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

4  
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16  
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19 *Strix aluco*, tawny owl.

## 22 **Abstract**

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

29

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

34

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

40

41 **4.** Owls laid larger clutches when food was more abundant. When owls were breeding in  
42 territories less exposed to goshawk predation, 99.5% of all breeding attempts reached the  
43 fledging stage. In contrast, the probability of breeding attempts reaching the fledging stage  
44 in territories more exposed to goshawk predation depended on the amount of resources an  
45 owl had already allocated towards reproduction (averaging 87.7% for owls with clutches  
46 of 1-2 eggs compared to 97.5% for owls with clutches of 4-6 eggs).

47

48 **5.** Overall, our results suggested that changes in extrinsic conditions (predominantly food  
49 availability, but also predator abundance) had the greatest influence on owl reproduction.

50 In response to deteriorating extrinsic conditions (fewer voles and more goshawks) owls  
51 appeared to breed more frequently, but allocated fewer resources per breeding attempt.

52 However, intrinsic attributes also appeared to have a relatively small influence on how an

53 individual responded to variation in extrinsic conditions, which indicates that reproductive

54 decisions were shaped by a complex series of extrinsic and intrinsic trade-offs.

55

## 56 **Introduction**

57 Understanding how different factors influence reproductive decisions is a central issue in  
58 ecology and conservation biology, as the number of offspring produced is a key driver of  
59 population dynamics (Nichols *et al.* 2004; Sedinger *et al.* 2008). The impact of some  
60 extrinsic factors on reproductive decisions, such as food availability, are well understood  
61 (reviewed in White 2008). In contrast the impact of others, such as predation risk is more  
62 equivocal, even when the same predator and prey species are examined (Sergio & Hiraldo  
63 2008). Quantifying the indirect effect of predation risk on prey reproductive decisions under  
64 natural conditions is difficult, but merits further investigation as it can theoretically  
65 destabilize predator-prey dynamics, under certain circumstances (Kokko & Ruxton 2000).  
66 Furthermore, despite the influence of food availability and predation risk on reproductive  
67 success being extensively studied, the extent to which these two extrinsic factors interact to  
68 affect reproductive decisions remains poorly understood (but see Sergio, Marchesi & Pedrini  
69 2003).

70

71 Food availability is frequently reported to have a positive influence on the proportion of  
72 individuals in the population breeding and the number of offspring produced (Arcese &  
73 Smith 1988; Pietiäinen 1989; Petty 1992; Millon *et al.* 2014). However, breeding individuals  
74 and individuals producing more offspring per breeding attempt are often more vulnerable to  
75 predation compared to non-breeding individuals (Magnhagen 1991; Hoogland *et al.* 2006) or  
76 those producing fewer offspring (Ercit, Martinez-Novoa & Gwynne 2014). Consequently, in  
77 years when predation risk is high, individuals of long-lived iteroparous species may attempt  
78 to minimize their vulnerability to predation by: i) refraining from breeding (Spaans, Blijleven  
79 & Popov 1998); ii) reducing the number or quality of offspring (Doligez & Clobert 2003;  
80 Zquette *et al.* 2011); or iii) abandoning the breeding attempt at an early stage (Sergio,

81 Marchesi & Pedrini 2003; Chakarov & Krüger 2010). Indeed, experimental studies have  
82 shown that individuals respond to variation in predation risk by making facultative decisions  
83 to alter their allocation of resources towards reproduction, so as to reduce their own, or their  
84 offspring's vulnerability to predators (Ghalambor & Martin 2001; Doligez & Clobert 2003;  
85 Fontaine & Martin 2006; Zanette *et al.* 2011). However, according to life history theory, such  
86 changes in reproductive strategies should arise only when the losses incurred from not  
87 breeding, or not completing a breeding attempt, are compensated for by future reproductive  
88 success (Stearns 1992).

89

90 This intrinsic trade-off between current reproductive success and future reproductive  
91 potential is thought to be an important factor shaping reproductive decisions (Stearns 1992).  
92 For many long-lived species, the strength of this trade-off is thought to vary over an  
93 individual's lifetime (Proaktor, Milner-Gulland & Coulson 2007), as both survival- and  
94 reproduction-related traits are age-dependant, often declining in later life (Nussey *et al.*  
95 2013). Furthermore, changes in extrinsic conditions can also cause the strength of this  
96 intrinsic trade-off to vary, via their influence on survival probabilities and ultimately the  
97 individual's future reproductive potential (Barbraud & Weimerskirch 2005; Hamel, Côté &  
98 Festa-Bianchet 2010). Consequently, an individual's reproductive response to changes in  
99 extrinsic conditions is predicted to vary according to their intrinsic attributes, with individuals  
100 becoming increasingly committed to their current reproductive attempt as they age, to  
101 compensate for the decline in future breeding prospects (Clutton-Brock 1984). However, few  
102 studies have examined whether intrinsic and extrinsic factors interact to explain variation in  
103 reproductive success (but see Wiklund 1990; Kontiainen *et al.* 2009; Rauset, Low & Persson  
104 2016), despite theory predicting such a link (Williams 1966; Ricklefs 1976).

105

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

126

127 We also investigated whether owl reproductive decisions were related to the following  
128 intrinsic attributes, current and previous allocation of resources towards breeding (clutch size  
129 and reproductive success the year before, respectively) and the age of the individual, as life-  
130 history theory predicts an intrinsic trade-off between current and future allocation of

131 resources towards reproduction (Williams 1966), as survival and reproductive rates are age-  
132 dependent in tawny owls (Millon *et al.* 2011).

133

134 Changes in extrinsic conditions are also likely to affect the probability of offspring being  
135 recruited into the breeding population, via their effect on juvenile owl survival (Sunde *et al.*  
136 2003; Sunde 2005; Koning, Koning & Baeyens 2009; Millon, Petty & Lambin 2010). Thus,  
137 the influence of extrinsic conditions on juvenile survival should influence the adaptive basis  
138 for reproductive decisions, for instance, how beneficial it is to allocate resources towards a  
139 reproductive attempt. Consequently, we also examined how juvenile survival varied in  
140 relation to temporal fluctuations in food availability and predation risk.

141

## 142 **Methods**

### 143 *Study site and owl monitoring*

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



156

157 Breeding females were captured every year using a modified angler's landing net which was  
158 placed over the entrance of the nestbox, when their chicks were 1-2 weeks old. The identity  
159 of breeding females was established from their metal ring numbers, and any unmarked  
160 breeding females (entering the population as immigrants) were ringed upon capture so that  
161 they would subsequently be individually identifiable. Tawny owls are highly site faithful, and  
162 in our study site >98% remained in the same territory where they first started breeding (Petty  
163 1992). Therefore we determined the identity of a female occupying a territory when no  
164 breeding took place or when the breeding attempt failed prior to trapping in the following  
165 way. When the same female was recorded breeding in a territory both before and after the  
166 year(s) where no female was caught, we assumed the same individual was involved.  
167 However, when different females were recorded either side of a year(s) when females were  
168 not caught, we deemed the identity of the breeder unknown and excluded such breeding  
169 attempts from our analyses. A total of 914 breeding attempts took place between 1985 and  
170 2013 where the identity of the female was known, or could be assumed in 89% of cases ( $N =$   
171 813).

172

### 173 *Analysis*

174 To determine the extent to which owl breeding decisions were affected by fluctuating  
175 extrinsic and intrinsic factors, we examined: i) breeding propensity, ii) clutch size and iii)  
176 whether breeding attempts were completed using generalised linear mixed effect models  
177 (GLMM) with the appropriate error structure in R version 3.0.3 (R Core Development Team  
178 2014). The identity of the breeding female and the year of a breeding attempt were fitted as  
179 random effects to account for individuals breeding in more than one year, and any residual  
180 temporal variation in response variables not attributable to the fitted temporal covariates of  
181 interest (food availability and predation risk). In all analyses both the additive and 2-way

182 interactive effects of fixed effect covariates were tested. We visually checked for any residual  
183 spatial-autocorrelation in all response variables not explained by the covariates included in  
184 the selected best models using correlograms (Zuur *et al.* 2009).

185

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

206

207 To determine the extent to which owls adjust the amount of resources they allocate towards  
208 reproduction in response to variation in food availability and predation risk, we modelled  
209 variation in clutch size. In addition, we examined the decision or capability to continue with a  
210 breeding attempt by classifying each breeding attempt as “complete”, if at least one chick  
211 fledged, or “incomplete” if not (fitted as a binary covariate). These two analyses were based  
212 on a different dataset to that used for the breeding propensity analysis, as it contained all  
213 breeding attempts by all known individuals ( $N = 241$ ), including first time-breeders between  
214 1985-2013.

215

#### 216 *Measures of food availability and predation risk*

217 Field voles are the main year-round prey of tawny owls in Kielder Forest, representing on  
218 average 62% of prey brought to the nestbox ( $N = 1423$ ; Petty 1999). As tawny owls are vole  
219 specialists in our study site, variation in the abundance of alternative food sources probably  
220 had only a limited impact on owl breeding decisions. Field vole densities were monitored in  
221 spring and autumn at 17-21 sites within the owl monitoring area, every year since 1985 (for  
222 methods see Lambin, Petty, & MacKinnon 2000). Vole densities in the spring and autumn  
223 were positively correlated ( $r = 0.65$ ,  $N = 27$ ,  $P < 0.001$ ). The amount of vole prey available in  
224 early spring (prior to egg laying) has previously been shown to affect owl reproduction; in  
225 years of high food availability more pairs attempted to breed and clutch sizes were larger  
226 (Petty 1992; Millon *et al.* 2014). Therefore, spring vole densities were used as a proxy for  
227 owl food availability in all analyses. Field vole densities were asynchronous but spatially  
228 structured across Kielder Forest (i.e. travelling waves; Lambin *et al.* 1998). However, this  
229 pattern has changed over time with a gradual loss of spatial structure (Bierman *et al.* 2006).  
230 Such changes in prey spatial synchrony may affect how easy it is for owls to predict the  
231 amount of food available in their territory, and hence influence their reproductive decisions.  
232 Therefore, we also examined the extent to which tawny owl breeding decisions were affected

233 by changes in the spatial synchrony of field vole densities. To do so, we first calculated  
234 spatial variation in field vole densities as the coefficient of variation (standard deviation  
235 divided by the mean) in spring vole densities between survey sites, each year. However,  
236 spatial variation in vole densities may be less important in years when food is abundant,  
237 compared to when it is scarce. Therefore, we classified years as either being of low overall  
238 food abundance if the averaged spring vole density was below the median value for all years,  
239 or high if not. We then included an interaction between spatial variation in vole densities and  
240 the categorical covariate of overall vole densities to test this hypothesis.

241

242 Northern goshawks (hereafter goshawks) have been continuously monitored since the first  
243 breeding attempt in 1973 (Petty & Anderson 1995). Each year occupied goshawk home-  
244 ranges were identified and over the last 40 years the number of occupied home-ranges has  
245 increased from one to 25-33. Goshawks are known predators of tawny owls, with breeding  
246 female owls being three times more likely to be killed than adult males; predation is also  
247 heavily biased towards juveniles (Hoy *et al.* 2014). Goshawk dietary data collected in Kielder  
248 Forest suggests that as the breeding population of goshawks increased, the mean number of  
249 owls killed each year by goshawks has also increased. An average of 5 [3-8; 95% CI] owls  
250 were killed each year when less than 15 goshawk home-ranges were occupied, compared to  
251 an average of 159 [141-176; 95% CI] owls killed each year when more than 24 goshawk  
252 home-ranges were occupied (see Appendix S1). Consequently, as predation on owls has  
253 increased with the abundance of goshawks in the forest, we used the total number of occupied  
254 goshawk home-ranges in a 964 km<sup>2</sup> area of Kielder Forest as a proxy of temporal variation in  
255 predation risk. However, as goshawks were monitored over a larger area than tawny owls, we  
256 also used an additional proxy of temporal variation in predation risk. Local goshawk  
257 abundance was measured as the number of goshawk home-ranges whose nest sites were

258 within 5.8 km (the estimated goshawk foraging distance) of the owl monitoring area,  
259 calculated in the same way described in Hoy *et al.* (2014).

260

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

279

### 280 *Intrinsic attributes*

281 When testing the hypothesis that the response of an individual to changes in extrinsic  
282 conditions varied according to age, we used the number of years elapsed since the individuals  
283 first recorded breeding attempt, because the exact age of 94 breeding females entering the

284 population as adult immigrants was unknown. However, most (89%) female owls had  
285 commenced breeding by the time they were 3 years old (Millon *et al.* 2010) and there had  
286 been no change in the mean age at first reproduction over the study period, neither  
287 for immigrants nor local recruits entering the owl population (unpublished data).  
288 Consequently, the number of years elapsed since an individual's first recorded breeding  
289 attempt is closely related to its age, and the length of an individual's breeding lifespan is also  
290 highly correlated with actual lifespan ( $r = 0.91$ ;  $N = 163$ ). We tested the hypothesis that  
291 previous investment in reproduction influenced an individual's current reproductive decisions  
292 in relation to changes in predation risk and food availability by fitting a binary covariate  
293 reflecting whether a female owl had successfully raised offspring to the fledgling stage the  
294 previous year. Lastly, we investigated whether the likelihood of an individual completing a  
295 breeding attempt to the fledging stage was related to clutch size, taking clutch size as a proxy  
296 for the extent to which an individual had already allocated resources towards the current  
297 reproductive attempt. All descriptive statistics are shown with the standard deviation (SD).

298

### 299 *Juvenile survival*

300 As recapture data were not available for male owls in all years, our analysis of juvenile owl  
301 survival was based on female owls only, ringed as chicks between 1985 and 2012 ( $N=1,082$ ),  
302 with the last recapture of individuals in 2013. The sex of individuals never recaptured as  
303 adults or sexed as chicks using DNA was unknown, as juvenile owls cannot be accurately  
304 sexed without molecular analyses. However, the sex ratio of chicks born in our study site was  
305 even 1:1 ( $N = 312$ , over 4 years; Appleby *et al.* 1997). Consequently, we randomly assigned  
306 half the number of chicks born each year minus the number known to be female as females,  
307 as done in previous analyses (Nichols *et al.* 2004; Millon *et al.* 2010). The rest of these chicks  
308 were assumed to be males and excluded from the analysis. Owls were only recaptured when  
309 breeding and owls usually starting to breeding between the ages 1-4 (89% before age 3;

310 (Millon *et al.* 2010). Recapture probabilities were therefore modelled as time-dependent and  
311 age-specific [(1, 2–3, 4+)] as done in Millon, Petty & Lambin (2010). This analysis was  
312 carried out in E-SURGE version 1.9.0 (Choquet *et al.* 2009). Goodness-of-fit tests were  
313 carried out in U-CARE 2.3.2 (Choquet *et al.* 2005). In this analysis only, rather than using  
314 spring vole densities (measured in March) as the measure of food availability, we used  
315 autumn densities of field voles (measured in September-October), as they have previously  
316 been shown to be more closely related to changes in juvenile tawny owl survival (Millon,  
317 Petty & Lambin 2010; Millon *et al.* 2011, 2014). Temporal proxies of predation risk were the  
318 same as those used in the previous analyses. Spatial proxies of predation risk were calculated  
319 as before, but using the natal nestbox, and were modelled as an individual covariate. Model  
320 selection in all of the above analyses was based on Akaike's information criterion corrected  
321 for small sample size (AICc; Burnham & Anderson 2002).

322

## 323 **Results**

### 324 *Breeding propensity*

325 When averaged across years, the probability of a female breeding after becoming  
326 reproductively active was  $0.78 \pm 0.17$  (range: 0.21-0.99). Variation in breeding propensity  
327 appeared most strongly related to changes in extrinsic conditions (Table 1). In years when  
328 local goshawk abundance was relatively low (fewer than 10 home-ranges occupied) breeding  
329 propensity increased from an average of  $0.33 \pm 0.18$ , when food availability was also low, to  
330 an average of  $0.95 \pm 0.06$  in years of high food availability (Fig. 1a). However, in years when  
331 goshawk abundance was high the relationship between breeding propensity and food  
332 availability was less apparent (Fig. 1a). Breeding propensity also appeared to vary according  
333 to intrinsic attributes (proxies of age and previous allocation of resources to reproduction);  
334 however the association between breeding propensity and intrinsic attributes was much

335 weaker in comparison to the relationship with extrinsic factors (Fig. 1b; Table 1; Appendix  
336 S4). Breeding propensity was estimated to increase slightly as owls aged. However this trend  
337 was only observed for individuals who had successfully fledged chicks the year before.

338

#### 339 *Clutch size*

340 Owl clutch size averaged  $2.85 \pm 0.82$  (range: 1-6;  $N = 850$ ), with 92.8% of clutches  
341 containing 2-4 eggs. The largest clutches were laid in years of high spring vole densities with  
342 clutch size increasing from an average of 2.38 [2.28-2.48; 95% CI] in years when vole  
343 densities were below 50 voles  $\text{ha}^{-1}$  to 2.98 [2.82-3.14; 95% CI] in years when vole densities  
344 were above 150 voles  $\text{ha}^{-1}$  (Fig. 2). There was no evidence to suggest that variation in clutch  
345 size was related to predation risk or female age (Table 2; Appendix S5).

346

#### 347 *Completing a breeding attempt to the fledging stage*

348 On average, 96% of breeding attempts ( $N = 813$ ) were completed. Clutch size and  
349 connectivity to goshawk nest sites explained the most variation in whether a breeding attempt  
350 was completed (Table 3; Appendix S6). Irrespective of clutch size, the percentage of a  
351 breeding attempts observed to reach the fledging stage was close to 100% ( $N = 193/194$ ) for  
352 owls breeding in territories not well connected to goshawk nest sites, hence less exposed to  
353 predation (i.e. in territories not in close proximity to many goshawks nest sites; Fig. 3).  
354 However, for owls breeding in territories relatively well connected to goshawk nest sites,  
355 hence exposed to predation (i.e. in close proximity to several goshawk nest sites in that year)  
356 the probability of breeding attempts being completed decreased from 97.5% ( $N = 39/40$   
357 breeding attempts) when owls had clutches containing four or more eggs to 87.7% ( $N =$   
358  $57/65$  breeding attempts) when clutches contained 1-2 eggs (Fig 3).

359

#### 360 *Juvenile survival*



361 Juvenile survival averaged  $0.18 \pm \text{SE } 0.02$ . Autumn vole densities explained the most  
362 variation in juvenile survival (slope on logit scale:  $\beta = 0.42 \pm 0.1$ ; %Deviation = 34.5).  
363 Juvenile survival was estimated to increase with autumn vole densities (Appendix S7). There  
364 was no evidence of a relationship between juvenile owl survival and any proxy of predation  
365 risk (Table 4).

366

## 367 **Discussion**

368 In this study we examined how reproduction in female tawny owls (breeding propensity,  
369 clutch size and nest abandonment) was influenced by both extrinsic (food availability and  
370 predation risk) and intrinsic factors (age, previous and current allocation of resources towards  
371 reproduction) and any interactions between these factors. Our main findings were as follows:  
372 i) breeding propensity was highest in years when food (field vole densities in spring) was  
373 abundant and predation risk (goshawk abundance) was low. However, in years when  
374 goshawk abundance was relatively high the association between breeding propensity and  
375 food availability was less apparent. Breeding propensity also appeared to be related to  
376 intrinsic attributes (but to a lesser extent than extrinsic factors), as owls which had  
377 successfully fledged chicks the year before were slightly more likely to breed as they aged  
378 compared to owls which had not fledged chicks. ii) Clutch size was positively associated with  
379 spring vole densities but was unrelated to predation risk or any intrinsic attributes examined.  
380 iii) On average 96% of breeding attempts were completed, however owls with small clutches  
381 (1-2 eggs), and breeding in territories more exposed to goshawk predation, were less likely to  
382 complete their breeding attempt compared to owls with larger clutches breeding in less  
383 exposed territories. iv) Juvenile owl survival was positively correlated with food availability  
384 in the autumn but was unrelated to predation risk. Overall, these findings represent rare

385 evidence about how extrinsic and intrinsic factors interact to shape reproductive decisions in  
386 a long-lived iteroparous predator.

387

### 388 *Breeding propensity*

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

411 the end of the study period) have made intermittent breeding a less beneficial strategy, as the  
412 cost of not breeding now is less likely to be compensated for in the future.

413

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

423

#### 424 *Clutch size*

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

436

437 *Completing a breeding attempt to the fledging stage*

438 As predicted by life-history theory, individuals who had allocated more towards reproduction  
439 (e.g. by laying larger clutches), were more likely to continue their breeding attempt to the  
440 fledging stage, a finding consistent with previous studies (e.g. Delehanty & Oring 1993).  
441 Predation risk was the only extrinsic predictor of whether breeding attempts reached the  
442 fledging stage, with individuals breeding in territories more exposed to predation risk being  
443 less likely to complete a breeding attempt (Fig. 3); a result congruent with another study  
444 examining the effect of spatial variation in predation risk on reproductive success (Sergio,  
445 Marchesi & Pedrini 2003). Goshawks start displaying over territories and building nests in  
446 late March and April in the UK (Kenward 2006), hence are likely to become even more  
447 conspicuous to owls, after owls have already committed to breeding. Furthermore, predation  
448 risk for both adult and fledgling owls increased throughout the breeding season (Petty *et al.*  
449 2003; Hoy *et al.* 2014). Therefore, the tendency of owls not to complete breeding attempts in  
450 territories where predation risk is presumably high, is consistent with females (having already  
451 commenced breeding), attempting to reduce their own vulnerability to predation as the  
452 breeding season progresses. Alternatively, as 23% of breeders which did not complete a  
453 breeding attempt were never recaptured in the study site again, the higher failure rates in  
454 territories well connected to areas of high goshawk activity could also reflect that some  
455 parents in those territories were predated by goshawks and hence were unable to complete the  
456 breeding attempt.

457

458 *Juvenile survival*

459 Our analysis confirmed that juvenile owl survival was positively related to food availability  
460 (Millon, Petty & Lambin 2010; Millon *et al.* 2011, 2014). Estimates of juvenile owl survival  
461 were lowest in low vole years (Appendix S7). If mothers were able to predict the food  
462 conditions that their offspring would experience they should be less inclined to allocate

463 resources towards reproduction in low vole years, due to the reduced probability of these  
464 offspring being recruited into the population. This may in part explain why individuals  
465 allocated relatively few resources towards reproduction (i.e. smaller clutch sizes) in years  
466 when food was scarce.

467

#### 468 *Reproductive strategies in relation to changing environmental conditions*

469 A reproductive strategy can be defined as the set of decisions which influence the number of  
470 offspring an individual produces. Owl breeding strategies appeared to change in response to  
471 extrinsic conditions. Individuals allocated more resources towards reproduction (in terms of  
472 breeding propensity and clutch size) in years when food was abundant (Fig. 1 & Fig. 2).  
473 Although we found no evidence to support our prediction that owls would attempt to  
474 minimise their vulnerability to predation by breeding less frequently or laying smaller  
475 clutches in years when predation risk was high, we did find evidence to suggest that owls  
476 responded to changes in predation risk, by making facultative decisions about whether to  
477 continue with their breeding attempt. However, the observed increase in incomplete nesting  
478 attempts with increasing predation risk also be partly due to parent(s) being killed, hence  
479 being unable to complete the breeding attempt, rather than a facultative decision not to  
480 continue the attempt. There was no year-to-year collinearity between our temporal covariates  
481 of predation risk and food availability. However, when averaged over a larger time scale (5  
482 years) these covariates were correlated, and hence both environmental conditions changed  
483 simultaneously in opposite ways, with spring vole densities decreasing and predation risk  
484 increasing over the course of the study period. Therefore, we were unable to fully disentangle  
485 the effects of food availability and predation risk on owl breeding decisions. As the overall  
486 percentage of failed breeding attempts was very low (4% on average), the main reproductive  
487 decisions influencing reproductive output were primarily breeding propensity then clutch  
488 size. Indeed, the proportion of the population breeding and average clutch size explained 83%

489 and 16% of the total variation in annual reproductive success (measured as the average  
490 number of chicks fledged per occupied owl territory) of the tawny owl population  
491 respectively. Whereas whether breeding attempts were completed only explained 0.1% of the  
492 total variation in reproductive success (see Appendix S8). Consequently, food availability  
493 seemed to have a greater impact on breeding propensity than changing predation risk (Fig. 1,  
494 Table 1) and be the main extrinsic factor driving variation in reproductive output, thus  
495 shaping reproductive strategies in tawny owls. However, the strength of the relationship  
496 between reproductive output and food availability weakened as predation risk increased.

497

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

508

509 Together our results suggest that extrinsic conditions and intrinsic attributes have a combined  
510 and interactive effect on reproductive decisions. Changes in extrinsic conditions, particularly  
511 food availability, were the main factors shaping owl reproductive decisions, as the association  
512 between intrinsic attributes and owl breeding decisions was relatively weak in comparison.  
513 This could in part be due to environmental variation in this system being relatively high  
514 because of the cyclical dynamics of vole populations, and the relatively recent recovery of an

515 apex predator, thus swamping the contribution of intrinsic attributes to reproductive  
516 strategies. Although many of our results were in line with previous studies and theoretical  
517 predictions, our comprehensive approach highlights the complex nature of how intrinsic and  
518 extrinsic trade-offs act in combination to shape tawny owl reproduction. Furthermore, the  
519 length of this study has enabled us to provide some empirical evidence, albeit correlative, of  
520 long-lived predators altering their life-history strategies in response to changes in multiple  
521 interacting environmental factors.

522

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533

### 534 **Data accessibility**

535 All data associated with the study which is not given in the text is available in the Dryad  
536 Digital Repository. <http://dx.doi.org/10.5061/dryad.6n579>.

537

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684

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

Model	<i>np</i>	Estimate	SE	$\Delta AIC_c$
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 x SVVD		0.03	0.60	
8. Breeding success previous year (BS)	4	0.34	0.22	27.81
9. Years since 1 <sup>st</sup> 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 x 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 x Y1st		0.14	0.06	
14. <b>Breeding success previous year</b>	<b>9</b>	<b>-0.34</b>	<b>0.35</b>	<b>0</b>
<b>Years since 1st reproduction</b>		<b>-0.01</b>	<b>0.05</b>	
<b>BS x Y1st</b>		<b>0.13</b>	<b>0.06</b>	
<b>Spring voles</b>		<b>1.17</b>	<b>0.23</b>	
<b>Local goshawk</b>		<b>0.13</b>	<b>0.22</b>	
<b>SV x LG</b>		<b>-0.69</b>	<b>0.26</b>	

693

694

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

Model	<i>np</i>	Estimate	SE	$\Delta AIC_c$
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
<b>6. Spring vole density</b>	<b>4</b>	<b>0.125</b>	<b>0.023</b>	<b>0.00</b>
7. Categorical spring vole density (CSV)	6	-0.130	0.059	6.52
Spatial variation in vole densities (SVVD)		-0.068	0.036	
CSV x 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

703

704

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

Model	<i>np</i>	Estimate	SE	$\Delta$ AICc
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 x SVVD		-0.08	0.48	
8. Successfully bred 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
<b>11. Connectivity to goshawks + Clutch size</b>	<b>5</b>	<b>0.84</b> <b>-0.60</b>	<b>0.28</b> <b>0.17</b>	<b>0.00</b>
12. Connectivity to goshawks (CG)	6	-0.35	0.59	1.85
Clutch size (CS)		0.89	0.31	
CG x CS		-0.10	0.23	

713

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

Models	Deviance	<i>np</i>	$\Delta AICc$
Null	2171.22	33	19.52
<b>Autumn vole density</b>	<b>2149.60</b>	<b>34</b>	<b>0.00</b>
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 x TG	2149.23	36	3.82
AV x LG	2148.98	36	3.57
AV x NG	2149.53	36	4.12
AV x CG	2148.32	36	2.91

719



720 **Figure Legends**

721

722 Fig. 1. Variation in the probability of adult female tawny owls breeding in relation to changes  
723 in: (a) the density of their main prey, (field voles), and the abundance of their main predator  
724 (northern goshawks). (b) The number of years since the individual's first reproductive  
725 attempt (a proxy for the age of the individual) and whether the individual had successfully  
726 fledged chicks the previous year. Solid and dashed lines represent model predictions when: a)  
727 goshawk abundance was fixed at the lower and upper quartile values respectively and b) for  
728 individuals which had and had not fledged chicks the previous year respectively (when spring  
729 vole densities and goshawk abundance were fixed at the median value). Shaded grey areas  
730 represent the 95% confidence intervals of model predictions. Points are the raw data showing  
731 the observed mean proportion of all females in the population breeding in a given year. Lines  
732 are predictions derived from individual level data, and so are not fitted to the illustrated  
733 points.

734

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

739

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

745 **Supporting Information**

746 The following supporting information is available for this article:

747

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

750

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

753

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

756

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

759

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

761

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

764

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

767

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