



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

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ABSTRACT

Environmental change often causes decreased food availability and/or increased foraging costs, putting wild animals at risk of starvation. Body-fat reserves can enable individuals to resist (buffer) periods of weather-driven food scarcity, improving their chances of survival and subsequent reproductive success. This capacity, however, is constrained by life-history factors and fixed long-term differences between individuals. Here, we use 29 years of data from a population of wild European badgers (*Meles meles*) to test how weather and population density affect individual body condition indices (BCIs), how BCI mediates survival rate and reproductive success, and whether long-term BCI phenotypes (fat vs. thin) provide life-history advantages. Maintaining body condition above a certain threshold was key to survival (reflecting a nonlinear relationship), especially when temperatures varied more between seasons (requiring greater tactical foraging and BCI adjustments) and following excessive rainfall (causing thermoregulative stress). BCI also affected survival more strongly in older individuals. Female reproductive success increased linearly with autumn BCI, and consistently fatter badgers (of both sexes) had higher lifetime reproductive success; however, substantial intra-individual body-condition variation remained after accounting for weather and individual factors, and 84% of individuals varied BCI substantially from year to year. Modelling BCI responses according to projected climate change through 2080 (Emissions Scenario RCP 8.5) revealed that even strong warming (as one-off events) would produce < 5% survival probability reductions, pushing few individuals below the BCI risk threshold. We thus demonstrate that life-history factors and individual body-condition tactics are fundamental to understanding population resilience under anthropogenic climate change.

1. Introduction

Environmental conditions affect food availability, food requirements, and foraging costs for wild animals [31,36]. Weather and primary productivity vary seasonally (and less predictably within seasons), and so longer-lived animals must adapt their energy budgeting accordingly [45], with many evolving body-fat reserves (“fasting tolerance”: [60]) and/or excess food caching [98] to resist or “buffer” [119] periods of food scarcity. Consequently, body-fat reserves generally provide a survival and/or reproductive advantage [68,69], especially among mammals (flight constrains somatic stores in birds: [58]). However, complicating matters, an individual's risk of incurring a net negative energy and thus losing body condition (increasing its risk of starvation) varies with life-history factors, such as sex, reproductive status (e.g., lactating

females, rutting males), and age class (e.g., young or geriatric individuals: [120]). Individuals in the same life-history stage can have different metabolic requirements relating to both transient factors (e.g., diet-derived gut microbiome: [59]) and fixed differences stemming from underlying physiology [46,67,114]. Furthermore, fat stores not only buffer food insecurity, but are also important for thermoregulation [39,40,43], and are thus vital to species engaging in hibernation/torpor [10,81]. These factors lead to a spectrum of individual energy allocation tactics (i.e., exhibiting different equilibria between investing in reproduction and prioritising survival through the conservation of body condition) often coexisting within populations experiencing the same environmental conditions [34].

Body-condition indices (BCIs, measuring body mass relative to skeletal size) are frequently used as surrogates of somatic fitness [5,54]; nev-

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ertheless, the relationship between fat stores and fitness, and particularly how this differs between individuals within a population, remains largely unexplored [22,36,38]. Importantly, any BCI metric has limited relevance if it relates poorly to lipid stores [84] or if these correlate weakly with fitness [113]. Fatter individuals can also suffer nutritional deficiencies [72], impaired physiology [85], and/or poor reproductive success [8], making nonlinear relationships between body condition and fitness metrics relevant when BCI varies substantially within wild populations.

Little is known about what selective advantages different individual body-fat storage tactics may have across populations subject to environmental stochasticity [108], and how sustained inter-individual differences in body-condition variability could benefit population resilience to rapid environmental change [91]. Here, we use 29 years of detailed demographic data from a European badger (*Meles meles* L., hereafter “badger”) population to investigate how prevailing weather conditions influence the interaction between body condition, survival probability, and reproductive success. Badgers provide a versatile model species for examining body-condition effects because of a) their dietary reliance on earthworms (at least in England: [53]), which surface only under appropriate weather conditions [123] their reliance on fat storage for withstanding seasonal fluctuations in energy constraints [66,71], and c) substantial life-history mediated constraints on optimal individual energy budgeting (see Appendix S1).

We examine how badger body condition (contrasting BCI with categorical fat score metrics) affects survival probability and reproductive success in relation to weather conditions, life-history factors, and population density. Specifically, we test:

- 1) Whether body condition provides a linear benefit to survival and female reproduction probability (where male reproductive success ultimately relies almost entirely on female success); or, alternatively,
- 2) If there is some minimum body-condition threshold (see [42,109]) above which individuals can invest energy tactically. In this case, body condition would only affect survival and reproduction (the latter is only tested in females; see Methods) below such a threshold.
- 3) Whether any threshold effects (*sensu* test 2) only become evident under energetically stressful conditions, either due to a) life-history (old age or post-reproductive females) or b) poor weather or social (high-density) population conditions.
- 4) If substantial inter-individual body-condition variation remains after accounting for weather and life-history energetic context, reflecting “fixed” heterogeneity (variation arising from sustained differences between individuals: [35,76]) rather than “dynamic” heterogeneity arising from changeable energy availability and requirements [108].
- 5) Whether any observed inter-individual body-condition variation takes the form of consistently higher or lower lifetime body-condition phenotypes, and if this form of fixed heterogeneity correlates with lifetime reproductive metrics.

Finally, in the context of resilience to anthropogenic climate change, we model how these relationships between weather, BCI, and survival would unfold in relation to climate projections for our study site under a severe carbon emissions scenario between 2021 and 2040 and 2061 and 2080.

2. Materials and methods

Fig. 1 provides an overview of the workflows in this analysis.

2.1. Badger trapping and biological data collection

We used individual-based data collected between 1990 and 2019 from a largely closed badger population (immigration/emigration rate = 3%: [64]) 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: [75]) for two-three nights, using string-trigger cage-traps (see [104,11]).

Individuals were given a unique inguinal tattoo on first capture; we assigned age continuously, based on year of birth for those first caught as cubs or inferred from tooth wear (scored 1–5 on each capture: [11]). In parallel, we interpret age effects by contrasting young badgers (choosing 2 years old, when sexual maturity occurs, as a benchmark) and old badgers (9 years old, largely post-reproductive: [105]). Body length (tip of snout to base of sacrum, to nearest 5 mm) and body mass (to nearest 0.1 kg) were recorded on each capture. We analysed two metrics of body condition: i) a direct subcutaneous fat score (categorical, 1–5, only recorded 1994–2019), assessed by palpating the belly-loin, with the badger laterally recumbent (after [99]), and ii) a body condition index (BCI) estimated using a ratio-based approach for each capture: $\log_e(\text{body mass})/\log_e(\text{body length})$ [73,74]. We compare how these metrics correlate, validating the use of BCI as an effective proxy for adiposity, in Appendix S2. We released badgers at their site of capture in the afternoon following processing. 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 (most recently PPL 30/3379). This resulted in 2073 captures for 751 distinct individuals during spring, 2295 captures for 777 individuals during summer, and 1498 captures for 584 individuals during autumn.

Following Dugdale et al. [25], we diagnosed lactation status (lactating, lactated, or not lactated) using teat size at the end of the suckling period (spring), to provide a robust year-to-year record of whether a female had endured pregnancy or not (1 = reproductive; 0 = non-reproductive). Any females only captured outside of the suckling period were assigned reproductive status for the year by comparing their teat size to females that were known to have lactated during that spring (Appendix S3). This approach is more comprehensive than pedigree data (available for the population: [3], updated through 2015 pers. comm.) because c. 25–36% of badger cubs die before they are caught and genotyped [2,64]; furthermore, the pedigree omits a substantial number of parentage assignments due to confidence limits. Once a female was assigned as having lactated/reproduced, she continued to hold that status throughout subsequent records for that year, irrespective of later teat status. Using this protocol, we assigned reproductive success to 592 females (1389 post-reproductive captures, 2420 non-reproductive captures).

In males, paternity success depends on the success of the female(s) they fertilised, and so instead we measured investment in reproductive capability, as badgers are highly promiscuous and therefore individuals may differ widely in their investments to secure mates [26,27]. To measure this investment, we used degree of testes descent as a proxy, as most (but not all) males ascend their testes outside of the breeding season [14,103]. We scored male testes seasonally (no carrying forward) as “descended,” “intermediate,” or “ascended” [103] for 540 individuals.

For both sexes, we computed lifetime reproductive success (LRS), defined as the total number of offspring assigned to an individual by pedigree (limited to parentage of cubs surviving to c. 16 weeks old, when we could first capture and genotype them). This analysis was limited to cohorts born up until 2007 (that could have reached age 8, realizing 80.6% of lifetime reproduction, by pedigree end in 2015: [25]).

LRS was used alongside realised lifespan (the last age at which an individual was captured) to investigate whether long-term life-history covariates correlated with high- or low-BCI phenotypes (see Section 2.7). Computing LRS required pedigree data because a) teat data only indicate that a litter was born, not number of offspring (range 1–4 cubs: [27]), where a lifetime series of singletons vs. multiparous litters would result in substantial LRS differences, and b) male reproductive success cannot be inferred from teat metrics. Despite the degree of missing assignments

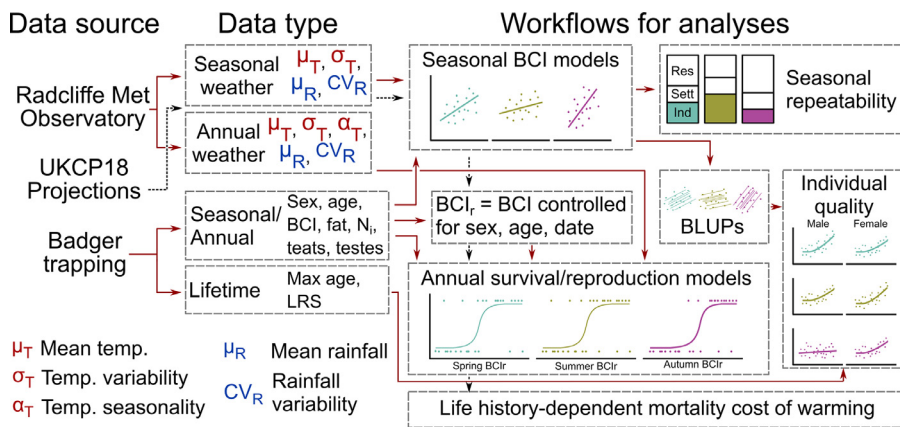


Fig. 1. Workflow and outputs. Real data not shown. Red arrows indicate data sources and types that feed into different components of analyses referenced in-text. Primary analysis centers around seasonal BCI models and annual survival/reproduction models. The first furthermore enables year-to-year individual repeatability analyses and investigation of individual quality through bootstrapped best linear unbiased predictors (BLUPs). Projections workflow uses both primary model sets, and is indicated through dashed black arrows.

in the pedigree (resulting in underestimates of LRS), this approach permits correlational analysis of life-history metrics (see [11]).

2.2. Weather covariates

Daily weather data were provided by the Radcliffe Meteorological Station (<https://www.geog.ox.ac.uk/research/climate/rms/>), 6 km from the field site. We calculated the mean and variance of weather variables, as both can affect success in wild animals ([16], including badgers: [77]): 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)—these metrics are listed in Fig. 1 for ease of reference. 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). We computed the same statistics for the driest 30-day and 90-day period in each year, where dry conditions reduce earthworm food availability (Appendix S1). 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.

2.3. Population density

We calculated total population density (N_i) annually, as an indicator of food competition in the study area, using a modified minimum number alive method, incorporating variable trapping efficiency [11]. Because this method is only robust to within 3 years of the end of these trapping data [11], we limited density-dependent analyses to 1990–2016.

2.4. Modelling survival as a function of body condition

We used generalized additive mixed models (GAMMs, used due to the high number of covariates tested and consequent challenges in using Cormack-Jolly-Seber alternative methods) 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 factors, weather, and density in each season (all continuous covariates standardised to mean = 0 and SD = 1). To detect a “true” signal of relative BCI on survival, beyond that caused by age-, sex-, or calendar date-related changes in BCI, in these models we used BCI_r—residuals from a generalised additive model (GAM) 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. Age-specific effects of reproductive investment could not be estimated for males, because few survival contrasts were available between testes descent categories at older ages, 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 S4).

We used a nearly identical procedure to model year-to-year survival as a function of fat score in each season. However, because the categorical fat score had to be modelled as a factor, we did not include two-way interactions with other covariates to avoid over-parameterising models. As only 8 springtime badgers had fat-score = 5, we only modelled the effects of springtime fat scores 1–4 on survival.

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 seasonal weather metrics for the seasons between the autumn BCI_r measurement and the next potential capture in May (winter and spring). These seasonal weather metrics were highly collinear and were thus modelled as 4 principal components that explained 84% of their variance (loadings in Appendix S5). 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, to avoid over-parameterisation).

2.6. Modelling drivers of seasonal BCI

To determine drivers of seasonal BCI patterns—and their variation—we built comprehensive GAMMs of BCI for each season. We modelled seasonal BCI 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 reproductive investment effects). Seasonal weather comprised: spring (including 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 winter period for the summer BCI model (Appendix S5); and metrics for the driest 30-day summer period and the entirety of autumn (including a quadratic effect for CV_R) for the autumn BCI model. As for survival models, Appendix S4 provides 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: [15]). If the model with the lowest AIC had exponential or power-dependent variance (homogeneous variance was nested within these variance structures), 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 (to control for group-based differences: [65]). 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. [122], Appendix S6.

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: [70]) of individual random effects, relative to total variance:

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

As density-dependent variance strongly skewed the magnitude of residual variance, we estimated ICC using density-independent variance. We bootstrapped GAMMs parametrically ($n = 1000$) to compute 95% confidence intervals for repeatability estimates.

To further test for 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. From seasonal models, we then used best linear unbiased predictors (BLUPs; individual random intercept estimates) as a measure of individuals' lifetime BCI profiles, and examined relationship with realised lifespan and LRS separately for males and females. This approach has received criticism because it ignores error in BLUP estimates [41]. 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 (see Appendix S7).

2.8. Climate projections

We used climate projections for our study site to examine potential BCI-mediated effects on life history-specific survival rates. We acknowledge that this approach does not account for potential further behavioral and physiological adaptation to sustained change; these projections aim simply to illustrate within-population differences in capacity for BCI tactics to buffer climate change, according to current constraints. To test whether BCI tactics could buffer survival even in the worst-case weather scenario (where implicitly all lesser cases should therefore be manageable), we modelled against the IPCC's Representative Concentration Pathway (RCP) 8.5 (a severe emissions scenario). These weather data comprise 12 projections of daily temperature, differing due to climate unpredictability and uncertainty (UKCP18, 2.2 km projections for RCP 8.5 from 2021 to 2040 and 2061–2080, avg. for 5 km centered at OS 447500, 207500: [50]). We used two arbitrary age points (ages 2 and 9) to contrast projected BCI changes under projected temperatures for young and geriatric badgers in summer and autumn (using males with descended testes in summer and ascended in autumn, the most common testes descent condition in each season) and reproductive and non-reproductive females in autumn (using age 4.5, the population mean,

for reproductive status contrasts), as these contrasts showed diverging effects of summer temperature on BCI (see Section 3.2.1).

We computed μ_T for the driest 30 summer days 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 the most vulnerable individuals, we then generated Gaussian distributions of 1000 individual BCI scores, with standard deviation equal to that of the "individual" random effect term in either the corresponding summer or autumn BCI models. We then predicted survival probability for these BCI values using our survival models (fixing all weather covariates to mean values, as μ_T did not have a direct effect on survival, see Section 3.2.1). To investigate the reduction in survival probability associated with BCI changes from increasing summer temperatures for each population sub-group, we performed quantile regression of the lowest fifth of survival probabilities from 1990 to 2080 for each of the 12 projections.

We constructed all models in R, version 3.5.3 (R [86]), presenting coding in full in the Wytham Woods Badger Project Dataverse (<https://dataverse.harvard.edu/dataverse/wytham-badgers>). Packages used: *emmeans* (for pairwise post-hoc Tukey tests: [55]); *gamma4* (for GAMMs: [117]); *quantreg* (for quantile regression: [52]); *standardize* (for covariate standardisation: [30]).

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_t had no significant unilateral effect on survival to the next year, with effects instead contingent on interactions with other energetic constraints (see Section 3.2; Fig. 2a,c). Autumn BCI_t exhibited a linear positive relationship with female probability of reproduction 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 from models predicting survival as a function of autumn BCI_t, fat scores in summer and autumn, and from the model predicting female reproductive probability from autumn fat scores. Below these thresholds, higher BCI_t/fat scores were associated with higher survival and female reproductive success probability, but body condition had little effect on these fitness metrics above the thresholds (Fig. 2d-f, h).

As significant effects differed little between BCI_t and fat score models, and because BCI_t models covered a wider year range, coefficients from BCI_t-based models are reported in Table 1, with fat score coefficients appended (for full fat score model coefficients, see Appendix S4).

3.2.1. Life history-dependent BCI thresholds

Age significantly and substantially strengthened the effect of spring (Fig. 2a) and summer (Fig. 2c) BCI_t 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_t did not have any unilaterally significant effects. Below a certain threshold, autumn BCI_t affected survival probability across all badgers ($p = 0.003$, $F = 4.65$; Fig. 3e); above that threshold, only older badgers benefitted from higher BCI_t, although the autumnal age-BCI_t 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*

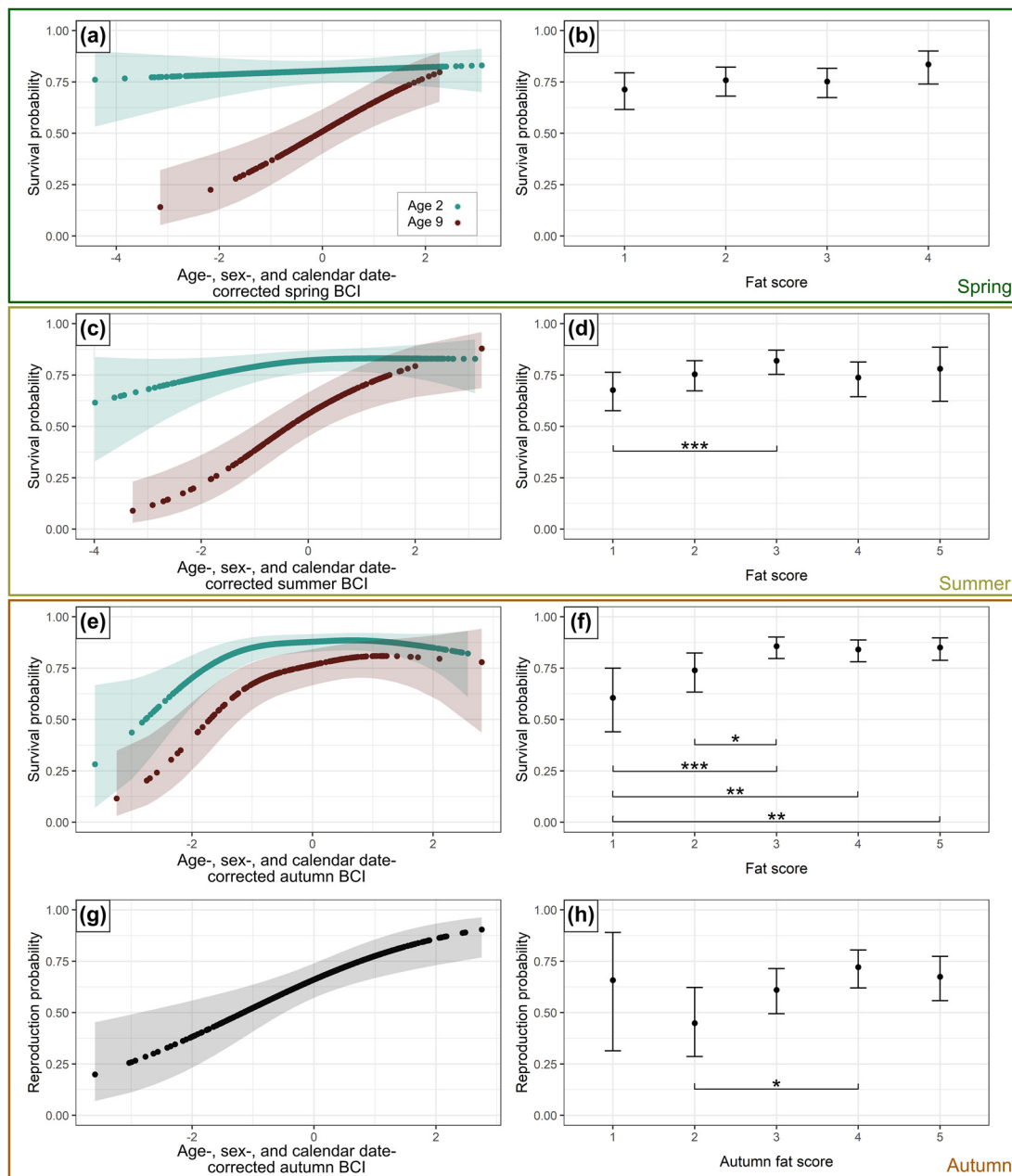


Fig. 2. Effect of body condition on individual fitness. Relationship between seasonal BCI_r (a, c, e, g) or fat scores (b, d, f, h) and the proportion of individuals surviving (a-f) or females reproducing (g-h) under average conditions (0 = 0%, 1 = 100%), with 95% confidence intervals. BCI_r-survival 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 BCI_r range coverage of the broader dataset, 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 ($p < 0.001$; $0.001 \leq p < 0.01$; $0.01 \leq p < 0.05$).

p -values: spring = 0.79, summer = 0.51, autumn = 0.30). In an unexpected reversal of expectations, females that had reproduced showed no relationship between spring or summer BCI_r and survival, while non-reproductive females showed a strong positive 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. Degree of testes descent did not affect survival probability in males (all $p > 0.05$).

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

Annual weather influenced the effect of BCI_r on survival. Models indicated that the positive effect of higher summer BCI_r on survival probability was stronger 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); and 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, when the

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 S4. 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
	BCI: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		
	Desc. testes	−0.658	0.532	−0.167	0.31	−0.572	0.346		
	BCI: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		
	BCI: μ_R	0.126	0.076	−0.017	0.08	0.253**	0.094		
	BCI: α_T	−0.082	0.092	0.19*	0.086	0.065	0.101		
	BCI: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

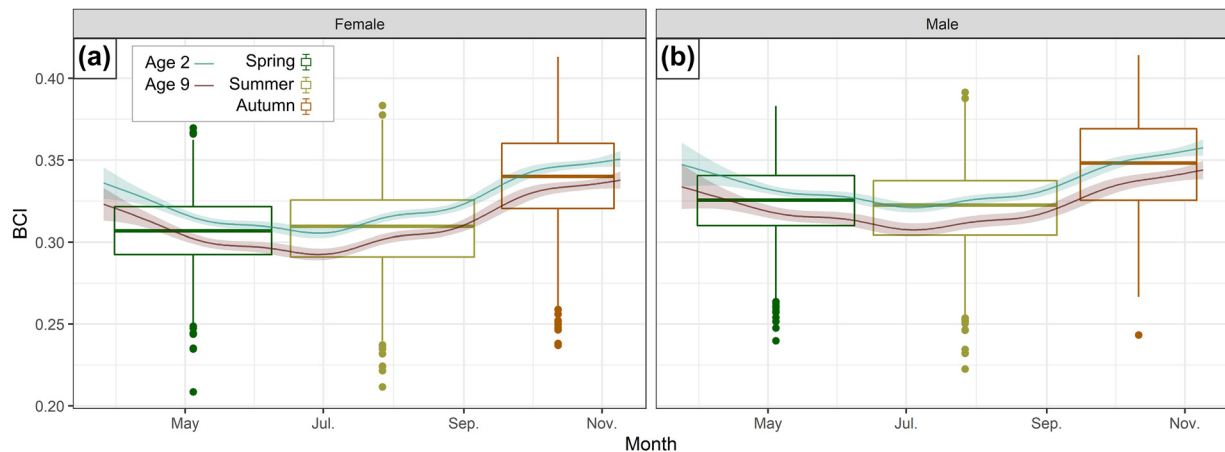


Fig. 3. Variation in body condition. Boxplots show variation in BCI by season (1990–2019); lines show population averages according to a best-fit GAM regression at age 2 (blue) or 9 (red). Boxplot width corresponds to the period considered in each season. Model controls for individual via random effect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

average badger (using male with descended testes as reference) under average weather conditions had an 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 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. Average population BCI was at its highest recorded level on the latest date trapped, November 28 (Fig. 3).

3.3.1. Weather drivers of seasonal BCI

Weather had substantial impacts on seasonal BCIs (Table 2): σ_T had a negative effect on BCI, and μ_T , μ_R , and CV_R drove season-specific effects largely according to season-specific energetic considerations. Warmer and wetter springs were associated with higher spring BCI (although effects were quadratic, with no further BCI gains above rainfall of 2 mm/diem and gains only above 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 ef-

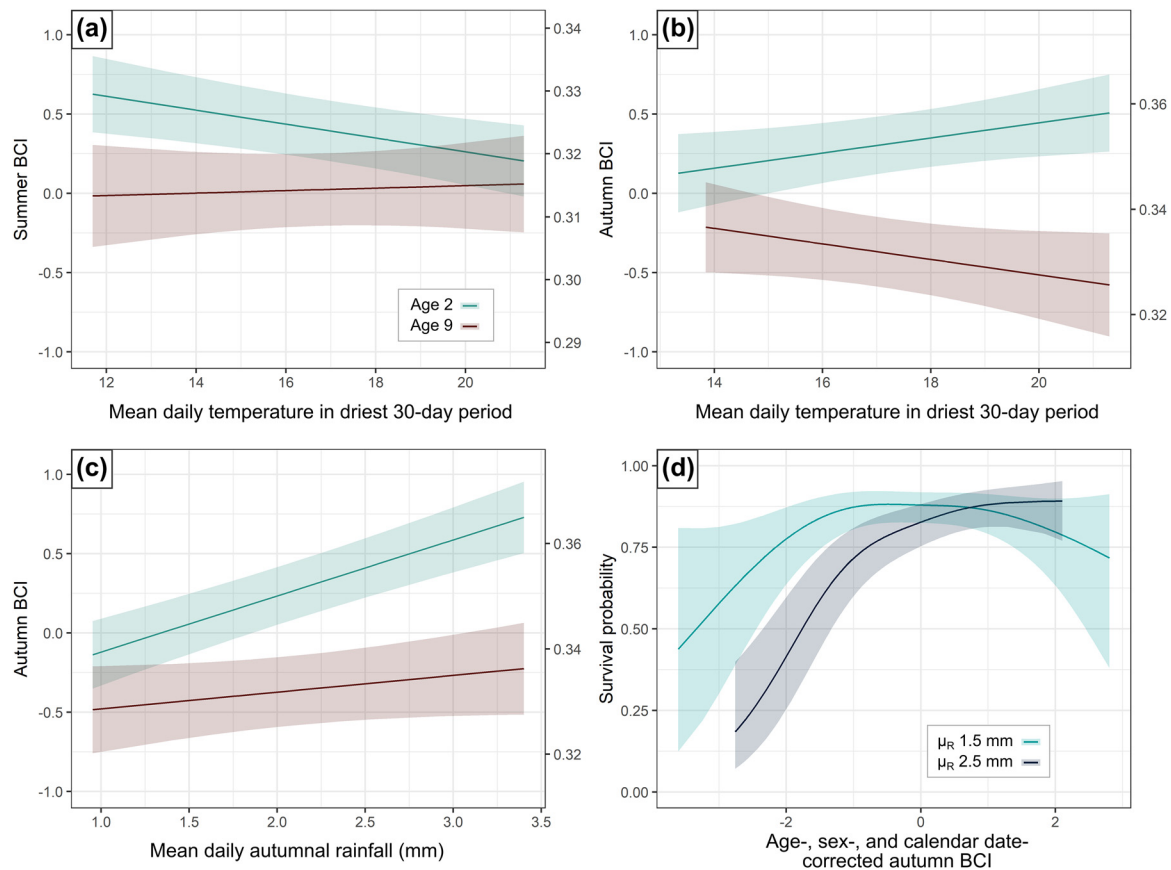


Fig. 4. Extrinsic-intrinsic interaction relationships. Effect of μ_T during the driest 30-day period in a given summer on a) summer BCI and b) autumn BCI for badgers of age 2 (young) and 9 (geriatric). Age-specific effects of autumn μ_R on BCI is shown in c), while d) illustrates the different effects of BCI_t on survival in relatively dry or relatively wet autumns (predicted for average-age badger, 4.5 years old). BCI for (a-c) is provided in both SDs (left axis) and real values (right axis).

fect was quadratic, with high BCIs following either particularly variable or consistent rainfall). Conversely, summer BCI was lower in years when the driest 30-day summer period 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

Overall, N_i did not influence seasonal BCI in either direction; however, it did affect BCI through life-history interactions. For older individuals, higher N_i values were associated with lower mean summer BCI, but higher autumn BCI. 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, $\Delta AIC = 2.9$, 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 $p = 0.086$). Moreover, females that reproduced had BCI even lower 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. Spring BCI among older reproductive females was higher than expected for their age.

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 ($p = 0.003$). There was no significant interaction between testes descent and age (all $p > 0.1$, Table S4.4).

Older badgers (of both sexes) had particularly low autumnal BCI 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 hotter summers and summer BCI.

3.4. Lifetime individual BCI variability

Despite the strong effects of life-history context and environmental conditions on seasonal BCI, these drivers cumulatively described less than half of the variance in BCI in any season (R^2 in spring = 0.35, summer = 0.18, autumn = 0.22). Individual year-to-year (spring-to-spring and so on) 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, Appendix S7), after accounting for weather and life-history, we detected three BCI “types” (Fig. 5): I) consistently low-condition individuals (11.2%); II) individuals with more variable BCI (84.3%); and III) consistently high-condition individuals (4.6%). These percentile patterns reflect those expected if each individual exhibited roughly the same BCI variability around different, fixed long-term means—simulations showed that

Table 2

Coefficients from condition modelling. Non-significant interaction terms are not shown; full set of coefficients available in Appendix S4. 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

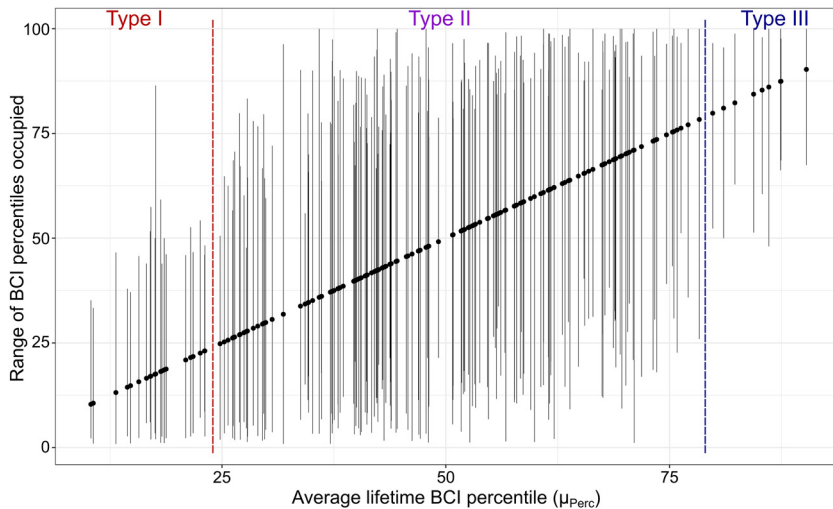


Fig. 5. Range of BCI percentiles occupied by average lifetime BCI percentile. Each line represents the full range of percentiles occupied by an individual, with dots located at their average lifetime percentile. Individuals loosely coalesce into low-BCI (Type I), variable-BCI (Type II), and high-BCI (Type III) phenotypes. Individuals only included with 10+ captures in their lifetime.

Gaussian random samplings of BCI with variance derived from our seasonal BCI models produced very similar results (Appendix S8).

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. S7.1, Appendix S7). 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—positive association with individual BLUP values (Fig. 6; see Appendix S7 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).

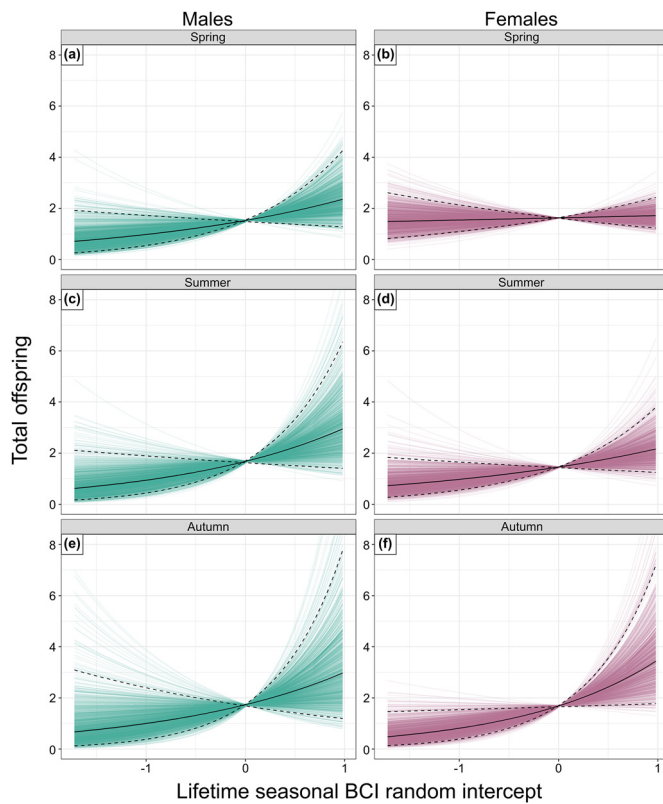


Fig. 6. Effects of BLUPs on lifetime reproductive success. Each line represents one iteration ($n = 1000$) of residual randomization. Mean slope provided by solid black line; 95% confidence intervals provided by the dotted lines.

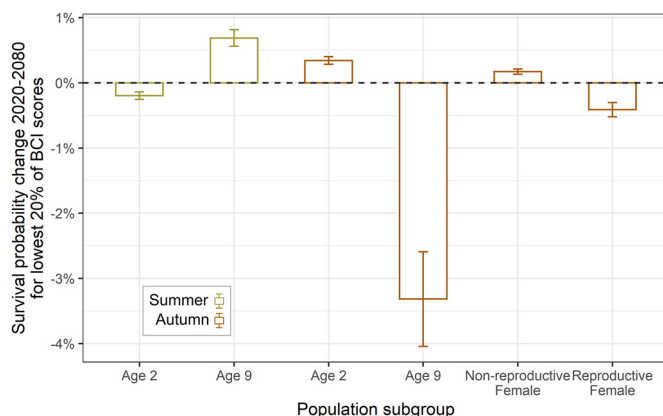


Fig. 7. Survival effects associated with climate change-driven BCI changes. 2020–2080 change in survival probability resulting from the life-history dependent BCI changes of 12 projections of climate change under a severe emissions scenario (RCP 8.5). Columns show average change across all 12 projections; error bars show standard deviation among projections. For age contrasts, we use males with the most common seasonal testes descent (summer = descended; autumn = ascended).

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 result in only small-to-moderate changes in survival probability under current BCI-survival relationships (Section 3.2) in even the lowest fifth of population subgroups—changes were even smaller for the remainder of population individuals (Fig. 7 and all subsequent numbers refer to this lowest fifth). In particular, threshold

BCI-survival relationships (Fig. 2) minimised predicted changes in survival probability. For instance, although geriatric badgers (9 year-olds) showed a narrow BCI safe zone in summer (Fig. 2c), the positive relationship between summer temperatures and their BCI resulted in an average survival probability increase of just 0.69% from 2020–2080 (projection range 0.19–1.07%), while their broader BCI safe zone in autumn (Fig. 2e) implied only a 3.32% (0.73–5.58%) survival probability reduction associated with BCI losses. For young badgers (2 year-olds), projected summertime BCI reduction corresponded to a miniscule 0.20% survival probability decrease (0.03–0.37%, Fig. 7). Concurrently, autumnal BCI costs from increasingly hot summers brought the survival probability of reproductive females (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 survival probability decrease (0.05–0.77%).

4. Discussion

Body condition had strong effects on individual fitness, mediating survival and female reproductive success probabilities. However, our non-linear modelling approach demonstrated a minimum body-condition threshold above which individuals can invest energy tactically. Badgers only exhibited significant risks associated with body-condition losses below these “safe-zone thresholds”. However, these minimum BCI thresholds depended on both life-history factors and prevailing environmental conditions (weather and density), as well as their interaction.

Broadly, fat indices produced stronger threshold effects on survival and reproduction than did BCI_t on its own (Fig. 2), with BCI_t effects becoming more evident through interactions with other model covariates. Although weather and life-history stage had strong effects on seasonal body condition, these described a relatively small percentage of the variance in BCI, suggesting that substantial variation in energy expenditure/storage tactics occurs above the safe-zone threshold. Nevertheless, those few individuals that maintained high body condition throughout their lives (Type III in Fig. 5) exhibited greater lifetime reproductive success (Fig. 6), suggesting at least some fixed heterogeneity in energy expenditure variation—i.e., some individuals were of higher “quality” [76]. Ultimately, the threshold-based relationship between BCI and survival appears capable of buffering individuals within the safe-zone from even the worst forecasted weather scenarios (as one-off events), making attaining the threshold body condition crucial for individual and population resilience under rapid change.

4.1. Weather and density drivers of body-condition safe-zone thresholds

In wild populations, weather conditions often determine both the availability of food [19,62] and the rate at which individuals expend energy (e.g., through heat loss: [36]; or elevated foraging costs: [79]). While food intake and fat storage is crucial for enduring periods of food scarcity, especially for more intrinsically vulnerable individuals (such as elderly ones), rationalizing efficient energy expenditure behaviors [82,116] and avoiding excessive heat loss [36] is also essential. Correspondingly, badgers not only exhibited lower BCI following poor foraging conditions, such as dry, cold springs and autumns, or hot summers, but also a stronger link between autumn BCI_t and survival during rainy years. Thinner badgers engage in compensatory autumn foraging, even during poor weather conditions [73,74]. Nevertheless, while moderately higher rainfall can increase earthworm availability, torrential rain can cause foraging badgers to experience hypothermia due to fur soaking [112], and poses a risk to cub survival [77]. This thermoregulatory trade-off was apparent from the quadratic relationship between spring rainfall and BCI, and likely explains why rainy years elevate the mortality risk of badgers with low BCI_t. We also found a stronger effect of summer BCI_t on survival probability—a narrowing of the energetic safe-zone—in years with higher seasonality (more extreme summers and

winters), likely because this larger transition requires a more extreme tactical adjustment in body condition and foraging activity.

4.2. Constraints of life-history frailty

Senescent declines in body condition are widespread among wild mammals [17,78,83], including badgers [28,105]—as a consequence, mortality among badgers aged 8+ contributes substantially to inter-annual population dynamics [11]. Not only did older badgers suffer consistently lower survival probabilities (throughout the year, not just in the food-scarce winter months), but their BCI were even lower in higher population-density years. This is consistent with other group-living animals, where greater geriatric sensitivity to body-condition effects may arise through reduced competitiveness [93] or exclusion from food acquisition [47]. While in some species, such marginalization might trigger terminal reproductive investment (with the animal then dying: [21]), we found no such effect, with a subset of older females retaining a high likelihood of reproductive success (see also [105]) but little increase in mortality risk (see also Section 4.3). Age brings both experience in food acquisition [4,20] and dominance in many social species [100], which may offset or exceed declining feeding competitiveness and senescent declines in anabolism [110]. In some badger populations, dietary specialization [89] and dominance [88] confer body-condition advantages in times of shortage. In our study, warmer summers were not detrimental to summer BCI in older badgers (unlike in 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 between summer BCI_t and survival than young badgers do, they may down-regulate metabolism in hot, dry summers (as noted for American badgers, *Taxidea taxus*: [37]), possibly explaining their lower autumnal BCI in such years (Fig. 4b).

The relationship between body-fat reserves and fitness can also depend on density-dependent competition for food between conspecifics [1,63] or within sympatric guilds [121], which exacerbates the risk of prioritizing reproductive investment over energy conservation [118]. While we did not find any direct effects of population density on most badgers' BCI, we did find that density exerted a significant constraining effect during the summer, with lower BCI variance during this season in high-density years and nearly 10% lower probability of surviving from summer through the next year at high compared to low population densities. The strength of intra-population competition is dependent on environmental carrying capacity [24,32]. If seasonal variation in food availability causes carrying capacity bottlenecks, especially by constraining the variety of dietary niches available [94], competition may have particularly severe consequences for more vulnerable individuals, as we found for old badgers, which exhibited lower than expected summer BCI during high-density years.

4.3. Fixed individual heterogeneity

Variation in lifetime reproductive success within a population arises from the additive contributions of stochastic environmentally-determined outcomes (dynamic heterogeneity) and explanatory differences between individual quality (fixed heterogeneity: [13]). In general, long-lived, iteroparous animals invest in survival over short-term reproductive success [80], where tactical energy allocation into survival allows for future reproductive success [1]. Investing stored capital in survival [95] likely explains why female badger reproductive success rose linearly with autumn BCI_t in our study. If some individuals in a population are of intrinsically lower quality—whether from early-life developmental constraints [56,61], genetic factors [115], or consistent metabolic disadvantages [59]—they may repeatedly postpone breeding, leading to lower lifetime reproductive output [17]. 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 drops in springtime BCI as a result of reproduction. Similarly, despite the BCI costs of descended testes (males with descended testes had seasonal BCI 5.0%, 3.6%, and 4.0% lower than those with ascended testes in spring, summer, and autumn, respectively), degree of testes descent did not have any significant effect on male survival probability.

4.4. Individual BCI variability

While some fixed heterogeneity occurred in this population, individuals with highly variable body-condition phenotypes (Type II in Fig. 5) comprised the largest share of highly-captured (10+) badgers 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—in other words, not all variation in body condition above safe-zone thresholds strictly implies differences in quality, but rather a broad range of roughly equivalent tactics.

Phenotypes with lower arithmetic mean fitness may persist in populations provided that environmental stochasticity enables them to maintain higher geometric mean fitness (a phenomenon termed “bet-hedging”: [87,101]). Thus, although consistently 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) consistently remained 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 [11] nor telomere dynamics [57] 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), suggests that, for the majority of individuals, tactical variation above the safe-zone threshold provides alternative paths to competitiveness.

Alternative tactics for balancing restricted energy allocation budgets can preserve competitiveness for lower-quality individuals. For example, roe deer (*Capreolus capreolus*) experiencing food limitation during development tend to grow to be smaller and lighter, but maintain typical body condition [106]. Thus, these “unlucky” (lower-quality) individuals prioritize survival in the short-term and may eventually get to reproduce, even if with a lower total lifetime reproductive output [33]. Under certain environmental conditions (e.g., low densities, under-represented in the present study but pertinent to fluctuating selection: [118]), such tactics could even have a selective advantage (fitness with lower need to insure against food supply insecurity), where heterogeneous fitness outcomes may ultimately represent dynamic [108] rather than fixed [76] heterogeneity.

4.5. Responses to projected climate change

Individuals exhibited relative robustness to BCI costs associated with even extreme climate change scenarios (6.5 °C in summer). Despite substantial projected warming, most associated BCI_t changes affected survival probabilities only slightly for individuals within the safe zone (Fig. 7). These projections provide insight into how individuals tailor energy budgeting according to intrinsic conditions (such as age) in order to buffer extrinsic fluctuations in environmentally-determined risk. For instance, geriatric badgers have an extremely narrow safe zone during summer (Fig. 2c). However, we found that older badgers had less of a relative BCI dip compared to younger badgers during hot summers (Fig. 4a)—old badgers may avoid activity to reduce energy expenditure and stay above the summer safe-zone threshold, but at some

cost to subsequent autumn BCI (Fig. 4b), in the hope that conditions will have improved by then. This avoidance of marginality during poor summer conditions minimizes total detriment to fitness for older individuals: where an equivalent reduction in BCI_t during summer would be severely detrimental to survival probability, current BCI-weather relationships project only a 3.3% survival probability reduction for old badgers under even extreme climate change (Fig. 7). It is highly unlikely that in such conditions foraging dynamics would persist unaltered and preserve existing individual buffering capacity, particularly subject to cumulative energy constraints as weather conditions continue to change [49,90]. Nevertheless, these projections illustrate how, particularly when not presented with additive challenges [97], flexible energy budgeting may have played a significant role in allowing populations to persist through previous periods of severe climatic change [7].

Shorter and less severe periods of food scarcity in winter are also likely to drive behavioral and physiological responses in badgers, which may reduce their need to accumulate fat or rely on torpor/hibernation [10,48,51]. Nevertheless, due to endocrine regulation [18,23], badgers—and other torpor-expressing species—may still deposit fat prior to the onset of even substantially milder winters. Accumulating excess fat unnecessarily under less stressful winter conditions represents a missed investment into reproduction, incurring a selective disadvantage [6,44]. Of concern is that increasing winter temperatures will result in greater badger activity during winter months [74], even as enduring summer weather becomes more energetically costly. If elevated activity is not matched by food availability, the costs of rousing frequently from torpor and subsequent winter activity may outweigh the benefits of foraging [18,44]. As these changes continue across wild populations, it will be important to develop an understanding of which individual energy-budgeting tactics can strike the optimal balance between stability and reproductive success, thus providing a template for successful adaptation to anthropogenic climate change.

5. Conclusion

Fluctuations in food supply, both predictable and stochastic, are part of the natural conditions to which species have evolved [107]. Increasingly, however, anthropogenic climate change and other forms of human-induced rapid environmental change [96] destabilize ecosystem dynamics, altering prey availability or foraging opportunities [12,74,92] and causing a mismatch between historical energetic demands and food supply [29,102]. The tactical adjustment of body-fat reserves provides a phenotypically plastic [9] mechanism for managing uncertainty, and both prevailing conditions and life history present further risk factors that make optimal body condition an ever-moving target. Ultimately, a better understanding of body-fat ecophysiology—and how this differs between individuals experiencing the same conditions—may be key to forecasting the resilience of many species and populations to ongoing changes [111].

Declaration of Competing Interests

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.

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Supplementary materials

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