Age-specific breeding success in a wild mammalian population: selection, constraint, restraint and senescence

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Abstract

The Selection, Constraint, Restraint and Senescence Hypotheses predict how breeding success should vary with age. The Selection Hypothesis predicts between-individual variation arising from quality differences; the other hypotheses predict within-individual variation due to differing skills or physiological condition (Constraint), residual reproductive lifespan (Restraint), or somatic and reproductive investment (Senescence). Studies tend to focus on either the initial increase in breeding success or later decrease; however, both require consideration when unravelling the underlying evolutionary processes. Additionally, few studies present genetic fitness measures and rarely for both sexes. We therefore test these four hypotheses, which are not mutually exclusive, in a high-density population of European badgers *Meles meles*. Using an 18-year data set (including 22 microsatellite loci), we show an initial improvement in breeding success with age, followed by a later and steeper rate of reproductive senescence in male than in female badgers. Breeding success was skewed within age-classes, indicating the influence of factors other than age-class. This was partly attributable to selective appearance and disappearance of badgers (Selection Hypothesis). Individuals with a late age of last breeding showed a concave-down relationship between breeding success and experience (Constraint Hypothesis). There was no evidence of abrupt terminal effects; rather, individuals showed a concave-down relationship between breeding success and residual reproductive lifespan (Restraint Hypothesis), with an interaction with age of first breeding only in female badgers. Our results demonstrate the importance of investigating a comprehensive suite of factors in age-specific breeding success analyses, in both sexes, to fully understand evolutionary and population dynamics.

Keywords: age-specific breeding success, constraint hypothesis, *Meles meles*, restraint hypothesis, selective disappearance, senescence

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Introduction

Reproductive lifespan and age-specific reproductive performance are key life-history traits affecting breeding success (Clutton-Brock 1988), providing insight into population dynamics and life-history evolution. Breeding success in iteroparous individuals generally shows an initial improvement with age, followed by a peak and then deterioration (Clutton-Brock 1988). Age-specific breeding success has been related to between-individual differences, due to selective appearance or disappearance of individuals, e.g. individuals that produce more offspring may first breed at a later age than individuals that produce fewer offspring; therefore, their selective appearance in the breeding population inflates the initial increase in breeding success with age (Van de Pol & Verhulst 2006). Age-specific breeding success has, however, also been linked to differences such as maturation (Krüger 2005), breeding experience

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(Bowen *et al.* 2006), physical condition (Robbins *et al.* 2006), dominance position (Cote & Festa-Bianchet 2001) and the number of helpers (Russell *et al.* 2007). These within-individual or between-individual processes provide the basis for four non-mutually exclusive hypotheses (the Selection, Constraint, Restraint, and Senescence Hypotheses) that may jointly explain age-specific variation in breeding success (reviewed in Forslund & Pärt 1995).

The Selection Hypothesis (Curio 1983; Nol & Smith 1987) predicts differential survival of individuals based on their phenotype, such that a cohort should consist of proportionally more 'good-quality' (i.e. fitter) individuals over time (Forslund & Pärt 1995). For example, New Zealand stitchbirds *Notiomystis cincta* show evidence of the loss of lower-fitness females with age (Low *et al.* 2007), and a similar loss under severe environmental conditions has been reported in Soay sheep *Ovis aries* (Tavecchia *et al.* 2005).

Within-individual processes could also lead to apparent improvement in breeding success with age, at the same time. The Constraint Hypothesis (Curio 1983) suggests that individuals may be constrained from breeding due to their physiological condition or their experience/skills. For example, individuals may gain experience from breeding or foraging, such that over time they improve their breeding performance. It predicts that individuals with breeding experience should perform better than inexperienced individuals of the same age, within the same breeding attempt (Nol & Smith 1987), as has been observed in grey seals *Halichoerus grypus* (Bowen *et al.* 2006) and captive chimpanzees *Pan troglodytes* (Fessler *et al.* 2005).

The Restraint Hypothesis (Williams 1966; Pianka 1976) proposes that reproductive effort varies according to an individual's residual reproductive lifespan. Younger individuals should refrain from breeding or reduce their effort, to improve their chances of survival and future reproduction (where this is possible), whereas older individuals should invest more in reproduction due to their diminished residual reproductive lifespan. This hypothesis predicts that inexperienced individuals will show increased reproductive expenditure with increased age at first reproduction (Forslund & Pärt 1995); weak evidence was found for the Restraint Hypothesis in female goshawks *Accipiter gentilis* (Krüger 2005). Within-individual differences consistent with both the Constraint and Restraint Hypotheses have been observed in Columbian ground squirrels *Spermophilus columbianus* (Broussard *et al.* 2003).

Within-individual deterioration, or senescence (the decrease in somatic or reproductive investment with age; in this article we focus on reproductive investment), also occurs, as documented in some wild-mammalian populations (Broussard *et al.* 2003, 2005; Bowen *et al.* 2006; Nussey *et al.* 2006; Robbins *et al.* 2006). There are two main theories for senescence, both of which rely on purifying selection being stronger on genes that act earlier rather than later in life (Hamilton 1966). The Mutation Accumulation Hypothesis (Medawar 1952) proposes that the gene pool accumulates weakly deleterious mutations that act late in life. The Antagonistic Pleiotropy Hypothesis (Williams 1957) suggests that traits selected to improve reproduction early in life have deleterious effects later in life when selection is weaker. There will, therefore, be positive selection favouring these genes, despite their negative effects late in life. For example, individuals that have been selected for an early age of first breeding (α) are expected under this hypothesis to have a faster rate of senescence, which will result in an earlier age of last breeding (ω). This prediction is not shared by the Mutation Accumulation Hypothesis (Charlesworth & Hughes 1996).

There has been a recent surge in studies that investigate this deterioration, or senescence (Nussey *et al.* 2008), with a bias towards documenting reproductive senescence in females (Bouwhuis *et al.* 2010; Hoffman *et al.* 2010; Sharp & Clutton-Brock 2010), and fewer studies in males (Brommer *et al.* 2007; Auld & Charmantier 2011), primarily because extra-pair paternity and plural breeding make it harder to quantify breeding success in males. It is important, however, to understand the complete pattern of how breeding success varies with age, in both males and females, to understand population dynamics and life-history evolution.

We examine the reasons underlying age-specific breeding success variation in both male and female European badgers *Meles meles* from a high-density population in Wytham Woods, Oxford, UK (Macdonald *et al.* 2009). This has not been possible previously, as genetic techniques are required to assign parentage, given that badger social-groups in lowland England contain more than one potential mother and father and, due to delayed implantation, mating can occur year-round (Yamaguchi *et al.* 2006) with cubs born and raised underground (Dugdale *et al.* 2010a). Two studies have shown that high-density badger populations exhibit a polygynandrous mating system, with plural breeding within groups, $\sim$ 50% extra-group paternity and multiple paternity within litters (Carpenter *et al.* 2005; Dugdale *et al.* 2007). Reproduction is slightly skewed within social groups; among females this is attributable to local resource availability and incomplete reproductive suppression (Dugdale *et al.* 2008).

Recruitment is low [42% of badgers with known lifetime breeding data, that reached breeding age, were not assigned any offspring (based on offspring that

survived to independence, of which 83% were assigned a father and 82% a mother), Dugdale *et al.* 2010b], and although alloparental care occurs no fitness benefits of this have been established (Dugdale *et al.* 2010a). Breeding success is reduced in young (2 years) and old (>8 years) badgers (Carpenter *et al.* 2005); however, the reasons for this are unknown.

We therefore quantify breeding success in European badgers and ask whether (i) breeding success is age-specific, with an initial increase and later decrease in breeding success with age. We then test whether our results are consistent with four hypotheses, by asking whether breeding success is correlated: (ii) positively with age of last breeding (selective disappearance) – the Selection Hypothesis (Curio 1983; Nol & Smith 1987); (iii) positively with the number of years that individuals had previously raised offspring successfully to independence – the Constraint Hypothesis (Curio 1983); (iv) positively with residual reproductive lifespan – the Restraint Hypothesis (Williams 1966; Pianka 1976); and (v) negatively with old age – the Senescence Hypothesis (Nussey *et al.* 2008), excluding the years prior to the peak in breeding success (i.e. to rule out a statistical artefact).

Materials and methods

Our study was conducted in Wytham Woods, Oxfordshire, UK (01°19′W, 51°46′N), a 4-km^2 area of deciduous woodland surrounded by mixed arable and permanent pasture (Macdonald *et al.* 2004). Between 1987 and 2005, badgers were trapped at least four times a year, over 1 week in January and 2 weeks in June, August and November. Badgers were sedated by an intra-muscular injection of ∼0.2 ml/kg ketamine hydrochloride, identified through a tattoo, sexed, and their tooth wear graded on a five-point scale. Upon first capture, badgers were classified as cubs or adults, according to their size and dentition; only individuals that were first trapped as cubs were included in our age analyses. Blood or guard hair samples were collected from 915 badgers, from which DNA was extracted, amplified and genotyped for 22 microsatellite loci as described in Dugdale *et al.* (2007).

We used parentage results, published previously (Dugdale *et al.* 2007), in which candidate mothers and fathers were selected for parentage analyses according to biological rules and trapping data. Female badgers give birth once a year, around February. Females are first capable of conceiving as yearlings and, due to delayed implantation (reviewed in Yamaguchi *et al.* 2006), they give birth in their second year. Candidate mothers were thus reproductive females (aged 2 years or more) present in the cub's social group in the year the cub was born. Candidate fathers were all males that were at least 1 year old and present in Wytham Woods in the calendar year before the cub was born. As badgers may be present but not trapped, adults and yearlings were included for two calendar years after their last date of capture, and cubs for 1 year (Macdonald & Newman 2002). Badgers first trapped as adults (261/915) with a tooth wear of 4–5 were considered to be at least 2 years old, otherwise they were classified as at least 1 year old (da Silva & Macdonald 1989).

CERVUS 3.0.1.8 (Kalinowski *et al.* 2007) and COLONY 1.2 (Wang 2004) were used to assign parent-pairs to and infer sibships among 630 genotyped cubs, from a total of 735 cubs born between 1988 and 2005 (Dugdale *et al.* 2007). These programs account for the presence of unsampled parents and genotyping error; additionally, CERVUS is currently the only parentage software that enables specification of the presence of relatives of the offspring among candidate parents, which is important as badgers are highly philopatric (Pope *et al.* 2006) such that many relatives will be present in the population (Dugdale *et al.* 2008). Both parents were assigned to 595 cubs (94% of those genotyped and 81% of those trapped), maternity to 602 (96% and 82%) and paternity to 611 (97% or 83%) with 80% confidence (Dugdale *et al.* 2007). A level of 80% confidence is commonly used in CERVUS analyses (Kalinowski *et al.* 2007) and within our study population this produced comparable estimates of litter size, as did assignments with 95% confidence (Dugdale *et al.* 2007). Only 53% of the genotyped cubs were assigned both parents with 95% confidence, however, which reduced the estimates of the number of breeders in a social group substantially. Breeding badgers were, therefore, interpreted to be those that were assigned offspring with at least 80% confidence, and whose offspring survived to independence (at least 12–15 weeks of age) and were then trapped and genotyped. This measure only includes breeding attempts that successfully reached the end of parental investment, as this is the first time-point at which we can count breeding attempts. Reproductive failure may, however, occur at all stages of pregnancy or rearing (Dugdale *et al.* 2008; discussed in: Yamaguchi *et al.* 2006). Badgers that were at least 2 years old and not assigned as a parent in a given year were assigned a breeding success of zero for that year. Although parents may gain some breeding experience by producing offspring that do not survive to independence, selection must be strongest for raising offspring successfully to independence.

We calculated age at first breeding (α – the age at which an individual was first assigned as a parent) for 233 badgers (126 males and 107 females) that were first trapped as cubs, and therefore of known age. Age of

last breeding (ω – the age at which an individual was last assigned as a parent) was estimated for 154 badgers (90 males and 64 females) that were caught as cubs and considered dead by the end of 2005. Lifetime breeding success (Brommer *et al.* 2004) was calculated for 337 badgers that were of known age, survived to breeding age (irrespective of whether they were assigned parent-age in their lifetime) and were considered dead by the end of 2005 (i.e. adults that were not trapped for 2 years, and cubs for 1 year, after their date of last capture). Lifetime breeding success was calculated as the number of trapped and genotyped offspring (i.e. cubs that at least reached independence, at 12–15 weeks of age, and were later trapped and genotyped) that were assigned to a badger over its lifetime.

We quantified the degree of reproductive skew (the proportion of individuals of each sex in a group that reproduced in that group) among age-categorized badgers by calculating the binomial skew index, *B* (Nonacs 2000) using methods described by Dugdale *et al.* (2008).

Statistical analyses

Statistical analyses were run in SAS 9.2 (Littell *et al.* 2006), unless otherwise stated, using a data set of the number of cubs assigned each year to known-age females ($n = 195$; 88 never bred; 64 had a known ω) and males ($n = 271$; 145 never bred; 90 had a known ω). Means are provided with the 95% confidence interval and sequential probability values are presented (due to the inclusion of higher-order effects), unless otherwise stated.

Age-specific breeding success. We first used the GLIMMIX procedure to model the number of cubs assigned each year to females ($n = 64$; 498 observations) and males ($n = 90$; 555 observations) of known age (i.e. first caught as a cub) and lifetime breeding success, separately for each sex. As the responses were count data we ran Generalized Linear Mixed Models (GLMMs) with Poisson-distributed error and log link. We used a residual pseudo-likelihood method, which iteratively applies linear mixed-model estimation based on an approximated model, where the fixed effects are generalized least-squares estimates, and the covariances are maximum-likelihood estimates (Littell *et al.* 2006). We included an over-dispersion parameter when the ratio of the generalized χ^2 statistic and its degrees of freedom to the Pearson statistic for the conditional distribution was greater than the Pearson-type residual (Littell *et al.* 2006); we checked that a negative binomial distribution did not provide a better fit than the Poisson distribution. We used a response-surface model (Box & Draper

1987), which specified linear and quadratic covariates of age, to test for within-individual differences, and α, α^2, ω and ω^2 to control for differences between individuals (Van de Pol & Verhulst 2006). Year was also included as a fixed effect to correct for year effects, and we included first-order interactions between age, α and ω.

In mixed models in SAS, random effects are specified to control for variance between individuals, and repeated effects are specified to control for covariance between pairs of observations taken on the same individual. Modelling the covariance structure between repeated measures is important, given that measures, taken on the same individuals, that are closer together in time are more likely to be highly correlated (Littell *et al.* 1998). Badger identity was therefore entered as a random effect, and as a repeated effect with autoregressive covariance structure. We used the Kenward-Roger denominator degrees of freedom method to correct for downward bias in the standard error estimates in the covariance matrix (Littell *et al.* 2006).

Parameter estimates from GLMMs with Poisson error-distribution and a pseudo-likelihood method can be biased, whereas Laplace approximation is more accurate but less flexible (Bolker *et al.* 2009). We therefore ran modified models [removing unsupported methods: R-matrix random effects (as a valid conditional distribution is required) and Kenward-Roger degrees of freedom method] with Laplace approximation; this did not alter our conclusions (results not presented). Additionally, as badgers were included as candidate parents for two calendar years after their last capture (Dugdale *et al.* 2007), we re-ran our models including individuals only until their year of last capture to ensure this did not bias our results.

We assessed whether factors other than age-class also influenced breeding success, by testing for *B* in breeding success within age-classes, among both males and females, using SKEW CALCULATOR 2003 1.2 (see: http://www.eeb.ucla.edu/Faculty/Nonacs/shareware.htm, Nonacs 2000) and methods described by Dugdale *et al.* (2008).

Terminal effects (individuals investing differently in their last breeding attempt) could alter conclusions about age-specific breeding success (Rattiste 2004), especially when there are fewer data points at older ages (Bouwhuis *et al.* 2009). We therefore ran the GLMMs again to test for terminal effects by including a binary term, scored as 1 for the last breeding attempt of an individual (whether or not this was successful) and 0 for all other times. We included the interaction between the terminal effect and age. This was run for the whole data set and the data set including candidate parents only until their year of last capture.

Testing the Selection Hypothesis. We included α and ω, in the previous analysis of age-specific breeding success, to control differences between individuals in selective appearance and disappearance, respectively (Van de Pol & Verhulst 2006). We also included first-order interactions between age, α and ω to test for age-specific effects in individuals with different reproductive lifespan.

Testing the Constraint Hypothesis. We tested whether the breeding success of badgers differed according to the number of years in which they had previously succeeded in raising offspring to independence. As the number of years of experience is highly correlated with age, we substituted the linear and quadratic covariates of age with the linear and quadratic covariates of the number of years of experience in our model of age-specific breeding success, and similarly re-ran the model excluding individuals after their last capture.

Testing the Restraint Hypothesis. For 24% males and 19% females, their estimated maximum age equalled ω; hence, residual reproductive lifespan (RRL) was ω minus age, so it was not possible to fit all of these effects in the same model (McCleery *et al.* 2008) as one would be effectively entering the same term twice. We, therefore, substituted age for RRL in our model of age-specific breeding success, and similarly re-ran the model excluding individuals after their last capture.

Reproductive Senescence Hypothesis. In a quadratic model, a decreased breeding success later in life may be an artefact of increased breeding success early in life, if breeding success asymptotes but does not then decline (McCleery *et al.* 2008; Bouwhuis *et al.* 2009). We, therefore, identified the age class with the highest breeding success (5 years; Fig. 1a) and analysed breeding success from this age onwards (*n* = 59 females and 72 males with complete lifetime breeding data) to test whether breeding success decreased with age. The model was similar to the first age-specific breeding success model described above, except that neither age[2] nor the non-significant interaction between α and ω were included.

Results

Age-specific breeding success

The age of both females and males had a significant negative quadratic effect on breeding success, showing that within individuals the number of cubs assigned increased with young age, peaked at 5 years in males and 3 years in females, and decreased with old age (Fig. 1a; Table 1). The same negative quadratic result
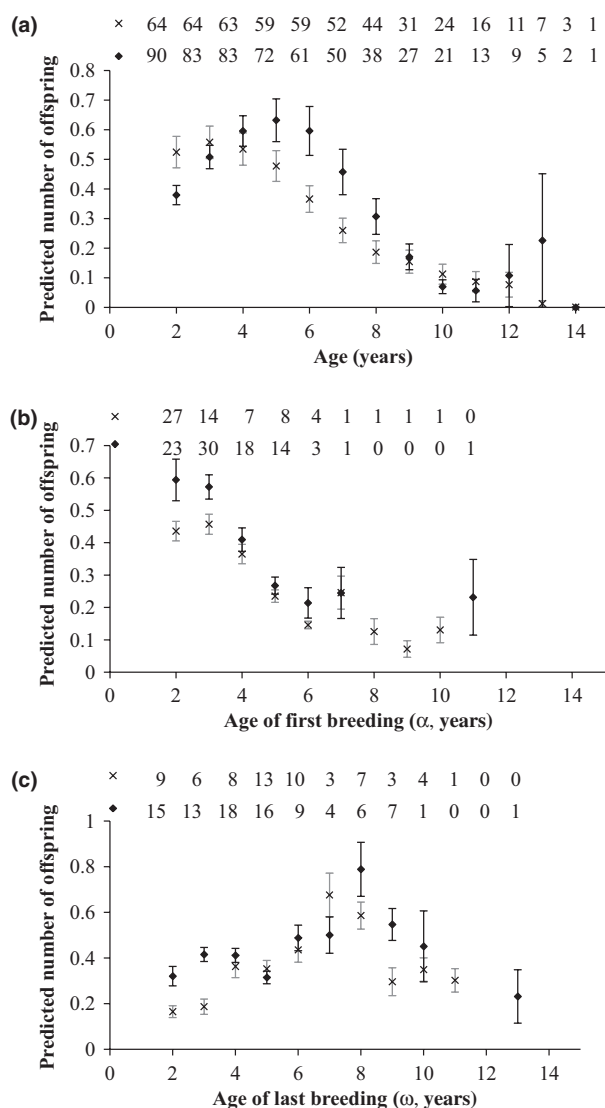
Fig. 1 The predicted mean number of cubs, from GLMMs, assigned to females and males according to: (a) age; (b) age of first breeding (α); and (c) age of last breeding (ω). Parentage was assigned with 80% confidence, and was based on 251 and 185 cubs whose fathers and mothers, respectively, had complete lifetime breeding success data. Error bars display the standard errors of the means. Data labels display the number of badgers present in each age category; the Generalized Linear Mixed Models control for repeated measures on the same individual. x = female; ♦ = male.

was observed when only data up to the last year of capture were included in both sexes (females: estimate = −0.12 ± 0.02, $F_{1,203.2}$ = 8.8, P = 0.0034; males: estimate = −0.23 ± 0.03, $F_{1,189.2}$ = 29.4, P < 0.0001; Table S1, Supporting information).

Variation in breeding success within age-classes, among males and females, however, indicated significant reproductive skew, such that factors other than the age influenced breeding success (Table 2).

Table 1 The effects of age at breeding, selective appearance (age of first breeding – α), selective disappearance (age of last breeding – ω) and their interactions, on the number of offspring assigned each year. Year of breeding was included as a fixed effect. Badger identity (individual variance) was included as a random factor and as a repeated factor with autoregressive covariance structure. Significant *P*-values are in bold

	Females					Males				
	Estimate	SE	d.f.	*F*	*P*	Estimate	SE	d.f.	*F*	*P*
Intercept	−14.85	54.79	—	—	—	78.95	48.02	—	—	—
Year	0.01	0.03	1,218.7	94.1	**<0.0001**	−0.04	0.02	1,537.8	41.4	**<0.0001**
Age	−0.64	0.14	1,217.7	31.3	**<0.0001**	−0.29	0.18	1,544.0	37.2	**<0.0001**
Age^2	−0.12	0.02	1,237.8	21.1	**<0.0001**	−0.23	0.03	1,511.3	43.9	**<0.0001**
α	−0.40	0.19	1,198.9	0.2	0.6993	−0.42	0.22	1,522.3	15.5	**<0.0001**
α^2	−0.10	0.03	1,198.7	24.2	**<0.0001**	−0.09	0.04	1,537.3	12.4	**0.0005**
ω	0.68	0.14	1,204.5	78.4	**<0.0001**	0.41	0.19	1,261.7	33.5	**<0.0001**
ω^2	−0.09	0.01	1,111.7	21.8	**<0.0001**	−0.08	0.02	1,142.1	4.0	**0.0474**
Age × α	0.20	0.03	1,205.0	68.0	**<0.0001**	0.28	0.05	1,512.1	64.0	**<0.0001**
Age × ω	0.16	0.02	1,215.5	49.2	**<0.0001**	0.25	0.03	1,515.3	59.0	**<0.0001**
α × ω	−0.02	0.03	1,113.4	0.5	0.4841	−0.10	0.05	1,88.0	3.8	0.0540
Individual variance	0.00	0.03	—	—	—	0.07	0.05	—	—	—
Autoregressive covariance	−0.11	0.05	—	—	—	−1.00	.	—	—	—
Residual variance	0.00	.	—	—	—	0.88	0.06	—	—	—
Overdispersion	0.68	0.05	—	—	—	0.00	.	—	—	—

Table 2 Reproductive skew (*B*), within age-categories (years), in the annual number of offspring assigned to badgers. Individuals included in the analysis were of known age and assumed dead by the end of 2005. Age was analysed up to 9 years, as there were too few breeders in the older categories to enable analysis. LCI and UCI = lower and upper confidence interval, respectively. Significant *P*-values are in bold

	Females				Males			
Age	*B*	LCI	UCI	*P*	*B*	LCI	UCI	*P*
2	0.010	0.002	0.027	**0.0071**	0.004	−0.038	0.023	0.1831
3	0.011	0.001	0.030	**0.0064**	0.017	0.009	0.032	**<0.0001**
4	0.006	−0.028	0.021	0.0665	0.015	0.006	0.029	**<0.0001**
5	0.009	−0.033	0.032	**0.0249**	0.036	0.021	0.057	**<0.0001**
6	0.029	0.005	0.077	**0.0037**	0.030	0.013	0.061	**<0.0001**
7	0.051	−0.123	0.224	**0.0412**	0.032	−0.076	0.100	**0.0389**
8	0.012	−0.082	0.075	0.1144	0.086	0.023	0.213	**0.0006**
9	0.035	−0.163	0.271	**0.0397**	0.022	−0.108	0.144	0.2009

There was no evidence of an abrupt terminal effect (females: estimate = −0.82 ± 0.88, $F_{1,477.5} = 0.0$, *P* = 0.92; males: estimate = −0.67 ± 0.48, $F_{1,528.5} = 3.2$, *P* = 0.07) or of an interaction of this with age (females: estimate = 0.03 ± 0.13, $F_{1,484.2} = 0.1$, *P* = 0.80; males: estimate = 0.05 ± 0.09, $F_{1,533} = 0.3$, *P* = 0.57; Table S2, Supporting information). Neither was there evidence of an abrupt terminal effect when we only included individuals until their last year of capture (females: estimate = −1.15 ± 0.54, $F_{1,344.6} = 0.6$, *P* = 0.46; males: estimate = −1.84 ± 0.54, $F_{1,333.9} = 0.0$, *P* = 0.98) nor was there an interaction between the terminal effect and age (females: estimate = 0.11 ± 0.10, $F_{1,342.6} = 1.4$, *P* = 0.24; males: estimate =

−0.17 ± 0.10, $F_{1,342.2} = 2.7$, *P* = 0.10; Table S3, Supporting information).

Selection Hypothesis

There was a negative effect of α on breeding success in both sexes, showing that, over all ages, badgers that had an earlier α were assigned more offspring; however, the smaller negative quadratic effect of α indicated a concave-down relationship such that the deterioration in breeding success with a later α becomes stronger with a later α (Fig. 1b; Table 1). Similarly, in both sexes the negative quadratic effect of ω on breeding success

indicated a concave-down relationship such that individuals of intermediate ω were assigned more offspring, with breeding success peaking when ω was 7 years in females and 8 years in males (Fig. 1c; Table 1). This demonstrates selective disappearance of lower-quality individuals (that are assigned fewer offspring in a year) with an early ω.

The relationship between breeding success and age in both sexes, however, differed for individuals of different α and different ω (Fig. 2). The positive interaction between α and age indicated that the decrease in breeding success with increased age was weaker with later α (Fig. 2a,b). The positive interaction between ω and age indicated that the concave-down relationship between breeding success and age became stronger with a later ω, such that there was a steeper increase in breeding success at early ages and a steeper decline in breeding success later in life with a later ω (Fig. 2c,d).

Constraint Hypothesis

There was a positive interaction between experience and ω in both males and females (Table 3), with a shallow decrease in breeding success for early ω and a concave-down relationship only apparent with late ω (Fig. 3; running a model with an interaction between experience-squared and ω confirmed this: female estimate = -0.08 ± 0.03, $F_{1,256.6} = 5.2$, $P = 0.0229$; male estimate = -0.11 ± 0.04, $F_{1,297.9} = 12.3$, $P = 0.0005$). The number of cubs sired decreased with an increase in the number of years that a male had previously been assigned paternity, but this was primarily due to a sharp decrease for

the one male with 6 years of experience (Fig. 3b). Excluding this data point, there was a marginal concave-down relationship between the number of cubs sired and experience (estimate = -0.21 ± 0.06; $F_{1,288.2} = 3.4$, $P = 0.0684$). The same relationships were seen when individuals were excluded after their last date of capture, for both sexes (Table S4, Supporting information).

Restraint Hypothesis

The RRL of both sexes had a significant negative quadratic effect on breeding success, showing that within individuals the number of cubs assigned was lower at large and small RRL (Table 4; Fig. 4a). This relationship was masked partially by selective appearance and disappearance of both sexes: females displayed a small positive linear relationship between breeding success and α (although the standard error was large), and a concave-down relationship between breeding success and ω; in males, breeding success increased with an earlier α and a later ω (Table 4). A negative interaction between RRL and α in females indicated that the relationship between breeding success and RRL differed for females of different α, such that females with an earlier α showed a more concave-down relationship between breeding success and RRL than females with a later α (Fig. 4b); this effect was not significant in males (Table 4).

The quadratic relationship between breeding success and RRL did not hold when data from 2 years after last capture were excluded (females: estimate = -0.01 ± 0.01,
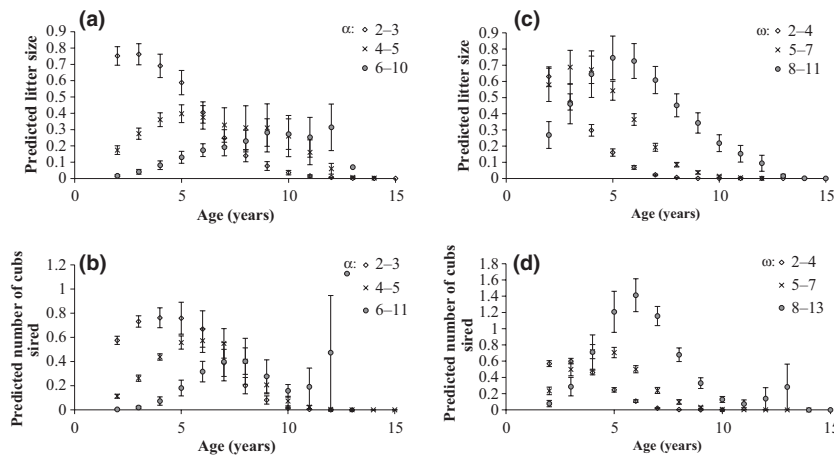

Fig. 2 The predicted mean number of cubs assigned to (a) females and (b) males classified by three categories of age of first breeding (α), and (c) females and (d) males classified into three categories of age of last breeding (ω). α and ω were categorized for ease of visualization; they were continuous effects in the Generalized Linear Mixed Models (GLMMs). Predicted values are from GLMMs controlling for year, repeated measures on the same individual, and either α (a & b) or ω (c & d). Error bars display the standard errors of the means. Individuals have predicted values before their age of first breeding and after their age of last breeding, as they were present in the population and sexually mature.

Table 3 The effects of the number of previous years of successful breeding experience (exp), selective appearance (age of first breeding – α), selective disappearance (age of last breeding – ω) and their interactions, on the number of offspring assigned each year. Year of breeding was included as a fixed effect. Badger identity (individual variance) was included as a random factor, and as a repeated factor with autoregressive covariance structure. n/a = not applicable. Significant *P*-values are in bold

	Females					Males				
	Estimate	SE	d.f.	*F*	*P*	Estimate	SE	d.f.	*F*	*P*
Intercept	50.15	56.66	—	—	—	60.33	50.89	—	—	—
Year	−0.03	0.03	1,159.1	37.1	**<0.0001**	−0.03	0.03	1,217.2	11.6	**0.0008**
Exp	−1.45	0.29	1,170.7	2.1	0.1515	−1.68	0.35	1,221.5	4.0	**0.0475**
Exp^2	−0.13	0.05	1,228.2	0.2	0.6482	−0.22	0.06	1,284.4	0.0	0.9912
α	−1.12	0.25	1,159.5	3.8	0.0543	−1.09	0.26	1,128.2	6.4	**0.0125**
α^2	−0.04	0.03	1,131.7	0.4	0.5167	−0.06	0.05	1,128.8	1.2	0.2696
ω	0.83	0.18	1,90.8	36.9	**<0.0001**	0.61	0.22	1,144.3	33.6	**<0.0001**
ω^2	−0.10	0.02	1,74.9	9.6	**0.0028**	−0.11	0.03	1,84.2	0.5	0.4725
Exp × α	−0.11	0.08	1,205.6	3.3	0.0731	−0.25	0.08	1,295.8	1.1	0.2857
Exp × ω	0.24	0.04	1,237.5	21.5	**<0.0001**	0.40	0.06	1,286.6	39.4	**<0.0001**
α × ω	0.15	0.04	1,108.2	12.0	**0.0008**	0.19	0.07	1,105.1	8.4	**0.0046**
Individual variance	0.02	0.05	—	—	—	0.14	0.07	—	—	—
Autoregressive covariance	0.04	0.05	—	—	—	−0.01	0.05	—	—	—
Residual variance	0.86	0.06	—	—	—	1.17	0.07	—	—	—
Overdispersion	n/a					n/a				

$F_{1,347.0} = 0.4$, $P = 0.52$; males: estimate = $−0.01 ± 0.02$, $F_{1,203.3} = 1.5$, $P = 0.23$), but there was a negative relationship, such that the number of offspring still decreased as sign-reversed RRL decreased (females: estimate = $−0.41 ± 0.14$, $F_{1,346.9} = 5.1$, $P = 0.0246$; males: estimate = $−0.11 ± 0.19$, $F_{1,143.7} = 9.6$, $P = 0.0024$; Table S5, Supporting information). The relationship between breeding success and RRL in females was still influenced by a negative interaction with α, but this was also significant in males (Table S5, Supporting information).

Reproductive Senescence Hypothesis

Restricting the analysis to badgers that were at least 5 years old confirmed the occurrence of reproductive senescence: reproductive output decreased with age for both females (estimate = $−2.10 ± 0.30$, $F_{1,163.3} = 5.7$, $P = 0.0184$) and males (estimate = $−2.74 ± 0.31$, $F_{1,117.7} = 4.0$, $P = 0.0492$; Table S6, Supporting information).

Discussion

Reproduction may be reduced within young individuals (due to reproductive restraint or constraint) and between young individuals (due to selection for superior reproductive performance, Curio 1983; Forslund & Pärt 1995; Williams 1966). It may also be reduced within older animals due to senescence (Medawar 1952; Williams 1957). We demonstrate that it is important to assess all of these processes, in both sexes, when analy-sing age-specific breeding success to gain a complete understanding of the underlying evolutionary processes.

The age of a male or female had a significant effect on the number of cubs that were assigned to them, with lower reproductive rates observed in younger and older individuals. This is consistent with general trends in other mammals (reviewed in Clutton-Brock 1988); however, very little was known about age-specific breeding success in badgers, given the need for genetic markers to assign parentage. In our analyses, components of age-specific breeding success are the probability of individuals breeding each year (badgers produce cubs only once a year) and the assigned litter-size of breeders. We, therefore, analysed the assigned litter-sizes of males and females, excluding individuals that were not assigned parentage in a given year (Supporting information). This showed a concave-down relationship with age in males, but this was not significant in females (Table S7, Supporting information). Litter size, therefore, does not vary with the age of a mother, but the number of offspring is reduced in younger and older fathers (pre-emergence litter size could vary but we were unable to investigate this with our data set). Both sexes, however, had a lower probability of being assigned parentage when younger or older, than at middle age (Table S8, Supporting information). The mean number of cubs that badgers were predicted to produce according to age is therefore low, given that breeding badgers were only assigned parentage in 36 ± 4% (males) and 29 ± 4% (females) of the years
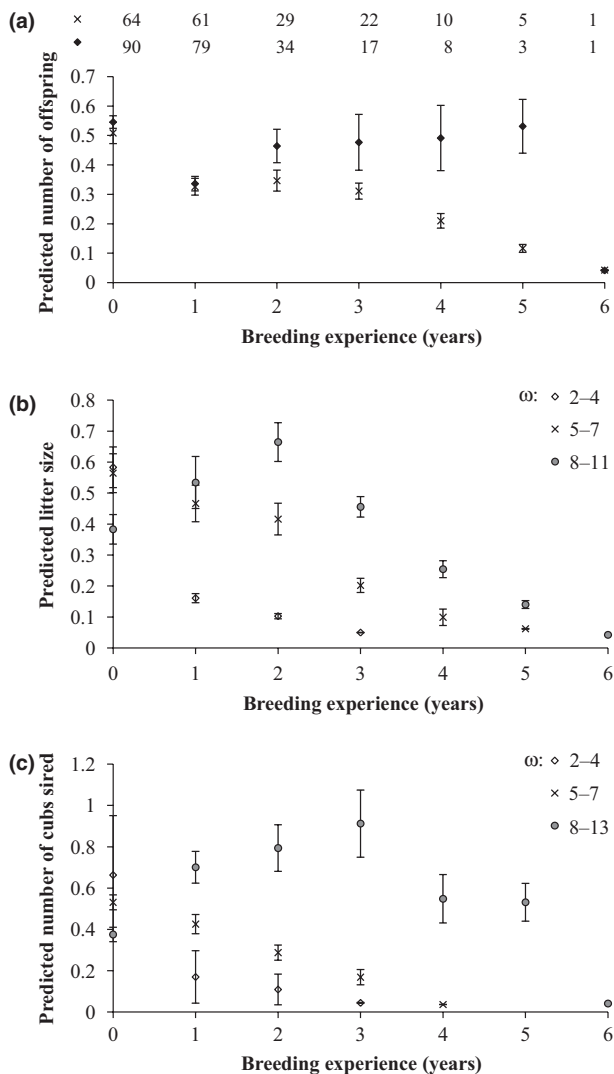
Fig. 3 The predicted mean number of cubs sired, from Generalized Linear Mixed Models (GLMMs), according to (a) the number of years of successful breeding experience for both males (♦) and females (x), and the number of years of successful breeding experience and age of last breeding (ω) for (b) females and (c) males. ω was categorized for ease of visualization; it was a continuous effect in the GLMMs. Error bars display the standard errors of the means. Data labels in (a) display the number of individuals present in each experience category.

in which they were included as potential breeders (Dugdale *et al.* 2010b).

Although cross-sectional patterns can differ from longitudinal patterns (Bouwhuis *et al.* 2009), our finding of an initial increase in breeding success with age is consistent with a cross-sectional field study that found that more two-year-old females than those 3 years or older failed to lactate (da Silva *et al.* 1994). This pattern has also been reported in field studies of other populations

(Cheeseman *et al.* 1987; Harris & Cresswell 1987; Revilla *et al.* 1999; Carpenter *et al.* 2005), post-mortem studies (Ahnlund 1980; Anderson & Trewhella 1985; Whelan & Hayden 1993) or both (Cresswell *et al.* 1992).

Our age-specific within-individual patterns of breeding success in badgers are consistent with the only previous longitudinal analysis of genetic breeding success, from a similarly high-density badger population in Woodchester Park (which controlled for repeated measures on the same individual, but not for α or ω, Carpenter *et al.* 2005). The inclusion of α and ω in our models, however, showed that, as well as being influenced by within-individual processes, performance at all ages was affected by between-individual processes, through selective appearance and disappearance of individuals (Curio 1983; Nol & Smith 1987). This was expected, given that lifetime fitness measures showed selection for an early α, and for a late ω up to 8 years of age in our population (Dugdale *et al.* 2010b). These between-individual processes therefore partially masked the overall pattern of age-specific breeding success. For example, individuals with low reproductive performance have a later α, so their selective appearance inflates reproductive senescence. Additionally, individuals with an earlier ω have decreased performance, so their selective disappearance inflates the initial improvement (Selection Hypothesis) and deflates reproductive senescence; however, individuals with a later ω also have reduced performance, producing the opposite effect. Selective disappearance of individuals with an early ω may be due to a cost of breeding at a young age, as lactating two-year-old females displayed a higher mortality rate than two-year-old females that did not lactate (Woodroffe & Macdonald 1995a).

Correlational selection-gradient analysis has shown that badgers are selected to breed at an early α independent of ω (Dugdale *et al.* 2010b); similarly, we did not find an interaction between α and ω. Interactions between age and both α and ω, however, showed the importance of accounting for how age-specific breeding success differs for individuals of different breeding lifespan. Our analyses assumed that the number of offspring assigned to a badger accurately reflected fitness (the relative contribution of a genotype to the next generation). This is reasonable, given that over the study period the number of offspring assigned correlated with the number of grand-offspring assigned (Dugdale *et al.* 2010b). The population size, however, did increase and then stabilized over the study period (Dugdale *et al.* 2007; Macdonald *et al.* 2009); therefore, future use of fitness measures that control for population growth rate may reduce noise in the analyses.

The Constraint Hypothesis predicts that an initial increase in breeding success with age is due to the

Table 4 The effects of residual reproductive lifespan (RRL), selective appearance (age of first breeding – α), selective disappearance (age of last breeding – ω) and their interactions, on the number of offspring assigned each year. Year of breeding was included as a fixed effect. Badger identity (individual variance) was included as a random factor and as a repeated factor with autoregressive covariance structure. Significant *P*-values are in bold

	Females					Males				
	Estimate	SE	d.f.	*F*	*P*	Estimate	SE	d.f.	*F*	*P*
Intercept	157.79	64.89	—	—	—	206.76	61.96	—	—	—
Year	−0.08	0.03	1,404.8	37.3	**<0.0001**	−0.10	0.03	1,236.0	5.8	**0.0168**
RRL	0.60	0.13	1,404.2	0.6	0.4582	0.25	0.13	1,222.5	1.7	0.1982
RRL^2	−0.02	0.01	1,410.8	7.0	**0.0085**	−0.03	0.01	1,294.5	5.7	**0.0172**
α	0.04	0.27	1,398.4	4.5	**0.0356**	−0.50	0.25	1,185.2	6.7	**0.0103**
$α^2$	−0.05	0.03	1,399.4	2.1	0.1488	−0.01	0.04	1,195.0	0.6	0.4579
ω	0.58	0.19	1,399.8	13.5	**0.0003**	0.30	0.21	1,198.2	19.0	**<0.0001**
$ω^2$	−0.05	0.02	1,401.1	8.8	**0.0032**	−0.03	0.03	1,199.4	0.2	0.6688
RRL × α	−0.08	0.02	1,405.7	13.2	**0.0003**	−0.06	0.03	1,244.4	3.4	0.0658
RRL × ω	−0.01	0.01	1,406.1	0.5	0.5040	0.02	0.02	1,268.4	1.1	0.3060
α × ω	0.07	0.04	1,400.8	3.7	0.0543	0.07	0.06	1,192.3	1.5	0.2302
Individual variance	0.00	.	—	—	—	0.00	.	—	—	—
Autoregressive covariance	−1.00	.	—	—	—	0.02	0.05	—	—	—
Residual variance	0.99	0.07	—	—	—	0.00	.	—	—	—
Overdispersion	0.02	0.04	—	—	—	1.55	0.09	—	—	—

acquisition of skills such as breeding experience (Curio 1983). An interaction between experience and ω showed that, for both sexes, only individuals with a late ω showed an initial improvement in breeding success with experience.

The Restraint Hypothesis predicts that individuals may vary their reproductive effort according to their RRL, Pianka 1976; Williams 1966). It predicts that younger individuals refrain from breeding to improve their chances of survival, whereas individuals with fewer reproductive events remaining should invest relatively more in reproduction. Initially there was an increase in performance within individuals as RRL decreased, in line with the Restraint Hypothesis; however, over the last 6 years of breeding attempts performance decreased, in both sexes. Our results, therefore, suggest that terminal effects occur gradually, as observed in mute swans *Cygnus olor* (McCleery *et al.* 2008); we found no evidence of abrupt terminal effects. Importantly, the Restraint Hypothesis assumes that individuals that restrain from breeding are equally capable of breeding as the same-sex same-age individuals that breed. This may not necessarily be the case, especially if other effects such as constraint are operating. Nevertheless, even though we detected constraint due to experience in individuals with a late ω, we still observed an initial increase in breeding success as RRL decreased.

Overall, our results suggest that reproductive constraints and restraints may influence breeding success within individuals, in both sexes. Constraints or restraints on breeding success could be imposed socially, physiologically or ecologically, and we have only considered a subset of these here. It may be that badgers are constrained due to their condition and further analyses are required to investigate this. Additionally, circumstantial evidence of infanticide in badgers (Lüps & Roper 1990; Roper 2010) implies socially imposed constraints on breeding, increased breeding success in young females when outlier setts (dens away from the main den) are present suggests female–female social competition (Cresswell *et al.* 1992), and reduced female breeding success following years with low food availability (Woodroffe & Macdonald 1995b) indicates ecological constraints. Social and ecological effects potentially interact in our study population with female–female competition possibly only occurring in years with high food availability (Dugdale *et al.* 2008), and further work is required to assess the extent of this in both sexes.

A significant quadratic relationship between annual breeding success and age was observed in both males and females, suggesting that reproductive senescence occurs in badgers. The negative relationship between breeding success and old age might be an artefact of the greater number of records of individuals at younger ages, if breeding success simply asymptotes with age, rather than decreases. Examining reproductive output from a general peak at age 5 confirmed that reproductive senescence did occur in both sexes (e.g. males sired 0.63 ± 0.07 cubs at age 5 vs. 0.07 ± 0.02 at age 10; females = 0.48 ± 0.05 vs. 0.11 ± 0.03, respectively). As
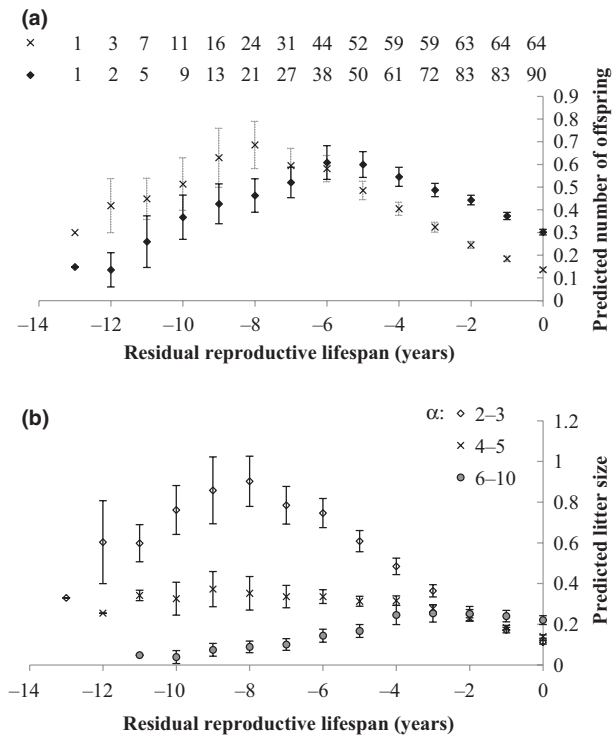
Fig. 4 The predicted mean number of cubs, from Generalized Linear Mixed Models (GLMMs), assigned to: (a) females (x) and males (♦) according to their residual reproductive lifespan (RRL), and (b) females according to their RRL and age of first breeding (α; categorized to aid visualization, but a continuous effect in the GLMM). Error bars display the standard errors of the means. Data labels in (a) represent the number of badgers present in each category. The GLMMs control for repeated measures on the same individual. The sign of RRL is reversed so that the last reproductive attempt is plotted on the right hand side.

only 154 badgers had known values of α and ω we did not have enough power to detect additive genetic variance using a bivariate animal model (discussed in Charmantier *et al.* 2006; Quinn *et al.* 2006) to test whether the Mutation Accumulation or the Antagonistic Pleiotropy Hypotheses best explained the decrease in annual breeding success that we observed in older badgers (see Dugdale 2007).

Reproduction peaked at an earlier age in females than in males and the rate of reproductive senescence was faster in males than in females. This peak was driven in both sexes by younger and older individuals having a lower probability of being assigned parentage, but also in males due to fewer offspring being assigned to younger and older than middle-aged breeders. A higher rate of reproductive senescence in males than females has been reported in red deer *Cervus elaphus* (Nussey *et al.* 2009), which is consistent with the prediction that, in polygynous species, senescence rates should be greater

in males (Clutton-Brock & Isvaran 2007) due to higher mortality rates in males (Williams 1957). In our study population the mating system is polygynandrous (Dugdale *et al.* 2007) and there is no overall sex-bias in mortality (Macdonald & Newman 2002). Investigations are required into the causes of variation in rates of senescence (Nussey *et al.* 2009), and also potential male–female interactions, which may influence patterns of senescence (Auld & Charmantier 2011). In our study population, males in poor condition gain more mountings around sett-entrances but males in better condition gain more paternity, after accounting for age effects (H. Dugdale, A. Griffiths & D. Macdonald, unpublished); therefore, male condition may be linked to rates of senescence.

In conclusion, unravelling the relationship between age and breeding success has enhanced our understanding of badger population dynamics. The age-specific patterns of breeding success, in both sexes, were each in part consistent with the Selection, Constraint, Restraint and Senescence Hypotheses. We provide strong evidence of variation in breeding success with age, with both sexes experiencing reproductive senescence; however, selective appearance and disappearance of individuals partially masked these effects. This is not new: selective disappearance has been found to mask some patterns of female senescence in species such as red deer (Nussey *et al.* 2006), mute swans (McCleery *et al.* 2008) and great tits *Parus major* (Bouwhuis *et al.* 2009). Additionally, selective appearance masked female age-specific performance in oystercatchers *Haematopus ostralegus* (Van de Pol & Verhulst 2006). Studies of males, however, are rarer (Auld & Charmantier 2011); our results, therefore, provide important insight into age-specific breeding success in both sexes. Additionally, this is one of the few studies to use genetic fitness estimates and incorporate the effects of both α and ω. We thus demonstrate the need for future studies to examine all of these effects, in both sexes, so that the evolutionary processes can be unravelled.

Acknowledgements

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Data accessibility

Data has been deposited under DRYAD doi:10.5061/dryad.9039.

Supporting information

Additional supporting information may be found in the online version of this article.

Materials and Methods

Table S1 The effects of age at breeding, selective appearance (age of first breeding—α), selective disappearance (age of last breeding—ω) and their first-order interactions, on the number of offspring assigned each year, excluding individuals after their last date of capture.

Table S2 Incorporation of a binary terminal effect in analyses of the effects of age at breeding, selective appearance (age of first breeding—α), selective disappearance (age of last breeding—ω) and their first-order interactions, on the number of offspring assigned each year.

Table S3 Incorporation of a binary terminal effect in analyses of the effects of age at breeding, selective appearance (age of first breeding—α), selective disappearance (age of last breeding—ω) and their first-order interactions, on the number of offspring assigned each year, excluding individuals after their last date of capture.

Table S4 The effects of the number of previous years of successful breeding experience (exp), selective appearance (age of first breeding—α), selective disappearance (age of last breeding—ω) and their first-order interactions, on the number of offspring assigned each year, excluding individuals after their last date of capture.

Table S5 The effects of residual reproductive lifespan (RRL), selective appearance (age of first breeding—α), selective disappearance (age of last breeding—ω) and their first-order interactions, on the number of offspring assigned each year, excluding individuals after their last date of capture.

Table S6 The effects of age at breeding (after four years of age), selective appearance (age of first breeding—α), selective disappearance (age of last breeding—ω) and their first-order interactions, on the number of offspring assigned each year.

Table S7 The effects of age at breeding, selective appearance (age of first breeding—α), selective disappearance (age of last breeding—ω) and their first-order interactions, on litter size (i.e., excluding data from non-breeders).

Table S8 The effects of age at breeding, selective appearance (age of first breeding—α), selective disappearance (age of last breeding—ω) and their first-order interactions, on the probability of being assigned parentage.

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