The effects of energetic expenditure tactics and life-history variability on European badger (*Meles meles*) ecology



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Abstract

Wild animals have evolved a diverse range of energy-budgeting tactics to cope *in situ* with rapid environmental change. My thesis investigates these tactics and their underlying mechanisms in a population of wild European badgers (*Meles meles*): 1) over the course of an individual's lifetime and 2) in response to fine-scale changes in energetic context.

Chapter 1 derives a novel minimum number alive abundance estimator, incorporating variable capture efficiency to more accurately quantify changing social context for subsequent analyses. Chapter 2 exposes how changing population metrics and weather drive sex-specific life-history responses, producing diverse co-occurring paces-of-life and potentially contributing to substantial sex ratio skew at higher densities. Chapter 3 uncovers a threshold-bounded relationship between body condition and survival probability, whereby most badgers exhibit flexible somatic phenotypes within what I term an "energetic safe zone"; adverse weather and life-history risk factors can tip individuals over the threshold, but a minority of high-quality individuals exhibit high reproduction probability and lower mortality risk despite reduced body condition.

Chapter 4 uses 3D printing to streamline production and reusability of bespoke multi-sensor collars, enabling simultaneous fine-scale quantification of overall dynamic body acceleration (ODBA, measuring mechanical energy expenditure) for multiple individuals. Chapter 5 applies this technology and finds season-specific fine-scale activity responses to prevailing weather conditions, according to individual energetic context; in particular, low body condition constrains energetic tactics. Chapter 6 combines ODBA with quantification of daily energy expenditure (DEE) using doubly-labelled water, demonstrating that individuals expend energy differently under the same conditions; ODBA/DEE, measuring proportional energy expenditure on activity, correlated negatively with next-season body condition.

The range of energetic expenditure tactics sustained in this population support the existence of adaptive heterogeneity. I present an argument predicated on Jensen's Inequality for the maintenance of this diversity, and reflect on implications for resilience to ongoing anthropogenic change.

Contents

Acknowledgments i

Abstract iii

Declaration of Authorship v

Ethics and Funding v

General Introduction – Energy expenditure: A heterogeneous affair 1

Part I – A life-history view of energetic heterogeneity

Chapter 1 – *Preserving identity in capture-mark-recapture studies: Increasing the accuracy of minimum number alive (MNA) estimates by incorporating inter-census trapping efficiency variation* 74

Chapter 2 – *What lies beneath? Population dynamics conceal pace-of-life and sex ratio variation, with implications for resilience to environmental change* 104

Chapter 3 – *A fat chance of survival: Body condition provides life-history dependent buffering of environmental change in a wild mammal population* 155

Part II – Fine-scale heterogeneity in energy expenditure

Chapter 4 – *3D-printing for bespoke, flexible, and reproducible wildlife collar designs: Best practices and lessons from field deployment on medium and large carnivores* 214

Chapter 5 – *Individual mechanical energy expenditure regimens vary seasonally with weather, sex, age, and body condition in a generalist carnivore population: Support for tactical diversity* 232

Chapter 6 – *Links between somatic condition, life history, and energy budgets reveal heterogeneous energy management tactics in a wild population of European badgers (Meles meles)* 290

General Discussion – Heterogeneous energy-budgeting: Evidence, distinctions, and maintenance 335

Appendices

Supplementary Chapter 1 – *Negative density-dependent parasitism in a group-living carnivore* 384

Supplementary Chapter 2 – *Early-life seasonal, weather and social effects on telomere length in a wild mammal* 421

Supplementary material for Chapter 2 467

Supplementary material for Chapter 3 476

Supplementary material for Chapter 4 496

Supplementary material for Chapter 5 519

Declaration of Authorship

I declare that this dissertation is primarily my own work. It was conceived and edited in a collaborative fashion, as credited in the respective chapter authorship lists (individual author contributions are specified at the end of each chapter); the primary analysis and writing, however, is my work alone. In keeping with the collaborative nature of much of the output, I have written the research chapters primarily in third person plural ("we"). Each research chapter has either been submitted for publication or has been prepared with journal submission in mind. Supplementary Chapters 1-2 are both collaborative papers with relation to my own work that I have been fortunate enough to contribute to during my PhD, but which were primarily led by their respective first authors. The work herein has not been submitted to meet the requirements of any degree or professional qualification, with the exception of Supplementary Chapter 2, which I do not claim primarily as my own work.

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Ethics and Funding

All badger captures were licensed under the Badger Act (1992) (most recently Natural England license 2019-2020-4417) and all handling procedures carried out under Animals (Scientific Procedures) Act (1986) license (currently PPL 30/3379).

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General Introduction

Energy expenditure: A heterogeneous affair

1 The question

Energy is the currency of fitness in wild populations. Just as with monetary currency, individual organisms must both acquire adequate energetic "income" (through chemosynthesis/photosynthesis, Dubilier et al. 2008, Vanlerberghe et al. 2020, or heterotrophy, Charnov 1976) and ensure it is invested optimally into growth and reproduction (Doughty and Shine 1997, Newbolt et al. 2017). Just as monopolies reduce the competitiveness of human enterprise, the allocation of limited energetic funds in wild populations is performed in a manner sensitive to the competitiveness of the fitness landscape (Gaillard et al. 1993, Stopher et al. 2008). Individuals must also weigh the fitness benefits of current reproduction against investing in an edge to current survival and/or growth, ideally to the advantage of future attempts at reproduction (Stearns 1992); these long-term investors are not mutually exclusive with short-term planners, a topic that we will return to in due course.

When energetic income cannot match outgoing expenditures, bankruptcy (mortality) will ultimately occur. Individuals can avoid this outcome by reining in voluntary expenditures (in animals, these can be as diverse as sexual advertisement, Weladji et al. 2005, or activity, Wilmers et al. 2017; these expenditures are further discussed later on) or incurring debt on accumulated capital (cached food, Humphries et al. 2003, fat and/or protein stores, Monteith et al. 2013), to a point. Ultimately, the conditions under which the environment overwhelms these coping mechanisms (e.g. when heat losses are untenable, Harding et al. 2005, or when predation risk exceeds food gain, Diserens et al. 2021) determine the Hutchinsonian niche of a species (Kearney et al. 2010). Of course, niches may be further limited by other currencies, such as nutrients (Raubenheimer et al. 2009) or time (Bergman et al. 2001). Nevertheless, just as we can study how fiscal fragility drives worse outcomes during economic recessions (e.g., Aiyemo

2020), the energetic niche is a useful concept for modelling the effects of large disruptions in the energetic landscape, such as those caused by anthropogenic climate change (Schloss et al. 2012, Foden et al. 2013).

Beyond the predictable and stochastic environmental variations that are routine in wild populations, species have evolved capacities to handle severe—even catastrophic—climate and habitat changes. The average mammalian species, for instance, persists for 1.5 million years (Barnosky 2001). Consequently, the average mammal species has coped with 14-15 of the Milankovitch cycles that, at least in the Pleistocene, have led to wide glaciation/inter-glacial cycles (Hays et al. 1976), and an order of magnitude more Dansgaard-Oeschger events (Dansgaard et al. 1993). Indeed, organisms carry this evolutionary history with them: it has been posited that stress induces elevated mutagenesis in bacteria (Foster 2007) as an adaptation to facilitate saltational evolution (Katsnelson et al. 2019). Therefore, we should only expect to see major changes in community composition through widespread extinction of maladapted guilds when the environment shifts beyond the scale of the average species' persistence—this concept is termed the Court Jester hypothesis (Barnosky 2001). The Court Jester is contrasted with the Red Queen hypothesis, which posits the consistent co-evolution of species as a result of short-term biotic interactions (Van Valen 1973, Strotz et al. 2018).

The diverse forms of human-induced rapid environmental change (HIREC, Sih 2013) present a unique challenge to populations. While many vagile populations are responding to anthropogenic climate change by moving to track it (e.g., Hickling et al. 2006, Kelly and Goulden 2008, Chen et al. 2011), its pace is too fast for many species (Schloss et al. 2012) and some, such as mountain-top species, have nowhere to go (Bell et al. 2014). The effects of climate change are in turn exacerbated by habitat degradation and destruction (Forister et al. 2010),

population exploitation by humans for food or resources (Pörtner and Peck 2010), introduction of pests and diseases (Pounds et al. 2006), and even the unanticipated effects of wildlife management (Bright Ross et al. 2021). Habitat fragmentation, while controversial in its unilateral effects on biodiversity (see Fahrig 2019), interferes with many of the ways that populations are pre-adapted to cope with rapid change, such as migration (Forister et al. 2010, Tucker et al. 2018) or gene flow (e.g., seed dispersal, Jump and Peñuelas 2005, Cui et al. 2018, offspring dispersal, Schwalm et al. 2016). The frequency and severity of the challenges that HIREC presents to populations has thus brought the processes of the Court Jester into the temporal domain of the Red Queen (Benton 2009).

Returning to the realm of economic analogy, two unique industry models in Japan can prove illustrative for how wild organisms can persist under the intense selective pressures of HIREC. Climate change is occurring, in the case of many longer-lived organisms, too quickly for genetic adaptation (Berteaux et al. 2004, Merilä and Hendry 2013); therefore, the first of these analogies relates to the ability to pivot within a single firm/organism. Following the disastrous aftermath of World War II, Japan recovered to boast the world's third largest economy by the late 1960s. Although the reasons for these are various (Gao 2007), Japanese firms were competitive on the world stage in part due to the predominant business model they came to follow, termed a "keiretsu" (McGuire and Dow 2002). The keiretsu firms (including widely-recognised names such as Mitsubishi and Toyota), through a horizontal and vertical integration process with grounding in historical inter-firm relationships, built less dependence on short-term returns for investors, permitting higher investment in flexibility in the marketplace (Aoki 1990)– a benefit that persists even as this traditional structure has been supplanted (Aoki and Lennerfors 2013). This type of flexibility is key, and analogous to plasticity in wild populations. Plasticity—

the capacity to change phenotypes within an individual lifetime in response to environmental cues—is crucial to weathering HIREC (Parmesan 2006, Chevin et al. 2010, Merilä and Hendry 2013). Nevertheless, different species will be unequally able to express plasticity—just as unique historical ties enabled the keiretsu to thrive, so too does dietary generalism (Davey et al. 2012), the capacity to leave central foraging places (Bhattacharyya and Ray 2015), and the ability to modulate energy requirements to cope with shortages (Geiser and Turbill 2009) shape a species' ability to respond plastically to change.

The second analogy we can draw upon relates to heterogeneity within a population of organisms (or businesses). Japan today boasts 40% of the world's current centenarian businesses (33,000), 140 businesses over 500 years old, and at least 19 with plausible claims of being a millennium old (Dooley and Ueno 2020). In the context of the tens of thousands of businesses that have folded after each major recession in the 21st century (Skeel 2020), the resilience of these shinise ("old shops") is amazing. This alternative business model can be explained using the biological concept of bet-hedging. Bet-hedging accepts that environmental stochasticity is a natural part of the fitness landscape, and can facilitate the persistence of phenotypes with lower arithmetic mean fitness (short-term competitiveness) if they either match or exceed other phenotypes' geometric mean fitness (long-term competitiveness) (Starrfelt and Kokko 2012). Thus, so long as the difference in arithmetic mean fitness does not drive the short-term competitive phenotype to fixation, slow and steady phenotypes can, ultimately, "win the race". Equally, the persistence of Japan's shinise has been explained through "kakun"—family-held values and dedication to the production of a trusted, consistent product, without a focus on competition and expansion (Dooley and Ueno 2020).

Together, Japan's keiretsu and shinise provide analogues to two of the most important tools that wild populations may have in the struggle for persistence under climate change: flexibility and heterogeneity. It is on these two features that this thesis will focus: how do animals in the wild cope with changing conditions, and how do these responses vary within a population?

Adopting an abstracted, mechanistic approach to energetic context is useful for grasping the scope of the challenges of the Anthropocene (e.g. bioclimate envelope modelling, Berry et al. 2002), but is too simplistic to truly understand how populations will respond to rapid change. Populations are not solely comprised of average individuals: some will succumb quicker than others (Harding et al. 2005, Richard et al. 2014); others will adopt tactics to persist even at the margins of energetic viability (Ganem and Nevo 1996, Parsons 2004). In every major evolutionary transition since the genesis of life on Earth, some traits have provided better coping capacity and consequently, shaped the succession biota: for instance, the capacity to withstand high levels of oxygen determined all the guilds to survive the Great Oxidation Event (Schirrmeister et al. 2013, Betts et al. 2018); a greater diversity of mobile animals replaced the end-Permian sessile biota (Clapham and Payne 2011); and the greater dietary diversity of Mesozoic mammals allowed them to supplant dinosaurs in most niches following the K/Pg extinction event (Wilson 2013). None of these extinctions occurred instantaneously; in all cases, organisms sought to survive—some succeeded, and some did for longer than others. Only by studying the diversity of energetic coping tactics already present within wild populations can we understand how best to help our present-day biodiversity withstand our very own mass extinction.

2 So you want to be different?

Differences between individuals within wild populations—individual heterogeneity (Hamel et al. 2018)—stem broadly from three sources: luck, pluck, and history. For this section, I will pause the use of economic analogy, as the vocabulary and concepts used hereafter carry problematic implications if applied to human society. If two animals are born simultaneously, after a given amount of time, the differences between them will be a product of both probabilistic happenstance (dynamic heterogeneity—luck, Tuljapurkar et al. 2009, Snyder and Ellner 2018) and deterministic quality (fixed heterogeneity—pluck, sometimes termed "individual quality", van Noordwijk and de Jong 1986, Hamel et al. 2009). These two categories of variation interact—for instance, two identical animals born in years of differing resource availability may develop different life-history strategies (e.g., Liedtke et al. 2015, concept developed further later), producing fixed life-long differences as a result of chance. For the purposes of this thesis, I will discuss fixed heterogeneity as that stemming from any life-long driver of difference, from maternal effects (Shine et al. 1997, Gangloff et al. 2018) and genetic differences (Meyers and Bull 2002, including the genetic drivers of plasticity, Nussey et al. 2005) to developmental effects (Stamps 2006, Bateson et al. 2014); dynamic heterogeneity will refer to variation caused by the environment that could be undone within an individual's lifespan (Steiner et al. 2010). To these sources of variation, we can add the consequences of evolutionary history, which shapes inter-individual differences at different ages (Clutton-Brock 1984, Zafon 2007, Richard et al. 2014), between sexes (Schindler et al. 2015b, Noonan et al. 2016, Petry et al. 2016), and between individuals with equivalent, non-deterministic behaviour (such as individual dietary niches, Svanbäck and Persson 2004, Sheppard et al. 2018), with species-specific context (Newman et al. 2011).

The ability of a population to endure disruption is dependent on its composition. In order to persist through repeated disruptions, a population must either exhibit resistance and/or resilience (Harrison 1979). The first of these, resistance, represents the ability to respond to change without experiencing demographic losses, typically through pre-adaptation ("exaptation", Gould and Vrba 1982), such as conservative reproductive investment (Svensson et al. 2005) or the behavioural plasticity required to cope with new conditions (Snell-Rood 2013). The second, resilience, is the ability to return rapidly to starting conditions, such as by increasing reproductive output (Capdevila et al. 2016) or adaptively maintaining some low-performing phenotypes that will persist even under adverse conditions ("diversified" bet-hedging, Ogura et al. 2017). This last point, in particular, illustrates the additive component of population persistence: although each gene will prioritise its own propagation (Dawkins 1976), the bundle of genes held in common by all individuals in a population will ensure their own persistence in some degree of population-level causality (see Millstein 2006, and debates therein). Therefore, the resilience of populations is very sensitive to the diversity of tactics and traits contained therein—a concept termed the "portfolio effect" (Schindler et al. 2015a) that will feature heavily in the chapters to come.

Also of import to understanding heterogeneous energetic budgeting within populations is the mechanistic basis for energy expenditure, storage, and trade-offs. First, it is important to understand the hormonal drivers of metabolism in mammals. In the brain, thyrotropin-releasing hormone (TRH) is released from the hypothalamus, which stimulates the anterior pituitary gland to produce thyroid-stimulating hormone (TSH, Harris et al. 1978). TSH, in turn, stimulates thyroxine (T_4) production in the thyroid gland (Mullur et al. 2014). In tissues, 5'-deiodinase type 2 (D2) enzymes convert T_4 to triiodothyronine (T_3), while another variant (D3) performs the

opposite role (Gereben et al. 2008). T_3 is the "active" form of thyroid hormone (TH), promoting expression of gene products that raise metabolism, such as through thermogenesis (Silva 1995), and lipid (Zhu and Cheng 2010) or carbohydrate (Klieverik et al. 2009) catabolism. Individual variation can occur at many points on this metabolic axis, with concentrations of readily-activated circulating plasma T_4 determining individual metabolism (Johnstone et al. 2005), different relationships between TSH and serum lipids in the sexes (implying differing feedbacks to lipid metabolism, Meng et al. 2015), and higher TSH levels in older humans (Wang et al. 2018)—likely to compensate for reduced capacity to oxidise fat in the respiring tissues of older individuals (Toth and Tchernof 2000).

The TH axis is very closely tied to the hormonal regulatory systems for various forms of energetic expenditure. TH up-regulates the transcription of the growth hormone (GH) axis (Evans et al. 1982), playing a role in development (Wen and Shi 2016) and muscle deposition (Jepson et al. 1988). This influence on the speed of development, for instance, facilitates precociality in some bird species through the provisioning of elevated maternal T_3 in yolk (Hsu et al. 2019). TH triggers cardiac vasodilation and increased blood flow to skeletal muscle (McAllister et al. 1995), providing one of the primary links between organ size, basal metabolic rate (BMR: formally, the energy expended by an adult, inactive, post-absorptive, nonreproductive, and thermoneutral animal), and maximum metabolic rate (MMR: the maximum energy an animal can expend while exercising) (Meerlo et al. 1997, Metcalfe et al. 2016, Vézina et al. 2017). The immune system, an oft-neglected energetic expenditure (Lochmiller and Deerenberg 2000, Cutrera et al. 2010), is dependent on TH action—diminished circulating T_4 inhibits T-cell responses (Silberman et al. 2002). And perhaps the most diverse category of energetic expenditures—those associated with reproduction—also communicate with TH, where

production of testosterone and luteinising hormone (LH) (both drivers of energetic responses, Day et al. 2005, Kim et al. 2021) are responsive to T_4 levels (Chiao et al. 1999). This is not a comprehensive accounting of the manner in which the hypothalamic-pituitary-thyroid axis affects energy expenditure, but rather an introduction to the diversity of endocrine pathways interacting to produce total energy expenditure—which can differ between individuals, even under the same conditions, by 5- to 15-fold in free-living animals (Williams 2008).

In order to accommodate the fact that energy intake is not constant, animals have developed robust regulatory endocrinology to balance energy storage and metabolism. At a fine scale, the concentration of glucose circulating in the blood (and thus available for metabolism) is kept in a narrow homeostatic band by the opposing effects of insulin (anabolic) and glucagon (catabolic) on glycogen storage in the liver (Gerich et al. 1976). Food intake is incentivised by ghrelin production in the stomach, which triggers hunger (Klok et al. 2007). External stressors (archetypically, encounters with predators) can require energy more acutely than feeding cycles can supply it; as such, these stressors activate the hypothalamo-pituitary-adrenal (HPA) axis (Sapolsky et al. 2000), mobilising glucose (through glucocorticoids, which reduce insulin sensitivity in the liver, Rizza et al. 1982) and augmenting cardiovascular capacity (through catecholamines such as epinephrine, Brown et al. 1979). Individuals can also exhibit stress-response phenotypes, with different HPA axis sensitivity to the same stressor (Ellis et al. 2006, Guimont and Wynne-Edwards 2006). At coarser timescales, adipose tissue produces leptin and adiponectin—leptin creates a satiation effect, while adiponectin increases insulin sensitivity, thus reducing food intake and switching to adipose catabolism when fat stores are available (Hewson et al. 2002, Meier and Gressner 2004). It is of note that this feedback system evolved to operate at relatively low levels of adiposity (Banks et al. 2001, 2006); under stable resource availability,

it therefore seems to be physiologically sub-optimal to accumulate more fat than necessary—a topic that will be explored in depth in Chapter 3. However, this physiological feedback is actively disrupted to cope with predictable shortage. Particularly in animals that experience seasonal shortage, large fat stores can be accumulated via a reduction in leptin sensitivity (Rousseau et al. 2003, Florant et al. 2004)—this same disruption prevents leptin from causing a satiation response in human obesity (Klok et al. 2007).

Foraging behaviour is the only manner by which animals acquire energy, but also rarely comes with guaranteed return rates. The efficiency of foraging can be determined by environmentally-determined food availability (Kneebone et al. 2018, DeSantis et al. 2020) or costs of movement (e.g. thermal loss or mechanical costs from wind, Williams et al. 2016, O'Mara et al. 2019), the need to account for predation risk (Dhellemmes et al. 2020, Diserens et al. 2021), and inter-individual differences in foraging efficiency (Grémillet et al. 2018, Cecere et al. 2020). Moreover, as mentioned in Section 1, there are other limiting currencies that can further constrain foraging efficiency (as their acquisition brings no additional energetic gain), such as the need to acquire water (key for evaporative heat loss in hyperthermic environments: Robertshaw 2006), balanced macronutrients (Remonti et al. 2011), or key micronutrients (e.g. selenium, needed for immune function: Flueck et al. 2012). An individual's energetic context will determine the trade-offs of engaging in voluntary behaviour in excess of this requisite maintenance foraging. For instance, a spectrum from capital- to income-breeding strategies determines whether species invest in either stored or concurrently acquired energy into reproductive costs (Jönsson 1997, Sainmont et al. 2014), including the energetically costly activities of mate searching (Swierk and Langkilde 2019), signalling to conspecifics (Allen et al. in prep), and intra-sex contests (Réale et al. 2009). However, this spectrum is plastic and not

fixed at the species scale: individuals within one population will invest different proportions of stored and concurrent energy into reproductive costs according to their body condition (Jaatinen et al. 2016, Williams et al. 2017). Other voluntary activities, such as exploration (Careau et al. 2009), territorial defence (Hurd 2006), hygiene and grooming (François 2021), and social interactions (Schino 2001), all have fitness benefits that must also be weighed against an individual's energetic capacity to engage in them (Wilmers et al. 2017).

In order to enable the study of the energetic trade-offs experienced by wild animals, it is necessary to be able to measure energy expenditure. Ideally, one would directly measure the instantaneous changes in caloric expenditure as an animal undergoes its standard behavioural responses to the environment. In practice, this is not possible, as such measurement would require respirometry (measurement of CO_2 respiration) or direct calorimetry (measurement of heat produced), both of which require the animal to be constrained to chambers that cannot suitably approximate the diversity of its natural environment (Levine 2005). Instead, respirometry has typically been used to measure resting metabolic rate (RMR, a less restrictive form of BMR that includes reproductive, growing, and/or digesting individuals, Careau et al. 2008) for wild animals (e.g., Krockenberger 2003, Bozinovic et al. 2004, Cutrera et al. 2010). Near-instantaneous resolution for energetic expenditure can be obtained using proxies from biologging data, such as body temperature (Hetem et al. 2019, which can also be measured remotely through thermography, McCafferty et al. 2011), heart rate (Clark et al. 2010), and accelerometry (e.g., Wilson et al. 2006, Noonan et al. 2014, 2018). Bi- and tri-axial accelerometry, in particular, provides a minimally-invasive measure of mechanical energy expenditure at a fine scale through the calculation of overall dynamic body acceleration (ODBA)—the sum of dynamic components for 2-3 axes of accelerometry (which narrowly

outperforms its vectorial counterpart, VeDBA, in predicting energy expenditure, Qasem et al. 2012). Nevertheless, ODBA only measures the energy expenditure associated with movement, and thus is an imperfect proxy for total energy expenditure (see Dalton et al. 2014, Jeanniard-du-Dot et al. 2017). The doubly-labelled water (DLW) method (Butler et al. 2004) can also account for the additional energy expenditure associated with physiological costs, by using the asymmetric elimination of known quantities of ^{2}H (eliminated through water loss) and ^{18}O (eliminated through both water loss and CO_2 respiration) isotopes to estimate the total CO_2 respired over a given period (Speakman 1997). While regular sampling can provide finer temporal measures of energy expenditure in subjects with ready access (such as humans, Berman et al. 2020), DLW can typically only estimate coarse total energy expenditure in field studies. These various approaches to measuring the components of energy budgets have demonstrated substantial inter-individual differences in energy expenditure (some examples provided in Table 1).

It has long been recognised that the availability of energy shapes the life history strategies available to wild animals. Historically, r/K selection theory proposed a spectrum of life-history traits in different species, and explained these as responding to differential selection depending on the availability of resources and competition in the environment (MacArthur and Wilson 1967, Pianka 1970, Reznick et al. 2002). If population growth is dependent on growth rate, "r", and a maximum carrying capacity, "K":

$$\Delta N = rN\left(1 - \frac{N}{K}\right) \quad (1)$$

then resource-rich, low-competition (or resource-stochastic, de-prioritising competition) environments would select for reproductive investments that maximise r, while resource-scarce,

Table 1. **Examples of inter-individual heterogeneity in energy expenditure**. Most of these studies were not designed specifically to quantify inter-individual heterogeneity, and therefore some metrics had to be estimated from figures. All spread percentages given represent the difference between the maximum and minimum values reported, divided by the minimum value.

Species	**Method**	**Heterogeneity documented**	**Reference**
Northern fur seal (*Callorhinus ursinus*)	Respirometry	Standard deviation of 18% of mean individual mass-specific O_2 consumption	Dalton et al. (2014)
Great tit (*Parus major*)	Respirometry	Approximately 100% spread (estimated from figure) in basal metabolic rates under the same conditions, partially explained by body mass and age	Broggi et al. (2007)
Bluegill sunfish (*Lepomis macrochirus*)	Respirometry	On average, 25% higher difference between mass-specific maximum and resting metabolic rate of bold and shy individuals	Binder et al. (2016)
Chevrier's field mouse (A*podemus chevrieri*)	Respirometry	On average, 21% higher resting metabolic rate in lactating than non-lactating individuals	Zhu et al. (2015)
South Georgian shag (*Phalacrocorax georgianus*)	Heart-rate monitoring	Up to 69% spread in resting heart rate (57.5% while diving) between individuals	Bevan et al. (1997)
Minke whale (*Balaenoptera acutorostrata*)	Modelling from blubber thickness and thermal conductance	Up to 49% more mass-specific heat lost in smallest whales	Folkow and Blix (1992)
Adélie penguin (*Pygoscelis adeliae*)	Tri-axial accelerometry	Approximately 60% spread (estimated from figure) in VeDBA under contemporaneous conditions; peak reproduction success at intermediate VeDBA values	Grémillet et al. (2018)
Lesser kestrel (*Falco naumanni*)	Tri-axial accelerometry	On average, 1.9 times as many foraging trips by males as by females while nestling	Hernández-Pliego et al. (2017)
Lesser kestrel (*Falco naumanni*)	Tri-axial accelerometry	Inter-individual differences in tendencies to adopt dynamic or static foraging tactics	Cecere et al. (2020)
Human (*Homo sapiens*)	Doubly-labelled water (review)	Males expend 11% more total energy than females, accounting for weight, height, and age	Black et al. (1996)
Field vole (*Microtus agrestis*)	Doubly-labelled wated; respirometry	Up to 150% spread in ratio of total energy expenditure to basal metabolic rate	Meerlo et al. (1997)
European badger (*Meles meles*)	Doubly-labelled water	Seasonal standard deviation of 36% of the seasonal mean individual daily energy expenditure	Barbour et al. (2019)

competitive (or resource-stable) environments would select for stability and reproductive investments that maximise each offspring's ability to persist at N ~ K (Pianka 1970). Demographic theory has largely supplanted r/K theory as the leading explanatory model for life history variation (but see Reznick et al. 2002), and conceptualises this variation as a product of the trade-off between current reproduction and future reproduction (survival, followed by reproduction) under differing degrees of survival uncertainty as a function of the environment (Stearns 1992, Roff et al. 2006). Much like r/K theory, this scheme places different species and populations along a gradient from "fast" (early reproduction with more, lower-quality offspring) to "slow" (delayed reproduction with fewer, higher-quality offspring) life histories (Read and Harvey 1989, Oli 2004, Bielby et al. 2007, Salguero-Gómez et al. 2016). As an illustrative example, urban blackbirds exposed to higher lifetime lead concentrations exhibit reduced individual reproductive output and higher survival probability than birds with lower Pb exposure, suggesting re-direction of energy towards survival and future reproduction (Fritsch et al. 2019).

Variability in environmentally-determined security has more recently been posited to drive the coevolution of life-history traits with a suite of physiological (metabolism, Careau et al. 2008, immune condition, Hegemann et al. 2013, but see also Tieleman 2018) and behavioural (Careau et al. 2010, Cole and Quinn 2012) traits, producing a characteristic pace-of-life (POL) for different populations (Ricklefs and Wikelski 2002, Dammhahn et al. 2018, Mathot and Frankenhuis 2018). These suites of traits can be selected for holistically in individuals, allowing use of a so-called pace-of-life syndrome (POLS) to study how energy budgeting varies consistently between individuals within wild populations, and the impacts of this variation on fitness and demographics (Réale et al. 2010, Cole and Quinn 2014, Hall et al. 2015). Thus, individual animals exhibit apparent "personality" types in line with consistent energy

expenditure phenotypes (Careau et al. 2009, Réale et al. 2010). Animal personalities range from "reactive" (shy, docile, sedentary) to "proactive" (bold, aggressive, exploratory) (Careau et al. 2008, Réale et al. 2010), with downstream implications for life-history and energetic state (Cole and Quinn 2012, Quinn et al. 2012, Firth et al. 2018). HPA stress-response phenotypes can underpin some of these behavioural variations, with reactive individuals exhibiting stronger glucocorticoid responses to stressors (and consequently, more fear, Cockrem 2007, 2013). Proactive lifestyles must be supported by elevated metabolism (Careau et al. 2008, 2010), and empirical tests have shown proactive individuals to have higher resting metabolic rates than reactive conspecifics (Metcalfe et al. 2016, Pettersen et al. 2016, but see also White et al. 2016).

Metabolism is a partially genetic trait, with a moderate heritability of 0.19 for RMR and a slightly higher rate of 0.21 for a range of active measures of metabolism (Pettersen et al. 2018). Pleiotropy of various genes associated with metabolism, therefore, can contribute to some genetic determination of pace-of-life (Immonen et al. 2018). However, phenotypic plasticity to early-life conditions through the hormonal pathways already discussed also plays a large role in an individual's lifetime reproductive success. Indeed, telomere length—a genomic measure of the physiological consequences of different individual experiences (Epel et al. 2004)—can differ substantially based solely on early-life conditions (van Lieshout et al. 2019, Supplementary Chapter 2). Individuals can benefit developmentally from beneficial environmental conditions early in life (the "silver spoon" hypothesis, Stamps 2006, Douhard et al. 2014, Pigeon et al. 2017) or by adopting phenotypes matching early environmental cues to benefit from later matching conditions (the "predictive adaptive response" hypothesis, Gluckman et al. 2005, Bateson et al. 2014). In accordance with these hypotheses, life-history strategies can be strongly shaped by early-life conditions (Garratt et al. 2015, Douhard et al. 2016), and enriched social,

physical, and resource-related early-life conditions have been shown to produce expected paces-of-life in experimental manipulations (Liedtke et al. 2015, Krause et al. 2017). Individuals may also exhibit different genetic predispositions to developmental plasticity: for example, rhesus macaques (*Macaca mulatta*) with a loss-of-function polymorphism in a serotonin transporter gene benefit more from supportive early-life maternal care than other macaques do (Madrid et al. 2018). Whether determined genetically or environmentally, the different paces-of-life represented in a population form an important—and under-explored—basis of diversity in modes of energy budgeting.

3 A tractable model

Since the early 19th century, ecology has bifurcated into two predominant approaches to the study of biodiversity. The (chronologically) first of these follows the tradition of the Reverend Gilbert White, whose 1789 book *The Natural History and Antiquities of Selborne* (today the fourth longest in-print book in the English language) epitomised an approach to ecology (a term not yet coined at the time) based on the careful study of one system (in White's case, the parish of Selborne, and in particular his own garden). Through these careful observations, White was able to form striking leaps in the understanding of ecological communities, such as of "how diversified are the modes of life not only of incongruous but even of con-generous animals" (White 1789), a crucial observation that forms the basis for speciation (e.g., Quattrini et al. 2013) and underpins the notions of divergence that would crystalise nearly a century later into Wallace and Darwin's theory of evolution (Wallace 1858, Darwin 1859). Furthermore, White was perhaps the first biologist to systematically record the behaviour of individual animals, recognising them as "beings in themselves, with rich inner lives and complex

behaviours, wants and needs" (Malhi 2021). Consider the following excerpt from *Selborne*, a description of the White's pet tortoise Timothy:

> *This creature not only goes under the earth from the middle of November to the middle of April, but sleeps great part of the summer; for it goes to bed in the longest days at four in the afternoon, and often does not stir in the morning till late. Besides, it retires to rest for every shower; and does not move at all in wet days… But as he avoids heat in the summer, so in the decline of the year he improves the faint autumnal beams by getting within the reflection of a fruit-wall.*

Thus, through observations of a tortoise from two and a half centuries prior to the writing of this thesis, White laid the basis for the systematic study of diverse aspects of individual energetic budgeting, from seasonal metabolic depression during times of shortage, to modification of activity when thermoregulatory conditions are sub-optimal, to behavioural thermoregulation.

Some decades after White published his *Natural History*, Alexander von Humboldt revolutionised the study of biodiversity with the advent of biogeography. Inspired by the commonalities he saw in diverse ecosystems through a life rife with travel, Humboldt gave rise to the concept that consistent environmental drivers would produce the same ecosystem responses in different biotopes (von Humboldt and Bonpland 1805, Fattorini et al. 2019, Pausas and Bond 2019). The resulting idea of comparative natural history underpins ecological theory as we know it today, and Humboldt's legacy still commands respect among ecologists (Schrodt et al. 2019, Malhi 2021). Indeed, notwithstanding the recognised value of long-term demographic studies (in the school of Gilbert White, see Clutton-Brock and Sheldon 2010), many high-impact ecological publications expect comparative approaches incorporating various taxa. For instance, the Journal of Animal Ecology currently cautions potential authors that its scope does not include "manuscripts in which the central focus is the ecology, behaviour or life history of a single species". Nevertheless, it seems reductive to expect that the inclusion of one—or even ten—

more species will appreciably increase the proportion of the ~8.7 million eukaryotic species on Earth represented in one's sample (Mora et al. 2011).

A focus on the universality of natural processes can be powerfully illuminating, but can have substantial drawbacks if it comes at the cost of nuanced, localised understanding. Humboldt's writings were key in building a global appreciation for the preservation of nature, counting among his ideological disciples John Muir, the father of the American preservationist movement (Zimmerer 2006). Indeed, Humboldt's propensity to view nature and human society as mutually informative (Malhi 2021) likely informs my ability to discuss the lessons that Japanese business practices can have for studying resilience in wild populations. Nevertheless, conservation following the Humboldtian model of assuming globally-applicable rules can backfire: for instance, his interpretation of mixed-woodland savannahs during his travels to the Neotropics has created a simplistic view of fire and degradation that plagued both conservation and ecology ever since (Bennett and Barton 2018, Pausas and Bond 2019), with the record only publicly being set straight over the past couple of decades through to the invaluable contributions of Indigenous scientists and land stewards (see, e.g., Mistry et al. 2016, Lake et al. 2017). Careful natural history observations have proved essential in challenging ecological orthodoxy in conservation before: in 1949, Aldo Leopold revolutionised wildlife management by suggesting, based on his extensive longitudinal experience with wolf extermination, that vegetation may also be regulated from the top-down, rather than simply by climatic limitation (Leopold 1949). In the spirit of Leopold, I aim for this thesis to challenge the existing orthodoxy that assumes monotonic population responses to anthropogenic stressors—an application of the so-called "Tyranny of the Golden Mean" (Williams 2008).

Even if a purely comparative approach to ecology may prove too simplistic in cases, it is also incumbent on the careful ecologist to ensure that their studied ecosystem, species, or population incorporates the context collected by others in their field, and is either generalisable or deliberately and illustratively specialised. Gilbert White himself was far from naïve in this respect, making use of the vast body of knowledge accumulated by other natural historians to build his understanding of Selborne (Menely 2004). In the effort to best contribute to my goal in this thesis—studying inter- and intra-individual heterogeneity in energy budgeting tactics—there are several features that should be prioritised in choosing a species to study carefully. First, animals with facultative behaviours likely have greater scope for flexible energy budgeting; for instance, facultative sociality in coyotes (*Canis latrans*) permits them to exploit a wide range of prey (Gese et al. 1988), while their congeneric cousins, grey wolves (*Canis lupus*), hunt almost exclusively large prey (Meachen and Samuels 2012). Second, dietary diversity itself can be an important marker of flexible energy budgeting: yellow-throated martens (*Martes flavigula*) can become facultative frugivores according to seasonal resource availability (Zhou et al. 2011), unlike, say, giant pandas (*Ailuropoda melanoleuca*), which only show variation in the species of bamboo that they use over the course of a year (Wu et al. 2017). Third, high conspecific density has been proposed to encourage individual niche diversification; this so-called Niche Variation Hypothesis (NVH) has been confirmed to drive increasing diet diversity in high-density populations (Svanbäck and Persson 2004, Bolnick et al. 2007). Finally, species with a broad biogeographical range exhibit a certain amount of flexible "pre-adaptation" to variation in energetic constraints (Payne and Finnegan 2007). The species upon which I focus in this thesis, the European badger (*Meles meles* L.), conforms to all of these criteria.

European badgers are medium-sized carnivores (in the population studied here, the average adult badger is 69.4 ± 3.0 cm long and weighs 8.4 ± 1.7 kg) in the family Mustelidae (superfamily Musteloidea), a diverse taxon of highly behaviourally plastic carnivorans (Macdonald et al. 2017). Badgers occur across a truly stunning geographic and environmental range, with representation in the arid Mediterranean chaparral (Rosalino et al. 2005b), the temperate countries of north-western Europe (Ireland: Byrne et al. 2012, England: Macdonald et al. 2015, Holland: Piza-Roca et al. 2018, France: François 2021), heathlands in Scotland (Kruuk and Parish 1982), the high Alps (Balestrieri et al. 2009), primeval forest in Poland (Kowalczyk et al. 2003), and has even recently been documented north of the Arctic circle (Bartra Cabré 2020). When including the European badger's three con-generics, which are ecologically similar enough to hybridise when co-occurring (Kinoshita et al. 2019), this range is expanded to the Middle-East and Caucasus mountains (*M. canescens*, the least-studied species, Abramov and Puzachenko 2013), the remainder of Central and East Asia, including Siberia and the Tibetan Plateau (*M. leucurus*, Zagainova and Markov 2011, Feng and Zhigang 2014), and the islands of Japan (*M. anakuma*, Kaneko et al. 2006).

The population studied for this thesis is broadly representative of badgers in temperate climes: the study site, Wytham Woods (Oxfordshire, UK, 51°46'N, 1°20'W, Savill 2011), is a 424-ha mix of pasture and closed-canopy forest, ranging from pure plantations of beech (*Fagus sylvatica*) and cedar (*Thuja* spp.) over previously open ground to ancient woodland with a mix of sycamore (*Acer pseudoplatanus*), common ash (*Fraxinus excelsior*), and interspersed common oaks (*Quercus robur*). Wytham is situated on a hill surrounded by the Thames river on three sides and the A-34 motorway on the fourth, making the population is more or less closed to migration and thus facilitating demographic analysis. Most badger setts (underground dens,

further discussed below) in Wytham are in a mid-elevation band of (well-drained) brown Frilford sand, but are widely distributed throughout the woods (Macdonald et al. 2004b, Taylor et al. 2011).

Badgers are facultatively social to differing degrees across their range, broadly as a function of how much of their local diet relies on earthworms (Johnson et al. 2002a). Badgers are dietary generalists (Roper 1994, Newman et al. 2011) that make ready use of seasonally plentiful foods, such as cereals (Remonti et al. 2011), fruits (Rosalino et al. 2005a), and even easily-captured prey (such as young rabbits, which can be important diet items in Spanish populations, Revilla and Palomares 2002). However, in regions such as the southern British Isles where anecic earthworms surface in dense patches according to microclimatic weather conditions (Macdonald 1980, Jiménez and Decaëns 2000), these can form an important component of the diet (in England, these are primarily the common earthworm, *Lumbricus terrestris* L., Kruuk 1978a, 1978b, Kruuk and Parish 1981, Macdonald 1983, Hofer 1988). The spatio-temporal variability in the surfacing rate and richness of these patches of earthworms ensure that, the territory required to consistently sustain a single badger is too large to effectively defend, and yet on balance provides sufficient food for multiple individuals. This relationship is formulated as the Resource Dispersion Hypothesis (RDH), which predicts that rudimentary sociality can occur under these conditions at low or no cost to individual fitness (Johnson et al. 2001b, 2001a, 2002b, Macdonald and Johnson 2015). As a result, in Ireland and southern England, where climatic conditions support substantial earthworm availability during parts of the year (Phillipson et al. 1978), badgers can reach very high densities for a carnivore of their size (Muldowney et al. 2003, Judge et al. 2017). At our study site, this results in a density of 43.8 badgers/km^2 (as of

2016), spread across a changeable number of social groups averaging 6.8 individuals (range 1-28).

The high density of the Wytham Woods population is a product of both environmental and social conditions. The population has been trapped systematically since 1987 (and studied since 1972, Kruuk 1978a), with three to four two-week trap-ups conducted annually; individuals are assigned unique inguinal tattoos on first capture and biometric data are collected on each capture, thus providing a "womb-to-tomb" accounting of the lives of these animals (see Macdonald et al. 2015 for a review; further details provided in research chapters). In the mid-1990s, the population experienced a sudden and drastic increase in size, from 160 individuals in 1990 to a peak of 328 in 1997. This growth seems to have been linked to a succession of mild winter conditions leading to higher body condition and consequent overwinter survival (see seasonal energy cycle below) (Macdonald and Newman 2002), but was facilitated by socio-spatial restructuring of the population, with the number of main setts expanding from 23 to 63 by 2004 (Macdonald et al. 2004b). Crucially, these newly-dug setts were not in poorer soil, and inhabitants did not exhibit lower body condition, suggesting the population growth was not a matter of increasing the number of marginal individuals, but rather an increase in the carrying capacity of the population (Macdonald et al. 2004b). Indeed, while the high densities were initially accompanied by an increase in bite wounds (Macdonald et al. 2004a), these bite wounds have become increasingly rare since the early 2000s (see Discussion), despite the population averaging 274.5 individuals since 2000. Aggression is not necessarily linked to population density in badgers (Delahay et al. 2006b), and this population exhibits little territorial exclusion (Ellwood et al. 2017) or feeding hierarchies (Macdonald et al. 2002b). Density-dependence seems to act either passively, with some reduction of body condition (Rogers et al. 1997a,

Macdonald et al. 2002a) and elevated exposure to parasites (which badgers avoid by redistributing themselves, Albery et al. 2020), or in a sex-specific manner, with proportionally fewer females breeding in large groups, particularly following poor foraging seasons (Woodroffe and Macdonald 1995a; for more details on reproduction, see below). Badgers can reach a maximum recorded age of 14 in our population, but exhibit steep (and sex-specific, see Rogers et al. 1997b, Macdonald and Newman 2002) survivorship curves: only 55% reach 2 years of age, and 18% reach age 8. This diversity in fitness outcomes, combined with the degree of social and environmental change encompassed by many badger lifetimes in this population, provide a unique opportunity to study long-term inter- and intra-individual life-history variability.

Resource availability changes substantially over the course of the year for badgers in England, driving the accumulation of adipose tissue during autumn in preparation for winter shortage (as they do across much of their range, Maurel and Boissin 1982, Virgós et al. 2011). This stored capital permits depression of BMR (McClune et al. 2015) and total energy expenditure through decreased activity during the winter months ("torpor", Newman et al. 2011). An individual badger may thus double its body weight in a given year (and vice-versa, halving overwinter), but a broad range of body weights exist concurrently within the population: during the summer, 25% of badgers weigh below 6.9 kg, while 25% are above 8.8 kg; the corresponding numbers in autumn are 8.2 kg and 11 kg. Badgers in high-density populations exhibit a primary mating season in early spring (late February to early April, Sugianto et al. subm.a, though some individuals remain reproductively active throughout the year, Buesching et al. 2009, Dugdale et al. 2011), but delay implantation of blastocysts until late December (Yamaguchi et al. 2006, Sugianto et al. subm.b). Births occur synchronously in February, and pregnancy is sensitive to autumn fat stores, with females in better body condition implanting developing blastocysts

earlier (Woodroffe 1995, Carpenter et al. 2005) and exhibiting higher reproductive success in the spring under certain conditions (Cresswell et al. 1992, Woodroffe and Macdonald 1995a, Delahay et al. 2006a). Subsequently, the energetic costs of lactation (until May, when cubs are weaned) reduce female badger condition through the following spring and summer (Woodroffe and Macdonald 1995b). While fat stores can be influential for survival and reproductive success (e.g., Milner et al. 2013, Monteith et al. 2013), the orthodoxy that "fat is good" has been challenged by the costs of fat to movement efficiency (Gosler 1996, Newman et al. 2011), predation risk (Gentle and Gosler 2001, Lind et al. 2010), thermal stress (Xu et al. 2013, although fat can also provide a supply of water through oxidation, Schweigert 1993), and health (Garaulet et al. 2010). Little attention has been paid to the changing seasonal context of body condition in wild populations, and what costs and benefits are involved in the heterogeneity of somatic stores seen under the same conditions in wild populations.

Badgers exhibit strong behavioural plasticity in response to environmental conditions. Badgers are semi-fossorial and nocturnal, spending the daytime sleeping in extensive (shared, where densities are high) underground dens termed "setts" (Noonan et al. 2014, 2015a). These setts act as thermal refugia (Kaneko et al. 2010, Tsunoda et al. 2018), and so emergence (and the nature of activity once emerged) is sensitive to the environmental conditions that affect both foraging efficiency (Kruuk 1978b, Noonan et al. 2014, 2018) and ability to withdraw from inclement weather (Noonan et al. 2015b). When activity is not accompanied by food availability, badgers exhibit elevated oxidative damage associated with this energetic stress (Bilham et al. 2018). In years with poor foraging conditions, therefore, accelerometry data demonstrate that thin badgers engage in more autumnal activity than fat badgers (Noonan et al. 2014), suggesting an individual energy context-dependent framework for badger behaviour. Similarly, badgers with

higher body-condition indices (BCIs) engage in more inter-sett visits than low-BCI badgers (Noonan et al. 2018), illustrating that badgers trade off social activity according to energetic security. Nevertheless, environmental conditions affect badger survival patterns (Macdonald and Newman 2002, Buesching et al. 2009, Montes et al. 2011), with adults suffering higher mortality in years with low rainfall (and low earthworm availability) or highly variable temperatures, and cubs suffering higher mortality during particularly dry or particularly wet years (Nouvellet et al. 2013). This non-linear effect of precipitation is expected to be a function of heat loss in the smaller cubs (due to scale-law allometry, as body size has a substantial effect on the proportional amount of energy produced that is lost as heat, Brown et al. 1993, Dodds et al. 2001) through fur-soaking under rainy conditions (Webb and King 1984). Badgers are therefore highly tractable for granularly studying how different individuals within the population are affected by and respond behaviourally to environmental conditions—and how these responses vary with different seasonal context.

Badgers exhibit sex-specific inter-individual heterogeneity in reproduction physiology and behaviour. Mating is polygynandrous (Dugdale et al. 2011) and superfoetation and multiple paternity are common (Dugdale et al. 2007, Sugianto et al. subm.b), which in combination with high densities and large territories makes mate defence impractical (Noonan et al. 2016). As a result, males must expend substantial energy on mating (where the mate search involved leads to seasonal peaks in road-traffic accidents, Macdonald and Newman 2002, Macdonald et al. 2010). Badgers (of both sexes) also communicate extensively through olfactory signals (largely deposited in communal latrines around setts and near group territory boundaries, Kilshaw et al. 2009) in the form of faeces (Roper et al. 1986), anal gland secretions (Davies et al. 1988), urine (Allen et al. 2019), and subcaudal secretions that are unique to badgers, which encode

individual-level information (Buesching et al. 2002) in calorie-dense fatty scent marks (Allen et al. in prep). These signals, the physiological costs of the reproductive status they advertise (Buesching et al. 2009), and the trips to deposit and receive them (Noonan et al. 2018) all incur energetic costs, and not all individuals meet these equally.

Reproductive heterogeneity in male badgers arises early in development. In medium- to high-density populations, testes weight (Ahnlund 1980), sperm production (Graf and Wandeler 1982), and circulating testosterone (Sugianto et al. 2019a) all exhibit bimodal development in males, with a portion of badgers reaching mating condition (and a greater fraction of adult body size, Sugianto et al. 2019a) at the end of their first year, while others do not reach this milestone until the end of their second. It is worth noting, however, that in resource-poor Russian populations, no males reach sexual maturity until their third year of life (Danilov and Tumanov 1972), suggesting a link between viable life-history strategies and resource availability. This heterogeneity persists in the adult male population, as both testis weight and testosterone levels increase in variability during the summer (Buesching et al. 2009, Stuart 2010)—it has been posited that this is to capitalise on the late entry of maturing females into the breeding population (Ahnlund 1980). Females exhibit reproductive heterogeneity that becomes evident at the point of reproduction itself: following years with good foraging conditions, enough females attempt to breed that female-female reproductive suppression occurs within social groups (Woodroffe and Macdonald 1995a, Dugdale et al. 2008), likely through infanticide (Agrell et al. 1998). The development pattern of early-life sexual size dimorphism makes clear that male badgers are more substantially affected by social conditions, while females are affected by environmental conditions: male cub growth is more sensitive to social group size, whereas female growth depends on food availability (Sugianto et al. 2019b). Reproduction peaks at age 3 in females at

the onset of somatic senescence, but reproductive hormone profiles only decline at 6 years of age; in males, reproduction does not decline until age 6, and declines thereafter with testosterone (Sugianto et al. 2020). Female badgers have exhibited post-reproductive lifespans, but very old female hormone profiles (age 9+) are highly variable, with some maintaining reproductive viability (Sugianto et al. 2020). These sex-specific patterns of heterogeneous life-history tactics will form the underpinning for much of our discussions ahead.

4 An overview of research chapters

The various questions set out thus far in this introduction align roughly with two temporal scales. The first of these is that of the individual life history, my analysis of which employs 32 years of demographic data from the Wytham badger population. In order to enable the ready examination of individuals within the context of a changing population, I needed to develop a method of demographic estimation that both incorporated the effects of variable environmental conditions on trappability (Noonan et al. 2015b, Martin et al. 2017) while maintaining a link to individual records. To do so, I modified the minimum number alive (MNA) population indicator to produce "enhanced" MNA (eMNA), which accounts for time-varying capture efficiency and pre-capture existence (Chapter 1). Armed with this tool, I was able to ask a series of questions about individual life histories: a) what shapes their development; b) how have variable life-histories interacted with the demographic changes this population has undergone; and c) how do males and females differ with regard to both of these aforementioned questions (Chapter 2)? In Chapter 3, I was then was able to investigate energetic variation more finely, examining how environmental conditions and individual traits shape body-condition variability within the population, both from season to season and across individual lifetimes. In particular, I examined why some individuals appear to deliberately opt to remain thin, making careful examination of

somatic-reproductive trade-offs and threshold-bounded relationships between body condition and survival.

Secondly, having established these broader boundaries for the context of energetic budgeting, I proceeded to investigate fine-scale variations in individual energy expenditure. First, I used 3D-printing technology and bespoke multi-sensor modules to develop the tools used thus far by our research group (Noonan et al. 2014, 2018) into inexpensive, reusable tri-axial accelerometry collars (enabling much larger sample sizes than previously obtained), with the additional capacity to record high-fidelity audio and Bluetooth Low-Energy readings (Chapter 4). I deployed these accelerometers on badgers alongside our seasonal trap-ups over two years to examine the seasonal drivers of fine-scale individual variation in mechanical energy expenditure (ODBA); during the first year of these deployments, I conducted a monthly diet analysis in parallel, to provide seasonal energetic context to these tactical energetic decisions (Chapter 5). I also focussed particularly on consistent individual activity phenotypes and individual energetic context for behavioural responses to environmental conditions. Finally, I used concurrent data from doubly-labelled water (administered to badgers at trapping) and accelerometry to investigate how individuals differ in their total energy budgets and their relative mechanical energy expenditure, while subject to the same extrinsic conditions (Chapter 6). I used context from other research chapters to relate investment into activity to body-condition losses, and in turn to downstream mortality risk.

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Part I

A life-history view of energetic heterogeneity

Chapter 1

Preserving identity in capture-mark-recapture studies: Increasing the accuracy of minimum number alive (MNA) estimates by incorporating inter-census trapping efficiency variation

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Abstract

Quantifying abundance is often key to understanding ecological and evolutionary processes in wild populations. Despite shortcomings in producing accurate abundance estimates, minimum number alive (MNA) remains a widely used tool, due to its intuitive computation, reliable performance as an abundance indicator, and linkage to individual life-histories. Here, we propose a novel "enhanced" MNA (eMNA) metric, which aims to preserve MNA's favourable aspects while remedying its flaws, by incorporating a) growth correlates to back-age individuals first captured as adults, and b) estimates of undetected persistence past last capture based on time-varying capture efficiency. We evaluate eMNA's performance as an abundance indicator (i.e., relative change) and estimator (i.e., absolute numbers) through simulated samplings of a baseline population parameterised using data from a long-term demographic study of European badgers (*Meles meles*), under three different levels of capture efficiency (low; intermediate /"real" based on badger field data; high). eMNA abundance estimates were negatively biased at all capture efficiencies, but negligibly so at intermediate-to-high capture efficiency, under-estimating abundance by only 3.5 badgers (1.5% of population) at intermediate (real) capture efficiencies. Moreover, at low capture efficiencies, eMNA performed as a precise abundance indicator, with half the standard deviation of Cormack-Jolly-Seber probabilistic estimates, proving robust to inter-sampling variation in capture efficiency. Using undetected persistence probabilities to parameterise survival regression, we recreated baseline age-based survival relationships, albeit with some negative bias of under-represented ages. We offer considerations on the continued limitations of using eMNA for abundance estimates, its benefits when individual identity is required, and potential for further improvement.

Keywords: *Badgers; calendar of catches; capture mark recapture; enumeration; minimum number alive; trappability.*

1 Introduction

Long-term individual based demographic studies are fundamental to ecology (Clutton-Brock and Sheldon 2010). The life-history and population contexts of an individual's birth, reproduction, and death shape the relationships between traits and fitness (Starrfelt and Kokko 2012, Sæther and Engen 2015, Wright et al. 2019, Chapter 3), and thus ultimately whether an individual's genes are passed on. The contextual information provided by linking individual life-history schedules with population dynamics underlies our understanding of much of ecology and evolution, from life-history theory (Stearns 1992) to density-dependence (Coulson et al. 2001) and the existence of diverse fitness strategies within populations (Réale et al. 2010, Wright et al. 2019).

Minimum number alive (MNA), also known as minimum number known alive, calendar of catches, or simply enumeration, has been used as an individual-linked abundance indicator for decades (Krebs 1966, Macdonald and Newman 2002, Smith and Nichols 2003, Johnson et al. 2016, *inter alia*). MNA, like many other capture-mark-recapture (CMR) metrics, does not require actual marking, so long as individuals are consistently distinguishable (Ellison and Swanson 2016). This enables MNA, as an intuitively constructed metric, to easily incorporate various stacked forms of identification (Palomares et al. 2005), ranging from DNA fingerprinting (Meijer et al. 2008) and camera trapping (Lazenby et al. 2014) to opportunistic tourism photography (Marnewick et al. 2014). We note, however, that although "minimum number alive" has been used to describe a measure of abundance based on a single coalescence of data (representing one sampling occasion, even if over several months, Morley and van Aarde 2007,

van den Hoven and Reilly 2012), here we define MNA strictly as the use of data from multiple sampling occasions to inform the presence of individuals not captured during intervening occasions.

Although clearly negatively biased (it is, after all, a "minimum"), MNA often correlates strongly with true abundance (Slade and Blair 2000, Pryde et al. 2005, Graipel et al. 2014, Johnson et al. 2016), particularly at higher degrees of population closure, capture frequency, and capture efficiency (the proportion of extant individuals captured or recaptured in a given capture session, Ruscoe et al. 2001, Pacheco et al. 2013). Therefore, while probabilistic approaches (ranging from simple Lincoln-Petersen estimators to multi-state CMR models, Pollock 2000, Lindberg 2012, Laake et al. 2013) may provide more accurate abundance *estimators* (accurate prediction of abundance), MNA can out-perform certain probabilistic metrics as an abundance *indicator* (precise correlation to changes in abundance, Davis et al. 2003), particularly when these approaches are hindered by obstructing terrain (as in transect distance sampling or double-observer abundance estimators) and/or cryptic animal behaviour (Corlatti et al. 2015, 2017), or under conditions that violate the assumption of equal catchability (Tuyttens 2000). Such an indicator can provide crucial information for ecological inquiry, such as abundance trends in different successional stages (Howe and Davlantes 2017) or in threatened populations (Pryde et al. 2005), comparative measures of abundance within a population over time (Chapter 2), or inter-specific (Fritts et al. 2017) and inter-population (Smith and Nichols 2003, Holloway et al. 2012) comparisons of abundance drivers. In the case of MNA, the indicator is also directly linked to individual life-history records, making it easy to test associations between population- and individual-scale processes (Chapters 2-3).

Nevertheless, MNA's usefulness as an abundance indicator belies significant shortcomings when it is used strictly to estimate abundance. As previously mentioned, MNA is a negatively-biased estimator (Bryja et al. 2001, Ramey et al. 2008, Mullican 2014); this bias is exacerbated under low capture efficiency (Hilborn et al. 1976, Tuyttens 2000). Downstream metrics suffer as a result: MNA yields positively biased trappability (Byrne and Do Linh San 2016), and survival estimates based on MNA alone (implying immediate death after last capture, which is almost universally a poor assumption in an uncontrolled population) can lead to improper selection of covariates (Viallefont et al. 1999). When governments use MNA-based metrics for species management interventions that require accurate estimates and not simply indicators, such as planning and evaluating pest control (Ramey et al. 2008, Lazenby et al. 2014, Johnson et al. 2016) or informing species conservation plans (Biggins et al. 2006), these shortcomings become important. Improvement to the MNA method's estimation ability would, therefore, improve the robustness of its use for such purposes while preserving the metric's intuitive computation and links to individual animals.

Here, we propose and evaluate the performance of a novel efficiency-modified minimum number alive metric (eMNA), which improves on standard MNA by a) back-aging individuals first captured as adults, based on growth correlates, and b) incorporating estimates of undetected survival beyond last capture, based on time-varying capture efficiency. We evaluate this metric's performance as both an abundance indicator and estimator in simulations parameterised with 32 years of data from a long-term demographic study on European badgers (*Meles meles*). Badgers are fossorial, nocturnal animals, presenting ecologists with considerable challenges when attempting to enumerate them for study (Noonan et al. 2015a). Their trappability varies substantially between sites, seasons, and years (Byrne et al. 2012, Noonan et al. 2015b), but

estimating their abundance accurately is often crucial, as they act as a reservoir of bovine tuberculosis (*Mycobacterium bovis*) in Britain and Ireland, and as such are widely controlled by government removal interventions (Donnelly et al. 2006, Byrne et al. 2014). Beyond their epidemiological importance, badgers have been used to study the effects of relative abundance on individual condition (Macdonald et al. 2002, Chapter 3), development (Sugianto et al. 2019b), life-history strategies (Chapter 2), mating physiology (Sugianto et al. subm.), energetics (Barbour et al. 2019), and social organisation (Johnson et al. 2001), among other topics, and in turn to study the effects of climate (Macdonald and Newman 2002, Macdonald et al. 2010) and habitat change (da Silva et al. 1993, Delahay et al. 2006) on abundance; they thus are a focal species for the need to optimise abundance indices and estimators. Nevertheless, capture efficiency is relatively high in the dataset we use here (average 73.8% annually, Chapter 2), and so we also evaluate the performance of eMNA at lower capture efficiencies better representative of many studies of small mammals (Parmenter et al. 2003), and at particularly high capture efficiencies, to evaluate whether eMNA could overestimate the "minimum" in near-optimal capture conditions.

2 Methods

To streamline further use of the method, we conducted all simulations, calculations, and analyses in R statistical software (R Core Team 2019); where relevant, we have indicated specific packages below. All code and data will be made available online upon publication.

2.1 Demographic data collection

We collected data for parameterising simulations from a largely closed (immigration/emigration rate = 3%: Macdonald and Newman 2002) badger population in Wytham Woods, a 424-ha mixed woodland in southern England (51°46'N, 1°20'W; for more

information, see Savill 2011). From 1987-2019, we trapped every active communal burrow system ("setts", comprising 1-10 holes, home to 5.5 badgers on average)—in the study area using string-trigger traps for two or (most commonly) three nights, three to four times per year, at regular seasonal intervals (for breakdown of seasonal dates, see Chapter 3). We transferred badgers to holding cages between 7:00-9:00 am, transported them to a central field station, and sedated them with 0.2 mL ketamine hydrochloride/kg body weight by intramuscular injection (Sun et al. 2015, Sugianto et al. 2019a). On first capture (typically as a cub or yearling), we gave each badger a unique numerical inguinal tattoo. On each capture, we estimated degree of molar tooth wear as a scaled value from 1-5, which has been shown to be useful for estimating age retrospectively in cases when individuals were first caught as adults (Hancox 1988, Chapter 2).

All badger captures were licensed under the Badger Act (1992) (currently Natural England license 2019-2020-4417) and all handling procedures carried out under Animals (Scientific Procedures) Act (1986) license (currently PPL 30/3379).

2.2 Generating baseline population

We used real badger data (henceforth, "real" data, subscript *r*) to generate a 30-year baseline time series of individual life-histories (henceforth, "baseline" data, subscript *b*) that could be iteratively sampled to simulate a range of capture efficiency scenarios. Hereafter, scalars will be indicated with italics, vectors will be indicated with bolded lowercase italics, and matrices with bolded uppercase italics. Subscripts will indicate firstly to which dataset a given value refers (real, baseline, or "captured" in simulations), and secondly to the corresponding timestep (if relevant)—where "t" refers to a generic timestep.

We generated a baseline population of individuals in the first time-step (N_{b1}), for which an age-distribution vector $\boldsymbol{n_{b1}}$ was initiated with the average number of badgers of each age in the

32 years of real data (Eq. 1). Although a small minority (4.5%) of individuals in this population survive beyond age 10 (with the oldest known-age individual reaching age 14, Macdonald et al. 2015), we capped our baseline population at age 10 to minimise the number of estimated parameters in CJS models (see Section 2.3 below). We adopt a post-reproductive census approach, because badgers are synchronous annual breeders, giving birth to cubs in February (Woodroffe and Macdonald 1995), and a majority of badger mortality occurs during the winter (Macdonald et al. 2010, Chapter 3), while the majority of our CMR capture regime occurs during spring-autumn (Chapter 3). Therefore, we simulated each subsequent N_{bt} value by vector-multiplying the previous age distribution by age- and sex-specific survival probabilities ($\boldsymbol{s_r}$), summing the number of surviving females in all age classes, then multiplying this number by the mean maternity rate m_r = mean($m_{r1} \ldots m_{r32}$). The cubs produced took the first position of the subsequent year's $\boldsymbol{n_b}$ vector, while the surviving badgers of other age classes moved down a position in the vector (gained a year of age). Although badgers display strong age dependence of maternity (and paternity) rates (Sugianto et al. 2020, Chapter 2), for simplicity's sake here we assume homogeneous maternity rates at all ages. So, for time t in 2-30:

$$\boldsymbol{n_{b1}} = mean(\boldsymbol{n_{r1}} \ldots \boldsymbol{n_{r32}}) \quad (1)$$

$$Survived_{b(t-1)} = \sum_{a=1}^{10} (\boldsymbol{n_{b(t-1)}} * \boldsymbol{s_r}) \quad (2)$$

$$Cubs\ produced_{bt} = females\ survived_{b(t-1)} * m_r \quad (3)$$

$$N_{bt} = Survived_{b(t-1)} + Cubs\ produced_{bt} \quad (4)$$

We estimated the constituent values of $\boldsymbol{s_r}$ by using generalised additive models (*mgcv* package, Wood 2011) to fit sex-specific age splines to individual survival (binomial, 1 = survived to time $t+1$; 0 = never detected past time t). Although this method is imperfect in

deducing true survival relationships, as it assumes death for individuals that were not detected (where these may persist, undetected, see Sections 2.4, 3.2 below), this is not problematic in this step of the analysis, as it simply provides us a baseline relationship to generate the population.

Given this series of $\boldsymbol{n_{bt}}$ vectors, we created a matrix of life histories ($\boldsymbol{LH_b}$), with a row for each individual that had ever been alive in the population, transacted by 30 columns, one for each year of the baseline time series (Fig. 1). In $\boldsymbol{LH_b}$, 1s represent years in which a badger was alive and 0s years in which it was not (whether for having died or not yet being born); thus, each row's sum gives the total number of years that individual was alive (in the simulated study), and each column's sum gives that year's N_{bt} value. We matched these individual life histories with context matrices (time-varying) and vectors (constant individual characteristics) representing individual information such as age ($\boldsymbol{A_b}$, known from $\boldsymbol{n_{bt}}$), sex, and tooth wear ($\boldsymbol{T_b}$). These matrices and vectors a) enable easy iterative sampling of the population and b) help pre-format the data for interfacing with MARK (White and Burnham 1999) or other related demographic analysis software. $\boldsymbol{T_b}$ values for any position $\{i,j\}$ were assigned by sampling the real tooth wear data for all badgers where age = $\boldsymbol{A_{b\{i,j\}}}$.

2.3 Computing abundance estimates with variable trapping efficiency

We sampled the baseline population 1,000 times under three different time-varying capture efficiency (ce_{bt}) regimes: "low" efficiency (each ce_{bt} drawn from a uniform distribution from 45-55%, characteristic of many small mammal trapping regimes, Parmenter et al. 2003); an intermediate "real" efficiency (each ce_{bt} drawn from a multi-modal distribution built to resemble that of real badger trapping efficiencies ce_{rt}, which averaged 74%); and "high" efficiency (ce_{bt} drawn from uniform distribution from 85-95%). For each ce_{bt} value, we "captured" that

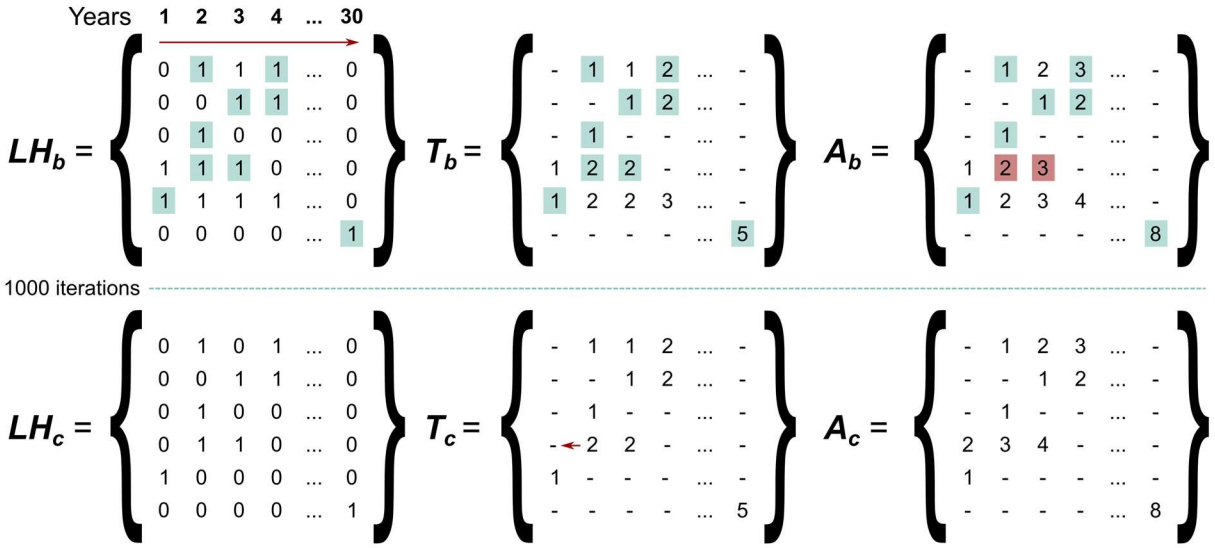


Figure 1. **Life-history and context matrices.** Top row shows baseline matrices (those data to be sampled); bottom row shows the outcomes of one sampling iteration, with boxed numbers indicating sampled badgers in a given year. Red boxes illustrate back-aging process: when individuals were first caught as adults, their first recorded tooth wear can be used to inform the first age record.

percentage of the "1" values in the corresponding year column of $\boldsymbol{LH_b}$ (and its context matrices), simulating the process of imperfect detection in a "captured" life history matrix, $\boldsymbol{LH_c}$ (Fig. 1).

We computed four different estimates of population abundance: three variants of minimum number alive (together, "enumeration" estimators) and one using a Cormack-Jolly-Seber (CJS) estimate of detection probability. MNA_{ct} represents simply adding "captured" (C_{ct}) individuals and those known from previous and subsequent captures to be alive but uncaptured in time t ("alive, uncaptured", AU_{ct}):

$$MNA_{ct} = C_{ct} + AU_{ct} \quad (5)$$

This number can be improved using context matrices to estimate ages at first capture for those individuals first caught as adults. In our case, we regressed real tooth wear against real age (using non-linear least squares in the *stats* package, see Chapter 2) to produce a relationship from which we could predict the age of unknown-age individuals based on their first sampled tooth wear (see Fig. 1 for example). For these individuals, life-history records could be back-projected to relevant years (BP_{ct}) to produce age-modified MNA ($aMNA_{ct}$):

$$aMNA_{ct} = MNA_{ct} + BP_{ct} \quad (6)$$

Time-varying capture efficiency itself (ce_{ct}, estimated as the proportion of known-alive individuals captured in time *t*) can also be used to estimate the probability that an individual *i* last captured at time *j-x* remained undetected but alive in the population at time *j* (we artificially lowered this probability to 0 past age 10, for reasons discussed above):

$$ce_{ct} = \frac{C_{ct}}{AU_{ct} + C_{ct}} \quad (7)$$

$$P(alive_{i,j}) = \prod_{t=j-x}^{j} (1 - ce_{ct}) \quad (8)$$

By summing these persistence probabilities for undetected-but-alive individuals in a given year, we calculated efficiency-modified MNA values ($eMNA_{ct}$):

$$eMNA_{ct} = aMNA_{ct} + \sum_{i=1}^{n} P(alive_{i,t}) \quad (9)$$

Finally, we also estimated abundance by implementing CJS models with the *marked* package (Laake et al. 2013) to provide a benchmark for the three stepwise varieties of MNA estimates. CJS models estimate two determinant parameters of detection: φ, the apparent survival (death and emigration) from time *t-1* to *t* (in these simulations, apparent survival = survival as no

emigration was modelled) and p, the probability of detection at time t given survival from $t-1$; both φ and p can be estimated as a function of time-varying and/or constant covariates. In each iterated sampling, we estimated p separately for each year (p_{ct}, an alternative estimate of ce_{ct}), and φ as a function of age, sex, and their interaction. Therefore, population abundance estimates (CJS_{ct}) using this method could be derived by dividing the captured individuals in time t by the detection probability:

$$CJS_{ct} = \frac{C_{ct}}{p_{ct}} \tag{10}$$

We could not compute this value for the first year of each iteration, as CJS models require a time $t-1$ for parameter estimation.

2.4 Estimating survival relationships using efficiency-modified persistence probabilities

Given a series of known life histories, individual survival probability can be expressed as a binomial linear regression, where case 1 represents known survival and case 0 represents known death. Imperfect capture efficiency (time-varying or otherwise), however, violates the assumption that an undetected individual at time t has died; therefore, the probability of undetected persistence must be considered. One possible solution to this issue is to use the probability an individual truly died after its final capture at time t (probability of "dead, uncaptured", DU_{ct}) to weight observations from different individuals in the survival regression:

$$Weight_i = DU_{ct} = 1 - AU_{ct} \tag{11}$$

We used these individual weightings to regress individual survival as a function of an individual's sex, age, and their interaction, producing a within-iteration estimate of these survival relationships to compare with the baseline relationships used to generate the population.

3 Results

3.1 Performance of different approaches as abundance estimators and indicators

Over the 30-year simulations, all enumeration estimators were negatively biased with regard to baseline abundance (Figs. 2a-c, 3); CJS probabilistic estimation was not (Fig. 2d-f). Moreover, MNA, aMNA, and eMNA underestimated the baseline population abundance most at lower average capture efficiencies (Figs. 2a-c, 3). Nevertheless, this negative bias was relatively consistent, with the exception of the first sampling occasion (in this case, year) and the final two (high capture efficiency) or three (low or real capture efficiency) occasions (Fig. 2g-i). eMNA provided a particularly informative abundance indicator, proving more robust to inter-annual fluctuations in time-varying capture efficiency than CJS estimates, with lower spread of abundance estimates over the 1,000 sampling iterations—particularly at low capture efficiencies and those modelled after real badger data (Fig. 2d-e). Following particularly rapid population dynamics shifts (see year 13 in Fig. 2), enumeration approaches exhibited an additional minor lagged negative bias.

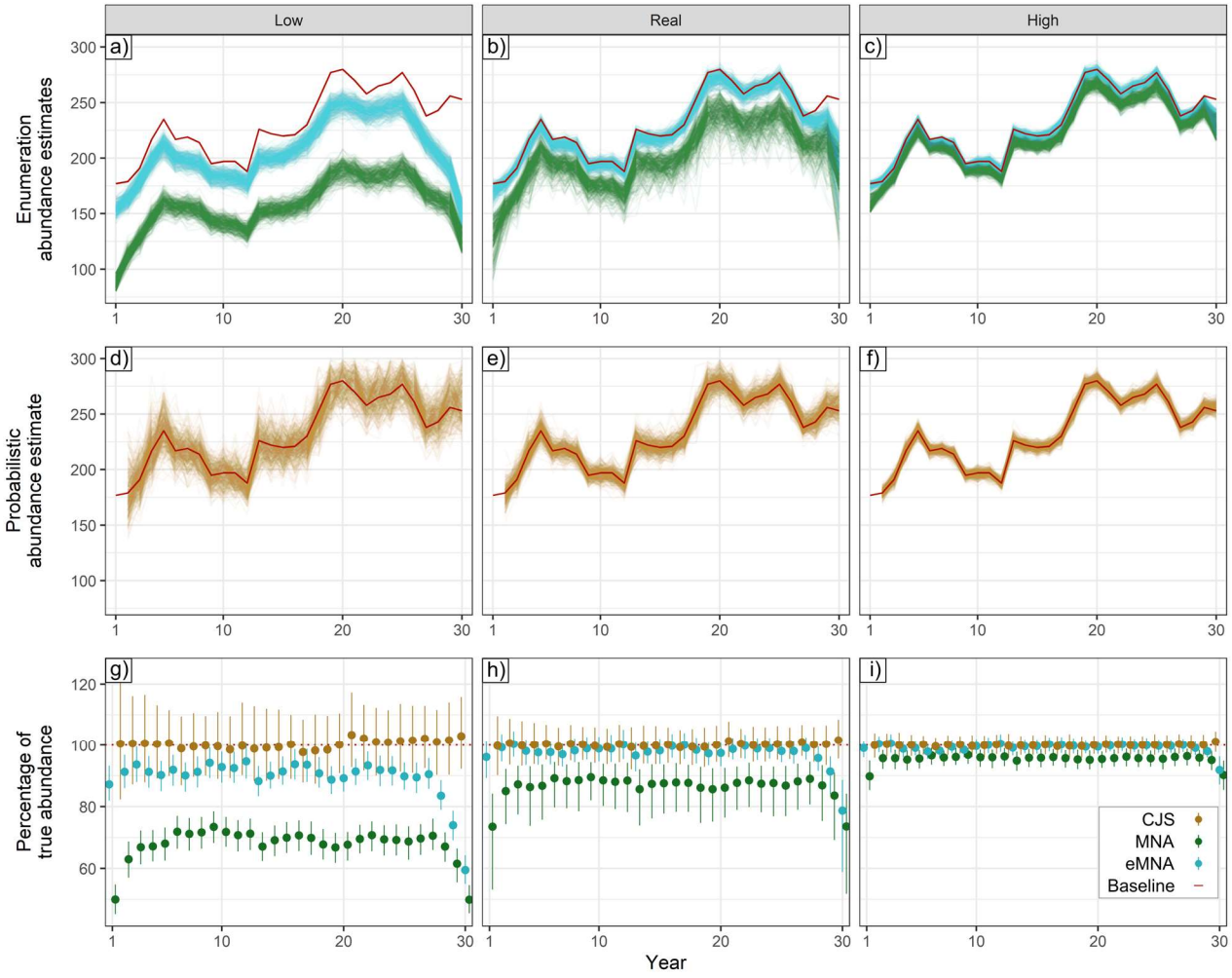


Figure 2. **Yearly simulation results.** For plots a-f, each line represents a single iteration (n = 1,000) of 30 years of sampling at low (45-55%), real (intermediate, based on badger rates), and high (85-95%) capture efficiency for either enumeration (MNA and eMNA) or probabilistic (CJS) methods. Panes g-h show mean iteration estimate and 95% percentage deviation from the baseline sampled data.

Each stepwise improvement to MNA reduced the negative bias of abundance estimates, with MNA, aMNA and eMNA estimates deviating from the baseline abundance by -12.5% (4.16%), -4.51% (SD = 2.91%) and -1.48% (SD = 2.25%), respectively, under intermediate capture efficiencies modelled after real badger data (Fig. 3; numbers calculated without first year and final 3 years of each sampling iteration). In the case of eMNA, this translates to an underestimation of only 3.5 badgers in an average year. While this negative bias was higher for eMNA at low average capture efficiencies (-8.58%), eMNA was far less susceptible to

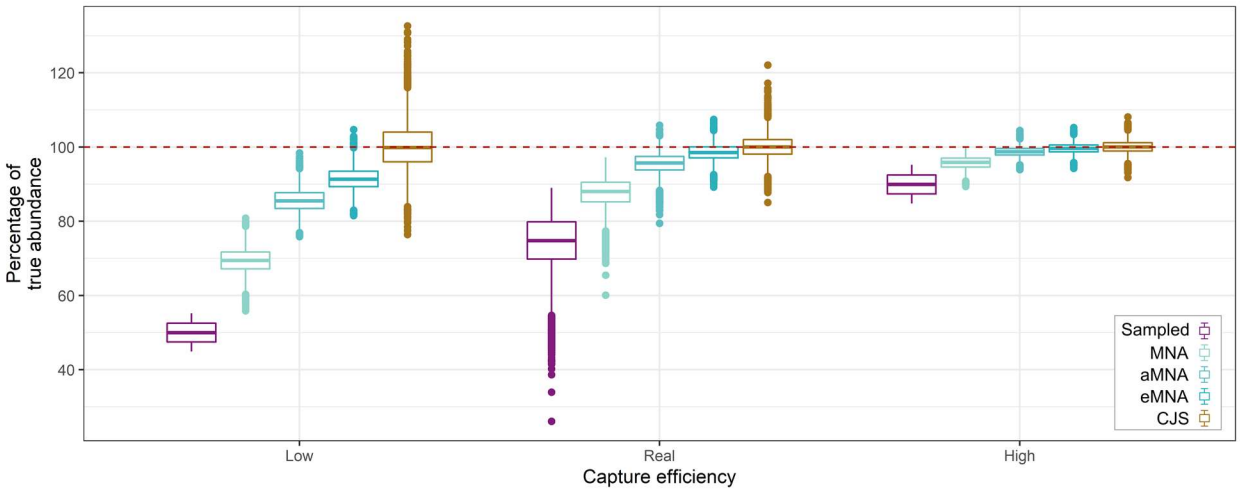


Figure 3. **Abundance estimation by method.** Boxplots display annual deviations from the baseline sampled population (with the exception of the first year and last three years of each iteration) for 1,000 samplings under either low, real, or high capture efficiency.

fluctuations from inter-annual capture efficiency variation than CJS, with the standard deviation of eMNA estimates being equivalent to only 3.07%, half of CJS' standard deviation of 6.18% under the same conditions (see the inter-annual "sawing" tendencies of CJS estimates in Fig. 2d).

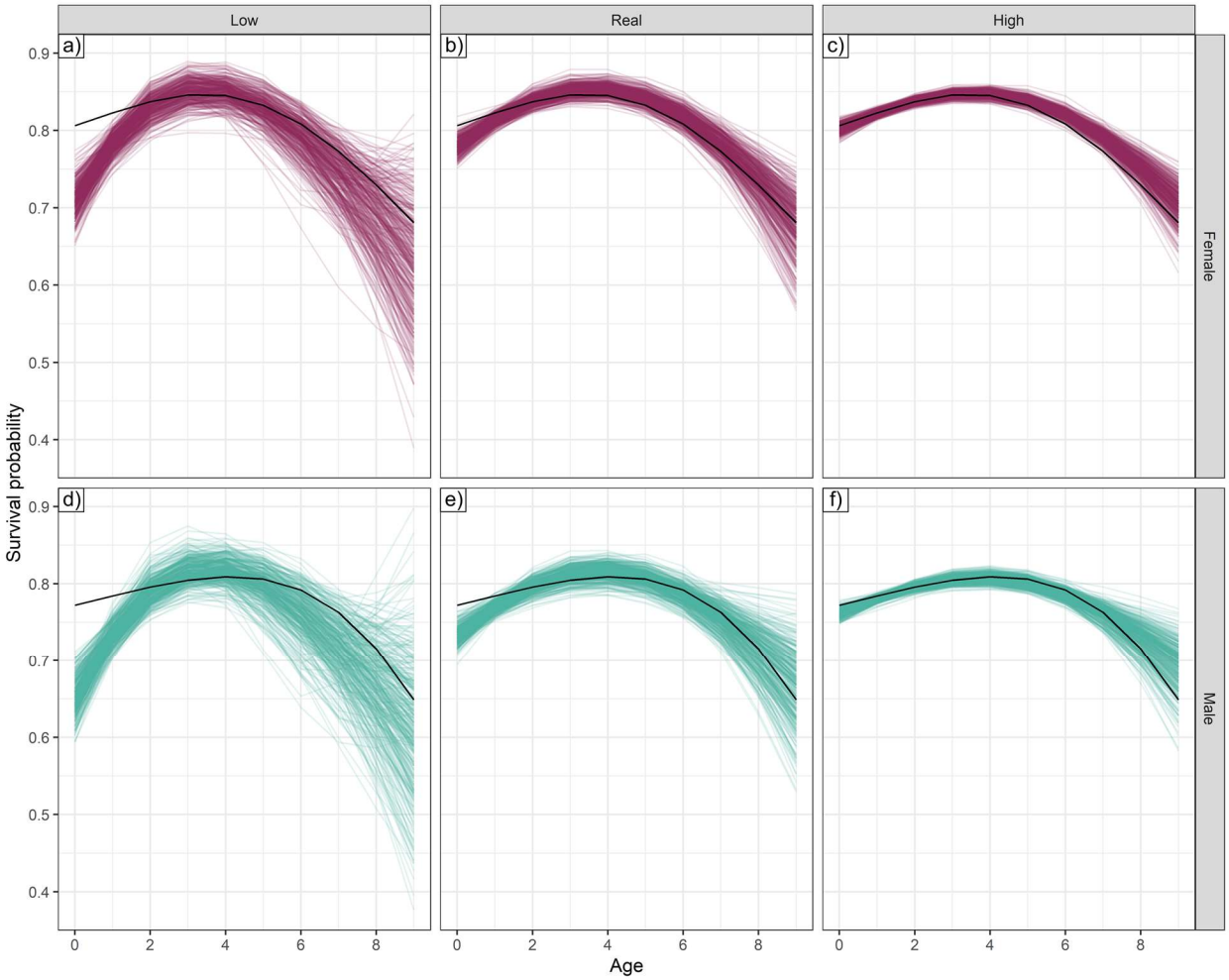


Figure 4. **Relationship between survival and age inferred from persistence probabilities.** Coloured lines show estimated relationships from 1,000 samplings under low, real, and high capture efficiencies; black lines show baseline relationship

3.2 Estimates of age-survival relationships from persistence probabilities

In nearly all sampling iterations under capture efficiencies modelled after real badger data, regressions weighting by probability of persistence beyond last detection recreated the baseline relationship between age and sex-specific survival (Fig. 4b, e). The validity of this regression method, however, was dependent on capture efficiency. First, a negative survival probability bias was evident at younger ages, particularly at low capture efficiency (Fig. 4a, d).

Second, survival probability at older ages was overestimated for high capture efficiencies (Fig. 4b-c, f).

4 Discussion

All forms of enumeration exhibited negative bias as abundance estimators, particularly at low capture efficiencies. However, under intermediate (based on real badger data) or high capture efficiencies, this negative bias was minimal in eMNA estimates. Moreover, even under low capture efficiency, enumeration methods (and particularly eMNA) provided abundance indices that were more robust to inter-annual variation in capture efficiency than probabilistic CJS outputs. The only instances in which eMNA underperformed CJS outputs as an abundance index were directly after abrupt changes in abundance, and during the last two (intermediate-high capture efficiency) or three (low capture efficiency) years of the sampling iterations. Finally, although estimating age-survival relationships through regression weighted with capture efficiency-modified persistence probabilities was hindered by the effects of imperfect capture efficiency on age representation in these data, most sampling iterations successfully approximated the baseline survival relationships, especially at intermediate capture efficiencies.

It has long been established that MNA's performance as an abundance estimator is sensitive to trapping efficiency (Hilborn et al. 1976). Nevertheless, its intuitive computation and usefulness as an abundance indicator have ensured its continued use for ecological studies (Smith and Nichols 2003, Holloway et al. 2012, Fritts et al. 2017, Howe and Davlantes 2017), conservation assessments (Sei and Porter 2003, Meijer et al. 2008), and governmental species management interventions (Ramey et al. 2008, Lazenby et al. 2014, Johnson et al. 2016). It is of particular use for endangered populations with small abundances (Sei and Porter 2003, Palomares et al. 2005, Meijer et al. 2008), as it provides a hard "floor" instead of the often wide

ranges associated with probabilistic estimates at low abundance (Meijer et al. 2008), and because its direct connection to individual life histories facilitates the computation of life tables and associated population parameters (Krebs 1985). The improvements we make here on MNA preserve this individual focus: rather than projecting a number of individuals with unknown features, it enables quantification of persistence probabilities for individuals with known features, benefitting from the careful design of most long-term demographic studies and the implicit additional information comprised in the resulting datasets. Using age-varying covariates to improve age estimation of individuals at first capture (Bird et al. 2019) and accounting for variable detection probabilities (White 2005) have both improved population parameter estimation in other methods. Here, by incorporating both factors in our eMNA formulation, we developed MNA's capacity to act not only as a valid density indicator, but also as a density estimator under intermediate-to-high capture efficiencies, while preserving the features that distinguish enumeration from probabilistic approaches.

Nevertheless, our results illustrate several of eMNA's persisting shortcomings under certain study conditions. First, as documented elsewhere for MNA (Pocock et al. 2004), eMNA's negative bias on our badger dataset was exacerbated during the first sampling and last two-three samplings of the population, making it of limited use as either an estimator or indicator unless in the context of either long-term datasets (Clutton-Brock and Sheldon 2010) or multiple populations under very similar capture efficiencies. Second, although eMNA handles inter-annual capture efficiency variation relatively well with animals such as badgers with lives that (on average) span multiple sampling recapture iterations (Fig. 2), consistently lower capture efficiency does introduce substantially higher negative bias (Fig. 2a). This risks low comparability if either inter-population habitat differences (Smith and Nichols 2003) or habitat

changes (Howe and Davlantes 2017) result in substantially different capture efficiencies. In these cases, methods such as CJS and closed-subpopulation models, the latter of which was developed using badger data (Tuyttens 2000), provide much more accurate abundance estimates (Byrne et al. 2012). Finally, estimation of survival rates and determinants thereof is risky when using approaches, such as MNA, that assume perfect detection of death (Viallefont et al. 1999). In addition to under-estimating survival rates, enumeration approaches ignore unmarked individuals (Graipel et al. 2014), which can lead to issues such as that seen in our estimates, which consistently underestimated juvenile survival (Fig. 4). Nevertheless, MNA methods have been used to calculate survival, particularly when populations are small (e.g., Sei and Porter 2003, Palomares et al. 2005). We caution that in such cases, researchers and conservation practitioners should carefully consider how certain sub-groups may be over- or under-represented in their capture data.

Despite its limitations, enumeration remains a powerful tool for wildlife ecologists. While model selection with probabilistic approaches can determine the drivers of individual survival and detection (Laake et al. 2013), eMNA directly connects individual persistence to population trends (Chapters 2-3). If this can be strengthened further by considering differential capture efficiency as a function of prevailing conditions (Noonan et al. 2015b), individual state markers (Noonan et al. 2014), and population sub-groups (Bryja et al. 2001)—all of which can substantially affect recapture probability—eMNA can continue to serve as a useful tool in wildlife studies. Moreover, individual heterogeneity presents one of the greatest challenges to studying wild populations (Davis et al. 2003), with individuals being trap-happy or trap-shy as a result of any number of determinants (Byrne et al. 2012). Ultimately, however, it is this individual heterogeneity that forms the basis for many ecological processes (Hamel et al. 2018),

and forming a detailed accounting of it remains crucial to growing our understanding of the "portfolio" that populations possess for tackling the challenges they face (Schindler et al. 2015, Beever et al. 2017).

5 Authors' Contributions

Conceptualization: Julius G. Bright Ross and Chris Newman; Data collection: Chris Newman, Christina D. Buesching, and David W. Macdonald; Coding and analysis: Julius G. Bright Ross; Writing: Julius G. Bright Ross; Editing: all authors.

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Chapter 2

What lies beneath? Population dynamics conceal pace-of-life and sex ratio variation, with implications for resilience to environmental change

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Abstract

Life-history and pace-of-life syndrome (POLS) theory predict that populations are comprised of individuals exhibiting different reproductive schedules and associated behavioural and physiological traits, optimised to prevailing social and environmental factors. Changing weather and social conditions provide *in situ* cues altering this life-history optimality; nevertheless, few studies have considered how tactical, sex-specific plasticity over an individual's lifespan varies in wild populations and influences population resilience. We examined the drivers of individual life-history schedules using 31 years of trapping data and 28 years of pedigree for the European badger (*Meles meles* L.), a long-lived, iteroparous, polygynandrous mammal that exhibits heterochrony in the timing of endocrinological puberty in male cubs.

Our top model for the effects of environmental (social and weather) conditions during a badger's first year on pace-of-life explained <10% of the ratio of fertility to age at first reproduction (F/α), and lifetime reproductive success (LRS). Conversely, sex ratio and sex-specific density explained 52.8% (males) and 91.0% (females) of variance in adult F/α ratios relative to the long-term population median F/α. Weather primarily affected the sexes at different life-history stages, with energy constraints limiting the onset of male reproduction but playing a large role in female strategic energy allocation, particularly in relation to ongoing mean temperature increases. Furthermore, the effects of social factors on age of first reproduction and year-to-year reproductive success covaried differently with sex, likely due to sex-specific responses to potential mate availability. For females, low same-sex densities favoured early primiparity; for males, instead, up to 10% of yearlings successfully mated at high same-sex densities. We observed substantial sex-ratio dynamism relating to differential mortality of life-

history strategists within the population, and propose that shifting ratios of "fast" and "slow" life-history strategists contribute substantially to population dynamics and resilience to changing conditions.

Keywords: *Life history, population resilience, HIREC, pace-of-life syndrome, demographic variability, individual strategies.*

1 Introduction

Threats imposed by Human Induced Rapid Environmental Change (HIREC: Sih 2013), and especially climate change (IPCC 2018), make it imperative to fully understand how vulnerable or resilient species and populations may be to both persistent and catastrophic events (Pacifici et al. 2015). This adaptability takes many forms (Kearney et al. 2009, Noonan et al. 2018), from genetic trait selection (Bårdsen et al. 2008) and behavioural plasticity (Loe et al. 2016, Beever et al. 2017) to changes in population dynamics (Walther et al. 2002). At the species level, fundamental life-history parameters are also important (Isaac 2009). Other plastic buffering (Vedder et al. 2013) mechanisms can, however, be more cryptic, such as how life-history strategies vary both between individuals and within individual lifespans, and in turn induce qualitative changes in population composition (Stenseth 1978).

Rapid, sustained periods of climatic change are neither exclusively anthropogenic nor particularly infrequent in the palaeontological record (e.g. Dansgaard-Oeschger events, Dansgaard et al. 1993). Environmental stochasticity, therefore, has shaped life-history evolution by shifting the "target" against which life history must be optimised (Tuljapurkar et al. 2009a), precluding individual behaviour and adaptive life-history traits from converging on a single optimum within populations (Stearns 1992). Consequently, *dynamic* (from stochastic environmental processes; Tuljapurkar et al. 2009b, Steiner et al. 2010) and *fixed* (differences in

individual quality; Stopher et al. 2008, Plard et al. 2018) heterogeneity cause life-history traits measured in populations to vary widely. Although in small populations, fixed heterogeneity can be maintained through weak selection and drift (Rozen et al. 2008), it is usually a product of shifting optima and consequent genotypic "bet-hedging", whereby lower longer-term fitness variance under environmental stochasticity redresses short-term fitness deficits (Starrfelt and Kokko 2012, Rajon et al. 2014).

This flexible fitness optimisation gives rise to "pace-of-life syndromes" (POLS), where different individual energetic investment profiles evolve along metabolic (Careau et al. 2008, Metcalfe et al. 2016) and behavioural (Careau et al. 2009) gradients to maximise each strategy's lifetime reproductive success (Réale et al. 2010, Dammhahn et al. 2018). Populations exhibiting "faster" composite life histories (early reproduction with high investment in producing offspring) are better adapted to stochastic conditions, where competitiveness at carrying capacity is rarely advantageous—analogous to r-selected species in community ecology (Pianka 1976). "Slower" life histories (delayed reproduction with fewer, often higher quality offspring) suit more stable, resource-limited niche conditions—analogous to K-selection (Dammhahn et al. 2018, Montiglio et al. 2018). Studies of extrinsic (weather and resource availability: Nilsen et al. 2009, Campbell et al. 2017, Krause et al. 2017) and intrinsic (social conditions: Kraus et al. 2005, Liedtke et al. 2015) drivers of population dynamics support these axes, but the relative contributions of each—providing either reproductive cues or constraints—to within-population pace-of-life (hereafter, "POL") variation (Réale et al. 2010) remains relatively under-investigated in the wild. Understanding how environmental conditions set and maintain not only mean life-history profiles but also the variance of these within populations (eschewing the "Tyranny of the Golden

Mean": Williams 2008), could therefore provide insights into population resilience to environmental change (Beever et al. 2017, Ogura et al. 2017, Noonan et al. 2018).

In this study, we therefore examine individual life-history variation with regard to: i) age of first reproduction, α; ii) annual reproductive success; and iii) two composite metrics that capture both early- and later-life life-history traits (overall "pace-of-life"): lifetime reproductive success (LRS), defined as the total number of offspring assigned to an individual; and the ratio of fertility to age of first reproduction (F/α), with "fertility" defined as the number of offspring produced per potential reproductive year of an individual's lifespan. This latter metric can position species along the fast-slow life-history continuum (Oli 2004, Dobson and Oli 2007), but has received some criticism at the population scale (Gaillard et al. 2005). On an individual scale, however, individual F/α values avoid the confounding effects of survival cautioned in that criticism, and both individual fertility rates and α are firmly linked to individual pace-of-life (Araya-Ajoy et al. 2018).

Energetic and strategic investment in reproduction and offspring care can also vary substantially between sexes; accordingly, the drivers of life-history tactics should vary (Hämäläinen et al. 2018). Males can potentially mate with multiple females, hedging the risk of failure to produce offspring against a typically higher mating investment (Kleiman and Malcolm 1981, Plard et al. 2018). Females must dedicate more energy to ensure successful brood production (Pontier et al. 1993), which, in mammals, includes gestation, lactation, and a degree of post-weaning care (Aloise King et al. 2013). Nevertheless, few studies have addressed differential plasticity in life-history traits between the sexes, potentially obscuring relationships at the population level (Royauté et al. 2018). We therefore examine (i) the relative contributions of weather and social drivers to pace-of-life variation; (ii) at what stage in an individual's

lifetime these drivers impact life-history strategies most; and (iii) how these relationships vary between the sexes.

For this analysis, we use long-term field data for the European badger (*Meles meles* L.; henceforth "badger"), which provide a tractable model species for long-term demographic studies. Badgers reach very high densities for a medium-sized carnivore in southern England (up to 45 individuals/km^2 at our site: Macdonald et al. 2015), with a high re-trappability rate (mean of 81.3% of known individuals trapped annually in our population: Noonan et al. 2015). Badgers exhibit substantial inter-individual realised lifespan variation, with a majority of individuals dying by age three in our population (largely due to cub mortality: ca. 25%) but with 4.4% living to age 10 (Macdonald and Newman 2002, Macdonald et al. 2015). Badgers are polygynandrous (Dugdale et al. 2008, Annavi et al. 2014b, 2014a) and females manage their reproductive investment through delayed (and selective) implantation, superfecundation, and superfoetation (Yamaguchi et al. 2006). In our population, an average of 45% of females produce one litter of 1-3 cubs per year (mean 1.46, Annavi et al. 2014b). This causes substantial variation in life-history decisions both between and within (year-to-year) individuals. Additionally, recent endocrinological work in our population has described two distinct phenotypes in male badgers, with some attaining sexual maturity and greater body size a year before others (Sugianto et al. 2019), inviting investigation into potential drivers for these diverging strategies. Moreover, badger population dynamics are sensitive to the effects of mean weather conditions and variation from the mean, which affect food availability (Kruuk 1978, Curry 2004), foraging activity (Noonan et al. 2014, 2018), and thus survival, with cubs in particular exhibiting higher mortality under very wet or dry conditions (Macdonald and Newman 2002, Macdonald et al. 2010, Nouvellet et al. 2013, see also Newman et al. 2017). Weather stochasticity therefore governs

survival likelihood, and thus may simultaneously signal future conditions, providing adults with cues on potential offspring survival. Over 31 years, this badger population also underwent a ca. 3-fold step-change in density (revised here as 137-328 individuals), principally from 1990-1995, with substantial annual fluctuations thereafter (Macdonald et al. 2009). However, there were no corresponding range or habitat changes, enabling examination of wide temporal variation in weather and social factors on POL. In turn, the long-term nature of the study (see Clutton-Brock and Sheldon 2010) permits coincident examination of demographic trends to provide insights into the effect of POL trends on population dynamics.

We test a series of hypotheses: a) if harsh weather is the primary driver of slower POL (Dammhahn et al. 2018), we predict that unsuitable weather during a cub's first year of life would be associated with lower F/α and LRS (**Harsh Conditions Hypothesis**). In contrast, b) if mating opportunities (relative abundance of mates and competitors in the "reproductive competition landscape") are a stronger driver of reproductive strategies, we predict lower F/α and LRS for cubs born at lower densities, and in years with population sex ratio skewed towards that individual's sex (**Reproductive Limitation Hypothesis**). This should be particularly evident in males, as badgers exhibit non-hierarchical scramble competition for mountings (Dugdale et al. 2011a), where reproductive opportunities scale with encounter rate (Annavi et al. 2014b, Swierk and Langkilde 2019). Therefore, under the Reproductive Limitation Hypothesis, we also predict that the distribution of sex-specific F/α will be skewed higher (faster POL) when population density is high and the sex ratio is skewed away from the sex in question (evidencing the effects of greater mating opportunities). With regard to timing of influences on life-history, we test c) whether early-life conditions (**Early Drivers Hypothesis**) adequately characterise lifetime F/α and LRS, with year-to-year environmental conditions contributing little to decisions

on whether or not to reproduce. Conversely, d) the **Later Drivers Hypothesis** predicts that age of first reproduction (and reproduction thereafter) results from year-to-year reproductive viability considerations. Finally, e) because females are more likely than males (which can spread out their investment between litters) to lose their entire reproductive investment if they fail to produce a surviving litter, and have a longer period of control over their reproductive investment, we predict that weather conditions should affect lifetime POL (F/α and LRS) and year-to-year life-history investments more in females than in males (**Cautious Females Hypothesis**). These hypotheses are summarised visually in Figure 1.

2 Methods

2.1 Study site and demographic data collection

Data were collected in Wytham Woods, a 424-ha semi-natural woodland in Oxfordshire, UK (51°46'N, 1°20'W; for more information, see Savill 2011). Beginning in 1987, each active badger sett in the study area was trapped for two or (most commonly) three nights, three to four times per year, at regular seasonal intervals. Individuals were transferred from string-trigger traps to holding cages, taken to a central field station between 7.00 – 9.00 am, and sedated with 0.2 ml ketamine hydrochloride/kg body weight by intramuscular injection (McLaren et al. 2005). On first capture, each individual was given a unique inguinal tattoo, allowing life-long recognition on recapture. Biometric data were recorded for each individual, including body length (to the nearest 5 mm), body weight (to the nearest 0.1 kg), and molar tooth wear (scale 1-5), a metric used for estimating the age of previously uncaptured adult badgers (Hancox 1988). For a comprehensive overview of the history of the Wytham badger project, please see Macdonald et al. (2015). All captures were made under Natural England license (currently 2019-38863, Badger Act 1992) and all animal handling procedures were made by qualified Personal Individual

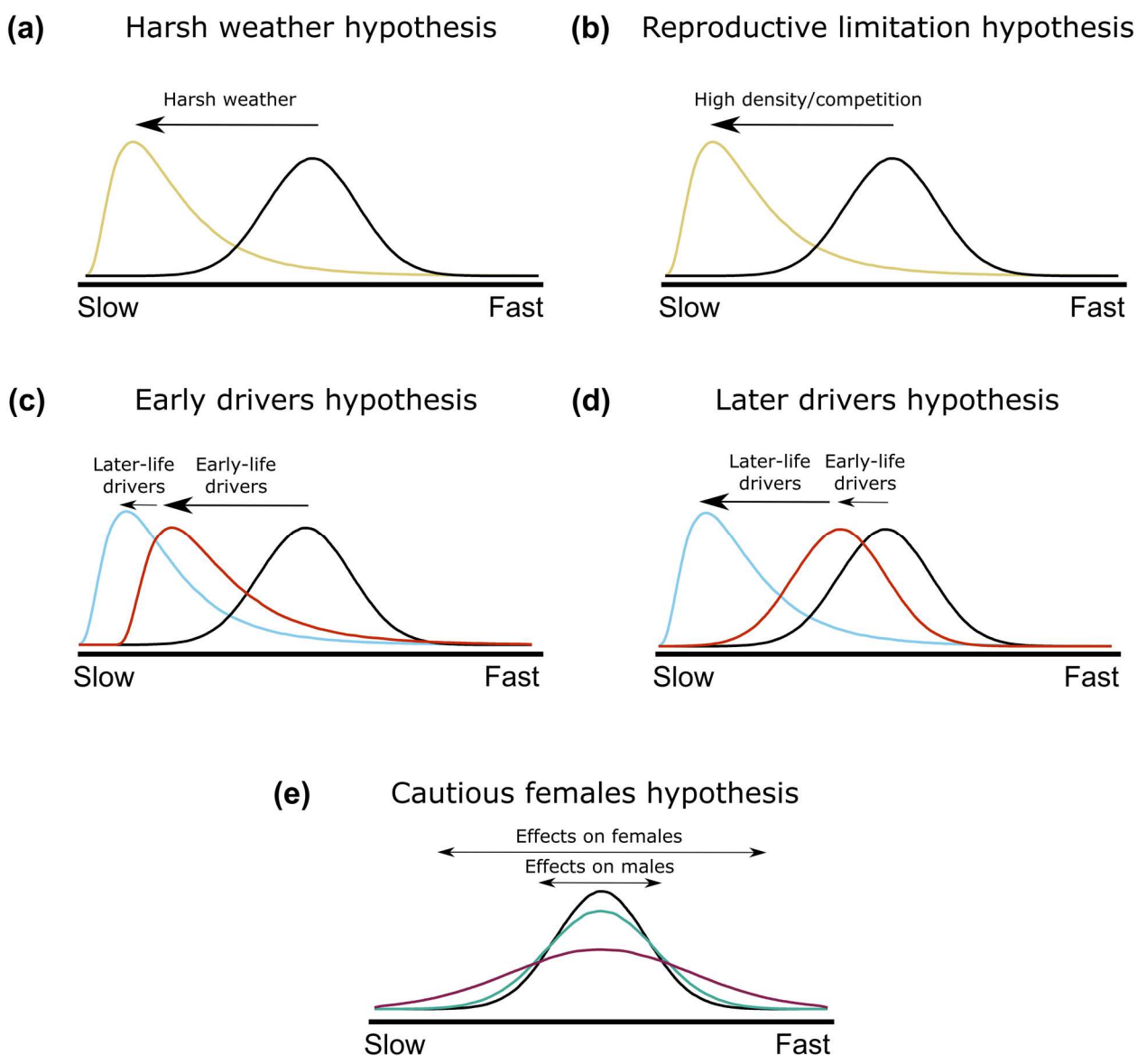


Figure 1. **Graphical summary of hypotheses advanced in this paper for the drivers of pace-of-life (POL) on a spectrum from slow (favouring somatic conservation) to fast (favouring reproductive investment).** The a) harsh weather and b) reproductive limitation hypotheses posit different primary environmental drivers of POL; the c) early drivers and d) later drivers hypotheses contrast the life-history stage at which environmental drivers produce most observable POL differences; and the e) cautious females hypothesis contrasts the magnitude of the effect of year-to-year weather drivers

on male and female POL. Panels a-d are given in one direction (with adverse conditions driving slower POL), but could also be represented in the other direction by favourable conditions.

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2.2 Trends in density and age-specific survival and fertility rates

Population density was estimated using a modified minimum-number alive (MNA) procedure, which has proven preferable to traditional capture-mark-recapture (CMR) models for our population (Macdonald and Newman 2002, Macdonald et al. 2009), which consistently overestimate density when trapping efficiency is high and migration is low (Rogers et al. 1997). This also meant that the identity of all individuals in our MNA design was known, and not implied. Traditionally (see Macdonald and Newman 2002), MNA for year *i* is estimated as the number of individuals trapped (T_i) plus un-trapped marked individuals known to be alive (KA_i) from subsequent trappings (as migration is very limited in this pop.: Macdonald and Newman 2002), as well as un-marked individuals inferred to be alive (IA_i) by back-projecting age according to tooth wear data (see Appendix S1 for formula) at first capture (for individuals not first caught as cubs):

$$MNA_i = T_i + KA_i + IA_i \quad (1)$$

Here, we modified this estimate by considering the effect of yearly trapping efficiency (TE_i, defined as T_i/MNA_i) on detection probability. Thus, the probability that an individual *j* (that was never caught again) remained alive in the population in each subsequent year *i* can be represented using the population-wide trapping efficiencies of the years between its last successful trapping ($t - 1$) and year *i*:

$$Prob(alive_{j,i}) = \prod_{t=1}^{i}(1 - TE_t) \quad (2)$$

These individual probabilities were then summed to the MNA_i estimate to derive an adjusted density estimate (N_i) more robust to inter-annual variation in trapping efficiency (Noonan et al. 2015, Byrne and Do Linh San 2016):

$$N_i = MNA_i + \sum_{j=1}^{n} Prob(alive_{j,i}) \quad (3)$$

N_i was computed for adults and cubs (cub N_i = cub MNA_i) of each sex over the course of the study (Fig. 3). In order to validate the use of N_i, a simulated population was created using demographic parameters drawn from our population. This population was then sub-sampled 1000 times according to plausible trapping efficiencies and the resulting sub-sampled "capture histories" used to create N_i estimates. N_i approximated the simulated "true" density very well for all but the first two and last three years of the simulated study (mean annual error for years 2-27 of 30 = -1.36 badgers, SD = 3.82); as a result, all analyses dependent on N_i are limited maximally to the years 1989-2015 (further limited for some models by pedigree data, see below). For more details on the N_i validation process, see Appendix S2 and Figure S2.1.

N_i was also computed separately for individuals in 4 age classes, according to life stages (juvenile: 1-2; young adult: 3-4; mature adult: 5-7; and senescent: 8+; Buesching et al. 2009, Sugianto et al. 2019, Sugianto et al. 2020). A genetic pedigree (detailed in Annavi et al. 2011, updated pers. comm.) was then used to assign parentage from 1987 to 2015 (n = 695 maternity assignments, 668 paternity assignments) and to compute the fraction of individuals in each age class to which parentage was assigned in each year. In order to provide a demographic context

for our POL modelling, we then used binomial GLMs to examine temporal trends in survival rate and in the proportion of reproductive individuals in the population.

2.3 Individual reproductive schedules and life-history metrics

Population pedigree was used to compute complete lifetime reproductive schedules for individuals that produced cubs surviving long enough to be recorded (minimally 12 weeks old; born in February, first trapped post-weaning in May). Limiting the analysis to individuals born in 2007 or earlier (8 years before the end of the pedigree) enabled us to incorporate ages comprising 80.6% of all recorded lifetime reproduction events (Dugdale et al. 2011b). With these filters, 269 individuals (128 females, 141 males) produced at least one detected cub.

We calculated age at first reproduction for males as the age at which they first mated to produce a genotyped cub, and for females as the age at which their first genotyped cub was born (given the 11 months of delayed implantation). This recognises that a) male badgers provide no input to reproduction beyond mating (and are therefore unaffected by future conditions); and b) males (but not females) may die after mating and still sire a viable litter the following spring. Individual LRS was computed as the sum of lifetime pedigree-assigned cubs (Vedder and Bouwhuis 2018), and F/α as the average number of cubs an individual produced per year of potential reproduction (beginning age 1 for males, age 2 for females, Sugianto et al. 2019) divided by age of first reproduction. Our genetic pedigree, though expansive, excludes assignments as a trade-off with accuracy; this presents a challenge for estimating lifetime reproductive metrics, as missing data could obscure "true" signals within noise. Therefore, we used the actual number of cubs in the population to simulate a "real" distribution of reproductive histories and computed individual F/α values after dropping different proportions of cub assignments. Simulated F/α values were relatively robust up to the degree of imprecision in our

dataset (R correlation coefficient at 60% missing assignments = 0.77). For further details on the simulation process and correlation curve, see Appendix S3.

2.4 Quantifying life-history trade-offs

Royauté et al. (2018) found highly equivocal support for the predictions of the POLS hypothesis in the literature, suggesting the assumption of reproductive-somatic trade-offs was not met among the studies reviewed (Dammhahn et al. 2018, Montiglio et al. 2018). Here, we therefore tested for such trade-offs among those badgers assigned parentage at least once by: i) modelling whether an earlier onset of reproduction covaried with realised lifespan; and ii) estimating the year-to-year probability of mortality associated with producing offspring.

Because variance in realised lifespan necessarily decreases as a function of age at first reproduction, we modelled this trade-off using linear mixed models (*nlme* package in R) to account for heterogeneity in variance. For both males and females, an exponential variance structure explained these data significantly better than not accounting for variance heterogeneity (L_{male} = 7.01, p = 0.008; L_{female} = 9.42, p = 0.002; both d.f. = 1). As the goal of these models was to establish trade-offs alone, no environmental drivers were considered in this model and a random intercept was instead evaluated for each cohort to control for developmental effects on realised lifespan. This intercept was retained for males (L = 4.48, d.f. = 1, p = 0.03), but not females (L = 0.012, d.f = 1, p = 0.91).

Logistic generalised linear mixed models (GLMM) were also used to model individual probability of year-to-year survival for all adults (age > 1, whether or not they were ever assigned offspring) based on i) whether or not a male mated successfully in a given year, or ii) the number of offspring a female produced in a given year (as female investment scales with

multiple offspring, but a polytocous litter costs a male no further investment), controlling for age as a fixed effect and for population-wide stochastic effects through a random intercept for year.

2.5 Computing covariates used in modelling life-history metrics

We modelled the influence of weather, social factors, and individual body condition on individual life history. Daily temperature and rainfall figures from 1987-2016 were provided by the Radcliffe Meteorological Station (https://www.geog.ox.ac.uk/research/climate/rms/), situated within 6 km of the field site. These figures were used to compute five weather covariates for each year (after Nouvellet et al. 2013, Byrne et al. 2015): mean temperature (μ_T), temperature variability (σ_T), seasonality (α_T), mean rainfall (μ_R), and the coefficient of variation of annual rainfall (CV_R). Annual σ_T was computed as the average annual squared difference between daily temperature measurements and a sinusoidal curve fitted to that year, while α_T of days within the year represented the amplitude of that curve (for details, see Nouvellet et al. 2013). CV_R was log-transformed to account for two years with particularly high rainfall variability. Of the weather covariates used, only μ_T exhibited a linear increase over time (1987-2016: 0.03 ºC/yr, $R^2 = 0.14$). For social factors, sex-specific adult population density (N_i) and sex ratio (SR, always given as adult male N_i/adult female N_i) were taken as measures of competition for food and reproductive opportunities, respectively. Additionally, in relevant models, we applied cohort size (CS) as a further measure of competition within cohorts.

Finally, individual condition was represented using a body-condition index ($BCI = \frac{\ln(body\ weight)}{\ln(body\ lengt\ )}$, established in Kruuk et al. 1987, Macdonald et al. 2002, Noonan et al. 2014). All BCI measurements were modelled using a generalised additive model (built with all individuals in the population) as a function of sex, season, and a smoothed spline of age (in years), allowing the spline to vary with season. Predicted values were subtracted from the fitted values, giving

residuals that were averaged within each year to produce an annual metric of individual condition relative to others of the same age and sex within a given season (BCI_r). Because this metric should covary to some degree with annual weather, all modelling procedures below include a check for collinearity between covariates.

2.6 Modelling drivers of life history

All modelling of life-history drivers was conducted separately for each sex using multi-model inference (*MuMIn* package in R, Barton 2019). We modelled all F/α ratios on the log scale, because a negative ratio is impossible but high values do occur, resulting in a right-skewed distribution prior to scaling. First, we scaled all covariates of interest to have a mean of 0 and a standard deviation of 1, for relative coefficient comparison. Second, we examined plots pairing the relevant response variable against each predictive covariate, to determine which might exhibit a quadratic relationship. Third, we computed orthogonal polynomial terms (function *poly()* in *stats* library, R) for each covariate identified in the prior step, in order to avoid collinearity between linear and squared terms. Fourth, we constructed correlation matrices of all considered covariates; covariates with a correlation coefficient of 0.6 or greater were never included together in a model. Finally, we conducted all-subsets model selection using these criteria, ranking models using Akaike's Information Criterion (AIC, Burnham and Anderson 2002). Among models with $\Delta AIC < 2$ from the lowest-AIC model, the most parsimonious model was selected and the coefficients reported in Table 1. Any deviations from this scheme are explained in the model-specific paragraphs below. Although p-values lose their statistical significance when conducting all-model selection, p-value levels are provided in Table 1 and the results using standard asterisk notation as an indication of how clear the covariate's signal was.

Although we draw attention to principal models designed to test each hypothesis, all model sets test multiple sets of hypotheses. The hypothesis that females should be more risk-averse in reproductive investment (Cautious Females Hypothesis) was tested in all models by splitting by sex.

To test between the Harsh Condition and Reproductive Limitation Hypotheses, we modelled individual life histories (F/α ratios and LRS values) as a function of social and weather conditions in the year a badger was born (model set 1a and 1b). For both sexes, a quadratic term for SR was included in the full model, and σ_T and μ_R were tested separately due to negative correlation; for males, σ_T and α_T were further tested separately. As this model set was cohort-based, cohort size (CS) was also included as a covariate.

To compare the Early Drivers and Later Drivers Hypotheses, we modelled annual individual cub production as a function of year-to-year weather and social conditions, controlling for individual BCI_r (model set 2). Because many individuals were not assigned a cub in most years, the model construction set contained many zeros; consequently, we used a zero-inflated model (Zeileis et al. 2008) to model separately the effect of covariates on reproduction probability (binomial) and on the number of offspring produced (Poisson). We controlled for age in the selection set; in males, a linear term performed best (ΔAIC linear-quadratic = 2.6), while in females, a cubic term was best (ΔAIC cubic-quadratic = 36.6), likely because some higher-quality females may persist to a later age than males while maintaining high hormone levels (Sugianto et al. in press), thus negating the downwards trend of senescence. Quadratic terms were included for μ_T; all other covariates were modelled linearly. We used Vuong tests (*pscl* library, Jackman 2017) to verify that the final selected zero-inflated models were better for fitting the data than basic Poisson models.

Table 1. **All models of the drivers of life history metrics, as described in the text.** If a covariate was not used in an analysis, this is indicated with "N/A"; if a covariate was included in model selection but not present in the final model, it is left blank. CS = cohort size; SR = male adults/female adults; N_i = sex-specific adult density; μ_T = mean annual temperature; σ_T = annual temperature variability; α_T = annual temperature seasonality; μ_R = annual mean rainfall; CV_R = annual coefficient of rainfall variation; BCI_r = sex, season, and age-controlled body condition. Significance levels provided for interpretability but should not be taken as traditional levels of significance. *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; . $p < 0.1$.

		Social					Weather						Condition
Model set	Sex	CS	SR	SR^2	N_i	N_i^2	μ_T	μ_T^2	σ_T	α_T	μ_R	$\ln(CV_R)$	BCI_r
First-year conditions (set 1)	Female (F/α)		-1.26	-1.97*		N/A		N/A					
	Female (LRS)		-1.04	-1.68**		N/A		N/A					
	Male (F/α)					N/A							
	Male (LRS)	0.18*	-0.27	-1.92**		N/A		N/A					
Annual cub production (set 2)	F(binomial)	N/A	-2.70***	N/A	10.97		-107.95***		0.96**	-1.48***			-0.71***
	F(Poisson)	N/A	-0.26**	N/A	-5.19*		-13.82***		0.08	0.01			~0
	M(binomial)	N/A	-0.68***	N/A	0.56**	N/A			0.44**			0.37	-0.13
	M(Poisson)	N/A	-0.07	N/A	-0.05	N/A			0.06			1.32***	0.39***
Successful first reproduction at each age (set 3)	F (age 2)	N/A			-15.59*								
	F (age 3)	N/A		N/A									0.41*
	F (age 4)	N/A	0.81**	N/A			21.00*						
	F (age 5)	N/A	0.76*	N/A								0.76*	
	M (age 1)	N/A			0.88*								
	M (age 2)	N/A		N/A		N/A							0.63**
	M (age 3)	N/A		N/A		N/A							0.64*
	M (age 4)	N/A		N/A		N/A	-32.13*		-0.94.				
Fraction above median F/α (set 4	Female	N/A	1.24**		-2.73***			N/A					
	Male	N/A	1.01**		-1.48***			N/A					

To further discern between the validity of the Early Drivers and Later Drivers Hypotheses, we modelled the effect of yearly weather, social factors, and individual condition on whether individuals mated productively (males) or produced offspring (females) for the first time in that year (model set 3). To do so, we compared annual covariates and BCI_r in individuals reaching their first reproduction to ones of the same age that delayed (by choice or circumstance) reproduction further (binomial glm, 1 = produced offspring for the first time, 0 = did not). Although some individuals bred for the first time only after age 4, sample sizes were small (6 males and 2 females produced offspring for the first time at age 5), resulting in convergence issues. The same series of terms were tested for these models as for the zero-inflated fertility models, by sex.

To further evaluate which limitation hypothesis was best supported (Harsh Condition or Reproductive Limitation) later in life, we modelled the effects of weather and social conditions on population-wide life history (model set 4). We pooled all individual life histories over the duration of the study and computed median male (0.167) and female (0.087) F/α (median chosen rather than mean due to a right-skewed distribution). For each year, we then tallied the number of males and females alive in the population with life histories above or below their respective median value. We used binomial models to test the effects of all weather covariates and the linear and quadratic forms of SR and N_i on the proportion of reproductive individuals in the population above the study-wide median life history.

All analyses were conducted using R (R version 3.5.3, R Core Team 2019). Full equations for all model sets are provided in Appendix S4.

3 Results

3.1 Descriptive natural history statistics

As annual breeders, badgers can only adjust breeding regimes by entire years. Any results depicting mean rates across the population that are not whole integers thus represent the composite of individuals following alternative life-history trajectories (e.g., shift in ratio of individuals first breeding at two or three years old). To address this statistical point, we present appropriate analyses and interpretations also as shifting ratios as predicted by our best-fit models between strategists.

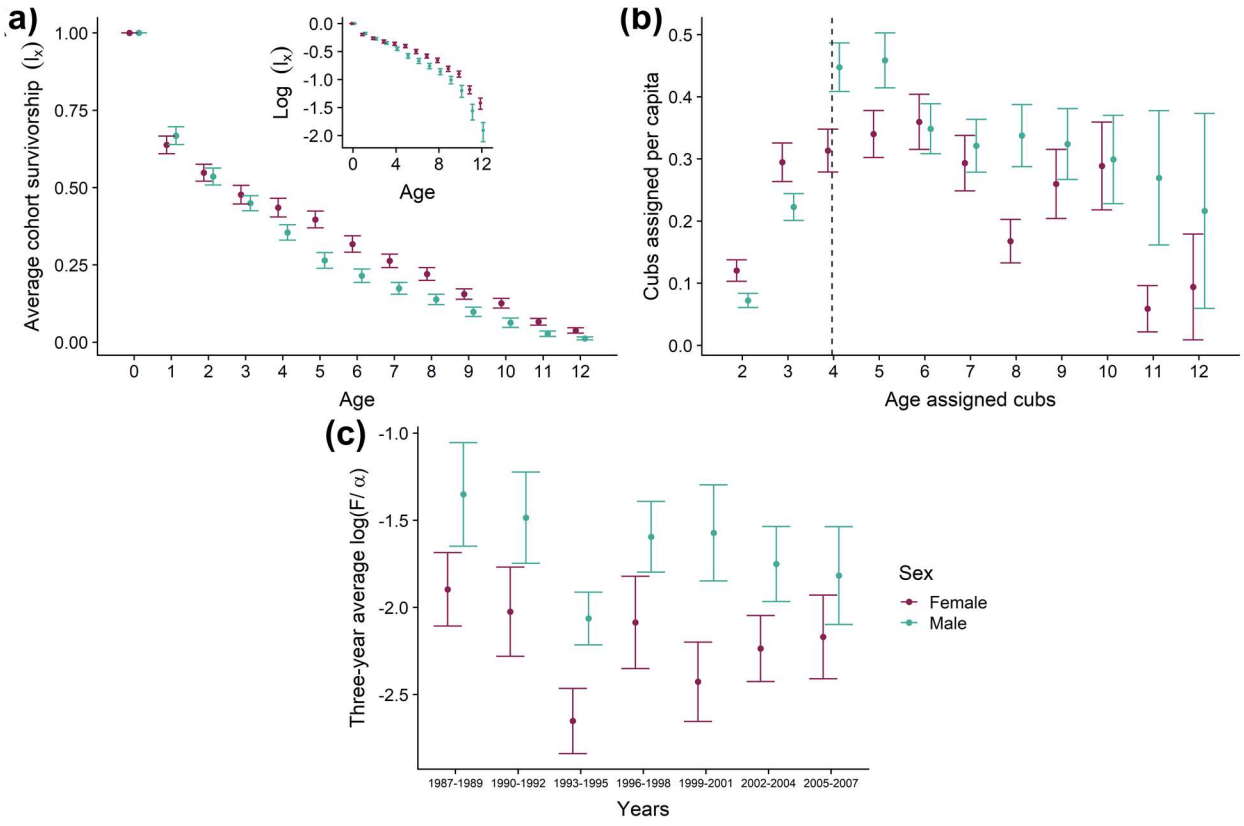


Figure 2. **Life-history dynamics.** Average a) cohort survivorship on a linear scale and (inset) on a logarithmic scale, b) annual per capita cub production by age, and c) tri-annual whisker plot of F/α values (on a log scale). Per capita cub production was estimated using a generalised additive model (GAM) with separate splines for males and

females; dotted line in (b) shows average age at first reproduction. Error bars for all panels display the standard errors of the means.

With this in mind, badgers exhibited considerable life-history variation. Males lived on average to 3.48 years and females to 4.08 years (median age at last capture = 2 for males, 3 for females) but with a long survivorship tail following high rates of mortality as cubs (Fig. 2a; see inset for logarithmic scale). Per capita cub assignments peaked at ages 4-5 for males and 5-6 for females (Fig. 2b); average age of first reproduction was similar between males and females (both on average aged 4 years), but varied widely in both sexes (SD_{male} = 1.61; SD_{female} = 1.76). F/α also varied substantially between individuals (Fig. 2c), and was on average higher for males than females (Mean F/α_{male} = 0.33, SD = 0.52; mean F/α_{female} = 0.16, SD = 0.17; Fig. 2c).

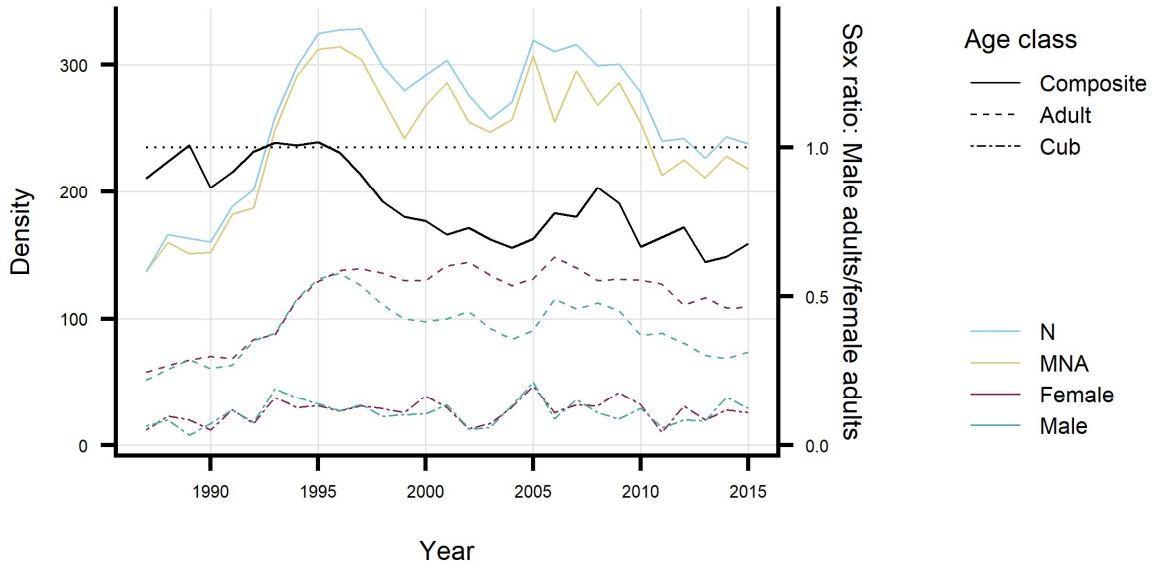


Figure 3. **Density estimates for the population from 1987-2015.** N_i and adult male and female density estimates are corrected for trapping efficiency. Sex ratio of male:female adults (black line) is also provided, with a null equal sex ratio indicated by the dotted black line.

3.2 Temporal trends

Annual trapping efficiency ranged from 50.0% to 82.6% ($\mu_{1988\text{-}2015}$ = 73.8%). Population density (N_i) increased threefold from 1987 to 1997, peaking at 328 individuals (63 cubs, 265 adults), followed by stabilisation between 250 and 300 individuals until 2010 and a subsequent decrease to a stable 230-240 individuals thereafter ($\mu_{2011\text{-}2015}$ = 191 adults, 47 cubs). From initial sex ratio parity (1987), the relative number of males decreased from 1997, remaining at 0.7-0.8 for the rest of the study. Survival rates also decreased over time in young and old badgers of both sexes over the study period (Fig. 4a); moreover, young males exhibited lower survival rates than did young females (age 1-2: $mean_m$ = 81%, $mean_f$ = 85%, p = 0.01; age 3-4: $mean_m$ = 78%, $mean_f$ = 87%, $p < 0.001$), likely driving the observed divergence in sex ratio (see Discussion). The oldest age class (age 8+) showed the steepest temporal decline in annual survival rates, from 77% (+/- 0.02 SE) in 1988 to just 61% (+/- 0.03 SE, p for trend < 0.001) in 2015. The proportion of females assigned offspring also declined in all age classes between 1988 and 2015 ($p < 0.001$ for all but age 2, p = 0.002); the reproducing proportion of males was lower for ages 5-7 (same slope as females), but temporal models for males aged 2, 3-4, and 8+ yielded a significantly flatter slope than those for females (age 2: p = 0.002; age 3-4: p = 0.045; age 8+: p = 0.001), indicating less of a decrease over the course of the study (Fig. 4b).

3.3 Life-history trade-offs

We found substantial evidence of life-history trade-offs, justifying the POLS framework for this study system. Realised lifespan was significantly related to age at first reproduction (females: p = 0.007; males: $p < 0.001$; Fig. 5a), with individuals that bred earlier living shorter lives than those that delayed reproduction, particularly in males (β_1 = 0.93 +/- 0.09 years of realised lifespan gained per year that the onset of reproduction was deferred; vs β_1 = 0.38 +/-

0.14 years in females, Fig. 5b). Models of the year-to-year survival costs of reproduction also showed that each cub produced had a significant negative effect on female survival probability, controlling for age and annual weather conditions ($\beta = -0.59$, $p < 0.001$). For males, siring a cub was negatively correlated with survival to the next year, although not significantly so ($\beta = -0.47$, $p = 0.14$). However, for both sexes, we found a significant positive interaction between age and higher survival probability when reproducing (males: $\beta = 0.13$*age*sired cubs, $p = 0.03$; females: $\beta = 0.07$*age*cubs in litter, $p = 0.003$).

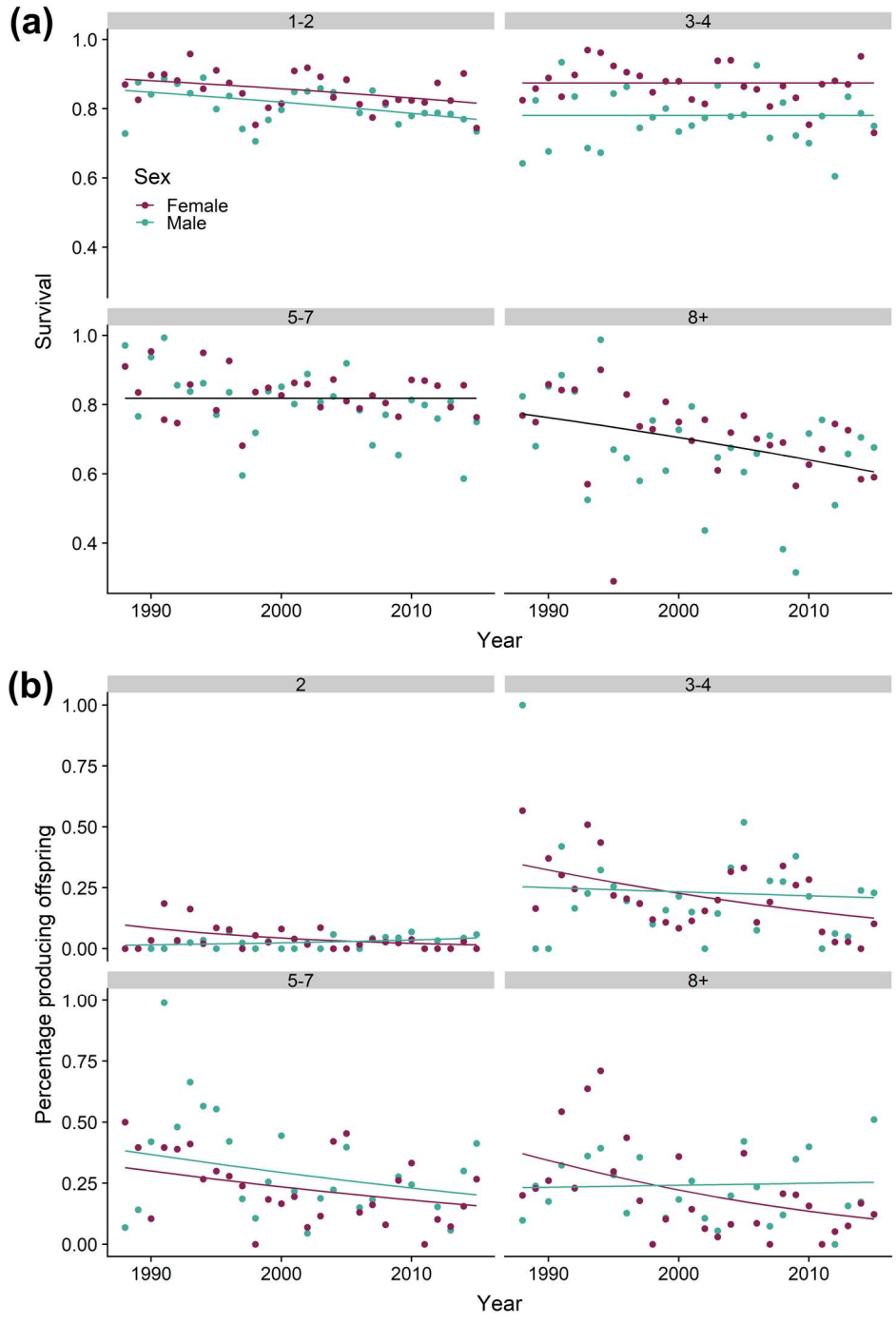


Figure 4. **Population dynamics.** Temporal trends in a) survival and b) percentage of individuals reproducing by age class and sex (male = cyan; female = magenta). Significant relationships shown by trend lines, with significant differences between sexes indicated by separate trend lines for each sex.

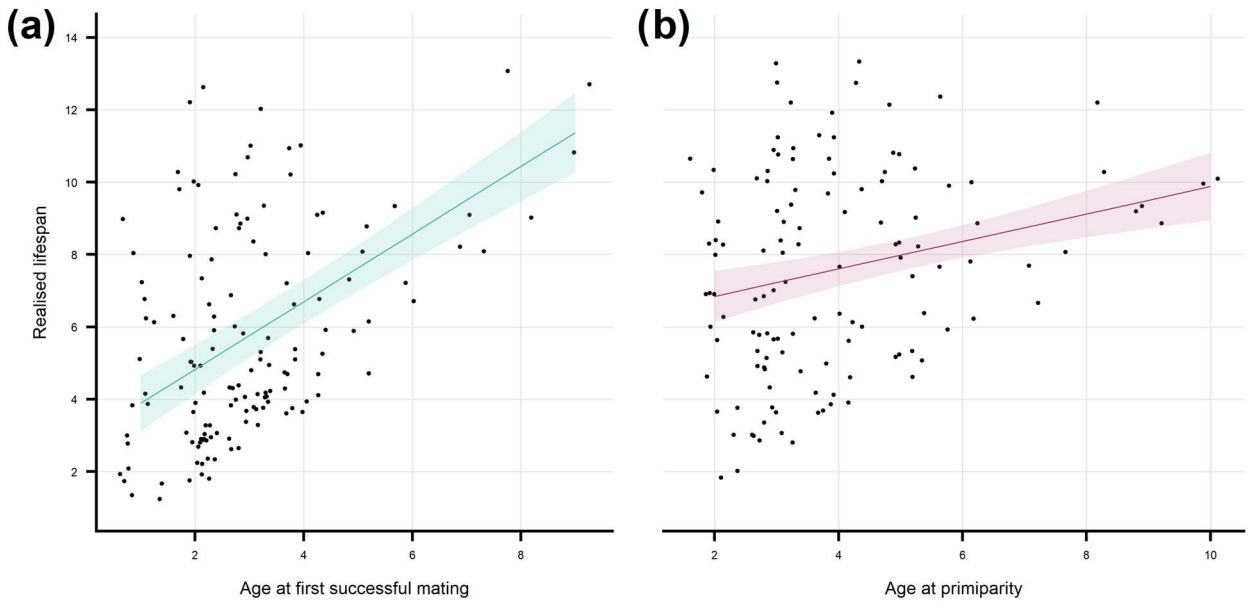


Figure 5. **Trade-off between age at first reproduction and realised lifespan by sex.** Regression lines for a) males and b) females shown with 95% confidence interval. Age at first reproduction represents age at first successful mating for males and age at first successful cub production for females. Points are jittered for clearer visualisation.

3.4 Drivers of life-history metrics

Our various hypotheses are tested simultaneously by multiple models, so here we first describe the results of model sets, later discussing insights that distinguish between competing hypotheses.

Model set 1 showed relatively little influence of natal conditions on the subsequent lifetime pace-of-life of an individual, with only social conditions retained in final models (variance explained: F/α_{male} = 0% (null model selected), F/α_{female} = 5.8%, LRS_{male} = 5.0%, LRS_{female} = 8.4%). Male cubs born in larger cohorts typically attained higher LRS while, for both sexes, pace of life was fastest (high LRS in males; high F/α and LRS in females) when cubs were born with the population at a SR of approximately 0.8, and slower at higher and lower SR (Table

1). For instance, 2.47 ± 0.32 SE cubs were predicted on average for a reproductive male born at the lowest SR of the study, compared to 4.21 ± 0.46 SE for a reproductive male born at an SR of 0.8.

Model set 2 provided insights into year-to-year reproductive outcomes, with both social and weather conditions retained in final models (zero-inflated models were significantly better fits for annual individual cub production than simple Poisson models; Vuong test, $p < 0.001$ for both sexes). Proportionally fewer individuals of both sexes reproduced at higher SR, and those that did reproduce produced fewer offspring. While higher female densities were typically associated with smaller litters per reproducing female, higher male densities, counter-intuitively, were associated with a greater likelihood that a given male would breed successfully (Table 1). Proportionally fewer females bred in seasonally extreme years (higher α_T), and in warmer years, which were also associated with smaller litter sizes per reproducing female; however, we also found a positive effect of temperature variability (σ_T) on female likelihood of breeding. Higher BCI_r had a negative effect on the likelihood of producing offspring, although this effect was small (Table 1). A higher proportion of males bred successfully in years with higher temperature variability, while higher rainfall variability (CV_R) covaried with more offspring sired in the following year. In males, we found a generally positive effect of BCI on the number of offspring sired the following year.

Model set 3 corroborated the role of social conditions in driving POL outcomes through substantial effects on the onset of reproduction. A greater proportion of males mated successfully (producing at least one cub) for the first time at age 1 at higher male densities (our models predicted 10.8% ± 0.5 SE at the highest N_i, but only 1.0% ± 0.5 SE at the lowest N_i); conversely, higher female densities led to fewer females commencing reproduction in their first viable year

(2.4% ± 1.3 SE of females producing cubs at age 2 at the highest N_i; 17.1% ± 8.7% at the lowest). Closer to SR parity, females were more likely to produce their first litter of cubs at ages 4 or 5 (as many as 36.6% ± 10.3 SE at age 4 and 37.8% ± 12.9% at age 5). While more females produced their first litter at age 4 following warmer years (38.3% ± 16.0 SE in the warmest years vs. 3.3% ± 2.2 SE in the coolest, holding SR constant at mean levels), higher mean temperatures were associated with fewer males beginning reproduction at that late an age (39.4% ± 15.5% at age 4 in the coldest years, 2.1% ± 1.9 SE in warm years, holding temperature seasonality constant at study average). More variable rainfall was also linked to higher likelihood of late-comer females beginning reproduction (41.8% ± 16.7 SE vs. 6.1% ± 3.3 SE at age 5, holding SR constant at mean levels), while more seasonality reduced the likelihood of latecomer males doing the same at age 4, although this effect was only borderline significant ($p = 0.054$, 1.3% ± 1.6 SE at lowest α_T, 35.2% ± 18.7 SE at highest α_T, holding temperature constant at study average). Higher BCI_r was associated with an earlier onset of reproduction in both sexes (females at age 3: 42.0% in highest condition; 6.3% in lowest; males: 32.3% ± 9.5 SE age 2, 39.4% ± 13.6 SE age 3 in best condition, 2.2% ± 1.7 SE age 2, 1.9% ± 1.9 SE age 3 in worst condition).

Model set 4 strongly supported the role of the reproductive competitive landscape in setting an individual's pace-of-life within long-term population demographics. Over the course of the study, SR parity was associated with a greater proportion (max 74% of males, 81% of females) of individuals above the long-term median F/α (indicating more "fast" life-history strategists); periods with higher sex-specific N_i had the opposite effect (indicating a preponderance of "slow" life-history strategists). High female density co-occurred with low SR (Fig. 3), leading to a substantial slow-down in population-wide female POL during these years (Fig. 6b). In males, the decrease in sex-specific density from 1997-2007 (and resulting increase

in females per reproductive male) meant that population F/α distribution remained relatively constant (notwithstanding a brief slowdown following the population peak) despite overall increases in density relative to the beginning of the study (Fig. 6a). Overall, these social factors alone explained substantial variance in model set 4, particularly for females (males: 52.8% of variance explained; females: 91.0%), reinforcing the role of relative mate and competitor abundance on setting long-term population pace-of-life.

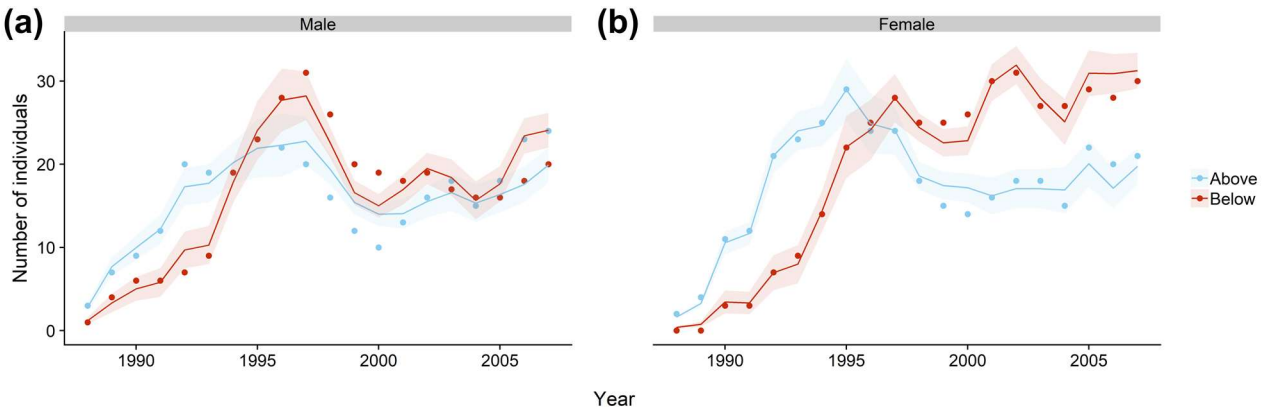


Figure 6. **Changing pace-of-life ratios over time.** Number of reproductive a) males and b) females in the population above (blue) and below (red) the long-term (1986-2007) individual median F/α value. Points represent real data, lines are model predictions based on population sex ratio (males/females) and sex-specific population density, with 95% confidence intervals.

4 Discussion

We found strong support for reciprocal mechanisms linking individual life histories to population dynamics, with population density and relative sex ratio driving sex-specific effects on reproductive outcomes. During a cub's first year, the population's demographic composition, but not weather, had an effect on individual lifetime POL for both sexes (model set 1, supporting

the Reproductive Limitation Hypothesis over the Harsh Conditions Hypothesis), although this effect accounted for only 0-8.4% of the variance in lifetime POL. Supporting the Later Drivers Hypothesis, year-to-year weather and demographic conditions subsequently had a much greater effect than early-life conditions in honing reproductive investment and life histories (better fit of model sets 2-4). We found that weather conditions (as a proxy for food availability and thermoregulatory costs), and the linked metric of BCI_r, were most influential in different life-history stages for males and females. Weather and BCI_r primarily affected the proportion of males reproducing successfully for the first time (model set 3); for females, the primary weather effect was on year-to-year reproductive output (model set 2; partially confirming the Cautious Females Hypothesis). Population dynamics drove differential reproductive investment responses in males and females, providing clues to differential survival observed between and within the sexes (Figs. 4a, 5). We reflect below on the potential for a density-dependent regulatory feedback on the frequency of precociously-breeding males and on its ability to generate the observed divergent sex ratio (Fig. 3).

While previous studies have focused on components of life histories determined by early-life drivers (Liedtke et al. 2015, Krause et al. 2017), any amount of environmental stochasticity over an individual's lifespan represents a "moving target" for reproductive success (Tuljapurkar et al. 2009a), especially for longer-lived iteroparous species. Even after early-life, factors such as weather (Coulson et al. 2001), population dynamics (Stopher et al. 2008), and body condition (Descamps et al. 2006, Albon et al. 2017) can continue to cue attempts at reproduction and determine the likelihood of success (Hamel et al. 2009). Therefore, maintaining life-history plasticity allows individuals to avoid canalisation and instead tailor reproductive investment to ongoing environmental stochasticity. Consequently, the relatively small role that early-life

factors played in badger life history exposes a dimension of resilience to change beyond the fixed behavioural phenotypes suggested by POLS theory (Dammhahn et al. 2018). Later-life conditions (model sets 2-4) were much more predictive than early-life environment of life-history traits, particularly in the case of the size and sex composition of the population.

The relative abundance of potential mates and competitors (measured by SR) shapes the marginal benefits of increased reproductive investment and therefore has far-reaching effects for individual life histories in animals (ranging from dendrobatid frogs, Pröhl 2002, to reindeer, Mysterud et al. 2003). In this study, we observed divergent effects of mate competition in males and females, with lower proportions of individuals breeding successfully in both sexes at SR closer to parity—expected due to mate limitation for males, but not females (keeping in mind SR was never male-skewed). Moreover, the reduced female reproductive output at higher female densities (Table 1, model set 2) implies a breeding constraint for females beyond encounters with males. This likely results from inter-female competition within social groups (Woodroffe and Macdonald 1995), which can manifest as a) a cryptic effect where blastocysts are lost or fail to implant during delayed implantation, b) abortion during pregnancy, or c) losses during weaning (Cresswell et al. 1992). These latter effects (b and c) are commonly seen in other stratified mammalian social reproductive systems (e.g. meerkats: Clutton-Brock et al. 2010) and, combined with the monopolisation of limited reproductive opportunities by more established individuals under conditions of intense reproductive competition (e.g. macaques: Kuester et al. 1995, reindeer: Røed et al. 2002), likely limited female reproductive opportunity at higher densities during our study.

Over the study period, the number of main sett sites increased from 23 in 1993 to 63 in 2002, in parallel with population density peaking in 1997 (Macdonald et al. 2004); inhabitants of

new setts, however, exhibited no reduction in weight or body condition. High densities (and an even sex ratio, see Fig 3) preceded, and thus drove, the increase in sett sites. Thereafter, this socio-spatial reorganisation likely alleviated female reproductive competition (and competition for other resources, according to the Local Resource Competition hypothesis; see Dugdale et al. 2003), facilitating the higher likelihood of an individual reproducing (for both sexes) at the female-skewed sex ratios (low SR) observed later in the study. Therefore, although ~15% fewer females reached early primiparity at higher densities, this sett proliferation likely also explains why older, previously nulliparous, females became nearly 40% more likely to begin reproduction at the later female-skewed SR, potentially having been constrained from breeding previously.

As expected from competition-mediated male investments (Lodé 2009, Newbolt et al. 2017), when SR was more male-skewed—rather than simply when male density was high—a reduced proportion of males reproduced successfully (model set 2). Conversely, high male densities were actually associated with higher proportions of males successfully breeding (model set 2). Of course, as multiple paternity in litters is common in badgers (Dugdale et al. 2007), more males do not necessarily imply exclusion from paternity. However, we also observed that a) a subset of males exhibited more reproductive success in more competitive environments, with as many as 10.8% of yearling males beginning reproduction at high male densities (model set 3, contrary to the effect seen in females, and in keeping with the "early-developer" endocrinological phenotype identified in Sugianto et al. 2019) and b) male LRS peaked when cubs were born at an intermediate, rather than a strongly female-skewed, sex ratio (0.86 males to each female, model set 1). Therefore, while crowding at high female densities—and associated food limitation—decreased female litter size (model set 2) and the proportion of young females breeding (model set 3), and resulted in fewer "fast" female POL strategists (model set 4; Fig.

6b), similar conditions actually increased reproductive output (and, presumably, reproductive investment) in a proportion of males.

Wild animals that invest disproportionately in reproduction over somatic conservation tend to "live fast" at the cost of "dying young" (Promislow and Harvey 1990, Hall et al. 2015). Males (particularly in scramble competition systems) often invest more in reproduction at higher relative competitor abundance (Weladji et al. 2005, Holwell et al. 2016), but at a price: in our study, males that reproduced early did so at nearly three times the cost to realised lifespan compared with females (Fig. 5) and, although the relationship was not significant, siring a cub was negatively associated with paternal survival probability. In addition to risking road traffic mortality (Macdonald et al. 2010, Canova and Balestrieri 2019) while searching for mates, the costs of elevated testosterone (Fargallo et al. 2007) have been linked to reduced survival probability in badgers (Buesching et al. 2009). Therefore, our findings emphasise the oft-ignored role reproductive effort can play in male survival (Bleu et al. 2016).

In relatively slow-lived animals, such as badgers (Macdonald et al. 2009), population growth is strongly dependent on adult survival (Oli and Dobson 2003). Therefore, the increased number of "fast-living" (and therefore, fast-dying; see Figs. 4 and 5) males observed at higher male densities (Figs. 2c, 6) likely contributed to the diverging sex ratio (up to 60.2% female) observed following the population peak in 1997 (Fig. 3), consistent with other high density badger populations (Rogers et al. 1997). If we characterise these males as following quicker, cheaper strategies, we see selection against this strategy in favour of "slow and steady" strategists as density increases (and slight compensatory recovery of the "fast" strategists later on, see Fig. 6), reflecting a form of density-dependent life-history selection (Wright et al. 2019). These long-term regulatory dynamics of density-dependent selection for increases and die-offs of

"fast-living" males support a risk-sensitive view of life-history strategy selection (Bårdsen et al. 2008).

Changing weather conditions frequently interact with population density and foraging efficiency to influence reproductive strategies (Bronson 2009, Richard et al. 2014), but often with sex-divergent effects (Yoccoz et al. 2002, Weladji et al. 2005). The strong effect of weather during a female's adult life on her life-history traits (model sets 2-4) was congruent with our expectation that females would tailor reproductive investment to their likelihood of being fit enough to carry a litter to term (Cresswell et al. 1992). We found that warmer years, particularly with more extreme summers and winters (negatively correlated with earthworm availability), had a negative effect on female reproduction probability (Table 1, model set 2). Linked to this, BCI among 3-year old females was correlated with the likelihood of achieving primiparity in the following year. Particularly as mean temperatures are expected to continue to rise (globally: IPCC 2018; documented for our study site in results), these effects emphasise the downstream effects of changing energetic conditions on life-history strategies in wild populations (Peterson et al. 2018).

Energy constraints, however, showed sex-specific effects, driving the age of first reproduction in males more strongly than in females. Earlier breeding (where conditions allow) can lead to a higher relative fitness advantage in males (*sensu* Oli and Dobson 2003). Age at first reproduction should be more sensitive to environmental conditions in polygynous males than in females because, once breeding, males can simultaneously invest in multiple litters and therefore achieve a faster overall pace-of-life (Hämäläinen et al. 2018). Overall, while more variable temperatures and rainfall were positively associated with male reproductive success in a given year (Table 1, model set 2; suggesting some effect on mating effort in relatively low-cub

mortality years, see Annavi et al. 2014a), warmer years were associated with virtually no "latecomer" males beginning reproduction at age 4 (compared with nearly 40% in colder years). Although this effect is difficult to separate from female litter failure, 30-40% younger males began reproduction as early as age 2 or 3 if they were in better body condition – a function of net energy gain. Parallel endocrinological work on this same population has found that male badgers require a minimum body size for the onset of puberty (Sugianto et al. 2019). Consequently, where weather and foraging conditions affect juvenile male growth, it can impede their "race to the starting line", whereas female strategies are governed more by maintaining a "steady pace" once there. This is consistent with the faster overall male POL expected in polygynous species (Tarka et al. 2018).

Our study exemplifies why it is important to consider the demographic composition of populations rather than simply population-wide metrics when estimating population resilience (Keith et al. 2008, Isaac 2009). Various studies report that climate change can affect the sexes differently (Petry et al. 2016, Gianuca et al. 2019), in ways likely to impact the plasticity and resilience of populations (Le Galliard et al. 2005, Miller and Inouye 2013). Particularly, where climate affects the distribution of fixed individual heterogeneity in populations, it may carry unforeseen consequences for population resilience and persistence (Jenouvrier et al. 2015). Ultimately, the extent to which a population is comprised of "fast" and "slow" individuals, and their associated sex ratio, will substantially affect how that population might respond to chronic or acute pressures in the form of altered weather regimes (Forister et al. 2010, Schloss et al. 2012) or habitat deterioration (Watson et al. 2018).

Maintaining multiple POL strategies (Starrfelt and Kokko 2012), rather than simply maximising proximate fitness (Day and Taylor 1996), provides an evolutionary stable strategy in

response to environmental stochasticity (Rajon et al. 2014, Ogura et al. 2017). In the present study, we documented a high-density wild population's ability to respond to varied environmental conditions over three decades (c. 7 generations) through plasticity in life history. However, HIREC risks exacerbating natural background selection pressures (Benton 2009), with the potential to drive maladaptive selection (Isaac 2009). Even if short-term benefits result from changing ratios of strategists, long-term instability may emerge (ecological "traps", *sensu* Le Galliard et al. 2005, Penteriani et al. 2018). Therefore, although adaptive plasticity to change is a key mechanism through which populations respond to rapid change (Berteaux et al. 2004, Silva et al. 2017), populations with high plasticity should be examined carefully for maladaptive selection. Ultimately, these types of cryptic qualitative changes in population composition must be incorporated into management programmes designed to minimise biodiversity loss under rapid climate change (Hoffmann and Sgrò 2011).

5 Data Availability Statement

The data that support the findings of this study are available on the Wytham Woods Badger Project Dataverse (host: Harvard Dataverse). DOI: 10.7910/DVN/OJ9GUJ.

6 Authors' Contributions

Conceptualization: Julius G. Bright Ross and Chris Newman; Data collection: Chris Newman, Christina D. Buesching, and David W. Macdonald; Coding and analysis: Julius G. Bright Ross; Writing: Julius G. Bright Ross; Editing: all authors.

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Chapter 3

A fat chance of survival: Body condition provides life-history dependent buffering of environmental change in a wild mammal population

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Under review by Climate Change Ecology

Abstract

Environmental change often causes decreased food availability and/or increased foraging costs, putting populations at risk of starvation. Body fat reserves can buffer periods of weather-driven food scarcity to ensure survival and reproductive success, but this capacity is affected by life-history factors and fixed inter-individual heterogeneity. Here, we use 29 years of data from a wild population of European badgers (*Meles meles*) as a model species to explore how body condition buffers weather-related variation in food availability and foraging costs. We found strong positive relationships between body condition and individual fitness. While female reproduction success probability increased linearly with autumn body-condition indices (BCIs), individual survival probability related nonlinearly to BCI, where maintaining body condition above "safe-zone thresholds" was key to survival. Thresholds were revealed and exacerbated by energetic risk factors. Survival of older individuals, for instance, was more contingent on BCI than that of young badgers, while high seasonality (poor foraging conditions) and excessive rainfall (thermoregulative stress) strengthened BCI-survival relationships. While consistently fatter badgers exhibited higher lifetime reproductive success, substantial body-condition heterogeneity remained after accounting for weather and individual factors, with 84% of individuals exhibiting highly variable BCI. Projected BCI changes through 2080 under severe climate change illustrate how the buffering effect of existing BCI-survival relationships enables this variability: even strong warming (as one-off events) produced < 5% survival probability reductions, with most individuals remaining above the safe-zone threshold. We thus demonstrate that life-history factors and individual tactical heterogeneity in body-condition are key to understanding population resilience under sustained environmental changes.

Keywords: *Body-condition index, climate change, human-induced rapid environmental change, individual heterogeneity, threshold effects, weather.*

1 Introduction

Few individuals fulfil their full potential lifespan in the wild (Simpson et al. 1995, Collins and Kays 2011), where mortality may arise due to accidents (Macdonald et al. 2010), predators (Arendt 2009, including humans: Collins and Kays 2011), competitors, or pathogens. Even without these factors, animals must avoid starvation by ensuring that their energy expenditure does not exceed intake (Anholt and Werner 1995). Increasingly variable and less predictable weather conditions due to anthropogenic climate change (Goodman et al. 2012), however, elevate the risk of unsustainable periods of food scarcity, straining the ability of animals to balance their energy budgets (Layton-Matthews et al. 2020).

An individual's risk of incurring a net negative energy balance varies with life-history factors, such as sex, reproductive status (e.g. lactating females; males with high circulating testosterone), age class (e.g. young or geriatric individuals may be more energetically "frail" than others, Zafon 2007), senescence and consequent terminal investments (Clutton-Brock 1984), social status (Heldstab et al. 2017), endocrine profiles (Williams 2008), immunological state (Norris and Evans 2000), gut microbiome (Lindsay et al. 2020), and underlying differences in metabolic rate (Johnstone et al. 2005). Therefore, a spectrum of individual energy allocation tactics often coexist within populations experiencing the same environmental conditions (Gangloff et al. 2018). Furthermore, spatio-temporal stochasticity in the environment drives unpredictable changes in food availability and energy requirements (Fietz et al. 2005, Harding et al. 2005) within seasonal patterns (Ims and Fuglei 2005), increasing the need for individuals to

maintain a “safety-net” body-fat reserve (Macdonald and Johnson 2015). The extent to which species and individuals can cache excess food (Smith and Reichman 1984) and/or store body-fat reserves (“fasting tolerance”; Lindstedt and Boyce 1985) is thus of considerable importance for resilience to rapid environmental change (Newton 2007).

Body-condition indices (BCIs, measuring body mass relative to skeletal size) are frequently used as surrogates of somatic fitness, or related traits (Aubry et al. 2013, Labocha et al. 2014). BCIs are easy to measure, but have limited relevance if not closely related to lipid stores (Peig and Green 2010), or if lipid stores correlate poorly with fitness (Wilder et al. 2016). Some individuals carry substantial body-fat stores, but still suffer nutritional deficiencies (Nie et al. 2015), impaired physiology (immunodeficiency, Ponton et al. 2013), and/or poor reproductive success (Batzli 1986). For temperate mammals in particular, white fat stores not only buffer food insecurity, but also reduce thermoregulatory costs (Heldmaier 1989, Hilderbrand et al. 2000, Humphries et al. 2003), and are essential to species engaging in hibernation/torpor (Ozgul et al. 2010). Nevertheless, especially among mammals (flight constrains somatic stores in birds: Lind et al. 2010), individuals with higher seasonal body-fat reserves typically exhibit a greater probability of reproducing and/or surviving (Milner et al. 2013, Monteith et al. 2013), strongly influencing population dynamics (Ronget et al. 2017). Nevertheless, the shape of the relationship between fat stores and fitness, and how this determines individual energetic context under different prevailing environmental and individual characteristics, remains largely unexplored (Harwood et al. 2000, Harding et al. 2005, Culina et al. 2019). Crucially, little is known of the diversity of capital storage phenotypes that wild populations exhibit under shifting conditions, and whether these reflect dynamic heterogeneity and shifting tactics to buffer environmental

stochasticity (Tuljapurkar et al. 2009b, Schindler et al. 2015) or fixed heterogeneity as a strict indicator of individual quality (Plard et al. 2018). The higher diversity of these tactics that a population can maintain without substantial fitness costs bears direct consequences for the population's resilience, especially under rapid environmental change (the "portfolio" concept, Schindler et al. 2015).

Here, we use the European badger (*Meles meles* L., hereafter "badger") as a model system, benefiting from 29 years of detailed demographic data. We investigate interactions between body condition, survival probability, and reproductive success in relation to prevailing weather conditions, with a focus on individual heterogeneity within "successful" tactics. Badgers provide a versatile model for examining fat storage: substantial inter-individual variation in body condition occurs within badger populations during all seasons, with concurrent behavioural variation (Noonan et al. 2014, 2018). Badgers live at high densities in southern England (Judge et al. 2017) and body-condition variation can be density dependent (Rogers et al. 1997a, Macdonald et al. 2002). Across much of their range, badgers undergo substantial seasonal weight gain (Virgós et al. 2011), accruing fat reserves in preparation for winter torpor (heavily reduced activity and depressed metabolism: Newman et al. 2011, McClune et al. 2015). Thus, individual body mass can more than halve/double intra-annually, from 6 kg in summer to 13 kg in late autumn. Badger autumnal fat deposition and consequent survival dynamics also depend on weather conditions (Macdonald et al. 2010, Byrne et al. 2015). This is particularly true in temperate northern regions like Britain and Ireland, where rainfall and mild temperatures encourage the surfacing of anecic earthworms (Johnson et al. 2001), a primary food source (particularly *Lumbricus terrestris*, Kruuk 1978, Rosalino et al. 2005, Silva et al. 2017). However,

badgers also opportunistically exploit seasonally super-abundant crops such as nut masts, cereals—particularly in dry summer months (Kruuk 1978)—and fruits (Rosalino et al. 2005).

Badgers exhibit substantial inter-individual variation in life-history mediated energetic constraints. Mortality is substantially age- and sex-sensitive, with higher mortality in young and geriatric badgers (Chapter 2) and female-biased survivorship with advancing age in high-density populations (Rogers et al. 1997b, Chapter 2). Males exhibit bimodal rates of juvenile sexual development, with larger male cubs attaining earlier puberty (Sugianto et al. 2019b). Further bimodality extends into maturity, with some males sustaining elevated testosterone titres into the summer at the expense of body condition (Buesching et al. 2009). In female badgers, low autumn body condition drives poor reproductive success following summers with adverse foraging conditions (Woodroffe and Macdonald 1995a). Furthermore, body condition determines small-scale differences in the timing of delayed implantation of developing blastocysts after onset of winter torpor (Woodroffe 1995, Carpenter et al. 2005), making autumnal fat deposition crucial to reproductive success (Cresswell et al. 1992, Delahay et al. 2006). Subsequently, the energetic costs of pregnancy and lactation affect female badger condition through the following spring and summer (Woodroffe and Macdonald 1995b). These various life-history considerations thus drive widely varying energy expenditure regimes and constraints within badger populations.

In this study, we examine how badger body condition (both BCI and fat score metrics) affects survival probability and reproductive success in relation to i) intrinsic sources of inter-individual energetic variation and ii) variation in extrinsic conditions that determine energy availability (annual/seasonal weather and population density). We test a series of predictions:

1) Foremost, we test whether body condition translates to a linear benefit to both survival and female reproduction probability (where male reproductive success ultimately relies almost entirely on female success).

2) Alternatively, we test whether there is some minimum body-condition threshold (*sensu* Tuomi et al. 1983, Huggett 2005) above which individuals can invest energy tactically to exploit equally viable alternative fitness tactics. This would result in survival probability and female reproduction probability correlating with body condition only below such a threshold.

3a) We predict that any thresholds might only become evident under energetically stressful conditions, either due to life-history (old age or post-reproductive females,) or to

3b) prevailing extrinsic determinants of energy availability and expenditure, with high densities and/or weather conditions that lead to adverse foraging/thermoregulatory effects resulting in a stronger effect of body condition on survival.

4) We next characterised the environmental (weather and density) and life-history drivers of individual BCI, and used these models to test the degree of inter-individual variability in the population; if, after accounting for the effects of weather and life-history energetic context, substantial body-condition variation remained in the population, it would imply that various BCI tactics can coexist and remain competitive in the population (i.e. variation from dynamic heterogeneity, Tuljapurkar et al. 2009b).

5) Conversely, if consistently higher- or lower- lifetime body-condition phenotypes produced differential survival and reproductive outcomes, this would support fixed variation in individual quality (i.e., fixed heterogeneity; van Noordwijk and de Jong 1986).

6) Finally, we use climate projections for our study site under a severe carbon emissions scenario from 2021-2040 and 2061-2080, and apply current relationships between weather, BCI, and survival, predicting that current BCI-survival relationships could affect life history-dependent (young vs. old; reproductive vs. non-reproductive) resilience to climate change.

2 Materials and methods

We tested the effects of weather and life-history (Fig. 1) as drivers of individual body condition, and, in turn, the effects of body condition on fitness outcomes (survival and female reproduction) using generalised additive mixed models (GAMMs, built using the *gamm4* package, Wood and Scheipl 2020).

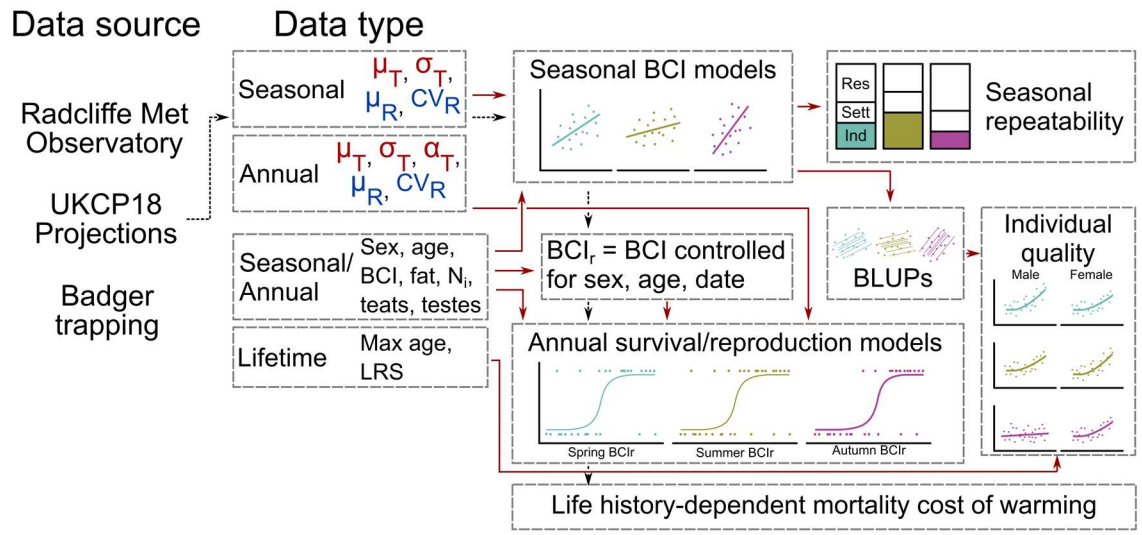


Figure 1. **Workflow and outputs.** Real data not shown. Projections workflow indicated through dashed black arrows.

2.1 Badger trapping and intrinsic data collection

We used data collected between 1990-2019 from a largely closed badger population (immigration/emigration rate = 3%: Macdonald and Newman 2002) in Wytham Woods; a 424-ha

mixed-woodland site in southern England (Oxfordshire, 51°46'N, 1°20'W). Each active sett (a shared burrow system used by groups averaging 5.6 individuals in Wytham, range 1-28) in the study area was trapped three-four times annually ("spring" = May-June; "summer" = July-September, primarily early September; "autumn" = October-November, primarily November; "winter" = January, excluded from models due to detection bias; Noonan et al. 2015) for two-three nights, using string-trigger cage-traps. Badgers were transferred to holding cages between 7.00 - 9.00 am, transported to a central field station and sedated them with 0.2 ml ketamine hydrochloride/kg body weight by intramuscular injection (Sun et al. 2015, Sugianto et al. 2019a). On first capture, each badger received a unique inguinal tattoo, typically as a cub or yearling; for individuals first caught as adults, we estimated age based on molar tooth wear, scaled 1-5 (Hancox 1988, detailed in Chapter 2 and supplements therein). Although we model age continuously, we also make particular reference to young badgers (choosing 2 year-olds as a reference point, around onset of sexual maturity) and older, geriatric badgers (choosing 9 year-olds for reference, which are largely post-reproductive; Sugianto et al. 2020) to contrast their energetic contexts.

On each capture, body length (tip of snout to base of sacrum, to nearest 5 mm) and body mass (to nearest 0.1 kg) were recorded.

We use two metrics of body-condition: (i) a direct subcutaneous fat score (1-5, only 1994-2019), assessed by palpating the belly-loin, with the badger laterally recumbent (after Speedy 1980), and (ii) a body condition index (BCI) estimated using a ratio-based approach for each capture: ln(body mass)/ln(body length) (Noonan et al. 2014, 2018). Because BCIs can be poor measures of fitness in some conditions (Peig and Green 2010, Wilder et al. 2016), we take

comprehensive steps to handle these shortcomings, which we detail in Appendix S1. We released badgers at their site of capture in the afternoon following processing. All badger captures were licensed under the Badger Act (1992) (currently Natural England license 2019-2020-4417) and all handling procedures carried out under Animals (Scientific Procedures) Act (1986) license (currently PPL 30/3379).

Although a pedigree exists for this population (Annavi et al. 2011, updated through 2015 pers. comm.), it was not used for scoring individuals' reproductive success because: a) substantial pre-emergence cub mortality (25-36%, Anderson and Trewhella 1985, Macdonald and Newman 2002) incurs pregnancy and lactation costs not detected by genotyping; and b) the pedigree omits a substantial number of parentage assignments due to confidence limits (see Chapter 2). Instead, we examined female mammary glands visually for lactation status (lactating, lactated, or not lactated) and recorded the length and diameter (in mm) of each teat (Dugdale et al. 2011a), then used these data to assign reproductive success (1 = reproductive; 0 = non-reproductive). Teat data from earlier in the same year (i.e., closer to lactation) are more reliable than from later captures; assigned reproductive status was therefore carried forward within a year. We thus assigned reproductive success to 592 females (1389 post-reproductive captures, 2420 non-reproductive captures); for further details, see Appendix S2. In males, paternity success depends on the success of the female they fertilised, and so we used degree of testes descent as a proxy for investment in reproductive capability; badgers are highly promiscuous (Dugdale et al. 2007, 2011b), but males ascend their testes outside of the breeding season according to age-related phenotypes (Buesching et al. 2009) and testes descent correlates with circulating testosterone, at least in spring (Sugianto et al. 2018). We scored male testes

seasonally (no carrying forward) as "descended," "intermediate," or "ascended" (Sugianto et al. 2018) for 540 individuals (Appendix S2).

We also computed lifetime reproductive metrics to test as correlates of consistently high- or low-BCI phenotypes. As teat data only indicate that a litter was born, not number of offspring (range 1-4 cubs, Dugdale et al. 2007), we used pedigree data to calculate: a) lifetime reproductive success (LRS); and b) age at first successful reproduction (α) (Chapter 2). We defined LRS as the total number of offspring assigned to an individual by pedigree, limited to cohorts up until 2007 (which could have reached age 8, realizing 80.6% of lifetime reproduction [Dugdale et al. 2011], by pedigree end in 2015). α denotes the age at which a female was first assigned offspring by the pedigree, or a males' age in the year prior to being assigned a cub (his "year of first investment"), due to delayed implantation in badgers (Yamaguchi et al. 2006); α was estimated for all individuals that were assigned at least one cub by the pedigree.

2.2 Weather covariates

We calculated mean and variance of weather, as both affect wild populations (Campbell et al. 2012, including badgers, Nouvellet et al. 2013): a) mean temperature (μ_T), b) mean rainfall (μ_R), c) annual temperature seasonality (α_T), the amplitude of a sinusoidal curve constructed for a year's temperature, d) temperature variability (σ_T), calculated as the squared sum of deviations from the year's sinusoidal temperature curve, and e) rainfall variability (CV_R), calculated as the coefficient of variation (SD/mean). We computed these statistics annually (Mar 1-Feb 28/29) and seasonally (spring: Mar 1-May 31; summer: Jun 1-Aug 31; autumn: Sep 1 - Nov 30; winter: Dec 1 - Feb 28/29; α_T only calculated annually). To capture the period of inferred lowest earthworm food availability in a year, we computed the same statistics for the driest 30-day and 90-day

period between May 1 and Aug 31. Unless otherwise specified, "weather" hereafter refers to all four seasonal (μ_T, μ_R, σ_T, and CV_R) or five annual (adding α_T) metrics. Weather data were provided by the Radcliffe Meteorological Station (https://www.geog.ox.ac.uk/research/climate/rms/), 6km from the field site.

2.3 Population Density

We calculated total population density (N_i) annually, using a modified minimum number alive method, incorporating variable trapping efficiency (Chapter 2), as an indicator of food competition in the study area. Because this method is only robust to within 3 years of the end of a trapping study (Chapter 2), we limited all density-dependent analyses to 1990-2016.

2.4 Modelling survival as a function of body condition

We constructed all models in R, version 3.5.3 (R Core Team 2019), and make full code available in the Wytham Woods Badger Project Dataverse (https://dataverse.harvard.edu/dataverse/wytham-badgers). We used GAMMs to model individual survival to the next year (binomial, 1 = captured again, 0 = never captured again; i.e. assuming worst-case detection probabilities) based on BCI, life-history characteristics, and extrinsic (weather and density) constraints in each season (all continuous covariates standardised to mean = 0 and SD = 1 using the *standardize* package, Eager 2017). To detect a "true" signal of relative BCI on survival, beyond that caused by age-, sex-, or calendar date-related changes in BCI, we used BCI_r—residuals from a GAM model of BCI in each season controlling for these covariates.

All survival models included: a) a spline for age (control); b) population density; c) annual weather conditions; d) a spline for BCI_r; e) female reproductive success in the preceding

spring; f) seasonal male testes descent (contrasting only most and least descended categories); g) two-way (linear) interactions between BCI_r and all other covariates, to test the contexts under which the BCI_r-survival relationship changes; and h) a random intercept for sett. All models also included different age splines for the sexes. We tested sex, female reproductive success, and degree of testes descent as a single factor (as each was mutually exclusive), and tested differences between the factor levels using post-hoc Tukey tests (*emmeans* package, Lenth 2020). Age-specific effects of reproductive investment could not be estimated, as survival contrasts between testes descent categories at older ages were few, precluding separate age spline computation. We report all one-way terms in the main text; however, we exclude non-significant interaction terms for brevity (reported in Appendix S3).

We used a nearly identical procedure to model year-to-year survival as a function of fat score in each season. However, because fat score had to be modelled as a factor, we did not include two-way interactions with other covariates to avoid over-parameterising models. Moreover, as only 8 springtime captures had fat-score = 5, we excluded this level from the spring fat model.

2.5 Modelling female reproduction as a function of body condition

We modelled springtime female reproductive success logistically as a function of BCI_r in the previous autumn. We performed modelling as for survival, except that instead of annual weather metrics this model incorporated weather in the intervening winter and spring. These weather metrics were highly collinear and were thus modelled as 4 principal components that explained 84% of their variance (loadings in Appendix S4). We only considered BCI_r interactions with N_i and age, as other interactions were less biologically plausible. However, we

included separate age splines for females that had not reproduced the year prior, to test whether terminal investment caused an uptick of reproductive investment at older ages. We also constructed a model predicting spring reproductive success as a function of fat score, without interactions (again, reducing over-parameterisation).

2.6 Modelling drivers of seasonal BCI

To determine drivers of seasonal BCI patterns—and their variation—we built comprehensive models of BCI for each season using GAMMs. We modelled seasonal BCI (spring n = 2,073 captures, 751 individuals; summer n = 2,295 captures, 777 individuals; autumn n = 1,498 captures, 584 individuals) as a function of a) sex, b) a spline for age (control); c) a spline for calendar date (control); d) N_i; e) seasonal weather conditions (specified below); f) female reproductive success in that year; g) male testes descent (all levels); h) two-way interactions between energetically stressful life-history markers (age and female reproductive success) and extrinsic covariates (weather, N_i); and i) two-way interactions between reproductive success/descended testes and age (to test for terminal investment effects). Seasonal weather comprised: spring (quadratic effects for μ_T and μ_R based on visual inspection) and preceding winter metrics for the spring BCI model; metrics for the driest 30-day summer period for the summer BCI model (see Appendix S4); and metrics for the driest 30-day summer period and the entirety of autumn (quadratic effect of CV_R) for the autumn BCI model. As for survival models, see Appendix S3 for full reporting of interaction effects. We also compared additional model variants that incorporated variance as a function (linear, exponential, or power) of N_i against the homogeneous variance model using Akaike's Information Criterion (AIC, Burnham and Anderson 2002). If the model with the lowest AIC had exponential or power-dependent variance

(homogeneous variance was nested), we tested the fit improvement from heterogeneous variance using a likelihood ratio test.

All BCI models included random intercepts for individual BCI, nested within sett. We verified that the capture distributions in our data (mean 5.9 captures per individual, 16% only captured once) were appropriate for accurate random effect determination after Zuur et al. (2014), detailed in Appendix S5.

2.7 Determining individual BCI variation/consistency

We used each final BCI model to calculate life-long seasonal repeatability as the intra-class correlation coefficient (ICC: Nakagawa and Schielzeth 2010) of individual random effects, relative to total variance:

$$ICC = \frac{var(Individual)}{var(Individual + Sett + Residual)} \quad (1)$$

As density-dependent variance seemed to strongly skew the magnitude of residual variance, we estimated ICC using density-independent variance. We bootstrapped GAMMs parametrically (n = 1,000) to compute 95% confidence intervals for repeatability estimates.

To further test for the existence of consistent body condition phenotypes, we extracted individual residuals from the three seasonal BCI models, averaged lifetime ranked percentile positions for individuals (μ_{Perc}), and examined their distribution. We then used best linear unbiased predictors (BLUPs; individual random intercept estimates) from seasonal models as a measure of individuals' lifetime BCI profiles, and examined their relationship with realised lifespan and LRS separately for males and females. This approach has received criticism because it ignores error in BLUP estimates (Houslay and Wilson 2017). In response, we adopted a novel

parametric bootstrapping approach, which produced semi-Bayesian "posterior-like" distributions for each BLUP to incorporate estimation errors into the analysis. For more details on μ_{Perc} estimation and BLUP modelling, see Appendix S6.

2.8 Climate projections

We used climate projections for our study site to examine potential effects of changing environmental conditions on life history-specific survival rates in the population. We acknowledge that this approach does not account for potential further behavioural and physiological adaptation to sustained change; these projections aim simply to illustrate within-population differences in buffering capacity according to current constraints. Similarly, we chose the IPCC's Representative Concentration Pathway (RCP) 8.5 (a severe emissions scenario) to subject these existing relationships to the worst-case scenario, rather than to make detailed predictions. The weather data used comprise 12 projections of daily rainfall and temperature, differing due to climate unpredictability and uncertainty (UKCP18, 2.2 km projections for RCP 8.5 from 2021-2040 and 2061-2080, avg. for 5 km centred at OS 447500, 207500, Kendon et al. 2019).

We selected two arbitrary age points (ages 2 and 9) to contrast young and geriatric badgers in summer and autumn (male, descended testes in summer, ascended in autumn) and reproductive and non-reproductive females in autumn (using solely age 4.5, the population mean, for reproductive status contrasts), as these groups showed diverging effects of summer temperature on BCI (see Section 3.3). We thus computed μ_{T} for the driest 30 days in each summer for each climate projection, and predicted average BCI using our seasonal BCI models for these subgroups (other covariates set to global mean). As we were interested in studying

survival of marginal individuals, we then generated Gaussian distributions of 1,000 individual BCI scores with standard deviation equal to the standard deviation of the individual random effect in either the summer or autumn BCI model, correspondingly. We predicted survival probability for these BCI scores using our survival models. For each of the 12 projections, we performed quantile regression (*quantreg* package, Koenker 2018) of the lowest quintile of survival probabilities from 1990-2080 to investigate the reduction in survival probability associated with BCI changes from increasing summer temperatures for each population sub-group.

3 Results

3.1 Linear effects of body condition on survival and female reproduction

Higher body condition (both BCI and fat score) had a positive effect on both individual survival probability and female reproductive success (Fig. 2). However, this survival effect was not consistent across all seasons, ages, or BCI ranges, and was rarely linear (see section 3.2 below). Notably, spring and summer BCI_r had no significant unilateral effect on survival to the next year, with effects instead contingent on interactions with other energetic constraints (in keeping with Predictions 3a-b, detailed in section 3.2; Fig. 2a-c). Autumn BCI_r exhibited a linear positive relationship with female reproductive success in the following spring, (Fig. 2g), while fat score acted non-linearly; the only significant contrast was between scores 2 and 4 (Tukey *post hoc* $p = 0.019$, Fig. 2h), with no further reduction at fat score 1, likely due to low autumn sample size for this score (n = 16).

3.2 Threshold Effects

There was strong support for threshold effects (Prediction 2) from models predicting survival as a function of autumn BCI_r, fat scores in summer and autumn, and from the model predicting female reproductive probability from autumn fat scores. Below these thresholds, higher BCI_r/fat scores were associated with higher survival and female reproductive success probability, but body condition had little effect above the threshold (Fig. 2d-f, h).

As significant effects differed little between BCI_r and fat score models, and because BCI_r models covered a wider year range, coefficients from BCI_r-based models are reported in Table 1, with fat score coefficients appended (for full fat score models coefficients, see Appendix S3).

3.2.1 Effects of life history-dependent energetic context on BCI thresholds

Reproductive status and age, as life-history risk factors, had substantial effects on the shape of the BCI_r-survival relationship (Prediction 3a). Age significantly and substantially enhanced the effect of spring (Fig. 2a) and summer (Fig. 2c) BCI_r on the probability of surviving to the next year, where spring ($p = 0.58$, F-statistic = 0.30) and summer ($p = 0.15$, $F = 2.97$) BCI_r did not have any unilaterally significant effects. Below a certain threshold, autumn BCI_r affected survival probability across all badgers ($p = 0.003$, $F = 4.65$; Fig 3e); above that threshold only older badgers benefitted from higher BCI_r, though the autumnal age-BCI_r interaction term was not quite significant (Table 1).

Survival probability for females that had reproduced was not significantly different from that of non-reproductive females (Tukey *post-hoc p*-values: spring = 0.79, summer = 0.51, autumn = 0.30). Similarly, degree of testes descent did not affect survival probability in males (all $p > 0.05$). Moreover, in an unexpected reversal of expectations, females that had reproduced

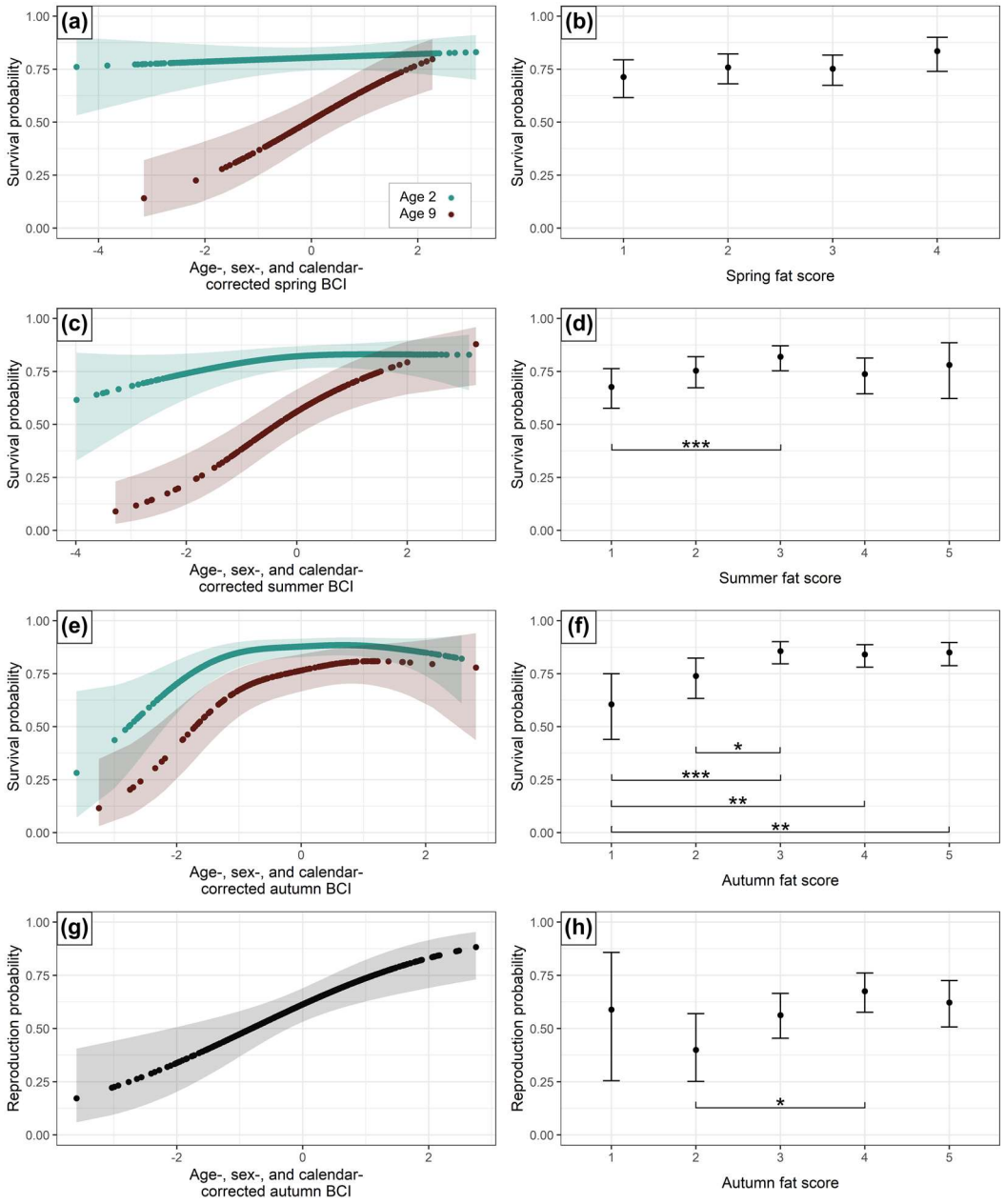


Figure 2. **Effect of body condition on individual fitness.** Relationship between seasonal BCI_r (a, c, e, g) or fat scores (b, d, f, h) and survival (a-f) or reproduction (g-h), with 95% confidence intervals. BCI_r-survival relationship is shown for young (age 2, blue) and old

(age 9, red) badgers to demonstrate the changing effects of body condition according to intrinsic factors; to illustrate data coverage, points show the (scaled) BCI_r values of individuals aged 1-8 (on the Age 2 line) or 9+ (on the Age 9 line). Standard asterisk notation shown for Tukey *post-hoc* comparison of fat score groups ($p < 0.001$; $0.001 \leq p < 0.01$; $0.01 \leq p < 0.05$).

showed no relationship between spring or summer BCI_r and survival, while non-reproductive females showed a strong linear effect of increasing BCI_r in these seasons, with the highest-BCI_r providing a 39% (spring, SE = 23-54%) or 55% (summer, SE = 38-68%) survival benefit over the lowest BCI_r.

Notably, females that had reproduced in the previous year were significantly and substantially more likely to reproduce again in the next (avg. 17%, SE = 7-26%). Moreover,

Table 1. **Coefficients from survival and reproduction modelling.** Interaction terms not significant in any model are not shown. Coefficients for models built from fat scores were not substantially different from those built from BCI; therefore, BCI model coefficients are reported here, and the effect sizes of fat scores are included at the bottom of the table (reference level = 4 for spring fat survival model; 5 for other fat models). Full set of coefficients available in Appendix S3. Significance levels shown using standard asterisk notation: ***$p < 0.001$; **$0.001 \leq p < 0.01$; *$0.01 \leq p < 0.05$.

	Spring		Summer		Autumn		Repr.	
	Coef	SE	Coef	SE	Coef	SE	Coef	SE
Female	-0.16	0.532	0.11	0.311	0.03	0.188		
Rep. female	0.048	0.545	0.393	0.331	0.495*	0.245	0.65***	0.105
BCIr:Rep. female	-0.187*	0.091	-0.206*	0.083	-0.064	0.1	0.178	0.109
Int. testes	-0.044	0.628	0.376	0.37	-0.304	0.28		

		Spring		Summer		Autumn		Repr.	
		Coef	SE	Coef	SE	Coef	SE	Coef	SE
	Desc. testes	-0.658	0.532	-0.167	0.31	-0.572	0.346		
	BCIr:Age	0.221***	0.062	0.215***	0.06	0.09	0.07	0.018	0.105
	N_i	-0.077	0.063	-0.137*	0.065	-0.055	0.087	0.004	0.103
Annual	μ_T	-0.052	0.066	-0.067	0.067	-0.111	0.094		
	μ_R	-0.096	0.074	-0.008	0.076	-0.184	0.101		
	α_T	0.107	0.086	0.028	0.085	0.087	0.111		
	σ_T	-0.117	0.087	0.067	0.084	-0.116	0.111		
	CV_R	0.057	0.068	-0.066	0.068	0.042	0.093		
	BCIr:μ_R	0.126	0.076	-0.017	0.08	0.253**	0.094		
	BCIr: α_T	-0.082	0.092	0.19*	0.086	0.065	0.101		
	BCIr:CV_R	-0.071	0.078	-0.159*	0.07	-0.015	0.098		
Winter-Spring	PC1							0.013	0.055
	PC2							0.104	0.077
	PC3							0.207*	0.086
	PC4							-0.131	0.108
	Fat 1	-0.286*	0.125	-0.395**	0.138	-0.904***	0.247	0.071	0.578
	Fat 2	-0.052	0.104	-0.018	0.12	-0.289	0.172	-0.694*	0.305
	Fat 3	-0.088	0.107	0.378**	0.122	0.453**	0.146	-0.036	0.215
	Fat 4			-0.101	0.142	0.334*	0.14	0.446*	0.216

while females that had not reproduced in the previous year exhibited a decreasing likelihood of reproducing with age (providing no evidence of terminal investment), females that had reproduced showed no such age-related trend ($p = 0.35$), so that by age 9, a female that had reproduced the previous year was 31% more likely to reproduce again than a non-parous female (SE = 18-42%).

3.2.2 Effects of environmental constraints on BCI thresholds

As predicted, annual weather influenced the effect of BCI_r on survival (Prediction 3b). Models indicated a stronger positive effect of higher summer BCI_r on survival probability in

years with higher seasonality (α_T); a positive effect of higher autumn BCI_r was particularly evident in rainy years (μ_R), which, conversely, were particularly detrimental to survival probability for individuals with low autumnal BCI_r, (Fig. 4d); higher summer BCI_r was positively correlated with survival in years with low rainfall variability (CV_R), but not in years with highly variable rainfall (Table 1). Density-dependence was only evident in summer, with the average badger (using male with descended testes as reference level) under average weather conditions having a 8.4% (SE = 1.1-15.7%) higher risk of mortality at $N_i = 320$ than at $N_i = 200$ (N_i range 160-328).

While neither of the first two principal components of weather had a significant effect on female reproductive success, the third principal component of winter and spring weather, representing years with high winter rainfall and low winter temperature variability, had a positive effect (Table 1).

3.3 Drivers of individual BCI

Badgers exhibited substantial BCI variation both seasonally and over the course of an individual's lifetime, with BCI declining with age (Fig. 3). Average seasonal BCI (1990-2019) was very similar between spring and summer (nadir in July), with subsequent fat deposition resulting in substantially higher autumn BCI. Males had higher BCI than females in both spring and summer, but not in autumn. BCI peaked by the latest date trapped, November 28 (Fig. 3).

3.3.1 Weather drivers of seasonal BCI

Weather had substantial impacts on seasonal BCI values (Table 2), with σ_T having a negative effect on BCI, and μ_T, μ_R, and CV_R driving season-specific effects largely according to

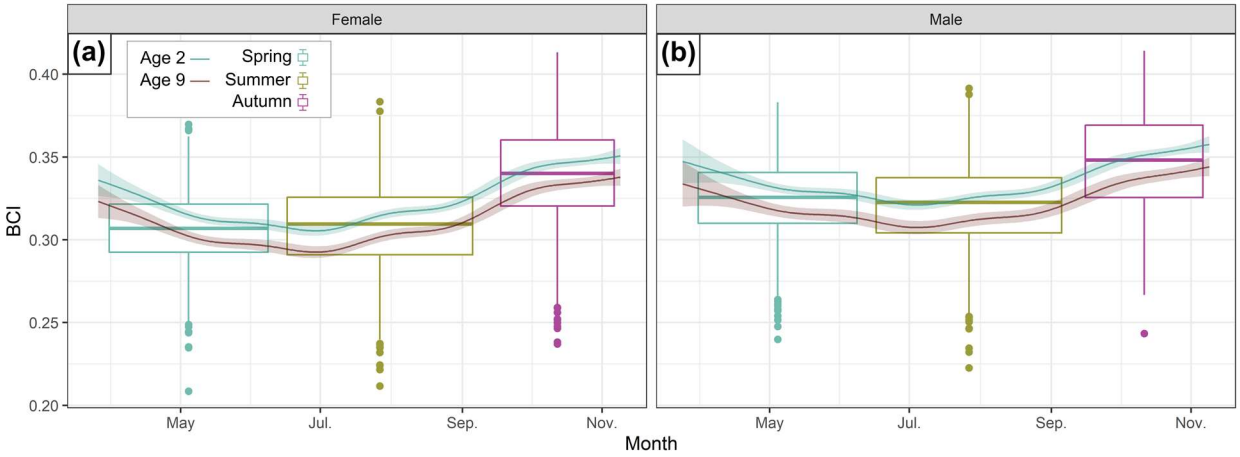


Figure 3: Variation in body condition. Boxplots show variation in BCI by season (1990-2019); lines show population averages according to a best-fit GAM regression at age 2 (blue) or 9 (red). Boxplot width corresponds to the period considered in each season. Model controls for individual *via* random effect and permits different splines by sex for age and day of year.

season-specific energetic considerations. Warmer and wetter springs (associated with higher earthworm availability) were associated with higher spring BCI (although effects were quadratic, with no further BCI gains above 2 mm rain/day and no costs below average temperatures of 9.5 °C). Similarly, higher autumnal μ_T and μ_R were associated with higher autumn BCI, as were autumns with consistent rainfall (low CV_R; although this effect was quadratic, with high BCI with either particularly variable or consistent rainfall). Conversely, summer BCI was lower in years when the driest 30-day summer period (lowest earthworm availability) was warmer than average, or consistently dry (low CV_R). However, and counter-intuitively, when this same 30-day period was wetter than average, badgers exhibited lower autumn BCI.

3.3.2 Density-dependent seasonal BCI effects

N_i did not influence seasonal BCI in either direction; however, it did affect BCI through life-history interactions. In older individuals, higher N_i values were associated with lower mean summer BCI, but higher autumn BCI. Additionally, summer BCI variance was lower at higher densities (exponential variance term, $L = 23.61$, $df = 1$, $p < 0.001$) while autumn BCI variance was higher at high densities (linear increase, ΔAIC = 2.9, non-nested so no LRT score).

3.3.3 Life-history and weather interactions in driving seasonal BCI

Life history and its interactions with seasonal weather had substantial effects on BCI. Females that had reproduced in a given year had lower BCI on average than non-reproductive females (Tukey *post-hoc* spring and summer $p < 0.001$), although by autumn this difference was marginal and not significant (autumn $p = 0.086$). Males with descended testes had significantly lower BCI than those with ascended testes in all seasons (Tukey *post-hoc* spring $p < 0.001$, summer $p = 0.001$, autumn $p = 0.034$), and lower BCI than those with intermediate testes descent in spring ($p = 0.003$). Moreover, females that had reproduced that year had even lower BCI than expected in both summer and autumn following warm summers, although winter σ_T did not negatively affect reproductive females' spring BCI as it did for other badgers. However, contrary to expectations of terminal investment, in males, no significant interaction was detected between testes descent and age (all $p > 0.1$, see Table S3.4), and older reproductive females actually had higher spring BCI than expected for their age. Older badgers had particularly low autumnal BCI

Table 2. **Coefficients from condition modelling.** Non-significant interaction terms are not shown; full set of coefficients available in Appendix S3. Significance levels shown using standard asterisk notation: ***$p < 0.001$; **$0.001 \leq p < 0.01$; *$0.01 \leq p < 0.05$.

		Spring model		Summer model		Autumn model	
		Coef	SE	Coef	SE	Coef	SE
	Female	-0.976***	0.12	-0.593***	0.096	-0.181**	0.064
	Rep. female	-1.692***	0.124	-1.024***	0.103	-0.358***	0.079
	Int. testes	-0.218	0.135	-0.205*	0.101	-0.177*	0.083
	Desc. testes	-0.531***	0.113	-0.341***	0.09	-0.293**	0.102
	N_i	0.019	0.024	0.03	0.03	-0.01	0.037
	N_i:Age	-0.001	0.018	-0.044*	0.021	0.051*	0.025
	Rep. female:Age	0.092***	0.023	0.021	0.027	0.014	0.032
Previous winter	μ_T	0.048	0.029				
	μ_R	-0.038	0.024				
	σ_T	-0.054*	0.028				
	CV_R	-0.04	0.023				
	σ_T:Rep. female	0.068**	0.023				
	μ_R:Age	-0.046*	0.02				
Spring	μ_T	0.059*	0.029				
	μ_T^2	0.089***	0.025				
	μ_R	0.054	0.035				
	μ_R^2	-0.068**	0.023				
	σ_T	-0.03	0.025				
	CV_R	-0.054	0.032				
Summer	μ_T			-0.135***	0.028	-0.047	0.039
	μ_R			-0.02	0.033	-0.161**	0.052
	σ_T			-0.071**	0.027	-0.15***	0.041
	CV_R			0.104**	0.035	0.188***	0.045
	μ_T:Rep. female			-0.08**	0.028	-0.072*	0.035
	μ_T:Age			0.045	0.023	-0.074**	0.026
Autumn	μ_T					0.061*	0.03
	μ_R					0.149***	0.037
	σ_T					-0.035	0.04
	CV_R					-0.042	0.031
	CV_R^2					0.105***	0.027
	μ_R:Age					-0.068**	0.024

following hot summers (Fig. 4b) and derived less autumnal BCI benefit from wet autumns than did young badgers (Fig. 4c)—similarly, wetter-than-average winters were associated with lower spring BCI in older individuals. However, older individuals did not exhibit the negative, marginally significant (p = 0.056, Fig. 4a) relationship seen in younger badgers between hot summers and summer BCI.

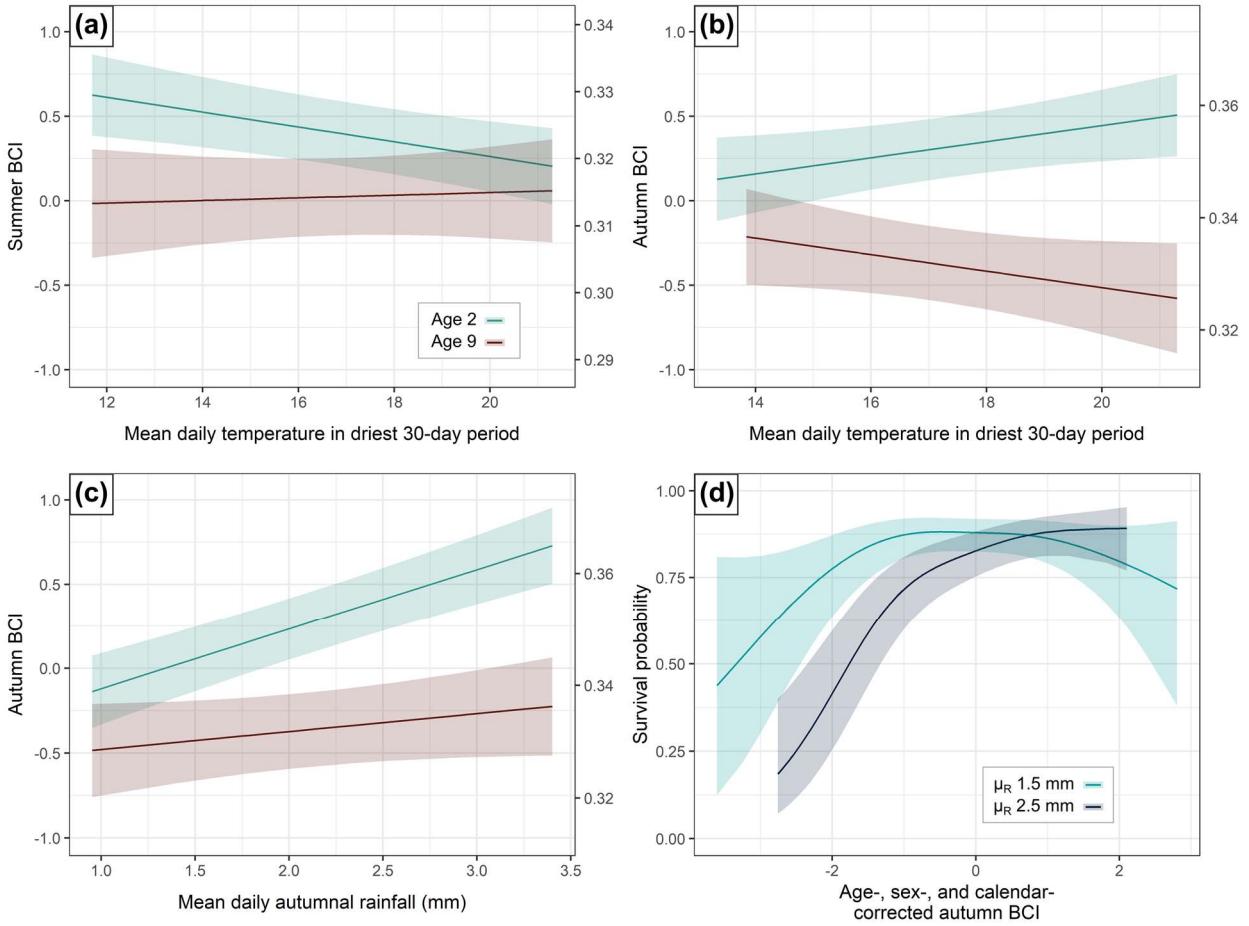


Figure 4. **Extrinsic-intrinsic interaction relationships.** Effect of μ_T during the driest 30-day period in a given summer on a) summer BCI and b) autumn BCI for badgers of age 2 (young) and 9 (geriatric). Age-specific effects of autumn μ_R on BCI is shown in c), while d) illustrates the different effects of BCI_r on survival in relatively dry or relatively wet autumns. BCI for (a-c) is provided in both SDs (left axis) and real values (right axis).

3.4 Lifetime individual BCI variability

Despite the strong signals of life-history context and environmental conditions determined by seasonal BCI modelling, these drivers cumulatively described less than half of the variance in BCI in all seasons (R^2 in spring = 0.35, summer = 0.18, autumn = 0.22). Individual BCI repeatability was intermediate, with the highest repeatability in spring (ICC = 0.32, 95% CI = 0.26-0.38) and somewhat lower in summer (ICC = 0.22, CI = 0.18-0.27) and autumn (ICC = 0.23, CI = 0.17-0.29). In all seasons, individual random effects significantly improved model fit (*L* spring = 171, summer = 166, autumn = 95; all $p < 0.001$).

Among frequently trapped individuals (10+ captures, see Appendix S6), after accounting for weather and life-history, we detected three BCI "types": I) consistently low-condition individuals (11.2%); II) individuals with more variable BCI, representing the majority of frequently trapped individuals (84.3%); and III) consistently high-condition individuals, the rarest type (only 4.6% of individuals, Fig. 5). These percentile patterns reflect those expected if each individual exhibited roughly the same BCI variability around different, fixed long-term means—simulations showed that Gaussian random samplings of BCI with variance derived from our seasonal BCI models produced very similar results (Appendix S7).

3.5 Lifetime effects of BCI phenotype

Among all individuals, our semi-Bayesian BLUP modelling procedure showed no effect of consistent BCI profile in any season on realised lifespan (Fig. S6.1, Appendix S6). Although only the relationship between autumn random intercepts and female LRS produced a 95% confidence interval that did not include 0 (Fig. 6f), LRS exhibited a clear—and sex- and season-specific—association with individual BLUP values (Fig. 6; see Appendix S6 for coefficients and

confidence intervals). LRS was more tightly linked to autumnal BCI profiles in females (with 0.48 lifetime offspring for the lowest BCI profile and 3.44 for the highest, 95% CIs 0.14-1.46 and 1.77-7.19, respectively) and to spring BCI profiles in males (0.71-2.36 lifetime offspring, 95% CIs 0.26-1.92 and 1.28-4.27), with females showing virtually no relationship between spring BCI profile and LRS (Fig. 6b).

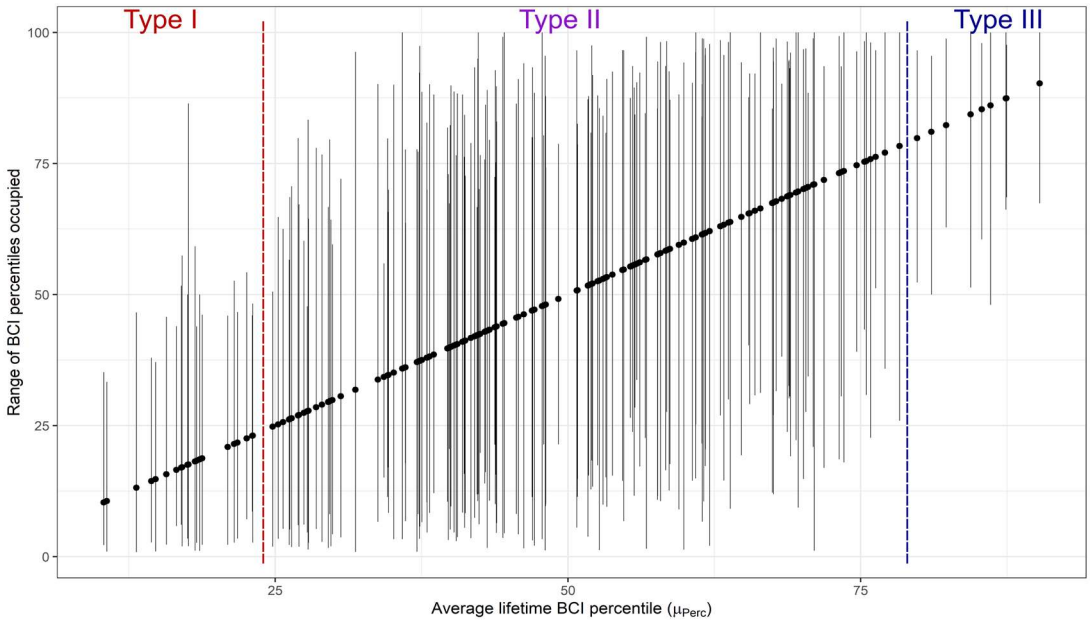


Figure 5. **Range of BCI percentiles occupied by average lifetime BCI percentile.** Each line represents the full range of percentiles occupied by an individual, with dots located at their average lifetime percentile. Individuals only included with 10+ captures in their lifetime.

3.6 Projected effects of climate change on life history-specific survival rates

Relative to 1990-2020, a mean increase of 6.47 °C is projected for the study site for the driest 30 summer days by 2075-2080. Corresponding BCI changes would predict only small-to-moderate changes in survival probability in even the lowest quintile of population subgroups—

changes were even smaller in the rest of predictions (Fig. 7 and all subsequent numbers refer to this lowest quintile). In particular, threshold BCI-survival relationships (Fig. 2) minimised the

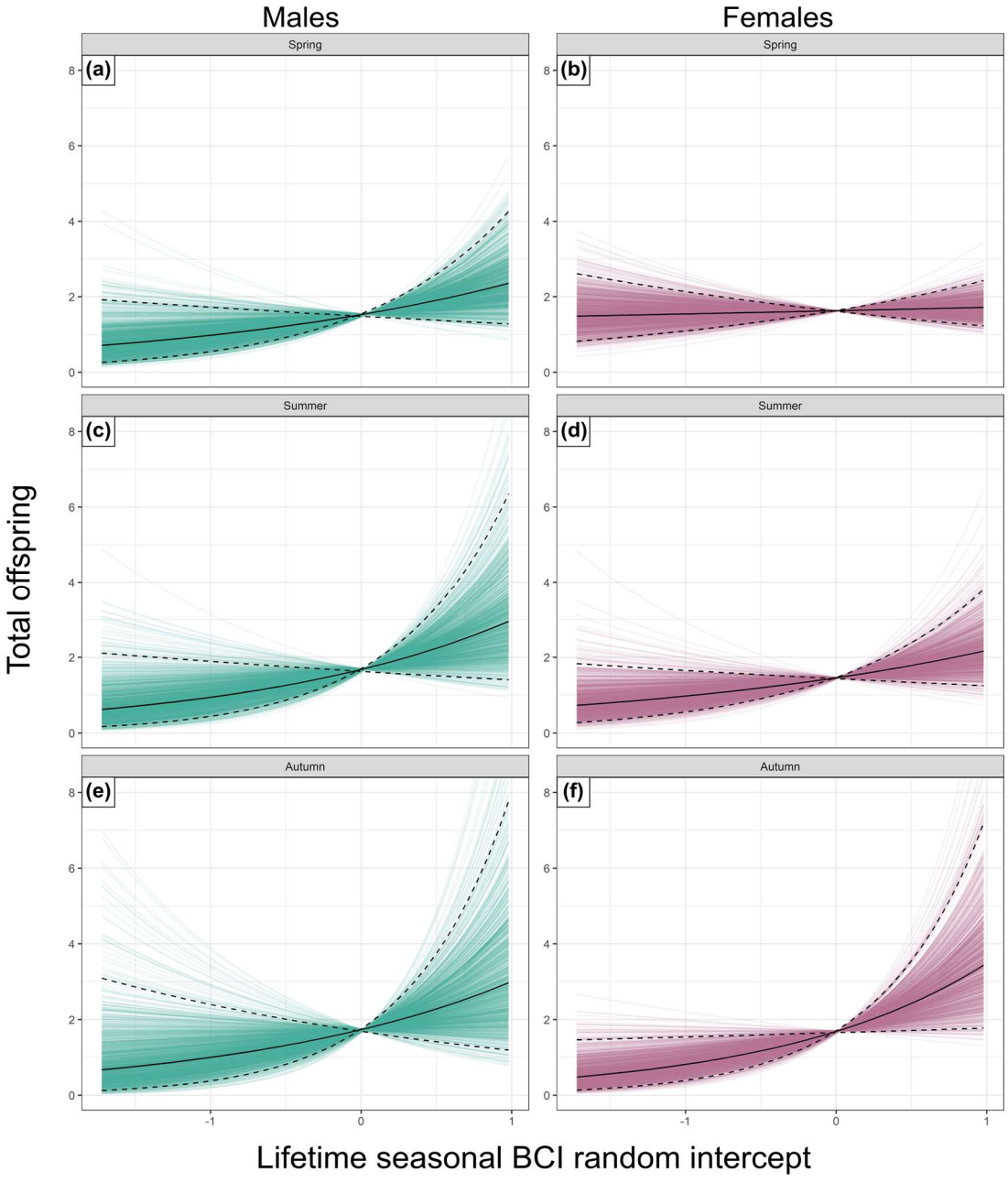


Figure 6. **Effects of BLUPs on lifetime reproductive success.** Each line represents one iteration (n = 1,000) of residual randomisation. Mean slope provided by solid black line; 95% confidence intervals provided by the dotted lines.

average changes in survival probability. For instance, although geriatric badgers showed a narrow BCI safe zone in summer (Fig. 2c), the positive relationship between summer temperatures and their BCI resulted in an average increase of just 0.69% survival probability from 2020-2080 (projection range 0.19-1.07%), while their broader BCI safe zone in autumn (Fig. 2e) meant autumnal BCI losses only carried on average 3.32% decreased survival probability (0.73-5.58%). Nevertheless, geriatric badgers were less well-buffered than youngsters, for which projected summertime BCI losses corresponded to a miniscule 0.20% survival probability decrease (0.03-0.37%, Fig. 7). Concurrently, autumnal BCI costs from increasingly hot summers brought reproductive female survival probability (which was sensitive to summer conditions, unlike that of non-reproductive females) only marginally closer to that of other females, corresponding to a 0.41% mean decrease in survival probability (0.05-0.77%).

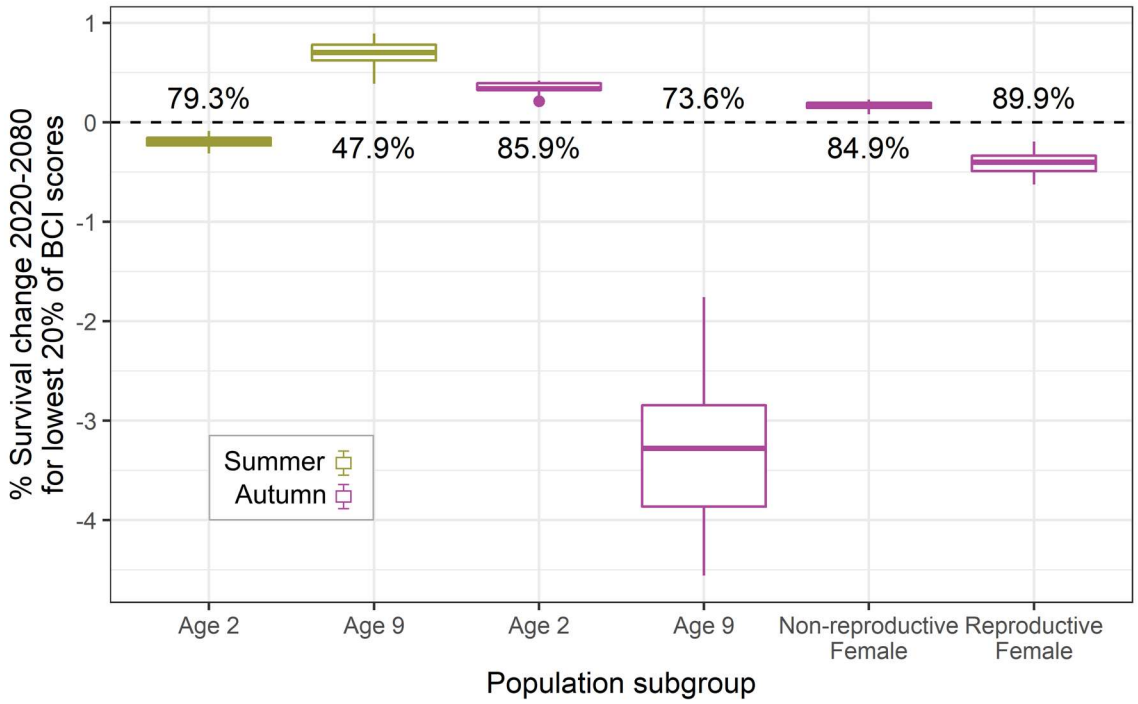


Figure 7. **Survival effects associated with climate change-driven BCI changes.** 2020-2080 change in survival probability (0-100%) resulting from the life-history dependent BCI changes of 12 projections of climate change under a severe emissions scenario (RCP 8.5). Average 1990-2020 survival for lowest quintile of each life-history category provided as a percentage, for context.

4 Discussion

In partial accord with our main prediction, we found that body condition had strong effects on fitness, mediating survival and female reproductive success probabilities. However, in support of Prediction 2, these effects largely emerged below what we term "safe-zone thresholds", which were related to and shaped by both life-history energetic context (Prediction 3a) and prevailing environmental conditions (weather and density, Prediction 3b), as well as their interaction. Broadly, fat indices produced stronger threshold effects on survival and reproduction

than BCI_r did on its own (Fig. 2), likely due to the ability to model interactions with energetic context covariates for the latter metric. Although we found strong effects of weather and life-history stage on seasonal BCI, these described a relatively small percentage of BCI variation, supporting our fourth prediction of substantial heterogeneity in energy expenditure/storage tactics above the safe zone threshold. Nevertheless, we found simultaneous support for Prediction 5, as those few individuals that maintained high BCI throughout their lives exhibited greater lifetime reproductive success, displaying a degree of higher individual quality. Finally, as we predicted, the threshold-based relationship between BCI and survival appears capable of buffering individuals within the safe-zone from even the worst forecasted weather conditions, making attaining the threshold BCI crucial for individual and population resilience.

4.1 Weather and density drivers of energetic safe-zone thresholds

In wild populations, weather conditions often determine both the availability of food (Linton and Macdonald 2018, Cecere et al. 2020) and the rate at which individuals expend energy (e.g. through heat-loss, Harding et al. 2005, or elevated foraging costs, O'Mara et al. 2019). While energy intake and storage is crucial for enduring periods of food scarcity, especially for marginal individuals, it is also paramount to rationalise efficient energy expenditure behaviours (Parker et al. 2009, Wilson et al. 2012) and avoiding excessive heat loss (Harding et al. 2005). In accord with these considerations, badgers exhibited lower BCI following poor foraging conditions, such as dry, cold springs and autumns, or hot summers, but also a stronger link between autumn body condition and survival during rainy years. In badgers, thinner individuals have been shown to engage in compensatory autumn foraging, even during poor conditions (Noonan et al. 2014, 2018). Nevertheless, while higher rainfall can increase

earthworm abundance, beyond a certain threshold, it can cause hypothermia from fur soaking (Webb and King 1984) and reduces badger cub survival (Nouvellet et al. 2013). This thermoregulatory trade-off was apparent from the quadratic relationship between spring rainfall and BCI, and likely explains why low-BCI badgers may suffer worse survival costs than otherwise expected during rainy years. We also found a stronger effect of summer BCI on survival probability—a narrowing of the energetic safe-zone—in years with higher seasonality (more extreme summers and winters). As summer temperatures are projected to increase by a median of 3.1 °C in the U.K. by 2100 (Murphy et al. 2018), this result points a constriction of the tactical energetic space that phenotypes can exploit under accelerating warming scenarios.

4.2 Interactions of environmental energetic context with life-history frailty

Senescent declines in body condition are widespread in wild mammals (Nussey et al. 2011, Paterson et al. 2016, Campbell et al. 2017), including badgers (Dugdale et al. 2011c, Sugianto et al. 2020)—as a consequence, mortality among badgers aged 8+ contributes substantially to inter-annual population dynamics (e.g., Chapter 2). Not only did older individuals in this study exhibit consistently lower survival probabilities (throughout the year, not just in the energetically-marginal winter months), but their BCIs were even lower in higher population-density years, when these older individuals were pushed to the margins. This is consistent with other group-living animals, where elevated geriatric sensitivity to BCI effects may arise through reduced competitiveness (Sharp and Clutton-Brock 2011) or exclusion from food acquisition (Jordan et al. 1967). While in some species, such marginalisation might trigger terminal investment among lower-quality individuals (Clutton-Brock 1984), we found no such

effect, with a subset of older females retaining high likelihood of reproductive success (see also Sugianto et al. 2020).

Age brings both experience in food acquisition (Atkinson and Ramsay 1995, Chang and Wiebe 2016) and dominance in many social species (Spong et al. 2008), which may offset or exceed declining feeding competitiveness and senescent declines in anabolism (Valenti and Schwartz 2008). In some badger populations, dietary specialisation (Robertson et al. 2015) and dominance (Revilla and Palomares 2001) confer body-condition advantages in times of shortage. In this study, warmer summers did not detrimentally affect summer BCI in older badgers (unlike young badgers, Fig. 4a), suggesting that older badgers may leverage their experience—or status—under particularly low-food conditions. Alternatively, as old badgers exhibit a stronger relationship than young badgers between summer BCI and survival, they may down-regulate metabolism in harsh summers (as in American badgers, *Taxidea taxus*, Harlow 1981), possibly explaining the lower autumnal BCIs they exhibit in such years (Fig. 4b).

The relationship between energy reserves and fitness can also depend on density-dependent competition for food between conspecifics (Albon et al. 1983, Macdonald and Johnson 2015) or within sympatric guilds (Zhou et al. 2013), which exacerbates the risk of energetically marginal strategies that prioritise reproduction over somatic conservation (Wright et al. 2019). While we did not find any direct effects of population density on individual badger body condition, we did find a significantly constraining effect of density during the summer, with lower BCI variance during high-density years, and a nearly 10% increase in mortality probability from low to high summer densities. Inter-population variation in carrying capacity and environmental stability can determine the strength of intra-population competition (Gaillard

et al. 1993, Dooley et al. 2013). If, therefore, seasonal energetic constraints temporarily vary environmental carrying capacity, individuals should logically be constrained in the variety of dietary niches they can occupy (Sheppard et al. 2018). These effects may be particularly detrimental for already-marginal individuals, as we found for old badgers, which exhibited even lower summer BCI than expected during high-density years.

4.3 Fixed individual heterogeneity

In general, long-lived, iteroparous animals invest in survival over short-term reproductive success (Oli and Dobson 2003), leading to tactical energy allocation into survival and a greater chance of future reproductive success (Albon et al. 1983). Investing capital in survival (Shero et al. 2015) likely explains why female badger reproductive success increased linearly with autumn BCI in our study. If some individuals in a population are of intrinsically lower quality—whether from early-life developmental constraints (Lindström 1999), genetic factors (Wilson et al. 2005), or consistent metabolic disadvantages (Lindsay et al. 2020)—they may continuously postpone breeding, leading to lower lifetime reproductive output (Campbell et al. 2017). This fixed heterogeneity manifested as bimodality in female badger life histories, where a) some females exhibited consistently higher autumn BCI and consequently higher lifetime reproductive success (Fig. 6f); b) females that had reproduced in year t were substantially more likely than other females to reproduce again in year $t+1$; and c) reproductive success in older females became even more confined to those with a previous reproductive history, with these experienced females also exhibiting smaller springtime BCI costs from reproduction. Similarly, despite the BCI costs of descended testes (males with descended testes had seasonal BCIs 5.0%, 3.6%, and

4.0% lower than with ascended testes), degree of testes descent did not have any significant effect on male survival probability—even in older individuals.

4.4 Individual BCI variability

While some fixed heterogeneity existed in this population, individuals with highly variable BCI phenotypes comprised the largest share of highly-captured (10+) badgers (Fig. 5) and BCI variance remained high after accounting for weather and life-history conditions. We infer, therefore, that individuals may contemporaneously exhibit widely differing body-fat storage tactics in wild populations without experiencing long-term selective disadvantages. Bet-hedging permits the persistence of phenotypes with lower arithmetic mean fitness in populations provided that environmental stochasticity enables them to maintain higher geometric mean fitness (Starrfelt and Kokko 2012, Rajon et al. 2014). Thus, although high-BCI phenotypes had an LRS advantage in the wider population (Fig. 6), on average 11.2% of individuals with over 10 captures (i.e., long-lived) persisted in the lowest quartile of the population ("Type I" in Fig. 5). Of these, 59% had LRS > 1; that is, individuals who were fit but not fat. While developmental constraint cannot be fully ruled out for these individuals, previous research has established that neither pace-of-life (Chapter 2) nor telomere dynamics (van Lieshout et al. 2019) are strongly affected by early-life conditions in badgers. Instead, the persistence of low-BCI phenotypes, and particularly the flexible, highly-prevalent Type II intermediate-BCI phenotypes (Fig. 5), suggest that, for the majority of individuals, varied tactics above the safe-zone threshold provide alternative paths to competitiveness.

Alternative tactics for balancing more constrained energy budgets can preserve competitiveness for individuals of lower quality. For example, roe deer (*Capreolus capreolus*)

experiencing food limitation during development tend to be smaller and lighter, but maintain typical body condition (Toïgo et al. 2006). Thus, these "unlucky" (lower-quality) individuals invest in survival and may eventually reproduce, even if with a lower total lifetime reproductive output (Gaillard et al. 2000). Under certain prevailing environmental conditions (e.g., low densities, under-represented in the present study but pertinent to fluctuating selection: Wright et al. 2019), such tactics could even have a selective advantage (fitness with minimal need to insure against food supply insecurity), such that heterogeneous fitness outcomes may ultimately represent dynamic (Tuljapurkar et al. 2009b) rather than fixed (van Noordwijk and de Jong 1986) heterogeneity.

4.5 Buffering of projected weather trends

For population resilience to be affected by an environmentally-determined trait, changes in the trait must affect demographic rates (Layton-Matthews et al. 2020). As the main determinant of individual resilience to short-term energy fluctuations, threshold-shaped BCI-survival relationships disengage small-scale BCI changes from mortality risk in badgers, even up to the costs associated with projected warmer summers. Despite substantial projected warming, most associated BCI changes affected survival probabilities only slightly (Fig. 7), as the sensitivity of mortality risk to BCI changes is low within the safe zone (Fig. 2). This is particularly important for energetically marginal individuals such as geriatric badgers, which have an extremely narrow safe zone during summer (Fig. 2c) and therefore high sensitivity. Buffering this sensitivity is therefore of crucial importance to continued fitness (Hilde et al. 2020) and a likely underlying explanation for why older badgers showed less or no BCI reduction compared to younger badgers during hot summers. Even if this plasticity comes at the

cost of autumn BCI, this is of less concern to old badgers, as by then their safe zone more closely resembles that of young badgers, and the 3.3% survival probability loss associated with even extreme climate change—while non-negligible—is less drastic (Fig. 7).

Nevertheless, mechanistically, cumulative energetic stress often explains mortality risk better than additive weather effects (Kautz et al. 2020), particularly in the context of sustained climate change (Rode et al. 2014). Thus, hot summers and high seasonality were not only associated with lower BCI in most badgers (Fig. 4a), but also with marginal individuals being pushed below the safe zone of BCI variation. While individuals showed relative robustness to BCI costs associated with even extreme climate change (6.5 °C in summer), it is highly unlikely that the associated year-to-year persistent constraint on summer food supply and/or changes in trophic choices and foraging dynamics would persist unaltered and preserve existing individual buffering capacity. This is particularly true for already-marginal individuals such as geriatric badgers, emphasising the importance of considering variability in individual resilience according to life-history stage in other animal populations.

Behavioural and physiological responses are also likely to be adaptive to shorter and less severe periods of food scarcity in winter, which may reduce the need for fat accumulation, caching, and/or hibernation strategies (Khan 2017). Torpor has evolved to cope with anticipated energy scarcity (Kato et al. 2018). Therefore, the degree to which badgers—and other torpor-expressing species—will still deposit fat prior to the onset of substantially milder winters, due to endocrine regulation (Caro et al. 2013, Doherty et al. 2014), is of great interest. Energetically cautious strategies such as accumulating excess fat under less stressful winter conditions would be at a selective disadvantage to those investing more heavily in reproduction (Humphries et al.

2002, Bårdsen et al. 2008). Broadly, however, increasing winter temperatures will result in an extension of badger activity into the winter months (Noonan et al. 2018), even as summers continue to become more energetically costly. If elevated activity is not matched by food availability, the costs of rousing from torpor and subsequent winter activity may outweigh the benefits of foraging (Humphries et al. 2002, Caro et al. 2013), counter-intuitively favouring phenotypes originally adapted to severe winters.

Fluctuations in food supply, both predictable and stochastic, are part of the natural conditions to which species have evolved (Tuljapurkar et al. 2009a). Increasingly, however, anthropogenic climate change and other forms of human-induced rapid environmental change (Sih 2013) destabilise ecosystem dynamics, altering prey availability or foraging opportunities (Noonan et al. 2018, Schulte-Hostedde et al. 2018), and mismatching historical energetic demands to extrinsic energetic supply (Stenseth and Mysterud 2002, Durant et al. 2007). The tactical adjustment of capital reserves by storage and expenditure of fat provides a phenotypically plastic (Boutin and Lane 2014) mechanism for handling much of this energetic uncertainty, but remains sensitive to life history-determined risk. Ultimately, phenotypic plasticity in body condition, and a full understanding of the relative selection pressures on different energetic phenotypes, will be key to forecasting the resilience of many species and populations to ongoing changes (Valladares et al. 2014).

5 Authors' Contributions

Conceptualization: Julius G. Bright Ross and Chris Newman; Data collection: Chris Newman, Christina D. Buesching, David W. Macdonald, Julius G. Bright Ross, Erin Connolly; Coding and

analysis: Julius G. Bright Ross, Shinichi Nakagawa; Writing: Julius G. Bright Ross; Editing: all authors.

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Part II

Fine-scale heterogeneity in energy expenditure

Chapter 4

3D-printing for bespoke, flexible, and reproducible wildlife collar designs: Best practices and lessons from field deployment on medium and large carnivores

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Abstract

Sophisticated biologging devices are increasingly important tools in modern wildlife ecology, but commercial equipment is often prohibitively expensive or limited in variation. Recent advances in affordable sensor components and 3D-printing enable researchers to produce bespoke multi-sensor units optimised to species-specific considerations, but techniques can be difficult to master, often resulting in repeated common mistakes. We describe an inexpensive multi-sensor collar (total cost per unit ~$100) designed for tracking activity, audio, and location, and present some recovered data. We offer a comprehensive guide on multi-sensor programme configurations, using 3D-printed housings for iterative and diverse design. We present lessons learned from deployments on wild European badgers (*Meles meles*, n = 81, eight deployments) and lions (*Panthera leo*, n = 11, two deployments: 1 wild, 10 captive). Our insights and techniques can inform designs for a wide range of wildlife studies. We make all design file iterations available and invite future practitioners to also share designs, to improve collaboration in designing replicable bespoke biologging equipment.

Keywords: *3D-printing, badgers, biologging, Internet of Things, lions, SensorTile, tri-axial accelerometry, wildlife ecology.*

1 Introduction

The near-continuous collection of wildlife data through biologging is a hallmark of twenty-first century ecology (Kays et al. 2015), enabling study of animal habitat selection using GPS- and radio-tracking (Bright Ross et al. 2021) or new technologies (Noonan et al. 2015), and energetics, physiology, and behaviour through remote sensors (Brown et al. 2013, Noonan et al. 2014).

Nevertheless, deploying large numbers of telemetry devices can be prohibitively expensive (Wilson et al. 2008, Kays et al. 2015), incentivising the development of custom designs (e.g., Noonan et al. 2014, Dewhirst et al. 2016, Foley and Sillero-Zubiri 2020). This hinges on:

1. Re-usability: Many bespoke designs preclude re-usability and capacity to fix minor hardware issues upon deployment (e.g. potting in resin, Noonan et al. 2014).
2. Reproducibility: Lack of design information (e.g. Dewhirst et al. 2016) or attempts to improve labour-intensive processes (e.g. Noonan et al. 2015), result in frequent reinvention and repeated mistakes.
3. Species considerations: Tools and techniques used should enable the adaptable development of robust, reliable, lightweight, and species-specific collar housings—crucial for animal welfare and accurate results (Coughlin and van Heezik 2014, Jung et al. 2018).

In this context, we therefore evaluate the considerable customisation potential of 3D-printing technology and commercially available sensing modules. We examine results from ten deployments of multi-sensor collars configured to return tri-axial accelerometry and other behavioural data (audio or Bluetooth Low-Energy, "BLE") on European badgers (*Meles meles*, hereafter deployments "B1-B8") and African lions (*Panthera leo*, "L1-L2"). Both species are social—conspecifics can incur collar damage—but span an order of magnitude in mass (mean lion = 154.3kg, badger = 7.3kg in deployments).

2 Materials

2.1 Sensor module assembly

Designs used SensorTile IoT turn-key sensor modules (STEVAL-STLK01V1, STMicroelectronics, 2016; hereafter "chipsets"). These are low-power, low-cost ($81.94), highly integrated, and sensor-rich platforms for development of "Internet of Things" prototypes. We based the module on a programmable ARM M4 Cortex microcontroller. Peripherals included: accelerometer, gyroscope, magnetometer, barometer, microphone, and a BLE wireless transceiver.

SensorTile component boards were soldered to the included cradle (Fig. 1a), incorporating a microSD card socket. Flexible cables were soldered either to a battery holder (deployments B2-8, L1-2) or directly onto battery terminals (B1, Fig. 1b); the latter is not recommended by manufacturers and is liable to damage battery cells unless performed with a spot-welder. In all deployments, runtime (battery capacity) was traded-off against weight (both from battery and casing) and unobtrusive design. For B1, we 3D-printed custom battery holders for a single CR123A battery (Fig. 2a). For B2-8, single battery holders were used (BHC-CR123A, PRO POWER; Fig. 1bi). For L1-2, two battery holders were soldered together (Fig. 1biii). Per-collar costs were $91.44-$93.26 for badgers, $106.90-$107.05 for lions (Appendix S1), with per-casing 3D-printed material only $1.48 (badgers)-$4.44 (lions).

2.2 3D-printed casing design

We used an iterative prototyping procedure to generate chipset casings for 3D-printing, using Fusion 360 CAD/CAM design software (Version 2.0, Autodesk 2018; detailed guide in Appendix S2). We rounded all external edges maximally without sacrificing structural integrity,

to minimise jaggedness (Fig. 2c). All deployed casings comprised a casing body (with perforated flanges for attachment), and a baseplate to seal the chamber.

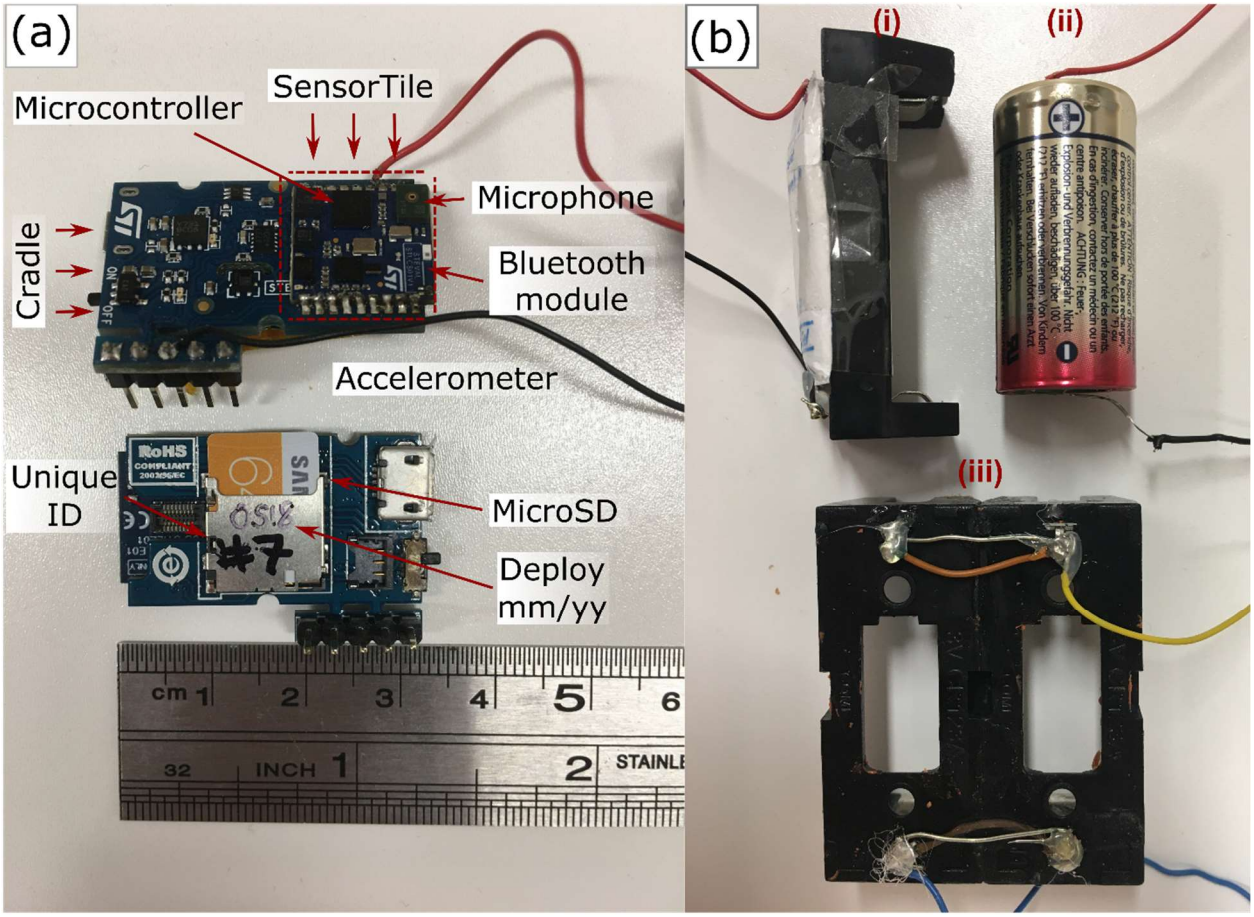


Figure 1. **Illustration of assembly.** Chip components (a) and battery soldering alternatives (b) as referred to in-text.

In badger casings, size constraints required stacking the chipset and battery holder, but in lion casings we designed a side slot for the chipset instead, resulting in less protrusion overall (Fig. 2d). We printed casings using a melted extrusion modelling (MEM) 3D printer (UPBOX+, Tiertime) using recyclable acrylonitrile butadiene styrene (ABS) plastic (Up Fila, Tiertime) on 99% infill, with autonomous print times from 2.6-3.2 hrs for badger collars (39-46 g) and 7.3 hrs for lions (113-117 g).

We used ABS plastic, based on experience from trials of a similar device on free-roaming dogs (*Canis familiaris*), where 11 3D-printed polylactic acid (PLA) plastic casings were deployed; all were damaged by conspecifics to the point of electronics failure. During subsequent deployments with ABS (n = 30), all casings lasted until recovery (14 days, Foley and Sillero-Zubiri 2020).

2.3 Programming

Code was written in C and compiled using ARM Keil MDK 5. A multi-threaded real-time operating system provided software modularity and real-time scheduling (ChibiOS 16.1). We could thus easily modify or enable/disable different components (e.g. accelerometer or microphone) without affecting the entire system architecture. This design and common code-base enabled rapid prototype re-configuration (e.g. adding Bluetooth in B7). We flashed compiled firmware to devices using a STLINKv2 programmer.

We trialled four different code versions (Table 1). In B1, version A, we programmed high-rate (80 Hz) full inertial sensing coupled with intermittent high-quality audio sampling (5s on, 95s off) to ground-truth behaviours (Wijers et al. 2018). Current consumption was high at 8mA, dominated by the gyroscope and magnetometer. Additionally, although high quality, intermittent audio sampling proved challenging to interpret. In version (B), audio was sampled continuously, but randomly down-sampled at 85% compression ratio under a compressive sampling approach (Christensen et al. 2009). Version C operated audio continuously but stored at 8-bit rather than 16-bit resolution, using a dynamic compander, with gyroscope disabled, and accelerometry and magnetometry sampled at 25 Hz. This reduced overall current consumption slightly, extending lifetime. In version D, we disabled audio entirely and used novel BLE contact

logging to assess feasibility of low-energy positioning. Current consumption was just c. 2mA, leading to estimated lifetime of c. 1 month.

3 Deployment and Iterative Design Changes

3.1 Assembly and deployment

For B1, we inserted batteries into 3D-printed battery holders (Fig. 2a) and soldered wires directly to battery terminals (Fig. 1bii). For all other deployments, we used pre-fabricated battery holders. We also inserted a silica gel pouch to safeguard against condensation. Except in B1, we beaded silicone sealant around the inner casing lip, fitted the baseplate and sealed it with an outer silicone layer. In B1-B8, we attached casings to padded nylon collars by running zip-ties through a slit between the nylon and padding. In L1, we attached casings to a leather collar using nyloc nuts and a custom-designed flat, rectangular metal plate bracket, welded to the heads of two bolts. In L2, we used polyester collars, necessitating a redesign so zip-ties could sit flush under the casing (Fig. 2e). Ability to rapidly adapt designs enabled small improvements between deployments, such as altering support structures to route wires better (Fig. 2f).

We fitted collars to sedated wild (B1-8, L1) or captive (L2) animals (Fig. 3) as part of ongoing studies (Table 1). For B7, we set out 79 Bluetooth beacons (Avvel X iBeacons, $25.55/ea) in two contrasting overlapping field grids (25x25m and 100x100m) to deduce appropriate spacing for adequate location detection.

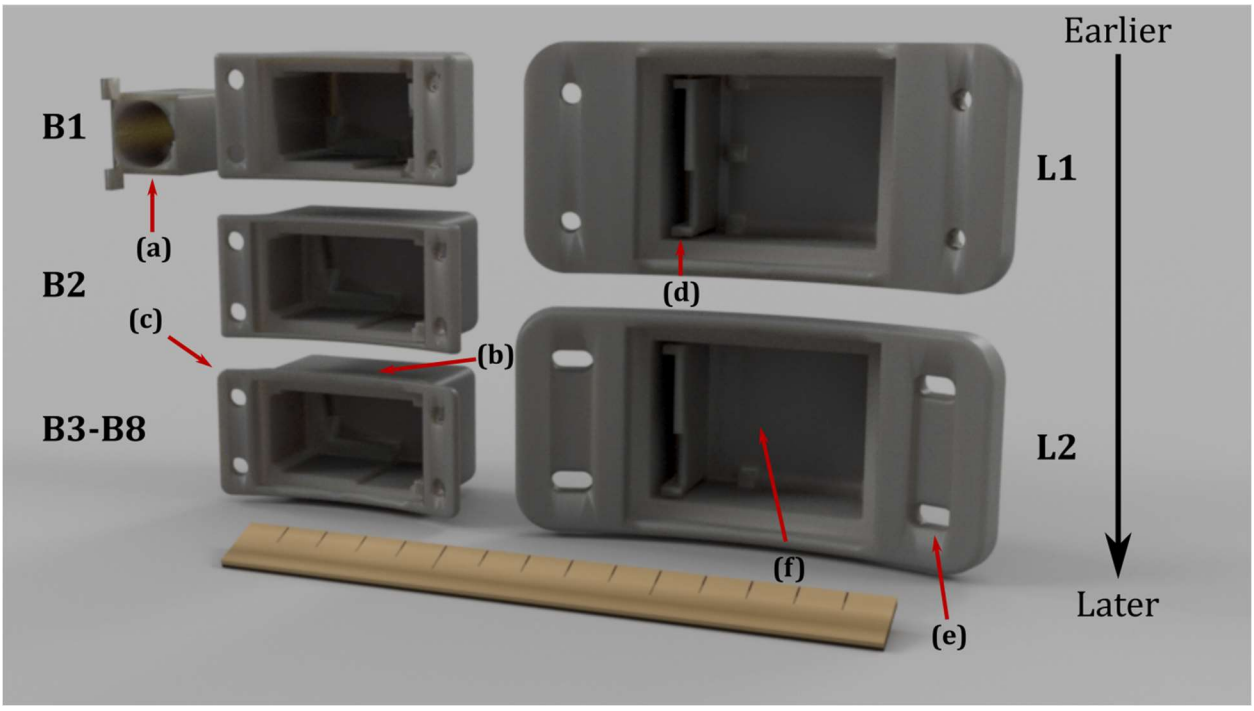


Figure 2. **Primary casing designs used in deployments.** Corresponding deployments indicated using uppercase letters—see Table 1. Design features referred to in the text shown with red arrows and bolded lowercase letters. Ruler in centimetres.

Table 1. **Collar deployments and corresponding programs.** Superscripts link deployments to program versions. Badger deployments were conducted in Wytham Woods, Oxfordshire, England; L1 in the Bubye Valley Conservancy, Zimbabwe; L2 at the Kevin Richardson Sanctuary, South Africa. Battery lifetime predicted for single 3V CR123a battery. *Some badger collars were recovered several months later than planned; this did not result in additional data, thus this is not reported. †All 10 L2 chips were recovered, but only 5 casings survived deployment.

Deployment	Animal	Date deployed	Deployment length	# deployed	# recovered	# returning data	Avg. data returned
B1[A]	*Badgers*	21/05/18	7 days*	9	7	5	7.02 days
B2[A]		03/09/18	7-10 days	10	10	10	6.62 days
B3[B]		09-10/09/18	65-82 days*	9	6	4	15.50 days

B4[B]		13/11/18	6-8 days*	12	11	0	0 days
B5[C]		27/05/19	7-8 days*	12	12	12	7.04 days
B6[C]		02/09/19	7-9 days*	12	12	10	7.98 days
B7[D]		09-10/09/19	63 days*	6	5		10.84 days
B8[C]		13/11/19	6-8 days	11	11	10	4.51 days
L1[C]	*Lions*	14/11/19	33 days	1	1	0	0 days
L2[C]		19/07/19	14-15 days	10	10[†]	6	3.88 days

Program version	Audio	Acc	Gyro	Mag	BLE	Mb data/day	Avg. current drain	Predicted lifetime
A	5s on, 95s off. 28kHz, 16-bit	80Hz	80Hz	80Hz	OFF	388	8mA	7.5 days
B	28kHz, 16- bit, 10% randomly sampled	80Hz	80Hz	80Hz	OFF	850	6mA	10.4 days
C	28KHz, 8bit, continuous	25Hz	OFF	25 Hz	OFF	2331	5mA	12.5 days
D	OFF	25Hz	OFF	25 Hz	500 msec scan/10 sec	24	2 mA	30 days

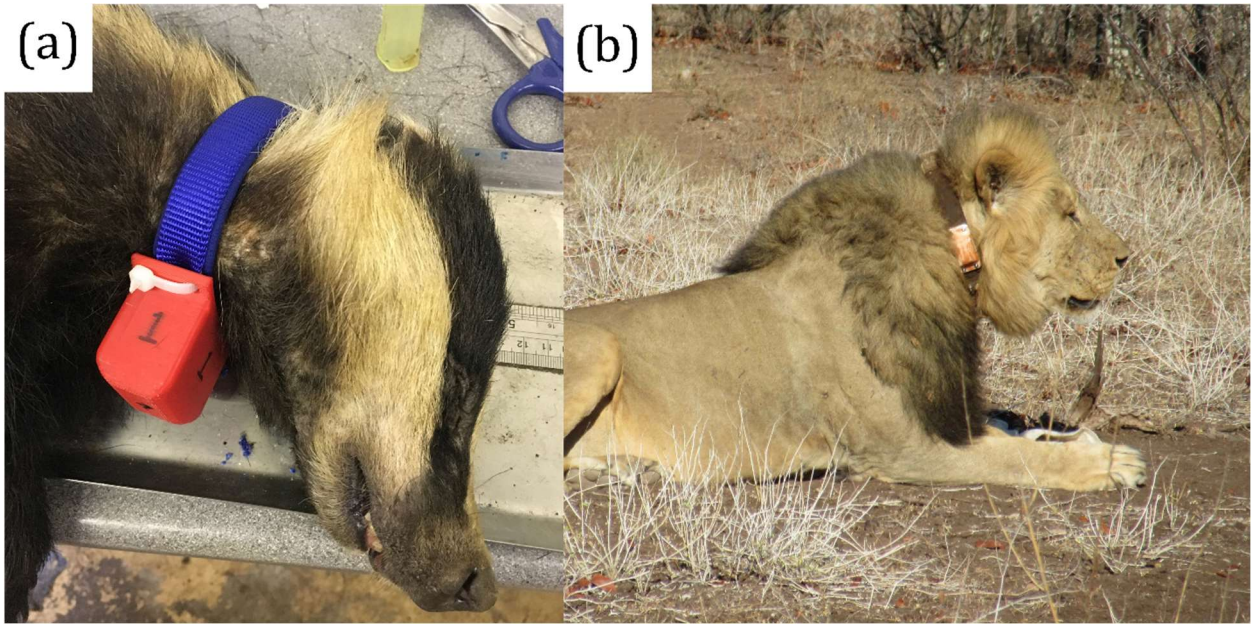


Figure 3. **Illustrations of equipment on test subjects.** Photographs taken of deployments on badgers (a – B1) and lions (b – L1).

4 Results

4.1 Deployment results

4.1.1 Badgers

We recovered 74/81 chipsets with casings intact. Only two B2 casing walls were chewed by conspecifics at the thinnest point; we reinforced subsequent designs accordingly (Fig. 2b) and successfully. Two B3/B4 collars recovered 6 months later than anticipated had lost their casings at the attachment flanges, implying limitations on ABS durability, although one intact B4 collar was recovered 10 months following deployment. Only 4 chipsets suffered water damage.

For B4, although only one chipset was not recovered, catastrophic data loss occurred due to data writing issues. Nevertheless, in other deployments, 51/64 of accelerometry chips returned data, mostly with full runtime. Switching to pre-fabricated battery holders improved accelerometry data recovery from 71.4% (B1) to 90.2% (B2-6, B8, excluding B4). Finally, BLE loggers lasted substantially less than their projected runtime but returned high-quality data.

4.1.2 Lions

The single L1 casing survived deployment on a wild male lion for over a month, but did not return data due to connection failure. Although all L2 chipsets were recovered, 50% of casings were destroyed within 24 hours of deployment, while the others lasted the entire deployment; casing survival was more likely on males with thick manes. Unfortunately, although the 6 chips recovered undamaged recorded data successfully for c. 4 days before deployment, they ceased recording within 2 hours of deployment, likely due to hardware failures associated with the double-battery rig.

4.2 Data collected

All chipset programs generated accelerometry and supplemental behavioural data sufficient to produce actograms and ethograms (e.g. Fig. 4a-b). Different audio programs produced data in accord with their settings; program C provided the best trade-off between interpretable data (Fig. 4b) and battery life. Furthermore, a coarse (100x100m) grid of BLE beacons was sufficient to generate biologically useful location data for central-place foragers like badgers (Campbell et al. 2013). This promotes the feasibility of BLE (by obviating the need for finer grids) for supporting advanced applications such as dead-reckoning (Bidder et al. 2015).

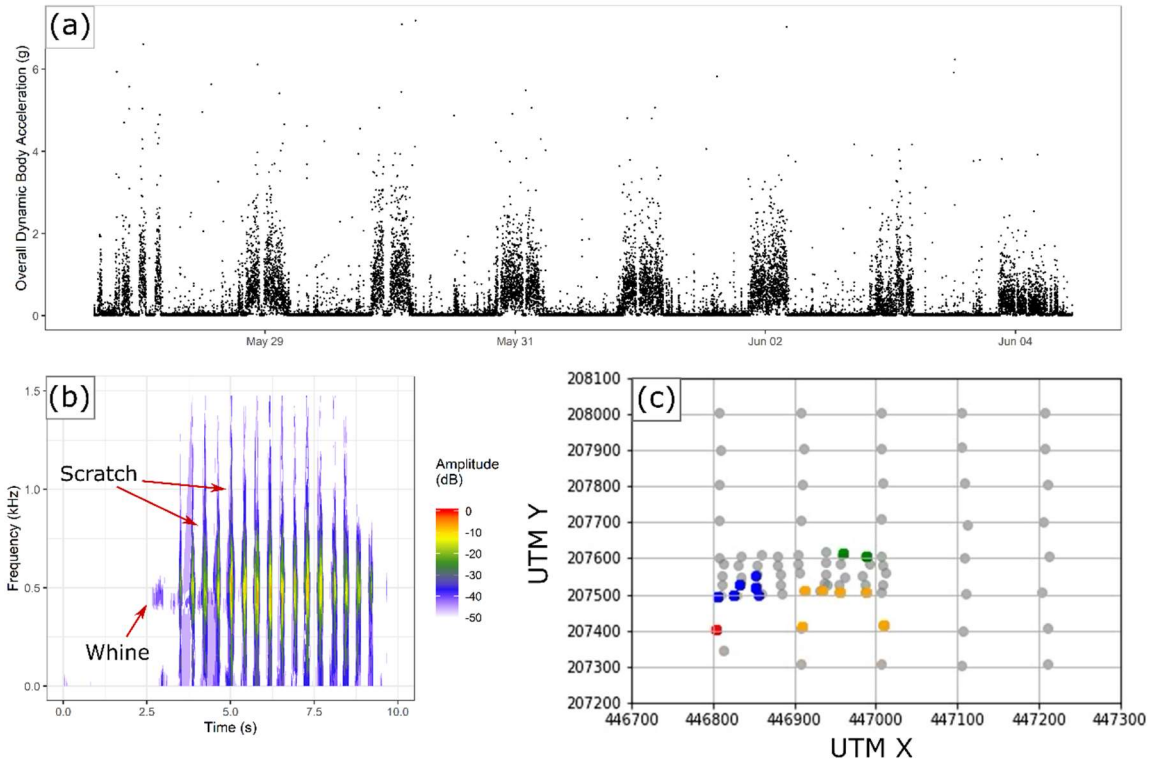


Figure 4. **Illustrations of data collected by deployments.** Examples are provided for: a) overall dynamic body acceleration from tri-axial accelerometry; b) audio data, illustrating recognisable behaviours; and c) BLE readings from different badgers (colours) by beacons during one 10-minute period.

5 Discussion and Recommendations

Although deploying biologging devices on diverse wild animals, from whale sharks (*Rhincodon typus*: Gleiss et al. 2009) to brushtail possums (*Trichosurus vulpecula*: Allan et al. 2013) has become commonplace, it remains an inexact science. High failure rates are commonplace (Zucco and Mourão 2009), even with commercial equipment (Cumming and Ndlovu 2011, Ruykys et al. 2011). Single-species deployments (e.g. Zucco and Mourão 2009, Allan et al. 2013), or a lack of field testing before full deployment (Fischer et al. 2018), limit generalisability of equipment performance. For example, we advocate the durability of 3D-printed casings for constraints inherent to badgers—exposed to moist fossorial conditions (Noonan et al. 2014, 2015)—but similar casings were not suitable for the bite force of lions. Future deployments should trial resin, ceramic, or metal 3D-printing, or computer numerically controlled (CNC) milling for stronger species with conspecifics that might do damage to casings; CNC milling is also much faster than 3D-printing while preserving flexible CAD-modelling techniques, but requires higher investment in machinery.

Crucially, our designs fully met chip-set reusability and reproducibility objectives, with some sensor modules used in 4 successful sequential deployments. Consequently, we could adapt programming (on the same hardware) and casings to optimise design—a costly process with pre-fabricated devices (Jung et al. 2018) or when deployment opportunities are limited (e.g. Ruykys et al. 2011). We recommend:

1. Testing even minimal component modifications and code iterations prior to deployment. The difference between B2 (good data recovery) and B4 (catastrophic data loss) deployments was purely due to a second SD card order—identically branded, but either made from a different factory/batch or sub-standard clones. Trials

on proxy animals and/or humans under field-like conditions can also reduce failure risk, as per L1-2.

2. Minimise assembly complexity. Fewer components and less field assembly reduce potential for equipment failure: 2/7 B1 collars failed early due to battery connection soldering; commercial battery holders reduced subsequent failure rate to 5/51. Silicone sealant and silica pouches—a simple sealing technique requiring ~5 minutes in the field—prevented water damage in nearly all deployments.

3. Use design logs to improve the reproducibility and generalisability of methods, explaining basis for modifications (Appendix S3).

Telemetry devices must not only be reliable and accurate, but designs should be continually refined to avoid encumbering or injuring focal animals, where collars have impaired body-condition (Tuyttens et al. 2002) and breeding success (Moorhouse and Macdonald 2005) in previous studies. A maximum 5% of study animal weight is mandated by various guidelines (see Sikes and Gannon 2011; UK Animals (Scientific Procedures) Act (1986), *inter alia*); our loggers (collars, casings, and components) averaged 1.34% bodyweight for badgers and 0.14% (L2) – 0.78% (L1) for lions and caused neither detectable impediment nor harm. The flexibility of our designs allows species-specific functionality, rather than "best fit available" off the shelf; the latter inevitably involving compromises on device shape, weight, and welfare considerations (c.f., Zucco and Mourão 2009). Specifically, we recommend:

4. Using materials with at least the tensile strength of ABS for casings, and at a thickness of > 4mm at any point (B3 and thereafter), with thicker walls for larger animals (7mm gave mixed results in L1-L2; >10mm should be trialled).

5. Rounding corners and avoiding points of weakness.

6. Modifying designs to reduce protrusion by rearranging components (Fig. 2, difference between B and L designs; Appendix S3).

Custom remote sensing equipment has become commonplace, user-friendly (Foley and Sillero-Zubiri 2020), and less expensive (e.g. < $300 Allan et al. 2013, < $200 Fischer et al. 2018 for GPS-enabled trackers). Our procedure—particularly 3D-printing, with high versatility for < $10 for each new casing—enabled rapid prototyping for four different data-collection programs on two substantially different species with a relatively small initial investment. We hope that the resources and recommendations we provide will prove instructive, and encourage future designers of custom equipment to refine, rather than reinvent, the proverbial wheel.

6 Authors' Contributions

Casing design: Julius G. Bright Ross, Andrew Markham, and Mattew Wijers; Sensor module programming: Andrew Markham; Data collection (badgers): Julius G. Bright Ross, Chris Newman, Christina D. Buesching; Data collection (lions): Genevieve Finerty and Matthew Wijers; Data collection (dogs): Conrad J. Foley; Writing: Julius G. Bright Ross and Chris Newman; Editing: all authors.

7 Data Availability Statement

Fusion 360 projects with deployment-ready casings are available online at: https://a360.co/2TskqUu (badgers) and https://a360.co/34xfp3d (lions). All casing designs (Appendix S3) and programs will be available upon publication at https://doi.org/10.7910/DVN/XXTWPF.

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Chapter 5

Individual mechanical energy expenditure regimens vary seasonally with weather, sex, age, and body condition in a generalist carnivore population: Support for tactical diversity

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In preparation for submission to a Special Issue in Animals entitled “The Adaptive Responses of Wildlife to Climate Change

Abstract

Diverse individual energy-budgeting tactics within wild populations enable resilience to natural fluctuations in food availability and expenditure costs. Although substantial inter-individual heterogeneity in activity-caused energy expenditure has been documented in wild populations, it is important to differentiate between responses to the environment and inter-individual differences stemming from life-history, allometry, or somatic stores. We use tri-axial accelerometer deployments across two years, complemented by a year-long diet analysis, to investigate how overall dynamic body acceleration (ODBA, a measure of activity intensity) and "Activity" (above an ODBA threshold) vary between individuals across three seasons in a high-density population of European badgers (*Meles meles*), a generalist mesocarnivore. Weather (including wind speed) affected badger ODBA and Activity according to predictors of earthworm (food resource) availability and potential for cooling effects. In spring, maximal ODBA was expended at intermediate rainfall and temperature values, suggesting that badgers traded off foraging success against thermoregulatory losses. Crucially, ODBA plasticity to temperature depended on individual body condition. Thinner badgers maintained high spring ODBA irrespective of temperature, while fatter badgers reduced ODBA at colder temperatures. Conversely, in summer, thin badgers modulated ODBA according to temperature, likely in response to super-abundant food supply. Moreover, between 35% (spring and summer) and 57% (autumn) of residual total daily ODBA related to inter-individual differences unexplained by top seasonal predictors, suggesting within-season activity phenotypes. We propose that this diversity among individual energy expenditure profiles may contribute to population resilience under rapid environmental change.

Keywords: *Activity profiles; age differences; behavioural plasticity; behavioural thermoregulation; dynamic heterogeneity; tri-axial accelerometry.*

1 Introduction

Vulnerability to human-induced rapid environmental change (HIREC, Sih et al. 2011) generally focuses on the species as the minimal unit of investigation (e.g. Pearson and Dawson 2003, Fuller et al. 2010), yet, fundamentally, natural selection operates on the individual (Darwin 1859, but see Wade and Kalisz 1990, Mayr 1997). Energy provides a common currency (Chimienti et al. 2020) for quantifying how individuals within the same population balance obligate and elective activities. Overarching constraints at the species-level determine the context within which this balancing occurs; among these, diet diversity (Bolnick et al. 2007), average body size (Mcnab 1979), climatic constraints in achieving thermoneutrality (Speakman 2005), reproductive strategies (González-Suárez et al. 2013), and predator pressures (Diserens et al. 2021). Ultimately, however, in order to optimise energy allocation between survival and reproduction, each individual aims to balance available energy inputs (food supply) with outputs (physiological homeostasis and activity) (Weiner 1992) according to its circumstances (sex, age, body-condition, social status, etc), and to have sufficiently predictable energy security to plan tactical energy budgets (Hall et al. 1992, Monteith et al. 2013, Chapter 3).

Under stable and consistent environmental conditions, directional selection should drive energy budgeting canalisation (e.g., Artacho and Nespolo 2009) after accounting for the variation stemming from intrinsic differences such as sex (Zhu et al. 2015), age (Even et al. 2001), and body condition (Monteith et al. 2013). This would result in a narrow range of optimised tactics prevailing across the entire population, or a small set of alternating strategies under density-dependent fluctuating selection (Wright et al. 2019). In reality, however,

environments are seldom so predictable (Tuljapurkar et al. 2009, Hoffmann and Sgrò 2011), and multiple pathways to equivalent fitness outcomes can produce tactical heterogeneity between individuals at both fine (daily, Williams et al. 2014) and coarse (e.g. seasonal, Humphries et al. 2003) timeframes. This can result in disruptive selection giving extreme phenotypes a stochastic fitness advantage over more intermediate phenotypes (Rueffler et al. 2006) or fluctuating selection for tactics that suit alternating environments (Bell 2010, Wright et al. 2019). In either case, tactical diversity provides a population with resilience to change, where some individuals will exhibit plastic variation in energy budgeting that may make them "pre-adapted" to newly emergent conditions (Rajon et al. 2014, Schindler et al. 2015).

Rapid anthropogenic climate change reduces environmental predictability and destabilises the selection pressures determining optimal energy allocation tactics (Thomas et al. 2001, Hetem et al. 2014, Bright Ross et al. 2021). These effects are compounded by other forms of HIREC disturbances, such as habitat loss (Segan et al. 2016); consequently, even vagile organisms may be unable to fully track their optimal bioclimatic niche (Jump and Peñuelas 2005, Schloss et al. 2012, but see also Bright Ross et al. 2021). Coping strategies *in situ* are therefore often essential for population and species persistence, but the short timescales involved limit the response effectiveness of genetic adaptation (Hoffmann and Sgrò 2011, Merilä and Hendry 2013, De Meester et al. 2018, Radchuk et al. 2019). Plastic changes in energy expenditure can, therefore, provide an essential coping strategy (Chevin et al. 2010, McCain and King 2014, Beever et al. 2017). Despite this importance, little attention has been given to how activity budgets, as the most pliable component of energy expenditure modification, are simultaneously a) constrained by a shared environmental context, once intrinsic context is accounted for; b) determined by intra-individual consistency (activity budgeting phenotypes); and c) affected by

inter-individual differences in responses to environmental conditions (differential plasticity, Hertel et al. 2020).

Energy intake and its environmental covariates are frequently characterised through diet analyses (e.g. Zhou et al. 2015, Hisano et al. 2017, Iwama et al. 2017), but quantifying how individuals deploy the energy assimilated from their diet is more challenging. Recently, however, advances in bi- and tri-axial accelerometry have enabled the intensity of activity to be quantified through overall dynamic body acceleration (ODBA, Wilson et al. 2006, Shepard et al. 2008). ODBA correlates with total metabolism in a wide range of species (Elliott et al. 2013, Lyons et al. 2013, Miwa et al. 2015), particularly at short timescales (Dalton et al. 2014), making it a good proxy for mechanical energy expenditure (Qasem et al. 2012).

Here we used collar-mounted custom tri-axial accelerometers (Chapter 4) to examine variability in individual activity regimens in a population of wild European badgers (*Meles meles* L., hereafter "badger"). Badgers provide a highly informative model system for studying individual activity, exhibiting strong weather-dependent foraging patterns according to prevailing conditions and food availability (Elliott et al. 2015, Noonan et al. 2018, Bartra Cabré 2020). At our high-density population study site, badgers live in social groups averaging 6.8 individuals (range 1-28), comprising an overall population of est. 248 individuals in 2016 (population estimates only accurate after 3 years of data, see Chapter 1). Moreover, badger groups occupy subterranean dens (setts) as refugia (Tsunoda et al. 2018), where fossoriality can provide an advantage to being active above ground in suboptimal conditions (Noonan et al. 2015, Williams et al. 2016)—particularly for fatter badgers with lower motivation to forage (Noonan et al. 2014). On fine timescales, the availability of earthworms (particularly *Lumbricus terrestris*), a primary though not obligate food item (Kruuk 1978, Hofer 1988, da Silva et al. 1993), also

varies extensively with weather conditions (Johnson et al. 2001). Additionally, badgers exhibit strong seasonal changes in body fat reserves, often nearly doubling their weight in autumn (going from 6-11 kg; see Chapter 3) and undergoing winter torpor (Newman et al. 2011, McClune et al. 2015) in anticipation of low food availability. Finally, delayed implantation until the onset of winter (Yamaguchi et al. 2006, Sugianto et al. subm.a) permits badgers to align parturition, lactation, and most mating activity with peak spring food abundance (Macdonald and Newman 2002, Buesching et al. 2009), focusing the majority of these costly reproductive investments into one season.

We investigated how weather affected daily activity in badgers (quantified at the hourly scale). We used "Activity" (binary, thresholded ODBA values—capital "A" to differentiate from general activity) and absolute "ODBA" (the intensity of activity), and tested whether either was linked to prevailing conditions. Rainfall and temperature affect survival probabilities in badgers non-linearly, where intermediate conditions are often optimal (Nouvellet et al. 2013); therefore, we also tested these two covariates for quadratic effects. We also examined whether under-evaluated weather covariates (wind speed, relative humidity, and a range of soil conditions) can influence Activity/ODBA. For instance, wind speed can reduce earthworm surfacing (Macdonald 1983), interferes with sensory perception (Allen et al. 2019), and acts additively with temperature to influence convective heat loss. For background seasonal energy intake context, we also conducted a year-long faecal dietary analysis.

Within the context imposed by environmental conditions—and their seasonal relevance—we quantified how activity budgeting changes according to intrinsic traits (sex, age, and body condition). Particularly, we predicted older badgers might exhibit risk-averse activity patterns due to the frailty associated with age (Chapters 2-3). Finally, we examined whether there

was intra-individual consistency in energy expenditure over deployments (i.e., energetic vs "lethargic" activity phenotypes), and whether there was substantial inter-individual environmental response heterogeneity, indicating potential for population resilience to changeable environmental conditions.

2 Methods

2.1 Badger data collection

Badger data were collected as part of a long-term demographic study in Wytham Woods (Oxfordshire, England; 51°46'N, 1°20'W; Macdonald et al. 2015). In May, September, and November of 2018 and 2019, we captured badgers at three setts using string-trigger traps and transported them to a central field station in holding cages between 07:00 – 09:00. We sedated badgers with 0.2 mL ketamine hydrochloride kg^{-1} body weight by intramuscular injection (Sun et al. 2015, Sugianto et al. 2019a) and equipped the first 9-12 adults captured each season with custom-built tri-axial accelerometers (SensorTile turn-key sensor modules, STEVAL-STLK01V1), attached to padded dog collars and zip ties, within 3D-printed ABS plastic casings (average mass of collars was 1.34% bodyweight; for more details see Chapter 4). In the collared subset, age was informed from the date of initial capture as a cub. Only one badger was first captured as an adult and its age was estimated from toothwear (see Chapter 2). We only collared adults, due to welfare considerations for growing cubs) After sedation, we measured each individual's weight (to nearest 0.1 kg) and body length (to nearest 5 mm), then computed a body-condition index ($BCI = \log_e(mass)/\log_e(length)$) as a measure of body fat stores (Labocha et al. 2014, see Chapter 3 and supplements therein). Female breeding success could not be deduced unequivocally, and so was not tested explicitly as an explanatory variable; however, we used teat

length and width and assessed recent lactation status visually, to deduce whether a female had lactated in the year captured (Dugdale et al. 2011, Chapter 2).

Badgers were released at the point of capture and recaptured to recover collars 6-10 days later (n = 66 deployed, 63 recovered, 3 badgers recaptured without collars). In four cases, individuals could not be recaptured within seasonal trapping sessions (12 days) and collars were recovered from subsequent trappings. A longer deployment was made from September 10, 2018 (n = 9 deployed, 6 recovered, 3 badgers recaptured without collars). Catastrophic data failure occurred from a hardware incompatibility in November 2018 (Chapter 4), resulting in only one year's data for autumn deployments.

All captures were licenced under the Badger Act (1992) (currently Natural England license 2019-2020-4417) and carried out by trained personnel with Animals (Scientific Procedures) Act (1986) licenses (currently PPL 30/3379).

2.2 Weather data collection

Hourly weather data were available from the Wytham Woods meteorological station (terrestrial site T08), managed by the UK Environmental Change Network (ECN, data upon request). We used: a) mean air temperature ("Temp", °C); b) total rainfall ("Rain", mm); c) wind speed ("Wind", m/S); d) mean relative humidity ("RH", in %); e) soil moisture at 20 cm ("SoilM", %); and f) soil temperature at 10 and 30 cm ("$SoilT_{10}$" and "$SoilT_{30}$", °C). During September 2019 deployments, the rainfall gauge was obstructed. We cross-referenced these days with data from the Radcliffe Meteorological Station 6 km away in Oxford; when total daily precipitation was 0 or trace amounts (7/9 days), we substituted hourly precipitation data with 0s, removing the two remaining days from the dataset. We compared each weather metric during the dates with recorded accelerometry data to the long-term average for the same dates (1991-2015,

Rennie et al. 2017); although many covariates were significantly different from the long-term mean (Appendix S1), most deviations were within one standard deviation of these means, making these periods broadly representative of seasonal values (Table S1.1). There were only two exceptions to this: $SoilT_{10}$ was 1.0 standard deviation higher than the long-term average in spring of 2018 ($p < 0.001$), and SoilM was 1.3 standard deviations lower than the long-term average in spring of 2019 ($p < 0.001$)—in other words, these seasons had unusually warm soil temperatures and dry soil, respectively. We found substantial seasonal correlations between several of these metrics (see Appendix S1), and so only evaluated models without collinear subsets of predictors in Sections 2.4-2.6.

2.3 Processing accelerometry data

We used overall dynamic body acceleration (ODBA) to quantify mechanical energy expenditure (Qasem et al. 2012). ODBA is calculated as the L1-norm of the three channels of acceleration:

$$ODBA = |A_x| + |A_y| + |A_z| \quad (1)$$

$A_{\{x,y,z\}}$ represent the difference between the mean and the midpoint of each channel over a 2-second window, divided by 2^{14}, the basis for *g* (g-force) programmed for these accelerometers. ODBA can then be summarised over any window of time to obtain a measure of total mechanical energy expenditure (Wilson et al. 2006); we averaged ODBA to one-hour and one-minute intervals. We used the first of these as a measure of hourly mechanical energy expenditure, and the second (which was more granular, to enable sensitivity analysis—see Appendix S2) to calculate Activity at both the hourly and daily scales. To calculate Activity, we used a sensitivity analysis to delimit an active/inactive threshold for minute-averaged ODBA (0.28, see Appendix S2) and computed hourly Activity (binary: active defined as above threshold

for >30 minutes in the hour) and the total number of active minutes (above the same threshold) per night (noon-to-noon), to characterise daily activity duration.

Collaring can produce behavioural changes, particularly shortly after release (Tuyttens et al. 2002, Moorhouse and Macdonald 2005, Chivers et al. 2016). In this study, we detected significantly lower activity during the first day after release compared to subsequent days, and so developed models using data only from the second day of deployment onwards. We also excluded data from the last day of each deployment, as the time of capture during the last night of activity was uncertain. Finally, we excluded one badger's data from spring 2018 due to a naturally occurring leg injury resulting in a severe limp (the badger in question expended only 73% of the population's average ODBA during the deployment period). Ultimately, this resulted in 6,238 "badger-hours" of usable data (spring: 1,933 hours from 14 individual deployments; summer: 3,585 hours from 23 individual deployments; autumn: 720 hours from 7 individual deployments).

2.4 Seasonal drivers of ODBA and activity

For each season, we constructed a full generalised additive mixed model (GAMM, *mgcv* package, Wood and Scheipl 2020) to describe ODBA expenditure. To do so, we modelled ODBA at the hourly scale (log_2-transformed, as higher values had more variance than lower values—see Appendix S2), as badgers exhibit clear circadian activity patterns, and their activity can respond to environmental covariates that vary at a finer scale than an entire night. For interpretation, we then summed hourly model predictions to infer total daily ODBA under given conditions. Therefore, we modelled hourly ODBA as a function of: a) a cyclic cubic regression spline of hour of day; b) weather covariates, including squared terms for rainfall and temperature; c) individual covariates (age, sex, and BCI); d) pairwise BCI interactions with sex,

temperature, and rainfall; and e) random intercepts for individuals. All continuous covariates were standardised to have a mean of 0 and a standard deviation of 1 (*standardize* package, Eager 2017). The autumn data included only two female badgers (out of a total of seven), which we judged too few to include sex as a covariate in that model.

We verified that random intercepts improved model fit for the full model structure (after Zuur et al. 2014, $\Delta AIC > 10$ in all seasons). We detected substantial autocorrelation in the residuals, and so we included an AR-1 autoregressive term in each seasonal model. We then performed all-subsets model selection for each season using Akaike's Information Criterion (AIC) (*MuMIn* package, Barton 2019), excluding models with collinear covariates (Appendix S1). We also carried out equivalent model selection for models constructed without autoregressive terms, and on thinned data, to evaluate the effects of autocorrelation on term selection. The results shown here were based on the model with lowest AIC from the model selection procedure with AR-1 terms; see Appendix S3 for models with $\Delta AIC < 2$ and full coefficients for top models from all three model selection approaches, which produced comparable results.

We performed the same procedure to select models predicting hourly Activity (binomial, 1/0) for each season. Due to the computational intensity of evaluating binomial models with autoregressive terms, we performed activity model selection on models without modelling residual autocorrelation (see Appendix S3 for full list of models with $\Delta AIC < 2$). We then included AR1 terms in the selected seasonal models.

2.5 Intra-individual consistency (activity regimen phenotypes)

There was substantial variance in hourly ODBA relating to the day/night cycle that dwarfed inter-individual variance. Therefore, it was not possible to adequately quantify

individual phenotypes using the random intercepts from hourly ODBA models (as constructed in Section 2.4). Instead, we used intra-class correlation (ICC) coefficients from seasonal models of total nightly ODBA (sum of hourly ODBA values from noon-to-noon—a cumulative measure of mechanical energy expenditure) as a function of the covariates selected in each seasonal hourly ODBA model (in these models, hourly weather covariates averaged between sunset and sunrise, derived from the *suncalc* package, Benoit and Achraf 2019). We performed an identical procedure with models of the total minutes each individual was active per night. We calculated ICC as the ratio of variance described by individual intercepts to total variance, after Nakagawa and Schielzeth (2010):

$$ICC = \frac{var(Individual)}{var(Individual + Residual)} \quad (2)$$

2.6 Inter-individual environmental response heterogeneity

We investigated inter-individual differences in ODBA expenditure per night in two ways: first, as detailed in Section 2.4, we included interactions between individual traits (age, sex, and BCI) and key environmental metrics in hourly ODBA and Activity models—thus investigating the potential drivers of differential plasticity. Second, we investigated further unexplained plasticity by re-computing the best seasonal model of hourly ODBA with random individual slopes for weather metrics. As very little activity occurs during daytime, we limited these re-computed models to data between sunset and sunrise. We built separate models with random slopes for each weather covariate in the model and compared these to the model without a random slope using AIC.

2.7 Diet analysis

As context for seasonal energy availability, we carried out a scat-based analysis of badger diet from Apr-Nov 2018 (spanning captures). We counted earthworm chaetae present in effluent washed through sieved scats, producing a measure of average chaetae found in 10 1-cm^2 squares on a Petri dish (after Kaneko et al. 2006, Cleary et al. 2009). We also calculated the monthly frequency of occurrence (FO = occurrences/samples) and relative frequency of occurrence (RFO = occurrences/total diet item occurrences) for each diet item. For further details, see Appendix S4.

3 Results

3.1 Individual and seasonal variation in ODBA and Activity patterns

Individuals exhibited substantially different total ODBA on the same nights, while subject to the same conditions (see Fig. 1). On average, the most active badger on a given night expended 1.9 times (range 1.1-5.9x) as much ODBA as the least active one.

Within this spread of individual energy expenditure patterns, badgers were active for the longest duration each night in autumn (mean minutes active per day = 569.8 ± 146.4 SD) and shortest in spring (502.3 ± 109.1 minutes), with intermediate values during summer (526.8 ± 110.0 minutes). Total nightly mechanical energy expended, however, was nearly identical in spring and summer (6.54 ± 1.58 and 6.51 ± 1.48, respectively) and somewhat higher in autumn (7.44 ± 2.29). Nightly ODBA schedules (from hourly ODBA models) exhibited two peaks, one around sunset and one before sunrise (Fig. 2a); Activity patterns were similar (Fig. 2b), although in autumn, Activity exhibited only a post-sunset peak, with no elevated probability of being

active before sunrise. While individuals were more likely than not to be active on any given night (Fig. 2b), 12.1% (spring), 20.9% (summer), and 27.3% (autumn) of all night-time

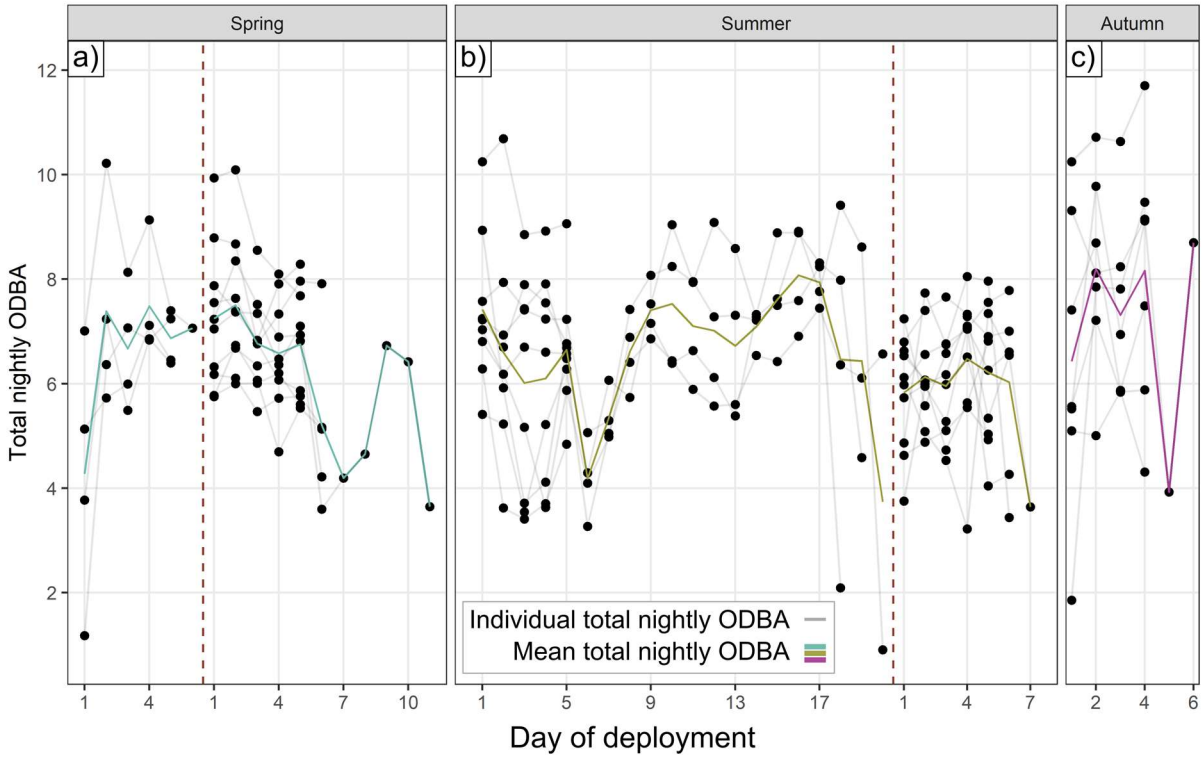


Figure 1. **Nightly ODBA variation**. Variation in total nightly ODBA expended by individual badgers (connected by grey lines) under the same environmental conditions in a) spring, b) summer, and c) autumn. Coloured lines show averages of nightly ODBA; vertical dotted lines separate datasets by year.

badger-hours (between ODBA peaks, inclusive) were below the Activity threshold, representing substantial incidence of episodes of nocturnal inactivity across all seasons. The converse was not true: we only found 2 cases of diurnal activity (09:00 – 15:00), both during summer. While summer and autumn post-sunset ODBA/Activity peaks occurred 1.5-2.5 hours after sunset, the spring peak coincided with the timing of sunset. Across all sampled individuals, spring and

summer post-sunset ODBA peaks were 36.9% and 37.2% higher than in autumn, respectively, while the pre-sunrise activity peak was only ODBA-intensive in spring, being 56.6% and 98.0% higher than in summer and autumn, respectively (Fig. 2a). Fewer seasonal differences between peaks were seen in the hourly Activity relationship, where >95% of badgers in all seasons were active during the sunset peak; in spring and summer, 90.9% and 85.1% of badgers, respectively, were active during the pre-sunrise peak, dropping to 66.4% at 03:00 (pre-inactivity; no second activity peak) in autumn (Fig. 2b).

Model fit was high for hourly ODBA in spring ($R^2 = 0.819$), slightly lower for summer ($R^2 = 0.718$), and lowest, though still explaining over 50% of variance, in autumn ($R^2 = 0.581$). Model fit was high for all hourly Activity models, with 94.6% (spring), 88.4% (summer), and 84.7% (autumn) of hours classified accurately as either active or inactive; Matthews correlation coefficients (MCCs), which measure correlations of classified data points while accounting for sensitivity and specificity (from -1 for perfect negative correlation to +1 for perfect classification), supported the high classification ability of seasonal models, with MCCs of 0.883 (spring), 0.761 (summer), and 0.701 (autumn). Five-fold cross-validation showed this classification success was robust to data sub-setting, producing accuracies of 94.3% (spring, MCC = 0.877), 88.3% (summer, MCC = 0.759), and 83.5% (autumn, MCC = 0.670).

3.2 Seasonal drivers of daily ODBA/Activity

3.2.1 Weather drivers

Figure 3 provides an overview of covariate coefficient values and presence in top models. Temp affected ODBA quadratically in both spring and summer, with a positive effect of higher temperatures below an optimum, and a negative effect beyond that (Fig. 4)—the particular

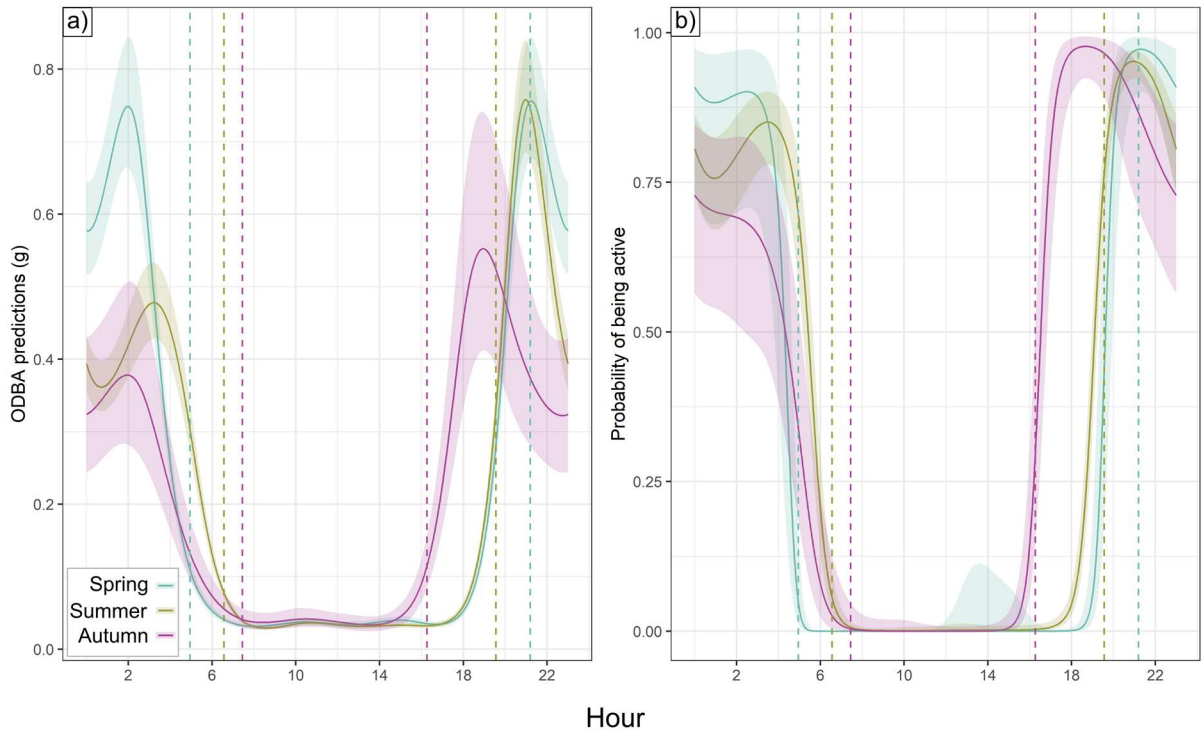


Figure 2. **Hourly trends by season**. Output predictions from smooth terms (cyclic cubic spline) in a) ODBA models and b) Activity models by season as a function of hour of day. Shaded region shows 95% confidence interval for hourly relationship; vertical dotted lines show average sunrise and sunset for deployment periods.

optimum was determined by BCI; see Section 3.4 for further details. In spring, higher temperatures were linearly associated with higher probability of activity, but summer activity probability peaked at intermediate temperatures (13.1 °C). In spring, Rain had a similar effect to Temp, with rainfall beyond an optimal point (0.8 mm hr^{-1}) reducing hourly ODBA. In autumn, higher rainfall correlated negatively with Activity, with a 25.6% lower probability of autumnal Activity (± SE, 2.2-47.4%) at the highest rainfall values (1 mm hr^{-1}). We did not find any effect of Rain on summer or autumn ODBA, or on spring or summer Activity.

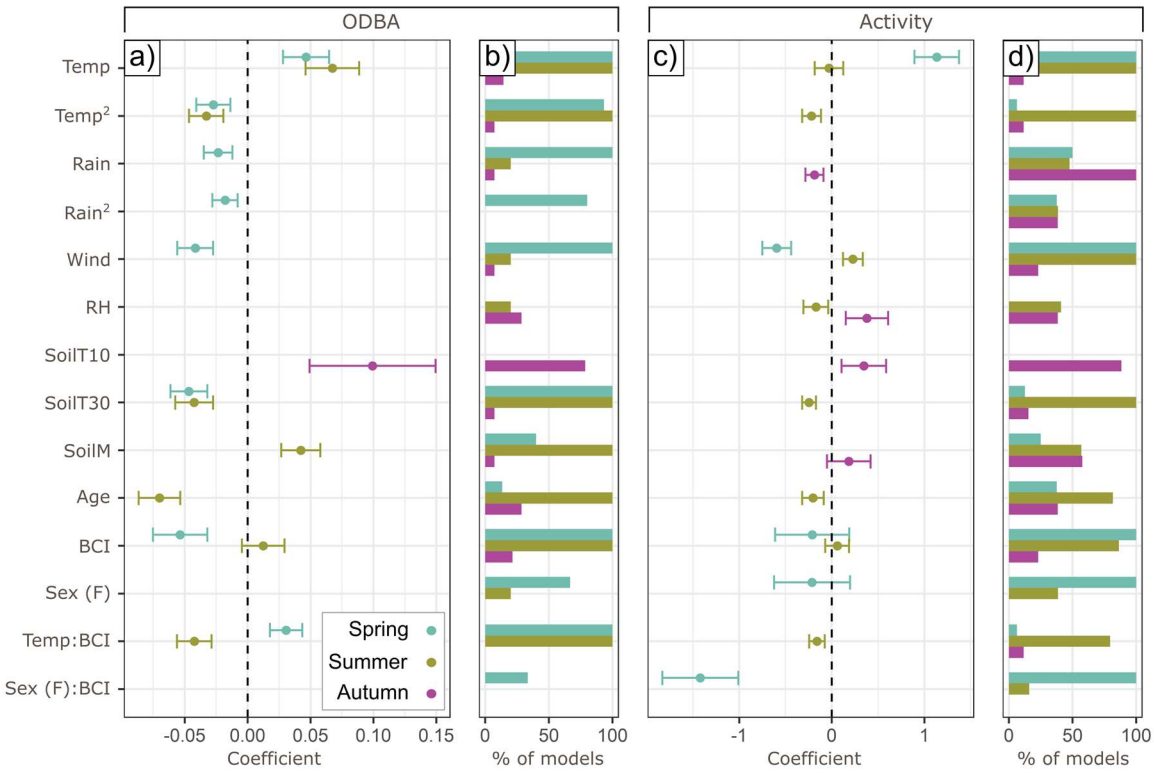


Figure 3. **Drivers of ODBA /Activity**. Panels a) and c) show the coefficients of lowest-AIC seasonal models for hourly ODBA and Activity (± SE); panels b) and d) show the percentage of models with ΔAIC < 2 of the best model that included the term.

Wind correlated negatively with both ODBA and Activity in spring, with the highest speeds (3.8 m s^{-1}) coinciding with a 24.2% ODBA reduction (12.1-34.7% SE) from that at lowest speeds (0.3 m s^{-1}), but correlated positively with summer Activity (modelled relationship predicts up to 19.4% higher likelihood of Activity at highest wind speeds—6.8 m s^{-1}, SE 9.2-28.7%). Although RH had a positive effect on Activity in autumn and a negative effect in summer, these effects lost statistical significance (p = 0.10 and 0.20, respectively) after accounting for autocorrelation and RH was not retained in the best ODBA model for any season.

$SoilT_{10}$ was only retained in autumn models (as it was collinear with Temp, and Temp was consistently selected over $SoilT_{10}$ in other models, Fig. 3b, d), with ODBA and

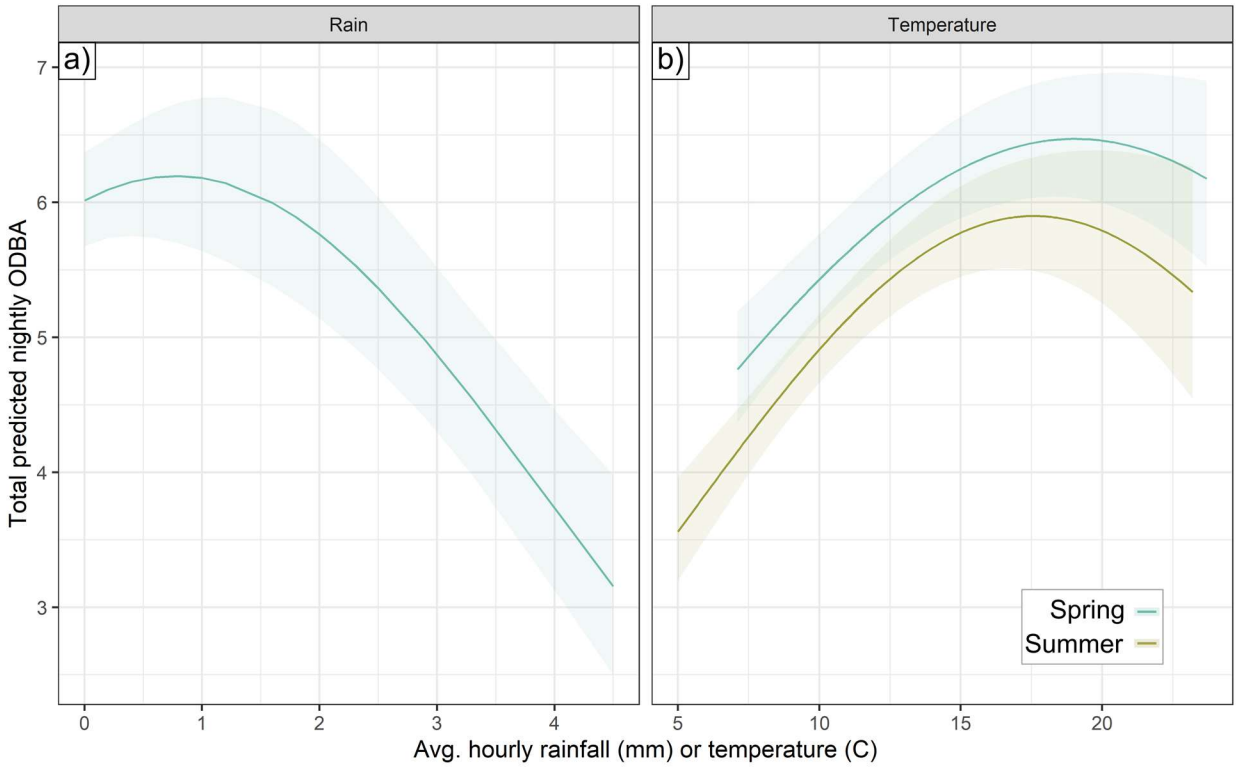


Figure 4. **Nonlinear effects of temperature and rainfall on nightly ODBA**. Total ODBA expended per day (sum of hourly predictions) as a function of a) Rain or b) Temp.

Activity being substantially higher at the highest soil temperatures (up to 44.3% higher activity probability, 9.2-71.6% SE, with total ODBA expended being 2.3-fold higher, 1.4-3.9x SE). SoilT_{30}, conversely, had a negative association with ODBA in both spring and summer (23.1%, 11.5-33.2% SE and 28.1, 15.6-38.8% SE reduction in nightly expenditure, respectively), and with Activity in summer. Higher SoilM values were associated with up to a 1.4-fold greater nightly summer ODBA (1.2-1.6x SE). SoilM was also retained in autumn Activity models, but fell below statistical significance after modelling residual autocorrelation ($p = 0.43$).

3.2.2 Intrinsic drivers of ODBA and Activity

An individual's age was related to ODBA and Activity only in summer, when it correlated strongly with lower ODBA (a 13 year-old badger's total per diem ODBA was 31.1% lower than a 1 year-old's, 21.0-39.9% SE) and slightly less strongly with lower Activity (only 12.8% reduction for the same contrast, 2.6-23.6% SE).

Sex was not retained in any ODBA models. However, in spring only, males (positive) and females (negative) had opposite relationships between BCI and Activity (Fig. 5). Although this negative female effect was in part shaped by one high-BCI female—the only one who had not lactated in the year of collaring—the interaction term remained significant ($p = 0.01$) after re-running the model to exclude that individual.

3.3 Intra-individual activity consistency (phenotypes)

After accounting for the terms retained in each seasonal ODBA model and accounting for sex, age and BCI, badgers still exhibited substantial intra-individual consistency with regards to both total nightly ODBA and the number of minutes active per night—that is, some badgers were consistently active for longer, and expended consistently more ODBA per night, than others.

ICCs for total nightly ODBA were highest in autumn (0.57) but also relatively high in spring and summer (both 0.35); for total nightly activity duration, spring and autumn ICCs were high (0.37 and 0.38, respectively) and somewhat lower in summer (0.27). These ICCs represent large differences between individual activity regimes that are not explicable by the modelled drivers of hourly ODBA, with a 1.25-, 1.49-, and 1.92-fold difference in average nightly ODBA expenditure from the most to the least ODBA-intensive badger (Fig. 6a, Fig. 7) and the most active badgers in spring, summer, and autumn being active for 2.2, 1.9, and 3.2 hours a night longer than the least active ones (Fig. 6b). For those individuals with data for multiple seasons,

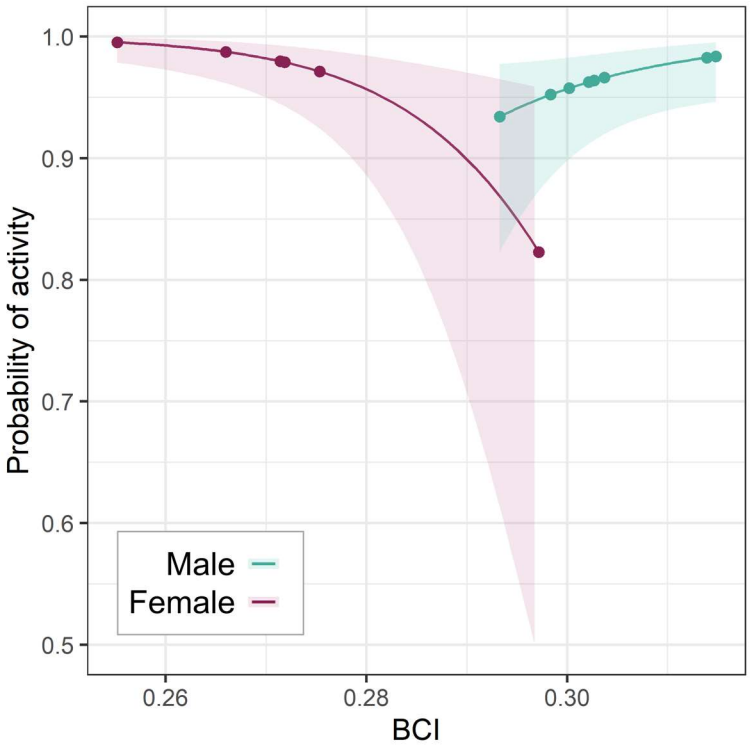


Figure 5. **Effect of BCI on spring activity probability**. Relationship between BCI and spring activity probability (with 95% CI) for the two sexes; points show the BCI values in the dataset.

there was no intra-individual correlation between spring and summer individual intercepts (Spearman rank correlation = 0.07 and -0.02 for total ODBA and minutes spent active, respectively); that is, the consistency of mechanical energy expenditure did not extend between seasons (sample size was too small to evaluate correlations with autumn intercepts).

3.4 Inter-individual response variability: explanatory factors

No model with a random slope for a weather metric had a lower AIC value than the best random-intercept model for each season. A random slope for temperature increased the log-likelihood of models in spring and summer, but not significantly so (p = 0.28 and 0.18, respectively). However, in spring and summer, individuals did differ substantially in their ODBA

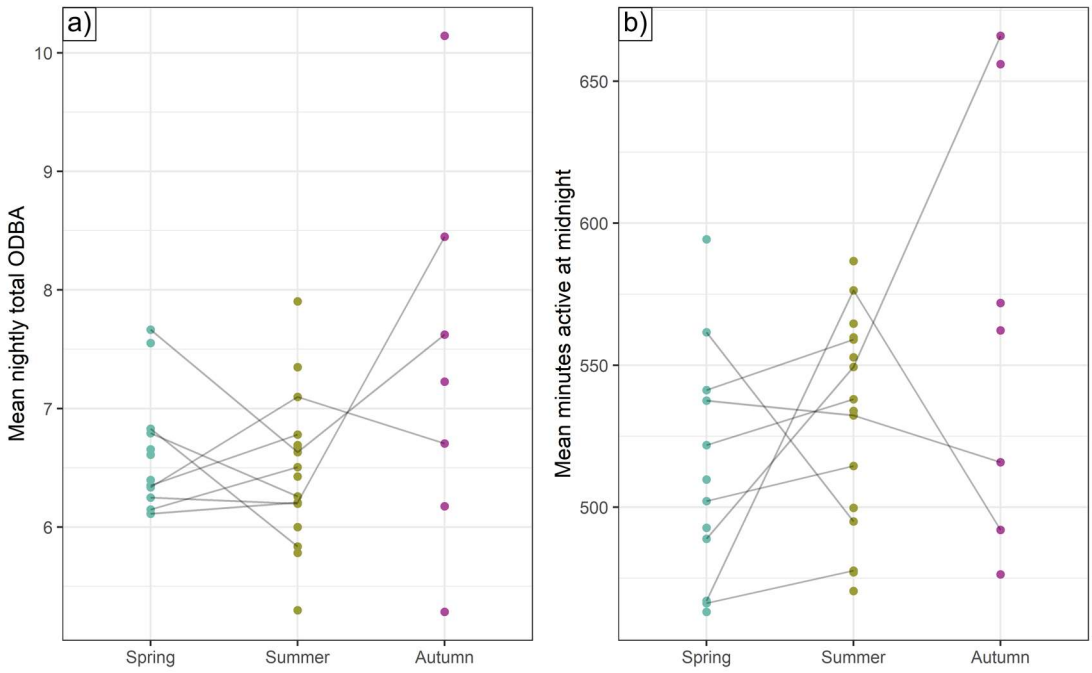


Figure 6. **Individual intercepts**. Under average seasonal environmental conditions and assuming average age and BCI, the expected a) total nightly ODBA and b) number of nightly minutes spent active for different individuals. Lines connect seasonal estimates for the same individual.

response to temperature as a function of BCI. In spring, the thinnest badgers collared (which exhibited BCIs in the 0.9th percentile for these social groups) had consistently high nightly ODBA (with predicted values from 6.0-7.2), while fatter badgers in our sample (61.3th percentile) had a positive relationship between Temp and ODBA, ranging from 3.9-6.4 (Fig. 8a); in summer (Fig. 8b), the relationship was the opposite, with thinner badgers (1.2th percentile) responding to Temp and ranging from total ODBA of only 2.6 to 7.0, while fatter badgers (97.4th percentile) remained more consistent around a mean of 5.6. This relationship was also evident for summer (but marginally significant, $p = 0.059$) but not spring Activity (Fig. 3c-d).

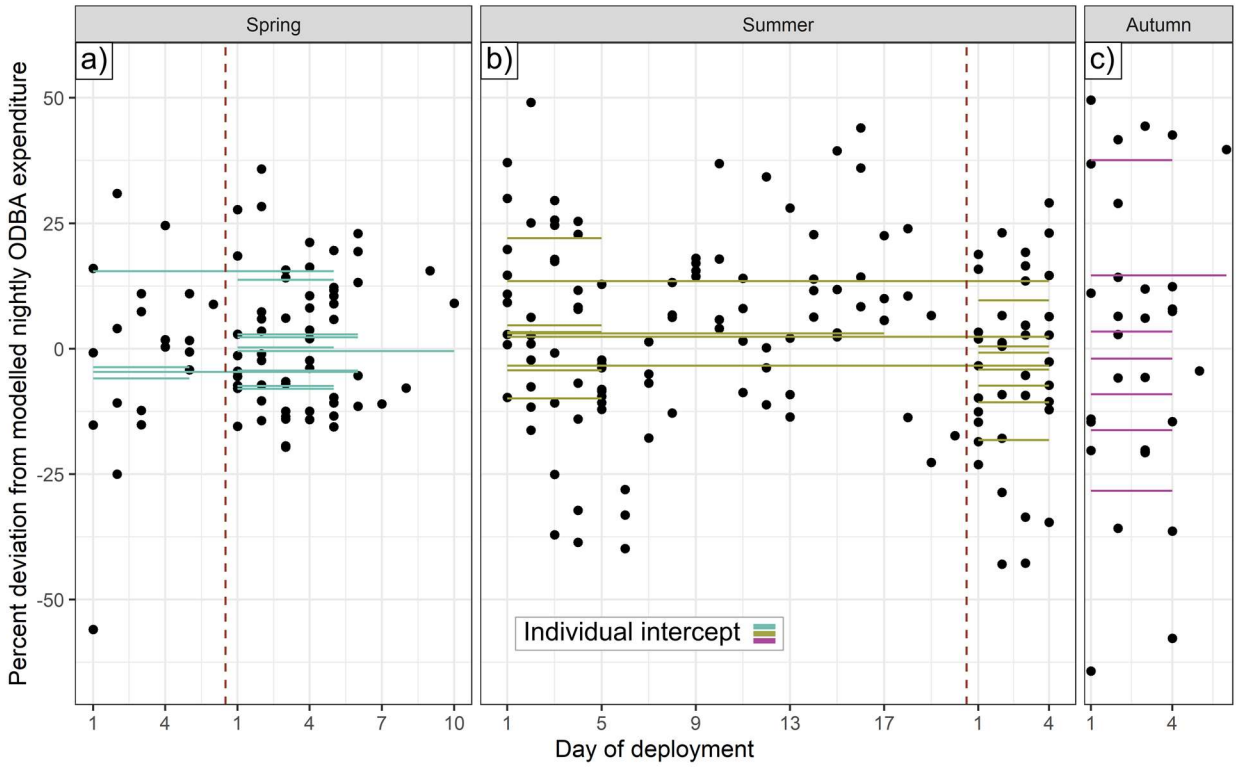


Figure 7. **Intra-individual consistency in nightly ODBA deviations.** Dots show residual deviations from average predicted nightly ODBA expenditure, in %, while horizontal lines show individual intercepts (average deviation from population mean). Vertical dotted lines separate datasets by year.

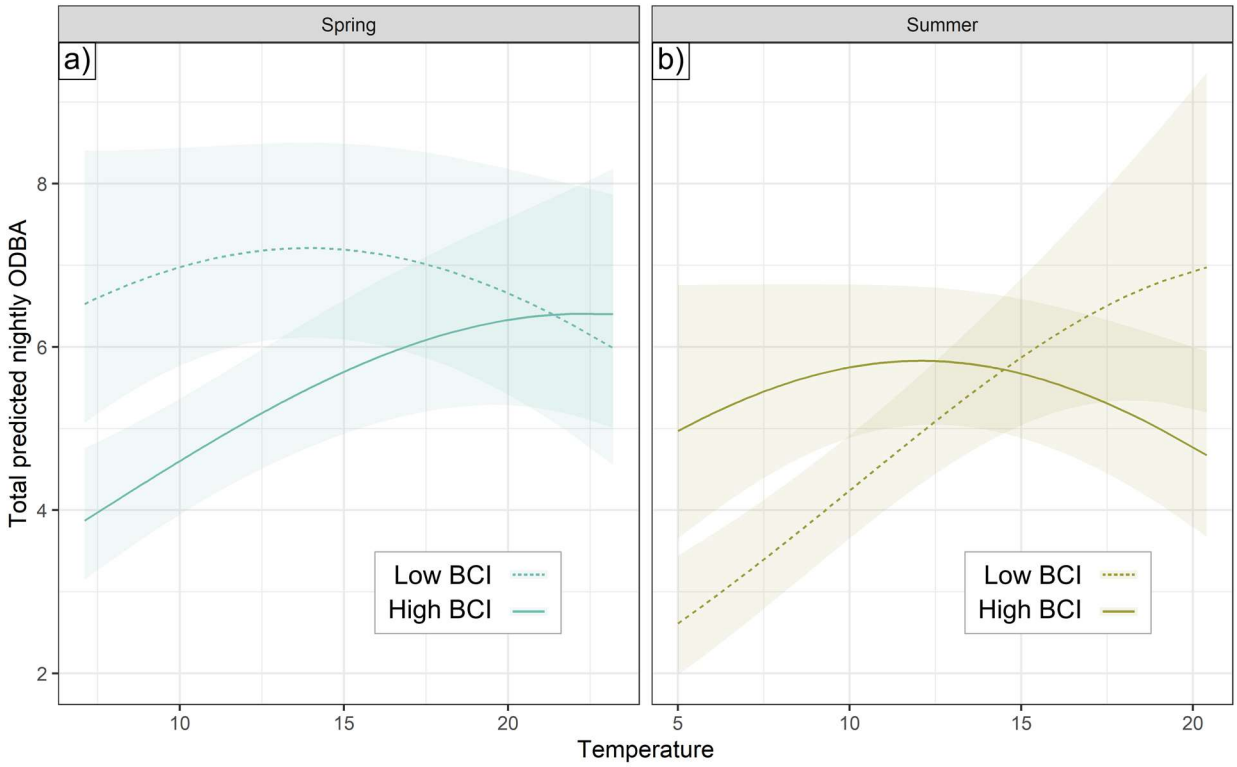


Figure 8. **Seasonal BCI-Temp interaction**. An individual's total ODBA in a) spring and b) summer (with 95% CI) varies differently according to temperature for low-BCI (dashed) and high-BCI (solid) individuals. Low and high BCI reflect the most extreme contrasts in our sample: see main text for values relative to population context. X-axis spans temperatures experienced by badgers between 17:00 – 7:00 hrs in seasonal data.

3.5 Diet

Badger diet varied opportunistically throughout 2018 (Fig. 9). We confirmed earthworms as the primary prey item for this population, with 77.9% average monthly FO (and 96% FO in March)—alongside year-long consumption of arthropods and snails (Fig. 9b)—but earthworm consumption was substantially lower during the summer months (Jun-Aug, Fig. 9a), with cultivated wheat (*Triticum aestivum var.*, FO = 76% in Jul) and the annual wild blackberry crop (*Rubus fruticosus*, FO = 84% in Aug) filling some of this gap. By September, blackberries were

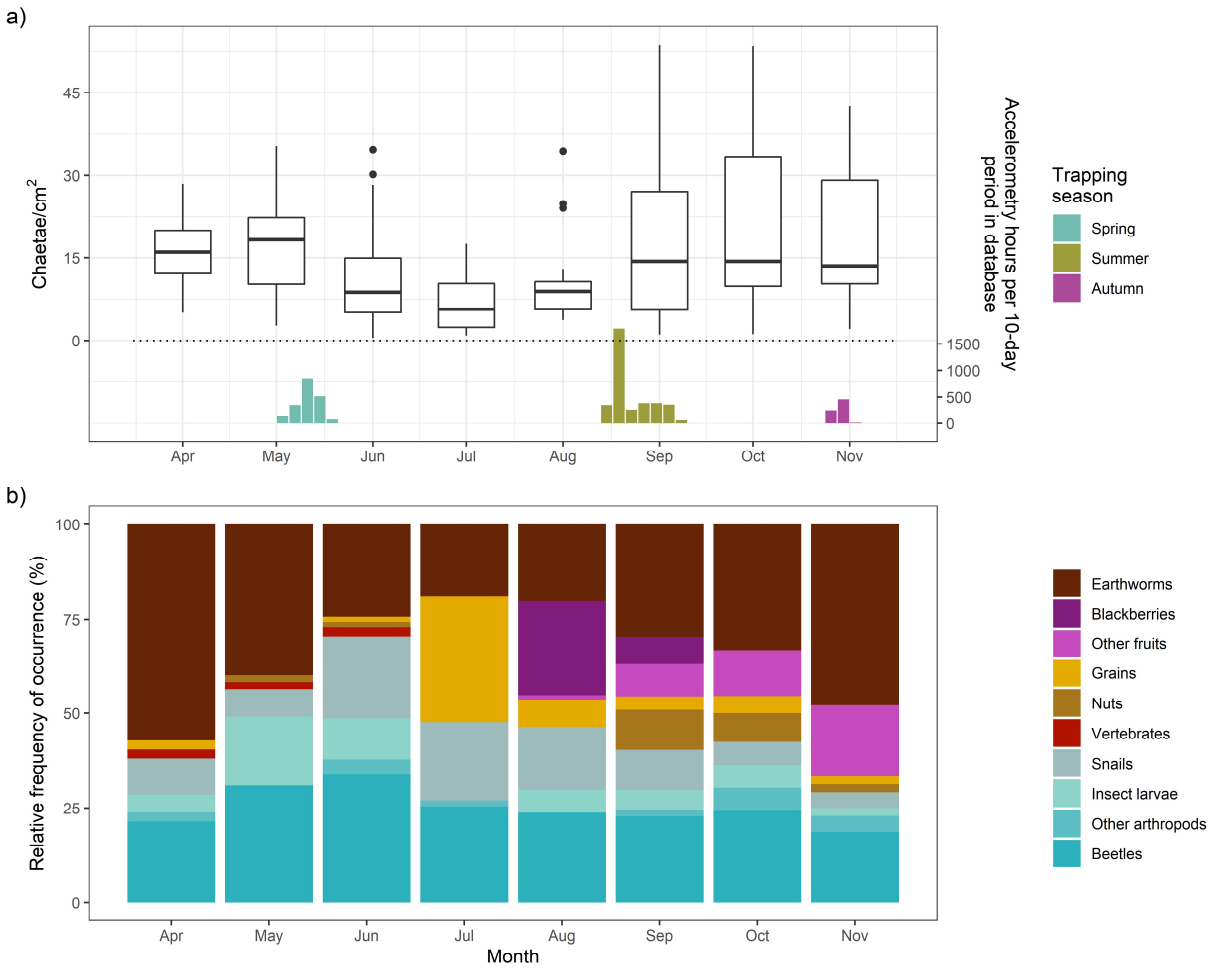


Figure 9. **Seasonal diet trends**. a) Average chaetae count in 10 1cm^2 squares for each scat sample collected and analysed, with bar plots indicating the timing and relative frequency of corresponding seasonal accelerometry data. Two observations from October were excluded from the plot due to particularly high chaetae count. b) Relative frequency of occurrence of diet categories in scats from a month.

supplemented with other fruits (FO = 32% in Sep) and hazelnuts (*Corylus avellana*), horse chestnuts (*Aesculus hippocastaneum*), and sweet chestnuts (*Castanea sativa*), which continued to be substantial diet components through the resumption of high earthworm consumption in autumn (Fig. 9b).

4 Discussion

Individual badgers, on the same day at the same site, and therefore under the same environmental and social conditions, exhibited substantially different daily ODBA and Activity expenditure, with some individuals expending almost twice as much mechanical energy as others on average (Fig. 1)—moreover, these differences remained consistent short-term within a season beyond the variance explained by intrinsic and extrinsic drivers (Figs. 6-7). Drivers explaining ODBA expenditure were complex (Fig. 3), involving responses at the hourly level to season-specific weather effects (Fig. 4), effects of life-history (Figs. 3, 5), and differential plasticity to prevailing weather according to individual body condition (Fig. 8).

Badgers in our study site forage predominantly on earthworms in spring (Fig. 9), which surface in an optimal mild temperature and humidity range (Macdonald 1983; Johnson et al. 2001). Accordingly, during our springtime deployments, Activity increased linearly with hourly temperature, while ODBA peaked at intermediate temperatures (optimum determined by BCI, see Fig. 8) and at precipitation levels of 0.8mm hr^{-1}. Activity during cooler and wetter conditions, exacerbated by wind chill (decreasing ODBA by up to 24.2% under the windiest conditions; see Williams et al. 2014), incurs higher thermoregulatory costs (Long et al. 2014, Williams et al. 2016), and thus warmer conditions are more conducive to activity. Strong winds may also disrupt badgers' ability to detect earthworms using scent or hearing (Macdonald 1980, 1983). The threshold-bounded effects of spring temperature and precipitation mirror non-linear relationships detrimental to badger body condition and survival (Nouvellet et al. 2013, Chapter 3), with the detrimental effects of high precipitation inferred to be linked to heat loss due to fur-soaking (Webb and King 1984). While shallow soil temperature ($SoilT_{10}$) in spring was not

influential on either ODBA or Activity (despite the spring models including a spring with unusually warm $SoilT_{10}$), warmer $SoilT_{30}$ was associated with up to a 23.1% decrease in ODBA.

During the summer deployments, ODBA again increased with temperature up to an optimum before declining (again, optimum determined by BCI). Unlike in spring, Activity also exhibited a tipping point, decreasing beyond 13.1 °C (just barely higher than the long-term average temperature for the period, see Table S1.1). We observed no effect of rainfall in summer; however, wind speed had a contrasting effect to spring, being associated with up to a 19.4% increase in activity probability under the windiest conditions (with no effect on ODBA expended). Consistent with the effects of $SoilT_{30}$ in spring, ODBA decreased by up to 28.1% with warmer $SoilT_{10}$ conditions, which also reduced Activity; in contrast, the highest SoilM conditions were associated with a 1.4-fold ODBA increase. We posit that moister, milder soil conditions, likely associated with greater earthworm availability, drove significant facultative ODBA increases; however, in summer, badgers depend less on earthworms in their diet and consume instead a greater proportion of berries and cereal crops (Fig. 9)—the availability of neither being affected by weather conditions. Unnecessary exertion in high ambient temperatures can lead to overheating, a major stressor for animals in the wild (Speakman and Król 2010). Therefore, heat often causes a hyperthermic lethargy response (Marino 2004, Nybo et al. 2014) in order to avoid serious sickness (e.g., Macy et al. 1985). The various summer weather effects observed suggest that, when freed from weather effects driving primary food availability, badgers instead sought to stay cool, reducing both ODBA and Activity when both the air and soil were warmer, and benefitting from a cooling breeze. Heat stress may be particularly pertinent to badgers, which evolved primarily as a cold-climate species (Madurell-Malapeira et al. 2011) and exhibit various physiological adaptations to minimise thermal loss (Newman et al. 2011).

In autumn, ODBA and Activity were less responsive to weather, especially air temperature, than in other seasons—although this likely stemmed at least in part from the smaller autumnal sample size. Only $SoilT_{10}$ (but not $SoilT_{30}$; and the effects of SoilM fell below significance after accounting for autocorrelation) had a significant influence, but this effect was substantial, associated with a 2.3-fold increase in ODBA and a 44% increase in Activity when soils were warmest—likely linked to conditions under which earthworms surfaced in the autumn (especially as the period studied had significantly colder $SoilT_{10}$ than the long-term mean for the same dates, $p < 0.001$, see Table S1.1). Badgers also sought to avoid heavy rain in the autumn, which reduced Activity by as much as 25.6%, corroborating patterns reported by Noonan et al. (2014). Henry (1984) reported that, when earthworms were scarce on frosty nights, the effectiveness of badger foraging was over ten times lower than during warmer nights, and thus badgers must reach a minimum autumnal body condition to mitigate overwinter survival risk (Chapter 2), enabling them to use fat reserves to support torpor. Accordingly, badgers in low body condition—those in need of foraging even under low likelihood of reward—have been found to be more active during years with poor autumn foraging conditions (Noonan et al. 2014).

Within the overarching context of extrinsic influences, we also established some clear effects of individual characteristics—sex, age, and body-condition—on mechanical energy expenditure. The limited number of sex contrasts in our dataset precluded rigorous analysis, but we detected no effect on ODBA, although we did find different relationships between BCI and springtime Activity in the sexes. Fatter females were less likely to be active than thinner ones in the spring, while males showed a (slight) positive BCI-Activity relationship (Fig. 5). Although the interaction term remained significant after excluding the highest-BCI female in the dataset, it was largely shaped by this individual, which was also the only female not to lactate for the year.

Reproduction takes a well-documented toll on female badger condition (Woodroffe and Macdonald 1995, Chapter 3). In this context, the higher Activity we observed in low-BCI reproductive females implies that residual effects of investments in reproduction reduce an individual's energy budget flexibility, as females must gain back the lost body condition or suffer reduced survival and reproduction probability for the next winter (Chapter 3). The elevated activity may relate to the slow rate of social integration for badger cubs relative to other social carnivores (Fell et al. 2006), during which time they are vulnerable to infanticide (Agrell et al. 1998) if their mother is not around to safeguard them (Macdonald et al. 2015). Although further effects of sex were not discernible from accelerometry, we were unable to trap and collar badgers during the peak post-partum mating period in mid-February (Sugianto et al. subm.b)—when sex-based activity might differ most (Macdonald and Newman 2002, Macdonald et al. 2010) due to welfare concerns (reflected in a legal closed season) linked to depriving neonatal cubs of maternal care.

While ODBA was not clearly related to sex, we found substantial inter-individual differences in plasticity tied to body condition: in spring, fatter badgers expended more ODBA with warmer temperatures, while low-BCI badgers exhibited consistently higher ODBA irrespective of temperature (Fig. 8a). Higher BCI might afford individuals some degree of buffering, enabling them to undertake less energy expenditure on cool spring nights, whereas thinner individuals must forage even under sub-optimal temperatures (Fig. 4). Individuals in poor condition may need to prioritise foraging activity irrespective of poor foraging conditions (Monteith et al. 2013), particularly if higher energy intake is required for energy-intensive life-history stages (e.g. lactation, breeding, Zhu et al. 2015, Iwama et al. 2017, Wascher et al. 2018). Alternatively, while early spring (~2 months prior to our springtime deployment) is the primary

mating season in badgers, individuals exhibit heterogeneous investments in social activity throughout the year (Noonan et al. 2018), and there is ample evidence that some individuals engage in more energy-intensive life-history strategies than others (Buesching et al. 2009, Chapters 2-3). Therefore, low BCI badgers in our sample may represent the outcome of an inflexible activity regime, whereby these individuals continue to expend energy during poor foraging conditions, but do so on social investments such as inter-sett visits (Ellwood et al. 2017, Noonan et al. 2018).

The BCI-plasticity relationship was reversed during summer (Fig. 8b). This resulted in a "down-shift" at higher BCIs of the inflection point temperature beyond which ODBA decreased, which implies that badgers, particularly fatter individuals, seek to avoid excess activity when well-insulated with fat because this may lead them to become too hot, with associated patho-physiological effects (Horowitz and Hales 1998). Not least, any insensible water loss due to panting to thermoregulate (Goldberg et al. 1981, Terrien et al. 2011) is challenging to replace in summer if puddles of water are scarce. Badgers generally acquire most of their fluid needs from an earthworm diet, but in summer a bias toward a cereal diet would require badgers to deliberately expend energy to search for water, which is a major constraint on badger distribution in arid Mediterranean regions (Rosalino et al. 2005). Such travel yields no energetic return or social benefit (see also Fuller et al. 2021). While diurnal animals may be able to partially compensate for warming conditions by shifting activity towards nocturnality (Levy et al. 2019), this is not an option for species that are already nocturnal, such as badgers, making reduced mechanical expenditure the only viable coping mechanism (Robertshaw 2006).

Ensuring food security is central to badger sociality (the Resource Dispersion Hypothesis, see Macdonald and Johnson 2015), and the super-abundant summer availability of cereals, fruits

and nuts is a certainty, irrespective of weather. In contrast, earthworm availability, the primary dietary item in the spring, is far less predictable and dependent on microclimate (Macdonald 1983). When food security is high, animals can simply rely on energy "income" (Atkinson and Ramsay 1995, Chang and Wiebe 2016), alleviating the need to carry substantial "capital" in the form of fat reserves, which can be burdensome, reducing agility (Gentle and Gosler 2001, Newman et al. 2011), and contributing to the possibility of overheating during warm conditions. While, as previously mentioned, somatic stores are necessary to sustain animals through low-food conditions (Chapter 3), these drawbacks likely dominate the energetic trade-offs of carrying excess fat stores during the plentiful summer months.

Further evidence suggesting that warm summer conditions may constrain mechanical energy expenditure in badgers was evident from the effects of age, where older badgers were both less likely to be active and expended less ODBA than young badgers during summer nights. The effects of heat stress on elderly individuals are well established from risks to human health (Kovats and Hajat 2008, Kenny et al. 2010, Kim et al. 2012). To mitigate this stress, hyperthermia triggers lethargy, largely through the generation of central fatigue involving changes in dopamine and serotonin levels (Nybo et al. 2014), resulting in reduced activity and consequently minimised thermogenesis (McKinley et al. 2018). Older badgers carry, on average, smaller fat stores (Chapter 3). The storage of fat is mediated by leptin in mammals (Meier and Gressner 2004), and so this may represent a physiological adaptation rather than a behavioural choice. Elsewhere (Chapter 3), we have reported that in badgers, somatic reserves in summer become more tightly linked to annual survival probability with advanced age, although it is not known whether the mortality occurs during summer or over winter. In terms of accessing food, it is unlikely that older badgers, or indeed badgers of any age, can monopolise feeding patches

because (i) badgers forage solitarily (da Silva et al. 1994), (ii) feeding hierarchies are not strongly expressed (Macdonald et al. 2002), and (iii) foraging patches are typically superabundant when available (e.g., worm patches, cereal fields, blackberry bushes: Macdonald 1983, da Silva et al. 1993). Therefore, the observed additional activity reductions seen in older badgers likely relate to a necessary avoidance of unsustainable loss of somatic condition during the summer.

Our data provide a window into the heterogeneity of "activity" schedules in wild populations. By way of technical corroboration, our observation of activity commencing before dusk and extending beyond dawn in our spring deployment (in May, during long days) matches direct observations of badgers reported elsewhere (Lloyd 1968, Kowalczyk et al. 2003). This relates to the duration over which badgers must be active to complete their nightly routines being relatively fixed and incompressible, to include not only foraging, but also mutual and self-grooming, scent marking, and territorial defence (see Macdonald et al. 2015). Although techniques such as camera-trapping can provide measures of activity schedules (e.g., Foster et al. 2013, Oberosler et al. 2017, Bartra Cabré 2020), fine-scale individual data are required to demonstrate the diversity of activity in wild populations (Brown et al. 2013). For instance, in our population, out of 271 badger-days of activity, only 126 (46.5%) involved one nonstop bout of activity—on a further 123 nights (45.4%), the badger became inactive for at least one hour and then active again (see dip in ODBA/Activity between peaks, Fig. 2), and one badger even became active, then inactive, then active again four full times in one night. The proportion of badgers without a break in activity was higher in spring (64.3%) than in the longer nights of the summer (35.7%) or autumn (53.3%) deployments. These varied activity patterns show how

individuals may tailor their energy budgeting not only from night to night, but also within a night, according to environmental constraints.

Ultimately, we demonstrated that substantial individual consistency occurred in the duration of nightly activity that could not be explained by these various extrinsic and intrinsic drivers. This finding underpins energy budgeting phenotypes beyond that captured by energy context—at least at the seasonal scale. Within seasonal deployments, high intra-class correlation coefficients for both the duration of nightly activity and total ODBA expended (Figs. 6-7) suggest that mechanical energy expenditure tactics were adaptive over a scale of weeks. This consistency did not extend between seasons; that is, a relatively high output individual might not remain so if instrumented in two successive deployments—although we stress our study was limited longitudinally. Crucially, however, after accounting for variation attributable to sex, age, and body condition, substantial heterogeneity in mechanical energy investment tactics was evident across the population: that is, given the exact same overarching conditions, two similar individuals might exhibit substantially different ODBA/Activity profiles (Fig. 7).

In addition to mechanical energy expenditure, an individual's total energy budget is also comprised by obligate basal metabolic rate (BMR) processes not measured by accelerometry (see Chapter 4), including homeostasis (Wilson 2015), immune responses (Cutrera et al. 2010) and thermoregulation (Oelkrug et al. 2015). Foraging incurs a necessary mechanical expenditure for sustaining these essential costs, and individuals must match their foraging regime to intrinsic differences in baseline requirements (Allison 1985). Moreover, inter-individual differences in the security with which these basal needs are met can lead to heterogeneous investment in "surplus" activities, such as exploration (Careau et al. 2009), social interactions (Schino 2001), territorial defence (Hurd 2006), sexual advertisement and other forms of communication (Allen et al.

2019), *inter alia*. For instance, high-BCI badgers in the studied population perform more inter-sett visits than do low-BCI badgers (Noonan et al. 2018), suggesting that badgers experiencing higher energy constraints reduce non-essential activities. Importantly too, many animals utilise inactivity (both sleep and torpor, Walker and Berger 1980, Boyles et al. 2020) in order to reduce energy expenditure (Lesku et al. 2006). This is particularly important as—at least as has been documented in humans (Hume et al. 2016)—low energy intake plus low energy expenditure (low energy flux), not energy surfeit, predicts future body fat gain.

According to the Niche Variation Hypothesis (Van Valen 1965), as the diets of individuals become more uniquely specialised, the cumulative niche breadth of a population increases (Svanbäck and Persson 2004, Bolnick et al. 2007). Niche specialisation is adaptive even within populations (Bolnick et al. 2007), and in badgers higher social group size militates for greater specialisation (Sheppard et al. 2018). The social groups in our current study were relatively large (avg. of 10.1 badgers from 2011-2016, vs. 4.3 avg. elsewhere in the population), even within this high-density population (Sugianto et al. subm.b, Chapter 2), promoting trophic niche specialisation. As a broader consideration, individuals must not only compete with conspecifics (Levis et al. 2020) to try to gain a selective advantage in how they translate lifetime energy efficiency into maximal fitness (Parsons 2005), but also within trophic guilds (e.g., Tsunoda et al. 2017).

Although plasticity to environmental change is generally associated with population resilience (Schindler et al. 2015, Beever et al. 2017), because individuals are simultaneously responding to existential selection pressures differently, it comes with costs to efficiency (Wolf et al. 2007, Pintor et al. 2014). Hypothetically, in stable environments, a single optimal strategy may become canalised; but for a generalist omnivore with a variable social system, such as the

badger (Macdonald et al. 2015), and in a seasonally temperate mosaic habitat (a multidimensional niche, Machovsky-Capuska et al. 2016), a single optimal solution to maximal fitness is not achievable—as opposed to species with a more specialised diet, or that benefit from group hunting, which promote higher activity fidelity among conspecifics (e.g., Prugh et al. 2008). Within populations with a wide niche breadth, substantial energy-balancing diversity can influence pace-of-life syndromes (POLS, Dammhahn et al. 2018)—the co-variation of behavioural and physiological traits (linking, for instance, energy requirements and engagement in surplus activity, Careau et al. 2008, Réale et al. 2010). In the studied badger population, there is demographic (Chapter 2), developmental (Sugianto et al. 2019b), and endocrinological (Buesching et al. 2009) evidence of variation in pace-of-life. While here we cannot link these various facets of POLS directly, POLS may explain the occurrence of substantial inter-individual differences, unaccounted for by mechanical energy expenditure.

In order for diverse tactics to persist within populations, they must either exhibit equivalent fitness or those that underperform under one environmental scenario must have a selective fitness advantage under different conditions (Kentie et al. 2020). As energy availability can vary substantially as a function of stochasticity in the environment, this balancing may occur through the minimisation of fitness variance (e.g., through elevated somatic stores at the cost of expenditure on reproductive competitiveness)—a phenomenon termed "bet-hedging" (Starrfelt and Kokko 2012, Rajon et al. 2014). Consequently, patterns can emerge when fluctuating selection pressures (Bell 2010) alternatively favour suites of energy expenditure tactics, potentially clustering populations into high- and low-competition phenotypes (e.g., Grémillet et al. 2018). This aligns well with the diversity of somatic storage tactics adopted in this studied population, despite the reproductive benefit of certain body-condition phenotypes (Chapter 3).

Although we observed low correlation between seasonal activity profiles in this study (Fig. 6), energy-balancing tactics may differ for the same individuals between seasons. For instance, female badgers typically exhibit relatively low BCI in spring, but both high autumnal BCI and having bred successfully in one year are positively predictive of reproductive success the following spring (Chapter 3). This suggests that these same individuals adopt tactics to maximally gain weight between spring and autumn.

Rapid environmental rapid change—and particularly climate change—exerts a disruptive selection pressure on populations (Pélabon et al. 2010), likely impacting the distribution of energy expenditure tactics. While more tactics will likely under-achieve, some options may deliver greater fitness under novel conditions—or, at least, superior fitness to other individuals (Schindler et al. 2015). Whether these alternatives become established (and thus constitute a long-term population adaptation, Chevin et al. 2010), however, depends on whether conditions resolve upon a new stable point, or continue to vary. Badgers, with their wide bioclimatic niche (Silva et al. 2017) and distribution (Johnson et al. 2002), provide a tractable model for considering the ramifications of such population changes. Outside of the UK, Ireland, and southern parts of Scandinavia, less consistent energy landscapes support much lower densities of badgers (Griffiths and Thomas 1993). Thus, although there is clearly sufficient potential plasticity for badgers to cope with a wide range of environmental constraints, this comes with substantial changes to the social structure of populations (see Macdonald et al. 2015, Sugianto et al. subm.b).

Here we focused on mechanical energy expenditure as a source of energy-budgeting diversity; however, it is crucial that the study of eco-energetics attempt to engage with measuring broader aspects of total daily energy expenditure (e.g., Green et al. 2009). Nevertheless, this

often proves challenging in free-living wild species, and entails a lower data resolution (Butler et al. 2004, Anderson and Jetz 2005, see also Chapter 4). This can preclude detailed analysis of how environmental constraints drive different responses in individuals. By integrating a more thorough understanding of the intrinsic and extrinsic variables affecting how an organism spends energy to ensure its survival and reproductive fitness—and building an understanding of how diverse responses to these are maintained—we may be better positioned to anticipate critical points in population and species viability (Humphries et al. 2004, Bonebrake et al. 2020), prior to catastrophic responses (Isaac 2009).

5 Authors' Contributions

Conceptualization: Julius G. Bright Ross and Chris Newman; Accelerometer programming: Andrew Markham; Data collection (biological): Julius G. Bright Ross, Chris Newman, Christina D. Buesching, Erin Connolly, and David W. Macdonald; Data collection (climatic): Denise W. Pallett; Analysis: Julius G. Bright Ross and Michael J. Noonan; Writing: Julius G. Bright Ross; Editing: all authors.

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Chapter 6

Links between somatic condition, life history, and energy budgets reveal heterogeneous energy management tactics in a wild population of European badgers (Meles meles)

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Abstract

Optimal management of voluntary energy expenditure is crucial to fitness among wild animals. Nevertheless, individuals from the same population undertake diverse energy-budgeting tactics under the same environmental conditions. Here we investigated individual drivers and heterogeneity of energy expenditure in a wild population of European badgers (*Meles meles*) by quantifying individuals' overall dynamic body acceleration (ODBA, from tri-axial accelerometry) and total daily energy expenditure (DEE, from doubly-labelled water). Both ODBA and DEE were highly variable and exhibited season-specific relationships with individual energetic context. DEE scaled allometrically with body weight, but only in summer and autumn; reproductive female badgers were lighter than other badgers during the spring but expended on average 350 kJ/day more than allometric scaling would have predicted. Older badgers expended significantly less energy on movement during the summer, which resulted in a marginally significant reduction of DEE. The ratio of ODBA to DEE (OD), a measure of proportional investment into movement, correlated more significantly with next-season body condition than did either energetic metric unilaterally ($p = 0.002$, $R^2 = 0.50$). However, the majority of individuals engaging in riskier tactics were either younger badgers or reproductive females; both life-history factors that partially—but not entirely—reduce the mortality risk associated with low body condition in badgers. The trade-offs associated with these risky energy-budgeting tactics illustrate how different energetic phenotypes are maintained within wild populations, potentially key to population resilience under current and future rapid environmental change.

Keywords: *Activity; doubly-labelled water; energy budgeting; individual heterogeneity; life-history energetics; tri-axial accelerometry; whole-organism energy expenditure.*

1 Introduction

In wild animal populations, energy is a limited currency (Chimienti et al. 2020), and maintaining a positive balance between intake and expenditure is key to survival (Anholt and Werner 1995, Monteith et al. 2013). Certain expenditures are involuntary, such as growth, development, and somatic maintenance (Rey-Rassat et al. 2002, Toïgo et al. 2006), thermoregulation (Oelkrug et al. 2015), and immune responses (Lochmiller and Deerenberg 2000, Cutrera et al. 2010). Even sleep, as a passive alternative to activity, plays an obligate role in energy budgeting (Lesku et al. 2006). Moreover, when animals reproduce, they must meet obligate costs from ovulation, gestation (Atkinson and Ramsay 1995), lactation in mammals (Zhu et al. 2015), and other forms of offspring provisioning (Regular et al. 2014). Energy budgets also include "voluntary" expenditures, such as activity not dedicated to foraging. These voluntary activities can provide individuals with fitness advantages, whether by securing resources through exploration (Careau et al. 2009) and territorial defence (Hurd 2006), or improving reproductive success by finding mates (Swierk and Langkilde 2019) and intra-sex contests (Réale et al. 2009). However, as with many non-motile reproductive costs (e.g., sexual advertisement/handicapping, Grose 2011, signalling to conspecifics, Allen et al. in prep), the degree and extent to which individuals engage in voluntary activity must be weighed against obligate expenditures.

The physiological processes underlying obligate energy expenditure are regulated extrinsically by exposure to environmental conditions (e.g., weather Nilsson et al. 2016, parasitism, Hicks et al. 2018, *inter alia*), but also by individual life-history traits (Stearns 1977, Nylin and Gotthard 1998) and somatic condition (Monteith et al. 2013). Physiologically, populations exhibit a wide variety of "energetic floors" determined by changes, or sustained

inter-individual differences, in the hormones regulating metabolism (thyroxine, insulin, and appetite regulators: leptin, ghrelin, adiponectin, and resistin; Meier and Gressner 2004, Johnstone et al. 2005), allometric relationships between basal metabolism and organ size (Meerlo et al. 1997, White et al. 2009), sex-specific endocrine expression (Wascher et al. 2018), age-related declines in basal metabolic rate (Even et al. 2001), and ability to reach normothermia autonomically (Terrien et al. 2011, Nybo et al. 2014). Body size is also pertinent to energetic demands and trade-offs, with basal metabolic rate (BMR) and mechanical costs of movement scaling allometrically (Bale et al. 2014, Thomas et al. 2019, but see also Cui et al. 2020). These various influences on involuntary costs produce individual-specific constraints on the optimisation of energy allocation to achieve maximal fitness (Elliott et al. 2014).

Energetic expenditure is supported by energy intake through foraging behaviour, which itself presents a further expenditure, where securing access to food may incur territory defence and marking costs (Rosell et al. 2008, Mares et al. 2012), and/or costs of competition or collaboration with conspecifics (Portier et al. 1998, Sheppard et al. 2018) or co-occurring species (e.g., Hisano et al. 2017, Tsunoda et al. 2017). Trophic niche breadth can also dictate different suites of energetic costs associated with carnivory, omnivory, and herbivory (Anderson and Jetz 2005). For many animals, predation or disturbance risk (real, or perceived, see Clinchy et al. 2016, Tsunoda et al. 2019) can preclude optimal foraging, although these risks are often predictable in time and space (Dhellemmes et al. 2020, Diserens et al. 2021). The temporal link between foraging and energy availability may be complicated by caching excess food, storing body-fat, and/or circumventing times of low food availability (or high activity cost) through torpor and hibernation (Iwasa and Kubo 1997, Humphries et al. 2003, Chapter 3). Ultimately, however, sub-optimal commitment of energy incurs a cumulative cost to an individual's survival

and reproductive probability (Mcnamara and Houston 1997). Therefore, characterising what proportion of whole-organism energy expenditure is committed to activity (i.e., mechanical expenditure), and what the fitness costs of this activity may be, is crucial for assessing the survival potential of the individual, population, or species (Grémillet et al. 2018).

Changes in food availability, foraging costs, or basal maintenance requirements due to environmental conditions force animals to attempt to rebalance their energy budgets accordingly (Elliott et al. 2014); their ability to do so successfully will vary depending on whether such changes are predictable, stochastic, or catastrophic. Predictable seasonal changes in food availability and the energetic costs of foraging under adverse conditions typically drive synchronised adaptations to cope with shortage and/or capitalise on abundance (Humphries et al. 2003, Ims and Fuglei 2005); this often includes changes in the intensity of voluntary activity (Fossette et al. 2012, Efrat et al. 2019, DeSantis et al. 2020). Animals support these changes in seasonal expenditure by either elevating total energy expenditure when possible (or depressing when necessary: the "Peak Demands" hypothesis, Zhu et al. 2015) or reallocating energy expenditure—including activity—to maintain equivalent expenditure as costs change (the "Reallocation" hypothesis, Krockenberger 2003, Bozinovic et al. 2004). Depending on seasonal food choices, weather condition stochasticity can affect both the mean optimal foraging regime and the range of viable options achievable (Amélineau et al. 2014, Hernández-Pliego et al. 2017, O'Mara et al. 2019). Inclement weather (too hot/cold; precipitation) can increase thermoregulatory costs (Kneebone et al. 2018)—though, particularly at fine timescales, animals can cope with these constraints behaviourally (Terrien et al. 2011), as seen in fossorial animals that can use dens as refugia (Williams et al. 2014, 2016, Noonan et al. 2015). Finally, extreme events (e.g., century droughts, Young et al. 2017, extreme predation events, Evans et al. 2020)

substantially affect energy budgeting, potentially causing large-scale demographic changes (Scheffer et al. 2001)—a risk factor exacerbated by human-induced rapid environmental change (HIREC, Sih 2013).

Within this framework, individuals can exhibit differences in their energy budgets and activity regimens under the same contemporaneous conditions, even after accounting for sex, age and body weight (Careau et al. 2008, Binder et al. 2016). The pace-of-life syndrome hypothesis (POLS, Réale et al. 2010) posits that the life-history trajectory each individual follows will dictate unfolding energetic profiles across their lifetimes (Dammhahn et al. 2018, Chapter 2). Different positions on the POLS variation axes represent trade-offs under various environmental conditions, where high energy expenditure can produce fitness advantages under favourable conditions but elevate risk under detrimental ones (Metcalfe et al. 2016). Of particular interest within this diversity of energy-allocation tactics found within populations is how individuals differ in activity profiles (Hertel et al. 2020), where individual behavioural plasticity often provides the best proximate response to ensure population resilience (Parmesan 2006, Chevin et al. 2010, Merilä and Hendry 2013, Beever et al. 2017).

Measuring energy expenditure in wild animals under natural conditions can be methodologically challenging (where respirometry techniques cannot be applied; Green et al. 2009, Halsey et al. 2009), limiting sample sizes. However, whole-organism energy expenditure ("daily energy expenditure", DEE) can be measured reliably in the field using doubly-labelled water (Speakman 1997), while mechanical energy expenditure ("overall dynamic body acceleration", ODBA) can be quantified using accelerometry (Wilson et al. 2006, Qasem et al. 2012). Here, we use these two methods to measure contemporaneous individual variation between mechanical and total energy expenditure within a wild population of European badgers

(*Meles meles*). Within the same population, badgers concurrently exhibit substantial variation in inter-individual life-history (Chapter 2), hormone profiles (Buesching et al. 2009, Sugianto et al. 2019b), activity regimes (Chapter 5), and consistent body condition profiles (Chapter 3).

We first examine (seasonally) which individual traits (sex, age, and body weight) affect the active component of energy expenditure (ODBA) and whole energy budgets (DEE). If all individuals partition voluntary and involuntary expenditures similarly, irrespective of their different life-history traits, both metrics should respond to the same drivers. Conversely, if individuals budget energy differently after accounting for individual traits, this would indicate a wide diversity of energetic tactics, or demands, under the same prevailing conditions. We use the "fraction of energy spent on activity" (ODBA/DEE, "OD", where ODBA is unitless) to characterise the variability in these energetic tactics. We also examine how these metrics interplay with next-season body condition—and how variation relates to mortality risk, using models constructed using past data from this population—potentially shaping selective advantages for long-term energetic phenotypes able to adapt to future climate (and habitat) change.

2 Methods

2.1 Study site and animal captures

All data were collected in Wytham Woods (Oxfordshire, England; 51°46'N, 1°20'W), in the context of a 32-year demographic badger study (Macdonald et al. 2015, Chapter 2). In May ("spring"), September ("summer"), and November ("autumn") of 2018-2019, we used string-trigger traps to capture badgers at three setts (dens), then transported them in holding cages between 7:00 – 9:00 am to a central field station. We sedated individuals with 0.2 mL ketamine hydrochloride/kg body weight by intramuscular injection (Sun et al. 2015, Sugianto et al. 2019a)

and recorded biometric information, including unique tattoo identity (assigned on first capture, see Chapter 2 for most recent overview of the study), weight (W, to 0.1 kg), body length (BL, to 5 mm), molar tooth wear (scale 1-5, to estimate ages of un-tattooed individuals, n = 1 in the present study), and for females, whether the badger was lactating/exhibited evidence of recent lactation. We computed a body condition index (BCI, Labocha et al. 2014; see also Chapter 3) as $\log_e(W)/\log_e(BL)$.

2.2 Doubly-labelled water administration and collaring

We quantified daily energy expenditure (DEE, kJ/day) using the doubly-labelled water (DLW) technique (Butler et al. 2004). The method has been validated by comparison to indirect calorimetry in a range of animals (e.g., Speakman and Racey 1988). In order to avoid repeated sedation of study animals, we estimated individual body weight prior to injection while in holding cages (deducting the weight of the cage and handler), and administered DLW (650,765 ppm ^{18}O, 342,395 ppm ^{2}H) via intramuscular injection according to the equation $Mass_{DLW\ (g)} = 0.31*W\ (kg) + 1.46$. We weighed syringes before and after injection (±0.0001g) to compute the precise mass of DLW injected. After 3-3.5 hours, we sedated badgers as in Section 2.1 and collected blood samples by jugular venipuncture into vacutainers with EDTA anticoagulant, then heat-sealed sub-samples into 100µL glass capillaries, stored at room temperature. Normally, a pre-injection blood sample would be used to deduce individual background isotope ratios. As we did not sedate animals prior to DLW injection, we could not collect these background samples and instead collected 5-9 samples from other individuals (sample size depending on availability) captured from the same social groups during that same 3-day trapping session, and used their average as a background enrichment level. We released badgers at the sett where they had been captured, then attempted to recapture these same individuals 6-10 days later (57/65 recaptured

within this DLW window, chosen as an estimate of the time before isotope elimination would reach background levels). All individuals were equipped with tri-axial accelerometers (SensorTile turn-key sensor modules, STEVAL-STLK01V1) attached to padded dog collars and zip ties (for further details, see Chapter 4). Upon recovery, we sedated individuals, identified them by tattoo, retrieved collars, and drew a further blood sample, which was sealed and stored as above. Time of isotope administration and blood sampling was carefully recorded.

2.3 DEE estimation

Analysis of isotopic enrichment of blood samples was performed blind, using a Liquid Isotope Water Analyser (Los Gatos Research, USA) (Berman et al. 2012). We vacuum-distilled blood from storage capillaries (Nagy 1983), then ran the resulting distillate alongside five lab standards for each isotope, using international standards to correct delta values to ppm. We estimated DEE using a single-pool model, as recommended for animals below 10kg and used elsewhere for badgers (Barbour et al. 2019). Specifically, we used equation 7.17 from Speakman (1997).

We analysed 57 samples from 30 badgers across two years (n spring = 17, summer = 21, autumn = 19). Of these, 2 samples had isotope enrichment at recovery too close to background to calculate DEE and a further 14 exhibited discrepancies consistent with improper dosing, likely related to the difficulties of injecting alert animals. Ultimately, we obtained reliable DEE estimates for 41 samples (30 different individuals with some repetition of the same individuals across seasons; n spring = 14, summer = 14, autumn = 13).

2.4 ODBA estimation

We used ODBA as a measure of mechanical energy expenditure (Wilson et al. 2006, Qasem et al. 2012). ODBA (in *g*, ms^{-2}) can be computed as the L1-norm of the three channels of acceleration:

$$ODBA = |A_x| + |A_y| + |A_z| \quad (1)$$

Where $A_{\{x,y,z\}}$ represent the difference between the mean and the midpoint of each channel over a 2-second window, divided by 2^{14}, the basis for *g* programmed for these accelerometers. We averaged these 2-second values over each day of collar data, then averaged these in turn to produce a mean daily ODBA value for each individual. We omitted first and last days of deployment from each average ODBA calculation, as we have detected a significant reduction in first-day post-release activity (Chapter 5) and the badger spends at least a fraction of the last day of deployment in a cage (mean days used for each ODBA deployment = 5.3).

Of the 65 accelerometry collars deployed, 63 were recovered and 41 returned adequate data (in particular, a hardware incompatibility resulted in no data recovered from autumn 2018; other failures stemmed from cable disconnections and/or water damage). This resulted in 41 ODBA data sets for 19 badgers (n spring = 15, summer = 15, autumn = 7; see Chapter 5).

2.5 Drivers of ODBA and DEE variation

We tested the intrinsic drivers of each of our energetic metrics using linear models. First, we explored whether either metric exhibited allometric scaling, permitting the scaling relationship and to change by season (where spring, summer, and autumn equal 1 in Eq. 2 if the data point derives from the respective season and 0 otherwise):

$$Metric\ (DEE\ or\ ODBA)\ =\ \alpha_1 W^{\gamma_1 Spring + \gamma_2 Summer + \gamma_3 Autumn} \quad (2)$$

To suit a linear modelling framework, we used a log-transformation of the response and predictor variables:

$$\log_e(metric) = \log_e(\alpha_1) + \beta_1 Spr \cdot \log_e(W) + \beta_2 Sum \cdot \log_e(W) + \beta_3 Aut \cdot \log_e(W) \quad (3)$$

We further permitted intercept to vary by season independent of this scaling equation, in order to relax the assumption that each metric necessarily exhibited a positive power relationship. However, as the range of weights spanned within this population was relatively small on a log-scale (0.76, see also Fig. 1 for approximate linearity of relationship), all further modelling used the more parsimonious linear scale.

We constructed models of DEE and ODBA as a function of body weight, age, season, and sex, as well as body weight:season and age:season interactions. As there were slight collinearities between body weight and age within season (see also Chapter 3), we did not include these two terms in the same models. This resulted in four full models, subject to stepwise selection.

2.6 Covariation of ODBA and DEE

ODBA and DEE data overlapped for 30 observations across 19 badgers (n spring = 12, summer = 13, autumn = 5). For these observations, we examined the relationship between the two metrics using linear models, at both the whole-study and seasonal scale. We controlled for the effects of weight on DEE in these models. We also computed the ratio of ODBA/DEE (OD) for each overlapping observation.

2.7 Energetic correlates of next-season body condition

We investigated the relationship between seasonal energy expenditure metrics (DEE, ODBA, and OD) and next-season body condition indices (BCI). Specifically, we modelled the

residual of individual BCI (BCI_{res}) after controlling for the effects of age, calendar date, and sex in a generalised additive model (GAM, package *mgcv*, Wood and Scheipl 2020) constructed using data from 27 years of badger captures from this population (n = 5,866; see Chapter 3 for further details). Badgers were re-captured the following season when possible, providing this value for 25/41 of ODBA records, 26/41 of DEE records, and 19/30 of the overlapping records. As accelerometers failed the first autumn and restrictions associated with the 2020 COVID-19 pandemic precluded spring 2020 trapping, we were unable to test the effects of autumn ODBA or OD on spring BCI.

Finally, we used BCI_{res}-survival relationships modelled previously within this population (Chapter 3) to quantify the cost in survival probability associated with the observed variability in individual BCI_{res}.

3 Results

3.1 Drivers of ODBA and DEE

Both ODBA and DEE varied extensively under the same environmental conditions. ODBA did not differ substantially from season to season and was highly variable between individuals in all seasons (SD = 15.9%, 18.4%, and 24.4% of the mean in spring, summer, and autumn, and the most active badger expending 1.6, 2.2, and 2.1 times as much as the least active badger in each season). DEE was not different between spring and summer (mean ± SD: spring = 3,013 ± 240 kJ/day; summer = 3,049 ± 630 kJ/day) but was significantly higher in autumn (3,483 ± 767 kJ/day, difference from spring $p = 0.046$). There was substantial intra-season variability, although intra-season variance was significantly lower (F-test for unequal variances) in spring (max difference of 1.3-fold in DEE) than summer (2.0-fold max difference, F = 0.15, $p = 0.001$)

or autumn (2.0-fold max difference, $F = 0.10$, $p < 0.001$). No significant overall difference was detected in either ODBA or DEE between 2018 and 2019 ($p_{ODBA} = 0.86$; $p_{DEE} = 0.10$).

DEE was significantly positively associated with body weight in summer and autumn (both $p < 0.001$), but not spring ($p = 0.64$; Fig. 1a). These relationships were similar when modelled exponentially, with DEE scaling allometrically with body weight to the -0.14-power in spring (not significantly different from no effect, $p = 0.64$), 0.90-power in summer ($p < 0.001$) and 0.65-power in autumn ($p < 0.001$). Pooling all seasons, DEE scaled to the 0.62 power ($p < 0.001$, $R^2 = 0.48$, dashed line in Fig. 1a). The deviation in spring was at least in part related to differential energy expenditure between females that had lactated that year (which on average expended high DEE and had low body weight, with a mean spring deviation from global allometric relationship of 350 kJ/day) and other individuals (mean deviation = -98 kJ/day). ODBA, conversely, exhibited a significant negative relationship with body weight in spring ($p = 0.02$) and autumn ($p = 0.04$), with heavier badgers expending less mechanical energy in these seasons (Fig. 1b); but not in summer ($p = 0.38$). The spring ODBA-weight relationship was again in part shaped by females that had lactated, which had relatively high ODBA values (on average 1.3-fold higher than other badgers) and low body weight (Fig. 1b).

Older badgers exhibited lower DEE than younger badgers in summer (e.g., 9-year olds expended 627 kJ/day less than 2-year olds, on average, Fig. 1c), although this effect was only marginally significant ($p = 0.054$). In summer, older badgers were significantly ($p < 0.001$) less active than younger badgers (e.g., 1.4-fold higher ODBA in 2-year olds than in 9-year olds, Fig. 1d). Sex was not retained in any model selection.

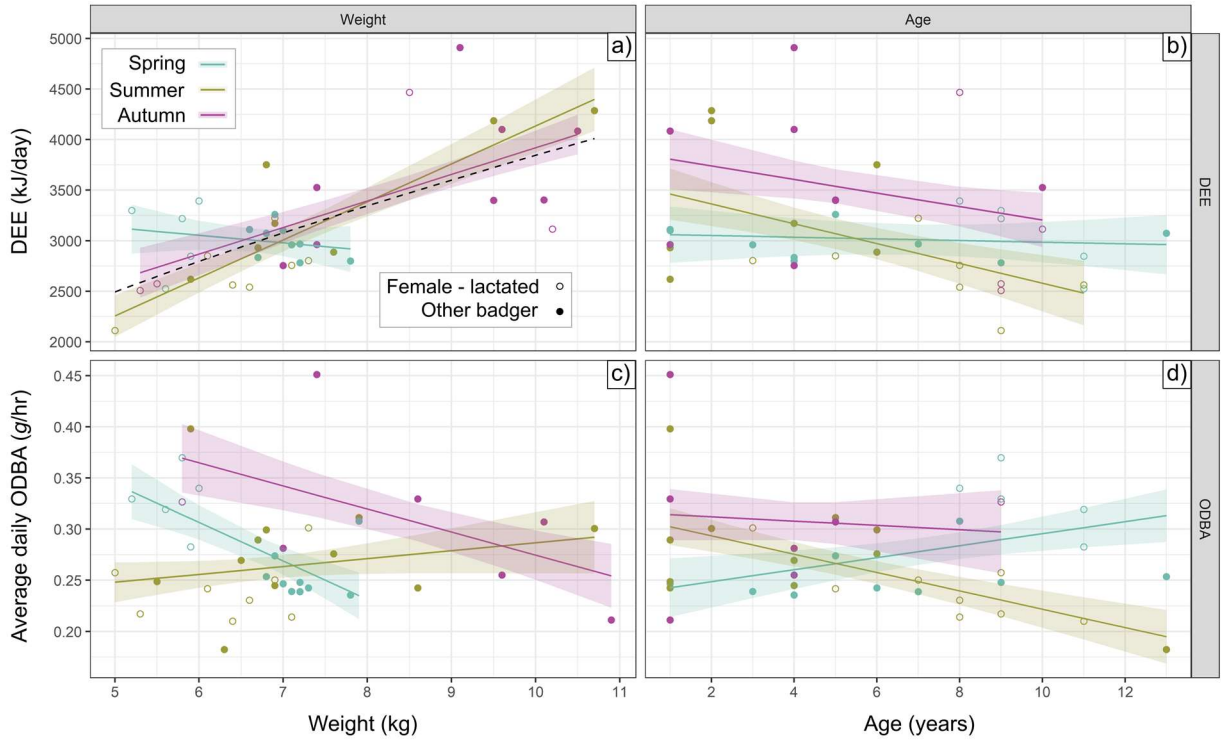


Figure 1. **Intrinsic drivers of energy budgeting.** Relationships between body weight (a, c) or age (b, d) and two energy metrics (total energy expenditure, a-b, and mechanical energy expenditure, c-d) are shown (± SE). Dashed line in panel (a) shows overall allometric scaling relationship, DEE α $W^{0.62}$; open circles show females that had lactated during the year studied, while closed circles represent all other badgers.

3.2 Covariation of DEE and ODBA

We did not detect a relationship between average daily ODBA and DEE ($p = 0.56$), even once weight had been accounted for ($p = 0.18$, Fig. 2), nor in any seasonal subset of the data. Consequently, the ratio of ODBA to DEE (OD) varied substantially between individuals, with the highest seasonal values representing 1.6x (spring), 2.2x (summer), or 2.4x (autumn) as much of their total energy allocation to activity as the lowest ones (Fig. 2). In spring, 71% of the variance in OD was explained by whether the badger in question was a female who had lactated:

females that had lactated expended 30% more of their total energy budget on ODBA than other badgers ($p < 0.001$).

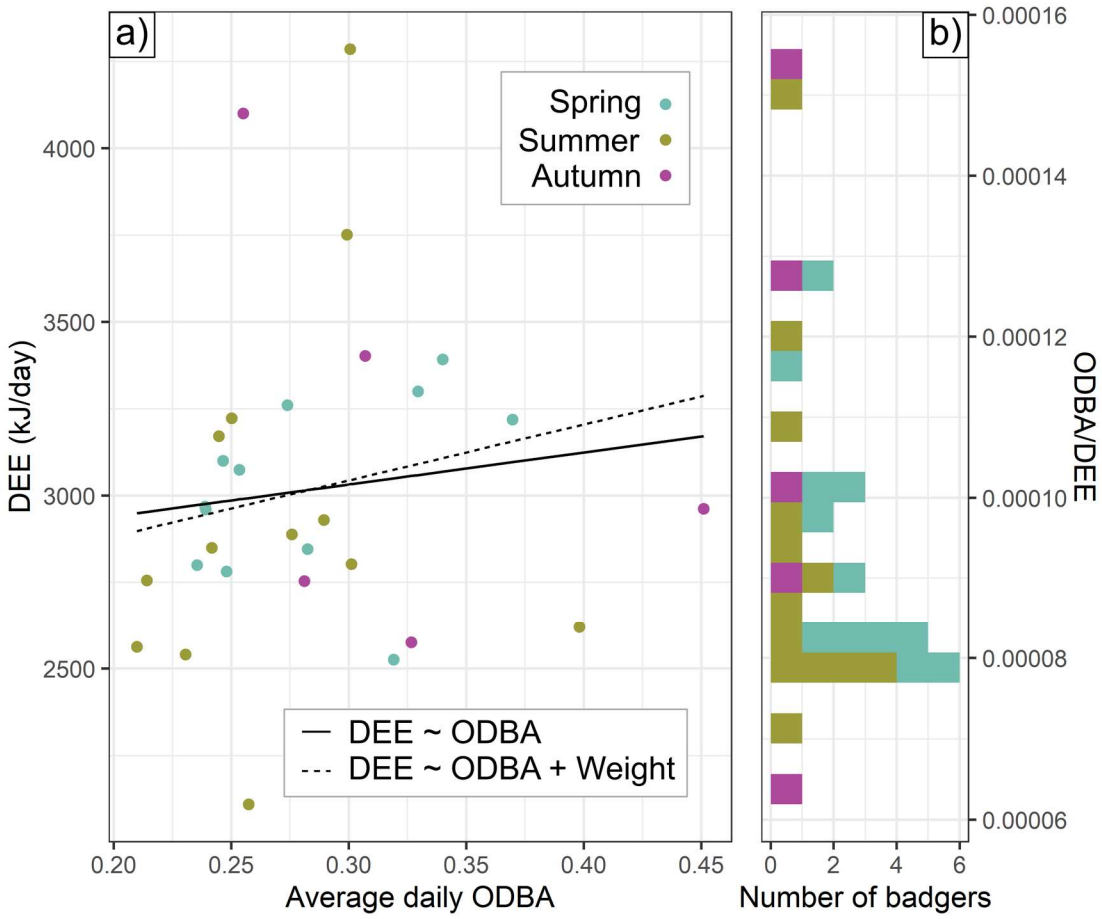


Figure 2. **Covariation of DEE and ODBA.** Individuals a) did not show a strong relationship between ODBA and DEE and b) consequently exhibited widely varying ratios of ODBA to DEE.

3.3 Drivers of next-season BCI

ODBA did not exhibit any relationship with next-season BCI_{res} ($p = 0.20$, Fig. 3a). DEE did show a positive (Fig. 3b), but marginally significant correlation ($p = 0.0496$). OD, however, exhibited a strongly significant negative correlation with next-season BCI_{res} (Fig. 3c, $p = 0.002$,

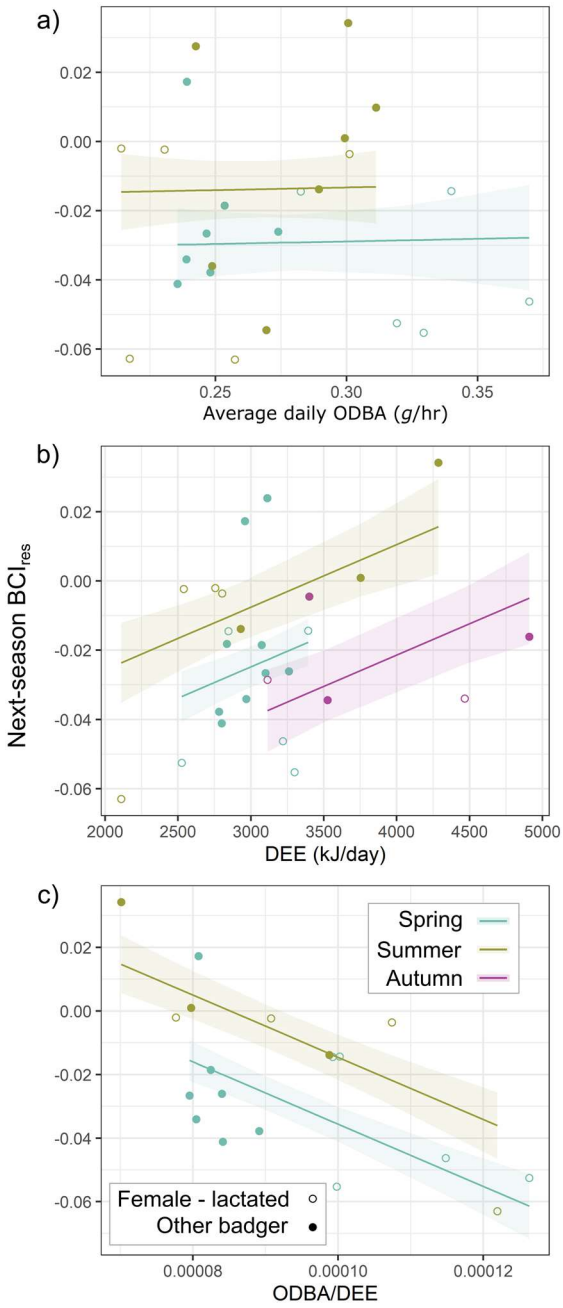


Figure 3. **Energetic drivers of next-season BCI_{res}.** Lines show seasonal relationships (± SE) between a) average daily ODBA, b) daily energy expenditure, and c) the ratio of ODBA to DEE and next-season BCI_{res}, while points show actual values. Open circles represent female badgers that had lactated during the year observed. BCI_{res} values are residuals from a GAM model of BCI as a function of sex, age, and calendar date.

$R^2 = 0.50$). Summer BCI_{res} in this sample were significantly higher than spring ones ($p = 0.03$). While there was a positive association between BCI_{res} in one season and the next, this association was not significant ($p = 0.10$).

The range of next-season BCI_{res} values predicted by the OD in the present study is associated with substantial differences in survival probability, depending on age—where survival probability is much more dependent on BCI_{res} for old badgers than for young badgers (Fig. 4). In a year with average population density and weather (see Chapter 3), the highest BCI_{res} predicted would have a 9.6% (in summer, prediction standard error -0.4-20.4%) or 23.1% (autumn, SE 13.6-33.1%) higher survival probability than the lowest BCI_{res} predicted for a 2-year old; for a 9-year old the same comparison spanned a much higher change in survival probability (summer: 29.8%, SE 17.5-40.5%; autumn: 44.9%, SE 31.0-57.2%). Figure 4 shows this relationship for all ages, with actual next-season BCI_{res} values shown on the badger's corresponding survival-age curve. Furthermore, as described in Chapter 3, reproducing (i.e., lactating, in our dataset) females exhibit higher survival probabilities for a given BCI_{res} than other badgers. Figure 4 shows the difference between a post-reproductive female's survival probability given their observed BCI_{res} and the expected average survival probability predicted for a non-reproductive female or male adult of the same age.

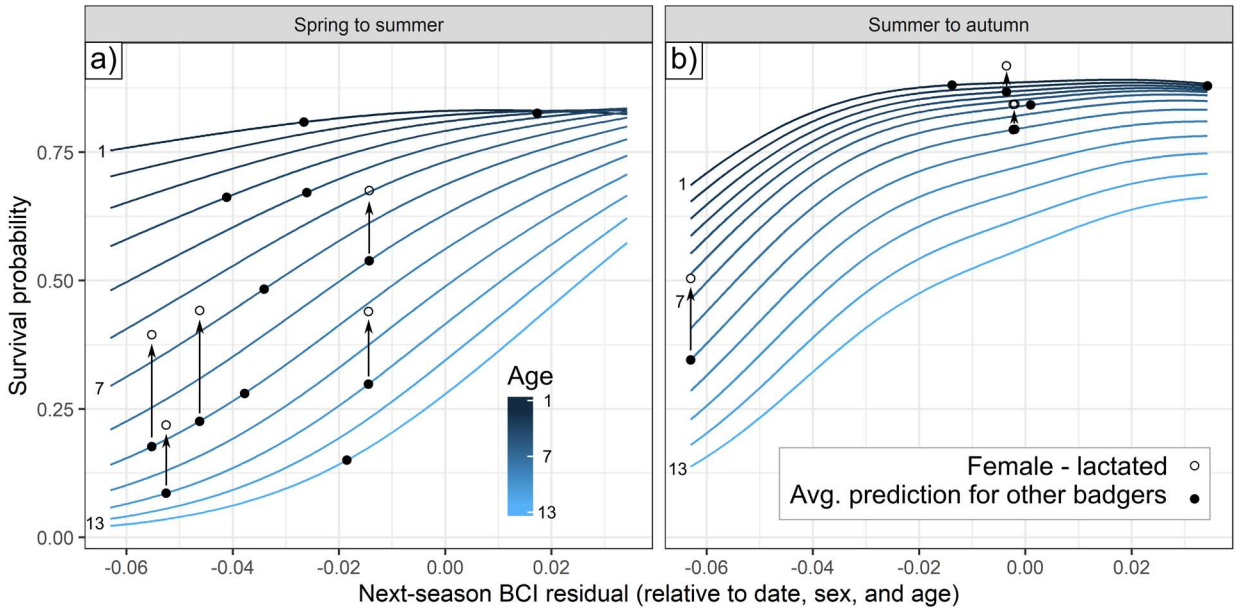


Figure 4. **Survival costs from OD-driven range of BCI_{res}.** Lines show age-dependent relationship between a) summer BCI_{res}, b) autumn BCI_{res} and probability of surviving to the next year for the median badger in the population under average weather and density conditions (average of males with seasonally-predominant scrotal testes descent condition, and non-reproductive female; see Chapter 3). Points show individual position on these curves from this study; arrows to open circles show positive survival probability change associated with being a reproductive female.

4 Discussion

Under identical extrinsic conditions, individual wild animals can exhibit widely differing energy budgeting tactics. Indeed, these different tactics provide the mechanistic underpinning for much of the variability in fitness observed within wild populations (Chimienti et al. 2020, Malishev and Kramer-Schadt 2021). In this study, we document substantial variability in both mechanical (ODBA) and total (DEE) energy expenditure in animals experiencing the same environment, as a result of different intrinsic traits (Fig. 2). Heavier badgers expended up to

~1,500 kJ/day more than lighter badgers did in summer and autumn. Younger badgers exhibited up to 1.4x higher mechanical energy expenditure than older badgers in summer. Females that had lactated in early spring exhibited high DEE and ODBA, driving a negative correlation between spring body weight and ODBA and cancelling out allometric scaling for spring DEE (Fig. 1). Crucially, we identified a link between individual energy budgeting and costs to somatic condition, whereby OD was more strongly correlated with next-season body condition than either the active (ODBA) or total (DEE) energy budget of a given individual (Fig. 3). However, interestingly, although body-condition costs associated with high OD values represent a substantial risk in terms of survival probability (Fig. 4), the badgers engaging in these "riskier" high relative ODBA strategies were predominantly those whose life-history (age or reproductive status) put them at less risk of mortality as a result.

Wild populations are not monoclonal, but comprised of shifting ratios of individuals with different life-histories (Bateson et al. 2014) and contemporary energetic contexts (Monteith et al. 2013). This heterogeneity favours different optimal responses to the same prevailing conditions, due to individual-specific sensitivity to stressors (Harding et al. 2005). For instance, in all populations, some individuals are older than others. Age presents varied thermoregulatory challenges that can affect energy budgeting, with diminished thermogenic capacity (McDonald and Horwitz 1999), reduced capacity to dissipate heat (Larose et al. 2014), and diminished physiological capacity to cope with hyperthermia (Kenney and Munce 2003). In addition, sarcopaenia (the age-related deterioration of muscle tissue, Rolland et al. 2008) reduces the efficiency of activity in older individuals; that is, an identical task takes more overall energy in the elderly. The impact of diminished efficiency should not be underestimated; as an illustrative example, one badger in our dataset had to be excluded from our data, as it developed a limp and

consequently was only able to expend 73% of the average population ODBA. Differences in the efficiency of activity, in fact, can drive substantial differences in fitness in wild populations (Parsons 2004, Grémillet et al. 2018).

Dens provide thermal refugia for fossorial animals (Noonan et al. 2015), making non-emergence a behavioural alternative to autonomic thermoregulation (Terrien et al. 2011, Williams et al. 2016, Tsunoda et al. 2018). Accordingly, reduced summer ODBA and (to a lesser extent) DEE in older badgers may reflect a reduction in non-essential activity during that season with them remaining underground in their sett; else higher ambient temperatures and lower water availability would otherwise incur greater energy costs and insensible water loss from panting, due to their reduced thermoregulatory physiology while attempting to forage (Robertshaw 2006). This is consistent with the combination of lower average body condition observed in older badgers (aged 8 years and up, see Chapters 2-3) and the greater cost to survival for older badgers from these low body conditions during summer (Chapter 3)—in other words, older badgers expend more energy when active, and also cannot dissipate heat as effectively when carrying fat, so therefore maintain a lower body condition, especially during the summer. This represents a substantial constraint on energy budgets: in older badgers, the loss of body condition associated with a higher fraction of total energy expenditure being spent on activity (evident as higher ODBA) would typically be associated with up to a 44.9% reduction in survival probability (Fig. 4).

The badgers exhibiting high and costly OD ratios were predominantly lactating females. Post-reproductive female badgers expended 350 kJ/day above allometric expectations in spring, even after lactation had ceased (Fig. 1). These same females were also more likely to exhibit relatively high OD ratios, and exhibit lower-than-average BCIs in subsequent seasons.

Pertinently, however, post-reproductive females suffer less reduction in survival probability from low body condition (Fig. 4, Chapter 3). While reproduction is an obligate component of fitness (since Darwin, biologists have recognised the potency of sexual selection, Darwin 1871), in longer-lived iteroparous species this substantial investment can be aborted and postponed until fairer conditions present themselves (Dugdale et al. 2011). Nevertheless, frailty to stressors increases with age even beyond that described by thermoregulatory potential (e.g. Richard et al. 2014), resulting in reduced reproductive potential and competitiveness (Cohen 2004, Møller et al. 2009). The trade-off between the contribution of current reproduction and postponed reproduction (through enhanced survival probability) to fitness changes as individuals approach senescence (Campbell et al. 2017), in some circumstances favouring a "terminal investment" (Clutton-Brock 1984).

In this same badger population, Sugianto et al. (2020) found a decreasing female per capita reproductive rate after age 3. This coincided with the onset of somatic decline but came earlier than hormonal decline (5.5 years onwards—an age attained by 31.8% of females, or 55.8% of those attaining sexual maturity). This gradual decline eventually results in near-complete reduction in oestrone production in the majority of females (functionally reaching menopause, Peccei 2001) around age 9, with an average post-reproductive lifespan (Cohen 2004) of 2.6 years, evidencing the difficulty of meeting both the endocrinological and somatic requirements of reproduction at advanced ages (Bérubé et al. 1999). Nevertheless, very old female badgers (age 9+) express heterogeneous endocrinological profiles (Sugianto et al. 2020), with some seemingly escaping the reproductive constraints of age; parallel research also provides evidence that reproductive older female badgers enjoy higher survival probability than other females of an equivalent age (Chapter 3). Congruent with this, we detected a moderate increase

in spring ODBA variability (this being the season most closely aligned with mating) in badgers aged 8 and above (Fig. 1d), suggesting some old females—particularly those marked as reproductive—engaged in energy budgets with more activity than others.

We found a direct somatic cost associated with elevated ratios of mechanical to total energy expenditure (OD; Fig. 3c). Expending energy on voluntary activity (ODBA) redirects resources from growth and somatic maintenance (Chimienti et al. 2020), but also tends to increase basal metabolic rate (Hume et al. 2016). These more costly energy budgets incur life-history costs: higher total energy expenditure (DEE) correlates negatively with longevity within taxa (Speakman 2005, Careau et al. 2010). Parsing causality in somatic-energetic correlative observations (Fig. 3) presents a challenge: do heavier badgers (with more somatic fat stores, see Chapter 3, and supplements therein) reduce activity because they do not need to forage, thus remaining heavier; or do heavier badgers possess somatic stores because they do not engage in excess voluntary activity? Both explanations are plausible. Heavier badgers expend up to twice as much total energy as light ones, despite no concurrent activity elevation (Fig. 1), due to allometric scaling effects (White et al. 2009). Conversely, a substantial portion of lighter badgers (with lower DEE) spent a higher fraction of their total energy expenditure on activity (Figs. 1, 3)—including all reproductive females during the spring. While excess fat hinders agility (Gentle and Gosler 2001, Newman et al. 2011) and presents health risks in humans (Bray 2004, Kopelman 2007, and more broadly, though less well-studied, see Garaulet et al. 2010), the elevated maintenance costs of excess somatic stores have received little attention in species for which fat stores are linked to survival at a coarser scale (compared with, for instance, small passerines: Gosler 2002). This is crucial because if the added bulk does not contribute to reproductive output, the additional maintenance costs over longer durations may not compare

favourably to the individual's proportional contribution of gene copies to the population (Dawkins 1976).

According to the Peak Demands model of energy budgeting, wild populations can elevate total energy expenditure to take advantage of either predictably high food availability or minimal seasonal energy losses—the elevated energy expenditure may be activity-based (e.g. enabling additional foraging, D'Amico and Hémery 2007, or mate-search, DeSantis et al. 2020) and/or physiological (e.g. aligning lactation with peak food availability, Zhu et al. 2015). In contrast, according to the Reallocation model, populations may rebalance allocations to maintain a steady expenditure throughout time, particularly when energy availability/losses do not vary predictably (Krockenberger 2003, Bozinovic et al. 2004). Ultimately, several studies have found substantial variation from these models, both between individuals (Zhu et al. 2015, Wascher et al. 2018) and between years (Regular et al. 2014). Populations are comprised of individuals with different energy ceilings (summit metabolic throughput, Elliott et al. 2014) and floors (basal requirements, Ricklefs et al. 1996), dictating diverse energy-budgeting tactics. For instance, in badgers, spring and summer body condition is only marginally influential on survival probability under average conditions for the majority of individuals (Chapter 3), reflecting a persistent range of viable activity and energy-budgeting phenotypes. While a certain amount of this variation can be attributed to individual quality (van Noordwijk and de Jong 1986, Hamel et al. 2009), it can also reflect heterogeneity due to equal viability of different energetic phenotypes over time (Hamel et al. 2018).

As metabolism and related metrics (basal requirements, summit metabolism, aerobic capacity; see Swanson et al. 2012) determine the efficiency and fitness benefits of different activities (e.g. Binder et al. 2016, Metcalfe et al. 2016), metabolic traits co-vary within

populations with a suite of behavioural types (the so-called "extended" pace-of-life syndrome hypothesis: Careau et al. 2008, Pettersen et al. 2016, Dammhahn et al. 2018, Gangloff et al. 2018). Behavioural types can have substantial effects on individual and offspring fitness (Gangloff et al. 2018, Cecere et al. 2020, Dhellemmes et al. 2020) because metabolism is heritable (particularly active metabolism, Pettersen et al. 2018). However, optimal metabolism—and consequently, energy-budgeting tactics—change with environmental conditions (Anderson and Jetz 2005). In the studied population, we have documented reproductive canalisation, whereby females that breed successfully are more likely to breed again (Chapter 3); this suggests the occurrence of "higher-quality" individuals (Hamel et al. 2018), especially as these reproductive females exhibit lower mortality rates in response to low summer BCI than the rest of the population (Fig. 4; Chapter 3). However, this relationship assumes equivalent distribution of body condition between reproductive and non-reproductive individuals. If instead—as we observe in this (albeit limited) sample—energy-budgeting tactics leading to lower body condition are more common in these reproductive individuals to begin with, then during years with harsh conditions (hot summers, particularly rainy autumns: Chapter 3), these tactics become "riskier", as individuals operate nearer to the margins of energy budgeting—and this energetic marginality is only liable to increase with the frailty of age. While not possible to confirm within the purview of this study, different males may also exhibit more and less risky tactics, as male cubs mature at different rates (Sugianto et al. 2019b, Chapter 2) and show heterogeneous testosterone profiles as adults (Buesching et al. 2009).

The risk of elevated energy investment in reproduction can be important under certain conditions. At higher population densities, for example, higher investment is required to remain competitive (Weladji et al. 2005). However, this "faster" pace of life typically incurs additional

survival costs (Metcalfe et al. 2016, Dhellemmes et al. 2020). In animals with particularly short generation times, this fluctuating selection for different paces-of-life at different densities (see Wright et al. 2019) can lead to population collapses as increasing numbers of individuals are driven to adopt energetically marginal strategies without concomitant resource increase (e.g., Stenseth 1978). In badgers, generation time buffers the intensity of this selection, but we have observed sex-ratio skew in part stemming from males over-investing in early reproduction at high densities (Chapter 2). Under normal environmental fluctuations, energetically marginal reproductively competitive tactics can co-exist with tactics that prioritise energetic stability through bet-hedging, which allows phenotypes with lower short-term fitness to persist if they achieve less variable fitness (Starrfelt and Kokko 2012). This is because under challenging conditions (typically, low food availability), less competitive traits may become favourable (Liedtke et al. 2015, Krause et al. 2017)—in great tits (*Parus major*), for instance, birds with lower feeding competitiveness have higher capacity for innovative problem-solving, allowing greater competitiveness in turn under stressful conditions (Cole and Quinn 2012). The regular occurrence of stochastic events in wild populations (Tuljapurkar et al. 2009b, 2009a) thus provides fluctuating selection that maintains diverse energy-budgeting tactics within the population (Nilsson and Nilsson 2016).

Under the more frequent and severe disturbances associated with human-induced rapid environmental change (HIREC: Sih 2013), fluctuating selection may give way to directional selection. Under these stressful conditions, energy efficiency is prioritised (Parsons 2004) and stability dominates selection (although populations may find diverse solutions to energy efficiency, providing diversifying or disruptive selection for energy-balancing tactics, Martin and Pfennig 2009). Whereas diversity is beneficial to the resilience of populations and communities

under strain (the "portfolio effect": Schindler et al. 2015, Sanders et al. 2018), populations that conversely lack sufficient phenotypic diversity to select from are more likely to undergo extirpation. Many species have survived rapid, sustained changes in environmental conditions in their palaeontological record without extinction (e.g. Dansgaard-Oeschger events, Dansgaard et al. 1993), and exhibit the hallmarks of that resilience today. For the conservation of present and future biodiversity, characterising the degree of energetic diversity within wild populations, as well as the generators of that diversity, will enable a better mechanistic accounting of population resilience to HIREC, and inform better targeted management interventions.

5 Authors' Contributions

Conceptualization: Julius G. Bright Ross and Chris Newman; Accelerometer programming: Andrew Markham; Doubly-labelled water assays: Catherine Hambly and John R. Speakman; Data collection: Julius G. Bright Ross, Chris Newman, Christina D. Buesching, and David W. Macdonald; Data analysis: Julius G. Bright Ross; Writing: Julius G. Bright Ross; Editing: all authors.

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General Discussion

Heterogeneous energy-budgeting:
Evidence, distinctions, and maintenance

1 The questions asked

I began this thesis asking: 1) how do animals in the wild cope with changing conditions; and 2) how do coping responses vary between individuals within a population? In answer to the first, for the Wytham Woods badger population, I exposed extensive plasticity—a term borrowed from material sciences to describe how a single genotype can, under different environmental contexts, produce different phenotypes (West-Eberhard 1989). In natural populations generally, the scale at which this plasticity is expressed can vary. Plastic responses to the environment may determine life-long phenotypes (Garratt et al. 2015, Douhard et al. 2016), relative allocation of energy based on ongoing environmental cues (Bårdsen et al. 2011, Fritsch et al. 2019), and even the extent, nature, and intensity of fine-scale behaviour (Williams et al. 2014, Kneebone et al. 2018, Cecere et al. 2020). At the first of these scales, I found relatively little influence of early-life conditions in establishing life-long pace-of-life (POL) in badgers, with POL instead being shaped by later, sex-specific, drivers (Chapter 2). Moreover, although weather effects influenced when males were able to start breeding, they were more influential in determining the year-to-year energetic context that shaped how female badgers invested in reproduction. At the inter-annual scale, I found broad variation in somatic fat stores—only 15.8% of badgers were consistently thin or consistently fat over their measured lifetimes (Chapter 3). Badgers depleted somatic stores according to individual energetic risk, where for instance, reproductive females had lower body condition indices (BCIs) than other females in spring and summer, but also exhibited no relationship between BCI and survival probability during these seasons. Conversely, old badgers, which exhibited a strong relationship between summer BCI and survival probability, did not suffer the additional BCI losses during hot summers seen in other badgers—likely as a result of conservative energy expenditure regimes. Indeed, at the finest

scale, plasticity in individual activity patterns was strongly weather-dependent, with responses to weather covariates inferred to determine diet and thermal constraint in each season (Chapter 5). The lack of individual activity phenotype consistency I found from one season to the next represents yet another form of plasticity, suggesting some degree of mutability in energy budgeting beyond that determined by fixed individual hormonal profiles, which should form the basis for future inquiry.

The answer to the second question this thesis posed must be split in two parts. First, the degree to which badgers were capable of expressing plastic responses was constrained by their energetic context, which varied between individuals. Once more applying an economic analogy, if one has little in their bank account and rent is high, avoiding bankruptcy leaves little budgetary flexibility, leading to prioritising income security. Congruent with this framework, I uncovered substantial differences in energy budgeting as a function of individual badger energetic considerations. Fatter badgers were able to decrease ODBA expenditure during cold springtime conditions (presuming poor foraging quality, Macdonald 1980, and potential for thermal losses, Harding et al. 2005, Williams et al. 2016), while thinner badgers were active irrespective of adverse temperatures, apparently recouping energetic losses (Chapter 5). During summer, this relationship was reversed, with fatter badgers actually decreasing ODBA expenditure in hot conditions (Chapter 5); I propose this relates in part to limitations on capacity to dissipate heat—further challenging the ecological orthodoxy that "fat is always good" (e.g., Gosler 1996, Garaulet et al. 2010, Lind et al. 2010). I found age was a critical to energetic context, where older badgers exhibited stronger relationships between BCI and survival probability than younger badgers (Chapter 3) and consequently more conservative summertime activity (Chapter 5) and overall energy expenditure (Chapter 6). The consequences of past life-history allocations

shaped future energy budgeting. This was particularly evident in reproductive females, which exhibited less flexibility in their springtime activity patterns (Chapter 5), likely as a result of depleting somatic stores (Chapter 3), and yet remained in low condition for the season to come (Chapter 6). This pattern of constraint and plasticity is crucial, as the capacity to adapt energy-budgeting tactics can alleviate an individual's exposure to potentially detrimental conditions (Hall and Chalfoun 2019). Indeed, despite the general capacity we find for reproductive females to recover BCI parity with other badgers, this is not the case following hot summers (Chapter 3), illustrating the hazards of induced inflexibility.

Despite the remarkable plasticity seen in phenotypes in this study population, a second source of variation in energetic coping strategies was evident in the form of some fixed energy budgeting profiles. At the finest scale, these encompassed consistently higher ODBA expenditure within a 2-week seasonal deployment, with differences in average expenditure ranging up to 1.9-fold in nightly ODBA expended and 3.2 hours of nightly activity (Chapter 5). As described in Chapter 5, my sample size made it impossible to authoritatively conclude whether these phenotypes were consistent from one season to the next, but the relationship between mechanical and total energy expenditure robustly linked individual somatic stores from one season to the next (Chapter 6), likely creating chain effects of constraints over energy budgeting. More coarsely, this can—in a non-trivial minority of individuals—coalesce into consistently low- or high-BCI profiles. In the right season (for males, spring; for females, autumn), these BCI profiles produce measurable fitness advantages in lifetime reproductive success (Chapter 3). The energy-budgeting strategies present in the population, however, are neither homogeneous nor static: over the course of demographic changes in the studied population, the ratios of fast and slow POL in the population shifted substantially and in a sex-

specific manner, possibly driving a divergence in sex ratio as more males adopted fast POL tactics at high densities, at the cost of earlier mortality (Chapter 2). This non-uniformity of wild populations is key to predicting how they will respond to external stressors.

2 What is a population parameter, anyway?

As with the economic analogies for energy budgeting used in this thesis, carrying capacity (K) originated from an anthropic parallel for ecological theory. Thomas Malthus (1798) warned that exponential human population growth would ultimately meet the limitation of food supply. Based on this premise, Pierre Verhulst (1838) developed a mathematical prediction of how effective growth would change as populations approached a fixed value K, giving us the logistic equation (*via* Seidl and Tisdell 1999). This origin is visible in early formulations of r/K selection theory, where K was conceptualised as differing between biomes (Pianka 1970), or in the theory of island biogeography, which models (among other things) colonisation and growth rates in unoccupied niche-space (MacArthur and Wilson 1967). In the majority of cases, however, real populations are neither colonising recently-vacated islands nor subject to one fixed carrying capacity indicative of their biome; K is, instead, an ever-changing target (Seidl and Tisdell 1999). The number of individuals supported by the energy available in a population's occupied niche varies according to stochastic changes in resource availability (e.g. fire's effects on forage availability, Joern 2004), as a result of adaptations that improve energy extraction efficiency (including through rapid cultural evolution, Kawai 1965), and as a result of anthropogenic manipulation (e.g., through supplemental feeding of ungulates, Bright Ross et al. 2021). The erroneous conception of carrying capacity as stationary can be highly detrimental. In human applications, the Malthusian myth contributed to the development of eugenics and post-WWII neo-colonial bio-political governance (Schlosser 2009, Carey 2012)—relying as it does on

a cynical view of carrying capacity that ignores both the ability of human innovation to increase K (Pulliam and Haddad 1994, Seidl and Tisdell 1999) and the effects of elite resource capture on reducing K (Motesharrei et al. 2014). Within ecology, carrying capacity becomes less useful to model population growth as environmental stochasticity increases (McLeod 1997) and is simply best assumed to be variable (Clark et al. 2010).

As populations change, density-dependent selection favours phenotypes that match the changing degree of competition. As an illustrative example, a broad diversity of wild populations undergo regular and drastic fluctuations in density (Kendall et al. 1998, including large mammals, Gunn 2003). As these cycles progress, selection pressures shift; at the low-water density mark, selection is strongest for individuals that can produce a high number of offspring, while at the highest densities, individuals are selected for the capacity to resist the fitness detriments of intra-specific competition (Wright et al. 2019). However, selection in these systems is lagged, as individuals selected for fast POL at low densities will typically either persist or pass on their genes until high densities are reached; consequently, the selection for stable, slow POL comes in the form of selective elimination of individuals with fast POL from the population (Stenseth 1978). The loss of a lag between low-density selection for fast POL and environmental stochasticity has, in fact, been proposed as the underlying mechanism for the collapse of many population cycles into low-density stable states since the advent of severe anthropogenic climate change (Ims et al. 2008). I argue that the results of Chapter 2 illustrate many of the features of these cycles: as environmental carrying capacity increased due to a succession of milder winter conditions throughout the 1990s (Macdonald and Newman 2002), the Wytham population came under selection favouring reproductively competitive phenotypes. In response (while sex ratio was at parity and the population was growing), males expressed fast

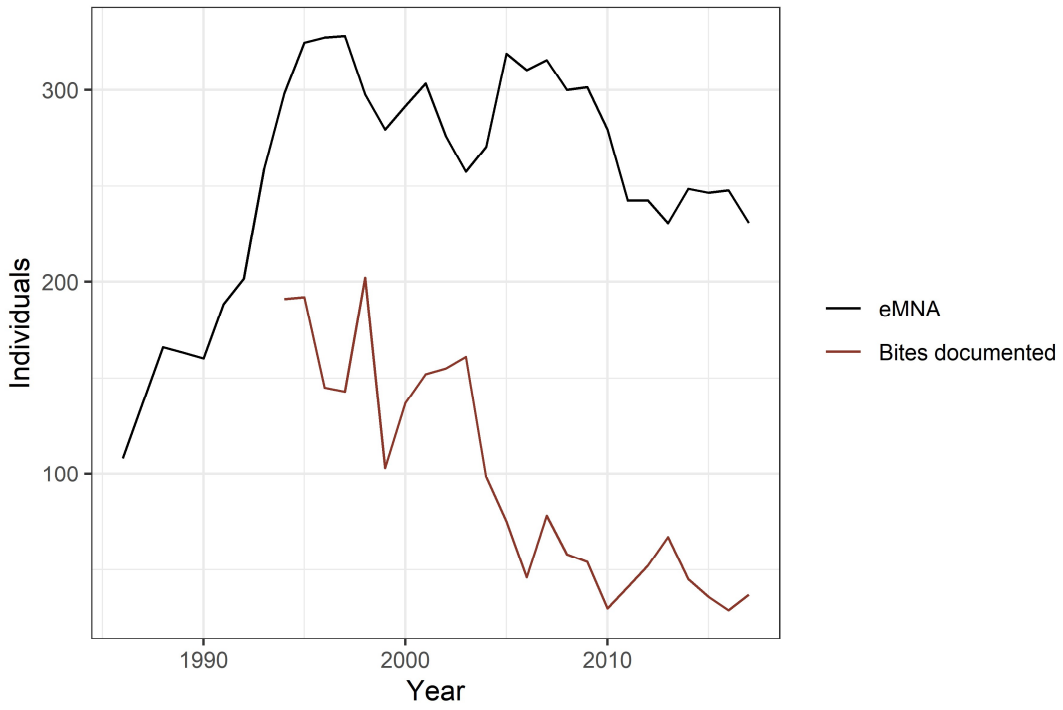


Figure 1. **Bite wounds and population density over time.** Total number of bite wounds documented in captures, starting with first records in 1994. eMNA computed as specified in Chapter 1.

POL, with early entry into the reproductive population and high investment in securing mating opportunities. This, however, led to stochastic elimination of many young males near peak population density, and a resulting skew in the sex ratio throughout the following half-decade. Crucially, however, it was the underlying diversity in POL tactics—including ones with lower short-term reproductive competitiveness—that permitted a new, higher baseline density for the population. This shift to a higher ratio of slow-POL strategists may have driven lower aggressiveness in the population: even as population density remained high, bite wounds decreased drastically in the population (Fig. 1).

The changes undergone by the Wytham Woods badger population reported in Chapter 2 illustrate that the endpoint of resilience need not be the population's starting point. The different social organisation observed in badger populations across Europe (Johnson et al. 2002) should not be understood as the outcome of seeding the continent uniformly with some primordial badger to produce the assemblages seen today, but rather as slight variations on neighbouring populations—mutable, and in the unending process of adapting to environmental energy supply and requirements. Thus, the reliance of badgers in Portugal on olives (*Olea europaea*, Rosalino et al. 2005) reflects a coping strategy for challenging resource-scapes (incidentally, by using a resource not native to the western Mediterranean, Besnard et al. 2013), which produces populations that differ substantially from the Wytham population—but remain within its adaptive capacity. Indeed, during the July sampling of the diet analysis in Chapter 5 (a month with little earthworm availability), I was nearly unable to find scats near the woodland setts, instead finding them concentrated by the few exit points bordering wheat fields outside the woods, challenging the notion that social structure remains static even across a year within a population.

The diversity of niches within populations is pertinent to the population's ability to shift to an alternative stable state. The Niche Variation Hypothesis (NVH) predicts that, as the cumulative niche breadth of a population increases, individual niche width will decrease (Van Valen 1965). Where higher densities increase the niche breadth of the population, this can be assumed to also correlate with niche divergence: in badgers, dietary niches tend to be narrower in larger social groups (Sheppard et al. 2018). However, high densities can drive niche divergence in two different ways: either fixed phenotypes can permit individual specialisation, or some individuals can be forced to exploit marginal niches as a result of limited resources. In the former

case, while some specialisations may provide exaptation for novel conditions, specialisation can come at the cost of behavioural plasticity (Wolf et al. 2007), potentially reducing a population's toolkit for handling rapid change. In the case of marginalisation, individuals existing at the periphery may be poised to adopt central roles in the eventuality that more favourable niches are vacated. Evidence from evaluation of the NVH points to this temporary nature of individual specialisation, as fixed morphological traits conform more poorly to the hypothesis' predictions than labile dietary ones in a range of species (Bolnick et al. 2007).

In badgers, it is unlikely that dietary specialisation occurs as a result of active competitive exclusion, as studies have shown little feeding exclusion (Macdonald et al. 2002) or territoriality (Ellwood et al. 2017). Nevertheless, female badgers seem to exhibit some within-group competition for reproductive opportunities: only a small number of females successfully breed within a social group (Woodroffe and Macdonald 1995), with some presumed role of infanticide in suppressing other litters (Cresswell et al. 1992). With this in mind, the Resource Dispersion Hypothesis' (RDH's) formulation of badger society provides an alternative conceptualisation of marginal individuals: according to the RDH, social-group ranges stem from the minimum territory required to sustain a *primary* individual (Kaneko et al. 2014), which when determined from heterogeneously available energy-dense food patches typically support multiple additional *secondary* individuals (typically philopatric offspring, Carr and Macdonald 1986, Macdonald and Johnson 2015). Thus, if a theatre metaphor may be employed, if those individuals that are excluded from reproduction can be thought of as the long-suffering understudies (secondaries) to the lead actor (primary), they might be called up to fill the lead role if the lead actor becomes indisposed (Martínez et al. 2008).

3 Concerning marginality—frailty and quality

In the discussion of "marginal" individuals within populations—those that find themselves at risk of being excluded from the gene pool, whether from mortality or competitive exclusion—it will be of use to differentiate between energetic marginality stemming from life history ("frailty") and that stemming from fixed phenotypes ("quality"). Over the course of an individual's life, there are stages when either energy expenditure is necessarily elevated (e.g., reproduction, Zhu et al. 2015) or energy acquisition potential is reduced (e.g., exclusion from pack hunting, Jordan et al. 1967). This heterogeneity can produce stage-specific adaptations to minimise the risk from energetic insecurity; in humans, Zafon (2007) demonstrates how this leads to three distinct fat-deposition life-history stages: infancy, pregnancy, and senescence. Where life-history marginality is concerned, my thesis has focused primarily on studying adult badgers, as the marginality of cubs has been extensively explored (e.g., Nouvellet et al. 2013, Bilham et al. 2018, van Lieshout et al. 2019, Sugianto et al. 2019a). Old animals, in particular, experience advancing marginalisation as a result of somatic and reproductive senescence (Nussey et al. 2011, Paterson et al. 2016, Campbell et al. 2017, Sugianto et al. 2020, van Lieshout et al. 2020); for this reason and because of the deteriorative effect of survivorship on population representation, old individuals are often a demographic afterthought. The extreme exception to this generalisation is in species that breed despotically, where age typically aids in securing limited breeding opportunities (e.g., in meerkats, *Suricata suricatta*: Kutsukake and Clutton-Brock 2006)—although even these despots eventually senesce (e.g., in giant otters, *Pteronura brasiliensis*: Davenport 2010), they play a key limiting role in demographics (Groenendijk et al. 2014). However, even in non-despotic species like badgers, old individuals may play a non-trivial role in population persistence: badgers aged 8 years or over (the oldest

recorded badger in the population reached age 14) still comprised 19% of the known-age and breeding-age population between 2000-2010, and produced 15% of the cubs detected by the pedigree over the same period. Indeed, badgers that last breed at age 8 exhibit the highest lifetime reproductive success (Dugdale et al. 2010b), indicative of directional selection to extend the reproductive lifespan past the onset of reproductive and somatic senescence (Sugianto et al. 2020). Old individuals, therefore, might be energetically marginal (Chapter 3), but are also important components of population resilience (Reichert et al. 2016).

Energetic marginality can differ substantially as a function of individual body mass, whether as a function of life history or fixed phenotypic differences. Basal metabolic expenditure scales allometrically with body mass in wild animals; theory variously predicts this relationship to scale to the 0.75-power (according to theories of nutrient transport through three-dimensional anatomical structures, Brown et al. 1993, West et al. 2002) or to the 0.67-power (according to the thermal equilibrium dictated by the relationship between surface area and volume, Dodds et al. 2001, see also Zhao 2015). Nevertheless, these relationships have been shown to be far from universal, even across similar taxa (Bokma 2004, White et al. 2007). However, some general rules may apply, such as that the greater the fraction of energy dissipated as heat by an organism, the closer allometry should follow the thermal equilibrium prediction of 0.67-scaling (Ballesteros et al. 2018). With this trend in mind, it is notable that across the entire weight range of badgers, total energy expenditure scaled to the 0.62-power, not far from that predicted if heat loss were a dominant regulator of badger energy expenditure (Chapter 6). This allometry is evident in the detrimental effects that overly rainy conditions can have on the survival of the smallest badgers in the population: cubs (Nouvellet et al. 2013). My thesis extends the role of thermal loss-related factors in governing somatic fat storage (Chapter 3) and activity patterns (Chapter 5) to adult

badgers as well, with the weight differences seen within the population spanning a substantial degree of difference in energy expenditure. The benefits of lower mass-specific heat loss at larger sizes, however, must be balanced with the drawbacks of greater absolute energy requirements (Chapter 6).

Nevertheless, my findings also illustrate an oft-neglected aspect of scale allometry—dissipation capacity. In particular, the inability to dissipate heat more efficiently than permitted by the available surface area coincides with life-history marginality: as animals age, their muscles become less efficient (Rolland et al. 2008) and their bodies become less capable of both dissipating heat (Larose et al. 2014) and enduring hyperthermia (Kenney and Munce 2003). Although these data cannot conclusively link the avoidance of summer activity in old badgers to thermal dissipation constraints, this provides a parsimonious explanation that underscores further targeted inquiry, particularly as ambient temperatures continue to rise under anthropogenic climate change. Diurnal species can become facultatively nocturnal during times of heat and water stress (e.g., Whitford et al. 1981, DeGregorio et al. 2014); this capacity has been theorised to provide an exaptation for coping with climate change (Levy et al. 2019). In nocturnal species, there is no such cooler temporal niche to shift to as temperatures rise. This does not necessarily imply nocturnal populations are doomed to extirpation—Mediterranean badger populations must experience warmer night-time conditions than British ones, after all. However, it raises further lines of inquiry as to how individuals with different levels of thermal marginality within populations may experience rising temperatures differently.

As semi-fossorial animals, badgers can utilise their setts (burrows) to avoid the detrimental effects of inclement weather; an advantage not all animals have. In burrowing animals, conditions that would lead to thermal losses typically prompt non-emergence (e.g., in

red squirrels, *Tamiasciurus hudsonicus*: Williams et al. 2014, and arctic ground squirrels, *Urocitellus parryii*: Williams et al. 2016). In other animals, muscular thermogenesis from increased movement can actually be an effective way to reach normothermia (e.g., in grey mouse lemurs, *Microcebus murinus*: Aujard and Vasseur 2001). Therefore, the same weather conditions may drive diverging responses in different species. Indeed, the benefits of burrows in decoupling inclement weather and individual thermal state has been posited to contribute to the evolution of sociality and high densities in carnivorans (Noonan et al. 2015). However, non-burrowing animals will still seek shelter when energy expenditure becomes untenable (Mysterud and Østbye 1999, Dussault et al. 2005), simply implying a different relationship between weather and activity below a given threshold of thermal loss. Moreover, burrow use involves some drawbacks: maintaining burrows can be energetically costly (Stewart et al. 1999); reproduction around multiple conspecifics can increase vulnerability to antagonistic infanticide (Agrell et al. 1998); and cohabitating can increase the density of both endo- (Newman et al. 2001) and ecto-parasites (Supplementary Chapter 1) with which an individual comes into contact. With parasite exposure in particular, it is worth considering to what degree differential use of setts by individuals as a result of energetic condition (Noonan et al. 2014, Chapter 5) results in unequal detriments to fitness.

While individuals can become energetically marginal through life history and/or scale allometry, this marginalisation can also occur through differential quality. Variance in reproductive success within animal populations is widespread in the wild (Cabana and Kramer 1991, Tatarenkov et al. 2008). When this variance stems from differences in individual quality, the orthodoxy that expending more energy on reproduction implies lower survival probability can fail to hold, as being able to acquire more energy can enable high-quality individuals to

secure survival *and* invest in reproduction (van Noordwijk and de Jong 1986). This notion is related to the "performance" model of energy management, whereby increased energy intake enables increased total expenditure (Mathot and Dingemanse 2015, Mathot et al. 2019). As the POLS hypothesis relies on trade-offs between current and future reproduction, the failure to account for individual quality and the tacit assumption of somatic-reproductive trade-offs can interfere with appropriate evaluation of the existence of POLS within populations (Jablonsky et al. 2018, Montiglio et al. 2018, Royauté et al. 2018). Verifying trade-offs between reproductive investment and decreased survival probability was, therefore, a primary goal of my research. I found that beginning reproduction earlier was correlated with a shorter realised lifespan, suggesting the existence of "fast" and "slow" life-history strategies (Chapter 2). The immediate survival costs of reproduction were less clear-cut: although I found in Chapter 2 that each additional cub a female produced decreased survival probability, in Chapter 3 I found no direct link between having been reproductive one spring and survival to the next year. Two factors may converge in explaining this discrepancy. First, the former chapter used pedigree data, while the latter used teat-derived evidence of lactation; while this has been validated as an approach to determining annual reproductive success (Dugdale et al. 2011, and where alloparental behaviour occurs but does not include allo-suckling, Dugdale et al. 2010a), it cannot fully capture the loss of cubs and therefore may not fully characterise the reproductive population. Second, although I controlled for mean annual BCI in Chapter 2, Chapter 3 modelled survival probability in context of seasonal BCI, suggesting that reproduction itself does not lead directly to mortality risk, but does so only when it is accompanied by unreplaced somatic loss.

This latter framework provides some evidence for individual quality, overwhelming the trade-offs associated with investing energy into current reproduction. First, reproductive females

exhibited a weaker effect of spring and summer BCI on survival probability than non-reproductive females did (Chapter 3). Second, reproductive success in one year was strongly predictive of successful reproduction in the next (among surviving females). Third, higher lifelong autumnal BCI averages were associated with higher lifetime reproductive success in females. The higher quality of those females that consistently reproduce may lead to heterochrony in senescence rates among older badgers: as badgers became older, I found that their survival cost of reproduction declined (Chapter 2). Moreover, nonreproductive females exhibited age-related declines in their probability of breeding the next year; this was not the case for females that had already reproduced in a given year, whose age was irrelevant to their reproductive probability the next (Chapter 3)—in fact, this finding is diametrically opposed to terminal investment theory (Clutton-Brock 1984). Together, these findings suggest that female badgers may begin reproductive senescence heterogeneously, with some lower-quality individuals, if they survive, eventually exhibiting a post-reproductive lifespan, while others continue to be reproductively active even at age 9 and above (explaining underlying endocrinological heterogeneity in old badgers, Sugianto et al. 2020).

Quantifying the reproductive inequality between individuals in a population—and consequently, the degree of marginalisation therein—is important. The Gini Index (GI), often used in the social sciences to measure inequality in societal resource distribution, particularly wealth and access to health care (e.g., Wan 2001), has also been employed in demography to characterise inequality of mortality rate in both human (Shkolnikov et al. 2003) and non-human populations (Archer et al. 2018), and even to compare inequality of reproductive success across populations (Dobson 1986). The number of offspring supported by a population's (non-static) carrying capacity is limited (Skogland 1985); therefore, offspring can be conceptualised as a

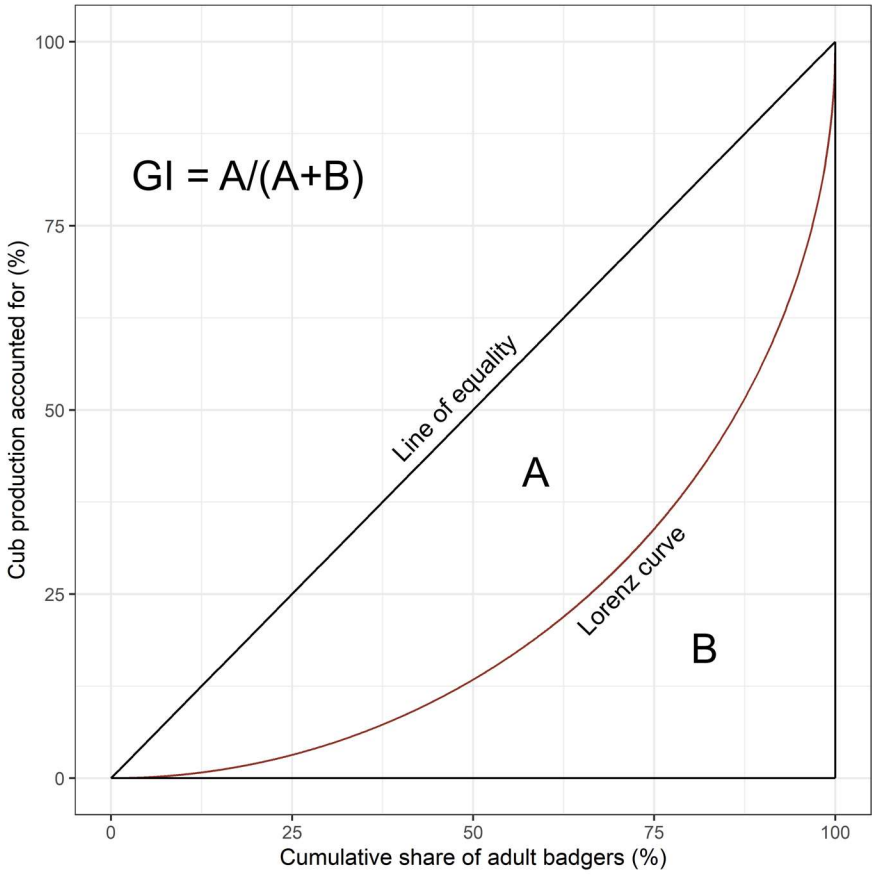


Figure 2. **Illustration of Lorenz curve and relationship to GI.** The Lorenz curve (red line) for a resource's distribution can be derived by sorting individuals from lowest to highest resource controlled, and plotting the cumulative resources (in this non-empirical example, cubs produced) controlled by each percentile of controllers. The Gini Index is equal to the proportion of the area below the line of equality (along which, no individual controls more resource than any other) that lies above the Lorenz curve.

limited resource for fitness. With regard to a given resource, the GI for a population is proportional to the concavity of that resource's Lorenz curve, which graphically represents the distribution of the resource among individuals in the population (Fig. 2). In the case of perfect egalitarianism, GI = 0; if one individual sequesters 100% of the resource, GI = 1.

For the Wytham Woods population, I computed annual (1988-2015) cub production GI using the population pedigree (Annavi et al. 2011, updated pers. comm.), and found very high reproductive inequality: mean annual GI for males was 0.87, and 0.84 for females. Over the years 2000-2010, this corresponds to the top 10% of fathers producing 74.5% of cubs, and the top 10% of mothers producing 67.3% of cubs (note, however, that pedigree included only ~60% of the cubs in the population—see Chapter 2, and supplements therein—so the real degree of inequality is likely to deviate non-trivially from these numbers). Examining GI against sex-specific population density demonstrates higher female inequality at higher female densities (β-regression, $p = 0.012$), but no such trend for males (Fig. 3). Substantial reproductive marginalisation existed for both sexes in all years, but the trend towards egalitarianism at lower female densities suggests that at least some marginal females were able to breed more easily when experiencing lower competition.

The greater degrees of male reproductive inequality seen over all years in Figure 3 warrants further discussion. The mechanisms underscoring the higher reproductive success of some males over others can be cryptic, and is thus not well understood (unlike other species with clearer competitive exclusion mechanisms, e.g. territoriality or harem defense in red deer *Cervus elaphus*: Carranza et al. 1990). Males have little control over whether a female carries their offspring to term; ultimately, it is female body condition (Chapter 3) and the prevailing conditions (Chapter 2) that determine cub production. Moreover, while in other species mate choice might permit males to choose females more likely to carry offspring to term (males can be choosy too: Edward and Chapman 2011), the highly promiscuous polygynandrous mating system of high-density badger populations (with no clear pattern in who mounts whom, Dugdale et al. 2011b), makes this explanation unlikely. Similarly, female badgers' ability to superfoetate litters,

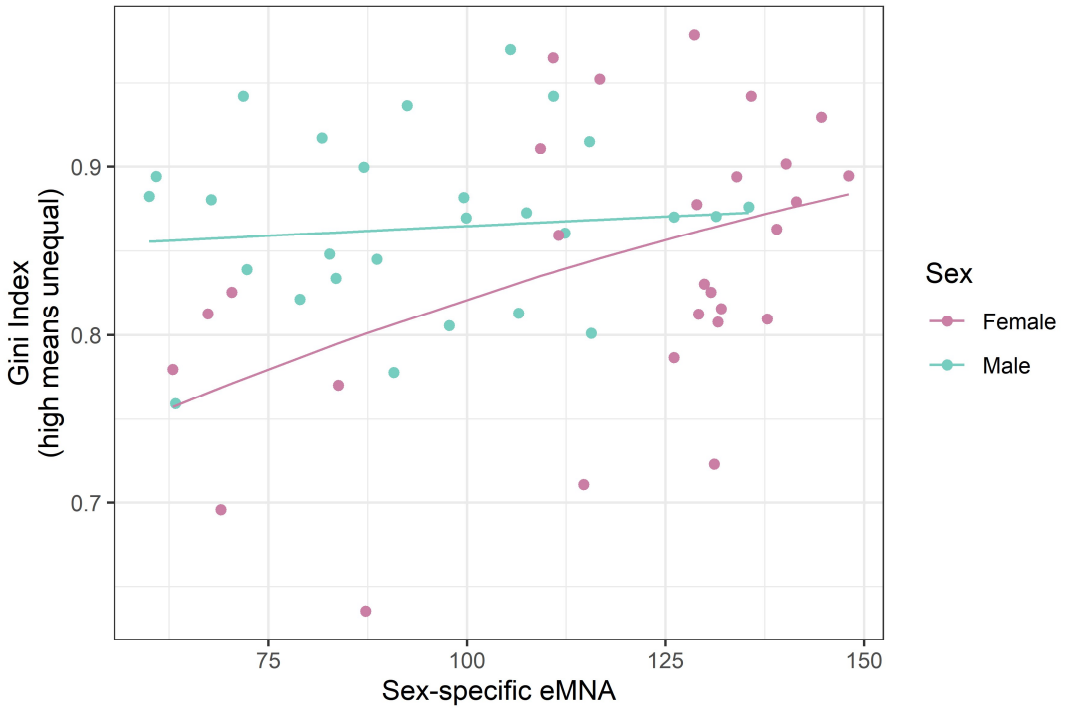


Figure 3. **GI over different sex-specific densities.** Trendlines show predictions from β-regression.

resulting in widespread multiple paternity (Dugdale et al. 2007), makes it unlikely that the successful male was necessarily the one with whom that female mated first. Indeed, because female badgers (like all mustelids, see Macdonald and Newman 2017) are induced ovulators (Yamaguchi et al. 2006), conceptive matings cannot occur until 48-72 hours after first intromission, where females solicit non-conceptive matings to ensure receptivity. Two non-exclusive mechanisms may explain the success of some male badgers over others. The first is post-mating selection through cryptic female choice (CFC, Firman et al. 2017); in badgers, high rates of extra-group paternity may reflect the use of CFC to ensure high heterozygosity and low inbreeding depression (linked to cub survival, Annavi et al. 2014b, 2014a). The second is high—and heterogeneous—investment in reproduction by males, through either sperm competition (Preston et al. 2003) or maximising total mating opportunities (Canal et al. 2012). The cost of

reproduction to males (in mammals, the non-lactating, non-offspring-bearing sex) is often an afterthought in ecology (Bleu et al. 2016). Nevertheless, male somatic-reproductive trade-offs were often detectable within this study badger population, from the stronger link they exhibit between early reproduction and realised lifespan and the male-biased mortality at high densities that led to a skewed population sex ratio (Chapter 2), to the direct somatic costs of degree of testes descent (Chapter 3), with observed (if non-significant) survival costs to successful reproduction (Chapter 2).

Broadly, different sexes rarely experience identical selective pressures. In most species, females bear the major burden of supporting offspring development—an ultimate product of the evolution of anisogamy (Schärer et al. 2012, Lehtonen et al. 2016). As a result, sex-specific behaviour is shaped by resource availability in females, and mating competition in males (Wrangham 1980). This is certainly the case in the Wytham Woods badger population, wherein social context drives compensatory life-history responses in males (Chapter 2), while female life history responds more strongly to proximate weather effects (Chapters 2-3). Nevertheless, the somatic condition of males—driven by weather (Chapter 3)—is also important for enabling them to be competitive, with juvenile BCI playing an influential role in enabling particularly "fast" young males to enter the breeding population (Sugianto et al. 2019b; increasing early reproduction probability by as much as 40%: Chapter 2). The stronger selection for reproductive competition in males is expected to drive, on balance, faster POL in males (Tarka et al. 2018). The Wytham Woods badgers corroborate this hypothesis, with males exhibiting higher F/α ratios (Oli 2004, see Chapter 2) and shorter mean realised lifespans (3.4 in males, 4.1 in females). Accounting for sex-specific demography is a vital tool in appropriately characterising population dynamics (Schindler et al. 2013, 2015, Plard et al. 2018); the evidence I present in this thesis

further supports this concept, and suggests that the process of coping with population change is likely to occur differently between males and females.

4 So how do marginal individuals persist?

Characterising individuals with consistently lower short-term fitness as "lower-quality" might be inadequate if lower fitness represents, instead, an alternative life-history strategy. Jensen's inequality (Denny 2017) provides a mathematical framework enabling us to better understand how phenotypes with low short-term fitness may persist in populations. Jensen's inequality is a mathematical law stating that the secant of a convex function lies above the graph (and vice-versa for a concave function); as the mean of two function outputs lies on the secant, this can be generalised to the statement that the mean of function outputs for different inputs is not equal to the function output for the mean input, if the function is non-linear. For instance, Jensen's inequality can mathematically capture the detrimental effects of increased stochasticity on long-run growth rates: as the relationship between growth rate (r) and proportional change (λ) is concave ($r = \log_e(\lambda)$), decreasing a population by 50% ($\lambda = 0.5$) in one year, then increasing it by 50% the next ($\lambda = 1.5$, or vice-versa) results in an overall decrease in population size, despite the mean λ for the period equalling 1 (Pickett et al. 2015). A wide variety of ecological phenomena adopt non-linear relationships with environmental conditions (Ruel and Ayres 1999, Denny 2017). When deviating from some optimum, these relationships are detrimental to fitness at various scales. Therefore, for a given nonlinear function d(w) that relates weather to a measure of fitness detriment; for instance, a (convex) parabola:

$$d(w) \propto w^2 \quad (1)$$

$$mean\big(d(w)\big) > d\big(mean(w)\big) \quad (2)$$

Given these equations, two rules are inferred from a convex weather-detriment relationship: 1) the greater the variance of weather, the higher the average, or sum (as sum is a linear transformation of the average) detriment; 2) the stronger the relationship, the higher the average or sum detriment for a given weather variance. Figure 4 represents these two rules visually with regard to d(w) and d'(w), where d'(w) represents a stronger link between fitness detriment and weather.

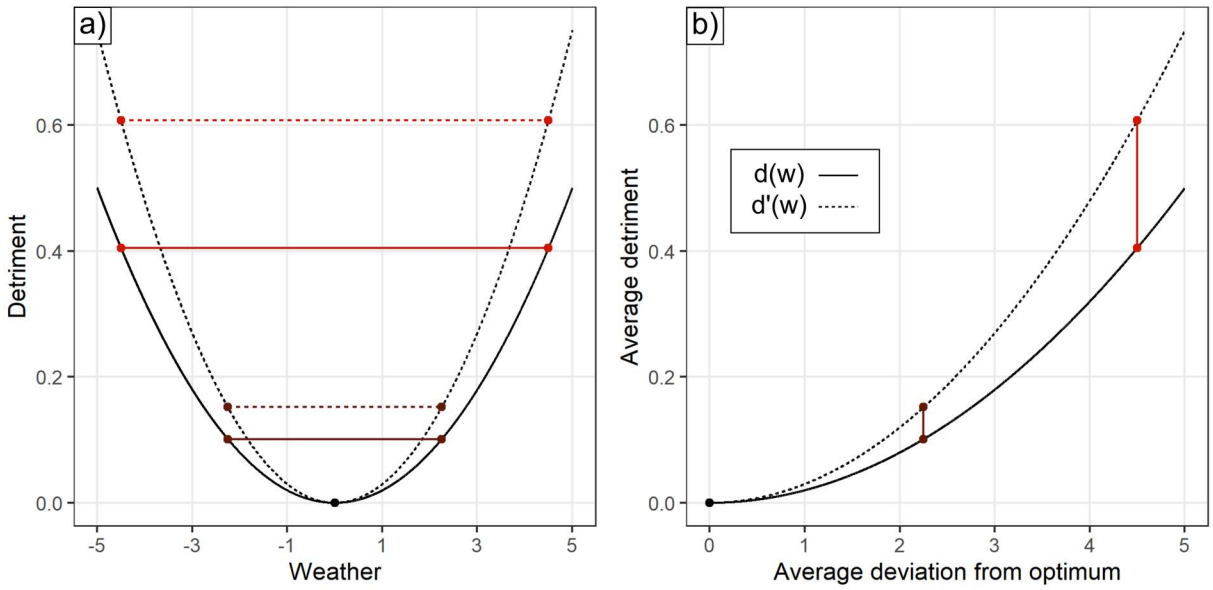


Figure 4. **Illustration of Jensen's inequality.** Dots indicate deviations from the optimum according to symmetrical weather fluctuations. These fluctuations a) result in average detriment (secant lines) above that predicted for the average weather and b) result in higher detriment the more closely tied fitness is to weather conditions.

The Wytham Woods badger population certainly fits the first of these rules. High seasonality (hot summers and cold winters) reduces per capita female cub production (Chapter 2), and increases the influence of summer BCI on survival probability (Chapter 3), while females have a higher probability of successful reproduction following winters with lower variability in

daily winter temperatures (Chapter 3). These effects are consistent with the adverse effects of temperature variability on badger survival reported previously (Nouvellet et al. 2013). Temperature and rainfall variability interacted unexpectedly with reproduction probability: males were more likely to breed in years with high rainfall variability; both sexes exhibited elevated reproduction probability at higher temperature variability; and temperature variability was associated with higher entry of late-breeding females into the population (Chapter 2). This relationship demands further scrutiny, but perhaps if autumnal earthworm availability is affected in a convex manner by weather (thus, the fitness detriment function is concave), then Jensen's inequality might result in a greater portion of females gaining enough fat to successfully reproduce (but with an associated drop in survival probability). While the predominantly non-linear effects I found in my studies are concave (exhibiting optima, such as activity responses to temperature or rainfall, Chapter 5—this results in a convex fitness detriment function), the existence of opposite relationships (where extreme conditions are preferable) should be thoroughly explored. Moreover, asymmetric fitness detriment functions can make deviations in one direction preferable to the other (Martin and Huey 2008), a crucial avenue of inquiry in the context of directional responses to climate change.

The second rule derived from Jensen's inequality may hold the key to understanding the long-run competitiveness of seemingly "lower-quality" phenotypes. The key advantage to a fast life history is to outcompete conspecifics; the effort to do this at cost to survival probability can validate the adage of living fast and dying young (Hall et al. 2015, Dhellemmes et al. 2020). In the most extreme cases, this can come to represent the entire reproductive strategy of a species: for instance, many species of the *Antechinus* genus (small dasyurid marsupials) exhibit a semelparous male breeding strategy whereby high circulating testosterone and cortisol levels do

irreparable harm to organ systems (Naylor et al. 2008). In long-lived species, however, fast life-history strategies may be less noticeably detrimental (Culina et al. 2019)—suggesting, instead, fixed differences in quality (van Noordwijk and de Jong 1986). Nevertheless, this may only hold under average conditions; if, instead, fast-living individuals are affected more drastically by suboptimal conditions, then applying Jensen's inequality might illustrate the long-run drawbacks of fast life histories (Fig. 4b). For instance, despite the many somatic advantages discussed for reproductive female badgers, they fail to recover somatic condition in autumns following hot summers (Chapter 3). If reduced survival probability in individuals with fast life-histories is contingent on only small detrimental deviations from average summer conditions, then the large expected summer temperatures increases under projected climate change (Murphy et al. 2018) should exert a selection pressure for increased representation of slow strategists that engage in reproduction only after meeting some higher security threshold.

Ultimately, individuals hedge their bets against harder times. At the individual scale, this can comprise plasticity to the environment that minimises detriment based on the individual's current energetic context and capacity to do so (Chapter 5). It can also comprise variable somatic strategies, gaining substantial fat stores when deemed necessary but expending that energy when it is advantageous (Chapter 3). More broadly, however, the population benefits from diversified bet-hedging—the production and maintenance of both high-performing (but potentially fragile under stressful conditions) fast strategists and low-performing (but stalwart) slower individuals (Starrfelt and Kokko 2012). This should not be thought of as reducing the average fitness of the population—rather, as previously discussed, the constituent individuals of a population also determine its carrying capacity, and Figure 3 shows that a population like the Wytham Woods badger population is apparently unable to sustain a full complement of fast individuals.

However, slow strategists represent an “each-way bet” (King 1985) at the genomic scale that likely fosters population persistence in the long run—buffering, to some extent, demographic stochasticity (Wilbur and Rudolf 2006, Hilde et al. 2020). This, ultimately, makes diversity in wild populations fundamentally adaptive and crucial to population resilience.

5 Future directions

While my research documented how energetic context affects energy budgeting differences between individuals, further inquiry is required to ascertain the physiological underpinnings of those differences. Pathology may play an under-explored role in determining individual energy context. For instance, in badgers, although bovine tuberculosis infection seems to incur no energetic cost (Barbour et al. 2019), endoparasites (Newman et al. 2001) and reactivation of (widespread) *Mustelid gammaherpesvirus 1* (MusGHV-1) infection (Tsai et al. 2020) carry pathological fitness costs (and, in the case of MusGHV-1, differentially affects individuals based on body condition: Tsai et al. 2021), and must be assumed to shape energy budgets given the substantial costs of mounting an immune response (e.g. 19% elevation of resting metabolic rate in tuco-tuco rodents, *Ctenomys talarum*: Cutrera et al. 2010). Particularly in the case of sexually-transmitted infections such as MusGHV-1, there is capacity for pathogen-induced behaviour alteration, either directly (an under-explored topic, but see Mackey and Immerman 2003) or to compensate for social avoidance (Paciência et al. 2019, but see also Nunn 2003). Pairing the technology developed in Chapter 4 with more rigorous video assays of behaviour (e.g., McClune et al. 2015 in captive animals) could permit both analysis of these behavioural shifts and tighter links between ethology and energetics (Jeanniard-du-Dot et al. 2017). In particular, this approach (particularly if paired with positioning approaches such as dead-reckoning, Bidder et al. 2015) would permit exploration of how individual foraging tactics

(underpinning individual dietary niches, Robertson et al. 2014, 2015) might shape heterogeneous microbiomes across the population. Differences in microbiota composition can substantially affect the efficiency of nutrient extraction and energy expenditure (Lindsay et al. 2020), and therefore present an under-explored form of both reversible (environmentally-determined: Ren et al. 2017, Wu et al. 2017) and irreversible (genetically-determined: Lindsay et al. 2020) inter-individual heterogeneity—especially as it relates to individual diet, which could not be ascertained in this work.

While my thesis has explored energetic plasticity at a variety of temporal scales, it is important to examine the mechanisms supporting reversible change in response to the environment. Epigenetic marks based on environmental conditions can affect thermoregulatory capacity (Weyrich et al. 2016), growth rates (Sinclair et al. 2007), and fat deposition (Martínez et al. 2012), often interacting with gene expression in homeostatic systems (Lillycrop et al. 2005, Tobi et al. 2009, Feil and Fraga 2012). Epigenetic markers should be longer-lasting when environmental heterogeneity is low (Herman et al. 2013); in studying their role in pre-adapting species to rapid change it will therefore be important to ascertain how flexible their codification into energetic strategies is in wild populations. Genetically, too, individuals can exhibit different capacities to develop plastically in response to the environment (e.g., Madrid et al. 2018), begging the question as to whether these plasticity phenotypes might correlate with any of the dominant POLS behavioural, endocrinological, and/or morphological pathways (Careau et al. 2009, Réale et al. 2010, Dammhahn et al. 2018). Finally, there is substantial inquiry to be done into the reversal of accumulated frailty. Torpor has been associated with a reduction in the shortening rate of telomeres (Turbill et al. 2013, but see also Nowack et al. 2019 for limitations) and even increases in telomere length (Supplementary Chapter 2)—a pattern also exhibited by

species that adopt restorative pauses in reproduction (Hoelzl et al. 2016). This raises important questions about the degree to which telomere lengthening through programmed downregulation of metabolism and activity may be able to restore the damage caused by adverse conditions (Zhang et al. 2018).

There is no single strategy that will guarantee resilience. When (not if) populations are presented with dramatic challenges—whether natural or anthropogenic in nature—their continued persistence relies on the responses of their constituent parts: individuals. My thesis has challenged orthodoxies in conceptualising populations. Individual niches are not static; new conditions will likely elicit adaptive plasticity and shifting life-history optima. The population is unlikely to respond to a challenge as a monolith; some individuals will have the capacity to adapt (at least to a point), while others will find themselves unable to, whether through frailty or over-competitive phenotypes. Once affected, the population is not doomed to continue its trend; the different phenotypes remaining may shift to a new equilibrium. The challenges facing wild populations in the 21st century are myriad and concerning. We have lost—and will continue to lose—untold numbers of species to anthropogenic causes (Ceballos et al. 2017, Otto 2018). Seeking the exceptions to this general trend may seem pointless—even hopeless. However, most of the findings of this thesis, and of others like it, point towards a more optimistic outlook, as we document the strikingly individual struggles that make up the bigger story of population change. It is my sincere hope that by striving to understand the natural toolbox populations possess to handle rapid change, by drawing back the heavy curtain of averages and unidirectional trends to reveal the diversity hidden therein, we can best identify how to shepherd our biodiversity through the challenges we have wrought.

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Appendices

Supplementary Chapters 1-2 and

Supplemental Materials for Research Chapters

Supplementary Chapter 1

Negative density-dependent parasitism in a group-living carnivore

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Abstract

Animals living at high population densities commonly experience greater exposure to disease, leading to increased parasite burdens. However, social animals can benefit immunologically and hygienically from cooperation, and individuals may alter their socio-spatial behaviour in response to infection, both of which could counteract density-related increases in exposure. Consequently, the costs and benefits of sociality for disease are often uncertain. Here, we use a long-term study of a wild European badger population (*Meles meles*) to investigate how within-population variation in host density determines infection with multiple parasites. Four out of five parasite taxa exhibited consistent spatial hotspots of infection, which peaked among badgers living in areas of low local population density. Combined movement, survival, spatial, and social network analyses revealed that parasite avoidance was the likely cause of this negative density dependence, with possible roles for localised mortality, encounter-dilution effects, and micronutrient-enhanced immunity. These findings demonstrate that animals can organise their societies in space to minimise parasite infection, with important implications for badger behavioural ecology and for the control of badger-associated diseases.

1 Introduction

A wild animal's infectious disease burden is determined by its exposure and susceptibility to infective pathogens. Typically, higher population density results in increased contact rates and thus greater exposure (Cote and Poulin 1995, Altizer et al. 2003); however, sociality carries immunological and hygienic benefits that can counteract this exposure-exacerbating effect (Kappeler et al. 2015, Ezenwa et al. 2016). For instance, cooperative foraging improves nutrition, alleviating infection costs (Almberg et al. 2015); mutual grooming removes ectoparasites (Stewart and Macdonald 2003, Madden and Clutton-Brock 2009, Poirotte et al. 2017); and "social immune responses" maintain collective group health (Cremer et al. 2007, Meunier 2015), e.g. through extirpating sick individuals (Baracchi et al. 2012). Additionally, the

environmental distribution of resources can influence spatial behaviour (Methion and Díaz López 2019, Bachorec et al. 2020, Webber et al. 2020) and determine local population densities (Webber and Vander Wal 2018), while altering susceptibility (Becker et al. 2019) and transmission efficiency (Albery et al. 2020). Sociality and disease may thus be confounded through shared causal origins rather than being mechanistically linked (Albery et al. 2020). Finally, individuals can minimise exposure by avoiding environmental cues (Curtis 2014, Weinstein et al. 2017) or infected conspecifics (Poirotte et al. 2017, Stockmaier et al. 2018), creating a population-level "landscape of disgust" analogous to predatory "landscapes of fear" (Buck et al. 2018, Weinstein et al. 2018). These processes could produce negative density effects, sometimes depending on parasite transmission mode (Cote and Poulin 1995, Albery et al. 2020, Hopkins et al. 2020), but their role in defining observed density-infection relationships is poorly understood.

Uncertainty concerning density-infection relationships largely arises because studies of social effects are often carried out across discrete groups (Cote and Poulin 1995, Ezenwa 2004), between populations (Brown and Brown 1986, Downs et al. 2015), or between species (e.g., Cote and Poulin 1995, Altizer et al. 2003, Ezenwa 2004, Rifkin et al. 2012). Continuous density measures are rarely linked to parasite burden within one contiguous host population, and studies that do so generally use purely social metrics rather than spatial density gradients (e.g., Drewe 2010, MacIntosh et al. 2012, VanderWaal et al. 2014). Continuous spatial density measures are advantageous because: density is a continuous, spatially explicit variable (Pullan et al. 2012, Kirby et al. 2017, Albery et al. 2019); for the many parasites that are spread through the environment, spatial density measures better represent transmission than direct (social network) metrics (Richardson and Gorochowski 2015, Manlove et al. 2018, Albery et al. 2020, Leu et al. 2020); and between-population and cross-species comparisons are fraught with confounding factors such as shared environmental causality or compensatory evolutionary changes (Cote and

Poulin 1995, Ezenwa et al. 2016), which within-population studies can more easily avoid or overcome. Furthermore, accounting for spatial effects may help anticipate or test the caveats of cooperation, environmental causality, and behavioural avoidance outlined above.

European badgers (*Meles meles*) are nocturnal, ground-dwelling mustelids with a pan-European distribution, eating a varied diet composed largely of earthworms (Macdonald et al. 2015). Badgers are of particular interest for cattle health in the United Kingdom because of their role in maintaining and spreading bovine tuberculosis (Macdonald et al. 2015, McDonald et al. 2018). Although intended as a control measure, intense culling perturbs badger social systems, causing stressed survivors to disperse, thereby spreading bovine tuberculosis to neighbouring farms (Tuyttens et al. 2000, Donnelly et al. 2007, Ham et al. 2019). Understanding badgers' socio-spatial behaviours and their epidemiological implications is therefore an important research priority (e.g., Weber et al. 2013, McDonald et al. 2018, Rozins et al. 2018, Silk et al. 2018). The demography, behaviour, and parasitism of badgers in Wytham Woods, Oxfordshire have been studied continuously since 1987 (Macdonald and Newman 2002, Macdonald et al. 2015). Dens (termed "setts") are situated dependent on soil composition and landscape topography (Macdonald et al. 2004). These badgers reside in cohesive mixed-sex social groups, with around 35% consistent philopatry; however, these groups are also fluid: 16.4% of individuals are trapped at a different social group to their previous capture history, and 19.8% away from their natal group (Macdonald et al. 2008). Furthermore, from genetic pedigree, 48% of cubs have extra-group paternity (Annavi et al. 2014). Badgers host several arthropod parasites, including badger-specific fleas (*Paraceras melis*) and lice (*Trichodectes melis*) and generalist ticks (*Ixodes* sp.) (Cox et al. 1999). They also carry two gastrointestinal protozoans: *Eimeria melis* and *Isospora melis*. *E. melis* predominantly infects young individuals, causing substantial mortality (Anwar et al. 2000, Newman et al. 2001). Although studies have examined social grooming effects on ectoparasite burden (Stewart and Macdonald 2003, Johnson et al. 2004) and

roles of denning behaviour in parasite transmission (Cox et al. 1999), the within-population spatial-social parasite epidemiology has yet to be investigated.

Here, we investigate parasite burdens in the Wytham badger population and their associations with spatial and social behaviour. We establish parasite distributions using spatial autocorrelation models. We quantify social drivers using both spatial density gradients and social network metrics, postulating that greater badger densities would drive higher parasite burdens through increased exposure. Finally, we examine survival effects, investigating whether parasite-linked mortality might alter spatial patterns of badger population density. We consider a range of potential social/spatial covariates of parasite burden, including density-related exposure changes, benefits of cohabitation, condition/susceptibility effects, encounter-dilution effects, and parasite avoidance behaviours.

2 Methods

2.1 Data collection

Badgers were sampled as part of a long-term study in Wytham Woods, Oxfordshire, UK (51.778°N, 1.313°W), established in 1987 and recording one of the highest local badger densities ever reported (Macdonald and Newman 2002, Macdonald et al. 2015). Badgers were trapped overnight at their setts in steel-mesh cages baited with peanuts, collected the next morning, transported to a handling facility and sedated. Individuals were identifiable by tattoo, applied on first trapping (typically as cubs). Measures were taken of head-body length (mm) and weight (to the nearest 0.1kg). We calculated a standardised index of body condition dividing $\log_e$(weight) by $\log_e$(body length). The population was trapped seasonally (winter: Jan/Feb/March; spring: April/May/June; summer: July/Aug/Sept; autumn: Oct/Nov/Dec) in 4 quadrants, for 3 days per quadrant. Our dataset included 9016 captures of 1369 badgers spanning 29 years (1990-2018).

The population currently comprises 23 social groups (mean group size=11; range 2-29 individuals), each using more than one sett, with sett/social group affiliation established using bait-marking (Macdonald et al. 2004, Buesching et al. 2016). Badgers were assigned to groups using established residency rules (Annavi et al. 2014). We computed social networks based on co-trapping using a "gambit of the group" approach, where individuals trapped in the same sett in the same year were assumed to have interacted (Franks et al. 2010).

Fleas were counted during a stereotyped 20-second inspection of the badger's full body, and ticks (*Ixodes* sp.) and lice (*Trichodectes melis*) were counted within a 4x4cm square of preferentially-parasitised skin near the groin (per Cox *et al.* 1999). Faecal sampling for two protozoan endoparasites, *Eimeria melis* and *Isospora melis,* was carried out through 1993-1997 and 2009-2017 (N = 1287 counts). Endoparasite were counted using salt flotation and microscopy (Newman et al. 2001, Sin et al. 2014). Each count was duplicated, and data were reduced to a binary infected/uninfected status (rather than counts) because of their highly overdispersed distribution.

2.2 Statistical Analysis

2.2.1 Covariates

Statistical analysis and data manipulation used R version 3.6.0 (R Core Team 2020). All data and code are available at https://github.com/gfalbery/Badgeworks. Models were constructed using the *inla* package (Lindgren et al. 2011, Lindgren and Rue 2015). Response variables included counts of fleas and lice (negative binomial distribution) and prevalence of ticks, *Eimeria*, and *Isospora*. Explanatory covariates included: Year (continuous); Month (categorical); Age Category (categorical: cub, yearling, and adult); Sex (male and female); and Body Condition (continuous). Continuous covariates were standardised (mean = 0; standard deviation = 1). Individual Identity and Year were fitted throughout as categorical random effects.

2.2.2 Spatial autocorrelation models

To identify generalised spatial patterns we first fitted models accounting for continuous spatial autocorrelation across the population (Lindgren et al. 2011, Lindgren and Rue 2015, Albery et al. 2019). We fitted a base model using only Year, Month, Age Category, and Sex, with individual and annual random effects. We then added an SPDE random effect controlling for spatial autocorrelation in the response variable in space, based on individuals' point locations. We then compared these models using Deviance Information Criterion (DIC) to establish whether accounting for spatial autocorrelation improved model fit; models within 2ΔDIC were judged competitive.

2.2.3 Density models

We then fitted models that replaced the SPDE effects with individual measures of local population density. Models included a range of social/spatial density measures, calculated using various methods. Spatial density metrics represent numbers of individuals in a given space, and therefore tread the line between social and spatial behavioural traits (Albery et al. 2020). We computed these by creating space use distribution kernels with the *adehabitathr* package in R (Calenge 2006). We rasterised the usage distribution, assigning each individual a local density based on the raster value for their map location (Fig. 1A-B). Measures included: 1) **Lifetime density**: the density of individuals' centroids across the study period. 2) **Trapping density**: the density of trapping events, incorporating multiple captures of the same individual per year. 3) **Annual density**: the density of individuals' centroids in the sampling year, calculated from annual density kernels. Only one spatial density measure was allowed in a given model, as the measures correlate ($R > 0.5$) and co-fitting several measures produced spurious, unexpected correlations in the opposite direction expected from data exploration. We also used two social metrics based on co-trapping patterns. **Degree centrality** was the number of unique badgers with whom each individual was trapped in the same sett per year. **Group size** was the total number of

individuals trapped in a given social group per year. Following spatial autocorrelation model procedures, we conducted a model selection procedure for behavioural metrics, using 2ΔDIC as the cutoff, and only including the best-fitting metric. We conducted these models for: the overall dataset (N = 9,016); adults only (age 2+, fitting age in years as a fixed covariate; N = 6,159); and juveniles only (N = 1,639). For these models, we display only the best-fitting metric, and for the overall dataset if it exhibited a significant trend (and a subset-only model otherwise).

2.2.4 Multi-response models

To investigate whether parasites covaried with badger density at the within- or between-individual level, we constructed multi-response models in MCMCglmm with an unstructured covariance matrix (Hadfield 2010, Brommer and Covarrubias-Pazaran 2019). We fitted parasites and local density as response variables, estimating their covariance when accounting for other fixed effects and decomposing this covariance at the within- and between-individual level. A negative within-individual (residual) correlation would imply that higher burden/prevalence individuals (compared to their baseline) moved to lower density areas during their lives, supporting either social ostracism or sickness behaviours. In contrast, negative between-individual covariance would imply that individuals inhabiting lower densities generally had inherently greater parasitism. We only constructed these models for parasite-host age category combinations that demonstrated density effects in the INLA models.

2.2.5 Survival models

To investigate parasites' mortality effects, we fitted models with survival as a binary response (1 = animal seen in any subsequent year; 0 otherwise). These models included the same covariates as the parasite models, plus parasite prevalence/count and badger density measures. Parasite measures were either log(x+1)-transformed integers (fleas, lice) or binary (ticks, *Eimeria*, and *Isospora*). We conducted another model selection procedure, adding parasite

metrics successively if they improved model fit. This was carried out for adults and juveniles separately.

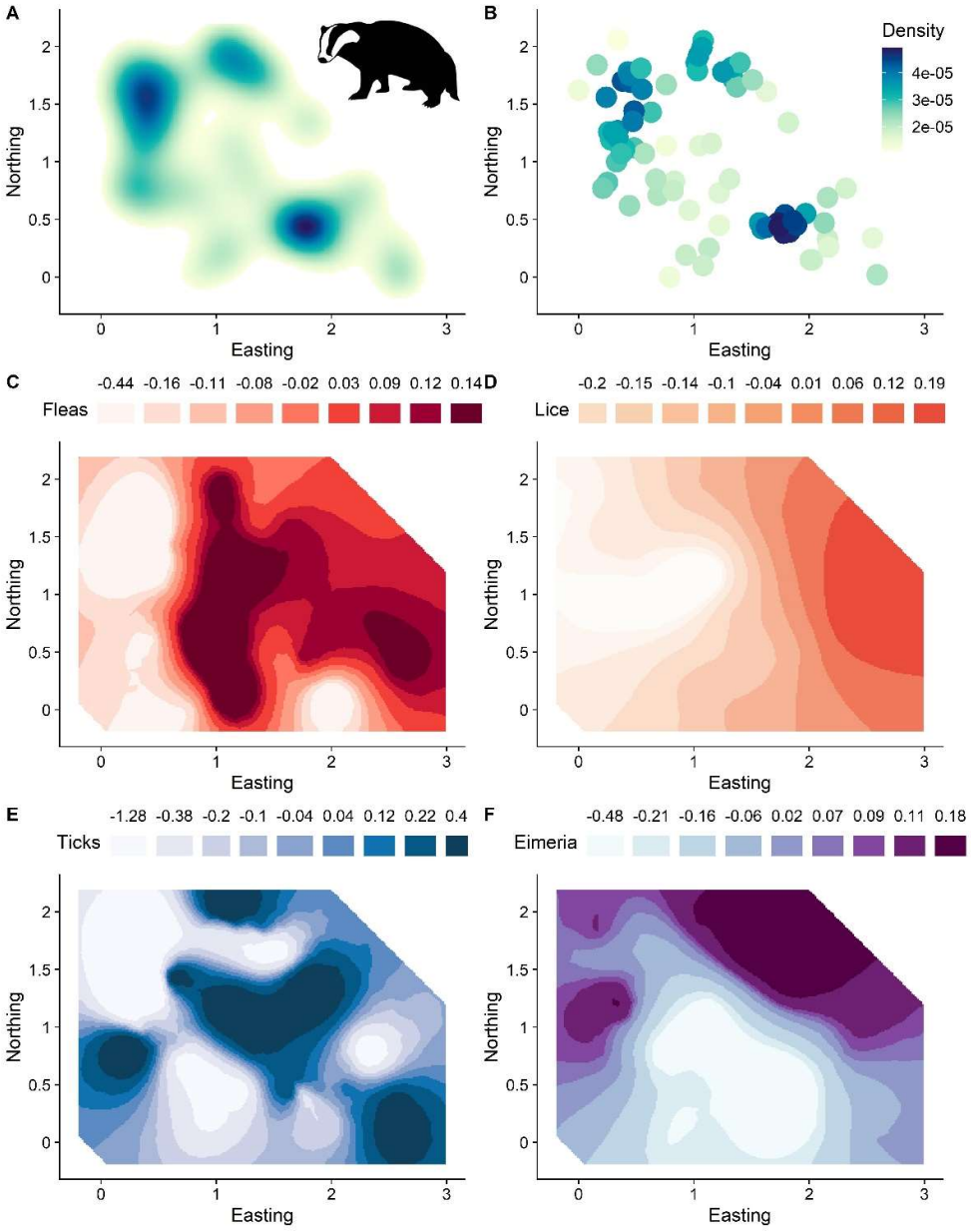


Figure 1. **Spatial distributions of badger population density and parasites in Wytham Woods, Oxfordshire, between 1989 and 2018.** A: badger population density distributed across Wytham Woods, calculated based on a space use kernel for individuals' annual centroids. B: Individual badgers trapped at setts (represented by

points) were assigned a local density value based on their location on the rasterised space use kernel. Darker blue colours in A and B correspond to greater population density. C-F: the spatial distribution of the four spatially distributed parasites, estimated using the INLA SPDE effect. Darker colours correspond to increased parasitism. The density values in B were fitted as covariates in linear models to explain individual parasite burdens, revealing a negative correlation between density and parasitism (see Fig. 2). All axes are in kilometres, with the 0,0 point at the bottom left of the study area. We examined a fifth parasite, *Isospora melis*, but it was not significantly spatially distributed (see Table 1). Badger silhouette is from phylopic.org, credit Anthony Caravaggi (CC BY-NC-SA 3.0).

3 Results

INLA autocorrelation models revealed considerable spatial structuring of parasite burdens. Models for 4/5 parasites were substantially improved by incorporating spatial effects (ΔDIC > 8; Table 1). Only *Isospora*'s model was not improved by spatial autocorrelation (Table 1).

Table 1. **DIC changes associated with spatial autocorrelation terms for the five examined parasites.** Lower numbers denote better models; best-fitting models ΔDIC = 0. All models except *Isospora* were improved by addition of spatial fields ("SPDE").

	Fleas	**Lice**	**Ticks**	**Eimeria**	**Isospora**
Base	153.03	36.57	49.25	8.28	0
SPDE	0	0	0	0	2.25

Density models provided substantial support for negative associations between badger density and parasite infection. Including at least one density measure as a covariate improved the model for at least one age category for 4/5 parasites; all had significant negative slopes for density effects (Fig. 2; Fig. SI1-4; Table SI1-3). Slopes were relatively shallow, but extremely significant and robust (Fig. 2). Flea counts were best described by Lifetime Density for the overall model (ΔDIC = -16.31; $p < 0.0001$; Fig. 2A), while lice burdens decreased with Trapping Density in the juveniles-only model (ΔDIC = -8.77; $p = 0.0017$; Fig. 2B). Tick prevalence was lower in areas of higher Lifetime Density (ΔDIC = -2.47; $p = 0.0038$; Fig. 2C), and *Eimeria* prevalence was lower with greater Trapping Density (ΔDIC = -5.83; $p = 0.0053$; Fig. 2D). Only one positive social effect was detected: adults with greater degree had slightly more lice (ΔDIC = -2.39; $p = 0.027$; Fig. SI2). All DIC changes associated with the model addition procedure are presented in Table SI1-3.

MCMCglmm multi-response models revealed similar trends to INLA univariate models (Fig. SI1-4), and allowed us to decompose density-parasite correlations into within- and between-individual changes (Fig. 3B). Correlations were greater and much more significant between- than within-individuals in all cases (Fig. 3B). This demonstrates that movement between high- and low-density areas was unlikely to produce changes in parasite burden over an individual's lifetime, but rather that individuals' home ranges exhibited inherently different local density-parasite relationships. Only louse infection predicted survival probability; the effect was relatively small, minimally significant, and specific to juveniles ($p = 0.038$; Fig. 3A).

Our models also revealed various other effects (Figs. SI1-4). Briefly, in the overall models, juveniles had fewer fleas, more lice, and greater *Eimeria* prevalence than did yearlings and adults, and lower *Isospora* prevalence than adults (Fig. SI1). Males had more lice than did

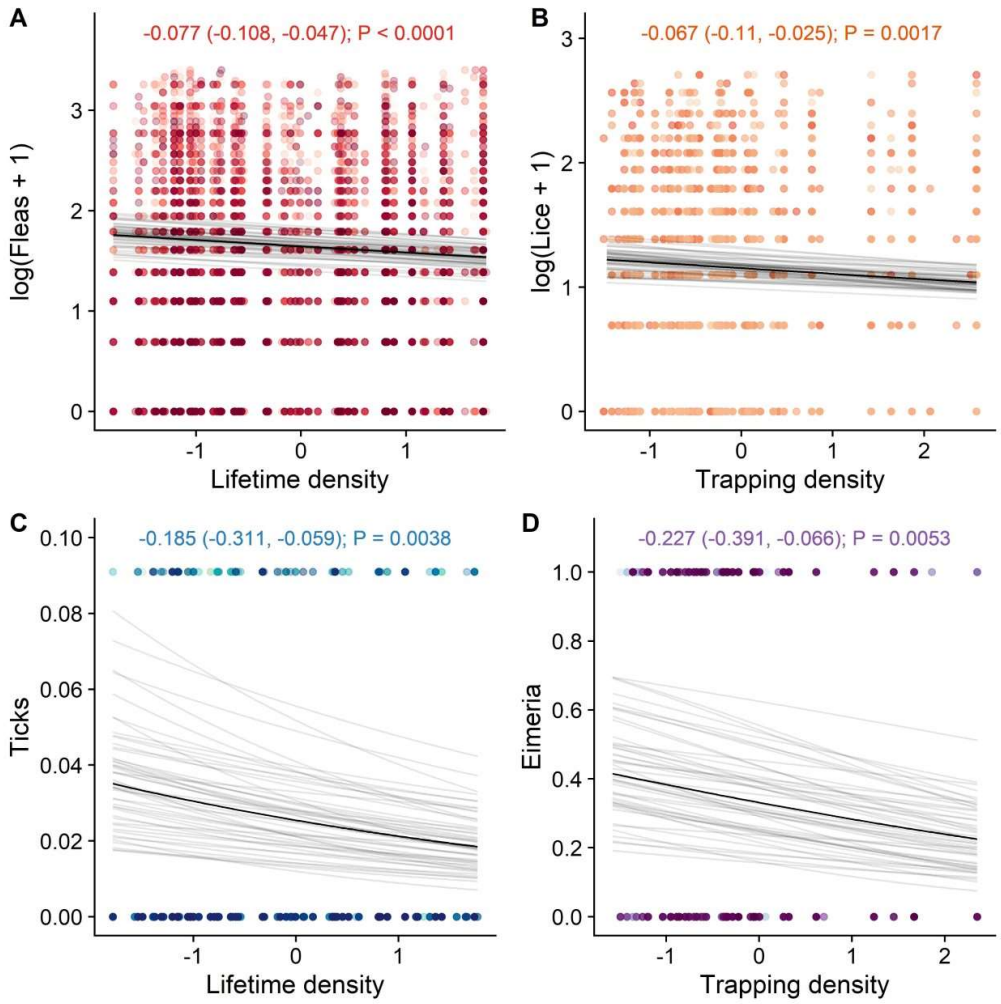


Figure 2. **Negative associations between population density and parasite infection.** Badgers living at higher densities had fewer fleas (A), fewer lice (B), lower tick prevalence (C), and lower *Eimeria melis* prevalence (D). B represents juveniles only. Points represent individual samples, with colours randomised along a colour palette for plotting clarity. Opaque black lines are derived from linear model fits, taking the mean of the posterior distribution. Transparent grey lines represent 100 fits drawn randomly from the posterior estimate distributions of each model, to demonstrate error in the slope and intercepts. Text at the top of the Figures communicates slope estimates, with lower and upper 95% credibility intervals in brackets, and P values. NB: in panel C, the y axis scale

and the location of the positive points have been altered for plotting clarity and to better visualise the slope, due to low tick prevalence.

females, with substantial monthly variation in all parasites (Fig. SI1). Additionally, body condition was negatively associated with fleas, lice, and *Eimeria* infection in all age/sex classes (Fig. SI1). The adults-only and juveniles-only models were very similar to the overall models (Fig. SI1-3); notably, in adults, lice burden increased with age in years, whereas *Eimeria* and *Isospora* prevalence decreased (Fig. SI2).

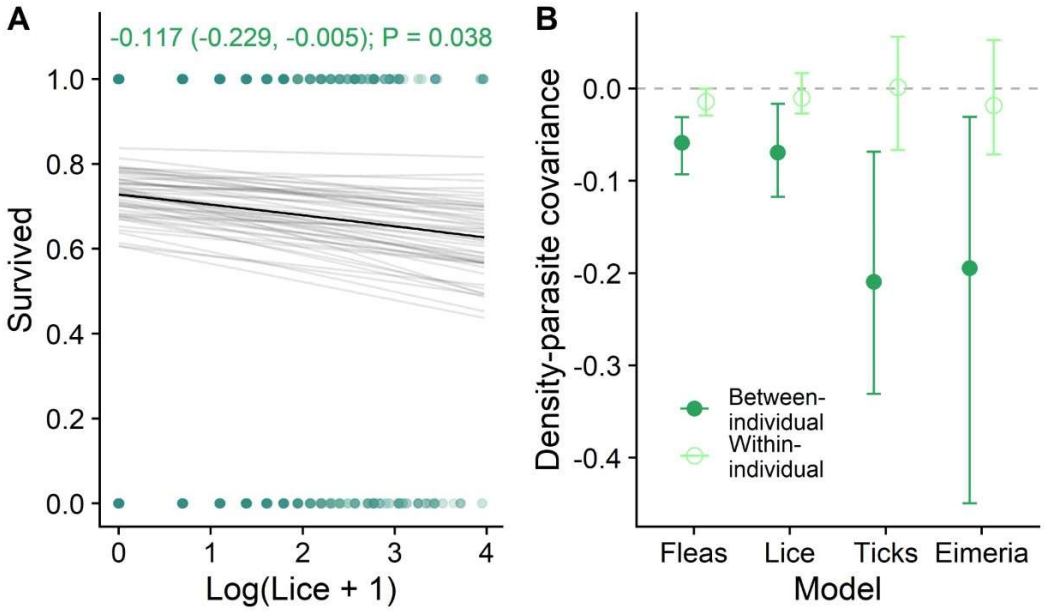


Figure 3. **Associations of parasitism with survival and density-parasitism covariance partitioning.** A) Louse burden was negatively associated with individual survival probability in juveniles. Opaque black line=linear model fit. Transparent grey lines = 100 fits drawn randomly from the posterior estimate distribution, to demonstrate error in the slope and intercept. Text at the top of panel A communicates slope estimate, with lower and upper credibility interval in brackets and P value. B) Estimates for within- and between-individual covariance between parasitism and density, taken from MCMCglmm

multivariate models. Points = posterior mean effect size estimates; error bars = 95% credibility intervals.

Table 2. **Reasoning surrounding our hypothesis testing.** We rejected most hypotheses for our observed negative density effects other than parasite avoidance.

Potential mechanism	Conclusion	Reason for conclusion
Co-habitation/ cooperation benefits	No	No direct social effects or competition with body condition effects (Model Set 2; Figure SI1-3)
Allo-grooming	No	Spatial rather than direct social effects; grooming not possible for endoparasites (Model Set 2; Figure SI1-3; Table SI1-3)
Nutrition-associated immune benefits	No	No competition with body condition effects (Model Set 2; Figure SI1-3)
Social ostracism/self-isolation	No	Low within-individual covariance of density and parasitism (Model Set 3; Figure 3B)
Encounter-Dilution	Untested	Possible for generalist ticks, but not for the other (badger-specific, non-mobile) parasites (Mooring and Hart 1992, Buck et al. 2017)
Micronutrient effects on immunity	Untested	Could be tested in the future by examining the landscape of immunity and correlations with parasites (Albery et al. 2019)
Local host die-offs	~No	Possible for lice, in juveniles, but no other mortality effects were evident (Model Set 4; Figure 3A)
Avoidance	Yes	Other possibilities eliminated; consistent with individual-level behavioural responses (Butler and Roper 1996)

4 Discussion

Using a combination of spatial and social network analysis, we uncovered negative associations between local population density and multiple parasites in this wild group-living carnivore. We found strong but contrasting spatial structuring of fleas, lice, ticks, and *Eimeria*, and, contrary to expectations, all four were most prevalent or abundant in areas of lowest badger density. Co-trapping network and grouping metrics were not predictive of parasitism, implying that "direct" social behaviours, such as mutual allo-grooming, were unlikely to explain the negative density effects. Additionally, badger density effects manifested independent of survival and body condition effects, implying that spatial structuring of the host population did not originate from: 1) localised host mortality, 2) reduced susceptibility arising from co-habitation and implied cooperation benefits (Almberg et al. 2015, Ezenwa et al. 2016), or 3) greater local resource availability influencing susceptibility (Strandin et al. 2018, Sweeny et al. 2019, Becker et al. 2019). Additionally, multi-response models revealed low within-individual covariance between density and parasites, providing little support for heavily-parasitised individuals becoming ostracised during the course of their lives (Baracchi et al. 2012). Taking spatial structuring together with setts' propensity to harbour parasites (Butler and Roper 1996, Cox et al. 1999), the most parsimonious interpretation is that badgers avoid infection behaviourally, preferring to inhabit areas poorly disposed to parasite transmission (Table 2). These individual-level avoidance behaviours amplify at the population level to produce patterns of badger density inversely related to parasite distributions in the environment, as expected under a "landscape of disgust" (Curtis 2014, Buck et al. 2018, Weinstein et al. 2018). As well as providing rare evidence of non-consumptive effects of parasites in a wild carnivore, these results imply that animals can arrange their society in space according to parasite transmission.

Our study demonstrates observationally that parasites can determine a society's structure in the environment, and that this phenomenon may counteract the more conventional prediction

that host density exacerbates parasitism through increased exposure (e.g., Cote and Poulin 1995, Altizer et al. 2003, Ezenwa 2016). Consequently, studies aiming to quantify social covariates of disease should explicitly seek to investigate individual movement and avoidance behaviours, socio-spatial structuring, and feedbacks between sociality and space use (Albery et al. 2020). Previous studies on other mammals have revealed avoidance of infected conspecifics (Poirotte et al. 2017) and faeces (Weinstein et al. 2017, Poirotte and Kappeler 2019), but it remained unclear whether animals avoid spatial hotspots of transmission themselves, and whether these could have population-level consequences (Buck et al. 2018, Weinstein et al. 2018). Badgers respond to social scent cues and may use these to detect and avoid infested or infectious individuals (Newman and Buesching 2019); furthermore, they move between setts regularly to avoid accumulating parasites (Butler and Roper 1996, Brøseth et al. 1997), abandoning highly infested setts and chambers (Cox et al. 1999); we posit that this behaviour has emergent population-level consequences. Wytham badgers preferentially establish their setts on northwest-facing slopes in areas with sandy soils (Macdonald et al. 2004), and variation in internal sett temperature and humidity are associated with reproductive success (Kaneko et al. 2010, Tsunoda et al. 2018). Our data suggest additional selection for sett traits and sites resistant to parasite infestation and transmission, which produce an emergent trend for fewer setts, with fewer occupants, in more highly parasitised areas. Quantifying parasites in the environment or inside setts and correlating them with badger behaviour could provide support for this hypothesis. Environmental (sett chamber-based) data on parasite presence would be needed to determine whether badgers avoid infection *actively* (pre-infection), using environmental cues that predict parasitism, or *reflexively* (post-infection), by moving away from areas of high parasitism due to irritation or sickness.

Four parasites exhibited negative density effects, which could impose tradeoffs on avoidance behaviour. The parasites' distributions were highly contrasting, likely driven by different environmental factors: for example, sett microclimates favouring flea survival will

facilitate their transmission (Butler and Roper 1996, Cox et al. 1999); similarly, *Eimeria* is transmitted faecal-orally, and oocysts are likely acquired from warm, moist sett chambers, which may explain the gradual decline moving away from the Thames river in the Northwest toward drier parts of the woods (Fig. 1F). Ultimately, in combination with other socio-ecological factors (e.g., finding suitable mates), badgers may be incapable of completely avoiding all parasites via denning decisions, which could mediate co-infection and promote diverse parasite communities, giving rise to local hotspots across the population. This may lead to parasite avoidance being traded off against foraging, reproductive success and survival (Hutchings et al. 2006, Buck et al. 2018). If badgers exhibit between-individual variation in movement and foraging specialisation (Robertson et al. 2014), avoidance of multiple co-infecting parasites could maintain between-individual immune heterogeneity (Sin et al. 2014). Notably, only cub density was negatively associated with lice. This observation could be linked to the detectable mortality effects in cubs, driving local cub mortality and/or motivating reproducing females to avoid spatial hotspots of lice.

All of the parasites we examined employ some degree of indirect transmission, likely yielding different relationships with host density than more directly transmitted parasites (Cote and Poulin 1995, Albery et al. 2020). Ultimately, only avoiding conspecifics can help avoid direct parasite transmission (e.g. (Poirotte et al. 2017)), which may not be achievable through purely spatial structuring. Future studies could examine sexually transmitted infections or aerosol-transmitted viruses to investigate whether individuals living in areas of lower density gain any benefit in terms of direct parasite transmission. This may be of particular importance for bovine tuberculosis (bTB), which has a complex, nonlinear relationship with badger sociality (Woodroffe et al. 2009, Delahay et al. 2013, Benton et al. 2016). Notably, previous bTB studies have generally used social group size as a metric of sociality; given that bTB has an

environmental transmission component, particularly between badgers and cattle (Woodroffe et al. 2016), spatial density metrics, such as those employed here, could be revealing.

We note two potential sources of negative density dependence untested by our modelling approach: the encounter-dilution effect (Mooring and Hart 1992, Buck et al. 2017) and micronutrient impacts on immunity (Calder and Jackson 2000). For the former, where parasites exhibit a constant attack rate in space, greater host densities actually drive a lower per-individual burden of disease because the same number of parasites is divided among more available hosts (Mooring and Hart 1992, Buck et al. 2017). Because this requires that the spatial distributions of parasites are not tightly linked to the host distribution (e.g. through reproducing on the host), it is unlikely to apply for any of the badger-specific parasites studied here. However, non-host-specific ticks (*Ixodes* sp.) could transmit from other species to badgers in a given area, producing an encounter-dilution effect; therefore, we are unable to rule out this mechanism (Table 2). Regarding nutritional status, we used body condition index as a coarse predictor of the ability to mount a healthy immune response. However, micronutrients are essential to effective immune function (Calder and Jackson 2000) and would not be detected from body condition indices; therefore, it is plausible that badgers might congregate in areas of high micronutrient availability. If this behavioural tendency functions to combat pathogens specifically, it amounts to a "landscape of disgust" acting through reduced susceptibility rather than reduced exposure. This possibility could be tested in this or similar systems by comparing the spatial distributions of high-resolution individual-level immune measures (i.e., the "landscape of immunity" (Albery et al. 2019)) with host density distributions.

Our findings have important implications for the socio-spatial dynamics of this system and its resilience to pathogens and ecological change. If badger populations are organised optimally to occupy areas of least parasite transmission, even small disturbances (e.g. setts lost to

forestry) could disrupt its socio-spatial structure and force individuals into unfavourable, more highly parasitised areas, exacerbating their disease burden. Therefore, disruptive anthropogenic activities such as culling-linked perturbation could have unseen consequences for badger disease beyond larger-scale movement impacts (e.g., Tuyttens et al. 2000, Ham et al. 2019). These findings further inform our understanding of the drivers of badger spatial behaviour, offering insights that may be invaluable for their conservation and disease control (Macdonald et al. 2004, McDonald et al. 2018).

5 Authors' Contributions

Gregory Albery conceived of the study, analysed the data, and wrote the manuscript. Christina Buesching, Chris Newman, and David Macdonald oversaw the system and data collection, and Julius Bright Ross and Gregory Albery collected some data. All authors commented on the manuscript and offered advice throughout.

6 Data Accessibility Statement

Data and code are available at zenodo.org (DOI:10.5281/zenodo.4283448)

7 Supplementary figures and tables

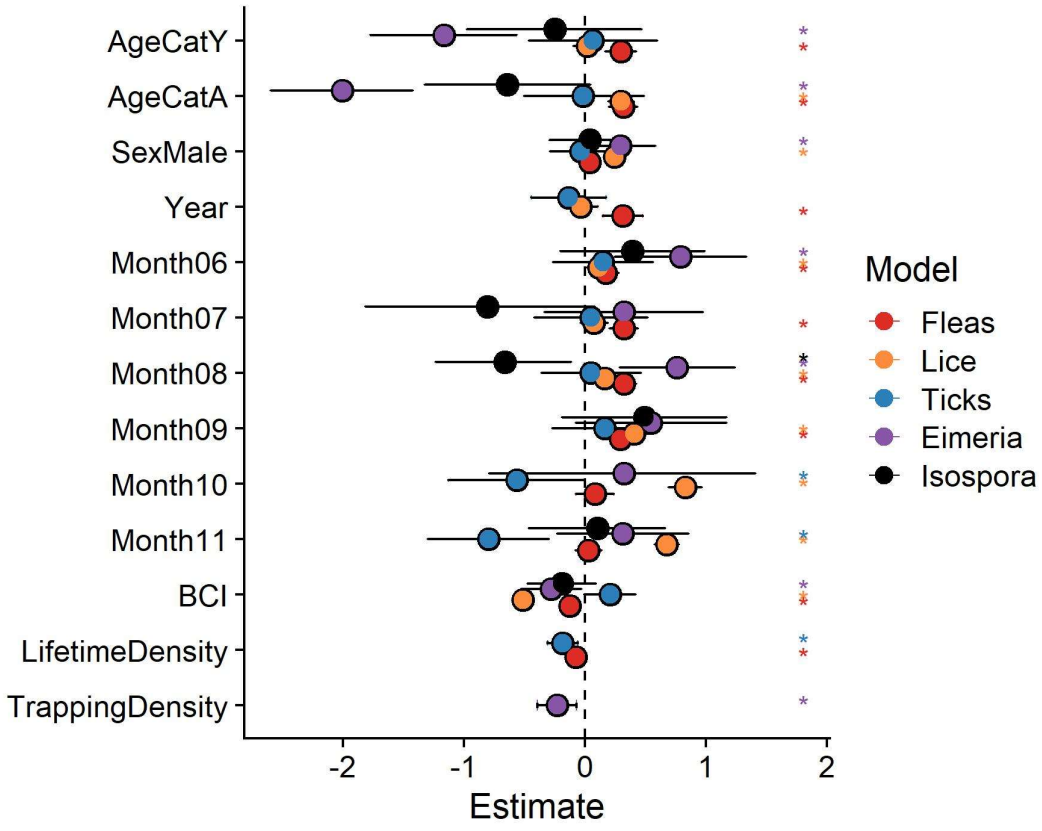


Figure SI1. **Model effect outputs for the full dataset INLA density models.** Points represent modes of the posterior distribution of the effect estimates; error bars represent the 95% credibility intervals. Asterisks denote significant results, whose 95% credibility intervals did not overlap with zero. Only the behavioural traits that improved the model fit ($\Delta DIC < -2$) and were kept in the final model are shown.

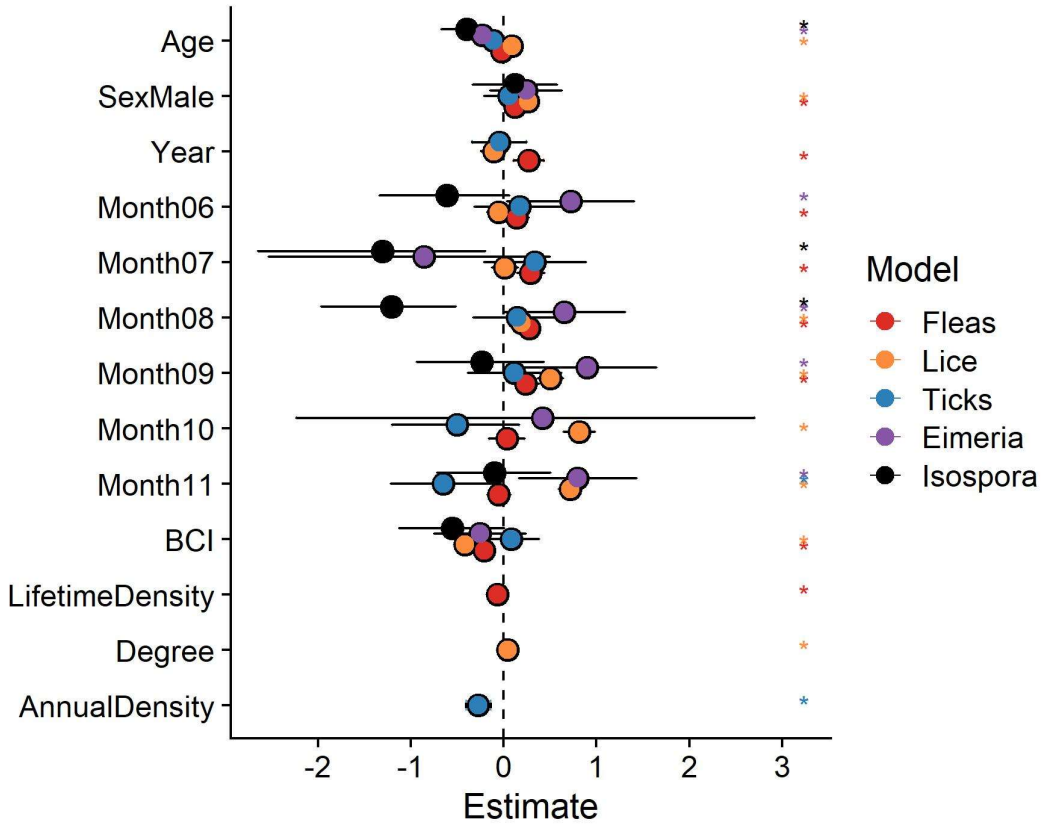


Figure SI2. **Model effect outputs for the adults-only dataset INLA density models.** Points represent modes of the posterior distribution of the effect estimates; error bars represent the 95% credibility intervals. Asterisks denote significant results, whose 95% credibility intervals did not overlap with zero. Only the behavioural traits that improved the model fit ($\Delta DIC < -2$) and were kept in the final model are shown.

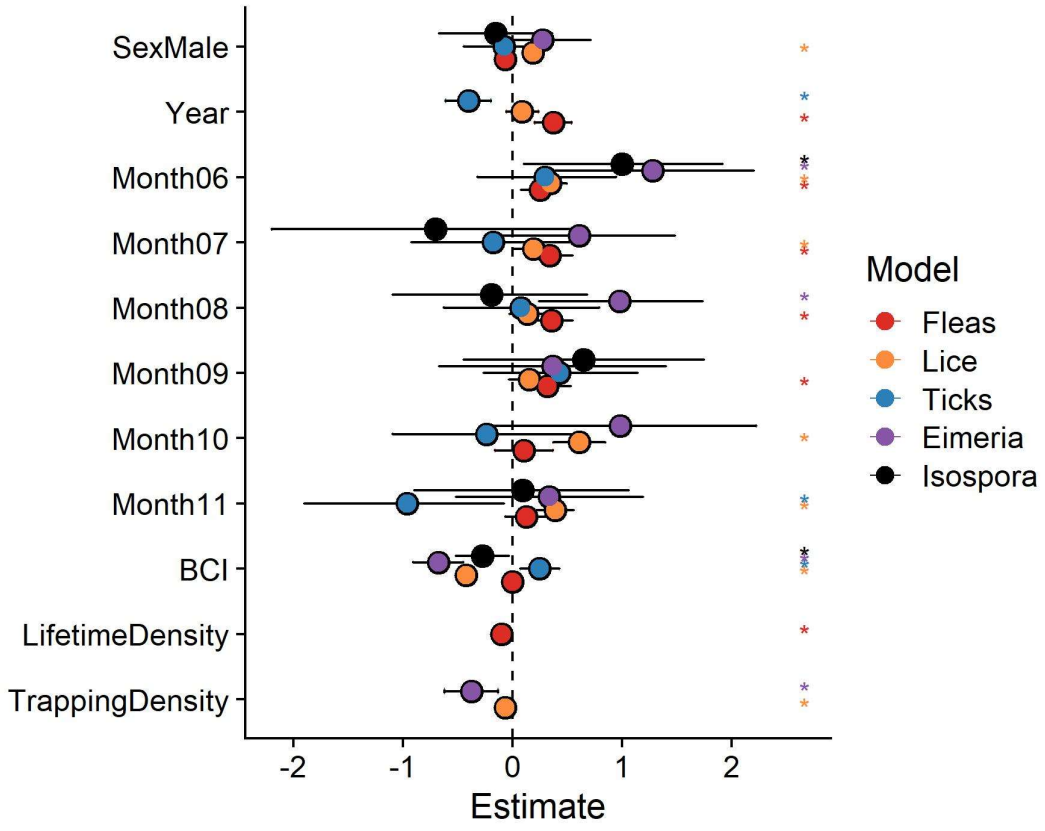


Figure SI3. **Model effect outputs for the juveniles-only dataset INLA density models.** Points represent modes of the posterior distribution of the effect estimates; error bars represent the 95% credibility intervals. Asterisks denote significant results, whose 95% credibility intervals did not overlap with zero. Only the behavioural traits that improved the model fit (ΔDIC < -2) and were kept in the final model are shown.

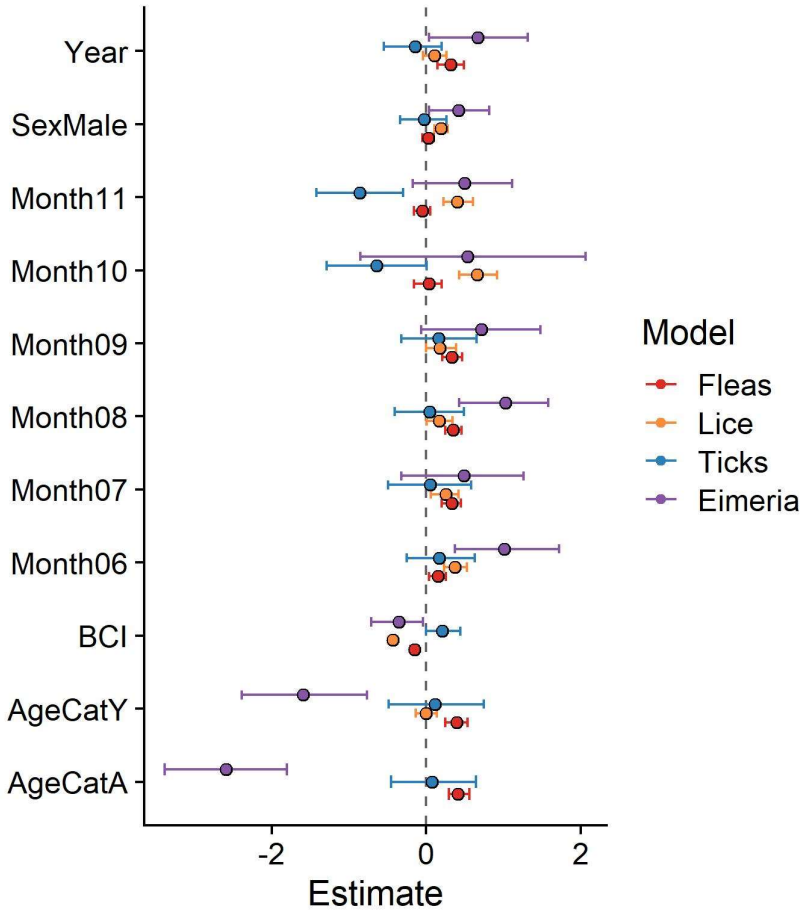


Figure SI4. **Model effect outputs for the multivariate MCMCglmm models closely represent the INLA univariate models.** Points represent modes of the posterior distribution of the effect estimates; error bars represent the 95% credibility intervals. Asterisks denote significant results, whose 95% credibility intervals did not overlap with zero. Only the behavioural traits that improved the model fit ($\Delta DIC < -2$) and were kept in the final model are shown.

Table SI1. **DIC Changes (ΔDIC) associated with density measure model addition for the full models.** Negative ΔDIC values correspnd to increased model fit. In each round, the variable that increased model the most was retained, and then the process was repeated, until no variables improved the model by decreasing ΔDIC by more than -2. Variables that were retained in each round are highlighted by asterisks.

PARASITE	ROUND	VARIABLE	DELTA	KEPT
FLEAS	1	Degree	2.08	0
	1	GroupSize	2.055	0
	1	**LifetimeDensity**	-16.001	1
	1	TrappingDensity	1.115	0
	1	AnnualDensity	-6.889	0
LICE	1	Degree	1.796	0
	1	GroupSize	1.3	0
	1	LifetimeDensity	1.694	0
	1	TrappingDensity	0.166	0
	1	AnnualDensity	1.117	0
TICKS	1	Degree	0.773	0
	1	GroupSize	3.644	0
	1	**LifetimeDensity**	-2.192	1
	1	TrappingDensity	1.007	0
	1	AnnualDensity	-0.266	0
EIMERIA	1	Degree	1.134	0
	1	GroupSize	1.79	0
	1	LifetimeDensity	1.084	0
	1	**TrappingDensity**	-6.035	1
	1	AnnualDensity	1.851	0
ISOSPORA	1	Degree	1.897	0
	1	GroupSize	1.861	0
	1	LifetimeDensity	1.873	0
	1	TrappingDensity	1.507	0
	1	AnnualDensity	1.717	0

Table SI2. **DIC Changes (ΔDIC) associated with density measure model addition for the adults-only models.** Negative ΔDIC values correspond to increased model fit. In each round, the variable that increased model the most was retained, and then the process was repeated, until no variables improved the model by decreasing ΔDIC by more than -2. Variables that were retained in each round are highlighted by asterisks.

PARASITE	ROUND	VARIABLE	DELTA	KEPT
FLEAS	1	Degree	1.835	0
	1	GroupSize	1.251	0
	1	**LifetimeDensity**	-8.444	1
	1	TrappingDensity	1.509	0
	1	AnnualDensity	-4.549	0
LICE	1	**Degree**	-2.388	1
	1	GroupSize	1.747	0
	1	LifetimeDensity	1.332	0
	1	TrappingDensity	1.943	0
	1	AnnualDensity	0.944	0
TICKS	1	Degree	1.93	0
	1	GroupSize	-12.573	0
	1	LifetimeDensity	-5.864	0
	1	TrappingDensity	1.2	0
	1	**AnnualDensity**	-14.067	1
EIMERIA	1	Degree	14.117	0
	1	GroupSize	1.964	0
	1	LifetimeDensity	1.817	0
	1	TrappingDensity	-0.283	0
	1	AnnualDensity	1.237	0
ISOSPORA	1	Degree	1.569	0
	1	GroupSize	0.882	0
	1	LifetimeDensity	1.9	0
	1	TrappingDensity	1.65	0
	1	AnnualDensity	1.8	0

Table SI3. **DIC Changes (ΔDIC) associated with density measure model addition for the juvenile-only models.** Negative ΔDIC values correspond to increased model fit. In each round, the variable that increased model the most was retained, and then the process was repeated, until no variables improved the model by decreasing ΔDIC by more than -2. Variables that were retained in each round are highlighted by asterisks.

PARASITE	ROUND	VARIABLE	DELTA	KEPT
FLEAS	1	Degree	0.985	0
	1	GroupSize	-2.362	0
	1	**LifetimeDensity**	-15.209	1
	1	TrappingDensity	1.337	0
	1	AnnualDensity	-10.016	0
LICE	1	Degree	-2.862	0
	1	GroupSize	1.747	0
	1	LifetimeDensity	-3.907	0
	1	**TrappingDensity**	-8.087	1
	1	AnnualDensity	-2.572	0
TICKS	1	Degree	1.602	0
	1	GroupSize	0.462	0
	1	LifetimeDensity	-0.244	0
	1	TrappingDensity	0.918	0
	1	AnnualDensity	-0.459	0
EIMERIA	1	Degree	1.42	0
	1	GroupSize	1.067	0
	1	LifetimeDensity	-0.127	0
	1	**TrappingDensity**	-7.465	1
	1	AnnualDensity	-0.945	0
ISOSPORA	1	Degree	1.73	0
	1	GroupSize	1.096	0
	1	LifetimeDensity	1.775	0
	1	TrappingDensity	1.567	0

	1	AnnualDensity	1.709	0

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Supplementary Chapter 2

Early-life seasonal, weather and social effects on telomere length in a wild mammal

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Under review by Molecular Ecology

Abstract

Early-life environmental conditions can provide a source of individual variation in life-history strategies and senescence patterns. Conditions experienced in early life can be quantified by measuring telomere length, which can act as a biomarker of survival probability in some species. Here, we investigate whether seasonal changes, weather conditions, and group size are associated with early-life and/or early-adulthood telomere length in a wild population of European badgers (*Meles meles*). We found substantial intra-annual changes in telomere length during the first three years of life (both between and within individuals), with shorter telomere lengths in the winter following the first spring and a trend for longer telomere lengths in the second spring compared to the first winter. In terms of weather conditions, cubs born in warmer, wetter springs with low rainfall variability had longer early-life (3–12 months old) telomere lengths. Additionally, cubs born in groups with more cubs had marginally longer early-life telomeres, providing no evidence of resource constraint from cub competition. We also found that our previously documented positive association between early-life telomere length and cub survival probability remained when social and weather variables were included. Finally, after sexual maturity, in early adulthood (i.e. 12–36 months) we found no significant association between same-sex adult group size and telomere length (i.e. no effect of intra-sexual competition). Overall, we show that controlling for seasonal effects, which are linked to food availability and foraging success, is important in telomere length analyses, and that variation in telomere length in badgers reflects early-life conditions and also predicts first year cub survival.

Keywords: *Telomere length, early-life environment, group size, weather conditions, senescence, season.*

1 Introduction

The early-life environment can affect individual fitness (Lindström 1999), with consequences for variation in life-history strategies (Metcalfe and Monaghan 2001) and senescence patterns (Nussey et al. 2007). For example, it has been hypothesised that senescence, the decline in performance in older age, is faster in individuals living in adverse early-life environments due to different energy allocation trade-offs between early- and later-life in response to the environment (Kirkwood and Rose 1991, Medawar 1952, Williams 1957). A more stressful early-life environment, either through a sub-optimal mean or more variable early-life environment, during this sensitive developmental period, could trigger early reproductive investment at the expense of somatic maintenance, leading to faster rates of senescence (Kirkwood and Rose 1991, Lemaitre et al. 2015). Empirical evidence for such detrimental effects has been found in various wild animal populations (Cooper and Kruuk 2018, Hammers et al. 2013, Reed et al. 2008).

Telomere length has been suggested as a non-causal biomarker of senescence in some species (López-Otín et al. 2013, Monaghan and Haussmann 2006), that facilitates quantification of physiological consequences of the conditions experienced (Monaghan 2014). Telomeres are highly conserved nucleoprotein structures at the end of chromosomes consisting of a non-coding sequence (5'-TTAGGG-3') and shelterin proteins (Blackburn 2000, de Lange 2005). Telomeres maintain genomic integrity by preventing chromosome degradation and fusion of chromosome ends by forming T-loops (de Lange 2004). Generally, telomeres shorten with each cell replication due to the end-replication problem (Olovnikov 1973), but telomere shortening can be accelerated potentially by oxidative damage (Boonekamp et al. 2017, Reichert and Stier 2017, von Zglinicki 2002) and through stressors (Epel et al. 2004, Heidinger et al. 2012). Telomeres can, however, elongate via the enzyme telomerase (Blackburn et al. 1989) – which shows a negative correlation with mammalian species' body mass (Tian et al. 2018) – and other telomere-

elongation pathways (Cesare and Reddel 2010, Mendez-Bermudez et al. 2012). Cells with critically short telomeres ultimately enter replicative senescence, where the accumulation of senescent cells can impair tissue function due to reduced renewal capacity (Campisi 2005, Campisi and di Fagagna 2007) and potentially lead to organismal senescence (Young 2018).

In some species, variation in early-life telomere length has been linked to season, specifically with winter effects when hibernation and torpor facilitate tolerance of winter food scarcity and reduction of thermoregulatory costs. During hibernation, more frequent arousal – which increases metabolic rate and potentially increases oxidative stress – is associated in arctic ground squirrels (*Urocitellus parryii*) with shorter telomere length (Wilbur et al. 2019) and in edible dormice (*Glis glis*) with increased telomere shortening (Turbill et al. 2013). Telomere shortening is reduced when the animals' core temperature difference between hibernation and arousal is smaller, in both edible and garden (*Eliomys quercinus*) dormice (Nowack et al. 2019). Conversely, the use of spontaneous daily torpor in non-hibernating Djungarian hamsters (*Phodopus sungorus*) is associated with telomere lengthening due to a relatively low energy investment to return to euthermia along with the benefits of reduced metabolic rate in torpor compared to hibernation (Turbill et al. 2012). In contrast, non-hibernating juvenile garden dormice that more frequently underwent fasting-induced torpor showed higher telomere shortening than individuals undergoing torpor less frequently (Giroud et al. 2014). Species that undergo facultative winter torpor may conserve energy for somatic maintenance that could potentially be invested in telomere restoration/elongation. Additionally, there is also evidence in non-hibernating rodents for seasonal effects of food availability on telomere dynamics (Criscuolo et al. 2020). However, since telomere length, season and body mass might be intercorrelated (Réale et al. 1999, Tian et al. 2018), body mass needs to be taken into account when studying seasonal effects.

In addition to these intra-annual changes in telomere length, extensive evidence links adverse early-life conditions to shorter telomeres (McLennan et al. 2016, Mizutani et al. 2013, Watson et al. 2015), where shorter telomeres are associated with reduced survival probability (Wilbourn et al. 2018). Food availability, often determined by weather conditions (e.g., Campbell et al. 2012), has been positively associated with early-life telomere length (e.g., Foley et al. 2020, Spurgin et al. 2017). Interestingly, early-life food availability may also impact life-history strategies (Chapter 2). It has been hypothesised that individuals in temporally stochastic environments should modulate their energy trade-offs (Erikstad et al. 1998, Reid et al. 2003, Weimerskirch et al. 2001) and adopt a bet-hedging strategy (Wilbur and Rudolf 2006). Since weather variability is predicted to increase in the future (IPCC 2018), it is important to understand the implications of variable early-life conditions for life-history strategies and early-life telomere length. The interplay between the mean of and variability in early-life environmental conditions, such as the availability and variation in food, foraging success and thermal stress for young individuals (Noonan et al. 2015, Nouvellet et al. 2013, Webb and King 1984), can thus impact developmental stress, longevity and may be reflected in early-life telomere length.

Social conditions in early-life can also shape life-history strategies and senescence due to increased competition for food and social stress. For example, female red deer (*Cervus elaphus*) that experienced high levels of resource competition in early-life showed faster rates of reproductive senescence (Nussey et al. 2007). Additionally, there is evidence for conspecific resource competition in early-life leading to greater telomere shortening in birds (Boonekamp et al. 2014, Nettle et al. 2015, Stier et al. 2015), and shorter telomere lengths in wild meerkats (Cram et al. 2017). Such patterns can be explained because stressors (including competition) are associated with both shorter telomere lengths and higher telomere shortening (Chatelain et al. 2020).

The effects of social conditions on senescence may also become apparent after sexual maturity, when individuals compete for mating opportunities (Andersson 1994, et al.Beirne et al. 2015). In polygynous species, sex differences in senescence may be attributable to intense intra-sexual competition between males (Clutton-Brock and Isvaran 2007, Promislow 1992, Williams 1957). Male investment for mating opportunities may trade off with self-maintenance (Kirkwood and Rose 1991). Intense male-male competition drives selection for shorter lifespan and faster senescence in males, compared to females (Clutton-Brock and Isvaran 2007, Williams 1957). While this prediction has been challenged (Bonduriansky et al. 2008, Graves 2007, Promislow 2003), and sex-specific senescence may be trait-dependent with respect to the underlying physiological processes (Nussey et al. 2009), higher rates of male-biased actuarial senescence in polygynous and sexual dimorphic species exist (Clutton-Brock and Isvaran 2007, Promislow 1992). While social effects may also contribute to senescence in females (Sharp and Clutton-Brock 2011, Woodroffe and Macdonald 1995), such sex-specific social effects on senescence are expected to be greater in males (Bonduriansky et al. 2008, Clutton-Brock and Isvaran 2007, Maklakov and Lummaa 2013). However, whether increased intra-sexual competition (e.g., higher local densities of same-sex individuals) is associated with shorter telomere lengths remains to be tested.

To test the effects of early-life social and environmental conditions on telomere length, we use a long-term dataset from a wild population of European badgers (*Meles meles*; henceforth 'badgers'). Badgers show reproductive senescence with males having a later onset but faster rate of senescence than females (Dugdale et al. 2011b). Additionally, early-life telomere length (3–12 months old) positively correlates with first-year survival and lifespan in badgers (van Lieshout et al. 2019). Badgers are natally philopatric and form large social groups (mean group size = 11.3, range = 2–29; da Silva et al. 1994) with latrine-marked borders (Buesching et al. 2016, Delahay

et al. 2000), although they do transgress these borders when foraging (Ellwood et al. 2017, Noonan et al. 2015) without any sex difference in foraging niche (Robertson et al. 2014).

Regardless of whether badgers undergo facultative winter torpor (Johansson 1957) or true hibernation (Ruf and Geiser 2015), badgers do reduce their body temperature by up to 8.9°C (Fowler and Racey 1988), thus reducing energy expenditure (Newman et al. 2011). Badgers in Britain mainly feed on earthworms (primarily *Lumbricus terrestris*: Johnson et al. 2001, Kruuk and Parish 1981). Earthworms are sensitive to microclimatic conditions (Edwards and Bohlen 1996, Gerard 1967, Newman et al. 2017), making their abundance and distribution highly dependent on weather conditions. High-density badger populations occur in mild areas with damp conditions where earthworms are available (Johnson et al. 2002, Kruuk 1978, Macdonald et al. 2015, Newman et al. 2017). Foraging efficiency is reduced in adverse weather conditions, due to reduced availability of earthworms, thermal stress when foraging in cold and wet conditions, and/or the choice to remain in thermally-stable underground dens, termed setts (Nouvellet et al. 2013, Noonan et al. 2014, 2018). Weather conditions can therefore impact survival probability where, for example, higher annual mean daily rainfall is positively associated with adult survival probability in badgers, whereas high annual variability in temperature has detrimental consequences for cub and adult survival (Nouvellet et al. 2013).

Badgers have one litter per year, with a mean litter size of 1.5 ± 0.3 (95% CI; range = 1–5; Annavi et al. 2014). Badger cub growth and maturation depends on the number of other cubs and adults present within the social group (Sugianto et al. 2019b), potentially indicating resource competition within social groups. Adult male badgers invest substantial energy into promiscuity and repeated mounting (Dugdale et al. 2011a) both within and outside their social group, resulting in high rates (i.e. 48%) of extra-group paternity, of which 85% were in neighbouring groups (Annavi et al. 2014, Dugdale et al. 2007). Males also exhibit substantial inter-individual variance in reproductive success (Dugdale et al. 2007, Dugdale et al. 2011b) and evidence of

reproductive skew among females within a group (Dugdale et al. 1995). With the polygynandrous system (Dugdale et al. 2011a), a slight sexual dimorphism and slight male-biased mortality (Johnson and Macdonald 2001, Sugianto et al. 2019a), and evidence of downstream effects of male–male competition on body mass senescence (Beirne et al. 2015), such intra-sexual competition may be reflected in telomere length in early adulthood.

Here, we investigate the relationships between early-life conditions and relative leukocyte telomere length (RLTL), by testing whether: (i) between-individual and within-individual variation in RLTL in early life and early adulthood can be explained by seasonal changes; (ii) adverse early-life weather, as a proxy for food availability and thermal stress, is associated with shorter early-life RLTL and the social conditions that cubs are exposed to (with more cubs potentially leading to resource competition and associated with shorter early-life RLTL, or more cubs reflecting more resources and thus being associated with longer early-life RLTL); (iii) the strength of the association between early-life RLTL and first-year survival probability is dependent on early-life conditions and (iv) adverse social conditions after sexual maturity (i.e. larger same-sex adult group size for females and, for males, more within-group and neighbouring-group adult (>1 year old) males), are associated with shorter RLTL in early post-maturity adulthood.

2 Methods

2.1 Study population and trapping

We conducted this study in a high-density population of European badgers (hereafter "badgers"; mean ± SE = 36.4 ± 2.55 badgers/km^2; Macdonald et al. 2009) in Wytham Woods, Oxfordshire, UK (51°46’24″N, 1°20’04″W); a 424 ha mixed semi-natural woodland surrounded by mixed arable and permanent pasture (Macdonald et al. 2015). The population consisted of 19 ± 2 (mean ± 95% CI; range = 14–26; Dugdale et al. 2008) mixed-sex social groups (Johnson et al. 2002, Newman et al. 2011) during the period that we analysed, 1987–2010, with a 50%

offspring sex ratio (Dugdale et al. 2003). The Wytham badger population is geographically discrete (Macdonald et al. 2009) with only ca. 3% annual immigration/emigration per year (Macdonald and Newman 2002).

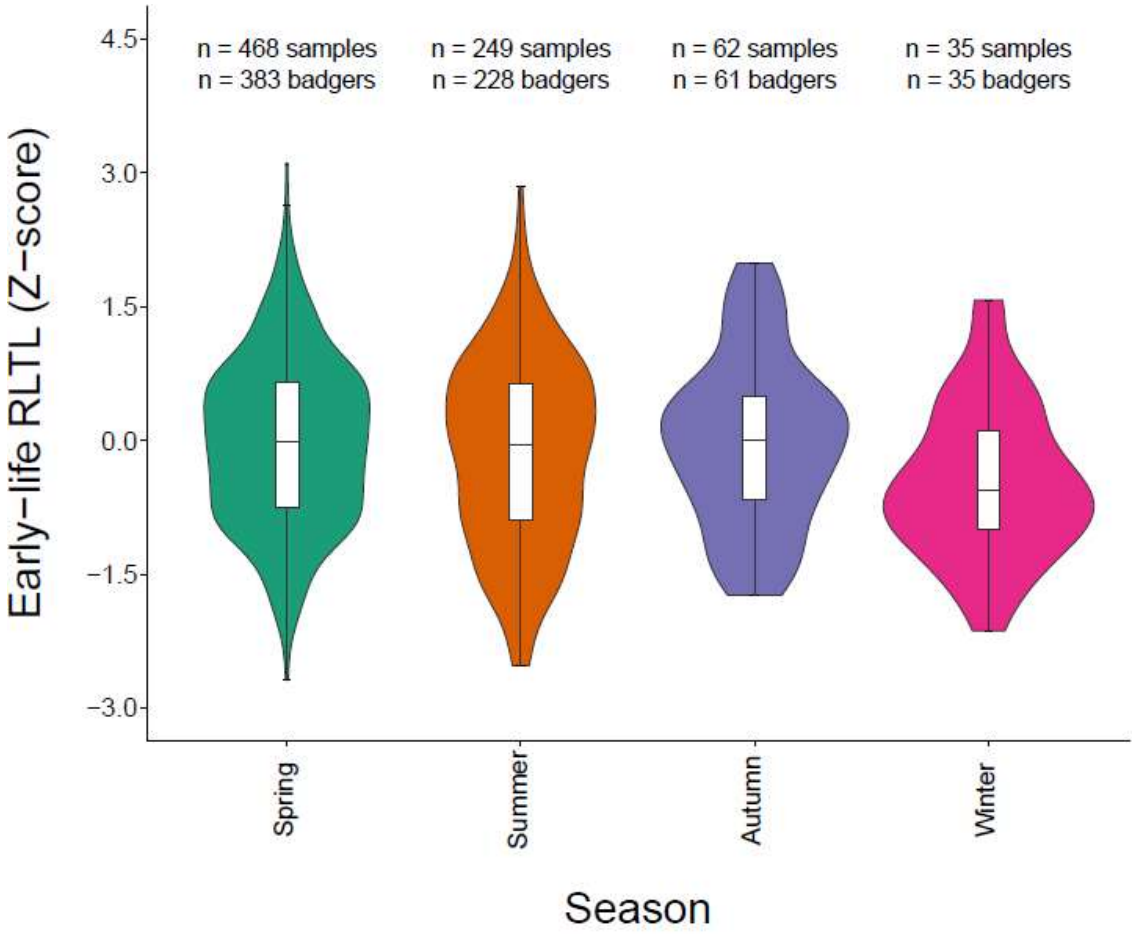


Figure 1. **Variation in early-life relative leukocyte telomere length (RLTL) among seasons in European badgers.** The data distributions and probability densities are shown (*n* = 814 samples; 533 badgers - the sum of badgers in the plot is >533 due to repeated measures). Data were collected in 24 years, across 66 trapping periods. The line in the boxplot represents the median, with first and third quartiles, and whiskers represent 1.57 times the inter-quartile range.

We used long-term data (1987 – 2016) from a badger population that was trapped over three two-week periods in May–June, August–September and November, with further trapping

in January in focal years (i.e. for specific experimental/research purposes only in specific years, see Fig. 1). Badgers were anaesthetised using an intra-muscular injection of 0.2 ml ketamine hydrochloride per kg body weight (McLaren et al. 2005). Upon first capture, badgers were assigned a unique inguinal tattoo for permanent identification. Sex, age class (cub <1 year old; adult ≥1 year old), capture date and social group were recorded. Age of badgers was defined as the number of days elapsed since the 14th of February, reflecting the average date of synchronised parturition, in the respective birth year (Yamaguchi et al. 2006). Age of badgers first caught as adults was inferred from tooth wear, which is commonly used and highly correlated ($r^2 = 0.80$) with known age in this population (da Silva and Macdonald, 1989, Hancox, 1988, Macdonald et al. 2009, Chapter 2). Only badgers that didn't have an already-known age and had a tooth wear of 2 (on a 1–5 scale) were included since these typically indicate a 1-year old adult (Chapter 2). Whole blood samples were collected from anaesthetised badgers through jugular venipuncture into vacutainers with an EDTA anticoagulant, and stored immediately at -20°C. Badgers were released after full recovery from anaesthesia. Additionally, bait-marking (Delahay et al. 2000, Macdonald and Newman, 2002) was conducted periodically to delimit group range sizes and deduce social groups.

2.2 Telomere analyses

Genomic DNA was extracted from whole blood samples (n = 814 samples; 533 badgers) using the DNeasy Blood and Tissue kit (Qiagen, Manchester, UK) according to the manufacturer's protocol, with changes by conducting a double elution step (2x 75 µl AE buffer) and using 125 µl of anticoagulated blood. DNA integrity was checked by running a random selection of DNA extracts (ca. 20%) on agarose gels to ensure high molecular weight. DNA concentration of all samples was quantified using the Fluostar Optima fluorometer (BMG Labtech, Ortenberg, Germany) and standardized to 20 ng/µl, after which samples were stored at -20 °C. We used monochrome multiplex quantitative PCR (MMqPCR) analysis to measure RLTL

(Cawthon, 2009). This is a measure that reflects the abundance of telomeric sequence relative to a reference gene, which are both analysed in the same well, and represents the mean telomere length across cells in a sample. We used a sub-set of 814 samples from the full dataset of 1248 samples detailed in van Lieshout et al. (2019). In the full dataset, Cq-values on the qPCR plates (n = 34) declined in a log-linear fashion ($r^2 > 0.99$). Reaction efficiencies were (mean ± SE) 1.793 ± 0.004 for IRBP and 1.909 ± 0.004 for telomeres. Inter-plate repeatability (intraclass correlation coefficient) calculated with the *rptr* 0.9.2 package (Stoffel et al. 2017) – by comparing variance among duplicates of the reference sample within a plate, to variance of the reference sample among plates – was 0.82 for RLTL measurements (95% CI = 0.76–0.87; n = 142 samples; 34 plates). Intra-plate repeatability calculated with duplicates of the same sample on the same plate, while controlling for plate effects, was 0.90 (95% CI = 0.86–0.93; n = 1,248 samples; 34 plates) for IRBP, 0.84 (95% CI = 0.79–0.90; n = 1,248 samples; 34 plates) for telomere Cq-values and 0.87 (95% CI = 0.82–0.91; n = 1,248 samples; 34 plates) for RLTL measurements. A detailed description of the MMqPCR analysis can be found in van Lieshout et al. (2019).

2.3 Weather conditions

Four weather metrics (mean daily temperature, temperature variability, mean daily rainfall, and rainfall variability) were calculated for each season (Spring = end of March to end of June, Summer = end of June to end of September, Autumn = end of September to end of December, Winter = end of December to end of March) from 1987 to 2010 to characterise the developmental stress associated with variation in earthworm food availability and thermoregulatory costs (Macdonald et al. 2010, Noonan et al. 2014, Nouvellet et al. 2013). Wytham Woods had a mean annual temperature of 10.6 °C (± 5.5 SD) and mean annual precipitation of 684 (± 129 SD) mm, 1987–2010. Mean daily temperature and rainfall were calculated using mean daily temperature and total daily precipitation values provided by the

Radcliffe Meteorological Station, School of Geography, University of Oxford (6 km from the field site). Daily temperatures followed a sinusoidal pattern, and so seasonal temperature variability was calculated as the sum of daily squared residuals from a sinusoidal fit to the corresponding year's temperatures (i.e., cumulative unpredictability). Rainfall did not show annual trends and its seasonal variability was therefore characterised simply as the coefficient of variation (SD/mean) in daily rainfall.

2.4 Group sizes

Natal group sizes were determined by the number of individuals (cubs and adults) that were present in a social group in the year of an individual's birth. Given high lifetime natal philopatry (35.8%), low permanent dispersal rates (19.1%), and high levels of short-term inter-group movements (Macdonald et al. 2008), individuals (n = 1,726) were assigned as a resident of a social group each year, according to published criteria (van Lieshout et al. 2020a). The number of individuals in a natal social group was then calculated as the sum of individuals present in the social group in that year.

Yearly social group size measures were then separated by age class (i.e., cub/adult) and sex (i.e., male/female) to determine sex- and age-specific group sizes per year. To measure intra-sexual competition in females, we calculated female adult group sizes, as females compete with other within-group females (Woodroffe and Macdonald 1995). However, for males, extra-group paternity is high (48%) and affected by the number of within-group and neighbouring-group candidate fathers (Annavi et al. 2014), so we combined both the number of within-group males and neighbouring-group males. The mean number of cubs in a social group for badgers in our dataset (n = 533 badgers) was 3.4 (± 2.3 SD; range 0–14), the mean number of female adults in a social group was 6.1 (± 3.4 SD; range 0–19) and the mean number of male adults in focal plus neighbouring social groups was 25.2 (± 11.5 SD; range 1–59).

2.5 Statistical analyses

Statistical analyses were conducted in R 3.3.1 (R Development Core Team, 2020), using parametric bootstrapping (n = 5,000) to estimate 95% confidence intervals and determine significance of predictors in *lme4* 1.1-14 (Bates et al. 2015). Model fit was assessed using standard residual plot techniques to ensure approximately normal distribution and constant variance, and fixed effects were ensured not to be collinear (VIF < 3). Relative leukocyte telomere length (RLTL) as response variable was first square-root and then Z-transformed (mean = 0, SD = 1) for comparability (Verhulst 2020). Quadratic fixed effects were included if such relationships were plausible *a priori*, and removed if $p > 0.1$ to test the significance of first-order effects.

In this study, we focus on early-life (3–12 months old) and since badgers typically reach sexual maturity by 2 years of age (Sugianto et al. 2019b), occasionally at age 1 year (Dugdale et al. 2007) and therefore first produce offspring when they are 2–3 years of age, due to delayed implantation resulting in a full year between conception and parturition, we define early adulthood as 12–36 months old.

2.5.1 Seasonal effects on RLTL in early-life and early adulthood

We first tested for an association between season and RLTL (≤36 months old) in early-life and early-adulthood in a Gaussian distribution model (identity link function) with RLTL as the response variable (n = 814 samples; 533 badgers). Including threshold functions of age at 29 months, such that the slope of the regression of RLTL with age differed for ≤29 months and >29 months of age best explained the relationship between RLTL and age (van Lieshout et al. 2019). Threshold age, age at last capture, season, weight and body length were included as fixed effects, and qPCR plate, row on qPCR plate, social group, cohort (i.e., birth year; 24 levels), year and individual ID as random effects as these may impact RLTL in badgers (van Lieshout et al. 2020b).

As we found a significant cross-sectional difference in RLTL between spring and winter, we then applied the 'within-subject centring' approach described by van de Pol and Wright (2009) to distinguish within- and between-individual effects between spring and winter. Following (Schroeder et al. 2012), we included two new fixed effects: 1) to estimate the within-individual variation component (β_W) we removed between-individual variation by subtracting the mean season value (coded as: spring = 0, winter = 1) for each individual across all years, from the season value for each RLTL measurement. So, if an individual was measured once in spring and once in winter, it was scored as -0.5 for spring and 0.5 for winter; and, 2) to estimate the between-individual variation between seasons (β_B), we included the mean season value for each individual (van de Pol and Wright 2009). We then ran a Gaussian distribution model (identity link function) with RLTL as the response variable (n = 503 samples; 402 badgers) and threshold age (van Lieshout 2019), age at last capture, within-individual season effect (β_W), between-individual season effect (β_B), weight and body length as fixed effects, and qPCR plate, row on qPCR plate, social group, cohort, year and individual ID as random effects. Subsequently, we tested whether the within-individual (β_W) and between-individual (β_B) slopes differed by including season and the between-individual effect (β_B; i.e. mean season value) in the same model (i.e. season now reflects the within-individual effect).

Lastly, to test whether telomere length decreases or increases from spring to winter we used a subset of individuals measured either in their first spring or first winter, plus 11 individuals measured in both their first spring and first winter (n = 214 samples; 203 badgers). For the direction of the effect from winter to spring we used a subset of individuals measured either in their first winter or second spring, plus 6 individuals measured in both their first winter and second spring (n = 84 samples; 78 badgers). In the two models (spring to winter and winter to spring) with a Gaussian distribution and RLTL as the response variable, we included age, age at last capture, season, weight and body length as fixed effects, and qPCR plate, row on qPCR

plate, social group, cohort, year (not in winter to spring model due to singularity) and individual ID as random effects. Subsequently, we used the within-subject centring approach again to separate within- and between-individual effects and test whether these slopes differ (van de Pol and Wright 2009).

2.5.2 Weather and natal group size effects on early-life RLTL

We tested whether weather and social conditions experienced as a cub (3–12 months old) were associated with early-life RLTL. We first used a GLMM to confirm the previous observation (van Lieshout et al. 2019) that early-life RLTL did not vary with age (in months), controlling for season, weight and body length (n = 406, $\beta = 0.154$, 95% CI = -0.158–0.464), and excluded age from subsequent analyses. The effects of first-year conditions on early-life RLTL were then modelled with early-life RLTL as the response variable in a Gaussian-distributed model (identity link function; n = 406, samples; 406 badgers). First, we determined the season in which the weather conditions (i.e., mean temperature, mean rainfall, temperature variability and rainfall variability) best explained the variation in early-life RLTL (AICc spring = 1,133.1 was lowest, versus summer ΔAICc = 11.3, autumn ΔAICc = 10.3, winter ΔAICc = 11.0), with models with ΔAICc < 7 from the top model being plausible (Burnham et al. 2011). The weather window of spring (end of March to end of June) is the season in which cubs grow the most and thus encounter the strongest developmental stress. This period includes when cubs first emerge above ground from the end of February, are weaned around mid-May, and reach independence at the start of June (Dugdale et al. 2010) during which time cubs exhibit high growth rates depending on food availability and social conditions (Sugianto et al. 2019a). Secondly, we determined whether the number of cubs, adults or the total number of individuals in the natal group best predicted early-life RLTL using AICc (the lowest AICc = 1,133.1 was for number of cubs, versus number of adults ΔAICc = 3.8, total number of individuals ΔAICc = 4.0, number of cubs plus number of adults ΔAICc = 5.8, number of cubs plus total number of individuals ΔAICc

= 5.6). Since ΔAICc < 7, and VIF > 3 for the other combinations in the same model, we ran five separate models with either the number of cubs, number of adults, the total number of individuals, number of cubs plus adults or number of cubs plus total number of individuals in the natal group as a fixed effect along with season, weight, body length, and mean daily temperature, temperature variability, mean daily rainfall and rainfall variability in spring. qPCR plate, row on qPCR plate, social group and cohort were included as random effects.

2.5.3 Covariation between early-life RLTL and weather conditions on cub survival probability

To understand whether the association between early-life RLTL and cub survival probability (van Lieshout et al. 2019) is due to or independent of weather effects, we tested whether the association between early-life RLTL and cub survival probability was still detected when social and weather conditions were included in the model. We first modelled survival to adulthood (≥1 year old) as a binary term in a binomially distributed model (logit link function; *n* = 406 samples; 406 badgers), where cubs only caught in their first year of life were coded as 0 and cubs that were caught when older than 1 year of age were coded as 1, with early-life RLTL, weight and body length as fixed effects and qPCR plate, row on qPCR plate, social group and cohort were included as random effects. We then also included as fixed effects: number of cubs in natal group, mean daily temperature, temperature variability, mean daily rainfall and rainfall variability in a given season. We determined the season in which weather conditions best explained the variation in cub survival probability, using AICc (the lowest AICc = 408.9 was in winter, versus spring ΔAICc = 21.6, summer ΔAICc = 16.3 and autumn ΔAICc = 22.5) where models with ΔAICc < 7 from the top model are plausible (Burnham et al. 2011). We checked whether the model was overdispersed. While cub survival is negatively impacted by endoparasitic coccidia infection (Newman et al. 2001), we did not have data to control for coccidia infection. We then applied model selection to test whether including weather and social variables knocked early-life RLTL out of the plausible models. This would indicate that the

early-life RLTL and survival probability relationship is driven by covariation between the environment and physiological state (early-life RLTL). As early-life RLTL was retained, we estimated the RLTL model-averaged parameter and 95% confidence interval using the natural averaged method (where the parameter was averaged over models in which it was present; Burnham and Anderson 2002). This avoids the parameter estimate shrinking towards zero, from inclusion of the relatively less important models where the parameter was not retained (Nakagawa and Freckleton 2011).

2.5.4 Same-sex group size effects on RLTL in early adulthood

We examined whether same-sex adult group sizes were reflected in RLTL in early adulthood (i.e., 12–36 months old). In a GLMM with RLTL in early adulthood as the response variable with one age threshold separating two periods of 12 to ≤29 months and >29 and ≤36 months (see van Lieshout et al. 2019) and season, weight and body length as fixed effects, we determined that RLTL did not vary with age (n = 376, 12 to ≤29 months, β = -0.064, 95% CI = -0.175–0.050; >29 and ≤36 months, β = -0.040, 95% CI = -0.184–0.110), and excluded age from the subsequent analysis. The effects of same-sex adult group sizes on RLTL in early adulthood were then modelled with RLTL in early adulthood as the response variable (n = 376 samples; 308 badgers). Same-sex adult group size (within-group for females and within- plus neighbouring-group for males), sex and its interaction with group size (to model differential strength in intra-sexual competition among the sexes), age at last capture (to control for selective disappearance), season, weight and body length were included as fixed effects, and qPCR plate, row on qPCR plate, social group, cohort, year and individual ID as random effects.

3 Results

3.1 Seasonal effects on RLTL in early-life and early adulthood

We found a cross-sectional effect of season, with badgers having shorter RLTL in winter compared to spring, controlling for age, weight and body length (Fig. 1; Table S1). We also found both a within- and between-individual effect of shorter RLTL in winter than in spring, with no significant difference between these slopes (Tables S2-S3). From spring to winter there was both a between-individual and within-individual decline in RLTL (Table S4 and Fig. S1), whereas from winter to the following spring there was marginally non-significant within-individual increase in RLTL (Table S5 and Fig. S1). For both spring to winter and winter to spring the slopes for within- and between-individual effects did not differ (Table S6).

3.2 Weather and natal group size effects on early-life RLTL

We found a positive association between spring temperature and early-life RLTL (Fig. 2; Tables 1, S7–S10), with cubs experiencing cooler-than-average first springs having shorter early-life RLTL. We also found that cubs experiencing intermediate-to-high mean daily rainfall had longer early-life RLTL (Fig. 3; Tables 1, S7–S10) than cubs developing during drier years. Cubs experiencing low rainfall variability also had longer early-life RLTL (Fig. 4; Tables 1, S7–S10). We found, while controlling for weather effects, a marginal effect where more cubs in the natal group leads to longer early-life RLTL. In contrast, we found no evidence for an association between the number of adults or total number of individuals in the natal group and early-life RLTL (Tables 1, S7–S10).

Table 1. **Parameter estimates** and 95% confidence intervals of fixed effects from a mixed model and parametric bootstrap tests of the number of cubs in natal group, season and weather effects in spring on early-life (3–12 months old) relative leukocyte telomere length (Z-score) in European badgers (full model and with $p > 0.10$ 2nd order effects removed). β = parameter estimate, S.E. = standard error, 95% CI = 95% confidence intervals; reference terms in brackets = reference level for factors. Significant parameter estimates (95% CI does not overlap zero) are in bold.

Parameter (reference level)	β	S.E.	95% CI
Intercept†	-0.009	0.118	-0.228 to 0.218
Number of cubs in natal group	**0.106**	**0.052**	**0.008 to 0.206**
Season (Spring)			
Summer	0.196	0.137	-0.072 to 0.464
Autumn	0.131	0.277	-0.409 to 0.656
Winter	**-1.001**	**0.383**	**-1.741 to -0.232**
Mean temperature	-4.036	3.767	-11.38 to 3.367
Mean temperature^2	4.519	3.830	-3.089 to 11.94
Daily temperature variability	0.588	1.709	-2.849 to 3.850
Daily temperature variability^2	-0.457	1.733	-3.780 to 3.044
Mean daily rainfall	**-1.894**	**0.810**	**-3.473 to -0.267**
Mean daily rainfall^2	**2.074**	**0.836**	**0.368 to 3.692**
Daily rainfall variability	-3.911	2.019	-7.818 to 0.014
Daily rainfall variability^2	3.790	2.041	-0.211 to 7.698
Weight	0.075	0.101	-0.124 to 0.275
Body length	-0.089	0.097	-0.274 to 0.100
Without non-significant 2nd order effects			
Intercept††	0.009	0.110	-0.197 to 0.216
Number of cubs in natal group	**0.100**	**0.051**	**0.001 to 0.200**
Season (Spring)			
Summer	0.178	0.136	-0.088 to 0.446
Autumn	0.097	0.274	-0.447 to 0.614
Winter	**-0.995**	**0.380**	**-1.726 to -0.237**
Mean temperature	**0.403**	**0.087**	**0.227 to 0.577**
Daily temperature variability	0.135	0.095	-0.053 to 0.321
Mean daily rainfall	**-1.225**	**0.559**	**-2.333 to -0.124**
Mean daily rainfall^2	**1.356**	**0.555**	**0.255 to 2.467**
Daily rainfall variability	**-2.843**	**1.414**	**-5.563 to -0.112**
Daily rainfall variability^2	**2.745**	**1.405**	**0.039 to 5.464**
Weight	0.072	0.100	-0.124 to 0.272
Body length	-0.082	0.096	-0.266 to 0.104

Random effect estimates (variance): †qPCR plate ($4.955*10^{-2}$), Row on qPCR plate ($1.861*10^{-3}$), Social group ($2.798*10^{-2}$), Cohort ($7.745*10^{-2}$), Residual ($7.537*10^{-1}$)
††qPCR plate ($4.911*10^{-2}$), Row on qPCR plate ($2.895*10^{-3}$), Social group ($2.642*10^{-2}$), Cohort ($5.287*10^{-2}$), Residual ($7.572*10^{-1}$)

3.3 Covariation between early-life RLTL and weather conditions on cub survival probability

We first replicated our published finding (van Lieshout et al. 2019) of a positive association between early-life RLTL and survival to adulthood, not controlling for social and weather effects (Table S11). Then we included social and weather conditions in the model: cub survival probability exhibited a negative quadratic relationship with mean daily temperature (Fig. S2; Table S12), a negative quadratic association with winter temperature variability (Fig. S3; Table S12), a marginal non-significant positive effect of mean daily rainfall (Table S12), a negative association with winter rainfall variability (Fig. S4; Table S12) but no significant effect of the number of cubs in a group (Table S12). Using model selection, early-life RLTL was

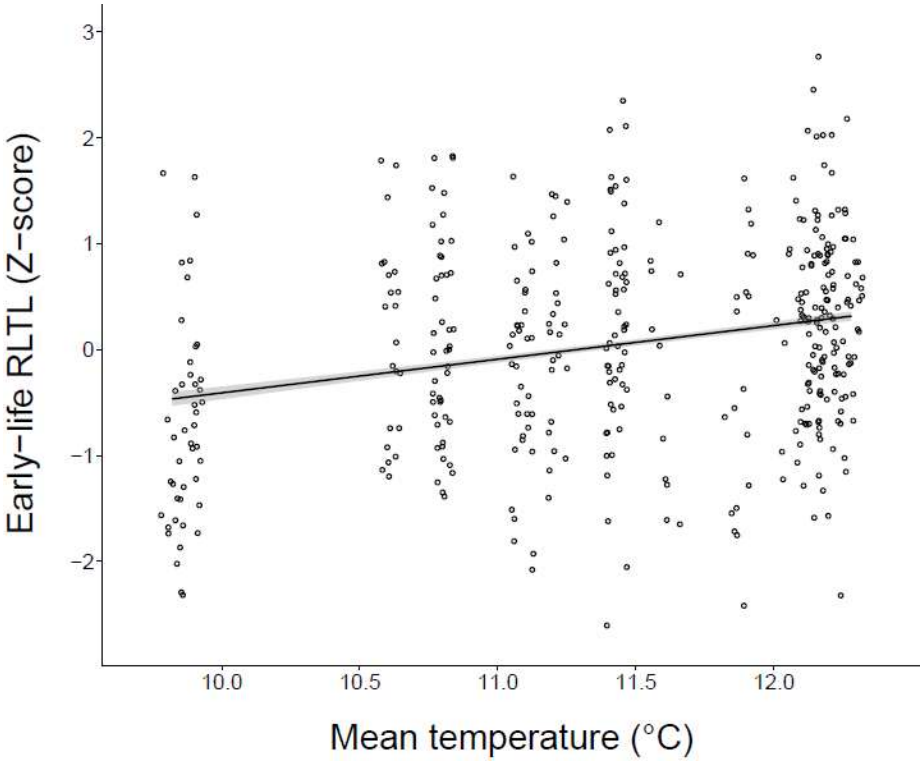


Figure 2. **The association between mean spring temperature and early-life relative leukocyte telomere length (RLTL).** Raw data points (n = 406 samples; 406 badgers) are shown, and jittered for clarity on the amount of data. The fitted line represents the regression from the mixed model, and the 95% confidence intervals as shaded areas.

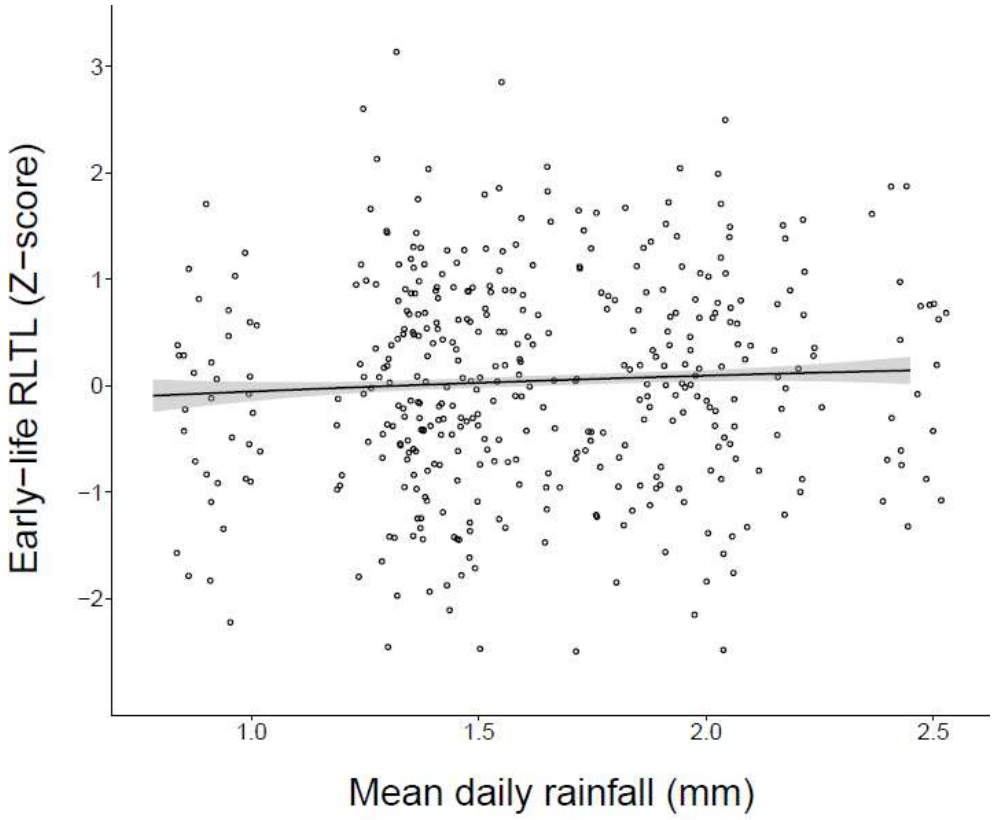


Figure 3. **The association between mean daily rainfall in spring and early-life relative leukocyte telomere length (RLTL).** Raw data points (n = 406 samples; 406 badgers) are shown, and jittered for clarity on the amount of data. The fitted line represents the quadratic regression from the mixed model, and the 95% confidence intervals as shaded areas.

present in the top 39 models and retained in 82/100 plausible models (Table S13). The naturally averaged estimate for RLTL in the plausible models was 0.366 (95% CI = 0.064 – 0.666; Table S14) and thus the 95% CIs of early-life RLTL overlapped between the models with and without (β = 0.386, 95% CI = 0.095 to 0.713, Table S11) early-life social and weather variables.

3.4 Same-sex group size effects on RLTL in early adulthood

We found no evidence of same-sex adult group size effects on RLTL in early adulthood for females or males (Table S15).

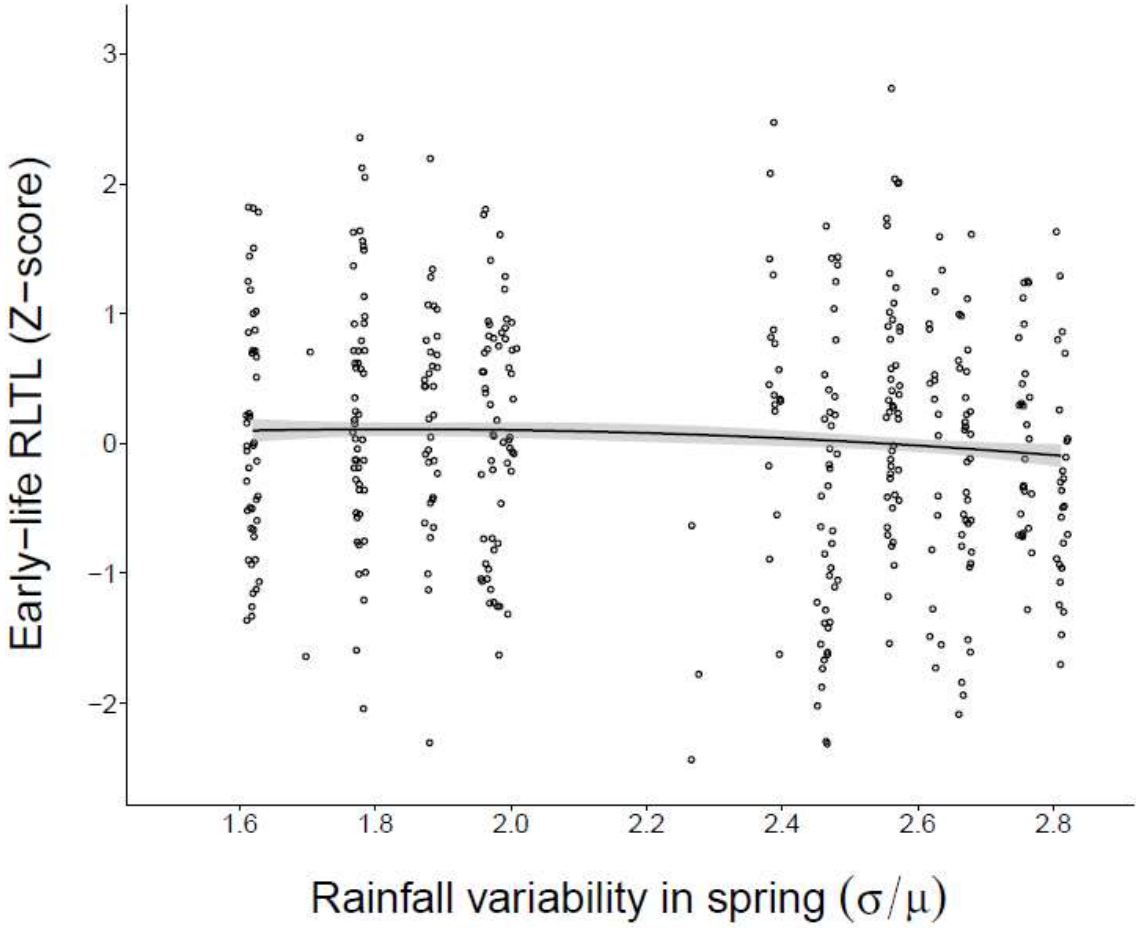


Figure 4. **The association between the rainfall variability in spring and early-life relative leukocyte telomere length (RLTL).** Raw data points (n = 406 samples; 406 badgers) are shown, and jittered for clarity on the amount of data. The fitted line represents the quadratic regression from the mixed model, and the 95% confidence intervals as shaded areas.

4 Discussion

Our results show both between-individual variation and within-individual changes in RLTL across seasons, where a cub's RLTL in their first spring was longer than in the following winter, and an indication that RLTL was longer again in the following spring compared to the preceding winter. Since the between- and within-individual slopes did not differ, the between-individual effect is driven by within-individual change and not selective (dis)appearance. We also found that cubs born in conditions that were warmer and wetter, with little variation in

rainfall, had longer early-life RLTL. Sociologically, the number of cubs had a positive effect on early-life RLTL, in contrast to the number of adults or total number of individuals. Our results also suggest that the link between early-life RLTL and cub survival probability is driven by conditions experienced in addition to the early-life social and weather conditions modelled. Additionally, we found no effect of the number of within-group adult females, or both within-group and extra-group adult males (i.e., intra-sexual competition) on RLTL in early adulthood.

Our finding that badgers had shorter early-life RLTL (both between and within individuals) in winter, compared to the preceding spring could be linked to the end-replication problem and stressful effects such as disease (Newman et al. 2001) and sub-optimal foraging conditions and food availability (Macdonald and Newman 2002, Newman et al. 2017). The within-individual effect means that between seasons there is an increase or decrease in telomere length for the same individual. Since there is no difference in the slopes for the within-individual and between-individual effect there is no selective disappearance of individuals and the between-individual effect is driven by within-individual change.

We then found a non-significant trend for positive within-individual changes in RLTL from the first winter to the following spring. Body temperatures in badgers fall from November to December (by a maximum of 8.9 °C compared to late-spring) and steadily rise until euthermic levels are reached by late April (Fowler and Racey 1988, Geiser and Ruf 1995). During harsh winter conditions, badgers use facultative torpor to reduce their core temperature and metabolic rate, conserving energy (Newman et al. 2011). This reduction of basal metabolic rates (Geiser 2004) can reduce mitosis (Kruman et al. 1988) and therefore potentially reduce telomere shortening. Similarly, daily torpor cycles in Djungarian hamsters had a positive effect on telomere length (Turbill et al. 2012). However, for species using torpor as a seasonal energy conservation strategy (e.g., edible dormice, garden dormice, and arctic ground squirrels; as do badgers), arousal and return to euthermia has been linked to telomere shortening; although this

appears to be in proportion to the extent that body temperature must be re-warmed (Giroud et al. 2014, Hoelzl et al. 2016, Turbill et al. 2013, Turbill et al. 2012, Wilbur et al. 2019). We postulate that badgers use torpor and their ability to remain within thermally stable setts (Tsunoda et al. 2018) to try to mitigate RLTL shortening that would otherwise be incurred by the stresses of maintaining activity during winter, when food is scarce and thermal losses are high. We need careful analyses to explore this further, for example, comparing badgers in different regions that experience different degrees of winter severity, with a large longitudinal sample size to disentangle within- and between-individual effects. Importantly, we need to track which badgers go into torpor, for how long and how often, and then calculate how much energy is conserved. We also do not yet know to what extent torpor-arousal cycles may affect telomere shortening, where there is likely an optimal balance. In this regard predicted increases in weather variability (IPCC 2018) that may cause more frequent warm–cold winter episodes, could add to the allostatic load of badgers, causing accelerated RLTL shortening. Since positive within-individual changes in badger telomere length occur, that are greater than measurement error (van Lieshout et al. 2019), such seasonal patterns may explain some of the variability in telomere length patterns across life in badgers. Indeed, there is also evidence of seasonal telomere dynamics in non-hibernating rodents (Criscuolo et al. 2020). Even though we accounted for body weight and length, other factors such as seasonal changes in leukocyte cell composition can also lead to apparent changes in telomere length (Beaulieu et al. 2017) this requires further investigation. For example, there is an increased proportion of neutrophils and lymphocytes that were lymphocytes from spring to autumn in badgers (van Lieshout et al. 2020a), and lymphocytes have shorter telomere lengths than neutrophils in humans and baboons (Baerlocher et al. 2007, Kimura et al. 2010). Nonetheless, our findings also highlight the importance of controlling for seasonal effects when analysing telomere dynamics.

Cubs born into more energetically favourable springs (warm, rainy, and low rainfall variability) had longer early-life RLTL. These weather conditions present optimal soil conditions for earthworm surfacing, enhancing food supply (Kruuk 1978, Newman et al. 2017). Dry conditions in spring have negative consequences for badger foraging success (Macdonald and Newman 2002). However, while we found no effect of spring temperature variability on early-life RLTL, cubs experiencing lower daily rainfall variability in spring had longer early-life RLTL. Greater rainfall variability can reduce the predictability of food availability and impact foraging activity (Noonan et al. 2014), and may require individuals to modulate their energy trade-offs (Erikstad et al. 1998, Reid et al. 2003, Weimerskirch et al. 2001) and adopt a bet-hedging strategy (Wilbur and Rudolf, 2006). The variability in spring rainfall and thus early-life conditions experienced shape life-history trade-offs, and since variability is likely to increase under current climate change (IPCC 2018), this can impact ecological and individual resilience.

Our estimate of post-dependence social effects was positive. An explanation for this positive effect may be that in badgers variation in parental resource acquisition is larger than variation in litter size, causing the per-offspring feeding rate to increase with litter size. In contrast, other species or experimental brood size enlargements may find variation in litter size that exceeds variation in parental resource acquisition, causing the per-offspring feeding rate to decrease with litter size (van Noordwijk and de Jong 1986, Vedder et al. 2017, Wilson and Nussey 2010). An increase in the per-offspring feeding rate with litter size can result in more available resources for cubs and thus longer early-life telomere length. Secondly, groups with more independent cubs may also potentially have more food available per capita which permits faster growth and cell replication without inducing stress, hence facilitating longer early-life telomere length. This result is in contrast with studies reporting that competition for food within litters and juvenile cohorts can cause telomere shortening (Boonekamp et al. 2014, Cram et al. 2017, Nettle et al. 2015). However, these studies were able to measure telomere length within the

first month of life. In contrast, we were unable to sample individuals until at least 3 months of age, due to welfare legislation (Protection of Badgers Act, 1992), when the weakest cubs could have already succumbed, reducing group sizes. We therefore do not have a measure of the number of dependent cubs in a group and could only measure RLTL in the first year from three to twelve months of age; thus, we cannot test for social effects during the dependent period, including selective disappearance which may also lead to similar positive associations between the number of cubs and early-life RLTL.

We found that the association between early-life RLTL and cub survival probability was retained in the top 39 most plausible models and 82/100 plausible models when including early-life weather and social variables. This indicates that, in badgers, the association between early-life RLTL and survival is not solely driven by covariation between the early-life environment and early-life RLTL (i.e., physiological state). While early-life RLTL in badgers appears to reflect the physiological consequences of conditions experienced, independent of the weather and social variables included in the models, there could still be a genetic component to telomere length or telomere length may genetically covary with survival as seen in other species (Froy et al. 2021, Vedder et al. 2021). Nonetheless, in badgers telomere length can be used as a comprehensive measure of the environmental consequences for physiology and survival probability.

There was no significant association between same-sex adult group size and RLTL in early adulthood. While female–female reproductive competition occurs in badgers (Sharp and Clutton-Brock 2011, Woodroffe and Macdonald 1995), in polygynous species, theory predicts intra-sexual competition for mating opportunities to be stronger among males than females. In Wytham badgers, there is slight sexual dimorphism (Johnson and Macdonald 2001) and slight male-biased mortality (Chapter 2). Reproductive skew is higher in sexually-mature males than females (Dugdale et al. 2008) and males with a higher body-condition index attain more

reproductive success (Dugdale et al. 2011a). High levels of polygynandrous and repeated mounting behaviour may however reduce male–male aggression and infanticide from males (Dugdale et al. 2011a, Wolff and Macdonald, 2004). Secondly, cryptic female choice (i.e., delayed implantation, superfecundation and superfetation) may promote sperm competition and mask paternity, and reduce pre-copulatory male–male competition (Birkhead and Pizzari 2002). Finally, group size and/or density could be a poor metric for competition due to foraging niches, variation in sex-ratio or larger groups having proportionally more available resources. In line with this, we found no evidence that variation in telomere length is due to intra-sexual competition in early adulthood. Early-life telomere length may reflect the consequences of the weather conditions experienced, thus with little impact of social conditions in early adulthood on badgers. However, in bad quality years only females in good condition breed, whereas in good quality years breeding success is related to status (Woodroffe and Macdonald 1995). We can therefore not exclude that there may only be female–female competition in good years. Additionally, early-adulthood male–male competition impacts on body mass senescence in a badger population at Woodchester Park (Beirne et al. 2015). While we detected no significant evidence of direct effects of early-adulthood intra-sexual competition on telomere length, there may be downstream effects on senescence.

In conclusion, we demonstrate the importance of accounting for seasonal variation when analysing telomere dynamics because of potential decreases as well as increases in telomere length across seasons. We also evidence that early-life adversity is reflected in shorter early-life telomere lengths in badgers, where the physical (weather) and social environment predict early-life telomere length. When accounting for these environmental effects, the positive association between early-life telomere length and survival probability remains. We conclude that variation in telomere length in badgers reflects early-life conditions, and in addition to this predicts first year cub survival.

5 Authors' contributions

This study was conceived by Sil van Lieshout, Amanda Bretman, and Hannah Dugdale; Samples were collected by Sil van Lieshout, Chris Newman, Christina Buesching, David Macdonald, and Hannah Dugdale; Sil van Lieshout conducted laboratory work with input from Terry Burke; environmental metrics were calculated by Sil van Lieshout, Elisa Badás, and Julius Bright Ross; statistical analyses were conducted by Sil van Lieshout with input from Elisa Badás and Hannah Dugdale; the paper was written by Sil van Lieshout and Hannah Dugdale with extensive input from all authors.

6 Data accessibility

Data are available from the Dryad Digital Repository (https://datadryad.org/stash/share/eh08mIrCX6fkQMH4nIjEOyewrWSg8BO5TpHGbzYB5Tg) (van Lieshout et al. 2021)

7 Supplementary figures and tables

Due to the large number of supplementary figures and tables for this paper, I have opted not to include them in this document; they can be accessed online at: doi.org/10.32942/osf.io/es5pc.

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Supplementary material for Chapter 2

S1 Age estimation for individuals first captured as adults based on tooth wear

The majority of individuals (1,268/1,763 individuals, 71.9%) were first caught as cubs, and thus age was known absolutely. A further 112 individuals (6.4%) were captured after their birth year and their age was estimated based on extensive field experience. For the remaining 383 individuals (21.7%, 100 of which were from the first three years of the study) with an unknown age at first capture, age was inferred using molar tooth wear on a 5-point scale (Hancox 1988). Although tooth wear in badgers can vary substantially within an age class and between populations (da Silva and Macdonald 1989), the number of captures for known-age individuals (n = 8,769) enabled use of a model to approximate inferred age for individuals without a known age. For each capture, tooth wear is marked independently of previous entries for a given individual, and therefore some error in estimation can occur. In 204 cases (2.4% of tooth wear data), an individual was marked as having a tooth wear score 2 or more points below a previous score; these scores were removed, as were 48 scores of 0 (0.6% of scores), an impossible value. We constructed i) a linear model and ii) a sigmoid model predicting individual age from these corrected tooth wear data, producing a marginally more robust fit from the sigmoid model ($R^2_{linear} = 0.679$; $R^2_{sigmoid} = 0.698$). Therefore, we used the sigmoid model (*SSLogis()* function in *stats* package, R core team 2019; asymptote = 9.66, x inflection point = 3.53, scale parameter = 0.79; see Fig. S1.1) to predict the age at first capture for the 383 individuals without a known age. These individuals' life records were then updated in minimum number alive (MNA) estimates to agree with these estimated ages (see Methods in main text).

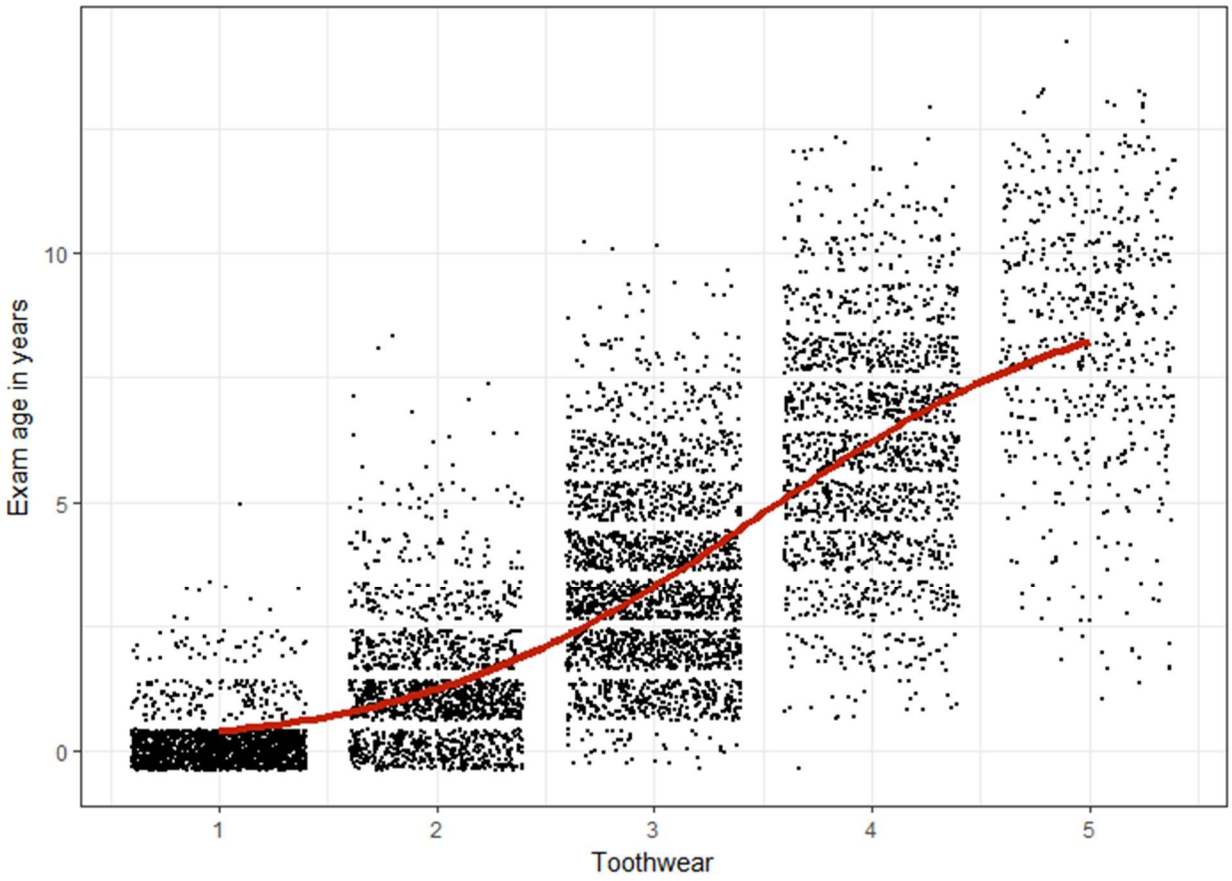


Figure S1.1 - Exam age in years as a function of molar tooth wear at time of capture on a scale of 1-5. Points are jittered on both axes for visual clarity. Red line indicates sigmoid fit to the data.

S2 Simulations of modified minimum number alive (N_i) estimates

To validate the accuracy of modified minimum number alive (N_i) figures, we simulated a series of life histories based on demographic parameters from our existing database and selectively sub-sampled these life histories according to trapping efficiencies similar to our study's values, then estimated N_i from these sub-sampled life histories. Much one-sex modelling is carried out using females, as these represent the reproductive potential of the population in

simplified cases (Miller and Inouye 2011); here, we decided to carry out simulations using only females for simplicity.

We began our simulated population with a vector of individuals representing the mean age distribution for females in our population (for this exercise, we limited the age of individuals between 0 and 10). We then created a data frame containing an entry for every year a female badger existed, her age in that year, the number of offspring she produced in that year, and the number of female badgers in the population at that time. Using this data frame, we estimated the relationship between a female's age and per capita cub production using a Poisson-link general additive model (GAM, *mgcv* package, Wood 2011). We also estimated the relationship between individual survival probability and age, including female density as a measure of density-dependence, using a binomial GAM (0 = never captured again, 1 = captured again). Because our genetic pedigree is conservative and does not assign every cub produced to one or both parents (see Appendix S3), we derived a ratio of total female cubs produced over the course of the study to the number of cubs in the dataset used to build the GAM model of per capita cub production (correction ratio = 1.40). We then applied the two GAM models, as well as the correction ratio, to iterate the starting population over 29 time-steps (total = 30 measurements). For every individual in the simulated population, we created a vector with 1s for years the individual was alive and 0s for the years a) before the individual's birth or b) following its death. For every year an individual was alive, we assigned it a randomly sampled tooth wear score from actual observations of individuals of that age.

For 1,000 iterations, we generated random trapping efficiencies for each year between 65-80% (a range similar to that of our existing trapping efficiency) and used each annual trapping efficiency to sub-sample the extant badgers in the population, obtaining a "capture

history" for that year. We then used each year's "capture history" to create N_i estimates as in the text, i) adding individuals known to be alive through prior and subsequent capture (KA_i from Eq. 1 in the main text), ii) back-projecting individuals' lifespans according to tooth wear when not captured as cubs (IA_i from Eq. 1 in the main text), iii) estimating annual trapping efficiency based on the individuals known to be alive that were missing from each year (blind to the original simulated population), and iv) applying these trapping efficiencies progressively to individuals that were never captured again ($Prob_{j,i}$ from Eq. 2 in the main text). Figure S2.1

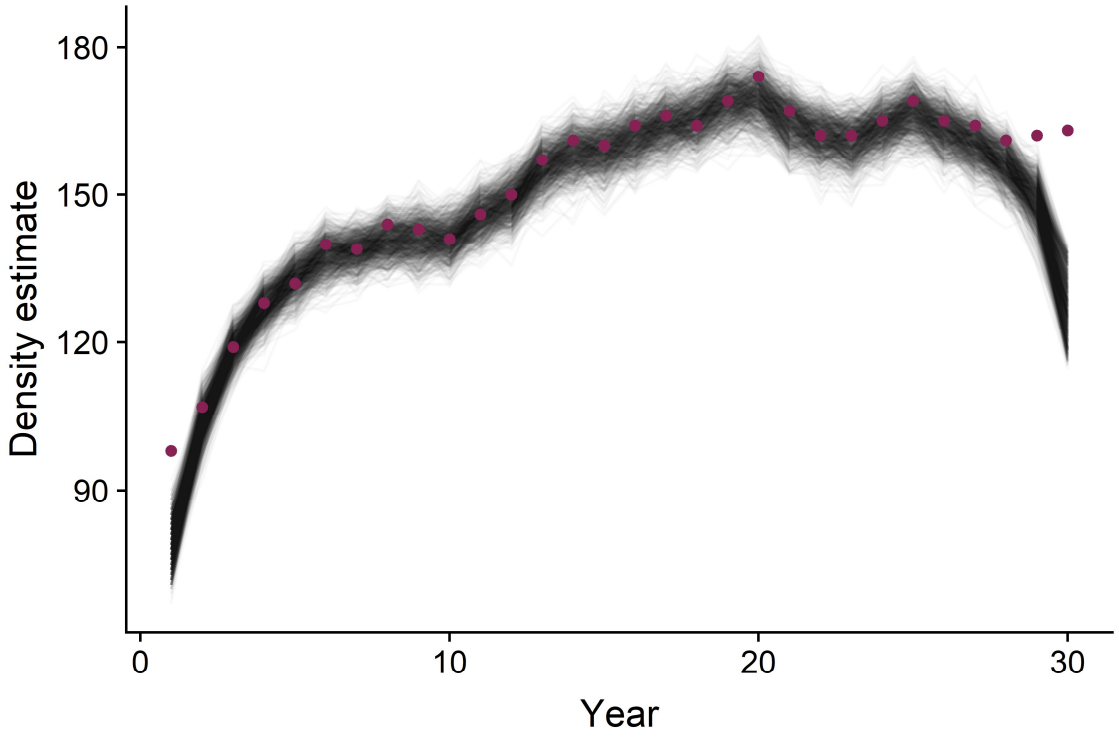


Figure S2.1 - Simulated population (purple dots) and N_i estimates derived from 1000 simulated trapping records (black lines) with imperfect trapping efficiency.

shows the results of this iterative process, with each black line representing an iteration. The "actual" population density was suitably approximated by most iterations even through abrupt changes, excepting the first two and last three years—which is typical for capture-mark-

recapture designs (mean residual with these years = -3.67 individuals, SD = 8.07; without them = -1.36 inds., SD = 3.82).

S3 Simulations of missing pedigree data

In order to validate the use of a pedigree with missing data to estimate individual lifetime reproductive metrics, we simulated realised lifespans and reproductive histories for 10,000 female badgers and selectively dropped different percentages of assigned cubs. To generate life histories, we constructed a model relating female realised lifespan to the natural log of age at first reproduction ($R^2 = 0.05$). We then drew a random maximum age from the distribution of real badgers in our population and used the model to predict an age at first reproduction (α), plus noise drawn from a normal distribution with standard deviation equal to that of the residuals from the model (0.324). Each maximum age value was then used to create an individual's life history (a series of 1s for years they were alive and 0s for years following death up to the 14th position, reflecting a maximum age of 14). All these life histories were compiled into a matrix where rows corresponded to individuals and columns corresponded to their ages. The total number of cubs to be distributed among simulated females in a column was calculated based on the ratio of cubs to female adults in our real population. Individuals with α falling in a given column were assigned a cub from the available pool first and the remainder distributed randomly among all individuals with α equal to or less than that age. Thus, we obtained a matrix with 10,000 rows representing individuals and 14 columns, representing cubs produced at a given age.

We then sub-sampled the cubs assigned to females in each column by 10-70%, in increments of 10%. For each increment of sub-sampling, we re-computed each individual's α and F value (LRS/number of potentially reproductive years) and used these to calculate F/α.

Correlation coefficients between the "real" values of these three metrics and their values at different increments of missing assignment are provided in Figure S3.1.

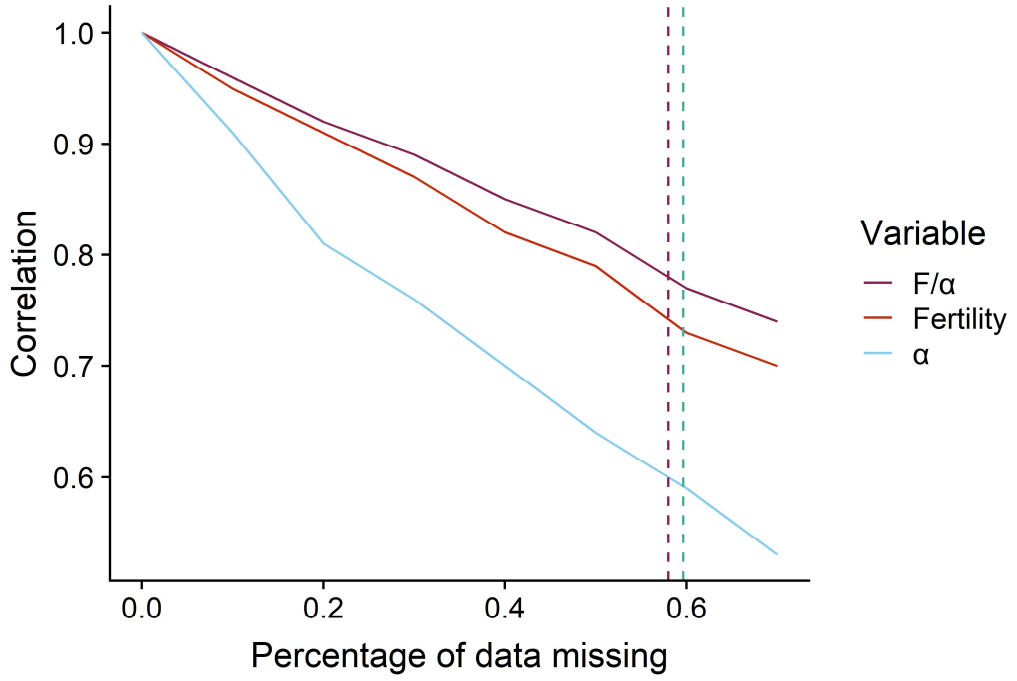


Figure S3.1 - Correlation coefficients between three lifetime reproductive metrics for a simulated population and the same values after dropping progressively more data. Vertical dashed lines indicate amount of data missing from the pedigree used in this study for males (green) and females (purple).

S4 Full model parameterisations

Table S4.1 All final models selected in the analyses described in the main text. Model type is specified and structure of the variance is provided in random effects column; if no heterogeneous variance or random effects were included, "-" is used. α = age at first reproduction; LRS = lifetime reproductive success; CS = cohort size; SR = male adults/female adults; N_i = sex-specific adult density; μ_T = mean annual temperature; σ_T = annual temperature variability; α_T = annual temperature seasonality; μ_R = annual mean rainfall; CV_R = annual coefficient of rainfall variation; BCI_r = sex, season, and age-controlled body condition.

Model	Response		Predictors	Model type	Random effects
Temporal survival trends (by sex and age class)	Annual (# survived)/(# died)	~	Year	Binomial	-
Temporal reproductive proportion trends (by sex and age class)	Annual (# assigned offspring)/(# not assigned offspring)	~	Year	Binomial	-
Trade-off models (by sex)	Realised lifespan	~	α	Linear	$Var \sim e^{\alpha}$ Cohort
	Survival to next year	~	Successful reproduction, age	Binomial	Year
Model set 1	Female LRS	~	SR, SR^2	Linear	-
	Male LRS	~	SR, SR^2, CS		
	Female F/α	~	SR, SR^2		
	Male F/α	~	-		
Model set 2	Female cub production	~	SR, N_i, μ_T, σ_T, α_T, BCI_r, age, age^2, age^3	Zero-inflated	-
	Male cub production	~	SR, N_i, σ_T, $\ln(CV_R)$, BCI_r, age		
Model set 3	Female (α = 2)/(α > 2)	~	N_i	Binomial	-
	Female (α = 3)/(α > 3)	~	BCI_r		
	Female (α = 4)/(α > 4)	~	SR, μ_T		
	Female (α = 5)/(α > 5)	~	SR, $\ln(CV_R)$		

	Male ($\alpha = 1$)/($\alpha > 1$)	~ N_i		
	Male ($\alpha = 2$)/($\alpha > 2$)	~ BCI_r		
	Male ($\alpha = 3$)/($\alpha > 3$)	~ BCI_r		
	Male ($\alpha = 4$)/($\alpha > 4$)	~ μ_T, σ_T		
Model set 4	Female (# of inds above longterm median F/α)/(# below)	~ SR, N_i	Binomial	-
	Male (# of inds above longterm median F/α)/(# below)	~ SR, N_i		

S5 Supplementary references

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da Silva, J., Macdonald, D. W. (1989). Limitations to the use of tooth wear as a means of ageing Eurasian badgers, *Meles meles*. Revue d Ecologie (Terre Vie). doi: http://hdl.handle.net/2042/55358.

Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. Journal of the Royal Statistical Society Series B (Statistical Methodology). doi: 10.1111/j.1467-9868.2010.00749.x.

Supplementary material for Chapter 3

S1 Meeting BCI assumptions

The issues with BCIs for studying fitness relationships, as identified by Peig and Green (2010) and Wilder et al. (2016) arise when three assumptions are violated:

1) BCI must appropriately estimate body fat mass.
2) BCI must avoid changing relationships between its constituent parts (e.g. body mass and body size).
3) Body fat mass (and, if assumption 1 is met, BCI) must affect fitness.

We handle assumption 1 by using a particular method of calculating BCI [$\log_e$(body mass)/$\log_e$(body length)] that has been shown to be better than either residual-based methods or scaled mass indices (*sensu* Peig and Green 2010) at estimating body fat mass, as it handles deviations from assumption 2 more readily (Labocha et al. 2014). We also performed ordinary least squares regression to confirm that subcutaneous fat score—which is a time-tested method for estimating fat in animal husbandry—was highly significantly correlated with BCI ($p < 0.001$, $R^2 = 0.52$).

In order to meet assumption 2, we limited our analysis to a) individuals from May-November, in order to exclude pregnancy- and lactation-based length-mass changes in females (Woodroffe 1995), and b) individuals aged 1+ year, as badger cubs undergo over 90% of skeletal growth during their first year (Sugianto et al. 2019a), during which time they also respond differently to weather-related stresses (Nouvellet et al. 2013). Finally, we also control in all models for multiple stage-based covariates (age, sex, and reproductive status) that might affect the relationship between body size and body weight.

Assumption 3 forms an explicit part of the questions we ask with our models, and therefore is not handled *a priori.*

S2 Female reproductive status based on teat data

S2.1 Assignment procedure

To assign reproductive status for females, we followed the following hierarchical procedure.

1) Age, where yearling females (n = 1,864) cannot have produced cubs and were therefore assigned non-reproductive status.
2) We scored females that were either actively lactating or had lactated (n = 349) in the spring as reproductive, and ones that were marked as not lactating (n = 425) as non-reproductive. We carried these assignments (total n = 812) forward through the summer for all females in this group.
3) Females with teat data but unassigned lactation data in the spring (n = 353) were assigned reproductive status based on teat metrics. Teat length and diameter measurements from step (2) (n = 774) were used to build a predictive model for reproductive status (case 1 = lactated/lactating, case 0 = not lactated) at the teat level (so as to incorporate data from individuals with incomplete sets of teat measurements). A generalised additive model (GAM, binomial) incorporating a spline of teat length or diameter (in mm), a fixed effect for the metric in question (length or diameter), and a fixed effect for teat position (anterior, middle, or posterior) was a substantially better fit for the data than a generalised linear model (GLM, binomial) with the same covariates (ΔAIC = 129.26).

4) For females caught in summer but not in spring, reproductive status was again assigned using summer teat metrics. A model was constructed using all females with known reproductive status that were also caught in the summer of the same year (n = 448 total, 197 reproductive, 251 not reproductive) to predict reproductive status based on summer teat metrics. Again, a GAM provided a superior fit to a GLM (ΔAIC = 17.57). 519 females were assigned reproductive status based on their summer teat metrics, with 7 of these providing information that could be used to assign their spring reproductive status (where the badger had been captured in spring but no teat data recorded).

S2.2 Validation of procedure

First, we report the fit of each teat-based model relative to the data used to construct it (true positives and true negatives). Second, we compare reproductive status as determined through our procedure to a more limited set of known assignments according to the population pedigree (Annavi et al. 2011; see main text).

The springtime teat model predicted reproductive females used to construct it with 91.4% accuracy and non-reproductive females with 82.1% accuracy. The summertime teat model was somewhat less accurate, but good nonetheless, predicting 79.7% of true reproductions and 82.1% of true non-reproductions. The procedure as a whole accurately classified 87.8% out of 625 female reproduction events identified by our pedigree for which the female had been captured in the year of reproduction.

S3 Full model results, with non-significant interactions, p-values, and all Tukey post-hoc pairwise comparisons for factor levels

Table S3.1. **Full coefficients from modelling effects of BCI_r on survival.** Reference level for sex/testes state is male with ascended testes. Significance levels shown using standard asterisk notation: ***$p < 0.001$; **$0.001 \leq p < 0.01$; *$0.01 \leq p < 0.05$.

	Spring			Summer			Autumn		
	Coef	SE	p	Coef	SE	p	Coef	SE	p
Female	-0.16	0.532	0.764	0.11	0.311	0.725	0.03	0.188	0.875
Rep. female	0.048	0.545	0.930	0.393	0.331	0.235	0.495*	0.245	0.043
BCI_r:Rep. female	-0.187*	0.091	0.041	-0.206*	0.083	0.014	-0.064	0.1	0.518
Int. testes	-0.044	0.628	0.944	0.376	0.37	0.310	-0.304	0.28	0.277
Desc. testes	-0.658	0.532	0.216	-0.167	0.31	0.590	-0.572	0.346	0.098
BCI_r:Desc. testes	-0.051	0.07	0.461	-0.113	0.064	0.077	-0.268	0.156	0.086
BCI_r:Age	0.221***	0.062	0.000	0.215***	0.06	0.000	0.09	0.07	0.198
N_i	-0.077	0.063	0.221	-0.137*	0.065	0.036	-0.055	0.087	0.528
BCI_r:N_i	0.051	0.069	0.456	-0.02	0.064	0.756	0.085	0.082	0.296
μ_T	-0.052	0.066	0.437	-0.067	0.067	0.322	-0.111	0.094	0.239
μ_R	-0.096	0.074	0.196	-0.008	0.076	0.913	-0.184	0.101	0.068
α_T	0.107	0.086	0.217	0.028	0.085	0.744	0.087	0.111	0.432
σ_T	-0.117	0.087	0.177	0.067	0.084	0.424	-0.116	0.111	0.294
CV_R	0.057	0.068	0.406	-0.066	0.068	0.333	0.042	0.093	0.651
BCI_r:μ_R	0.032	0.068	0.640	-0.025	0.071	0.724	0.014	0.091	0.878
BCI_r:μ_T	0.126	0.076	0.097	-0.017	0.08	0.833	0.253**	0.094	0.007
BCI_r:σ_T	0.015	0.096	0.877	-0.09	0.088	0.302	0.037	0.106	0.728
BCI_r:α_T	-0.082	0.092	0.374	0.19*	0.086	0.026	0.065	0.101	0.523
BCI_r:CV_R	-0.071	0.078	0.360	-0.159*	0.07	0.023	-0.015	0.098	0.876

Table S3.2. **Full coefficients from modelling effects of fat score on survival.** Reference level for sex/testes state is male with ascended testes; for fat scores is 4 (spring) or 5 (summer and autumn). Significance levels shown using standard asterisk notation: ***p < 0.001; **0.001 ≤ p < 0.01; *0.01 ≤ p < 0.05.

	Spring			Summer			Autumn		
	Coef	SE	p	Coef	SE	p	Coef	SE	p
Female	-0.696	0.797	0.383	0.168	0.307	0.585	0.019	0.185	0.918
Rep. female	-0.494	0.805	0.540	0.418	0.327	0.201	0.414	0.235	0.078
Int. testes	-0.434	0.864	0.615	0.341	0.362	0.346	-0.238	0.276	0.390
Desc. testes	-1.218	0.795	0.126	-0.178	0.307	0.562	-0.286	0.332	0.390
N_i	-0.056	0.065	0.395	-0.048	0.066	0.470	0.022	0.083	0.789
μ_T	μ_T	0.068	0.839	-0.002	0.07	0.979	0.021	0.09	0.820
μ_R	μ_R	0.072	0.330	-0.008	0.075	0.915	-0.195*	0.093	0.037
α_T	0.144	0.088	0.104	0.073	0.085	0.395	0.157	0.11	0.152
σ_T	s_T	0.088	0.126	0.04	0.084	0.637	-0.112	0.105	0.289
CV_R	CV_R	0.07	0.428	-0.063	0.069	0.359	0.036	0.09	0.690
Fat 1	-0.286*	0.125	0.023	-0.395**	0.138	0.004	-0.904***	0.247	0.000
Fat 2	-0.052	0.104	0.613	-0.018	0.12	0.880	-0.289	0.172	0.093
Fat 3	-0.088	0.107	0.412	0.378**	0.122	0.002	0.453**	0.146	0.002
Fat 4	NA	NA	NA	-0.101	0.142	0.475	0.334*	0.14	0.017

Table S3.3. **Full coefficients from modelling effects of autumn fat score on female reproduction.** Reference level for fat is score 5. Significance levels shown using standard asterisk notation: ***p < 0.001; **0.001 ≤ p < 0.01; *0.01 ≤ p < 0.05.

	Coef	SE	p
Ni	0.025	0.102	0.810
Rep. female	0.622***	0.104	0.000
PC1	0.015	0.055	0.788
PC2	-0.076	0.077	0.324
PC3	-0.298***	0.087	0.001
PC4	-0.081	0.108	0.457
Fat 1	0.071	0.578	0.902

	Coef	SE	p
Fat 2	-0.694*	0.305	0.023
Fat 3	-0.036	0.215	0.869
Fat 4	0.446*	0.216	0.039

Table S3.4. **Full coefficients from condition modelling.** Reference level for sex/testes descent is male with ascended testes. Significance levels shown using standard asterisk notation: ***$p < 0.001$; **$0.001 \leq p < 0.01$; *$0.01 \leq p < 0.05$.

		Spring model			Summer model			Autumn model		
		Coef	SE	p	Coef	SE	p	Coef	SE	p
	Female	-0.976***	0.12	0.000	-0.593***	0.096	0.000	-0.181**	0.064	0.005
	Rep. female	-1.692***	0.124	0.000	-1.024***	0.103	0.000	-0.358***	0.079	0.000
	Int. testes	-0.218	0.135	0.107	-0.205*	0.101	0.043	-0.177*	0.083	0.033
	Desc. testes	-0.531***	0.113	0.000	-0.341***	0.09	0.000	-0.293**	0.102	0.004
	N_i	0.019	0.024	0.416	0.03	0.03	0.317	-0.01	0.037	0.781
	N_i:Age	-0.001	0.018	0.938	-0.044*	0.021	0.038	0.051*	0.025	0.041
	N_i:Rep.female	0.003	0.019	0.870	-0.035	0.025	0.163	0.021	0.035	0.551
	Rep.female:Age	0.092***	0.023	0.000	0.021	0.027	0.427	0.014	0.032	0.659
	Desc. testes:Age	0.027	0.018	0.137	~0	0.02	0.989	-0.007	0.047	0.885
Winter	μ_T	0.048	0.029	0.096	NA	NA	NA	NA	NA	NA
	μ_R	-0.038	0.024	0.111	NA	NA	NA	NA	NA	NA
	σ_T	-0.054*	0.028	0.049	NA	NA	NA	NA	NA	NA
	CV_R	-0.04	0.023	0.076	NA	NA	NA	NA	NA	NA
	μ_T:Rep.female	-0.015	0.028	0.577	NA	NA	NA	NA	NA	NA
	μ_R:Rep.female	0.01	0.023	0.665	NA	NA	NA	NA	NA	NA
	σ_T:Rep.female	0.068**	0.023	0.003	NA	NA	NA	NA	NA	NA
	CV_R:Rep.female	-0.029	0.021	0.176	NA	NA	NA	NA	NA	NA
	μ_T:Age	0.02	0.025	0.423	NA	NA	NA	NA	NA	NA
	μ_R:Age	-0.046*	0.02	0.021	NA	NA	NA	NA	NA	NA
	σ_T:Age	-0.012	0.02	0.553	NA	NA	NA	NA	NA	NA
	CV_R:Age	0.017	0.019	0.376	NA	NA	NA	NA	NA	NA
Spring	μ_T	0.059*	0.029	0.043	NA	NA	NA	NA	NA	NA
	μ_T^2	0.089***	0.025	0.000	NA	NA	NA	NA	NA	NA
	μ_R	0.054	0.035	0.118	NA	NA	NA	NA	NA	NA
	μ_R^2	-0.068**	0.023	0.004	NA	NA	NA	NA	NA	NA

		Spring model			Summer model			Autumn model		
		Coef	SE	p	Coef	SE	p	Coef	SE	p
	σ_T	-0.03	0.025	0.224	NA	NA	NA	NA	NA	NA
	CV_R	-0.054	0.032	0.096	NA	NA	NA	NA	NA	NA
	μ_T:Rep.female	0.009	0.027	0.744	NA	NA	NA	NA	NA	NA
	μ_R:Rep.female	-0.011	0.03	0.719	NA	NA	NA	NA	NA	NA
	σ_T:Rep.female	-0.012	0.024	0.609	NA	NA	NA	NA	NA	NA
	CV_R:Rep.female	0.049	0.026	0.057	NA	NA	NA	NA	NA	NA
	μ_T:Age	0.002	0.025	0.925	NA	NA	NA	NA	NA	NA
	μ_R:Age	0.011	0.025	0.673	NA	NA	NA	NA	NA	NA
	σ_T:Age	0.004	0.021	0.842	NA	NA	NA	NA	NA	NA
	CV_R:Age	0.043	0.022	0.056	NA	NA	NA	NA	NA	NA
Summer	μ_T	NA	NA	NA	-0.135***	0.028	0.000	-0.047	0.039	0.231
	μ_R	NA	NA	NA	-0.02	0.033	0.552	-0.161**	0.052	0.002
	σ_T	NA	NA	NA	-0.071**	0.027	0.008	-0.15***	0.041	0.000
	CV_R	NA	NA	NA	0.104**	0.035	0.003	0.188***	0.045	0.000
	μ_T:Rep.female	NA	NA	NA	-0.08**	0.028	0.004	-0.072*	0.035	0.040
	μ_R:Rep.female	NA	NA	NA	0.02	0.031	0.530	-0.045	0.045	0.311
	σ_T:Rep.female	NA	NA	NA	-0.021	0.026	0.428	-0.012	0.04	0.770
	CV_R:Rep.female	NA	NA	NA	0.018	0.032	0.579	0.047	0.043	0.272
	μ_T:Age	NA	NA	NA	0.045	0.023	0.056	-0.074**	0.026	0.005
	μ_R:Age	NA	NA	NA	-0.012	0.026	0.648	-0.017	0.034	0.615
	σ_T:Age	NA	NA	NA	-0.002	0.023	0.928	0.009	0.028	0.746
	CV_R:Age	NA	NA	NA	-0.011	0.025	0.650	0.004	0.031	0.901
Autumn	μ_T	NA	NA	NA	NA	NA	NA	0.061*	0.03	0.040
	μ_R	NA	NA	NA	NA	NA	NA	0.149***	0.037	0.000
	σ_T	NA	NA	NA	NA	NA	NA	-0.035	0.04	0.375
	CV_R	NA	NA	NA	NA	NA	NA	-0.042	0.031	0.171
	CV_R^2	NA	NA	NA	NA	NA	NA	0.105***	0.027	0.000
	μ_T:Rep. female	NA	NA	NA	NA	NA	NA	0.003	0.03	0.924
	μ_R:Rep. female	NA	NA	NA	NA	NA	NA	-0.028	0.034	0.425
	σ_T:Rep. female	NA	NA	NA	NA	NA	NA	0.01	0.04	0.799
	CV_R:Rep. female	NA	NA	NA	NA	NA	NA	0.032	0.029	0.271
	μ_T:Age	NA	NA	NA	NA	NA	NA	-0.001	0.022	0.951
	μ_R:Age	NA	NA	NA	NA	NA	NA	-0.068**	0.024	0.004
	σ_T:Age	NA	NA	NA	NA	NA	NA	-0.041	0.027	0.135
	CV_R:Age	NA	NA	NA	NA	NA	NA	0.032	0.027	0.247

All pairwise comparisons for Table S3.5 were performed using the *emmeans* package in R (Lenth 2020).

Table S3.5. **All pairwise comparisons for factor means in modelling procedures.** Model response is specified; where response is used in multiple models, the corresponding differentiator is provided to the right of the tilde. p-values are adjusted for number of comparisons in each factor set.

Model	Contrast	Difference	SE	df	T-ratio	p (adj.)
Spring BCI~	Desc. testes - Rep. female	1.16	0.06	2023	19.66	< 0.001
	Desc. testes - Asc. testes	-0.53	0.11	2023	-4.69	< 0.001
	Desc. testes - Int. testes	-0.31	0.09	2023	-3.63	0.003
	Desc. testes - Nonrep. female	0.45	0.05	2023	8.57	< 0.001
	Rep. female - Asc. testes	-1.69	0.12	2023	-13.69	< 0.001
	Rep. female - Int. testes	-1.47	0.10	2023	-14.89	< 0.001
	Rep. female - Nonrep. female	-0.72	0.05	2023	-15.75	< 0.001
	Asc. testes - Int. testes	0.22	0.14	2023	1.61	0.49
	Asc. testes - Nonrep. female	0.98	0.12	2023	8.17	< 0.001
	Int. testes - Nonrep. female	0.76	0.10	2023	7.93	< 0.001
Summer BCI~	Desc. testes - Rep. female	0.68	0.07	2258	10.45	< 0.001
	Desc. testes - Asc. testes	-0.34	0.09	2258	-3.81	0.001
	Desc. testes - Int. testes	-0.14	0.07	2258	-1.99	0.27
	Desc. testes - Nonrep. female	0.25	0.05	2258	4.65	< 0.001
	Rep. female - Asc. testes	-1.02	0.10	2258	-9.98	< 0.001
	Rep. female - Int. testes	-0.82	0.09	2258	-9.57	< 0.001
	Rep. female - Nonrep. female	-0.43	0.06	2258	-7.76	< 0.001
	Asc. testes - Int. testes	0.21	0.10	2258	2.03	0.25
	Asc. testes - Nonrep. female	0.59	0.10	2258	6.16	< 0.001
	Int. testes - Nonrep. female	0.39	0.08	2258	5.00	< 0.001
Autumn BCI~	Desc. testes - Rep. female	0.07	0.12	1451	0.54	0.98
	Desc. testes - Asc. testes	-0.29	0.10	1451	-2.87	0.034
	Desc. testes - Int. testes	-0.12	0.12	1451	-0.96	0.87
	Desc. testes - Nonrep. female	-0.11	0.11	1451	-1.03	0.84
	Rep. female - Asc. testes	-0.36	0.08	1451	-4.51	< 0.001
	Rep. female - Int. testes	-0.18	0.10	1451	-1.73	0.42
	Rep. female - Nonrep. female	-0.18	0.07	1451	-2.52	0.086

Model	Contrast	Difference	SE	df	T-ratio	p (adj.)
	Asc. testes - Int. testes	0.18	0.08	1451	2.14	0.20
	Asc. testes - Nonrep. female	0.18	0.06	1451	2.83	0.038
	Int. testes - Nonrep. female	0.00	0.09	1451	0.04	1.00
Survival ~ Spr. BCI	Rep. female - Nonrep. female	0.21	0.18	2048	1.12	0.79
	Rep. female - Desc. testes	0.68	0.21	2048	3.31	0.008
	Rep. female - Asc. testes	0.02	0.56	2048	0.04	1.00
	Rep. female - Int. testes	0.07	0.41	2048	0.17	1.00
	Nonrep. female - Desc. testes	0.47	0.19	2048	2.54	0.083
	Nonrep. female - Asc. testes	-0.18	0.55	2048	-0.33	1.00
	Nonrep. female - Int. testes	-0.14	0.40	2048	-0.35	1.00
	Desc. testes - Asc. testes	-0.66	0.53	2048	-1.24	0.73
	Desc. testes - Int. testes	-0.61	0.38	2048	-1.63	0.48
	Asc. testes - Int. testes	0.04	0.63	2048	0.07	1.00
Survival ~ Sum. BCI	Rep. female - Nonrep. female	0.28	0.18	2269	1.58	0.51
	Rep. female - Desc. testes	0.51	0.20	2269	2.55	0.081
	Rep. female - Asc. testes	0.35	0.34	2269	1.01	0.85
	Rep. female - Int. testes	-0.03	0.29	2269	-0.10	1.00
	Nonrep. female - Desc. testes	0.23	0.18	2269	1.27	0.71
	Nonrep. female - Asc. testes	0.06	0.33	2269	0.19	1.00
	Nonrep. female - Int. testes	-0.31	0.28	2269	-1.13	0.79
	Desc. testes - Asc. testes	-0.17	0.31	2269	-0.54	0.98
	Desc. testes - Int. testes	-0.54	0.25	2269	-2.15	0.20
	Asc. testes - Int. testes	-0.38	0.37	2269	-1.01	0.85
Survival ~ Aut. BCI	Rep. female - Nonrep. female	0.47	0.24	1472	1.94	0.30
	Rep. female - Desc. testes	0.94	0.40	1472	2.31	0.14
	Rep. female - Asc. testes	0.36	0.27	1472	1.36	0.65
	Rep. female - Int. testes	0.67	0.34	1472	1.96	0.29
	Nonrep. female - Desc. testes	0.47	0.37	1472	1.26	0.72
	Nonrep. female - Asc. testes	-0.10	0.22	1472	-0.47	0.99
	Nonrep. female - Int. testes	0.20	0.31	1472	0.66	0.96
	Desc. testes - Asc. testes	-0.57	0.35	1472	-1.66	0.46
	Desc. testes - Int. testes	-0.27	0.41	1472	-0.66	0.97
	Asc. testes - Int. testes	0.30	0.28	1472	1.09	0.81
Survival ~ Spr. Fat score	Fat 1 - Fat 2	-0.23	0.16	1908	-1.44	0.48
	Fat 1 - Fat 3	-0.20	0.17	1908	-1.15	0.66
	Fat 1 - Fat 4	-0.71	0.29	1908	-2.48	0.063
	Fat 2 - Fat 3	0.04	0.14	1908	0.25	0.99
	Fat 2 - Fat 4	-0.48	0.27	1908	-1.79	0.28
	Fat 3 - Fat 4	-0.51	0.27	1908	-1.93	0.22

Model	Contrast	Difference	SE	df	T-ratio	p (adj.)
	Nonrep. female - Rep. female	-0.20	0.18	1908	-1.10	0.81
	Nonrep. female - Asc. testes	-0.66	0.81	1908	-0.82	0.92
	Nonrep. female - Desc. testes	0.55	0.18	1908	3.03	0.021
	Nonrep. female - Int. testes	-0.23	0.40	1908	-0.58	0.98
	Rep. female - Asc. testes	-0.46	0.81	1908	-0.57	0.98
	Rep. female - Desc. testes	0.76	0.19	1908	3.89	< 0.001
	Rep. female - Int. testes	-0.03	0.40	1908	-0.07	1.00
	Asc. testes - Desc. testes	1.22	0.80	1908	1.53	0.54
	Asc. testes - Int. testes	0.43	0.86	1908	0.50	0.99
	Desc. testes - Int. testes	-0.78	0.38	1908	-2.08	0.23
Survival ~ Sum. Fat score	Fat 1 - Fat 2	-0.38	0.16	2174	-2.34	0.13
	Fat 1 - Fat 3	-0.77	0.17	2174	-4.45	< 0.001
	Fat 1 - Fat 4	-0.29	0.20	2174	-1.44	0.60
	Fat 1 - Fat 5	-0.53	0.39	2174	-1.36	0.65
	Fat 2 - Fat 3	-0.40	0.15	2174	-2.60	0.071
	Fat 2 - Fat 4	0.08	0.18	2174	0.45	0.99
	Fat 2 - Fat 5	-0.15	0.38	2174	-0.41	0.99
	Fat 3 - Fat 4	0.48	0.18	2174	2.60	0.070
	Fat 3 - Fat 5	0.24	0.38	2174	0.64	0.97
	Fat 4 - Fat 5	-0.24	0.38	2174	-0.62	0.97
	Nonrep. female - Rep. female	-0.25	0.18	2174	-1.42	0.61
	Nonrep. female - Asc. testes	0.15	0.32	2174	0.47	0.99
	Nonrep. female - Desc. testes	0.33	0.18	2174	1.85	0.34
	Nonrep. female - Int. testes	-0.19	0.27	2174	-0.70	0.96
	Rep. female - Asc. testes	0.40	0.34	2174	1.20	0.75
	Rep. female - Desc. testes	0.58	0.20	2174	2.95	0.026
	Rep. female - Int. testes	0.06	0.28	2174	0.22	1.00
	Asc. testes - Desc. testes	0.18	0.31	2174	0.58	0.98
	Asc. testes - Int. testes	-0.34	0.36	2174	-0.94	0.88
	Desc. testes - Int. testes	-0.52	0.25	2174	-2.11	0.22
Survival ~ Aut. Fat score	Fat 1 - Fat 2	-0.62	0.35	1415	-1.78	0.39
	Fat 1 - Fat 3	-1.36	0.33	1415	-4.06	< 0.001
	Fat 1 - Fat 4	-1.24	0.33	1415	-3.72	0.002
	Fat 1 - Fat 5	-1.31	0.35	1415	-3.76	0.002
	Fat 2 - Fat 3	-0.74	0.24	1415	-3.04	0.021
	Fat 2 - Fat 4	-0.62	0.24	1415	-2.58	0.075
	Fat 2 - Fat 5	-0.70	0.26	1415	-2.67	0.059
	Fat 3 - Fat 4	0.12	0.20	1415	0.59	0.98
	Fat 3 - Fat 5	0.05	0.23	1415	0.21	1.00

Model	Contrast	Difference	SE	df	T-ratio	p (adj.)
	Fat 4 - Fat 5	-0.07	0.21	1415	-0.34	1.00
	Nonrep. female - Rep. female	-0.40	0.23	1415	-1.70	0.43
	Nonrep. female - Asc. testes	-0.10	0.21	1415	-0.48	0.99
	Nonrep. female - Desc. testes	0.19	0.35	1415	0.52	0.99
	Nonrep. female - Int. testes	0.14	0.30	1415	0.46	0.99
	Rep. female - Asc. testes	0.29	0.25	1415	1.16	0.77
	Rep. female - Desc. testes	0.58	0.38	1415	1.51	0.55
	Rep. female - Int. testes	0.53	0.33	1415	1.61	0.49
	Asc. testes - Desc. testes	0.29	0.33	1415	0.86	0.91
	Asc. testes - Int. testes	0.24	0.28	1415	0.86	0.91
	Desc. testes - Int. testes	-0.05	0.39	1415	-0.12	1.00
Rep. success ~ Aut. Fat score	Fat 1 - Fat 2	0.76	0.78	549	0.98	0.86
	Fat 1 - Fat 3	0.11	0.73	549	0.15	1.00
	Fat 1 - Fat 4	-0.37	0.74	549	-0.51	0.99
	Fat 1 - Fat 5	-0.14	0.75	549	-0.19	1.00
	Fat 2 - Fat 3	-0.66	0.37	549	-1.76	0.40
	Fat 2 - Fat 4	-1.14	0.38	549	-3.02	0.022
	Fat 2 - Fat 5	-0.91	0.39	549	-2.33	0.14
	Fat 3 - Fat 4	-0.48	0.24	549	-1.99	0.27
	Fat 3 - Fat 5	-0.25	0.26	549	-0.95	0.88
	Fat 4 - Fat 5	0.23	0.25	549	0.93	0.88

S4 Season-specific weather covariates

Principal components were used to model effects of winter and spring weather on female badger reproductive success, without incurring the penalties of collinearity. Loadings of principal components are shown in Table S4.1.

Table S4.1. **Loadings and proportion of variance described by different principal components of winter and spring weather covariates.** PC3 is highlighted with dotted lines as the only component to display a significant effect in reproductive modelling.

Season	Covariate	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
Winter	μ_T	0.39	0.00	0.19	0.73	-0.08	0.04	-0.13	-0.51
	μ_R	-0.14	-0.43	0.64	0.04	-0.24	-0.43	-0.28	0.26
	σ_T	-0.30	0.01	-0.63	0.34	-0.24	-0.29	-0.48	0.15
	CV_R	-0.42	-0.09	0.15	0.22	0.78	0.23	-0.29	0.02
Spring	μ_T	-0.28	0.52	0.27	0.37	-0.30	0.33	0.18	0.45
	μ_R	0.49	0.03	-0.11	0.27	0.40	-0.38	0.23	0.56
	σ_T	0.11	-0.70	-0.20	0.16	-0.16	0.57	0.12	0.28
	CV_R	-0.48	-0.23	-0.09	0.26	0.02	-0.32	0.70	-0.23
Standard deviation		1.75	1.26	1.13	0.91	0.75	0.55	0.48	0.40
Proportion of variance		0.38	0.20	0.16	0.10	0.07	0.04	0.03	0.02
Cumulative variance		0.38	0.58	0.74	0.84	0.91	0.95	0.98	1.00

We also considered the possibility that during the energetically-limiting summer season, cumulative stress captured by weather covariates during an already-extreme period might constrain BCI more than season-long weather characteristics. Accordingly, we designed three models of summer BCI as specified in the main text, one using season-long weather covariates, one using those covariates computed for the driest 90-day period in the summer, and one using them computer for the driest 30-day period. Of these, the 30-day driest window metrics provided the lowest AIC (ΔAIC = 14.77 from the next-lowest AIC model), and we proceeded using these metrics.

S5 Estimating random effects with this study's number of unique records

As recommended by Zuur et al. (2014), we verified that the relatively high rate of single-observation individuals in our dataset did not invalidate the use of individual-level random

effects in BCI models. To do so, we generated an imaginary response variable (BCI_{sim}) for individual *i* on sampling occasion *j* to be a function of three independent covariates:

$$BCI_{sim\ i,j} = 1 + 0.2*X_1 - 0.75*X_2 + 0.51*X_3 + Ind_i + \epsilon_j \quad \text{S1}$$

where Ind_i is a Gaussian-distributed individual intercept with standard deviation equal to that estimated for the spring BCI model (0.49). Similarly, noise (ϵ) was generated as a normal distribution with standard deviation equal to that observed in the spring BCI model (0.56). 50 observations were generated according to this relationship for each of 751 individuals (the number used in spring BCI modelling), representing a highly sampled population (good ability to detect the "true" individual intercept).

We then subsampled this hypothetical population to have the same number of observations per individual as observed in the actual badger population used to model spring BCI. We modelled $BCI_{sim\ i,j}$ as a function of X_1, X_2, and X_3, with a random intercept for individual, and extracted the resulting SD for individual intercepts. We repeated this subsampling and modelling process 1000 times, producing the distribution of SD values in Figure S4.1. Although the "real" SD value was slightly higher than the average of the estimated values (65.4% of estimates were below the modelled SD value), the average difference was quite small (0.013), and 95% of iterations returned a derived individual intercept SD value with 93-105% of the magnitude of the original, leading us to judge that our degree of individual sub-sampling did not affect our ability to detect a honest intercept.

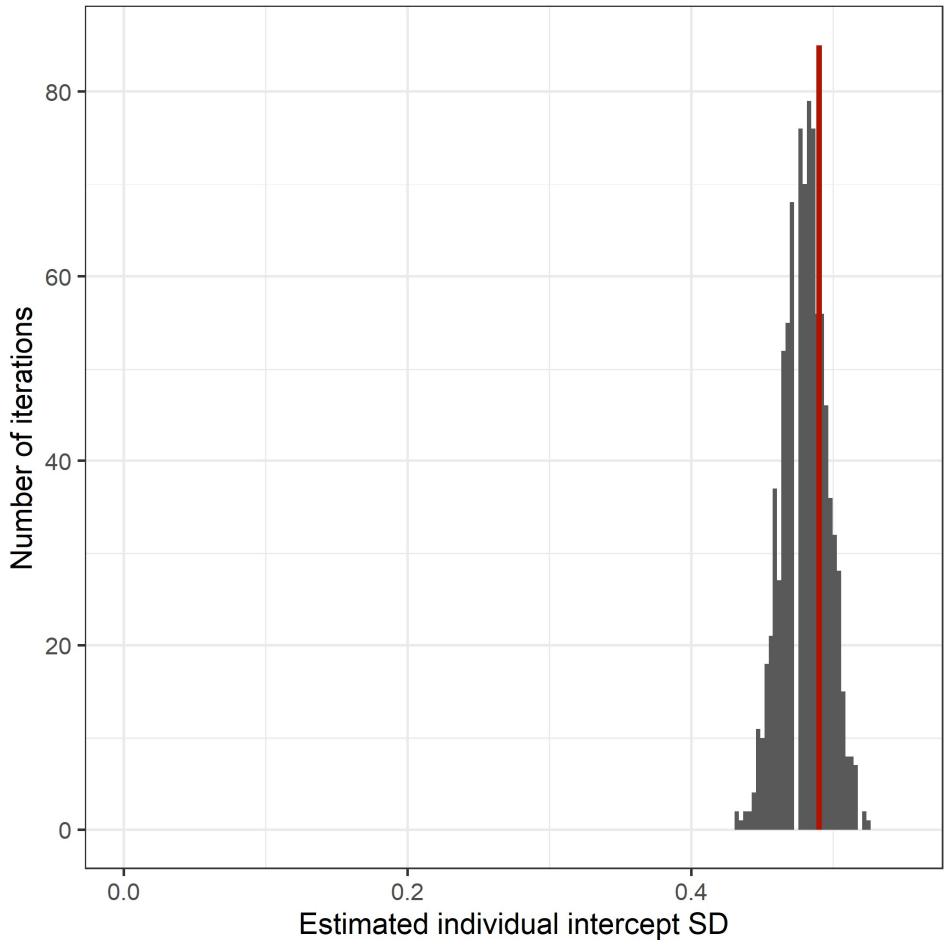


Figure S5.1. **Outcome of simulated random intercept generation.** Y-axis shows number of iterations that produced an estimated individual intercept SD value within a given 0.03 bin. Red line shows the actual intercept produced from BCI modelling. X-axis bounded at 1 to demonstrate the ability to detect a random effect that is different from 0.

S6 Individual BCI consistency estimation, BLUP bootstrapping procedure, and full BLUP modelling results

To evaluate the existence of consistent BCI phenotypes, we extracted individual residuals from the three seasonal BCI models above (from fixed predictions alone, not accounting for

random individual and sett intercepts). We then ranked all individual residuals within year *i* and season *j* to derive individual percentiles for each season ($Perc_{i,j}$). For each individual, we calculated lifetime average of $Perc_{i,j}$ (μ_{Perc}). To avoid issues with extremely large or small averages due to small individual sample size, we then subsetted these data to individuals with at least 10 captures in their lifetime (n = 197) and examined the distribution of percentile positions and μ_{Perc} values for patterns.

We then tested the effect of lifetime BCI profiles on realised lifespan and LRS using best linear unbiased predictors (BLUPs; measures of individual random intercepts) from seasonal models. In order to incorporate error in these measures, we carried out a modified parametric bootstrapping procedure (n = 1,000), fixing the individual and sett levels of bootstrapped response variables at their respective random intercept estimates, but permitting residuals to vary according to each seasonal model's residual variance. We then re-estimated individual random effects, and used these estimated values to model lifetime metrics, thus producing 95% confidence intervals of the slope of the relationship between lifetime BCI and fitness metrics (by season). Due to sex-specific patterns of badger survivorship (Chapter 2) and reproductive phenology (Sugianto et al. 2019b, 2020), we constructed models for males and females separately. Realised lifespan was recorded as the age of the individual at last capture, limited to individuals last trapped in or before 2017 (n_{male} = 334, 341, and 273 for spring, summer, and autumn, n_{female} = 356, 379, 267) to avoid accidentally marking undetected individuals as deceased. LRS (n_{male} = 286, 284, 236, n_{female} = 302, 322, 234) was calculated as specified above. Both LRS and realised lifespan were modelled using Poisson links.

Table S6.1. **All coefficients from BLUP modelling procedure.** Coefficients provided in exponential scale.

Response variable	Season	Sex	Intercept	Slope	95% CI
LRS	Spring	Male	0.43	0.44	-0.15 – 1.03
		Female	0.48	0.05	-0.28 – 0.40
	Summer	Male	0.49	0.58	-0.15 – 1.35
		Female	0.36	0.40	-0.14 – 0.97
	Autumn	Male	0.52	0.55	-0.35 – 1.52
		Female	0.50	0.73	0.07 – 1.47
Realised lifespan	Spring	Male	1.61	0.14	-0.05 – 0.33
		Female	1.84	0.01	-0.14 – 0.15
	Summer	Male	1.65	0.06	-0.18 – 0.29
		Female	1.80	0.03	-0.17 – 0.22
	Autumn	Male	1.73	0.18	-0.11 – 0.50
		Female	1.90	0.01	-0.22 – 0.26

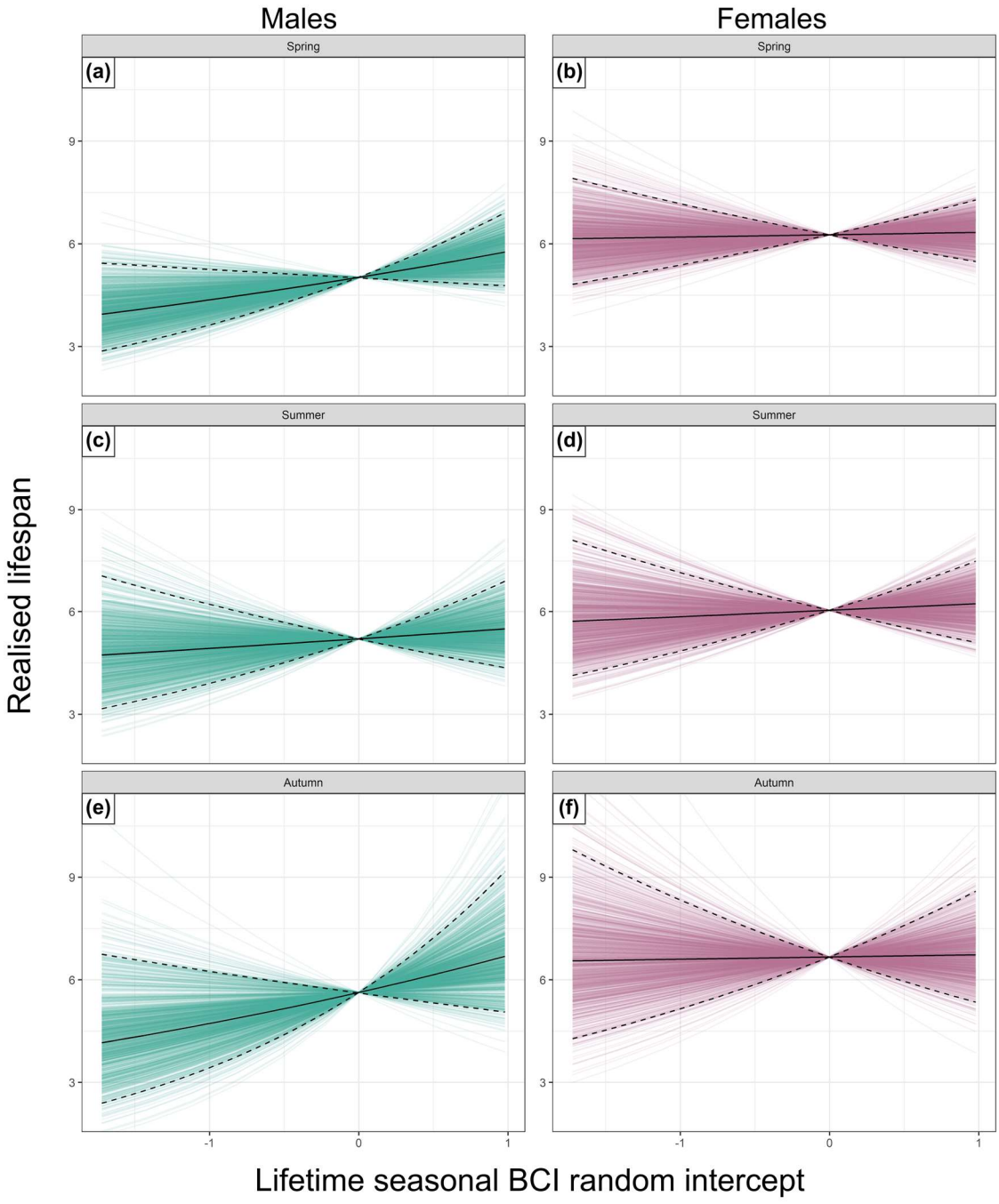


Figure S6.1. **Effects of BLUPs on realised lifespan.** Each line represents one iteration (n = 1000) of residual randomization. Mean slope provided by solid black line; 95% confidence intervals provided by the dotted lines.

S7 Simulation of $Perc_{i,j}$ for random samplings of BCI

To evaluate whether the BCI phenotypes observed in the main text could be generated by chance (absent of active efforts by individuals to escape their body condition percentile), we recalculated $Perc_{i,j}$ for a hypothetical population where individuals' lifetime BCI variation was simply a normal distribution around their mean lifetime BCI residual (calculated as the actual observed means from the population). The assumption was made that all individuals' BCI distributions would share the same standard deviation (calculated as the mean actual SD value). Individuals were assigned to one of 79 starting positions (equivalent to the number of seasons in the dataset) according to the number of actual captures from that season. Each individual was then assigned a mean BCI model residual drawn from the real population and a number of captures drawn from the real distribution of individual capture numbers (mean = 5.98, range 1-35). The resulting BCI residual values were then ranked within a season (as in the main text) and average lifetime percentile (μ_{Perc}) was calculated. Moreover, for both the real data and this simulated data, we computed the within-lifetime standard deviation of percentile position (σ_{Perc}) as a means to test the effects of random variation on the emergence of BCI types. The resulting plot shows that real data (Fig. S7.1a) and simulated data (Fig. S7.1b) show very similar patterns, even if the average variability in real data is slightly higher for a given μ_{Perc} value.

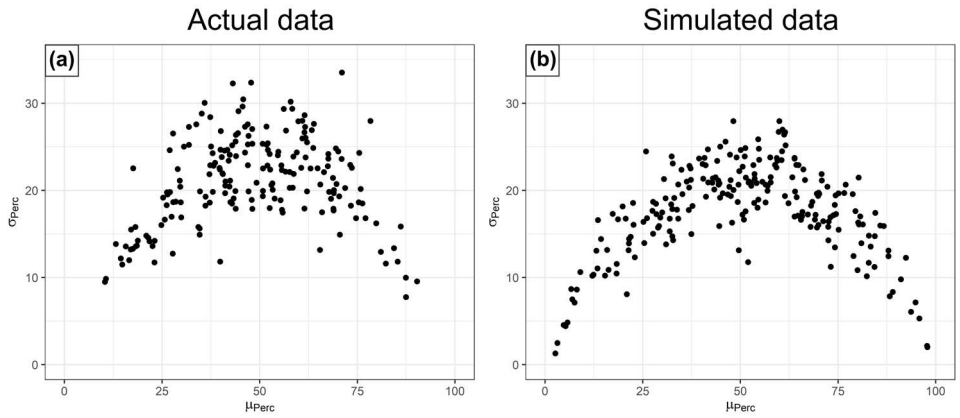


Figure S7.1 **Comparison of a) data-derived and b) simulated $Perc_{i,j}$ values.** Individual lifetime BCI residual position standard deviation as a function of average position within the population.

Supplementary material for Chapter 4

S1 Component costs and details

Final weight of badger logger: 53g chipset, battery, and casing combined, 45g collar. Final weights of lion loggers: 107g chipset, batteries, and casing combined, 1093g L1 collar, 113g L2 collar. Costs per core component are provided in Table S1.

Table S1. **Costs of core components and total cost per deployed design (in USD).**

Grams of ABS filament used in printing provided after product code 4 for a given design.

Component	**Code**	**Product**		**Cost**
Chipset	1	STEVAL-STLK01V1, STMicroelectronics		$81.87
Micro SD card	2a	Transcend 4 GB Class 4		$9.02
	2b	Transcend 16 GB UHS-I U1		$7.46
	2c	Transcend 32 GB		$19.48
Battery holder	3	BHC-CR123A, PRO POWER		$0.63
3D-printing plastic	4	UP fila ABS plastic		$37.96/kg
Deployment	**Product codes**		**Printing time**	**Total cost**
B1	1, 2a, 4 (46 g)		3.5 hrs	$93.26
B2-3	1, 2b, 3, 4 (39 g)		2.8 hrs	$91.44
B4-8	1, 2b, 3, 4 (40 g)		2.8 hrs	$91.48
L1	1, 2c, 3 (x2), 4 (117 g)		7.3 hrs	$107.05
L2	1, 2c, 3 (x2), 4 (113 g)		7.2 hrs	$106.90

All costs converted from GBP at a 1.31:1 conversion ratio (Aug 23, 2020).

S2 3D modelling guide

This guide provides an introduction to making modular, flexible designs in 3D-modelling computer-aided design (CAD) software. This project used Fusion 360 (Autodesk, 2020), software available for free for students and educators, which integrates the simple structural design used here with advanced design tools (not covered in this guide). However, many of the techniques described herein will be applicable to most CAD software currently on the market. The skills in this guide can be developed further using Autodesk's own comprehensive (and, in

our opinion, well-designed) tutorials, available at https://www.autodesk.co.uk/products/fusion-360/learn-support.

S2.1 Basics – sketches, bodies, and best practices

Fusion 360 permits the creation of 3D bodies from 2D sketches. These sketches and bodies are free to shift in three-dimensional space, and therefore must be constrained by affixing them to some fixed component of the workspace. The easiest way to begin this is to make some part of the first sketch coincident with the {x, y, z} origin of the workspace (Fig. S2.1).

Fusion 360 adopts a sequential approach to design. This is pertinent because, where bodies present flat surfaces, sketches and new bodies can be created with reference to the body surface; this is best avoided in most cases for two reasons:

1) Sketches form the "skeleton" of the design, and can be constrained by various parametric measurements, thus providing a smaller number of templates on which to modify the design according to evolving needs.
2) As designs evolve, bodies are likely to change substantially, and it is more difficult to keep track of how a change in three dimensions will affect downstream features.

Some exceptions to this general rule exist, and will be described where relevant below. It is universally true, however, that operating on simple geometric shapes is easier than on curves. Therefore, we strongly recommend finding geometric solutions to ensure consistency in the design, even when dealing with curves (see Fig. S2.4 below, for instance).

Here, we will describe the design process for a collar casing meant to be affixed to an animal at the neck. Specifically, we will present the design used in deployments L1-L2.

Therefore, some features (such as a curved interior edge to the base) will be specific to the considerations of this design.

S2.2 Design process

To begin, we recommend starting a sketch along the {x, z} or {y, z} plane. This sketch will provide information on the base of the casing (from which the main body will extrude). At a distance equal to the radius of the neck of a particularly large individual of the intended study species, draw a rectangle with the casing base's desired height and thickness (Fig. S2.1).

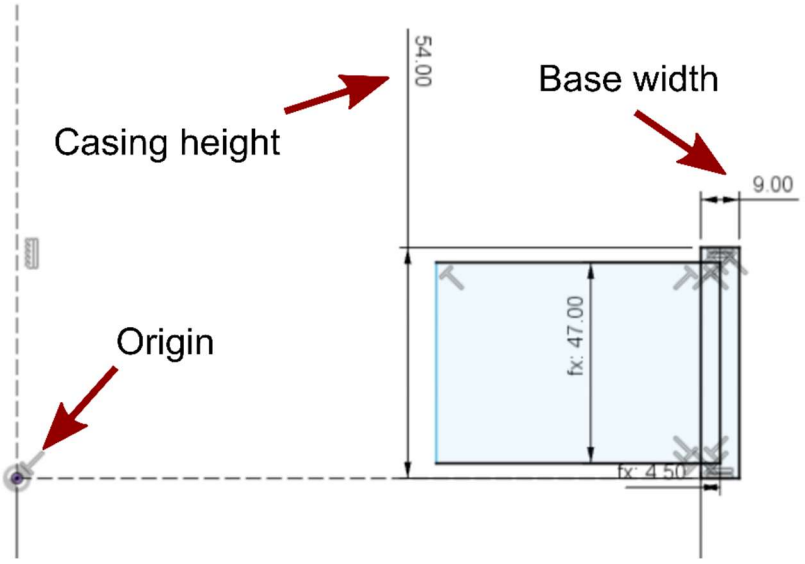


Figure S2.1. **Sketch of casing base.** Figure shows difference between "sketch" lines (solid) and "construction" lines (dashed). Sketch lines form shapes that can be acted upon, while construction lines exist solely to constrain the sketch (such as, here, to set it a certain distance from the origin).

The rectangle that forms the casing's base should then be selected and "revolved" in both directions with the line protruding from the origin as its focal axis (representing the centre of the animal's neck) until it produces the desired extent. A new sketch can then easily be created

perpendicular to the centre of the base. To do so, create a new plane at the bisecting line of the base's sketch, rotated 90 degrees (Fig. S2.2a). Then create a new sketch in that plane; this sketch will provide the main measurements for the casing body (Fig. S2.2b). By enabling the visibility of other sketches while working on this new sketch, the design can be constrained according to the existing sketch of the base.

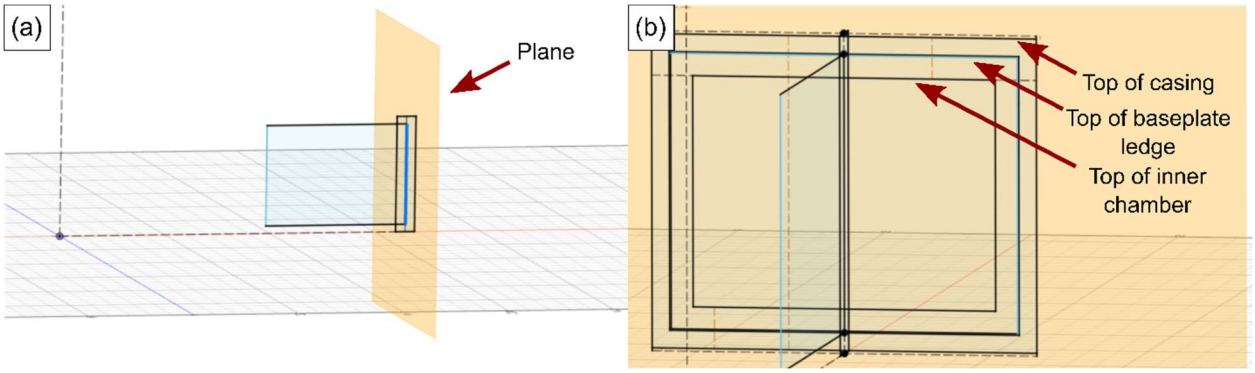


Figure S2.2. **Establishment of the main casing body sketch.** Panel (a) shows the new plane perpendicular to the centre of the base (highlighted in blue). Panel (b) shows the new sketch created on the plane (with base sketch still visible). The new sketch is constrained to the dimensions of the base sketch (black dots show constrained points), and thus any changes to the parameters of the base will affect the dimensions of the casing body.

A new extruded body should be created from this sketch (in both directions, to close the gap between the edges of the sketch and the casing base, which is curving away from the sketch's plane). These extrusions provide the main body of the casing, so long as the designed selects to "join" them to the existing body. New extrusions that intersect an existing body will, as a default, cut away at the existing solid (as, again, Fusion 360 is a sequential design program). Therefore, the same sketch can also be used to make the ledge for the casing's baseplate (done

by extruding through the base away from the main body) and the main chamber of the casing (Fig. S2.3a). By accessing the "Modify" toolbar, one can pre-define parameters to specify in the design (e.g., the depth of the main chamber, or the thickness of the baseplate ledge). This is strongly recommended, as it provides a central hub for tweaking the design without having to recall which sketch or operation uses a given parameter (Fig. S2.3b).

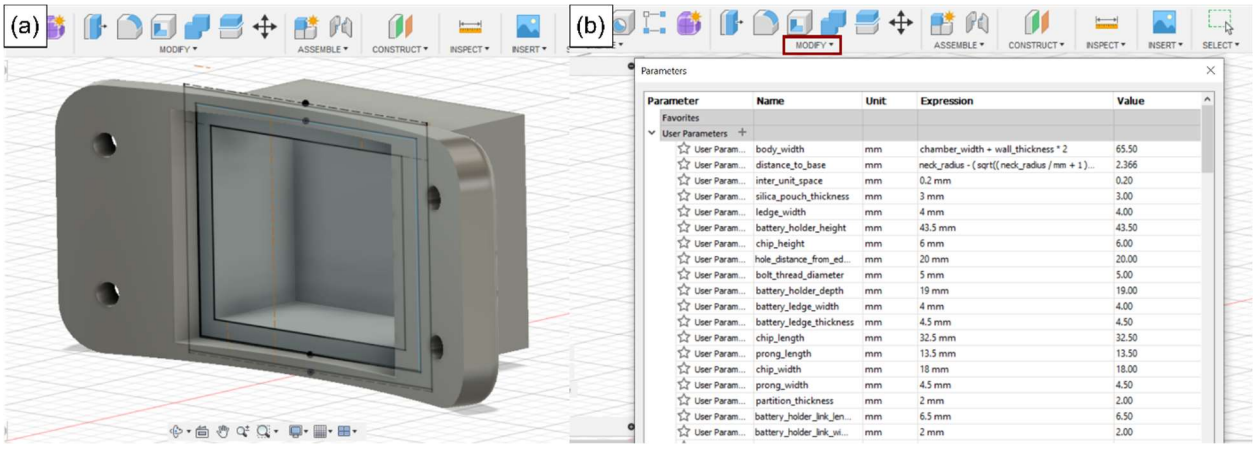


Figure S2.3. **Extrusions from sketches.** Panel (a) shows how multiple extrusions from the same sketch can, depending on their order, generate a body and then cut from it. Panel (b) shows the parameter menu, with some examples of both pre-set parameters and parameters that depend on other values.

For the flanges, a new difficulty presents itself: to create fixture holes that will be perpendicular to the collar itself (see Fig. S2.3a, where this has already been done). This can be done by creating new construction planes tangential to the curve of the flange (assuming this will reflect the curvature of the animal's neck), then creating new sketches on those planes and extruding holes through the flanges. These sketches can be set equidistant from the centre of the casing by fixing the tangential point of the construction planes to points in a sketch based on the top of the "base" sketch (Fig. S2.4).

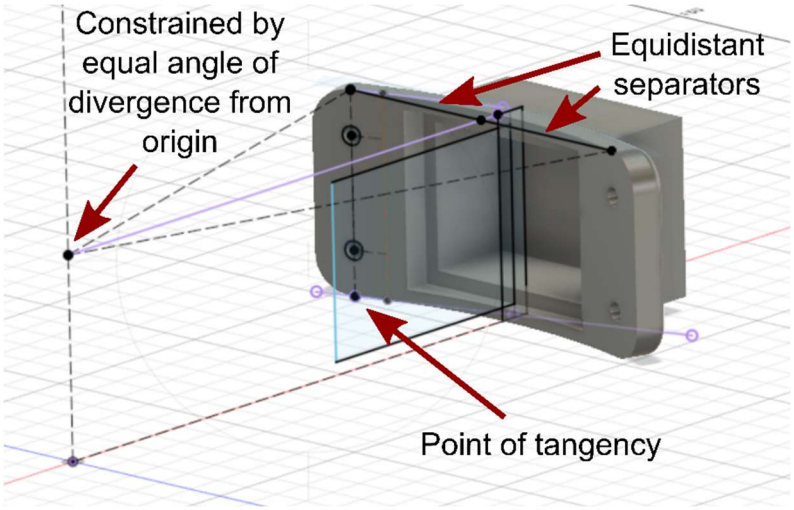


Figure S2.4. **Perpendicular attachment holes.** This figure illustrates how constraining new sketch planes by the properties set out in other sketches can produce consistency.

The next step is one of the rare occasions in which we advocate starting a sketch on the face of a body. For structures whose position depends on that of surfaces in non-curved space, such as internal structures within the casing's (right rectangular prismatic) main chamber, establishing the sketch on the body's surface ensures good agreement between extruded structures and the existing 3D body. We therefore recommend beginning a new sketch on the surface of interest (in this case, the far wall of the main chamber), then (while the 3D body is visible, thus permitting body-feature-dependent constraints) establishing outer bound lines that are constrained by the dimensions and positions of the existing chamber (Fig. S2.5a). Thus, one can extrude a variety of fine structures to support the internal components of the casing (Fig. S2.5b).

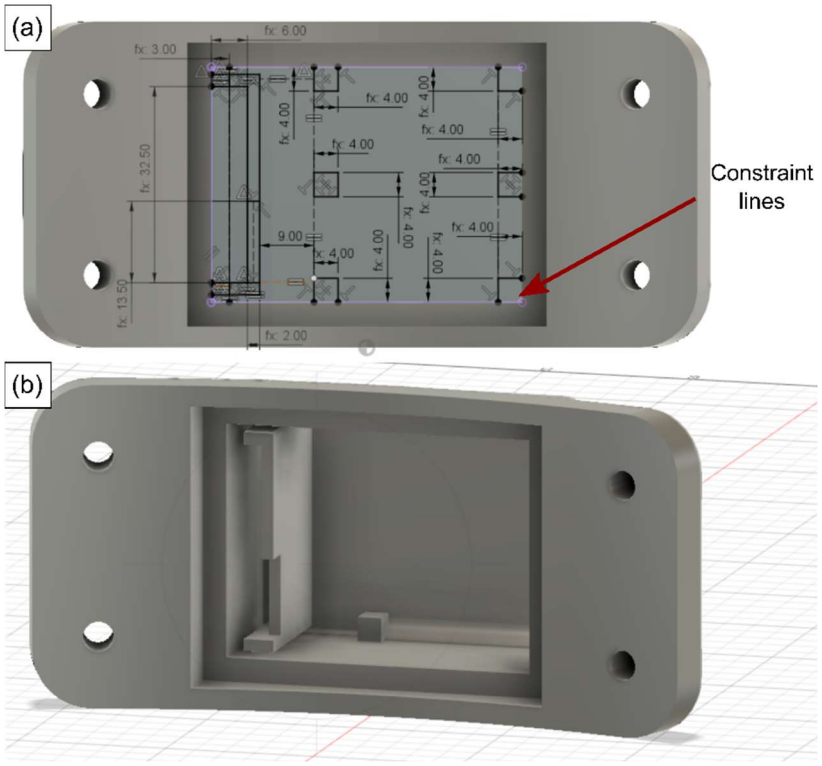


Figure S2.5. **Internal structures.** Panel (a) shows the many detailed components that can be sketched onto the inner surface of the main chamber, while panel (b) shows how those sketches can be extruded differentially to create heterogeneous surfaces within the chamber.

Once the main casing design possesses all the required characteristics, features should be rounded using the "fillet" tool. This tool can round faces ("1" in Fig. S2.6) or edges (inc. groups of edges—all other numbers in Fig. S2.6). We recommend rounding the elements that will present the largest difference in shape to the design first—as an example, we have numbered Figure S2.6 in sequential order of fillet tool use. After rounding, we strongly recommend turning on "hidden edges" in the display settings, to visually inspect how close the newly-rounded outer edge comes to the inner corners of the main chamber; less rounding may be necessary if the remaining material is too thin for structural integrity.

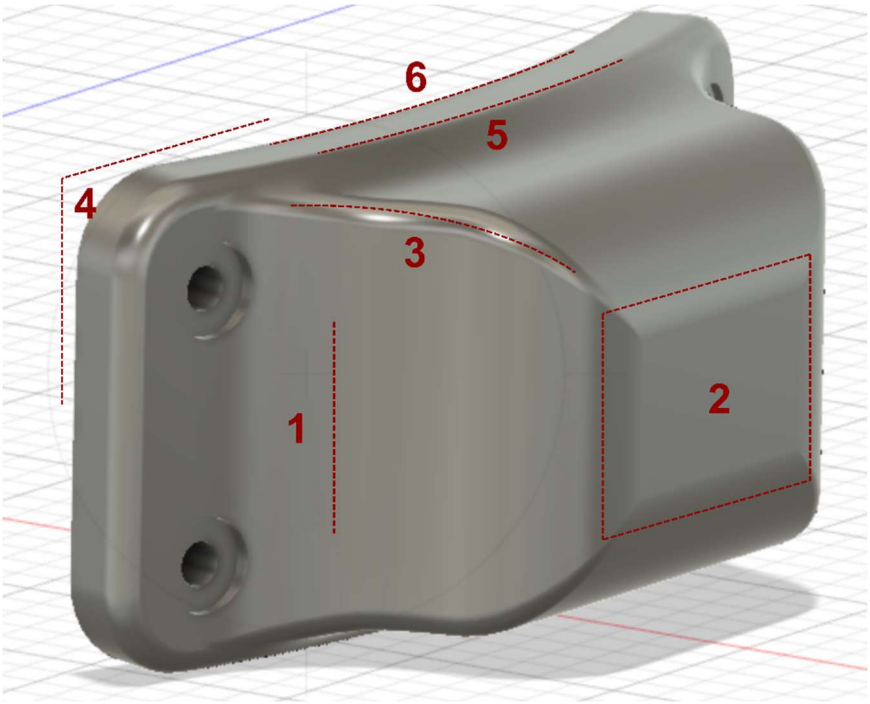


Figure S2.6. **Order of rounding operations.** All edges should be rounded to the greatest degree possible without sacrificing structural integrity, but doing so in order of decreasing impact will provide best results. This figure provides some guidance as to the best order, which will vary according to the design.

Finally, the baseplate must be created. This can be done by first extruding (backwards) a rectangle from the sketch used to create the main body of the casing. However, this time the extrusion must be specified to form a new body, rather than fusing with the existing body. It is inadvisable to re-use the exact rectangle used to create the baseplate ledge, because very minor inaccuracies in printing (which are common) would preclude a snug fit. Therefore, we recommend "fudging" the dimensions of the baseplate by extruding from a new rectangle ~0.25 mm inside the ledge rectangle. The precise degree of fudging will depend on each 3D-printer and the overall dimensions of the casing, but in the case of limited prototyping opportunities, the designer could err on the side of caution and overestimate the error, planning for a 0.5 mm gap

and making up the difference with silicone. Once the baseplate is extruded as a right rectangular prism, the origin-ward rectangle in the very first sketch (the base, Fig. S2.2a) can be "revolved" around the origin to cut the baseplate into the exact same curve as the rest of the casing base.

We hope that these detailed instructions, along with the design notes to follow (Appendix S3) and the design files available online will provide future researchers with the toolkit required to design their own species-specific casings.

S3 Design notes

Fusion 360 projects with deployment-ready casings are available online at: https://a360.co/2TskqUu (badgers) and https://a360.co/34xfp3d (lions). All casing designs as named in logs below are available at https://doi.org/10.7910/DVN/XXTWPF.

S3.1 BADGE: BADGER AUTOMATIC DATA-GATHERING EQUIPMENT

A note on retrospective/proactive records: Changes in the 16 iterations of BADGE were not recorded comprehensively. We have retrospectively added in broad changes from each design to the next, in order to illustrate the iterative nature of refining a design for deployment in the wild—noting that in the absence of these flexible design opportunities, our first deployment would likely have suffered catastrophic failure.

The proactive records (BADGE 17.0 and thereafter) include far more detail than the first 16, including the corresponding Fusion 360 data panel, making them far more accessible for replication. We encourage this level of record-keeping for any future project with a similar scope.

S3.1.1 BADGE: Retrospective records:

Added on Apr 1, 2020, as keeping a design log was not carried out until following the B1 deployment. Logs will be substantially less detailed.

STL version: BADGE 1.0

Initial design meant only to provide a rough building block for structure. Rounded rectangular chamber flanked by two flanges that could be affixed to a collar.

STL version: BADGE 2.0

First practical design, with shallower curve of the casing base (accommodating larger necks than had originally been anticipated). Large holes in wings for what had been assumed to be either rivet plates or bolts for affixing to collar. Columnar structures in each corner of the inner chamber with screw holes, allowing the baseplate to be screwed in.

Design was in four STL parts: main casing, baseplate, chip tray (a specific tray to hold the Sensortile chip), and battery holder. Battery holder had one large opening for the battery to slot in and a small opening for the positive terminal to protrude from. The battery holder and the chip tray were meant to slot in around the gaps created by the main casing's screw columns.

STL version: BADGE 3.0

Thickened walls of main casing, enlarged screw holes, and shrank the flange bolt holes.

STL version: BADGE 4.0

Widened (cross-throat axis) inner chamber of main casing.

STL version: BADGE 5.0

First design without a chip tray. Instead, added complexity to the inside of the main chamber, including a recess in which the chip could sit while the battery holder rests on a ledge above the highest level of the chip. This permitted the casing to be narrower (cross-throat axis).

STL version: BADGE 6.0

Added two flanges to the battery holder at the negative terminal end, which could be slotted into new recesses in the casing's screw columns in order to hold the battery holder in place with the same screws used to affix the baseplate.

STL version: BADGE 7.0

Changed structure of chip recess, to fit the chip more snugly by extending the ledges around the recess asymmetrically to fit the chip, then cutting a slight recess out of the main chamber wall to allow part of the chip to slide down into the chamber. Similarly, a very small recess was cut out of the main chamber wall to allow the switch on the side of the chip to slide into the chamber.

Added recesses into both terminal faces of the battery holder to allow the wire to extend below the battery holder and connect to the chip.

STL version: BADGE 8.0

Cut out an additional recess from the main chamber wall to allow a part of the chip that hadn't fit properly before to slide uninterrupted down into the casing.

Increased width of wire recesses on battery holder, as previous design had not allowed the wire enough space.

STL version: BADGE 9.0

Only discernible change is a widening of the slot in the main chamber wall that permitted the chip switch to slot into the chamber.

Further increased width of wire recesses on battery holder.

STL version: BADGE 10.0

Alternative design to permit attachment without any fastening devices. The notion was to create a new component (an "anchor") that would go on the other side of the collar and slot together

firmly with the main casing. This required that the main casing be expanded in the head-tail axis and that two grooves be designed along the flange in the cross-throat axis. The anchor was then a solid plate with two jutting ridges that would slot into the grooves on the flange.

This sort of design was never used in the field, because of a) the concern that the anchor would chafe against the animal (unlike the padded collars used in real deployments) and b) issues with printing the groove successfully—scaffolding proved very difficult to remove from the inside of the small groove.

This design was also the first one without screw holes in the baseplate, screw columns, or battery holder. It was determined that silicone would be a better sealant than screws for the baseplate, and that the flanges on the battery holder would hold it in place in any case.

STL version: BADGE 11.0

In an attempt to circumvent the issue of extracting scaffolding from a too-small groove, this design took BADGE 10.0 and made the groove larger, also changing it over to the anchor rather than being on the main casing, and dropping down to a single groove along the upper flange (on the side of the animal's head).

As the inner dimensions of this design were identical to those of BADGE 10.0, no separate STL files were created for the battery holder or baseplate, with these meant to be printed from the BADGE 10.0 designs.

STL version: BADGE 12.0

This design was a further variant for attachment style. It also incorporated an anchor, but due to the difficulties with extracting scaffolding from printed grooves, an alternative attachment style was designed. This comprised slots cut in the main casing's flanges that could accommodate columns extending from the anchor plate, which in turn had bolt-holes. The idea was to run bolts through the holes and thus hold the casing in place on the collar.

This design, like the previous attachment style, was never used in the field. The reason for this was twofold: a) we worried that the bolt-holes would provide too much structural weakness to the attachment, resulting in lost casings; b) the columns protruded too much and we worried this would either provide a hindrance to animals or provide a tempting target to worry at, thus resulting in casing loss.

Again, as the inner dimensions of this design were identical to those of BADGE 10.0, no additional STL files were included for the battery holder or baseplate.

STL version: BADGE 13.0

This design attempted to remedy the issues with structural weakness in BADGE 12.0 by making the anchor columns (and their corresponding slots in the main casing flanges) thicker. This, however, resulted in the protrusion of the columns being even more of a danger to the animals and the aims of the study.

Identical inner chamber to BADGE 10.0, no STL files included for battery holder or baseplate.

STL version: BADGE 14.0

This version represented a return to the original design (last represented in BADGE 9.0), without any anchor. Primary changes from BADGE 9.0 represented by additional rounding of edges, to reduce both wear on the collar itself and to minimise the chance that it would chafe against the animal.

STL version: BADGE 15.0

Not a substantial change from BADGE 14.0, primarily shortening the flanges to minimise unnecessarily constraining the curvature of the collar.

STL version: BADGE 16.0

Design used for B1 deployment. Primary change from BADGE 15.0 was a widening of the groove for the pins on the chipset cradle to slide down into the main chamber, as it had been getting caught on the ledge previously, resulting in a poor fit.

3.1.2 BADGE: Proactive records:

The following were recorded in real time as edits were made, and are therefore far more detailed than the preceding logs. Each record contains the date the edit was made, the Fusion 360 data panel in which the changes were made, the STL version on which the new design was built, and the STL file it was saved as.

Date: 23-07-18

Data panel model used: BADGE 10

STL version based off of: BADGE 16.0

Saved as: BADGE 17.0

Added an extrusion (Extrude 52) to give more room for metal bit sticking off short end of chip.
Added a rectangle to the chip tray sketch and extruded it (Extrude 53) to cut out a chunk to allow extra room for the prong set on the chip.

Date: 23-07-18

Data panel model used: BADGE 10

STL version based off of: BADGE 17.0

Saved as: BADGE 18.0

Created new sketch (Hollow for battery holder) to hollow out space for a CR123a battery holder.
Lengthened casing to accommodate the battery holder.
Hollowed out a spot for the battery holder, leaving silica pouch space identical.

Date: 31-07-18

Data panel model used: BADGE 11

STL version based off of: BADGE 18.0

Saved as: BADGE 19.0

Solved a few disjunction issues that came from modifying the design too much when adding in the battery holder.

Added 1 mm to the battery holder length, as it currently doesn't fit into the casing.

Date: 01-08-18

Data panel model used: BADGE 11

STL version based off of: BADGE 19.0

Saved as: BADGE 20.0

Added 0.5 mm to battery holder height, to ensure baseplate will fit.

Added 0.5 mm to battery holder width, to allow better fit.

Subtracted 5 mm from silica pouch height to keep it from having too much space to rattle around.

Subtracted 0.3 mm from chip prongs hollow because of extra space.

Date: 02-08-18

Data panel model used: BADGE 11

STL version based off of: BADGE 20.0

Saved as: BADGE 21.0

Added 3 mm to battery holder height, to accommodate bulge of battery.

Subtracted 0.5 mm from batter holder length, to keep from sliding too much.

Increased chamber width by 1 mm to give a bit more of a lip for the silicone.

Date: 03-08-18

Data panel model used: BADGE 11

STL version based off of: BADGE 21.0

Saved as: BADGE 21.1

Added 0.5 mm to both battery holder height and silica pouch thickness, to hopefully allow the battery holder to rest better on the ledge made for it and to keep the baseplate from being just slightly raised up.

BADGE 21.1 WAS DEPLOYED IN SEPTEMBER 2018, FOR BOTH THE 7-10 DAY AND EXTENDED DEPLOYMENTS

Date: 22-09-18

Data panel model used: BADGE 11

STL version based off of: BADGE 21.1

Saved as: BADGE 22.0

Increased battery holder height by 1 mm, to allow for more flexibility when inserting components. Added 1 mm to height of the base on top and bottom, to solve issue of badgers biting through to the baseplate.

Date: 29-10-18

Data panel model used: BADGE 11

STL version based off of: BADGE 22

Saved as: BADGE 22.1

Rounded corners slightly more (fillet from 1.5 mm to 3 mm radius; added fillet on inner corner as well) to avoid scratching animals.

3.2 ROAR: RANGED ORDINATION AND ACCELEROMETRY RIGS

3.2.1 ROAR: Proactive records

Date: 03-10-18

Data panel model used: Based on TRUMPET 2, saved as ROAR 1

STL version based off of: None

Saved as: ROAR 1.0

Created brand new casing design for lions, based originally on elephant template. Spaced bolt holes 21 mm apart, as is already set on the collars; re-sized holes and washer hollows to fit M5 gear. Re-sized to accommodate a 222 mm-diameter neck. Fixed height of casing to 54 mm because of the size of the belting. Designed a hollow for two side-by-side battery holders, with ledges for them to sit on to allow pins to drop below them and remain stable.

Date: 09-10-18

Data panel model used: ROAR 1

STL version based off of: ROAR 1.0

Saved as: ROAR 1.1

Increased depth of chip hollow by 4.5 mm to allow for the width of the prongs. Spaced holes 30 mm apart from centre to centre, according to Matt's specifications. Increased circumference of lion neck to 100 cm (radius = 160 mm). Added a fillet to chamber floor, allowing slightly thicker walls, and decreased thickness of bottom wall to 8 mm (allowing less protrusion). Finally, set distance along curve between holes to 90 mm.

Date: 10-10-18

Data panel model used: ROAR 1

STL version based off of: ROAR 1.1

Saved as: ROAR 1.2

Removed lion logo imprint. Kept it in the data panel, but drew back progress to before the extrudes were done.

Date: 16-10-18

Data panel model used: ROAR 1

STL version based off of: ROAR 1.2

Saved as: ROAR 1.3

Removed 0.2 mm from all around the baseplate, to allow a slightly looser fit.

VERSION 1.3 USED FOR DEPLOYMENT L1 ON NOV 14TH, 2018

Date: 02-05-19

Data panel model used: ROAR 1

STL version based off of: ROAR 1.3

Saved as: data panel ROAR 2, STL ROAR 2.0

Specifically for use with zip-ties, included a groove for the zip-tie to lie flush against the tab. Also filleted the outer edge of the base where it comes into contact with the belting, to reduce rub.

Date: 10-05-19

Data panel model used: ROAR 2

STL version based off of: ROAR 2.0

Saved as: STL ROAR 2.1

Modification of zip-tie design to allow for two zip-ties per side and for the zip-ties to run around the outer edge of the casing. Widened hole, created grooves along new path of the zip-ties, and filleted all edges that would contact a zip-tie.

Date: 11-06-19

Data panel model used: ROAR 2

STL version based off of: ROAR 2.1

Saved as: STL ROAR 2.2

Removed central props for joined battery holders, as they interfere with the battery connection.

Increased space around baseplate from 0.2 mm to 0.4 mm, to allow a smoother fit.

Date: 11-06-19

Data panel model used: ROAR 2

STL version based off of: ROAR 2.2

Saved as: STL ROAR 2.3

Moved chip-end supports for battery holder further towards the centre of the chamber to allow better access for wires to curve around the partition.

Date: 12-06-19

Data panel model used: ROAR 2

STL version based off of: ROAR 2.3

Saved as: STL ROAR 2.4

Decreased space around baseplate back to 0.25 mm, as 0.4 mm was far too loose.

VERSION 2.4 USED FOR DEPLOYMENT L2, ON JULY 19, 2019

Supplementary material for Chapter 5

S1 Evaluation of weather covariates within seasonal deployments: Deviations from long-term average and within-season collinearity

First, we evaluated whether the weather covariates tested differed significantly or substantially from the long-term (1991-2015, Rennie et al. 2017) mean for the site in question. To do so, we performed seasonal one-way ANOVA differences-of-means tests (2018 or 2019 vs. 1991-2015) for hourly weather metrics between sunset and sunrise (*suncalc* package, Benoit and Achraf 2019) on the dates with recorded accelerometry data. In the case of hourly air temperature (Temp), we controlled for the contribution of the day-night cycle by using a generalised additive model (GAM, *mgcv* package, Wood and Scheipl 2020) with a 5-k spline for hour (1-24). The long-term mean, annual deviations from this mean (from models), and long-term standard deviation are provided for each covariate in Table S1.1.

Table S.1.1 **Weather covariate characterisations.** Deviation shown in same units as average and SD. Significance levels shown using standard asterisk notation: ***$p <$ 0.001; **$0.001 \leq p < 0.01$; *$0.01 \leq p < 0.05$. Bolded cells indicate when seasonal deviation for a covariate equals or exceeds long-term standard deviation.

		Spring			Summer			Autumn		
	Year	Average 1991-2015	Deviation	SD 1991-2015	Average 1991-2015	Deviation	SD 1991-2015	Average 1991-2015	Deviation	SD 1991-2015
Temp.	2018	10.1 °C	+2.3***	2.9 °C	12.1 °C	+0.1	2.7 °C	-	-	-
	2019	11.0 °C	+0.1	2.7 °C	12.9 °C	-1.4***	2.6 °C	6.1 °C	-1.9***	3.6 °C
Rainfall	2018	0.10 mm	+0.15*	0.47 mm	0.08 mm	-0.02	0.48 mm	-	-	-
	2019	0.08 mm	-0.05	0.38 mm	-	-	-	0.07 mm	+0.09*	0.34 mm
Wind speed	2018	1.84 m/s	+0.13	0.97 m/s	1.66 m/s	+0.23***	0.92 m/s	-	-	-
	2019	1.64 m/s	+0.02	0.86 m/s	1.60 m/s	-0.16	0.87 m/s	2.22 m/s	-0.29*	1.34 m/s
Soil temp. (10 cm)	2018	**14.5** °C	**+2.3*** **	**2.3** °C	15.5 °C	-0.1	1.8 °C	-	-	-
	2019	15.7 °C	-0.5*	2.1 °C	16.7 °C	-1.4***	1.6 °C	7.5 °C	-1.6***	2.0 °C
Soil temp. (30 cm)	2018	14.1 °C	+0.6**	1.3 °C	16.0 °C	-0.2*	1.2 °C	-	-	-
	2019	15.1 °C	-0.7***	1.3 °C	16.8 °C	-0.9***	1.0 °C	8.8 °C	-0.9***	1.5 °C
Soil moisture	2018	31.1%	-2.8**	7.3%	25.7%	-4.0***	6.8%	-	-	-
	2019	**30.1%**	**-10.8*** **	**8.2%**	25.8%	-5.2%***	7.2%	35.4%	+3.2%***	5.2%
Relative humidity	2018	84.8%	+6.7***	10.2%	88.0%	+0.1%	8.9%	-	-	-
	2019	86.8%	+2.3	10.3%	87.1%	-1.4%	9.6%	92.1%	+2.7%***	7.0%

For each seasonal hourly ODBA model selection, we carried out an independent assessment of collinearity between explanatory variables. To do so, we used correlations between standardised predictors (mean = 0, SD = 1), and considered any covariates with R values of 0.6 or greater to be too collinear to include in the same model. Figures S1.1-S1.3 were constructed using the *corrplot* package in R (Wei and Simko 2017).

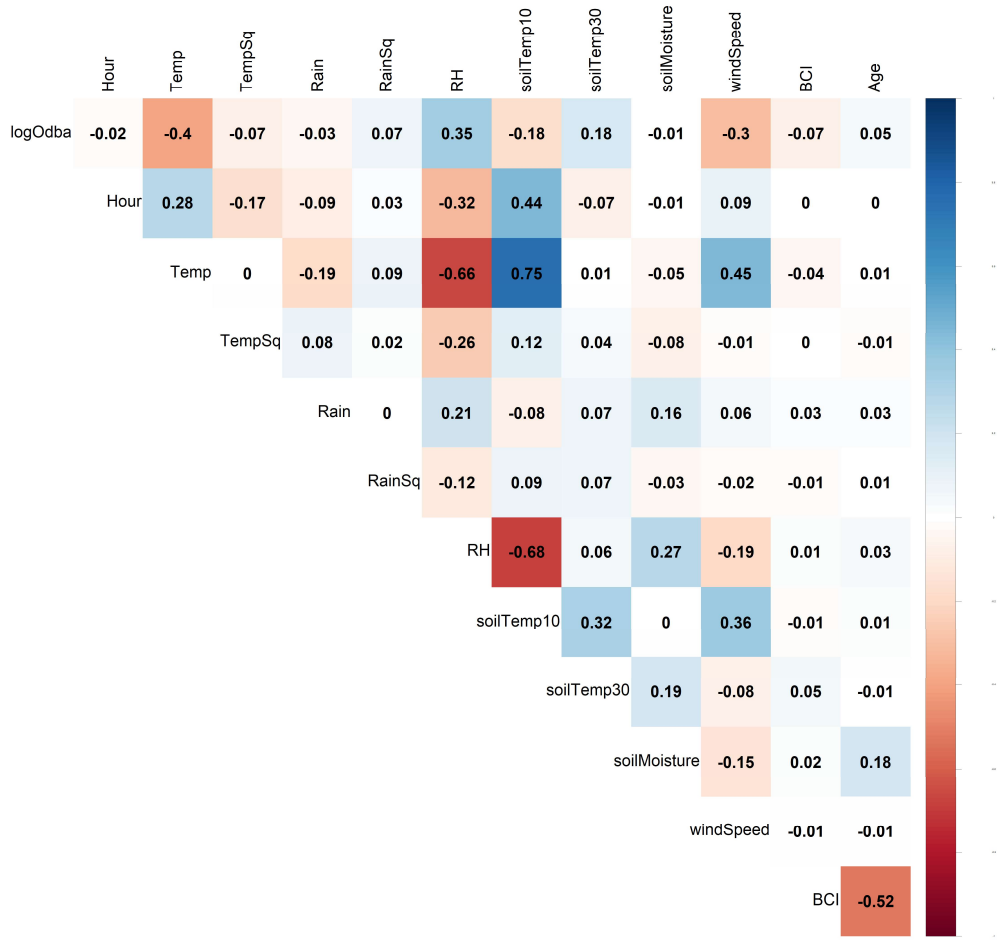


Figure S1.1 **Correlations between covariates during spring study period**. Colours denote degree of correlation, with red indicating negative correlation and blues indicating positive correlation.

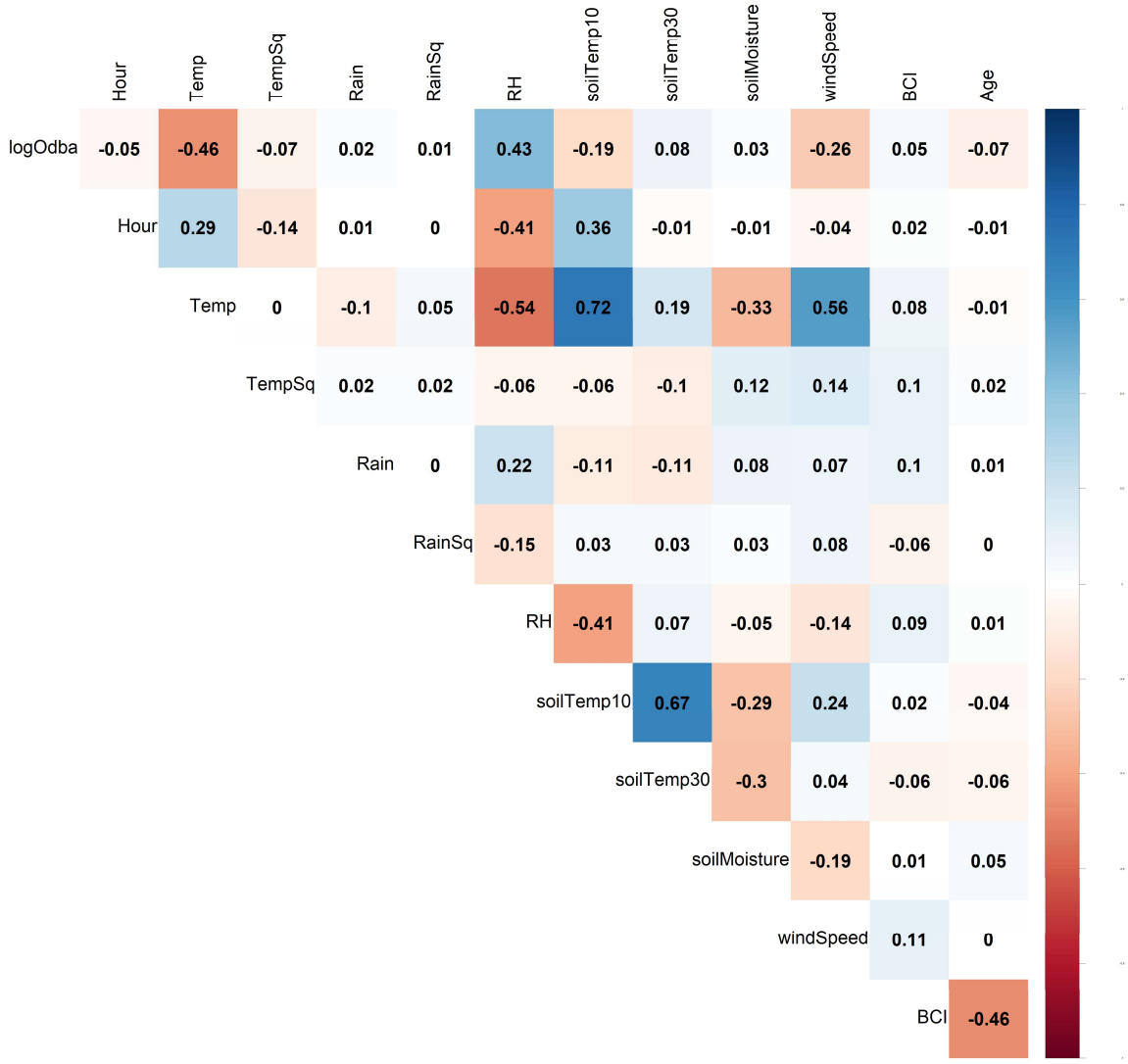


Figure S1.2 **Correlations between covariates during summer study period**. Colours denote degree of correlation, with red indicating negative correlation and blues indicating positive correlation.

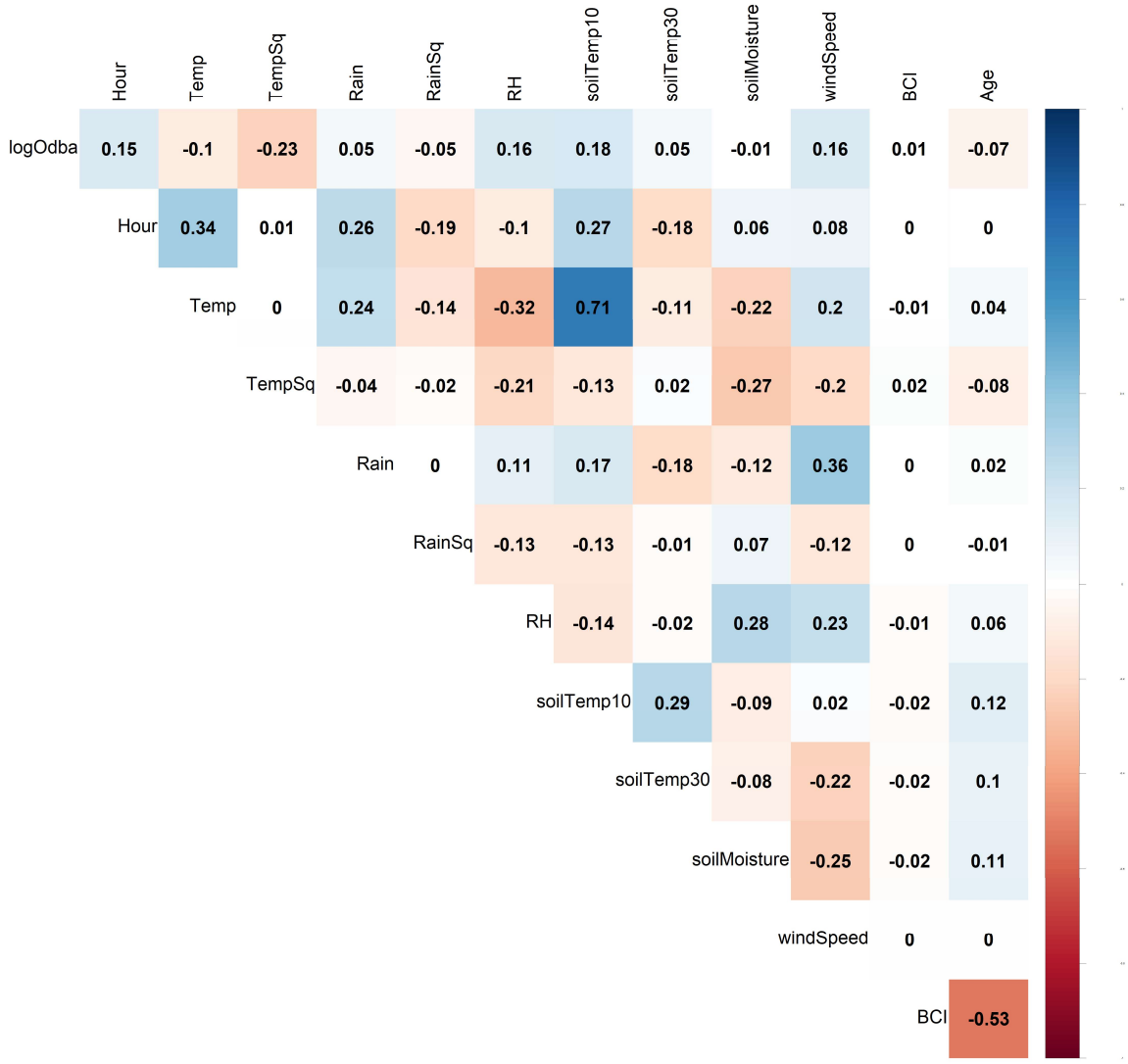


Figure S1.3 **Correlations between covariates during autumn study period**. Colours denote degree of correlation, with red indicating negative correlation and blues indicating positive correlation.

S2 Determining accelerometry threshold for activity

Overall dynamic body acceleration (ODBA) is a multi-modally distributed metric, with most animal time budgets breaking down into two primary "modes": those times when individuals are active, and when they are not. The first of these modes lies near 0; the second lies at some positive nonzero value that will be determined by study-specific parameters (individual conditions, extrinsic conditions, species, etc.). Nonzero values can still be confidently assigned to "inactivity" if they represent sampling noise or low-level motion from respiration, especially at a fine timescale (Noonan et al. 2014). Some threshold value T separates the two distributions, where activity in minute k (a_k) is equal to the signum function (1 for positive values; 0 for negative ones) of the difference between that minute's ODBA score and T:

$$a_k = sgn(ODBA_k - T) \quad \text{(S2.1)}$$

We determined the value of T through sensitivity analysis: we found the value of T where the above equation exhibited the lowest sensitivity (smallest difference in the proportion of minutes classified as "active") to a change (± 0.05) in the value of T. For our study, across all badgers in all seasons, this produced a value of T equal to 0.278, which partitioned our data into 63.4% "inactive" and 36.6% "active" minutes (Fig. S2.1, n = 390,300).

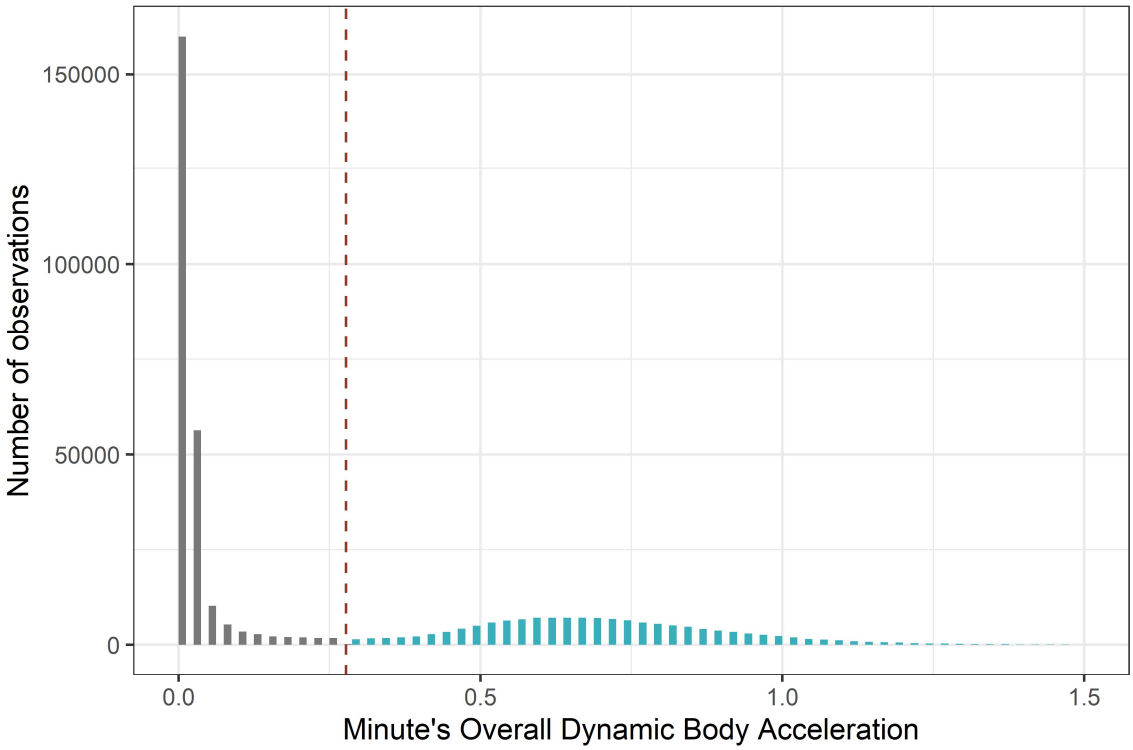


Figure S2.1 **Distribution of active/inactive samples**. Red dashed line indicates value of *T* identified by sensitivity analysis; values to the left are classified as "inactive", to the right as "active".

S3 Model selection with varied approaches to handling autocorrelation

We compared three separate approaches to selecting a top model for seasonal hourly ODBA. The first of these was to perform all-subsets selection on models incorporating an AR-1 autoregressive structure (*gamm4* library, Wood and Scheipl 2020). The second approach was to perform all-subsets selection without accounting for autocorrelation. The third was to thin the data and perform all-subsets selection on the thinned data. To thin the data, we created a tracker that began each badger's data on a different number from 1-10. We then continued the sequence to 10, then starting again at 1, until that badger's hourly ODBA data had been numbered start-to-finish. Then, we could create 1/2, 1/5, and 1/10-scale datasets without worrying about over-

sampling a specific time of day for any given badger, and without under-sampling any hours in the dataset. After examining autocorrelation function (ACF) estimates of top models, all relevant autocorrelation was accounted for after halving the data, so we did not proceed with all-subsets selection of 1/5 and 1/10-scale datasets.

As can be seen in Table S3.1, all-subsets selection on the original dataset not only inflated term significance, but also led to the selection of additional terms that no longer retained significance once autocorrelation had been accounted for. Halving the data produced comparable selection of terms to the other two approaches, but showed a tendency to produce terms with less fidelity to the other estimates, and consistently selected marginally or non-significant terms. Therefore, we proceeded in the main text by reporting the results from all-subsets selection on models with AR-1 terms, which produced similar estimates to those of models without an autoregressive term, but proved more conservative in its selection of terms.

Table S3.1. **Top model coefficients for seasonal ODBA model selection approaches.** All covariates are standardised within-season to mean = 0, standard dev. = 1. Terms not included in top model indicated with a dash ("-"); terms not evaluated in model selection indicated with "NA". A spline for hour was significant in all models, and is not shown here. "Sex" represents a binomial factor, where the baseline sex is male. Significance levels shown using standard asterisk notation: ***$p < 0.001$; **$0.001 \leq p < 0.01$; *$0.01 \leq p < 0.05$; .$0.05 < p < 0.10$.

	Spring			Summer			Autumn		
	AR-1	Null	Halved	**AR-1**	Null	Halved	**AR-1**	Null	Halved
Intercept	**0.003**	-0.043	-0.026	**-0.002**	-0.009	0.001	**-0.006**	-0.007	-0.02
Temp.	**0.046***	0.047***	0.025	**0.067****	0.06***	0.097 ***	-	0.083**	0.097*
Temp.^{2}	**-0.027***	-0.031**	-0.035 *	**-0.033***	-0.034***	-0.032*	-	-0.099***	-0.085*
Rainfall	**-0.024***	-0.027*	-0.029 .	-	-	0.019	-	-	-
Rainfall^2	**-0.018.**	-0.022*	-	-	-	-	-	-	-
Wind speed	**-0.042****	-0.039***	-0.027.	-	0.018	-	-	-	-
Relative humidity	**-**	-	-	-	-	-	-	-	-
Soil temp. (10 cm)	**-**	-	-	-	-	-	**0.099***	-	-
Soil temp. (30 cm)	**-0.047****	-0.046***	-0.047**	**-0.043****	-0.043***	-0.042 **	-	0.043.	0.053
Soil moisture	-	0.034*	0.037*	**0.042****	0.041***	0.045 **	-	-	-
Age	-	-	-	**-0.07*****	-0.072***	-0.075***	-	-0.102	-0.091.
BCI	**-0.054***	0.029	0.057	**0.012**	-0.002	0.006	-	-0.044	-
Sex	-	0.078*	0.105**	-	-	-	NA	NA	NA
BCI:Temp.	**0.031***	0.032***	0.035**	**-0.042****	-0.046***	-0.051***	-	-0.049.	-
BCI:Rainfall	-	0.028.	0.037	-	-	-	-	-	-
BCI:Sex	-	-0.075*	-0.070.	-	-	-	NA	NA	NA

Table S3.2. **Models with ΔAIC < 2 from top model for all-subsets selection with AR-1 term for hourly springtime ODBA.** All covariates are standardised within-season to mean = 0, standard dev. = 1. A spline for hour was significant in all models, and is not shown here, nor is intercept. " Sex" represents a binomial factor, where the baseline sex is male.

Temp.	Temp.^{2}	Rainfall	Rainfall^2	Wind speed	Relative humidity	Soil temp. (10 cm)	Soil temp. (30 cm)	Soil moisture	Age	BCI	Sex	BCI:Temp.	BCI:Rainfall	BCI:Sex	ΔAIC
0.046	-0.027	-0.024	-0.018	-0.042	-	-	-0.047	-	-	-0.054	-	0.031	-	-	0
0.044	-0.026	-0.024	-0.017	-0.038	-	-	-0.047	0.033	-	0.021	0.076	0.03	-	-0.072	0.31
0.046	-0.028	-0.023	-0.018	-0.042	-	-	-0.046	-	-	-0.019	0.046	0.03	-	-	0.53
0.041	-0.028	-0.025	-	-0.041	-	-	-0.047	-	-	-0.054	-	0.03	-	-	1.18
0.039	-0.026	-0.025	-	-0.037	-	-	-0.047	0.034	-	0.022	0.076	0.03	-	-0.073	1.27
0.046	-0.027	-0.026	-0.018	-0.041	-	-	-0.047	-	-	-0.052	-	0.032	0.014	-	1.35
0.044	-0.028	-0.022	-0.018	-0.043	-	-	-0.044	-	-	-0.005	0.052	0.03	-	-0.041	1.35
0.046	-0.026	-0.024	-0.018	-0.039	-	-	-0.048	0.018	-	-0.011	0.056	0.03	-	-	1.44
0.043	-0.026	-0.026	-0.017	-0.038	-	-	-0.047	0.034	-	0.024	0.078	0.032	0.016	-0.073	1.47
0.047	-0.027	-0.024	-0.018	-0.042	-	-	-0.047	-	0.016	-0.047	-	0.031	-	-	1.53
0.047	-0.026	-0.024	-0.018	-0.04	-	-	-0.048	0.012	-	-0.054	-	0.031	-	-	1.55
0.04	-0.028	-0.025	-	-0.041	-	-	-0.046	-	-	-0.019	0.046	0.03	-	-	1.73
0.045	-0.027	-0.025	-0.018	-0.042	-	-	-0.046	-	-	-0.016	0.047	0.032	0.015	-	1.81
0.046	-0.028	-0.023	-0.018	-0.042	-	-	-0.046	-	0.019	-0.009	0.048	0.031	-	-	1.84
0.044	-	-0.025	-0.017	-0.036	-	-	-0.05	0.036	-	0.021	0.076	0.031	-	-0.073	1.9

Table S3.3. **Models with ΔAIC < 2 from top model for all-subsets selection with no accounting for autocorrelation for hourly springtime ODBA.** All covariates are standardised within-season to mean = 0, standard dev. = 1. A spline for hour was significant in all models, and is not shown here, nor is intercept. " Sex" represents a binomial factor, where the baseline sex is male.

Temp.	Temp.^{2}	Rainfall	Rainfall^2	Wind speed	Relative humidity	Soil temp. (10 cm)	Soil temp. (30 cm)	Soil moisture	Age	BCI	Sex	BCI:Temp.	BCI:Rainfall	BCI:Sex	ΔAIC
0.047	-0.031	-0.027	-0.022	-0.039	-	-	-0.046	0.034	-	0.029	0.078	0.032	0.028	-0.075	0
0.048	-0.031	-0.022	-0.023	-0.04	-	-	-0.046	0.032	-	0.021	0.073	0.029	-	-0.072	1.43
0.049	-0.032	-0.025	-0.024	-0.043	-	-	-0.045	-	-	-0.008	0.052	0.032	0.027	-	1.64
0.05	-0.032	-0.026	-0.024	-0.043	-	-	-0.046	-	-	-0.045	-	0.032	0.026	-	1.67
0.048	-0.031	-0.027	-0.023	-0.04	-	-	-0.047	0.019	-	0.004	0.066	0.032	0.028	-	1.93
0.047	-0.031	-0.027	-0.022	-0.039	-	-	-0.046	0.033	0.005	0.03	0.078	0.032	0.028	-0.073	1.94

Table S3.4. **Models with ΔAIC < 2 from top model for all-subsets selection on halved data for hourly springtime ODBA.** All covariates are standardised within-season to mean = 0, standard dev. = 1. A spline for hour was significant in all models, and is not shown here, nor is intercept. " Sex" represents a binomial factor, where the baseline sex is male.

Temp.	Temp.^{2}	Rainfall	Rainfall^2	Wind speed	Relative humidity	Soil temp. (10 cm)	Soil temp. (30 cm)	Soil moisture	Age	BCI	Sex	BCI:Temp.	BCI:Rainfall	BCI:Sex	ΔAIC
0.025	-0.035	-0.029	-	-0.027	-	-	-0.047	0.037	-	0.057	0.105	0.035	0.037	-0.07	0
0.03	-0.035	-0.02	-0.019	-0.029	-	-	-0.047	0.034	-	0.048	0.1	0.032	-	-0.068	0.47
0.025	-0.035	-0.022	-	-0.028	-	-	-0.047	0.035	-	0.05	0.102	0.032	-	-0.07	0.54
0.029	-0.034	-0.026	-0.016	-0.028	-	-	-0.047	0.035	-	0.054	0.103	0.035	0.032	-0.069	0.58
0.031	-0.037	-	-	-0.032	-	-	-0.048	0.032	-	0.05	0.102	0.032	-	-0.07	0.76
0.014	-0.032	-0.034	-	-	-	-	-0.047	0.043	-	0.061	0.108	0.035	0.038	-0.073	0.85
0.027	-0.037	-0.027	-	-0.032	-	-	-0.045	-	-	0.015	0.072	0.035	0.036	-	0.9
0.032	-0.037	-0.017	-0.021	-0.034	-	-	-0.045	-	-	0.007	0.069	0.033	-	-	0.97
0.027	-0.035	-0.03	-	-0.028	-	-	-0.049	0.023	-	0.025	0.085	0.035	0.038	-	1.15
0.031	-0.036	-0.024	-0.018	-0.033	-	-	-0.045	-	-	0.013	0.071	0.035	0.031	-	1.18
0.033	-0.039	-	-	-0.036	-	-	-0.047	-	-	0.009	0.071	0.033	-	-	1.19
0.027	-0.038	-0.02	-	-0.033	-	-	-0.045	-	-	0.008	0.07	0.032	-	-	1.37
0.014	-0.033	-0.027	-	-	-	-	-0.047	0.041	-	0.054	0.105	0.032	-	-0.073	1.53
0.032	-0.035	-0.02	-0.02	-0.03	-	-	-0.048	0.021	-	0.015	0.08	0.033	-	-	1.57
0.018	-0.032	-0.031	-0.015	-	-	-	-0.047	0.042	-	0.058	0.106	0.035	0.034	-0.072	1.6
0.031	-0.034	-0.026	-0.017	-0.029	-	-	-0.048	0.022	-	0.022	0.083	0.035	0.033	-	1.62
0.019	-0.032	-0.024	-0.019	-	-	-	-0.047	0.04	-	0.051	0.103	0.032	-	-0.072	1.65
0.027	-0.036	-0.022	-	-0.029	-	-	-0.048	0.022	-	0.017	0.081	0.032	-	-	1.79
0.031	-0.04	-	-	-0.037	-	-	-0.044	-	-	0.026	0.08	0.033	-	-0.041	1.9
0.031	-0.038	-0.016	-0.021	-0.034	-	-	-0.043	-	-	0.022	0.077	0.033	-	-0.038	1.91
0.026	-0.038	-0.026	-	-0.033	-	-	-0.043	-	-	0.029	0.079	0.035	0.036	-0.037	1.93
0.025	-0.035	-0.029	-	-0.027	-	-	-0.047	0.037	0.001	0.057	0.105	0.035	0.037	-0.069	2

Table S3.5. **Models with ΔAIC < 2 from top model for all-subsets selection with AR-1 term for hourly summertime ODBA.** All covariates are standardised within-season to mean = 0, standard dev. = 1. A spline for hour was significant in all models, and is not shown here, nor is intercept. " Sex" represents a binomial factor, where the baseline sex is male.

Temp.	Temp.^{2}	Rainfall	Rainfall^2	Wind speed	Relative humidity	Soil temp. (10 cm)	Soil temp. (30 cm)	Soil moisture	Age	BCI	Sex	BCI:Temp.	BCI:Rainfall	BCI:Sex	ΔAIC
0.067	-0.033	-	-	-	-	-	-0.043	0.042	-0.07	0.012	-	-0.042	-	-	0
0.055	-0.035	-	-	0.019	-	-	-0.041	0.042	-0.071	0.011	-	-0.043	-	-	0.6
0.068	-0.033	0.009	-	-	-	-	-0.042	0.042	-0.07	0.011	-	-0.042	-	-	1.31
0.068	-0.033	-	-	-	-	-	-0.043	0.042	-0.07	0.01	-0.005	-0.043	-	-	1.93
0.068	-0.033	-	-	-	0.004	-	-0.043	0.043	-0.07	0.012	-	-0.042	-	-	1.9

Table S3.6. **Models with ΔAIC < 2 from top model for all-subsets selection with no accounting for autocorrelation for hourly summertime ODBA.** All covariates are standardised within-season to mean = 0, standard dev. = 1. A spline for hour was significant in all models, and is not shown here, nor is intercept. " Sex" represents a binomial factor, where the baseline sex is male.

Temp.	Temp.^{2}	Rainfall	Rainfall^2	Wind speed	Relative humidity	Soil temp. (10 cm)	Soil temp. (30 cm)	Soil moisture	Age	BCI	Sex	BCI:Temp.	BCI:Rainfall	BCI:Sex	ΔAIC
0.060	-0.034	-	-	0.018	-	-	-0.043	0.041	-0.072	-0.002	-	-0.046	-	-	0
0.072	-0.032	-	-	-	-	-	-0.044	0.042	-0.071	0	-	-0.046	-	-	0.32
0.073	-0.032	0.012	-	-	-	-	-0.043	0.042	-0.072	-0.002	-	-0.046	-	-	0.64
0.062	-0.034	0.01	-	0.016	-	-	-0.043	0.041	-0.072	-0.003	-	-0.046	-	-	0.82
0.06	-0.034	-	-	0.018	-	-	-0.044	0.041	-0.072	-0.004	-0.014	-0.047	-	-	1.54
0.058	-0.034	-	-	0.018	-0.005	-	-0.043	0.041	-0.071	-0.001	-	-0.047	-	-	1.88
0.072	-0.032	-	-	-	-	-	-0.044	0.042	-0.072	-0.003	-0.013	-0.046	-	-	1.93

Table S3.7. **Models with ΔAIC < 2 from top model for all-subsets selection on halved data for hourly summertime ODBA.** All covariates are standardised within-season to mean = 0, standard dev. = 1. A spline for hour was significant in all models, and is not shown here, nor is intercept. " Sex" represents a binomial factor, where the baseline sex is male.

Temp.	Temp.^{2}	Rainfall	Rainfall^2	Wind speed	Relative humidity	Soil temp. (10 cm)	Soil temp. (30 cm)	Soil moisture	Age	BCI	Sex	BCI:Temp.	BCI:Rainfall	BCI:Sex	ΔAIC
0.097	-0.032	0.019	-	-	-	-	-0.042	0.045	-0.075	0.006	-	-0.051	-	-	0
0.096	-0.032	-	-	-	-	-	-0.043	0.046	-0.074	0.008	-	-0.052	-	-	0.1
0.081	-0.034	-	-	0.021	-	-	-0.042	0.045	-0.074	0.007	-	-0.052	-	-	0.44
0.085	-0.034	0.016	-	0.018	-	-	-0.041	0.045	-0.075	0.005	-	-0.051	-	-	0.84
0.094	-0.033	0.017	0.012	-	-	-	-0.042	0.044	-0.074	0.007	-	-0.051	-	-	1.01
0.098	-0.032	0.019	-	-	-	-	-0.043	0.045	-0.075	0.002	-0.01	-0.051	-	-	1.76
0.097	-0.032	0.016	-	-	-	-	-0.042	0.046	-0.074	0.006	-	-0.05	0.005	-	1.83
0.096	-0.032	0.02	-	-	-0.007	-	-0.042	0.045	-0.074	0.007	-	-0.051	-	-	1.88
0.096	-0.032	-	-	-	-	-	-0.044	0.046	-0.074	0.004	-0.009	-0.052	-	-	1.88
0.082	-0.035	0.015	0.012	0.017	-	-	-0.041	0.044	-0.074	0.006	-	-0.051	-	-	1.92

Table S3.8. **Models with ΔAIC < 2 from top model for all-subsets selection with AR-1 term for hourly autumn ODBA.** All covariates are standardised within-season to mean = 0, standard dev. = 1. A spline for hour was significant in all models, and is not shown here, nor is intercept.

Temp.	Temp.^{2}	Rainfall	Rainfall^2	Wind speed	Relative humidity	Soil temp. (10 cm)	Soil temp. (30 cm)	Soil moisture	Age	BCI	BCI:Temp.	BCI:Rainfall	ΔAIC
-	-	-	-	-	-	0.099	-	-	-	-	-	-	0
-	-	-	-	-	-	0.101	-	-	-0.075	-	-	-	0.22
-	-	-	-	-	0.054	0.105	-	-	-	-	-	-	0.28
-	-	-	-	-	0.054	0.107	-	-	-0.078	-	-	-	0.46
-	-	-	-	-	-	0.101	-	-	-0.099	-0.045	-	-	1.66
-	-	-	-	-	-	-	-	-	-	-	-	-	1.68
-	-	-	-	-	-	0.107	-0.018	-	-	-	-	-	1.83
-	-	-	-	-	-	0.106	-	0.018	-	-	-	-	1.84
-	-	-	-	-	0.054	0.107	-	-	-0.104	-0.046	-	-	1.89
0.055	-0.06	-	-	-	-	-	-	-	-	-	-	-	1.94
0.081	-	-	-	-	0.066	-	-	-	-	-	-	-	1.97
-	-	0.003	-	-	-	0.099	-	-	-	-	-	-	1.98
-	-	-	-	0.005	-	0.099	-	-	-	-	-	-	1.98
-	-	-	-	-	-	0.099	-	-	-	0.007	-	-	1.9

Table S3.9. **Models with ΔAIC < 2 from top model for all-subsets selection with no accounting for autocorrelation for hourly autumn ODBA.** All covariates are standardised within-season to mean = 0, standard dev. = 1. A spline for hour was significant in all models, and is not shown here, nor is intercept.

Temp.	Temp.^{2}	Rainfall	Rainfall^2	Wind speed	Relative humidity	Soil temp. (10 cm)	Soil temp. (30 cm)	Soil moisture	Age	BCI	BCI:Temp.	BCI:Rainfall	ΔAIC
0.083	-0.099	-	-	-	-	-	0.043	-	-0.102	-0.044	-0.049	-	0
0.082	-0.096	-	-	-	-	-	0.043	-	-	-	-	-	0.1
0.083	-0.099	-	-	-	-	-	0.043	-	-	0.009	-0.049	-	0.29
0.083	-0.096	-	-	-	-	-	0.043	-	-0.076	-	-	-	0.37
0.087	-0.09	-	-	-	-	-	-	-	-	-	-	-	0.86
0.088	-0.093	-	-	-	-	-	-	-	-0.097	-0.042	-0.049	-	0.88
0.088	-0.092	-	-	-	-	-	-	-	-	0.008	-0.049	-	1.1
0.087	-0.09	-	-	-	-	-	-	-	-0.073	-	-	-	1.19
0.101	-0.097	-	-	-0.031	-	-	-	-	-0.098	-0.043	-0.049	-	1.39
0.099	-0.093	-	-	-0.031	-	-	-	-	-	-	-	-	1.41
0.092	-0.101	-	-	-0.02	-	-	0.037	-	-0.102	-0.044	-0.049	-	1.46
0.091	-0.097	-	-	-0.02	-	-	0.037	-	-	-	-	-	1.58
0.101	-0.096	-	-	-0.031	-	-	-	-	-	0.008	-0.049	-	1.62
0.086	-0.098	-	-	-	0.014	-	0.045	-	-0.103	-0.045	-0.049	-	1.71
0.1	-0.094	-	-	-0.031	-	-	-	-	-0.073	-	-	-	1.73
0.092	-0.1	-	-	-0.02	-	-	0.037	-	-	0.009	-0.049	-	1.76
0.083	-0.097	-	-	-	-	-	0.043	-	-0.102	-0.047	-	-	1.8
0.092	-0.093	-	-	-	-	-	0.043	0.014	-0.103	-0.045	-0.049	-	1.81
0.085	-0.095	-	-	-	0.014	-	0.045	-	-	-	-	-	1.82
0.091	-0.098	-	-	-0.02	-	-	0.037	-	-0.076	-	-	-	1.85
0.091	-0.09	-	-	-	-	-	0.043	0.013	-	-	-	-	1.94
0.083	-0.099	0	-	-	-	-	0.043	-	-0.102	-0.044	-0.049	-	2

Table S3.10. **Models with ΔAIC < 2 from top model for all-subsets selection on halved data for hourly autumn ODBA.** All covariates are standardised within-season to mean = 0, standard dev. = 1. A spline for hour was significant in all models, and is not shown here, nor is intercept.

Temp.	Temp.^{2}	Rainfall	Rainfall^2	Wind speed	Relative humidity	Soil temp. (10 cm)	Soil temp. (30 cm)	Soil moisture	Age	BCI	BCI:Temp.	BCI:Rainfall	ΔAIC
0.097	-0.085	-	-	-	-	-	0.053	-	-0.091	-	-	-	0
0.103	-0.077	-	-	-	-	-	-	-	-0.087	-	-	-	0.08
-	-	-	-	-	-	0.126	-	-	-0.09	-	-	-	0.16
0.096	-0.084	-	-	-	-	-	0.052	-	-	-	-	-	0.56
0.102	-0.076	-	-	-	-	-	-	-	-	-	-	-	0.57
0.094	-0.093	-	-	-	-	-	0.056	-	-0.114	-0.039	-0.061	-	0.58
-	-	-	-	-	-	0.125	-	-	-	-	-	-	0.74
0.101	-0.084	-	-	-	-	-	-	-	-0.108	-0.037	-0.059	-	0.93
0.114	-0.08	-	-	-0.028	-	-	-	-	-0.087	-	-	-	1.49
0.097	-0.085	-	-	-	-	-	0.053	-	-0.114	-0.042	-	-	1.49
0.094	-0.091	-	-	-	-	-	0.055	-	-	0.02	-0.061	-	1.58
0.103	-0.078	-	-	-	-	-	-	-	-0.108	-0.039	-	-	1.61
-	-	-	-	-	-	0.127	-	-	-0.112	-0.04	-	-	1.67
0.1	-0.083	-	-	-	0.02	-	0.056	-	-0.092	-	-	-	1.71
-	-	-	-	-	-	0.133	-	0.022	-0.093	-	-	-	1.8
0.1	-0.083	-	-	-	-	-	-	-	-	0.02	-0.059	-	1.81
0.107	-0.076	-0.017	-	-	-	-	-	-	-0.087	-	-	-	1.87
0.103	-0.085	-	-	-0.013	-	-	0.049	-	-0.091	-	-	-	1.88
-	-	-	-	-	0.018	0.128	-	-	-0.091	-	-	-	1.92
0.099	-0.084	-0.007	-	-	-	-	0.051	-	-0.091	-	-	-	1.97
0.105	-0.076	-	-	-	0.012	-	-	-	-0.087	-	-	-	1.99
0.113	-0.079	-	-	-0.028	-	-	-	-	-	-	-	-	1.99
0.097	-0.085	-	-	-	-	-	0.053	0	-0.091	-	-	-	2

Table S3.11. **Models with ΔAIC < 2 from top model for all-subsets selection for hourly springtime Activity (binomial, 0 = inactive, 1 = active).** All covariates are standardised within-season to mean = 0, standard dev. = 1. A spline for hour was significant in all models, and is not shown here, nor is intercept. " Sex" represents a binomial factor, where the baseline sex is male.

Temp.	Temp.^{2}	Rainfall	Rainfall^2	Wind speed	Relative humidity	Soil temp. (10 cm)	Soil temp. (30 cm)	Soil moisture	Age	BCI	Sex	BCI:Temp.	BCI:Rainfall	BCI:Sex	ΔAIC
1.16	-	-	-	-0.604	-	-	-	-	-	-0.198	-0.215	-	-	-1.532	0
1.17	-	-	-	-0.612	-	-	-	-	0.313	-0.076	-0.192	-	-	-1.394	0.71
1.09	-	0.025	-0.156	-0.56	-	-	-	-	-	-0.175	-0.191	-	-	-1.566	0.95
1.165	-	-	-	-0.59	-	-	-0.125	-	-	-0.22	-0.239	-	-	-1.482	0.98
1.083	-	0	-0.148	-0.556	-	-	-	-	-	-0.104	-0.145	-	0.197	-1.591	1.09
1.187	-	-	-	-0.606	-	-	-	-0.195	-	-0.386	-0.373	-	-	-1.286	1.12
1.204	-	-	-	-0.615	-	-	-	-0.249	0.362	-0.284	-0.378	-	-	-1.077	1.26
1.122	-	-0.08	-	-0.573	-	-	-	-	-	-0.144	-0.177	-	0.187	-1.536	1.34
1.132	-	-0.059	-	-0.579	-	-	-	-	-	-0.221	-0.232	-	-	-1.503	1.44
1.175	-	-	-	-0.598	-	-	-0.132	-	0.322	-0.094	-0.216	-	-	-1.341	1.58
1.124	-	0.042	-0.173	-0.566	-	-	-	-0.247	-	-0.409	-0.388	-	-	-1.262	1.61
1.14	-	0.04	-0.175	-0.574	-	-	-	-0.301	0.378	-0.302	-0.394	-	-	-1.047	1.64
1.098	-	0.02	-0.154	-0.567	-	-	-	-	0.32	-0.055	-0.173	-	-	-1.422	1.65
1.09	-	-0.004	-0.147	-0.562	-	-	-	-	0.316	0.008	-0.132	-	0.193	-1.448	1.89
1.164	-	-	-	-0.604	-	-	-	-	-	-0.213	-0.216	-0.032	-	-1.531	1.96
1.141	-0.017	-	-	-0.604	-	-	-	-	-	-0.197	-0.213	-	-	-1.534	1.99

Table S3.12. **Models with ΔAIC < 2 from top model for all-subsets selection for hourly summertime Activity (binomial, 0 = inactive, 1 = active).** All covariates are standardised within-season to mean = 0, standard dev. = 1. A spline for hour was significant in all models, and is not shown here, nor is intercept. " Sex" represents a binomial factor, where the baseline sex is male.

Temp.	Temp.^{2}	Rainfall	Rainfall^2	Wind speed	Relative humidity	Soil temp. (10 cm)	Soil temp. (30 cm)	Soil moisture	Age	BCI	Sex	BCI:Temp.	BCI:Rainfall	BCI:Sex	ΔAIC
-0.025	-0.221	-	-	0.222	-0.188	-	-0.255	-	-0.213	0.048	-	-0.164	-	-	0
-0.032	-0.234	-0.065	0.106	0.208	-	-	-0.268	-	-0.216	0.045	-	-0.162	-	-	0.15
-0.019	-0.22	-	-	0.202	-	-	-0.26	-	-0.22	0.026	-	-0.16	-	-	0.3
0.03	-0.221	-	-	0.209	-0.177	-	-0.238	0.099	-0.219	0.046	-	-0.144	-	-	0.32
0.039	-0.219	-	-	0.19	-	-	-0.242	0.106	-0.225	0.025	-	-0.139	-	-	0.34
0.024	-0.233	-0.065	0.103	0.196	-	-	-0.25	0.102	-0.222	0.044	-	-0.142	-	-	0.37
0.033	-0.24	-	-	0.19	-	-	-0.238	0.138	-0.261	-	-	-	-	-	0.59
-0.034	-0.233	-0.052	0.096	0.221	-0.141	-	-0.263	-	-0.212	0.059	-	-0.165	-	-	0.95
-0.021	-0.218	-	-	0.223	-0.184	-	-0.258	-	-0.22	0.022	-0.145	-0.168	-	-	0.98
-0.034	-0.226	-	-	0.225	-0.199	-	-0.255	-	-	0.096	-	-0.163	-	-	1
-0.028	-0.231	-0.064	0.106	0.21	-	-	-0.271	-	-0.223	0.019	-0.144	-0.167	-	-	1.12
0.058	-0.208	-	-	0.188	-	-	-0.243	0.115	-0.204	0.079	-0.129	-0.157	-	-0.166	1.14
0.023	-0.252	-0.055	0.098	0.195	-	-	-0.246	0.135	-0.264	-	-	-	-	-	1.14
0.045	-0.216	-	-	0.191	-	-	-0.245	0.108	-0.232	-0.002	-0.149	-0.143	-	-	1.15
-0.014	-0.216	-	-	0.204	-	-	-0.263	-	-0.227	-0.001	-0.149	-0.164	-	-	1.17
0.035	-0.239	-	-	0.191	-	-	-0.24	0.139	-0.26	-	-0.165	-	-	-	1.2
0.028	-0.241	-	-	0.206	-0.145	-	-0.236	0.134	-0.263	-	-	-	-	-	1.2
0.036	-0.217	-	-	0.21	-0.172	-	-0.242	0.101	-0.226	0.019	-0.146	-0.148	-	-	1.24
-0.041	-0.24	-0.067	0.108	0.211	-	-	-0.27	-	-	0.091	-	-0.161	-	-	1.28
0.03	-0.229	-0.064	0.102	0.197	-	-	-0.253	0.103	-0.229	0.018	-0.145	-0.147	-	-	1.29
0.049	-0.209	-	-	0.206	-0.168	-	-0.24	0.108	-0.197	0.101	-0.126	-0.161	-	-0.164	1.33
-0.012	-0.21	-	-	0.22	-0.18	-	-0.258	-	-0.192	0.103	-0.126	-0.181	-	-0.157	1.34
0.02	-0.232	-0.053	0.094	0.208	-0.13	-	-0.246	0.097	-0.218	0.057	-	-0.146	-	-	1.35
-0.03	-0.234	-0.094	0.104	0.208	-	-	-0.266	-	-0.214	0.059	-	-0.159	0.059	-	1.35

Table S3.12 continued. **Models with ΔAIC < 2 from top model for all-subsets selection for hourly summertime Activity (binomial, 0 = inactive, 1 = active).** All covariates are standardised within-season to mean = 0, standard dev. = 1. A spline for hour was significant in all models, and is not shown here, nor is intercept. " Sex" represents a binomial factor, where the baseline sex is male.

Temp.	Temp.^{2}	Rainfall	Rainfall^2	Wind speed	Relative humidity	Soil temp. (10 cm)	Soil temp. (30 cm)	Soil moisture	Age	BCI	Sex	BCI:Temp.	BCI:Rainfall	BCI:Sex	ΔAIC
0.042	-0.221	-0.064	0.101	0.194	-	-	-0.251	0.111	-0.2	0.099	-0.126	-0.159	-	-0.165	1.35
0.015	-0.248	-	-	0.187	-	-	-0.23	0.13	-0.221	0.125	-	-	-	-	1.43
-0.006	-0.209	-	-	0.201	-	-	-0.263	-	-0.199	0.078	-0.13	-0.178	-	-0.157	1.44
-0.02	-0.223	-0.064	0.105	0.207	-	-	-0.27	-	-0.195	0.099	-0.126	-0.18	-	-0.157	1.45
-0.023	-0.224	-0.054	-	0.209	-	-	-0.265	-	-0.217	0.031	-	-0.162	-	-	1.52
0.017	-0.226	-	-	0.214	-0.191	-	-0.241	0.091	-	0.093	-	-0.145	-	-	1.58
-0.028	-0.226	-	-	0.205	-	-	-0.262	-	-	0.07	-	-0.158	-	-	1.59
0.034	-0.224	-0.052	-	0.197	-	-	-0.246	0.105	-0.224	0.031	-	-0.142	-	-	1.59
-0.027	-0.224	-0.039	-	0.225	-0.175	-	-0.258	-	-0.213	0.05	-	-0.165	-	-	1.59
0.001	-0.262	-0.061	0.102	0.192	-	-	-0.238	0.127	-0.217	0.145	-	-	-	-	1.6
0.026	-0.233	-0.092	0.101	0.196	-	-	-0.249	0.1	-0.219	0.057	-	-0.139	0.056	-	1.63
0.006	-0.251	-	-	0.204	-0.167	-	-0.227	0.125	-0.215	0.147	-	-	-	-	1.63
0.011	-0.239	-0.067	0.105	0.199	-	-	-0.253	0.094	-	0.089	-	-0.143	-	-	1.77
0.024	-0.251	-0.055	0.097	0.196	-	-	-0.248	0.136	-0.263	-	-0.166	-	-	-	1.79
0.03	-0.24	-	-	0.206	-0.144	-	-0.238	0.135	-0.262	-	-0.167	-	-	-	1.85
-0.043	-0.238	-0.053	0.097	0.225	-0.152	-	-0.264	-	-	0.106	-	-0.163	-	-	1.88
0.026	-0.225	-	-	0.194	-	-	-0.245	0.098	-	0.068	-	-0.14	-	-	1.91
0.028	-0.223	-0.039	-	0.212	-0.164	-	-0.242	0.099	-0.219	0.048	-	-0.146	-	-	1.92
-0.03	-0.23	-0.052	0.095	0.222	-0.137	-	-0.266	-	-0.219	0.033	-0.142	-0.169	-	-	1.98
-0.021	-0.216	-	-	0.224	-0.192	-	-0.258	-	-	0.179	-0.11	-0.18	-	-0.195	2

Table S3.13. **Models with ΔAIC < 2 from top model for all-subsets selection for hourly autumn Activity (binomial, 0 = inactive, 1 = active).** All covariates are standardised within-season to mean = 0, standard dev. = 1. A spline for hour was significant in all models, and is not shown here, nor is intercept.

Temp.	Temp.^{2}	Rainfall	Rainfall^2	Wind speed	Relative humidity	Soil temp. (10 cm)	Soil temp. (30 cm)	Soil moisture	Age	BCI	BCI:Temp.	BCI:Rainfall	ΔAIC
-	-	-0.255	-	-	-0.254	0.785	-	0.308	-	-	-	-	0
-	-	-0.322	0.182	-	-	0.82	-	0.237	-	-	-	-	0.14
-	-	-0.301	0.157	-	-0.221	0.835	-	0.3	-	-	-	-	0.32
-	-	-0.347	0.18	-	-	0.736	-	-	-	-	-	-	0.36
-	-	-0.272	-	-	-	0.759	-	0.234	-	-	-	-	0.48
-	-	-0.254	-	-	-0.254	0.787	-	0.311	-0.39	-	-	-	0.59
-	-	-0.296	-	-	-	0.677	-	-	-	-	-	-	0.68
-	-	-0.322	0.183	-	-	0.822	-	0.239	-0.392	-	-	-	0.72
-	-	-0.301	0.157	-	-0.221	0.837	-	0.303	-0.393	-	-	-	0.9
-	-	-0.347	0.181	-	-	0.738	-	-	-0.353	-	-	-	1
-	-	-0.272	-	-	-	0.762	-	0.237	-0.387	-	-	-	1.07
-	-	-0.295	-	-	-	0.679	-	-	-0.348	-	-	-	1.33
-	-	-0.29	-	-	-0.169	0.673	-	-	-	-	-	-	1.47
0.402	-0.368	-0.284	-	-	-	-	0.411	-	-0.554	-0.455	-0.455	0.204	1.53
-	-	-0.339	0.165	-	-0.137	0.729	-	-	-	-	-	-	1.59
-	-	-0.255	-	-	-0.254	0.785	-	0.309	-0.575	-0.331	-	-	1.68
-	-	-0.277	0.174	-0.117	-	0.837	-	0.231	-	-	-	-	1.7
-	-	-0.218	-	-0.143	-	0.785	-	0.227	-	-	-	-	1.81
-	-	-0.322	0.182	-	-	0.82	-	0.237	-0.577	-0.331	-	-	1.81
-	-	-0.295	0.171	-0.132	-	0.757	-	-	-	-	-	-	1.82
-	-	-0.235	-	-0.159	-	0.709	-	-	-	-	-	-	1.86
-	-	-0.23	-	-0.069	-0.236	0.795	-	0.299	-	-	-	-	1.86
0.401	-0.367	-0.283	-	-	-	-	0.41	-	-	-0.163	-0.453	0.201	1.92
0.527	-0.372	-0.214	-	-0.254	-	-	0.356	-	-0.558	-0.452	-0.45	0.199	1.93
-	-	-0.259	-	-	-0.257	0.799	-0.028	0.305	-	-	-	-	1.97
-	-	-0.255	-	-	-0.254	0.784	-	0.308	-	-0.027	-	-	1.99

S4 Diet analysis methods

Forty-one latrines at five setts were examined once a month from April to November 2018 for scat samples. On the first day of each sampling period, the freshest scats found at each latrine were collected, and a light layer of sand was sprinkled over the remaining samples (in order to ensure only the freshest samples were collected), taking care to switch gloves between latrines (after Kilshaw et al. 2009). Latrines were then visited for three days and up to two fresh scats collected per sett per day, again sprinkling any surplus samples. Five samples were analysed for each sett per month for dietary content (n = 25/month, total = 200). Each sample was weighed, oven-dried for 48 hours, and weighed again, then dissolved in approx. 1L of water, before being rinsed through a 0.5 mm stainless steel sieve, large enough to allow earthworm chaetae to flow through (Kaneko et al. 2006, Cleary et al. 2009). Earthworm chaetae in badger scats have been shown to correlate with the number of earthworms consumed (Kruuk and Parish 1981) and have therefore been used in various studies to quantify the role of earthworms in badger diets (e.g. Goszczyński et al. 2000, Zabala and Zuberogoitia 2003, Kaneko et al. 2006, Balestrieri et al. 2009). After Kruuk and Parish (1981), the flow-through was allowed to settle for ten minutes and 1.5 mm of sediment was drawn up from the bottom and examined in a petri dish; ten 1-cm^2 squares were then examined under 10x magnification and the number of chaetae in each were averaged. The sieved material was examined for other diet items, and these were sorted and once again oven-dried. Dry weights were recorded for each diet item, as well as for the remaining matrix. Fragments of beetle elytra were counted and summed, rounding up to whole beetles where applicable. In some cases, diet items comprised a significant enough fraction of the matrix that a subsample was taken, the diet item in question completely sorted

from it, and weighed. The fraction of the subsample matrix the diet item comprised was considered to be representative of the entire matrix.

Occurrence was decided differently for different diet items. For earthworms, a score of "2" or higher on the scale provided in Kruuk and Parish (1981) was determined to be a minimum requirement for occurrence, representing at least 6 chaetae/cm^2 in a sample's wash-through. For beetles, detection of at least one eighth of an elytron or one leg was sufficient for occurrence; for other arthropods, occurrence of some digested arthropod material that was identifiably not coleopteran qualified for occurrence. For all other categories, a non-zero weight of the given category was taken to indicate occurrence.

Frequency of occurrence (FO, occurrences/total samples) and relative frequency of occurrence (RFO, occurrences/total occurrences of all diet items) were calculated monthly for each diet item. We then summed RFO for related diet objects (e.g., hymenoptera + dermaptera = non-beetle arthropods).

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