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Age and sex-selective predation moderate the overall impact of predators

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Summary

1. Currently, there is no general agreement about the extent to which predators impact prey population dynamics and it is often poorly predicted by predation rates and species abundances. This could, in part be caused by variation in the type of selective predation occurring. Notably, if predation is selective on categories of individuals that contribute little to future generations, it may moderate the impact of predation on prey population dynamics. However, despite its prevalence, selective predation has seldom been studied in this context.

2. Using recoveries of ringed tawny owls (*Strix aluco*) predated by 'superpredators', northern goshawks (*Accipiter gentilis*) as they colonized the area, we investigated the extent to which predation was sex and age-selective. Predation of juvenile owls was disproportionately high. Amongst adults, predation was strongly biased towards females and predation risk appeared to increase with age. This implies age-selective predation may shape the decline in survival with age, observed in tawny owls.

3. To determine whether selective predation can modulate the overall impact of predation, age-based population matrix models were used to simulate the impact of five different patterns of age-selective predation, including the pattern actually observed in the study site. The overall impact on owl population size varied by up to 50%, depending on the pattern of selective predation. The simulation of the observed pattern of predation had a relatively small impact on population size, close to the least harmful scenario, predation on juveniles only.

4. The actual changes in owl population size and structure observed during goshawk colonization were also analysed. Owl population size and immigration were unrelated to goshawk abundance. However, goshawk abundance appeared to interact with owl food availability to have a delayed effect on recruitment into the population.

5. This study provides strong evidence to suggest that predation of other predators is both age and sex-selective and that selective predation of individuals with a low reproductive value may mitigate the overall impact of predators on prey population dynamics. Consequently, our results highlight how accounting for the type of selective predation occurring is likely to improve future predictions of the overall impact of predation.

Key-words: *Accipiter gentilis*, mesopredator, northern goshawk, population dynamics, predatory interactions, recruitment, senescence, *Strix aluco*, superpredator, tawny owl

Introduction

Despite being a fundamental issue in ecology, the extent to which predators can impact prey population dynamics remains controversial, with some studies finding only a weak impact, whilst others reporting that an increase in predator abundance can cause up to a fourfold decrease in prey abundance (reviewed in Ritchie & Johnson 2009). This highlights the complex nature of predator–prey interactions and suggests that the impact of predators on prey dynamics is moderated by factors other than predation rates and species abundances alone. The composition of

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many communities is currently changing, as species distributions shift in response to climate (Walther *et al.* 2002) and with the restoration of ecosystems (Maehr, Noss & Larkin 2001; Deinet *et al.* 2013). Consequently, improving predictions of the potential demographic impact of predation has become increasingly important for conservation and wildlife management purposes. Especially as many top predator species are of conservation interest (Sergio & Hiraldo 2008; Ritchie & Johnson 2009). However, in order to improve predictions, the mechanisms involved in moderating the impact of predators on prey population growth rates (λ) need to be identified.

In theory, variation in the degree of selectivity in predation occurring, defined here as the degree to which categories of prey are predated disproportionally to their relative abundance, is one mechanism which could cause a variety of demographic responses to predation. For example, in many long-lived species, the relative contribution made by different categories of individuals to population growth rates is likely to vary, as survival and reproductive output are both age and condition-dependent (Jones *et al.* 2008). Thus, if predation disproportionately affects categories of individuals with low survival and reproductive values, those that have a proportionally smaller effect on population dynamics, such as young, senescent and low-quality individuals, then the impact of predators on prey population dynamics may be different to that predicted from predation rates only. Furthermore, depending on the mating system of the prey species, sex-selective predation has the potential to destabilize predator–prey dynamics (Boukal, Berec & Křivan 2008). Therefore, in some circumstances, sex-selective predation may also have modulate the impact that predators have on prey populations. However, empirical evidence supporting this hypothesis remains scant (Gervasi *et al.* 2012).

From the predator's point of view, optimal foraging theory predicts that predation should be biased towards categories of individuals that are easy to catch, either because they are encountered more frequently, are easy to detect, or because they are less able to escape predators (Werner & Hall 1974). For example, juveniles are known to be predated at disproportionately high rates (e.g. Hammill & Smith 1991), which could have a knock-on effect on recruitment (Koning, Koning & Baeyens 2009). The ability to escape predators also varies amongst adults, with individuals in substandard condition being disproportionally predated (reviewed in Temple 1987). Furthermore, breeders are thought to be more vulnerable to predation than non-breeders (Magnhagen 1991 and references therein). As poor condition is associated with a higher predation risk, the physiological decline in condition after breeding could be one mechanism which explains why breeding often results in reduced future survival (Williams 1966). In long-lived species, if the cost of previous breeding attempts and accompanying decline in condition accumulates with age, age-dependent vulnerability to predation in adults may arise conditionally on past

reproductive decisions. Consequently, predation might increase the age-specific cost of reproduction and this mechanism of increasing predation risk with age could contribute to the decline in survival observed in most vertebrates (Jones *et al.* 2008; Nussey *et al.* 2013). However, few studies have examined whether predators select older individuals (Spalding & Lesowski 1971; Kunkel *et al.* 1999).

'Superpredation' is a special type of predation where larger 'superpredators' kill smaller 'mesopredators'. In theory, mesopredators can defend themselves against superpredators using the teeth, claws or talons they use to kill prey. Consequently, the risk of injury associated with attacking other predators may be higher than when superpredators attack other prey. This could lead to different patterns of selective predation occurring. For example, sex-selective predation of sexually dimorphic species can be caused by size differences, as the larger sex may be a greater nutritional reward (Hairston, Walton & Li 1983). However, in cases where both sexes are within the prey size range of the predator, if there is a higher risk of injury associated with attacking the larger mesopredator sex it might outweigh any nutritional benefit. Despite this, except for a higher vulnerability of juveniles, we know of no study that has quantified age and sex-selective patterns of superpredation. As mesopredators play an important role in the top–down control of ecosystems, the impact that superpredators can have on mesopredator dynamics can also have a 'cascade effect' on lower trophic levels (Paine 1980). Thus, superpredation can affect the structure of whole communities and biodiversity of ecosystems (Ripple & Beschta 2004; reviewed in Ritchie & Johnson 2009). Despite this, interactions between superpredators and mesopredators are often ignored.

In spite of many studies suggesting that predation is selective on certain classes of individuals, the role of selective predation in moderating the overall impact of predators remains poorly known. Research linking selective predation to its subsequent effects on populations is needed to help determine whether such biases are responsible for variation in the impact of predators on population dynamics. Here, we take an empirical approach combined with a simulation exercise to determine whether predation of other predators (superpredation) is selective and examine the role of selective predation in moderating the overall impact of predators on prey populations. To do this, we take advantage of long-term longitudinal data collected on individuals of an established population of mesopredators, spanning the colonization and increase in abundance of a superpredator. Northern goshawks (*Accipiter gentilis*; hereafter goshawks) are known superpredators of several other avian predator species, such as tawny owls *Strix aluco* (Mikkola 1976; Petty *et al.* 2003). Goshawks have been shown to selectively predate individuals of other prey species based on condition, sex and age (Kenward 1978; Kenward, Marcström & Karlbom 1981; Hoogland *et al.* 2006). However, whether goshawk

predation on other predators is selective remains undetermined. Tawny owls are a sexually dimorphic long-lived mesopredator. Juvenile owls have a relatively low probability of survival and adult owl survival and reproduction declines with age (Millon *et al.* 2011). Consequently, as both survival and reproduction are age-dependent, the relative contribution of each owl age class to λ is likely to vary. Therefore, goshawk predation of tawny owls provides a suitable model for testing the hypothesis that if predation is disproportionally biased (selective) towards certain age classes, it will alter the overall impact of predation on prey population dynamics.

The objectives of this study are threefold. Firstly, using recoveries of ringed tawny owls predated by goshawks, we test whether superpredation is selective. More specifically, we tested the common belief that young inexperienced and elderly individuals are disproportionately taken by predators. We also predicted that predation would be biased towards males, because they are smaller than females and because males are more active they are generally thought to be more vulnerable to predation (Boukal, Berec & Křivan 2008 and references therein). Secondly, we aimed to determine whether selective predation modulates the overall impact of predation. We used age-specific population matrix models to simulate and compare the relative impact of several different patterns of selective predation on the tawny owl population, including the pattern observed in the first part of the study. Lastly, we explored whether the increase in goshawk abundance and concomitant predation had actually impacted tawny owl population characteristics, by testing for correlations between tawny owl population size, recruitment and immigration and goshawk abundance.

## Materials and methods

STUDY SYSTEM

The study took place in Kielder Forest, northern England (55°13′N, 2°33′W); a man-made conifer forest. As the forest largely lacks natural tree cavities, the preferred nesting sites for tawny owls, owls readily started using the nest boxes which were provided in excess to the number of potential territories in a 176 km² central subsection of the forest (Petty, Shaw & Anderson 1994). Each year, since 1979, occupied owl territories were identified and nearly all birds were uniquely marked with rings. Most breeding adults were caught each year (for details see Petty 1992a); females throughout the study period (1979–2012) and males between 1988–1998 and 2008–2012. Adult owls were sexed by wing length, mass and the presence of a brood patch (Petty 1992a), and for 4 years, all chicks were sexed using DNA fingerprinting (Appleby *et al.* 1997). Un-ringed owls caught as adults were aged using primary feather moulting patterns from 1985 onwards (Petty 1992a,b). Therefore, the age of 98·5% (N = 2216) of breeding owls in the population was known. Owl population size was measured as the total number of occupied territories, estimated for all except 6 years during the study period. Owl population dynamics may be influenced by food availability as

the amount of vole prey available prior to the egg-laying stage (early spring) is positively associated with the number of owl pairs which attempt to breed and clutch size (Petty 1992a; Millon *et al.* 2014). In Kielder, field voles (*Microtus agrestis*) are the main prey species for tawny owls in the study site (Petty 1987, 1999), and their densities hereafter referred to as owl food availability have been monitored bi-annually since 1985 (for methods see Lambin, Petty & MacKinnon 2000).

Goshawks were absent in Kielder Forest until 1973 (Petty & Anderson 1995). Their subsequent spread has been continuously monitored over an area of 964 km², and approximately, 30 home ranges are currently occupied (Fig. 1). On average, goshawks (females: 1500 g, males: 850 g) are 2–3 times heavier than tawny owls (females: 520 g, males: 420 g) and are known to regularly kill them (Mikkola 1976; Petty *et al.* 2003). Each year goshawk territories were searched for the remains of prey items, including tawny owl rings and when possible, nests were also searched for additional prey items. The goshawk monitoring area is more than five times larger than the tawny owl monitoring area. Goshawk pairs are known to have home ranges averaging 64 km² ± 16 (SE; Boal, Andersen & Kennedy 2003) and territories are known to overlap (Kenward 1977). Consequently, the entire tawny owl study site lay within the hunting range of goshawks. As goshawk home range size is highly variable (Kenward 1982) and is unknown in our study site, we used two proxies of predation risk for tawny owls (i) total goshawk abundance (the total number of goshawk territories known to be occupied); and (ii) local goshawk abundance (the number of occupied goshawk territories whose nests sites were within the estimated goshawk foraging distance of the owl monitoring area). Goshawk foraging distance was estimated as 5·8 km, 85% of the maximal distance from the nest box last used by an owl to the goshawk nest where the owl ring was recovered.

AGE AND SEX-SELECTIVE PREDATION ANALYSES

In order to determine whether goshawk predation was selective, the age and sex-selective pattern of ring recovered from goshawk nest sites were compared to those from other causes of mortality,
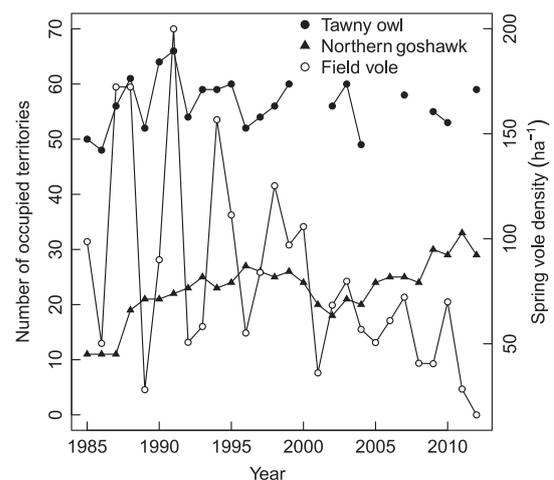
Fig. 1. Amongst-year variation in the estimated number of territories occupied by tawny owls and northern goshawks, and spring (March–April) field vole densities in Kielder Forest, UK.

such as starvation and collisions with vehicles, fences and buildings. As goshawk nest sites were deliberately targeted to recover owl rings, recoveries from other causes of mortality were only used to examine goshawk prey selectivity, not to infer the relative contribution of goshawk predation to owl mortality. The age at death was estimated for owls whose rings were recovered at goshawk nest sites. When carcasses were recovered with rings, the freshness of the carcass was used to estimate the month and year of death. The exact year at death could be determined for 92% (46) of the recoveries. Thus, a minimum age at death was estimated for 4% of the remaining recoveries using the date the owl was last captured alive, the year the goshawk nest was constructed and subsequently used and the years the goshawk territory was occupied. The remaining 4% of recoveries were from owls known to have died as adults, but the age at death could not be estimated. Such recoveries were excluded from the analysis specifically examining age-dependent predation of adults.

The first analysis tested whether goshawk predation was selective on juveniles (owls under 1 year old) or adults (owls over 1 year old). Fisher's exact test was used to determine whether the actual number of rings recovered for each age class (juveniles vs. adult) differed significantly from the number of rings expected to be recovered, if goshawk predation was random. The number of rings expected to be recovered was estimated by calculating the proportion of juveniles and adults in the population, using the age distribution of the owl population at equilibrium, predicted by the population matrix model (see Appendix S1, supporting information for details) and then multiplying it by the number of rings recovered from goshawk nest sites. The analysis was repeated on recoveries from other causes of mortality, and the results of the two analyses were compared. As the number of recoveries from adults was small, to determine whether predation on adult owls was age-selective, the proportion of all recoveries that were goshawk-related was analysed in relation to the owls' age at death using generalized linear models (GLMs) with a binomial error structure.

Sex-selective predation was determined using a binomial test to detect deviation of the sex ratio of predated recoveries from an expected even sex ratio. The same analysis was then repeated on recoveries from other causes of mortality and the results compared. Male and female owls were fitted with identically sized rings, so that a bias in ring detection probability between sexes can be ruled out. To identify whether activities related to breeding could be responsible for any sex bias in predated recoveries, these analyses were repeated using owls that died as adults only.

SIMULATED IMPACT OF SELECTIVE PREDATION

A post-breeding population matrix model with 17 age classes (juvenile and adults aged 1–16 years old) was parameterized using the survival parameters estimated by Millon, Petty & Lambin (2010) and Millon *et al.* (2011) (see Appendix S2, Supporting information for methods). This matrix model was used to estimate the age distribution of the population at equilibrium and simulate the effect of contrasted scenarios of selective goshawk predation on owl population size. Goshawk predation was simulated by removing a constant number of owls ($N = 5$) from the population each year. The initial population vector contained 200 adult females (over 1 year old) and the corresponding number of juveniles (i.e. fledglings) to match the age distribution at equilibrium. The age of the five individuals removed remained

constant throughout the simulation and was set according to five contrasted patterns of selective predation: (i) the pattern of age-specific predation actually observed in Kielder Forest, determined by the ring recovery analysis; (ii) even where an equal number of individuals across all ages were removed; (iii) predation of juveniles only, where only juveniles (<1 year old) were removed; (iv) predation on young (prime-age) adults only, where an even distribution of young adult owls (aged 1–8 years old) were removed; and (v) predation of old adults only, where an even distribution of adults aged 9 years and older were removed. The cut-off for young (prime-aged) and old owls was set at 9 years of age because a previous analysis found some support for a threshold in female survival at 8 years of age after which survival was significantly lower than at age one, and female owls are also reproductively senescent at this age (Millon *et al.* 2011).

OBSERVED CHANGES IN OWL POPULATION SIZE AND STRUCTURE

As variation in food availability is also likely to impact tawny owl population dynamics, it was included as an explanatory variable when analysing the observed changes in owl population size and structure. To detect any impact that the selective goshawk predation actually occurring had on owl population size, variation in the number of territories occupied each year was analysed over time and in relation to the increase in goshawk abundance (measured as either total or local goshawk abundance) and changes in owl food availability. This was analysed over a 22-year period between 1985 and 2012 (excluding the 6 years where occupancy estimates were unavailable) using GLMs with a Poisson error structure.

The effect of goshawk predation on owl population size could potentially be masked by compensatory mechanisms such as increased recruitment or immigration. Therefore, variation in both were analysed in relation to goshawk abundance and food availability. Additionally, we tested for a temporal trend in both recruitment and immigration over a 28-year period between 1985 and 2012. To determine whether recruitment or immigration had changed, interannual variation in the proportion of newly recruited breeders in the population (those which had not recorded breeding previously) and the proportion of local recruits amongst all newly recruited breeders were analysed using GLMs with a Binomial error structure. If newly recruited owls into the population were ringed as chicks in Kielder Forest they were classified local recruits, or as immigrants if not. These analyses were restricted to females only as males were not caught throughout the entire study period. Descriptive statistics in the results section are the mean and standard deviation unless otherwise stated.

The additive and interactive effects of both owl food availability and goshawk abundance on owl population size, recruitment and immigration were tested. Explanatory variables were standardized so as to compare their effect sizes. We hypothesize that goshawk predation mainly occurs during the peak of the goshawk breeding season, which is after owl population size has been measured and recruitment of breeding owls has taken place. If this is the case, any effect of goshawk predation in that year may not become apparent until the following year. Consequently, the analyses looking at variation in owl population size and recruitment were repeated to test for the effect of a 1-year time lag. The probability of owls being recruited into the population

in their first year is very small and the majority of owls start breeding between 2–3 years of age (Millon, Petty & Lambin 2010). Consequently, any effect of goshawk predation and food availability on juvenile survival and thus the number of locally born owls available to be recruited is only likely to become evident after a 2–3 year lag. Therefore, the proportion of local recruits was analysed against explanatory variables after a 2-year and 3-year time lag. Model selection was based upon Akaike's information criterion corrected for small sample size (AICc, Burnham & Anderson 2002). As total and local goshawk abundances were correlated ($r = 0.82$, $N = 28$, $P < 0.001$), their effects were examined in separate models. Neither measure of goshawk abundance was highly correlated with owl food availability ($r = -0.35$, $N = 28$, $P = 0.07$ for total goshawk abundance and $r = -0.17$, $N = 28$, $P = 0.39$ for local goshawk abundance). All analyses were carried out in R 3·0·3 (R Core Team 2014).

Results

AGE AND SEX-SELECTIVE PREDATION

During the study period, 2153 ringed tawny owl chicks fledged. Overall, 16% of these fledglings were subsequently recaptured in the study area after reaching 1 year old and 3% were seen after 10 years old. The maximum age was 20 and 17 years for females and males respectively. A total of 108 ringed tawny owls were recovered, of which 50 (46%) were retrieved from goshawk nest sites. Of these, 34 (68%) were predated as juveniles. An exact age at death could be determined for 12 of the remaining 16 rings from adult owls recovered from goshawks nest sites and a minimum age at death for two others. The month of death could also be estimated for 12 of the adult recoveries. All of the owls were predated in June or July with the exception of one being predated in November. This peak in detected instances of adult predation coincides with when breeding tawny owls have large, fledged but dependant chicks whilst goshawks still have chicks in the nest. Collisions (mainly with vehicles) were the main cause of mortality for the 30 (52%) recoveries known to have died from other causes.

At equilibrium, the population matrix model estimated that juveniles made up 36% of the tawny owl population. Significantly, more juveniles were predated by goshawks than expected from their relative abundance in the population, 34 juvenile owl recoveries compared to the 18 expected (Fishers exact test: $P < 0.003$, $N = 50$, odds ratio = 3·7). In contrast, there was no discrepancy between the observed and expected number of juvenile recoveries (21 vs. 20) from other causes of mortality. The age distribution of adult owl recoveries from goshawk predation differed to that of other causes of mortality. The proportion of the owl population known to reach each age which were predated by goshawks increased with age, whereas recoveries from other causes of mortality did not (Fig. 2). The proportion of ringed owls recovered as goshawk kills amongst all causes of mortality, increased significantly with owl age ($F_{10} = 2.48$, $P < 0.01$), with
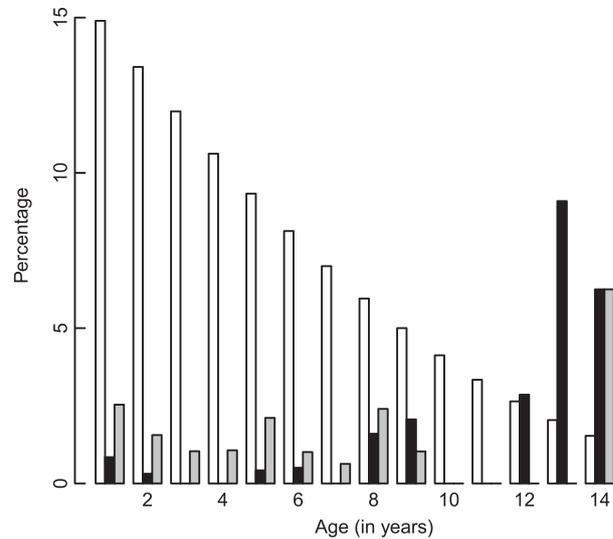
Fig. 2. Expected age distribution at equilibrium of adult tawny owls aged 1–14 years predicted by a population matrix model (white bars).The percentage of tawny owls known to reach each age that were predated by northern goshawks or died from other causes are shown by black and grey respectively.

recoveries from birds estimated to have died over 9 years old three times more likely to have been predated by goshawks than dying from other causes of mortality.

Amongst adults, recoveries of predated owls differed significantly from an even sex ratio (Exact binomial test: $P = 0.04$, $N = 15$). Recoveries were three times more likely to be from females than males (12 females and three males). Nine (75%) of adult females predated were recorded as breeding in the year they were predated. There was no excess of females amongst predated owls when an additional 12 rings from owls that died as juveniles (four females and eight males) were included in the analysis ($P = 0.44$, $N = 27$, 16 females, 11 males). There was no departure from an even sex ratio of recoveries from other causes of mortality, irrespective of whether recoveries from juvenile were included ($P = 0.56$, $N = 26$, 15 females and 11 males) or not ($P = 0.54$, $N = 24$, 13 females and 11 males).
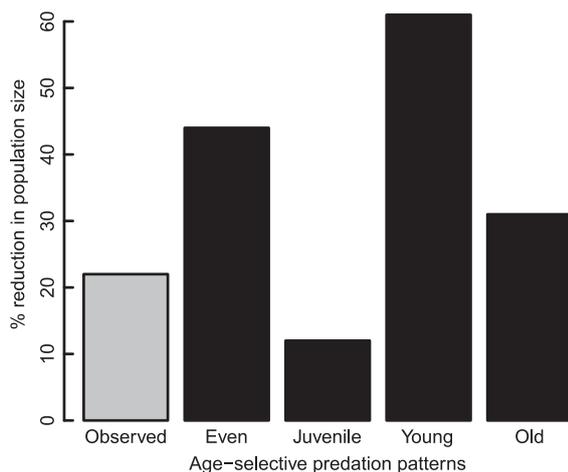
SIMULATED IMPACT OF SELECTIVE PREDATION

The simulated impact of predation varied greatly between predation patterns from an 11% to 61% reduction in initial population size (percentages relate respectively to the simulation of predation on juveniles and predation of young adults only). The observed pattern of selective predation had a relatively small impact on population size, 12% more than the simulation of predation on juveniles alone, but less impacting than any of the other predation scenarios. Simulations of predation on young adults and even predation on all ages had the greatest impact, 50% and 28% more than the observed pattern of predation respectively. The simulated effect of predation on old

adult owls (aged 9 years old and over) had a moderate impact on population size, 11% more than that of the observed pattern of predation but 18% less impacting than even predation on all ages (Fig. 3). For a full description of the population matrix model used and the estimated elasticity of tawny owl age-dependent demographic transitions see Appendices S2 and S3 (Supporting information) respectively.

OBSERVED CHANGES IN OWL POPULATION SIZE AND STRUCTURE

There was little interannual variation in the number of owl territories estimated to be occupied (56 ± 4.07; Fig. 1). Variation in the number of occupied owl territories was not associated with either food availability or goshawk abundance and the null model performed best (see Table 1), irrespective of whether the effect of a time lag was included. There was no overall temporal trend in the proportion of newly recruited breeders in the owl population, suggesting recruitment has not changed overall. The null model performed best in terms of AICc when no time lag was considered. However, 50% of the variation in recruitment was explained by an interaction between local goshawk abundance and food availability when a 1-year time lag was included (see Table 1). The proportion of newly recruited breeders in the population was relatively high when food availability and goshawk abundance were low in the preceding year. However, when goshawk abundance was high, the relationship between food availability and recruitment was weaker (Fig. 4). The proportion of local recruits in the population

Fig. 3. The predicted impact, in terms of the percentage reduction in initial population size for five different patterns of age-selective predation on a theoretical tawny owl population simulation over 20 years. Observed relates to the simulation of the actual pattern of selective predation observed in the study site. Even is the simulated effect of equal predation on all ages; juvenile, the simulation of predation only on individuals less than 1 year old; young, the simulated effect of even predation on adult owls aged 1–8 years. Old represents even predation on owls aged 9 years and over.

decreased significantly ($F_{26} = -3.15$, $P < 0.01$) by 38% from 0.48 ± 0.25 in the first 5 years of the study period to an average of 0.30 ± 0.19 in the last 5 years. There was a positive correlation between the proportion of new recruits that were born locally and food availability, which explained 20% and 15% of the variation in immigration when a 2 and 3-year time lag was considered respectively (Fig. 5).

Discussion

Predation of tawny owls was sex and age-selective, with juveniles more vulnerable to goshawk predation than adults. Predation of adults was also selective towards females and older individuals, especially those over 8 years old. A result consistent with predation contributing to the senescence in survival observed in tawny owls. These results contrast with those from other causes of mortality, which showed no indication of any age or sex-selection and suggest that goshawks selectively predate individuals of low reproductive value (juveniles and older individuals) that contribute relatively little to λ. The simulation experiment supported the hypothesis that age-selective predation can moderate the overall impact of predation, as there was up to a 50% difference in overall impact between the contrasted patterns of age-selective predation. The simulated impact of the observed pattern of selective predation on owl population size was relatively small, particularly when compared to the simulation of no age-selective predation or predation of young adults. The number of occupied owl territories (owl population size) remained constant throughout the study period in Kielder Forest and was seemingly unaffected by changes in goshawk abundance. Overall, these results match our hypothesis that if predators primarily target individuals which contribute less to λ the actual impact of goshawk predation on the tawny owl population should be relatively small.

AGE AND SEX-SELECTIVE PREDATION

As expected, predation of juveniles was disproportionately high; a result concordant with other studies investigating superpredation in birds of prey (Petty *et al.* 2003; Sunde 2005; Koning, Koning & Baeyens 2009). Fledgling tawny owls may be more vulnerable to goshawk predation than adults as they are unable to fly properly when they first leave the nest (Petty & Thirgood 1989; Sunde, Bølstad & Møller 2003). Additionally, they produce begging calls during the day, making them more conspicuous to diurnal predators, such as goshawks (Petty *et al.* 2003). Therefore, fledglings may be easier to locate than adult owls which generally only call at night (Mikkola 1983).

Predation of adult owls was strongly female biased, despite male-biased predation being 2·3 times more common across a range of taxonomic groups (reviewed in Boukal, Berec & Křivan 2008). This result contrasts with

Table 1. Results of analysis and model selection examining the effect of food availability (field vole densities in spring) and goshawk abundance on (a) tawny owl population size (number of occupied territories) and recruitment (the proportion of female breeders newly recruited) each year, modelled against explanatory variables from the same year and with 1 year delayed effect (1-year lag effect). (b) Immigration (the proportion of newly recruited breeders into the tawny owl population which were born locally) with a 2 and 3-year delayed effect. As models with each measure of goshawk abundance performed very similarly, only one measure for each analysis is presented in the table. For each analysis, the model with the lowest AICc is in bold

a) Response variable		Explanatory variable	Same year					1-year lag effect			
			Estimate	S.E	d.f.	ΔAICc		Estimate	S.E	d.f.	ΔAICc
Owl population size (Number of occupied owl territories)	1.	**Null**	–	–	**21**	**0·00**	1.	–	–	**20**	**0·00**
	2.	Food availability	0·041	0·028	20	0·25	2.	0·003	0·029	19	2·44
	3.	Total goshawk	0·022	0·029	20	1·83	3.	−0·010	0·029	19	2·35
	4.	Food availability + Total goshawk	0·054 0·039	0·029 0·030	19	1·26	4.	0·001 −0·009	0·030 0·030	18	5·09
	5.	Food availability Total goshawk Interaction	0·053 0·039 −0·003	0·030 0·031 0·029	18	4·27	5.	0·001 −0·010 −0·002	0·030 0·031 0·031	17	8·18
Recruitment (Proportion of breeding females newly recruited)	1.	**Null**	–	–	**27**	**0·00**	1.	–	–	26	14·89
	2.	Food availability	−0·049	0·071	26	1·84	2.	−0·308	0·094	25	5·64
	3.	Local goshawk	−0·008	0·083		2·32	3.	−0·148	0·085	25	14·14
	4.	Food availability + Local goshawk	−0·055 −0·026	0·074 0·086	25	4·27	4.	−0·311 −0·153	0·094 0·083	24	4·75
	5.	Food availability Local goshawk Interaction	−0·049 −0·020 0·044	0·076 0·087 0·099	24	6·82	**5.**	**−0·279** **0·026** **0·389**	**0·100** **0·105** **0·144**	**23**	**0·00**

b) Response variable		Explanatory variable	2-year lag effect					3-year lag effect			
			Estimate	S.E	d.f.	ΔAICc		Estimate	S.E	d.f.	ΔAICc
Immigration (Proportion of newly recruited females born locally)	1.	Null	–	–	25	5·50	1.	–	–	24	3·55
	2.	**Food availability**	**0·410**	**0·151**	**24**	**0·00**	**2.**	**0·347**	**0·146**	**23**	**0·00**
	3.	Total goshawk	−0·113	0·140	24	7·19	3.	−0·187	0·156	23	4·44
	4.	Food availability + Total goshawk	0·401 −0·047	0·153 0·142	23	2·46	4.	0·329 −0·049	0·158 0·170	22	2·51
	5.	Food availability Total goshawk Interaction	0·458 −0·042 0·253	0·162 0·142 0·203	22	3·73	5.	0·343 −0·096 0·068	0·161 0·202 0·157	21	5·19

the lack of any such sex-selection in owl recoveries from other causes of mortality and contradicts our prediction that predation of owls would be male biased, as males are more active doing the majority of hunting during the breeding season. Sex-selective predation can be caused by differences in parental roles that make one sex more vulnerable to predation (Götmark *et al.* 1997; Svensson 1997). For example, increased vulnerability of females during incubation and brooding was cited as the main cause of sex-selection in game birds predated by goshawks (Kenward 1977; Widén 1987). However, as tawny owls are cavity-nesters, females are unlikely to be vulnerable (in terms of exposure) to avian predation during the majority of this period. However, after fledging, juvenile begging calls may make female owls easier to detect than males as they remain closer to their offspring once the chicks have left the nest box (Sunde, Bølstad & Møller 2003). Additionally, females may become vulnerable to predation when protecting their brood (Mikkola 1983). Such differences in parental roles are thought to cause sex-selective predation in other species. For example, male Malagasy giant rats, *Hypogeomys antimena,* have a higher risk of being predated as they remain closer to and invest more in the welfare of their offspring than females (Sommer 2000).

The high proportion of adult owls recorded as breeding in the year they were predated supports the hypothesis that reproduction increases vulnerability to predation. Given most recorded instances of adult owls being predated were in June and July, after owl chicks have fledged, it suggests that vulnerability to predation is related to reproductive costs incurred before the fledgling stage or changes in behaviour at the fledging stage. In birds, the cost of previous reproduction can manifest itself as fewer feathers being replaced by breeding birds (Pietiäinen, Saurola & Kolunen 1984; Petty 1994) or poorer quality plumage produced by breeders (Dawson *et al.* 2000). Female tawny owls moult fewer primary feathers per year than males after breeding and moult *c.* 30% fewer primaries than non-breeding owls (Petty 1994). This suggests the cost of reproduction is higher for females and, as a consequence, female flight ability may be lower than males after breeding. Furthermore, female flight feather condition may degrade more than males during
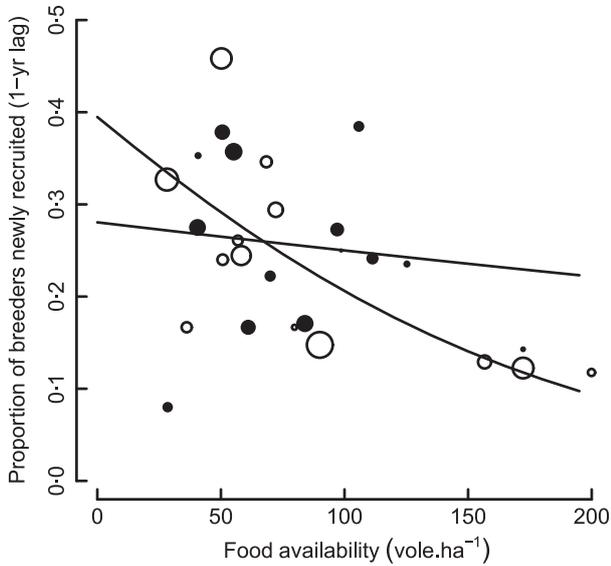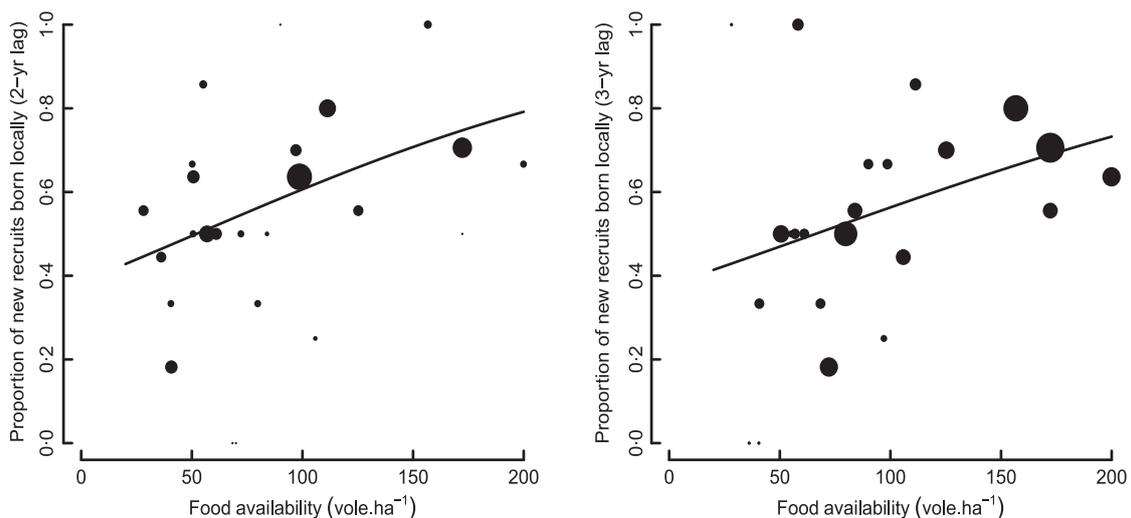
Fig. 4. Annual proportion of breeding female tawny owls which were newly recruited according to mean vole density in spring the previous year. Solid black points represent proportions when local goshawk abundance was relatively high (10 or more occupied territories) in the previous year. White points represent proportions when goshawk abundance was low (<10 occupied territories) in the preceding year. Point size is proportional to the number of pairs breeding in the current year (range: 4–61).

the breeding season, due to abrasion against the sides of the nest-cavity and spending less time preening and exercising flight muscles whilst incubating eggs and brooding young chicks. All of which is likely to result in females having reduced feather condition after breeding. Given poor-quality plumage can result in inferior flying performance (Swaddle *et al.* 1996), we propose that, after breeding, females have a reduced ability to escape predators. The above conjectures could explain why no

sex-selectivity was observed when recoveries from juveniles were also included.

Predation of adult owls also appeared age-dependent, as the proportion of all ring recoveries that were goshawk-related increased with age. For species, like tawny owls which do not do a full moult annually, the cost of reproduction in terms of reduced feather quality (fewer feathers replaced by breeders) is likely to accumulate with age following successive breeding attempts. This could potentially be the mechanism causing the observed increase in vulnerability to predation with age and thus contribute to the pattern of senescence in survival observed in tawny owls. After 8 years of age, the proportion of all recoveries that were predated was higher than that of other causes of mortality. This implies that after this age, the risk of being predated increases for female owls. This coincides with a decline in female owl survival, as survival of 9-year-old females was significantly lower than at age one (Millon *et al.* 2011). Consequently, these results provide some support for our hypothesis that age-dependent predation risk contributes to the decline in survival observed in long-lived species.

Overall, our results support the hypothesis that the accumulation of reproductive costs over a lifetime and subsequent decline in condition leads to increased vulnerability to predation with age. Interestingly, it implies that the cost of reproduction for this long-lived species is fully evident in the presence of a predator, and conversely, that the trade-off between reproduction and moulting may not be visible in environments lacking top predators. Thus, we posit that the observed age and sex-selective predation were caused by a combination of (i) juveniles and females being easier to detect; and (ii) the ability to escape predator attacks being age and sex-dependent due to the accumulation of reproductive costs, with age.

Fig. 5. Variation in the proportion of newly recruited breeding female tawny owls which were born locally each year according to mean vole density in spring the previous (a) 2 years (b) 3 years. Point size is proportional to the number of new recruits in the current year (range: 1–22).

SIMULATED AND OBSERVED IMPACT OF SELECTIVE PREDATION ON OWL POPULATION SIZE AND STRUCTURE

Despite goshawks predating owls relatively frequently in our study site, tawny owl population size seemed unaffected by the increasing goshawk population. Our simulations of contrasted selective predation patterns indicates that the observed pattern of predation by goshawks is very close the least harmful scenario, having a relatively small impact on total population size. This combined with the observation that goshawks appeared to selectively predate individuals with low reproductive values (juveniles and older females) matches the prediction that, if predation is restricted to categories of individuals with low reproductive values, the overall impact of predators on prey population dynamics will be lower than that predicted by predation rates alone. A conclusion further supported by the lack of a relationship between goshawk abundance and owl population size.

There was no evidence to suggest that an increase in recruitment into the population could be masking the effect of goshawk predation on the population, as there was no overall change in the proportion of breeders newly recruited into the population during the study period. However, goshawk abundance did appear to interact with owl food availability to have a combined effect on recruitment in the following year. We posit that when food is highly abundant and predation risk is low, more breeders survive to the following year, thus fewer territories become available for new breeders resulting in a low proportion of new recruits in the breeding population. However, when goshawk abundance is high, presumably so is the risk of owls being predated, which may reduce any positive effect of high food availability on owl survival. This could explain why the proportion of new recruits in the population was relatively low when owl food availability was high and goshawk abundance was low in the preceding year and why the effect of food availability and recruitment was weaker when goshawk abundance was high. Although owl population size and overall recruitment appeared to remain constant, there was a significant decrease in local birds being recruited into the population; this implies there is a shortage of local recruits. The positive correlation between owl food availability and the proportion of local recruits after a 2- and 3-year lag is consistent with the findings of Millon, Petty & Lambin (2010). This suggests that the decline is most likely caused by a reduction in owl productivity and potentially juvenile survival due to declining food availability in spring and changing climate (Millon *et al.* 2014). Although predation of juveniles may also contribute to a shortage of local recruits, our analyses suggest it does not exacerbate the effect of declining food availability on local owl recruitment significantly.

Overall, our results imply that selective predation can alter the impact of predators on prey populations and highlight the importance of examining the type and extent of selective predation occurring when assessing and predicting the potential impact of predators. We conclude that superpredation, goshawk predation of adult owls is both age and sex-selective; however, the pattern of selective goshawk predation occurring in our study system is insufficient to affect tawny owl population size. Thus, selective predation combined with other compensatory mechanisms such as immigration may play an important role in modulating and buffering the overall impact of predators.

Data accessibility

All data associated with the study which have not already been given in the text are available from the Dryad Digital Repository: http://doi.org/10.5061/dryad.h1289 (Hoy *et al.* 2014).

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Supporting Information

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

Appendix S1. Expected age distribution of the population at equilibrium.

Appendix S2. Population matrix model.

Appendix S3. Elasticities of tawny owl demographic transitions.