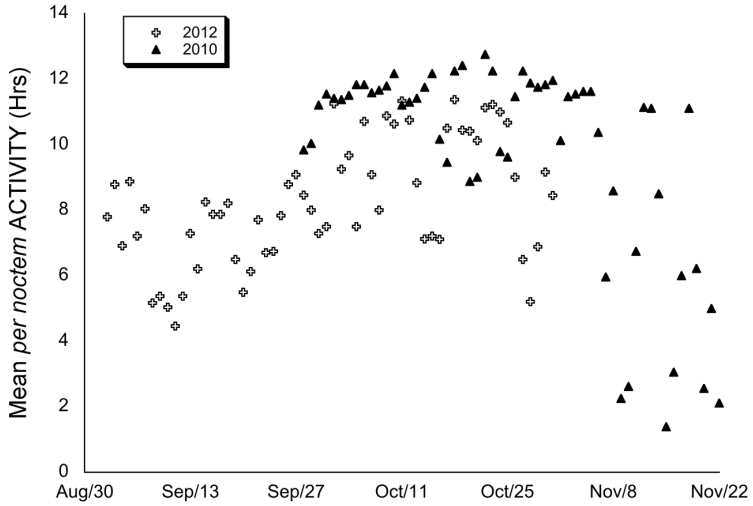

Figure 3.2: Mean *per noctem* ACTIVITY over the study periods. Mean *per noctem* ACTIVITY over the course of the study periods in 2010 and 2012. The duration of *per noctem* ACTIVITY was significantly more variable in 2010 than it was in 2012 (CV = 35.3%, $n = 58$; CV = 22.7%, $n = 60$ respectively; Levene's: $F_{[1,116]} = 8.46$, $p < 0.005$), this was also true when compared on the same calendar dates, to control for night length, significantly longer (ANOVA: $F_{[1,1454]} = 13.51$, $p < 0.0005$) in 2010.

Interaction between activity and climatic variables

To explore how the weather conditions influenced *per noctem* ACTIVITY between years specifically, we determined the relationship between the climatic variables and ACTIVITY using ANCOVAs. The study period in 2010 was comparatively drier than 2012, with a pronounced cold interlude, and more variable soil temperatures. In 2010, we observed no correlation between mean badger ACTIVITY and RH (Fig. 3.3a) ($F_{[1,216]} = 0.46$, $p = 0.50$).

There also was no correlation between activity and RAIN ($F_{[1,216]} = 0.09$, $p = 0.77$), but a positive correlation between ACTIVITY and TEMP (Fig. 3.4a), 10cmTEMP, 30cmTEMP, and WATER ($F_{[1,216]} = 86.49$, $p < 0.0005$; $F_{[1,216]} = 8.94$, $p < 0.005$; $F_{[1,216]} = 120.51$, $p < 0.0005$; $F_{[1,216]} = 7.02$, $p = 0.008$ respectively). In all

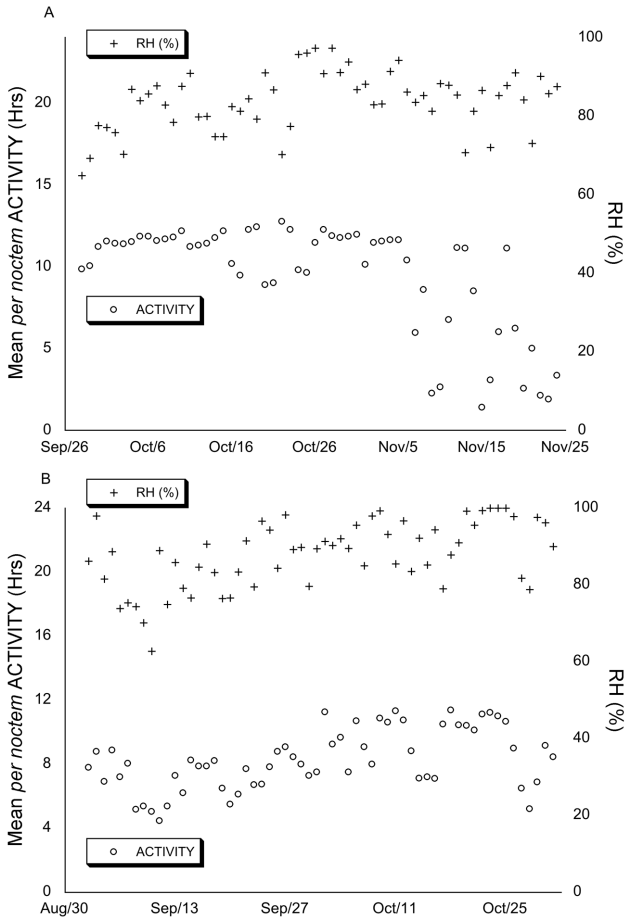

Figure 3.3: Mean *per noctem* ACTIVITY and RH over the study periods. Mean *per noctem* ACTIVITY and relative humidity (RH) over the course of the study periods in 2010 (A) and 2012 (B). In 2010, there was no correlation between ACTIVITY and RH ($F_{[1,216]} = 0.46$, $p = 0.50$). In 2012, ACTIVITY correlated significantly and postively with RH ($F_{[1,230]} = 102.59$, $p < 0.0005$).

cases, there was no significant difference between individuals (all p values >0.06).

As well as being wetter than 2010, soil temperatures were also less variable during the 2012 study period, and we found that ACTIVITY correlated significantly and positively with RH ($F_{[1,230]} = 102.59$, $p < 0.0005$) (Fig. 3.3b), WATER ($F[_{1,230]} = 71.52$, $p < 0.0005$), and RAIN ($F_{[1,230]} = 13.37$, $p < 0.0005$). In addition, we found a negative correlation between ACTIVITY and 10cmTEMP, and 30cmTEMP ($F_{[1,230]} = 22.21$, $p < 0.0005$; $F_{[1,230]} = 62.26$, $p < 0.0005$ respectively), but no correlation between mean ACTIVITY and TEMP (Fig. 3.4b; $F_{[1,230]} = 2.46$, $p = 0.12$). Again, in all cases, there was no significant difference between individuals (all p values >0.062).

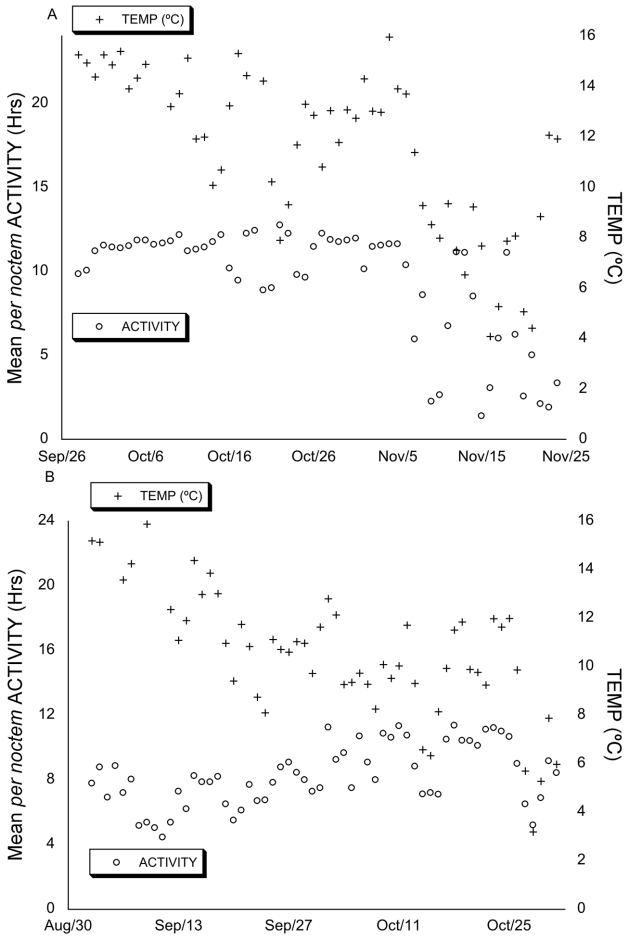

Figure 3.4: Mean *per noctem* ACTIVITY and TEMP over the study periods. Mean *per noctem* ACTIVITY and daily air temperature (TEMP) over the course of the study periods in 2010 (A) and 2012 (B). In 2010 ACTIVITY correlated significantly and postively with TEMP ($F_{[1,216]} = 86.49$, $p < 0.0005$), where in 2012, there was no correlation between ACTIVITY and TEMP ($F_{[1,230]} = 2.46$, $p = 0.12$).

Modelling Activity-climate variable interactions

Informed by our observation that the relationship between these environmental variables and ACTIVITY varied between years, we used information-theoretic models, and finer-scale hourly measures, to ascertain the strongest predictors of *per noctem* ACTIVITY. For 2010, the most supported model included the SOLAR*RH interaction, RAIN, and 30cmTEMP ($w = 0.557$), however a model that included the SOLAR*RH interaction, and the RAIN*30cmTEMP interaction also had some support ($w = 0.442$). Δi values indicated too much information loss to warrant consideration of other models. For 2012, the most supported model included the SOLAR*RH interaction, and the RAIN*10cmTEMP interaction ($w = 0.999$). Again, Δi values

indicated too much information loss (Table 3.2) to warrant consideration of other models. Thus, while our uni-variate analyses revealed that the relationship between each environmental variable and ACTIVITY varied inter-annually, this modelling showed that measures of daylight, rain/humidity, and soil temperature were the most supported predictors of ACTIVITY in both years.

Table 3.2: Climatic variables as predictors of *per noctem* ACTIVITY. Model selection using Akaike's information criterion (AIC) to assess variation in hourly ACTIVITY in 2010, and 2012. The parameter β_0 provides an estimate of the model intercept of the angular transformed ACTIVITY in a linear function, with standard error in parentheses. In addition, $var_{\text{INDIVIDUAL}}$, an estimate of the variation between individuals for each climatic prediction model, and parameter estimates for each model are also presented; as all models included only one measure of temperature, $\beta_{\text{Temperature}}$ refers to the parameter used (i.e., TEMP, 10cmTEMP, 30cmTEMP). Akaike differences (Δi), and weight ($w\text{AIC}i$) relative to the best model are also provided. For clarity, only the top 10 models in each year are listed, including the intercept.

2010									
Model	ΔAIC_i	w_{AIC_i}	β_0	$var_{\text{INDIVIDUAL}}$	$\beta_{\text{SOLAR*RH}}$	β_{SOLAR}	β_{RH}	$\beta_{\text{Temperature}}$	β_{RAIN}
SOLAR*RH+RAIN+30cmTEMP a	0	0.557	-46.78 (3.94)	0.14	-0.002 (<0.001)	0.070 (0.01)	0.24 (0.03)	4.39 (0.18)	-6.12 (0.88)
SOLAR*RH+RAIN*30cmTEMP	0.46	0.442	-46.25 (3.97)	0.63	-0.002 (<0.001)	0.071 (0.01)	0.24 (0.03)	4.35 (0.18)	-13.44 (6.84)
SOLAR*RH+30cmTEMP	47.18	<0.001	-43.91 (3.94)	0.13	-0.002 (<0.001)	0.065 (0.01)	0.19 (0.03)	4.41 (0.18)	-
SOLAR*RH+RAIN*10cmTEMP	124.32	<0.001	-22.82 (3.56)	0.63	-0.002 (<0.001)	0.069 (0.01)	0.28 (0.03)	2.60 (0.12)	-7.19 (0.90)
SOLAR*RH+RAIN+10cmTEMP	126.75	<0.001	-23.36 (3.55)	0.14	-0.002 (<0.001)	0.065 (0.01)	0.26 (0.06)	2.58 (0.19)	-7.11 (1.55)
SOLAR*RH+10cmTEMP	190.68	<0.001	-19.14 (3.53)	0.14	-0.002 (<0.001)	0.062 (0.01)	0.23 (0.03)	2.55 (0.19)	-
SOLAR*30cmTEMP	227.83	<0.001	- 42.87 (3.01)	0.71	-	0.058 (0.02)	-	5.46 (0.21)	-
SOLAR+RAIN+30cmTEMP	254.46	<0.001	-28.59 (2.59)	0.13	-0.002 (<0.001)	-0.099 (0.002)	-	4.49 (0.18)	-5.39 (0.89)
SOLAR+RH*30cmTEMP	272.53	<0.001	62.69 (18.00)	0.24	-	-0.102 (0.002)	-1.09 (0.21)	-1.26 (1.23)	-
Intercept	2710	<0.001	24.28 (0.38)	-	-	-	-	-	-
2012									
Model	ΔAIC_i	w_{AIC_i}	β_0	$var_{\text{INDIVIDUAL}}$	$\beta_{\text{SOLAR*RH}}$	β_{SOLAR}	β_{RH}	$\beta_{\text{Temperature}}$	β_{RAIN}
SOLAR*RH+RAIN*10cmTEMP a	0	0.999	-9.74 (3.84)	0.23	-0.002 (<0.001)	0.08 (0.01)	0.29 (0.03)	0.98 (0.13)	48.89 (5.76)
SOLAR*RH+RAIN*30cmTEMP	17.1	<0.001	-5.01 (4.22)	0.23	-0.002 (<0.001)	0.08 (0.01)	0.26 (0.03)	0.77 (0.17)	64.46 (6.91)
SOLAR*RH+TEMP*WATER	58.24	<0.001	19.90 (8.69)	0.23	-0.002 (<0.001)	0.07 (0.01)	0.25 (0.03)	-1.75 (0.70)	-
SOLAR*RH+RAIN+10cmTEMP	67.89	<0.001	-7.45 (3.86)	0.23	-0.002 (<0.001)	0.08 (0.01)	0.28 (0.03)	0.83 (0.13)	0.96 (0.58)
SOLAR*RH+RAIN*WATER	68.21	<0.001	8.19 (3.48)	0.22	-0.002 (<0.001)	0.08 (0.01)	0.23 (0.03)	-	-19.51 (3.81)
SOLAR*RH+10cmTEMP	69.38	<0.001	-8.00 (3.84)	0.23	-0.002 (<0.001)	0.08 (0.01)	0.29 (0.03)	0.82 (0.13)	-
SOLAR*RH+TEMP+WATER	70.67	<0.001	-6.33 (6.93)	0.23	-0.002 (<0.001)	0.07 (0.01)	0.27 (0.03)	0.59 (0.10)	-
SOLAR*RH+TEMP*RAIN	78.74	<0.001	-1.69 (3.49)	0.23	-0.002 (<0.001)	0.07 (0.01)	0.28 (0.03)	0.54 (0.10)	-
SOLAR*RH+TEMP	78.89	<0.001	-2.25 (3.46)	0.23	-0.002 (<0.001)	0.07 (0.01)	0.28 (0.03)	0.55 (0.09)	-
Intercept	1918	<0.001	20.38 (0.36)	-	-	-	-	-	-

3.4.3 Individual differences in badgers activity regimes

Within this climatic framework, in both years ACTIVITY also differed significantly between individuals (ANOVA: $F_{[3,5280]} = 4.87$, $p < 0.005$; $F_{[3,5496]} = 3.38$, $p = 0.017$ respectively). We therefore compared BCI, as a proxy of nutritional state, against individual activity regimes, as well as the population mean (PM) values for BCI $\pm$ the standard deviation (SD).

In 2010, badgers with higher BCI, exhibited less *per noctem* activity than badgers with lower BCI. When first captured in September, only one badger (N30) had a significantly poorer BCI than the PM. This individual also exhibited the longest

mean ACTIVITY duration *per noctem* compared to all other badgers tracked that year, being active on average 30 min longer than conspecifics; this greater activity was statistically significant when compared to badgers N31 and N34 (Tukey *post-hoc*: $p = 0.003$; $p = 0.020$ respectively). N31 and N34 had BCIs significantly higher than the PM. N33 was, on ave5age, also active for 30 min longer *per noctem* than N34, however this was not statistically significant (ANOVA: $F_{[1,2789]} = 2.80$, p = 0.09). When recaptured in November, N33 had a lower BCI than N34, and was within the PM, while N34's BCI had increased, and was still well above the PM (Fig. 3.5a).

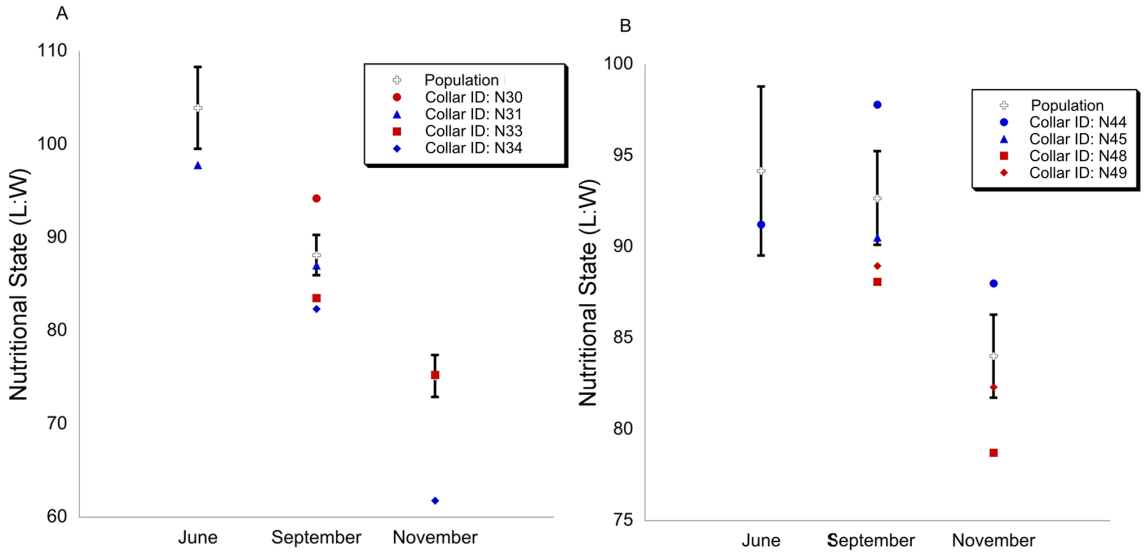

Figure 3.5: Variation in individual nutritional states from the population. Individual measures of nutritional state (L:W) in comparison to the population mean (PM) ± the standard deviation (SD) in June, September, and November in 2010 (A) and 2012 (B). Red points indicate badgers with comparatively long ACTIVITY, where blue points indicate badgers with comparatively short ACTIVITY.

In contrast in 2012, badgers with the longest per noctem activity exhibited higher BCIs when recaptured in November. BCI for N48 and N49 both exceeded the PM when collared in September. When recaptured in November, only N48 remained above the PM, and had been more active (on average 20 minutes longer per noctem) than N49, for which BCI had fallen to within the PM. Badger N44 had a lower BCI than both N48 and N49, and was below the PM in both September and November. On a per noctem basis, N44 was, on average, active for 40 min less than N48 and 20 min less than N49. Badger N45 was the least active over the course of the study period, and was within the PM when collared in September, however it was not

recaptured in November, and so no conclusions can be drawn for that individual concerning autumnal changes in BCI (Fig. 3.5b).

3.5 Discussion

Badgers are particularly sensitive to climatic conditions (Johnson et al., 2002*a*; Macdonald and Newman, 2002; Nouvellet et al., 2013) and, in this study population, autumnal conditions have been found to present a critical period for all aspects of badger population dynamics (Macdonald et al., 2010), testing the ability of badgers to balance energy budgets. Applying fine-scaled measures of activity allowed us to determine with high resolution that individual badger activity regimes varied in response to proximate weather, and with respect to body-condition. These clear inter-annual differences in the way individuals responded to varying climatic conditions evidence that biological responses, phenology and cyclicities in annual physiological and behavioural regimes should not be assumed to follow the same course each year.

Although there are various factors that can influence badger activity (for example Goransson (1983) found that, in autumn, badgers spent over 2–5 h daily digging and collecting material for bedding), our modelling indicates that interactions between solar radiation and humidity, rainfall, and soil temperatures were significant drivers of badger *per noctem* autumnal activity. In relation to Nouvellet et al's (2013) observation that survival rates decline outside of the typical annual range of daily predicted temperature norms in this population, we found that badgers were significantly more active in the drier year (2010) than a wetter one (2012).

Furthermore, we identified the generality for those badgers attaining the highest BMI to also be the most active individuals in 2012; the wetter of the two years. This implies that whatever specific activities contributed to their nightly regime, foraging must have being among these, and returned net-positive energetic gains. In 2010, with drier conditions, we observed a more subtle response: 'thinner' badgers (BCI $<$ PM) were more active than 'fatter' badgers (BCI $>$ PM).

Given that badgers in this region (Kruuk and Parish, 1981; Hofer, 1988; Kruuk, 1989; da Silva et al., 1993; Muldowney et al., 2003), as well as in others (e.g., Goszczyński et al., 2000; Kowalczyk et al., 2003), favour earthworm prey (see above), and given that earthworms surface and become most available to predators under

mild, moist microclimatic conditions (Macdonald, 1983*a*; Johnson et al., 2001; Kowalczyk et al., 2003), this syllogism leads us to strong inference that activity relates in major part to foraging success. Badgers with higher BCI prove freer to obviate the risk of net-negative energy returns under less optimal conditions by reducing their nightly activity levels.

Our tri-axial accelerometry results resonate with other studies that report increased badger foraging-related activity under sub-optimal climatic conditions (e.g., in Spain – Revilla and Palomares, 2002, Poland –Kowalczyk et al., 2003, and Switzerland – Do Linh San et al., 2007). Under conditions that limit earthworm availability (i.e., below 2°C: Macdonald, 1983*a*; Holmstrup and Zachariassen, 1996; Kowalczyk et al., 2003; Nuutinen and Butt, 2009), Kowalczyk et al. (2003) report that badgers attempt to compensate by devoting over 2.5 hrs more to foraging. In addition, maintaining body-temperature is more energetically expensive when active in cold, wet conditions (Webb and King, 1984; Kimmel et al., 1991; Macdonald et al., 2010; Nouvellet et al., 2013). This defines a suite of optimal weather conditions that can influence badger foraging success (Kruuk and Parish, 1985), ability to improve/maintain body condition (Macdonald and Newman, 2002) and thus ultimately survival probability (Macdonald et al., 2010; Nouvellet et al., 2013).

Based on the inter-individual differences in activity regimes we observed, we emphasise that a 'one size fits all' approach cannot be applied to ecological responses. State-dependent risk-taking is well documented across a diversity of taxa (Lima, 1998), where changes in behaviour to maintain positive energy budgets have been linked to climate variability (e.g., caribou, *Rangifer tarandus*, Lenart et al., 2002; badgers, Macdonald et al., 2010; Eurasian beavers, *Castor fiber*, Campbell et al., 2013). According to Clark (1994), individuals with greater reproductive value – a function of body condition in badgers (Woodroffe, 1995; Macdonald and Newman, 2002), should increase risk aversion in comparison to individuals with less reproductive value, in order not to jeopardise survival and future reproduction. Conversely, some individuals will take greater risks to achieve future fitness returns than individuals with greater reproductive value (Roff 2002). We infer that predictable conditions seem to be important for optimal survival dynamics, allowing individual badgers to prospect risk most effectively (McDermott et al., 2008) and optimise their annual routines (Feró et al., 2008).

In conclusion, these accelerometry data further advance understanding of badger-climate interactions, with detail allowing us to begin to dissect the causal mechanisms involved. This level of resolution is essential – beyond identifying indicative trend relationships – in order to identify the ecological consequences of weather patterns (or indeed other influential factors in other systems) and understand individual-specific adaptive responses, in turn better informing ability to devise conservation policy (Newman and Macdonald, 2013).

3.6 Appendix to Chapter 3: Climate and the individual: Inter-Annual Variation in the Autumnal Activity of the European Badger (*Meles meles*)

Note: The version of the Appendix to Chapter 3 presented in this thesis represents an amendment to the version published in the journal PLoS One (2014; 9, e83156). Here, ODBA values have been scaled to g.

Triaxial accelerometry provides a wealth of data about fine scale motion and can be used to infer behaviour and energetics. In this work we propose a method to determine how active an animal is, on a normalized scale with 0 (0%) corresponding to inactive and 1 (100%) corresponding to continuous activity. This method is scale-invariant and hence is useful to contrast the ratio of active to inactive time in animals.

3.6.1 Approach

1. Acceleration is sampled at 8 Hz on 3 axes simultaneously to provide a fine-scale record of animal behaviour.

2. The vector measurements are transformed to observed dynamic body acceleration (ODBA; in g) as per the method in Wilson et al. (2006), here using a window length of 2 seconds to obtain the direction of g, followed by taking the L1 (absolute value) norm of the dynamic component.

3. ODBA is averaged over a 10 minute bin to give a metric of overall activity. In this way, brief spikes in acceleration, which are due to knocks and bumps, are filtered out, leaving the trend itself.

4. The mean ODBA is thresholded to determine if the animal was active (1) or inactive (0) during the window. Formally:

$$a_k = \text{sgn}(\text{ODBA}_k - T) \tag{3.1}$$

where a_k [0:1] is the activity in the k^{th} window, sgn() is the signum function, ODBA_k is the time averaged ODBA value and T is a threshold value.

T should be chosen such that sampling noise and low-level motion from respiration is treated as being inactive and only dynamic motion that would contribute to energetic load above a baseline being regarding as being active. The value of T that best partitions the set into active and inactive subsets is determined using sensitivity analysis, a technique commonly used in robust control theory. Formally, this can be regarded as finding the value T that minimizes the gradient of the sensitivity function. Intuitively, if the threshold is too low, then the animal will be reported as being active 100% of the time. Conversely is the threshold is too high, then the animal will be reported as being active 0% of the time. The objective is to find an operating point where large changes in the threshold value lead to small changes in the overall duty cycle (ratio of active to inactive; e.g., see Fig 3.6).

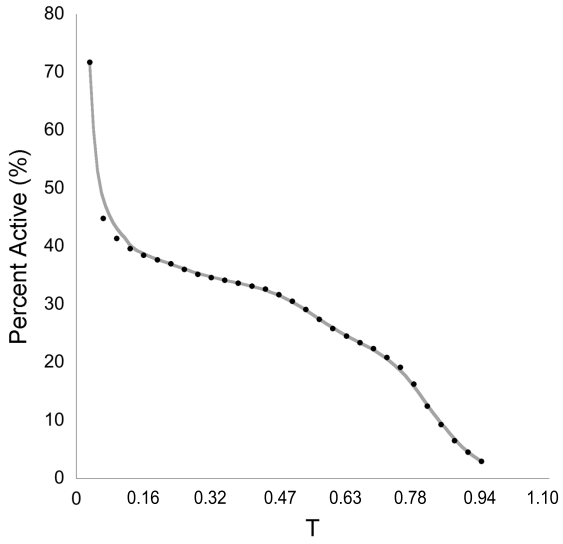

Figure 3.6: Perceived activity as a function of the threshold value. Percent active as a function of the threshold ODBA value (T) for badger N44 over the course of the study period. The threshold value chosen for this individual was 0.313.

Chapter 4

Avoiding verisimilitude when modelling ecological responses to climate change: The influence of weather conditions on trapping efficiency in European badgers (*Meles meles*)

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4.1 Abstract

The signal for climate change effects can be abstruse; consequently, interpretations of evidence must avoid verisimilitude, or else misattribution of causality could compromise policy decisions. Examining climatic effects on wild animal population dynamics requires ability to trap, observe or photograph and to recapture study individuals consistently. In this regard, we use 19 years of data (1994–2012), detailing the life histories on 1179 individual European badgers over 3288 (re-) trapping events, to test whether trapping efficiency was associated with season, weather variables (both contemporaneous and time lagged), body-condition index (BCI) and trapping efficiency (TE). PCA factor loadings demonstrated that TE was affected significantly by temperature and precipitation, as well as time lags in these variables. From multi-model inference, BCI was the principal driver of TE, where badgers in good condition were less likely to be trapped. Our analyses exposed that this was enacted mechanistically via weather variables driving BCI, affecting TE. Notably, the very conditions that militated for poor trapping success have been associated with actual survival and population abundance benefits in badgers. Using these findings to parameterize simulations, projecting best-/worst-case scenario weather conditions and BCI resulted in 8.6% ± 4.9 SD difference in seasonal TE, leading to a potential 55.0% population abundance under-estimation under the worst-case scenario; 38.6% over-estimation under the best case. Interestingly, simulations revealed that while any single trapping session might prove misrepresentative of the true population abundance, due to weather effects, prolonging capture–mark–recapture studies under sub-optimal conditions decreased the accuracy of population estimates significantly. We also use these projection scenarios to explore how weather could impact government-led trapping of badgers in the UK, in relation to TB management. We conclude that population monitoring must be calibrated against the likelihood that weather conditions could be altering trap success directly, and therefore biasing model design.

4.2 Introduction

The ability to recognise verisimilitude – untruths appearing as being true or real – is fundamental to the philosophy and practice of science (Niiniluoto, 2014). There is explicit need to explore the falsifiability of theories and correlations (Popper, 1963; Stamos, 1996; Popper, 2014), and to avoid inductive bias (Hume, 1748; Howson, 2000), in order to establish the apodicticity (logical certainty) of propositions in the Aristotelean sense (Frede, 1996). Explanations that temporarily appear to fit facts well, even from empirical testing, only later to be superseded, have played an important role in the history and ontology of scientific enquiry. From the theory of 'Phlogiston' (Bennett, 1988) to 'Lamarkianism' (Koonin and Wolf, 2009), Popper's application of the 'survival of the most fit' explanation (Popper, 1972) alerts us to the need continuously to question sources of bias, or logical fallacy (Jungwirth, 1987), and to apply *modus tollens* (L. 'the way that denies by denying') to deny the consequent, and *reductio ad absurdum* (L. 'reduction to absurdity') to infer contradiction (Byrne and Johnson-Laird, 2009).

Climate ecology is particularly susceptible to implying correlation without causality – '*cum hoc ergo propter hoc*'. As Bobby Henderson's much promulgated internet spoof (Comfort, 2006) illustrates, global warming, earthquakes, hurricanes, and other natural disasters can all be attributed as a direct effect of the shrinking numbers of Pirates since the 1800s. Spurious correlations between climate change variables and animal ecology population dynamics are especially vulnerable to misinterpretation. Aside from failure to fully acknowledge other environmental covariates (Newman and Macdonald, 2013), Kellner and Swihart (2014) report that only 23% of 537 ecological articles they reviewed accounted for imperfect detection. Crucially, there is a risk that weather conditions could alter ability to detect the target species directly. This has the potential to corrupt inference from climate-ecology studies, resulting in the misattribution of causality and thus compromised policy decisions. Climate ecologists should, therefore, remain alert for counterfactual explanations (Weber, 1999).

The ability to trap, observe, or photograph and to recapture study individuals consistently and reliably is central to accurate population monitoring (Krebs and Boonstra, 1984; Gibbs et al., 1998; Efford, 2004; Royle and Dorazio, 2008;

Kellner and Swihart, 2014). Ultimately, this is a function of an animal's activity regimes and denning habitats (e.g., Rowe and Moll, 1991); where detecting rodents or small carnivores utilising arboreal or subterranean refugia is fundamentally more difficult than large ungulates on open plains (MacKenzie et al., 2003). Furthermore, individuals make the decision to engage in active behaviours based on an algorithm balancing the costs of energy expenditure against their current physiological condition, in relation to prospective energetic (or fitness) returns (Norberg, 1977; Clark, 1994; Noonan et al., 2014). If the availability of target animals varies substantially between capture sessions, or if operations are scheduled during periods likely to achieve poor trapping (or observational) success, reasoning from the observed to the unobserved (*sensu* Hume, 1748) could potentially induce biases, due to inconsistent data veracity (Gerber and Parmenter, 2015). Even if differential trapping efficiency can be modelled into capture-mark-recapture (CMR) estimates or Minimum Number Alive (MNA) enumerations (Clobert, 1995; Sollmann et al., 2011, 2013; Gerber and Parmenter, 2015), it is essential to understand the basis for doing so, by establishing how controlling factors operate. In this regard, the capacity for weather (both prevailing conditions while trapping, or observing, and those preceding the deployment) to influence the activity regimes, nutritional status, and motivation of target animals is an often over-looked extrinsic component of trapping success.

European badgers (*Meles meles*) have proven highly instructive for exploring climate change effects (e.g., Macdonald and Newman, 2002; Macdonald et al., 2010; Nouvellet et al., 2013, see also Macdonald et al. in press). Across much of their range, European badgers exhibit trophic specialisation towards earthworms (*Lumbricus terrestris*) (Kruuk and Parish, 1982; Johnson et al., 2002*a*; Muldowney et al., 2003), which only surface under specific microclimatic conditions (Jiménez and Decaëns, 2000; Curry, 2004). Weather conditions, and especially resultant soil conditions, are therefore crucial for the distribution and availability of earthworms (Macdonald, 1983*b*; Kowalczyk et al., 2003), with direct affects on badger nutritional status (Macdonald and Newman, 2002; Macdonald et al., 2010). Consequently, badgers exhibit substantial variation in body-weight and -condition through the year, in relation to food supply (Macdonald and Newman, 2002) and to annual cycles of winter torpor (Kowalczyk

et al., 2003).

Our detailed long-term study of the population dynamics of a geographically discrete population of badgers in central England (Wytham Woods, Oxford; see Macdonald et al. in press) has been subject to imperfect detection (Tuyttens et al., 1999*b*), which we have quantified at 83.7% (SE = 1.32) captured *per annum* of the contemporaneous Minimum Number Alive (MNA) estimate (see Macdonald et al., 2009). Furthermore, our previous work has exposed facets of interactions with seasonal weather patterns that have stimulated us to evaluate more precisely how badgers respond to climatic conditions. For example, extrapolating the mean litter size observed among females caught in January and diagnosed with ultrasound (Woodroffe, 1995) onto the subsequent number of lactating females (Dugdale et al., 2011) does not adequately account for the actual annual cohort size. This would only be explained if those females trapped in January are not truly representative of mean litter size. Noonan et al. (2014) cast further light on the phenomenon of the changing availability of individuals with the observation that badger emergence from their underground dens (termed setts) is dictated by proximate weather conditions, reflecting the energetic effectiveness of foraging versus remaining in the sett – where badgers are capable of tolerating extended periods of living off fat reserves in a torpid state (Newman et al., 2011).

Using 19-years of data, detailing the life-histories on 1179 individuals, our aim here was to illustrate how the absence of an individual from observational or trapping records may in-and-of-itself be the product of variation (and thus trends) in weather conditions. Such an absence might be capable of skewing measures of demographic rates (natality, age-specific mortality) or population means (e.g., seasonal mean weight / body-condition, in utero litter size, parasitic infection rate, etc). Consequently, a misattribution of exactly what aspect of the species' biology is being driven by climate could lead to faulty syllogism. Furthermore, there is an important conservation issue involved here; failure to interpret the true interaction of a population with climatic drivers may well have a negative influence on intervention efficacy (Nichols and Williams, 2006; Seddon et al., 2007; Byrne et al., 2012), especially in light of climate change (Walther et al., 2002; Davis et al., 2005; Newman and Macdonald, 2013). Objectively, we test for any interaction between weather variables, season and the

trappability of badgers, also examining interactions with time-lagged weather, to establish if swings between 'good' and 'bad' foraging conditions exacerbate trapping error. We then explore interactions with badger body-condition, as a proxy for nutritional state, positing that this might influence whether badgers risk foraging or not under different weather conditions (see Noonan et al., 2014). Finally, we use these findings to parameterise simulations, illustrating how any single trapping session, or trapping year, might prove misrepresentative of the true population abundance.

4.3 Methods

4.3.1 Study Site & Trapping protocol

This study used long-term population data collected at Wytham Woods, a 424 ha mixed semi-natural woodland site, located approximately 5km north-west of Oxford, UK (GPS reference: 51°46'26"N; 1°19'19"W); mean annual temperature 10.1°C; mean annual precipitation 644.8 mm (for details see Savill et al., 2010). The resident badger population is discrete geographically, due to landscape features, with a stable range (Macdonald et al., 2009) and <3 % annual immigration / emigration (Macdonald and Newman, 2002). The fact that the parentage of individuals within this population are well accounted for by genetic pedigree further corroborates that this is essentially a closed population (Dugdale et al., 2008; Annavi et al., 2014).

As part of a broad research programme, this population has been trapped and marked systematically since 1987 (for full details see Macdonald et al. in press). Trapping sessions were conducted three to four times per annum, over two weeks in May- June (Spring), August-September (Summer) and November (Autumn), with trapping in January (Winter) in focal years. For reasons of logistics, the site was divided into 4 even-sized quadrants; each including 7-8 badger social groups. Complete trapping sessions ran over 12 days, with three days in each quadrant. Up to 30 badgers were still caught per day (mean: 9.5 ± 5.3 SD), each requiring 10-20 minutes to process. Badgers were trapped in steel mesh cage traps (850 x 370 x 380 mm) sited at all of the active setts (including outlying holes) associated with each social-group and baited with ca. 150g peanuts

(but without pre-baiting). Traps were set between 15:00 and 18:00; more traps were set at each sett than the anticipated number of badgers (inferred from previous trapping records), providing saturation trapping.

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 (0.2 mL/kg body weight; McLaren et al., 2005) to facilitate handling. Upon first capture, all badgers were tattooed with a unique number on the left inguinal region, for permanent individual identification. Sex, age-class (cub or adult) and Body Condition Index (BCI) (subcutaneous fat score scaled 1 (thin) – 5 (fat); after Speedy, 1980) were recorded. Badgers were then released at their capture site after a 3-hour recovery period.

4.3.2 Demographic Data

We restricted our analyses to data collected between 1994-2012, over which period the trapping regime was consistent. Previous studies on this population found mean annual trap success of ca. 83.7% (S.E. = 1.32%; Macdonald et al., 2009), each extant badger tending to be caught within a 525 day period (Dugdale et al., 2007). We therefore excluded the two most recent years (2013 and 2014) from analyses, because abundance estimates in these years would have yielded under-estimates (Macdonald et al., 2009). Because it was essential to pair annual population size with specific individual biometric data (notably BCI), it was not feasible to use inferential statistical techniques for generating capture-mark-recapture estimates (see Macdonald et al., 2009) and we therefore used minimum number alive (MNA) enumeration techniques to calculate robustly the proportion of badgers that were trapped. Also, capture-mark recapture models consistently over-estimate badger numbers in high-density populations where trapping efficiency is high (Rogers et al., 1997; Tuyttens et al., 1999*a*). We excluded cubs from our analyses because their trappability varies with their formative experience (Tuyttens et al., 1999*b*) and they are subject to high rates of juvenile mortality (Macdonald et al., 2009), in turn linked to prevailing weather conditions (Macdonald et al., 2010; Nouvellet et al., 2013).

To explore interactions with badger nutritional state and trappability (*sensu* Noonan et al., 2014), we calculated the mean population BCI corresponding with each trapping session as a proxy for contemporaneous nutritional state. In addition, we calculated the female to male ratio (F:M) to test for any sex-related differences in trappability.

4.3.3 Weather variables

We began with an exploration of minimum and maximum air temperature (°C), soil temperature (°C) at 10cm and 30cm below ground, and precipitation (mm), using data obtained from the Oxford Radcliffe Meteorological station (School of Geography, University of Oxford) 6km from Wytham Woods. These temperature variables proved to be inter-correlated (Pearson's r >0.9), and so we restricted our analyses to daily-maximum air temperature (TEMP), supplemented with precipitation (RAIN). We calculated both contemporary mean values for these weather variables during the two-week trapping sessions and also the effects of preceding weather over two-week time periods stepped at two, four, six, eight, ten, and twelve weeks prior to the trapping session. In addition, we included year and season as categorical variables.

4.3.4 Response variable

The high rate (ca. 20%) of short-term, inter-group movement in this population, as evidenced from long-term trapping data (Macdonald et al., 2008) and recent radio-tracking studies (Dyo et al., 2010; Noonan et al., 2015*b*), prevented us from computing, with certainty, what proportion of the population was actually present and available in each quadrant of the woods being trapped on any given trap-night. Accordingly, we defined Trapping Efficiency (TE) as the proportion of adult badgers trapped during each trapping session, relative to the MNA enumeration for that year. To satisfy assumptions of normality, TE values were subject to angular transformations according to:

$$\sin^{-1}\sqrt{\mathrm{TE}} \tag{4.1}$$

4.3.5 Descriptive analyses

We undertook an initial analysis of these data, using analyses of variance (ANOVA) and covariance (ANCOVA), as well as Pearson's correlations ($\alpha = 0.05$), to describe the relationships between TE and our predictive variables. To summarise the variance in TE contingent on weather and BCI we ran a Principal Component Analysis (PCA), performed over the individual trapping sessions ($n = 68$). Here, year and season were included as supplementary qualitative factors, and TE as a supplementary quantitative factor, without using any rotation; cases with missing values were excluded. We then employed a one-way ANOVA, using TE as a factor, to test for variation in these PCA scores following Johnson et al. (2000).

4.3.6 Multi-model inference

From a global model predicting variance in TE that included the variables year, season, BCI, along with weather variables TEMP and RAIN (both contemporaneous and time-lagged), we specified a subset of candidate models comprised of all possible combinations of fixed effects. We then used Akaike's information criterion (AIC), to rank these candidates according to their statistical support (Burnham et al., 2011), additionally calculating the delta AIC (Δ_{i}), in relation to the highest-ranking model, and the Akaike weight (w) for each model using the R package *MuMIn* (v. 1.12.1; Barton, 2012). Following Anderson (2008), rather than using Δ_{i} cut-off values, we applied Akaike weight based averaging over all candidate models. We derived estimates of the coefficients (θ) associated with all candidate models, and their 95% confidence intervals (CI). Mean θ values were then calculated by averaging their values over all candidate models that included the θ of interest, weighted by w. We then calculated the 'Relative Influence' (RI) of each variable as the summation of w across all models that included the variable of interest (Burnham and Anderson, 2002). The variable with the largest RI was inferred to be the most influential predictor; the variable with the lowest RI, the least.

4.3.7 Abundance simulations

This modelling framework enabled us to parameterise simulations of the number of badgers that would have been captured under a series of weather scenarios for

each season. We constructed a global model predicting variance in TE, which included the principal predictors of TE from our multi-model inference (Season; BCI; RAIN 6-8 weeks prior; TEMP 4-6 weeks prior; and TEMP 8-10 weeks prior: see below). We then used the 'predict' function in the R environment (R Core Team, 2014) to estimate the TE of each trapping session, had these been carried out under the weather conditions associated with our best, and worst seasonal TE. Applying these estimated TEs onto our long-term MNA estimates thus yielded (re-)capture projections for each trapping session. These capture projections were calculated using an estimate of implied population abundance, following Huggins (1989):

$$\widehat{N} = \frac{M_{t+1}}{1 - (1 - p_1) \cdots - (1 - p_n)} \tag{4.2}$$

Where; $\widehat{N}$ represents the estimated population size; M_{t+1} the total number of unique animals marked; and p_n the capture probability during each trapping session n.

By manipulating the values of M_{t+1}, and p_n we projected $\widehat{N}$ under best- and worst-case weather scenarios persisting for either one ($n = 4$ trappings), or two ($n = 8$) years. We then compared these estimates to our long-term MNA estimates, demonstrating how any single trapping session, subject to a weather extreme, might prove misrepresentative of the actual population size.

All statistical analyses were conducted in the R environment (version 3.0.3; R Core Team, 2014). Although statistical analyses were performed on transformed data, we depict original data in graphical representations.

4.4 Results

3288 adult badger (re-)trapping events were achieved between 1994 - 2012, with a mean annual TE of 81.3% ± 6.1 SD, compared with same year MNA, which differed significantly between years (ANOVA: $F_{[18,46]} = 3.53$, $P < 0.001$). Mean TE per session (39.9% ± 13.3 SD) also differed significantly between seasons (ANOVA: $F_{[3,46]} = 37.45$, $P < 0.001$); summer trapping sessions yielded the

greatest TE (50.5% ± 9.3 SD) and winter sessions the lowest (20.89% ± 6.6 SD) (Fig. 4.1).

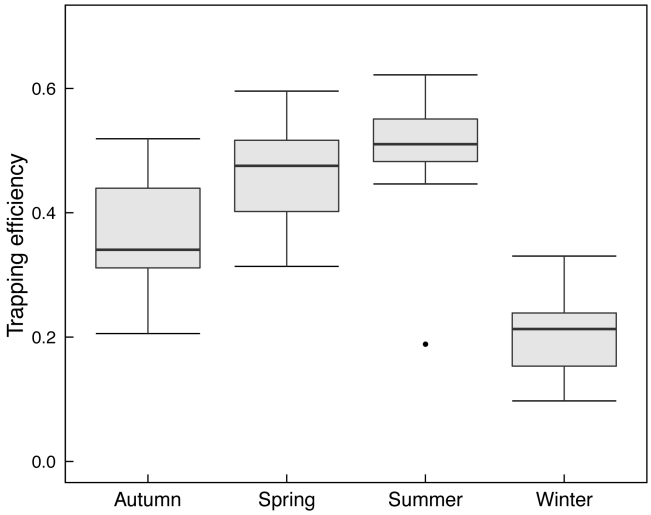

Figure 4.1: Box plots showing the proportion of adult badgers trapped in each season (trapping efficiency) in relation to contemporaneous Minimum Number Alive (MNA) estimates.

Notably, although the mean sex ratio of captured badgers was, overall, near parity (mean F:M: 1.13 ± 0.31 SD), this differed significantly between years (ANOVA: $F_{[18,46]} = 4.05$, P <0.001; Fig. 4.2a), ranging from 0.73 to 1.59 and between seasons (ANOVA: $F_{[3,46]} = 20.63$, P <0.001; Fig. 4.2b). When *ad hoc* winter trapping sessions, during which females proved less trappable (mean F:M: 0.77 ± 0.31 SD), were excluded, the seasonal effect became non-significant (ANOVA: $F_{[2,35]} = 2.51$, P = 0.10).

4.4.1 The effect of weather variation on trapping efficiency

When controlling for season, weather variables correlated significantly with TE (Table 4.1). Crucially, the relationship between TE and weather was not consistent between seasons. For example, RAIN during the spring trapping session had a significant negative effect, but a positive, albeit non-significant effect during summer trappings. Similarly, RAIN 6-10 weeks prior to the trapping in autumn had a significant negative effect, with no contemporaneous RAIN effect.

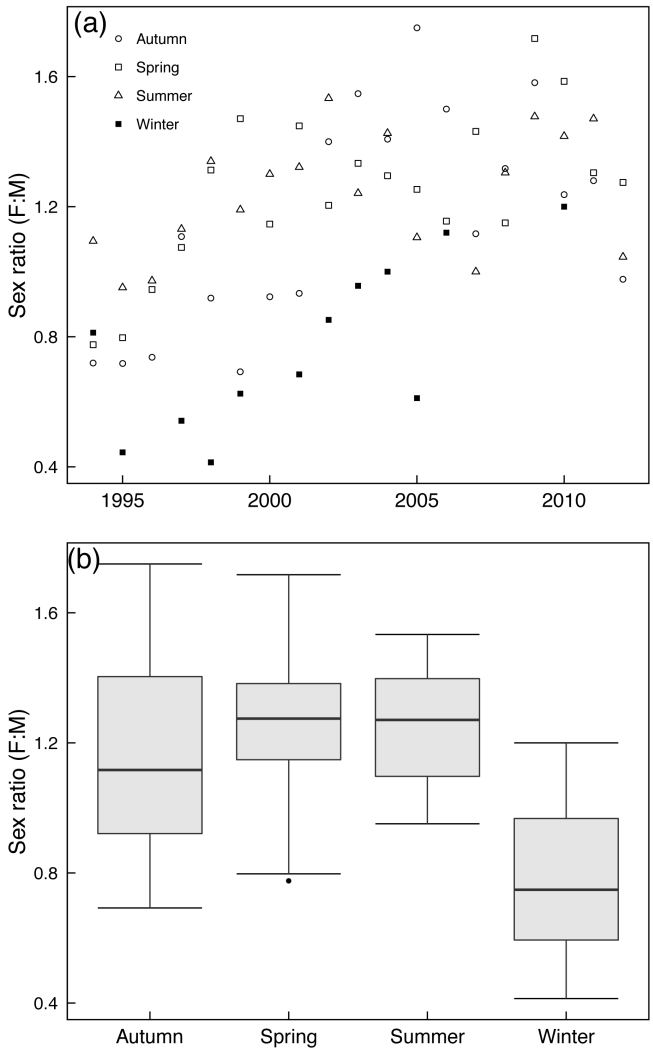

Figure 4.2: The sex ratio (F:M) of captured badgers in (a) individual trapping sessions over the 19-year study period and (b) box plots showing seasonal trends in the sex ratio.

In the PCA, only the first four of 15 components had Eigenvalues >1, and explained a cumulative 68.5% of the variance (Table 4.2).

Projecting trapping sessions into the reduced dimension space defined by PC 1 and PC 2, revealed that each season grouped into a unique cluster; that is, there were consistent seasonal influences across years, with minimal overlap between these (Fig 4.3). From the factor loadings TE was affected significantly by the differential effects of TEMP and RAIN (PC 1: ANOVA: $F_{[1,66]} = 55.20$, P <0.001) and by time lags in these variables (PC 2: ANOVA: $F_{[1,66]} = 10.20$, P <0.005). None of the other components had a significant effect on TE (all P

values >0.05).

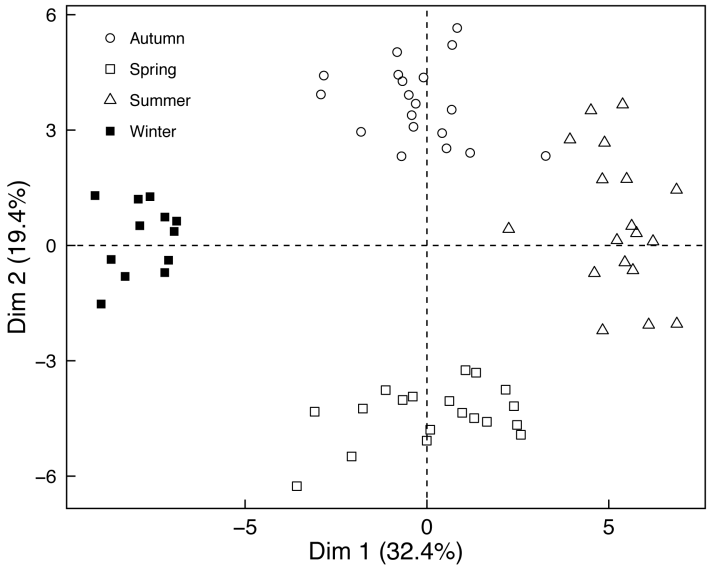

Figure 4.3: Factor map of all trapping sessions ($n = 68$) projected in a reduced dimension space, defined by component 1 (x-axis) and component 2 (y-axis) of our principal component analysis. Percentages represent the amount of variation in these data that was accounted for by the respective components.

4.4.2 Body-condition and trapping efficiency

In accord with previous research, BCI exhibited significant seasonal variation ($F_{[3,64]} = 78.68$, P <0.001), ranging from a mean seasonal minimum of 2.19 ± 0.21 SD in spring trappings to a maximum of 3.52 ± 0.33 SD in autumn. BCI correlated significantly and negatively with TE (ANCOVA: $F_{[1,63]} = 88.0$, P <0.001), with a significant seasonal effect (ANCOVA: $F_{[3,63]} = 16.40$, P <0.001) (Fig. 4.4).

4.4.3 Principal predictors of TE

Multi-model inference (Table S1) revealed that BCI was the principal driver of TE, where the most supported model predictive of TE included mean BCI, season, and time-lagged measures of temperature and precipitation ($w = 0.004$). A similar construct resulted from model averaging (Table 4.3), which revealed that although TE per season exhibited significant relationships with weather variables, the effect was actually enacted through associated changes in BCI; that

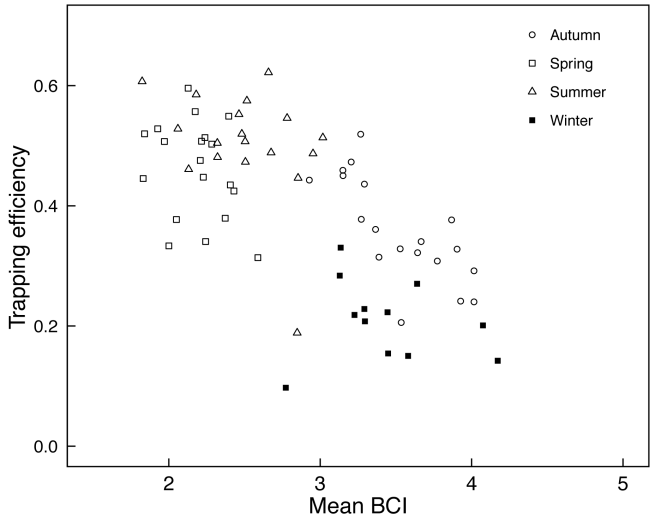

Figure 4.4: Scatter plot representing the relationship between the proportion of adult badgers trapped within each trapping session (trapping efficiency) and the mean BCI of captured animals – a subcutaneous fat score scaled 1 (thin) - 5 (fat).

is, BCI, season, and time-lagged weather variables were the primary predictors of TE.

4.4.4 Abundance simulations

Projecting best/worst-case weather conditions and BCI for each trapping session, over time, resulted in a mean difference of 8.6% ± 4.9 SD in the seasonal TE between the two scenarios (Fig. 4.5).

Abundance estimates derived from these seasonal projections established that weather-induced variability had the potential to generate a four-fold difference in estimates, with 55.0% under-estimation, with respect to long term MNA estimates, under the worst-case scenario; 38.6% over-estimation under the best-case (Fig. 4.6). Interestingly, the results of our worst-case scenarios suggest that prolonging capture-mark-recapture studies under sub-optimal conditions may actually drive population estimates significantly (and falsely) lower (t-test: $t_{51} = 6.21$, P <0.001), by disproportionately influencing the denominator of associated formulae. When estimating the population abundance under differing timelines, a two-year study duration simulation could only achieve par with our long-term MNA estimates (t-test: t_{51} = -0.98, P = 0.33) if carried out under the best trapping conditions scenario.

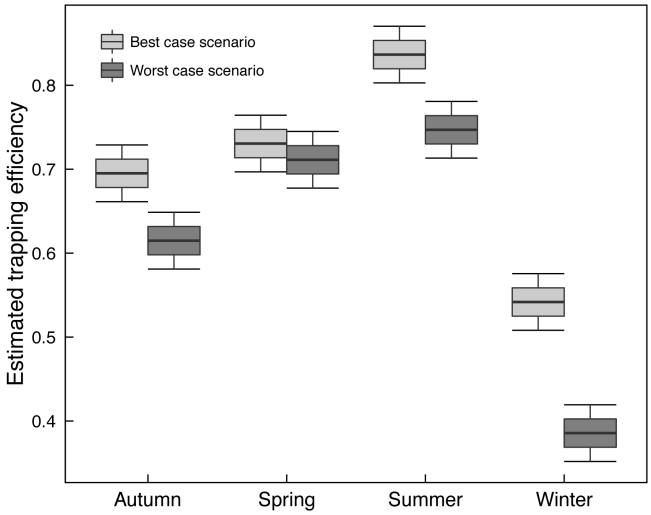

Figure 4.5: Box plots depicting the estimated trapping efficiency (i.e., the proportion of the adult badger population trapped during each trapping session) under the best- and worst case weather scenarios for each season, projected over the 19-year study period.

4.5 Discussion

The signal for climate change effects can be abstruse (Ladle et al., 2005), either because of interactive ecological covariates (Walther et al., 2002) or, in terms of the popular understanding of consequences, due to media sensationalism (Weingart et al., 2000) combined with disasters exacerbated by poor, or unsustainable civic planning (Smit and Wandel, 2006). A corollary is that, in order to achieve and maintain credibility (Lorenzoni et al., 2007), interpretations of evidence must account for data biases comprehensively, unimpeded by biased implication. Furthermore, this approach is a fundamental prerequisite for effective ecological management in response to climate change (Hulme, 2005). When monitoring a natural population, it is thus essential to attempt to model differential trapping efficiency into abundance estimates (Clobert, 1995; Sollmann et al., 2011, 2013; Gerber and Parmenter, 2015).

In terms of simple seasonal variation in trappability, this has been established for badgers previously (Tuyttens et al., 1999*b*; Byrne et al., 2013), and related to phenological differences in activity (Kowalczyk et al., 2003). Our study elaborates on this pattern by demonstrating that even with consistent effort, there was not only intra-seasonal variation in TE between years, but also – crucially –

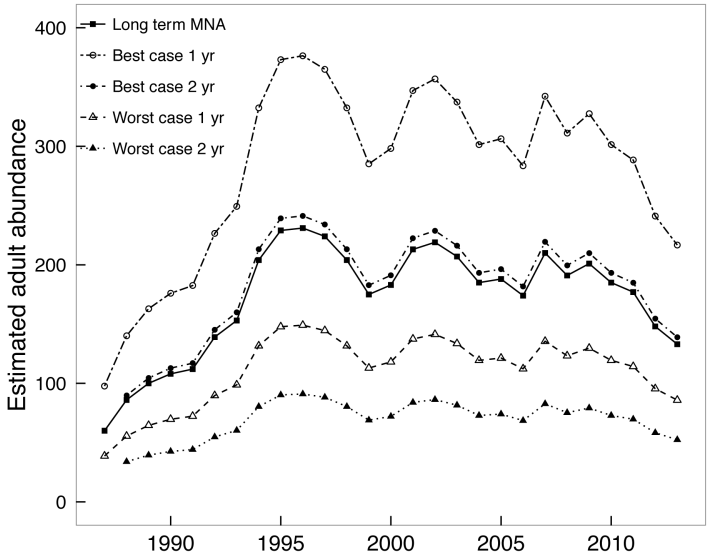

Figure 4.6: The annual abundance of adult badgers present in Wytham Woods, estimated from both long-term capture records (MNA), and the predicted number of (re-)captures based on the trapping efficiency of each trapping session under theoretical best- and worst case weather scenarios. One-year estimates (1 yr) were generated from the weather scenarios for each season projected over a full year; two-year estimates (2 yr) from the same scenarios projected two years.

this was related to proximate and time-lagged weather conditions. Furthermore, individual responses were also influenced by body-condition; in-and-of-itself a function of weather-mediated food availability for badgers (Macdonald et al., 2010; Noonan et al., 2014). Although the precept of consistent trappability is central to population estimation techniques (Efford, 1992), the majority of capture-mark-recapture studies fail to acknowledge imperfect detection (Kellner and Swihart, 2014), where surveys associating species abundance to climate tend to imply causality (reviewed in Newman and Macdonald, 2013). Biases resulting from this issue are compounded by the fact that temporal variations in trapping efficiency are only apparent retrospectively (as with this study), making short-term studies and *ad hoc* surveys particularly susceptible to inductive bias (Pocock et al., 2004). Our weather-extreme simulations highlighted this effect, demonstrating that these could induce variability in trapping efficiency generating a four-fold difference in abundance estimates, dependent on study length. Moreover, under simulation, a two-year study could only match our long-term study accuracy if conducted over two 'optimal-weather' trapping years. Undertaking a short-term trapping study under sub-optimal conditions can lead not only to considerable and significant population under-/over-estimation, but

also prolonging a capture-mark-recapture study under sub-optimal conditions may actually drive population estimates significantly lower; a particular issue if species management is the objective.

Important too is to appreciate the mechanism behind this weather effect on badger trapping efficiency. Because badgers reside in burrows, non-emergence above ground prohibits cage trapping (and notably would also prohibit camera trapping). For all animals, the decision to engage in active behaviours is based on an algorithm balancing the costs of energy expenditure against prospective energetic (or fitness) returns (MacArthur and Pianka, 1966; Norberg, 1977). Although badgers are versatile generalist omnivores, in the southern UK they have a strong dietary preference for earthworms. The sensitivity with which badger population dynamics are governed by weather conditions (e.g., Macdonald and Newman, 2002; Macdonald et al., 2010; Nouvellet et al., 2013) arises partly because microclimate affects the availability of these earthworms (Jiménez and Decaëns, 2000; Curry, 2004), which are drought and frost averse. As a consequence, the warm, dry conditions of spring and summer lead to badgers being seasonally thin – indeed often badly emaciated (Macdonald and Newman, 2002) – which has negative implications for their survival dynamics (Macdonald and Newman, 2002; Macdonald et al., 2010). Because individuals adjust activity budgets (Noonan et al., 2014) and risk taking behaviour (*sensu* Clark, 1994) against a balance of energetic costs and benefits, badgers are at their most trappable when in a famished and desperate condition – simply, bad weather = high TE. Specifically, body condition, our proxy for nutritional state, was the most influential predictor of trapping efficiency. In the autumn, mild, and humid conditions in the UK promote earthworm availability (supplemented by seasonal fruit availability); badgers are fat, more satisfied, and thus less disposed to entering traps – good weather = low TE. Winter is a special case: in the UK badgers do not hibernate, but become less active according to a seasonal regime (Noonan et al., 2014). This leads to a very restricted availability, limiting trap success to the extent that we only conduct winter trapping on an '*ad hoc*' basis to include mostly favourable conditions. Elaborating on our previous findings that cub cohort size extrapolated from ultrasound performed on females caught in January does not account for the actual annual cohort size adequately (Dugdale et al., 2011), we speculate that this is misrepresentative due to these being thinner, more desperate and trappable pregnant mothers

with sub-average embryonic litter sizes. This elucidates the complexities of climate-mediated variation in trappability, because poor conditions that lead to high TE will bias population estimates positively, while they simultaneously drive actual population size down.

In addition to the direct effects of proximate weather conditions on trapping efficiency, we also found that time-lagged weather variables were highly influential in our models. Indeed, temperature and rainfall up to two and a half months prior to a trapping session proved more influential than both proximate weather conditions and seasonal variation. This is likely because extended 'good' or 'bad' foraging conditions prior to trapping establish the badgers' predisposition toward risk-taking Noonan et al. (2014), i.e., entering a trap. Importantly, we emphasise here an essential juxtaposition: previous work detecting weather/climate influences on badger population dynamics (detailed above) did so 'despite' the influence of weather on TE.

Practical Implications

The influence of weather conditions on trappability is particularly pertinent to the recent failure of badger culling initiatives, undertaken by the UK government, to achieve culling targets during trials of methods intended to alleviate the spread of bovine tuberculosis in cattle (DEFRA, 2014*b*; IEP, 2014). Even after extension into late autumn, projected targets of 70% removal were not met in 2013, and eventually culling operations were suspended due to 'bad weather' and resultant low culling rate. In 2014, only 341 of the targeted 316-435 badgers were culled in Somerset and only 174 of the targeted 615-1091 in Gloucestershire (DEFRA, 2014*a*). This was achieved under sub-mean autumnal weather conditions in relation to TE (colder, and with rainfall exceeding our autumnal means), where we conjecture that this weather variability contrived to impair TE, yielding fewer individuals than would have been achieved under more optimal weather conditions. Plausibly, applying our coefficients, a potential string of conditions militating for higher TE (warmer and with less rainfall) would have resulted in the Somerset cull getting close to its upper quota target – though TE in Gloucestershire would still have been far from minimum quota

targets.

Few other studies have quantified the direct effect of weather on trapping efficiency of any species (but see Stokes et al., 2001; Spence-Bailey et al., 2010). Although there are a variety of intrinsic (e.g., age / sex / temperament) and extrinsic (e.g., habitat type / extent of cover / topography) factors that can influence trappability, which cannot be altered or adapted to, we demonstrate here that both prevailing and preceding weather conditions can influence seasonal TE significantly, interactive with individual body-condition. These types of weather effects will undoubtedly modify the trappability of many species, especially (but not exclusively) those utilising inaccessible refugia.

The risk of verisimilitude that climate ecologists face when interpreting data is especially challenging in the light of ever-more variable weather patterns (Hulme, 2005; Harrison et al., 2006; IPCC, 2007, 2014). Changes in the apparent distribution and abundance of species subject to short-term monitoring must be calibrated against the likelihood that weather conditions could be altering trap success directly, and therefore biasing model design. We recommend that, in-so-far as study design and practicality permit, investigators exercise *modus tollens* to differentiate genuine weather correlates from weather artifacts.

Table 4.1: Linear correlations between seasonal trapping efficiency (i.e., the proportion of the adult badger population trapped during each trapping session) and weather variables (both contemporaneous, and time-lagged). Asterisks denote statistically significant correlations.

Spring	**TEMP**		**RAIN**	
	P	r	P	r
During trapping	0.686	0.099	0.046*	-0.462
0-2 weeks prior	0.675	-0.103	0.844	-0.049
2-4 weeks prior	0.924	-0.023	0.366	0.220
4-6 weeks prior	0.396	0.213	0.496	-0.167
6-8 weeks prior	0.587	0.133	0.138	-0.353
8-10 weeks prior	0.670	0.105	0.937	0.020
10-12 weeks prior	0.251	0.277	0.457	0.182
Summer	**TEMP**		**RAIN**	
	P	r	P	r
During trapping	0.916	-0.268	0.675	0.106
0-2 weeks prior	0.193	0.321	0.576	-0.141
2-4 weeks prior	0.336	0.241	0.167	-0.340
4-6 weeks prior	0.023*	-0.532	0.803	0.063
6-8 weeks prior	0.101	-0.399	0.447	0.191
8-10 weeks prior	0.522	-0.160	0.984	-0.005
10-12 weeks prior	0.555	-0.149	0.753	0.080
Autumn	**TEMP**		**RAIN**	
	P	r	P	r
During trapping	0.696	0.096	0.929	-0.022
0-2 weeks prior	0.724	0.087	0.755	-0.077
2-4 weeks prior	0.117	-0.372	0.481	-0.172
4-6 weeks prior	0.206	-0.304	0.600	-0.129
6-8 weeks prior	0.522	0.156	0.013*	-0.554
8-10 weeks prior	0.771	0.072	0.046*	-0.462
10-12 weeks prior	0.156	-0.338	0.618	-0.122
Winter	**TEMP**		**RAIN**	
	P	r	P	r
During trapping	0.650	0.146	0.418	0.258
0-2 weeks prior	0.794	-0.085	0.344	-0.300
2-4 weeks prior	0.819	0.074	0.270	-0.346
4-6 weeks prior	0.046*	-0.584	0.005*	-0.752
6-8 weeks prior	0.082	-0.522	0.220	-0.382
8-10 weeks prior	0.250	0.360	0.330	-0.306
10-12 weeks prior	0.954	0.019	0.921	0.032

Table 4.2: Summary of the first four components of a principal components analysis performed over the individual trapping sessions ($n = 68$). Year and season were included as supplementary qualitative factors, and trapping efficiency (i.e., the proportion of the adult badger population trapped during each trapping session) as a supplementary quantitative factor. TEMP represents daily-maximum air temperature (°C); RAIN daily precipitation (mm); and BCI a subcutaneous fat score scaled 1 (thin) – 5 (fat).

Variable	**PC 1**	**PC 2**	**PC 3**	**PC 4**
Eigenvalue	4.86	2.90	1.28	1.23
% of variance explained	32.4	19.4	8.5	8.2
Cumulative % of variance explained	32.4	51.8	60.3	68.5
Factor Loadings				
TEMP during trapping	0.81	-0.46	0.04	0.14
TEMP 0-2 weeks prior	0.85	-0.28	0.17	0.17
TEMP 2-4 weeks prior	0.92	-0.13	0.04	0.12
TEMP 4-6 weeks prior	0.90	0.22	-0.06	0.16
TEMP 6-8 weeks prior	0.79	0.50	0.06	0.10
TEMP 8-10 weeks prior	0.64	0.68	0.06	-0.04
TEMP 10-12 weeks prior	0.29	0.88	-0.04	-0.08
RAIN during trapping	-0.25	0.10	0.73	0.19
RAIN 0-2 weeks prior	-0.15	0.42	0.20	-0.03
RAIN 2-4 weeks prior	0.16	0.28	0.20	-0.14
RAIN 4-6 weeks prior	-0.32	-0.04	0.70	0.23
RAIN 6-8 weeks prior	-0.27	0.17	-0.10	0.75
RAIN 8-10 weeks prior	-0.22	0.28	-0.31	0.55
RAIN 10-12 weeks prior	-0.45	0.21	-0.16	0.33
BCI	-0.40	0.81	0.00	-0.21

Table 4.3: Model averaging for the variables predictive of trapping efficiency (i.e., the proportion of the adult badger population trapped during each trapping session) within the linear model. The Relative Influence of each parameter (based on Akaike weights) is presented along with model-averaged estimated values of their coefficients (θ), and the 95% confidence intervals (CI). Asterisks denote coefficient estimates that differed significantly from zero (based on 95% confidence intervals).

Weather Metric	**Relative Influence**	θ	**95% CI**	
Intercept	-	1.005*	0.014	1.995
BCI	0.98	-0.119*	-0.236	-0.002
RAIN 6-8 weeks prior	0.79	-0.013*	-0.026	<0.001
TEMP 4-6 weeks prior	0.71	-0.009	-0.017	<0.001
Season	0.69	-0.030	-0.117	0.058
TEMP 8-10 weeks prior	0.65	0.011	0.000	0.023
RAIN 4-6 weeks prior	0.50	-0.013	-0.026	<0.001
TEMP 0-2 weeks prior	0.39	0.004	<0.001	0.007
RAIN 2-4 weeks prior	0.38	-0.007	-0.014	<0.001
RAIN 8-10 weeks prior	0.34	-0.007	-0.015	<0.001
TEMP 2-4 weeks prior	0.31	0.002	<0.001	0.003
TEMP 6-8 weeks prior	0.30	-0.001	-0.003	<0.001
TEMP 10-12 weeks prior	0.30	0.001	<0.001	0.003
RAIN 10-12 weeks prior	0.30	0.004	<0.001	0.008
RAIN during trapping	0.29	-0.003	-0.007	<0.001
RAIN 0-2 weeks prior	0.28	-0.002	-0.005	<0.001
TEMP during trapping	0.28	0.001	<0.001	0.002

Chapter 5

In situ behavioral plasticity as compensation for weather variability modeled in the European badger: implications for future climate change

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Submitted to Ecology.

5.1 Abstract

Climate change places species in evolutionarily novel conditions that could result in serious population declines, or extinctions, over the coming 50-100 years. Despite climatic effects on species biogeographic distributions being well documented, far less research has considered individuals' capacity to accommodate altered conditions *in situ*. Here, we utilize high-resolution tracking of the European badger, as a model species, to examine weather-driven modification of activity and behavior through the critical autumn season. This study was conducted in Wytham Woods, UK (GPS reference: 51°46'26"N; 1°19'19"W); a 424-ha mixed semi-natural woodland designated a Site of Special Scientific Interest (SSSI). Badgers live in underground burrows, termed setts, which provide thermal refugia; thus exposure to unfavorable conditions can be adjusted to optimize energy budgets. Activity was assessed using new accelerometer and active-RFID transponder technology. We first applied Bayesian mixed models to investigate the relationship between weather variables and: i) activity duration; ii) Overall Dynamic Body Acceleration (ODBA); and iii) ranging behavior. We then used behavioral response models to parameterise simulations of how future climate change scenarios might affect behavior. Bayesian inference showed that inter-individual differences in activity were promoted significantly by temperature, but inhibited by day length, relative humidity, and rainfall. Furthermore, warm, humid conditions led badgers to make significantly more visits to neighbouring group dens, especially individuals in better body-condition. Modeled against IPCC climate change scenarios, the milder and drier conditions projected for the next century would likely cause badgers to maintain elevated activity levels into winter months. According to our projections, this would necessitate an increase in energetic expenditure by as much as 31% per day.

Less mobile species must compensate for climate change *in situ* via behavioral plasticity, rather than relocating to maintain continuity with their current bioclimatic niche. Badgers proved versatile, although projected behavioral responses did not follow a linear trajectory. Future climate change will likely drive substantial additional autumnal activity, and ultimately winter food supply limitations will cease to satisfy increased energy requirements, defining a tolerance threshold.

5.2 Introduction

Rapid, anthropogenic climate change (IPCC, 2014) risks exposing species to evolutionarily novel situations they may be unable to accommodate (Palumbi, 2001). This may ultimately force range shifts (Walther et al., 2002), or cause serious population declines, and even extinctions (Stork, 2010). Although even quite rapid rates of natural climate change are not unprecedented in the paleontological record (Dansgaard et al., 1993), species' capacities to accommodate current climate change are also impacted by other Human-Induced Rapid Environmental Change (HIREC) pressures (Sih et al., 2011), such as habitat loss, fragmentation, and/or loss of ecosystem biodiversity (Venter et al., 2006; Sih et al., 2011; Bellard et al., 2012). Failure to compensate climatic change adequately will result in impaired energetic balance (Chevin et al., 2010), and/or reduced fitness (Hellmann and Pineda-Krch, 2007), potentially impacting the species' realised niche (Quintero and Wiens, 2013). Furthermore, responses are typically non-linear, where exceeding 'tipping points' can trigger disproportionately severe consequences (Doak and Morris, 2010). Despite well documented coarse-scale adaptations to global climate change (Walther et al., 2002), a finer-scale understanding of more nuanced individual behavioral responses is lacking (discussed by Newman and Macdonald, 2015). It is therefore crucial to understand species immediate behavioral responses to changing conditions from a mechanistic perspective (Sih et al., 2011).

To maintain bioclimatic niche continuity, and to allow existing behaviors to continue to function, more mobile species tend to shift their use of habitat mosaics, or relocate entirely (reviewed in Walther et al., 2002; Barnosky and Kraatz, 2007); a trend also prevalent in the fossil record (Fernández and Peláez Campomanes, 2005; Lister and Stuart, 2008). In contrast, less mobile species, and/or those tied to specific habitats (e.g., semi-aquatic, -fossorial, and -scansorial specialists, or central-place foragers), must contend with changing local conditions *in situ* (e.g., Campbell et al., 2012). These species must accommodate change either through differential genetic trait selection (Visser, 2008), changes in population dynamics (Walther et al., 2002; Macdonald et al., 2010), or through behavioral plasticity (Kearney et al., 2009; Noonan et al., 2014).

Genotypic adaptation, via Darwinian selection, takes generations to occur (Barnosky and Kraatz, 2007). Species already near their physiological limits (Hoffmann and Sgrò, 2011), or with longer inter-generational times (Rosenheim and Tabashnik, 1991), are therefore especially vulnerable to environmental change. Consequently, behavioral plasticity provides the most immediate tactical response to changed conditions (Bradshaw and Hardwick, 1989; Walther et al., 2002; Kearney et al., 2009; Sih et al., 2010, 2011). Behavioral responses are also less permanent than genetic selection, and thus better suited to temporary, or stochastic changes (Bradshaw and Hardwick, 1989). Not all behaviors can be modified, however, particularly those tied tightly to ensuring reproduction/ fitness (Visser, 2008), or dependent on inter-specific relationships (Cahill et al., 2012). In this respect, generalist species are more likely to respond through individual plasticity within their lifetimes, while rigid strategists are biased toward differential selection for phenotypes better fitting transformed conditions (Visser, 2008).

5.2.1 Model species: The European badger

European badgers (*Meles meles*, henceforth 'badgers') have provided an informative model for studying how population dynamics (Macdonald and Newman, 2002; Macdonald et al., 2010; Nouvellet et al., 2013; Byrne et al., 2015) and behavior (Noonan et al., 2014, 2015*a*) respond to weather variation and climate change. They have a pan-European distribution, (Johnson et al., 2002*a*), with ecologically similar congenerics occurring through northern Asia (*M. leucurus*; *M. canescens*) into Japan (*M. anakuma*). In lowland Britain, badgers live in groups of 5 to 25 individuals (Macdonald et al., 2015). They are adaptable generalists (Newman et al., 2011), tied to fossorial dens (termed 'setts') within forest and forest/agrarian mosaic habitats (Macdonald et al., 2015), and generally not prone to extensive dispersal (Macdonald et al., 2008; but see Byrne et al., 2014). Much of their climatic sensitivity is a result of their feeding ecology, where earthworms (principally *Lumbricus* spp.) are a major component of their diet (Goszczyński et al., 2000; Macdonald et al., 2015). Earthworms are sensitive to micro-climatic conditions (Curry, 2004; Nuutinen and Butt, 2009), and their distribution and availability to consumers is highly dependent

on prevailing conditions (Macdonald, 1983*a*; Kowalczyk et al., 2003). Furthermore, badgers can decide to remain underground in their thermally-stable setts (Kaneko et al., 2010) during harsh weather conditions (Noonan et al., 2014, 2015*b*) and enter torpor if poor weather and low food availability persist (Newman et al., 2011). In addition to foraging, there are other individual-specific drivers motivating badger activity, such as territorial (Tinnesand et al., 2015), social (Buesching et al., 2003), and mating (Annavi et al., 2014) interactions. Therefore, each individual must trade-off these behaviours against net losses to body-condition incurred by activity on thermally challenging nights (Kowalczyk et al., 2004; Noonan et al., 2014, 2015*b*).

Badger survival dynamics are particularly sensitive to autumnal conditions (Macdonald et al., 2010; Nouvellet et al., 2013) linked to their need to accumulate fat reserves (Noonan et al., 2014), prior to potential winter frost, snow and low(er) food supply (Kowalczyk et al., 2003). Failure to gain sufficient body-condition during the autumn reduces their potential to use torpor to see them through winter periods, when activity carries a high energetic cost (Fowler and Racey, 1988; Newman et al., 2011). On this account, we conducted this study across the autumnal months.

To investigate fine-scale effects of weather conditions on individual activity patterns, we equipped badgers with tri-axial accelerometers (Wilson et al., 2008), able to derive overall dynamic body acceleration (ODBA; Wilson et al., 2006) as a measure of energy expenditure. It should be noted however that although ODBA exhibits a significant correlation with V_{O_2}, it is derived mechanically, and is therefore limited by a number of factors including for instance the effect of specific ligament and tendon elasticity, differences in gaits, and the influence of weather conditions on metabolic rate (for a discussion on this topic see Wilson et al., 2006). Furthermore, the land's gradient will likely influence V_{O_2} disproportionately more than ODBA values, thus, the ODBA value of an animal moving up a steep slope may not be an accurate reflection of V_{O_2}. Nonetheless, collar-borne accelerometers are well-suited for providing estimates of energy expenditure patterns in free-ranging animals (Wilson et al., 2006). We also used an animal-borne active-RFID tracking system, combined with a sensor network across the landscape, to log the locations of multiple badgers in near real-time

(Noonan et al., 2015*b*). In addition, we inserted thermal probes into setts, to measure their potential as thermal refugia (Kaneko et al., 2010).

We posit that, to maintain energetic equilibrium, badgers will adjust their above-ground activity versus remaining within the refuge of their setts, and alter their roaming behavior, in response to prevailing conditions. Because badgers cannot survive within their setts indefinitely without leaving to forage, we anticipate that individuals with lower fat reserves will be more motivated to feed under sub-optimal weather conditions than fatter badgers (*sensu* Noonan et al., 2014). We also consider how behavioral responses are modified by sex, and reproductive status.

5.2.2 Climate change predictions

We proceed to model what effects future projected climate change scenarios (Murphy et al., 2009; IPCC, 2014) might have on badger activity regimes. We consider whether these behavioral changes are sustainable with regard to food supply thresholds, or if modified activity regimes risk exposing badgers to other mortality factors, such as road traffic accidents (Macdonald et al., 2010). From these findings, we extrapolate to similar vulnerabilities other low-mobility species may encounter in response to climate change.

5.3 Materials and methods

This study was conducted in Wytham Woods, Oxfordshire (GPS reference: 51°46'2"N; 1°19'19"W); a 424-ha mixed semi-natural woodland designated as a Site of Special Scientific Interest (SSSI), and managed by the University of Oxford. The resident, high-density badger population comprised 23 social groups with ca.145 adults and 52 cubs in 2014 (Noonan et al., 2015*a*).

As part of a long-term research program, a subset of 15 badgers (6 males and 9 females; Table 5.1), resident at three adjacent social groups, were caught, sedated, sampled, and measured (for details see Macdonald et al., 2009, 2015).

From these morphometrics, we calculated the ratio of body weight to length (ln mass:ln length), to generate Body-Condition Indices (BCI) as a measure of stored body-fat (Noonan et al., 2014). Following Woodroffe and Macdonald (1995*a*, ; see also Tinnesand et al., 2015, female reproductive status was inferred from vulva condition; classified as oestrus (vulva swollen and moist), or non-oestrus (vulva flat and dry). All males had scrotal testes when collared in August and inferred to be in breeding condition (Buesching et al., 2009). In autumn, however, both sexes enter a period of reproductive quiescence (Woodroffe and Macdonald, 1995*a*; Buesching et al., 2009), thus reproductive motivation likely changed over the study period. Nevertheless, there are distinct physiological costs associated with maintaining reproductive condition (Woodroffe and Macdonald, 1995*a*; Buesching et al., 2009) that persist after the mating season itself, incurring ongoing costs throughout this study.

Table 5.1: Summary information of collared animals. BCI represents log scaled mass:length, reproductive status was determined by testes decent in males, and vulva condition in females.

Deployment Date	Collar Number	Sex	BCI	Reproductive Status	Operational Days
12/08/14	1	M	0.326	Descended	50
14/08/14	2	F	0.333	Non-Oestrus	23
14/08/14	3	M	0.297	Descended	64
15/08/14	4	M	0.331	Very descended	-
15/08/14	5	M	0.331	Descended	65
15/08/14	6	M	0.342	Very descended	54
15/08/14	7	F	0.304	Non-Oestrus	84
16/08/14	8	F	0.271	Non-Oestrus	33
16/08/14	9	F	0.333	Oestrus	-
16/08/14	10	F	0.310	Non-Oestrus	-
16/08/14	11	F	0.325	Non-Oestrus	-
19/08/14	12	M	0.303	Very descended	54
19/08/14	13	F	0.331	Non-Oestrus	47
19/08/14	14	F	0.322	Oestrus	48
19/08/14	15	F	0.288	Oestrus	-

Captured badgers were fitted with custom-built tracking tags [39 mm (l) x 22 mm (w) x 12 mm (h)], including tri-axial accelerometers and active radio-frequency identification (aRFID), powered by CR123A lithium batteries (see Noonan et al., 2015*b*). Tags were hermetically sealed in epoxy resin, and mounted onto commercially available padded leather dog collars, with a complete assembly weight of 95 g. Henceforth, individual badgers are referred to by their unique collar ID. After handling and collaring, badgers were held in a

recovery room for 3 h, before being released at the locations where they were captured (Macdonald et al., 2015).

5.3.1 Quantifying energy expenditure

Accelerometers sampled relative acceleration continuously, at a frequency of 8 Hz, across each of three axes (heave, surge, and sway). Data were compressed and stored onboard collars, and communicated wirelessly to base-stations (see below), making it unnecessary to recapture individuals for data collection. From these accelerometer data, we calculated two inter-dependent variables, which addressed distinct behavioral decisions: i) ODBA (in g), which provides an accurate proxy for energy expenditure (see Wilson et al., 2006); and ii) 'activity', which gives a binary measure of the badgers' pattern of above-ground activity versus inactivity below ground. Activity was calcuated based on an ODBA threshold value of 0.313 g (Noonan et al., 2014). Above this threshold, readings were consistent with activity; below it individuals were inactive (for full details see Appendix S1). Data were collected from August 16, 2014, until Nov 7, 2014, by which point all batteries had run out. Across all 10 animals, over $3.5\text{x}10^8$ accelerometer data points were generated over 522 badger days.

5.3.2 Quantifying movement patterns

Due to the limitations of utilising Lagrangian tracking technologies (i.e., following individuals continuously) in dense vegetation and when underground (Noonan et al., 2015*b*), we used a Eulerian sampling approach (i.e., logging visits to specific receivers in the environment, positioned at all setts used by this sub-population).

The three neighbouring focal social groups occupied ca. 49 ha and included nine setts (three main, and six outlying; Fig. 5.1). Each group had a fairly stable membership and distinct range, delineated by a series of inter-group latrines (Tinnesand et al., 2015) From trapping histories, all groups within the Wytham Woods population exhibit high inter-conectivity (Macdonald et al., 2008), and badgers frequently trespass temporarily into neighbouring group ranges (Macdonald et al., 2008, 2015); also evidenced by genetic analyses, revealing 48%

extra-group paternity (Annavi et al., 2014). Therefore, these specific focal groups were selected because each had direct access to earthworm-rich pasture, decreasing the likelihood that inter-group visits were related to foraging and instead implying a social function.

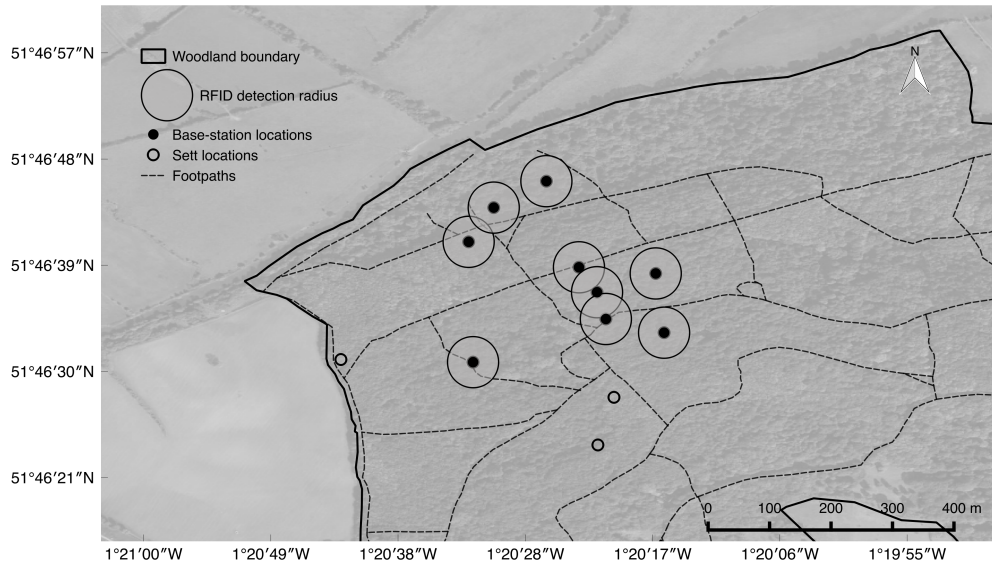

Figure 5.1: Map of the study site (Wytham Woods; GPS reference: 51°46'2"N; 1°19'19"W) depicting the locations of aRFID base-stations at monitored sett sites, as well as unmonitored, nearby sett sites

The 2.4 GHz 802.15.14 (Zigbee) base-station receivers we installed at each sett were powered by a 12 V battery (Noonan et al., 2015*b*). Base-stations received aRFID tag signals, broadcast every 3 s, whenever an animal was within a 20-25 m radius detection range. When a collar was detected, an entry (consisting of collar ID, time-stamp, and received signal strength) was generated. Buffered data were transferred from collars to base-stations, with two-way handshaking (i.e., a network transmission control protocol where data packets are exchanged reciprocally between devices) and saved for later retrieval. Due to the way setts were distributed within the study area, it was possible for an individual to be within the detection range of multiple base-stations simultaneously. In these instances, a badger was recorded at the location where it registered the strongest signal. In total, 103,797 (re-)visits to setts were recorded.

Given the importance of photoperiod on badger activity (Noonan et al., 2014), we apply the term '*per diem*' to designate a full circadian cycle, avoiding confu-

sion with the dual meaning of the term 'per day'. Because there was substantial variation in the number of sett sites individuals visited each night, and their frequency of (re-)visits, we used sett proximity data to calculate *per diem* utilisation distributions (henceforth 'inter-sett visits'), using the kernel Brownian bridge method in the *R* package '*AdehabitatHR*' (Calenge, 2011). For each badger, the smoothing parameter σ^1 was calculated using the maximum likelihood approach developed by Horne et al. (2007), while σ^2, a measure of the imprecision of relocations, was set to 50 m (i.e., the maximum aRFID detection diameter). Although limited by the sub-sampling inherent in the Eulerian tracking approach, these utilisation distributions provide a robust minimum estimate of inter-sett visit rate.

5.3.3 Autumnal weather conditions

Meteorological records were obtained from the UK Environmental Change Network (ECN) weather station in Wytham Woods (terrestrial site T08). To quantify the effects of contemporaneous weather on badger activity, we decomposed these weather data into four variables, known to influence badger behavior (Johnson et al., 2002*a*; Macdonald et al., 2010; Noonan et al., 2014, 2015*a*): (1) hourly solar radiation, providing a measure of photoperiod (in W/m^2), with the additional subtle benefit of including cloud cover influences on dusk emergence; (2) mean hourly relative humidity (in %); (3) mean hourly air temperature (in °C); and (4) total hourly rainfall (in mm).

In addition, in Appendix S2 we present analyses of trends in historic autumnal weather data from 1853 to 2015, providing the range of conditions this population's ancestors were exposed to, shaping their selection. In Appendix S3, we present analyses of the sett micro-climate over the course of the study period.

5.3.4 Descriptive analyses

All statistical analyses were conducted in the *R* environment (version 3.0.3; R Core Team, 2014). We undertook an initial descriptive analysis, using analyses

of variance (*ANOVA*) and covariance (*ANCOVA*), as well as Pearson's correlations ($\alpha = 0.05$). To summarise the variance contingent on weather, activity, and energy expenditure variables, as well as individual traits, we ran a principal component analysis (PCA), performed over mean *per diem* data ($n = 362$). Here, sex was included as a supplementary qualitative factor, without rotation; instances with missing values were excluded.

5.3.5 Bayesian inference

To investigate the relationship between behavioral response variables and weather variables, we applied a Bayesian mixed models approach across mean hourly data (n = 12,546), using the *R* package '*MCMCglmm*' (Hadfield, 2010). Due to the uneven spatial distribution of monitored setts, behavioral decisions had the potential to be biased by geography and relative proximity of neighbouring base-stations. Similarly, sett visits involving longer distances require more energy. To address this, we included the random effect of group membership in all of our models. To test whether activity and energy expenditure responded to variation in weather or individual BCI, sex, and reproductive condition, two predictive models were fitted, with 'individual' and 'group' included as random effects:

i) activity = f(solar radiation + temperature + humidity + rainfall + sex + reproductive status + BCI)

ii) ODBA = f(solar radiation + temperature + humidity + rainfall + sex + reproductive status + BCI)

To examine movement patterns and inter- sett visits, the following model was fitted, with individual, and group included as random effects:

iii) inter-sett visits = f(solar radiation + temperature + humidity + rainfall + sex + reproductive status + BCI)

Following Hadfield (2010), we used uninformative, inverse-gamma prior distributions. We used a binomial distribution to model activity data, whereas ODBA, and inter-sett visits were modeled against a Gaussian distribution with an identity link function. All parameters were mean centred prior to analyses. To correct for a positive skew, inter-sett visit data were log-transformed. The

number of iterations, thinning interval and the burn-in period were determined using diagnostic tests in the *R* package '*coda*' (Plummer et al., 2006). Convergence between model chains was verified using the Geweke diagnostic (Geweke, 1992).

5.3.6 Climate change projections

We used activity data to parameterise simulations of how future climate change might affect badgers. Based on the IPCCs SRES emissions scenarios (Nakicenovic Swart, 2000), we obtained UK Climate Projections 2009 (Murphy et al., 2009) for the 25 km^2 area around Wytham Woods. These data exist as mean monthly values for seven overlapping, 2-decade time-periods (from 2010 to 2099), over a wide probability range. We simulated responses to both, a low emissions (i.e., the B1 scenario, which predicts 500 to 600 ppm CO_2, a 1.1 to 2.9 °C rise in mean temperature, and no significant trends in precipitation) and a high emissions scenario (i.e., the A1F1 scenario, which predicts 550 to 750 ppm CO_2, a 2.4 to 6.4 °C rise in mean temperature, a 0 to 5% decrease in relative humidity, and no significant trends in precipitation).

We then applied the '*predict*' function in the *R* environment (R Core Team, 2014) to our three models to predict how these activity variables would respond to projected weather conditions per period, detailed in Appendix S4. We note, however, that although response trends can be considered as robust, both our parameter estimates and climate predictions are subject to modelling error, and therefore interpretations should be made cautiously.

5.4 Results

5.4.1 Summary of activity and movement data

Badgers were active on average 9.7 ± 2.1 SD hours *per diem*, and, superficially (but see below) there was no evidence of a trend in mean activity over the study period (r = -0.01, n = 86, P = 0.94; Fig. 5.2a). There were significant differences in duration of *per diem* activity between individuals ($F_{[9,512]}$ = 9.16,

P <0.005; Fig. 5.3a), but no difference between sexes ($F_{[1,520]} = 0.01$, $P = 0.92$).

Individuals exhibited significant differences in *per diem* ODBA expenditure ($F_{[9,512]} = 41.91$, P <0.005), with a significant sex effect ($F_{[1,520]} = 22.8$, P <0.005), where males had a lower *per diem* ODBA than females. As autumn progressed, badgers visited significantly fewer setts (r = -0.24, n = 78, P = 0.03; Fig. 5.2b). Inter-sett visit rates differed significantly between individuals ($F_{[9,648]} = 17.09$, P <0.005; Fig. 5.3b), with males visiting significantly more setts than did females ($F_{[1,715]} = 25.33$, P <0.005).

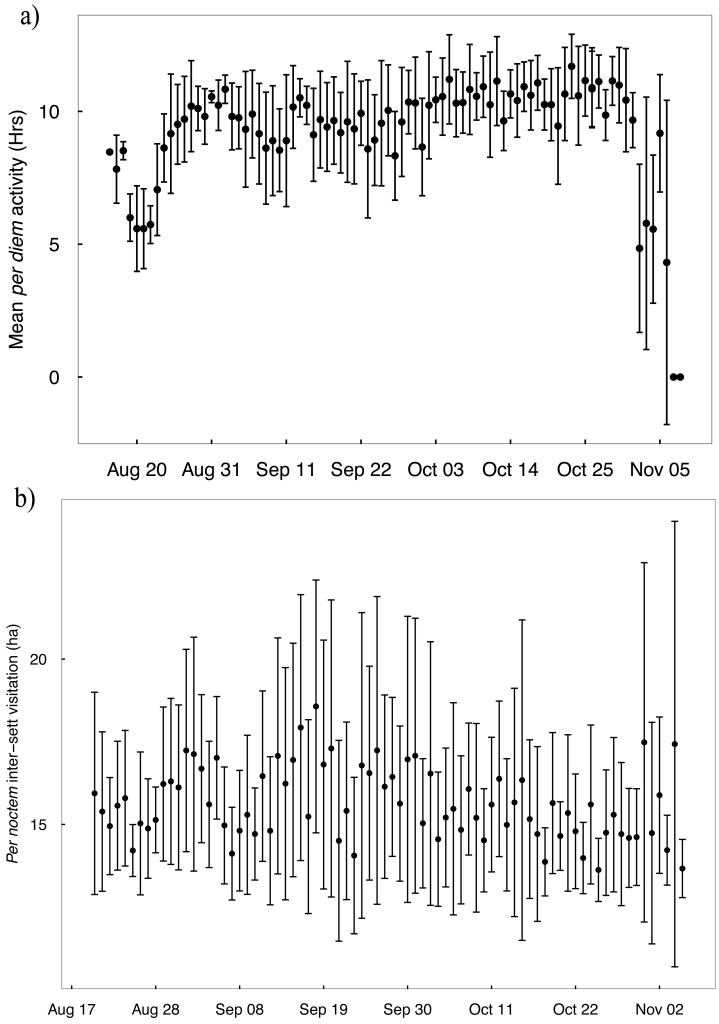

Figure 5.2: Mean ± SD *per diem* a) activity; and b) inter-sett visitation across all collared badgers over the study period.

Only the first four components warranted retention in a PCA across mean per

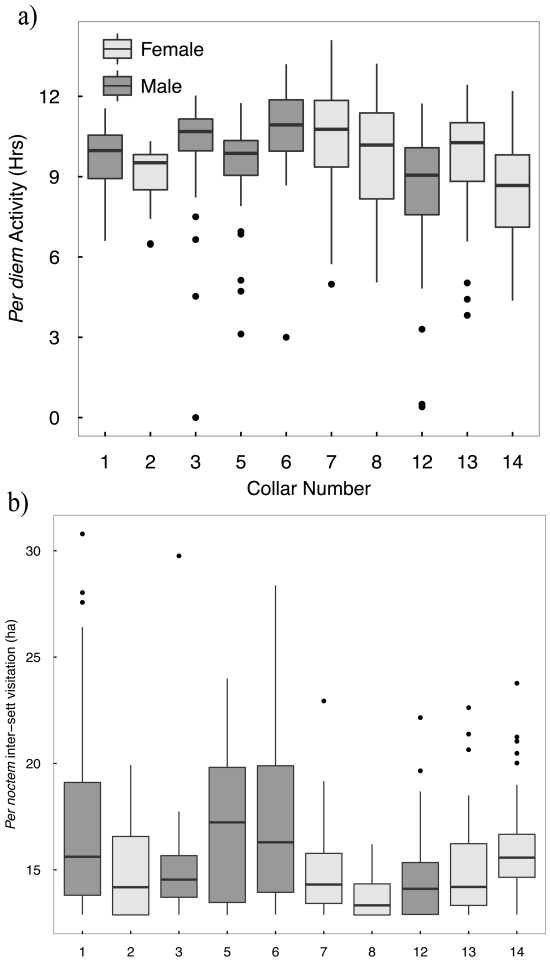

Figure 5.3: Boxplots of *per diem* (a) activity; and (b) inter-sett visits of each collared badger.

diem data, which explained a cumulative 68.7% of the variance (Table 5.2). From component factor loadings, reproductive status, activity/ODBA budgets, and weather variables were the most influential parameters. Projecting these data into the reduced dimension space defined by PC 1 (termed the 'energy budget component') and PC 2 (termed the 'weather component') revealed minimal overlap between sexes, within which individuals in different reproductive condition grouped into relatively distinct clusters (Fig. 5.4).

5.4.2 Modeling movement patterns

From Bayesian inference, weather conditions were crucial for predicting the amount of time spent active. Posterior parameter estimates revealed that du-

Table 5.2: Summary of the first four components of a principal component analysis performed over mean *per diem* data, with sex included as a supplementary qualitative factor.

	PC 1	**PC 2**	**PC 3**	**PC 4**
Eigenvalue	2.49	2.14	1.44	0.91
% of variance explained	24.94	21.42	14.42	9.07
Cumulative % of variance explained	24.46	45.36	60.78	69.84
Factor loadings				
Individual	-0.17	-0.25	-0.17	0.77
Body condition	0.05	<0.01	0.65	-0.07
Reproductive status	-0.34	-0.31	0.20	0.20
Hours active	0.29	0.46	<0.01	0.41
ODBA	0.41	0.48	0.02	0.11
Temperature	0.35	-0.20	0.15	0.37
Relative humidity	-0.43	0.33	0.06	<0.01
Rainfall	-0.36	0.35	0.02	0.06
Solar radiation	0.39	-0.36	-0.07	-0.18
Inter-sett visitation	0.02	-0.02	0.69	0.09

ration of activity was promoted significantly by temperature and inhibited significantly by solar radiation, relative humidity, and rainfall (Table 5.3).

In contrast, when modeling ODBA, although the significant negative relationship with solar radiation, relative humidity and rainfall persisted, the positive effect of temperature became non-significant (Table 5.4).

From posterior parameter estimates, temperature, humidity and BCI had significant positive effects on the rate of *per diem* inter-sett visits. Individuals with higher BCI tended to visit more setts, where warm, humid conditions promoted inter-sett visits (Table 5.5).

5.4.3 Climate change projections

The changes predicted by climate scenarios through the 21st Century appear likely to drive a substantial change in badgers' autumnal behavioral phenology (detailed in Appendix S4). Under the low emissions scenario, milder and less humid conditions could cause a 4% ± 22.7 SD mean increase in activity duration

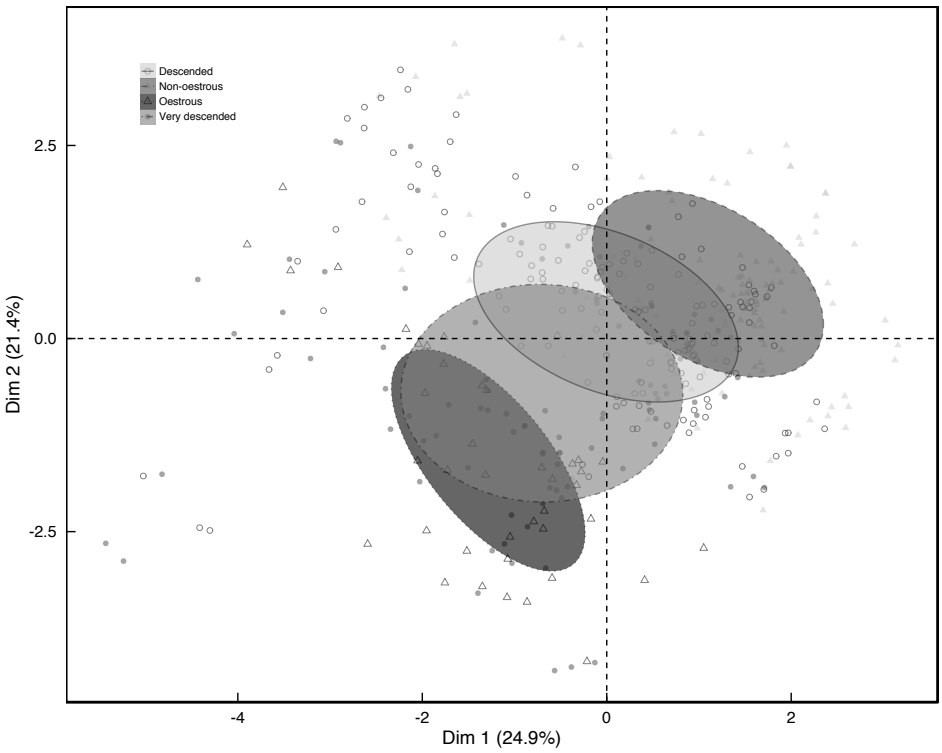

Figure 5.4: Factor map of *per diem* data projected in a reduced dimension space, defined by PC 1 (x-axis) and PC 2 (y-axis) of our principal component analysis. Percentages represent the amount of variation in these data that were accounted for by the respective components.

to be maintained into the winter months (Figure 5.5a). This would necessitate summer levels of ODBA being maintained into winter, requiring 6% ± 8.9 SD more ODBA '*per diem*' than present day (Figure 5.5b). Under this scenario, activity and ODBA adjustments were accompanied by only a mean 1% ± 7.2 SD increase in inter-sett visits (Figure 5.5c).

In contrast, under a high emissions scenario, only a 2% ± 23.8 SD mean increase in activity duration was predicted (Figure 5.5d), but, counter-intuitively, accompanied by a 7% ± 8.9 SD increase in ODBA expenditure (Figure 5.5e). Interestingly, this scenario predicted a 3% ± 9.0 decrease in inter-sett visits (Figure 5.5f).

Table 5.3: Relationship between weather metrics, individual attributes; sex, Body Condition Indices (BCI), and reproductive status (see details in text), and activity in the linear model. Posterior coefficient estimates (β), and their 95% confidence intervals (CI) are presented. Asterisks denote variables that differed statistically from zero (based on 95% confidence intervals). Note: 6.0 x 10^7 iterations, with a 2.4 x 10^3 burn-in period and a thinning interval of 3.3 x 10^2.

	β	**lower CI**	**upper CI**
Fixed terms			
Intercept	-3.90**	-5.76	-2.00
Solar radiation	-0.04***	-0.05	-0.04
Temperature	0.09***	0.07	0.11
Humidity	-0.05***	-0.06	-0.04
Rainfall	-0.29*	-0.54	-0.04
BCI	4.73	-34.64	45.06
Reproductive status	-0.73	-1.96	0.48
Sex	0.08	-1.43	1.54
Random terms			
Individual	0.48**	0.06	1.25
Group	2.04*	0.06	5.89
Residual variance	0.15***	0.06	0.28

5.5 Discussion

Ultimately, how populations cope with climate change is a function of how individuals respond to cumulative, contemporary weather stresses (Visser, 2008; Noonan et al., 2014; Blumstein and Berger-Tal, 2015). Schloss et al. (2012) predict that, for the western hemisphere, an average of 9.2% of mammals at any given location will be unable to respond to climate change adequately – in some regions up to 39% may be unable to keep pace. Similarly, the biogeographic ranges of 87% of mammalian species are expected to undergo reductions, where for many this will be due to limited dispersal abilities, as opposed to reductions in area with suitable climate (Newman and Macdonald, 2015). Within these predictions, however, lies a core assumption; that species will go on trying to operate in the same way as at present, despite changes to their bioclimatic niche. This assumption is clearly invalid – tactically, all species will, to some degree, attempt to exploit their innate behavioral plasticity to accommodate the cascade of stressors resulting from climate change (Bradshaw and Hardwick, 1989; Chevin et al., 2010; Noonan et al., 2014). Studies quantifying how behavioral plasticity underlies mechanistic responses to climatic change are, however, few

Table 5.4: Relationship between weather metrics, individual attributes; sex, Body Condition Indices (BCI), and reproductive status, and ODBA (g) in the linear model. Posterior coefficient estimates (β), and their 95% confidence intervals (CI) are presented. Asterisks denote variables that differed statistically from zero (based on 95% confidence intervals). Note: 6.0 x 10^7 iterations, with a 2.0 x 10^3 burn-in period and a thinning interval of 1.1 x 10^2.

	β	**lower CI**	**upper CI**
Fixed terms			
Intercept	0.01	-1.60	1.65
Solar radiation	-0.06***	-0.08	>-0.01
Temperature	<0.01	>-0.01	<0.01
Humidity	>-0.01***	>-0.01	>-0.01
Rainfall	-0.06***	-0.08	-0.04
BCI	-0.06	-34.48	32.87
Reproductive status	-0.08	-1.10	0.99
Sex	-0.01	-1.29	1.23
Random terms			
Individual	0.34**	0.05	0.87
Group	1.51*	0.06	4.56
Residual variance	0.05***	0.05	0.05

(Blumstein and Berger-Tal, 2015). Ultimately, this leads to a lack of understanding how weather conditions affect behavior and activity at the individual level for many species (reviewed in Newman and Macdonald, 2015).

To begin to redress this information gap, we describe how the European badger, a K-selected generalist with a wide biogeographic range, uses behavioral plasticity to accommodate variation in weather. Even given the small geographic extent occupied by this sub-population, and the relative homogeneity of their forest habitat, we observed significant response heterogeneities between individuals not explained by BCI, sex, reproductive status, or group membership. Badgers exhibited three primary responses: first, when conditions were mild and humid, but without heavy rainfall, they were active for less time. This implies they could satisfy their dietary needs quickly and effectively (e.g., Kowalczyk et al., 2003) when conditions were conducive to earthworm emergence (Macdonald, 1983*a*; Curry, 2004). Second, when it was drier and mild, badgers were active for extended periods – likely because more foraging effort was required when earthworms were less abundant, but without activity incurring substantial

Table 5.5: Relationship between weather metrics, individual attributes; sex, Body Condition Indices (BCI), and reproductive status, and per diem inter-sett visits in the linear model. Posterior coefficient estimates (β), and their 95% confidence intervals (CI) are presented. Asterisks denote variables that differed statistically from zero (based on 95% confidence intervals). Note: 4.0 x 10^7 iterations, with a 2.0 x 10^3 burn-in period and a thinning interval of 1.0 x 10^2.

	β	**lower CI**	**upper CI**
Fixed terms			
Intercept	-0.03	-0.09	0.03
Solar radiation	>-0.01	>-0.01	<0.01
Temperature	0.01**	<0.01	0.02
Humidity	<0.01*	<0.01	<0.01
Rainfall	-0.01	-0.01	<0.01
BCI	3.12**	1.48	4.63
Reproductive status	0.02	-0.03	0.08
Sex	0.05	-0.03	0.12
Random terms			
Individual	<0.01*	<0.01	<0.01
Group	<0.01*	<0.01	<0.01
Residual variance	0.03***	0.02	0.03

thermoregulatory costs. Finally, under colder conditions, badgers were significantly less active – extended periods of activity risk net-negative energetic returns during conditions of low(er) earthworms availability, particularly under harsh conditions (Noonan et al., 2014). These tactical responses suggest badgers attempt to optimise their activity in response to prey availability and the risks of thermoregulatory losses above-ground.

Nevertheless, irrespective of prevailing weather and the need to forage, badgers must weigh decisions on commitments to social and territorial activities. For example, up to four hours difference in individual activity per night often occurred between dyads. Furthermore, on some nights, certain badgers did not emerge from their thermally stable burrows (see Appendix S3) at all, while others were active for a normal (ca. 8 hrs) duration. These differences may reflect differences in energy-based motivation, and/or differences in behavioral objectives. In this regard, we also found a positive relationship between temperature, humidity and the rate of inter-sett visits. This suggests that when badgers can readily meet their energetic requirements, but without thermoregulatory costs,

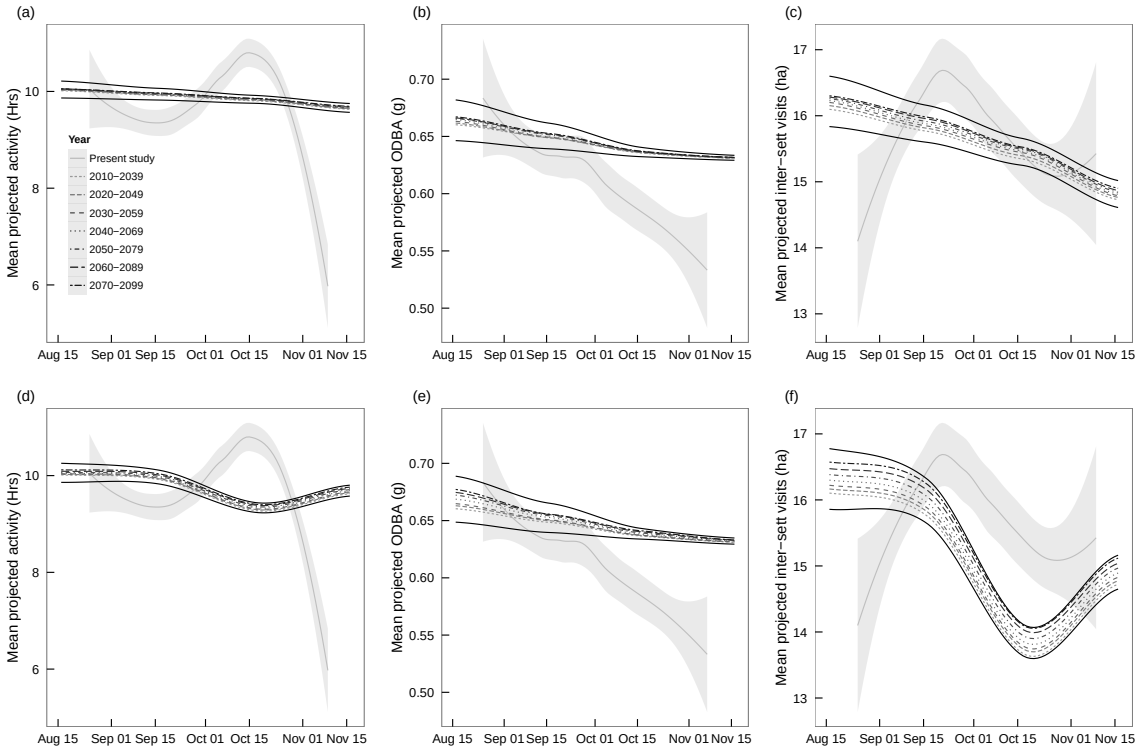

Figure 5.5: Mean projected *per diem* activity (Hrs); ODBA (g); and inter-sett visits (ha) under future climate projections over seven over-lapping time periods. Panels (a) – (c) depict projected behaviour under a low emissions scenario (IPCC SRES B1); (d) – (f) depict behaviour under a high emissions scenario (IPCC SRES A1F1). Trend lines depict Loess smoothed regressions. Shaded areas represent the standard error of the fit to behavioral data from the present study, whereas solid lines represent the error associated with projected responses.

they can invest more time in social activities. Furthermore, although we found no significant relationship between BCI and activity; those badgers with higher BCI, of both sexes, tended to make more inter-sett visits; where extra-group mating is known to enhance breeding success (Annavi et al., 2014). In this respect however, we note that the lack of a relationship between BCI and activity in this study fails to replicate the BCI-sensitive risk taking evidenced by Noonan et al. (2014). With a total of only three years between these two studies, investigating a collective 18 animals, inter-annual, and -individual differences in risk sensitivity could have been due to a range of confounding variables not adequately accounted for in these studies (e.g., small sample size, differences in densities/social contexts between years/groups, differences in environmental conditions that weren't recorded such as local agricultural practices and variance in the availability of secondary food sources, etc). Furthermore, although

animals on a positive energy budget are generally expected to take fewer risks (Kacelnik and Bateson, 1997), the study design employed here made it impossible to determine the exact relationship between BCI at the time of capture and longer-term trajectories. As such, no firm conclusions can be arrived at regarding the presence of condition-sensitive risk taking in this population.

The tactical reliance on innate behavioral plasticity evidenced in this study reveals, mechanistically, how badger responses to prevailing weather have, thus far, been sufficient to ensure the perpetuation of this population (see also Macdonald et al., 2010; Nouvellet et al., 2013). Badgers have a recorded history of occupying this study-site for centuries (Macdonald et al., 2015), likely since the Holocene interglacial began (Sommer and Benecke, 2004). Although our current study took place in a comparatively low weather-stress year, meteorological records for this site commencing in 1853 reveal a number of extreme weather event years (i.e., mean values of weather parameters falling more than two standard deviations from long-term means; see Appendix S1). These harsh years likely impacted the population severely (Nouvellet et al., 2013), but illustrate the resilience with which this species can survive weather stress at the population level. In terms of trends, there has been an incremental, 1.7 °C increase in temperature (consistent with global trends; IPCC, 2014), which, to date, has generally benefited population success (Macdonald and Newman, 2002; Macdonald et al., 2015).

Few projections of future species-success take behavioral plasticity into account (e.g., Keith et al., 2008). We demonstrate that warming conditions in the future may promote extended periods of autumnal badger activity. Crucially, however, we found that the activity responses we modeled did not follow a linear trajectory (Doak and Morris, 2010) across both IPCC emissions scenarios. Based on these data, we anticipate the low emissions scenario will result in increased activity, ODBA, and inter-sett visits, whereas the high emissions scenario involves a relative decrease in activity and inter-sett visits, but an increase in ODBA. This ODBA increase would amount to 31% more energy expenditure *per diem* than current levels. In this respect, Turbill et al. (2011) highlight that hibernation is generally associated with higher annual survival, longer life spans, slower reproductive rates, later maturity, and longer generation times

when compared with similar sized non-hibernating species. This strategy, however, is being compromised by winters warming beyond the point at which metabolic rates can remain sufficiently suppressed (Newman and Macdonald, 2015). For instance, Pretzlaff and Dassmann (2012) found that dormice (*Muscardinus avellanarius*) do not compensate for changes in ambient temperature, and are thus more likely to deplete fat reserves before the end of hibernation with warmer temperatures. Furthermore, arousal also occurred more frequently during warmer winters, resulting in significantly increased energy expenditure. Similarly, climate change effects can also cause bats to awaken from hibernation during periods of low food availability, depleting their energy reserves and leading to mortality (Foley et al., 2011). Changes in phenology via the mechanisms evidenced in this study could therefore put specific calorific requirements out of synchrony and/or balance (Walther et al., 2002) with seasonal food availability. If food supply cannot keep pace with this heightened rate of energy expenditure through the winter months, this could ultimately compromise population dynamics and reduce population density (Walther et al., 2002). It should be noted however, that there are other complicating factors that are not captured in these models; hibernation/torpor are not only a response to weather conditions. These processes are also under endocrinological control via day-length, operating through the pineal hormone melatonin (Bechtold et al., 2012). Ability to respond to changing autumnal weather would thus have an interactive hormonal component, where day-length variation stays fixed with latitude.

There are also confounding corollaries of greater winter activity. By modifying activity patterns, and ranging behaviour, Macdonald et al. (2010) describe how milder winter temperatures are linked to higher rates of badger road traffic accidents (RTAs) in the urban UK, which are the primary cause of adult mortality. Similarly, an analysis by Glista et al. (2008) of more than 60 vertebrate species revealed that temperature was the primary predictor of RTA mortality. Interestingly however, Rolandsen et al. (2011) found that in moose (*Alces alces*) populations, warmer winters result in fewer RTAs. They speculate that this negative relationship is because moose are cold-adapted, and thus maintain higher levels of activity at lower temperatures, demonstrating the importance of accounting for species- and situation-specific behavioural plasticity, and a '*one size does not fit all*' approach generally.

A meta-analysis by Hendry et al. (2008), examining over 3000 instances of phenotypic change rates, concluded that behavioral plasticity proved the most important response to climate change. Understanding the ability to compensate climate change *in situ*, through plastiticity in behavioral tactics (Hendry et al., 2008), must become a climate-ecology and conservation priority (Sih et al., 2010; Newman and Macdonald, 2015; Wong and Candolin, 2015; Blumstein and Berger-Tal, 2015). As we have shown, this is especially important in regions where proximate weather conditions are highly variable, such as the UK (UKCP09; Murphy et al., 2009), where the flexibility afforded by behavioral responses are most effective (Tuljapurkar, 2010; Nouvellet et al., 2013).

5.6 Appendix S1

In this appendix, we provide further information relating to the calculation of the behavioral parameter 'activity'. In this work we apply the threshold method developed by Noonan et al. (2014) to determine how active an animal was, on a binary scale with 0 corresponding to inactive and 1 corresponding to active. This method was applied across all collared animals however, for clarity, we only present details for the badger wearing collar number 1.

5.6.1 Quantifying 'activity'

Approach

(a) Acceleration was sampled at 8 Hz on 3 axes (i.e., heave; surge; and sway) simultaneously to provide a fine-scale record of animal behavior.

(b) The vector measurements were transformed to observed dynamic body acceleration (ODBA; in g) as per the method in Wilson et al. (2006), here using a window length of 2 seconds to obtain the direction of g, followed by taking the L1 (absolute value) norm of the dynamic component.

(c) ODBA values were then averaged over 1 minute bins, providing a metric of mean acceleration for each 1 minute time period. In this way, brief spikes in acceleration, which are due to knocks and bumps, are filtered out, leaving the trend itself. Applying this method, a total of 75,124 ODBA values were obtained for this badger over the 50 day sampling period. These values ranged from <0.01 to 11.19 g, with a mean value of 0.32 g $\pm$ 0.47 SD.

(d) Mean ODBA values for each time period were then compared to a threshold value as per the method in Noonan et al. (2014) to determine if the animal was active (1) or inactive (0). Formally:

$$a_k = \text{sgn}(\text{ODBA}_k - T) \tag{5.1}$$

where a_k [0:1] is the activity in the k^{th} window, sgn() is the signum function, $ODBA_k$ is the time averaged ODBA value and T is a threshold value.

The threshold value used in this study was 0.313. For badger 1, this resulted in 33.5% of ODBA values being categorised as 'active'; 66.5% as 'inactive'. Subsequently, this measure was used to calculate *per diem* activity (i.e., the duration of time per 24hr period that an individual was categorised as 'active'), as well as to investigate broad patterns in badgers' activity regimes (see below).

5.6.2 Activity and location

This binary activity measure was used to investigate an individual's willingness to engage in above-ground activity. This required a degree of certainty that the parameter 'activity' corresponded with the badger being above-ground. Although a total of 75,124 ODBA values were obtained for this badger, only 3,691 of these corresponded to a time when the badger was known to be within a monitored sett; 4,033 to a time when the badger was above-ground and within the detection range of a base-station. In contrast, 67,400 values corresponded to a time when the badger was at an unknown location either above-ground, or within an unmonitored sett. As such, limiting our analyses to ODBA values generated when the animal was at a known location would have resulted in a data loss of 89.7%.

For this reason, we make the assumption here that the majority of badger 'activity' occurs above-ground. Of the 3,691 ODBA values recorded while the badger was known to be within the sett, only 4.4% of these involved the badger being categorised as active. In contrast, of the 4,033 ODBA values recorded while the badger was known to be above-ground, it was categorised as being active 82.9 % of the time. Of the ODBA values recorded when the badger was at an unknown location, 39.8 % of these were catagorised as periods of 'activity' (e.g., Fig. 5.6).

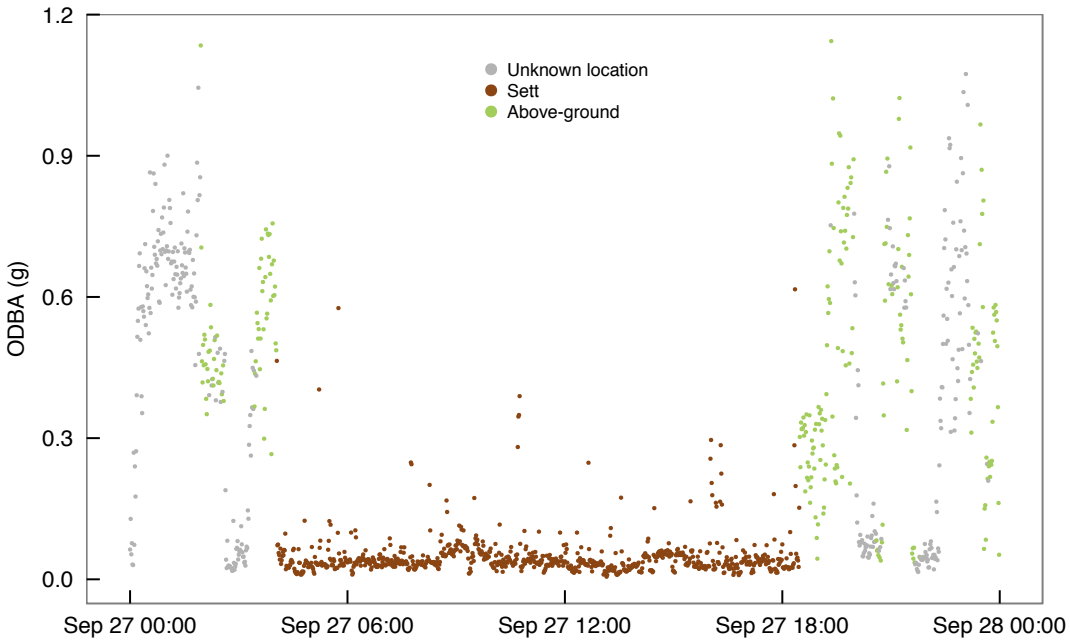

Figure 5.6: Scatterplot depicting ODBA values over the course of a 24 hour period. Colours indicate the individual's location categorised as i) sett (i.e., the badger was recorded within a monitored sett; ii) above-ground (i.e., above-ground and within the detection range of a base-station); and at an unknown location

5.7 Appendix S2

In this appendix, we provide analyses of trends in historical autumnal weather data (1853 – 2015). For these analyses, we used historical records of daily mean temperatures and total rainfall, as well as days of air frost, obtained from the University of Oxford's Radcliffe Meteorological Station. Although located 6 km from the study site, weather parameters correlate between the ECN and Radcliffe Meteorological stations (Savill et al., 2010), where the latter was used due to requiring longer-term data. These records are available freely.

5.7.1 Temperature

Because of the sinusoidal nature of annual temperature fluctuations (Fig. 5.10a), we characterised autumnal temperatures in each year according to the trigonometric function:

$$T_m = \beta_0 + r_T \sin(\frac{2\pi}{\phi} m) \tag{5.2}$$

Where β_0 represents the model intercept for each year; ϕ the phase (which was set to 12 such that each cycle has a period of one year); r_T the amplitude of temperature change; and T_m the mean temperature for calendar month m in °C. To examine trends in the extent of seasonal temperature changes, we calculated r_T over the autumnal period (Sep – Dec) for each year.

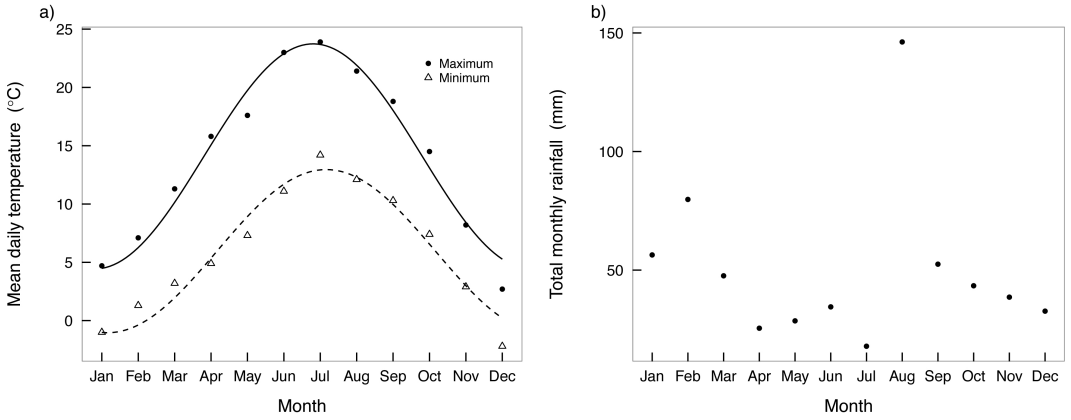

Figure 5.7: Scatterplots depicting; (a) sinusoidal functions based on mean daily maximum and minimum temperatures; and (b) total monthly rainfall for the year 2010.

Mean daily maximum temperature in autumnal months (Sep – Dec) averaged 12.44 C ± 4.58 SD (range: 0.2 to 23.2 °C), with 11 years having mean maximum temperatures that fell more than two standard deviations from the long-term mean (henceforth classified as 'extreme'; Table 5.8). Mean daily minimum temperature averaged 6.08 °C ± 3.41 SD (range: -2.2 to 13.5 °C), and only 4 years had mean minimum temperatures classified as extreme. There was a significant positive warming trend in long-term mean autumnal daily maximum temperature ($F_{[1,161]} = 48.20$, $P < 0.001$, $R^2 = 0.23$; Fig. 5.8a), as well as a significant warming in minimum temperature ($F_{[1,161]} = 58.11$, $P < 0.001$, $R^2 = 0.27$; Fig. 5.8b), equivalent to an overall increase of ca. 1.7 °C over the 162 year period.

Table 5.6: Descriptive statistics for weather parameters in autumnal months, at the University of Oxford's Radcliffe Meteorological Station, between 1853 – 2015. Months were categorised as 'extreme' when values in a given year were greater (positive extreme events), or less (negative extreme events) than two standard deviations from long-term means.

	Mean	SD	Range	Positive Extreme Events	Negative Extreme Events
Maximum temperature (°C)					
September	18.54	1.53	15.2 – 23.2	7	1
October	14.19	1.37	11.0 – 18.9	7	5
November	9.7	1.45	6.1 – 13.5	4	6
December	7.34	1.92	0.2 – 13.6	1	4
Minimum temperature (°C)					
September	9.9	1.17	7.0 – 13.5	3	3
October	6.93	1.59	2.3 – 11.1	5	3
November	3.74	1.58	0.0 – 8.4	3	5
December	2.32	1.83	-2.2 – 8.3	1	7
Days of air frost					
September	0.01	0.08	0 – 1	1	0
October	1.25	1.93	0 – 9	11	0
November	5.23	3.97	0 – 17	6	0
December	8.25	5.2	0 – 25	6	0
Rainfall (mm)					
September	55.83	34.07	2.6 – 156.1	7	0
October	66.97	37.23	5.0 – 192.9	6	0
November	60.85	32.07	4.8 – 175.5	6	0
December	60.1	32.4	7.8 – 147.9	9	0

There were, on average, 3.3 ± 4.55 SD days of frost per autumnal month (range: 0 to 25), with 17 years exhibiting extreme frost patterns. Congruent with long-term temperature trends, there was a significant decrease in the number of days with air frost over time ($F_{[1,161]} = 13.96$, $P < 0.001$, $R^2 = 0.08$; Fig. 5.8c).

Long-term temperature increases were relatively consistent across all the autumnal months. Consequently, the amplitude of difference between months exhibited a negative, albeit non-significant trend (maximum: $F_{[1,161]} = 2.39$, $P = 0.12$, $R^2 = 0.015$; Fig. 5.8d; minimum: $F_{[1,161]} = 2.02$, $P = 0.16$, $R^2 = 0.012$; Fig. 5.8e) temperatures.

5.7.2 Rainfall

Total monthly rainfall in autumnal months averaged 60.94 mm ± 34.16 SD (range: 2.6 to 192.9 mm), with 26 years exhibiting extreme rainfall patterns (Table 5.8). Autumn rainfall did not exhibit any predictable intra-annual trends (Fig. 5.10b), nor was there any significant trend in mean autumnal rainfall (Sep

– Dec) over the 162 year period ($F_{[1,161]} = 0.53$, $P = 0.47$, $R^2 = 0.003$; Fig. 5.8f).

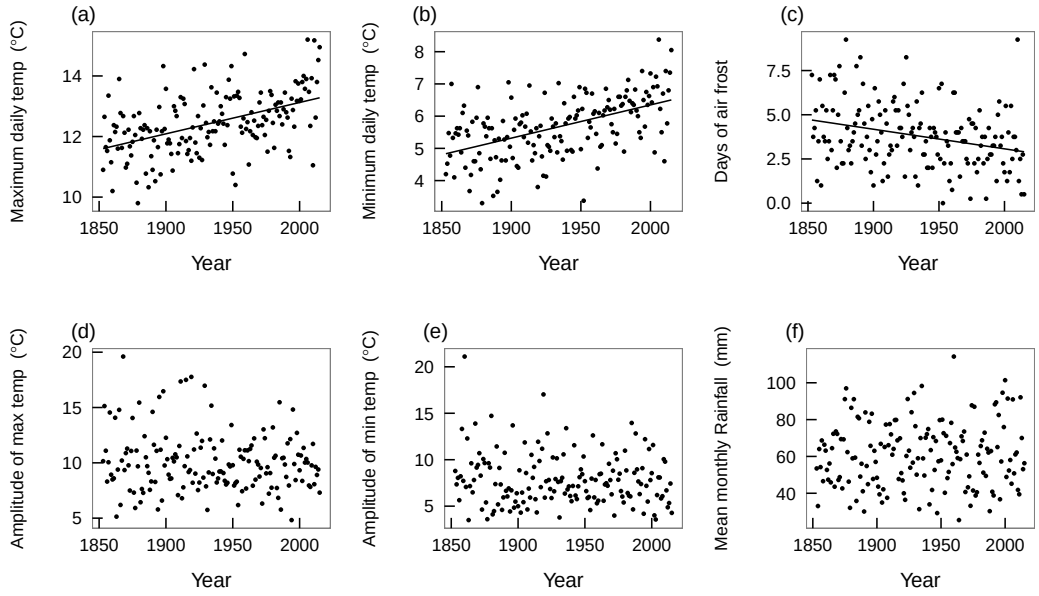

Figure 5.8: Scatterplots depicting autumnal (Sep – Dec) trends in weather parameters over the 162 years for which data were available (1853 – 2015). Trend lines denote statistically significant correlations.

5.7.3 Temporal trends in extreme weather events

Extreme weather events occurred at a mean frequency of 1.88 ± 1.76 SD times *per annum* (range: 0 to 11). There was no evidence for a trend in the frequency of extreme weather *per annum* ($F_{[1,161]} = 1.08$, $P = 0.30$, $R^2 = 0.01$; Fig. 5.9a). There was however, a significant increase in the frequency of temperature events that were warmer than long-term means ($F_{[1,161]} = 25.51$, $P < 0.001$, $R^2 = 0.14$; Fig. 5.9b), and a significant decrease in the frequency of temperature events that were colder than long-term means ($F_{[1,161]} = 18.60$, $P < 0.001$, $R^2 = 0.10$; Fig. 5.9c). In contrast the frequency of extreme rainfall events did not vary with time ($F_{[1,161]} = 0.19$, $P = 0.67$, $R^2 < 0.01$; Fig. 5.9d). It should be noted however, that as rainfall could never be lower than 0mm, all extreme events were the result of rainfall exceeding long-term means.

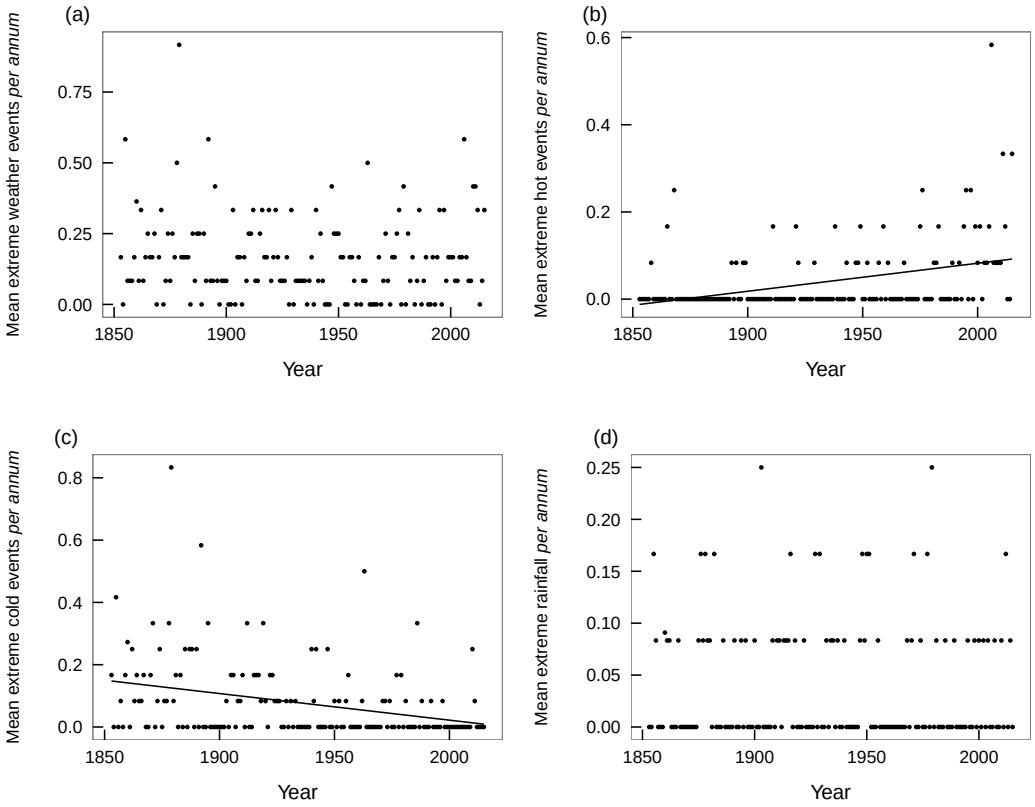

Figure 5.9: Scatterplots depicting; (a) the mean frequency of extreme events for all weather parameters; (b) instances where temperature parameters were two SD greater than long-term means, or days of air frost two SD less than the mean; (c) instances where temperature parameters were two SD less than long-term means, or days of air frost two SD greater than the mean; and (d) rainfall events that were classified as extreme. Trend lines denote statistically significant correlations.

5.8 Appendix S3

In this appendix we provide analyses on the sett microclimate over the course of the study period, establishing setts as thermal refugia.

Sett entrance microclimate was measured at six of the nine sett sites monitored; three main setts ($\geq$ 10 entrance holes); and three outlying setts (two entrance holes). Temperature and humidity data loggers (Lascar Electronics, Salisbury, UK), set at a 5 min sampling rate, were secured 1m inside of sett entrances. Although conditions within the sett differ asymptotically from above-ground conditions up to a depth of 3 m (Kaneko et al., 2010), a depth of 1 m was selected here as this represents the depth at which both main, and outlying setts begin to reach a thermal plateau. Thus, a tunnel depth of 1 m has sufficient thermal stability to provide an accurate estimate of deeper internal temperature. This depth and also represents the point inside the sett from which badgers consider the suitability of external weather when making their decisions on whether to leave the sett or not (Noonan et al., 2014; 2015a).

Due to main setts including more burrow entrances, data loggers were placed at two entrances, selected at random, versus a single data logger at outlying setts. Temperature and humidity records at main setts were then averaged between loggers. Data were collected continuously from September 2, 2014 to December 10, 2014, with a gap between October 8 to 14, 2014 when logger batteries were changed and the equipment was re-calibrated, generating a total of 26,817 data points per sett logger.

On a *per diem* basis, mean above-ground temperature did not differ significantly from temperatures 1m inside sett entrances at main setts (paired t-test: t_{93} = -1.72, $P = 0.089$), or outliers (paired t-test: t_{93}= -0.74, $P = 0.46$). There was also no significant difference in temperature stability at a depth of 1m between outliers and main setts (Levene's: $F_{[1,187]} = 0.30$, $P = 0.584$). Over time, however, sett temperatures were significantly more stable than above-ground temperatures (Levene's: $F_{[1,187]} = 2.64$, $P <$0.005; Table 5.7); where the proportion of time per diem that temperatures in sett entrances remained warmer

than above-ground temperatures increased significantly over the autumnal period (sett: $r = 0.579$, $n = 94$, $P < 0.005$; outlier: $r = 0.613$, $n = 94$, $P < 0.005$; Fig. 5.10).

Table 5.7: Mean ± SD, and variance (CV) in temperature (°C), and humidity (RH) over the study period (2 September 2014 to 10 December 2014). Setts were sampled at a depth of 1m.

	Above-ground	**Main sett**	**Outlying sett**
Mean temp	10.7 ± 4.1	11.1 ± 2.5	11.0 ± 2.7
Temp CV	41.80%	22.70%	24.50%
Mean RH	96.8 ± 6.1	105.0 ± 1.8	103.5 ± 2.3
RH CV	7.50%	1.80%	2.50%

Mean *per diem* humidity was also significantly higher in both main setts and outliers than above-ground (paired t-test: $t_{93} = -14.5$, $P < 0.005$; $t_{93} = -13.6$, $P < 0.005$, respectively). As with temperature, at a 1m depth, relative humidity was significantly more stable in main and outlying setts than above-ground (Levene's: $F_{[1,187]} = 114.95$, $P < 0.005$; $F_{[1,187]} = 4.30$, $P = 0.040$, respectively). Unlike temperature, sett conditions were consistently more humid than those above-ground, and therefore it was impossible to investigate any trends in proportional differences.

Implicitly, it cannot rain within setts, thus no comparison between conditions within the sett and above-ground was made.

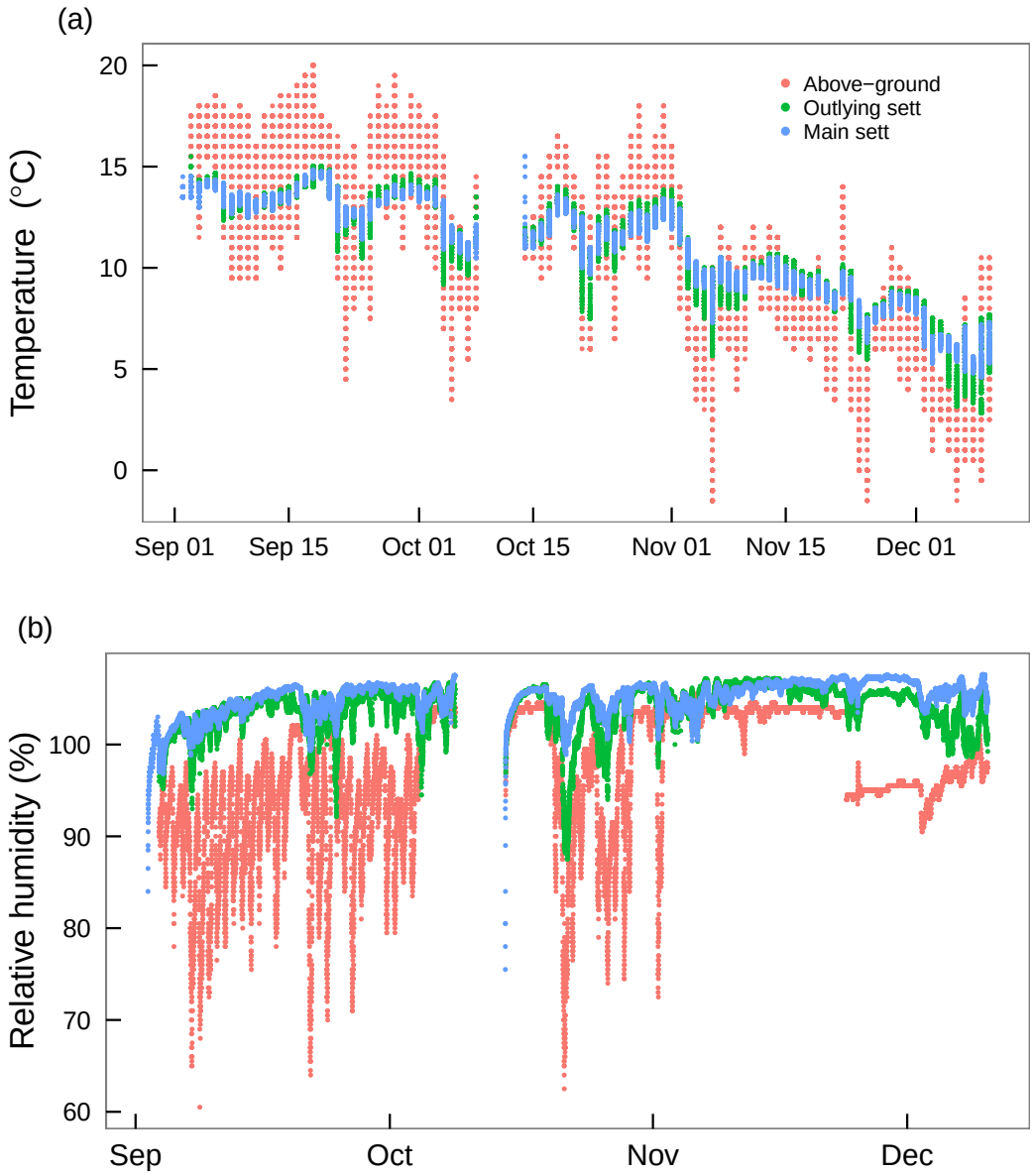

Figure 5.10: Scatter plots depicting a) temperatures, and b) relative humidity in main setts, outlying setts, and the above-ground environment over the 2014 study period (2 September to 10 December), sampled at 5 minute intervals. Main, and outlying setts were sampled at a depth of 1m.

5.9 Appendix S4

In this appendix, we provide details of predicted proportional changes in badger activity (Table 5.8) and energy expenditure (Table 5.9) in relation to climate projections under the IPCCs low emissions scenario SRES B1, and high emissions scenario SRES A1F1. The B1 scenario predicts an increase in atmospheric CO_2 to 500 to 600 ppm over the next century, resulting in a 1.1 to 2.9 °C rise in mean temperature and with no significant trends in precipitation. The A1F1 scenario predicts an increase in atmospheric CO_2 to 550 to 750 ppm over the next century, resulting in a 2.4 to 6.4 °C rise in mean temperature and a 0 to 5% decrease in relative humidity, with no significant trends in precipitation. These data exist as mean monthly values for seven overlapping time-periods; 2010 – 2039; 2020 – 2049; 2030 – 2059; 2040 – 2069; 2050 – 2079; 2060 – 2089; 2070 – 2099. Predictive models were parameterised based on the models presented in text.

Table 5.8: Proportional change in the duration (in hours) of *per diem* activity predicted under the IPCCs low emissions scenario SRES B1 climate projections for each time-period in comparison to *per diem* means exhibited by collared badgers in the present study. The standard deviation (SD) of means from the present study are also presented.

			Proportional Change						
Date	**Hrs**	**SD**	**2010 - 2039**	**2020 - 2049**	**2030 - 2059**	**2040 - 2069**	**2050 - 2079**	**2060 - 2089**	**2070 - 2099**
14-08-25	9.16	2.25	1.09	1.09	1.10	1.10	1.10	1.10	1.10
14-08-26	9.51	1.50	1.05	1.05	1.06	1.06	1.06	1.06	1.06
14-08-27	9.71	1.61	1.03	1.03	1.03	1.03	1.04	1.04	1.04
14-08-28	10.20	1.71	0.98	0.98	0.98	0.98	0.99	0.99	0.99
14-08-29	10.11	0.83	0.99	0.99	0.99	0.99	0.99	0.99	0.99
14-08-30	9.81	1.05	1.02	1.02	1.02	1.02	1.02	1.02	1.02
14-08-31	10.55	0.22	0.95	0.95	0.95	0.95	0.95	0.95	0.95
14-09-01	10.23	0.95	0.97	0.97	0.97	0.97	0.97	0.97	0.97
14-09-02	10.83	0.53	0.92	0.92	0.92	0.92	0.92	0.92	0.92
14-09-03	9.81	1.26	1.01	1.01	1.01	1.01	1.01	1.02	1.02
14-09-04	9.76	1.17	1.02	1.02	1.02	1.02	1.02	1.02	1.02
14-09-05	9.33	2.18	1.06	1.06	1.07	1.07	1.07	1.07	1.07
14-09-06	9.90	1.65	1.00	1.00	1.00	1.00	1.01	1.01	1.01
14-09-07	9.16	1.89	1.08	1.08	1.08	1.09	1.09	1.09	1.09
14-09-08	8.62	2.11	1.15	1.15	1.15	1.15	1.15	1.16	1.16
14-09-09	8.90	2.07	1.11	1.12	1.12	1.12	1.12	1.12	1.12
14-09-10	8.54	1.56	1.16	1.16	1.16	1.16	1.17	1.17	1.17
14-09-11	8.90	2.48	1.11	1.12	1.12	1.12	1.12	1.12	1.12
14-09-12	10.17	1.56	0.98	0.98	0.98	0.98	0.98	0.98	0.98
14-09-13	10.51	0.72	0.94	0.94	0.95	0.95	0.95	0.95	0.95
14-09-14	10.23	0.72	0.97	0.97	0.97	0.97	0.97	0.97	0.97
14-09-15	9.12	1.75	1.09	1.09	1.09	1.09	1.09	1.09	1.09
14-09-16	9.69	1.82	1.02	1.02	1.03	1.03	1.03	1.03	1.03
14-09-17	9.41	1.67	1.05	1.05	1.06	1.06	1.06	1.06	1.06
14-09-18	9.65	1.64	1.03	1.03	1.03	1.03	1.03	1.03	1.03
14-09-19	9.20	1.52	1.08	1.08	1.08	1.08	1.08	1.08	1.08
14-09-20	9.61	2.28	1.03	1.03	1.03	1.03	1.04	1.04	1.04
14-09-21	9.34	2.07	1.06	1.06	1.06	1.06	1.07	1.07	1.07
14-09-22	9.93	1.21	1.00	1.00	1.00	1.00	1.00	1.00	1.00
14-09-23	8.59	2.60	1.15	1.16	1.16	1.16	1.16	1.16	1.16
14-09-24	8.92	1.71	1.11	1.11	1.11	1.11	1.12	1.12	1.12
14-09-25	9.56	2.36	1.04	1.04	1.04	1.04	1.04	1.04	1.04
14-09-26	10.04	1.71	0.99	0.99	0.99	0.99	0.99	0.99	0.99
14-09-27	8.33	1.67	1.19	1.19	1.19	1.19	1.19	1.20	1.20
14-09-28	9.60	2.05	1.03	1.03	1.03	1.04	1.04	1.04	1.04
14-09-29	10.35	1.19	0.96	0.96	0.96	0.96	0.96	0.96	0.96
14-09-30	10.32	1.73	0.96	0.96	0.96	0.96	0.96	0.97	0.97

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Table 5.8 – continued from previous page

			Proportional Change						
Date	**Hrs**	**SD**	**2010 - 2039**	**2020 - 2049**	**2030 - 2059**	**2040 - 2069**	**2050 - 2079**	**2060 - 2089**	**2070 - 2099**
14-10-01	8.66	1.83	1.13	1.13	1.14	1.14	1.14	1.14	1.14
14-10-02	10.23	2.02	0.96	0.96	0.96	0.96	0.96	0.96	0.96
14-10-03	10.44	0.85	0.94	0.94	0.94	0.94	0.94	0.94	0.94
14-10-04	10.56	1.45	0.93	0.93	0.93	0.93	0.93	0.93	0.93
14-10-05	11.21	1.68	0.88	0.88	0.88	0.88	0.88	0.88	0.88
14-10-06	10.31	1.27	0.95	0.95	0.95	0.95	0.96	0.96	0.96
14-10-07	10.33	1.15	0.95	0.95	0.95	0.95	0.95	0.95	0.95
14-10-08	10.83	1.69	0.91	0.91	0.91	0.91	0.91	0.91	0.91
14-10-09	10.56	0.89	0.93	0.93	0.93	0.93	0.93	0.93	0.93
14-10-10	10.93	1.15	0.90	0.90	0.90	0.90	0.90	0.90	0.90
14-10-11	10.25	1.98	0.96	0.96	0.96	0.96	0.96	0.96	0.96
14-10-12	11.14	1.67	0.88	0.88	0.88	0.88	0.88	0.88	0.88
14-10-13	9.64	1.12	1.02	1.02	1.02	1.02	1.02	1.02	1.02
14-10-14	10.66	0.91	0.92	0.92	0.92	0.92	0.92	0.92	0.92
14-10-15	10.41	1.38	0.94	0.94	0.94	0.95	0.95	0.95	0.95
14-10-16	10.93	0.93	0.90	0.90	0.90	0.90	0.90	0.90	0.90
14-10-17	10.61	1.31	0.92	0.93	0.93	0.93	0.93	0.93	0.93
14-10-18	11.07	1.03	0.89	0.89	0.89	0.89	0.89	0.89	0.89
14-10-19	10.26	0.96	0.96	0.96	0.96	0.96	0.96	0.96	0.96
14-10-20	10.25	1.36	0.96	0.96	0.96	0.96	0.96	0.96	0.96
14-10-21	9.45	2.19	1.04	1.04	1.04	1.04	1.04	1.04	1.04
14-10-22	10.65	1.75	0.92	0.92	0.92	0.92	0.92	0.92	0.93
14-10-23	11.70	1.21	0.84	0.84	0.84	0.84	0.84	0.84	0.84
14-10-24	10.59	1.86	0.93	0.93	0.93	0.93	0.93	0.93	0.93
14-10-25	11.16	1.34	0.88	0.88	0.88	0.88	0.88	0.88	0.88
14-10-26	10.85	1.30	0.90	0.91	0.91	0.91	0.91	0.91	0.91
14-10-27	10.89	1.51	0.90	0.90	0.90	0.90	0.90	0.90	0.91
14-10-28	11.12	1.00	0.88	0.88	0.88	0.88	0.89	0.89	0.89
14-10-29	9.86	0.96	0.99	1.00	1.00	1.00	1.00	1.00	1.00
14-10-30	11.15	0.92	0.88	0.88	0.88	0.88	0.88	0.88	0.88
14-10-31	10.99	1.42	0.89	0.89	0.90	0.90	0.90	0.90	0.90
14-11-01	10.42	1.94	0.92	0.93	0.93	0.93	0.93	0.93	0.93
14-11-02	9.67	1.03	1.00	1.00	1.00	1.00	1.00	1.00	1.00
14-11-03	4.85	3.16	1.99	1.99	1.99	1.99	2.00	2.00	2.00
14-11-04	5.79	4.75	1.66	1.67	1.67	1.67	1.67	1.67	1.67
14-11-05	5.57	2.79	1.73	1.73	1.73	1.73	1.74	1.74	1.74
14-11-06	9.18	2.21	1.05	1.05	1.05	1.05	1.05	1.05	1.06
14-11-07	4.32	6.10	2.23	2.23	2.24	2.24	2.24	2.24	2.25

Table 5.9: Proportional change in the duration (in hours) of *per diem* activity predicted under the IPCCs high emissions scenario SRES A1F1 climate projections for each time-period in comparison to *per diem* means exhibited by collared badgers in the present study. The standard deviation (SD) of means from the present study are also presented.

			Proportional Change						
Date	**Hrs**	**SD**	**2010 - 2039**	**2020 - 2049**	**2030 - 2059**	**2040 - 2069**	**2050 - 2079**	**2060 - 2089**	**2070 - 2099**
14-08-25	9.16	2.25	1.09	1.09	1.10	1.10	1.10	1.10	1.10
14-08-26	9.51	1.50	1.05	1.05	1.06	1.06	1.06	1.06	1.06
14-08-27	9.71	1.61	1.03	1.03	1.03	1.04	1.04	1.04	1.04
14-08-28	10.20	1.71	0.98	0.98	0.98	0.99	0.99	0.99	0.99
14-08-29	10.11	0.83	0.99	0.99	0.99	0.99	1.00	1.00	1.00
14-08-30	9.81	1.05	1.02	1.02	1.02	1.02	1.03	1.03	1.03
14-08-31	10.55	0.22	0.95	0.95	0.95	0.95	0.95	0.96	0.96
14-09-01	10.23	0.95	0.97	0.97	0.97	0.97	0.98	0.98	0.98
14-09-02	10.83	0.53	0.92	0.92	0.92	0.92	0.92	0.92	0.93
14-09-03	9.81	1.26	1.01	1.01	1.01	1.02	1.02	1.02	1.02
14-09-04	9.76	1.17	1.02	1.02	1.02	1.02	1.02	1.03	1.03
14-09-05	9.33	2.18	1.06	1.07	1.07	1.07	1.07	1.07	1.08
14-09-06	9.90	1.65	1.00	1.00	1.01	1.01	1.01	1.01	1.01
14-09-07	9.16	1.89	1.08	1.08	1.09	1.09	1.09	1.09	1.10
14-09-08	8.62	2.11	1.15	1.15	1.15	1.16	1.16	1.16	1.17
14-09-09	8.90	2.07	1.11	1.12	1.12	1.12	1.12	1.13	1.13
14-09-10	8.54	1.56	1.16	1.16	1.17	1.17	1.17	1.17	1.18
14-09-11	8.90	2.48	1.11	1.12	1.12	1.12	1.12	1.13	1.13
14-09-12	10.17	1.56	0.98	0.98	0.98	0.98	0.98	0.98	0.99
14-09-13	10.51	0.72	0.94	0.95	0.95	0.95	0.95	0.95	0.95
14-09-14	10.23	0.72	0.97	0.97	0.97	0.97	0.98	0.98	0.98
14-09-15	9.12	1.75	1.09	1.09	1.09	1.09	1.10	1.10	1.10
14-09-16	9.69	1.82	1.02	1.03	1.03	1.03	1.03	1.03	1.04
14-09-17	9.41	1.67	1.05	1.06	1.06	1.06	1.06	1.06	1.07
14-09-18	9.65	1.64	1.03	1.03	1.03	1.03	1.03	1.04	1.04
14-09-19	9.20	1.52	1.08	1.08	1.08	1.08	1.09	1.09	1.09
14-09-20	9.61	2.28	1.03	1.03	1.04	1.04	1.04	1.04	1.04
14-09-21	9.34	2.07	1.06	1.06	1.07	1.07	1.07	1.07	1.07
14-09-22	9.93	1.21	1.00	1.00	1.00	1.00	1.01	1.01	1.01
14-09-23	8.59	2.60	1.16	1.16	1.16	1.16	1.16	1.17	1.17
14-09-24	8.92	1.71	1.11	1.11	1.12	1.12	1.12	1.12	1.13

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Table 5.9 – continued from previous page

			Proportional Change						
Date	Hrs	SD	2010 - 2039	2020 - 2049	2030 - 2059	2040 - 2069	2050 - 2079	2060 - 2089	2070 - 2099
14-09-25	9.56	2.36	1.04	1.04	1.04	1.04	1.04	1.05	1.05
14-09-26	10.04	1.71	0.99	0.99	0.99	0.99	0.99	1.00	1.00
14-09-27	8.33	1.67	1.19	1.19	1.19	1.20	1.20	1.20	1.21
14-09-28	9.60	2.05	1.03	1.03	1.04	1.04	1.04	1.04	1.05
14-09-29	10.35	1.19	0.96	0.96	0.96	0.96	0.96	0.97	0.97
14-09-30	10.32	1.73	0.96	0.96	0.96	0.97	0.97	0.97	0.97
14-10-01	8.66	1.83	1.07	1.07	1.08	1.08	1.08	1.09	1.09
14-10-02	10.23	2.02	0.91	0.91	0.91	0.91	0.92	0.92	0.92
14-10-03	10.44	0.85	0.89	0.89	0.89	0.90	0.90	0.90	0.90
14-10-04	10.56	1.45	0.88	0.88	0.88	0.89	0.89	0.89	0.89
14-10-05	11.21	1.68	0.83	0.83	0.83	0.83	0.84	0.84	0.84
14-10-06	10.31	1.27	0.90	0.90	0.90	0.91	0.91	0.91	0.91
14-10-07	10.33	1.15	0.90	0.90	0.90	0.90	0.91	0.91	0.91
14-10-08	10.83	1.69	0.86	0.86	0.86	0.86	0.87	0.87	0.87
14-10-09	10.56	0.89	0.88	0.88	0.88	0.88	0.89	0.89	0.89
14-10-10	10.93	1.15	0.85	0.85	0.85	0.86	0.86	0.86	0.86
14-10-11	10.25	1.98	0.91	0.91	0.91	0.91	0.91	0.92	0.92
14-10-12	11.14	1.67	0.83	0.84	0.84	0.84	0.84	0.84	0.85
14-10-13	9.64	1.12	0.96	0.97	0.97	0.97	0.97	0.97	0.98
14-10-14	10.66	0.91	0.87	0.87	0.87	0.88	0.88	0.88	0.88
14-10-15	10.41	1.38	0.89	0.89	0.90	0.90	0.90	0.90	0.90
14-10-16	10.93	0.93	0.85	0.85	0.85	0.86	0.86	0.86	0.86
14-10-17	10.61	1.31	0.88	0.88	0.88	0.88	0.88	0.89	0.89
14-10-18	11.07	1.03	0.84	0.84	0.84	0.84	0.85	0.85	0.85
14-10-19	10.26	0.96	0.91	0.91	0.91	0.91	0.91	0.92	0.92
14-10-20	10.25	1.36	0.91	0.91	0.91	0.91	0.91	0.92	0.92
14-10-21	9.45	2.19	0.98	0.98	0.99	0.99	0.99	0.99	1.00
14-10-22	10.65	1.75	0.87	0.87	0.88	0.88	0.88	0.88	0.88
14-10-23	11.70	1.21	0.79	0.80	0.80	0.80	0.80	0.80	0.81
14-10-24	10.59	1.86	0.88	0.88	0.88	0.88	0.88	0.89	0.89
14-10-25	11.16	1.34	0.83	0.83	0.84	0.84	0.84	0.84	0.84
14-10-26	10.85	1.30	0.86	0.86	0.86	0.86	0.86	0.87	0.87
14-10-27	10.89	1.51	0.85	0.85	0.86	0.86	0.86	0.86	0.86
14-10-28	11.12	1.00	0.83	0.84	0.84	0.84	0.84	0.84	0.85
14-10-29	9.86	0.96	0.94	0.94	0.95	0.95	0.95	0.95	0.96
14-10-30	11.15	0.92	0.83	0.83	0.84	0.84	0.84	0.84	0.84
14-10-31	10.99	1.42	0.84	0.85	0.85	0.85	0.85	0.86	0.86
14-11-01	10.42	1.94	0.92	0.93	0.93	0.93	0.93	0.93	0.94
14-11-02	9.67	1.03	1.00	1.00	1.00	1.00	1.00	1.01	1.01
14-11-03	4.85	3.16	1.99	1.99	1.99	2.00	2.00	2.01	2.01
14-11-04	5.79	4.75	1.66	1.67	1.67	1.67	1.68	1.68	1.69
14-11-05	5.57	2.79	1.73	1.73	1.74	1.74	1.74	1.75	1.75
14-11-06	9.18	2.21	1.05	1.05	1.05	1.06	1.06	1.06	1.06
14-11-07	4.32	6.10	2.23	2.24	2.24	2.24	2.25	2.26	2.26

Table 5.10: Proportional change in *per diem* hourly ODBA (in g) expenditure predicted under the IPCCs low emissions scenario SRES B1 climate projections for each time-period in comparison to *per diem* means exhibited by collared badgers in the present study. The standard deviations (SD) of mean ODBA expenditure from the present study are also presented.

			Proportional Change						
Date	ODBA	SD	2010 - 2039	2020 - 2049	2030 - 2059	2040 - 2069	2050 - 2079	2060 - 2089	2070 - 2099
14-08-25	0.64	0.12	1.04	1.04	1.04	1.04	1.04	1.05	1.05
14-08-26	0.70	0.12	0.94	0.95	0.95	0.95	0.95	0.95	0.95
14-08-27	0.67	0.10	0.98	0.99	0.99	0.99	0.99	0.99	0.99
14-08-28	0.69	0.07	0.96	0.96	0.96	0.97	0.97	0.97	0.97
14-08-29	0.68	0.10	0.97	0.97	0.98	0.98	0.98	0.98	0.98
14-08-30	0.67	0.03	0.98	0.99	0.99	0.99	0.99	0.99	0.99
14-08-31	0.73	0.07	0.90	0.90	0.91	0.91	0.91	0.91	0.91
14-09-01	0.73	0.03	0.89	0.89	0.89	0.89	0.89	0.89	0.89
14-09-02	0.76	0.05	0.86	0.86	0.86	0.86	0.86	0.86	0.86
14-09-03	0.66	0.10	0.99	0.99	0.99	0.99	0.99	0.99	0.99
14-09-04	0.64	0.09	1.01	1.01	1.02	1.02	1.02	1.02	1.02
14-09-05	0.62	0.14	1.04	1.04	1.04	1.04	1.05	1.05	1.05
14-09-06	0.61	0.13	1.06	1.06	1.06	1.06	1.06	1.06	1.06
14-09-07	0.61	0.12	1.06	1.06	1.06	1.06	1.06	1.06	1.06
14-09-08	0.61	0.12	1.07	1.07	1.07	1.07	1.07	1.07	1.07
14-09-09	0.63	0.12	1.03	1.03	1.03	1.03	1.04	1.04	1.04
14-09-10	0.65	0.11	1.00	1.00	1.00	1.00	1.00	1.00	1.00
14-09-11	0.65	0.09	0.99	0.99	0.99	0.99	1.00	1.00	1.00
14-09-12	0.64	0.12	1.02	1.02	1.02	1.02	1.02	1.02	1.03
14-09-13	0.64	0.12	1.02	1.02	1.02	1.02	1.02	1.02	1.02
14-09-14	0.66	0.06	0.98	0.98	0.98	0.99	0.99	0.99	0.99
14-09-15	0.65	0.13	1.00	1.00	1.00	1.00	1.00	1.00	1.01
14-09-16	0.59	0.12	1.10	1.10	1.10	1.10	1.11	1.11	1.11
14-09-17	0.63	0.08	1.02	1.02	1.02	1.02	1.03	1.03	1.03
14-09-18	0.62	0.13	1.05	1.05	1.05	1.06	1.06	1.06	1.06

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Table 5.10 – continued from previous page

			Proportional Change						
Date	ODBA	SD	2010 - 2039	2020 - 2049	2030 - 2059	2040 - 2069	2050 - 2079	2060 - 2089	2070 - 2099
14-09-19	0.61	0.14	1.06	1.06	1.06	1.06	1.06	1.06	1.06
14-09-20	0.66	0.12	0.98	0.98	0.98	0.98	0.98	0.98	0.98
14-09-21	0.68	0.11	0.96	0.96	0.96	0.96	0.96	0.96	0.97
14-09-22	0.65	0.14	0.99	0.99	0.99	0.99	0.99	1.00	1.00
14-09-23	0.63	0.14	1.03	1.03	1.04	1.04	1.04	1.04	1.04
14-09-24	0.64	0.14	1.02	1.02	1.02	1.02	1.02	1.03	1.03
14-09-25	0.64	0.14	1.02	1.02	1.02	1.02	1.02	1.02	1.02
14-09-26	0.62	0.12	1.05	1.05	1.05	1.05	1.05	1.05	1.05
14-09-27	0.58	0.11	1.12	1.12	1.12	1.12	1.12	1.12	1.12
14-09-28	0.61	0.11	1.07	1.07	1.07	1.07	1.07	1.07	1.07
14-09-29	0.61	0.11	1.06	1.06	1.06	1.06	1.07	1.07	1.07
14-09-30	0.63	0.14	1.03	1.03	1.03	1.03	1.04	1.04	1.04
14-10-01	0.61	0.13	1.04	1.04	1.04	1.04	1.04	1.04	1.04
14-10-02	0.62	0.10	1.02	1.03	1.03	1.03	1.03	1.03	1.03
14-10-03	0.63	0.12	1.01	1.01	1.01	1.01	1.01	1.01	1.01
14-10-04	0.66	0.12	0.96	0.97	0.97	0.97	0.97	0.97	0.97
14-10-05	0.68	0.14	0.94	0.94	0.94	0.94	0.94	0.94	0.94
14-10-06	0.61	0.15	1.04	1.04	1.04	1.04	1.04	1.04	1.04
14-10-07	0.58	0.13	1.10	1.10	1.10	1.10	1.10	1.10	1.10
14-10-08	0.58	0.12	1.10	1.10	1.10	1.10	1.10	1.10	1.10
14-10-09	0.58	0.13	1.09	1.09	1.09	1.09	1.09	1.09	1.09
14-10-10	0.59	0.11	1.08	1.08	1.09	1.09	1.09	1.09	1.09
14-10-11	0.62	0.10	1.02	1.02	1.03	1.03	1.03	1.03	1.03
14-10-12	0.62	0.11	1.02	1.03	1.03	1.03	1.03	1.03	1.03
14-10-13	0.53	0.10	1.19	1.20	1.20	1.20	1.20	1.20	1.20
14-10-14	0.54	0.08	1.17	1.17	1.17	1.17	1.17	1.17	1.17
14-10-15	0.52	0.09	1.21	1.21	1.21	1.21	1.22	1.22	1.22
14-10-16	0.55	0.08	1.16	1.16	1.16	1.16	1.16	1.16	1.16
14-10-17	0.55	0.08	1.15	1.15	1.15	1.15	1.15	1.15	1.15
14-10-18	0.55	0.08	1.15	1.15	1.15	1.15	1.15	1.15	1.15
14-10-19	0.54	0.13	1.18	1.18	1.18	1.18	1.18	1.18	1.18
14-10-20	0.57	0.11	1.11	1.11	1.11	1.11	1.12	1.12	1.12
14-10-21	0.65	0.12	0.97	0.97	0.97	0.97	0.97	0.97	0.98
14-10-22	0.62	0.11	1.03	1.03	1.03	1.03	1.03	1.03	1.03
14-10-23	0.57	0.11	1.12	1.12	1.12	1.12	1.12	1.12	1.13
14-10-24	0.61	0.12	1.04	1.04	1.04	1.04	1.04	1.04	1.04
14-10-25	0.60	0.13	1.06	1.06	1.06	1.06	1.06	1.06	1.06
14-10-26	0.61	0.15	1.04	1.04	1.04	1.04	1.04	1.04	1.04
14-10-27	0.61	0.17	1.04	1.04	1.04	1.04	1.04	1.04	1.05
14-10-28	0.53	0.09	1.20	1.20	1.20	1.20	1.20	1.20	1.20
14-10-29	0.50	0.12	1.26	1.26	1.27	1.27	1.27	1.27	1.27
14-10-30	0.51	0.12	1.24	1.24	1.24	1.24	1.24	1.24	1.24
14-10-31	0.51	0.09	1.25	1.25	1.25	1.25	1.26	1.26	1.26
14-11-01	0.56	0.10	1.13	1.13	1.13	1.13	1.13	1.13	1.13
14-11-02	0.53	0.11	1.18	1.18	1.18	1.18	1.18	1.18	1.18
14-11-03	0.56	0.20	1.12	1.12	1.12	1.12	1.12	1.12	1.12
14-11-04	0.50	0.15	1.26	1.26	1.26	1.26	1.26	1.26	1.26
14-11-05	0.56	0.20	1.12	1.12	1.12	1.12	1.13	1.13	1.13
14-11-06	0.48	0.09	1.30	1.30	1.30	1.30	1.30	1.30	1.30

Table 5.11: Proportional change in *per diem* hourly ODBA (in g) expenditure predicted under the IPCCs high emissions scenario SRES A1F1 climate projections for each time-period in comparison to *per diem* means exhibited by collared badgers in the present study. The standard deviations (SD) of mean ODBA expenditure from the present study are also presented.

			Proportional Change						
Date	ODBA	SD	2010 - 2039	2020 - 2049	2030 - 2059	2040 - 2069	2050 - 2079	2060 - 2089	2070 - 2099
14-08-25	0.64	0.12	1.04	1.04	1.04	1.05	1.05	1.06	1.06
14-08-26	0.70	0.12	0.94	0.94	0.94	0.96	0.96	0.96	0.97
14-08-27	0.67	0.10	0.98	0.98	0.98	1.00	1.00	1.00	1.01
14-08-28	0.69	0.07	0.96	0.96	0.96	0.97	0.98	0.98	0.98
14-08-29	0.68	0.10	0.97	0.97	0.97	0.99	0.99	0.99	1.00
14-08-30	0.67	0.03	0.98	0.98	0.98	1.00	1.00	1.00	1.01
14-08-31	0.73	0.07	0.90	0.90	0.90	0.92	0.92	0.92	0.93
14-09-01	0.73	0.03	0.89	0.89	0.89	0.89	0.90	0.90	0.90
14-09-02	0.76	0.05	0.86	0.86	0.86	0.86	0.87	0.87	0.87
14-09-03	0.66	0.10	0.98	0.99	0.99	0.99	0.99	0.99	1.00
14-09-04	0.64	0.09	1.01	1.02	1.02	1.02	1.02	1.02	1.03
14-09-05	0.62	0.14	1.04	1.04	1.05	1.05	1.05	1.05	1.05
14-09-06	0.61	0.13	1.06	1.06	1.06	1.06	1.07	1.07	1.07
14-09-07	0.61	0.12	1.06	1.06	1.06	1.06	1.07	1.07	1.07
14-09-08	0.61	0.12	1.07	1.07	1.07	1.07	1.08	1.08	1.08
14-09-09	0.63	0.12	1.03	1.03	1.04	1.04	1.04	1.04	1.04
14-09-10	0.65	0.11	1.00	1.00	1.00	1.00	1.01	1.01	1.01
14-09-11	0.65	0.09	0.99	0.99	1.00	1.00	1.00	1.00	1.00
14-09-12	0.64	0.12	1.02	1.02	1.02	1.03	1.03	1.03	1.03
14-09-13	0.64	0.12	1.02	1.02	1.02	1.02	1.03	1.03	1.03

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Table 5.11 – continued from previous page

			Proportional Change						
Date	ODBA	SD	2010 - 2039	2020 - 2049	2030 - 2059	2040 - 2069	2050 - 2079	2060 - 2089	2070 - 2099
14-09-14	0.66	0.06	0.98	0.99	0.99	0.99	0.99	0.99	0.99
14-09-15	0.65	0.13	1.00	1.00	1.00	1.01	1.01	1.01	1.01
14-09-16	0.59	0.12	1.10	1.10	1.11	1.11	1.11	1.11	1.11
14-09-17	0.63	0.08	1.02	1.02	1.03	1.03	1.03	1.03	1.03
14-09-18	0.62	0.13	1.05	1.06	1.06	1.06	1.06	1.06	1.07
14-09-19	0.61	0.14	1.05	1.06	1.06	1.06	1.06	1.07	1.07
14-09-20	0.66	0.12	0.98	0.98	0.98	0.98	0.99	0.99	0.99
14-09-21	0.68	0.11	0.96	0.96	0.96	0.97	0.97	0.97	0.97
14-09-22	0.65	0.14	0.99	0.99	0.99	1.00	1.00	1.00	1.00
14-09-23	0.63	0.14	1.03	1.04	1.04	1.04	1.04	1.05	1.05
14-09-24	0.64	0.14	1.02	1.02	1.02	1.03	1.03	1.03	1.03
14-09-25	0.64	0.14	1.02	1.02	1.02	1.02	1.02	1.03	1.03
14-09-26	0.62	0.12	1.05	1.05	1.05	1.05	1.06	1.06	1.06
14-09-27	0.58	0.11	1.12	1.12	1.12	1.12	1.13	1.13	1.13
14-09-28	0.61	0.11	1.06	1.07	1.07	1.07	1.07	1.08	1.08
14-09-29	0.61	0.11	1.06	1.06	1.07	1.07	1.07	1.07	1.07
14-09-30	0.63	0.14	1.03	1.03	1.03	1.04	1.04	1.04	1.04
14-10-01	0.61	0.13	1.04	1.04	1.04	1.04	1.04	1.04	1.05
14-10-02	0.62	0.10	1.03	1.03	1.03	1.03	1.03	1.03	1.03
14-10-03	0.63	0.12	1.01	1.01	1.01	1.02	1.02	1.02	1.02
14-10-04	0.66	0.12	0.97	0.97	0.97	0.97	0.97	0.97	0.97
14-10-05	0.68	0.14	0.94	0.94	0.94	0.94	0.94	0.94	0.95
14-10-06	0.61	0.15	1.04	1.04	1.04	1.05	1.05	1.05	1.05
14-10-07	0.58	0.13	1.10	1.10	1.10	1.10	1.10	1.11	1.11
14-10-08	0.58	0.12	1.10	1.10	1.10	1.10	1.11	1.11	1.11
14-10-09	0.58	0.13	1.09	1.09	1.09	1.10	1.10	1.10	1.10
14-10-10	0.59	0.11	1.09	1.09	1.09	1.09	1.09	1.09	1.09
14-10-11	0.62	0.10	1.03	1.03	1.03	1.03	1.03	1.03	1.03
14-10-12	0.62	0.11	1.03	1.03	1.03	1.03	1.03	1.03	1.03
14-10-13	0.53	0.10	1.20	1.20	1.20	1.20	1.20	1.20	1.20
14-10-14	0.54	0.08	1.17	1.17	1.17	1.17	1.17	1.18	1.18
14-10-15	0.52	0.09	1.21	1.22	1.22	1.22	1.22	1.22	1.22
14-10-16	0.55	0.08	1.16	1.16	1.16	1.16	1.16	1.16	1.17
14-10-17	0.55	0.08	1.15	1.15	1.15	1.16	1.16	1.16	1.16
14-10-18	0.55	0.08	1.15	1.15	1.15	1.15	1.16	1.16	1.16
14-10-19	0.54	0.13	1.18	1.18	1.18	1.18	1.18	1.18	1.19
14-10-20	0.57	0.11	1.11	1.12	1.12	1.12	1.12	1.12	1.12
14-10-21	0.65	0.12	0.97	0.98	0.98	0.98	0.98	0.98	0.98
14-10-22	0.62	0.11	1.03	1.03	1.03	1.04	1.04	1.04	1.04
14-10-23	0.57	0.11	1.12	1.13	1.13	1.13	1.13	1.13	1.13
14-10-24	0.61	0.12	1.04	1.04	1.04	1.05	1.05	1.05	1.05
14-10-25	0.60	0.13	1.06	1.06	1.06	1.06	1.06	1.06	1.07
14-10-26	0.61	0.15	1.04	1.04	1.04	1.04	1.04	1.04	1.05
14-10-27	0.61	0.17	1.04	1.05	1.05	1.05	1.05	1.05	1.05
14-10-28	0.53	0.09	1.20	1.20	1.20	1.20	1.21	1.21	1.21
14-10-29	0.50	0.12	1.27	1.27	1.27	1.27	1.27	1.27	1.28
14-10-30	0.51	0.12	1.24	1.24	1.24	1.24	1.24	1.25	1.25
14-10-31	0.51	0.09	1.25	1.26	1.26	1.26	1.26	1.26	1.26
14-11-01	0.56	0.10	1.13	1.13	1.13	1.13	1.13	1.13	1.13
14-11-02	0.53	0.11	1.18	1.18	1.18	1.18	1.18	1.18	1.18
14-11-03	0.56	0.20	1.12	1.12	1.12	1.12	1.12	1.13	1.13
14-11-04	0.50	0.15	1.26	1.26	1.26	1.26	1.26	1.26	1.26
14-11-05	0.56	0.20	1.12	1.12	1.13	1.13	1.13	1.13	1.13
14-11-06	0.48	0.09	1.30	1.30	1.30	1.31	1.31	1.31	1.31

Table 5.12: Proportional change in *per diem* sett visits (ha) expenditure predicted under the IPCCs low emissions scenario SRES B1 climate projections for each time-period in comparison to *per diem* means exhibited by collared badgers in the present study. The standard deviations (SD) of mean inter-sett visitation from the present study are also presented.

			Proportional Change						
Date	Sett Visits	SD	2010 - 2039	2020 - 2049	2030 - 2059	2040 - 2069	2050 - 2079	2060 - 2089	2070 - 2099
14-08-25	14.27	0.51	1.13	1.13	1.14	1.14	1.14	1.14	1.14
14-08-26	13.79	1.35	1.17	1.17	1.18	1.18	1.18	1.18	1.18
14-08-27	14.36	1.19	1.12	1.13	1.13	1.13	1.13	1.13	1.14
14-08-28	15.85	0.71	1.02	1.02	1.02	1.02	1.03	1.03	1.03
14-08-29	15.18	1.22	1.06	1.06	1.07	1.07	1.07	1.07	1.07
14-08-30	14.79	1.07	1.09	1.09	1.10	1.10	1.10	1.10	1.10
14-08-31	14.51	1.42	1.11	1.11	1.12	1.12	1.12	1.12	1.12
14-09-01	15.51	0.68	1.02	1.02	1.02	1.02	1.03	1.03	1.03
14-09-02	15.35	1.02	1.03	1.03	1.03	1.03	1.04	1.04	1.04
14-09-03	16.87	2.20	0.93	0.94	0.94	0.94	0.94	0.95	0.95
14-09-04	15.09	1.63	1.04	1.05	1.05	1.05	1.05	1.06	1.06
14-09-05	16.51	1.42	0.95	0.96	0.96	0.96	0.96	0.97	0.97
14-09-06	14.97	1.77	1.05	1.06	1.06	1.06	1.06	1.07	1.07
14-09-07	14.12	1.40	1.12	1.12	1.12	1.12	1.13	1.13	1.13
14-09-08	14.81	1.82	1.06	1.07	1.07	1.07	1.07	1.08	1.08

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Table 5.12 – continued from previous page

			Proportional Change						
Date	Sett Visits	SD	2010 - 2039	2020 - 2049	2030 - 2059	2040 - 2069	2050 - 2079	2060 - 2089	2070 - 2099
14-09-09	15.29	2.41	1.03	1.03	1.04	1.04	1.04	1.04	1.05
14-09-10	14.71	1.39	1.07	1.07	1.08	1.08	1.08	1.08	1.09
14-09-11	16.92	2.75	0.93	0.93	0.94	0.94	0.94	0.94	0.94
14-09-12	14.85	2.39	1.06	1.06	1.07	1.07	1.07	1.07	1.08
14-09-13	17.07	3.57	0.92	0.93	0.93	0.93	0.93	0.93	0.94
14-09-14	16.44	3.69	0.96	0.96	0.96	0.97	0.97	0.97	0.97
14-09-15	16.95	3.53	0.93	0.93	0.93	0.94	0.94	0.94	0.94
14-09-16	17.93	4.02	0.88	0.88	0.88	0.89	0.89	0.89	0.89
14-09-17	15.50	2.99	1.02	1.02	1.02	1.02	1.03	1.03	1.03
14-09-18	18.57	3.82	0.85	0.85	0.85	0.86	0.86	0.86	0.86
14-09-19	16.81	3.76	0.94	0.94	0.94	0.94	0.95	0.95	0.95
14-09-20	17.83	4.48	0.88	0.89	0.89	0.89	0.89	0.89	0.90
14-09-21	14.77	3.23	1.07	1.07	1.07	1.07	1.08	1.08	1.08
14-09-22	15.41	2.69	1.02	1.03	1.03	1.03	1.03	1.04	1.04
14-09-23	14.06	2.37	1.12	1.12	1.13	1.13	1.13	1.13	1.14
14-09-24	17.22	4.68	0.92	0.92	0.92	0.92	0.92	0.93	0.93
14-09-25	17.20	3.27	0.92	0.92	0.92	0.92	0.93	0.93	0.93
14-09-26	18.04	4.88	0.87	0.88	0.88	0.88	0.88	0.88	0.89
14-09-27	16.27	2.94	0.97	0.97	0.97	0.98	0.98	0.98	0.98
14-09-28	16.87	2.16	0.93	0.94	0.94	0.94	0.94	0.95	0.95
14-09-29	15.52	2.48	1.02	1.02	1.02	1.02	1.03	1.03	1.03
14-09-30	16.97	4.33	0.93	0.93	0.93	0.94	0.94	0.94	0.94
14-10-01	17.46	4.27	0.88	0.88	0.88	0.89	0.89	0.89	0.89
14-10-02	15.27	1.95	1.01	1.01	1.01	1.01	1.01	1.02	1.02
14-10-03	17.00	4.00	0.90	0.91	0.91	0.91	0.91	0.91	0.91
14-10-04	14.73	2.09	1.04	1.05	1.05	1.05	1.05	1.05	1.05
14-10-05	15.50	2.04	0.99	0.99	1.00	1.00	1.00	1.00	1.00
14-10-06	15.80	3.27	0.97	0.97	0.98	0.98	0.98	0.98	0.98
14-10-07	15.03	2.44	1.02	1.02	1.03	1.03	1.03	1.03	1.03
14-10-08	15.97	2.13	0.96	0.96	0.97	0.97	0.97	0.97	0.97
14-10-09	16.01	3.08	0.96	0.96	0.96	0.97	0.97	0.97	0.97
14-10-10	15.22	1.31	1.01	1.01	1.01	1.02	1.02	1.02	1.02
14-10-11	15.70	2.18	0.98	0.98	0.98	0.99	0.99	0.99	0.99
14-10-12	16.39	2.54	0.94	0.94	0.94	0.94	0.95	0.95	0.95
14-10-13	14.87	2.13	1.03	1.04	1.04	1.04	1.04	1.04	1.04
14-10-14	16.57	3.57	0.93	0.93	0.93	0.93	0.94	0.94	0.94
14-10-15	16.72	5.11	0.92	0.92	0.92	0.93	0.93	0.93	0.93
14-10-16	15.63	2.65	0.98	0.98	0.99	0.99	0.99	0.99	0.99
14-10-17	15.05	3.13	1.02	1.02	1.03	1.03	1.03	1.03	1.03
14-10-18	14.44	1.34	1.06	1.07	1.07	1.07	1.07	1.07	1.08
14-10-19	16.08	2.07	0.95	0.96	0.96	0.96	0.96	0.96	0.97
14-10-20	15.00	0.84	1.02	1.03	1.03	1.03	1.03	1.03	1.04
14-10-21	15.68	2.41	0.98	0.98	0.99	0.99	0.99	0.99	0.99
14-10-22	15.26	1.69	1.01	1.01	1.01	1.01	1.02	1.02	1.02
14-10-23	14.17	1.19	1.08	1.09	1.09	1.09	1.09	1.09	1.10
14-10-24	15.58	2.56	0.99	0.99	0.99	0.99	0.99	1.00	1.00
14-10-25	13.63	1.23	1.13	1.13	1.13	1.14	1.14	1.14	1.14
14-10-26	15.07	1.96	1.02	1.02	1.03	1.03	1.03	1.03	1.03
14-10-27	14.15	1.71	1.08	1.09	1.09	1.09	1.09	1.10	1.10
14-10-28	14.60	2.31	1.05	1.05	1.06	1.06	1.06	1.06	1.06
14-10-29	14.49	1.62	1.06	1.06	1.07	1.07	1.07	1.07	1.07
14-10-30	14.63	1.63	1.05	1.05	1.06	1.06	1.06	1.06	1.06
14-10-31	15.09	1.95	1.02	1.02	1.02	1.03	1.03	1.03	1.03
14-11-01	13.38	0.84	1.10	1.10	1.11	1.11	1.11	1.11	1.11
14-11-02	15.04	2.62	0.98	0.98	0.98	0.98	0.99	0.99	0.99
14-11-03	14.34	1.33	1.03	1.03	1.03	1.03	1.03	1.04	1.04
14-11-04	14.47	2.43	1.02	1.02	1.02	1.02	1.03	1.03	1.03
14-11-05	14.18	0.74	1.04	1.04	1.04	1.04	1.05	1.05	1.05
14-11-06	16.99	3.69	0.87	0.87	0.87	0.87	0.87	0.87	0.88

Table 5.13: Proportional change in *per diem* sett visits (ha) expenditure predicted under the IPCCs high emissions scenario SRES A1F1 climate projections for each time-period in comparison to *per diem* means exhibited by collared badgers in the present study. The standard deviations (SD) of mean inter-sett visitation from the present study are also presented.

			Proportional Change						
Date	Sett Visits	SD	2010 - 2039	2020 - 2049	2030 - 2059	2040 - 2069	2050 - 2079	2060 - 2089	2070 - 2099
14-08-25	14.27	0.51	1.13	1.13	1.14	1.14	1.15	1.15	1.16
14-08-26	13.79	1.35	1.17	1.17	1.18	1.18	1.19	1.19	1.20
14-08-27	14.36	1.19	1.12	1.13	1.13	1.14	1.14	1.15	1.15
14-08-28	15.85	0.71	1.02	1.02	1.02	1.03	1.03	1.04	1.05
14-08-29	15.18	1.22	1.06	1.06	1.07	1.07	1.08	1.09	1.09
14-08-30	14.79	1.07	1.09	1.09	1.10	1.10	1.11	1.11	1.12
14-08-31	14.51	1.42	1.11	1.11	1.12	1.12	1.13	1.14	1.14
14-09-01	15.51	0.68	1.02	1.02	1.02	1.03	1.03	1.04	1.05
14-09-02	15.35	1.02	1.03	1.03	1.03	1.04	1.05	1.05	1.06
14-09-03	16.87	2.20	0.93	0.94	0.94	0.95	0.95	0.96	0.96

Continued on next page

Table 5.13 – continued from previous page

			Proportional Change						
Date	**Sett Visits**	**SD**	**2010 - 2039**	**2020 - 2049**	**2030 - 2059**	**2040 - 2069**	**2050 - 2079**	**2060 - 2089**	**2070 - 2099**
14-09-04	15.09	1.63	1.04	1.05	1.05	1.06	1.06	1.07	1.08
14-09-05	16.51	1.42	0.95	0.96	0.96	0.97	0.97	0.98	0.98
14-09-06	14.97	1.77	1.05	1.06	1.06	1.07	1.07	1.08	1.09
14-09-07	14.12	1.40	1.12	1.12	1.13	1.13	1.14	1.14	1.15
14-09-08	14.81	1.82	1.06	1.07	1.07	1.08	1.08	1.09	1.10
14-09-09	15.29	2.41	1.03	1.03	1.04	1.04	1.05	1.06	1.06
14-09-10	14.71	1.39	1.07	1.08	1.08	1.09	1.09	1.10	1.10
14-09-11	16.92	2.75	0.93	0.94	0.94	0.94	0.95	0.95	0.96
14-09-12	14.85	2.39	1.06	1.07	1.07	1.07	1.08	1.09	1.09
14-09-13	17.07	3.57	0.92	0.93	0.93	0.94	0.94	0.95	0.95
14-09-14	16.44	3.69	0.96	0.96	0.97	0.97	0.98	0.98	0.99
14-09-15	16.95	3.53	0.93	0.93	0.94	0.94	0.95	0.95	0.96
14-09-16	17.93	4.02	0.88	0.88	0.89	0.89	0.90	0.90	0.91
14-09-17	15.50	2.99	1.02	1.02	1.03	1.03	1.04	1.04	1.05
14-09-18	18.57	3.82	0.85	0.85	0.86	0.86	0.86	0.87	0.87
14-09-19	16.81	3.76	0.94	0.94	0.94	0.95	0.95	0.96	0.97
14-09-20	17.83	4.48	0.88	0.89	0.89	0.90	0.90	0.91	0.91
14-09-21	14.77	3.23	1.07	1.07	1.08	1.08	1.09	1.09	1.10
14-09-22	15.41	2.69	1.02	1.03	1.03	1.04	1.04	1.05	1.05
14-09-23	14.06	2.37	1.12	1.13	1.13	1.14	1.14	1.15	1.16
14-09-24	17.22	4.68	0.92	0.92	0.92	0.93	0.93	0.94	0.94
14-09-25	17.20	3.27	0.92	0.92	0.92	0.93	0.93	0.94	0.94
14-09-26	18.04	4.88	0.87	0.88	0.88	0.89	0.89	0.90	0.90
14-09-27	16.27	2.94	0.97	0.97	0.98	0.98	0.99	0.99	1.00
14-09-28	16.87	2.16	0.93	0.94	0.94	0.95	0.95	0.96	0.96
14-09-29	15.52	2.48	1.02	1.02	1.02	1.03	1.03	1.04	1.05
14-09-30	16.97	4.33	0.93	0.93	0.94	0.94	0.95	0.95	0.96
14-10-01	17.46	4.27	0.78	0.79	0.79	0.79	0.80	0.81	0.81
14-10-02	15.27	1.95	0.90	0.90	0.90	0.91	0.91	0.92	0.92
14-10-03	17.00	4.00	0.81	0.81	0.81	0.82	0.82	0.83	0.83
14-10-04	14.73	2.09	0.93	0.93	0.94	0.94	0.95	0.95	0.96
14-10-05	15.50	2.04	0.88	0.89	0.89	0.90	0.90	0.91	0.91
14-10-06	15.80	3.27	0.87	0.87	0.87	0.88	0.88	0.89	0.89
14-10-07	15.03	2.44	0.91	0.92	0.92	0.92	0.93	0.94	0.94
14-10-08	15.97	2.13	0.86	0.86	0.86	0.87	0.87	0.88	0.88
14-10-09	16.01	3.08	0.86	0.86	0.86	0.87	0.87	0.88	0.88
14-10-10	15.22	1.31	0.90	0.90	0.91	0.91	0.92	0.92	0.93
14-10-11	15.70	2.18	0.87	0.88	0.88	0.88	0.89	0.90	0.90
14-10-12	16.39	2.54	0.84	0.84	0.84	0.85	0.85	0.86	0.86
14-10-13	14.87	2.13	0.92	0.93	0.93	0.93	0.94	0.95	0.95
14-10-14	16.57	3.57	0.83	0.83	0.83	0.84	0.84	0.85	0.85
14-10-15	16.72	5.11	0.82	0.82	0.83	0.83	0.84	0.84	0.84
14-10-16	15.63	2.65	0.88	0.88	0.88	0.89	0.89	0.90	0.90
14-10-17	15.05	3.13	0.91	0.91	0.92	0.92	0.93	0.93	0.94
14-10-18	14.44	1.34	0.95	0.95	0.96	0.96	0.97	0.97	0.98
14-10-19	16.08	2.07	0.85	0.86	0.86	0.86	0.87	0.87	0.88
14-10-20	15.00	0.84	0.91	0.92	0.92	0.92	0.93	0.94	0.94
14-10-21	15.68	2.41	0.87	0.88	0.88	0.89	0.89	0.90	0.90
14-10-22	15.26	1.69	0.90	0.90	0.91	0.91	0.92	0.92	0.93
14-10-23	14.17	1.19	0.97	0.97	0.97	0.98	0.99	0.99	1.00
14-10-24	15.58	2.56	0.88	0.88	0.89	0.89	0.90	0.90	0.91
14-10-25	13.63	1.23	1.00	1.01	1.01	1.02	1.02	1.03	1.04
14-10-26	15.07	1.96	0.91	0.91	0.92	0.92	0.93	0.93	0.94
14-10-27	14.15	1.71	0.97	0.97	0.98	0.98	0.99	0.99	1.00
14-10-28	14.60	2.31	0.94	0.94	0.95	0.95	0.96	0.96	0.97
14-10-29	14.49	1.62	0.95	0.95	0.95	0.96	0.96	0.97	0.97
14-10-30	14.63	1.63	0.94	0.94	0.94	0.95	0.95	0.96	0.97
14-10-31	15.09	1.95	0.91	0.91	0.92	0.92	0.93	0.93	0.94
14-11-01	13.38	0.84	1.10	1.10	1.11	1.11	1.12	1.12	1.13
14-11-02	15.04	2.62	0.98	0.98	0.99	0.99	0.99	1.00	1.00
14-11-03	14.34	1.33	1.03	1.03	1.03	1.04	1.04	1.05	1.05
14-11-04	14.47	2.43	1.02	1.02	1.02	1.03	1.03	1.04	1.04
14-11-05	14.18	0.74	1.04	1.04	1.05	1.05	1.06	1.06	1.07
14-11-06	16.99	3.69	0.87	0.87	0.87	0.88	0.88	0.89	0.89

Part III

Burrow Use and Group-Living In The European Badger

'Once well underground,' he said, 'you know exactly where you are. Nothing can happen to you, and nothing can get at you. You're entirely your own master, and you don't have to consult anybody or mind what they say. Things go on all the same overhead, and you let 'em, and don't bother about 'em. When you want to, up you go and there things are, waiting for you.'

The Badger simply beamed...

– Kenneth Grahame

Chapter 6

The pervasive artefact of rigid social-group structure and spatial segregation: Evidence from European badgers (*Meles meles*)

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6.1 Introduction

Inductive inference is perhaps the greatest risk in scientific inquiry (*sensu* Hume, 1748; see also Popper, 2014). The assumption that a known process or outcome should invariably apply to an unknown threatens the logical certainty (termed 'apodicticity') of the scientific process, from the conception and design of experiments, to the (mis)interpretation of results (Frede, 1996), potentially leading to verisimilitude (e.g., Noonan et al., 2015*a*). Explanations that appear to fit facts well, and appear true, even from empirical testing, are vulnerable to being falsified (Popper, 2014), and alert us to the continuous need to question sources of bias, or logical fallacy (Jungwirth, 1987).

Studies on the social organisation of species are particularly prone to inductive, and anthropocentric bias. Although animal societies exhibit a substantial range of organisational complexity (e.g., Leyhausen, 1965; Eisenberg, 1966; Powell, 1979; Lukas and Clutton-Brock, 2013; Macdonald and Johnson, 2015), they are often classified (perhaps forced) into generalised categories, based either on human conceptions of 'society', or the organisation applied in similar species studied previously (e.g., Trivers, 1971; Kruuk, 1989; Conradt and Roper, 2005; Smith et al., 2012). Technological advances are, however, increasingly revealing that former 'classical' models of social organisation are unnecessarily rigid and even misrepresentative, for example genetic evidence of extra-pair paternity in 'monogamous' species (Griffith et al., 2002; Fossøy et al., 2008); high-resolution tracking data revealing unprecedented levels of intergroup conectivity in 'group-living' species (Schauber et al., 2007; Drewe et al., 2009; Dyo et al., 2010); and social contact networks revealing societal organisation in species categorised as 'solitary' (Yoerg, 1999; Mourier et al., 2012).

Related to misinterpretation of socio-spatial geometries is the conceptual understanding of territorial borders (Powell, 2000). Many truly territorial species actively defend borders (Stamps and Buechner, 1985) – a term derived from the geo-political divides that segregate human societies (of Germanic origin, from the root 'board'; first known use in 14th century naming the boundary between England and Scotland) – for other species, borders increasingly appear not to be rigid territorial boundaries, but permeable contact zones (e.g., Stewart et al., 1997*a*). Application of the generic term 'border' across a range of interface types

has, however, led to ambiguity and the presumption of a particular type of exclusivity, often inconsistent with empirical evidence (Powell, 2000; Tinnesand et al., 2015). In this study we begin with a clean slate (i.e., a '*tabula rassa*' approach; Haig, 1995), grounded in the consilient and pragmatic interpretation of evidence (Thornberg, 2012), seeking to establish the extent to which the interface between groups is permeable, or impermeable, to neighbours. We do so using a group-living mustelid, the European badger (*Meles meles*; henceforth 'badger') as a model species (Stopka and Johnson, 2000), benefitting from how this species, which resides in discrete colonial burrows (termed 'setts' Noonan et al., 2015*b*), demarcates the contact zone between groups with latrines (Roper et al., 1986; Stewart et al., 2001).

Although the fundamental socio-spatial arrangement in mustelids is solitary (Powell, 1979), when local food supply support high local population densities, intra-sexual territoriality develops (Powell, 1979; Johnson et al., 2000). In badgers, if local resource abundance/dispersion are such that territories can further support secondary individuals at little/no cost to the primary occupants (Macdonald, 1983*b*; Macdonald and Johnson, 2015) then group-living, though not necessarily reliant upon cooperative benefits, can persist (reviewed in Johnson et al., 2002*a*). This socio-spatial arrangement, however, has long been considered anomalous within the Family (Powell, 1979), where inconsistencies regarding the role of latrines have resulted in widely varying definitions of badger societies (e.g., Roper et al., 1986; Doncaster and Woodroffe, 1993; Stewart et al., 1997*a*; Blackwell and Macdonald, 2000; Doncaster, 2001; Buesching and Macdonald, 2001; Newman et al., 2011; Tinnesand et al., 2015).

Badgers deploy their faeces systematically, using shared latrines (i.e., a series of localised pits into which faeces are egested, sometimes over-marking preceding faeces left by conspecifcs; Roper et al., 1986; Kilshaw et al., 2009), where anal gland secretion coats faeces and encodes information on both the identity (sex, reproductive condition, etc), and diet of the depositor (Brinck et al., 1983; Buesching et al., 2002*a*,*b*). Saturation of the depositor's home range with indicators that food in this area is being consumed thus signals the extent to which that range is fully exploited (e.g., Roper et al., 1986; Pigozzi, 1990; Stewart et al., 1997*a*; Kilshaw et al., 2009), as well as the identity and condition of the inhabitant(s) (Buesching et al., 2002*a*,*b*; Tinnesand et al., 2015). Badgers also use

subterranean burrows and, in high density regions where groups form (reviewed in Johnson et al., 2002*a*), individuals cohabit in setts (Roper et al., 2001) – although the extent to which badgers share chambers is still relatively unknown (Noonan et al., 2015*b*). Territoriality is typically tested via bait-marking surveys (e.g., Roper et al., 1993; Doncaster and Woodroffe, 1993; Kilshaw et al., 2009), a technique derived from monitoring spotted hyenas (*Crocuta crocuta*; Kruuk, 1989). These inevitably link latrines to the coloured bait provisioned at each sett, but an error rate with respect to strict territorial borders is always found – where the accepted methodology is to discard 'erroneous' data (see Delahay et al., 2000). The combination of badgers residing in a 'central-place', and an interface with surrounding groups at shared latrines (Roper et al., 1986; Delahay et al., 2000; Kilshaw et al., 2009), leads to a tessellated socio-spatial geometry across inhabited landscapes (Doncaster and Woodroffe, 1993; Blackwell and Macdonald, 2000; Doncaster, 2001; Stewart et al., 2001).

Two mutually exclusive hypotheses have been proposed to account for this spatial arrangement of latrines: i) the Active Territorial Defence Hypothesis (ATDH; Stewart et al., 1997*a*) which states that latrines serve as 'scent fences', demarcating the borders between groups (Kruuk, 1978; Roper et al., 1993; Doncaster and Woodroffe, 1993; Delahay et al., 2000), where trespassing individuals are expected to be subject to aggressive eviction (Roper et al., 1993); or ii) the Passive Range Exclusion Hypothesis (PREH; Stewart et al., 1997*a*), which states that latrines serve as informations sites (Buesching and Macdonald, 2001; Tinnesand et al., 2015), and accumulate at borders as these are the isopleths of resource depletion between groups (Stewart et al., 2001). Badger movement patterns within this 'territorial' framework however, challenge predictions of the ATDH (e.g., Christian, 1995; Woodroffe et al., 1995; Byrne et al., 2014; Noonan et al., 2015*b*). For example, long-term trapping records show that on any given night, ca. 20% of the population are on a temporary inter-group visit (Macdonald et al., 2008). A lack of fighting wounds on 'trespassing' individuals (Macdonald et al., 2015), and 50% extra-group paternity, within a polygynandrous and promiscuous framework (Carpenter et al., 2005; Dugdale et al., 2007; Annavi et al., 2014), further suggest that as 'hard borders' latrines are totally ineffective. Indeed, the passive range exclusion hypothesis (Stewart et al., 1997*a*), and the individual advertisement function of latrines (Buesching

and Macdonald, 2001) are proving increasingly plausible; where latrines function as 'signposts', as opposed to 'keep out signs' (Tinnesand et al., 2015).

Here, we test for rational consistency (*sensu* Schick, 1963) in the way badger society is actually structured; permitting this to be more intricate, and flexible than previous bounds have compelled (e.g., Kruuk, 1978; Roper et al., 1993; Delahay et al., 2000). Specifically, we examine i) whether the organisation of badger latrines demark spatially explicit territories; and ii) whether individuals are restricted to these bait-marked territories with respect to a) their above-ground movement; and b) their patterns of sett use. Deviations from strict territoriality (i.e., regular transgressions beyond latrine-marked 'borders', and visits to neighbouring group setts) would refute the predictions of the ATDH in favour of the null-hypotheses that badgers are unimpeded by any inferred group structure, and a secondary functions of latrines (Buesching and Macdonald, 2001). We then contrast these results with pre-established models of badger socio-ecology to demonstrate that caution is required when studying group-living species to avoid the application of assumptions and inductive inference (*sensu* Popper, 2014).

6.2 Methods

This study was conducted in Wytham Woods, Oxfordshire (GPS reference: 51°46'26"N; 1°19'19"W); a 424-ha mixed semi-natural woodland designated a Site of Special Scientific Interest (SSSI), and maintained by the University of Oxford (for a detailed description of the study site see Savill et al., 2010). The resident, high-density population comprised 23 spatial groups with ca. 145 adults and 52 cubs in 2014 (Noonan et al., 2015*a*). For simplicity, individuals affiliating with an established group of conspecifics, based on recent trapping history (for details see Macdonald et al., 2008), which showed fidelity to a suite of setts within historical bait marking ranges (Kilshaw et al., 2009), are henceforth termed 'spatial groups'.

As part of a long-term trapping regime (for details see Macdonald et al., 2009, 2015), 15 adult badgers (6 males and 9 females; Table 5.1), a subset of the

ca. 32 residents from three adjacent spatial groups (see below), were caught in steel mesh traps (85x37x38 cm), baited with 150g of peanuts placed near the entrances of setts and outlying holes (outliers). Captured animals were transferred to holding cages, between 06:30h and 08:00h, and transported to a field station using an ATV and trailer. There, individuals were sedated by an intramuscular injection of ketamine hydrochloride (0.2 mL/kg body weight; McLaren et al., 2005), sexed, measured to the nearest mm (tip of snout to base of sacrum, laid dorsally), and weighed to the nearest 100 g. From these morphometrics, we calculated the ratio of body mass to length (ln mass:ln length), to generate Body Condition Indices (BCI; Kruuk et al., 1987; Noonan et al., 2014). Following Woodroffe and Macdonald (1995*a*; see also Tinnesand et al., 2015; Chapter Five), female reproductive status was inferred via vulva condition and classified as oestrous (vulva swollen and moist), or non-oestrous (vulva flat and dry). Although all collared males had scrotal testes and were assumed to be in breeding condition, the extent of descent varied between: i) descended into the scrotum, but with restricted lateral movement (classified as 'descended'); and ii) fully scrotal and mobile (classified as 'fully descended').

Captured badgers were then instrumented with custom built tracking tags [39 mm (l) x 22 mm (w) x 12 mm (h)], equipped with magneto-inductive (MI) tracking components, as well as active radio-frequency identification (aRFID), and powered by CR123A lithium batteries (for full details see Noonan et al., 2015*b*). Tags were hermetically sealed in epoxy resin, and mounted onto commercially available leather dog collars (with padded undersides to reduce abrasion), having a complete assembly weight of 95 g. Henceforth, individual badgers are referred to by their unique collar ID.

After handling and collaring, badgers were held in a recovery room for 3 h, before being released at the locations where they were captured (Sun et al., 2015). When recaptured during subsequent trapping events, collars were removed, and animals showed no signs of detrimental wounds or hair loss in response to the collars. All procedures undertaken for this study were covered by both Natural England (2014-5710-SCI-SCI), and Home Office licenses (PPL 30/2385), and approved by the University of Oxford's Animal Welfare and Ethical Review Board.

6.2.1 Bait marking survey

In April 2015, to coincide with the peak in latrine use (Roper et al., 1993), a bait marking survey was carried out to determine patterns of latrine use by badgers (for details see Delahay et al., 2000). This built on historic surveys in which the relatively stable positions of many latrines (Roper et al., 1986) were mapped previously (Kruuk, 1978; Stewart et al., 2001; Kilshaw et al., 2009). Bait consisted of a mixture of peanuts, golden syrup, and indigestible, coloured plastic (alkathene) pellets, 2 mm in diameter (Greyland Plastics, Evesham, United Kingdom), mixed at a ratio of approximately 15:1. Each day, for a period of three weeks, a small amount of bait was placed into burrow entrances at all known sett sites in the ca. 49 ha study (sub-)area. Although Delahay et al. (2000) suggest provisioning bait of a single colour to all setts within one social group, here each sett site was provisioned with different coloured bait, allowing us to retrace the origin of faecal deposits without any assumptions regarding the cohesion among badgers using each sett. In this regard, although we apply the terms 'main sett' and 'outlying sett' throughout, these are in relation to their relative sizes (where main setts had $\geq$ 10 entrance holes, and outlying setts ca. 2-3 entrance holes; see Roper, 1992), as opposed to any inferred social function (e.g., Roper et al., 2001; Weber et al., 2013). After the third week of bait deployment, the surrounding area was surveyed for badger latrines systematically. When a latrine was found, its location, and the number of coloured, and non-coloured faecal deposits were recorded.

For consistency with previous methods (Roper et al., 1993; Delahay et al., 2000), data on the locations of bait-marked latrines were analysed using a minimum-area convex polygon (MCP) approach, via the *R* package '*AdehabitatHR*' (Calenge, 2011), to determine the area marked by individuals from each spatial group. In addition, we also applied a kernel estimation approach, which factors in both the location and number of faecal deposits, to determine the area marked by individuals occupying each sett site (i.e., 'main setts', and 'outliers' separately, independently of any inferred group structure). It should be noted, however, that due to very few latrines occurring in the northernmost section of the survey site, those boundaries were not resolved as robustly.

6.2.2 Quantifying above-ground movements

Badger home ranges can extend beyond the area encompassed by conterminous neighbouring sett sites (e.g., Cheeseman et al., 1988; Kowalczyk et al., 2006; Macdonald et al., 2008; Byrne et al., 2014), however, our focus here concerned overlap with direct neighbours. As such, we used a Eulerian sampling approach to track movement between sett sites, as Lagrangian tracking technologies exhibit limited capabilities in dense vegetation and the subterranean environment (Dyo et al., 2010; Markham et al., 2012; Noonan et al., 2015*b*). All nine setts (three main, and six outlying; Fig. 5.1) in the 49 ha study (sub-)area occupied by three neighbouring spatial groups, were fitted with base-stations equipped with a 2.4 GHz 802.15.14 (Zigbee) receiver, and powered by a 12V battery. These spatial groups were selected for two primary reasons; i) each bordered pastureland and so had direct access to feeding sites, reducing the likelihood that inter-group visits were related to feeding ecology; and ii) despite the presence of latrine marked borders (Kilshaw et al., 2009; Tinnesand et al., 2015), recent analyses indicate a high rate of connectivity (Dugdale et al., 2007; Macdonald et al., 2008; Dyo et al., 2010; Annavi et al., 2014).

Base-stations allowed above-ground detection of animals via aRFID receivers, and the initiation of data transfer. Base stations received collar signals continuously, which were broadcast every 3-s, over a detection range of 15-20m. When a tag was detected, an entry (consisting of a collar id, timestamp, and received signal strength) was generated, stored onboard the collar, and data transfer was initiated. Buffered data were transferred reliably, with two-way handshaking, and saved on a micro-SD card within the base station unit for later retrieval. Proximity data were collected from August 20 2014 until the final collar batteries failed on Nov 5 2014, generating 103,797 relocations across all animals.

We used these proximity data to calculate individual 95% utilisation distributions (henceforth 'inter-sett ranges') within the detection area, as well as both the percentage, and probability of overlapping distributions between individuals (Fieberg and Kochanny, 2009). Inter-sett ranges were calculated with the *R* package '*AdehabitatHR*', using the kernel Brownian bridge method, which accounts for both the utilisation distribution, and the time between successive relocations. For each badger, the smoothing parameter σ^1 was determined using

the maximum likelihood approach developed by Horne et al. (2007), while σ^2, a measure of the imprecision of relocations, was set to 50m (i.e., the maximum aRFID detection diameter). Note, these movement data were limited by the sub-sampling inherent in the Eulerian approach, and are unlikely representative of a badger's complete 'home range' (Powell, 2000). Nonetheless, while the complete range and frequency of these movements will have been higher, these utilisation distributions provide a consistent inter-individual measure of 'inter-sett' visitation.

6.2.3 Quantifying underground sett use

Each of the nine sett sites was equipped with MI detection antennae, which measured entry into the sett, and subsequent time spent therein (for details see Noonan et al., 2015*b*). Antennae consisted of wire loops buried 5 cm below the soil surface, and attached to base units. Base units consisted of a PIC24F48GA002 micro-controller, and ten half-bridge TC4421 MOS-FET drivers, powered by the same 12V battery as aRFID receivers. Operating at a frequency of 125 kHz (Markham et al., 2010*b*), these generated weak magnetic fields directly above the burrows, allowing the presence of collared animals within the sett to be determined at a frequency of one fix per minute. Fixes were stored on-board collars and transferred to base stations using the same two-way handshaking as aboveground fixes. Underground proximity data were collected from August 20 2014 until the final collar batteries failed on Nov 5 2014, generating 176,788 relocations across all animals.

We used these data to calculate individual 95% utilisation distribution between equipped setts, as well as the percentage, and probability of spatial overlap between individuals. Sett-use was calculated using the utilisation distribution kernel method (Worton, 1989) in the *R* package '*AdehabitatHR*'. As with above-ground proximity data, these data were limited by the Eulerian tracking approach employed in this study, and should be considered as representing a minimum estimate of sett use patterns.

6.3 Results

6.3.1 Latrine spatial pattern

157 bait-marked faecal deposits were recorded at 27 latrine sites, within 1 to >40 unique pits at each site. Linking latrines used by individuals originating from each spatial group gave MCPs depicting contiguous territories, (Fig 6.1a).

Interestingly, territories defined by applying kernel estimation to faecal deposits originating from outlying setts and main setts separately, resulted in bait-marked ranges failing to cluster into distinct territories (Fig. 6.1b). Indeed, two setts classified as 'outliers' were encompassed within the marked territories defined for not one, but multiple main setts.

6.3.2 Individual sett use patterns

Congruent with predictions of the ATDH, both males and females predominantly occupied the main sett on which their spatial group's MCP was centred (Fig. 6.2).

There was only a 3.9% (± 9.6%) overlap in sett use among individuals assigned to neighbouring spatial groups. Indeed, only one badger was responsible for this overlap (collar 14, a female in oestrus), which used the main setts encompassed within two neighbouring MCPs. There was no significant difference between sexes in the frequency with which they used monitored setts; $F_{[1,7]} = 3.28$, $p = 0.11$). Although the use of outlying setts increased with BCI in females, but decreased with BCI in males (Fig. 6.3b), small sample size precluded formal statistical analyses.

6.3.3 Above-ground movement patterns

In contrast to patterns of sett use, there was little evidence of active territoriality/exclusivity in above-ground movement; that is, badgers moved regularly between MCP bound spatial groups (Fig. 6.4).

Above-ground, inter-sett ranges exhibited significantly more overlap with badgers resident in their own spatial group than with neighbouring individuals ($\bar{x}$ = 76.0 ± 17.3% vs. $\bar{x}$ = 15.4 ± 17.0%, respectively; $F_{[1,43]} = 129.2$, $p < 0.001$; Fig. 6.5). When compared to patterns of underground sett use however, above-ground, badgers were significantly more likely to have overlap with individuals from neighbouring spatial groups ($F_{[1,51]} = 5.94$, $p = 0.02$), and significantly less likely to have overlap with individuals from their own spatial group ($F_{[1,26]} = 50.77$, $p < 0.005$). Female inter-sett ranges ($\bar{x}$ = 7.06 ± 0.15ha) did not typically include setts outside of their resident MCP, and exhibited only 4.0 ± 5.1% overlap with neighbouring females, driven primarily by female number 14. In contrast, although there was no significant difference in sett visitation patterns between males and females ($\bar{x}$ = 8.67 ± 2.33ha; $F_{[1,8]} = 2.40$, $p = 0.16$), males tended to overlap multiple females, from multiple spatial groups, with a mean overlap of neighbouring females of 12.7 ± 11.1%. In addition to overlapping multiple females however, the suite of setts visited by males resulted in significantly more overlap with extra-group males than the extra-group overlap exhibited between females ($\bar{x}$ = 23.9 ± 16.1%; $F_{[1,29]} = 15.98$, $p < 0.001$). Furthermore, there was a positive relationship between the number of setts used by males and BCI, but no evidence of an allometric relationship in females (Fig. 6.3a), however sample size again prevented any statistical analyses of these relationships.

6.4 Discussion

"Society exists only as a mental concept;
in the real world there are only individuals."

– Oscar Wilde

While melodramatic, Wilde's quip does have some bearing on the examination of animal societies. An unbiased understanding of how individuals – the functional units within these societies – behave allows for the deduction of how their societies operate, avoiding the application of inductive inference (Hume, 1748; Popper, 2014). In this respect, we evidence that although MCPs drawn around bait-marked latrines can depict the semblance of spatially-explicit territories

(*sensu* Delahay et al., 2000), badger movement was not congruent with this territorial framework. Individuals made regular visits to setts outside of their MCP, irrespective of putative borders. Applying the *modus tollens* rule here: if the MCP implies a border, but the border does not restrict movement, then the MCP is artifactual and does not represent a true border. Consequently we reject the hypothesis that badger latrines function as range delimiters (e.g., Doncaster and Woodroffe, 1993; Roper et al., 1993; Delahay et al., 2000), in favour of less agonistic, communicative possibilities (e.g., Buesching and Macdonald, 2001; Tinnesand et al., 2015), and more fluid socio-spatial dynamics generally.

6.4.1 Latrines and 'hard boundaries'

Badgers rely primarily on olfaction to acquire information about their environment (Buesching and Macdonald, 2001). Without any evidence of their function (*sensu* Tinbergen, 1963), it is illogical to infer territoriality based on the position of latrines alone (Jungwirth, 1987). Indeed, the depiction of contiguous, non-overlapping boundaries via latrine locations proved highly dependent on the methodological/statistical procedures employed (see also Blackwell and Macdonald, 2000). For example, while MCPs drawn around latrines supported the appearance of strict (i.e., exclusive) territoriality, kernel estimation, which factors in both the location and number of faecal deposits, did not support clear (i.e., non-overlapping) territorial boundaries. Indeed, multiple setts classified as 'outliers' by MCP standards fell within the marked territories of multiple 'spatial groups'. In short, these two approaches revealed significantly different spatial systems, and exactly why badgers deploy their faeces in these locations can not be deduced from these analyses alone.

Here, investigation into the way latrines are used in parts of their geographic range where badgers are less gregarious proves insightful. Pigozzi (1990) for example, reports that in Italy, where food dispersion results in solitary life-histories, latrine use varied seasonally, and faeces were deposited disproportionately at seasonally limited food source. In addition, the area marked by females

exhibited minimal evidence of seasonality, whereas males extended their territories to coincide with the autumnal breeding season. Similarly, Revilla and Palomares (2002) report that in Spain, where trophic dispersion supports mother-offspring groups resulting from delayed dispersal, latrine use peaked during the mating season, and periods of food scarcity. As such, latrine positioning better supports the 'book keeping' hypothesis (Henry, 1977; see also Remonti et al., 2012; Zhou et al., 2015), where latrines serve to demarcate locations where valuable resources were obtained, rather than the ATDH (Stewart et al., 1997*a*). Interestingly, a similar situation occurs in ecologically similar, albeit solitary hog badgers (*Arctonyx collaris*), which position latrines at scarce, valuable food supplies within their home ranges, rather than at territorial borders (Zhou et al., 2015). In this respect, investigation into the function of olfactory cues, rather than their location, overwhelmingly evidences an 'independent advertisement' role of badger scent marks (Buesching and Macdonald, 2001), where latrines serve to indicate individual presence, condition, and diet (Buesching et al., 2002*a*,*b*), with minimal support for any defensive role (Buesching et al., 2003; Tinnesand et al., 2015).

6.4.2 Above-ground ranging behaviour

By definition, inter-territorial ranging in a species exhibiting active territorial defence should be rare (Stamps and Buechner, 1985; Stewart et al., 1997*a*; Powell, 2000). Inter-group ranging behaviour has been observed previously in badgers (e.g., Woodroffe et al., 1995; Roper et al., 2003; Vicente et al., 2007), however it is often treated as anecdotal evidence of unusual behaviour. Similarly, but in contrast to the ATDH, half of the animals collared here made frequent visits to setts outside of their MCP bound territory; and all collared animals made at least occasional visits to neighbouring spatial groups. Females cohabiting the same main sett occupied a fixed range size, and exhibited minimal range overlap with females from neighbouring spatial groups, whereas male ranges overlapped multiple female ranges from multiple spatial groups. Specifically, we found that male range size tended to increase with BCI, whereas female ranges were independent of BCI. Furthermore, individuals that would classically be defined as constituting a group (i.e., occupying setts within the same MCP; Kruuk, 1989; Doncaster and Woodroffe, 1993; Roper et al., 1993; Delahay et al., 2000), engaged in significantly different ranging behaviour. The 'extra-group'

movement observed in this study further indicate a substantially higher rate of connectivity than would be expected in a classically exclusive territorial species (see also Macdonald et al., 2008; Dugdale et al., 2007, 2008; Annavi et al., 2014).

Again, investigation into the spatial arrangement of badgers in low-density populations proves insightful. For example, Revilla and Palomares (2002) report that in Spain females occupied discrete territories, and their ranging behaviour coincided with latrine marked territories at all times of the year. In contrast, males extended their home ranges during the breeding season to overlap multiple female ranges, irrespective of the spatial arrangement of latrines. Similar patterns are evident in the congeneric Japanese badger (*Meles anakuma*), where females occupy discrete ranges of fixed size, whereas males expand their ranges during the mating season (Kaneko et al., 2014). Indeed intra-sexual territoriality is the most commonly reported socio-spatial arrangement of badgers living in low density populations (Pigozzi, 1990; Kowalczyk et al., 2000; Johnson et al., 2002*a*; Do Linh San et al., 2007); where females are 'obstinate' territorial strategists (*sensu* von Schantz, 1984) occupying territories of constant size to maintain access to resources sufficient to allow them to raise offspring reliably. Although living at much higher densities (>36 badgers/km2 versus <1 badger/km^2 across much of Continental Europe; Johnson et al., 2002*a*), the trends we observed in this population are concordant with the ranging behaviour observed in low density populations.

6.4.3 Patterns of sett use

Although the presence of excavatable sett sites, even at density extremes, tends not to be a limiting factor for badgers (Macdonald et al., 2004*b*), communal denning is common when territories are shared with conspecifics (Roper et al., 2001; Newman et al., 2011; Noonan et al., 2015*b*). Use of underground space has thus been implicated as a fundamental component of badger socio-ecology (Butler and Roper, 1996; Roper et al., 2001; Rogers et al., 2003; Weber et al., 2013; Noonan et al., 2015*b*,*c*), where setts are the focal point of latrine bound territories (Doncaster and Woodroffe, 1993; Doncaster, 2001; Stewart et al., 2001, but see Blackwell and Macdonald 2000). Interestingly, although badgers visited the proximity of neighbouring setts frequently, we found that they

rarely actually entered these setts, evidencing a spatial dichotomy in badger social dynamics (*sensu* Hinze et al., 2013). Indeed, in comparison to the extent of overlap in above-ground ranges. individuals from neighbouring spatial groups were significantly less likely to exhibit overlapping patterns of sett use. This dichotomy likely reflects the interaction between local resource availability/dispersion (Macdonald, 1983*b*; Johnson et al., 2002*b*; Macdonald and Johnson, 2015) on the one hand, versus the benefits of large established setts (Kaneko et al., 2010) and the energetic cost of burrowing (Vleck, 1981; Stewart et al., 1999) on the other. It should also be noted that the allometric relationships we found in above-ground ranging behavior were not repeated in patterns of sett use, however small samples size precludes any firm conclusions of these trends. Although badgers may disperse from their natal group (Woodroffe et al., 1995; Roper et al., 2003; Macdonald et al., 2008; Byrne et al., 2014), Kaneko et al. (2010) found that individuals residing in large, established setts had improved survival and were more philopatric. As such, when local resources can support the energetic requirements of multiple adults (Macdonald, 1983*b*), dispersal can be obviated entirely in favour of shared ranges (reviewed in Johnson et al., 2002*a*). Thus, at higher densities, philopatry at natal setts can result in spatial congregations, albeit the independent nature of their behavioural patterns (Noonan et al., 2014, 2015*b*).

6.4.4 Conclusion

The results of our study demonstrate that the pattern of intra-sexual territoriality badgers exhibit at low-density (e.g., Pigozzi, 1990; Kowalczyk et al., 2000; Revilla and Palomares, 2002; Do Linh San et al., 2007; Kaneko et al., 2014) seems to be conserved within this high-density population. Here, local resources allow for over-laying ranges (*sensu* Macdonald, 1983*b*), creating a mosaic of individualistically motivated patterns, but at high densities present the verisimilitude of sociality. Crucially, this paradigm shift in our understanding of the geometry of badger societies at high densities has practical implications for species management in relation to the control of bovine tuberculosis (*Mycobacterium bovis;* DEFRA, 2014*a*,*b*). While current culling operations and disease transmission models operate under the inference of strict territoriality (Carter et al., 2007; Böhm et al., 2008; Riordan et al., 2011), the behavioural

patterns elucidated here will undoubtedly improve the understanding of these failing (IEP, 2014) practices.

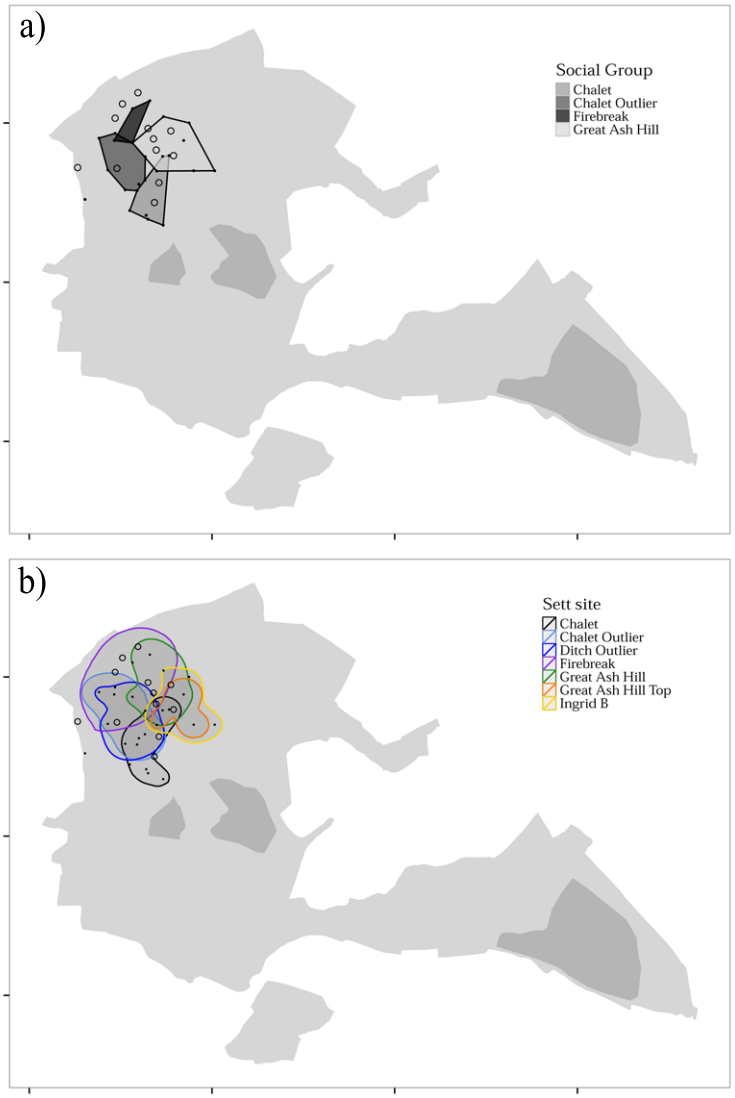

Figure 6.1: Map of the study site depicting; a) Minimum convex polygons (MCPs); and b) kernel utilisation distributions drawn around bait-marked latrine sites. Hollow circles represent sett sites within the surveyed area, and solid circles the location of latrines. Latrines with unmarked faeces were excluded from analyses

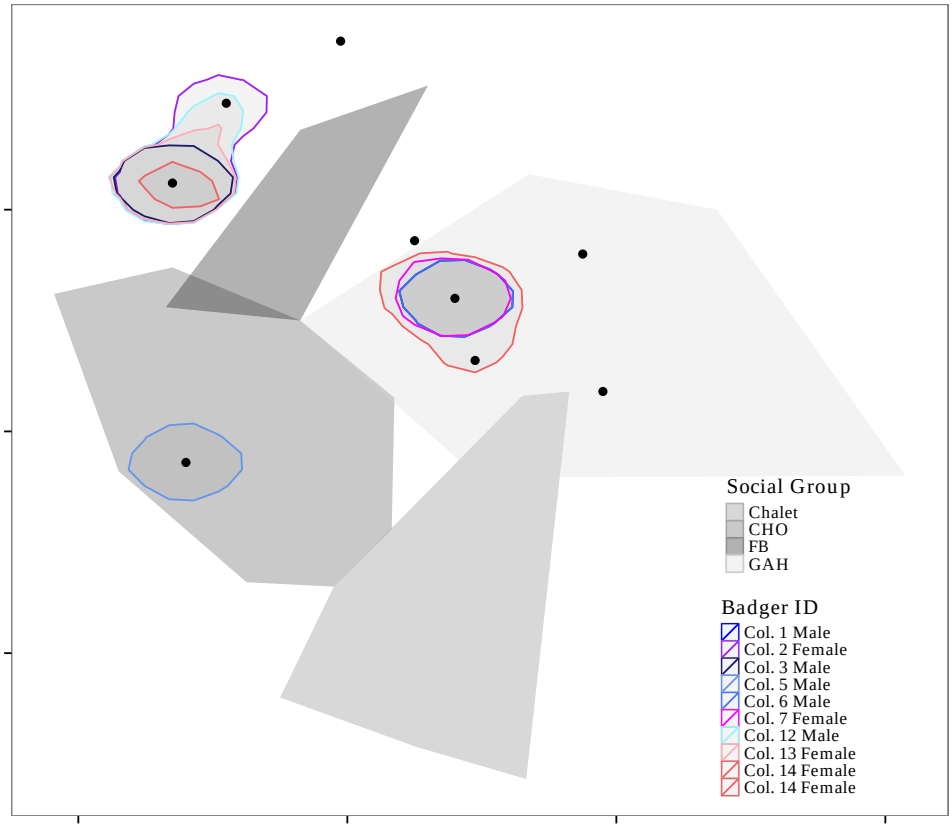

Figure 6.2: Underground 95% utilization distributions collared animals. Solid circles depict the locations of sett sites equipped with MI detection antennae, and shaded areas represent bait marked MCP territories (see Fig. 6.1).

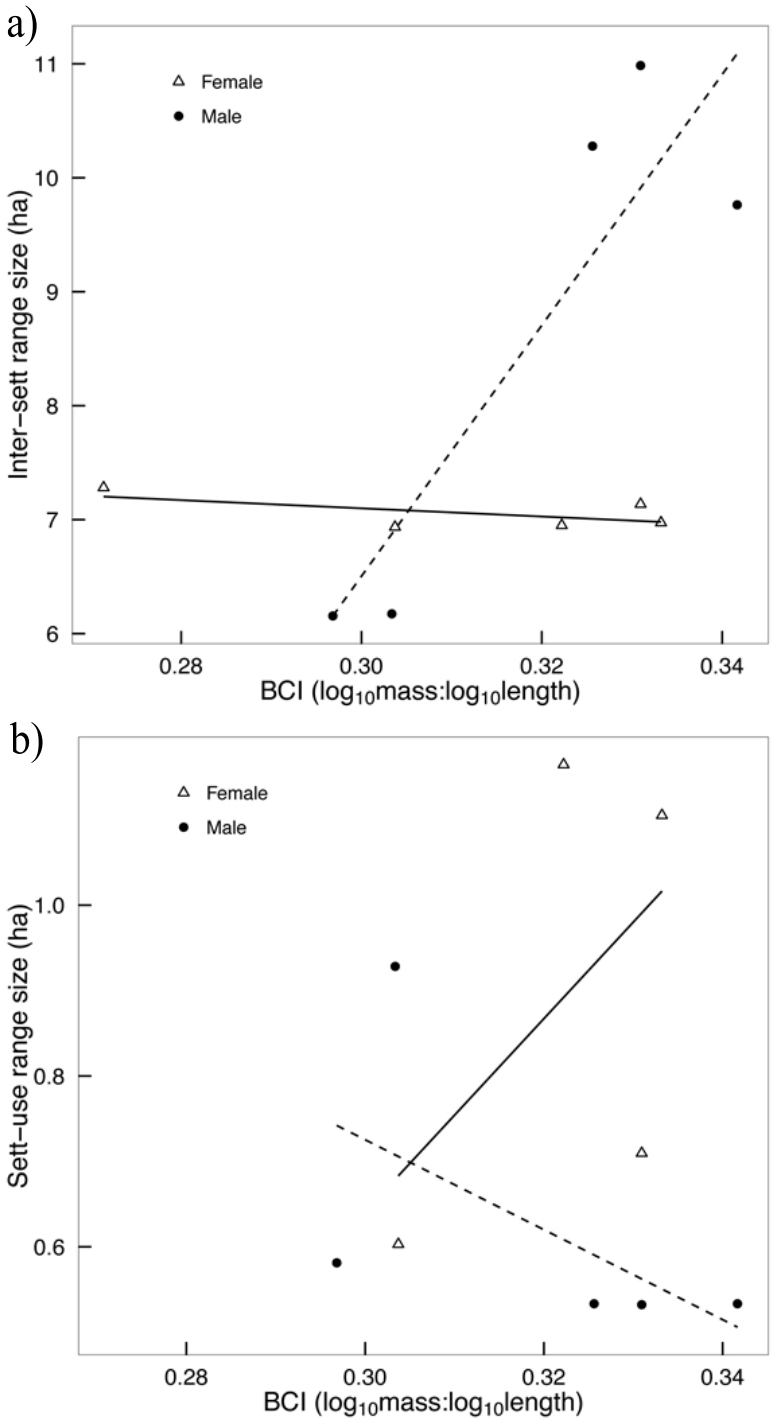

Figure 6.3: Scatter plots depicting; a) above-ground; and b) underground range size as a function of body condition indices (BCI).

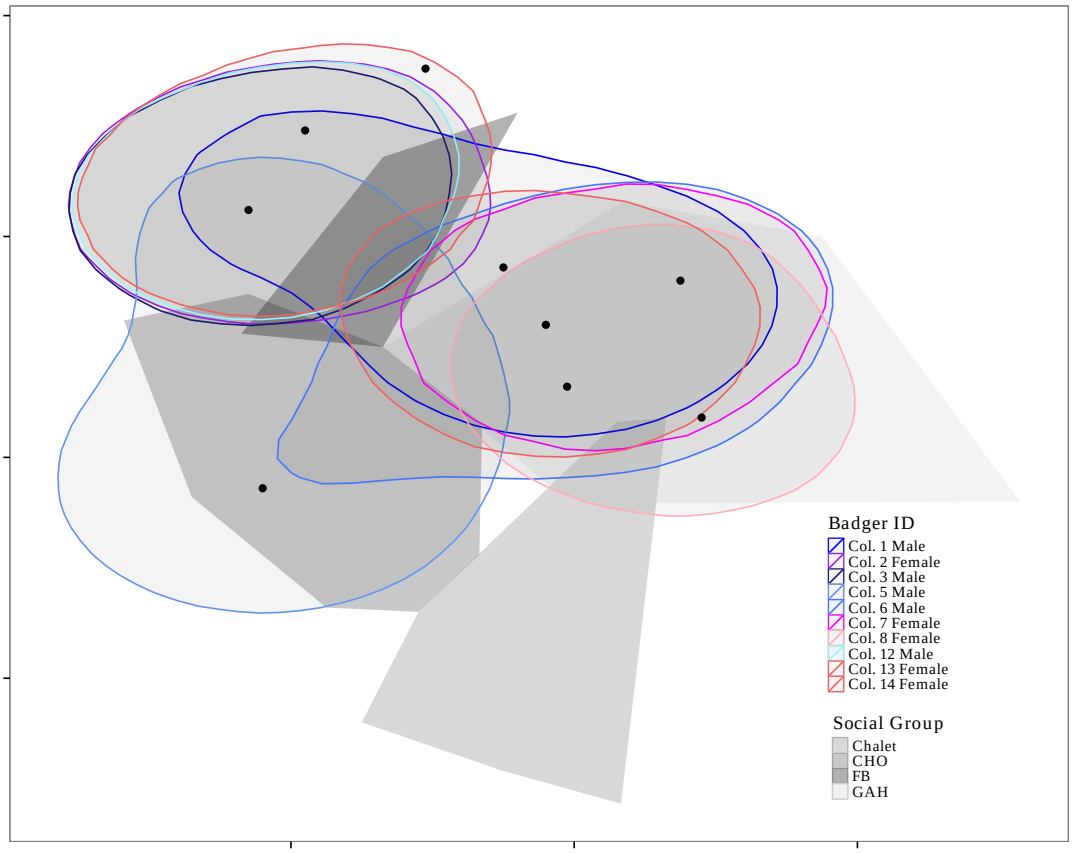

Figure 6.4: Above-ground 95% utilization distributions of collared animals. Solid circles depict the locations of sett sites equipped with aRFID basestations, and shaded areas represent bait marked MCP territories.

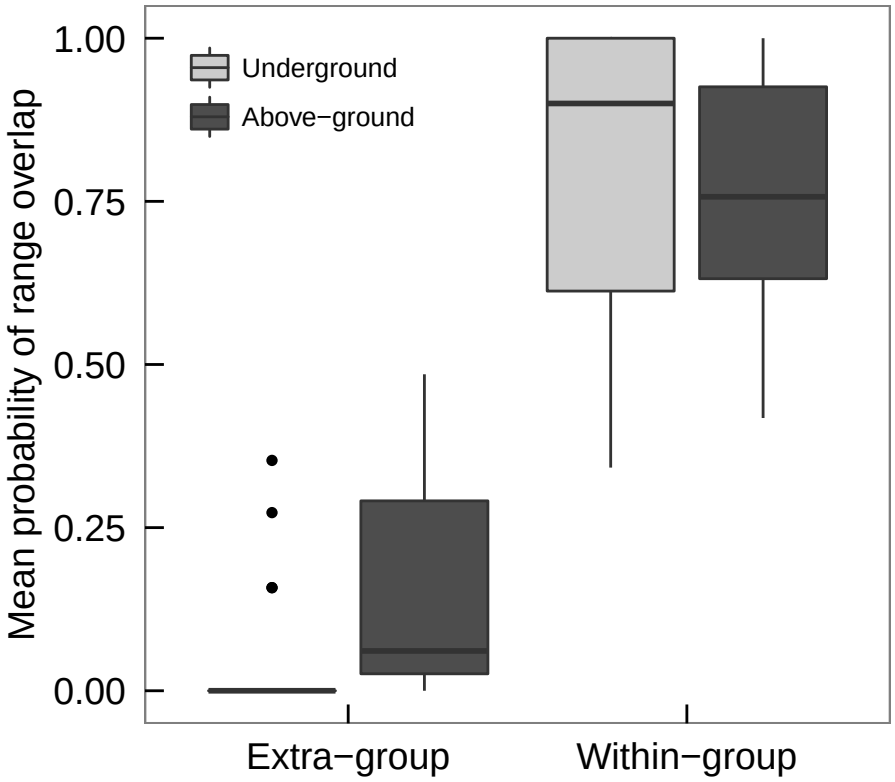

Figure 6.5: Mean ± SD probability of two badgers having overlapping space use over the study period.

Chapter 7

A new Magneto-Inductive tracking technique to uncover subterranean activity: What do animals do underground?

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7.1 Abstract

1. Despite the importance of the subterranean ecotope, knowledge of underground movement and behaviour has been extremely limited. Previous technologies have relied upon techniques with very low spatial or temporal resolution, such as VHF telemetry. Rather incongruously, therefore, relatively simple underground activity regimes have often been assumed, with insufficient attention to the ecological importance of burrow use.

2. We test the capability of Magneto-Inductive (MI) tracking, recording underground movement within a European badger sett over a 2 week period in February. These data allowed us to: quantify subterranean movement; extrapolate the three-dimensional burrow architecture; simultaneously track multiple individuals; and establish the function of specific movement patterns; demonstrating the technique's utility. Contrasting data generated using MI tracking, against the resolution achievable with VHF tracking, we establish how sampling frequency can influence the perception of movement.

3. Taking 20 locational fixes per minute, MI collars operated for 1 year before on-board batteries failed, resulting in an average five billion data points per collar deployment. Socio-ecologically we found that rather than foraging continuously throughout the night, badgers returned to the sett an average of 2.2 times, approximately every 3 – 4 h. From burrow mapping, badgers tended to use peripheral chambers for ca. 45 min on these return visits. These outlying chambers were used less by day, when badgers selected deeper chambers, suggesting each chamber type fulfils a different function. This technology also exposed that badgers exhibited a far greater extent of underground movement than revealed by former technologies, which by comparison captured <0.5% of subterranean activity. Importantly, these high-resolution data showed that individuals left, returned to, and moved about the sett independently, with no tendency for synchronous subterranean activity.

4. In overview, Magneto-Inductive tracking proved relatively simple and cost-effective to deploy, it provided very detailed and accurate subterranean fixes, and was robust enough for long-term field deployment. Furthermore, the capabilities of MI are highly transferable, enabling a better understanding of underground activity and the ecological importance of subterranean burrows for the conservation and management of a wide range of species.

7.2 Introduction

Underground dens and burrow systems are ecologically and sociologically important for a wide range of species. 447 of the 777 genera of extant terrestrial mammals spend a significant proportion of their lives underground (Kinlaw, 1999), varying along a continuum from the totally subterranean naked mole rats (*Heterocephalus glaber*) to species only excavating dens for specific phases of their life-cycle. Burrows are particularly important for various rodents, insectivores and lagomorphs, providing refuge from adverse weather conditions, as well as terrestrial and aerial predators (Reichman and Smith, 1990). In addition, for some of these small burrowers, subterranean tunnels also provide foraging space (e.g., multiple *Rodentia* and *Talpidae spp.* – see Nevo, 1999).

Numerous carnivores also exhibit a critical reliance on underground dens (Case, 1978*a*). Many small-medium sized carnivores are adapted to either excavate prey (exhibiting forelimb anatomy and claws adapted to digging; Hildebrand, 1985), or to pursue prey within burrow networks (e.g., mustelids – Roper, 1992; Zhang et al., 2010; viverids – Jennings et al., 2010; and herpestids – Doolan and Macdonald, 1997; Rathbun and Cowley, 2008). Even larger, less fossorial, carnivores often benefit from the shelter burrows provide and require the protection of dens for key periods, such as during hibernation/torpor (e.g., black bears, *Ursus americanus*, Immell et al., 2013; raccoon dogs, *Nyctereutes procyonoides*, Kitao et al., 2009; and striped skunks, *Mephitis mephitis*, Doty and Dowler, 2009) or while caring for altricial young (typically 6-10 weeks until weaning – Gittleman, 1986); indeed, this neo-natal security function is paramount for juvenile survival and recruitment in a number of species (Derrickson, 1992; Kinlaw, 1999).

Furthermore, either by extension of philopatry (Isbell, 2004) and/or through delayed dispersal (Kokko and Ekman, 2002), dens can facilitate communal aggregation, often being associated with 'social-group' formation; for example, meerkats (*Suricata suricatta*; Manser and Bell, 2004); European badgers (*Meles meles*; Doncaster and Woodroffe, 1993); banded mongooses (*Mungos mungo*; Cant et al., 2013); and spotted hyaenas (*Crocuta crocuta*; Kolowski and Holekamp, 2009). For these social burrowers, dens may also serve as an 'information centre' (Ward and Zahavi, 1973), where frequent returns to a central

place could provide individuals with information on the activities of conspecifics.

Subterranean living is, however, not without challenges – such as hypoxia/hypercapnia, permanent darkness, and conditions of high infectivity (Nevo, 1999), which can lead to the spread of diseases and parasites within communal burrows communicable to humans or livestock. For example, den sharing has been implicated in the incidence of bovine tuberculosis (bTB) infecting a number of social burrowers (e.g., yellow-bellied marmots, *Marmota flaviventris*, Van Vuren, 1996; brushtail possums, *Trichosurus vulpecula*, Whyte et al., 2014; wombats, *Vombatus ursinus*, Skerratt et al., 2004; and European badgers, Weber et al., 2013).

Given these important functions of the subterranean ecotope, den living often plays a key role in life-history evolution, and population structure, making it important to develop more effective and precise tools for investigating fossorial ecology. Competing contemporary techniques, such as GPS, are not effective underground, and because high frequency electromagnetic waves are heavily attenuated by soil and moisture, with path losses of 50 dB/m at 700 MHz (Vuran and Akyildiz, 2010), UHF/VHF methods (e.g., Biggins, 2012; Weber et al., 2013) offer very low spatial or temporal resolution. This typically restricts the application of VHF signals to provide just basic daily fixes for the presence of radio-collared individuals with a burrow system – a labour intensive method. In addition, walking over the burrow surface to detect radio-signals can disturb animals, altering their behaviour. Destructive methods are also typically required to map the architecture of burrow systems (e.g., Roper, 1992). Hitherto, and rather incongruously, in the absence of techniques for depicting underground behaviour accurately, 'inactivity' has often been implied, but without substantive evidence (e.g., Roper, 1992; Broseth et al., 1997; Kowalczyk et al., 2003) – exemplifying 'argument through ignorance' (a fallacy in formal logic; see Walton, 2010).

The aim of this study was to develop technology capable of investigating the knowledge gaps pertaining to underground activity, with high spatial and temporal resolution, and able to detect the position of multiple individuals simultaneously. Objectively, we targeted a cascade of capabilities:

(a) To measure location at a scale capable of distinguishing between fossorial activity/inactivity.

(b) To extrapolate the three-dimensional architecture of complex burrow systems from the movement trajectories recorded.

(c) To generate temporal data able to establish the function of specific underground activity patterns.

(d) To test the capacity of this system to track the subterranean movements of multiple individuals for group-living species, enabling investigation of underground social contacts, pertinent to socio-ecology, disease epidemiology and mating systems.

7.2.1 Proof of concept: A deployment using the European badger

To fulfill our objectives, and cognisant of typical limitations, we investigate here the utility of low frequency magnetic fields for providing subterranean localisation capability; able to penetrate soil, rock and vegetation with negligible attenuation, while being harmless to the subject animal (Markham et al., 2012). We tested our novel Magneto-Inductive (MI) tracking technique on a widely distributed fossorial Carnivore, the European badger, which exhibits varying degrees of sociality over its wide biogeographic range (Johnson et al., 2002*a*). In the UK, groups of up to 25 badgers (Buesching et al., 2003) use often extensive dens, termed 'setts', typically with around 12 entrances (some >80; Roper, 1992). Sett architecture is believed to be quite varied, although investigation has been limited by the need to use destructive mapping (Roper, 1992), where a sett might comprise over 15 m^3 of internal volume, representing around 25 tonnes of soil (Neal and Roper, 1991). Badgers spend a large proportion of their lives underground (see Noonan et al., 2014), and exhibit morphological, physiological and behavioural adaptations for fossoriality (Long and Killingley, 1983). Furthermore, badger setts are often exploited by other mammal species, (i.e., 'kleptoclaustromy'), either commensally (e.g., red foxes, *Vulpes vulpes*, Goszczyński and Wójtowicz, 2001; raccoon dogs, Kowalczyk et al., 2008) or once vacated (e.g., crested porcupines, *Hystrix cristata*, Monetti et al., 2005), and so badgers are in a sense 'keystone' (Mills and Doak, 1993) to the subterranean ecotope.

Despite badger behaviour having been monitored extensively above ground, using video observation (Stewart et al., 1997*b*), and tracking with GPS (Mullen et al., 2013), VHF (Rosalino et al., 2005*a*), and RFID (Dyo et al., 2010), little is known about the patterns and extent of their underground activity and chamber use, and studies tend to opperate under the assumption that each individual utilises only a single chamber during diurnal sett occupation. Indeed, while there is limited existing evidence suggesting that sett excavation and maintenance is influenced by sex and reproductive status (Stewart et al., 1999), and that subterranean chamber use is influenced by season (Kowalczyk et al., 2004) ectoparasitic load (Butler and Roper, 1996; Roper et al., 2001) and bTB infection status (Weber et al., 2013), no study has yet quantified within-sett, multiple-individual, movements on a fine temporal and spatial scale.

Here, we use MI to test this null-hypothesis of relatively simple underground space use and social contact (Roper et al., 2001; Kowalczyk et al., 2003). Our measures of success were to prove able to determine interactions between individuals underground with precision and to quantify the relative use of chambers situated within the sett architecture, as well as transitions between chambers; in turn, enabling the complex burrow system to be plotted in 3-D. We then illustrate how sampling frequency can influence the perception of movement; that is, we contrast our raw data rate of sampling every 3 seconds, which we sub-sampled to yield fixes every 10 minutes, against perceived movement based on the resolution achievable with typical VHF tracking, i.e., positional fixes once *per diem*, or once per hour.

7.3 Methods

7.3.1 Study site

We worked with badgers within the high-density Wytham Woods (Oxfordshire; GPS reference: 51°46'26"N; 1°19'19"W) badger population (36.4 badgers/km^2, SE = 2.55 badgers/km^2 – Macdonald et al., 2009). To maximise potential to record underground movements, we investigated a sett with 12 active holes, excavated on a relatively level surface, bordering permanent pasture and unmanaged woodland, known to have been in existence since at least 1973 (Kruuk,

1978). From concurrent trapping records 15 adult badgers (9 male and 6 female) were resident at this sett.

7.3.2 System development and deployment

The tracking system used lightweight receivers measuring 39mm (l) x 22mm (w) x 12mm (h), (henceforth MI-tags), which we designed and produced ourselves, mounted on commercially available, leather dog collars (with padded undersides to prevent abrasion), with a complete assembly weight of 105g. The receiver component was comprised of a Zigbit A-2 wireless sensor module (consisting of an Atmega-1281V microcontroller and an AT86RF230 2.4 GHz Zigbee compliant radio transceiver), along with an on-board 4 Mbyte flash chip for data storage, powered by a CR123A lithium battery. Because collars can rotate around the animal's neck, MI-tags were also equipped with three, orthogonally mounted detector coils, in a tri-axial arrangement. Each coil detected the magnitude of the received magnetic field independently, decoupling orientation from position, allowing measurements to be made invariant to collar rotations (for detailed calculations, see Markham et al., 2012). MI-tags operated at very low frequencies (f <250 kHz), therefore active power consumption was miniscule (60 – 110 μA) permitting a 100% duty cycle.

We fitted four adult badgers (three males and one female) with MI-tags, during routine trapping in September 2010, following the sedation and handling protocols described by (Macdonald et al., 2009). We allowed 2 cm greater circumferential collar length than the badger's neck size, as not to constrict the airway or cause discomfort (Tuyttens et al., 2002) (Fig. 7.1). When recaptured during subsequent trapping events collars were removed, and animals showed no signs of detrimental wounds or hair loss as a consequence of the collars.

These MI-tags record and store the magnetic field strengths generated by an array of time-multiplexed and digitally coded transmitting antennae, driven by a base unit (see below). Antennae consisted of a rectangular loops of wire that produce a very weak magnetic field directly above an animals' burrow system, allowing the position of the MI-tags within the field to be determined. Through experimental validation (Markham et al., 2010*a*), we found that a carrier frequency of 125 kHz was appropriate, with negligible attenuation even

Figure 7.1: A sedated adult badger wearing an assembled MI tracking collar. Arrow indicates the tag and battery.

when tracking an animal through a few metres of conductive soil.

The number, size and shape of the antennae dictates the system's accuracy. For example, a single coil can infer proximity or 'presence' within a certain region, whereas simultaneous field measurements from multiple spatially displaced coils permit location in two or three dimensions. Simultaneously, the trajectories followed underground map the architecture of the subterranean burrow system. Our base units could accommodate up to 10 antennae, and were comprised of a PIC24F48GA002 microcontroller, and ten half-bridge TC4421 MOSFET drivers, powered by a 12V battery. Initially, in September 2010, we instrumented the sett with four proximity detection coils (i.e., smaller antennae) to determine overall usage. Once the system was calibrated and we had established a coarse image of sett use, an array of eight, full sized antennae was installed, four aligned horizontally and four aligned vertically (Fig. 7.2). Each antenna extended over 15 m x 2 m, suspended 1.2 m above the ground. Antennae were energized sequentially, such that only one was transmitting actively at any point in time.

Base-station receivers were then placed close to the burrow system, powered by the same battery as the antenna driver. These base-stations listened for collar beacons continuously, which were broadcast every three seconds. If a base-station detected a beacon, a download was initiated, and buffered data were transferred reliably, with two-way handshaking, over the 2.4 GHz 802.15.4 link. Downloaded data were saved on a micro-SD card for later retrieval. Note that

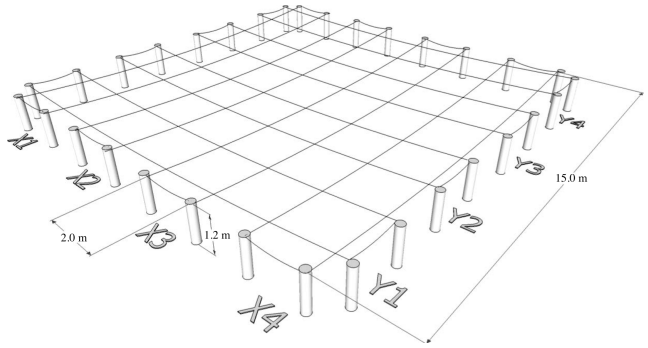

Figure 7.2: Layout of the antenna array. There were a total of eight loops, four aligned horizontally, and four aligned vertically. Each loop was 15 m x 2 m large and was suspended 1.2 m above the ground.

a major advantage of these base-stations is that they serve the dual purpose of data transfer initiation, making recapture for data collection unnecessary, and also allow for the detection of the position of animals when they are above ground, either using radio based Received Signal Strength Indicator (RSSI) or Link Quality Indication (LQI). All data were thus time-stamped and the LQI and RSSI were recorded. Base-stations were also equipped with sensors measuring ambient air temperature and humidity.

Prior to deployment, the system was ground-truth tested to determine the positional error/accuracy of the antenna array. An MI tag was moved along two perpendicular transects through the array of antennae, and lowered down an entrance hole at fixed depths. These known trajectories were then compared to the reconstructed trajectories generated by the tracking system. Additionally, MI performance was validated after collar deployment by placing four small antennae, with a 25 cm detection radius, at known locations within the full tracking array. The locations estimated by the full array were then compared with these four known positions. From these performance tests, we found that the MI system had a 2-D tracking error of just 0.25 – 0.37 m and a 3-D tracking error of 0.42 – 0.45 m. Raw data were in the form of magnetic field strengths records; these were processed using a particle filter estimator (sequential Monte Carlo) and knowledge of the spatial distribution of the magnetic field, to provide the animal's location in 3-D (i.e., x, y, z coordinates; for full details see Markham et al., 2012)

In a socio-ecological context, it is also important to be able to determine if two animals are close together. We verified that the system could identify the proximity of multiple collars, by placing two receivers in the same location. We found good correspondence between two devices, with a 3-D RMS error of 0.07 – 0.21 m, giving us confidence that this system could identify social contacts.

Though capable of continuous tracking, the primary purpose of this deployment was system development (Markham et al., 2010*a*, 2012). As such, data collection here were not continuous, but occured over a series of scenarios, each limited by the battery life of above-ground components (approximately two weeks), with calibration occuring between scenarios. Nevertheless, we were still able to test the biological potential of a subset of continuous positional fixes collected between January 27 and February 8 2011, sampling at a rate of one fix per three seconds. For consistent accuracy we restricted analyses to positional fixes established from five, or more, antennae and used only fixes with Z coordinates of less than zero, that is, when a badger was below ground. The resulting 13-day data set comprised 717,008 fixes, which represents at least a 55,000-fold increase in resolution compared to previous studies using one VHF-derived location per day. To explore how this could influence the perception of movement, we contrasted raw data from one badger, sampled every 3 seconds, and sub-sampled locations measued every 10 minutes, against perceived movement attainable using typical VHF tracking, i.e., positional fixes once per diem, or once per hour.

For more complete technical details of infra-structure research and development, including explanation of the differences between localisation/communication using a propagating electromagnetic wave (traditional radio) versus a quasi-static magnetic field, see Markham et al. (2012).

7.3.3 Spatial and statistical analyses

Following Butler and Roper (1996), we used clusters of positional fixes within a 1 m radius to define eight chambers (see Results) visited by collared animals. Due to the planar internal structure of this sett (see fig. 5.4), we were able to calculate the Euclidean distance to the midpoint of each chamber from the X and Y coordinates of each positional fix. Occupation of a chamber was defined

as a fix within a threshold distance of 1 m from the chamber midpoint; other below-ground fixes implied a badger was in a connecting tunnel (assigned as 'within the sett'). 99.6% of fixes related to chambers, and in no instance did the system assign a badger to two chambers simultaneously.

Given the high resolution of these data, we could disambiguate between temporary chamber visits and active use, applying the Manly-Chesson index α (Chesson, 1978; Manly et al., 1992):

$$\alpha_i = \frac{\frac{r_i}{p_i}}{[\sum_{i=1}^{m} \frac{r_i}{p_i}]} \tag{7.1}$$

Where r_i represents the proportion of time spent in chamber i, p_i represent the proportion of time an individual spent within chambers, and m represents the number of chambers within the sett (here 8). Output values, α, for individual *per diem* chamber use could range from 0 (complete avoidance) to 1 (complete fidelity). If $\alpha = 1/\text{m}$ (i.e., 0.13), the badger was allocated as using the chamber at random; $\alpha >$0.13 indicated greater than random and $\alpha <$0.13 less than random use.

To analyse chamber transitions and sett ingress/egress we sub-sampled badger locations at biologically appropriate ten-minute intervals (3,670 fixes for four animals). Since individuals typically made use of the entire sett, these transitions satisfied the assumptions of an ergodic Markov chain (i.e., transitions between all states were possible) (Guttorp, 1995). To elaborate further on underground space use, we considered individuals as extrinsic factors, assessing differences in inter-individual transitions between locations. We applied a first-order Markov chain model (Guttorp, 1995), calculating n x n transition matrices (T) using:

$$T = (p_{ij} : i, j \in I) \,\text{with}\, p_{ij} \geq 0 \,\text{for all}\, i, j \,\text{and} \sum_{j \in I} p_{ij} = 1 \tag{7.2}$$

Where each $i \in I$ represents a state in the state-space I (i.e., presence at a location), n signifies the number of possible states i (here 10, from transitions between eight chambers, non-chamber locations within the sett, and the external

environment), and p_{ij} gives the probability of transition between state i and j, determined from:

$$p_{ij} = \frac{\alpha_{ij}}{\sum_{(j=1)}^{10} \alpha_{ij}} \tag{7.3}$$

Where a_{ij} represents the number of transitions observed from location i to j.

Because the availablity of chambers was interpreted from sampling, we used chi-square tests for homogeneity, rather than goodness-of-fit, to reduce type I error (Thomas and Taylor, 1990). We used a Z-test for proportions to examine differences between the transition matrices (Fleiss, 1981). All statistical analyses were performed using R v. 3.0.3 (R Core Team, 2014).

7.4 Results

This MI tracking system proved capable of resolving underground activity in great spatial and temporal detail and collars exceeded their target field-deployment lifetime of six months, typically operating for almost one year before we removed them. We were also able to map the sett's underground structure in both 2-D (Fig. 7.3a), and 3-D (Fig. 7.3b), based on individual positional fixes.

At a coarse scale MI tracking established that badgers spent on average, 12.3 $\pm$ 1.69 SD hrs in the sett per diem (Fig. 7.4); indeed we actually detected no significant difference between time spent within the sett during daylight hours ($\bar{x}$ = 6.4 $\pm$ 1.0 SD) and during darkness ($\bar{x}$ = 5.8 $\pm$ 0.88 SD; paired sample t-test: $t_6 = 0.90$, $p = 0.40$). Notably, this deployment also had the resolution to expose fine-scale behaviour, and inter-individual differences in activity patterns. One badger (1300) spent three nights away from the focal sett, while the other three were absent for only 2.2 $\pm$ 3.1 SD consecutive hours.

Throughout the night, badgers returned to the sett 2.3 $\pm$ 1.45 times, residing for 0.77 $\pm$ 0.91 hrs per visit. On returns, they tended to use peripheral chambers located near the outer perimeter of the sett; they occupied central chambers for longer periods diurnally (Table 7.1).

Table 7.1: Number of occasions where badgers selected a chamber located centrally vs. peripherally when returning for a brief ($\bar{x} = 45$ min) nocturnal period or a longer diurnal period, compared with values expected from a random chamber selection.

	Central		**Peripheral**				
	Obs	Exp	Obs	Exp	χ^2	df	p
Diurnal	43	27	5	21	21.7	1	<0.001
Nocturnal	60	76	72	56	7.94	1	<0.005

Spatially, from Manly-Chesson indices, badgers used 1.55 ± 0.61 ($n = 49$, range: 1-3) chambers *per diem* (i.e., α exceeding 0.13; Fig. 7.5).Though no individual used more than three chambers *per diem*, a chamber of primary fidelity could be identified for each badger, which was favoured for 2.7 ± 1.7 consecutive days ($n = 16$, range: 1-7 days) before moving to a different chamber.

While each badger used a unique subset of the chambers available ($\chi^2 = 115.4$, d.f. $= 7$, p <0.0001), they made some use of the entire set, visiting up to seven chambers *per diem*, typically transitioning between chambers 7.6 ± 4.6 times *per diem* ($n = 46$, range: 1-19; Fig. 7.6).

While most chamber transitions occurred nocturnally ($\chi^2 = 281.3$, d.f. $= 7$, p <0.0001), all four instrumented badgers also changed chambers diurnally (22 instances); with 12 instances of a single and five instances of double diurnal relocation; nine of these 22 observations involved badger 1400. Transition matrices computed for each collared individual showed that apart from their infrequent use of chamber 1 (only visited 11 times cumulatively), and the 0.4% of fixes attributed to tunnels, all individuals exhibited a unique pattern of sett and chamber use (Table 7.2; Fig. 7.7), leaving, returning to, and moving about the sett independently.

Our manipulation of sampling rate exposed that, had we sampled the location of badger 1100 once daily at 12:00, we would have observed four chamber changes over the 13 day study period (Fig. 7.8a). This is in emphatic contrast to the 110 transitions the MI system was able to record for this badger when sampled every 10 minutes (Fig. 7.8c), and the 802 transitions when sampled every three

Table 7.2: The results of a Z-test for proportions, derived via Markov chain transition matrices, on inter-individual variation in sett use.

	χ^2	df	p
Chamber 1	6.98	3	0.072
Chamber 2	27.4	3	<0.0001
Chamber 3	133.9	3	<0.0001
Chamber 4	196.9	3	<0.0001
Chamber 5	198.8	3	<0.0001
Chamber 6	358.4	3	<0.0001
Chamber 7	18.1	3	<0.0005
Chamber 8	31.3	3	<0.0001
Sett	0.590	3	0.90
Outside	257.5	3	<0.0001

seconds (Fig. 7.8d). This implies that previous protocols have captured less than 0.5% of underground movement.

7.5 Discussion

Conventionally, burrows have been considered shelters from environmental stresses, or predation (Kinlaw, 1999), and a number of hypotheses have been suggested to explain burrow complexity (e.g., predator confusion – Bronner, 1992, improved gas exchange – Meyer, 1999), and patterns of use (e.g., parasite avoidance – Hart, 1990, or social hierarchy – Kruuk, 1989). Substantiating these claims has been difficult, however, in the absence of technologies and methods appropriate for detailed investigation. The autonomous, non-invasive MI tracking system we present here resulted in a 55,000-fold increase in resolution compared to previous methods, and is capable of answering a variety of questions about the activity and burrow structure of subterranean animals in their natural habitat (as exemplified here by the European badger). In addition, MI is not limited to underground deployments, and can be used for terrestrial/arboreal studies where precise positioning is required, as well as underwater tracking in freshwater ecosystems.

In terms of the accessibility of this new system, we benefitted from manufacturing our own equipment, however the costs of components, and time needed for assembly, were already competitive with VHF and GPS tracking. Collars

operated for close to one year, where parts currently cost about $100 USD, and antennae are standard, low cost, off-the-shelf single core cables. Although for reasons of technical development we chose to fit collars to badgers, if one assumes a maximum collar weight of 5% of the instrumented animal's mass (Hubrecht and Kirkwood, 2010), even in its current form, this system is suitable for burrowing mammals weighing as little as 2 kg, though weight refinements are easily achievable.

MI benefits from flexibility in the scale of deployments; this same system can be tuned for either fine-scale 3-D, or proximity (presence/absence) tracking. Detection range can be set to cover entire burrows, portions of burrows, or even precise foci of interest (e.g. 10 cm volume). Deploying MI proximity tracking is simple, involving just placing an antenna loop around the area of interest and trapping and collaring target animals. Even high-resolution tracking is straightforward; installation of an array of eight antennae over a 400 m^2 area took a single researcher around 6 hours per burrow system. Furthermore, automatic data downloading means that, apart from periodic equipment checks, MI tracking involves relatively little maintenance; ideal for monitoring burrows in remote, and/or poorly accessible locations.

Our array of eight antennae clearly satisfied our primary objective, being able to distinguish between basic fossorial activity/inactivity. By contrast, using VHF telemetry, Kowalczyk et al. (2004) noted just two instances of diurnal badger movement in a four year study spanning 2015 days of tracking. Here, we were able to observe a high, and previously unrealised, rate of dirunal chamber transition. Equally, this system also met our second objective, namely fine-scale underground positional fixes could also be used to reconstruct an internal sett map; MI thus negates the need for destructive burrow mapping (e.g., Roper, 1992), allowing potential to track the ontogeny of burrow architecture over time. Note, however, while it was simple to map well-used chambers, mapping tunnel layout proved more challenging, as the three second fix rate chosen was too coarse, i.e., there is a trade-off between battery life and sampling rate. Because collars can be reprogrammed wirelessly, however, it is possible to manipulate sampling rate remotely for a short period, to facilitate mapping.

The resolution achievable with MI also facilitates a far greater capability for linking underground activity patterns to function than achievable previously (e.g., Butler and Roper, 1996; Broseth et al., 1997), For example, our finding that badgers returned to the sett an average of 2.2 times *per noctem*, every 3-4 hours for on average 45 minutes suggests that there could be both energetic (Noonan et al., 2014), or information sharing (Ward and Zahavi, 1973) benefits to returning to the sett between foraging bouts. That outlying chambers were selected for these short returns while deeper chambers were selected for longer periods of diurnal use further implies the involvement of thermal/energetic benefits (Kaneko et al., 2010).

The array used in this deployment also performed well when tracking the precise subterranean movements of multiple individuals simultaneously, revealing social contacts in a way highly generalisable to other group-living species. For example, we observed contemporaneous chamber co-habition among collared individuals, primarily within central chambers, during diurnal sett occupation. While we are unable to comment with certainty on possible social interactions with other un-collared sett residents, it was noteworthy that those badgers we did track exhibited no greater tendency for synchronous subterranean activity than when above ground (Carr and Macdonald, 1986; da Silva et al., 1994) that is, all instrumented individuals left, returned to and moved around within the sett autonomously. This reinforces that group-living, indeed co-habiting, does not intrinsically equate to, or act as a precursor for intigrated social behaviour (*sensu* Eisenberg, 1966).

In terms of potential to test hypotheses connected with subterranean ecology empirically, these MI data offered support for the parasite avoidance hypothesis (see Roper et al., 2001), with badgers known to be infested with host-specific fleas (*Paraceras melis*) and lice (*Trichodectes melis*) changing primary chamber every 3 days or so, possibly to mitigate these infestations (Neal and Roper, 1991; Butler and Roper, 1996). These nidiculous infestations are non-trivial, because badger ectoparasites can vector other pathogens (e.g., Macdonald et al., 1999; Newman et al., 2001; Lizundia et al., 2011). As well as ectoparasite loads, subterranean chambers are also often contaminated with other sources of disease. In the case of badgers, helminths and coccidia (*Eimeria spp.*) contribute significantly to mortality rate among more immunologically vulnerable neonates and

juveniles (Newman et al., 2001) – a trait generally associated with the altricial young of fossorial carnivores (Wolff, 1997). Furthermore, interactions within setts could potentially be involved in bovine tuberculosis transmission between badgers (Gallagher and Clifton-Hadley, 2000, or other important diseases in other fossorial species) – where, suprisingly, despite the economic and political importance of this disease (Zinsstag et al., 2006) pertinent literature is lacking (but see Courtenay et al., 2006; Weber et al., 2013).

In overview, we present here a new underground tracking technology, with broad potential to elucidate the underground activities of diverse species. It is relatively simple to deploy, low maintenance, cost effective, provides very detailed and accurate fixes, is robust enough for long-term field deployment, and is demonstrably capable of addressing previously intractable questions concerning fossorial ecology.

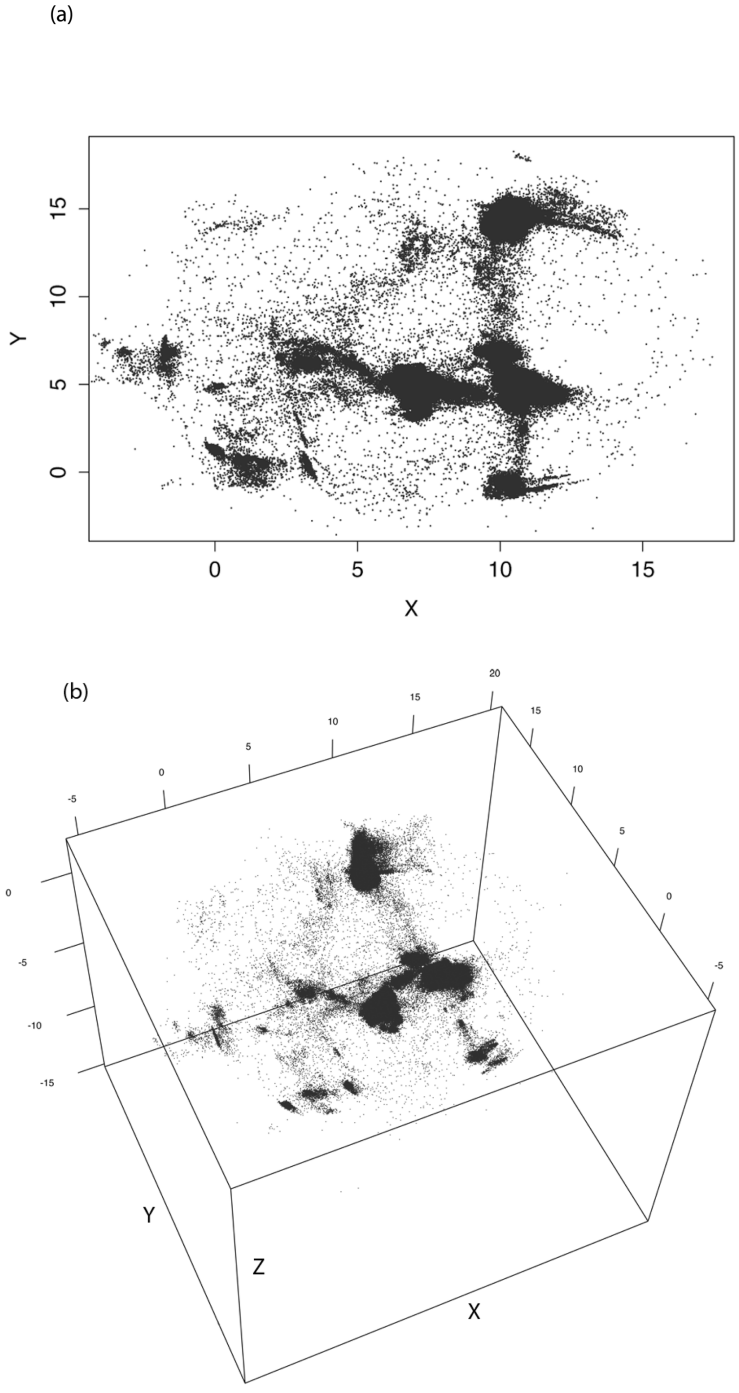

Figure 7.3: X, Y, Z coordinates of underground positional fixes, for all instrumented badgers, over the course of the study period presented in (a) 2-D and (b) 3-D. Axes are in metres.

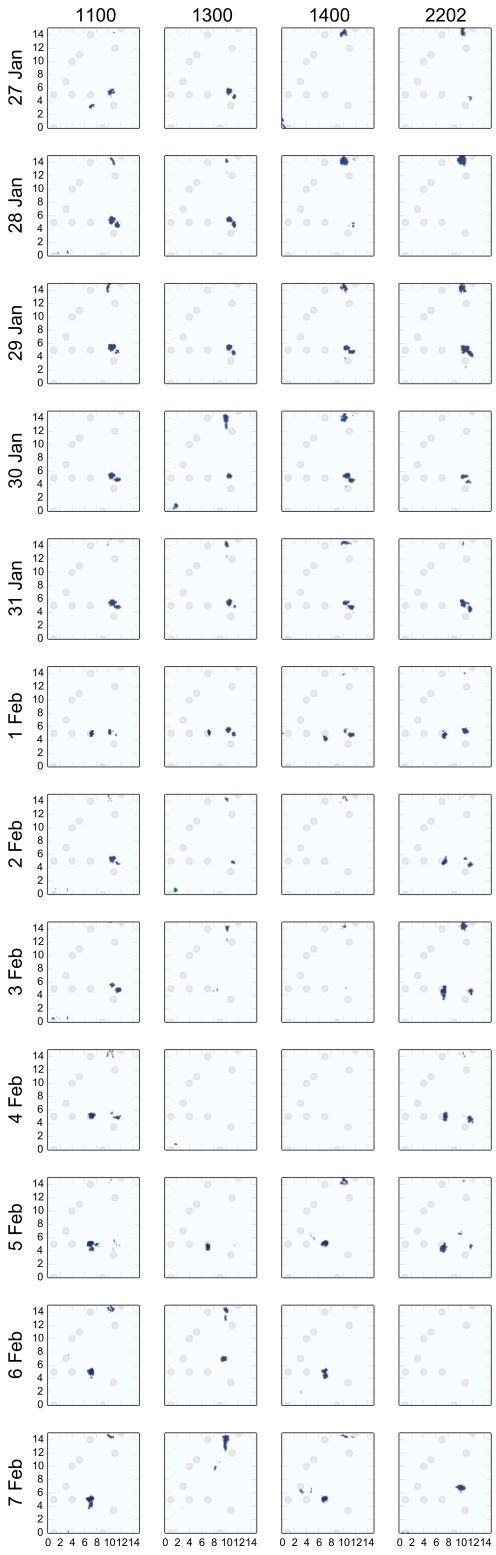

Figure 7.4: 24 hour density histograms of sett occupancy for each collared animal over a 13-day study period. Cell sizes are 10 cm x 10 cm, for any depth below 0 m. For clarity, any cell with less than 30 seconds of occupancy over a 24 hour period was ignored.

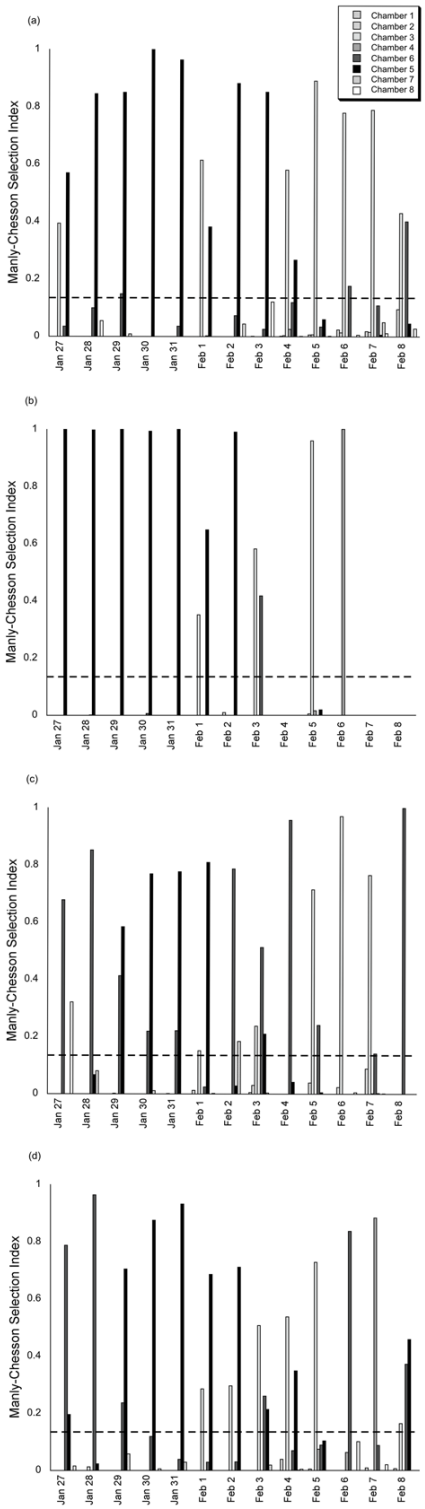

Figure 7.5: Manly-Chesson *per diem* chamber use indices for badgers: (a) 1100 (b) 1300 (c) 1400 and (d) 2202. The dashed line represents the threshold of random use (0.13; i.e., 1/m), bars extending above and below the line indicate more and less used chambers respectively.

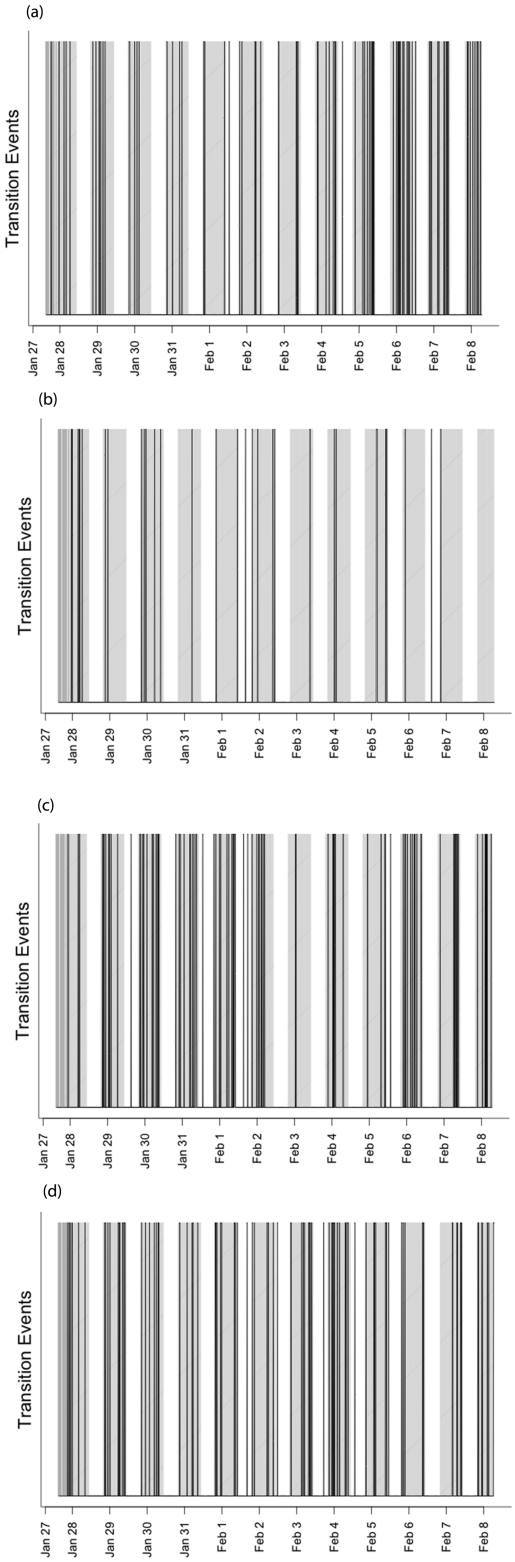

Figure 7.6: Transition events over time for badgers: (a) 1100 (b) 1300 (c) 1400 and (d) 2202, where black bars represent a transition, white bands represent sunlight hours, and grey bands represent night time.

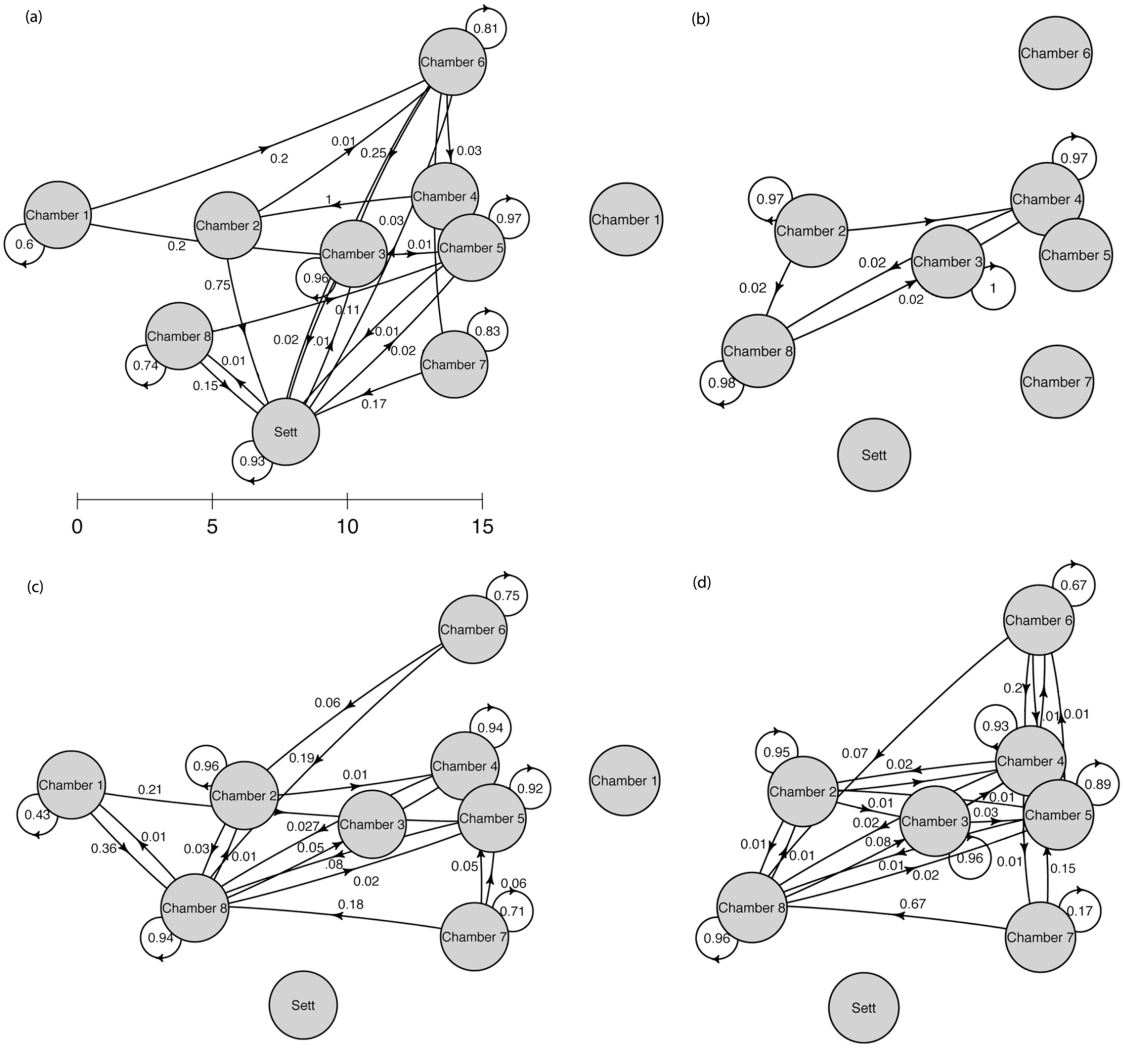

Figure 7.7: Markov chains representing probabilities of transition between chambers for badgers: (a) 1100 (b) 1300 (c) 1400 and (d) 2202 at a resolution of one fix per 10 min. Only transitions between chambers within the sett and tunnels are presented. The position of each chamber depicts the actual architecture of the sett (see Fig. 7.3). Scale is in meters.

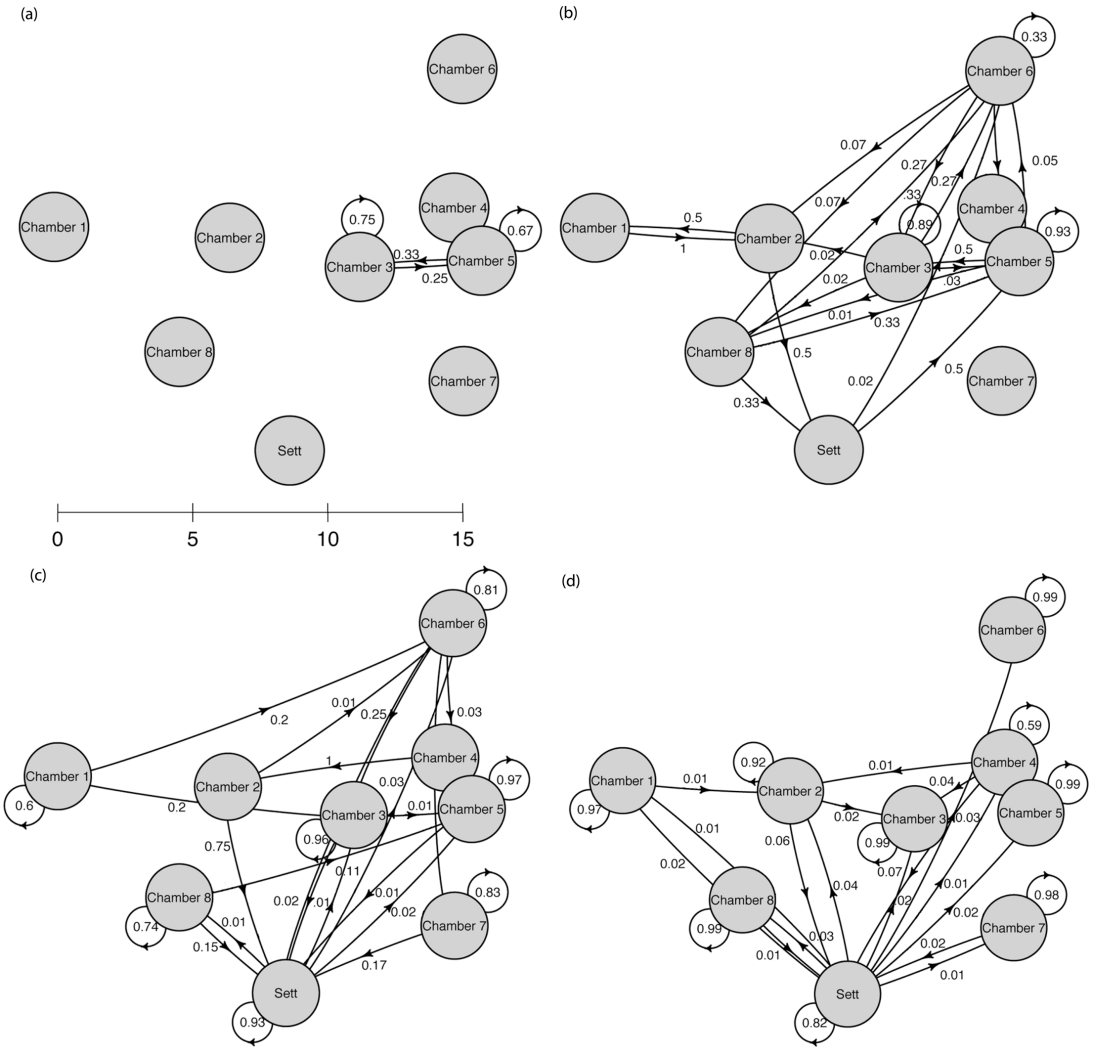

Figure 7.8: Markov chains representing probabilities of transition between chambers for badger 1100 sampled: (a) per diem at 12:00 h (b) hourly (c) once every ten-minutes and (d) once every three seconds. Only transitions between chambers within the sett and tunnels are presented. The position of each chamber depicts the actual architecture of the sett (see Fig. 7.3). Scale is in meters.

Part IV

Synthesis

'We are drowning in information, while starving for wisdom. The world henceforth will be run by synthesizers, people able to put together the right information at the right time, think critically about it, and make important choices wisely.'

– E. O. Wilson

Chapter 8

What does fossoriality contribute to the paradigm of group-living?

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Group-living is rare in the Carnivora, occurring in only 10-15% of species (Bekoff et al., 1984; Gittleman, 1989; Johnson et al., 2000; Noonan et al., 2015*c*). Indeed, solitary life-histories appear to be the basal socio-spatial arrangement amongst the Mammalia generally, whereas sociality is the derived response to specific selection pressures (Lukas and Clutton-Brock, 2013). Axiomatically, for group-living to present an evolutionary stable strategy (ESS; Maynard Smith and Price, 1973), the benefits of living with conspecifics must outweigh the costs (Alexander, 1974). A precise understanding of the mechanisms involved however, has proven challenging (e.g., Eisenberg, 1966; Alexander, 1974; Clutton-Brock, 2009; Macdonald, 1983*b*; von Schantz, 1984; Bacon et al., 1991; Koenig et al., 1992; Kokko and Ekman, 2002; Newman et al., 2011; Smith et al., 2012; Lukas and Clutton-Brock, 2013), particularly in instances where individuals living in groups do not interact cooperatively, and forage alone. In this respect, a number of recent studies have observed that fossorial mammals are typically more gregarious than otherwise ecologically similar epigean (living above-ground) species (Ebensperger and Blumstein, 2006; Sobrero et al., 2014; Smorkatcheva et al., 2014; Noonan et al., 2015*c*). In this thesis, I set out to investigate the role played by fossoriality in group-formation positing that by providing a 'safe-haven' (*sensu* Kokko and Ekman, 2002), fossorial dens promote group-living by leveraging delayed dispersal and natal philopatry (i.e., the Fossorial Benefits Hypothesis: FBH).

In this synthesis I first propose a framework for the FBH, explaining the key mechanisms of how fossoriality promotes philopatry at various life-history stages, driving group formation and the subsequent evolution of sociality. I then demonstrate formally how the survival benefits associated with philopatry at natal dens can contribute to adult group formation. Finally, I review how the FBH fits with empirical studies that have investigated how fossoriality shapes spatial/social groups, ending with a case study of the FBH mechanisms and group-living in European badgers (*Meles meles*). While the focus of this synthesis is drawn from the specific evidence presented in each chapter of this thesis, I draw heavily upon ancillary evidence from the broader literature, demonstrating the significance of fossoriality to group formation across a range of taxa.

8.1 Demonstrating how fossoriality promotes group-living: A framework

I begin by noting a crucial caveat; that fossoriality alone does not provide a sufficient explanation for group-living, particularly when the influence of factors encouraging dispersal (e.g., competition for local food resources, or breeding opportunities) is significant. Indeed, in Part I of this thesis I drew focus on the observation that even species with similar reliance on the subterranean environment can exhibit substantially different socio-spatial geometries (Noonan et al., 2015*c*; Ebensperger and Blumstein, 2006; Sobrero et al., 2014; Smorkatcheva et al., 2014). For example, while the European badger exhibits facultative group-living (Johnson et al., 2002*a*) the taxonomically related and equally fossorial American badger (*Taxidea taxus*) is solitary (Long, 1973) – a contrast seen across various taxonomic dyads (see Noonan et al., 2015*c*). Nonetheless, this paradox exposes how a suite of factors inter-play with the extent of fossoriality to promote, or constrain group-living relative to the FBH. I posit that of primary importance are: i) phylogenetic inertia and the ability to dig; ii) the extent of neonate altriciality; iii) allometric constraints; iv) local resource abundance and dispersion; v) the benefits to the adult life-stage; and vi) the influence of reproductive suppression. Collectively these factors provide a comprehensive framework with which to examine the contribution made by fossoriality to group-living, and a set of predictable outcomes regarding how fossoriality promotes philopatry mechanistically (Fig. 8.1).

8.1.1 Phylogenetic inertia

Ancestral specialisation limits which species are capable of digging (Martin, 1989; Andersson, 2004; Samuels et al., 2013), and, therefore, the extent to which fossoriality can promote group-living (Noonan et al., 2015*c*). Digging requires extensive forelimb supination, and elongated humeri and ulnae to provide stable elbow joints (Van Valkenburgh, 1987; Andersson, 2004; Samuels et al., 2013). In this respect, Andersson (2004), highlights two opposing evolutionary trajectories pertaining to forelimb form and function in the Carnivora: i) elongated limbs, adapted to cursoriality; and ii) forelimbs capable of extensive supination, adapted to manual dexterity. Species unable to excavate burrows themselves

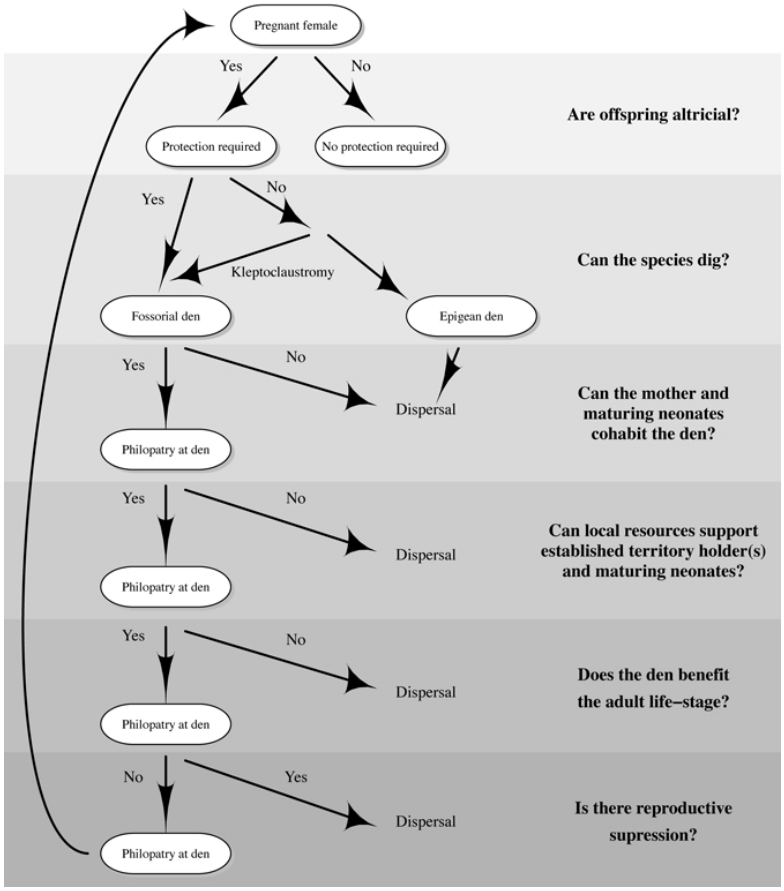

Figure 8.1: Diagram depicting the ontogeny of the FBH route to spatial groups. Each grey band represents a crucial stage in the establishment, and continued, philopatric use of fossorial dens. Arrows indicate which behavioural trajectory would be favoured by FBH predictions at each step.

however, can often rely on '*kleptoclaustromy*' (i.e., den theft; Noonan et al., 2015*c*), and so burrowing species are 'keystone' (Mills and Doak, 1993) to the subterranean environment (e.g. Whittington-Jones and Bernard, 2011). As a result, chapter Two (Noonan et al., 2015*c*) demonstrated that fossorial exaptations ('pre-adaptations', *sensu* Gould and Vrba, 1982) for digging, and/or the availability of pre-excavated dens for those species unable to dig, can impose limits on the extent to which burrows promote group formation (see also Ebensperger and Blumstein, 2006; Sobrero et al., 2014; Smorkatcheva et al., 2014).

8.1.2 Neonate altriciality

The extent of neonate development at birth interacts with fossoriality to predict the propensity for group-living. Offspring are born along a continuum of altriciality to precociality (Derrickson, 1992). While precocial young achieve independence more rapidly than altricial neonates, they require longer gestation periods and greater pre-natal energetic investment (reviewed in Martin and MacLarnon, 1985). Furthermore, precociality is a trade-off against litter size and the need to maintain agility (Case, 1978*b*; Woodroffe and Ginsberg, 1997). As noted by Case (1978*a*) however, altricial species require a protective environment to rear young (see also Case, 1978*b*; Wolff, 1997). In this respect, chapter Two (Noonan et al., 2015*c*) detailed an evolutionary link between the use of subterranean natal dens and neonate altriciality (see also Kinlaw, 1999; Nevo, 1999). The substantial benefits of fossorial dens improve survival probability of neonates (Kinlaw, 1999; Nevo, 1999; Kaneko et al., 2010), and thus philopatry at natal dens will be under positive selection until opposing forces drive maturing offspring to disperse (Macdonald, 1983*b*; von Schantz, 1984; Koenig et al., 1992). Consequently, different extents of delayed dispersal can be observed, with some species dispersing immediately after weaning (e.g., Sheffield and King, 1994; Gorsuch and Larivière, 2005), usually leading to solitary life-histories, through to offspring remaining philopatric until sexual maturity (e.g., Clark Jr, 2005; Kaneko et al., 2014), leading to temporary maternal-offspring groups, to the retention of breeding adults (e.g., Woodroffe et al., 1995; Hinze et al., 2013), leading to stable adult groups.

8.1.3 Allometric constraints

In addition to phylogenetic constraints, significant allometric constraints limit burrowing capacity. I posit that only those carnivores small enough to maintain burrow use into adulthood (i.e., less than ca. 15kg; Noonan et al., 2015*c*), can delay dispersal in favour of a prolonged denning period. Although the cost associated with burrow construction scale with body mass (M) according to $\alpha M^{0.54}$ (Vleck, 1981), the force an animal can exert scales according to $\alpha M^{0.25}$ (Biewener, 2005). As such, there is an upper body mass limit on burrowing, beyond which individuals cannot exert the force necessary to dig (Fig. 8.2).

Burrow size also scales allometrically according to $\alpha M^{0.33}$ (Vleck, 1981) and there is an upper limit on burrow size imposed by structural stability (White, 2005). Consequently, although even 300+ kg *Ursidae* spp. have a morphology compatible with burrowing (Andersson, 2004), it is smaller species that tend to rely more frequently and more substantially on underground space (Kinlaw, 1999; Nevo, 1999; Noonan et al., 2015*c*).

As a result of these allometric constraints, the neonates of many mammals will out-grow their natal den as they mature, surpassing the mass threshold of continued excavation (Vleck, 1981; White, 2005). In addition, when multiple neonates begin to approach adult size, crowding may further limit their capacity to cohabit burrows, especially for larger species. These larger species will abandon natal dens in favour of more epigean life histories, precluding an FBH route to group-formation.

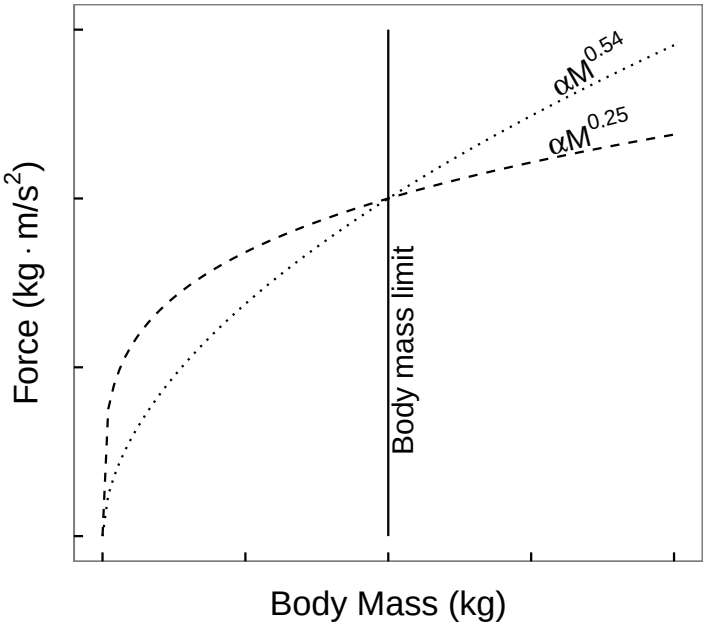

Figure 8.2: Allometric relationships between the cost of burrowing and muscle force. The dotted line depicts the force required to dislodge soil as a function of body mass (M). The dashed line depicts the muscular force available to an animal of mass M. The maximum body mass for fossorial mammals is that at which the force required to excavate a burrow, and the available muscular force are equal.

8.1.4 Local resource abundance and dispersion

Whether the adaptive value of fossorial dens can promote philopatric behaviour in maturing juveniles will also depend on the dispersion of resources (i.e., the Resource dispersion hypothesis, RDH; Macdonald, 1983*b*), and environmental carrying capacity (*sensu* von Schantz, 1984) in the vicinity of the natal den (i.e., the natal territory). Regardless of their ability to cohabit burrows, if local food supply cannot support the energetic requirements of offspring as they mature and grow (West et al., 2001; Hou et al., 2008), the inability to achieve minimum food security will drive individuals to disperse (Macdonald, 1983*b*; von Schantz, 1984; Macdonald and Johnson, 2015). For instance, from an economic standpoint, predatory species must be less numerous than prey items (Eisenberg, 1966), and non-cooperative hunters tend to space themselves out as local food resources can rarely support the requirements of multiple adults (Eisenberg, 1966; von Schantz, 1984; Macdonald et al., 2004*a*; Macdonald and Johnson, 2015). A notable caveat however, is that resource abundance in-and-of-itself (*sensu* von Schantz, 1984) does not intrinsically promote group-living (Johnson et al., 2002*b*; Macdonald and Johnson, 2015). Rich territories can be contracted and split (Kruuk and Macdonald, 1985). Species consuming an omnivorous/ insectivorous diet however, can exploit a broader trophic base with a more heterogeneous dispersion, and so this more extensive use of resources effectively reduces competition (Gittleman, 1986); conditions favouring range sharing (Macdonald, 1983*b*).

Importantly, morphology also plays a role in whether individuals can cope with sharing their range with conspecifics, which typically lowers their individual food security (Macdonald and Johnson, 2015). Due to instability in food supply (Caraco, 1980) individuals must also be capable of enduring food paucity driven by weather patterns and seasonality (e.g., Kowalczyk et al., 2003; Zhou et al., 2013), as well as sustaining energetic expenditure while foraging in inclement conditions (Boyce, 1979; Noonan et al., 2014, 2015*a*, Chapter Five *in prep*). As a consequence, the ability of individuals to store food during times of abundance, either through accumulating body-fat (Storey and Storey, 1990; Newman et al., 2011), or through caching food (Macdonald, 1976; Post et al., 2006), proves influential to their capacity to share ranges.

8.1.5 Benefits of fossoriality at the adult life-stage

As Johnson et al. (2002*b*) explain, a food supply driven basis to group formation (e.g., Macdonald, 1983*b*; von Schantz, 1984) implicitly requires at least some marginal cost of dispersal, and/or benefit of philopatry, to encourage maturing juveniles to delay dispersal (see also Carr and Macdonald, 1986). This leads to the question of: 'why should multiple adults want to maintain overlapping home ranges?' – where the FBH proposes that it is burrow fidelity that unites individuals into a spatial-group. Subterranean dens must therefore maintain an adaptive value into adulthood (*sensu* Tinbergen, 1963) otherwise, provided there are no costs to dispersal (Hatchwell and Komdeur, 2000; Kokko and Lundberg, 2001), offspring would disperse as they mature. I posit that in instances where the survival benefits of fossorial dens are also present at the adult life-stage, the integration of subsequent generations into natal groups will be favoured (e.g., Roper et al., 2001; Dahle and Swenson, 2003; Ferreras et al., 2004; Hwang et al., 2007; Kitao et al., 2009; Hinze et al., 2013; Kaneko et al., 2014). In this respect, two primary benefits of fossorial dens prove pertinent to the benefits adults accrue from continuing to reside in them. Burrows provide; i) protection from predators for inhabitants (Alexander et al., 1991; Kinlaw, 1999; Nevo, 1999); and ii) stable refugia from surface conditions with more constant internal temperature, protection from wind, rain, etc (Kinlaw, 1999; Fløjgaard et al., 2009; Noonan et al., 2014, 2015*a*,*b*,*c*, Chapter Five *in prep*).

8.1.6 Reproductive suppression

As juveniles approach reproductive maturity, they can be forced to disperse from their natal territory if the opportunity to breed independently cannot be realised (Koenig et al., 1992; Kokko and Ekman, 2002). For instance, if the resource security necessary to breed are limited, reproductive suppression of female subordinates can occur (Creel and Creel, 1991; Creel and Macdonald, 1995). I posit however, that the survival benefit of fossorial dens will act to promote the perpetuation of natal groups to form persistent (sub-)adult groups (Noonan et al., 2015*c*). The number of descendents an individual leaves (its 'fitness') is the product of how much it invests in each breeding cycle and, crucially for this argument, how many cycles it survives for and participates in.

For iteroparous species, fitness can increase with age provided the individual; i) survives until the next reproductive season; ii) remains reproductively active; iii) is in sufficiently good condition to reproduce at this time; and iv) is at the front of the breeding 'queue' (Kirkwood and Rose, 1991; Clark, 1994; Kokko and Ekman, 2002). Mathematically, this relationship can be represented as the summation of the probability of survival to age x (l_x), and age-specific reproduction (m_x; Pianka, 2000):

$$R_o = \sum l_x \; m_x \tag{8.1}$$

Mechanistically therefore, fitness (R_o) can accrue via direct investment in reproduction, maximising m_x (Gittleman and Thompson, 1988; Stearns, 1992), or indirectly through investment in survival maximising l_x (Charnov, 1991; Kirkwood and Rose, 1991; Vaupel et al., 2004). When resources in the natal territory can support breeding among philopatric offspring (Gittleman and Thompson, 1988; Speakman, 2008), by acting as a 'safe haven' (*sensu* Kokko and Ekman, 2002) the benefits of fossorial dens reduce the mortality probability of philopatric individuals, increasing the probability of accruing future reproductive success. I further posit that this benefit will be most evident under conditions where there are ecological constraints on dispersal (Emlen, 1982).

8.2 Fossoriality and the benefits of philopatry

As natal individuals mature, they are faced with two alternatives: i) remain within the natal territory; or ii) disperse and attempt to acquire a new territory outside of the natal group. Ultimately, the outcome of this choice is determined according to the relative costs and benefits of each option (e.g., Emlen, 1982; Stacey and Ligon, 1991; Creel and Macdonald, 1995; Kokko and Lundberg, 2001), where, as I have just demonstrated, the benefits of fossorial dens can serve to tip the balance in favour of philopatry (Ebensperger and Blumstein, 2006; Sobrero et al., 2014; Smorkatcheva et al., 2014; Noonan et al., 2015*c*). To demonstrate the importance of the survival benefits associated with fossorial

dens, I employ Kokko and Ekman's (2002) formalisation of this cost-benefit relationship:

$$\frac{\beta T_D}{\mu_D} > \frac{\alpha + T_P}{\mu_P} \tag{8.2}$$

The left-hand side of this inequality is termed the benefits of dispersal (D), where β represents the probability of securing a territory outside of the natal group, where β <1 means a disperser is unlikely to acquire a territory; β >1 and dispersers can readily establish territories. T_D represents the number of neighbouring territories dispersers can test their opportunity against, and μ_D the mortality probability associated with dispersing. Conversely, the right-hand side of the inequality is termed the benefits of philopatry (P), where α represents the probability of breeding in the natal territory; when α <1 reproductive suppression occurs; α >1 and breeding within the group is possible. T_P represents the number of neighbouring territories philopatric individuals can test their opportunity against, and μ_P the mortality probability associated with philopatry.

Crucially, due to local habitat saturation (von Schantz, 1984) and/or dominance hierarchy (Sapolsky, 2005) the relative benefits of philopatry will likely differ between individuals. For subordinate individuals of rank n, P must be adjusted according to the factor 'q_n' (Kokko and Ekman, 2002), where:

$$q_n = \frac{\sum_{i=0}^{n-1} \gamma^{\mathrm{i}}}{\sum_{i=0}^{n} \delta_{\mathrm{i}}} \tag{8.3}$$

Here, the parameter γ represents the extent of social hierarchy within the natal territory; thus $\gamma = 0$ implies territorial inheritance is strictly hierarchical, and with $\gamma = 1$ territory acquisition is independent of rank. Survival probability may also be a function of social rank in societies with dominance hierarchies, where the parameter δ_n denotes a non-decaying, rank dependent mortality factor (i.e., $\delta_n \mu_P$); if $\delta_n = 1$ for all n, mortality is independent of rank. P/D thus represents the relative benefit of philopatry for the primary territory holder;

Pq_n/D the relative benefit for a subordinate of rank n.

From equation (8.2) we see that the relationship between μ_P and μ_D is essential to determining the value of P/D. Under otherwise ecologically comparable scenarios, if fossoriality improves the survival probability within the natal territory, delayed dispersal is favoured for a greater number of individuals (Fig. 8.3a). Interestingly, when reproductive suppression is factored into the equation (i.e., $\alpha = 0.5$), the survival benefits required to promote group formation become significantly higher, and, generally, smaller group sizes are favoured (Fig. 8.3b). It should be noted however, that these predictions do not factor in any inclusive fitness benefits (Herre and Wcislo, 2011), but present only the 'baseline' benefits of philopatry (for details see Kokko and Ekman, 2002).

8.3 Empirical evidence of the FBH

Although the formalisation of the FBH is novel to this thesis, empirical studies that have investigated the role of fossoriality in shaping spatial/social groups provide varying degrees of support for the FBH framework, while also highlighting potential problems.

8.3.1 Phylogenetic analyses

Perhaps the most consilient evidence in support of the FBH comes from comparative analyses (*sensu* Harvey and Pagel, 1991) within the Rodentia. A relationship between rodent societies and fossoriality was first proposed by Nevo (1979), however Ebensperger and Blumstein (2006) were the first to provide strong empirical evidence linking the two. They demonstrated that in New World hystricognath rodents group-living is positively correlated with the evolution of burrowing behaviour. Building on this, Smorkatcheva and Lukhtanov (2014) demonstrated that in the evolutionary history of subterranean rodents, group-living was nearly always selected for. They speculate that in these taxa, the secondary loss of sociality arises due to the subsequent influence of factors extrinsic of fossoriality. Conversely, they found that epigean rodents exhibited

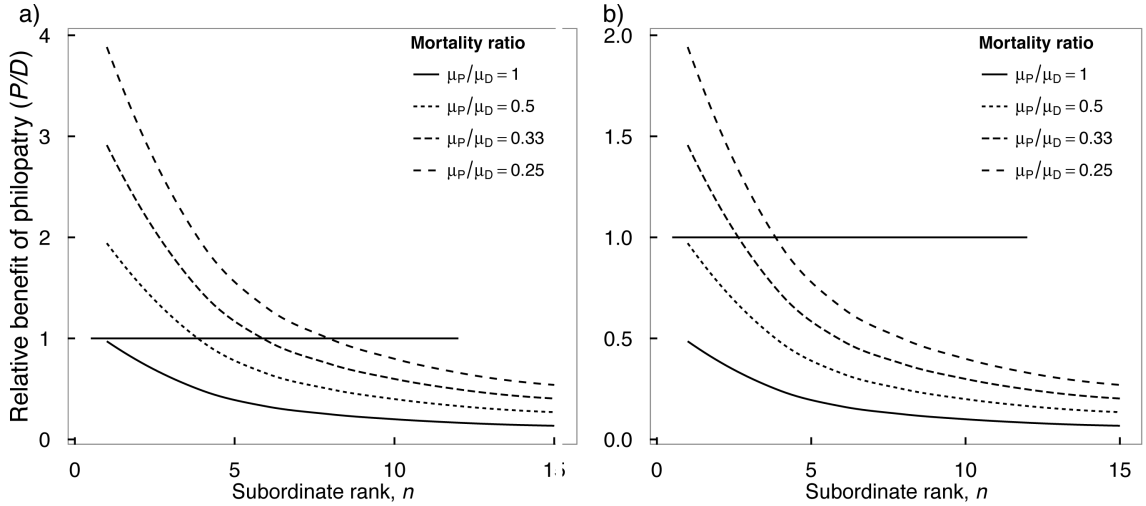

Figure 8.3: The relative benefit of dispersal (P/D) for a series of subordinate individuals (n) cohabiting a burrow. The solid horizontal line depicts the tipping point between philopatry and dispersal: when P/D >1 philopatry is favoured; <1 and dispersal is favoured. Group size is determined by the last n for which P/D >1. In a) I parameterised the model such that mortality is not influenced by rank ($\delta_n = 1$ for all n), that the probability of securing mating opportunities is equal for both philopatric and dispersing individuals (α and $\beta = 1$), but that territory acquisition depends partly on rank ($\gamma = 0.5$), that philopatry benefits via territorial inheritance ($T_P = 0$), and that dispersers cannot observe more territories than philopatric individuals ($T_D = 1$). Here we see that if the mortality of dispersing individuals (μ_D) is equal to that of philopatric individuals (μ_P), groups are not favoured. When the benefits of natal dens improve survival however ($\mu_D > \mu_P$), a greater number of individuals can benefit from philopatry, promoting group formation. In b) I adjusted the model to account for reproductive suppression of subordinates ($\alpha = 0.5$). Here we see that groups only form via FBH mechanisms when the benefits to survival are substantially higher (i.e., mortality is three times higher for dispersers), and that groups tend to be smaller.

significantly less predictable patterns in their evolution of sociality.

In the Rodentia however, attention has focused primarily on the role of fossorial dens as predator-free refugia, with minimal consideration of any further benefits – although Sobrero et al., (2014) do draw attention to the potential energetic benefits of communal den maintenance. In this respect, Healy et al. (2014) demonstrated that, in mammals generally, there is a significant positive phylogenetic relationship between fossoriality and longevity. Here, the findings of Chapter Two (Noonan et al., 2015*c*) prove pertinent. I found that fossoriality and group-living are linked in the Carnivora. In this Order however, the extent

of neonate altriciality and the northernmost latitude of species' distributions predominantly promoted fossoriality, with no evidence of a predator defence role.

8.3.2 Field studies

The energetic benefits of communal denning are perhaps the best studied FBH prediction. For example, Hwang et al., (2007) report that, when compared to individuals that den alone, communal-denning in the striped skunk (Mephitis mephitis) leads to 16.2% more body fat conservation over the winter period; thus congregation brings thermoregulatory (energetic) benefits. Similarly, Hinze et al. (2013) found that although African ice rats (*Otomys sloggetti robertsi*) compete with each other for food above-ground, they huddled in groups below-ground during cold periods, evidencing the fossorial foundation of their society. Similar group-huddling benefits have been observed in European badgers (Fowler and Racey, 1988), and raccoon dogs (*Nyctereutes procyonoides* Kitao et al., 2009), supporting a benefit to cohabiting fossorial dens in challenging environments (see also Kinlaw, 1999; Fløjgaard et al., 2009).

The interaction between fossoriality, local resources, and group-living has also received support from a number of studies. For instance, Vagen et al. (2001) report that for wolverines (*Gulo gulo*), years of high prey abundance allow for delayed dispersal and offspring retention at sub-nivean natal dens, whereas in years of low prey availability juveniles are forced to disperse as they mature. Interestingly, even American badgers, with solitary life-histories (Long, 1973), may delay dispersal where resource availability enables offspring to persist at natal dens for extended periods (Kinley and Newhouse, 2008).

Schradin et al. (2010) present further evidence in support of the FBH in African striped mice (*Rhabdomys pumilio*), where, albeit the presence of female-female competitive infanticide, the survival benefits of communal denning promote philopatric groups, even at low densities.

8.3.3 Circumstantial evidence

There are also a number of studies where a role of fossoriality in group-formation is implied, but is not central to the empirical analyses performed. While circumstantial evidence must be approached with caution to avoid 'just-so stories' (Gould and Lewontin, 1979), these broadly corroborate the role of fossoriality in group formation, as well as highlighting ecological situations warranting further investigation.

For example, Larivire (2002) reports that in Fennec foxes (*Vulpes zerda*), while individuals forage alone, groups of as many as 10 individuals can result from philopatry at fossorial natal dens; although the factors ultimately influencing dispersal were not investigated. In comparison, albeit being semi-fossorial, the Sechura fox (*Pseudalopex sechurae*) rarely forms groups, where food availability is thought to drive dispersal patterns (Cossíos, 2010).

Although black bears (*Ursus americanus*) utilise fossorial natal dens (Larivière, 2001), and congregate at rich food patches such as salmon runs (Reimchen, 2000), they appear to surpass the body-size threshold permitting philopatry at natal dens (Vleck, 1981; Noonan et al., 2015*c*). Similarly, albeit consuming an omnivorous diet, the marsh mongoose (*Atilax paludinosus*) makes no use of fossorial dens, and exhibits a solitary life-history (Baker, 1992). Pertinently, Taylor and Meester (1993) note that yellow mongooses (*Cynictis penicillata*), meerkats (*Suricata suricatta*), and ground squirrels (*Xerus inaurus*) all cohabit extensive burrow systems, which provide significant thermoregulatory and anti-predator advantages to the occupants.

8.4 The European badger: A case study

There is a substantial body of research examining the socio-ecology of European Badgers enabling me to use them to investigate the role of fossoriality in group formation (Stopka and Johnson, 2000).

Badgers are semi-fossorial, spending more than half of their lives underground (Roper et al., 2001; Noonan et al., 2015*b*) in extensive burrows (termed 'setts' Roper, 1992), which are used for diurnal rests (Noonan et al., 2015*b*); the rearing of young (Stewart et al., 1999); and, in regions with harsh winters, as hibernaculae (Kowalczyk et al., 2003). Local resource dispersion (*sensu* Macdonald, 1983*b*) is pivotal to badgers' capacity for range sharing. Badger densities, and group-living tendencies exhibit a positive correlation with the extent of vermivory (Goszczyński et al., 2000), which all increase towards the northwest of their geographic distribution (Johnson et al., 2002*a*). Research from low-density badger populations outside of the United Kingdom and Ireland reveals that although maternal-offspring groups may persist temporarily (Revilla and Palomares, 2002; Kaneko et al., 2014), when food availability becomes a limiting factor (Macdonald, 1983*b*; von Schantz, 1984; Macdonald and Johnson, 2015), less gregarious social systems arise (Roper, 1994; Rosalino et al., 2005*b*; Roper, 2010).

Congruent with the Magneto-Inductive tracking carried out in Chapter Six (Noonan et al. *in prep*) research into badger spacing patterns has consistently drawn attention to the central role that setts play (Kruuk and Parish, 1982; Doncaster and Woodroffe, 1993; Stewart et al., 1997*a*; Roper et al., 2001; Doncaster, 2001; Rogers et al., 2003; Weber et al., 2013, but see Blackwell and Macdonald 2000), where in the United Kingdom, stable congregations of up to 30 individuals co-habit the same setts (Macdonald et al. 2015). In the high-density population in Wytham Woods, 10-15% badgers disperse in their first year (Macdonald et al., 2008). In this respect, Kaneko et al. (2010) found that large, established setts had greater thermal stability than smaller, outlying setts, which was associated with higher cub survival probability through their first year (83.3% versus 27.3% respectively). In addition to the survival advantage, cubs born in large main setts were also significantly more philopatric than those born in smaller, less thermally stable outliers. Where local resources allow for range sharing (Johnson et al., 2002*b*), philopatry at established setts can thus promote the maintenance of groups into adulthood.

Badgers are also strategic in how they expend energy (Noonan et al., 2014, 2015*a*,*b*, Chapter Five, *in prep*), and will avoid unfavourable conditions risking

net energy loss where possible. Analyses of activity budgets (Noonan et al., 2014; Chapter Five, *in prep*; see also Kowalczyk et al., 2003) revealed that when conditions inside the sett were warmer on average than conditions outside the sett, both activity, and ranging behaviour were significantly reduced in favour of subterranean inactivity. As a corollary, Chapter Two (Noonan et al., 2015*c*) found that latitude, a proxy for winter severity, was influential in predicting the importance of fossoriality across carnivore species of all body size (irrespective of Bergmann's rule, *sensu* Blackburn et al., 1999). Similarly, Kowalczyk et al. (2003) found that across their range, the duration of badgers' winter torpor was directly proportional to local winter severity. It is important to note however that badgers have the capacity to employ facultative torpor to drastically reduce their metabolic rate (Newman et al., 2011; McClune et al., 2015), and this mode of risk avoidance is unlikely to occur in species unable to store body-fat to provide food security (Newman et al., 2011). Chapter Seven (Noonan et al., 2015*b*) provides further insight towards the thermoregulatory role of setts, where, in mid-winter, individual badgers made frequent returns to their sett – indeed they were never away from the sett for more than ca. 3-4 hrs. On these return visits, badgers tended to occupy outlying chambers, while deeper chambers were selected for longer periods of diurnal use, further implying the involvement of thermal/energetic benefits (Kaneko et al., 2010). Collectively these lines of evidence demonstrating the importance of setts in maintaining an energetic balance through adulthood, supporting fossoriality as a playing a causative role in the maintenance of spatial groups.

It is important to note however, that many studies of badger socio-ecology often apply the unsubstantiated inference of active territorial defence (see Stewart et al., 1997*a*), and infer a defensive role of latrine arrangement (e.g., Roper et al., 1993; Doncaster and Woodroffe, 1993; Delahay et al., 2000). Interestingly, above-ground tracking in Chapter Six (Noonan et al. *in prep*) revealed a more independent nature of badger movement consistent with the spacing patterns of solitary mustelids generally (see Powell, 1979), and, crucially, that of badgers at low densities (e.g., Pigozzi, 1990; Kowalczyk et al., 2000; Revilla and Palomares, 2002; Do Linh San et al., 2007; Newman et al., 2011; Kaneko et al., 2014). Furthermore, where Chapter Six (Noonan et al. *in prep*) evidenced a significant extent of inter-group range overlap despite the presence of latrine

marked 'borders', the findings presented in Appendix A evidence an 'independent advertisement' role of badger scent marks (where latrines serve to indicate presence and condition; see also Buesching et al., 2002*a*,*b*, 2003), with minimal support for any defensive role.

8.5 Conclusions and a future for the fossorial benefits hypothesis

In conclusion, I propose that fossorial dens can act as a precursor to, and contribute to the perpetuation of stable congregations of adults in suitable resource-scapes. Crucially, I emphasise that cohabitation does not imply co-operation (Kruuk, 1972; Clutton-Brock, 2009; Smith et al., 2012; Macdonald and Johnson, 2015). Individuals can den communally but without the presence of over-arching group-level patterns of individual behaviour (e.g., Hinze et al. 2013), resulting in 'spatial' though not necessarily 'social' -groups (*sensu* Eisenberg, 1966). Given that nearly three quarters of extant vertebrates engage in at least some form of burrowing behaviour (Kinlaw, 1999; Nevo, 1999; Noonan et al., 2015*c*) fossoriality may be influential in shaping the spacing patterns of a large number of species. Importantly, understanding the factors that promote philopatry at fossorial dens requires not only quantifying the cost-benefit balance of den-living, but also consideration of interactions with extrinsic factors such as the local carrying capacity (Macdonald, 1983*b*; von Schantz, 1984), the specific capacity to tolerate secondary food security (Newman et al., 2011; Macdonald and Johnson, 2015), reproductive suppression (Creel and Macdonald, 1995; Kokko and Ekman, 2002), and/or constraints on dispersal (Koenig et al., 1992; Kokko and Lundberg, 2001). Furthermore, subterranean living is not without its challenges, including the high energetic cost of burrowing (Vleck, 1979, 1981), hypoxia/ hypercapnia, permanent darkness, and conditions of high pathogen infectivity, which can lead to the spread of parasites and disease (Nevo, 1999). Consequently, it should not be presumed that fossorial dens always provide a net-benefit to occupants. Nonetheless, although the precise mechanism may differ inter-specifically, the threads of evidence presented in this review provide consilient support in favour of fossoriality as a route to

sociality.

Part V

Appendices

'...whoever read it would find what there was there and have it always.'

– Ernest Hemingway

Appendix A

Will Trespassers Be Prosecuted or Assessed According to Their Merits? A Consilient Interpretation of Territoriality in a Group-Living Carnivore, the European Badger (*Meles meles*)

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A.1 Introduction

The socio-spatial interactions of Carnivores have conventionally been described using the vocabulary of friend or foe, manifesting through territoriality and aggression (Macdonald, 1983*b*). This resulted in the strict differentiation between two types of habitat use. While the term 'home range' refers to the area, which an animal or social group uses for its day-to-day activities, 'territory' refers to the area within the animal's or group's home range over which it has exclusive (or at least priority) use; a territory is, by definition, defended and can encompass the home range in part or completely (Powell, 2000). Such socio-spatial relationships are most complex in group-living species, where individuals permit certain familiar conspecifics to co-share their territory while excluding others (Clutton-Brock, 2009). This involves a trade-off between costs of defence versus resource security benefits (Johnson et al., 2002*b*). Yet, the mechanisms involved, and the role of heterogeneities in individual costs and benefits linked to participation in group defence, are still not fully understood (Schradin, 2004). Crucially, residents must be able to recognise, remember and discriminate other own-group members from extra-group individuals (i.e., neighbours and strangers: Fisher, 1954; Müller and Manser, 2007). Ability to determine individual-specific characteristics, group membership and familiarity then aids in the formation of more complex animal societies (Carazo et al., 2008).

Olfactory signals are particularly effective in this context due to their latency (i.e., their persistence in the environment over time), where the signalling individual does not need to be present to convey information (Bossert, 1968), nor do they need to encounter conspecifics directly to gain information (Gosling, 1990; Johnston, 2008). Consequently, olfactory cues such as faeces and urine play a critical role in defining the activity range of an individual (e.g., Hutchings and White, 2000), or group (e.g., Jordan et al., 2010). Scent-matching of scent-marks to resident individuals therefore allows intruders to identify territory holders, alleviating potentially costly aggressive conflicts (e.g., Gosling et al., 1996; Lewis and Moorcroft, 2001). Scent marks are thus often referred to as a form of territorial defense and conventionally interpreted as 'keep-out signs' (e.g., Richardson, 2010) or 'scent fences' (e.g., Sun and Müller-Schwarze,

1998).

Game theory (Potts and Lewis, 2014) predicts that the outcome of territorial disputes hinges on two factors: (i) the value that the defended resource has for each individual's fitness (Gosling et al., 1996), and (ii) the contestant's fighting ability (resource holding power: Smith and Parker, 1976; Kelly, 2008). Accordingly, territorial animals are expected to react in a context-specific manner. The Dear Enemy Phenomenon (DEP) (Fisher, 1954) predicts that, by evaluating the relative threat posed by interlopers, residents can direct attention towards individuals that pose the greatest risk, while being more tolerant of others (Threat-level hypothesis: Temeles, 1994)). Thus, when competition with neighbours is intense, residents are predicted to respond more strongly to their neighbours, or to their olfactory cues, than to strangers (Carazo et al., 2008). In situations where strangers pose the greater threat than neighbours (e.g., dispersers intent upon territory acquisition), residents will respond more strongly to them. The resulting geometry of individual- or group-territories manifests as a contiguous socio-spatial network, maintained primarily by scent-marking rather than direct aggression (Gosling et al., 1996).

This conceptual framework can, however, lead to interpretive bias because it implies that all same-group conspecifics (own-group: OG) are 'friends', that is, conspecifics against which no aggression will be shown; whereas all individuals belonging to other groups (extra-group: EG) are 'enemies', potentially subject to aggressive exclusion/ repulsion (Johnston, 2008). This discounts social nuances, where OG-individuals may also be threatening (e.g. dominance; reproductive suppression, food competition) and EG may have positive intent (e.g. seeking mating opportunities), or benign consequences under different resource scenarios (e.g., Ostfeld, 1985).

Of particular interest is range use and territoriality in group-living solitary foragers – typically a spatial aggregation of individuals best explained by the particular dispersion of their key resources, as described by the Resource Dispersion Hypothesis (RDH: reviewed in Macdonald and Johnson, 2015). This social system is more common than previously understood, often involving a common denning site. Functionally, there is little basis for these spatial groups

to operate in isolation. The formation of obligate social groups is determined by bottom-up drivers (*sensu* Hunter and Price, 1992), such as collaborative and cooperative social behaviours between group members. In RDH-based spatial-groups, these social behaviours are not predicted to be intrinsic to group formation, rather the tolerance of a limited number of conspecifics (often kin) is less costly than trying to maintain an exclusive range under key resource conditions (see Macdonald and Johnson, 2015). Consequently the population will undergo top-down segregation into social-group units, determined by the most economic division of resources that allows necessary resource security (Macdonald and Johnson, 2015; Hunter and Price, 1992).

An example of an RDH-based facultative group-living, solitary forager is the European badger *Meles meles* (Macdonald and Johnson, 2015), for which a consilient understanding of socio-spatial segregation and territoriality has proven challenging, as new data contradict traditional views of territorial exclusivity in this species (Bradshaw and Hardwick, 1989). Understanding the details of badger sociality, however, is particularly important as, in the UK, this species is implicated as a wildlife reservoir in bovine tuberculosis (bTB) breakdowns in cattle herds (reviewed in Carter et al., 2007). The government-implemented large-scale culling operations of badgers as bTB management strategies rely largely on the notion of territoriality by specifically targeting infected social groups (Carter et al., 2007).

Badgers rely primarily upon olfaction to gain information about their environment and conspecifics (Buesching and Macdonald, 2001), and – like many carnivores – establish composite latrines containing faeces, urine, subcaudal and anal gland secretions, the location of which can remain stable over decades (Roper et al., 1986). Bait-marking surveys (Delahay et al., 2000) separate these latrines into two types: 'hinterland latrines', which are used exclusively by members of the resident social group, and 'border latrines', which are shared between neighbouring groups (Roper et al., 1993). Since Kruuk's formative descriptions of badger society (Kruuk, 1978), these border latrines are conventionally assumed to link up into defended perimeters, which divide group-territories via 'scent fences' (Stewart et al., 2001). This, however, is interpretative and a potential source of bias in the role of latrines: Simply because the bait-marking procedure

(Roper et al., 1993) draws hard lines linking latrines to segregate groups, does not mean that badgers perceive the resultant 'borders' in such a rigid way. In actuality, there is scant evidence of active territorial defence in badgers (Stewart et al., 1997*a*), with little aggression between neighbours observed at border latrines (Christian, 1995). Consequently, although the conventional 'active territorial defence' hypothesis (Stewart et al., 1997*a*), would interpret latrine use in badgers at territory borders as a stand-off in terms of each group's resource holding potential, signalling encounter likelihood across the boundary (Stewart et al., 2001), explanations based on non-agonistic but resource-pragmatic mechanisms of range separation between groups, such as the Passive Range Exclusion Hypothesis (Stewart et al., 1997*a*) appear increasingly plausible.

New data show that badgers from different social groups meet at latrines frequently, and pass by each other amicably, proceeding into their neighbour's range (Christian, 1995). Trapping records (Macdonald et al., 2008) and underground telemetry (Noonan et al., 2015*b*) evidence that individual badgers can reside within the main den ('sett') of other (primarily neighbouring) social groups for several days, with some individuals disappearing from their home sett for weeks, presumably residing with more distant groups (Noonan et al., 2015*b*). In Ireland, Byrne et al. (2014) observed badgers making long-distance movements, crossing the implied territories of others and likely staying temporarily in setts occupied by less familiar conspecifics. Genetic pedigree has revealed that badgers breed frequently between groups (Carpenter et al., 2005; Dugdale et al., 2008; Annavi et al., 2014), undermining territory defence by the inference that it is ineffective. Truly co-operative behaviours are few (Fell et al., 2006; Stewart and Macdonald, 2003; Stewart et al., 1999), and hence badger groups cannot be defined as 'eusocial', 'breeding' or 'spatial' (Bradshaw and Hardwick, 1989).

In a previous study, Palphramand and White (2007) demonstrated that badgers are able to discriminate between faeces from OG, neighbours and strangers, but interpreted this only in the context of territoriality and DEP. The interpretative power of their study, however, was limited because they were not able to identify the sex, age or group affiliation of either the donor or recipient animal. Here, we used anal gland secretion (AGS, which coats faecal deposits: Roper et al., 1986)

isolate to investigate the broader context of scent function in badger society.

Mustelid AGS encodes idiographic as well as nomothetic (Brinck et al., 1983) parameters (e.g., group-membership and individual-specific information such as age, sex, reproductive status), independent of faecal odour cues associated with foraging success. AGS from known individuals was presented to identifiable wild recipients to assess responses to familiar and unfamiliar scent-marks, and whether these vary according to context expectation in different regions of badger group-ranges. This framework permitted to test the predictions of three different (not necessarily mutually exclusive) hypotheses:

(a) The **familiarity hypothesis** (Fisher, 1954; Temeles, 1994), which posits that residents will react to the degree of familiarity of scent cues, unaffected by any individual-specific information encoded. Thus, corresponding with increasing familiarity, badgers would show a lesser response to OG-AGS than to neighbours or strangers.

(b) The **threat-level hypothesis** (Temeles, 1994), which posits that residents will modify their response according to the perceived level of threat, implied by the spatial-context of the cue (Mayeaux and Johnston, 2002). Thus, AGS from non-residents at the resident's sett, rather than at the territory perimeter, and AGS from neighbours at unshared, as opposed to shared borders, would elicit a greater response, as these scenarios might signify territory incursion.

(c) The **individual advertisement hypothesis** (Buesching and Macdonald, 2001), which posits that scent-marks advertise individual-specific characteristics, such as sex, age and/or reproductive status. Thus, the response of residents would be predicated upon the relevance of the encoded information, relative to their own physiological status and motivation, and largely independent of spatial context.

The findings of this study are used to advance conceptual understanding of badger socio-spatial ecology, and are placed into the general context of territoriality.

A.2 Materials and Methods

A.2.1 Study population

This study was carried out in a high-density badger population at Wytham Woods, Oxfordshire, England (51°46'26"N; 1°19'19"W; a designated Site of Special Scientific Interest (SSSI), owned by the University of Oxford) between 30th May – 8th June 2012 and 3rd – 15th June 2013, when latrines are particularly active (Delahay et al., 2000). Since 1987, a long-term trapping programme has documented the life histories and social-group affiliations of all individuals in this population from birth until death (usually indicated by disappearance from trapping records) over seasonal trapping sessions each year (Macdonald et al., 2009). The population comprised 23 social groups with ca. 182 adults and 39 cubs in 2012, and ca. 215 adults and 40 cubs in 2013 (estimated after Macdonald et al., 2009), permitting good statistical power. Social group ranges, and thus the affiliation of badgers caught at setts in each group range, were inferred from bait-marking and latrine surveys (Delahay et al., 2000).

A.2.2 Trapping protocol

All field work and data collection for this study was covered by our Natural England license 2014-5710-SCI-SCI and Home Office license PPL 30/2385; and all work was approved and supervised by the University of Oxford's Zoology Ethical Review Committee. Badgers (protected in the UK under the Badger Act 1992) were caught and sedated for handling and sampling, following the methodology detailed in Macdonald et al. (2009) as part of an ongoing population study. All trapped badgers were identifiable from a permanent individual tattoo number on the left inguinal region. In addition, all juveniles ($<$ 2 years, sexually immature) and adults ($\geq$ 2 years) were fur-clipped at every trapping (Stewart and Macdonald, 1997), permitting visual identification of individuals for behavioural analyses to cross-reference against their life-history records in the trapping record. Cubs ($<$ 1 year) were not clip-marked and were excluded from all analyses.

Sex, age-class (juvenile and adult), and reproductive status were recorded for each capture as 'individual characteristics'. For adult females, oestrus was in-

ferred from vulva condition and classified as oestrous (vulva swollen and moist), or non-oestrous (vulva flat and dry). Although all males had scrotal testes and were assumed to be in breeding condition during the field trials (Woodroffe and Macdonald, 1995*a*), the degree of testes descent varied between descended (testes descended into the scrotum, but lateral movement restricted) and fully descended (testes fully scrotal and mobile).

The social group affiliation of the individual (i.e. its capture site) defined its 'status', i.e., its group affiliation relative to the responding individual.

A.2.3 Sample collection

AGS samples (n = 50; 22 adult males; 6 yearling males; 18 adult females; and 4 yearling females) were collected in sterile 2.0ml glass vials with Teflon lined caps by gently everting and palpating the left anal gland papilla while the badger was sedated. Secretion was stored at -20°C until used in the trials. Only samples obtained within 10 days of the scent presentation experiment were used to maintain contemporaneous context.

A.2.4 Scent-presentation experiments

In total, we conducted 117 trials in 11 different social groups (for details of donors see Table A.1). In each trial, a sample vial, containing approximately 0.1g of AGS, was pushed into the ground until the rim was level with the surrounding soil, and an empty control vial was placed 50cm (i.e., approximately one badger head-body length) from the sample. Vials were deployed between 18:00 and 19:00, approximately 1 hour before badger emergence. New latex gloves were worn whenever samples were handled to avoid scent-contamination. To identify sample and control vial location on the camera footage, the researcher took a photo of themselves with the in situ camera immediately after vial deployment, pointing to both vials.

Familiarity treatments

AGS from three different donor categories were presented:

Table A.1: Scent samples used in the behavioural trials varying in levels of familiarity (own- group, neighbour, stranger), spatial-context (sett, shared border, unshared border) and sex and age class of the scent donor ($n = 117$).

Treatment	Location	n_{Total}	$n_{\text{Female Adult}}$	$n_{\text{Female Yearling}}$	$n_{\text{Male Adult}}$	$n_{\text{Male Yearling}}$
Own group	Sett	13	4	1	7	1
	Border	17	6	1	8	2
Neighbour	Sett	17	5	1	8	3
	Border	15	5	1	8	1
	Unshared border	13	5	1	6	1
Stranger	Sett	22	6	2	12	2
	Border	20	6	1	11	2

- OG (i.e., donor resident in the same social group where its AGS was presented; $n = 30$)
- Neighbour (i.e., donor resident in a neighbouring group to the group where its AGS was presented; $n = 45$)
- Stranger (i.e., donor resident in a social group at least 2 territories apart; $n = 42$).

AGS was presented either at the main sett or at a border latrine:

- OG presented at main sett ($n_{\text{Own}} = 13$) or at border latrine ($n_{\text{Own}} = 17$).
- Neighbour presented at main sett ($n_{\text{Neighbour}} = 17$), at a shared border latrine ($n_{\text{Neighbour-shared}} = 15$) or at a latrine on a different sector of the responder's group's border (i.e., not shared with that particular neighbour: $n_{\text{Neighbour-unshared}} = 13$).
- Stranger presented at main sett ($n_{\text{Stranger}} = 22$) or at border latrine (i.e., always unshared: $n_{\text{Stranger}} = 20$).

AGS from each scent donor was used only once in each category to avoid habituation. Trials were conducted at each social group for three days, with one AGS sample presented per night at each location. Treatment order was randomised.

A.2.5 Behavioural Observations

Responses were recorded using infra-red ReconyxHyperFireHC600 cameras (Reconyx Inc., Wisconsin, USA; one camera per site) taking two frames per second. At each site, one camera was set up in a nearby tree, approximately 1.5m off the ground and – depending on tree-availability – between 1.5m and 3.5m distance

from the sample, a minimum of 12 hours before the start of each 3-day-trial-period, and checked every morning. If badgers investigated a sample during the previous night, the respective sample and control vial were removed and a new sample and control vial presented at this location in a different spot (ca. 50cm away from previous sample) the following evening. If no badger responded, the sample and control were removed in the morning and replaced with a new control vial and a fresh sample from the same donor the following evening to maintain social-contact continuity.

Response measurements

A **potential response** was defined as a badger ('responder') approaching the sample to $\leq$50cm (ca. one head-body length), from where the badger would be capable of detecting the scent.

As a subset of these potential response events, an **actual response** was defined as progression to a badger positioning its nose within $\leq$10cm of the sample ('sniffing' the sample; the exact extent to which badgers may have licked samples was hard to discern consistently and was not used as a variable in the analyses, but tongue-contact with the sample was observed in some instances, indicating use of the vomero-nasal organ: Lüps and Wandeler, 1993).

For each response, (i) the number of times an individual sniffed the sample (potential response = 0 sniffing; actual response $\geq$ 1 sniffing) was recorded; (ii) the sniff-duration in seconds; (iii) the number of times an individual responded with subcaudal-marking within a 50cm radius of the sample (noting that badgers cannot scent-mark with AGS unless they defecate); and (iv) whether this subcaudal marking involved over-marking on top of the sample, or proximity-marking within 50cm of the sample (Buesching and Macdonald, 2004) were recorded for each actual response.

A.2.6 Statistical analyses

To test the predictions of the familiarity-, threat-level-, and individual advertisement hypotheses, the entire dataset (all responses regardless of identifiability

of responder; $n = 351$) was first evaluated with analyses of variance (ANOVA).

The relative importance of individual-specific characteristics of the scent donor (as established during the recent trapping session when AGS was collected) on sniff-duration and over-marking responses was then analysed using an information-theoretic (IT) approach employing Akaike Information Criteria (AIC) on the complete dataset ($n = 351$; see Stephens et al., 2005).

To further understanding of potential individual advertisement information encoded in AGS, IT-modelling was then expanded to investigate the influence of individual responder characteristics (age-class, sex, relative group-affiliation) as well as their interaction with scent-donor characteristics on sniff-duration and over-marking responses (restricting the dataset to those observations where the responder could be identified individually; $n = 187$).

To satisfy assumptions of normality, data on sniff-duration were log-transformed in all analyses.

i) Effects of scent familiarity on interest levels of the responder: The Familiarity hypothesis

To evaluate how residents responded to treatments at group-level, cumulative group-level responses (i.e. the mean of responses of individuals affiliated to that group) were analysed by testing the mean duration of sniffing events across all potential and actual responses, as well as the mean number of scent-marking events across all actual responses, against the 'category of the donor' (levels: own-group, neighbour, stranger).

Responses to AGS from neighbours at unshared borders were excluded from these analyses, as they are implicitly always 'out-of-context'. Following the approach of Palphramand and White (2007), social group, rather than individual, was treated as a random, repeated effect in these analyses.

ii) Effect of socio-spatial context on interest levels of the responder: The Threat-level hypothesis

To test the threat-level hypothesis, familiarity was controlled for by presenting AGS from neighbours in three different socio-spatial-contexts (levels: shared border, sett, unshared border). The mean duration of sniffing events and the mean number of scent-marking events was then tested against these socio-spatial-contexts levels. Responses to 'own-group' (implicitly always 'in-context') and 'strangers' (implicitly always 'out-of-context') were excluded. As before, social group was treated as a random, repeated effect.

iii) Effects of relevance of individual-specific information encoded in AGS on the interest-levels of the responder: Individual advertisement hypothesis

AIC model selection was applied to reference effects of individual-specific fitness-related information encoded in the AGS, against the characteristics of the responder (Burnham and Anderson, 2002; Burnham et al., 2011). These analyses used sniff-duration per potential response, as well as number of scent-marking events per actual response, as treatment response variables. Model selection does not support missing data, because this invalidates between-model contrasts. As individuals could not be identified from their clip-marks in 46% of observations due to the camera-angle, model selection was performed using the complete dataset initially, including unidentifiable responders. This global model included the variables 'age' of the donor (levels: yearling, adult); 'sex' of the donor (levels: male, female); 'reproductive status of the female donor' (levels: oestrous, non-oestrous); and 'reproductive status of the male donor' (levels: descended, fully descended), as well as interaction terms. Trial ID was included as a random effect in these models.

Subsequently, and restricting the dataset to those observations where the responder clip-marks could be identified unambiguously ($n = 187$), individual responses were evaluated, based on a global model that included the same variables as above, but also including the characteristics of the responder. Responder and trial ID were included as random effects in these models (Bates, 2010).

The AIC was derived to rank the support for each model, and the Δ AIC (Δ_i) calculated in relation to the highest-ranking model and Akaike weight (w) (Burnham et al., 2011). Model averaging was applied to derive estimates of the coefficients (θ) associated with all sets of models, and their 95% confidence intervals (CI). To take into account uncertainty in model selection (Burnham and Anderson, 2002), mean coefficient values were calculated by averaging their values over all models that included the coefficient of interest, weighted by w. The 'Relative Influence' of each predictive variable was calculated as the summation of w across all models that included the variable of interest (Burnham and Anderson, 2002).

All statistical analyses were performed in R-v.3.0.3 (R Core Team, 2014) using the '*lme4*', '*nlme*', and '*MuMIn*' packages. Although statistical analyses were performed on transformed data, for visual purposes, figures are based on untransformed data.

A.3 Results

From a total of 117 trials, 85 ($n_{\text{Own}} = 20$, $n_{\text{Neighbour}} = 35$, $n_{\text{Stranger}} = 30$) produced 351 potential responses ($n_{\text{Own}} = 112$; $n_{\text{Neighbour}} = 125$, $n_{\text{Stranger}} = 126$), including 196 actual responses involving sniffing ($n_{\text{Own}} = 27$, $n_{\text{Neighbour}} = 81$, $n_{\text{Stranger}} = 88$) and 141 involving subcaudal-scent-marking responses (n$n_{\text{Own}} = 9$, $n_{\text{Neighbour}} = 49$, $n_{\text{Stranger}} = 83$). Sniff-duration could not be determined accurately for 13 responses. There was no potential response in 32 trials, which were excluded from all analyses. Badgers never responded to blank control vials.

When badgers sniffed AGS, their noses generally made direct contact with the sample ($n = 188/196$). AGS from strangers was dug out more often (26.7%, $n = 8/30$), compared to neighbours at unshared borders (15.4%, $n = 2/13$) and at setts (7.6%, $n = 1/13$), whereas OG- and neighbour-AGS at shared borders was never interfered with; there were, however, insufficient data to analyse these digging responses systematically.

i) Effects of scent familiarity on interest levels of the responder: The Familiarity hypothesis

Cumulative group-responses to introduced scent were stronger when AGS was less familiar (weakest to OG-AGS, with intermediate responses to neighbouring-group samples, and strongest to stranger-AGS). The duration of sniffing responses at the group-level differed significantly between all levels of familiarity (ANOVA: $F_{[2,67]} = 14.17$, $P < 0.0001$; Tukey *post hoc* test: all P-values < 0.027; Fig. A.1a), and were longer in response to AGS from both strangers ($\bar{x} = 4.29$s $\pm$ 2.60 SD, $n = 32$), and neighbours ($\bar{x} = 2.71$s $\pm$ 2.56 SD, $n = 33$), than to OG ($\bar{x} = 1.44s\pm$ 2.58 SD, $n = 19$). Similarly, over-marking responses differed significantly between all levels of familiarity (ANOVA: $F_{[2,67]} = 15.45$, $P < 0.0001$; Tukey *post hoc* test: all P-values < 0.03; Fig. A.1b), and were more frequent to AGS from both strangers ($\bar{x} = 0.77 \pm 0.51$ SD, $n = 32$), and neighbours ($\bar{x} = 0.48 \pm 0.50$ SD, $n = 33$), compared to OG-AGS ($\bar{x} = 0.07 \pm 0.50$ SD, $n = 19$).

ii) Effect of socio-spatial context on interest levels of the responder: The Threat Level hypothesis

Across the complete dataset including all levels of familiarity, sniff-duration differed significantly between locations (ANOVA: $F_{[2,67]} = 4.73$, $P = 0.012$). Neighbour-AGS provided out-of-context, at either the sett or at an unshared border, however, received no greater interest from the responder (ANOVA: $F_{[1,18]} = 2.88$, $P = 0.11$) than at an in-context location (shared border).

This pattern was also apparent in subcaudal-over-marking responses that, across all levels of familiarity, were affected significantly by location ($F_{[2,67]} = 12.08$, $P < 0.0001$); although neighbour-AGS presented out-of-context was not over-marked more often than at an expected location (ANOVA: $F_{[2,18]} = 0.73$, $P = 0.41$).

iii) Effects of relevance of encoded individual-specific information content on the interest levels of the responder: Individual advertisement hypothesis

In general, individual-level responses followed the same overarching patterns as those at the group-level: sniff-duration differed significantly with familiarity (two-way ANOVA: $F_{[2,330]} = 37.70$, $P < 0.0001$), where the duration of responses decreased with greater familiarity (Fig. A.2a) with no significant effect of AGS-location on sniff-duration ($F_{[3,330]} = 1.96$, $P = 0.12$). Conversely, subcaudal-marking responses differed significantly between levels of familiarity (two-way ANOVA: $F_{[2,343]} = 19.76$, $P < 0.0001$), as well as location ($F_{[3,343]} = 3.05$, $P = 0.029$; Fig. A.2b).

Responding individuals could be identified in 54% of observations ($n = 187$; Total number of identifiable individuals = 45 of which $n_{\text{Male Adult}} = 14$, $n_{\text{Male Yearling}} = 3$, $n_{\text{Female Adult}} = 25$, $n_{\text{Female Yearling}} = 3$). In 12.9% of trials ($n = 11$) an identifiable individual returned a second, and in one case also a third time, to respond to the same AGS sample. In 63.6% ($n = 7$) of these instances, the donor was a stranger ($n_{\text{Male}} = 4$, $n_{\text{Female}} = 3$), a neighbour at an unshared location in 27.3% ($n = 3$, $n_{\text{Male}} = 1$, $n_{\text{Female}} = 2$), while in only one case the scent donor was a young female from the responding female's own group.

When examined in more detail, individual responses were moderated by the relevance of individual-specific information encoded in the donor AGS to the physiological state of the responder.

Overall, males tended to sniff for longer than did females ($\bar{x} = 2.38$s $\pm$ 3.08 SD; $\bar{x}= 1.73$s $\pm$ 3.12 SD respectively), bordering significance (ANOVA: $F_{[1,79]} = 3.83$, $P = 0.054$), but there were no sex-related differences in the frequency of over-marking responses (ANOVA: $F_{[1,80]} = 1.30$, $P = 0.26$; Fig. A.2a). Similarly, there were no age-class related differences in sniff-duration or over-marking responses (ANOVA: $F_{[1,72]} = 1.31$, $P = 0.26$; $F_{[1,72]} = 0.13$, $P = 0.72$ respectively).

Interestingly, animals in reproductive condition sniffed AGS significantly longer and subcaudal over-marked it more often, although the latter effect was not

significant (ANOVA: $F_{[1,59]} = 3.99$, $P = 0.012$; $F_{[1,59]} = 2.52$, $P = 0.066$ respectively). Whereas males tended to over-mark oestrous female AGS more than non-oestrous female AGS (Fig. A.2b; bordering significance: ANOVA: $F_{[1,17]} = 4.09$, $P = 0.059$), females exhibited no noticeable difference in inter-individual over-marking responses in relation to donor's reproductive status. Subcaudal-proximity-marking occurred significantly more often than direct over-marking (Sign test: $P < 0.0001$, n = 141; 84.4% vs. 15.6% respectively), but without any significant effect of familiarity (ANOVA: $F_{[2,136]} = 1.04$, $P = 0.36$), location ($F_{[1,136]} = 0.520$, $P = 0.47$), or (donor-) sex ($F_{[1,136]} = 0.45$, $P = 0.51$; Table A.2).

Table A.2: Subcaudal over-marking (i.e., marking on top of the introduced AGS), and proximity-marking (i.e., within 50cm) in response to different levels of familiarity (own group, neighbour, stranger), spatial-context (sett, shared border, unshared border) and sex of donor ($n = 141$).

	Treatment	**Neighbour location**	n_{Total}	n_{Female}	n_{Male}
Over-mark ($n = 22$)	Own		-	-	-
	Neighbour	Shared border	2	2	-
		Sett	-	-	-
		Unshared border	5	2	3
	Stranger		15	7	8
Proximity-mark ($n = 119$)	Own		9	8	1
	Neighbour	Shared border	7	3	4
		Sett	-	-	-
		Unshared border	35	19	16
	Stranger		68	41	27

A.3.1 Sniffing

While familiarity and location were the most supported parameters determining the time spent investigating introduced AGS, the influence of age and sex of the scent donor were also important (Table A.3). Donor reproductive status as well as the interaction terms, however, had relatively little influence. Indeed, the most supported model for sniff-duration included level of familiarity, location at which the sample was presented, donor sex and age, and interaction terms between these ($w = 0.118$). The model that excluded individual characteristics (i.e., including only status: familiarity and location) had little biological significance ($\Delta_i = 4.15$, $w = 0.006$) indicating the importance of considering the individual-specific information encoded in scent when predicting responses.

Table A.3: Model averaging for the parameters linking sniffing and over-marking responses of badgers for the complete dataset ($n = 351$). The Relative Influence of each parameter (based on Akaike weights) is presented along with model-averaged estimated values of their coefficients (θ), and 95% confidence intervals (CI). Asterisks (*) denote interaction terms.

	Sniff duration				Over-marking response			
Metric	**Relative Importance**	θ	**95% CI**		**Relative Importance**	θ	**95% CI**	
Treatment	1.00	-0.192	-0.384	-0.001	1.00	0.256	-0.035	0.548
Location	0.98	-0.173	-0.345	-0.001	1.00	0.316	0.001	0.632
ScAge	0.95	0.125	0.000	0.250	0.90	0.249	0.001	0.498
ScSex	0.89	0.036	0.000	0.072	0.88	0.108	0.000	0.216
ScSex*Treatment	0.55	0.003	-0.094	0.100	0.13	0.157	0.001	0.313
Location*ScSex	0.50	-0.080	-0.249	0.090	0.42	-0.171	-0.656	0.313
ScAge*ScSex	0.45	-0.155	-0.310	-0.001	0.29	-0.149	-0.298	0.000
ScAge*Treatment	0.42	0.003	-0.094	0.100	0.14	0.100	0.000	0.200
Location*ScAge	0.39	0.035	-0.114	0.184	0.42	0.099	-0.223	0.420
ScRep	0.30	0.027	-0.001	0.055	0.99	0.264	0.001	0.527
Location*Treatment	0.22	0.154	0.000	0.308	0.30	-0.637	-1.271	-0.002
ScAge*ScRep	0.05	-0.019	-0.136	0.098	0.09	0.004	-0.122	0.131
Location*ScRep	0.05	-0.011	-0.178	0.125	0.99	-0.335	-1.072	0.402
ScRep*Treatment	0.01	-0.012	-0.113	0.089	0.07	-0.208	-0.599	0.184

A.3.2 Over-marking

Familiarity and location were also the most influential parameters affecting subcaudal-marking responses when analysing the complete dataset. Unlike sniffing responses, however, the reproductive status of the scent-donor, and its interaction with location were highly influential. The influence of donor age and sex were of moderate importance, while the interaction terms had relatively little influence (Table A.3). The model that excluded individual characteristics had little biological significance ($\Delta_i = 16.77$, $w = 0.00$), while the most supported models all included these characteristics and their interaction with location.

When models based on the restricted dataset were ranked, familiarity and location remained the most influential parameters, with the responder's reproductive status being highly influential (Table A.4). Unlike sniffing responses, the most supported model predictive of subcaudal-marking response included familiarity as well as location of the AGS sample in addition to the responder's reproductive status, ($w = 0.113$).

A.4 Discussion

Sun Tzu (6^{th} Century BCE) wrote: "If you know your enemies and know yourself, you will not be imperilled in a hundred battles? if you do not know your enemies nor yourself, you will be imperilled" – a pervasive philosophical concept

Table A.4: Model averaging for the parameters linking sniffing and over-marking responses of badgers for the restricted dataset ($n = 187$) including responder characteristics within the linear model. The Relative Influence of each parameter (based on Akaike weights) is presented along with model-averaged estimated values of their coefficients (θ), and 95% confidence intervals (CI). Asterisks (*) denote interaction terms.

	Sniff duration				**Over-marking response**			
Metric	**Relative Importance**	θ	**95% CI**		**Relative Importance**	θ	**95% CI**	
Treatment	1.00	-0.104	-0.207	-0.001	1.00	0.083	-0.233	0.398
RespRep	0.74	-0.043	-0.156	0.070	0.68	-0.160	-0.452	0.132
RespAge	0.51	0.185	0.001	0.370	0.27	-0.059	-0.118	0.000
RespAge*Treatment	0.38	-0.161	-0.374	0.052	0.01	-0.006	-0.054	0.041
Location	0.33	-0.142	-0.284	-0.001	0.990	0.177	-0.039	0.392
RespSex	0.30	-0.078	-0.155	-0.001	0.34	0.183	0.001	0.365
ScAge	0.28	0.103	0.001	0.205	0.14	0.034	0.000	0.067
RespRep*Treatment	0.27	0.029	-0.167	0.226	0.01	0.080	-0.176	0.336
ScSex	0.25	0.077	0.000	0.154	0.36	0.116	0.001	0.232
Location*Treatment	0.14	-0.274	-0.274	-0.002	0.13	-0.185	-0.369	-0.002
RespSex*Treatment	0.06	0.022	-0.118	0.163	0.05	0.321	0.002	0.640
Location*ScSex	0.05	0.064	-0.152	0.280	0.19	0.153	-0.245	0.551
RespAge*RespRep	0.05	-0.319	-0.635	-0.003	0.08	-0.865	-1.722	-0.007
ScSex*Treatment	0.04	-0.207	-0.413	-0.002	0.02	-0.242	-0.483	-0.002
RespAge*ScAge	0.02	-0.472	-0.940	-0.003	0.01	0.665	0.005	1.324
RespRep*ScSex	0.01	-0.092	-0.183	-0.001	0.01	-0.200	-0.398	-0.002
ScAge*Treatment	0.01	-0.032	-0.063	0.000	0.01	0.201	0.002	0.401
RespSex*ScSex	0.01	-0.198	-0.395	-0.002	0.00	-0.081	-0.162	-0.001
RespRep*ScAge	0.01	-0.033	-0.080	0.014	0.00	-0.243	-0.484	-0.002
Location*RespSex	0.01	0.021	-0.211	0.254	0.14	-0.283	-0.721	0.154
RespAge*RespSex	0.01	-0.067	-0.134	-0.001	0.01	-0.485	-0.965	-0.004
RespSex*ScAge	0.01	0.100	0.001	0.199	0.00	-0.328	-0.653	-0.003
Location*RespRep	0.01	0.133	-0.201	0.468	0.04	-0.012	-0.278	0.255
ScAge*ScSex	0.00	-0.173	-0.344	-0.001	0.00	-0.397	-0.792	-0.003
Location*RespAge	0.00	-0.135	-0.268	-0.001	0.01	0.060	0.000	0.120
Location*ScAge	0.00	-0.184	-0.366	-0.002	0.01	-0.348	-0.694	-0.003
RespAge*ScSex	0.00	0.086	0.001	0.171	0.01	0.665	0.005	1.324

in political and military theory.

This study evidences that, for badgers, and by extension other species with a comparable RDH-based social system, interpretations of territoriality depicting rigid and potentially agonistic discrimination between OG-members and members of foreign groups are overly-simplistic. As expected, we found no support for indiscriminate attempts at Active Territorial Defence (Stewart et al., 2001). The notion of 'enemy' therefore is increasingly contrary to the Schengen-type (movement without borders: Schutte, 1991) badger society proposed by Macdonald, Newman and Buesching (2015). Instead, individuals and their scent-marks might well be recognised as non-residents; however, they are not treated as a threat at carte blanche level, but assessed on their individual-specific characteristics. Receiver responses to conspecifics are driven by the interplay of three factors: (i) the status (degree of familiarity) of the signaller, (ii) the characteristics of the signaller, and (iii) the relevance of the scent-signal to the responder. In the following, we evaluate this cascade of evidence through a filter of progressively more refined functions.

A.4.1 Familiarity Hypothesis

Badgers were clearly able to discriminate between OG- and EG-AGS, reacting significantly less to more familiar individuals. Evidence of DEP (Müller and Manser, 2007) was also apparent in our study.

DEP is an evolved response to minimise costs associated with territoriality (Ydenberg et al., 1988), and in badgers it could likely be the mechanism allowing certain animals to visit neighbouring territories. In this same population, the lifetime reproductive output of 193 females examined involved exclusively EG-paternity for 39%, OG for 36%, with the remaining 25% following a mixed strategy (Annavi et al., 2014). Similarly, over 5255 trapping events, 36% of badgers were never caught visiting a different social group, while at any one seasonal trapping 16.4% of the population was at a group differing from its primary affiliation (Macdonald et al., 2008).

Palphramand and White (Palphramand and White, 2007) found that badgers responded more strongly to faeces from strangers, but not neighbours, compared to OG-samples, when presented in the single context of main setts. Their results, however, are challenging to interpret because they deliberately selected faeces not to contain any visible glandular secretions. Faeces cannot encode information about group-membership per se, but only about the food consumed (as a potential cue for optimal foraging: Galef Jr and Wigmore, 1983)) or the donor's endocrinological status (Schwarzenberger et al., 1996). In contrast, here residents also reacted stronger to neighbours, compared to OG-AGS.

A.4.2 Threat level hypothesis

Although out-of-context signals from neighbours have been reported to evoke greater responses in a variety of species (Müller and Manser, 2007), there was little support that scent-location moderated reaction in this badger population. Instead, badgers appeared to modify their response according to the relevance of encoded individual-specific scent-donor information relative to their own characteristics and status. This indicates that badgers did not assess the level of threat posed by apparent interlopers by the positioning of their scent-marks, but rather by individual characteristics and familiarity. Notably, some responses to strangers were very intense: Stranger-AGS was repeatedly dug up, and evoked significantly elevated responsive subcaudal-marking compared with OG- and neighbour-AGS. As observed by Palphramand and White (Palphramand and White, 2007), longer sniff-duration was associated with less familiar AGS, likely connected to time required to attempt to identify the individual donor and their implied threat-level (Sliwa and Richardson, 1998) and/or decode individual-specific information (Buesching and Macdonald, 2001).

A.4.3 Individual advertisement

Due to the large sample size of individually-known AGS donors and responders in this present study, the individual-specific mechanisms underscoring these group-level effects became apparent.

Mustelid-AGS encodes a variety of fitness-related individual-specific information such as sex, age and reproductive condition (Zhang et al., 2003; Apps, 2013). Although Davies, Lachno and Roper (1988) report limited variability in AGS-profiles of badgers, new techniques indicate that the chemical composition of badger-AGS does differ between males and females, and varies with age, reproductive status and individuality (Buesching et al., 2003). Field observations confirm that badgers can decipher this individual-specific information; mirroring responses to chemical variation in subcaudal gland secretions (Buesching and Macdonald, 2004). Nevertheless, although responsive subcaudal marking rates by males and females were similar, their motivation was likely different: in mammals females typically sequester (and thus scent-mark) food resources necessary to raise offspring, whereas males sequester access to females (Greenwood, 1980). From their more limited data, Palphramand and White (2007) reported no evidence of differences in the responses of male or female badgers to faeces deposited by an individual of unknown sex and age. Aided by knowing the sex of both, the donor and the receiver, the present study highlighted that males investigated AGS more thoroughly than did females, and sniffed and over-marked AGS from oestrous females significantly longer than AGS from non-oestrous females. This is in strong contrast to previous studies (Palphramand and White, 2007), and suggests an epigamic role of the female AGS signal triggering male interest (Buesching and Macdonald, 2004). Interestingly, complementary work in this same study population found that badgers, instead of simply defecating at the section of boundary closest to their current foraging site often traverse the entire group-range to place their faeces at a latrine chosen very deliberately, again implying self-advertisement (Kilshaw et al., 2009).

A.4.4 Conclusions

In overview, this study demonstrates that badgers have a thorough operational knowledge of individuals well beyond their own social group, and the apparent ability to ascertain quickly the characteristics (sex, age, etc) of unfamiliar individuals. Our findings give support to the familiarity hypothesis as well as individual advertisement. The results highlight that (a) AGS encodes information pertaining to fitness-relevant parameters, and (b) that individuals have a diverse and adaptable knowledge of their neighbouring conspecifics, as well as

the ability to distinguish strangers from OG and neighbours. The presented observations of how social communication is mediated in badger society reconcile well with mounting evidence of more complex inter-group interactions than realised previously (Macdonald et al., 2015), from both genetic pedigree (e.g., Dugdale et al., 2008; Annavi et al., 2014) and high-resolution tracking (Noonan et al., 2015*b*), which highlight that individual heterogeneities govern socio-spatial interactions.

The ability to exchange information between all conspecifics sharing a space is crucial for the maintenance of stable socio-spatial landscapes (Dall et al., 2005). If plotted on a map, scent-sites, such as latrines, which are used for communication amongst neighbours, can easily generate the – potentially false – appearance of co-ordinated group territories, although they might not fulfil a role in central control or explicit defence (Delahay et al., 2000). Nevertheless, the resulting extent of social network connectivity affects how social and/or genetic information (Krause et al., 2007), as well as infection (Perkins et al., 2009), can flow between individuals.

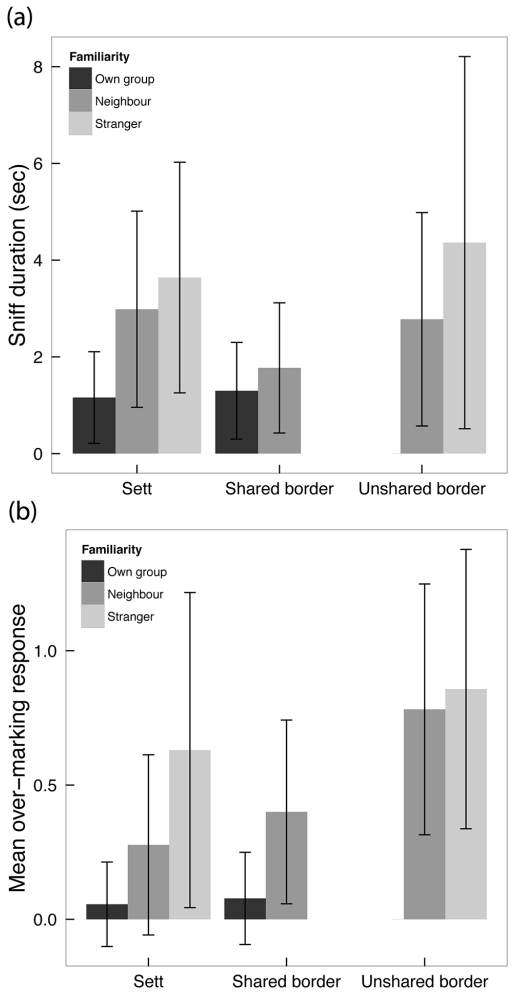

Figure A.1: Group-level variation in responses to AGS from donors of different levels of familiarity. Mean (± SD) group level (a) duration of sniffing responses in seconds; and (b) number of subcaudal-marking responses per potential response to AGS from own-group ($n = 20$ trials), neighbours ($n = 35$) and strangers ($n = 30$) presented at either the responding group's sett, or a border (shared or unshared) between the responding group and the scent donor.

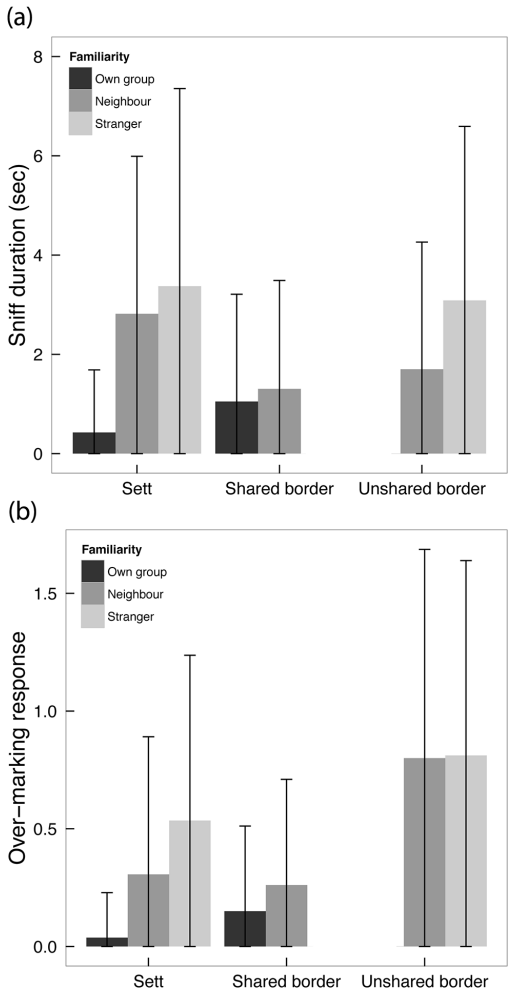

Figure A.2: Individual-level variation in responses to AGS from donors of different familiarity levels. Individual level (± SD) (a) duration of sniffing responses; and (b) number of subcaudal-marking responses per potential response to AGS from own-group (n = 20 trials), neighbours (n = 35) and strangers (n = 30) presented at either the responder's sett, or a border (shared or unshared) between the responder and the scent donor.

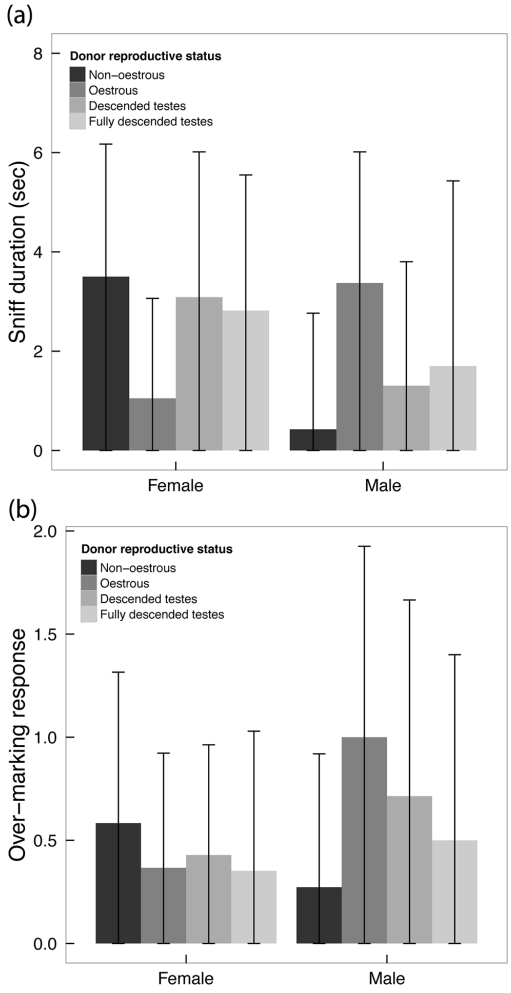

Figure A.3: Variation in responses to AGS according to the reproductive status of the donor. Individual male and female (± SD) (a) duration of sniffing responses; and (b) number of subcaudal-marking responses per potential response to AGS in relation to the reproductive status of female (levels: oestrous, non-oestrous) and male (levels: descended testes, fully descended testes) scent.

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