Food availability and predation risk, rather than intrinsic attributes, are the main factors shaping the reproductive decisions of a long-lived predator

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Summary

1. Deciphering the causes of variation in reproductive success is a fundamental issue in ecology, as the number of offspring produced is an important driver of individual fitness and population dynamics. Little is known, however, about how different factors interact to drive variation in reproduction, such as whether an individual's response to extrinsic conditions (e.g. food availability or predation) varies according to its intrinsic attributes (e.g. age, previous allocation of resources towards reproduction).

2. We used 29 years of reproductive data from marked female tawny owls and natural variation in food availability (field vole) and predator abundance (northern goshawk) to quantify the extent to which extrinsic and intrinsic factors interact to influence owl reproductive traits (breeding propensity, clutch size and nest abandonment).

3. Extrinsic and intrinsic factors appeared to interact to affect breeding propensity (which accounted for 83% of the variation in owl reproductive success). Breeding propensity increased with vole density, although increasing goshawk abundance reduced the strength of this relationship. Owls became slightly more likely to breed as they aged, although this was only apparent for individuals who had fledged chicks the year before.

4. Owls laid larger clutches when food was more abundant. When owls were breeding in territories less exposed to goshawk predation, 99·5% of all breeding attempts reached the fledging stage. In contrast, the probability of breeding attempts reaching the fledging stage in territories more exposed to goshawk predation depended on the amount of resources an owl had already allocated towards reproduction (averaging 87·7% for owls with clutches of 1–2 eggs compared to 97·5% for owls with clutches of 4–6 eggs).

5. Overall, our results suggested that changes in extrinsic conditions (predominantly food availability, but also predator abundance) had the greatest influence on owl reproduction. In response to deteriorating extrinsic conditions (fewer voles and more goshawks), owls appeared to breed more frequently, but allocated fewer resources per breeding attempt. However, intrinsic attributes also appeared to have a relatively small influence on how an individual responded to variation in extrinsic conditions, which indicates that owl reproductive decisions were shaped by a complex series of extrinsic and intrinsic trade-offs.

Key-words: *Accipiter gentilis*, breeding decisions, breeding propensity, clutch size, juvenile survival, life-history trade-offs, northern goshawk, reproductive strategies, *Strix aluco*, tawny owl

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Introduction

Understanding how different factors influence reproductive decisions is a central issue in ecology and conservation biology, as the number of offspring produced is a key driver of population dynamics (Nichols *et al.* 2004; Sedinger *et al.* 2008). The impact of some extrinsic factors on reproductive decisions, such as food availability, is well understood (reviewed in White 2008). In contrast, the impact of others, such as predation risk, is more equivocal, even when the same predator and prey species are examined (Sergio & Hiraldo 2008). Quantifying the indirect effect of predation risk on prey reproductive decisions under natural conditions is difficult, but merits further investigation as it can theoretically destabilize predator–prey dynamics, under certain circumstances (Kokko & Ruxton 2000). Furthermore, despite the influence of food availability and predation risk on reproductive success being extensively studied, the extent to which these two extrinsic factors interact to affect reproductive decisions remains poorly understood (but see Sergio, Marchesi & Pedrini 2003).

Food availability is frequently reported to have a positive influence on the proportion of individuals in the population breeding and the number of offspring produced (Arcese & Smith 1988; Pietiäinen 1989; Petty 1992; Millon *et al.* 2014). However, breeding individuals and individuals producing more offspring per breeding attempt are often more vulnerable to predation compared to non-breeding individuals (Magnhagen 1991; Hoogland *et al.* 2006) or those producing fewer offspring (Ercit, Martinez-Novoa & Gwynne 2014). Consequently, in years when predation risk is high, individuals of long-lived iteroparous species may attempt to minimize their vulnerability to predation by: (i) refraining from breeding (Spaans, Blijleven & Popov 1998); (ii) reducing the number or quality of offspring (Doligez & Clobert 2003; Zanette *et al.* 2011); or (iii) abandoning the breeding attempt at an early stage (Sergio, Marchesi & Pedrini 2003; Chakarov & Krüger 2010). Indeed, experimental studies have shown that individuals respond to variation in predation risk by making facultative decisions to alter their allocation of resources towards reproduction, so as to reduce their own, or their offspring's vulnerability to predators (Ghalambor & Martin 2001; Doligez & Clobert 2003; Fontaine & Martin 2006; Zanette *et al.* 2011). However, according to life-history theory, such changes in reproductive strategies should arise only when the losses incurred from not breeding, or not completing a breeding attempt, are compensated for by future reproductive success (Stearns 1992).

This intrinsic trade-off between current reproductive success and future reproductive potential is thought to be an important factor shaping reproductive decisions (Stearns 1992). For many long-lived species, the strength of this trade-off is thought to vary over an individual's lifetime (Proaktor, Milner-Gulland & Coulson 2007), as both survival- and reproduction-related traits are age-dependent, often declining in later life (Nussey *et al.*

2013). Furthermore, changes in extrinsic conditions can also cause the strength of this intrinsic trade-off to vary, via their influence on survival probabilities and ultimately the individual's future reproductive potential (Barbraud & Weimerskirch 2005; Hamel, Côté & Festa-Bianchet 2010). Consequently, an individual's reproductive response to changes in extrinsic conditions is predicted to vary according to their intrinsic attributes, with individuals becoming increasingly committed to their current reproductive attempt as they age, to compensate for the decline in future breeding prospects (Clutton-Brock 1984). However, few studies have examined whether intrinsic and extrinsic factors interact to explain variation in reproductive success (but see Wiklund 1990; Kontiainen *et al.* 2009; Rauset, Low & Persson 2016), despite theory predicting such a link (Williams 1966; Ricklefs 1976).

In this study, we used 29 years of breeding data collected on an intensively monitored population of individually identifiable female tawny owls (*Strix aluco*) to examine the extent to which owl reproductive decisions varied in relation to two extrinsic factors, natural variation in the abundance of their main prey (field vole, *Microtus agrestis*; Petty 1999), and their main predator (a diurnal raptor, northern goshawk, *Accipiter gentilis*; Hoy *et al.* 2014). In another study site, predation by diurnal raptors was found to account for 73% of natural tawny owl mortality after the fledging stage, when parents are still provisioning food for their young (Sunde, Bølstad & Desfor 2003), and in our study site, predation on adult owls was biased towards breeding females (Hoy *et al.* 2014). It is expected that breeders and parents of larger broods spend more time hunting to provision food for their offspring, which may make these parents more exposed to predation by goshawks. Consequently, in years when predation risk is high, individuals may attempt to minimize their vulnerability to predation by reducing the amount of resources they allocate towards reproduction (breeding less frequently or laying smaller clutches). However, as the seasonal peak in goshawk predation on tawny owls occurs after owls have already initiated breeding attempts (Petty *et al.* 2003), the main response of individuals to variation in predation risk may manifest itself as an increased tendency to abandon breeding attempts at an early stage. Therefore, in this study we examined how three different reproductive decisions: (i) breeding propensity; (ii) clutch size; and (iii) whether breeding attempts were completed to the fledging stage, varied in relation to fluctuations in food availability and predation risk.

We also investigated whether owl reproductive decisions were related to the following intrinsic attributes: current and previous allocation of resources towards breeding (clutch size and reproductive success the year before, respectively) and the age of the individual, as life-history theory predicts an intrinsic trade-off between current and future allocation of resources towards reproduction (Williams 1966), and because survival and reproductive rates are age-dependent in tawny owls (Millon *et al.* 2011).

Changes in extrinsic conditions are also likely to affect the probability of offspring being recruited into the breeding population, via their effect on juvenile owl survival (Sunde, Bølstad & Desfor 2003; Sunde 2005; Koning, Koning & Baeyens 2009; Millon, Petty & Lambin 2010). Thus, the influence of extrinsic conditions on juvenile survival should influence the adaptive basis for reproductive decisions, for instance, how beneficial it is to allocate resources towards a reproductive attempt. Consequently, we also examined how juvenile survival varied in relation to temporal fluctuations in food availability and predation risk.

Materials and methods

STUDY SITE AND OWL MONITORING

Tawny owl reproduction has been continuously monitored in a 176 km² central section of Kielder Forest (55°13′N, 2°33′W) since 1979, using nest boxes (Petty, Shaw & Anderson 1994). Kielder Forest, mainly planted with Sitka Spruce (*Picea sitchensis*), lacks natural tree cavities; therefore, owls breed almost exclusively in nest boxes (Petty, Shaw & Anderson 1994). Each year, all nest boxes were checked for occupancy, to record clutch size, the number of chicks fledging and to ring chicks. Tawny owls do not breed every year after becoming reproductively active and only breed once per year, but can re-lay if the first breeding attempt fails early (during laying or the early incubation period; Petty 1992). In such cases, we only included the second breeding attempt, such that each individual contributed only one breeding attempt per year to our analysis. In some cases, the monitoring of a nest box resulted in owls abandoning their breeding attempts. We therefore excluded all such breeding attempts ($N = 51/965$) from all our analyses.

Breeding females were captured every year using a modified angler's landing net which was placed over the entrance of the nest box, when their chicks were 1–2 weeks old. The identity of breeding females was established from their metal ring numbers, and any unmarked breeding females (entering the population as immigrants) were ringed upon capture so that they would subsequently be individually identifiable. Tawny owls are highly site faithful, and in our study site, > 98% remained in the same territory where they first started breeding (Petty 1992). Therefore, we determined the identity of a female occupying a territory when no breeding took place or when the breeding attempt failed prior to trapping in the following way. When the same female was recorded breeding in a territory both before and after the year(s) where no female was caught, we assumed the same individual was involved. However, when different females were recorded either side of a year(s) when females were not caught, we deemed the identity of the breeder unknown and excluded such breeding attempts from our analyses. A total of 914 breeding attempts took place between 1985 and 2013 where the identity of the female was known, or could be assumed in 89% of cases ($N = 813$).

ANALYSIS

To determine the extent to which owl breeding decisions were affected by fluctuating extrinsic and intrinsic factors, we examined (i) breeding propensity, (ii) clutch size and (iii) whether breeding

attempts were completed using generalized linear mixed-effect models (GLMM) with the appropriate error structure in R version 3.1.0 (R Core Team 2014). The identity of the breeding female and the year of a breeding attempt were fitted as random effects to account for individuals breeding in more than 1 year, and any residual temporal variation in response variables not attributable to the fitted temporal covariates of interest (food availability and predation risk). In all analyses, both the additive and two-way interactive effects of fixed-effect covariates were tested. We visually checked for any residual spatial autocorrelation in all response variables not explained by the covariates included in the selected best models using correlograms (Zuur *et al.* 2009).

We examined causes of variation in breeding propensity by analysing whether an individual bred or did not breed each year after becoming reproductively active, up until its last recorded breeding attempt (fitted as a binary covariate). We examined breeding propensity in this way for the following reasons. We excluded first-time breeding attempts as the breeding propensity of such attempts would necessarily be one and this may bias the results. We did not include the years prior to the first breeding attempt because there is no way to identify a new recruit in a territory before it first bred and it was unknown whether individuals had made a facultative decision not to breed the year(s) before they first bred, or whether they were incapable of breeding regardless of extrinsic conditions. Furthermore, some individuals were only recorded breeding once; thus, we had no way of determining whether such individuals were alive and had decided to not to breed in the subsequent year(s) after their only recorded breeding attempt or whether these individuals were dead. When at least one egg was laid in a territory known to be occupied by a particular female, we recorded that as a breeding attempt. Less than 2% ($N = 5$) of the 268 different females recorded breeding in Kielder Forest were known to have skipped breeding for three or more consecutive years. Therefore, we assumed an individual was dead if it had not been re-captured in the last 3 years of the study (i.e. after 2010). In this analysis, we excluded all individuals that could not be assumed dead or were known to be alive (i.e. were recorded breeding) in 2013 ($N = 40$), to remove any bias that unknown non-breeding events occurring in the last few years of the study period could induce.

To determine the extent to which owls adjust the amount of resources they allocate towards reproduction in response to variation in food availability and predation risk, we modelled variation in clutch size. In addition, we examined the decision or capability to continue with a breeding attempt by classifying each breeding attempt as 'complete', if at least one chick fledged, or 'incomplete' if not (fitted as a binary covariate). These two analyses were based on a different data set to that used for the breeding propensity analysis, as it contained all breeding attempts by all known individuals ($N = 241$), including first-time breeders between 1985 and 2013.

MEASURES OF FOOD AVAILABILITY AND PREDATION RISK

Field voles are the main year-round prey of tawny owls in Kielder Forest, representing on average 62% of identifiable prey items brought to the nest box ($N = 1423$; Petty 1999). As tawny owls are vole specialists in our study site, variation in the abundance of alternative food sources probably had only a limited impact on owl breeding decisions. Field vole densities were moni-

tored in spring and autumn at 17–21 sites within the owl monitoring area, every year since 1985 (for methods see Lambin, Petty & MacKinnon 2000). Vole densities in the spring and autumn were positively correlated ($r = 0.65$, $N = 27$, $P < 0.001$). The amount of vole prey available in early spring (prior to egg laying) has previously been shown to affect owl reproduction; in years of high food availability, more pairs attempted to breed and clutch sizes were larger (Petty 1992; Millon *et al.* 2014). Therefore, spring vole densities were used as a proxy for owl food availability in all analyses. Field vole densities were asynchronous but spatially structured across Kielder Forest (i.e. travelling waves; Lambin *et al.* 1998). However, this pattern has changed over time with a gradual loss of spatial structure (Bierman *et al.* 2006). Such changes in prey spatial synchrony may affect how easy it is for owls to predict the amount of food available in their territory, and hence influence their reproductive decisions. Therefore, we also examined the extent to which tawny owl breeding decisions were affected by changes in the spatial synchrony of field vole densities. To do so, we first calculated spatial variation in field vole densities as the coefficient of variation (standard deviation divided by the mean) in spring vole densities between survey sites, each year. However, spatial variation in vole densities may be less important in years when food is abundant, compared to when it is scarce. Therefore, we classified years as either being of low overall food abundance if the averaged spring vole density was below the median value for all years, or high if not. We then included an interaction between spatial variation in vole densities and the categorical covariate of overall vole densities to test this hypothesis.

Northern goshawks (hereafter goshawks) have been continuously monitored since the first breeding attempt in 1973 (Petty & Anderson 1995). Each year occupied goshawk home ranges were identified, and over the last 40 years, the number of occupied home ranges has increased from 1 to 25–33. Goshawks are known predators of tawny owls, with breeding female owls being three times more likely to be killed than adult males; predation is also heavily biased towards juveniles (Hoy *et al.* 2014). Goshawk dietary data collected in Kielder Forest suggests that as the breeding population of goshawks increased, the mean number of owls killed each year by goshawks has also increased. An average of 5 [3–8; 95% CI] owls were killed each year when < 15 goshawk home ranges were occupied, compared to an estimated average of 159 [141–176; 95% CI] owls killed each year when more than 24 goshawk home ranges were occupied (see Appendix S1, Supporting information). Consequently, as predation on owls has increased with the abundance of goshawks in the forest, we used the total number of occupied goshawk home ranges in a 964 km² area of Kielder Forest as a proxy of temporal variation in predation risk. However, as goshawks were monitored over a larger area than tawny owls, we also used an additional proxy of temporal variation in predation risk. Local goshawk abundance was measured as the number of goshawk home ranges whose nest sites were within 5.8 km (the estimated goshawk foraging distance) of the owl monitoring area, calculated in the same way described in Hoy *et al.* (2014).

Spatial variation in predation risk has also been found to influence reproductive decisions (Sergio, Marchesi & Pedrini 2003). Therefore, we investigated the extent to which owl reproductive decisions varied in relation to two spatial proxies of predation risk: (i) distance from an owl's nest to the nearest goshawk nest site; and (ii) the location of an owl's territory in relation to all goshawks nest sites (i.e. connectivity of an owl territory to all goshawk nest sites). The connectivity measure of predation risk takes into account all goshawk nest sites, but weights the influence each goshawk nest site has on this index of predation risk, according to its distance from the focal owl nest site (for further details and method see Appendix S2). These spatial covariates of predation risk were calculated for each owl territory, every year. Common buzzards *Buteo buteo* are abundant in our study site and are known to kill tawny owls (Mikkola 1976). However, we did not include buzzards in any of our measures of owl predation risk, because dietary data indicated that buzzard predation on owls was negligible in our study site (M. Davison, personal communication). None of the temporal proxies of food availability were significantly correlated with the temporal covariates of predation risk. However, no two proxies of predation risk or two proxies of food availability were included in the same model as they were collinear (see Appendix S3 for all cross correlation coefficients). All temporal and spatial covariates were standardized (had a mean of 0 and a standard error of 1) to enable their effect sizes to be compared.

INTRINSIC ATTRIBUTES

When testing the hypothesis that the response of an individual to changes in extrinsic conditions varied according to age, we used the number of years elapsed since the individuals first recorded breeding attempt, because the exact age of 94 breeding females entering the population as adult immigrants was unknown. However, most (89%) female owls had commenced breeding by the time they were 3 years old (Millon, Petty & Lambin 2010) and there had been no change in the mean age at first reproduction over the study period, neither for immigrants nor local recruits entering the owl population (S.R. Hoy, unpublished data). Consequently, the number of years elapsed since an individual's first recorded breeding attempt is closely related to its age, and the length of an individual's breeding lifespan is also highly correlated with actual lifespan ($r = 0.91$; $N = 163$). We tested the hypothesis that previous investment in reproduction influenced an individual's current reproductive decisions in relation to changes in predation risk and food availability by fitting a binary covariate reflecting whether a female owl had successfully raised offspring to the fledgling stage the previous year. Lastly, we investigated whether the likelihood of an individual completing a breeding attempt to the fledgling stage was related to clutch size, taking clutch size as a proxy for the extent to which an individual had already allocated resources towards the current reproductive attempt. All descriptive statistics are shown with the standard deviation (SD).

JUVENILE SURVIVAL

As recapture data were not available for male owls in all years, our analysis of juvenile owl survival was based on female owls only, ringed as chicks between 1985 and 2012 ($N = 1082$), with the last recapture of individuals in 2013. The sex of individuals never recaptured as adults or sexed as chicks using DNA was unknown, as juvenile owls cannot be accurately sexed without molecular analyses. However, the sex ratio of chicks born in our study site was even 1:1 ($N = 312$, over 4 years; Appleby *et al.* 1997). Consequently, we randomly assigned half the number of chicks born each year, minus the number known to be female as females, as done in previous analyses (Nichols *et al.* 2004; Millon,

Petty & Lambin 2010). The rest of these chicks were assumed to be males and excluded from the analysis. Owls were only recaptured when breeding and owls usually starting breeding between the ages 1 and 4 (89% before age 3; (Millon, Petty & Lambin 2010). Recapture probabilities were therefore modelled as time-dependent and age-specific [(1, 2–3, 4+)] as done in Millon, Petty & Lambin (2010). This analysis was carried out in E-SURGE version 1.9.0 (Choquet, Rouan & Pradel 2009). Goodness-of-fit tests were carried out in U-CARE 2.3.2 (Choquet *et al.* 2005). In this analysis only, rather than using spring vole densities (measured in March) as the measure of food availability, we used autumn densities of field voles (measured in September–October), as they have previously been shown to be more closely related to changes in juvenile tawny owl survival (Millon, Petty & Lambin 2010; Millon *et al.* 2011, 2014). Temporal proxies of predation risk were the same as those used in the previous analyses. Spatial proxies of predation risk were calculated as before, but using the natal nest box, and were modelled as an individual covariate. Model selection in all of the above analyses was based on Akaike's information criterion corrected for small sample size (AICc; Burnham & Anderson 2002).

Results

BREEDING PROPENSITY

When averaged across years, the probability of a female breeding after becoming reproductively active was 0·78 ± 0·17 (range: 0·21–0·99). Variation in breeding propensity appeared most strongly related to changes in extrinsic conditions (Table 1). In years when local goshawk abundance was relatively low (fewer than 10 home ranges were occupied), breeding propensity increased from an average of 0·33 ± 0·18, when food availability was also low, to an average of 0·95 ± 0·06 in years of high food availability (Fig. 1a). However, in years when goshawk abundance was high the relationship between breeding propensity and food availability was less apparent (Fig. 1a). Breeding propensity also appeared to vary according to intrinsic attributes (proxies of age and previous allocation of resources to reproduction); however, the association between breeding propensity and intrinsic attributes was much weaker in comparison with the relationship with extrinsic factors (Fig. 1b; Table 1; Appendix S4). Breeding propensity was estimated to increase slightly as owls aged. However, this trend was only observed for individuals who had successfully fledged chicks the year before.

CLUTCH SIZE

Owl clutch size averaged 2·85 ± 0·82 (range: 1–6; *N* = 850), with 92·8% of clutches containing 2–4 eggs. The largest clutches were laid in years of high spring vole

Table 1. Parameter estimates and model selection examining how tawny owl breeding propensity varied in relation to fluctuations in predation risk (total goshawk abundance; local goshawk abundance; connectivity of the owls territory to all goshawk nest sites; distance the owl was nesting from the nearest goshawk nest site) and food availability (spring vole densities; spatial variation in vole densities across the study site). Breeding propensity was also analysed in relation to whether the individual had successfully bred the previous year and the number of years elapsed since the owl first started breeding (a measure of age). The most parsimonious model is emboldened

|	Model	*np*	Estimate	SE	ΔAkaike's information criterion
1.	Null	3			27·99
2.	Total goshawk	4	0·40	0·24	27·37
3.	Local goshawk	4	0·45	0·25	27·08
4.	Connectivity to goshawks	4	−0·03	0·12	29·97
5.	Nearest goshawk	4	0·05	0·10	29·75
6.	Spring voles density	4	1·09	0·26	16·20
7.	Categorical spring vole density (CSV)	6	−0·83	0·56	23·87
	Spatial variation in vole densities (SVVD)		−0·62	0·44	
	CSV × SVVD		0·03	0·60	
8.	Breeding success previous year (BS)	4	0·34	0·22	27·81
9.	Years since 1st reproduction (Y1st)	4	0·07	0·03	24·45
10.	Spring voles	5	1·14	0·23	10·84
	+Local goshawk		0·51	0·18	
11.	Spring voles (SV)	6	1·15	0·23	6·29
	+Local goshawk (LG)		0·14	0·21	
	SV × LG		−0·68	0·26	
12.	Breeding success previous year	5	0·34	0·23	24·33
	+Years since 1st reproduction		0·07	0·03	
13.	Breeding success previous year	6	−0·30	0·35	21·03
	Years since 1st reproduction		−0·01	0·05	
	BS × Y1st		0·14	0·06	
14.	**Breeding success previous year**	**9**	**−0·34**	**0·35**	**0**
	Years since 1st reproduction		**−0·01**	**0·05**	
	BS × Y1st		**0·13**	**0·06**	
	Spring voles		**1·17**	**0·23**	
	Local goshawk		**0·13**	**0·22**	
	SV × LG		**−0·69**	**0·26**	
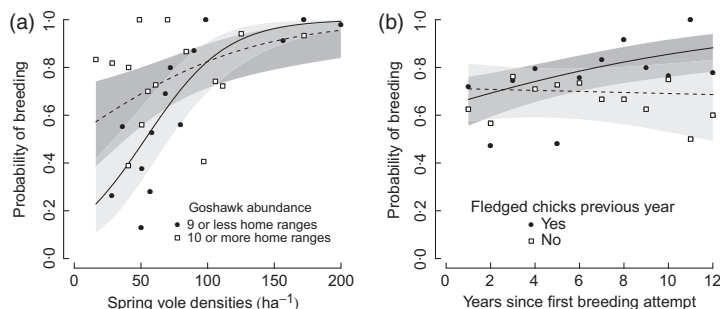
Fig. 1. Variation in the probability of adult female tawny owls breeding in relation to changes in: (a) the density of their main prey (field voles) and the abundance of their main predator (northern goshawks). (b) The number of years elapsed since the individual's first reproductive attempt (a proxy for the age of the individual) and whether the individual had successfully fledged chicks the previous year. Solid and dashed lines represent model predictions when (a) goshawk abundance was fixed at the lower and upper quartile values, respectively, and (b) for individuals which had and had not fledged chicks the previous year, respectively (when spring vole densities and goshawk abundance were fixed at the median value). Grey-shaded areas represent the 95% confidence intervals of model predictions. Points are the raw data showing the observed mean proportion of all females in the population breeding in a given year. Lines are predictions derived from individual level data and so are not fitted to the illustrated points.
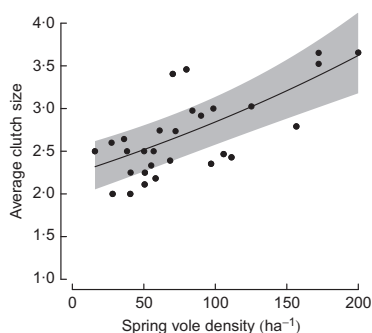

Fig. 2. Variation in the observed mean clutch size of tawny owls according to the density of their main prey, field voles in the spring, just prior to laying in Kielder Forest each year between 1985 and 2013. Points are the raw data while the line represents the predicted value from our best model. The 95% confidence intervals of model predictions are shaded in grey.

densities with clutch size increasing from an average of 2·38 [2·28–2·48; 95% CI] in years when vole densities were below 50 voles ha^{-1} to 2·98 [2·82–3·14; 95% CI] in years when vole densities were above 150 voles ha^{-1} (Fig. 2). There was no evidence to suggest that variation in clutch size was related to predation risk or female age (Table 2; Appendix S5).

COMPLETING A BREEDING ATTEMPT TO THE FLEDGING STAGE

On average, 96% of breeding attempts ($N = 813$) were completed. Clutch size and connectivity to goshawk nest sites explained the most variation in whether a breeding attempt was completed (Table 3; Appendix S6). Irrespective of clutch size, the percentage of breeding attempts observed to reach the fledging stage was close to 100% ($N = 193/194$) for owls breeding in territories not well connected to goshawk nest sites, hence less exposed to predation (i.e. in territories not in close proximity to many goshawks nest sites; Fig. 3). However, for owls

Table 2. Parameter estimates and model selection to determine whether variation in tawny owl investment in reproduction (clutch size) was related to proxies of predation risk (total goshawk abundance; local goshawk abundance; connectivity of the owls territory to all goshawk nest sites; distance the owl was nesting from the nearest goshawk nest site), food availability (spring vole densities; spatial variation in vole densities across the study site) and intrinsic attributes (whether the individual had successfully bred the previous year and the number of years elapsed since the individuals first breeding attempt). The most parsimonious model is highlighted in bold

	Model	np	Estimate	SE	ΔAkaike's information criterion
1.	Null	3			17·11
2.	Total goshawk	4	−0·035	0·032	17·99
3.	Local goshawk	4	−0·017	0·033	18·88
4.	Connectivity to goshawk	4	0·007	0·024	19·04
5.	Nearest goshawk	4	−0·007	0·022	19·02
6.	**Spring vole density**	**4**	**0·125**	**0·023**	**0**
7.	Categorical spring vole density (CSV)	6	−0·130	0·059	6·52
	Spatial variation in vole densities (SVVD)		−0·068	0·036	
	CSV × SVVD		−0·020	0·060	
8.	Breeding success previous year	4	0·028	0·046	18·75
9.	Years since 1st reproduction	4	0·002	0·006	18·97

breeding in territories relatively well connected to goshawks hence were more exposed to predation (i.e. in close proximity to several goshawk nest sites in that year), the probability of breeding attempts being completed decreased from 97·5% ($N = 39/40$ breeding attempts) when owls had clutches containing four or more eggs to 87·7% ($N = 57/65$ breeding attempts) when clutches contained 1–2 eggs (Fig 3).

Table 3. Model estimates and selection for analyses investigating the relationship between the probability of tawny owl breeding attempts being completed to the fledgling stage and proxies of predation risk (total goshawk abundance; local goshawk abundance; connectivity of the owls territory to all goshawk nest sites; distance the owl was nesting from the nearest goshawk nest site), food availability (spring vole densities; spatial variation in vole densities across the study site) and attributes intrinsic to the breeder (whether they had successfully bred the previous year and the number of years elapsed since their first breeding attempt) and the breeding attempt (clutch size). The most parsimonious model is emboldened

	Model	np	Estimate	SE	ΔAkaike's information criterion
1.	Null	3			18·76
2.	Total goshawk	4	−0·21	0·20	19·72
3.	Local goshawk	4	−0·26	0·19	18·96
4.	Connectivity to goshawks	4	−0·58	0·16	8·74
5.	Nearest predator	4	0·48	0·20	14·93
6.	Spring voles	4	−0·26	0·20	19·02
7.	Categorical spring vole density (CSV)	6	0·55	0·49	23·35
	Spatial variation in vole densities (SVVD)		−0·02	0·26	
	CSV × SVVD		−0·08	0·48	
8.	Breeding success previous year	4	0·08	0·38	20·73
9.	Years since 1st reproduction	4	0·02	0·00	20·68
10.	Clutch size	4	0·89	0·29	9·54
11.	**Connectivity to goshawks**	**5**	**0·84**	**0·28**	**0**
	+ Clutch size		**−0·60**	**0·17**	
12.	Connectivity to goshawks (CG)	6	−0·35	0·59	1·85
	Clutch size (CS)		0·89	0·31	
	CG × CS		−0·10	0·23	

JUVENILE SURVIVAL

Juvenile survival averaged 0·18 ± SE 0·02. Autumn vole densities explained the most variation in juvenile survival (slope on logit scale: β = 0·42 ± 0·1; %Deviance = 34·5). Juvenile survival was estimated to increase with autumn vole densities (Appendix S7). There was no evidence of a relationship between juvenile owl survival and any proxy of predation risk (Table 4).

Discussion

In this study, we examined how reproduction in female tawny owls (breeding propensity, clutch size and nest abandonment) was influenced by both extrinsic (food availability and predation risk) and intrinsic factors (age, previous and current allocation of resources towards reproduction) and any interactions between these factors. Our main findings were as follows: (i) breeding propensity was highest in years when food (field vole densities in spring) was abundant and predation risk (goshawk
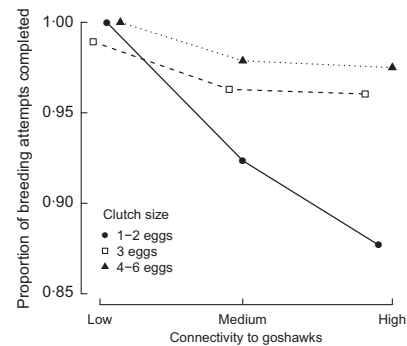

Fig. 3. The mean proportion of tawny owl breeding attempts, which were observed to reach the fledgling stage, shown in relation to how connected the owls breeding territory was to the surrounding goshawk nest sites (a measure of exposure to goshawk predation) and clutch size, a proxy of the amount of resources an individual had already allocated towards the current breeding attempt. Points represent the raw data.

Table 4. Model selection for annual survival of female tawny owls in their first year of life between 1985 and 2013 in relation to predation risk (total goshawk abundance; local goshawk abundance; connectivity of the owls territory to all goshawk nest sites; distance the owl was nesting from the nearest goshawk nest site) and food availability (autumn vole density). Recapture probability was modelled as [a(1,2-3,4 +) + t]. The most parsimonious model is emboldened

Models	Deviance	np	ΔAkaike's information criterion
Null	2171·22	33	19·52
Autumn vole density	**2149·60**	**34**	**0**
Total goshawk	2171·09	34	21·49
Local goshawk	2171·14	34	21·54
Nearest goshawk	2170·96	34	21·36
Connectivity to goshawks	2169·57	34	19·97
Autumn vole density + Total goshawk (TG)	2149·52	35	2·01
Autumn vole density + Local goshawk (LG)	2148·98	35	1·47
Autumn vole density + Nearest goshawk (NG)	2149·55	35	2·04
Autumn vole density (AV) + Connectivity to goshawks (CG)	2148·64	35	1·14
AV × TG	2149·23	36	3·82
AV × LG	2148·98	36	3·57
AV × NG	2149·53	36	4·12
AV × CG	2148·32	36	2·91

abundance) was low. However, in years when goshawk abundance was relatively high the association between breeding propensity and food availability was less apparent. Breeding propensity also appeared to be related to intrinsic attributes, but to a lesser extent than extrinsic factors, as owls which had successfully fledged chicks the year before were slightly more likely to breed as they aged compared to owls which had not fledged chicks. (ii) Clutch size was positively associated with spring vole

densities but was unrelated to predation risk or any intrinsic attributes examined. (iii) On average, 96% of breeding attempts were completed; however, owls with small clutches (1–2 eggs) and breeding in territories more exposed to goshawk predation were less likely to complete their breeding attempt compared to owls with larger clutches breeding in less exposed territories. (iv) Juvenile owl survival was positively correlated with food availability in the autumn but was unrelated to predation risk. Overall, these findings represent rare evidence about how extrinsic and intrinsic factors interact to shape reproductive decisions in a long-lived iteroparous predator.

BREEDING PROPENSITY

Breeding propensity was closely correlated with food availability (measured as field vole densities in spring) in the early years of the study, when predation risk (goshawk abundance) was relatively low (Fig. 1a). However, as predator abundance increased over the study period, the positive effect of food availability on breeding propensity diminished. These results indicate that breeding propensity is not purely constrained by the amount of food available prior to the breeding season. They also suggest that owls may be capable of assessing changes in predation risk and make facultative decisions about whether to allocate resources to reproduction, as shown for other species (Sih 1988; Candolin 1998; Ghalambor & Martin 2001; Zanette *et al.* 2011). Unfortunately, we were unable to determine the exact nature of the link between food availability, predation risk and the observed changes in owl reproduction, as our approach was necessarily correlative, given the spatial scale of the processes considered. Therefore, we cannot rule out the possibility that changes other than average vole density in spring or goshawk abundance may have co-occurred to cause the observed variation in breeding propensity. However, we also examined whether changes in the spatial dynamics of food availability and predation risk were related to breeding propensity. Life-history theory predicts that individuals should only forgo breeding when the cost of not breeding is compensated for by future reproductive gains (Stearns 1992). An analysis of breeding female owl survival in our study site suggests that it was lowest in years when goshawk abundance was relatively high and owl food availability was low (S.R. Hoy, unpublished data). Consequently, we suggest that the higher breeding propensity observed in years when goshawks were abundant and food was scarce could plausibly reflect that these environmental conditions (being adverse for owls for a number of consecutive years towards the end of the study period) have made intermittent breeding a less beneficial strategy, as the cost of not breeding now is less likely to be compensated for in the future.

We also found evidence suggesting that a detectable but relatively small amount of variance in breeding propensity was associated with the age of the female owl and their previous allocation of resources towards reproduction, as breeding propensity increased slightly with age for females which had fledged chicks the previous year. This could indicate that some individuals are inherently of 'high quality' and do not face a strong trade-off between current and future investment in reproduction. While the effect sizes were relatively small in comparison with the strength of the correlations between breeding propensity and extrinsic conditions (food availability and predation risk; Fig. 1), our results demonstrate the dual intrinsic and extrinsic influences on the decision to reproduce.

CLUTCH SIZE

The strong positive effect of food availability on clutch size is concordant with results from several other studies (Fig. 2; Ballinger 1977; Crawford *et al.* 2006; Lehikoinen *et al.* 2011). However, we found no evidence of an association between clutch size and any proxy of predation risk. Due to the latitude of our study site, nights are relatively long prior to the breeding season. Hence, there is little overlap in the activity periods of nocturnal tawny owls and diurnal goshawks, compared to late spring and summer when nights are relatively short. Furthermore, female goshawks are thought to leave Kielder Forest in winter, returning in February, just prior to owls laying (S.J. Petty, unpublished data). Therefore, predation risk for owls might potentially be relatively low prior to the breeding season, when female owls are building up the body reserves needed for breeding, which could, in part, explain why we found no evidence of a relationship between clutch size and predation risk.

COMPLETING A BREEDING ATTEMPT TO THE FLEDGING STAGE

As predicted by life-history theory, individuals who had allocated more towards reproduction (e.g. by laying larger clutches) were more likely to continue their breeding attempt to the fledging stage, a finding consistent with previous studies (e.g. Delehanty & Oring 1993). Predation risk was the only extrinsic predictor of whether breeding attempts reached the fledging stage, with individuals breeding in territories more exposed to predation risk being less likely to complete a breeding attempt (Fig. 3), a result congruent with another study examining the effect of spatial variation in predation risk on reproductive success (Sergio, Marchesi & Pedrini 2003). Goshawks start displaying over territories and building nests in late March and April in the UK (Kenward 2006), hence are likely to become even more conspicuous to owls, after owls have already committed to breeding. Furthermore, predation risk for both adult and fledgling owls increased throughout the breeding season (Petty *et al.* 2003; Hoy *et al.* 2014). Therefore, the tendency of owls not to complete breeding attempts in territories, where predation risk is presumably high, is consistent with females (having

already commenced breeding), attempting to reduce their own vulnerability to predation as the breeding season progresses. Alternatively, as 23% of breeders which did not complete a breeding attempt were never recaptured in the study site again, the higher failure rates in territories well connected to areas of high goshawk activity could also reflect that some parents in those territories were killed by goshawks and were therefore unable to complete the breeding attempt.

JUVENILE SURVIVAL

Our analysis confirmed that juvenile owl survival was positively related to food availability (Millon, Petty & Lambin 2010; Millon *et al.* 2011, 2014). Estimates of juvenile owl survival were lowest in low vole years (Appendix S7). If mothers were able to predict the food conditions that their offspring would experience, they should be less inclined to allocate resources towards reproduction in low vole years, due to the reduced probability of these offspring being recruited into the population. This may in part explain why individuals allocated relatively few resources towards reproduction (i.e. smaller clutch sizes) in years when food was scarce.

REPRODUCTIVE STRATEGIES IN RELATION TO CHANGING ENVIRONMENTAL CONDITIONS

A reproductive strategy can be defined as the set of decisions which influence the number of offspring an individual produces. Owl breeding strategies appeared to change in response to extrinsic conditions. Individuals allocated more resources towards reproduction (in terms of breeding propensity and clutch size) in years when food was abundant (Figs 1 and 2). Although we found no evidence to support our prediction that owls would attempt to minimize their vulnerability to predation by breeding less frequently or laying smaller clutches in years when predation risk was high, we did find evidence to suggest that owls responded to changes in predation risk, by making facultative decisions about whether to continue with their breeding attempt. However, the observed increase in incomplete nesting attempts with increasing predation risk also be partly due to parent(s) being killed, hence being unable to complete the breeding attempt, rather than a facultative decision not to continue the attempt. There was no year-to-year collinearity between our temporal covariates of predation risk and food availability. However, when averaged over a larger time-scale (5 years) these covariates were correlated, and hence, both environmental conditions changed simultaneously in opposite ways, with spring vole densities decreasing and predation risk increasing over the course of the study period. Therefore, we were unable to fully disentangle the effects of food availability and predation risk on owl breeding decisions. As the overall percentage of failed breeding attempts was very low (4% on average), the main

reproductive decisions influencing reproductive output were primarily breeding propensity then clutch size. Indeed, the proportion of the population breeding and average clutch size explained 83% and 16% of the total variation in annual reproductive success (measured as the average number of chicks fledged per occupied owl territory) of the tawny owl population, respectively. Whereas whether breeding attempts were completed only explained 0·1% of the total variation in reproductive success (see Appendix S8). Consequently, food availability seemed to have a greater impact on breeding propensity than changing predation risk (Fig. 1, Table 1) and be the main extrinsic factor driving variation in reproductive output, thus shaping reproductive strategies in tawny owls. However, the strength of the relationship between reproductive output and food availability weakened as predation risk increased.

As food availability declined (specifically as vole populations switched from high- to low-amplitude cycles; Cornulier *et al.* 2013) and predation risk increased, tawny owls seemed to breed more frequently, but invested less per breeding attempt. By spreading reproductive effort more evenly across years, a 'bet-hedging' reproductive strategy minimizes variation in reproductive success and can actually increase an individual's fitness in certain situations (Slatkin 1974; Starrfelt & Kokko 2012). Consequently, given that owl survival was lowest in years when food was scarce and goshawk abundance was high, our results could reflect that owls have switched from an intermittent reproductive strategy of saving resources to invest more in one, or a few reproductive attempts in the future, to a 'bet-hedging' reproductive strategy.

Together, our results suggest that extrinsic conditions and intrinsic attributes have a combined and interactive effect on reproductive decisions. Changes in extrinsic conditions, particularly food availability, were the main factors shaping owl reproductive decisions, as the association between intrinsic attributes and owl breeding decisions was relatively weak in comparison. This could in part be due to environmental variation in this system being relatively high because of the cyclical dynamics of vole populations, and the relatively recent recovery of an apex predator, thus swamping the contribution of intrinsic attributes to reproductive strategies. Although many of our results were in line with previous studies and theoretical predictions, our comprehensive approach highlights the complex nature of how intrinsic and extrinsic trade-offs act in combination to shape tawny owl reproduction. Furthermore, the length of this study has enabled us to provide some empirical evidence, albeit correlative, of long-lived predators, altering their life-history strategies in response to changes in multiple interacting environmental factors.

Data accessibility

All data associated with the study which is not given in the text are available in the Dryad Digital Repository. http://dx.doi.org/10.5061/dryad.6n579 (Hoy *et al.* 2016).

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 B: Biological Sciences*, **264**, 1111–1116.

Arcese, P. & Smith, J.N.M. (1988) Effects of population density and supplemental food on reproduction in song sparrows. *Journal of Animal Ecology*, **57**, 119–136.

Ballinger, R. (1977) Reproductive strategies: food availability as a source of proximal variation in a lizard. *Ecology*, **58**, 628–635.

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

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.

Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd edn. Springer-Verlag, New York, NY, USA.

Candolin, U. (1998) Reproduction under predation risk and the trade-off between current and future reproduction in the threespine stickleback. *Proceedings of the Royal Society B: Biological Sciences*, **265**, 1171–1175.

Chakarov, N. & Krüger, O. (2010) Mesopredator release by an emergent superpredator: a natural experiment of predation in a three level guild. *PLoS ONE*, **5**, e15229.

Choquet, R., Rouan, L. & Pradel, R. (2009) *Program E-SURGE:* a software application for fitting multievent models. *Modeling Demographic Processes in Marked Populations. Springer Series: Environmental and Ecological Statistics*, Vol. 3 (eds D.L. Thomson, E.G. Cooch & M.J. Conroy). pp. 845–865. Springer, Dunedin.

Choquet, R., Reboulet, A.M., Lebreton, J.-D., Gimenez, O. & Pradel, R. (2005) *U-CARE 2.2 User's Manual*. CEFE, Montpellier, France.

Clutton-Brock, T.H. (1984) Reproductive effort and terminal investment in iteroparous animals. *The American Naturalist*, **123**, 212.

Cornulier, T., Yoccoz, N.G., Bretagnolle, V., Brommer, J.E., Butet, A., Ecke, F. *et al.* (2013) Europe-wide dampening of population cycles in keystone herbivores. *Science*, **340**, 63–66.

Crawford, R.J.M., Barham, P.J., Underhill, L.G., Shannon, L.J., Coetzee, J.C., Dyer, B.M. *et al.* (2006) The influence of food availability on breeding success of African penguins Spheniscus demersus at Robben Island, South Africa. *Biological Conservation*, **132**, 119–125.

Delehanty, D.J. & Oring, L.W. (1993) Effect of clutch size on incubation persistence in male Wilson's Phalaropes (Phalaropus tricolor). *The Auk*, **110**, 521–528.

Doligez, B. & Clobert, J. (2003) Clutch size reduction as a response to increased nest predation rate in the collared flycatcher. *Ecology*, **84**, 2582–2588.

Ercit, K., Martinez-Novoa, A. & Gwynne, D.T. (2014) Egg load decreases mobility and increases predation risk in female black-horned tree crickets (Oecanthus nigricornis). *PLoS ONE*. doi: 10.1371/journal.pone.0110298.

Fontaine, J.J. & Martin, T.E. (2006) Parent birds assess nest predation risk and adjust their reproductive strategies. *Ecology Letters*, **9**, 428–434.

Ghalambor, C.K. & Martin, T.E. (2001) Fecundity-survival trade-offs and parental risk-taking in birds. *Science*, **292**, 494–497.

Hamel, S., Côté, S.D. & Festa-Bianchet, M. (2010) Maternal characteristics and environment affect the costs of reproduction in female mountain goats. *Ecology*, **91**, 2034–2043.

Hoogland, J.L., Cannon, K.E., DeBarbieri, L.M. & Manno, T.G. (2006) Selective predation on Utah prairie dogs. *The American Naturalist*, **168**, 546–552.

Hoy, S.R., Petty, S.J., Millon, A., Whitfield, D.P., Marquiss, M., Davison, M. *et al.* (2014) Age and sex-selective predation as moderators of the overall impact of predation. *Journal of Animal Ecology*, **84**, 692–701.

Hoy, S.R., Millon, A., Petty, S.J., Whitfield, D.P. & Lambin, X. (2016) Data from: Food availability and predation risk, rather than intrinsic attributes are the main factors shaping the reproductive decisions of a long-lived predator. *Dryad Digital Repository*, http://dx.doi.org/10.5061/dryad.6n579.

Kenward, R.E. (2006) *The Goshawk*. T & A D Poyser, London, UK.

Kokko, H. & Ruxton, G.D. (2000) Breeding suppression and predator-prey dynamics. *Ecology*, **81**, 252–260.

Koning, F.J., Koning, H.J. & Baeyens, G. (2009) Long-term study on interactions between tawny owls Strix aluco, jackdaws Corvus monedula and northern goshawks Accipiter gentilis. *Ardea*, **97**, 453–456.

Kontiainen, P., Pietiäinen, H., Huttunen, K., Karell, P., Kolunen, H. & Brommer, J.E. (2009) Aggressive ural owl mothers recruit more offspring. *Behavioral Ecology*, **20**, 789–796.

Lambin, X., Elston, D.A., Petty, S.J. & MacKinnon, J.L. (1998) Spatial asynchrony and periodic travelling waves in cyclic populations of field voles. *Proceedings Biological Sciences/The Royal Society*, **265**, 1491–1496.

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.

Lehikoinen, A., Ranta, E., Pietiäinen, H., Byholm, P., Saurola, P., Valkama, J. *et al.* (2011) The impact of climate and cyclic food abundance on the timing of breeding and brood size in four boreal owl species. *Oecologia*, **165**, 349–355.

Magnhagen, C. (1991) Predation risk as a cost of reproduction. *Trends in Ecology and Evolution*, **6**, 183–186.

Mikkola, H. (1976) Owls killing and killed by other owls and raptors in Europe. *British Birds*, **69**, 144–154.

Millon, A., Petty, S.J. & Lambin, X. (2010) Pulsed resources affect the timing of first breeding and lifetime reproductive success of tawny owls. *Journal of Animal Ecology*, **79**, 426–435.

Millon, A., Petty, S.J., Little, B. & Lambin, X. (2011) Natal conditions alter age-specific reproduction but not survival or senescence in a long-lived bird of prey. *Journal of Animal Ecology*, **80**, 968–975.

Millon, A., Petty, S.J., Little, B., Gimenez, O., Cornulier, T. & Lambin, X. (2014) Dampening prey cycle overrides the impact of climate change on predator population dynamics: a long-term demographic study on tawny owls. *Global Change Biology*, **20**, 1770–1781.

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.

Nussey, D.H., Froy, H., Lemaitre, J.F., Gaillard, J.M. & Austad, S.N. (2013) Senescence in natural populations of animals: widespread evidence and its implications for bio-gerontology. *Ageing Research Reviews*, **12**, 214–225.

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

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*, **248**, 451–465.

Petty, S.J. & Anderson, D.I.K. (1995) Goshawks Accipiter gentilis. *The Atlas of Breeding Birds in Northumbria* (eds J.C. Day, M.S. Hodgson & B.N. Rossiter), pp. 44–45. Northumberland and Tyneside Bird Club, Newcastle upon Tyne, UK.

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

Petty, S.J., Anderson, D.I.K., Davison, M., Little, B., Sherratt, T.N., Thomas, C.J. *et al.* (2003) The decline of common kestrels Falco tinnunculus in a forested area of northern England: the role of predation by Northern Goshawks Accipiter gentilis. *Ibis*, **145**, 472–483.

Pietiäinen, H. (1989) Seasonal and individual variation in the production of offspring in the Ural owl, Strix uralensis. *Journal of Animal Ecology*, **58**, 905–920.

Proaktor, G., Milner-Gulland, E.J. & Coulson, T. (2007) Age-related shapes of the cost of reproduction in vertebrates. *Biology Letters*, **3**, 674–677.

R Core Team (2014) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Rauset, G.R., Low, M. & Persson, J. (2016) Reproductive patterns result from age-related sensitivity to resources and reproductive costs in a mammalian carnivore. *Ecology*, **96**, 3153–3164.

Ricklefs, R.E. (1976) On the evolution of reproductive strategies in birds: reproductive effort. *The American Naturalist*, **111**, 453–478.

Sedinger, J.S., Chelgren, N.D., Ward, D.H. & Lindberg, M.S. (2008) Fidelity and breeding probability related to population density and individual quality in black brent geese *Branta bernicla nigricans*. *Journal of Animal Ecology*, **77**, 702–712.

Sergio, F. & Hiraldo, F. (2008) Intraguild predation in raptor assemblages: a review. *Ibis*, **150**, 132–145.

Sergio, F., Marchesi, L. & Pedrini, P. (2003) Spatial refugia and the coexistence of a diurnal raptor with its intraguild owl predator. *Journal of Animal Ecology*, **72**, 232–245.

Sih, A. (1988) The effects of predators on habitat use, activity and mating behaviour of a semi-aquatic bug. *Animal Behaviour*, **36**, 1846–1848.

Slatkin, M. (1974) Hedging one's evolutionary bets. *Nature*, **250**, 704–705.

Spaans, B., Blijleven, H. & Popov, I. (1998) Dark-bellied Brent geese *Branta bernicla bernicla* forego breeding when arctic foxes *Alopex lagopus* are present during nest initiation. *Ardea*, **86**, 11–20.

Starrfelt, J. & Kokko, H. (2012) Bet-hedging-a triple trade-off between means, variances and correlations. *Biological Reviews*, **87**, 742–755.

Stearns, S.C. (1992) *The Evolution of Life Histories*. Oxford University Press, Oxford, UK.

Sunde, P. (2005) Predators control post-fledging mortality in tawny owls, *Strix aluco*. *Oikos*, **110**, 461–472.

Sunde, P., Bølstad, M.S. & Desfor, K.B. (2003) Diurnal exposure as a risk sensitive behaviour in tawny owls *Strix aluco*? *Journal of Avian Biology*, **34**, 409–418.

White, T.C.R. (2008) The role of food, weather and climate in limiting the abundance of animals. *Biological Reviews*, **83**, 227–248.

Wiklund, C.G. (1990) The adaptive significance of nest defence by merlin, *Falco columbarius*, males. *Animal Behaviour*, **40**, 244–253.

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

Zanette, L.Y., White, A.F., Allen, M.C. & Clinchy, M. (2011) Perceived predation risk reduces the number of offspring songbirds produce per year. *Science*, **334**, 1398–1401.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009) *Mixed Effects Models and Extensions in Ecology with R*. Springer Science & Business Media, New York, NY, USA.

Supporting Information

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

Appendix S1. Estimating the number of tawny owls killed each year by the goshawk population.

Appendix S2. Method used to calculate the connectivity measure of predation risk for each owl territory.

Appendix S3. Correlation between temporal covariates of predation risk and food availability.

Appendix S4. A full list of all model estimates and selection for the breeding propensity analysis.

Appendix S5. A full list of all model estimates and selection for the clutch size analysis.

Appendix S6. A full list of all model estimates and selection for the probability of breeding attempts being completed.

Appendix S7. Variation in the probability of a tawny owl surviving through their first year of life in relation to the availability of their main prey (field voles) in autumn.

Appendix S8. Analysis of inter-annual variation in the reproductive success of the Kielder Forest tawny owl population between 1985 and 2013.