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Effects of weather and social factors on hormone levels in the European badger (*Meles meles*)

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ABSTRACT

Animals in the wild continually experience changes in environmental and social conditions, which they respond to with behavioural, physiological and morphological adaptations related to individual phenotypic quality. During unfavourable environmental conditions, reproduction can be traded-off against self-maintenance, mediated through changes in reproductive hormone levels. Using the European badger (*Meles meles*) as a model species, we examine how testosterone in males and oestrogens in females respond to marked deviations in weather from the long-term mean (rainfall and temperature, where badger earthworm food supply is weather dependent), and to social factors (number of adult males and females per social group and total adults in the population), in relation to age, weight and head-body length. Across seasons, testosterone levels correlated postively with body weight and rainfall variability, whereas oestrone correlated positively with population density, but negatively with temperature variability. Restricting analyses to the mating season (spring), heavier males had higher testosterone levels and longer females had higher oestradiol levels. Spring oestrone levels were lower when temperatures were above normal. That we see these effects for this generally adaptive species with a broad bioclimatic niche serves to highlight that climatic effects (especially with the threat of anthropogenic climate change) on reproductive physiology warrant careful attention in a conservation context.

1. Introduction

To maximise individual fitness, animals in the wild adapt to environmental and social changes through behavioural, physiological, and morphological responses, according to their individual phenotypic quality (i.e. body size, age) (Whitten and Turner, 2009; Gesquiere et al. 2011). Stressful environmental factors, such as climate variability (i.e., temperature and rainfall outside of the normal range) can impinge on food availability and/or enhance thermoregulatory costs, which can significantly impair somatic condition and subsequent survival (Hansen, 2009; Mumby et al. 2015). In this context, reproduction requires a substantial energy investment (Wade and Schneider, 1992), and during unfavourable conditions may be compromised or traded-off to give precedence to somatic self-maintenance (Crews, 1992; Gesquiere et al. 2011). This trade-off is regulated by the endocrine system through changes in reproductive hormone levels (Wade and Schneider, 1992; Gesquiere et al. 2011).

Among male Merino sheep (*Ovis aries*; Martin et al. 1994), tufted capuchin monkeys (*Cebus apella nigritus*; Lynch et al. 2002), yellow baboons (*Papio cynocephalus*; Gesquiere et al. 2011) and olive baboons (*Papio anubis*; Sapolsky, 1986) all exhibit reduced testosterone levels under difficult foraging conditions. Similarly, among wild female mammals, environmental conditions (such as population density and seasonal resource cycles) induce stress (observed through corticosteroid hormone levels) in Asian elephants (*Elephus maximus;* Charbonnel et al. 2008) and voles (*Arvicola scherman;* Mumby et al. 2015), with negative consequences for reproductive fitness. Captive female Syrian hamsters (*Mesocricetus auratus;* Wade and Schneider, 1992) and beef cows (*Bos taurus*) exhibit lower reproductive hormone levels (oestrone and oestradiol; Rasby et al. 1990) when food/nutrition is restricted.

In seasonal habitats, climatic factors synchronize the phenology of mating and parturition so that gestation and offspring provisioning occur during the most suitable conditions, and/or so that offspring have optimal conditions in which to mature (Rawlins & Kessler, 1985; Crews,

Table 1

Coefficients (Estimate, SE, and t-value) and significance of parameters (Df, AIC, X2, and p-value) of the male model with testosterone levels across seasons as response.

Parameters	Across season testosterone model Coefficients			Across season testosterone model parameter significance			
	Estimate	SE	T	DF	AIC	X^2	P
Across season testosterone model (T)					63.227		
(Intercept)	-1.742	0.987	-1.765				
Head Body Length (HBL)	0.035	0.039	0.884	1	61.969	0.742	0.389
Age (AG)	-0.002	0.032	-0.047	1	61.227	0.000	0.998
Body weight (BW)	**0.052**	**0.027**	**1.923**	**1**	**65.271**	**4.044**	**0.044**
Total adult males in SG (NM)	0.005	0.015	0.326	1	61.245	0.018	0.893
Total adult females in SG (NF)	-0.008	0.013	-0.627	1	61.457	0.230	0.631
Total adults in population (NT)	-0.0002	0.004	-0.068	1	61.243	0.016	0.900
Avg. temperature deviation (DT)	0.023	0.035	0.657	1	61.660	0.433	0.511
Avg. rainfall deviation (DR)	**0.169**	**0.080**	**2.111**	**1**	**64.465**	**3.238**	**0.072**
Season				**3**	**87.526**	**30.299**	**< 0.001**
Season Spring	0.402	0.082	4.917				
Season Summer	0.134	0.089	1.503				
Season Winter	0.921	0.317	2.908				

Note: number of samples = 114, Avg.= Average, SG= Social group. Threshold of significance is p < 0.05. Significance based on drop 1 function

Table 2

Coefficients (Estimate, SE, and t-value) and significance of parameters (Df, AIC, X2, and p-value) of the male model with testosterone levels during the mating season in spring as response.

Parameters	Spring testosterone model Coefficients			Spring testosterone model parameter significance			
	Estimate	SE	T	DF	AIC	X^2	P
Spring testosterone model (T)				1	48.109		
(Intercept)	-2.713	2.094	-1.296	1			
Head Body Length (HBL)	0.043	0.088	0.490	1	46.275	0.166	0.684
Age (AG)	0.058	0.070	0.831	1	46.814	0.704	0.401
Body weight (BW)	**0.121**	**0.077**	**1.573**	**1**	**50.128**	**4.019**	**0.045**
Total adult males in SG (NM)	0.009	0.029	0.318	1	46.139	0.030	0.863
Total adult females in SG (NF)	0.007	0.028	0.255	1	46.279	0.170	0.680
Total adults in population (NT)	0.0009	0.006	0.157	1	46.204	0.094	0.759
Avg. temperature deviation (DT)	-0.003	0.063	-0.055	1	46.111	0.001	0.973
Avg. rainfall deviation (DR)	0.036	0.226	0.159	1	46.253	0.1432	0.705

Note: number of samples = 40, Avg.= Average, SG= Social group. Threshold of significance is p < 0.05. Significance based on drop 1 function

1992; Campbell et al. 2013). Such synchronicity has been observed in the reproductive hormone levels of Suffolk rams (*Ovis aries*; Dufour et al., 1984), white-tailed deer (*Odocoileus virginianus borealis*; Plotka et al. 1977) and the European badger (*Meles meles*; Sugianto et al. 2018; 2021a). Exposure to high ambient temperatures can also influence reproductive processes directly through heat stress (Hansen, 2009), inducing lower testosterone levels in wild boar (*Sus domesticus*; Wettemann and Desjardins, 1979) and lower oestradiol levels in Shiba goats (*Capra hircus*; Ozawa et al. 2005). Even in tropical ecosystems where changes in photoperiod are minor, subtle changes in ambient temperature provide an adaptive basis regulating reproductive cycles (McNutt et al. 2019). In this regard, climate change that destabilizes this reproductive endocrinological synchronicity or causes such extreme and stressful conditions that the endocrinology of individuals is compromised, risks potentially catastrophic population failures (Bronson, 2009; Milligan et al. 2009).

Environmental stressors interact with social factors (i.e., mate availability, intra-specific competition for mates and/or resources) and also affect reproductive hormone levels significantly (Strier et al. 1999). In rhesus monkeys (*Macaca mulatta*), the presence of females is necessary to stimulate elevated testosterone levels in males (Gordon et al. 1978). Similarly, testosterone levels in male gray-cheeked mangabeys (*Lophocebus albigena*) increase with the number of receptive females present, reflecting that mating investment is tied to perceived opportunities for mating success (Arlet et al. 2011). Competition for resources also elevates testosterone levels, linked to increased male aggression in antagonistic interactions (Cristóbal-Azkarate et al., 2006; Arlet et al. 2011). In contrast, intra-female reproductive suppression can impair the endocinological performance of subordinate rivals (Montgomery et al.

2018), which is central to reproductive despotism among various group-living carnivores (Creel and Creel, 1991) such as meerkats (*Suricata surciata*) (O'Riain et al. 2000). Within this framework of extrinsic stressors, intrinsic factors such as age, body size, disease status and idiopathic glucocorticoid responses can then subsequently modify individual endocrinological responses (Bronson, 1989).

Understanding how climatic and social factors can affect reproduction is particularly pertinent for the European badger (*Meles meles*; hereafter 'badger'). Badgers are polygynandrous and promiscuous (Dugdale et al. 2007), but without any clear mating hierarchy (Hewitt et al. 2009), leading to opportunistic mating related to contact rates (Annavi et al. 2014). Furthermore, their mating season can be extended, due to ongoing conception during delayed implantation in lower density populations (Corner et al. 2015; Sugianto et al. 2021a). This prolonged opportunity for multiple mating (Dugdale et al. 2011) can impact male body-condition (Buesching et al. 2009; Bright Ross et al. 2021). Woodroffe and Macdonald (1995a) reported lower female breeding success in denser social groups, linked to resource competition and social status. Moreover, Bright Ross et al. (2021) found that reproductive success in female badgers increased linearly with autumn body-condition indices (BCIs) and that consistently fatter badgers had higher lifetime reproductive success. Maintaining body condition above a threshold was key to badger survival (reflecting a nonlinear relationship), especially when temperatures varied more between seasons (requiring greater tactical foraging and BCI adjustments) and when there was excessive rainfall (causing thermo-regulative stress). This relates to badger diet, which, in some parts of the UK (such as Wytham Woods, Oxfordshire and other regions in the south and west of England), includes a high proportion of earthworms (*Lumbricus terrestris*), and thus badger bodyweight is
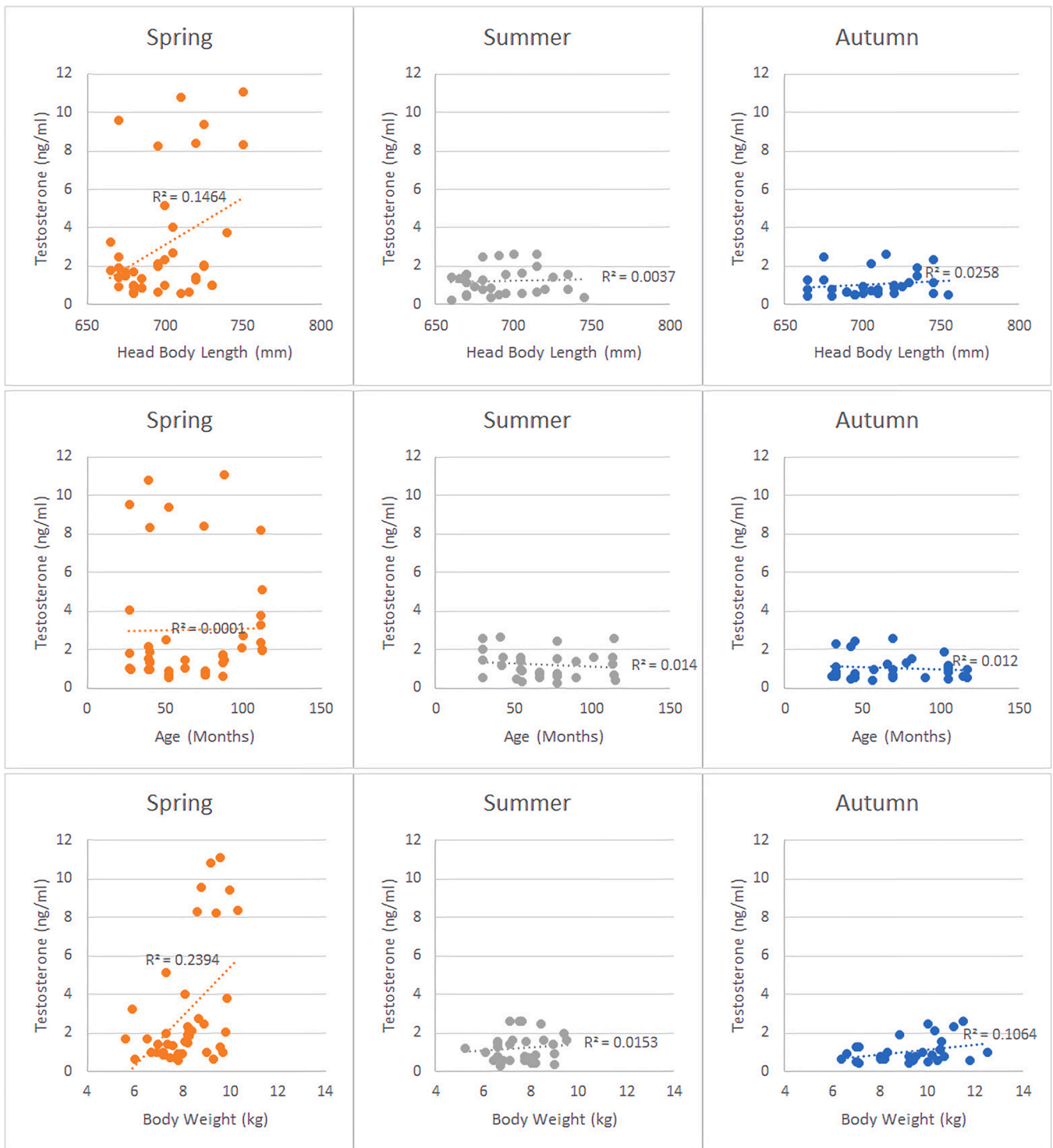
Fig. 1. Testosterone in males across seasons for phenotypical parameters (head body length, age and weight).

substantially a function of suitable climatic conditions that promote earthworm abundance at the soil surface (see Newman et al. 2017). Those factors affecting badger reproductive success and survival rates also have applied relevance because of efforts to control their populations, linked to the role badgers play as a wildlife host of *Mycobacterium bovis* sustaining bovine tuberculosis in cattle herds within the British Isles (Carter et al. 2007). Indeed, specific attention has been given to fertility control to reduce badger numbers (Swinton et al. 1997).

In this specific context, as well as in the general context of ongoing climate change (Fuller et al. 2020), we examine how male testosterone

and female oestrogens respond to weather (rainfall and temperature) and social factors (number of male and female adult badgers per social group and total adult badgers in the population), as a function of an individual's age, weight and head-body length. We hypothesize that in conditions that are not ideal (such as unfavourable weather conditions or high social competition), reproduction may be negatively impacted (to differing degrees depending on an individual's phenotype) and can be observed through hormonal measures. We benefit from established links between badger population dynamics and weather (see Newman et al. 2017) and from recent advances in the understanding of badger
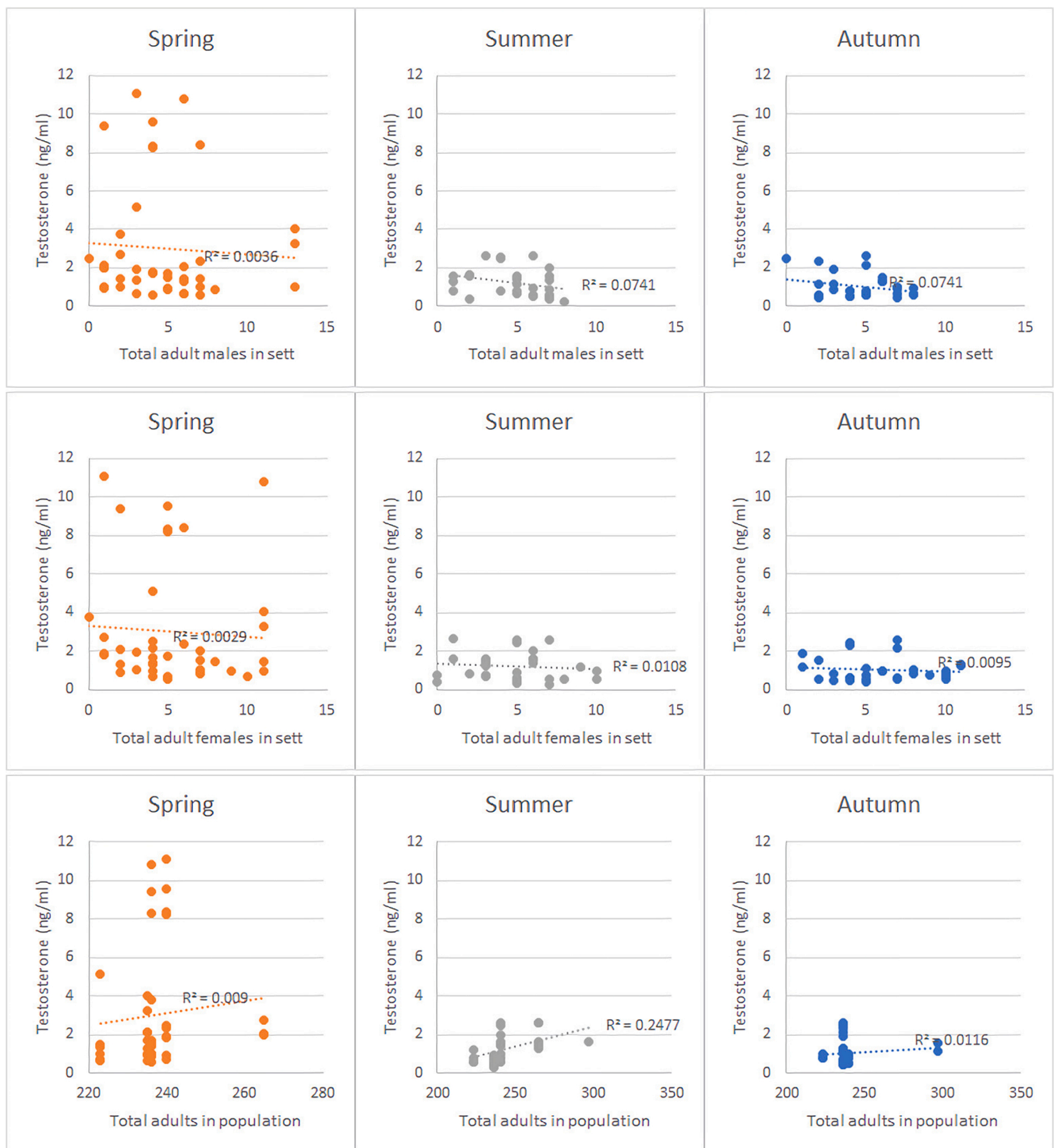
Fig. 2. Testosterone in males across seasons for social parameters (total adult males, total adult females and total adults).

reproductive physiology (Sugianto et al. 2019a,b).

2. Materials and methods

2.1. Badger trapping and data collection

Data were collected from a high-density badger population in Wytham Woods, Oxfordshire, UK (51°46:26 N, 1°19:19 W; for details see Macdonald et al. 2015) between 1995 and 2016, as part of a long-term research project. Following the methodology described in

Sugianto et al. 2019c, traps baited with peanuts were checked the next day between 6.30 and 8.00 am and captured animals were transferred to holding cages and transported to a central field station before being sedated with 0.2 ml ketamine hydrochloride / kg body weight via intramuscular (quadriceps) injection. A typical procedure from initial sedation to completion of data collection and handling required 10–15 min per badger and processing of all captured badgers was typically completed before noon. After processing, badgers were given 3 h (from the last procedure) to fully recover from sedation in a dark, quite recovery room, before being returned to their setts of capture. Badgers

Fig. 3. Testosterone in males across seasons for weather parameters (average temperature and rainfall deviation).

Table 3

Coefficients (Estimate, SE, and t-value) and significance of parameters (Df, AIC, X2, and p-value) of the female model with oestrone levels across seasons as response.

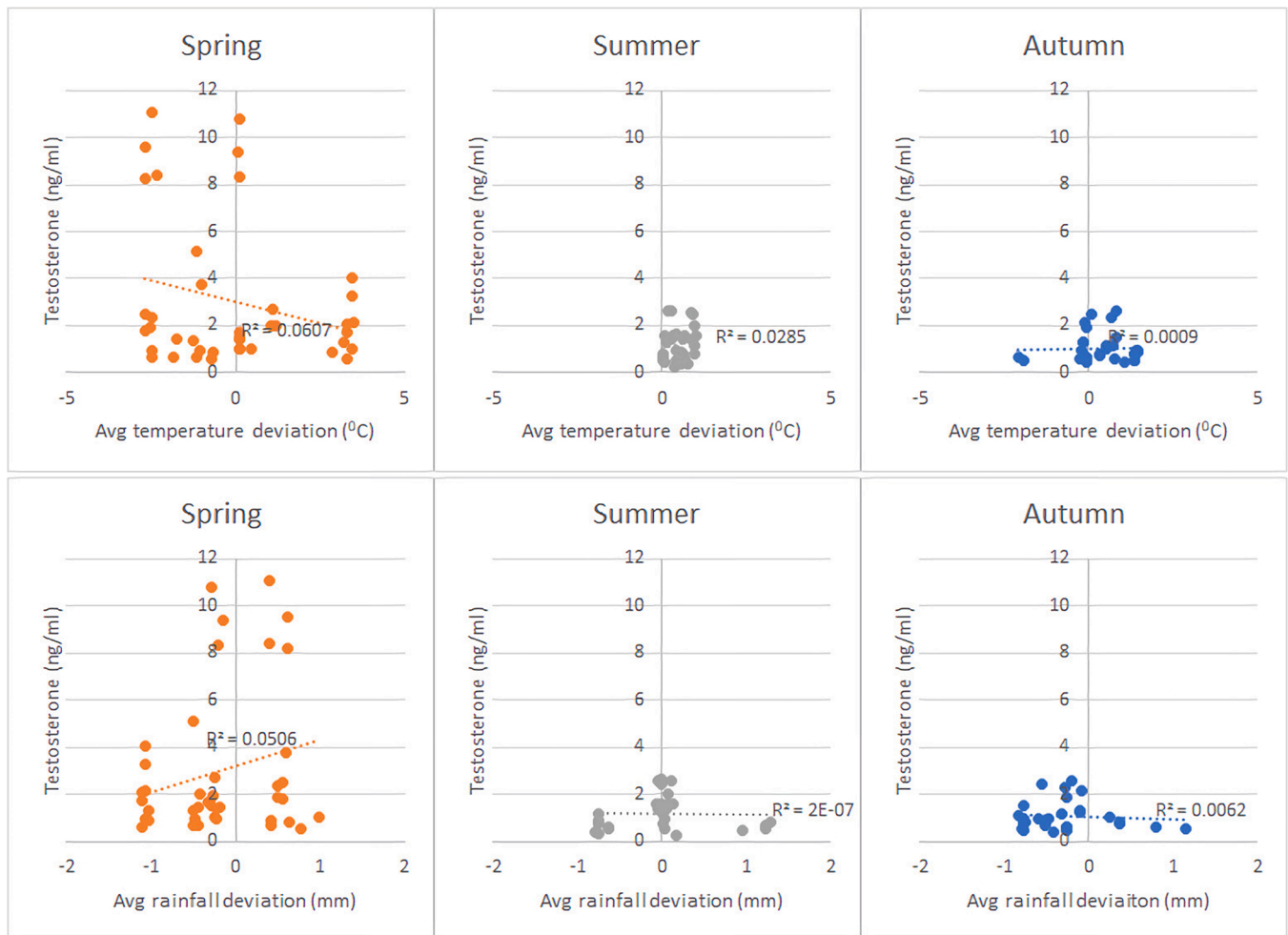| Parameters	Across season oestrone model Coefficients			Across season oestrone model parameter significance			
	Estimate	SE	T	DF	AIC	X^2	P
Across season oestrone model (E1)					18.665		
(Intercept)	0.089	0.860	0.103				
Head Body Length (HBL)	-0.013	0.029	-0.449	1	16.889	0.224	0.636
Age (AG)	0.034	0.024	1.399	1	18.825	2.160	0.142
Body Weight (BW)	0.015	0.024	0.641	1	17.122	0.458	0.499
Total adult males in SG (NM)	0.0003	0.014	0.023	1	16.666	0.001	0.981
Total adult females in SG (NF)	0.012	0.010	1.136	1	18.093	1.428	0.232
Total adults in population (NT)	**0.003**	**0.002**	**1.766**	**1**	**20.089**	**3.424**	**0.064**
Avg. temperature deviation (DT)	**-0.042**	**0.024**	**-1.736**	**1**	**19.974**	**3.309**	**0.069**
Avg. rainfall deviation (DR)	-0.045	0.048	-0.929	1	17.622	0.957	0.328
Season				**3**	**61.674**	**49.009**	**< 0.001**
Season Spring	-0.089	0.083	-1.081				
Season Summer	-0.369	0.075	-4.924				
Season Winter	-1.287	0.271	-4.752				

Note: number of samples = 117, Avg.= Average, SG= Social group. Threshold of significance is p < 0.05. Significance based on drop 1 function

were trapped 3–4 times annually: (1) in *spring* (May/June) at the end of the main mating period, (2) in *summer* (August/September) during the second mating peak previously reported in other high-density badger populations (Cresswell et al. 1992; Page et al. 1994; Carpenter et al. 2005), (3) in *autumn* (October/November) during reproductive quiescence, and (4) in winter (December/January) when badgers implant blastocysts initiating gestation (Sugianto et a. 2021a). Badgers have a

post-partum oestrus and induced ovulation (Macdonald and Newman, 2017), and thus trapping was suspended during the actual mating season (late January – end of April) to preclude capturing females late in gestation or with dependent neonates. Upon first capture, typically as cubs, all badgers received a permanent unique tattoo allowing reliable aging (AG) and individual identification (ID) (see Bright Ross et al. 2020). All animals included in this study were adults (older than 2 years;

Table 4

Coefficients (Estimate, SE, and t-value) and significance of parameters (Df, AIC, X2, and p-value) of the female model with oestrone levels during the mating season in spring as response.

Parameters	Spring oestrone model Coefficients				Spring oestrone model parameter significance		
	Estimate	SE	T	DF	AIC	X^2	P
Spring oestrone model (E1)					7.702		
(Intercept)	-0.659	1.241	-0.531				
Head Body Length (HBL)	0.023	0.041	0.560	1	6.079	0.377	0.539
Age (AG)	0.024	0.040	0.602	1	6.139	0.437	0.509
Body Weight (BW)	-0.041	0.048	-0.868	1	6.606	0.904	0.342
Total adult males in SG (NM)	0.024	0.021	1.173	1	7.341	1.639	0.200
Total adult females in SG (NF)	0.005	0.016	0.296	1	5.808	0.106	0.745
Total adults in population (NT)	0.003	0.003	1.093	1	7.128	1.425	0.233
Avg. temperature deviation (DT)	**-0.069**	**0.030**	**-2.283**	**1**	**11.650**	**5.948**	**0.015**
Avg. rainfall deviation (DR)	-0.055	0.084	-0.652	1	6.213	0.511	0.475

Note: Number of samples = 33, Avg.= Average, SG= Social group. Threshold of significance is p < 0.05. Significance based on drop 1 function

Sugianto et al. 2019b) below 10 years of age (to exclude senescent individuals; Sugianto et al. 2020). Badger capture was licensed under the Badger Act (1992) and all handling procedures licensed under the Animals (Scientific Procedures) Act (1986).

2.2. Social group parameters

Badgers make frequent temporary visits between groups (Macdonald et al. 2008), and so the primary social group of residence for each individual was assigned annually according to rules given in Sugianto et al. (2019a). The annual total number of adult male (NM) and female (NF) badgers per social group, as well as the total adult population (NT) were calculated using minimum number alive estimates (following Macdonald et al. 2009).

2.3. Somatic metrics

Two somatic parameters were used: head-body length (HBL, in mm), which provides a stable metric, independent of environmental factors, and body weight (BW, in kg), which fluctuates with season, food supply, and energy expenditure (Bright Ross et al. 2021). HBL was measured from the snout tip to the sacrum base to the nearest 5 mm, with the sedated and relaxed badger laid dorsally. BW was measured to the nearest 100 g using electronic scales.

2.4. Weather data

Daily weather data, from 1987 to 2016 inclusive, were obtained from the Radcliffe Meteorological Station (https://www.geog.ox.ac.uk/research/climate/rms/), situated 6 km from the field site. For each badger capture event, daily weather data over the prior 70 days were compared to the long-term mean (1987–2016) to produce a daily deviation score, following Nouvellet et al. (2013; see also Byrne et al., 2015). The 70 day period represents the immediate weather condition that an individual has cumulatively experienced up to the point of capture (since the effect of daily weather may not be immediately reflected physiologically, Nouvellet et al. 2013). The daily deviation score over these 70 days was then averaged to produce mean temperature deviation (DT) and mean rainfall deviation (DR), where positive values refer to conditions warmer/ wetter than expected. The long term mean provides a base point to which we assume the badgers have adapted to and the deviations relative to this long term mean indicates how extreme the immediate weather being experienced is.

2.5. Blood sampling and hormone assays

Blood samples were collected for endocrinological analyses via jugular venipuncture into K2-EDTA (ethylene diamine tetraacetic acid) vaccutainer tubes (Becton-Dickinson). Blood samples were centrifuged within 30 min of sampling at 10 °C for 10 min under 2500 rpm. Plasma was transferred into Eppendorf tubes and frozen at − 20 °C immediately (Sugianto et al. 2018). Sampling times were standardized to account for circadian variation in hormonal profiles (Buesching et al. 2009; Sugianto et al. 2021b). Sex steroid titres were analysed using Enzyme-immunoassays (EIA), measuring testosterone level (T) in males (n = 114) and oestrone (E1, n = 117) and oestradiol (E2, n = 18) levels in females. Oestrone and testosterone levels were analysed at the Chester Zoo Endocrinology Laboratory, UK (see Sugianto et al. 2018; 2021a); while oestradiol was analysed at the Endocrinology Laboratory at the German Primate Centre, Germany (see Sugianto et al. 2021a). The intra-assay coefficient of variation (CV) for oestrone (calculated as the average CV across all individuals and sample duplicates), relative to high and low-value quality controls were 8.21% (high) and 6.05% (low), and inter-assay variation (repeated measurements of high and low-value quality controls across plates) was 13.96% (high) and 13.62% (low) respectively. For oestradiol, inter-assay CVs were 4.5% (high) and 7.4% (low), and the intra-assay CV was 6.2%. For testosterone intra-assay CVs were14.69% (high) and 6.18% (low), and inter-assay CVs were 9.15% (high) and 5.23% (low).

2.6. Statistical analyses

A linear mixed model was used to assess sex-steroid levels (testosterone [T, n = 114] and oestrone [E1, n = 117]) in relation to headbody length (HBL), age (AG), body weight (BW), number of adult males in social group (NM), number of adult females in social group (NF), total adults in population (NT), mean temperature deviation (DT), and mean rainfall deviation (DR), with season as a covariate. Year (when badger was captured) and ID (Tattoo number) were assigned as random factors. A drop1 function was used to determine which factors influenced sex-steroid levels in the mixed models significantly. Oestrone data from pregnant females (identified via ultrasound) were excluded from this cross-season analyses, given that pregnant females have higher oestrone levels than non-pregnant individuals due to oestrone's function in sustaining implanted blastocysts, thus not comparable with non-pregnant individuals (Sugianto et al. 2021a). Oestradiol (E2, n = 18) was not modelled in this way because levels are only high in spring when E2 regulates mating behaviour (Sugianto et al. 2021a), and thus is not comparable with other seasons.

We then repeated the same analytical procedure for Testosterone (T, n = 40) and Oestrone (E1, n = 33) with data restricted to spring only to assess effects restricted to the main mating season (Sugianto et al. 2018; 2021a), and also modelled oestradiol levels (E2) during the spring mating period. In this spring only analysis, all oestradiol levels (E2) were independent data points, and therefore a linear model was applied using the same parameters as in the testosterone (T) and oestrone (E1) models.
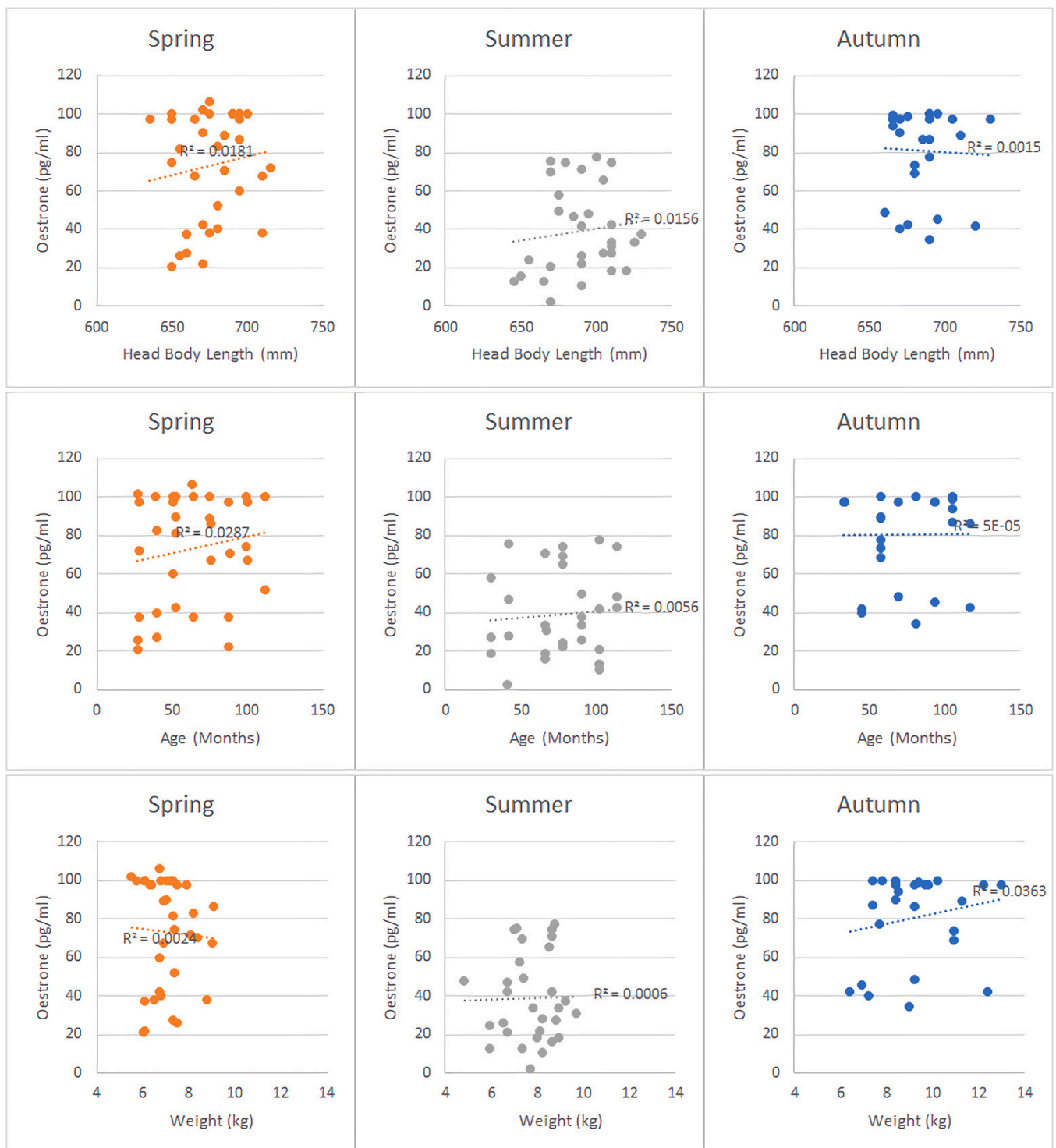
Fig. 4. Oestrone in females across seasons for phenotypical parameters (head body length, age and weight).

Before models were run, a Pearson correlation test was used to test for correlation between continuous parameters. All model parameters were independent. Patterns of residuals, normality, and mean variance relationship for each model were checked using diagnostic plots in R. All statistical analyses were performed using RStudio (0.99.896; RStudio, 2015) and R (R-3.2.4; R Core Team, 2013).

3. Results

3.1. Males

Across all seasons, only body weight (BW) significantly and positively affected testosterone levels in males; although a non-significant positive trend (p = 0.072) was also noted for mean rainfall deviation (DR) (Table 1). Limited to the spring mating season, heavier males had significantly higher testosterone levels (Table 2). No social factors were significant in either analysis. Figs. 1–3 provide visualization of the data
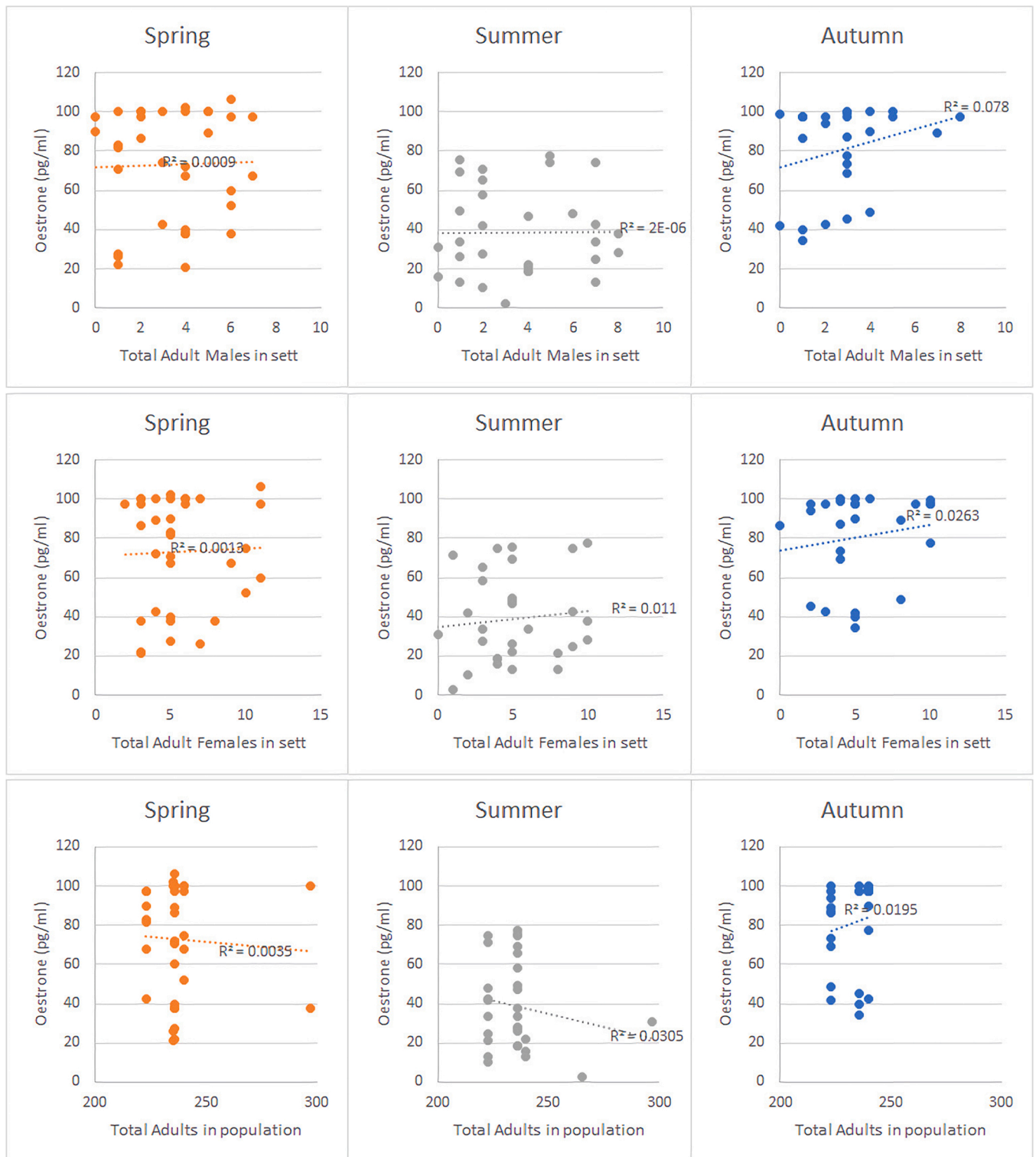
Fig. 5. Oestrone in females across seasons for social parameters (total adult males, total adult females and total adults).

to accompany the analysis results.

3.2. Females

3.2.1. Oestrone

Across all seasons, female oestrone levels showed non-significant trends with both total adults in population (NT, positive correlation, p = 0.064) and average temperature deviation (DT, negative correlation, p = 0.069) (Table 3). Limiting analyses to the spring mating season revealed a significant effect of average temperature deviation, such that higher temperatures were associated with lower oestrone levels (Table 4). No social factors were significant in either analysis. Figs. 4–6 provide visualization of the data used in the analysis.

3.2.2. Oestradiol

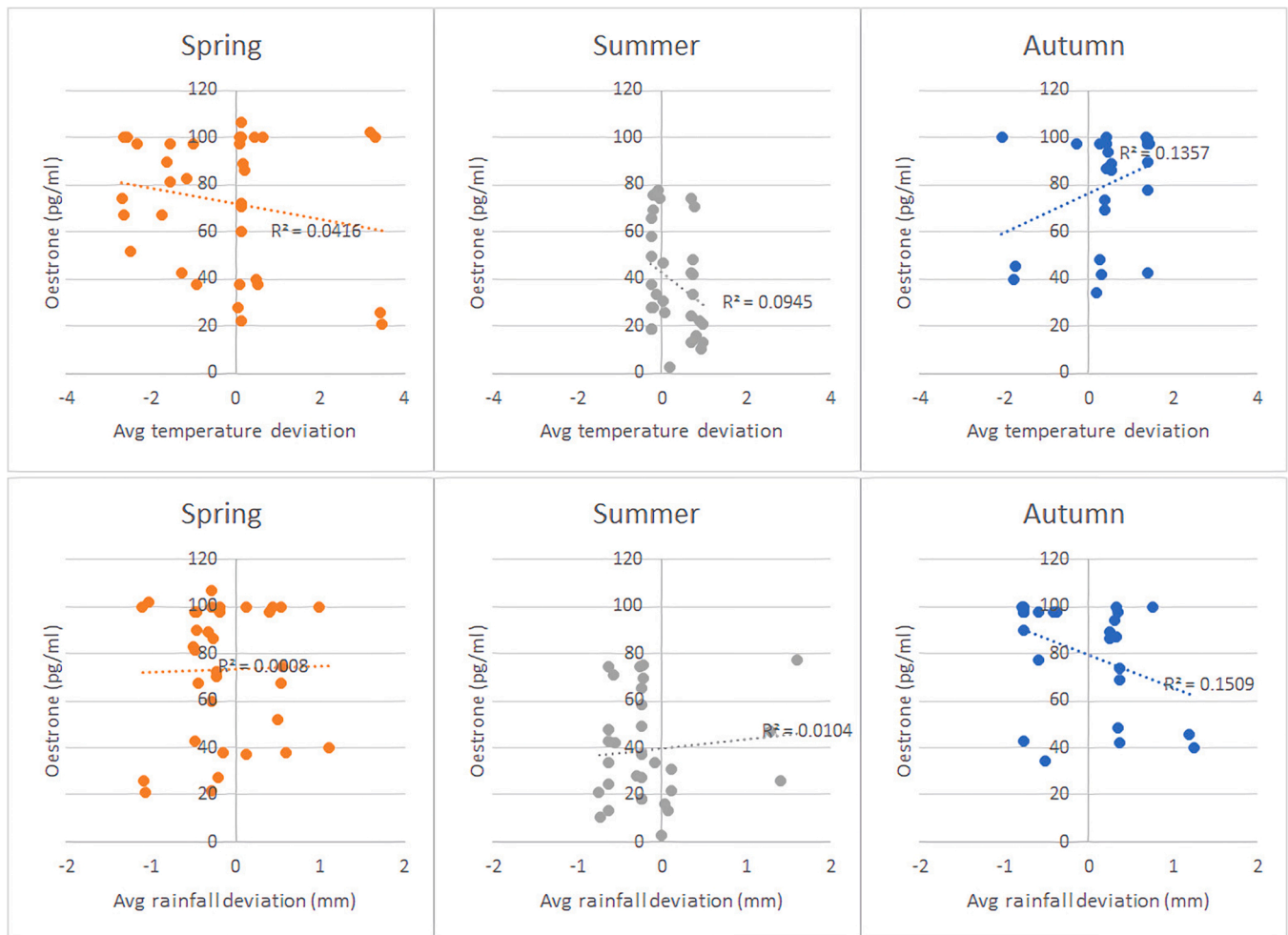Oestradiol (E2) levels in spring correlated positively and

Fig. 6. Oestrone in females across seasons for weather parameters (average temperature and rainfall deviation).

Table 5
Coefficients (Estimate, SE, and t-value) and significance of parameters (Df, AIC, X2, and p-value) of the female model with oestradiol levels during the mating season in spring as response.

Parameters	Spring oestradiol model Coefficients			Spring oestradiol model parameter significance				
	Estimate	SE	T	DF	Sum Sq	Mean Sq	F	P
Spring oestradiol model (E2)								
(Intercept)	-8.953	11.683	-0.766					
Head Body Length	**0.127**	**0.174**	**0.732**	**1**	**0.953**	**0.953**	**5.435**	**0.045**
Age (AG)	-0.034	0.124	-0.276	1	0.037	0.037	0.208	0.659
Body weight (BW)	0.010	0.206	0.049	1	0.016	0.016	0.094	0.766
Total adult males in SG (NM)	0.034	0.059	0.579	1	0.234	0.234	1.334	0.278
Total adult females in SG (NF)	-0.026	0.061	-0.426	1	0.012	0.012	0.071	0.796
Total adults in population (NT)	**0.044**	**0.097**	**0.450**	**1**	**0.613**	**0.613**	**3.499**	**0.094**
Avg. temperature deviation (DT)	0.119	1.488	0.080	1	0.0006	0.001	0.003	0.957
Avg. rainfall deviation (DR)	0.781	1.016	0.769	1	0.104	0.104	0.591	0.462
Residuals				9	1.578	0.175		

Note: Number of samples 18, Avg.= Average, SG= Social group. Threshold of significance is p < 0.05. Significance based on drop 1 function

significantly only with the individual's head body length, with a marginal positive trend (p = 0.094) related to the total number of adults in the population (NT) (Table 5). Fig. 7 provides visualisation of the data.

4. Discussion

The effects of environmental and somatic factors on circulating sex-steroid levels in male and female badgers in Wytham Woods were mixed. Heavier males had higher testosterone levels. There was also a weaker positive effect of rainfall deviation on testosterone levels, possibly linked to more extreme rainfall promoting earthworm food availability, with positive benefits for body weight (Newman et al. 2017). Male badgers tend to lose body condition through the mating season (Woodroffe and Macdonald 1995b; Buesching et al. 2009) and thus those able to retain weight may be able to invest more energy into testosterone production. Similar interactions between rainfall, food availability, subsequent body condition and testosterone levels have been noted for males in other mammal species, such as baboons (*Papio*
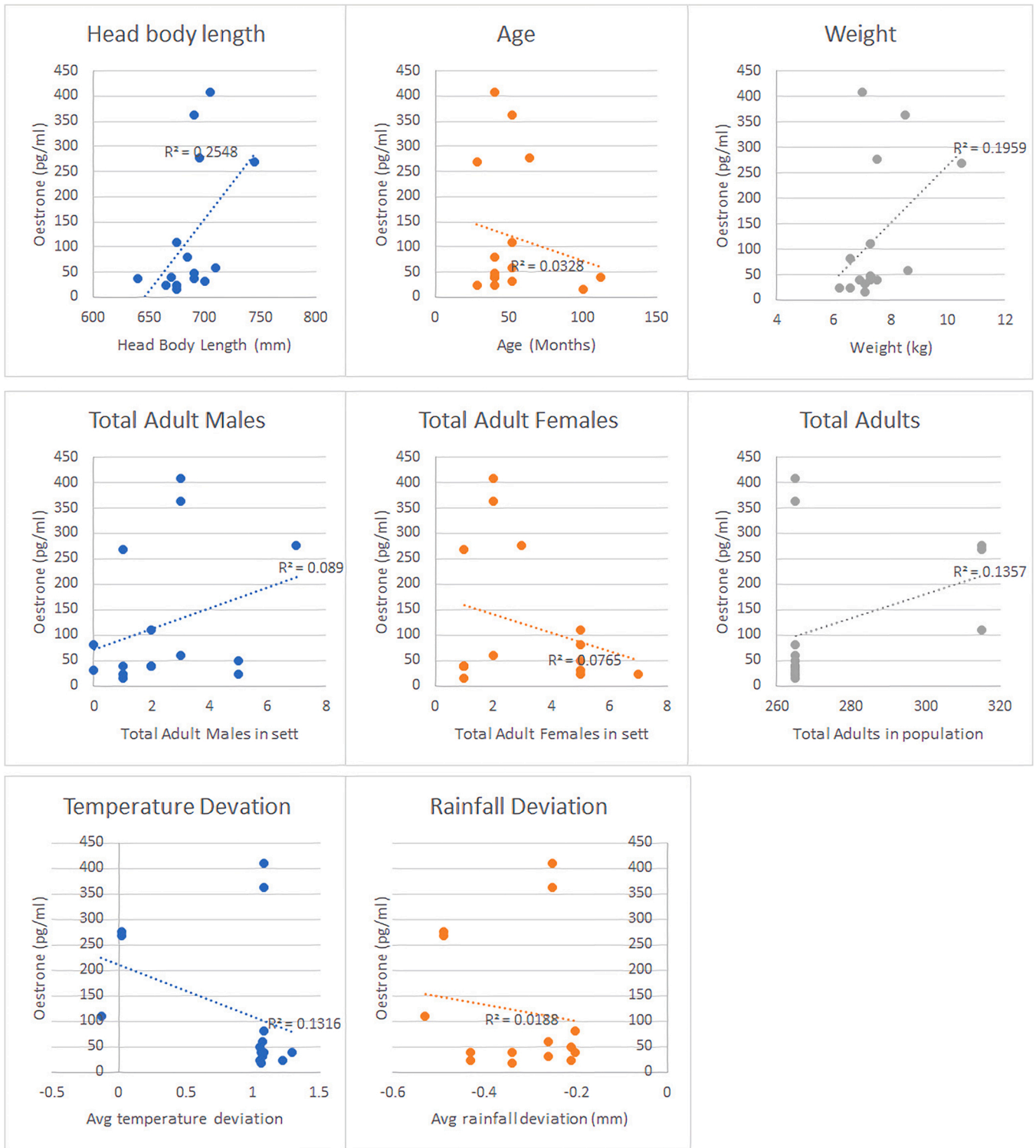
Fig. 7. Oestradiol in females in spring for all parameters.

cynocephalus; Gesquiere et al. 2012), white rhinoceros (*Ceratotherium simum simum*; Kretzschmar et al. 2004), tufted capuchin monkeys (*Cebus apella nigritus*; Lynch et al. 2002), European rabbits (*Oryctolagus cuniculus*; Monclús et al., 2006; Cabezas et al. 2007) and orangutans (*Pongo sp.*; Knott, 2005). Understanding how weather may affect testosterone secretion, mediated by foraging success acting on body weight, is important because this will affect male reproductive behaviour and fertility (and subsequent breeding success) through spermatogenesis, sperm quality and quantity (Minter and DeLiberto, 2008).

In females, lower oestrone levels were associated with higher temperature deviation, especially in the spring mating season, but unaffected by rainfall deviation (thus differing from males). Oestrone is secreted by the ovaries and is necessary to maintain a suitable uterine environment for pre-implanted blastocyst survival (and thus provides a proxy for blastocyst presence; Sugianto et al. 2021a). Oestrone then prepares the uterus for implantation and extends the life-span of the corpora lutea (CL) (Heap et al. 1975; Heap et al. 1979), (see Sugianto et al. 2018). High temperatures may cause heat stress and exacerbate

thermoregulatory costs (Gesquiere et al. 2012; Bright Ross et al. 2021), where thermoregulatory stress can slow follicle maturation rate, reduce ovulation frequency, and raise embryo mortality rate (Hansen, 2009). These effects can alter hormone secretion (Roth et al. 2000; Ozawa et al. 2005); for example, heat stress causes reduced plasma oestradiol and Luteinizing Hormone (LH) concentrations in goats (*Capra aegagrus hircus*), delaying ovulation (Ozawa et al. 2005). In black rats (*Rattus rattus*) heat stress reduces oestradiol levels in folicullar fluids, and reduces gonadotropin reception in granulosa cells (Shimizu et al. 2005). Even pre-implanted blastocysts can be susceptible to maternal heat stress (see Ealy et al. 1993; Matsuzuka et al. 2005).

In contrast to males, the only somatic parameter that significantly affected female sex-steroid levels was head body length (and not body weight) where longer females produced more oestradiol during the mating season. This is likely because females benefit more from longer-term investments in reproduction, such as skeletal size, compared to males (Gesquiere et al. 2012). Woodroffe and Macdonald (1995a,b) found that body size gives female badgers an advantage in terms of breeding success, possibly due to being more competitive during periods of food scarcity – also manifesting in other female mammals (Stockley and Bro-Jørgensen, 2011). In contrast, females may lose body-weight (but not length) quickly during gestation and lactation, due to somatic trade-offs with reproductive investment (Glazier, 1999). This may also explain why reproductive hormone levels in female badgers are less susceptible to changes in rainfall which generate variability in food availability.

The only group size effect on reproductive hormones was an indicative but non-significant trend for females in larger groups to have higher oestrone and oestradiol levels. Social stimuli caused by conspecific presence may promote endocrine changes in individuals, possibly through mate availability or resource competition factors (Gonzalez et al. 1988; Lott, 1991; Kotrschal et al. 2000). When females encounter a larger number of potential mates, this can result in increased oestradiol levels functioning to promote fertilization. For instance, male presence promotes oestrogen secretion and ovulation in American mink (*Neogale vison*, Amstislavsky and Ternovskaya, 2000). Badgers are highly promiscuous and females tend to mate with males according to encounter rate, including with males from outside their own social group (Annavi et al. 2014). Alternatively, female fertility may be affected by density dependent competition (see Albon et al., 1983), causing females to invest more in reproduction. In support of this proposition, longer females tended to have higher oestradiol levels; that is, being larger with higher hormone levels might reflect a benefit for female breeding success in denser groups, where female badgers can be subject to intra-sexual reproductive suppression (Woodroffe and Macdonald 1995a; Dugdale et al., 2008). This may reflect the different dimensions of crowding stress versus weather-driven resource limitation for badgers, where Macdonald et al. (2004) reported that the socio-spatial redistribution for this same population in the 1990 s, which reduced functional group sizes, allowed more females the opportunity to breed successfully, resulting in higher natality (Macdonald et al. 2009; Bright Ross et al. 2020). Furthermore, George et al. (2014) found that cortisol levels were higher in adult badgers with poor body condition, especially in spring, where decreased body weight causes 'energetic stress' (Pérez-Rodríguez et al., 2006; Cabezas et al. 2007) and glucocorticoids tend to suppress the secretion of reproductive hormones (Geraghty and Kaufer, 2015; Whirledge and Cidlowski, 2010).

Rapid anthropogenic climate change (Sih et al. 2011) threatens many species with extinction (Urban, 2015). It is thus crucial to understand better the extent to which those adaptive behaviours (Noonan et al. 2014), life-history strategies (Bright Ross et al. 2020), physiological responses (Bilham et al. 2018) and genetic adaptations (van Lieshout et al. 2021) that badgers and other species have evolved may cope with accelerated rates of climate change, and to anticipate the point at which these mechanisms may be overwhelmed (see Noonan et al. 2018). Animals are exposed to a variety of environmental changes that may be

unfavorable (McEwen and Wingfield, 2003; Wingfield, 2004), and individuals may self-regulate their hormonal levels according to their concurrent physical state to maximize fitness. If more extreme weather impairs sex hormone secretion and thus impedes reproduction, either directly or by exerting selection for body-size benefits (Bright Ross et al. 2021), then clearly this risks population decline. Badgers can buffer inclement and extreme weather conditions somewhat by remaining underground in their burrows, termed 'setts' (Tsunoda et al. 2018; Noonan et al. 2014) and by manipulating their body-fat reserves (Newman et al. 2011; Bright Ross et al. 2021). That we see these effects for this generally adaptive species with a broad bioclimatic niche (Johnson et al. 2002; Silva et al. 2017), serves to highlight that climatic effects on reproductive physiology warrant careful attention in a conservation context (Fuller et al. 2010; Butt and Gallagher, 2018).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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