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A. Millon[1], S. J. Petty[1,2] and X. Lambin[1]*

[1]Institute of Biological and Environmental Sciences, Aberdeen University, Zoology Building, Tillydrone Avenue, Aberdeen AB24 2TZ, UK; and [2]Centre for Human and Ecological Sciences, Forest Research, Northern Research Station, Roslin, Midlothian EH25 9SY, UK

Summary

1. According to life-history theory, environmental variability and costs of reproduction account for the prevalence of delayed reproduction in many taxa. Empirical estimates of the fitness consequences of different ages at first breeding in a variable environment are few however such that the contributions of environmental and individual variability remains poorly known.

2. Our objectives were to elucidate processes that underpin variation in delayed reproduction and to assess lifetime consequences of the age of first breeding in a site-faithful predator, the tawny owl *Strix aluco* L. subjected to fluctuating selection linked to cyclical variation in vole density (typically 3-year cycles with low, increasing and decreasing vole densities in successive years).

3. A multistate capture–recapture model revealed that owl cohorts had strikingly different juvenile survival prospects, with estimates ranging from 0·08 to 0·33 respectively for birds born in Decrease and Increase phases of the vole cycle. This resulted in a highly skewed population structure with > 75% of local recruits being reared during Increase years. In contrast, adult survival remained constant throughout a vole cycle. The probability of commencing reproduction was lower at age 1 than at older ages, and especially so for females. From age 2 onwards, pre-breeders had high probabilities of entering the breeding population.

4. Variation in lifetime reproductive success was driven by the phase of the vole cycle in which female owls started their breeding career (26–47% of variance explained, whether based on the number of local recruits or fledglings), more than by age at first breeding or by conditions experienced at birth. Females who postponed reproduction to breed for the first time at age 3 during an Increase phase, produced more recruits, even when accounting for birds that may have died before reproduction. No such effects were detected for males.

5. Sex-specific costs of early reproduction may have accounted for females being more prone to delay reproduction. Contrary to expectations from a best-of-a-bad job strategy, early-hatched, hence potentially higher-quality females were more likely to breed at age 1, but then experienced rapidly declining food resources and so seemed caught in a life-history trap set by the multiannual vole cycle.

Key-words: age at first breeding, cost of reproduction, information-theoretic approach, population cycles, survival

Introduction

Even if they produce equal numbers of offspring over their lifetime, individuals who breed early in life contribute more to a growing population than those delaying reproduction, whereas the reverse is true in a decreasing population (Houston & McNamara 1999). Age at first breeding (AFB) is thus likely to be under strong, possibly fluctuating, selective pressure contributing to the diversity of breeding strategies across

*Correspondence author. E-mail: x.lambin@abdn.ac.uk

species and environmental conditions (Charmantier *et al.* 2006). Life-history strategies which include facultative delayed maturity are widespread among a variety of taxa suggesting that organisms may benefit from retaining a plastic response to environmental conditions such as with diapause in insects (Bradford & Roff 1993), reproduction skipping in small mammals (Ruf *et al.* 2006) or co-operative breeding in birds (Pasinelli & Walters 2002). Empirically, within-population variation in reproductive strategy is particularly useful for exploring the fitness consequences associated with the timing and cost of first breeding. For instance, the estimated

contribution to population growth of female Townsend's voles *Microtus townsendii* Bachman delaying reproduction was *c*. 50% lower than that of precocious females breeding before reaching adult body size during the summer population growth phase, although the latter category suffered severely reduced survival following reproduction early in life (Lambin & Yoccoz 2001). Indeed, due to inexperience or elevated energetic demands of combining somatic growth with reproduction, first time breeders in iteroparous species may suffer elevated costs of reproduction in terms of survival or future breeding probability (Curio 1983; Hadley, Rotella & Garrott 2007).

Temporal variability in environmental conditions affects the fitness expectations of commencing reproduction early in life and may lead to the evolution of delayed reproduction (Tuljapurkar 1990; Wilbur & Rudolf 2006). In temporally auto-correlated environments such as those generated by cyclic prey populations, predators must trade the cost of breeding early in life when prey abundance may be low against the risk of not breeding at all if they choose to postpone reproduction until the next pulse in prey abundance. For instance, in Ural owl *Strix uralensis* Pallas, females delaying first reproduction so as to breed in an Increase phase of the vole cycle had similar estimated fitness to females breeding in other years of the vole cycle but at younger ages, suggesting alternative breeding strategies were seemingly maintained in the population because of their equal long-term fitness outcomes (Brommer, Pietiäinen & Kolunen 1998).

Empirical evidence matches life-history theory predictions and suggests that individuals are indeed facing a strong evolutionary trade-off between early and late investment in reproduction (e.g. Charmantier *et al*. 2006; Descamps *et al*. 2006). However, even when confronted with similar environmental conditions, individuals may optimize their reproductive effort over their lifetime according to their intrinsic quality by opting for different breeding strategies, including AFB (Williams 1966; Pianka & Parker 1975; Curio 1983; Cam & Monnat 2000). However, covariates characterizing individual quality have hitherto rarely been assessed in relation to the timing of reproduction (but see Ens, Weissing & Drent 1995; Lambin & Yoccoz 2001), such that the contributions of environmental and individual variability in the evolution of alternative reproductive strategies remains poorly known.

The tawny owl *Strix aluco* L. is a nocturnal predator of Eurasian forests and some individuals are known to delay reproduction for several years (Petty 1992a). In Kielder Forest, northern Britain, this site-faithful predator mainly feeds on field voles *Microtus agrestis* L. Populations of this microtine rodent displayed high amplitude 3–4 year cycles in abundance (Lambin, Petty & MacKinnon 2000), thus providing strikingly different year types in terms of prey available for the owls. This constitutes an ideal system in which investigating the causes and consequences of AFB, which are likely to be influenced by both the external environment (e.g. territory vacancy, food resource) and an individual's internal state. Hereafter, we took advantage of complete individual life his-

tories collected from both male and female tawny owls, over 11 and 17 years respectively, to (i) investigate to what extent prey dynamics influence breeding decisions, (ii) estimate the fitness of individuals adopting different breeding strategies by starting their breeding career at different ages and/or phases of the vole cycle, and (iii) test whether individuals opt for different breeding schedules according to conditions experienced early in life.

Materials and methods

STUDY SYSTEM AND DATA COLLECTION

The tawny owl is a sexually dimorphic (female heavier than male), medium sized, territorial, nocturnal predator. Both sexes can breed at age 1 but they have distinct reproductive roles. Females undertake all incubation and brooding of chicks until they are around 15 days old, while during this period males provide food for female and chicks.

This study took place in Kielder Forest, northern England (55°13′N, 2°33′W), is a large conifer forest planted with mainly Sitka spruce *Picea sitchensis* and Norway spruce *Picea abies*. Unplanted river margins and a 40–60-year rotational clear-cutting system (size range: 5–100 ha) both provide suitable open habitats for field voles. Replanted areas remain occupied by voles for up to 15 years, after which the young trees shade out the ground vegetation. Field voles show cyclical changes in density in Kielder Forest spanning multiple years (data published by Lambin *et al*. 2000) and are the most important prey species year round for tawny owls (Petty 1999). Field vole densities were assessed three times (in spring, summer and autumn) each year using a Vole Sign Index calibrated against trapping-derived density estimates (Lambin *et al*. 2000). On this basis, we categorized each owl breeding season in one of the following three vole classes: Low (constantly low numbers during the owl breeding season but starting to increase in autumn), Increase (numbers increasing throughout the year) and Decrease (numbers high in spring followed by a rapid decline in summer; Table 1, insert in Fig. 1).

Forty tawny owl territories were identified during 1975–1979 in a 176 km² area by listening for calling birds and finding roost locations, nest sites and fledged broods. Nestboxes were then erected near each territory centre, with an additional box placed between territories. Additional boxes were sited in parts of the forest that lacked owls, at a similar spacing to boxes in the forest with owls. Most nestboxes were erected during winters 1979/1980 and 1980/1981, and at any one time there were at least twice as many boxes available as pairs of owls (Petty 1992a). All pairs breeding in natural nest sites prior to

Table 1. Average parameters for vole density in different seasons (mean number of voles ha⁻¹ ± SD) and total number of chicks fledged in Kielder Forest (mean ± SD) in relation to the phase of the vole cycle

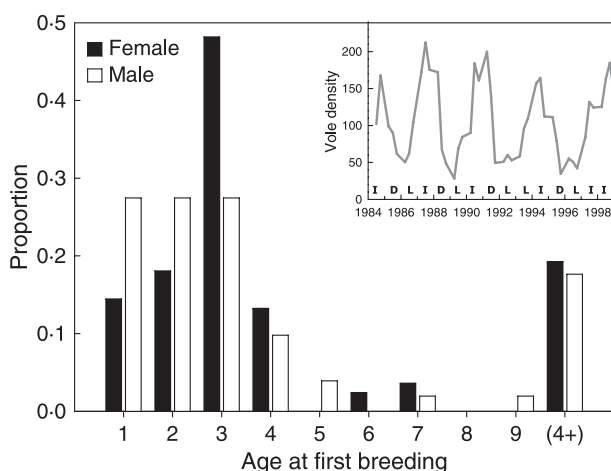|	Phase of the vole cycle		
	Low	Increase	Decrease
Spring vole density	48·5 ± 11·8	125·6 ± 39·2	145·5 ± 48·4
Summer vole density	67·3 ± 17·0	159·4 ± 38·7	94·5 ± 32·8
Autumn vole density	78·7 ± 30·2	154·2 ± 29·2	48·6 ± 11·1
Number of chicks fledged	27·4 ± 16·6	117·8 ± 25·2	97·0 ± 45·8

Fig. 1. Distribution of age at first breeding according to sex ($N = 83$ females and 51 males). Data from individuals ringed as chicks in Kielder Forest only. The category 4+ gathers all birds starting their breeding career at age 4 and older (as used in analyses). Inserted panel: density (ind ha^{-1}) of field vole in Kielder Forest, and classification of years into the three different phases of the vole cycle (Low: L, Increase: I, Decrease: D).

1980 (including sites on the ground) had switched to nestboxes within the 3 years after their erection (Petty, Shaw & Anderson 1994). After the first breeding attempt, the vast majority of owls stayed in the same territory for life. All nestboxes were monitored each year to check for territory occupancy, and, if breeding occurred, to record clutch size and ring chicks. Trapping of breeding adult females was carried out between 1982 and 1998 in nestboxes when chicks were 1–2 weeks old. Over this period, 619 pairs laid ≥1 egg, 532 females raised fledglings (85·9%), and 567 females were caught (91·6%). A similar effort was applied to males between 1988 and 1998 (433, 363 [83·8%], 339 [78·3%]). The proportions of breeding adults caught were constant through the different phases of the vole cycle. Although still ongoing, the trapping effort was reduced after 1998, precluding accurate assignment of AFB. To reduce the bias inherent to the finite study period, the data set was restricted to cohorts born between 1981 and 1995 for females and 1987–1995 for males, as most owls started breeding during their three first years of life (Petty 1992a). Age at first breeding was known for 83 females and 51 males born in Kielder Forest and subsequently recruited into the study population. Furthermore, nestbox occupancy data suggest that only one female and five males might have bred undetected prior to first capture as breeder in the same territory. Changing AFB for these six birds did not alter the results (not shown). Thus, while assuming AFB of wild animals may suffer from several sampling biases, such biases were minimal here.

CAPTURE–RECAPTURE ANALYSES

We used the multi-state capture–recapture framework to estimate age-specific apparent survival and probabilities of access to reproduction or recruitment (Pradel & Lebreton 1999). The term recruitment hereafter is used for owls breeding for the first time. However, some birds may have occupied a territory or formed a pair bond without laying eggs in preceding years. A total of 851 individuals were ringed as chicks in Kielder Forest between 1987 and 1997 (encountered until 1998), and assigned as pre-breeders (PB, or immature state) in the year of ringing. Only breeders have ever been caught in nestboxes. Individuals subsequently recaptured were therefore

unambiguously assigned as breeders (B), and recapture of individuals in state PB was fixed at 0 (unobservable state). Once in state B, individuals were assumed to stay in this state for the remainder of their life, such that the transition from B to PB was impossible (see also Lebreton *et al.* 2003). However, adult tawny owls (in state B) are prone to skip reproduction and the subsequent breeding probability was then accounted for by recapture parameters.

The sex of chicks was unknown except for 312 individuals sexed by molecular techniques (Appleby *et al.* 1997) between 1994 and 1998. The sex ratio among this subset was exactly 1 : 1 (156 males and 156 females), and did not differ from parity in any of these years (binomial tests for each year, all P's $> 0·66$). We therefore assumed an even sex ratio for the rest of the years and randomly assigned the sex of birds that have never been recaptured subsequently as in Nichols *et al.* (2004).

The parameterization of recapture, apparent survival and transition was carried out in E-SURGE 1.4.4 (Choquet, Rouan & Pradel 2009). Goodness-of-fit tests for multistate models were performed in U-CARE 2.2.5 (Choquet *et al.* 2003), following recommendations of Pradel, Wintrebert & Gimenez (2003).

LIFETIME REPRODUCTIVE SUCCESS

We used lifetime reproductive success (LRS) as a proxy for fitness. Lifetime reproductive success was calculated using two different types of offspring counts: lifetime fledgling production (LFP) or lifetime recruit production (LRP), for owls known to have started and ended their breeding career during the study period. An individual was considered to have died if it was not caught for three consecutive years (only three of 70 males and two of 110 females have been recorded after a gap of 3 years in their encounter histories). We considered owls that fledged in Kielder Forest ($N = 41$ females and 30 males) but also owls first caught as unringed adults and therefore likely to be immigrants born outside the study area (23 females and four males). Such individuals can be aged as 1-, 2- or 3 year old, based on the number of juvenile flight feathers remaining in their plumage. However, at 3 years of age, some birds have already replaced all juvenile feathers on both wings and cannot be aged accurately (Petty 1992b). Such birds (aged 3+) were therefore discarded from the data set. As local recruits and immigrants may adopt distinct breeding strategies (Julliard, Perret & Blondel 1996), we considered the dispersal status (disp) in all analyses.

We tested the expectation of equal LRS between males and females for a diploid population with an assumed operational sex ratio of 1 : 1 (Kokko & Jennions 2003) to test whether the study period was long enough for males to obtain reliable estimates of their fitness. Considering owls born in Kielder Forest only, LFP was slightly higher for females compared to males (mean ± SD, females: 6·39 ± 4·52; males: 5·13 ± 3·33). However, LRP was much higher for females (0·95 ± 1·36) than for males (0·40 ± 0·62). We therefore analysed males and females separately and ignored LRP for males.

In an attempt to account for the striking difference in survival prospects between fledglings born in different phases of the vole cycle, we considered a third type of offspring count. Specifically, we estimated the number of fledgling expected to survive to their first winter (sc-LFP), multiplying LFP by empirical estimates for juvenile survival (see Results). To ensure these estimates were robust to the uncertainty inherent to the binomial nature of survival, the number of fledglings alive after the first winter was estimated drawing death or survival outcomes from a binomial distribution with a mean survival rate corresponding to the phase of the vole cycle at birth. These numbers were then summed over the lifetime for each tawny owl with

a complete life history. This procedure was repeated 5000 times to provide 95% confidence sampling intervals for sc-LFP.

Statistical analyses were conducted using the information-theoretic approach, and model selection was based on Akaike's information criterion corrected for small sample size (AICc, Burnham & Anderson 2002). Square-root transformation successfully normalized the distribution of LFP ($+1$) and sc-LFP ($+0.1$) for females (Shapiro-Wilk tests; P's > 0.15), and regression models with Gaussian distribution of error and identity link were run. A Poisson distribution of error with log link was used for LRP. For males, LFP and sc-LFP were slightly bimodal though did not deviate from normality acutely ($P = 0.03$ for LFP, $P = 0.09$ for sc-LFP). These two variables were not satisfactorily normalized by any transformation and were analysed untransformed. All analyses were carried out with R 2.5.1 (R development Core Team, 2006).

Results

AGE AT FIRST BREEDING

The AFB for local recruits ranged from 1 to 9 years old (Fig. 1). Males tended to breed earlier (median = 2) than females (median = 3). AFB was more variable for males than females, as a clear modal AFB was visible for females (48% at age 3), while an even proportion of males (27%) bred at age 1, 2 or 3. There was a strong dependence between AFB and the phase of the vole cycle at first breeding (VFB) as shown by the results from a log-linear model (see the increase in deviance between models 5 and 6 in Table 2). Indeed, most tawny owls of either sex were recruited into the breeding population in two phases of the vole cycle, i.e. either at age 1 in a Decrease phase or at age 3 in an Increase phase (56.7% of females, 49% of males, Appendix S1, Supporting Information). There was also a slight interaction between sex and AFB (or VFB, compare models 2–3 and 5). Indeed, females were more prone to delay reproduction (36 birds with AFB3 in Increase vs. 11 birds with AFB1 in Decrease) than males (12 vs. 13, Table 3).

Owl cohorts born during Increase years accounted for 79.5% (66/83) of female and 76.5% (39/51) of male local recruits (Appendix S1, Supporting Information). In comparison, 52.6% of chicks were reared during an Increase phase (Table 1).

SURVIVAL AND ACCESS TO REPRODUCTION

We considered the Arnason–Schwarz model

$$\{S[(PB, B) \times t \times sex], P[(PB, B) \times t \times sex], \Psi_{PB \to B}(t \times sex)]\}$$

as the starting model. This model fitted adequately the data ($\chi^2 = 31.48$, d.f. = 50, $P = 0.98$). The most parsimonious model included time-dependent recapture rates for breeders, reflecting annual variation in breeding propensity for adults, with a sex-specific parameterization (additive model), accounting for the slightly lower capturability of males.

Juvenile survival rates (from model averaging) varied considerably according to the phase of the vole cycle experienced at birth (compare models 2 and 3 in Table 4): chicks born

Table 2. Model selection from log-linear modelling of the three-way contingency table, testing for conditional dependence between age at first breeding (AFB), phase of the vole cycle at first breeding (VFB) and sex (see Table 3)

No.	Model	Deviance	d.f.	ΔAIC
1	AFB × VFB + AFB × sex + VFB × sex	5·05	6	3·0
2	**AFB × VFB + AFB × sex**	**6·01**	**8**	**0**
3	AFB × VFB + VFB × sex	8·90	9	0·9
4	AFB × sex + VFB × sex	110·04	12	96·0
5	AFB × VFB	13·51	11	1·5
6	AFB + VFB + sex	122·16	17	98·2

The most parsimonious model is in bold.

Table 3. Distribution of age at first breeding according to the phase of the vole cycle experienced during the first breeding event

Age at first breeding	Voles at first breeding		
	Low	Increase	Decrease
Females			
AFB1	0	1	11
AFB2	9	4	2
AFB3	4	36	0
AFB4 +	1	11	4
Total (%)	14 (16·9)	52 (62·7)	17 (20·5)
Males			
AFB1	0	1	13
AFB2	5	8	1
AFB3	2	12	0
AFB4 +	1	3	5
Total (%)	8 (15·7)	24 (47·1)	19 (37·3)

Data from individuals ringed as chicks in Kielder Forest ($N = 83$ females and 51 males).

during an Increase phase had the highest survival (0.33 ± 0.04), whereas those born in a Decrease phase, thus experiencing the crash in vole densities during their first autumn, suffered a fourfold reduction in survival (0.08 ± 0.02). For local survival, an age-dependent model (two age classes: juvenile vs. adult survival) received considerably more support than a model accounting for different survival probabilities between pre-breeder and breeder states (compare models 1 and 2). The survival of chicks belonging to the small cohort born during Low years was intermediate (0.18 ± 0.05). Female and male juveniles had very similar survival rates in the three different vole phases (0–3.7%, model 8) such that a model ignoring sex performed much better (model 3), and averages of these estimates across models were not altered by considering sex.

In contrast to juvenile survival, adult survival (from age 2, i.e. one-year-old birds and older) was not influenced by vole dynamics (compare models 3 and 4 in Table 4). The most parsimonious model included sex-specific adult survival rates (model 9). Unfortunately, we cannot test properly for an interaction between age of breeders and the vole cycle, as

Table 4. Model selection for juvenile and adult survival, and transition (from pre-breeder [PB] to breeder [B] stages) from tawny owls ringed as chicks

No.	Model	Deviance	np	ΔAICc	w_i
Survival					
1	(PB, B)	1486·04	19	56·8	0
2	a_{0-1+}	1483·25	19	39·1	0
3	$a_{0 \times (phase)} + a_{1+}$	1443·54	21	3·5	0·10
4	$a_{0 \times (phase)} + a_{1+ \times phase}$	1443·19	23	7·3	0·01
5	$a_{0 \times (phase)} + a_{1-2+}$	1443·50	22	5·6	0·04
6	$a_{0 \times (phase)} + a_{1-2+,fem} + a_{1+,male}$	1437·66	23	1·8	0·24
7	$sex \times (a_{0 \times (phase)} + a_{1+})$	1437·71	27	6·0	0·03
8	$sex \times a_{0 \times (phase)} + a_{1+}$	1442·14	24	8·4	0·01
9	$a_{0 \times t(phase)} + sex \times a_{1+}$	**1437·95**	**22**	**0**	**0·58**
Access to reproduction ($\Psi_{PB \to B}$)					
10	t	1432·12	30	10·9	0
11	sex	1450·49	21	10·5	0
12	a_{1-2+}	1442·46	21	2·4	0·13
13	$sex + a_{1-2+}$	1439·60	22	1·6	0·20
14	$sex \times a_1 + a_{2+}$	**1437·95**	**22**	**0**	**0·45**
15	$phase + a_{1-2+}$	1439·12	23	3·2	0·09
16	$phase + a_{1-2+} + sex$	1436·77	24	3·0	0·10
17	$cohort(phase) \times a_{1-2+}$	1437·32	25	5·6	0·03
18	constant	1451·58	20	9·5	0

The most parsimonious parameterization for survival and access to reproduction is indicated in bold. ΔAICc and AICc weights (w_i) were calculated separately for survival and transition, using the best parameterization for the other step (i.e. models 9 and 14 are the same).

np, number of estimable parameters; t, time-dependent model; phase, a three-level factor categorizing years according to the dynamics of field voles (Low, Increase, Decrease) used to categorize time and cohort; a_{0-1+} two age classes, juvenile and adult; a_{1+} and a_{1-2+}, one and two adult age classes respectively; '+' and '×' denote respectively additive and interactive models.

1-year-old birds bred exclusively during Decrease years. However, we did test this indirectly by comparing a model including a phase effect on adult survival (all ages pooled in model 4, no support) to a model contrasting survival of 1-year-old breeders with older ones. We found some support for survival of 1-year-old birds being lower compared to older ones, but only for females (female survival from model 5, $a_1 = 0.80 \pm 0.13$, $a_{2+} = 0.88 \pm 0.03$; compare models 5, 6 and 9). Model averaging provided the following survival estimates for females aged 2: 0.85 ± 0.03, and aged 3+: 0.87 ± 0.03, and for males aged 2+: 0.79 ± 0.03.

The probability of being recruited at age 1, for birds that survived until that age, was lower than at older ages, and especially so for females (PB to B transition probability estimates for female aged 1: 0.14 ± 0.05, male aged 1: 0.26 ± 0.08, female aged 2+: 0.44 ± 0.08, male aged 2+: 0.49 ± 0.11, model 14 in Table 4). As a consequence of the strong dependence between age and voles at first breeding generating low sample size for certain conditions of AFB and VFB, models including four age-classes or the complete interaction between age, vole phase and sex did not provide reliable estimates.

LIFETIME CONSEQUENCES OF FIRST BREEDING

The phase of the vole cycle during the first breeding attempt (voles at first breeding: VFB), more than AFB *per se*, drove the variation in LRS, with female tawny owls starting to breed during an Increase phase of the vole cycle being the most successful (Table 5, Fig. 2). Models including AFB explained 14–28% of the variance in LRS according to the type of offspring count, while models with VFB systematically performed better and explained 20–48% of the variance. There was no support for models including AFB (all w_i < 0·01) compared to models with VFB. Model selection, whether based on LFP, sc-LFP or LRP, consistently identified the model including an additive effect of voles at first breeding and dispersal status (VFB + disp) as the most supported, with AICc weights ranging 0·60–0·81. Nearly half of the between-individual variation in sc-LFP was explained by this model. Bootstrapped results of sc-LFP revealed that females who started reproducing at age 3 (and to a lesser extent at age 2) had higher fitness prospect than females who started to breed at age 1 or age 4+ ([95% CI]: AFB1 [0·44–1·06], AFB2 [0·92–1·85], AFB3 [1·25–1·84], AFB4+ [0–1]). Females that started to breed in an Increase phase had strik-

Table 5. Summary of model selection considering female lifetime reproductive success expressed as number of fledglings (LFP), number of fledglings expected to survive over the first winter (sc-LFP) and number of recruits (LRP)

Model	LFP			sc-LFP			LRP		
	AICc	w_i	R^2	AICc	w_i	R^2	AICc	w_i	R^2
Null	153·36	0	–	74·39	0	–	168·52	0	–
AFB × disp	153·33	0	20·2	67·46	0	28·4	160·88	0	21·8
AFB + disp	149·71	0	18·3	64·06	0	26·4	158·88	0·01	18·9
AFB	150·58	0	14·0	64·57	0	22·9	161·31	0	14·1
VFB × disp	138·33	0·09	34·3	44·89	0·09	47·6	151·41	0·27	29·1
VFB + disp	**133·97**	**0·77**	**33·6**	**40·42**	**0·81**	**47·2**	**149·84**	**0·60**	**25·9**
VFB	137·26	0·15	27·5	44·52	0·10	41·5	153·20	0·11	20·2

LFP (+1) and sc-LFP (+0·1) were square root-transformed before being analysed with a Gaussian distribution of error. LRP was analysed using a Poisson distribution of error. Explanatory factors were age at first breeding (AFB: 1, 2, 3 & 4+), voles at first breeding (VFB: Increase, Decrease & Low) and dispersal status (disp: local vs. immigrant). The most parsimonious model is in bold.
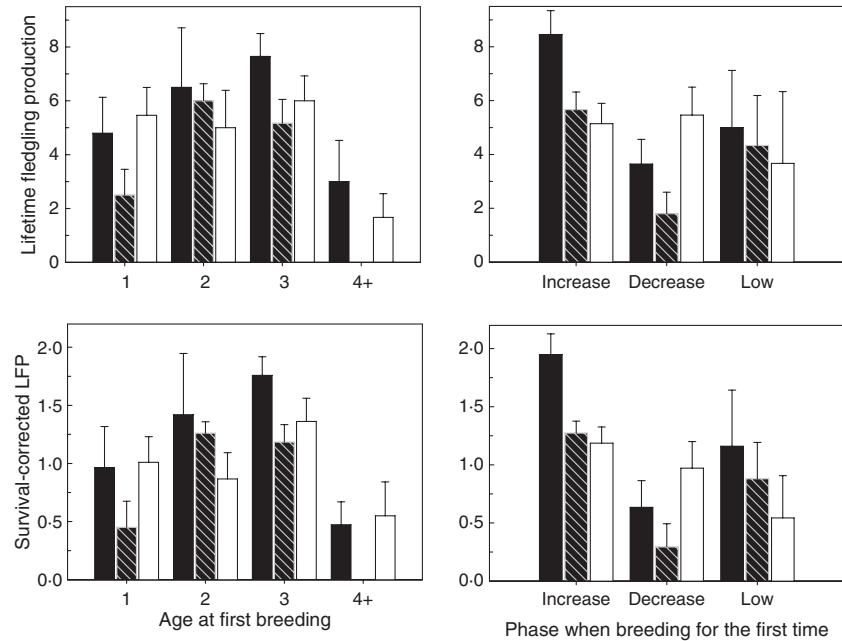
Fig. 2. Lifetime reproductive success (mean ± SE) based on number of fledglings (LFP, top raw) and number of fledglings expected to survive their first winter (sc-LFP, bottom raw) according to age at first breeding (AFB, left column) and phase of the vole cycle during the first breeding attempt (VFB, right column). Black bars refer to females either being local recruits ($N = 41$, filled bars) or immigrants ($N = 23$, hatched bars), and white bars to males ($N = 30$, local recruits only).

ingly higher sc-LFP [1·38–1·97] than females starting in a Decrease year [0·32–0·79]. The few females starting to reproduce in Low vole years had intermediate success [0·5–1·63]. This pattern remained broadly true when considering local recruits vs. immigrants (compare models VFB × disp and VFB + disp, see also Fig. 2), although females born locally consistently produced more fledglings (6·4 ± 4·5 vs. 4·7 ± 2·9), more fledglings expected to survive the first winter (1·4 ± 1·0 vs. 1·0 ± 0·6), and more local recruits (median: 1 vs. 0) than immigrants into Kielder Forest.

No consistent pattern was found for males, and null models were always preferred (Table 6). In striking contrast with females, males breeding for the first time in a Decrease or an Increase performed equally well over their lifetime (Fig. 2). Too few immigrant males precluded any inference on the effect of DISP. The difference in LFP or sc-LFP between AFB1 and AFB3 was less marked than for females (Fig. 2). As for females, males that recruited late (AFB4+) suffered reduced LRS.

Restricting the data set to female local recruits only, allowed us to test whether the phase of the vole cycle experienced during the post-fledgling period affected LRS. The vole phase at birth had virtually no effect on LRS (using sc-LFP) for owls that survived their first winter (ΔAICc = 21·8, $R^2 = 3\%$). As for the entire data set, most of the variation in LRS was driven by VFB (ΔAICc = 0, $R^2 = 43\%$), compared to AFB (ΔAICc = 15·2, $R^2 = 22·5\%$).

The measure of LRS used above only considers birds that successfully recruited, but ignores those that failed to ever breed. So as to overcome the bias induced by this 'invisible fraction', we used age-specific adult survival rates to estimate the number of females (to the nearest integer born during an Increase year) that postponed reproduction but died before breeding (i.e. sc-LFP = 0). From this, we then re-calculated average LRS for first breeders at age 2 (in a Low year, $N = 5$

Table 6. Summary of model selection considering male lifetime reproductive success expressed as number of fledglings (LFP), and number of fledglings expected to survive over the first winter (sc-LFP), and number of recruits (LRP). LFP and sc-LFP were analysed untransformed (see Methods) with a Gaussian distribution of error

	LFP			sc-LFP		
Model	AICc	w_i	R^2	AICc	w_i	R^2
Null	**179·19**	**0·73**	–	**70·59**	**0·62**	–
AFB + disp	185·63	0·03	11·8	77·44	0·02	10·8
AFB	182·70	0·13	11·7	74·50	0·09	10·7
VFB + disp	186·15	0·02	2·3	75·40	0·06	8·3
VFB	183·39	0·09	2·3	72·65	0·22	8·3

See Table 4 for abbreviations. The most parsimonious model is in bold. Note that the low number of immigrants precluded the run of interactive models.

observed + 1 female expected to have died before breeding) or age 3 (Increase, $N = 29 + 10$, assuming equal proportions of immigrant amongst the invisible fraction as in the observed sample). Even though delayed strategies still had higher LFP and sc-LFP, the difference in LRS was not large enough to demonstrate an effect of AFB on fitness (null models having the lowest AICc). Nevertheless, voles at first breeding did still affect the number of recruits (LRP), with females starting to breed at age 3 in an Increase phase producing more recruits (predicted number of additional recruits compared to AFB1: −0·05 ± 0·84 for AFB2, 0·94 ± 0·48 for AFB3; model AFB + DISP: ΔAICc = 2·8 with the null model, $R^2 = 11·3\%$, note in this case that AFB and VFB are strictly equivalent, as only females from Increase cohorts were considered). Interestingly, females starting to breed in an Increase phase produced fledglings that had a higher chance of being recruited (Fig. 3). In contrast, none of the
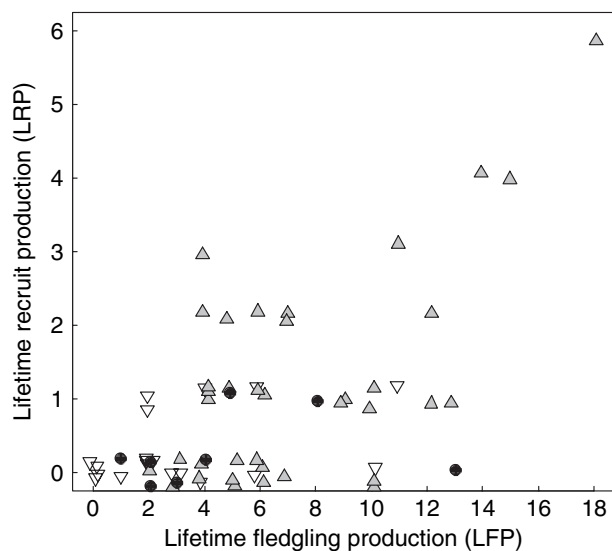
Fig. 3. Relationship between the number of local recruits and the number of fledglings produced over lifetime by tawny owl females. The different symbols indicate the phase of the vole cycle when breeding for the first time (VFB; grey triangle: Increase, open triangle: Decrease, black circle: Low). For a given number of fledglings produced, females starting their breeding career during an Increase year could expect more recruits than those breeding for the first time in Decrease or Low years. Points were slightly moved to facilitate viewing.

females that started to breed in either Decrease or Low phases produced more than one recruit, whatever the number of fledglings produced (competing models with LRP as the response variable: [VFB + LFP] vs. LFP, ΔAICc = 1·6, R^2 = 42·6 vs. 36·5% respectively).

Finally, the proportion of owls failing to breed ever again after the first breeding attempt was much higher for females that started to breed at age 1 (55·6%, N = 18) compared to those that postponed breeding until age 2 or older (17·9%, N = 84). This suggests a high survival cost for reproducing at age 1 (modelling the probability to breed ever again after the first attempt as a binary variable, binomial distribution of error, competing models: null vs. AFB [1, 2+], ΔAICc = 8·0). There was no such difference for males (age 1: 25%, N = 16; older: 21·8%, N = 55; ΔAICc = −2·0).

DO NATAL CONDITIONS AFFECT THE DECISION OF FIRST BREEDING?

Hatching date is often used as proxy of individual quality in many avian systems. Using owls born during Increase years for which sample size is largest, we found that females who started to breed at age 1 had hatched 6–15 days earlier relative to females that postponed breeding (modelling the probability to breed at age 1 or later as a binary variable, binomial distribution of error, competing models: null vs. hatching date, ΔAICc = 5·5). There was no such pattern in males (ΔAICc = −0·3). The proportion of deviance explained by hatching date was however relatively low (R^2 = 12·8%). The number of brood mates had no effect on the probability to

breed at age 1 (ΔAICc = −0·9 and ΔAICc = −0·7 for females and males respectively).

Discussion

This study demonstrated that decision of first breeding in tawny owls, equivalent to recruitment to the breeding population, was contingent upon three different phases of the prey cycle, and entailed dramatic consequences in terms of LRS for females. Tawny owls have evolved strategies with delayed reproduction, and females appeared to be more constrained by environmental variation and reproductive costs than males, and therefore enter the breeding segment of the population at older ages.

AGE-SPECIFIC SURVIVAL AND ACCESS TO REPRODUCTION

Field vole densities in the first autumn/winter of life acted as a bottleneck for vole predators (see also Korpimäki & Lagerström 1988; Brommer, Pietiäinen & Kolunen 2002b). Juvenile survival rates varied greatly between phases of the vole cycle. A comparison between the two most productive cohorts was particularly revealing. While about the same number of chicks fledged during a Decrease or an Increase year, mortality rate was about 90% for the former cohort, but less than 70% for the latter, as a consequence of differences in vole density during the post-fledgling period. As a result, the breeding population structure of tawny owls in Kielder Forest was highly biased, with most local recruits (>75%) being reared during an Increase phase. Adult survival was not affected by prey density, thus confirming previous findings on tawny owls in Finland (Francis & Saurola 2004; Karell *et al.* 2009), in contrast with other owl species in the same area (Ural owl, Brommer *et al.* 2002b; Tengmalm's owl *Aegolius funereus* L., Hakkarainen *et al.* 2002).

Multistate capture-recapture modelling emphasized that access to reproduction was mostly affected by age, 1-year-old birds having lower recruitment rates than older ones, and this age effect was particularly pronounced in females. The probability of transition from pre-breeding to breeding stage was higher for birds aged 2 and older, with nearly half of the birds alive at a given age entering the breeding population. This suggests that relatively few tawny owls liven as floaters in Kielder Forest. In comparison, recruitment rates for the white stork *Ciconia ciconia* L. were much lower (from 0·06 to 0·21 between age 2 and age 4; Nevoux, Barbraud & Barbraud 2008), indicating a larger proportion of floaters in the population. Interestingly, for this species with similar vital rates to tawny owl, first breeding never occurred at age 1.

LIFETIME CONSEQUENCES OF FIRST BREEDING

How to estimate fitness has long been debated (Grafen 1988), particularly so in the context of timing of reproduction (Brommer, Merilä & Kokko 2002a). Here, we deliberately used LRS instead of the rate-sensitive method (λ_{ind})

proposed by McGraw & Caswell (1996) which explicitly accounts for AFB. This is because the effect of the timing of first reproduction is contingent upon whether λ_{ind} exceeds 1, i.e. whether average individuals produce two or more offspring over their lifetime, and is affected by the type of counts used (e.g. nestling or recruit; Brommer *et al.* 2002a). This threshold in LRS determines whether individuals are analogous to either declining populations (then delayed reproduction is favoured), or to increasing populations (then reproduction early in life is favoured), and therefore may alter the ranking between different breeding strategies taken from rate-sensitive and rate-insensitive methods (see Supporting Information Appendix S2). Furthermore, Brommer *et al.* (2004) provided empirical evidence that LRS was a better proxy for long-term genetic contributions than λ_{ind} when counting fledglings. The challenge of estimating fitness becomes even more complex when such populations are subjected to environmentally-driven fluctuating selection pressures (Benton & Grant 1996; Brommer, Kokko & Pietiäinen 2000), as we have demonstrated in this study. Indeed, LRS based on the count of fledglings implausibly assumes invariant recruitment probabilities for offspring. While counting recruits is expected to provide a more accurate measure of fitness, such a method requires exceptionally long-term and large-scale data sets to obtain unbiased estimates, hence limiting its applicability (e.g. with males in this study; see also Tinbergen 2005). In an attempt to overcome this issue, we calculated an alternative estimate for individual fitness (sc-LFP) by estimating the number of fledglings surviving the first winter, according to juvenile survival rates expected from the prevailing vole dynamics. While it requires combining population-level survival estimates with individual breeding histories, this method may provide useful insights when survival prospects of offspring vary to a large extent among years, but in a relatively predictable manner according to environmental covariates (e.g. Reid *et al.* 2003). Interestingly, the three types of count provided qualitatively similar results, but the proportion of variance explained was noticeably higher with sc-LFP (Table 5; Fig. 3).

The phase of the vole cycle during the first breeding attempt (VFB) was the main driver of the variation in fitness for female tawny owls in Kielder Forest (Table 5, Fig. 2). Models incorporating VFB consistently received more support than models with AFB, and the former explained a substantial amount of the variance (26% when counting recruits, 47% when counting fledglings corrected for juvenile survival). Also, females recruited locally always performed better than immigrant females (see also Bouwhuis *et al.* 2009), providing evidence for costs associated with dispersal in this species. Considering the fitness of females born locally, we did not find evidence for a carry-over effect of vole densities experienced early in life. Owls surviving the harsh conditions during their first winter were not any longer affected and had similar fitness to those born during an Increase or a Low year who had experienced rising prey densities during their first winter. Focusing on females from the Increase cohort further revealed that, even when accounting for hypothetical individuals who postponed reproduction but died before recruiting, a delayed reproduction strategy remained the most successful (but only when counting recruits, Fig. 3). Brommer *et al.* (1998) found similar results with Ural owl although the difference between females using the first opportunity to breed and females postponing breeding was no longer significant with LRS accounting for the invisible fraction, possibly due to a lack of power.

As most females breeding at age 1 did so in a Decrease year, it is not possible to tease apart the relative contribution of age and environmental conditions on fitness. A study on tawny owls in Finland suggests however that the cost of the first reproduction remains high even under favourable conditions (Karell *et al.* 2009). In this population, > 50% of new recruits were 1-year-old birds that bred for the first time during the Increase phase of the vole cycle, and inexperienced breeders (pooling birds with different AFB however) suffered a severe reduction in survival. In contrast to our results however, the two sexes were equally affected and had strikingly lower survival. The moulting vs. reproduction resource allocation trade-off (Dawson *et al.* 2000) may be a plausible mechanism by which a cost of reproduction arises in tawny owls. Indeed, breeding birds allocated fewer resources to moulting wing and tail feathers, a key process in maintaining fight ability, than non-breeding birds. Tawny owls breeding at age 1 replace none of their juvenile flight feathers (remiges and rectrices) before breeding commences (Petty 1994). Such birds might struggle to replace feathers later on, a process that could impair their survival or their breeding capabilities. As a fact, females breeding at age 1, but not males, drastically reduced their chance of breeding ever again.

Most previous studies on AFB and costs of reproduction have, for practical reasons, focused solely on females (e.g. Viallefont, Cooke & Lebreton 1995), or even pooled individuals of unknown sex (e.g. Barbraud & Weimerskirch 2005). This is despite life-history theory predicting that sex-specific roles in reproduction should affect the pattern of selection between males and females. Although our analyses are based on a smaller sample, neither AFB nor VFB seems to alter male fitness, and 1-year-old males breeding in Decrease years did not suffer the additional mortality seen in females. Costs of reproduction might have contributed to the evolution of delayed breeding in females whereas males appeared less constrained (Tavecchia *et al.* 2001; Hawn, Radford & du Plessis 2007).

PREY CYCLICITY: A LIFE-HISTORY TRAP FOR TAWNY OWLS?

Organisms may have evolved life-history strategies such as bet-hedging and delayed reproduction when confronted with temporally varying environment (Wilbur & Rudolf 2006). However, and contrary to previous assertions, recent theoretical work reveals that temporal environmental variability alone cannot select for delayed reproduction in classic iteroparous organisms (i.e. with adult survival higher than juvenile survival; Koons, Metcalf & Tuljapurkar 2008). Costs associated with early reproduction must therefore be large to

make delayed reproduction evolutionarily beneficial. Indeed, we have provided here evidence of high costs of early reproduction that translates into lower realized fitness. This, in turn, begs the question of why did some tawny owl females start to breed at age 1 in a Decrease vole year? Obviously, individuals typically differ in intrinsic quality and it could be hypothesized that owls breeding at age 1 were individuals with lower survival prospects opting for a best-of-a-bad job strategy. Surprisingly, we found just the opposite. Females that recruited at age 1 were those that hatched relatively early in the previous year, a trait classically assumed to reflect better offspring internal state as a consequence of higher parental quality and/or investment (e.g. Spear and Nur, 1994). High prey densities during spring of Decrease years might have lured young females into a life-history trap, by encouraging breeding in a year where resources later collapsed. Such a trap effect may be magnified by the low number of potential recruits available in a Decrease phase. Indeed, the fact that recruits were mostly yearlings reared during the previous Increase phase indicated a lack of older birds in the non-breeding pool.

Finally, given the marked impact of cyclical prey dynamics on life-history decisions of tawny owls, it would be interesting to investigate whether early conditions (phase of the vole cycle) at birth or during the first breeding event, or AFB, affect individual age-specific performance throughout lifetime, and potentially population dynamics. This is particularly relevant given the decreasing amplitude of prey multi-annual cycles seen in Kielder Forest as well as elsewhere in Europe (Bierman *et al.* 2006; Ims, Henden & Killengreen 2008).

Acknowledgements

References

Appleby, B.M., Petty, S.J., Blakey, J.K., Rainey, P. & MacDonald, D.W. (1997) Does variation of sex ratio enhance reproductive success of offspring in tawny owls (*Strix aluco*)? *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **264**, 1111–1116.

Barbraud, C. & Weimerskirch, H. (2005) Environmental conditions and breeding experience affect costs of reproduction in blue petrels. *Ecology*, **86**, 682–692.

Benton, T.G. & Grant, A. (1996) How to keep fit in the real world: elasticity analyses and selection pressures on life histories in a variable environment. *The American Naturalist*, **147**, 115–139.

Bierman, S.M., Fairbairn, J.P., Petty, S.J., Elston, D.A., Tidhar, D. & Lambin, X. (2006) Changes over time in the spatiotemporal dynamics of cyclic populations of field voles (*Microtus agrestis* L.). *The American Naturalist*, **167**, 583–590.

Bouwhuis, S., Sheldon, B.C., Verhulst, S. & Charmantier, A. (2009) Great tits growing old: selective disappearance and the partitioning of senescence to stages within the breeding cycle. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **276**, 2769–2777.

Bradford, M.J. & Roff, D.A. (1993) Bet hedging and the diapause strategies of the cricket *Allonemobius fasciatus*. *Ecology*, **74**, 1129–1135.

Brommer, J.E., Pietiäinen, H. & Kolunen, H. (1998) The effect of age at first breeding on Ural owl lifetime reproductive success and fitness under cyclic food conditions. *Journal of Animal Ecology*, **67**, 359–369.

Brommer, J.E., Kokko, H. & Pietiäinen, H. (2000) Reproductive effort and reproductive values in periodic environments. *The American Naturalist*, **155**, 454–472.

Brommer, J.E., Merilä, J. & Kokko, H. (2002a) Reproductive timing and individual fitness. *Ecology Letters*, **5**, 802–810.

Brommer, J.E., Pietiäinen, H. & Kolunen, H. (2002b) Reproduction and survival in a variable environment: Ural owls (*Strix uralensis*) and the three-year vole cycle. *The Auk*, **119**, 544–550.

Brommer, J., Gustafsson, L., Pietiäinen, H. & Merilä, J. (2004) Single-generation estimates of individual fitness as proxies for long-term genetic contribution. *The American Naturalist*, **163**, 505–517.

Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference*, 2nd edn. Springer-Verlag, New-York.

Cam, E. & Monnat, J.Y. (2000) Apparent inferiority of first-time breeders in the kittiwake: the role of heterogeneity among age classes. *Journal of Animal Ecology*, **69**, 380–394.

Charmantier, A., Perrins, C., McCleery, R.H. & Sheldon, B.C. (2006) Quantitative genetics of age at reproduction in wild swans: support for antagonistic pleiotropy models of senescence. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 6587–6592.

Choquet, R., Reboulet, A.M., Pradel, R., Gimenez, O. & Lebreton, J.-D. (2003) *User's Manual for U-CARE.*, pp. ftp://ftp.cefe.cnrs-mop.fr/biom/Soft-CR/. CEFE/CNRS, Montpellier.

Choquet, R., Rouan, L. & Pradel, R. (2009). *Modeling Demographic Processes in Marked Populations* (eds D.L. Thomson, E.G. Cooch & M.J. Conroy), pp. 845–865. Environmental and Ecological Statistics Series, Vol. 3, Springer US.

Curio, E. (1983) Why do young birds reproduce less well? *Ibis*, **125**, 400–404.

Dawson, A., Hinsley, S.A., Ferns, P.N., Bonser, R.H.C. & Eccleston, L. (2000) Rate of moult affects feather quality: a mechanism linking current reproductive effort to future survival. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **267**, 2093–2098.

Descamps, S., Boutin, S., Berteaux, D. & Gaillard, J.M. (2006) Best squirrels trade a long life for an early reproduction. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **273**, 2369–2374.

Ens, B.J., Weissing, F.J. & Drent, R.H. (1995) The despotic distribution and deferred maturity: two sides of the same coin. *The American Naturalist*, **146**, 625–650.

Francis, C.M. & Saurola, P. (2004) Estimating components of variance in demographic parameters of Tawny Owls, *Strix aluco*. *Animal Biodiversity and Conservation*, **27**, 489–502.

Grafen, A. (1988). On the uses of data on lifetime reproductive success. *Reproductive Success*. (ed. T.H. Clutton-Brock), pp. 538. University of Chicago Press, Chicago.

Hadley, G.L., Rotella, J.J. & Garrott, R.A. (2007) Evaluation of reproductive costs for Weddell seals in Erebus Bay, Antarctica. *Journal of Animal Ecology*, **76**, 448–458.

Hakkarainen, H., Korpimäki, E., Koivunen, V. & Ydenberg, R. (2002) Survival of male Tengmalm's owls under temporally varying food conditions. *Oecologia*, **131**, 83–88.

Hawn, A.T., Radford, A.N. & du Plessis, M.A. (2007) Delayed breeding affects lifetime reproductive success differently in male and female green woodhoopoes. *Current Biology*, **17**, 844–849.

Houston, A.I. & McNamara, J.M. (1999) *Models of Adaptive Behaviour*. Cambridge University Press, Cambridge.

Ims, R.A., Henden, J.-A. & Killengreen, S.T. (2008) Collapsing population cycles. *Trends in Ecology & Evolution*, **23**, 79–86.

Julliard, R., Perret, P. & Blondel, J. (1996) Reproductive strategies of philopatric and immigrant blue tits. *Acta Oecologia*, **17**, 487–501.

Karell, P., Ahola, K., Karstinen, T., Zolei, A. & Brommer, J.E. (2009) Population dynamics in a cyclic environment: consequences of cyclic food abundance on tawny owl reproduction and survival. *Journal of Animal Ecology*, **78**, 1050–1062.

Kokko, H. & Jennions, M. (2003) It takes two to tango. *Trends in Ecology & Evolution*, **18**, 103–104.

Koons, D.N., Metcalf, C.J.E. & Tuljapurkar, S. (2008) Evolution of delayed reproduction in uncertain environments: a life-history perspective. *The 'merican Naturalist*, **172**, 797–805.

Korpimäki, E. & Lagerström, M. (1988) Survival and natal dispersal of fledglings of Tengmalm's owl in relation to fluctuating food conditions and hatching date. *Journal of Animal Ecology*, **57**, 433–441.

Lambin, X. & Yoccoz, N.G. (2001) Adaptive precocial reproduction in voles: reproductive costs and multivoltine life-history strategies in seasonal environments. *Journal of Animal Ecology*, **70**, 191–200.

Lambin, X., Petty, S.J. & MacKinnon, J.L. (2000) Cyclic dynamics in field vole populations and generalist predation. *Journal of Animal Ecology*, **69**, 106–118.

Lebreton, J.D., Hines, J.E., Pradel, R., Nichols, J.D. & Spendelow, J.A. (2003) Estimation by capture-recapture of recruitment and dispersal over several sites. *Oikos*, **101**, 253–264.

McGraw, J.B. & Caswell, H. (1996) Estimation of individual fitness from life-history data. *The American Naturalist*, **147**, 47–64.

Nevoux, M., Barbraud, J.-C. & Barbraud, C. (2008) Nonlinear impact of climate on survival in a migratory white stork population. *Journal of Animal Ecology*, **77**, 1143–1152.

Nichols, J.D., Kendall, W.L., Hines, J.E. & Spendelow, J.A. (2004) Estimation of sex-specific survival from capture-recapture data when sex is not always known. *Ecology*, **85**, 3192–3201.

Pasinelli, G. & Walters, J.R. (2002) Social and environmental factors affect natal dispersal and philopatry of male red-cockaded woodpeckers. *Ecology*, **83**, 2229–2239.

Petty, S.J. (1992a) *The Ecology of the Tawny Owl Strix aluco in the Spruce Forests of Northumberland and Argyll*. Open University, Milton Keynes.

Petty, S.J. (1992b) A guide to age determination of tawny owl *Strix aluco*. *The Ecology and Conservation of European Owls* (eds C.A. Galbraith, I.R. Taylor & S. Percival), pp. 89–91. Joint Nature Conservation Committee, UK Nature Conservation, No.5, Peterborough.

Petty, S.J. (1994). Moult in tawny owls *Strix aluco* in relation to food supply and reproductive success. *Raptor Conservation Today* (eds B.-U. Meyburg & R.D. Chancellor), pp. 521–530. World Working Group on Birds of Prey and Owls & Pica Press, Bodmin.

Petty, S.J. (1999) Diet of tawny owls (*Strix aluco*) in relation to field vole (*Microtus agrestis*) abundance in a conifer forest in northern England. *Journal of Zoology, London*, **248**, 451–465.

Petty, S.J., Shaw, G. & Anderson, D.I.K. (1994) Value of nest boxes for population studies of owls in coniferous forest in Britain. *Journal of Raptor Research*, **28**, 134–142.

Pianka, E.R. & Parker, W.S. (1975) Age-specific reproductive tactics. *The American Naturalist*, **109**, 453–464.

Pradel, R. & Lebreton, J.D. (1999) Comparison of different approaches to the study of local recruitment of breeders. *Bird Study*, **46**, S74–S81.

Pradel, R., Wintrebert, C.M.A. & Gimenez, O. (2003) A proposal for a goodness-of-fit test to the Arnason-Schwarz multistate capture-recapture model. *Biometrics*, **59**, 43–53.

R development Core Team (2006) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Reid, J.M., Bignal, E.M., Bignal, S., McCracken, D.I. & Monaghan, P. (2003) Environmental variability, life-history covariation and cohort effects in the red-billed chough Pyrrhocorax pyrrhocorax. *Journal of Animal Ecology*, **72**, 36–46.

Ruf, T., Fietz, J., Schlund, W. & Bieberm, C. (2006) High survival in poor years: life history tactics adapted to mast seeding in the edible dormouse. *Ecology*, **87**, 372–381.

Spear, L. & Nur, N. (1994) Brood size, hatching order and hatching date: effects on four life-history stages from hatching to recruitment in western gulls. *Journal of Animal Ecology*, **63**, 283–298.

Tavecchia, G., Pradel, R., Boy, V., Johnson, A.R. & Cézilly, F. (2001) Sex- and age-related variation in survival and cost of first reproduction in greater Flamingos. *Ecology*, **82**, 165–174.

Tinbergen, J.M. (2005) Biased estimates of fitness consequences of brood size manipulation through correlated effects on natal dispersal. *Journal of Animal Ecology*, **74**, 1112–1120.

Tuljapurkar, S. (1990) Delayed reproduction and fitness in variable environments. *Proceedings of the National Academy of Sciences of the United States of America*, **87**, 1139–1143.

Viallefont, A., Cooke, F. & Lebreton, J.-D. (1995) Age-specific costs of first-time breeding. *The Auk*, **112**, 67–76.

Wilbur, H.M. & Rudolf, V.H.W. (2006) Life-history evolution in uncertain environments: bet hedging in time. *The American Naturalist*, **168**, 398–411.

Williams, G.C. (1966) Natural selection, the costs of reproduction, and a refinement of Lack's principle. *The American Naturalist*, **100**, 687–690.

Supporting Information

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

Appendix S1. Age at first breeding pyramids according the phase of the vole cycle at birth for locally recruited tawny owls in Kielder Forest.

Appendix S2. For comparative purpose, we extended the analysis on fitness consequences of age at first breeding in tawny owls using the rate-sensitive method proposed by McGraw & Caswell (1996).

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