



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

Journal:	<i>Global Change Biology</i>
Manuscript ID	GCB-20-0066
Wiley - Manuscript type:	Primary Research Articles
Date Submitted by the Author:	13-Jan-2020
Complete List of Authors:	Bright Ross, Julius; University of Oxford, Zoology Newman, Chris; Oxford University, Zoology Buesching, Christina; Oxford University, Zoology Macdonald, David; Oxford University, Zoology
Keywords:	Life history, Population resilience, HIREC, Individual strategies, Demographic variability, Pace-of-life syndrome, European badger
Abstract:	<p>Life-history and pace-of-life syndrome (POLS) theory predict that populations are comprised of individuals exhibiting different reproductive schedules and associated behavioural and physiological traits, optimised to prevailing social and environmental factors. Changing weather and social conditions provide in situ cues altering this life-history optimality; nevertheless, few studies have considered how tactical, sex-specific adaptation over an individual's lifespan varies in wild populations and influences population resilience. We examined the drivers of individual life history schedules using 31 years of trapping data and 28 years of pedigree for the European badger (<i>Meles meles</i> L.), a long-lived, iteroparous, polygynandrous mammal that is known to exhibit early and late development phenotypes.</p> <p>Our top model for the effects of environmental conditions during a badger's first year of life on pace-of-life only explained &lt;10% of the ratio of fertility to age at first reproduction (<math>F/a</math>), and lifetime reproductive success (LRS). However, sex ratio and sex-specific density explained 52.8% (males) and 91.0% (females) of variance in adult pace-of-life balance relative to the long-term population median <math>F/a</math>. Weather primarily affected the sexes at different life-history stages, with energy constraints limiting the onset of male reproduction but playing a large role in female strategic energy allocation, particularly in relation to ongoing mean temperature increases. Furthermore, the effects of social factors on individual age of first reproduction and year-to-year reproductive success covaried differently with sex, likely due to sex-specific responses to potential mate availability. For females, low same-sex densities favoured early primiparity; for males, instead, up to 10% of yearlings reached an early onset of reproduction at high same-sex densities. We observed substantial sex-ratio dynamism relating to differential mortality of life-history strategists within the population, and propose that shifting ratios of "fast" and "slow" life-history strategists contribute substantially to population dynamics and resilience to</p>

	changing conditions.

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## 1. Title Page

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

**ii Running head:** Drivers of life-history variability

**iii Authors:** Julius G. Bright Ross,<sup>1</sup> Chris Newman,<sup>1</sup> Christina D. Buesching,<sup>1</sup> and David W. Macdonald<sup>1</sup>

**iv Institutes:** 1. Wildlife Conservation Research Unit, The Recanati-Kaplan Centre, Department of Zoology, University of Oxford, Oxford, U.K.

**v Contact Information:** Corresponding author: Julius G. Bright Ross. Telephone: +44 (0) 7480 328287. Email: julius.brightross@zoo.ox.ac.uk

## 2. Abstract

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

Our top model for the effects of environmental conditions during a badger's first year of life on pace-of-life only explained <10% of the ratio of fertility to age at first reproduction ( $F/\alpha$ ), and lifetime reproductive success (LRS). However, sex ratio and sex-specific density explained

52.8% (males) and 91.0% (females) of variance in adult pace-of-life balance relative to the long-term population median  $F/\alpha$ . Weather primarily affected the sexes at different life-history stages, with energy constraints limiting the onset of male reproduction but playing a large role in female strategic energy allocation, particularly in relation to ongoing mean temperature increases. Furthermore, the effects of social factors on individual age of first reproduction and year-to-year reproductive success covaried differently with sex, likely due to sex-specific responses to potential mate availability. For females, low same-sex densities favoured early primiparity; for males, instead, up to 10% of yearlings reached an early onset of reproduction at high same-sex densities. We observed substantial sex-ratio dynamism relating to differential mortality of life-history strategists within the population, and propose that shifting ratios of “fast” and “slow” life-history strategists contribute substantially to population dynamics and resilience to changing conditions.

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

### 3. Introduction

Threats imposed by Human Induced Rapid Environmental Change (HIREC: Sih 2013), and especially climate change (IPCC 2018), make it imperative to fully understand how vulnerable or resilient species and populations may be to both persistent and catastrophic events (Pacifi et al. 2015). This adaptability takes many forms (Kearney et al. 2009, Noonan et al. 2018), from genetic trait selection (Bårdsen et al. 2008) and behavioural plasticity (Loe et al. 2016, Beever et al. 2017) to changes in population dynamics (Walther et al. 2002). At the species

level, fundamental life-history parameters are also important (Isaac 2009). Other plastic adaptive (Vedder et al. 2013) mechanisms, however, can be more cryptic, such as how life-history strategies vary both between individuals and within individual lifespans, and in turn induce qualitative changes in population composition (Stenseth 1978).

Rapid, sustained periods of environmental change are neither exclusively anthropogenic nor particularly infrequent in the palaeontological record (e.g. Dansgaard-Oeschger events, Dansgaard et al. 1993). Environmental stochasticity, therefore, has shaped life history evolution by shifting the “target” against which life-history must be optimised (Tuljapurkar et al. 2009a), precluding individual behaviour and adaptive life-history traits from converging on a single optimum within populations (Stearns 1992). Consequently, *dynamic* (from stochastic environmental processes; Tuljapurkar et al. 2009b, Steiner et al. 2010) and *fixed* (differences in individual quality; Stopher et al. 2008, Plard et al. 2018) heterogeneity cause measured life history traits in populations to vary widely. Fixed heterogeneity is maintained by shifting optima and consequent genotypic “bet-hedging”, whereby lower longer-term fitness variance under environmental stochasticity redresses short-term fitness deficits (Starrfelt and Kokko 2012, Rajon et al. 2014).

This flexible fitness optimisation gives rise to “pace-of-life syndromes” (POLS), where different individual energetic investment profiles evolve along metabolic (Careau et al. 2008, Metcalfe et al. 2016) and behavioural (Careau et al. 2009) gradients to maximise each strategy’s lifetime reproductive success (Réale et al. 2010, Dammhahn et al. 2018). Populations exhibiting “faster” composite life histories (early reproduction with high investment in producing offspring) are better adapted to stochastic conditions, where carrying capacity is frequently under-exploited—analogous to r-selected species in community ecology (Pianka 1976). “Slower” life

histories (delayed reproduction with fewer, often higher quality offspring) suit more stable, resource-limited niche conditions—analogueous to K-selection (Dammhahn et al. 2018, Montiglio et al. 2018). Studies of extrinsic (weather and resource availability: Nilsen et al. 2009, Campbell et al. 2017, Krause et al. 2017) and intrinsic (social conditions: Kraus et al. 2005, Liedtke et al. 2015) drivers of population dynamics support these axes, but the relative contributions of each—providing either reproductive cues or constraints—to within-population pace-of-life (hereafter, “POL”) variation (Réale et al. 2010) remains relatively unexplored in the wild. Understanding how environmental conditions set and maintain not only mean life-history profiles but also the variance of these within populations (eschewing the “Tyranny of the Golden Mean”: Williams 2008), could therefore provide insights into population resilience to environmental change (Beever et al. 2017, Ogura et al. 2017, Noonan et al. 2018).

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

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

For this analysis, we use long-term field data for the European badger (*Meles meles* L.; henceforth “badger”), which provide a tractable model species for long-term demographic studies. They reach very high densities for a medium-sized carnivore in southern England (up to 45 individuals/km<sup>2</sup> at our site: Macdonald et al. 2015), with a high re-trappability rate (mean of 81.3% of known individuals trapped annually in our population: Noonan et al. 2015). Badgers exhibit substantial inter-individual realised lifespan variation, with a majority of individuals dying by age three in our population (largely due to cub mortality: ca. 25%) but with 4.4% living to age 10 (Macdonald and Newman 2002, Macdonald et al. 2015). Badgers are polygynandrous (Dugdale et al. 2008, Annavi et al. 2014b, 2014a) and females manage their reproductive investment through delayed (and selective) implantation, superfecundation, and superfoetation (Yamaguchi et al. 2006). In our population, an average of 45% of females produce one litter of

1-3 cubs per year (mean 1.46, Annavi et al. 2014b). This causes substantial variation in life-history decisions both between and within (year-to-year) individuals. Additionally, recent endocrinological work in our population has found two distinct phenotypes in male badgers, with some attaining sexual maturity and greater body size a year before others (Sugianto et al. 2019), inviting investigation into potential drivers for these diverging strategies. Moreover, badger population dynamics are sensitive to the effects of mean weather conditions and variation from the mean, which affect food availability (Kruuk 1978, Curry 2004), foraging activity (Noonan et al. 2014, 2018), and thus survival, with cubs in particular exhibiting higher mortality under very wet or dry conditions (Macdonald and Newman 2002, Macdonald et al. 2010, Nouvellet et al. 2013, see also Newman et al. 2017). Weather stochasticity therefore governs survival likelihood, and thus may simultaneously signal future conditions, providing adults with cues on potential offspring survival. Over 31 years, this badger population also underwent a ca. 3-fold step-change in density (revised here as 137-328 individuals), principally from 1990-1995, with substantial annual fluctuations thereafter (Macdonald et al. 2009). However, there were no corresponding range or habitat changes, enabling examination of varied weather and social factors on POL.

We test a series of hypotheses: a) if harsh weather is the primary driver of slower POL (Dammhahn et al. 2018), we predict that unsuitable weather during a cub's first year of life would be associated with lower  $F/\alpha$  and LRS (**Harsh Conditions Hypothesis**). In contrast, b) if mating opportunities (how abundant mates and competitors are in the "reproductive competition landscape") are a stronger driver of reproductive strategies, we predict lower  $F/\alpha$  and LRS for cubs born at lower densities, and in years with population sex ratio skewed towards that individual's sex (**Reproductive Limitation Hypothesis**). This should be particularly evident in males, as badgers exhibit non-hierarchical scramble competition for mountings (Dugdale et al.



2011a), where reproductive opportunities scale with encounter rate (Annabi et al. 2014b, Swierk and Langkilde 2019). Therefore, under the Reproductive Limitation Hypothesis, we also predict that the distribution of sex-specific  $F/\alpha$  will be skewed higher (faster POL) when population density is high and the sex ratio is skewed away from the sex in question (evidencing the effects of greater mating opportunities). With regard to timing of influences on life-history, we test c) whether early-life conditions (**Early Drivers Hypothesis**) adequately characterise lifetime  $F/\alpha$  and LRS, with year-to-year environmental conditions contributing little to decisions on whether or not to reproduce. In opposition, d) the **Later Drivers Hypothesis** predicts that age of first reproduction (and reproduction thereafter) results from year-to-year reproductive viability considerations. Finally, e) because females are more likely than males (which can spread out their investment between litters) to lose their entire reproductive investment if they fail to produce a surviving litter, and have a longer period of control over their reproductive investment, we predict that weather conditions should affect lifetime POL ( $F/\alpha$  and LRS) and year-to-year life history investments more in females than in males (**Cautious Females Hypothesis**).

#### 4. Methods

##### *Study site and demographic data collection*

Data were collected in Wytham Woods, a 424-ha semi-natural woodland in Oxfordshire, UK (51°46'N, 1°20'W, for more information, see Savill 2011). Beginning in 1987, each active badger sett in the study area was trapped for two or three nights, three to four times per year, at regular seasonal intervals. Individuals were transferred from string-trigger traps to holding cages, taken to a central field station between 7.00 – 9.00 am, and sedated with 0.2 ml ketamine hydrochloride/kg body weight by intramuscular injection (McLaren et al. 2005). On first capture, each individual was given a unique inguinal tattoo, allowing life-long recognition on recapture.

Biometric data were recorded for each individual, including body length (to the nearest 5 mm), body weight (to the nearest 0.1 kg), and molar tooth wear (scale 1-5), a metric used for estimating the age of previously uncaptured adult badgers (Hancox 1988). All captures were made under Natural England license (currently 2019-38863, Badger Act 1992) and all animal handling procedures were made by qualified Personal Individual License (PIL) holders under Home Office license (current PPL 30/3379, Animals (Scientific Procedures) Act 1986).

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

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

$$MNA_i = T_i + AU_i \tag{1}$$

Here, we modified this estimate by considering the effect of yearly trapping efficiency ( $TE_i$ , defined as  $T_i/MNA_i$ ) on detection probability. Thus, the probability that an individual  $j$  that was never caught again but remained alive in the population in each subsequent year  $i$  can be

represented using the population-wide trapping efficiencies of the years between its last successful trapping ( $t - 1$ ) and year  $i$ :

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

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

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

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

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

parentage was assigned in each year. We then used binomial GLMs to determine if there were unidirectional time trends in survival rate and in the proportion of reproductive individuals in the population.

#### *Individual reproductive schedules and life-history metrics*

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

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

relatively robust up to the degree of imprecision in our dataset (R correlation coefficient at 60% missing assignments = 0.77). For further details on the simulation process and correlation curve, see Appendix S3.

### *Quantifying life history trade-offs*

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

Because variance in realised lifespan necessarily decreases as a function of age at first reproduction, we modelled this trade-off using linear mixed models (*nlme* package in R) to account for heterogeneity. For both males and females, an exponential variance structure explained these data significantly better than not accounting for variance heterogeneity ( $L_{male} = 7.01$ ,  $p = 0.008$ ;  $L_{female} = 9.42$ ,  $p = 0.002$ ; both  $d.f. = 1$ ). A random intercept by cohort was retained for males ( $L = 4.48$ ,  $d.f. = 1$ ,  $p = 0.03$ ), but not females ( $L = 0.012$ ,  $d.f. = 1$ ,  $p = 0.91$ ).

Logistic generalised linear mixed models (GLMM) were also used to model individual likelihood of year-to-year survival for all adults (age > 1, whether or not they were ever assigned offspring) based on i) whether or not a male mated successfully in a given year, or ii) the number of offspring a female produced in a given year (as female investment scales with multiple offspring, but a multiparous litter costs a male no further investment), controlling for age as a fixed effect and for population-wide stochastic effects through a random intercept for year.

## 246 *Computing covariates used in modelling life history metrics*

247       We modelled the influence of weather, social factors, and individual body condition on  
 248 individual life history. Daily temperature and rainfall figures from 1987-2016 were provided by  
 249 the Radcliffe Meteorological Station (<https://www.geog.ox.ac.uk/research/climate/rms/>), within  
 250 6 km of the field site. These figures were used to compute five weather covariates for each year  
 251 (after Nouvellet et al. 2013, Byrne et al. 2015): mean temperature ( $\mu_T$ ), temperature variability  
 252 ( $\sigma_T$ ), seasonality ( $\alpha_T$ ), mean rainfall ( $\mu_R$ ), and the coefficient of variation of annual rainfall  
 253 ( $CV_R$ ). Annual  $\sigma_T$  was computed as the average annual squared difference between daily  
 254 temperature measurements and a sinusoidal curve fitted to that year, while  $\alpha_T$  of days within the  
 255 year represented the amplitude of that curve (for details, see Nouvellet et al. 2013).  $CV_R$  was log-  
 256 transformed to account for two years with particularly high rainfall variability. Of the weather  
 257 covariates used, only  $\mu_T$  exhibited a linear increase over time (1987-2016:  $0.03\text{ }^{\circ}\text{C/yr}$ ,  $R^2 = 0.14$ ).  
 258 For social factors, sex-specific adult population density ( $N_i$ ) and sex ratio (SR, always given as  
 259 adult male  $N_i$ /adult female  $N_i$ ) were taken as measures of competition for food and reproductive  
 260 opportunities, respectively. Additionally, in relevant models, we applied cohort size (CS) as a  
 261 further measure of competition within cohorts.

262       Finally, individual condition was represented using body-condition index ( $BCI =$   
 263  $\frac{\ln(\text{body weight})}{\ln(\text{body length})}$ , established in Kruuk et al. 1987, Macdonald et al. 2002, Noonan et al. 2014). All  
 264 BCI measurements were modelled using a generalised additive model (built with all individuals  
 265 in the population) as a function of sex, season, and a smoothed spline of age (in years), allowing  
 266 the spline to vary with season. Predicted values were subtracted from the fitted values, giving  
 267 residuals that were averaged within each year to produce an annual metric of individual  
 268 condition corrected for age, sex, and season ( $BCI_r$ ). Because this metric should covary to some

degree with annual weather, all modelling procedures below include a check for collinearity between covariates.

### *Modelling drivers of life history*

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

Although we draw attention to principal models designed to test each hypothesis, all model sets test multiple sets of hypotheses. The hypothesis that females should be more risk-

291     averse in reproductive investment (Cautious Females Hypothesis) was tested in all models by  
292     splitting by sex.

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

299             To compare the Early Drivers and Later Drivers Hypotheses, we modelled annual  
300     individual cub production as a function of year-to-year weather and social conditions, controlling  
301     for individual  $BCI_r$  (model set 2). Because many individuals were not assigned a cub in most  
302     years, the model construction set contained many zeroes; consequently, we used a zero-inflated  
303     model (Zeileis et al. 2008) to model separately the effect of covariates on reproducing/not  
304     reproducing (binomial) and on the number of offspring produced (Poisson). We controlled for  
305     age in the selection set; in males, a linear term performed best, while in females, a cubic term  
306     was best. Quadratic terms were included for  $\mu_T$ ; all other covariates were modelled linearly. We  
307     used Vuong tests (*pscl* library, Jackman 2017) to verify that the final selected zero-inflated  
308     models were better for fitting the data than basic Poisson models.

309             To further discern between the validity of the Early Drivers and Later Drivers  
310     Hypotheses, we modelled the effect of yearly weather, social factors, and individual condition on  
311     whether individuals productively mated (males) or produced offspring (females) for the first time  
312     in that year (model set 3). To do so, we compared annual covariates and  $BCI_r$  in individuals  
313     reaching their first reproduction to ones of the same age that delayed (by choice or circumstance)



reproduction further (binomial glm, 1 = produced offspring for the first time, 0 = did not). Although some individuals bred for the first time only after age 4, sample sizes were small (6 males and 2 females produced offspring for the first time at age 5), resulting in convergence issues. The same series of terms were tested for these models as for the zero-inflated fertility models, by sex.

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

All analyses were conducted using R (R version 3.5.3, R Core Team 2019).

## 5. Results

### *Descriptive natural history statistics*

As annual breeders, badgers can only adjust breeding regimes by entire years. Any results depicting mean rates across the population that are not whole integers thus represent the composite of individuals following alternative life-history trajectories (e.g., shift in ratio of individuals first breeding at two or three years old). To address this statistical point, we present

appropriate analyses and interpretations also as shifting ratios as predicted by our best-fit models between strategists.

With this in mind, badgers exhibited considerable life history variation. Males lived on average to 3.48 years and females to 4.08 years (median age at last capture = 2 for males, 3 for females) but with a long survivorship tail following high rates of mortality as cubs (Fig. 1a; see inset for logarithmic scale). Per capita cub assignments peaked at ages 4-5 for males and 5-6 for females (Fig. 1b); average age of first reproduction was similar between males and females (both on average aged 4 years), but varied widely in both sexes ( $SD_{\text{male}} = 1.61$ ;  $SD_{\text{female}} = 1.76$ ).  $F/\alpha$  also varied substantially between individuals (Fig. 1c), and was on average higher for males than females (Mean  $F/\alpha_{\text{male}} = 0.33$ ,  $SD = 0.52$ ; mean  $F/\alpha_{\text{female}} = 0.16$ ,  $SD = 0.17$ ; Fig. 1c).

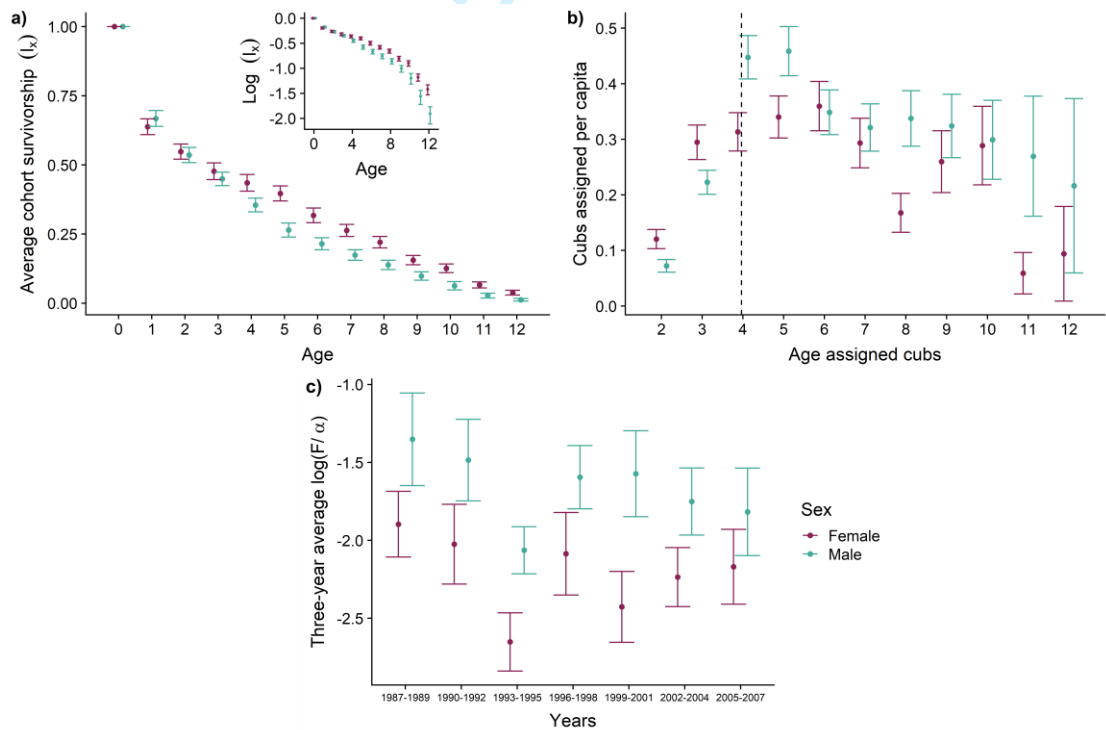
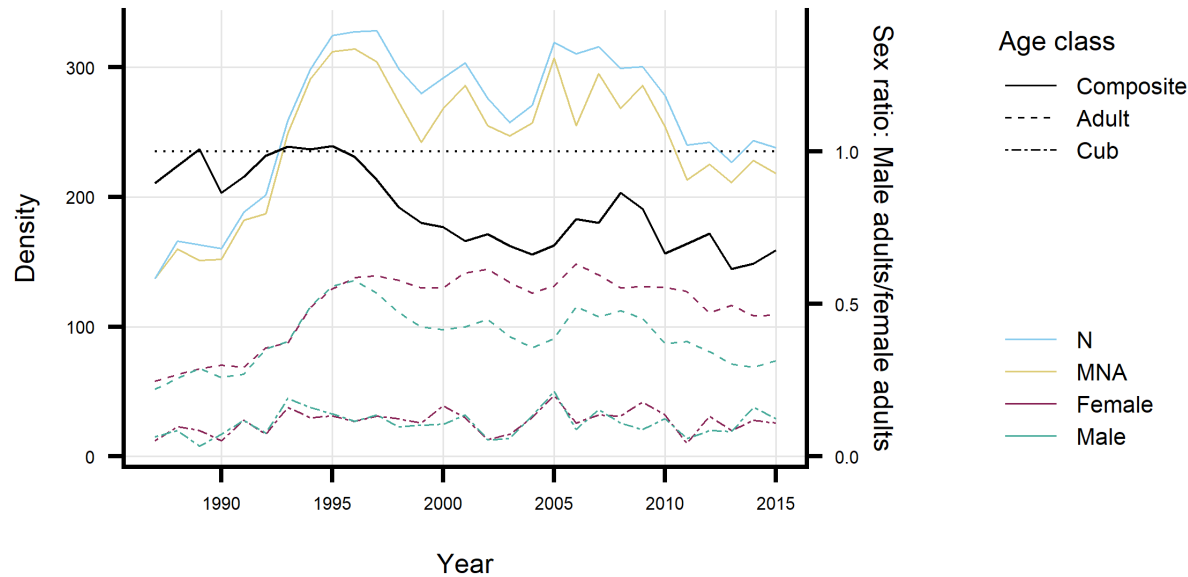


Figure 1 - Average a) cohort survivorship on a linear scale and (inset) on a logarithmic scale, b) annual per capita cub production by age, and c) tri-annual whisker plot of  $F/\alpha$  values (on a log scale). Per capita cub production was estimated using a generalised additive model (GAM) with separate splines for males and females; dotted line in second panel shows average age at first reproduction. Error bars for all panels display the standard errors of the means.

351 *Temporal trends*

352 Annual trapping efficiency ranged from 50.0% to 82.6% ( $\mu_{1988-2015} = 73.8\%$ ). Population  
353 density ( $N_i$ ) increased threefold from 1987 to 1997, peaking at 328 individuals (63 cubs, 265  
354 adults), followed by stabilisation between 250 and 300 individuals until 2010 and a subsequent  
355 decrease to a stable 230-240 individuals thereafter (mean 189 adults). From initial sex ratio  
356 parity (1987), the relative number of males decreased from 1997, remaining at 0.7-0.8 for the  
357 remainder of the study. Survival rates also decreased in young and old badgers of both sexes  
358 over the study period (Fig. 2a); young males exhibited lower survival rates than did young  
359 females (age 1-2:  $\text{mean}_m = 81\%$ ,  $\text{mean}_f = 85\%$ ,  $p = 0.01$ ; age 3-4:  $\text{mean}_m = 78\%$ ,  $\text{mean}_f = 87\%$ ,  $p$   
360  $< 0.001$ ), likely driving the observed divergence in sex ratio (see discussion). The oldest age  
361 class (age 8+) showed the steepest temporal decline in annual survival rates, from 77% ( $\pm 0.02$   
362 SE) in 1988 to just 61% ( $\pm 0.03$  SE,  $p$  for trend  $< 0.001$ ) in 2015. The proportion of females  
363 assigned offspring also decreased in all age classes between 1988 and 2015 ( $p < 0.001$  for all but  
364 age 2,  $p = 0.002$ ); the reproducing proportion of males decreased in ages 5-7 (same slope as  
365 females), but temporal models for males aged 2, 3-4, and 8+ yielded a significantly flatter slope  
366 than did females (age 2:  $p = 0.002$ ; age 3-4:  $p = 0.045$ ; age 8+:  $p = 0.001$ ), indicating less of a  
367 decrease over the course of the study (Fig. 2b).

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Figure 2 – Density estimates for the population from 1987-2015.  $N_i$  and adult male and female density estimates are corrected for trapping efficiency. Sex ratio of male:female adults (black line) is also provided, with a null equal sex ratio indicated by the dotted black line.

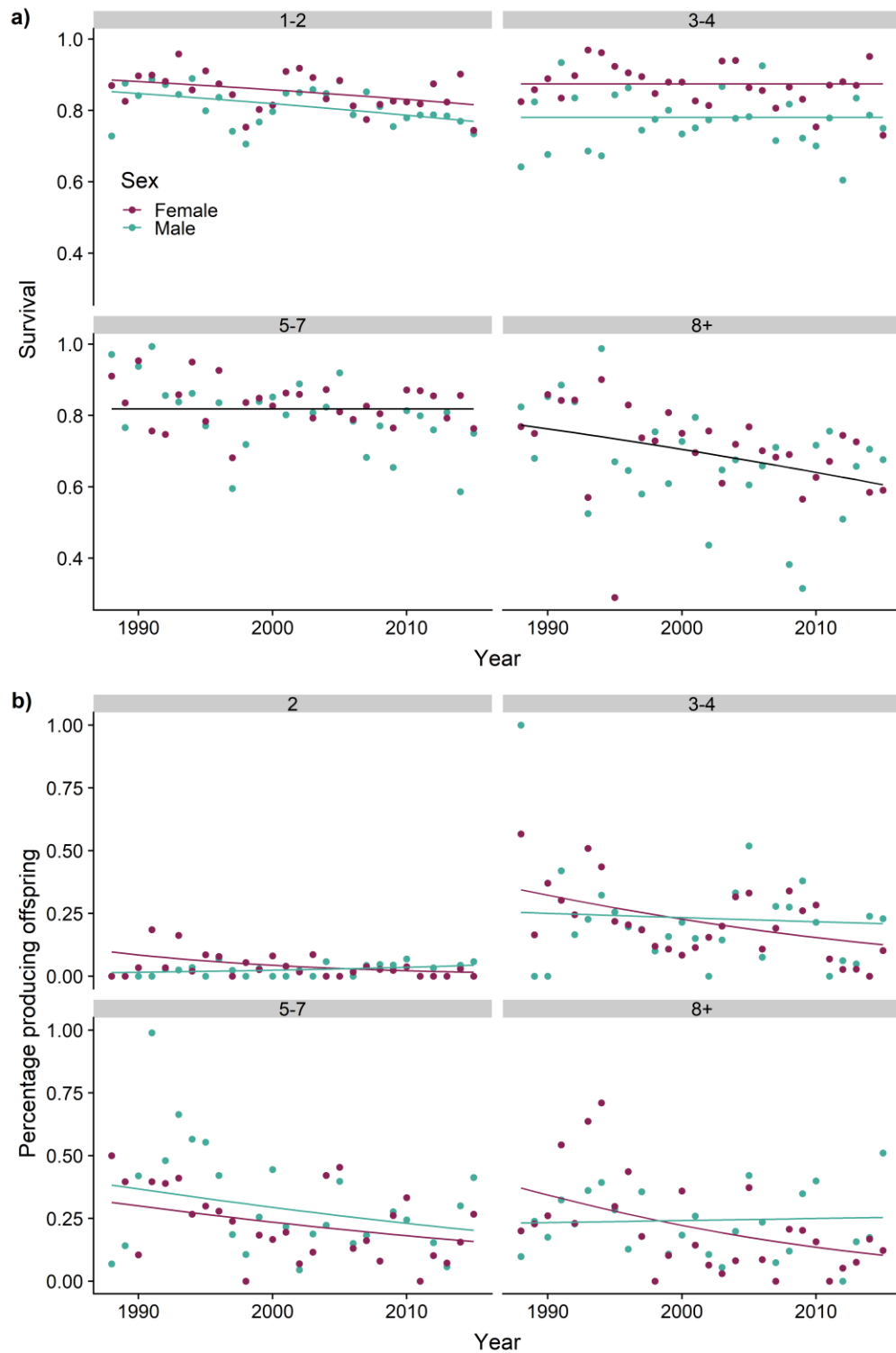


Figure 3 – Temporal trends in a) survival and b) percentage of individuals reproducing by age class and sex (male = cyan; female = magenta). Significant relationships shown by trend lines, with significant differences between sexes indicated by separate trend lines for each sex.

*Life history trade-offs*

We found substantial evidence of life history trade-offs, justifying the POLS framework for this study system. Realised lifespan was significantly related to age at first reproduction (females:  $p = 0.007$ ; males:  $p < 0.001$ ; Fig. 3a), with individuals that bred earlier living shorter lives than those that delayed reproduction, particularly in males ( $\beta_1 = 0.93 \pm 0.09$  years of realised lifespan gained per year that the onset of reproduction was deferred; vs  $\beta_1 = 0.38 \pm 0.14$  years in females, Fig. 3b). Models of year-to-year survival costs of reproduction also showed that each cub produced had a significant negative effect on female survival probability, controlling for age and annual weather conditions ( $\beta = -0.59$ ,  $p < 0.001$ ). For males, siring a cub was negatively correlated with survival to the next year, although not significantly so ( $\beta = -0.47$ ,  $p = 0.14$ ). However, for both sexes, we found a significant positive interaction between age and higher survival probability when reproducing (males:  $\beta = 0.13 \times \text{age} \times \text{sired cubs}$   $p = 0.03$ ; females:  $\beta = 0.07 \times \text{age} \times \text{cubs in litter}$ ,  $p = 0.003$ ).

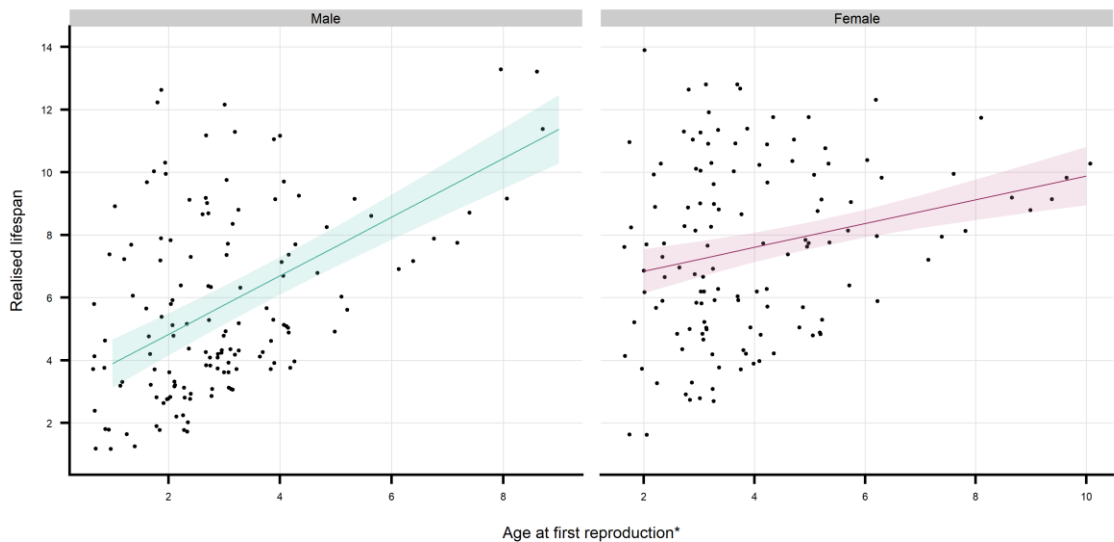


Figure 4 - Trade-off between age at first reproduction and realised lifespan by sex. Regression lines shown with 95% confidence interval.

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

Table 1 – All models of the drivers of life history metrics, as described in the text. If a covariate was not used in an analysis, this is indicated with “N/A”; if a covariate was included in model selection but not present in the final model, it is left blank. CS = cohort size; SR = male adults/female adults; N<sub>i</sub> = sex-specific adult density;  $\mu_T$  = mean annual temperature;  $\sigma_T$  = annual temperature variability;  $\alpha_T$  = annual temperature seasonality;  $\mu_R$  = annual mean rainfall; CV<sub>R</sub> = annual coefficient of rainfall variation; BCI<sub>T</sub> = sex, season, and age-controlled body condition. Significance levels provided for interpretability but should not be taken as traditional levels of significance. \*\*\* p < 0.001; \*\* p < 0.01; \* p < 0.05; . p < 0.1.

*Drivers of life history metrics*

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

Model set 1 showed relatively little influence of natal conditions on the subsequent lifetime pace-of-life of an individual, with only social conditions retained in final models (variance explained:  $F/\alpha_{\text{male}} = 0\%$  (null model selected),  $F/\alpha_{\text{female}} = 5.8\%$ ,  $\text{LRS}_{\text{male}} = 5.0\%$ ,  $\text{LRS}_{\text{female}} = 8.4\%$ ). Male cubs born in larger cohorts typically attained higher LRS while, for both sexes, pace of life was fastest (high LRS in males; high  $F/\alpha$  and LRS in females) when cubs were born with the population at a SR of approximately 0.8, and slower at higher and lower SR (Table 1). For instance,  $2.47 \pm 0.32$  SE cubs were predicted on average for a reproductive male born at the lowest SR of the study, compared to  $4.21 \pm 0.46$  SE for a reproductive male born at an SR of 0.8.

Model set 2 provided insights into year-to-year reproductive investment, with both social and weather conditions retained in final models (zero-inflated models were significantly better fits for annual individual cub production than simple Poisson models; Vuong test,  $p < 0.001$  for both sexes). Proportionally fewer individuals of both sexes reproduced at higher SR, and those that did reproduce produced fewer offspring. While higher female densities were typically associated with smaller female litters, higher male densities, counter-intuitively, were associated with a greater likelihood that a given male would breed successfully (Table 1). Proportionally fewer females bred in seasonally extreme years (higher  $\alpha_T$ ), and in warmer years, which were also associated with smaller litter sizes per reproducing female; however, we also found a positive effect of temperature variability ( $\sigma_T$ ) on female likelihood of breeding. Higher  $\text{BCI}_T$  had



a negative effect on the likelihood of producing offspring, although this effect was small (Table 1). A higher proportion of males bred successfully in years with higher temperature variability, while higher rainfall variability ( $CV_R$ ) covaried with more offspring sired in the following year. In males, we found a generally positive effect of BCI on the number of offspring sired.

Model set 3 corroborated the role of social conditions in driving POL outcomes. A greater proportion of males (productively) mated successfully for the first time at age 1 at higher male densities (our models predicted  $10.8\% \pm 0.46$  SE at the highest  $N_i$ , but only  $1.0\% \pm 0.5$  SE at the lowest  $N_i$ ); conversely, higher female densities led to fewer females commencing reproduction in their first viable year ( $2.4\% \pm 1.3$  SE of females producing cubs at age 2 at the highest  $N_i$ ;  $17.1\% \pm 8.7\%$  at the lowest). Closer to SR parity, females were more likely to produce their first litter of cubs at ages 4 or 5 (as many as  $36.6\% \pm 10.3$  SE at age 4 and  $37.8\% \pm 12.9\%$  at age 5). While more females produced their first litter at age 4 following warmer years ( $38.3\% \pm 16.0$  SE in the warmest years vs.  $3.3\% \pm 2.2$  SE in the coolest, holding SR constant at mean levels), higher mean temperatures were associated with fewer males beginning reproduction that late ( $39.4\% \pm 15.5\%$  at age 4 in the coldest years,  $2.1\% \pm 1.9$  SE in warm years, holding temperature seasonality constant at study average). More variable rainfall was also linked to higher likelihood of late-comer females beginning reproduction ( $41.8\% \pm 16.7$  SE vs.  $6.1\% \pm 3.3$  SE at age 5, holding SR constant at mean levels), while more seasonality reduced the likelihood of latecomer males doing the same at age 4, although this effect was only borderline significant ( $p = 0.054$ ,  $1.3\% \pm 1.6$  SE at least seasonal,  $35.2\% \pm 18.7$  SE at most seasonal, holding temperature constant at study average). Higher  $BCI_T$  was associated with an earlier onset of reproduction in both sexes (females at age 3:  $42.0\%$  in highest condition;  $6.3\%$  in lowest;

males:  $32.3\% \pm 9.5$  SE age 2,  $39.4\% \pm 13.6$  SE age 3 in best condition,  $2.2\% \pm 1.7$  SE age 2,  $1.9\% \pm 1.9$  SE age 3 in worst condition).

Model set 4 strongly supported the role of the reproductive competitive landscape in setting an individual's pace-of-life within long-term population demographics. Over the course of the study, SR parity was associated with a greater proportion (max 74% of males, 81% of females) of individuals above the long-term median  $F/\alpha$  (indicating more "fast" life history strategists); periods with higher sex-specific density ( $N_i$ ) had the opposite effect (indicating a preponderance of "slow" life history strategists). High female density co-occurred with low SR (Fig. 2), leading to a substantial slow-down in population-wide female POL during these years (Fig. 5a). In males, the decrease in sex-specific density from 1997-2007 (and resulting increase in females per reproductive male) meant that population  $F/\alpha$  distribution remained relatively constant (notwithstanding a brief slowdown following the population peak) despite overall increases in density relative to the beginning of the study (Fig. 5b). Overall, these social factors alone explained substantial variance in model set 4, particularly for females (males: 52.8% of variance explained; females: 91.0%), reinforcing the role of relative mate and competitor abundance on setting long-term population pace-of-life.

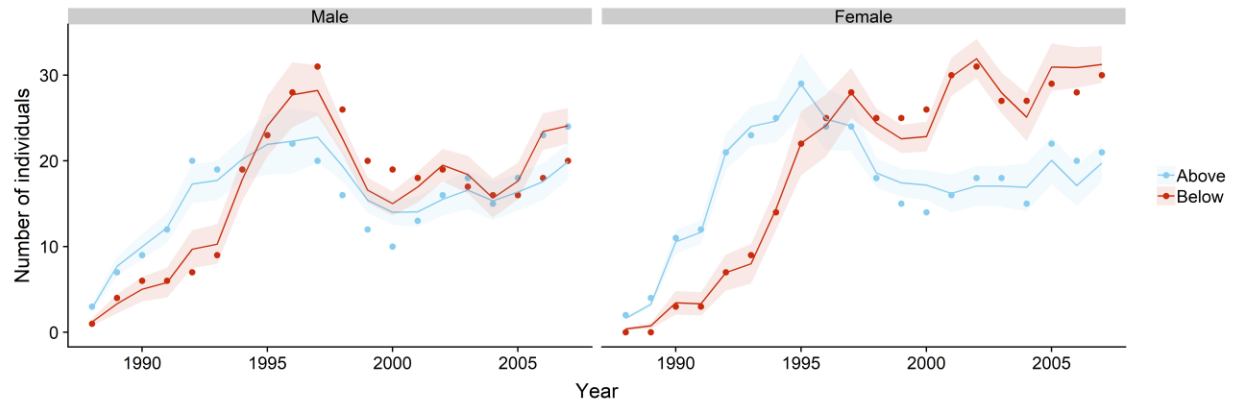


Figure 5 - Number of reproductive a) females and b) males in the population above (blue) and below (red) the long-term (1986-2007) individual median  $F/\alpha$  value. Points represent real data, lines are model predictions based on population sex ratio (males/females) and sex-specific population density, with 95% confidence intervals.

## 6. Discussion

We found strong support for reciprocal mechanisms linking individual life histories to population dynamics, with population density and relative sex ratio driving sex-specific effects. During a cub's first year, the population's demographic composition, but not weather, had an effect on individual lifetime POL for both sexes (model set 1, supporting the Reproductive Limitation Hypothesis over the Harsh Conditions Hypothesis), although this effect accounted for less than 10% of the variance in lifetime POL. Supporting the Later Drivers Hypothesis, year-to-year weather and demographic conditions subsequently had a much greater effect, honing reproductive investment and life histories (better fit of model sets 2-4). We found that weather conditions (as a proxy for food availability and thermoregulatory costs), and the linked metric of  $BCI_r$ , were differentially influential in males and females in relation to life history stage. Weather and  $BCI_r$  primarily affected the proportion of males successfully reproducing for the first time (model set 3); for females, the primary weather effect was on year-to-year reproductive investment (model set 2; partially confirming the Cautious Females Hypothesis). Differential

reproductive investment responses in relation to population dynamics were apparent in a regulatory feedback in the frequency with which early-breeding occurred in males, with implications for differential survival between and within the sexes.

While previous studies have focused on components of life histories set early in life (Liedtke et al. 2015, Krause et al. 2017), any amount of environmental stochasticity over an individual's lifespan represents a "moving target" for reproductive success (Tuljapurkar et al. 2009a), especially for longer-lived iteroparous species. Even after early-life, in longer-lived species environmental factors such as weather (Coulson et al. 2001), population dynamics (Stopher et al. 2008), and body condition (Descamps et al. 2006, Albon et al. 2017) can continue to cue attempts at reproduction and determine the likelihood of success (Hamel et al. 2009). Therefore, variation in life-history tactics allows "pivoting" to accommodate ongoing environmental stochasticity. The relatively small role that early-life factors played in badger life history exposes a dimension of resilience to change beyond the fixed behavioural phenotypes suggested by POLS theory (Dammhahn et al. 2018). Later-life conditions were much more predictive in model sets 2-4, particularly the size and sex composition of the population.

Generally, the relative abundances of potential mates and competitors (measured by SR) shape the marginal benefits of increased reproductive investment and therefore have far-reaching effects for individual life histories in animals (ranging from dendrobatid frogs, Pröhl 2002, to reindeer, Mysterud et al. 2003). However, we observed lower proportions of individuals breeding in both sexes at SR closer to parity—expected due to mate limitation for males, but not females (keeping in mind SR was never male-skewed). Moreover, the reduced female reproductive output at higher female densities (Table 1, model set 2) implies a breeding constraint for females beyond encounters with males. This likely results from inter-female competition within social

groups (Cresswell et al. 1992, Woodroffe and Macdonald 1995)—as seen in other stratified social mammal reproductive systems (e.g. meerkats: Clutton-Brock et al. 2010)—and the monopolisation of reproductive opportunities by more established individuals under conditions of intense reproductive competition (e.g. macaques: Kuester et al. 1995, reindeer: Røed et al. 2002).

Over the study period, the number of main sett sites increased from 23 in 1993 to 63 in 2002, in parallel with population density peaking in 1997 (Macdonald et al. 2004); inhabitants of new setts, however, exhibited no reduction in weight or body condition. High densities (and an even sex ratio, see Fig 2) preceded, and thus drove, the increase in sett sites. Thereafter, this socio-spatial reorganisation likely reduced female reproductive competition (and competition for other resources, according to the Local Resource Competition hypothesis; see Dugdale et al. 2003), facilitating the higher likelihood of an individual reproducing (for both sexes) at the female-skewed sex ratios observed later in the study. Therefore, although ~15% fewer females reached early primiparity at higher densities, this sett proliferation likely also explains why older, previously nulliparous, females became nearly 40% more likely to begin reproduction at the later female-skewed SR, potentially having been constrained from breeding previously.

As expected from competition-mediated male investments (Lodé 2009, Newbolt et al. 2017), when SR was more male-skewed—rather than simply when male density was high—a reduced proportion of males reproduced successfully (model set 2). Conversely, high male densities were actually associated with higher proportions of males successfully breeding (model set 2). Of course, as multiple paternity in litters is common in badgers (Dugdale et al. 2007), more males do not necessarily imply exclusion from paternity. However, we also observed that a) a subset of males exhibited more reproductive success in more competitive environments, with

as many as 10% of yearling males beginning reproduction at high male densities (contrary to the effect seen in females, and in keeping with the “early-developer” endocrinological phenotype identified in Sugianto et al. 2019) and b) male LRS peaked when cubs were born at an intermediate, rather than a strongly female-skewed, sex ratio (0.86 males to each female, model set 1). Therefore, while crowding at high female densities—and associated food limitation—decreased female litter size (model set 2) and the proportion of young females breeding (model set 3), and resulted in fewer “fast” female POL strategists (model set 4; Fig. 5), similar conditions actually increased reproductive output (and, presumably, reproductive investment) in a proportion of males.

Wild animals that invest disproportionately in reproduction over somatic conservation tend to “live fast” at the cost of “dying young” (Promislow and Harvey 1990, Hall et al. 2015). Males (particularly in scramble competition systems) often invest more in reproduction at higher relative competitor abundance (Weladji et al. 2005, Holwell et al. 2016), but at a cost: in our study, males that reproduced early did so at nearly three times the detriment to realised lifespan as females (Fig. 4) and, although the relationship was not significant, siring a cub was negatively associated with paternal survival probability. In addition to risking road traffic mortality (Macdonald et al. 2010, Canova and Balestrieri 2019) while searching for mates, the costs of elevated testosterone (Fargallo et al. 2007) have been linked to reduced survival probability in badgers (Buesching et al. 2009). Therefore, our findings emphasise the oft-ignored role reproductive effort can play in male survival (Bleu et al. 2016).

In relatively slow-lived animals, such as badgers (Macdonald et al. 2009), population growth is strongly dependent on adult survival (Oli and Dobson 2003). Therefore, the increased number of “fast-living” (and therefore, fast-dying; see Figs. 3 and 4) males observed at higher

male densities (Figs. 1c, 5) likely contributed to the diverging sex ratio (up to 60.2% female) observed following the population peak in 1997 (Fig. 2), consistent with other high density badger populations (Rogers et al. 1997). If we characterise these males as following quicker, cheaper strategies, we see selection against this strategy in favour of “slow and steady” strategists as density increases (and slight compensatory recovery of the “fast” strategists later on, see Fig. 5). These long-term regulatory dynamics of density-dependent selection for increases and die-offs of “fast-living” males support a risk-sensitive view of life-history strategy selection (Bårdsen et al. 2008).

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

Energy constraints, however, showed sex-specific effects, driving the age of first reproduction in males more strongly than in females. Earlier breeding (where conditions allow) can lead to a higher relative fitness advantage in males (*sensu* Oli and Dobson 2003). Age at first

reproduction should be more sensitive to environmental conditions in polygynous males than in females because, once breeding, males can simultaneously invest in multiple litters and therefore achieve a faster overall pace-of-life (Hämäläinen et al. 2018). Overall, while more variable temperatures and rainfall were positively associated with male reproductive success in a given year (Table 1, model set 2; suggesting some effect on mating effort in relatively low-cub mortality years, see Annavi et al. 2014a), warmer years were associated with virtually no “latecomer” males beginning reproduction at age 4 (compared with nearly 40% in colder years). Although this effect is difficult to separate from female litter failure, 30-40% younger males began reproduction as early as age 2 or 3 if they were in better body condition – a function of net energy gain. Parallel endocrinological work on this same population has found that male badgers require a minimum body size for the onset of puberty (Sugianto et al. 2019). Consequently, where weather and foraging conditions affect juvenile male growth, it can impede their “race to the starting line”, whereas female strategies are governed more by maintaining a “steady pace” once there. This is consistent with the faster overall male POL expected in polygynous species (Tarka et al. 2018).

Our study exemplifies why it is important to consider the demographic composition of populations, not simply population-wide metrics, when estimating population resilience (Keith et al. 2008, Isaac 2009). Various studies report that climate change can affect the sexes differently (Petry et al. 2016, Gianuca et al. 2019), in ways likely to impact the adaptive plasticity and resilience of populations (Le Galliard et al. 2005, Miller and Inouye 2013). Particularly, where climate applies fitness pressures that shift the distribution of fixed individual heterogeneity in populations, it may carry unforeseen consequences for population resilience and persistence (Jenouvrier et al. 2015). Ultimately, the extent to which a population is comprised of “fast” and



“slow” individuals, and their associated sex ratio, will substantially affect how that population might respond to chronic or acute pressures in the form of altered weather regimes (Forister et al. 2010, Schloss et al. 2012) or habitat deterioration (Watson et al. 2018).

Maintaining multiple POL strategists (Starrfelt and Kokko 2012), rather than simply maximising proximate fitness (Day and Taylor 1996), provides an evolutionary stable strategy in response to environmental stochasticity (Rajon et al. 2014, Ogura et al. 2017). However, HIREC risks exacerbating natural background selection pressures (Benton 2009), with the potential to drive maladaptive selection (Isaac 2009). Even if short-term benefits result from changing ratios of strategists, long-term instability may emerge (ecological “traps”, Le Galliard et al. 2005, Penteriani et al. 2018). Therefore, although adaptive plasticity to change is a key mechanism through which populations respond to rapid change (Berteaux et al. 2004, Silva et al. 2017), if anthropogenic selective pressures drive populations into maladaptive strategic compositions, it should also be examined as a potential liability. Ultimately, these types of cryptic qualitative changes in population composition must be incorporated into management programmes designed to minimize biodiversity loss under rapid climate change (Hoffmann and Sgrò 2011).

## 7. Acknowledgments

The authors would like to thank the People’s Trust for Endangered Species (PTES) for their support of the Wytham Badger Project for the first two decades of its operation. JGB was supported by a Marshall Scholarship during the design and execution of the manuscript and CN was funded by the H.N. Southern Fellowship in Ecology. The authors would furthermore like to thank Profs. Roberto Salguero-Gomez, Tim Coulson, and Michael Bonsall for their incisive and helpful advice in the design of the analyses.

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