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Summary

1. Natal conditions and senescence are two major factors shaping life-history traits of wild animals. However, such factors have rarely been investigated together, and it remains largely unknown whether they interact to affect age-specific performance.

2. We used 27 years of longitudinal data collected on tawny owls with estimates of prey density (field voles) from Kielder Forest (UK) to investigate how prey density at birth affects ageing patterns in reproduction and survival.

3. Natal conditions experienced by tawny owls, measured in terms of vole density, dramatically varied among cohorts and explained 87% of the deviance in first-year apparent survival (annual estimates ranging from 0·07 to 0·33).

4. We found evidence for senescence in survival for females as well as for males. Model-averaged estimates showed that adult survival probability declined linearly with age for females from age 1. In contrast, male survival probability, lower on average than for female, declined after a plateau at age 1–3.

5. We also found evidence for reproductive senescence (number of offspring). For females, reproductive performance increased until age 9 then declined. Males showed an earlier decline in reproductive performance with an onset of senescence at age 3.

6. Long-lasting effects of natal environmental conditions were sex specific. Female reproductive performance was substantially related to natal conditions (difference of 0·24 fledgling per breeding event between females born in the first or third quartile of vole density), whereas male performance was not. We found no evidence for tawny owls born in years with low prey density having accelerated rates of senescence.

7. Our results, combined with previous findings, suggest the way natal environmental conditions affect senescence varies not only across species but also within species according to gender and the demographic trait considered.

Key-words: cyclic prey dynamics, field vole, life-history optima, natal environment effect, tawny owl

Introduction

Conditions experienced during the early stages of life, whether originating from parental investment and/or environmental conditions can have profound effects on the performance of individuals throughout their lifetime. When environmentally driven, this leads to among-cohort variation in fitness-related traits (Lindström 1999; Metcalfe & Monaghan 2001; Monaghan 2008) and such delayed or long-lasting effects are expected to alter population dynamics as well as the evolution of life-history traits (Beckerman *et al.* 2002; Lindström & Kokko 2002). For instance, cohort effects have been shown to influence growth (Madsen & Shine 2000), age at first breeding (AFB) (Millon, Petty & Lambin 2010), reproductive performance (Brommer, Pietiäinen & Kolunen 1998; Reid *et al.* 2003) and survival (Daan, Dijkstra & Tinbergen 1990; Descamps *et al.* 2008b). However, whether natal environmental conditions influence the pattern of ageing has been rarely investigated.

Senescence has been only recently acknowledged as a process commonly occurring in wild populations (Brunet-

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Rossinni & Austad 2006; Jones *et al.* 2008). The evolutionary theory of senescence is built upon the key concept that the force of selection declines with age, even if mortality arises from age-independent causes, and not from physiological processes of ageing *per se* (Medawar 1952; Williams 1957; Hamilton 1966). Schedules and rates of mortality are therefore crucial in determining the optimal spread of reproductive investment over a lifetime and the onset and intensity of senescence (Williams 1966; Partridge & Barton 1993; Williams *et al.* 2006). The disposable soma theory suggests that because the strength of selection weakens with age, an optimal resource allocation should favour reproduction as individuals age, at the expense of somatic maintenance that prevents lethal deterioration (Kirkwood 1977; Kirkwood & Rose 1991). The degree to which reproduction is favoured over somatic maintenance is expected to vary according to environmental conditions, but to date, very few studies have investigated the relationship between senescence and early environmental conditions for free-living populations. Female red deer *Cervus elaphus* L. on the Isle of Rum born in years of high population density, and therefore exposed to greater competition, showed faster rates of senescence in both survival and reproduction (Nussey *et al.* 2007). Pulse of food resource induced cohort effects in American red squirrels *Tamiasciurus hudsonicus* Erxleben were associated with age-specific reproduction but not survival (Descamps *et al.* 2008a). Lastly for female great tit *Parus major* L., none of the proxies used for natal environmental conditions were found to influence the rate of reproductive senescence, although immigrant individuals (therefore with unknown natal conditions) suffered accelerated senescence relative to locally born females (Bouwhuis *et al.* 2010).

Several mechanisms have been hypothesised to link an early environmental effect to alteration in individual life-history strategy and the onset of ageing (Mangel 2008). Harsh environmental conditions can affect early development and impair physiological functions in adulthood, such as the dynamics of telomere erosion (Monaghan & Haussmann 2006) or the assimilation of antioxidants (Blount *et al.* 2003). Besides these constraints, individuals experiencing adverse early conditions might also operate an adaptive shift in developmental processes, and so doing, change the schedule and/or the trade-off between early growth and reproduction (Brakefield *et al.* 2005; Monaghan 2008). Even though field studies are unlikely to tease apart the contribution of proximate processes, characterising the relationship between early environment and age-specific performance, using data on both reproduction and survival, are clearly important issues for life-history studies in order to establish out the prevalence of natal environment effects and to what extent their importance varies across species (Monaghan *et al.* 2008).

In this article, we investigated the consequences of variation in prey abundance experienced early in life on age-specific survival and fecundity in a 27-year-long study of tawny owls *Strix aluco* L. in northern England. Like other vole-eating predators, the study population was subjected to dramatic among-cohort variation in vole abundance that drove first-year survival (Brommer, Pietiäinen & Kolunen 2002; Millon, Petty & Lambin 2010). However, little is known about how such large variation in natal prey conditions affects the performance of predators later in life (Lindström 1999). This lack of knowledge stems from the high dispersal propensity of predators in response to the cyclic prey dynamics, and associated low local recruitment rate (e.g. Korpimäki & Lagerström 1988), which typically impairs the collection of data from individuals with information on natal conditions. Here, we take advantage of the particularly high rate of local recruitment in our study population (60% compared with 19% in a Finnish population, Karell *et al.* 2009), which provided a unique opportunity to investigate how among-cohort heterogeneity influenced lifetime performance.

Specifically, we hypothesise that tawny owls that experienced low vole density during the first months of life should reduce reproductive performance and/or survival during adulthood and suffer faster rates of senescence compared with individuals born in years with high vole density. In contrast to most studies on the enduring effect of early conditions and ageing, which focus either on females only or combined data from both sexes, we test this prediction separately for males and females as sex-specific survival rates and reproductive costs have been documented in this sexually dimorphic species (Millon, Petty & Lambin 2010).

Materials and methods

STUDY SPECIES AND STUDY SITE

The tawny owl is a nocturnal raptor with sex-specific reproductive duties. Females are 46% heavier than males during the brooding period (Petty 1992), and undertake all incubation and brooding until the chicks are *c.* 15 days old, while males provide most of the food for females and chicks.

Reproduction and survival in tawny owls have been monitored continuously in Kielder Forest since 1980, within a study area of 176 km^2 where breeding occurred almost exclusively in nest-boxes. Annual checks of nest-boxes were carried out to record territory occupancy, ring chicks and the number of fledglings. Adults were trapped when chicks were 1–2 weeks old, using a landing net for females and a trap fixed to the entrance of the nest-box for males (Petty 1992). Trapping of females was carried out throughout the study period, but male trapping only took place between 1988–1998 and 2008–2010. Although of a shorter period compared with that for females, the male data set encompasses the whole life-span range, as all chicks have been ringed since 1980.

Field voles *Microtus agrestis* L. are the primary food source for tawny owls in Kielder Forest, typically representing 40–70% of prey brought to nestlings (Petty 1999), and are the main determinant of owl breeding success (Petty 1992). Abundance of field voles was estimated in autumn (September–October) from 1984 to 2010 by recording the presence/absence of vole sign in 25 quadrats (25 × 25 cm) within 14–36 early-stage clear cuts dominated by grass. Vole densities (individuals ha^{-1}) were derived from this index after calibration against vole live trapping and CMR analysis (Lambin, Petty & MacKinnon 2000). Field vole densities in Kielder Forest displayed multi-annual fluctuations of 3–4 years with contrasting within-year dynamics (Lambin, Petty & MacKinnon 2000). We used two distinct measures of natal environmental conditions: (i) autumn vole density

at the nearest vole site (hereafter local density, range: 23–291 vole ha^{-1}) and (ii) autumn vole density averaged across the study site (global density, range: 35–175 vole ha^{-1}), because young tawny owls leave the natal territory towards the end of summer to find profitable hunting areas (Coles *et al.* 2003), and a spatially averaged measure of vole density may provide a more relevant index of environmental conditions.

Recruitment of new breeders in Kielder Forest consisted mainly of birds born in the study area (for 1988–2010: 56% of female recruits, $N = 220$ and 61% of male recruits, $N = 177$). This remarkably high local recruitment rate is at least partly because of the semi-isolated nature of Kielder Forest, allowing us to concentrate on birds where the exact birth place and time was known, and for which we can derive natal conditions, expressed in terms of vole density measured in early autumn. Our data set of local recruits consisted of 132 females (maximal age = 20) and 102 males (maximal age = 16). We grouped individuals from the oldest ages to reduce possible biases because of low sample size (three records ≥16 years old for females; and three records ≥12 years old for males for reproduction, six records ≥9 years old for survival analysis).

AGE-SPECIFIC ANALYSES: SURVIVAL AND REPRODUCTION

In order to characterise the relationship between age and either reproductive performance or survival, we fitted a variety of functions (null, linear, linear + quadratic, allowing for the existence of age thresholds with separate slopes each side of the threshold). We did not find any support for models considering two thresholds (results not shown). The selective appearance or disappearance of individuals that differ in phenotypic quality can create spurious age-specific variation at the population level (Vaupel & Yashin 1985; Cam & Monnat 2000; van de Pol & Verhulst 2006). Therefore, we tested the influence of AFB (for selective appearance) and life span (or age at last breeding for selective disappearance), using the best age function, on age-specific reproduction. As AFB and life span were not available for all individuals (e.g. life span for individuals recorded over the last 2 years of the study), corresponding models were run separately on data sets with different sample size. AFB and life span were treated as covariates and fitted additively and in interaction with the age function.

Based on the best parameterisation from this first step (age function, AFB and life-span effect potentially), we further investigated the potential long-lasting effects of natal prey conditions on age-specific performance by fitting vole density (local or global) as a continuous covariate. Specifically, additive models (age function + vole density) tested for the occurrence of a cohort effect, while models with an age function × vole density interaction tested for an effect of natal conditions on the rate of ageing.

Capture–recapture analyses were conducted in two steps to estimate age-specific survival. First, the effect of vole density at birth on first-year survival was measured for 11 cohorts between 1987 and 1997 (recapture up to 1998), a period when both adult females and males were caught intensively (91·8% and 78·3% of breeding individuals respectively, Millon, Petty & Lambin 2010). As the sex of chicks was unknown over most of this period, survival analyses were performed for both sexes combined (*c-hat* = 3·26). The regression coefficient of first-year survival against vole densities was estimated on a logit scale ($\beta \pm$ SE), and the proportion of deviance explained by vole densities was calculated (%Dev, Skalski, Hoffmann & Smith 1993). Then, adult survival rates were estimated separately for females and males born in Kielder Forest (between 1984 and 2009,

with recapture spanning to 2010 for females; 1987–1997 with recapture between 1988 and 1998 for males, *c-hat* of 1·298 and 1 respectively). Recapture probabilities were modelled as time dependent and age specific [(1, 2–3, 4 +) for females; (1, 2 +) for males] so as to account for delayed recruitment (Millon, Petty & Lambin 2010). Breeding tawny owls are highly site-tenacious, with the vast majority of adults staying in the same territory for life (> 98%; Petty 1992), such that adult survival rates can be considered as true survival. In contrast, an unknown proportion of juveniles disperse outside the study area, so that first-year survival refers to local survival and includes permanent emigration (e.g. Francis & Saurola 2002).

Concerning reproduction, a total of 435 and 226 breeding events by known age parents and with the number of fledglings recorded (range: 0–5) are available for females ($N = 132$) and males ($N = 102$) respectively. The average number of fledglings (among pairs that laid at least one egg) varied greatly by year in relation to vole density (range of annual averages: 1·14–3·23). To overcome this while keeping our models tractable, we analysed residual individual number of fledglings each year after subtracting the annual average. In this manner, we retained a biologically meaningful unit of variation, while accounting for inter-annual variation in vole densities. Generalised Linear Mixed Models (GLMM) were fitted with normally distributed errors, and individual identities as random intercepts to account for the repeated nature of the data and possible heterogeneity among individuals.

Models of survival were implemented in E-SURGE 1.6.0 (Choquet, Rouan & Pradel 2009) and goodness-of-fit tests using U-CARE v.2.3.2 (Choquet *et al.* 2003). Over-dispersion was accounted for when required by adjusting the *c-hat*. Models for age-specific reproduction were run in R 2.10.0 using *nlme* package (R Development Core Team 2009), and effect sizes are expressed as mean ± SE. Models were ranked according to Akaike Information Criterion corrected for small sample size (*AICc*). Multi-model inference was based on Akaike's weights (*w*) to produce mean estimates averaged across several models, associated with standard errors obtained by the delta method (Burnham & Anderson 2002).

Results

INFLUENCE OF VOLE DENSITY ON FIRST-YEAR SURVIVAL

Local first-year survival of tawny owls varied considerably among cohorts, ranging from 0·07 to 0·33 (from time-dependent model, females and males combined, Fig. 1). This variation was largely explained by global vole density in the autumn following birth (slope on logit scale: $\beta = 0·597 \pm 0·196$, %Dev = 86·9, Anodev: $F_{1,9} = 59·92$, $P < 0·01$) and alternative models received virtually no support (time-dependent fist-year survival: $\Delta AICc = 8·22$, $w = 0·01$; constant: $\Delta AICc = 16·80$, $w < 0·001$). Local vole density (fitted as an individual covariate) provided similar results ($\beta = 0·495 \pm 0·195$), but the model performed less well ($\Delta AICc = 3·51$, $w = 0·15$ vs. $w = 0·84$ for the model fitting global vole density as a yearly covariate).

PATTERN OF AGEING IN ADULT SURVIVAL

Adult survival declined with age for both sexes (Table 1, Fig. 2). For females, survival declined linearly from age 1
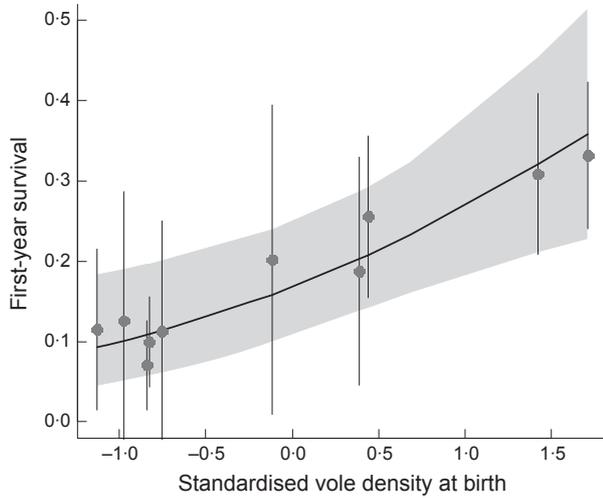
Fig. 1 First-year apparent survival of tawny owls born in Kielder Forest in relation to global vole density in the year of birth. Annual estimates ($\pm$ SE) from a time-dependent model are shown together with predicted values (solid line $\pm$ 95% CI, within grey area) from a model fitted with standardised vole density (linear on logit scale). Global vole densities, averaged across the study site, ranged from 35 to 175 vole ha^{-1}.

(slope on logit scale: $\beta = -0.480 \pm 0.180$, with standardised age) with only a weak support for an age threshold (at 8 years, Tables 1 and S1, Supporting Information). For males, stronger support was for constant survival, although limited sample size compared with females might have affected model selection. Nevertheless, there was some support for a linear decrease of survival ($\beta = -0.125 \pm 0.101$), and for the existence of a threshold at age 3 after which survival dropped steeply ($\beta = -0.509 \pm 0.388$; Table 1, Fig. 2).

Natal conditions (global vole densities, following model selection on first-year survival) did not affect survival, and this result was consistent between sexes. In Fig. 2 are shown age-specific estimates averaged across all models (see Table 1), and the slight positive effect of natal conditions on survival of either sex (contrast between first and third quartiles of vole density measured at birth) falls well within standard error bars.

PATTERN OF AGEING IN REPRODUCTIVE PERFORMANCE

Both female and male reproductive performance varied with age, with an initial increase, followed by a decline in performance after a threshold (Fig. 3). Threshold models were favoured for both sexes (Table 2 and S1, Supporting Information). For females, reproductive performance increased slightly until age 9 (0.039 ± 0.020) and declined afterwards (-0.072 ± 0.037). For males, peak reproductive performance occurred much earlier (3 years), with a relatively steep initial increase (0.305 ± 0.108), followed by a decline comparable to that of females (-0.065 ± 0.025). Age-specific variation in the number of fledglings raised seemed to be more marked in males than in females (correlation between averaged observed and fitted values: $r = 0.71$ for males, $P < 0.001$, $r = 0.52$ for females, $P = 0.04$; compare also AICc between age threshold and null models in Table 2).

We found no evidence for selective appearance or a selective disappearance of individuals to underpin ageing patterns for either sex. Neither AFB (all $\Delta AICc > 1.5$ and > 4.5, respectively for females and males) nor life span (all $\Delta AICc > 2.1$ and > 3.8) improved the fit of models and, as a consequence, were not retained for further modelling.

Vole density at birth did affect age-specific reproductive output for female tawny owls but not for males (Fig. 3). Local vole density outperformed vole density averaged at the landscape level ($\Delta AICc = 4.92$ between the two additive models) in explaining variation in female reproduction, but effect size were similar between the two measures (coefficient from the additive model: 0.0020 ± 0.0006 for local density; 0.0023 ± 0.0011 for global density; see Materials and methods for range of vole densities). A female born in the first quartile of local vole density (77 vole ha^{-1}) faced an expected reduction of about 0.24 fledglings per breeding attempt compared with a female born in the third quartile (197 vole ha^{-1}; Fig. 3). However, the slope of the relationship between age and reproduction was not affected by vole density at birth for either sex, as shown by the weak support for a model fitting the interaction between age and vole density at birth (full interaction for both sides of the threshold, Table 2). Thus, adults that experienced harsher natal

Table 1. Model selection for annual adult survival of female and male tawny owls. Deviance, number of parameters (*np*), difference of *AICc* with the best model (*ΔAICc*) and Akaike's weights (*w*) are shown. Recapture was modelled as [(a₁, ₂₋₃, ₄₊) + *t*] for females and as [(a₁, ₂₊) + *t*] for males and kept identical for all models. Age threshold was 8 years for females and 4 years for males. Vole.birth refers to global vole density at birth
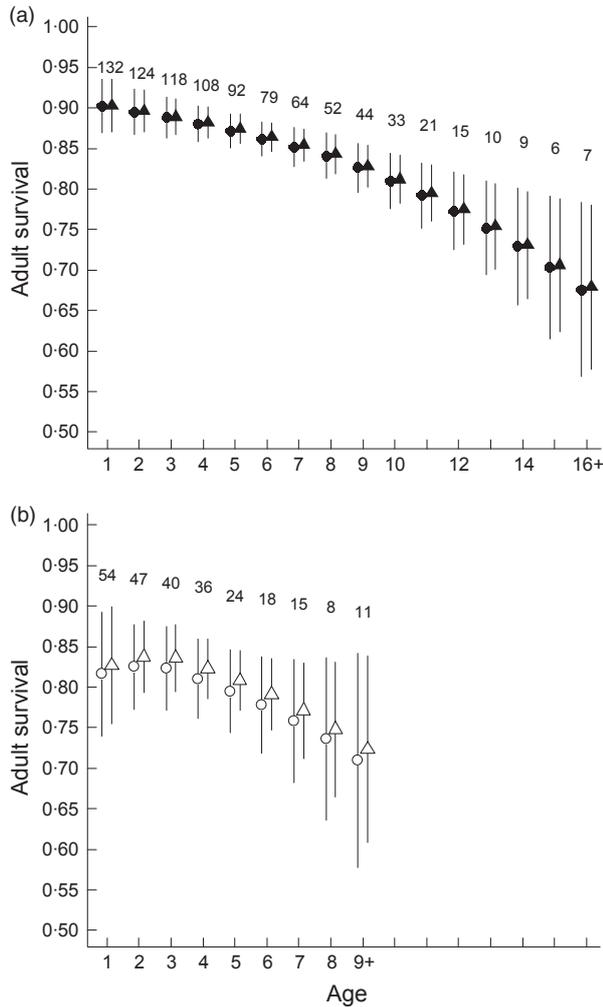
| Models for adult survival	Females				Males			
	Deviance	np	ΔAICc	w	Deviance	np	ΔAICc	w
1. Constant	2127·05	31	4·83	0·036	701·15	15	0·00	0·327
2. Linear effect of age	2118·07	32	0·00	0·403	699·65	16	0·61	0·241
3. Linear + quadratic	2117·34	33	1·53	0·188	699·35	17	2·44	0·097
4. Age threshold	2117·54	33	1·68	0·160	698·25	17	1·34	0·167
5. Linear + vole.birth	2117·79	33	1·88	0·157	698·87	17	1·96	0·123
6. Linear × vole.birth	2117·77	34	3·96	0·056	698·73	18	3·95	0·045

Fig. 2. Age-specific adult survival of (a) female and (b) male tawny owls. The last age categories (16 + and 9 +) gather individuals up to age 20 and 11 for females and males respectively. Annual survival estimates (± SE) are averaged across all models considered in Table 1. Circles and triangles show predicted survival for tawny owls born in a year with low and high global vole densities respectively (first and third quartiles). Sample size is indicated for each age.

conditions did not suffer faster rates of senescence. Figure 3 shows predictions averaged across all models presented in Table 2.

Discussion

Using 27 years of longitudinal data on predator demography combined with prey density, we showed that prey density experienced in the first year of life is a primary determinant of pre-reproductive mortality for both sexes, with first-year survival rates (apparent survival) ranging from 0·07 to 0·33 (Fig. 1). These figures are particularly low for a raptor species but may be partly because of vole-dependent permanent emigration outside the study area. Vole density after youngsters dispersed from their natal territories acted as a bottleneck for survival and biased population structure towards individuals subjected to favourable environmental at this
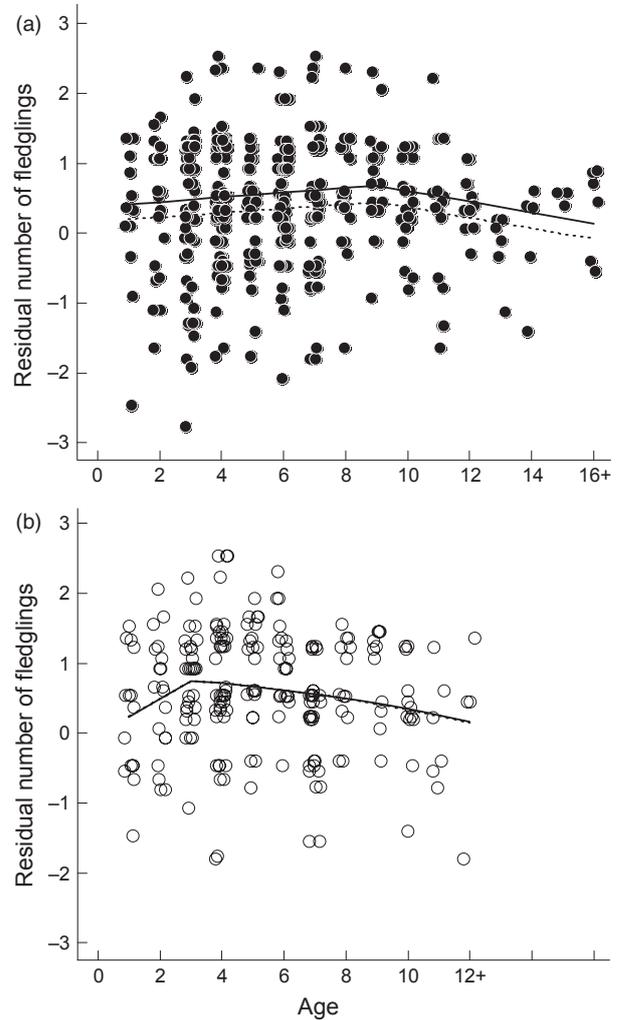
Fig. 3. Age-specific reproductive performance (residual number of fledglings accounting for vole density during reproduction) for (a) female ($N = 435$ breeding events for 121 individuals) and (b) male tawny owls ($N = 226$ breeding events for 102 individuals). Lines are predictions averaged across all models considered in Table 2, for owls born in a year with low local vole density (first quartile, dotted line) or with high local vole density (third quartile, solid line). Note these two lines are almost indistinguishable for males. A small degree of jitter has been added on the *x*-axis for improving sample size visualisation.

time. This appears to be typical for resident predators feeding on cyclic rodents (Korpimäki & Lagerström 1988; Brommer, Pietiäinen & Kolunen 2002). Our results, accounting for individual heterogeneity, provide further support for the occurrence of senescence in the wild, as tawny owls suffered reduced reproductive performance and survival as they aged. We showed that this large amplitude in natal environmental conditions had a long-lasting effect on owls by affecting individual performance, but not the way individuals senesce. Thus, the enduring effects of natal conditions did not interact with the processes leading to senescence. Interestingly, the magnitude of the natal environment effect differed not only between survival and reproduction, but also between the sexes (Figs 2 and 3).

Table 2. Model selection for reproductive performance (annual residual number of fledglings) of female and male tawny owls. Individuals were fitted as random factors to account for the pseudo-replicated nature of the data. Age threshold was 9 years for females and 3 years for males. Vole.birth refers to local vole density at birth. Other abbreviations are as in Table 1

Models for reproduction	Females				Males			
	Deviance	np	$\Delta AICc$	w	Deviance	np	$\Delta AICc$	w
1. Constant	1117·77	3	8·19	0·013	560·17	3	6·34	0·022
2. Linear effect of age	1117·57	4	10·03	0·005	559·06	4	7·30	0·014
3. Linear + quadratic	1114·52	5	9·02	0·009	551·62	5	1·95	0·202
4. Age threshold	1112·42	5	6·92	0·025	549·67	5	0·00	0·535
5. Age threshold + vole.birth	1103·44	6	0·00	0·808	549·66	6	2·11	0·187
6. Age threshold × vole.birth	1102·81	8	3·52	0·139	548·47	8	5·19	0·040

THE EXPRESSION OF SENESCENCE

Reproductive performance peaked at age 9 for females, whereas males' performance peaked earlier, with their prospects decreasing from age 3. This meant that 18% of breeding events involved females that were potentially senescent, with this proportion reaching up to 72% for males (Fig. 3). The rate of decline following the peak in performance was similar between sexes. The peak in reproductive performance matched the peak occurring in survival for males, whereas for females, no clear peak was detected for survival (Fig. 3). Such a difference in the onset of senescence between females and males supports the prediction from classical theory that reduced life expectancy should drive the evolution of a more rapid senescence (Williams 1957; Hamilton 1966). To date, potential differences in ageing patterns between males and females have been studied mainly in polygynous mammals (Mysterud *et al.* 2001; Clutton-Brock & Isvaran 2007; Nussey *et al.* 2009), in line with predictions from sexual selection theory (Promislow 2003; Bondurianky *et al.* 2008). Our results provide further evidence of differences in senescence and life-history trajectories between sexes in a monogamous species (see also Catry *et al.* 2006; Reed *et al.* 2008).

Our sex-specific survival rates for tawny owls are consistent with conclusions from a comparative analysis of birds pointing out the sex providing food for nestlings is subject to higher mortality (accounting for difference in body mass; Owens & Bennett 1994), as male tawny owls provide food during most of the breeding period.

LONG-LASTING EFFECTS OF NATAL CONDITIONS

Assuming that surviving the first year with low prey density is associated with some degree of physiological impairment, we expected individuals from low-prey cohorts to pay a cost later in life (Metcalfe & Monaghan 2001). Female reproductive performance was affected by vole density experienced in the year of birth, extending earlier findings on tawny owls in Kielder Forest, based on only 2 years (Appleby *et al.* 1997). However, no such effect was detected for males. Some of the few studies on wild populations that have looked at sex-specific natal effect have already pointed out that cohort effects

can differ between females and males (Kruuk *et al.* 1999; Wilkin & Sheldon 2009; but see Reid *et al.* 2003).

From these results, two main questions arise: First, why are females affected by natal conditions but not males? Available evidence indicates that they have very similar first-year survival rates according to vole densities, making the hypothesis of males being unaffected by prey availability after fledging unlikely (Millon, Petty & Lambin 2010). In great tit *Parus major,* both longevity and lifetime reproductive success were affected by the natal environment for males but not for females (Wilkin & Sheldon 2009). The authors suggested that the absence of an effect in females might have resulted from high pre-reproductive mortality that could have imposed strong selection promoting a plastic response to environmental variation. Male great tits were also subjected to strong selection, yet they were affected by long-lasting effects of their natal environment. Furthermore, the probability of local recruitment is lower for tawny owls than for great tits (*c.* 7% vs. 12%), suggesting the strength of early selection is important for these species. In the light of our results, we suggest that sexual size dimorphism and associated growth trajectories early in life might account for sexual differences in susceptibility to natal conditions. Specifically, the larger sex (male great tits are heavier than females, whereas female tawny owls are substantially larger than males) appears to be more susceptible to adverse natal conditions (or benefit more from enhanced conditions) and thus more likely to suffer long-lasting effects from natal conditions.

The second question is why natal conditions affected reproduction but not survival? Tawny owl can be categorised as a long-lived species with annual survival rates of 0·79–0·87 for adults (Millon, Petty & Lambin 2010; this study), and as such, might trade reproduction for longer survival, and particularly so where prey cycles generate years with few resources. Breeding skipping is indeed common in Kielder Forest (ranging from 5 to 92%; S.J. Petty's unpublished data), and considering this behaviour in the light of senescence theory might be fruitful (McNamara *et al.* 2009). Interestingly, preliminary results for tawny owls in Kielder Forest suggest that females have a decreasing tendency to skip reproduction as they age (S.J. Petty's unpublished data).

Natal conditions are expected to have long-lasting effects and to affect the expression of traits in adulthood, including the pattern of ageing or senescence (Brakefield *et al.* 2005; Nussey *et al.* 2007; Mangel 2008; Monaghan *et al.* 2008). However, in tawny owls variable natal conditions did not translate into differential rates of ageing. This lack of an interactive effect may conceivably have been the consequence of high first-year mortality rates which could have reduced the power to detect any carry-over effect. However, the proportion of females reaching at least 8 years old was not different between the quartiles of vole density at birth (from lowest to highest: 47%, 37%, 37% and 39%), confirming our finding of similar adult survival rates among cohorts. Therefore, we are confident of our ability to detect differences in rates of senescence among cohorts and can safely refute our prediction of faster senescence for owls that encountered harsher conditions early in life. The handful of studies that looked at the relationship between natal environmental conditions and senescence provide no clear picture. Harsher natal environments accelerate reproductive and actuarial senescence in female red deer (Nussey *et al.* 2007), but reproductive senescence only in female red squirrel (Descamps *et al.* 2008a). In female great tit, natal environment had no effect on senescence but immigrant birds suffered higher rates of ageing compared with locally born individuals (Bouwhuis *et al.* 2010). For the latter species, it would be interesting to replicate the analysis with males, as they show a much stronger natal environment syndrome than females (Wilkin & Sheldon 2009).

In conclusion, our results showed that despite strong selection occurring early in life, natal conditions still impose long-lasting effects on the reproductive performance of female, but not male tawny owls. Together with previous results on the effect of AFB and vole density during the first breeding attempt (Millon, Petty & Lambin 2010), our results suggest that females (the larger sex) are much more sensitive to varying environmental conditions than males in a sexually dimorphic, monogamous species like the tawny owl. In contrast to the few previous studies, natal environmental effects did not affect the pattern of senescence.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Values of $\Delta AICc$ (difference of *AICc*, or AIC corrected for small sample size, between the model considered and best model) from the threshold model selection concerning reproduction and adult survival in female and male tawny owls born in Kielder Forest.

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