The impact of increasing predation risk and declining food availability on the population dynamics and demography of a long-lived mesopredator

Sarah Rose Hoy

MSc Ecology, Evolution & Conservation, Imperial College London

BSc Zoology (hons), University of Manchester

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DECLARATION OF AUTHENTICITY

I, *Sarah Rose Hoy* declare that the work presented in this thesis is my own, and has not been accepted in any previous applications for a degree. All quotations have been distinguished by quotation marks and all sources of information have been specifically acknowledged.

Signed ______________________________ date_____________________

AUTHOR CONTRIBUTIONS

I am the first author of all chapters; Xavier Lambin, Alex Millon, Phil Whitfield and Steve Petty are contributing authors on Chapters 2-5. Mick Marquiss and Martin Davison were also contributing authors to Chapter 3. Jane Reid and Steve Redpath also made helpful suggestions on drafts of Chapter 3 and Jane also commented on Chapter 4.

While the data used in the analyses has been collected by many people over the years (most notably by Steve Petty, David Anderson, Martin Davison and Brian Little), I collected all data on tawny owls and field voles between October 2011-October 2014 and also assisted with data collection on goshawks during this time. Steve Petty initiated the monitoring of goshawks, tawny owls and field voles and along with myself, Alex Millon and Xavier Lambin he played a role in designing the research carried out in this thesis.

The chapters in this thesis have been written as a sequence of manuscripts, in preparation for publication and each has several smaller objectives, summarised below. Chapter 3 was published in 2014, as a research article entitled ‘*Age and sex-selective predation moderate the overall impact of predators*’ in the Journal of Animal Ecology.

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THESIS ABSTRACT

Understanding the role that extrinsic processes play in shaping animal population dynamics is a central tenet of population ecology and an issue of vital importance for conservation and wildlife management. The top-down impact of predation and bottom-up influence of food availability are thought to be two of the most important extrinsic processes affecting the population dynamics and demography of species occupying middle trophic levels. However, many studies only focus on quantifying the impact of one of these processes in isolation and it is not clear whether the impact of one extrinsic factor on population dynamics and demographic rates is augmented or lessened by changes in other extrinsic factors. Furthermore, little is known about the extent to which the impact of extrinsic conditions on populations is modulated by attributes intrinsic to the individuals. In this thesis I examine the extent to which both top-down and bottom-up processes shape population dynamics (population size, recruitment and immigration) and demography (survival, reproduction, life-history trade-offs and reproductive strategies) in a long-lived species, the tawny owl, by taking advantage of a ‘natural experiment’ whereby predation risk (goshawk abundance) increased and food availability (field vole densities) declined.

The salient findings of this thesis are as follows. Goshawks were selectively preying upon on juvenile and older owls, which I posit is due to these classes of individuals being less able to evade predators once detected. There was a per capita increase in predation on tawny owls over time as goshawk abundance increased, which I hypothesise, is due to the goshawk population becoming increasingly food limited and switching to preying upon less profitable prey species, such as tawny owls to make up the shortfall in the diet. However, despite the increase in predation, the owl population remained stable, which is most likely due to goshawk predation being selective on individuals with a low reproductive value (juveniles and old individuals) and an increase in the number of immigrants entering the population. Food availability and predation risk interacted to have a combined impact on the recruitment of new breeders into the population. Further analysis supports the hypothesis that recruitment of new breeders is proximately mediated by the impact of food availability and predation on the survival of existing breeders in the population and thus the number of territories which become available for new recruits. Food availability was the main factor influencing the recruitment of local breeders into the population, due to its impact on juvenile owl survival (i.e. survival in the 1st year of life) and the productivity of the owl population. Juvenile owl survival was strongly influenced by food availability; but there was no evidence to suggest that it was affected by changes in goshawk abundance, hence predation by goshawks did not appear to be an additive cause of mortality for juvenile owls. However, selective predation on older owls (over 8 years old) did have a negative impact on the survival of this age class and appeared to be shaping the pattern of actuarial senescence observed in the Kielder Forest tawny owl population in my study site. I also found evidence supporting the prediction that extrinsic causes of mortality, such as predation, influence the strength of the intrinsic trade-off between survival and reproduction. Food availability was the main extrinsic factor influencing owl breeding decisions and consequently reproductive strategies; however both predation risk and food availability interacted to have a combined effect on whether individuals bred or did not breed. Furthermore, increasing predation risk led to an overall increase in the number of owl breeding attempts being abandoned. Overall, my results suggest that owl reproductive strategies are shaped by a complex series of trade-offs between intrinsic and extrinsic factors. As food availability declined and predation risk increased owls appeared to be switching from an ‘eggs in one basket strategy’ of saving resources to invest more in fewer breeding attempts in the future, to a ‘bet-hedging’ strategy of reproducing more often, but investing less per breeding attempt. These analyses also provide some evidence suggesting that changes in extrinsic conditions are increasing the incentive for owls to terminally invest in reproduction.

In a broader context, I show that top-down and bottom-up processes interact to affect the population dynamics and demographic rates of individuals occupying middle trophic levels. I also demonstrate that the impact that extrinsic factors have on demography depends on attributes intrinsic to the individuals. The findings made throughout this thesis provide empirical support for several long-standing theoretical predictions which have hitherto been largely lacking, most notably the increased vulnerability of old individuals to predation being one mechanism shaping senescence and influencing the strength of life-history trade-offs. This work highlights the importance of considering the top-down impact of predation on mesopredators, which is particularly important for conservation and wildlife management in both North America and Europe, as several large predator populations are currently increasing in abundance and recolonising their former ranges.

CHAPTER 1

GENERAL INTRODUCTION

Adult female tawny owl

General background

Understanding the extent to which extrinsic (environmental) processes influence animal population dynamics and demography is the cornerstone of population ecology and an issue of vital importance for conservation and wildlife management. Two of the main extrinsic processes that have been identified as important drivers of population dynamics and demography are the bottom-up impact of food availability and the top-down effect of predation (White 2001; Meserve *et al.* 2003; Fox 2007; Laundré *et al.* 2014). Historically, a long-standing debate exists about the relative importance of top-down and bottom-up processes in shaping the population dynamics of species occupying middle trophic levels, with some ecologists arguing that food availability is the dominant force (Mattson & Addy 1975; White 2008), whilst other protagonists championed the idea that top-down forces are the main driver (for example see Hairston *et al.* 1960). However, in recent years, most ecologists have a more balanced view, accepting that both top-down and bottom-up processes have a role and act in combination (Hunter, Varley & Gradwell 1997). Yet despite this, only a relatively small number of studies have focused on whether the impact that one extrinsic factor has on population dynamics is augmented or lessened by changes in other extrinsic factors. Furthermore, whether the response of populations to changes in extrinsic factors is dependent on attributes intrinsic to individuals is poorly understood.

While there is a general consensus that increasing food availability has a positive effect on population growth rates (reviewed in White 2008), the impact of predation on population dynamics remains more controversial, with some studies suggesting that predation only has a weak impact, whilst others report that predators have a disproportionately large impact on prey dynamics, relative to the amount of predation actually occurring (reviewed in Ritchie & Johnson 2009). Given that predators are known to selectively kill certain classes of individuals (Temple 1987; Hammill & Smith 1991; Boukal, Berec & Křivan 2008), and the relative contribution of different categories of individuals to population growth rates is predicted to vary according to their reproductive value (Fisher 1930), the disproportionate impact that predation can sometimes have on prey populations dynamics, could be the result of predators selectively predating certain individuals. For example, if predators are selectively predating juveniles then this may have a smaller impact on population dynamics than predation rates alone might suggest (Gervasi *et al.* 2012). Yet despite the number of studies providing evidence to suggest that predation is selective on certain classes of individuals (e.g. Temple 1987; Hammill & Smith 1991; Boukal *et al.* 2008), to the best of my knowledge, only one study has attempted to ascertain whether selective predation actually modulates the impact predators have on wild prey populations (Gervasi *et al.* 2012).

Alternatively, the disproportionate effect that predators can have on prey populations could be mediated through indirect processes which are often hard to detect. In addition to the direct impact that killing individuals can have on prey population dynamics, by eliciting anti-predator behaviours in their prey, such as avoidance of risky areas or being less active at the same time as their predators (Rudolph 1978; Buchanan 1996, 2012; Sergio *et al.* 2007). Such predator induced behavioural changes can reduce the prey's food intake and result in a reduction in the survival and reproductive output of prey individuals. For example, when redshank *Tringa tetanus* perceived there was a high risk of being predated by sparrowhawks *Accipiter nisus* they were found to reduce the amount of time they spent foraging to such an extent that it ultimately resulted in some individuals starving to death (Cresswell & Whitfield 2008). Furthermore, given physiological and behavioural changes associated with breeding can make individuals more vulnerable to predation (Magnhagen 1991), individuals can alter their reproductive decisions in response to changes in predation risk to increase their probability of survival. Indeed, there is evidence to suggest that birds can assess predation risk and make facultative decisions about the extent to which they allocate resources to reproduction to increase their probability of survival (Ghalambor & Martin 2001). For example, variation in predation risk has been shown to influence: the number of individuals which attempt to breeding (Spaans, Blijleven & Popov 1998); the number of offspring an individual produces (Zanette *et al.* 2011) and whether an individual abandons their breeding attempt or not (Krüger 2002). Such indirect effects of predation on prey survival and reproduction are ultimately likely to have a knock-on effect on prey population dynamics and in theory, the indirect effect of predators on prey populations has been shown to destabilize predator-prey dynamics, under certain circumstances (Kokko & Ruxton 2000). Consequently, even when actual predation rates are very low, the threat of predation alone can still exert a strong effect on the behaviour of potential prey species which can incur a substantial demographic cost (Lima & Dill 1990; Preisser, Bolnick & Benard 2005; Moura, Vieira & Cerqueira 2009; Zanette *et al.* 2011). Indeed a meta-analysis revealed that indirect effects can account for up to 85% of the total impact that predators have on prey populations (Preisser *et al.* 2005). Therefore, although such indirect effects by nature can be difficult to detect, they are still an important factor worth considering when assessing the impact of predators on prey population dynamics. Thus, together with other processes such as selective predation on certain classes of individuals, the strength of indirect effects of predation could in part explain the lack of consensus about the importance of predation in shaping prey population dynamics and demography.

How an individual responds to changes in extrinsic conditions, such as predation risk is likely to vary according to attributes intrinsic to the individual and the extent to which the individuals age/sex class is likely to be affected by the change in extrinsic conditions. For example, an experimental study revealed that in response to an increase in predation risk during the breeding season, parents of long-lived species (high probability of adult survival) with small clutches responded more strongly to minimise their own vulnerability to predation, even at a cost to their reproductive output, when predation was directed towards adults (Ghalambor & Martin 2001). Whereas parents of short-lived species (low probability of adult survival) with relatively large clutches, responded more strongly to minimise the risk of their offspring being killed by predators, even though this increased the parents risk of being preyed upon. The results of these experiments therefore support the hypothesis that the impact of extrinsic conditions on breeding decisions and the trade-off between survival and reproduction is dependent on attributes intrinsic to individuals. Furthermore, they also highlight the importance of understanding the pattern of age-dependent predation when investigating the impact of predation on such life-history trade-offs.

The trade-off between the level of investment in reproduction and somatic maintenance is a fundamental part of life-history theory (Williams 1966). Due to competing energetic demands, reproduction is thought to reduce the amount of resources an individual allocates to somatic maintenance at the cellular level (Metcalfe & Alonso-Alvarez 2010; Sudyka *et al.* 2014). Such trade-offs at the cellular level are thought to translate into survival costs at the individual level. For example, the amount an individual allocates to reproduction when young has been shown to alter the onset and rate of senescence in later life, in several wild vertebrate species (e.g. Lambin & Yoccoz 2001; Orell & Belda 2002). Given the cost of reproduction (in terms of reduced somatic maintenance) results in a decline in an individual's condition, it should increase the individual's vulnerability to predation, as individuals in poor condition are disproportionally predated by predators (Temple 1987). Therefore, variation in extrinsic factors such as predation pressure has the potential to influence the strength of such life-history trade-offs. Consequently, the survival cost of reproduction (the extent to which reproduction at age x reduces the probability of surviving to age $x+1$) is predicted to vary with changes in predation risk. However, most studies only examine the short term impact of changes in extrinsic conditions on the trade-off between reproduction and survival, in the same year or one year following a breeding attempt and do not examine any longer term cumulative effects on survival and senescence.

The term 'superpredation' is used to describe predatory interactions between two predator species (Lourenço *et al.* 2013). Superpredation is a sized-based phenomenon, whereby larger 'superpredators' kill smaller 'mesopredators', and has been documented in both terrestrial and aquatic systems; in amphibians, reptiles, mammals, fish, invertebrates and birds of prey (Polis, Myers & Holt 1989; Polis & Holt 1992; Holt & Polis 1997; Palomares & Caro 1999; Arim & Marquet 2004; Barton & Roth 2008; Sergio & Hiraldo 2008; Webb, Pringle & Shine 2009; Davenport & Chalcraft 2012). Given mesopredators play an important role in the top-down control of their prey populations, the impact of superpredation on mesopredator population dynamics is thought to 'cascade' to effect lower trophic levels (Paine 1980). Indeed, under some circumstances by influencing mesopredator population dynamics, superpredation can affect the structure and biodiversity of ecosystems (Ripple & Beschta 2004; reviewed in Ritchie & Johnson 2009). Given the far-reaching effects that superpredation can have on communities, improving our understanding of the role that superpredation plays in shaping the population dynamics and demography of mesopredator species is important. Indeed, it has become increasingly important issue for conservation and wildlife management, as populations of several large predator species are currently increasing in abundance and recolonising their former ranges, in both North America and Europe (Maehr, Noss & Larkin 2001; Deinet *et al.* 2013). However, until relatively recently, researchers investigating how extrinsic factors influence predator population dynamics and demography have largely ignored the role of top-down processes.

Superpredation is particularly well documented in birds of prey, with several species of raptors and owls known to regularly predate other predators such as other birds of prey (Mikkola 1976; Sergio & Hiraldo 2008; Zuberogoitia & Prommer 2011; Lourenço *et al.* 2013). Northern goshawk (*Accipiter gentilis*, hereafter goshawk) is one such avian predator known to kill smaller predator species, particularly smaller bird of prey species (Mañosa 1994; Petty *et al.* 2003; Kenward 2006; Zuberogoitia & Prommer 2011). Goshawks are native to the UK, but were heavily persecuted until they were extirpated in the late 19th century. However, scattered populations were re-established in the 1960's after some captive individuals escaped and were released by falconers (Marquiss & Newton 1982; Petty 1996). Despite illegal persecution still occurring, over the last few decades these goshawk populations have continued to increase as the species recolonises it former range and at least 500 pairs are currently thought to be breeding in the UK (Robinson 2005). The recovery of goshawks in the UK is therefore likely to have increased predation risk for smaller predators known to be preyed upon by goshawks. Consequently, the sustained and relatively recent recovery of goshawks in the UK presents a unique opportunity to examine the impact that an increase in predation risk has on the population dynamics and demography of mesopredators.

At the same time that predation risk has presumably increased for smaller bird of prey species known to be preyed upon by goshawks, food availability has also changed dramatically for those which specialise in killing voles, such as Eurasian kestrel (*Falco tinnunculus*), tawny owl (*Strix aluco*), long-eared owl (*Asio otus*) and short-eared owl (*Asio flammeus*). In the UK field voles (*Microtus agrestis*) are the main prey species for the aforementioned species (Petty *et al.* 2003). Field vole populations are cyclical, however these population cycles switched from being high-amplitude to low-amplitude in the mid-90's both in the UK and throughout the rest of Europe, which has resulted in an overall decline in vole densities in more recent years (Cornulier *et al.* 2013). Consequently, this temporal variation in both food availability and predation risk for vole specialist avian predators therefore presents a useful model system to quantify and examine the relative importance that changes in top-down and bottom-up forces have on population dynamics and demography in a natural setting. Examining the impact that extrinsic factors, such as predation have on populations in natural settings is important, as it is difficult to simulate a realistic level of predation risk (Lambin *et al.* 1995). Furthermore, the behavioural response typically elicited in some experiments has later been shown to be an artefact of extreme stimuli and unrepresentative of natural responses to predation risk (Wolff & Davis Born 1997; Mappes, Koskela & Ylonen 1998).

Thesis objectives & structure

The overarching aim of this PhD was to assess the extent to which both top-down and bottom-up processes shape population dynamics and demographic rates in a long-lived mesopredator species, the tawny owl, by taking advantage of this natural increase in predation risk (goshawk abundance) and decline in food availability (field vole densities). Although competition and disease are also thought to play an important role in regulating population dynamics (White 2001, 2008), this thesis only focuses on the role of predation and food availability. Before the influence of predation on mesopredator dynamics and demography can be examined, an important first step is to quantify how much predation is occurring and whether this has indeed increased along with goshawk abundance. Therefore, the main aim of the Chapter 2 was to calculate how much predation on tawny owls has actually occurred. Then the remaining chapters focus on the impact of variation in food availability and predation risk on tawny owl population dynamics and demographic rates. I chose to focus specifically on the impact of goshawks on tawny owls given the extent of predation on tawny owls found in Chapter 2 and the level of demographic data available for tawny owls in the study site. For brevity, the term raptor will hereafter be used to refer to all diurnal and nocturnal Falconiformes, Accipitriformes and Strigiformes.

Chapter summaries

Chapter 2

Main objective: Quantify the amount of goshawk predation on mesopredators. However, as the mechanisms driving superpredation are not well understood (Sergio & Hiraldo 2008), in this first data chapter I also evaluate which mechanisms are most likely to be driving superpredation in this system. The more specific aims of this chapter are as follows:

1) Establish how much predation on avian mesopredators has occurred and examine whether this has changed as goshawks continued to colonise the study site.
2) Investigate whether there is evidence to suggest that the goshawk population has become food-limited during the colonisation process to identify which mechanisms might be driving variation in the amount of superpredation occurring in this system.

3) Quantify the potential impact that goshawk predation has had on the local kestrel, tawny owl and sparrowhawk populations, by estimating the number of individuals killed each year by the goshawk population.

I had also planned to assess the extent to which variation in the amount of goshawk predation on other raptors is influenced by the individual goshawks present in the population, as goshawk diet has been shown to change with age (Rutz, Whittingham & Newton 2006) and there is some anecdotal evidence in raptors to suggests that certain individuals specialise in killing other raptors (Rudebeck 1951). Understanding whether the extent of superpredation occurring is dependent on individual goshawks specialising in taking certain types of prey or a change in their diet with age is important because predation risk for mesopredators will not just be influenced by the number of goshawks in the population but also by the individual hawks present in the population and the age distribution of the goshawk population. Consequently, individual dietary specialisation has important implications for management, given that predator abundance and the ratio of predators to prey densities are the most commonly used predictors of the impact of predators on prey populations. Unfortunately, little is known about the foraging behaviour of individual goshawks in the forest, as physically capturing adult goshawks is both difficult and time consuming. Furthermore wing tags and colour rings are ineffective methods of collecting individual re-sighting data in this species, due to the elusive nature of goshawks and how difficult they are to observe freely in their wooded habitats (Opdam & Muskens 1976). However, it is thought that individual goshawks can be identified by the phenotypic characteristics of moulted primary feathers (Opdam & Muskens 1976). Primary feathers from female goshawks are relatively easy to collect, as they are usually moulted in the area around the nest. Indeed a number of goshawk primary feathers have been collected in the study site over the years, which could be used to identify individuals and test the hypothesis that certain individuals specialise in taking particular prey species. However, there is some degree of variation in the characteristics of feathers between subsequent moults which could potentially lead to misidentification. Consequently, before this inexpensive phenotypic method is relied upon to identify individuals, its accuracy needs to be ascertained. Therefore, during this PhD I also sought to validate the method of using the phenotypic characteristics of moulted feathers to identify individual goshawks, by examining the extent to which phenotypic assignment of individuals matched genetic assignment of individuals using DNA-fingerprinting. The results of this can be found in Appendix 1. Unfortunately, there was not sufficient time within this PhD to collate all the old moulted feather samples, assigned them to individuals using the phenotypic characteristics and analyse the data. However, the work that was done to validate the phenotypic method of identifying individuals lays a solid foundation for future studies. Although molecular methods could have been used to genetically identify all individuals from moulted feathers, the quality of DNA from some moulted feather samples (particularly old ones) was not always of sufficiently high quality to do so. Furthermore, it is also expensive to genetically identify the large number of samples needed.

Chapter 3

Main objective: Quantify the overall impact that temporal variation in food availability and predation/predation risk (i.e. both the direct and indirect effect of predation) has on tawny owl population dynamics. Recruitment and immigration rates also influence population dynamics (Koning, Koning & Baeyens 2009; Millon *et al.* 2014). Therefore, I also examined whether these two demographic rates had changed over the study period. I also examine the extent to which predation by goshawks is selective on particular individuals, and theoretically test the prediction that selective predation modulates the overall impact that predation has on owl dynamics. More specifically in this chapter I aimed to:

1) Establish whether the increase in goshawk abundance and concomitant predation on owls has: (i) impacted tawny owl population size; (ii) influenced recruitment of new breeders into the owl population; (iii) altered immigration rates.
2) Identify whether vulnerability to predation by goshawks is dependent on the age or sex of the individual.
3) Determine whether the type of selective predation occurring can modulate the overall impact of predation.

Chapter 4

Main objective: Determine the extent to which variation in predation and food availability has influenced tawny owl survival. In this chapter I also discuss the potential role that the age-selective predation found in Chapter 3 could be having on the pattern of senescence previously observed in tawny owls (Millon *et al.* 2011). Given that: i) predation and food availability are thought to influence both survival and reproduction and ii) life-history theory predicts that there is an intrinsic trade-off between reproduction and survival (Williams 1966). I also examined whether the strength of life-history trade-offs are influenced by changes in predation risk and food availability. In summary the hypotheses tested in this chapter were that:

1) Tawny owl survival will decline as goshawks increase in abundance and food availability declines.
2) Age-selective predation by goshawks will shape the age-dependent pattern of adult tawny owl survival.
3) Age-selective predation shapes the age-specific survival cost of reproduction in tawny owls.
4) Reproductive costs have a cumulative impact on survival in later life.
5) The trade-off between reproduction and survival in later life is affected by increasing predation pressure.

The results of the analyses examining the impact of goshawk predation and food availability on the survival of juvenile owls are presented in Appendix 2.

Chapter 5

Main objective: Establish the role that food availability and predation risk play in shaping breeding decisions and consequently life-history strategies in tawny owls, given there is a growing body of evidence to suggest that predation risk can have a strong indirect effects on breeding decisions in birds (Lima & Dill 1990; Lima 2009; Zanette *et al.* 2011). To accomplish this I examined the impact that temporal variation in both food availability and predation risk had on:

1) The probability that a female owl breeds.
2) The amount an individual allocates to reproduction (clutch size).
3) Whether an individual completed their breeding attempt.
4) In addition, I also examined whether the behavioural response of an individual to temporal variation in predation risk and food availability varied according to intrinsic factors (the reproductive value of the breeder, clutch size).

Chapter 6

In the last chapter of this thesis I recapitulate the main results of each chapter and give my interpretation of what they signify when reviewed in synthesis.

Study system

Kielder Forest

All the research carried out herein took place in Kielder Forest, northern England (55°13´N, 2°33´W; Fig 1). Kielder is the largest man-made coniferous forest in England and is managed for timber production by the Forestry Commission (state owned forestry department). Kielder is primarily comprised of Sitka Spruce *Picea sitchensis* (77%) and Norway spruce *Picea abies* (8%), the rest is mainly pines and larches (Shuttleworth *et al.* 2012). Planting started in Kielder in 1933, and was largely completed by 1980, however clear cutting and replanting started in 1968. Kielder Forest covers an area approximately 650km² and together with several other man-made coniferous forests, it forms part of the much larger 'Border Forests'. Due to the clear cutting rotation management system (the average rotation length is between 45-60 years) the forest is made up of a mosaic of different-aged stands. Despite its continually changing structure, Kielder Forest is home to at least 10 species of raptor; goshawk, sparrowhawk, buzzard *Buteo buteo*, Merlin *Falco columbarius*, kestrel, peregrine *Falco peregrinus*, osprey *Pandion haliaetus*, tawny owl, long-eared owl and barn owl *Tyto alba*. Short-eared owls also used to be found in the forest, but have not been recorded breeding here since 2003; however many breeding pairs have been recorded elsewhere in Northumberland. Remarkably, all raptor species present in the forest have been monitored to varying degrees for over 40 years by ornithologists employed by Forest Research and the Forestry Commission, most notably by Steve Petty, Dave Anderson, Ian Yoxall, Martin Davison, Brian Little and Paul Hotchin (Newton, Meek & Little 1986; Little, Davison & Jardine 1995; Petty *et al.* 1995, 2003).

Northern goshawk

Goshawks are an elusive, impressively agile and powerful diurnal avian predator, found across the entire Holarctic region (Kenward 2006). Female goshawks are considerably larger than males (females: 1500g, males: 850g; Robinson 2005). Prior to 1973, goshawks had not been recorded breeding in Kielder Forest (Petty & Anderson 1996); however the population increased rapidly and now approximately 26-33 home-ranges are estimated to be occupied. The present goshawk population in Kielder Forest derives from Fennoscandia hawks released by falconers in the late 1960'/ early 70's (Petty & Anderson 1995). Goshawks hunt over both open areas and within woodland, but the majority of goshawk hunting takes place within 200m of the forest edge (Kenward 1982).

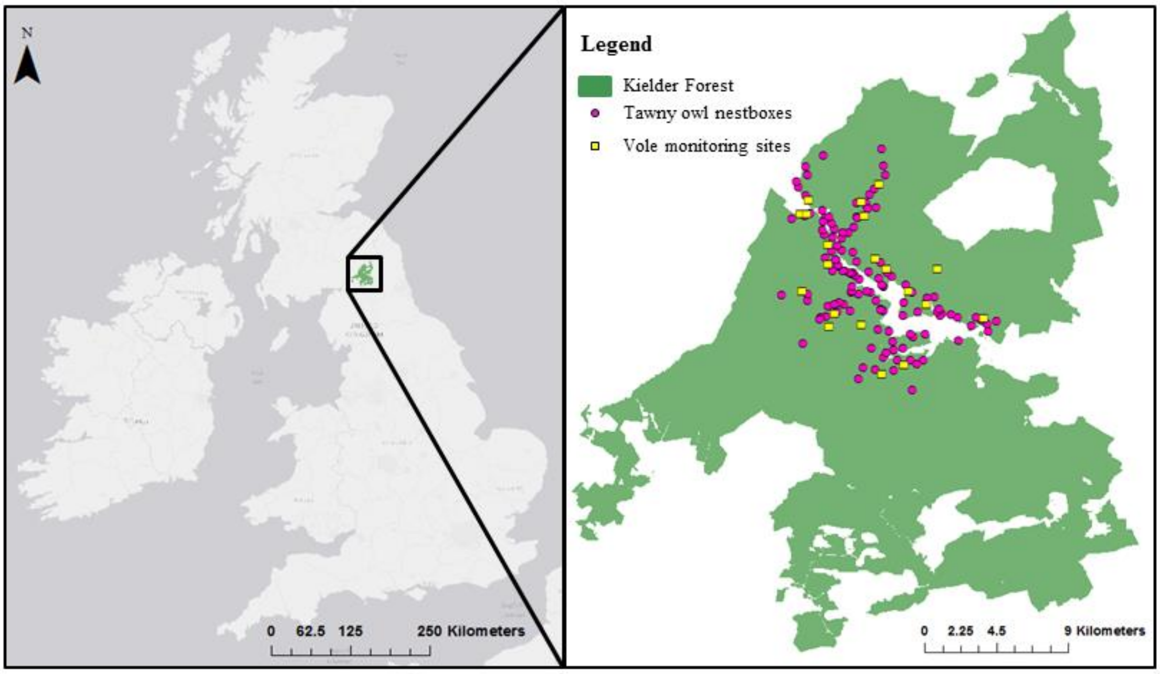

Figure 1. The location of the study site, Kielder Forest in the UK and the locations within the forest where vole densities have been monitored since 1984 and the current location of all tawny owl nest boxes.

In the UK goshawks feed largely on birds, namely pigeons, corvids and grouse and pheasants but also prey on other species, such squirrels and rabbits and occasionally on field voles (Marquiss & Newton 1982; Petty *et al.* 2003). Goshawks are a tree nesting species and generally only breed in large blocks of mature forest in the UK; however they are known to breed in wooded parks in some cities in Europe (Petty 1996). Although goshawks defend the area around the nest site against other goshawks and predator species they have large home-ranges, which are known to overlap with other goshawk pairs (Kenward 1977, 2006; Boal, Andersen & Kennedy 2003).

Tawny owls

Tawny owls are a sedentary, nocturnal, cavity nesting species (Mikkola 1983). In Kielder Forest the occupied tawny owl territories were first identified between 1975-1978 (Petty 1992a; Petty, Shaw & Anderson 1994). The tawny owl population has been continuously monitored since 1979, in a 176 km² central subsection of the study site (Petty *et al.* 1994). As Kielder Forest is managed for timber production, trees do not develop natural cavities, the preferred nest sites for tawny owls. Consequently, in the winters of 1979-1980 owl nestboxes were erected near the centre of each territory. Additional boxes were placed between territories, and in areas which lacked owl territories, such that at any one time there were at twice as many boxes available as there were occupied territories. Within three years of their erection, all tawny owls had switched to using these nestboxes and breeding occurred almost exclusively in nestboxes thereafter (Petty *et al.* 1994). The current location of the 126 owl nest boxes in Kielder Forest is shown in Figure 1. It is possible to ascertain whether a territory is occupied, even when breeding attempts do not take place, by checking for the appearance of a nest cup in the material (spruce needles and soil) lining the bottom of the nestbox. Even when tawny owls do not lay eggs, territorial birds still leave a clearly detectable nest cup and unlike other species which occasionally occupy nest boxes in this study site, tawny owls do not add additional nesting materials to the box. Therefore, if a nest cup appeared, unaccompanied by the addition of other nesting materials it was assumed that the territory was occupied.

Tawny owls can be seen as a vole specialist in Kielder Forest as field voles on average represent 62% of the prey brought to the nest during the breeding season (Petty 1999). Tawny owls have been known to live up to 21 years (Robinson 2005), and in our study site have been known to successfully reproduce at 20 years of age. Tawny owls are sexually dimorphic (females: 520g, males: 420g) and on are average 2-3 times lighter than goshawks (Robinson 2005). Both sexes have distinct reproductive roles; the females incubate and brood chicks until the chicks are roughly two weeks old, during this time the male provides food for both the female and their chicks (Mikkola 1983). Almost all breeding females were caught annually during 1984–2014 (> 90%; Millon *et al.* 2011). Breeding males were also caught, except between 1999-2007. Tawny owls are highly site faithful, remaining in their territory year round and the vast majority of owls stay in the same territory for life once they have started breeding (>98%; Petty 1992). Thus the recapture rate of breeding adults is high (Petty 1992a; Millon, Petty & Lambin 2010; Millon *et al.* 2011). The reproductive success of individuals in the population has also been continuously monitored since 1979. Given nearly all chicks have been ringed since 1981, it is possible to identify whether breeding owls were been born in the study site. Consequently, there is detailed demographic data available on the Kielder Forest tawny owl population from 1980 onwards.

Field voles

Field voles are one of the most common mammals in Europe. They mainly feed on grasses, but also eat other vegetation and are generally found in moist grassy habitats (Zima 1999). Within 2-3 years of an area of forest being felled; clear cuts grass over and become suitable vole habitat and remain suitable for up to 12 years (Lambin, Petty & Mackinnon 2000). These clear cuts and grass verges along forest roads are the main habitat for voles in Kielder Forest. Since the autumn of 1984 field vole densities have been assessed twice a year, in spring (March) and autumn (September) at 17-21 sites within the forest (Figure 1), using sign indices calibrated against the densities of field voles estimated from snap-trapping (for methods see Lambin *et al.* 2000).

Proxies of food availability and predation risk

In natural systems it is difficult to directly measure how much food is available, the amount of predation occurring and the level of predation risk to which individuals/populations are exposed to. Consequently, proxies of food availability and predation/predation risk are inevitably used instead. An essential first step before attempting to understand the role that food availability and predation play in shaping population dynamics and demography was therefore to find suitable proxies for them. Field vole densities seemed an obvious and appropriate proxy for food availability given that: i) field voles are the main year-round prey species for tawny owls (Petty 1999); ii) previous studies on tawny owls have found that reproduction success is strongly correlated with field vole densities (Petty 1987; Millon *et al.* 2014) and experimental studies have shown that reproductive success is tightly associated with food availability (Lenski 1984; Arcese & Smith 1988).

Previous studies have used predator abundance or distance from the preys nest to the nearest predators nest as a proximate measure of predation risk, based on the assumption that predation risk increases along with predator abundance and that individuals living in close proximity to predators have a higher risk of being killed (Kostrzewa 1991; Sergio & Newton 2003; Koning *et al.* 2009). However, before using these two measures of predation risk I wanted to assess whether these were appropriate proxies in our system. To test whether goshawk abundance was a suitable proxy for temporal variation in predation risk, I first sought to establish how much goshawk predation on tawny owls was occurring and establish whether this had changed over the study period as goshawk abundance increased (Chapter 2). I tested the assumption that individuals living in relatively close proximity to goshawks had a higher risk of being killed using tawny owl ring recovery data. The rings of 50 tawny owls ringed in our study site have been recovered in goshawk nest sites (Chapter 3). I used these rings to estimate the distance between the nestbox an owl was last observed using and the goshawk nest site the ring was recovered in, i.e. the distances goshawks travelled to predate owls (Appendix 5a). If the number of tawny owls killed increased along with goshawk abundance and owl ring recoveries indicate that goshawks were mainly killing owls living in close proximity to them, then using these two measures as proxies of predation risk seemed justifiable. However, goshawks are not uniformly distributed across the forest and some owls were living in relatively close proximity to several goshawk nest sites, whilst other owls were not (for a visual description see Figure 2), To take this into account I used a third proxy for predation risk, connectivity of an owls territory to all goshawk nest sites, a measure of predation risk based on both goshawk abundance and the spatial distribution of goshawks across the forest relative to the location of the focal tawny owl nest site (for methods see Appendix 5a).

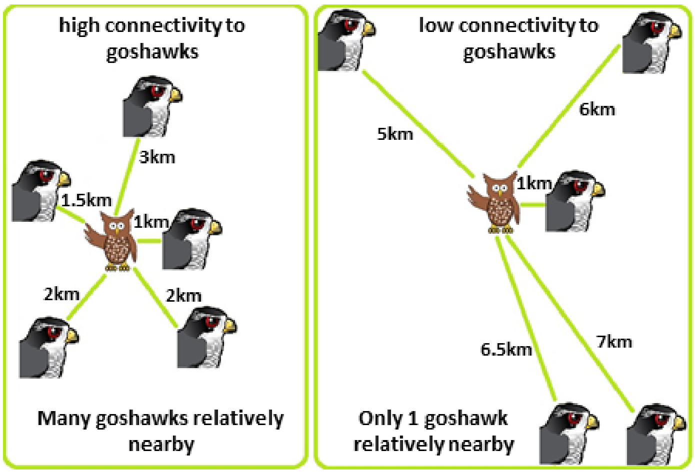

Figure 2. Diagram representing the connectivity of a tawny owl territory to their main predator, northern goshawk. In both the right and left hand side of the diagram the owls have the same number of goshawks nesting around them and the distance to the nearest goshawk nest site is the same. However, the diagram on the left-hand side shows an owl nesting in relatively close proximity to several goshawk nest sites, hence is in a territory which is highly connected to goshawks. Whereas, the diagram on the right-hand side shows an owl nesting in close proximity to only one northern goshawk, hence is in a territory with relatively low connectivity to goshawks.

CHAPTER 2

IS FOOD-LIMITATION CAUSING A RECOVERING POPULATION OF NORTHERN GOSHAWKS *ACCIPITER GENTILIS* TO PREY MORE ON RAPTORS?

Adult goshawk plucking on a partridge

Abstract

Superpredation, the killing of smaller mesopredators by larger superpredators, is thought to play a crucial role in shaping the structure of some communities. One hypothesis put forward to explain the occurrence of superpredation is the food-limitation hypothesis, whereby predators kill smaller mesopredators to make up the shortfall in their diet, when the availability of their preferred prey declines. In theory populations should become increasingly food-limited as population densities increase, due to an increase in competition and depletion of prey. Consequently, if food-limitation influences superpredation rates, then as predator densities increase there should be a per capita increase in predation on mesopredators. Here we use dietary data collected on a recovering population of northern goshawks, a superpredator known to kill other smaller 'mesopredators' to test this prediction by: 1) assessing whether the goshawk population has become food-limited during the colonisation process; 2) determining whether the extent of superpredation occurring has changed as the goshawk population increased. We also quantified the potential impact of goshawk predation on local mesopredator populations, as any impact on mesopredator dynamics could have a cascade effect on lower trophic levels. As goshawks increased in abundance, the reproductive success of the goshawk population decreased and the proportion of goshawk diet comprised of the three main prey species/groups declined. Goshawk diet also became more diverse and the extent of predation on raptors increased over the study period, to such an extent that raptors represented 10% of goshawk diet in terms of abundance by the end of the study period. We posit that these results suggest that as the goshawk population increased, the availability of their preferred prey declined, which forced goshawks to switch to less profitable prey species, such as raptors, which also had a negative knock-on effect on the reproductive success of the goshawk population. We estimated that the number of kestrels, tawny owls and sparrowhawks killed each year by goshawks increased substantially. However, despite this increase in predation, local tawny owl and sparrowhawk populations remained stable, but we posit that increasing goshawk predation on kestrels is at least in part responsible for the local kestrel population declining.

Introduction

Superpredation, defined here as the killing of smaller 'mesopredator' species by larger 'superpredators' (Polis, Myers & Holt 1989) occurs in a wide range of taxa, and is particularly well documented in birds of prey (Mikkola 1976; Sergio & Hiraldo 2008; Lourenço *et al.* 2013). Understanding the mechanisms driving superpredation is important, as superpredation can impact mesopredator population dynamics which then 'cascades' to affect lower trophic levels (Paine 1980). Indeed in some circumstances superpredation is thought to play a crucial role in structuring whole communities and shaping the biodiversity of ecosystems (Palomares & Caro 1999; Caro & Stoner 2003; Ripple & Beschta 2004; and reviewed in Ritchie & Johnson 2009). Yet, despite the far-reaching effects which superpredation can have, it is still not clear what mechanism (or combination of mechanisms) causes one predator to kill another and what drives variation in the prevalence of superpredation in wild populations.

Optimal foraging theory predicts that the energy gained by consuming prey should outweigh the energy used when searching and capturing the prey (MacArthur & Pianka 1966). Thus large and abundant species and those which are relatively easy and of low risk to catch are expected to be preferentially preyed upon by predators. If mesopredators are killed because they are a profitable prey source, then predation rates on mesopredators are predicted to vary according to the size and availability of the mesopredator species. Indeed, based on their body mass alone many mesopredators (which fall within the preferred prey size range of superpredators) should be a profitable prey item for top predators. However, given that the density of mesopredator populations are relatively low compared with other prey species, the time and energy needed to find and capture them presumably makes mesopredators a less profitable prey source (Lourenço *et al.* 2010). Furthermore, capturing and handling other predators may be associated with a higher risk, compared to other prey species, as mesopredators have evolved to kill other species and are equipped with sharp claws, teeth and talons. This might reduce the benefit of preying upon mesopredators and make them a less preferable food source, which are only preyed upon when predators become food-limited, due to their preferred prey being scarce. Thus, one potential explanation for predators killing mesopredators is that they do so to make up the shortfall in their diet (Polis *et al.* 1989; Rutz & Bijlsma 2006; Lourenço *et al.* 2010). Stable populations of predators should become food-limited following a decline in the abundance of their preferred prey species (Rutz & Bijlsma 2006). Alternatively, populations may become food-limited if the abundance of individuals exploiting these preferred food sources increases and leads to an increase in competition for food (Malthus 1798).

Populations of many large predator species are currently increasing in abundance and recovering their former ranges, in both North America and Europe (Maehr *et al.* 2001; Deinet *et al.* 2013; Chapron *et al.* 2014). Consequently, if superpredation is driven by predators being food-limited, then the level of superpredation occurring is predicted to increase as these large predator populations increase in abundance, even if mesopredators are not a preferred prey species. However, whether such an increase in superpredation has actually occurred and whether it coincides with or follows the colonisation process is as yet unknown.

The northern goshawk (*Accipiter gentilis*, hereafter goshawk) is a medium sized raptor, whose diet predominantly consists of birds (mainly Columbiformes, Corvidae, Phasianidae and Tetraonidae), but also includes other predators, such as raptors and owls (reviewed in Rutz *et al.* 2006; Lourenço *et al.* 2010). Although native to the UK, goshawks were extirpated in the late 19th century, largely due to persecution (Marquiss & Newton 1982; Petty 1996). However, scattered populations were subsequently established after birds escaped and were released by falconers in the 1960s and 70s and in some areas the size of these goshawk populations increased rapidly (Marquiss & Newton 1982; Petty & Anderson 1995; Petty 1996). Consequently, the recovery of goshawk in the UK presents an opportunity to test the prediction that superpredation will increase during the colonisation process as goshawk populations expand and competition for preferred food resources increases.

Here we use data collected on a recovering population of goshawks as they first started to colonise Kielder Forest, northern England to evaluate support for the prediction that as superpredator populations recover the concomitant increase in competition for food resources will result in the population becoming food-limited and an increase in superpredation. Goshawks were absent in the forest prior to 1973, therefore goshawks occupying home-ranges in the early part of the study period would presumably have had little competition for food. However, as goshawk population densities increased, goshawks may have started to deplete populations of their preferred prey species. Furthermore, increasing densities of predators may have elicited anti-predator behaviours in their prey, such as spatial or temporal avoidance of risky areas, which could have made the prey more difficult to catch. Both of these processes are likely to result in a reduction in the availability of preferred prey species. In this study we first aimed to determine whether the goshawk population had become food-limited, by examining goshawk diet and the productivity of the population. Our second aim was to use goshawk dietary data to test the prediction that superpredation would increase during the colonisation process. In addition, we also reviewed evidence supporting the other proposed determinants of superpredation in this system. If goshawk predation on mesopredators (and any changes in its prevalence) was sufficient enough to deplete mesopredator populations, it is likely to have a cascading impact on mesopredator prey species. Consequently, the last objective of this study was therefore to quantify the potential impact of goshawk predation on populations of the three raptor species killed most frequently, and determine how this has changed during the colonisation process, by estimating the number of individuals killed by the goshawk population.

Methods

Study system

Goshawks have been continuously monitored in Kielder Forest over an area of 964 km² ever since the first recorded breeding attempt in 1973 (Petty & Anderson 1995). Over the last 41 years approximately 30 home ranges have become occupied by goshawks, and the population has become stable, reaching saturation around the mid-1990s. Each year active goshawk home ranges were located by watching birds displaying over their territories in February and March. Suitable blocks of timber were then searched for active nests, and the location of all nests was recorded. Active goshawk nest sites were visited multiple times (minimum 4) to establish whether a breeding attempt took place and record the number of chicks fledged. The number of chicks that fledged was established either by climbing up to the nest and counting chicks, just prior to fledging or by counting the number of large feathered young in or close to the nest from a suitable vantage point. Many other raptor and owl species have also been monitored in the study site over a long period of time. Counts of territorial pairs of kestrel *Falco tinnunculus,* short-eared owl *Asio fammeus,* long-eared owl *Asio otus* and Merlin *Falco columbarius* have been assessed annually since 1975 (Newton, Meek & Little 1986; Little, Davison & Jardine 1995; unpublished data). In a 176 km² central subsection of the forest tawny owls have also been monitored continuously since 1979 (Petty *et al.* 1994; Millon *et al.* 2014). The number of occupied sparrowhawks *Accipiter nisus* territories has been monitored since 1974 (Petty 1979; Petty *et al.* 1995; unpublished data). Buzzards have been continuously monitored, since they began colonising the forest in 1996, using the same methods described above for monitoring goshawks. For brevity, the term raptor will hereafter be used to refer to all diurnal and nocturnal Falconiformes, Accipitriformes and Strigiformes.

Assessing whether the goshawk population has become food limited

In practice it is difficult to directly measure the extent to which generalist predators are food-limited in wild populations, without doing a comprehensive series of prey abundance surveys. However, several experimental studies in birds found that there was a strong positive correlation between food availability and reproductive success (Hogstedt 1981; Arcese & Smith 1988; Dhindsa & Boag 1989; Siikamäki 1998; Millon, Arroyo & Bretagnolle 2008). Furthermore, a previous study on a stable population of goshawks in the Netherlands found that as goshawks became food limited, following the simultaneous decline in three of their preferred prey species, the reproductive success of the goshawk population declined (Rutz & Bijlsma 2006). Given that reproductive success in goshawks and other bird species is tightly associated with food availability, we proximately assessed whether the Kielder Forest goshawk population had become food-limited during the colonisation process, by examining changes in the reproductive success of the population. The observed decline in the reproductive success of the Dutch goshawk population was mediated by an increase in the proportion of nests which failed (Rutz & Bijlsma 2006). Therefore, we calculated both the proportion of goshawk breeding attempts which failed and the average number of chicks fledged per breeding attempt each year, and then averaged these proportions across 4-5 year time periods. We examined the relationship between the number of occupied goshawk territories and the proportion of goshawk breeding attempts which failed each year and the average number of chicks fledged per breeding attempt using a generalised linear model (GLM) with the appropriate error structure. Unfortunately, it was not possible to determine whether the quality of goshawk offspring has changed during the colonisation period as morphometric data was not available for all chicks.

In addition, we used dietary data to examine whether there had been a decline in preferred prey species in the diet during the colonisation process, as this could also indicate that the goshawk population had become food limited. To characterise goshawk diet, blocks of timber surrounding nest sites were searched multiple times for the remains of prey (feathers, bones and fur) between March-August, 1975-2014, except in 1999-2001, in the same way as described in (Petty *et al.* 2003). When possible the nesting material of active nests was also searched for additional prey remains at the end of the breeding season. Prey remains were removed to avoid double counting in subsequent searches. Prey remains were identified to species level by comparing them with reference collections. We were unable to identify 50 prey items to species level and excluded these from our analysis. It was not always possible to differentiate carrion crow (*Corvus corone*) remains from rook (*Corvus frugilegus*) remains. Therefore in this analysis crow/rook refers to the abundance of both species in the diet. We identified and quantified the minimum number of individuals of medium to large prey species by counting skeletal remains, while small avian prey (less than 100g) were identified and quantified by plucked feathers. Collecting and quantifying dietary data in this way is likely to underestimate the contribution of small prey items to diet, as they are harder to detect (Rutz 2003). However, such species will be relatively unimportant to overall diet in terms of biomass and such a bias is unlikely to vary across years, therefore should not affect the results of our analyses.

Some species and taxonomic groups are known to make up a substantial proportion of goshawk diet. For example, pigeons are the preferred prey for goshawks across most of Europe, comprising between 7- 69% of diet (reviewed in Rutz *et al.* 2006). However, at more northerly latitudes, grouse are the most important prey, comprising almost 80% in some years, and in the south of Europe rabbits are an important prey source (reviewed in Kenward 2006). We therefore categorised prey into the following 6 groups: pigeons (Columbiformes), corvids (Corvidae), game birds (Phasianidae and Tetraonidae); mammals (mainly Lagomorpha, and *Sciuridae*); raptors (Accipitridae, Falconidae, Strigidae) and ‘other’. This ‘other’ group largely consists of passerines, but also includes prey species which are only occasionally preyed on and do not fit into the other categories. We estimated the frequency contribution of each prey species/group to goshawk diet for the entire study period. We also calculated the contribution of each prey species/group to goshawk diet in terms of biomass by multiplying the number of each species killed by its respective body mass and then dividing this by the total value for biomass for all prey items collected over the entire study period. A full list of all the species killed by goshawk and those comprising each prey group can be found in Appendix 3a, along with the body mass used in the biomass calculations.

The number of prey items collected each year ranged from 10 in the early years of the study period, when only a few territories were occupied, to 678 prey items when the goshawk population became stable. Consequently, when analysing whether goshawk diet had changed over time we pooled annual data into two time periods, "colonisation"1975-1996 and "stable" 1997-2014, at the home-range scale. We used 1996 as a cut-off point as the goshawk population was stable by 1996. However, as well as splitting the data into two time periods, we also split it into shorter 4-5 year periods to visually check whether the above cut-off point was influencing our results. In addition, we also examined how the proportion of prey groups in the diet varied with altitude, as prey species such as grouse are mostly found at higher altitudes in our study site, whereas species such as tawny owls and rabbits are mostly found at lower altitudes. Furthermore, the relative contribution of prey groups to breeding season diet has previously been shown to change with altitude, presumably reflecting changes in the abundance and diversity of the prey species available at different altitudes elsewhere in the UK and Europe (Marquiss & Newton 1982; Toyne 1998). Goshawk home-ranges were grouped into three altitudinal categories as follows: 'low' altitude if the nest site was 225m or below; 'medium' if the nest site was between 226-354m; 'high' if the nest site was 355m or above. We used these cut-offs as goshawk home-ranges above 355m tended to be surrounded by more open moorland habitat, whereas home-ranges below 225m tended to be surrounded by more farmland. Unfortunately, we were unable to assess whether changes in goshawk diet were related to changes in the abundance of prey species, as regional population trends for many species were not available.

Several studies have shown that as raptor populations became food-limited, the diversity of their diet increased (Rutz & Bijlsma 2006; Lourenço *et al.* 2010). Consequently, we also compared how diet diversity changed between the two time periods using abundance-biomass-comparison curves (ABC curves; Rutz & Bijlsma 2006; Millon *et al.* 2009). For each of the two time periods, species were ranked from most to least important and then the cumulative contribution of each species to overall diet in terms of abundance and then again separately for biomass were plotted against these ranks.

Quantifying changes in the extent of superpredation on raptors over time

To determine whether the extent of goshawk predation on raptors had changed over the study period, we analysed how the proportion of all raptor species in goshawk diet varied between the two time periods and with altitude, using generalised linear mixed effect models (GLMM) with a binomial error structure. The identity of goshawk home-ranges and year were both fitted as random effects to account for variation in diet between years and between home-ranges. We then repeated this analysis to see whether the proportion of goshawk diet comprised of each of the most commonly preyed upon raptor species (kestrel, tawny owl and sparrowhawk; Petty *et al.* 2003) had changed over time in our study site.

Potential impact of goshawk predation on raptor populations

To quantify the impact of goshawk predation on local kestrel, tawny owl and sparrowhawk populations, and determine whether this changed over the study period we estimated the average number of individuals of each species killed per pair of goshawks every year for each of the two time periods, using the same equation as Petty *et al.* (2003).

$$IK = (CF + CM + CY) * (PT)/ M$$

IK is the estimated number of individuals killed by a pair of goshawks between March and August (184 days). CF = estimated total food consumption of a female goshawk during the breeding season (189g of food per day * 184 days). CM = total food consumption of a male goshawk during the breeding season (133g of food per day * 184 days). The daily food consumption values used for male and female goshawk are the same as those used by Petty *et al.* (2003), originally calculated by Kenward *et al.* (1981). CY = total food consumption of young goshawks during the breeding season (161g of food per day (CF+CM/2) * 108 days * mean fledged brood size of breeding pairs). The CY estimate assumes that young goshawk hatch around mid-May and do not leave their natal territory until August and that overall, young goshawks have the same food intake as adults. Although young nestlings require less food than adults, older nestlings require more, such that we assume that when averaged over the entire period their food intake is equivalent to adults. M = average mass of the prey species. We used an average mass of 208g for kestrel (Ratcliffe 1993); 470g for tawny owl and 205g for sparrowhawk (Robinson 2005). PT =

proportion biomass of the prey species in the diet. To reduce any sampling bias in our estimate of the proportion biomass of each of the three mesopredator species in the diet for each period, we used a bootstrapping approach. We randomly sampled (with replacement) the dietary data collected in occupied goshawk home ranges in a particular year within that period and then calculated the proportion of goshawk diet comprised of each of the three raptor species for this random sample. We repeated this process 500 times for each period and then calculated the average proportion of these replicates for each of the two time period. This average proportion was then used in the above equation to calculate the number of individuals of each species eaten during the breeding season by a goshawk pair. To get an estimate of the total number of each species killed each year by the entire goshawk population, we multiplied our estimate of the number of individuals killed by a pair of goshawks (IK) by the average number of home ranges occupied by goshawks in that time period. As the area over which the local tawny owl population is monitored is smaller than the goshawk monitoring area, to estimate the number of tawny owls killed each year we only used dietary data collected from goshawk home ranges within 5.8km of the owl monitoring area, which we hereafter refer to as the core study area. The distance of 5.8km was selected as it is 85% of the maximal distance between the nestbox an owl was last observed using and the goshawk nest site that the ring of a predated tawny owl was recovered in. We assumed that this distance roughly reflects the distance goshawks travel when foraging in Kielder Forest. The mean fledged brood size of goshawks nesting in the entire study area was 2.05 in the early period, 1.19 in the later period and 1.72 over the entire study period, whereas in the core study area the mean fledged brood size was estimated to be 2.08, 1.27 and 1.54 in the early, late and entire study period respectively.

Descriptive statistics are presented as the mean ± SD. GLMM analyses were carried out using the *lme4* package (Bates *et al.* 2014) in R version 3.0.3 (R Core Development Team 2014). Model selection was based on Akaike's information criterion corrected for small sample size, AICc (Burnham & Anderson 2002).

Results

Assessing whether the goshawk population has become food-limited

Variation in the reproductive success of the goshawk population

The reproductive success of the goshawk population declined over the study period, in terms of both the proportion of breeding attempts which were successful and the number of chicks fledged per breeding attempt (Figure 3). The percentage of breeding attempts which were successful declined by 15%, from 73.31 ± 26.86% in the early period, to 57.62 ± 11.67% in the late period and was negatively associated with the number of occupied goshawk home-ranges (Figure 4a). The number of chicks fledged per breeding attempt declined by 38% from 2.05 ± 0.78 in the early period to 1.28 ± 0.31 in the late part of the study period and was also negatively correlated with the number of occupied home-ranges increased (Figure 4b).

Quantifying goshawk diet and variation in the contribution of main prey species

In total 7763 prey items were recorded between 1975-2014, almost half of which (48%) were pigeons (Table 1). Wood pigeon and feral pigeon were the most common prey items. In terms of biomass, the percentage of goshawk diet comprised of wood pigeon increased by 6% from 26.06% in the early period to 30.50% in the later period, whereas the percentage of goshawk diet comprised of feral pigeon decreased by 9% from 18.48% to 9.20%. Corvids and game were the two next most common prey groups making up 19.15% and 15.55% of goshawk diet in terms of biomass, respectively. In terms of frequency, the proportion of game and pigeon in the diet averaged over 4-5 year periods gradually declined over the study period, whereas the proportion of corvids in the diet increased until the mid-1990s and then declined thereafter (Figure 5). In terms of biomass the percentage of goshawk diet comprised of pigeons, corvids and game also declined between the two periods, by 4.8%, 3.7% and 6.4% respectively (Table 1). The decline in pigeon in the diet was driven by a decline in feral pigeon.

Crow/rook and jay ranked within the top-10 most important prey species, both in terms of biomass and frequency (Table 2). The proportion of goshawk diet comprised of crow/rook decreased by 5% from 18.88% in the early period to 13.95% in the late period (Table 1). There was no apparent difference in the proportion of corvids in the diet of goshawks occupying home-ranges in different altitudinal categories. However, goshawks occupying home-ranges at higher altitudes had a lower proportion of pigeon and a relatively high proportion of game birds in the diet compared to goshawks nesting at lower altitudes (Figure 5b and d). The higher proportion of game in the diet at relatively high altitudes was driven by a higher proportion of red grouse in the diet.

Figure 3. The decline in the reproductive success of the Kielder Forest goshawk population averaged over 4-5 year time periods between 1975 and 2014 in terms of a) the proportion of breeding attempts which were successful b) the averaged number of chicks fledged per breeding attempt.

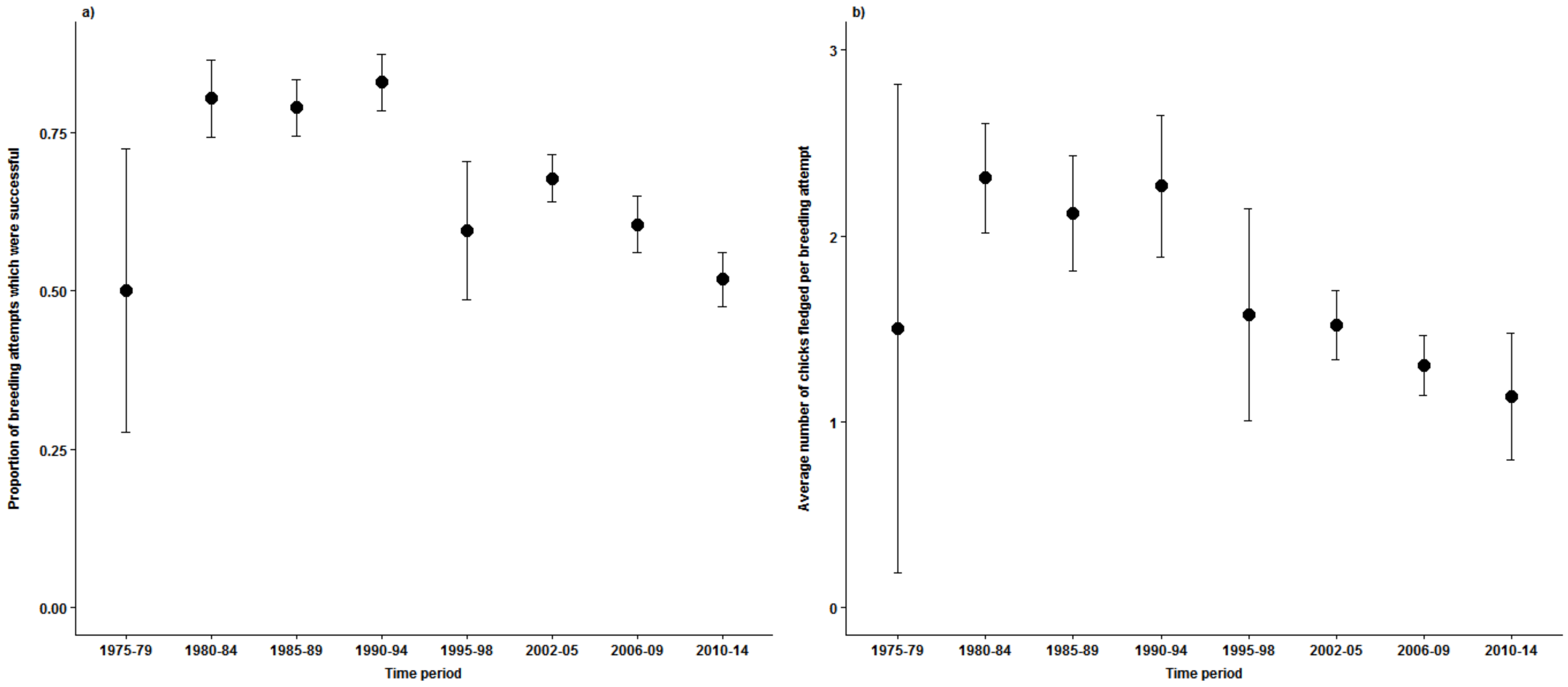

Figure 4. The decline in the breeding success of the Kielder Forest goshawk population as the number of occupied goshawk home-ranges increased. Point size is proportional to the number of breeding attempts (range: 1–33). a) shows the decline in the proportion of breeding attempts which were successful. b) shows the decline in the average number of goshawk chicks fledged per breeding attempt.

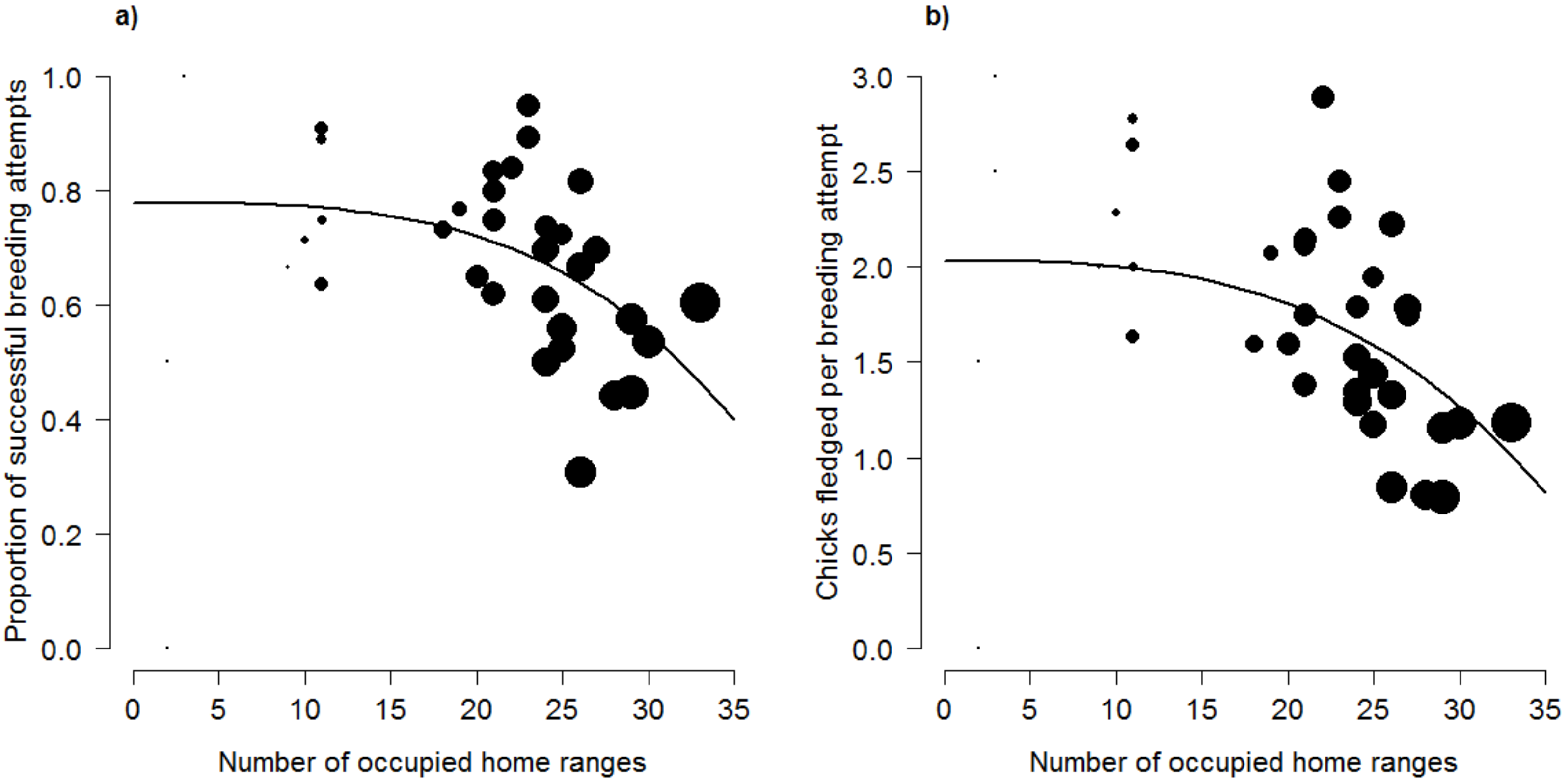

Table 1. Overall proportion of northern goshawk diet made up different prey groups. Total refers to goshawk dietary data collected over the entire study period (1973-2014), whereas early and late respectively refer to dietary data collected between 1973-1996 and 1997-2014.

Prey group	*n*			% Biomass			% Frequency		
	Total	Early	Late	Total	Early	Late	Total	Early	Late
Pigeon (Columbidae)	3724	2953	771	43.37	44.53	39.72	47.97	50.57	40.07
Corvid (Corvidae)	1379	1062	317	19.15	20.04	16.33	17.76	18.19	16.48
Game (Phasianidae, Tetraonidae)	748	642	106	15.55	17.10	10.67	9.64	11.00	5.51
Mammal	541	365	176	14.08	12.59	18.78	6.97	6.25	9.15
Raptor (Accipitridae, Falconidae, Strigidae)	465	262	203	4.35	2.90	8.91	5.99	4.49	10.55
Other	906	555	351	3.50	2.84	5.59	11.67	9.51	18.24
Total	7763	5839	1924	100	100	100	100	100	100

Figure 5. Changes in the proportion of goshawk diet (in terms of frequency, between March and August) comprised of a) raptors; b) pigeon; c) corvids; d) game birds; e) mammals; f) other species over the study period as the goshawk population colonised Kielder Forest. Error bars are the 95% confidence intervals.

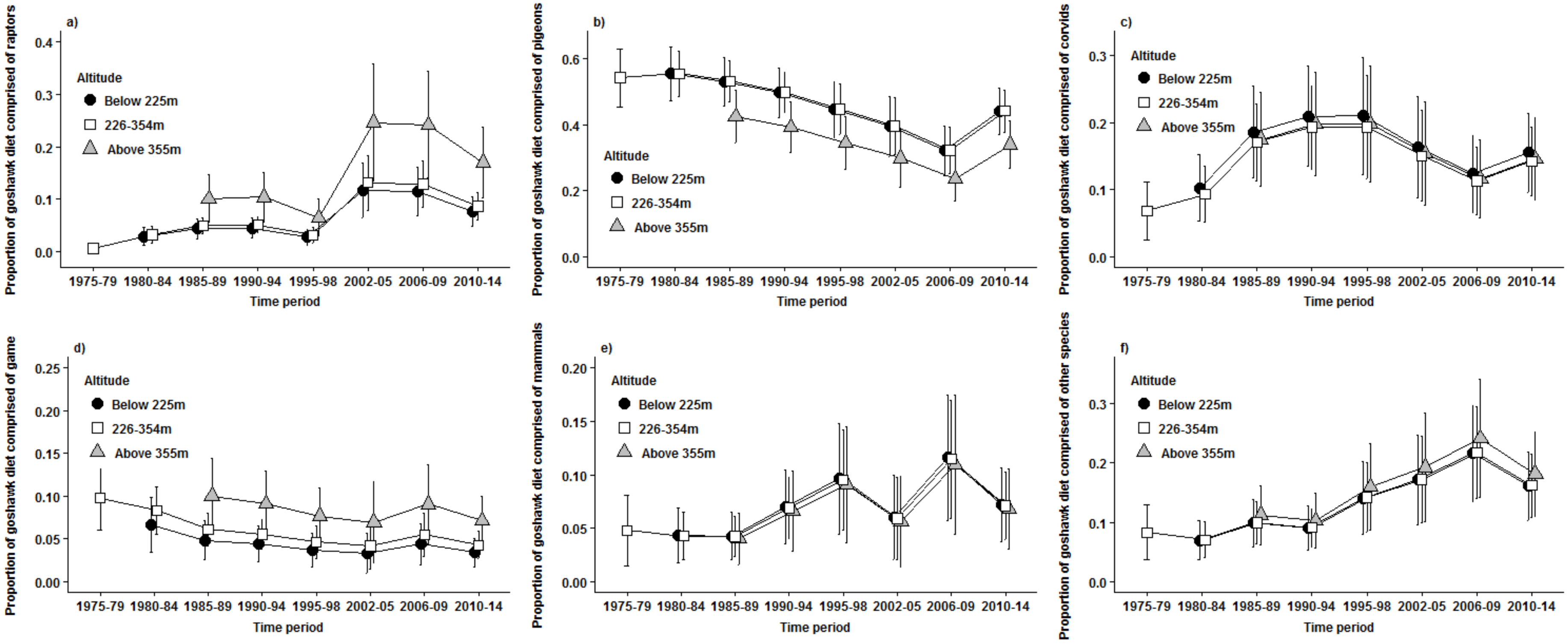

Table 2. The 10 most important prey species in northern goshawk breeding season diet, in terms of both biomass and abundance in both the early (1975-1996) and late (1997-2014) part of the study period, ranked in order of decreasing importance from 1-10.

Species rank	Biomass		Species rank	Frequency			
	1975-1996	1997-2014		1975-1996	*n*	1997-2014	*n*
1.	Wood pigeon (*Columba palumbus*)	Wood pigeon	1.	Feral pigeon	1522	Wood pigeon	530
2.	Crow/rook	Rabbit	2.	Wood pigeon	1431	Feral pigeon	240
3.	Feral pigeon (*Columba livia*)	Crow/rook	3.	Crow/rook	915	Crow/rook	214
4.	Red grouse (*Lagopus lagopus scotica*)	Feral pigeon	4.	Red grouse	561	Red squirrel	87
5.	Rabbit (*Oryctolagus cuniculus*)	Red grouse	5.	Rabbit	172	Mistle thrush	85
6.	Pheasant (*Phasianus colchicus*)	Pheasant	6.	Kestrel	151	Jay	81
7.	Kestrel (*Falco tinnunculus)*	Tawny owl	7.	Mistle thrush (*Turdus viscivorus*)	115	Rabbit	80
8.	Red squirrel (*Sciurus vulgaris*)	Red squirrel	8.	Red squirrel	108	Kestrel	77
9.	Tawny owl (*Strix aluco*)	Kestrel	9.	Song thrush (*Turdus philomelos*)	105	Red grouse	70
10.	Jay (*Garrulus glandarius*)	Jay	10.	Jay	95	Song thrush	10

Red grouse and pheasants were consistently in the top-10 most important prey species, in terms of biomass (Table 2). The percentage biomass of grouse in goshawk diet decreased by 7%, from 13.61% in the early period to 5.37% in the late period, whereas the percentage of pheasant in the diet increased from 2.98% to 5.17%. The contribution of mammals to goshawk diet increased by 6% from 12.59% to 18.78% in terms of biomass between the two time periods (Table 1). There was no evidence to suggest that the proportion of mammals in the diet (in terms of frequency) varied according to the altitude of the goshawk home range (Figure 5e). Rabbit and red squirrel were the only mammal species which ranked within the top-10 prey species. The importance of red squirrels to goshawk diet in terms of biomass remained the same between the two study periods. However, the importance of rabbits in the diet increased from rank 5 (11% of diet) to rank to 2 (16% of diet; Table 2). The average proportion of other prey species in the diet gradually increased over the study period until around 2010 in terms of frequency, but did not vary according to the altitude of the goshawk home range (Figure 5f). The difference in the abundance and biomass contribution of the different prey groups to goshawk diet between spring and summer months can be found in Appendix 3b. The ABC curves differ between the two study periods, particularly in terms of abundance and indicate that the diversity of goshawk diet increased between the early and late part of the study period (Figure 6).

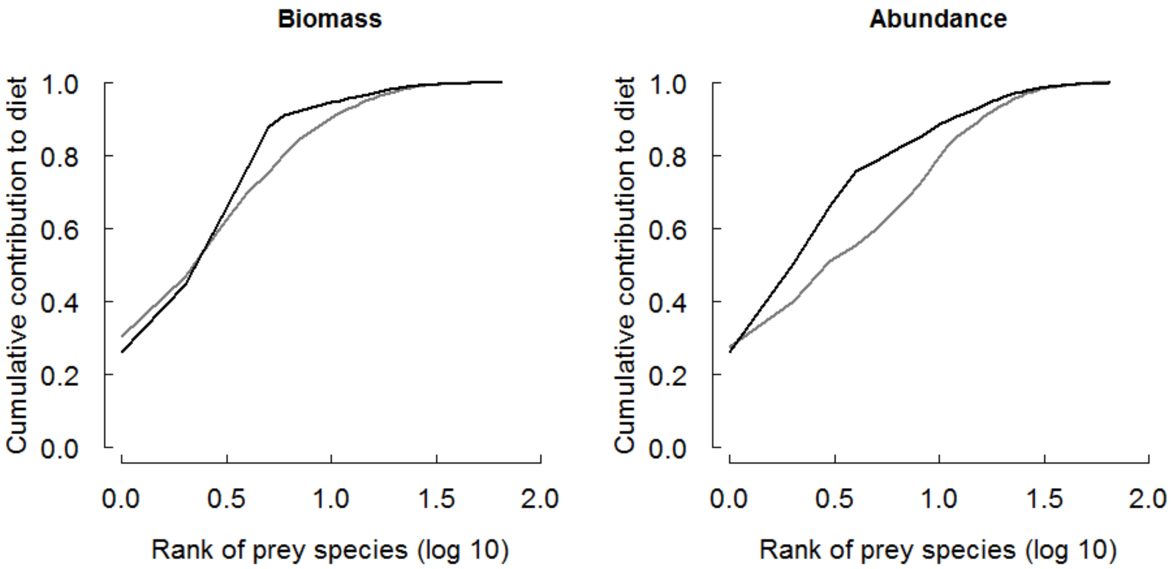

Figure 6. Changes in the diversity of northern goshawk diet in the breeding season (March-August), between the early (1975-1996, black line) and late (1997-2014, grey line) part of the study period using ABC curves in terms of both biomass and abundance.

Quantifying changes in the prevalence of superpredation on raptors over time

Overall raptors comprised 5.99% (645) of all identifiable prey killed by goshawks and 4.35% of prey in terms of biomass (Table 1). The percentage of goshawk diet comprise of raptors increased by 6% from 2.9% to 8.91% in terms of biomass. In terms of frequency, variation in the proportion of goshawk diet comprised of raptors was best modelled with an interaction between altitude and time period (Table 3). The contribution of raptors to goshawk diet was greater in home-ranges in the highest altitudinal category (above 350m), and at this altitude the proportion of raptors in the diet did not change between the two time periods. In contrast, in home-ranges at lower elevations, the contribution of raptors to diet increased between the two study periods, such that in the late part of the study period, the proportion of raptors in the diet was similar in all altitudinal categories (Figure 7a). The higher proportion of raptors being killed at high altitudes was driven by kestrels (see Appendix 3c). Variation in the proportion of goshawk diet comprised of raptors showed a gradual increase and was also higher at high altitudes, when examined over a 4-5 year time period (Figure 5a). The numbers of all raptor species predated, the percent biomass and frequency contribution to goshawk diet between the early and late time periods is shown in Table 4. Overall, the most commonly predated raptor species was kestrel, which represented almost 50% of the raptors killed by goshawks, however this declined by 20% from 57.63% to 38.12% between the early and late time periods (Table 4). Tawny owls were the second most commonly predated raptor species. Both kestrels and tawny owls were ranked amongst the top-10 most important prey species in terms of biomass (Table 2). Whilst the importance of tawny owls to goshawk diet increased from rank 9 to rank 7, the importance of kestrels decreased from rank 7 to rank 9 (Table 2).

Over the entire study period tawny owls represented 22.8% of all raptors killed by goshawks, however the proportion of all raptors killed which were tawny owls increased from 14.89% in the early part of the study period to 33.17% in the late period (Table 4). Overall tawny owls represented 1.5% and 1.37% of goshawk diet in terms of biomass and frequency respectively (Table 4). The percentage of goshawk diet comprised of tawny owls showed over a 3-fold increase from 0.52% to 3.12% between the two study periods (Figure 8a). There was no evidence of a relationship between the proportion of tawny owls in goshawk diet and the altitude of the goshawk home range (Table 3).

Sparrowhawks were the third most commonly predated raptor species, representing 9.9% of all raptor species killed in the early part of the study period and 10.9% in the late period. The average frequency of sparrowhawk in the diet gradually increased throughout the study period and was highest in the late time period (Figure 8b). There was no apparent difference in the proportion of sparrowhawk in the diet between goshawk home-ranges in different altitudinal categories (Table 3). The change in the proportion of goshawk diet comprised of all raptor species, kestrels, tawny owls and sparrowhawks averaged over 4-5 year time periods can be found in Appendix 3d.

Potential impact of goshawk predation on raptor populations

We estimated that the Kielder Forest goshawk population killed 145 ± CI 2.57 kestrels each year when averaged over the entire study period, this increased 2-fold from 96 ± CI 1.34 kestrels killed to 195 ± CI 4.17 kestrels killed in the early and later part of the study period respectively (Table 5). There was a 10-fold increase in the number of tawny owls killed each year in the core study area, which averaged 12 ± 0.23 in the early part of the study period to 119 ± 2.66 in the late period (Table 5). The number of sparrowhawks killed by the entire goshawk population each year also increased, by 35% over the study period from 15 ± 0.41 to 50 ± 1.16 in the late part of the study period (Table 5).

Figure 7. The proportion of northern goshawks breeding season diet comprised of a) all raptor species and b) kestrels in between 1975-1996 and 1997-2014.

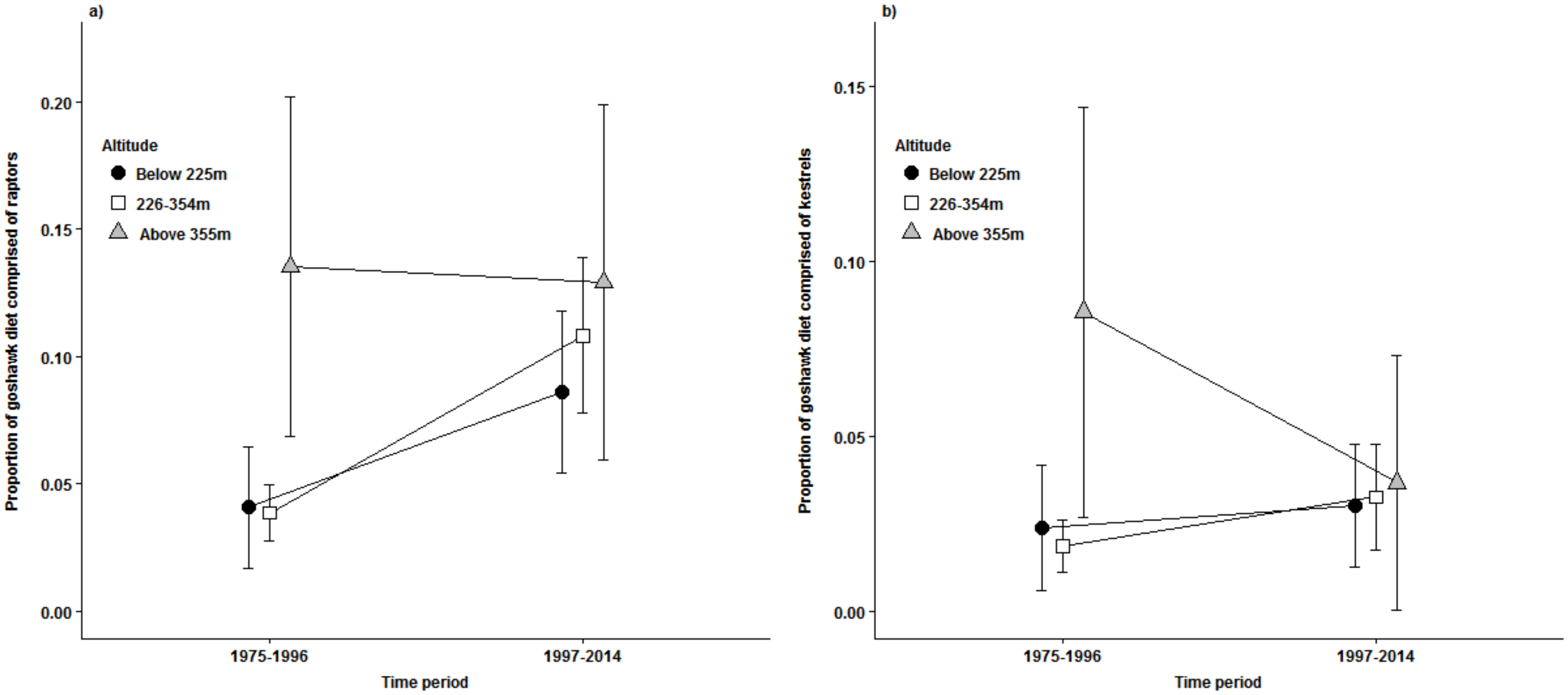

Figure 8. The proportion of a) tawny owls and b) sparrowhawk in the breeding season diet of northern goshawks between 1975-1996 and 1997-2014.

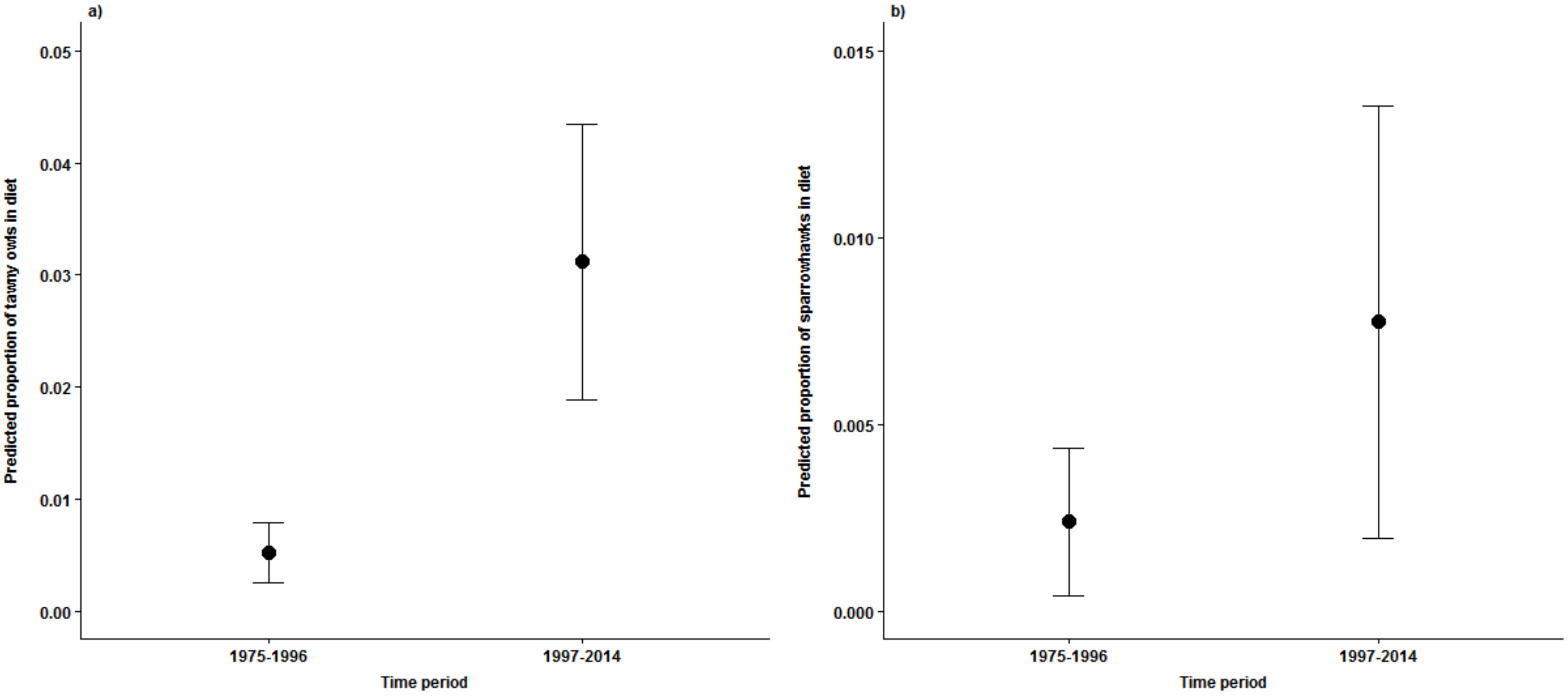

Table 3. Model estimates and selection of variation in the proportion of goshawk diet comprised of all raptor species, kestrels, tawny owls and sparrowhawks between two time period (1975-1996 vs 1997-2014) and three altitudinal categories (below 225m, 226-354m and above 355m). The most parsimonious model is emboldened.

			All raptors				Kestrel				Tawny owl				Sparrowhawk		
	Model	*np*	Estimate	SE	ΔAICc		Estimate	SE	ΔAICc		Estimate	SE	ΔAICc		Estimate	SE	ΔAICc
1.	Null	2			38.70	1.			10.65	1.			30.90	1.			4.42
2.	Time period	4	0.96	0.17	16.70	2.	0.36	0.001	10.37	**2.**	**1.82**	**0.27**	**0**	**2.**	**1.18**	**0.45**	**0**
3.	Altitude (226-354m)	5	-0.01	0.19	25.15	3.	-0.18	0.26	1.48	3.	0.15	0.35	34.48	3.	-0.20	0.49	4.94
	Altitude (above 355m)		0.95	0.28			0.96	0.38			0.36	0.52			0.92	0.76	
4.	Altitude (226-354m)	6	0.11	0.18	4.63	4.	-0.11	0.26	1.53	4.	0.37	0.34	2.75	4.	0.07	0.50	1.42
	Altitude (above 355m)		0.96	0.27			1.01	0.38			0.45	0.52			1.03	0.76	
	+ Time period		0.93	0.17			0.36	0.25			1.87	0.28			1.09	0.45	
5.	Altitude (226-354m)	8	**-0.06**	**0.31**	**0**	**5.**	**-0.25**	**0.38**	**0**	5.	-0.07	0.82	5.53	5.	0.30	0.89	4.89
	Altitude (above 355m)		**1.30**	**0.39**			**1.35**	**0.49**			0.69	1.03			1.61	1.16	
	Time period		**0.80**	**0.35**			**0.25**	**0.46**			1.45	0.84			1.40	0.94	
	Altitude (226-354m) x Time period		**0.31**	**0.35**			**0.33**	**0.47**			0.54	0.89			-0.26	1.01	
	Altitude (above 355m) x Time period		**-0.85**	**0.49**			**-1.14**	**0.72**			-0.40	1.13			-0.95	1.30	

Table 4. Contribution of raptors to the breeding season diet of northern goshawk in Kielder Forest, total refers to the period between 1973-2014, early refers to the period 1973-1996, whilst late refers to 1997-2014.

Species	*n*			% Biomass			% Frequency			% of raptors		
	Total	Early	Late	Total	Early	Late	Total	Early	Late	Total	Early	Late
Common kestrel (*Falco tinnunculus*) [d]*	228	151	77	1.46	1.27	2.05	2.94	2.59	4.0	49.03	57.63	38.12
Tawny owl (*Strix aluco*) [n]*	106	39	67	1.53	0.74	4.03	1.37	0.67	3.48	22.80	14.89	33.17
Sparrowhawk (*Accipiter nisus*)[d]	48	26	22	0.30	0.22	0.58	0.62	0.45	1.14	10.32	9.92	10.89
Short-eared owl (*Asio flammeus*)[d]*	23	22	1	0.23	0.29	0.04	0.30	0.38	0.05	4.95	8.40	0.50
Barn owl (*Tyto alba*)[n]*	14	0	14	0.13	0.00	0.54	0.18	0	0.73	3.01	0	6.93
Long-eared owl (*Asio otus*)[n]*	17	6	11	0.15	0.07	0.41	0.22	0.10	0.57	3.66	2.29	5.45
Merlin (*Falco columbarius*)[d]	14	13	1	0.09	0.11	0.03	0.18	0.22	0.05	3.01	4.96	0.50
Northern goshawk (*Accipiter gentilis*)[d]	13	5	8	0.40	0.20	1.02	0.17	0.09	0.42	2.80	1.91	3.96
Common buzzard (*Buteo buteo*)[d]	2	0	2	0.05	0.00	0.23	0.03	0	0.1	0.43	0	0.99

[d] = species which are predominantly diurnal

[n] = species with are nocturnal

* Denotes raptor species which are dependent on voles

Table 5. Estimated number of kestrels and sparrowhawks killed during the breeding season (March-August) by the entire goshawk population each year and the number of tawny owls killed by goshawks nesting in the core area of the study site in the early (1975-1996) and late (1997-2014) part of the study period. Total refers to the number of each species killed averaged over the entire study period.

Species	Time period	Estimated % biomass of goshawk diet	CI	Average number killed per pair	Number of occupied goshawk territories	Estimated total killed each year	Lower CI	Upper CI
Kestrel	Early	1.49	0.02	6.81	14.05	95.58	94.25	96.92
	Late	1.98	0.04	7.74	25.19	195.00	190.83	199.17
	Total	1.81	0.03	7.74	18.74	144.99	142.42	147.57
Tawny owl	Early	0.97	0.02	1.98	5.81	11.50	11.27	11.68
	Late	6.38	0.14	10.85	11.00	119.37	116.71	122.02
	Total	3.89	0.13	7.12	7.91	56.29	54.42	58.17
Sparrowhawk	Early	0.23	0.01	1.05	14.05	14.75	14.34	15.15
	Late	0.50	0.01	1.97	25.19	49.73	48.58	50.89
	Total	0.40	0.01	1.74	18.74	32.68	31.88	33.49

Discussion

The reproductive success of the goshawk population both in terms of the number of breeding attempts which were successful and the average number of chicks fledged per breeding attempt declined over the study period as the number of occupied goshawk territories increased, suggesting that reproduction in this population is density dependent. The principal prey species for goshawk in Kielder Forest were wood pigeon, feral pigeon, crow/rook, red grouse and rabbit. The percentage of goshawk diet comprised of the three main prey groups (pigeons, corvids and game), all declined over the study period, whereas the percentage of mammals and raptors increased. Goshawk diet was more diverse in the later part of the study period compared to the early part. Goshawks nesting in home-ranges at relatively high altitudes had a greater proportion of game and raptors in the diet and a lower proportion of pigeon compared to goshawks nesting at lower elevations. Goshawks killed a minimum of 465 raptors between 1975-2014, and the overall percentage of goshawk diet comprised of raptors was 5.99% in terms of abundance and 4.35% in terms of biomass. Kestrel was the most commonly predated raptor species, followed by tawny owl, then sparrowhawk. The contribution of raptors, kestrels, tawny owls and sparrowhawks to goshawk diet all increased over the study period, as the number of occupied goshawk home-ranges increased and was highest after the goshawk population had become stable.

Evidence suggesting the goshawk population has become food limited

Overall, our results suggest that goshawk diet has changed during the colonisation process. Together the decline in the three main prey groups (pigeon, game, corvid) in goshawk diet and the increase in the diversity of goshawk diet between the two periods could plausibly reflect that the amount of preferred prey available has declined and goshawks are making up this shortfall in their diet by switching to alternative prey (Rutz & Bijlsma 2006). In the north east of England breeding bird surveys suggest that both carrion crow and rook populations have declined (by 9% and 21% respectively) since 1995 (Baillie *et al.* 2014). This could in part explain the observed decline in corvids in the diet after 1995. The decline in pigeon and grouse in the diet was driven by a decline in feral pigeon and red grouse respectively. Unfortunately, regional population trends for feral pigeon and red grouse are not available. As a plantation, the majority of feral pigeons in Kielder Forest are likely to be stray racing pigeons. Pigeon racing is a traditional pastime in the north east of

England, however the Royal Pigeon Racing Association (RPRA) reported a decline in the number of people participating in the sport, the number of races and number of entrants over the years (RPRA 2012). Fewer birds being raced may lead to fewer strays ending up in the forest, which could account for the decreasing proportion of feral pigeons in the diet. There is also anecdotal evidence to suggest that the numbers of all game species in the area have decreased (Martin Davison, personal communication). Consequently, we posit that the decline in three main prey species in the diet (feral pigeon, red grouse, and crow/rook) reflects a local decline in the abundance of these prey species, hence fewer preferred prey species being available per goshawk pair. We also suggest that the increase in diet diversity is the result of goshawks switching to alternative prey to make up the shortfall in their diet, as another study on goshawk diet reported that the diversity of goshawk diet increased, following a decline in the abundance of three main prey species (Rutz & Bijlsma 2006).

In line with our prediction, as the number of occupied home-ranges increased there was a substantial decline in the reproductive success of the goshawk population (both in terms of an increase in the proportion of nesting attempts failing and a decrease in the number of chicks fledging), which suggests that goshawk reproduction is density dependent. Experimental studies have shown a strong link between population densities, competition for food resources and reproductive success (Lenski 1984; Arcese & Smith 1988). Therefore we posit that these results suggest that as the goshawk population increased the concomitant increase in competition for food resulted in the goshawk population becoming increasingly food-limited during the colonisation process which had a knock-on effect on the reproductive success of the goshawk populations.

The prevalence of superpredation has increased over time

Whilst reviews of the breeding season diet of goshawk in Europe have suggested that on average only 1.9-2% of goshawk diet was composed of raptors (Rutz *et al.* 2006; Lourenço *et al.* 2010) we found raptors comprised 10.6% of goshawk diet in terms of frequency in the late part of the study period. Hence, the amount of superpredation in Kielder Forest seems exceptionally high compared to elsewhere in Europe. We also found that goshawks living in home ranges at relatively high altitudes had a higher proportion of raptors in the diet, which we suggest might be a result of lower pigeon and crow availability (particularly wood pigeon) in the surrounding area, due to the habitat being more open. As predicted the proportion of raptors in goshawk diet increased over the study period, which in combination with our other results is consistent with the hypothesis that goshawks switch to alternative, less profitable prey species, such as raptors when the availability of preferred prey declines and goshawks become food limited. However, we also discuss the level of support our results give to alterative hypotheses put forward to explain the occurrence of superpredation.

If superpredation is a purely opportunistic process, then changes in the relative frequency of mesopredator species in the diet should reflect changes in mesopredator abundances (Polis *et al.* 1989). Yet, this was not the case in our system. A previous study revealed that as kestrel numbers declined, goshawk killed a progressively greater proportion of the population (Petty *et al.* 2003). Indeed, the contribution of kestrels to goshawk diet was higher in the late part of the study period, despite the kestrel population continuing to decline after 1996, both in the study area and at a national level (Baillie *et al.* 2014 & unpublished data). Moreover, there has been an increase in the proportion of goshawk diet comprised of tawny owls, despite no increase in the number of territories occupied by tawny owls, in the central part of the forest (Millon *et al.* 2014). Furthermore, despite a substantial increase in the abundance of buzzards in the forest (now over 80 home-ranges are occupied, unpublished data), only 2 buzzard chicks were killed by goshawks in the latter part of the study period. We posit that the relatively small amount of goshawk predation on buzzards could in part be due to buzzards being more difficult and risky to capture and kill, as they are a predator of a similar size to goshawks (buzzard M: 780 g F: 1000 g vs goshawk M: 850 g F: 1500 g; Robinson 2005). However, given that variation in goshawk predation on different raptor species did not mirror the population trends of the raptor species in our study site, superpredation does not appear to be a purely opportunistic process.

Previous studies have suggested that the extent to which different mesopredator species are predated depends on how active mesopredators are at the same time as their predators, with species more active at the same time as their predators being killed more often than those which aren’t (Petty *et al.* 2003; Lourenço *et al.* 2010). As 70.5% of all raptors killed were diurnal and therefore active at the same time as goshawks, our results do support this hypothesis. However, nocturnal tawny owls were the second most commonly preyed upon raptor species, representing 33% of all raptors killed by goshawks in the later part of the study period. The latitude of our study site means that in summer nights are relatively short (less than 7 hours of darkness) and tawny owls have been observed hunting during the day in the summer, particularly in years when vole-densities declined during the breeding season and owls had offspring to feed, (Steve Petty, personal communication). Consequently, given the majority of tawny owls were killed between June-August (see Chapter 3), predation on adult tawny owls might have occurred when owls were forced to hunt in daylight. Furthermore, tawny owl chicks are known to make food-begging calls during the day after they have fledged (Petty *et al.* 2003). These food-begging calls could plausibly make fledged chicks conspicuous to goshawks. Consequently, the relatively high proportion of tawny owls killed in summer might be due to goshawk predation on newly fledged tawny owl chicks, as hypothesised by Petty *et al.* (2003).

In contrast to the hypothesis that superpredation is opportunistic, there are two further hypotheses for superpredation which suggest it is an adaptive response to the presence of other predators. The first is the competitor-removal hypothesis suggests that predators kill potential competitors to free up shared prey resources (this hypothesis only applies to a special type of superpredation, called intra-guild predation; Serrano 2000). The second is the predator-removal hypothesis, suggests that predators kill other predators to decrease the probability of either themselves or their offspring being killed (Lourenço *et al.* 2011). Although it is difficult to directly measure competition for resources in wild populations, examining the extent of dietary overlap between species can give some indication of the potential food resources that the two species might compete for. Given 83% of the raptors killed by goshawks were largely dependent on voles, and voles only make up a relatively small proportion (0.06%) of goshawk diet in terms of biomass, our results provide very little support for the competitor-removal hypothesis of superpredation. Owls are known to take a greater proportion of avian prey when vole densities are low (Petty 1999), which in theory would increase the degree of dietary overlap between owls and goshawks. However, the shared prey species are likely to be relatively unimportant to goshawk diet in terms of overall biomass (Petty *et al.* 2003). Our results also do not provide any support for the predator-removal hypothesis, given 97% of the raptors killed by goshawks were of no threat either to adult or juvenile goshawks. Consequently, we conclude that neither the predator-removal nor competitor-removal is the mechanism driving superpredation in this system.

We conclude that the food-limitation is the most likely cause of the increase in superpredation on raptors we observed given that: 1) the decrease in the reproductive success of the goshawk population and decline in three main prey species suggests that the goshawk population has become food-limited; 2) superpredation does not appear to be purely opportunistic, as raptor species are not killed relative to their abundance; 3) there is no evidence supporting the predator-removal hypothesis, as almost all of the raptors killed by goshawks posed no threat to goshawks or their offspring; 4) the extent of dietary overlap between goshawks and the majority of the raptor species they killed makes the competitor-removal hypothesis unlikely.

Potential impact of goshawk predation on tawny owl population dynamics

Our crude estimate of the number of kestrels killed each year by the Kielder Forest goshawk population suggested it had increased from 96 in the early part of the study period to 195 in the late part of the study period. The results of a previous study, specifically investigating the impact of goshawk predation on kestrels in our study site prior to 1996 implicated goshawk predation as a major cause of the decline in the kestrel population (Petty *et al.* 2003). Consequently, it is highly likely that such a large increase in the number of kestrels being killed each year would have had a further negative effect on kestrel populations since then. Indeed as mentioned previously, kestrel populations in and around the study area have continued to decline. Given that an average of only 6 kestrel home-ranges have been known to be occupied in our study site since 2002, our findings support the conclusion of Petty *et al.* (2003) that goshawks are continually removing immigrant kestrels and thus have created a ‘sink’ habitat for kestrels.

We estimated that there was a 10-fold increase in the number of tawny owls killed by the goshawk population in the core-part of the study area where the owl population has been monitored. It is therefore surprising that such a large increase in the number of owls being killed has not resulted in an overall decline in the local owl population (Millon *et al.* 2014). The reason for this is as yet unclear, but given the number of immigrant owls entering the local population has increased in recent years (Millon *et al.* 2014), it could potentially be mitigating the negative impact of goshawk predation on owl population dynamics. However, we also acknowledge that a proportion of the owls killed by goshawks used in this estimate could have originated from owl populations outside of the area or be non-territorial owls, which we are unable to monitor, hence this might also account for the apparent lack of an effect on owl population dynamics. The number of sparrowhawks estimated to be killed each year by the goshawk population increased by 35%. However, as the number of sparrowhawk home-ranges occupied in the late part of the study period (range 7-16) is similar to that estimated between 1974-1979 (range 7-14; Petty 1979), this increase in predation on sparrowhawks appears to be insufficient to impact local population trends.

Overall our analyses suggest that as the goshawk population increased in abundance the reproductive success of the population declined and the proportion of preferred prey species in the diet decreased, which we posit is due to the goshawk population becoming food-limited. We also found that goshawk diet diversified and that the amount of predation on raptors increased during the study period, which we suggest is a result of goshawks making up the shortfall in their diet by switching to alternative prey species, such as other raptors, as the goshawk population became food limited. Consequently, based on these results and an evaluation of alternative mechanisms, we suggest that the most-likely driver of superpredation in this system is food-limitation. We estimated that the number of kestrel; tawny owl and sparrowhawk killed each year by the goshawk population has increased substantially over the study period. Although the increase in predation on kestrels could be responsible for the decline in kestrel populations around the study area, local populations of tawny owls and sparrowhawks appear to have remained stable, in spite of this increase in predation. The reasons for this are not clear; however an increase in the number of immigrants entering the owl population could be helping to mitigate the impact of increased predation on tawny owls. Now that the level of predation on each raptor species has been quantified, they can be used to assess how the structure of the whole raptor community has changed as goshawks colonised the forest, and predict how other mesopredator populations and guilds will be affected in areas where goshawks are only just starting to recover.

Acknowledgements

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CHAPTER 3

AGE AND SEX-SELECTIVE PREDATION MODERATE THE OVERALL IMPACT OF PREDATION

Brood of goshawk chicks in the nest

Abstract

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. Using recoveries of ringed tawny owls (*Strix aluco*) predated by 'superpredators', northern goshawks (*Accipiter gentilis*) as they colonised 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. 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 of predation 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. The actual changes in owl population size and structure, observed during goshawk colonisation 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. 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.

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 four-fold decrease in prey abundance (reviewed in Ritchie and 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 many communities is currently changing as species distributions shift in response to climate (Walther *et al.* 2002) and with the restoration of ecosystems (Maehr *et al.* 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 reproductive values (i.e. 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 alone. Furthermore, depending on the mating system of the prey species, sex-selective predation has the potential to destabilise predator-prey dynamics (Boukal *et al.* 2008). Therefore, in some circumstances sex-selective predation will also 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 *et al.* 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 & Pletscher 2001; Wright *et al.* 2006).

‘Superpredation’ is a special type of predation where larger ‘superpredators’ kill smaller ‘mesopredators’ (Lourenço *et al.* 2013). 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. Given that mesopredators play an important role in the top-down control of ecosystems, the impact that superpredators can have on mesopredator demography can also ‘cascade’ to effect 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 colonisation 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 *et al.* 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 in tawny owls the relative contribution of each owl age class to λ is likely to vary. Therefore goshawk predation on 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. First, 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 *et al.* 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 this 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.

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 nestboxes which were provided in excess to the number of potential territories in a 176 km² central subsection of the forest (Petty *et al.* 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 1992); 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 four 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 six 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). 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 (Figure 9). On average goshawks (females: 1500g, males: 850g) are 2-3 times heavier than tawny owls (females: 520g, males: 420g; Robinson 2005) 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 $64km^2$ ± SE 16 (Boal *et al.* 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 nestbox last used by an owl to the goshawk nest site that the owl ring was recovered.

Age and sex-selective predation analyses

To determine whether goshawk predation was selective, the age and sex-selective pattern of rings recovered from goshawk nest sites were compared to those from other causes of mortality, 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 on adult owls.

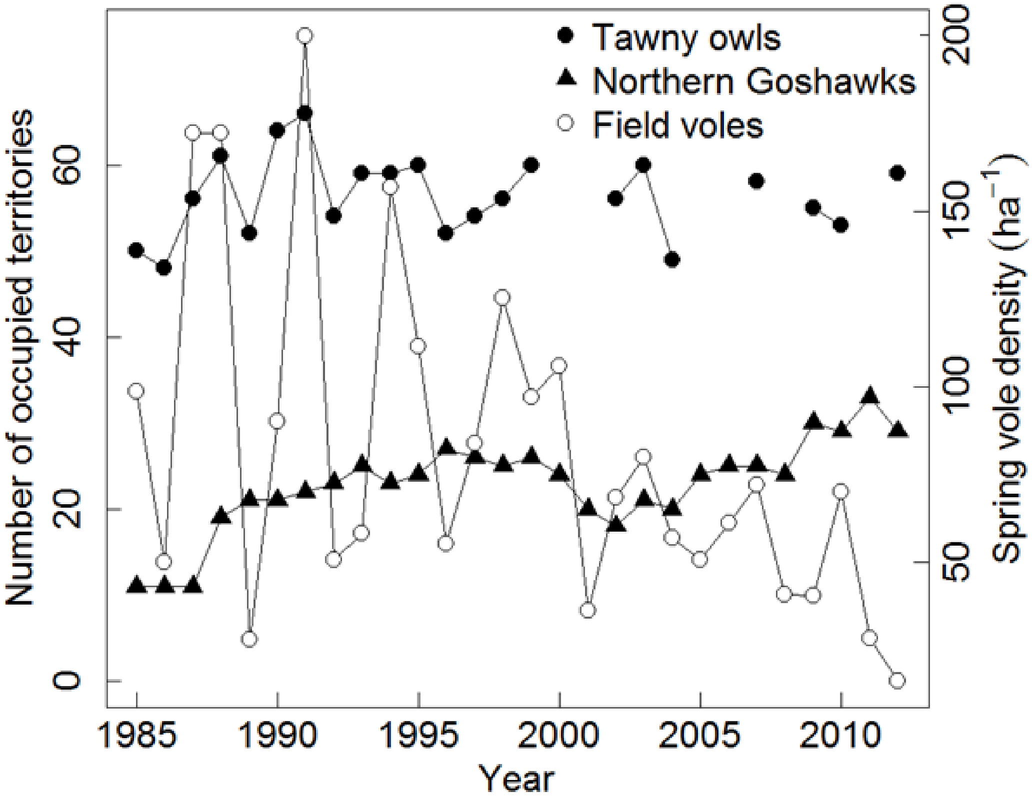

Figure 9. Among-year variation in the estimated number of territories occupied by tawny owls and northern goshawks, and field vole densities in spring (March-April) in Kielder Forest, UK.

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 4a, 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 owl’s age at death using generalised 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 was repeated using owls that died as adults only.

Simulated impact of selective predation

A post-breeding population matrix model with 17 age classes (juvenile <1 year old and adults ages 1-16 years old) was parameterised using the survival parameters estimated by Millon, Petty & Lambin (2010) and Millon *et al.* (2011) (see Appendix 4b for details). 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 adult owls (aged 1-8 years old) were removed; 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 six years where owl territory 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, inter-annual variation in the proportion of newly recruited breeders in the population (those which had not recorded breeding previously) and the proportion of local recruits among 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 standardised so as to compare their effect sizes. We hypothesise that goshawk predation mainly occurs during the peak of the goshawk breeding season (June to Aug), as a previous study found that owls occurred most frequently in goshawk diet during these months (Petty *et al.*2003). As this is after owl population size has been measured and recruitment of breeding owls has taken place, any effect of goshawk predation in that year will 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 *et* *al.* 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 Development 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 old 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 in 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 30 (52%) ring recoveries from owls 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 ring recoveries (21 vs 20) from owls dying of other causes of mortality. The age distribution of adult owl rings recovered from goshawk nest sites 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 (Figure 10). The proportion of ringed owls recovered as goshawk kills among all causes of mortality, increased significantly with owl age ($F_{10} = 2.48$, $P < 0.01$), with 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 3 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, (4 females and 8 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 a 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.

Observed changes in owl population size and structure

There was little inter-annual variation in the number of owl territories estimated to be occupied (56 ± 4.07; Figure 9). Variation in the number of occupied owl territories was not associated with either food availability or goshawk abundance and the null model performed best, irrespective of whether the effect of a time lag was included (see Table 6). 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 one year time lag was included (see Table 6). 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 (Figure 12). The proportion of local recruits in the population decreased significantly (F_{26} = -3.15, $P < 0.01$) by 38% from 0.48 ± 0.25 in the first five years of the study period to an average of 0.30 ± 0.19 in the last five 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 (Figure 13).

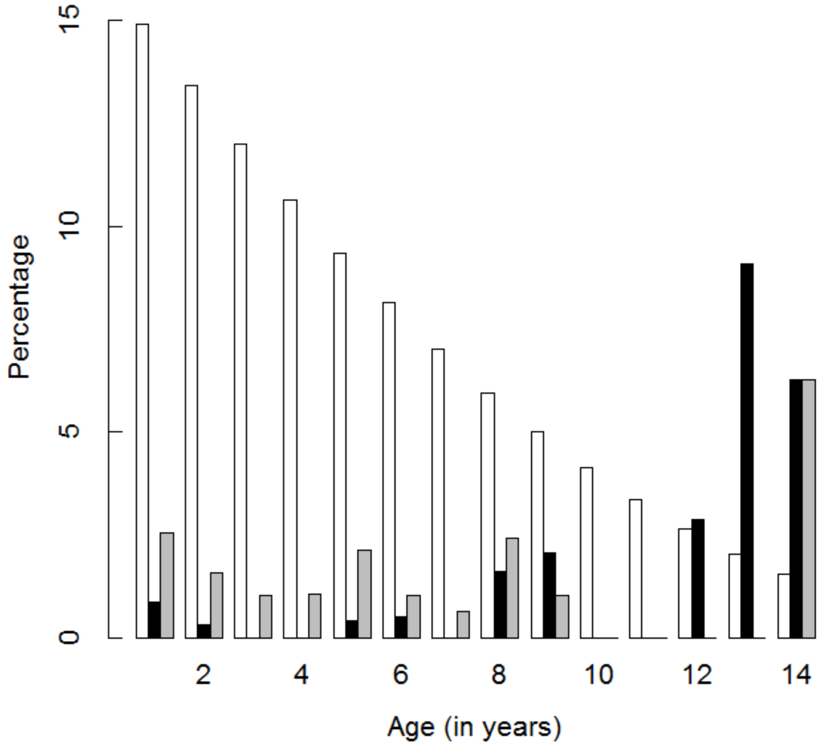

Figure 10. Expected age distribution at equilibrium of adult tawny owls aged 1-14 years predicted by a population matrix model (white bars).The percentage of tawny owls known to reach each age that were predated by northern goshawks or died from other causes are shown by black and grey respectively.

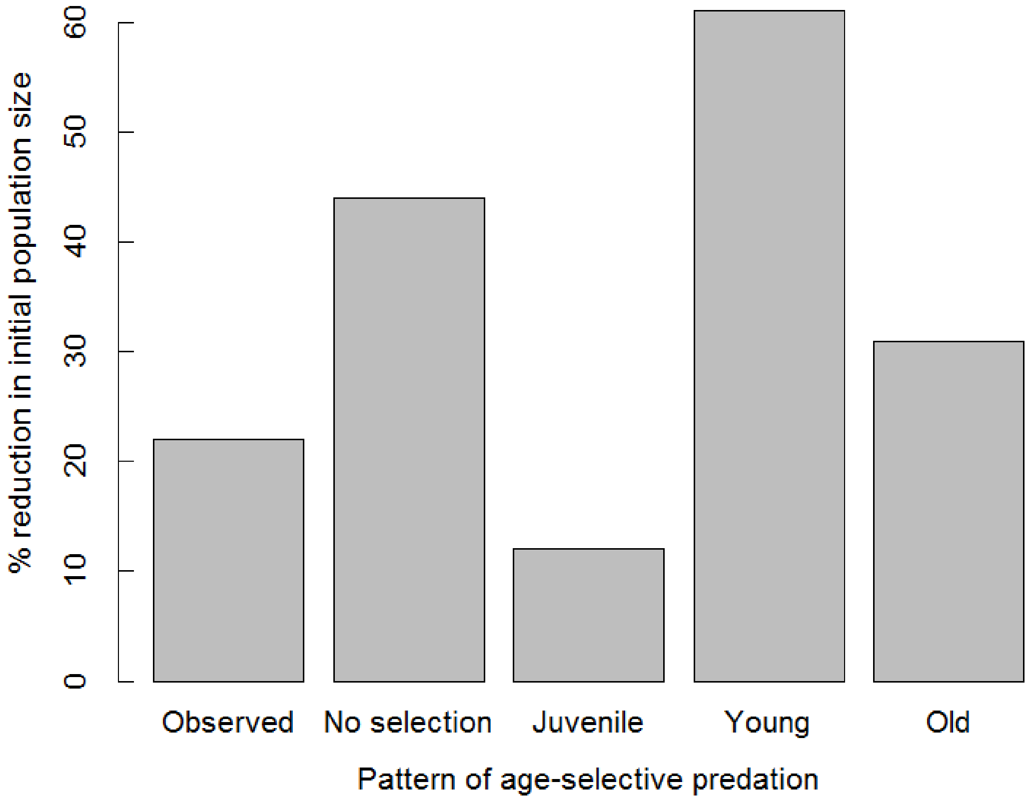

Figure 11. The predicted impact, in terms of the percentage reduction in initial population size for five different patterns of age-selective predation on a theoretical tawny owl population simulation over 20 years. Observed relates to the simulation of the actual pattern of selective predation observed in the study site. Even is the simulated effect of equal predation on all ages; juvenile, the simulation of predation on individuals less than one year old only; young, the simulated effect of even predation on adult owls aged 1-8; old represents even predation on owls aged 9 years and over.

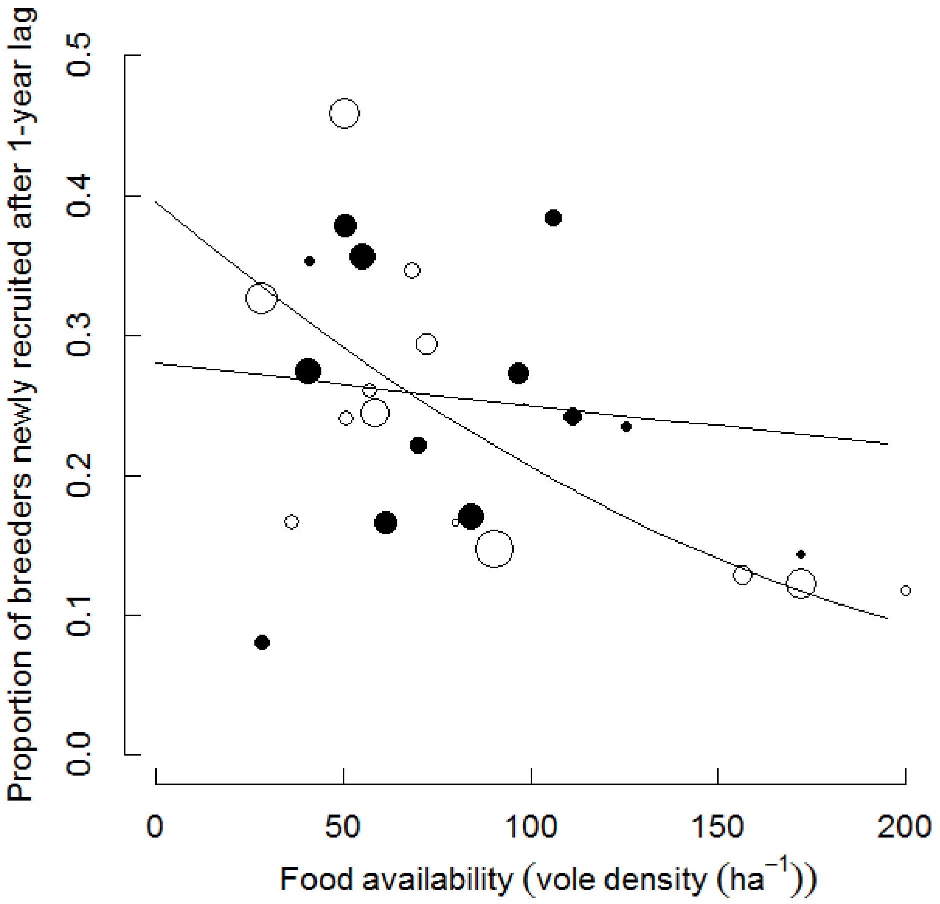

Figure 12. Annual proportion of breeding female tawny owls newly recruited according to mean vole densities in spring the previous year. Solid black points represent proportions when local goshawk abundance was relatively high (10 or more occupied territories) in the previous year. White points represent proportions when goshawk abundance was low (less than 10 occupied territories) in the preceding year. Point size is proportional to the number of pairs breeding in the current year (range: 4-61).

Table 6. 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 one years delayed effect (one 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)			Same year					One year lag effect			
Response variable		Explanatory variable	Estimate	S.E	df	ΔAICc		Estimate	S.E	df	ΔAICc
Owl population size (Number of occupied owl territories)	**1.**	**null**	**-**	**-**	**21**	**0.000**	1.	**-**	**-**	**20**	**0.000**
	2.	food availability	0.041	0.028	20	0.251	2.	0.003	0.029	19	2.443
	3.	total goshawk	0.022	0.029	20	1.829	3.	-0.010	0.029	19	2.347
	4.	food availability +	0.054	0.029	19	1.255	4.	0.001	0.030	18	5.091
		total goshawk	0.039	0.030				-0.009	0.030		
	5.	food availability	0.053	0.030	18	4.266	5.	0.001	0.030	17	8.175
		total goshawk	0.039	0.031				-0.010	0.031		
		interaction	-0.003	0.029				-0.002	0.031		
Recruitment (proportion of breeding females newly recruited)	**1.**	**null**	**-**	**-**	**27**	**0.000**	1.	-	-	26	14.890
	2.	food availability	-0.049	0.071	26	1.843	2.	-0.308	0.094	25	5.640
	3.	local goshawk	-0.008	0.083		2.318	3.	-0.148	0.085	25	14.142
	4.	food availability +	-0.055	0.074	25	4.274	4.	-0.311	0.094	24	4.750
		local goshawk	-0.026	0.086				-0.153	0.083		

a)			Same year					One year lag effect			
Response variable		Explanatory variable	Estimate	S.E	df	ΔAICc		Estimate	S.E	df	ΔAICc
Recruitment (proportion of breeding females newly recruited)	5.	food availability	-0.049	0.076	24	6.815	5.	**-0.279**	**0.100**	**23**	**0**
		local goshawk	-0.020	0.087				**0.026**	**0.105**		
		interaction	0.044	0.099				**0.389**	**0.144**		

b)			Two year lag effect					Three year lag effect			
Response variable		Explanatory variable	Estimate	S.E	df	ΔAICc		Estimate	S.E	df	ΔAICc
Immigration (proportion of newly recruited females born locally)	1.	null	-	-	25	5.496	1.	-	-	24	3.549
	2.	**food availability**	**0.410**	**0.151**	**24**	**0**	2.	**0.347**	**0.146**	**23**	**0**
	3.	total goshawk	-0.113	0.140	24	7.185	3.	-0.187	0.156	23	4.436
	4.	food availability +	0.401	0.153	23	2.458	4.	0.329	0.158	22	2.513
		total goshawk	-0.047	0.142				-0.049	0.170		
	5.	food availability	0.458	0.162	22	3.733	5.	0.343	0.161	21	5.185
		total goshawk	-0.042	0.142				-0.096	0.202		
		interaction	0.253	0.203				0.068	0.157		

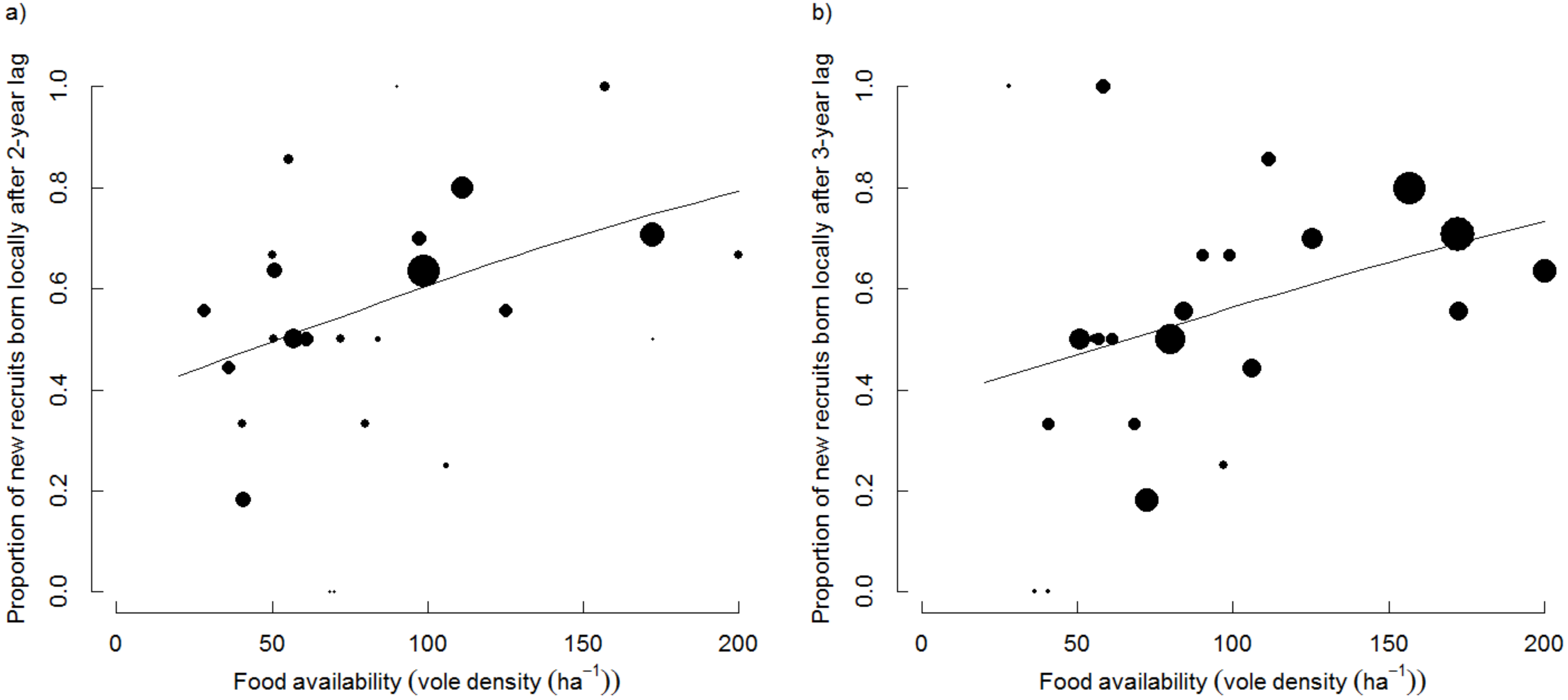

Figure 13. Variation in the proportion of newly recruited breeding female tawny owls which were born locally each year according to mean vole density in spring the previous (a) 2 years (b) 3 years. Point size is proportional to the number of new recruits in the current year (range: 1-22).

Discussion

Goshawk predation on 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 eight 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 the 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 *et al.* 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 *et al.* 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 *et al.* 2008). This result contrasts with 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). Given that 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 nestbox (Sunde *et al.* 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 that 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 (Pietiäeinen, 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 approximately 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 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 on 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 eight years of age, the proportion of all recoveries that were predated was higher than that of other causes of mortality, which 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 nine 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 results in 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 was 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.

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 indicate 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, the risk of owls being predated is also presumably high, 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 *et al.* (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 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.

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CHAPTER 4

INCREASING PREDATION RISK ALTERS THE TRADE-OFF BETWEEN REPRODUCTION AND SURVIVAL FOR SENESCENT INDIVIDUALS

Adult female tawny owl

Abstract

Predation, as a major cause of extrinsic mortality has the potential to shape senescence and drive selection on life-history strategies. Yet, research linking predation to the strength of trade-offs between reproduction and senescence is lacking, despite evidence showing that: 1) reproduction alters the rate of actuarial senescence; 2) predation influences reproductive decisions; 3) vulnerability to predation depends on the age, reproductive status and condition of individuals. Here, we investigate the impact of a recolonising predator (northern goshawk) on age-dependent survival and the reproduction-survival trade-off of a long-lived prey species (tawny owl). Our results suggest that increasing vulnerability to predation with age shaped senescence, as increasing predation risk (goshawk abundance) negatively affected the survival of senescent owls but not of younger individuals. In addition, we provide unique empirical evidence linking the strength of the intrinsic reproduction-survival trade-off with extrinsic mortality. The full extent of the trade-off between reproductive costs accumulated over an individual's lifetime and survival only became apparent when predator abundance increased. Additionally, the impact of predation on survival depended on the reproductive output of the individual, thereby suggesting age-dependent predation may drive selection on life-history strategies.

Introduction

Actuarial senescence, the decline in survival with age, occurs due to the accumulation of somatic damage; damage predominantly caused by oxidative stress reducing the capability of telomeres to protect the ends of chromosomes during DNA replication (Von Zglinicki 2002; Cawthon *et al.* 2003; Hofer *et al.* 2005 and references therein). Due to competing energetic demands, reproduction reduces an individual's allocation of resources to somatic maintenance at the cellular level (Metcalfe & Alonso-Alvarez 2010; Sudyka *et al.* 2014). This intrinsic trade-off between reproduction and maintenance is thought to influence survival and the rate of senescence (Williams 1966). In particular, the level of investment in reproduction in early life has been shown to alter the onset and rate of actuarial senescence, in several wild vertebrate species, such as Townsend's voles (*Microtus townsendii*; Lambin & Yoccoz 2001) and willow tits (*Parus montanus*: Orell & Belda 2002). Additionally, the cumulative effect of experimentally increasing reproductive effort in jackdaws (*Corvus monedula*) throughout their lifetime led to a dramatic, three-fold, increase in mortality in later life (Boonekamp *et al.* 2014). Such studies suggest that the physiological cost of previous reproductive attempts accumulates over an individual's lifetime, exacerbating the effect of ageing on condition, to accelerate senescence in later life, in accordance with general life history theory (Kirkwood & Holliday 1979; McNamara *et al.* 2009).

Understanding how extrinsic factors influence senescence and life-history trade-offs is a central issue in ecology as they will have a knock-on effect on population dynamics. Any impact of extrinsic factors on such trade-offs can have a knock-on effect on population dynamics in the short term and can ultimately act as a selective force on strategies over evolutionary timescales. As a main extrinsic cause of natural mortality in wild populations (Sullivan 1989; Sandercock *et al.* 2011), predation directly impacts survival and it has been suggested that variation in predation pressure can affect the rate of senescence (Williams 1957; Williams & Day 2003; Williams *et al.* 2006). However, Abrams (1993) demonstrated theoretically, that extrinsic mortality can only influence senescence in certain situations, for example if causes of mortality are themselves age-dependent, as later highlighted by Caswell (2007). Given individuals in poor condition are disproportionally predated (reviewed in Temple 1987), vulnerability to predation should increase with age, as somatic condition deteriorates, and should also be conditional on an individual's previous reproductive output. Therefore, age/condition-dependent vulnerability to predation could be one extrinsic factor mediating the trade-off between reproduction and survival in later life. In support of this hypothesis, there is some empirical evidence to suggest that predation is biased towards older individuals (presumably those in poor condition; Spalding & Lesowski 1971; Wright *et al.* 2006; Chapter 3). However, the extent to which age-dependent causes of adult mortality, such as predation, affect senescence and the role predation plays in mediating the trade-off between reproduction and survival in later life have yet to be fully examined.

Here we address this crucial knowledge gap and examine the impact of predation on the pattern of senescence and the strength of the intrinsic trade-off between reproduction and survival in later life using longitudinal data collected on a population of tawny owls (*Strix aluco)* in Kielder Forest (UK), as the abundance of their main predator, northern goshawk, *Accipiter gentilis* dramatically increased. Northern goshawk (hereafter goshawk) dietary data collected in Kielder Forest suggests that there has been over a 4 fold increase in the number of tawny owls killed during the breeding season, from an average of 12 ± CI 0.23 tawny owls killed each year between 1975-1996, when goshawk abundance was relatively low to an average of 119 ± CI 2.66 killed between 1997-2014 when goshawk abundance was high (see Chapter 2). Therefore, we took advantage of the recovery of an important predator of owls (the northern goshawk *Accipiter gentilis*; Chapter 3) and concomitant increase in predation to address the following questions: (1) does age-dependent predation shape adult owl survival? Based on the assumption that predation risk would increase with predator abundance (Chapter 2), and given goshawk predation on adult owls is biased towards senescent female owls (Chapter 3), we predicted that survival of adults in later life would be negatively related to predator abundance. (2) Does predation risk alter the trade-off between reproduction and survival in later life? Assuming the accumulation of reproductive costs over a lifetime increases an individual's vulnerability to predation and influences survival in later life, we predicted that the survival cost of reproduction (the degree to which reproduction at age x reduces the probability of surviving to age x+1) should increase with age for a long-lived iteroparous species like the tawny owl. Furthermore, we also predicted that the impact of increasing predation risk would be more pronounced in individuals investing more in reproduction.

Methods

Study system

Tawny owls are long-lived, territorial, nocturnal predators, which have previously been shown to be senescent after age eight, both in terms of survival and reproduction (Millon *et al.* 2011). Owl survival and reproduction have been continuously monitored since 1979, in a 176 km² central subsection of Kielder Forest, northern England (55°13′N, 2°33′W) using nest boxes (Petty *et al.* 1994). Each year, owl nest boxes were checked for occupancy, to ring chicks and to record the number of chicks that fledged. When chicks were 1-2 weeks old, breeding female owls were trapped using landing nets, yielding 33 years of female recapture data (1980-2013). Tawny owls are highly site-faithful, facilitating high recapture rates (> 90%) and readily estimable survival and reproductive success (Petty 1992a; Millon *et al.* 2011). Unfortunately, it was not possible to estimate age- and cause-specific survival probabilities as unbiased ring-recovery data on cause-specific owl mortality was not available.

Northern goshawks, hereafter goshawks, are diurnal predators, known to frequently predate other birds of prey, such as tawny owls (Mikkola 1976) and selectively predate individuals in poor condition (Kenward 1978). Goshawks were extirpated from the UK in the late 19th century due to persecution; however the species began to recover and recolonize its former range in the 1960s after birds escaped or were released by falconers (Marquiss & Newton 1982). Goshawks have been continuously monitored in Kielder Forest since they began colonising the area in 1973 (Petty & Anderson 1995). Each year occupied goshawk territories were identified and over the last 40 years, the goshawk population has gone from a single pair to approximately 26-33 pairs. Goshawks have large, variable, and overlapping home-ranges, averaging 64km² ± 16 SE (Kenward 1977, 1982; Boal *et al.* 2003). Therefore, goshawk abundance was used as one proxy of owl predation risk, and was included as a yearly covariate (i.e. with the same value for all owls in a given year) in all survival analysis. Predation risk also is also likely to depend on how predator and prey species are distributed spatially relative to one another. Therefore, we used two additional spatial proxies for goshawk predation risk: distance from an owl's nest to the nearest occupied goshawk nest site and connectivity of an owl's nest to all occupied goshawk nest sites. The connectivity measure of predation risk takes into account all occupied goshawk home ranges, but weights the influence each goshawk nest site has on this index according to the distance it is from the focal owl nest site. These proxies were calculated each year, for every individual, and then averaged so they could be modelled as an individual covariate (for further details see Appendix 5a). As proxies of predation risk are not independent of each other, the effect of each was examined in separate models to avoid any issues caused by any multi-collinearity.

Field voles (*Microtus agrestis*) are the main prey for tawny owls in Kielder Forest (Petty 1999). Variation in autumn vole densities influence owl survival (Millon *et al.* 2010, 2011, 2014). Therefore, autumn vole densities were averaged across the whole study area (see (Lambin *et al.* 2000) for the vole sampling method) and fitted as a yearly covariate affecting owl survival, as in (Millon *et al.* 2014). This covariate will hereafter be referred to as "food availability". To discriminate between the impact of annual fluctuations in food availability and predation risk on owl survival, both were included as temporal covariates potentially affecting adult survival and the interactive effect of these covariates was also examined. Owl food availability was not significantly correlated with goshawk abundance (r = -0.27, N = 28, P = 0.14).

Analysis 1: Does age-dependent predation shape owl survival?

All survival analyses involved female owls, as detected instances of predated adult female owls were three times more common than males and adult males were only caught during the early and later parts of the study period (Hoy *et al.* 2014). In order to maximise sample size, we used a pooled dataset containing recapture-data from both owls ringed as chicks (of known age), born between 1980 and 2012, which were subsequently recruited into the breeding population (N = 163), and also immigrant female owls ringed as breeding adults, but of unknown age (N = 109). The first capture of owls ringed as chicks (i.e. the birth year) was removed, such that the first capture for all individuals represented the first recorded breeding attempt. Occupancy data suggests that only 1.2% of female owls could have bred undetected prior to their first capture (Millon *et al.* 2010). Therefore, the first recorded breeding attempt represented the first actual breeding attempt by an individual in almost all cases. Although age was effectively modelled as time since first reproductive attempt in our analysis, the length of breeding lifespan is highly correlated with actual lifespan (r = 0.91) as the majority of female owls start breeding between 1-4 years old (89% by age 3; Millon *et al.* 2010). Therefore this analysis still reflects the impact that predation has on survival as owls age. For brevity, years since first reproductive attempt will hereafter be referred to as ‘age’.

To determine whether age-dependent predation by goshawks could be shaping the pattern of senescence in tawny owl survival, we first sought the most parsimonious model characterising age-dependent survival. This model was then used as a basis to test for significant statistical associations between the proxies of goshawk predation risk and age-dependent survival. We evaluated models which tested for the presence of a threshold in survival (where survival was allowed to differ either side of this threshold) 1-7 years after the first reproductive attempt (Millon *et al.* 2011).

Analysis 2: Does predation risk alter the trade-off between reproduction and survival in later life?

Firstly, we calculated the age-specific survival cost of reproduction using the formula proposed by (Caswell 1982), to determine whether such costs did increase with age:

$$C_i = \frac{v_1}{v_i + 1}$$

The age-specific survival cost of reproduction averaged across the population (C_x) is estimated from the left eigenvector (v_x, age-specific reproductive value) of a Leslie matrix model. We used the matrix model and parameterisation used to project population dynamics for this same tawny owl population (Chapter 3). To determine whether selective predation of older individuals might be causing this pattern, we then compared the shape of the age-specific survival cost of reproduction predicted for tawny owls with the pattern predicted for other similar, long-lived species, where predation was not a main driver of adult survival (Proaktor, Milner-Gulland & Coulson 2007).

To determine whether variation in the trade-off between reproduction and survival in later life was affected by predation risk, we compared models which tested whether reproductive output and predation risk had an additive or interactive effect on owl survival in later life. The proxy of goshawk predation risk used in this analysis was the one which performed best in the first analysis. The effect of reproduction on survival was examined by adding a covariate for reproductive output to the model which best characterised the age-dependent pattern of survival. We used the number of chicks fledged annually, averaged across all years after becoming reproductively active, as one proxy of lifetime reproductive output, as other measures of lifetime reproductive output, such as the total number of chicks fledged, are highly correlated with lifespan and therefore unsuitable for this analysis.

The propensity of tawny owls to skip reproduction in Kielder Forest (Millon *et al.* 2014) suggests that there is an inherently high cost or physiological constraint for female owls in attempting to breed. If reproductive costs are cumulative and the survival cost of reproduction increases with age, then the frequency of breeding attempts when ‘old’ should have a strong impact on survival. Therefore, breeding frequency when ‘old’, measured as the proportion of years when an owl was senescent, where breeding attempts took place, was used as an alternative proxy for reproductive output. For brevity, we refer to this covariate as a proxy of reproductive output, even though not all breeding attempts are successful, because measuring reproductive effort is intrinsically difficult. These two proxies for reproductive output were calculated for each individual, and modelled as individual covariates. As these two proxies are not independent, the effect of each was analysed in separate models.

All survival analyses were carried out in E-SURGE version 1.9.0 (Choquet, Rouan & Pradel 2009). U-CARE 2.3.2 was used for goodness-of-fit tests for each dataset (Choquet *et al.* 2005). Model selection was based on Akaike's information criterion corrected for small sample size (AICc; Burnham & Anderson 2002). Both the additive and interactive effects of proxies of food availability, predation risk and reproductive output on owl survival were tested. All covariates were standardised (to have mean of zero and standard deviation of one), so that their effect sizes could be compared. Slope estimates (β ± 1SE) are given on the logit scale. The proportion of deviance explained by each covariate was calculated according to (Skalski, Hoff & Smith 1993).

Results

Analysis 1: Does age-dependent predation shape owl survival?

Survival of breeding female tawny owls declined by 9.5% from an average of 0.84 ± 0.01 in the first five years after breeding to 0.77 ± 0.02 six years or more after commencing breeding. The best parameterisation of the pattern of female owl survival indicated a threshold in survival occurring six years after becoming reproductively active (see Appendix 5b). Survival was estimated to be statistically lower for individuals six or more years after starting breeding compared to younger individuals (before this threshold) and 86% of individuals were estimated to be nine or more years old after this threshold, the age at which tawny owls become reproductively senescent (Millon *et al.* 2011). Therefore we used this threshold (of six years after first reproductive activity) to classify 'prime-age individuals' and 'senescent individuals'. Survival rates did not differ between locally-born and immigrant individuals (ΔAICc = 1.22; 0.86 ± 0.13 prime-age local vs 0.82 ± 0.12 prime-age immigrant; 0.76 ± 0.18 senescent local vs 0.78 ± 0.2 senescent immigrant).

Survival of prime-aged individuals was not associated with any proxy of predator or food availability (Table 7). However, survival of senescent individuals declined as goshawk abundance increased (β = -0.62 ± 0.33), and was positively associated with food availability (β = 0.31 ± 0.20; Figure 14). Together, the additive effects of goshawk abundance and owl food availability explained 28% of the deviance in senescent owl survival. There was weak evidence to suggest that food availability and goshawk abundance interacted to have a combined effect on the survival of senescent owls (Table 7). There was no evidence to suggest that the survival of either prime-age or senescent owls were related to the distance they nested from the nearest goshawk nest site or how well connected their nest sites were to all surrounding goshawk nest sites.

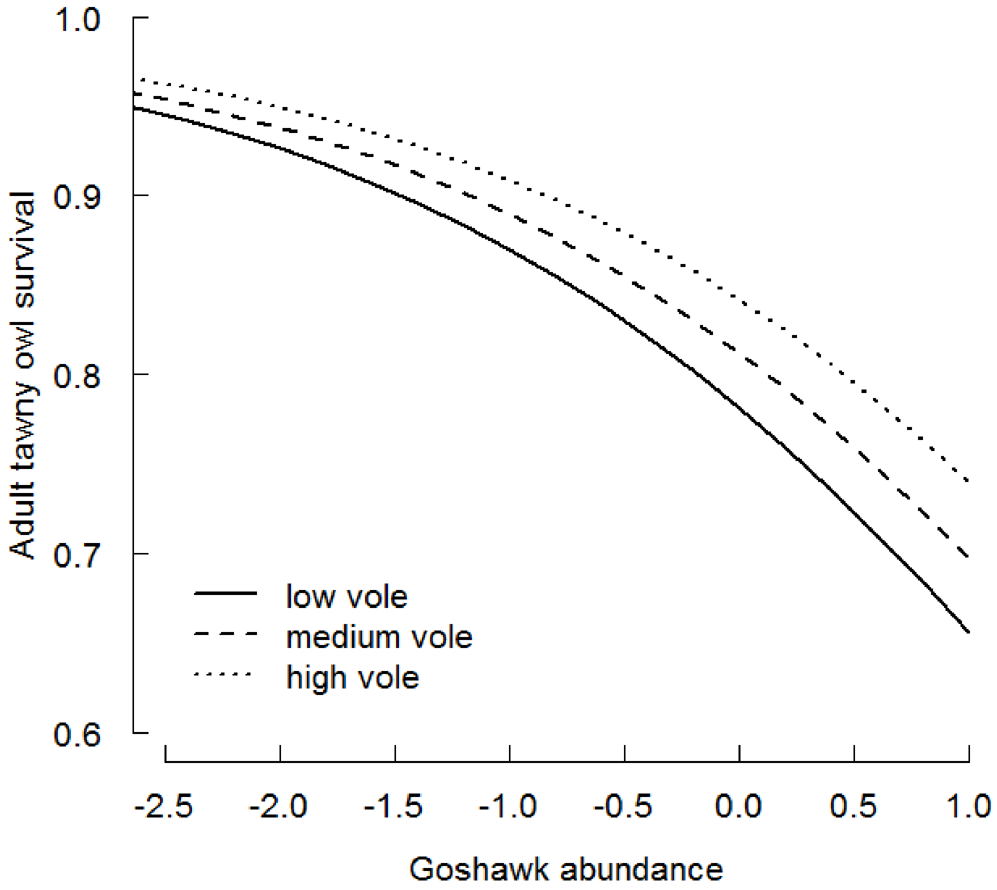

Figure 14. The additive effect of goshawk abundance and owl food availability (vole densities ha^{-1}) on the survival of older breeding female tawny owls (6 years after first starting breeding). Low, medium and high voles represent predicted adult owl survival when vole densities (food availability) are fixed to the lower, median and upper quartile values of the standardised range. Goshawk abundance (number of occupied home ranges) are also shown as standardised values.

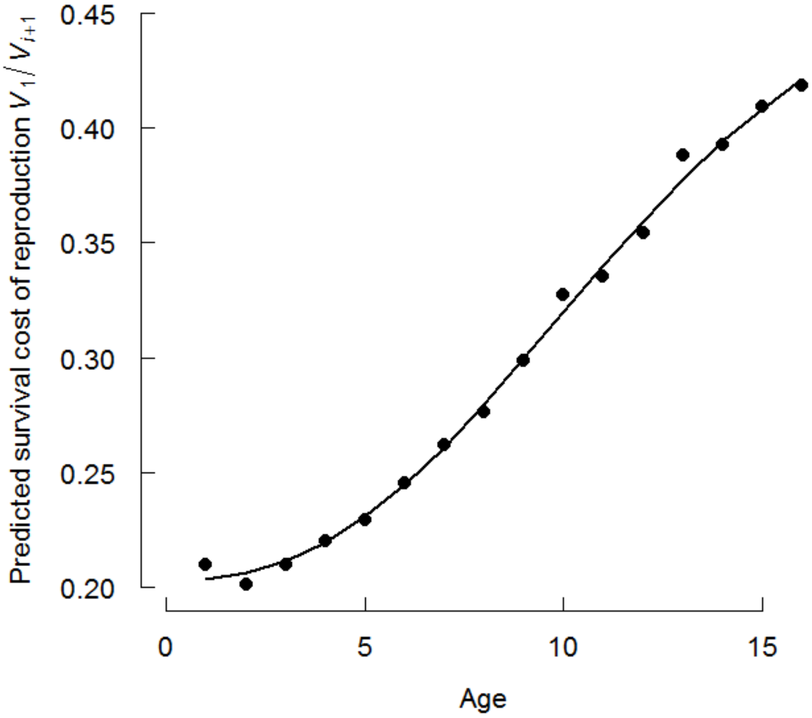

Figure 15. Age-specific survival cost of reproduction estimated for the tawny owl population of Kielder Forest from a post-breeding population matrix model with 17 age-classes. Solid line represents the predicted increase in the survival cost of reproduction with age, smoothed using a Generalised Additive Model.

Analysis 2: Does predation risk alter the trade-off between reproduction and survival in later life?

At the population level, the predicted survival cost of reproduction increased with age, doubling from C_1 = 0.21 to C_{16} = 0.42 (Figure 15). At the individual level, variation in survival of senescent owls was best explained by an interaction between reproductive output and goshawk abundance plus an additive effect of owl food availability, regardless of the covariate for reproductive output used (Table 8). This model explained 76% of the deviance in survival of senescent individuals when the average number of chicks was used as the reproductive covariate (Table 8a) and 80% of the deviance when breeding frequency in later life was used (Table 8b). Survival of senescent owls was positively associated with owl food availability (see contrast between Figure 16a/c and Figure 16b/d) and negatively associated with goshawk abundance and reproductive output (see Figure 16a and Figure 16b for the average number of chicks produced and Figure 16c and Figure 16d for breeding frequency). Overall, survival was highest for individuals producing fewer chicks and breeding less frequently when goshawk abundance was relatively low and food availability was high. The decline in senescent owl survival as goshawk abundance increased was greater for individuals with relatively low reproductive outputs (i.e. those individuals producing fewer chicks on average; Figure 16a and Figure 16b; and those breeding relatively less frequently in later life; Figure 16c and Figure 16d).

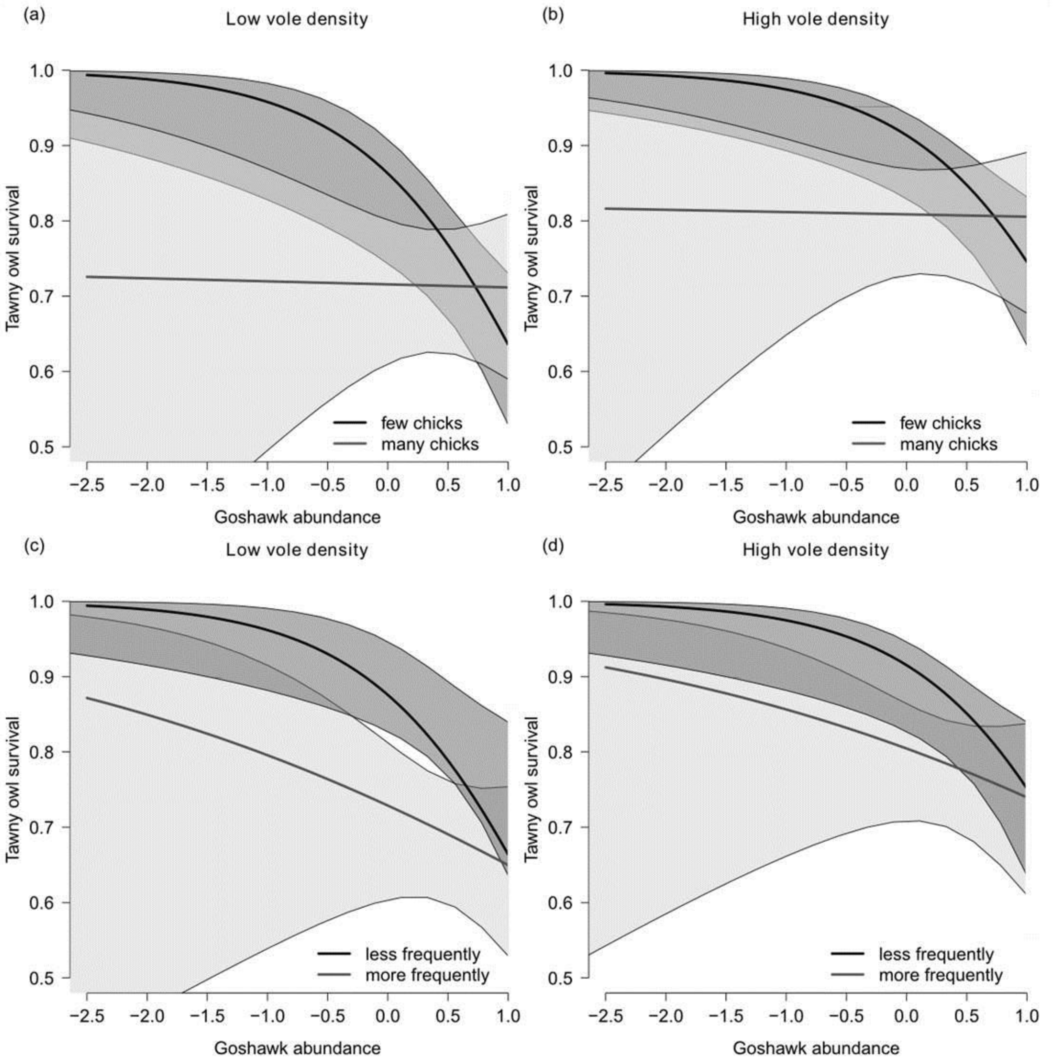

Figure 16. Survival of older breeding tawny owls as predicted by a model which includes an interaction between reproductive output and predator (goshawk) abundance. Reproductive output was measured as the average number of chicks produced per year since they began breeding (a and b) and also breeding frequency in later life (c and d). The additive effect of owl food availability (vole densities) on owl survival can be seen by comparing (a and c) when vole densities are fixed at the lower quartile value with (b and d) when vole densities were fixed at the upper quartile value. Black line represents the lower quartile value of the reproductive output covariate and the grey line represents the upper quartile.

Table 7. Model selection to determine how the survival of adult female tawny owls of two age-classes varied in relation to proxies of food availability and predation risk. The most parsimonious model is indicted by bold text. This analyses using a dataset which included all breeding females, where age was modelled as time since first reproductive attempt. ‘Prime age class’ and ‘senescent age class’ refer respectively to the results of analyses where the survival of owls below and above the threshold in survival (6 years after starting breeding) were modelled as a function of the each set of covariates listed**.**

	Prime age class			Senescent age class		
Models	Deviance	np	ΔAICc	Deviance	np	ΔAICc
null	**2054.75**	**35**	**0.00**	2054.75	35	3.88
Food	2053.88	36	1.28	2050.33	36	1.61
Predator abundance	2054.65	36	2.06	2049.24	36	0.52
Nearest predator	2054.71	36	2.11	2054.74	36	6.02
Connectivity to predators	2054.52	36	1.92	2054.73	36	6.01
Food + Predator abundance	2053.85	37	3.41	**2046.56**	**37**	**0.00**
Food + Nearest Predator	2053.83	37	3.39	2050.33	37	3.77
Food + Connectivity to predators	2053.61	37	3.17	2050.29	37	3.72
Food x Predator abundance	2053.78	38	5.50	2045.13	38	0.73
Food x Nearest predator	2053.59	38	5.31	2050.31	38	5.91
Food x Connectivity to predators	2053.40	38	5.12	2049.12	38	4.72

Table 8. Model selection evaluating the relationship between proxies of reproductive output, food availability and predation risk on the survival of all breeding tawny owls in later life. Owl food availability is measured as vole densities, predation risk measured as goshawk abundance. Two proxies of reproductive output were used as covariates in separate analyses: (a) where the average number of chicks produced per year since becoming reproductively active was used as the covariate for reproductive output; (b) when breeding frequency in later life was used as the covariate.

	a) Average number of chicks			b) Frequency of breeding attempts		
Models	Deviance	np	ΔAICc	Deviance	np	ΔAICc
null	2054.75	35	13.44	2054.75	35	14.50
Reproductive output	2054.11	36	14.94	2053.48	36	15.39
Reproductive output & Predator	2047.98	37	10.98	2040.42	37	4.48
Reproductive output x Predator	2036.93	38	2.09	2034.66	38	0.89
Reproductive output & Food	2049.71	37	12.71	2041.64	37	5.70
Reproductive output x Food	2049.55	38	14.71	2037.03	38	3.26
Reproductive output & Predator & Food	2045.50	38	10.67	2037.65	38	3.88
Reproductive output x Predator & Food	**2032.67**	**39**	**0**	**2031.6**	**39**	**0**

Discussion

Our results support the hypothesis that age-dependent predation affects owl survival and ultimately contributes to the pattern of senescence. Firstly, the age at which goshawk predation on owls increased coincided with the age of a significant decline in owl survival. Secondly, there was no evidence of a relationship between survival of prime-aged owls and goshawk abundance; whereas survival of senescent owls was negatively related to increasing predator abundance. Thus, age-dependent predation by a large colonising diurnal predator has impacted the survival of a smaller nocturnal predator, but only for senescent individuals. We also found indirect evidence supporting our hypothesis that increased vulnerability to predation with age causes the survival cost of reproduction to increase with age. Crucially, we provide hitherto lacking empirical evidence showing that predation influences the trade-off between reproduction and survival for senescent individuals. Indeed, the impact of predation on the survival of a long-lived prey species depended on the average reproductive output of the individual over its breeding lifespan. Our results also revealed that the intrinsic trade-off between reproduction and survival in later life only became apparent when the impact of variation in predation was considered; an unexpected but important finding.

Age-dependent predation affects the pattern of senescence in survival

We found support for the life history theory prediction that age-dependent extrinsic causes of mortality, such as predation, influence senescence in prey species (Abrams 1993; Caswell 2007). Firstly, we found that the pattern of senescence in owl survival was inversely related to the age-dependent pattern of predation risk, as owl survival became significantly lower six years after starting breeding (when almost all owls would be at least nine years old) and goshawk predation on adult female owls became disproportionately high after eight years of age (Chapter 3). Additionally, survival of senescent breeders was negatively related to goshawk abundance whereas the survival of prime-age individuals remained unaffected. This depression of old owl survival by increasing predator abundance implies that age-dependent predation is one extrinsic factor which contributes to senescence in this species.

Under some circumstances increasing mortality for senescent individuals can select against the evolution of senescence (Abrams 1993; Williams & Day 2003). However, Williams &

Day (2003) predicted that if there is a time-lag between incurring reproductive costs and paying them, in response to an increase in age/condition dependent extrinsic mortality, the optimal pattern of senescence should be decreased age-specific deterioration in early life, but with a greater deterioration in later life. As the survival cost of reproduction is predicted to be relatively small for young tawny owls, yet the cumulative cost of previous reproductive attempts results in lower survival in later life, our results provide some empirical support for William and Day's theoretical predictions (Williams & Day 2003).

Predation risk alters the trade-off between reproduction and survival in later life

The survival cost of reproduction for tawny owls was estimated to increase sharply with age (Figure 15). In stark contrast, the survival cost of reproduction was predicted to be highest when young, and declined exponentially with age for all the other bird of prey species in which it has been previously examined, where predation was seemingly not a main driver of adult survival (Proaktor *et al.* 2007). These contrasting patterns provide tenuous evidence supporting the hypothesis that increasing vulnerability to predation with age causes a concomitant increase in the survival cost of reproduction. The prediction that the cost of reproduction can be changed by the prevailing pattern of predation could be further tested by examining whether other long-lived species, such as elk (*Cervus elaphus*) in Yellowstone national park display a similar age-specific survival cost of reproduction pattern, to that documented here, as they are subject to a similar pattern of increasing predation risk with age (Wright *et al.* 2006).

The trade-off between reproduction and survival only became apparent when examined in combination with increasing predation risk, as reproductive output alone explained relatively little variation in the survival of older individuals. This suggests that the balance of reproductive costs accumulated over an individual's lifetime is only fully settled by predators. Therefore, this result not only highlights the importance of considering the role of extrinsic causes of mortality when examining life-history trade-offs and senescence in future studies, but also has implications for how the results of previous studies examining life-history trades-offs in relatively predator-free systems should be interpreted. Owl survival in later life declined as goshawk abundance increased, which is consistent with more old owls being predated as the number of goshawks increased. However we found that the extent to which predation influenced owl survival in later life depended on the average reproductive output of the individual. Whereas previous observational and experimental studies on birds found individuals breeding less frequently and producing fewer offspring had higher survival in later life (Orell & Belda 2002; Reid *et al.* 2003; Boonekamp *et al.* 2014), our study shows that although this was the case when predation risk was low, increasing predation risk altered the reproduction-survival trade-off for senescent individuals. When goshawk abundance was low, survival during the senescent portion of an owl's lifespan (six or more years after starting breeding) was lower for individuals with a greater reproductive output (i.e. those fledging more chicks on average throughout their lifetime and breeding more frequently). This suggests reproductive costs are long-term, having a negative effect on survival in later life (Williams 1966; Kirkwood & Holliday 1979).

However, the strength of the reproduction-survival trade-off altered as goshawk abundance increased. The impact of increasing predator abundance was greatest on individuals only able or willing to invest relatively little in reproduction, compared to individuals with higher reproductive outputs (Figure 16). Predation of adult female owls by goshawks mainly occurs in June and July, when owl chicks born that year have fledged the nest but are still dependent on their parents for food (Petty *et al.* 2003; Chapter 3). We therefore posit that owls with relatively low reproductive outputs are likely to be inefficient hunters, unable to provision enough food to raise large broods and are also more conspicuous to predators after breeding. Firstly, less efficient hunters will need to spend more time foraging to compensate for their reduced capacity to provide food and may be forced to hunt in daylight, particularly in late spring and summer when nights are short, thus making them more conspicuous to diurnal goshawks. Secondly, experiments on avian species with altricial offspring demonstrated that the intensity of food begging calls made by chicks is inversely related to their body condition and the amount of food they receive (Sacchi, Saino & Galeotti 2002). Given that female owls stay close to their broods after fledging (Sunde *et al.* 2003), if broods raised by less efficient hunters produce more intense food begging calls, remaining in the proximity of hungry and vocal offspring may make the parents easier for goshawks to detect. Both of which could result in inefficient hunters, with relatively low reproductive outputs being vulnerable to predators and hence more strongly affected by increasing predation risk compared to efficient hunters.

Together, our results suggest that age-dependent predation is an extrinsic factor shaping owl survival and is one extrinsic mechanism ultimately influencing actuarial senescence. In addition, we reveal a link between the strength of the intrinsic trade-off between reproduction and survival in later life and extrinsic causes of mortality. We provide evidence showing that the full extent of the trade-off between reproductive costs accumulated over an individual’s lifetime and survival only become apparent as predator abundance increased. Additionally, our results provide some indirect evidence to suggest that age-dependent predation is causing the survival cost of reproduction to increase with age and that predation may therefore be an important driver of selection on life-history strategies. The importance of predation in driving selection on life-history strategies could be examined in populations of long-lived prey in this and other ecosystems where large predators are increasing in abundance and recolonising former ranges (Maehr *et al.* 2001; Deinet *et al.* 2013).

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CHAPTER 5

THE INFLUENCE OF INTRINSIC AND EXTRINSIC (FOOD AVAILABILITY AND PREDATION RISK) PROCESSES ON THE REPRODUCTIVE DECISIONS OF A LONG-LIVED PREY SPECIES

Juvenile tawny owl almost ready to fledge

Abstract

How extrinsic factors, such as predation and food availability, drive demographic changes in populations is a fundamental issue in ecology. However, little is known about the extent to which extrinsic factors interact to have a combined effect on reproduction and whether an individual’s response to such extrinsic factors varies according to their intrinsic attributes. By taking advantage of a decline in food (field vole) availability and an increase in predator (northern goshawk) abundance, we quantify the extent to which intrinsic attributes and extrinsic factors (food availability and predation risk) influence breeding decisions (breeding propensity, clutch size and nest abandonment) and reproductive strategies of a long-lived predator and prey species (tawny owl), using breeding data collected on known individuals, between 1985-2013. The decision to breed was shaped by a complex trade-off between extrinsic and intrinsic factors. For a given amount of food, breeding propensity varied by up to 8% according to predation risk, which suggests that owls assessed food availability and predation risk and made a facultative decision to breed. Unexpectedly, when food was scarce breeding propensity was higher when goshawks were abundant, compared to when they were uncommon. Breeding propensity was higher for older individuals; however this was only the case when they had successfully bred the year before. Owls laid larger clutches when food was abundant. Individuals with small clutches and breeding in locations well connected to goshawk nest sites were 15% less likely to complete their breeding attempt compared to individuals with large clutches breeding in territories not well connected to goshawks. Thus, the decision to complete a breeding attempt was a trade-off between the intrinsic reproductive value of the breeding attempt (clutch size) and the extrinsic impact of predation risk. Predation and food availability interacted to have a combined effect on owl reproductive decisions; however an individuals’ response to variation in extrinsic conditions depended on intrinsic attributes. As food availability declined and predation risk increased, owls appeared to switch from an ‘all eggs in one basket’ to a ‘bet-hedging’ strategy of reproducing more often, but investing less per breeding attempt. Thus here we provide empirical evidence supporting the hypothesis that extrinsic factors interact to drive selection on life-history strategies.

Introduction

The way in which individuals’ breeding decisions and consequently their reproductive success are influenced by extrinsic factors is a central issue in ecology, as they will ultimately impact population dynamics (Nichols *et al.* 2004; Sedinger *et al.* 2008). While the bottom-up effect of food availability on reproduction is well understood (reviewed in White 2008), the top-down impact that predation can have on reproductive decisions remains less clear. In addition to directly removing breeders and their offspring from populations, predators can indirectly impact the reproductive success of their prey by eliciting anti-predator behaviours in their prey, such as avoidance of risky areas or being less active at the same time as their predators. Such anti-predator behaviours can reduce the prey's foraging efficiency and possibly the amount of resources they could otherwise allocate to reproduction (Lima & Dill 1990; Buchanan 1996, 2012; Cresswell 2008). Alternatively, individuals may respond to predation risk by making a facultative decision to alter the amount they allocate to breeding, to reduce either their own or their offspring's vulnerability to predators (Ghalambor & Martin 2001; Fontaine & Martin 2006). In theory, such indirect effects could destabilize predator-prey dynamics, under certain circumstances (Kokko & Ruxton 2000). However, the actual indirect effects of predation on reproductive decisions are not well understood, as they are difficult to quantify under natural conditions.

Fundamental to our understanding of life-histories is an intrinsic trade-off between investing in reproduction and survival (Williams 1966). However, the strength of such intrinsic trade-offs should be related to the level of predation risk, as reproduction makes individuals more vulnerable to predation than non-breeders (Magnhagen 1991; Hoogland *et al.* 2006), and producing more offspring per breeding attempt can make individuals more vulnerable to predators in some cases (for example see Ercit, Martinez-Novoa & Gwynne 2014). Given predation risk fluctuates temporally, in years when predation risk for adults is high, individuals of long-lived iteroparous species (with relatively high adult survival) should attempt to reduce their vulnerability to predation, either by refraining from breeding (Spaans *et al.* 1998), or by abandoning their breeding attempt (Chakarov & Krüger 2010). Alternatively, in years when offspring have a high risk of being predated, individuals may respond by reducing investment in reproduction (e.g. in terms of the number or quality of offspring; Doligez & Clobert 2003). This strategy of reducing current investment in reproduction to increase the probability of successfully reproducing in the future, under better circumstances is a central part of research on life-history trade-offs (Williams 1966). There is some experimental evidence showing that birds can assess predation risk and make facultative decisions about the extent to which they allocate resources to reproduction (Ghalambor & Martin 2001; Fontaine & Martin 2006). However, it is difficult to simulate a realistic level of predation risk (Lambin *et al.* 1995). Indeed the behavioural response elicited in some experiments was later shown to be an artefact of extreme stimuli and unrepresentative of natural responses to predation risk (Wolff & Davis Born 1997; Mappes *et al.* 1998). Furthermore, how behavioural responses translate into demographic responses is often indeterminate.

According to life-history theory, an individual’s response to changes in extrinsic conditions should vary according to attributes intrinsic to the breeder or the reproductive attempt, such as their reproductive value. Reproductive value is the contribution an average individual of a given age/stage makes to future population growth rates and is dependent on the probability of them surviving, successfully reproducing and the number of offspring produced per breeding attempt (Fisher 1930). Life-history theory predicts that, as an individual’s reproductive value declines, it should be more dedicated to its current reproductive attempt, as its probability of surviving and producing offspring in the future decreases (Clutton-Brock 1984). Senescence affecting both survival and reproduction has been observed in individuals of a wide-range of species (Nussey *et al.* 2013). Consequently, as an individual ages (and their reproductive value declines), it is predicted that they should become increasingly committed to their current reproductive attempt (i.e. the individual should terminally invest; Clutton-Brock 1984). In addition, individuals who have produced relatively large broods or litters are also predicted to be more dedicated to ensuring their reproductive attempt is successful, as it has an intrinsically high reproductive value. Thus, attributes intrinsic to the breeder and their current breeding attempt should influence the way in which individuals respond to extrinsic conditions (Williams 1966; Ricklefs 1976). However, there is little empirical evidence supporting these theoretical predictions in birds, with the exception of Wiklund (1990) and Kontiainen *et al.* (2009).

Although a plethora of studies have examined the impact of food and predation on reproduction in isolation, little is known about the extent to which they interact to effect on reproductive decisions under natural conditions, and the validity of some of the experimental work in this field has been debated (Wolff & Davis Born 1997; Mappes *et al.* 1998). Furthermore, it is not yet clear whether an individual’s response to variation in extrinsic factors is dependent on intrinsic attributes. Here we address these knowledge gaps using data from a population of tawny owls (*Strix aluco*) collected over a 28 year period (1985-2013) and encompassing a 3-fold increase in the abundance of their main predator, northern goshawks (*Accipiter gentilis*, hereafter goshawks), and a gradual decline in the amplitude of field vole (*Microtus agrestis*) population cycles (Cornulier *et al.* 2013), the main prey species for owls in our study site (Petty 1999). Although goshawk predation on tawny owls appears selective on juveniles, predation on adult owls also occurs and is biased towards females (Chapter 3). Adult female tawny owls have a relatively high reproductive value compared to their offspring, due to their high survival probability (average survival probability for adult females is 0.83 compared to an average of 0.19 for young owls in their 1st year of life; Millon *et al.* 2011). Therefore, we predicted that adult females facing relatively high levels of predation risk would attempt to decrease their vulnerability to predation by breeding less often or allocating less to the current reproductive attempt, assuming that owls can assess predation risk, as do other avian species (Fontaine & Martin 2006). We examined how owl breeding propensity (i.e. the probability of mature females breeding in a given year) and the extent to which owls invested in reproduction (clutch size) varied in relation to temporal fluctuations in food availability and predation risk. We also examined the extent to which an individual's decision to complete a breeding attempt varied in relation to food availability and predation risk, given that predation on owls increases throughout the owl breeding season (Petty *et al.* 2003). Additionally, we tested the hypothesis that the behavioural response of an individual to temporal variation in predation risk and food availability varied according to the reproductive value of the individual and the breeding attempt (clutch size). Lastly, given life-history theory predicts an intrinsic trade-off between the amount of effort previously allocated to reproduction and the amount they can allocate to future reproductive attempts (Williams 1966), we also tested whether an individual's reproductive success the year before influenced their current reproductive decisions.

Methods

Study site and owl monitoring

Tawny owl reproduction has been continuously monitored in a 176 km² central subsection of Kielder Forest (55°13′N, 2°33′W) since 1979, using nest boxes (Petty *et al.* 1994). Kielder Forest lacks natural tree cavities, the preferred nesting sites for tawny owls.

Consequently, owls breed almost exclusively in nestboxes, making it relatively easy to monitor their reproduction (Petty *et al.* 1994). Each year nest boxes were checked for occupancy, to record clutch size, the number of chicks fledged and to ring chicks. Tawny owls are a suitable species for this study as they exhibit sufficient reproductive plasticity to be able to respond to changes in extrinsic conditions, as clutch size can vary between 1-6 eggs and individuals do not breed every year after becoming reproductively active (Petty 1992). Owls usually only breed once per year; however they are occasionally known to re-lay and have a second breeding attempt if the first breeding attempt fails early on in the breeding season. To account for this, in cases where a re-lay occurred we only included the second breeding attempt, such that each individual contributed only one breeding attempt per year to our analysis.

In some cases observer disturbance during monitoring visits resulted in owls abandoning breeding attempts. To determine whether an owl had returned to incubate their eggs after a monitoring visit, we marked eggs with a pen/pencil and checked whether the mark remained clear on a subsequent visit. If it did, we assumed the egg/s had not been incubated since the last visit, and inferred the observer had caused the owl to desert. Additionally, if the carcasses of dead chicks were estimated to be the same size as they were at the last visit, we also assumed that the breeding attempt had been abandoned due to human disturbance. We excluded all such breeding attempts (N = 51/965) from all our analyses.

The identity of breeding female owls was known in most years, as they were caught using landing nets when chicks were 1-2 weeks old throughout the study period. Tawny owls are highly site faithful, and in our study site 98% remained in the same territory where they first started breeding (Petty 1992a). The identity of a female occupying a territory when no breeding took place or when the breeding attempt failed prior to trapping was determined as follows; when the same female was recorded breeding in a territory both before and after the year/s where no female was caught; we assumed the same individual was involved. When different females were recorded either side of a year/s when females were not caught, we deemed the identity of the breeder unknown and excluded such cases from our analyses. A total of 914 breeding attempts took place between 1985 and 2013 and the identity of the female was known or could be assumed in 93% of cases (N = 850).

Analysis

To determine which breeding decisions were affected by extrinsic conditions (food availability and predation risk) and how the response of individuals to extrinsic conditions varies according to intrinsic attributes, we examined owl i) breeding propensity, ii) clutch size and iii) whether breeding attempts were completed. These response variables were analysed in relation to covariates reflecting predation risk and food availability and intrinsic attributes (breeding success the previous year, the age/reproductive value of the breeder and the reproductive value breeding attempt), using generalised linear mixed effect models (GLMM) with the appropriate error structure, using the *lme4* package (Bates *et al.* 2014) in R version 3.0.3 (R Core Development Team 2014). As some individuals bred in multiple years, the identity of the breeding female was fitted as random effect in all analyses to account for any variation caused by individual differences. Additionally, the year of a breeding attempt was also fitted as a random effect to account for the residual temporal variation in response variables not attributable to fitted temporal covariates of interest (food availability and predation risk). In all analyses both the additive and 2-way interactive effects of fixed effect covariates were tested. Model selection for each analysis was based on Akaike’s information criterion corrected for small sample size, AICc (Burnham & Anderson 2002). We visually checked for any residual spatial-autocorrelation in all response variables not explained by the covariates included in selected best models using correlograms.

We examined breeding propensity by analysing whether an individual bred or did not breed each year after becoming reproductively active, up until its last recorded breeding attempt (fitted as a binary covariate). If at least one egg was laid in a territory known to be occupied by a particular female, we recorded that female as having attempted to breed. Less than 2% (N= 5) of the 268 different females recorded breeding in Kielder Forest were known to have skipped breeding for more than three consecutive years. Therefore, we assumed an individual was dead if they had not been re-captured in the last 3 years of the study (i.e. after 2010). In this analysis, we excluded all individuals which could not be assumed dead or were known to be alive (i.e. were recorded breeding) in 2013 (N = 40) to remove any bias that unknown non-breeding events occurring in the last few years of the study period could induce. To determine the extent to which owls adjusts their investment in reproduction in response to variation in food availability and predation risk, we modelled variation in clutch size. The clutch size analysis was based on a different dataset to that used for the breeding propensity analysis as it contained all breeding attempts by all known individuals. In addition, we examined the decision to continue a breeding attempt to completion by classifying each breeding attempt as "complete", if at least one chick fledged or "incomplete" if not (fitted as a binary covariate).

Measures of food availability & predation risk

Field voles are the main year round prey species of tawny owls in Kielder Forest, representing 62% of diet on average (Petty 1999). Consequently, as tawny owls can be seen as a vole specialist in our study site, variation in the abundance of alternative food sources should only have a limited impact on owl breeding decisions. Field vole densities were monitored in spring and autumn at 17-21 sites within the owl monitoring area, every year since 1985 (for methods see Lambin, Petty, & MacKinnon 2000). The amount of vole prey available prior to the egg laying stage (early spring) has previously been shown to affect owl reproduction; in years of high food availability more pairs attempt to breed and clutch sizes are larger (Petty 1992a; Millon *et al.* 2014). Therefore, we used spring vole densities as a proxy for owl food availability in all analysis. Field vole densities were spatially synchronous across Kielder Forest (Lambin *et al.* 1998). However, this pattern has changed over time (Bierman *et al.* 2006). Such changes in spatial synchrony are also likely to impact owl reproductive decisions, because low synchrony could make it harder for owls to predict how much food is available. Therefore, we also examined the extent to which tawny owl breeding decisions were affected by changes in the spatial synchrony in field vole densities across the forest. To this effect, we first calculated spatial variation in field vole densities as the coefficient of variation (standard deviation divided by the mean) in spring vole densities between survey sites, each year. However, spatial variation in vole densities is likely to have less of an effect on owl breeding decisions when food is abundant. Therefore, we classified years as either being of low overall food abundance if the spatially averaged spring vole density was below the median value for all years, or high if not. We then included an interaction between spatial variation in vole densities and the categorical covariate of overall vole densities to test this hypothesis.

Goshawks were estimated to kill an average of 56 tawny owls each year in the central part of Kielder Forest (Chapter 2), with 70% of the owls killed being juveniles and adult female owls were three times more likely to be killed than adult males (Chapter 3). Goshawks have been continuously monitored since the first breeding attempt in 1973 (Petty & Anderson 1995). Each year occupied goshawk territories were identified and over the last 40 years the Kielder Forest goshawk population has grown from one to approximately 26-33 occupied home ranges. Given that predation on owls increased with the abundance of goshawks in the forest (Chapter 2), we used the total number of occupied goshawk territories in a 964 km² area of Kielder Forest as a proxy of temporal variation in predation risk. However, as goshawks are monitored over a larger area than tawny owls, we used an additional proxy of temporal variation in predation risk, local goshawk abundance, measured as the number of goshawk territories whose nests sites were within 5.8km (the estimated goshawk foraging distance) of the owl monitoring area, calculated in the same way described in (Chapter 2 & Chapter 3).We also investigated the extent to which owl reproductive decisions varied in relation to two spatial proxies of predation risk: (i) distance from an owl's nest to the nearest goshawk nest site; (ii) the location of an owl's territory in relation to all goshawks nest sites, i.e. connectivity of an owl territory to all goshawk nest sites. The connectivity measure of predation risk takes into account all goshawk nest sites, but weights the influence each goshawk site has on this index of predation risk, according to its distance from the focal owl nest site. It assumes no inter-individual variation in diet and the propensity to predate owls. To calculate the connectivity indices, we used the formula proposed by (Hanski 1994).

$$S_i = \sum \exp(-\alpha d_{ij})$$

Si is the connectivity of tawny owl territory *i* to all the surrounding goshawk nest sites. The distance in km *d*, between the owl's nestbox *i* and goshawk nest site *j*, is weighted by α following a negative exponential. We set the value of α to reflect the distances goshawks travelled to predate owls and estimated it as the distance between the nestbox an owl last used, and the goshawk nest site where the owl's ring was recovered (Hoy *et al.* 2014). Based on the distribution of 46 owl ring recovery distances, we estimated that the influence each goshawk nest site had on the probability of an owl being eaten by a goshawk halved at a 1.4 km (α =0.49). These spatial covariates of predation risk were calculated separately for each owl territory, every year (in the same way as described in Chapter 4). We assumed nest locations were the activity centres for owls and goshawks during the breeding season. None of the temporal proxies of food availability were significantly correlated with the temporal covariates of predation risk. However, no two proxies of predation risk or two proxies of food availability were included in the same model as they were not all independent (see Appendix 6a for all cross correlation coefficients). All temporal and spatial covariates were standardised (had a mean of 0 and a standard error of 1) to enable their effect sizes to be compared.

Intrinsic attributes

The age-specific reproductive value for female tawny owls has been calculated previously and is known to decline with age (Chapter 3, but also see Appendix 6b). Unfortunately, the exact age of 94 breeding females entering the population as adult immigrants was not known. However, the length of an individual's breeding lifespan is highly correlated with actual lifespan (r = 0.91; Chapter 4), as most females commence breeding between 2-4 years of age (Millon *et al.* 2010). Consequently, we tested the hypothesis that the response of an individual to changes in extrinsic conditions varied according to their own reproductive value, using the number of years elapsed since their first recorded breeding attempt as a proxy for an individual's age and reproductive value at the time of a breeding attempt. We tested the hypothesis that previous investment in reproduction influenced an individual's current reproductive decisions in relation to changes in predation risk and food availability by fitting a binary covariate reflecting whether an individual had bred successfully the previous year (i.e. had raised offspring to the fledgling stage). Lastly, we investigated whether the likelihood of an individual completing a breeding attempt was related to clutch size, taking clutch size as a proxy for the reproductive value of the breeding attempt.

Results

Breeding propensity

On average, the probability of a female breeding after becoming reproductively active was 0.78 ± SD 0.17 (range 0.21-0.99). Breeding propensity appeared to be mediated by a trade-off between vole densities and local goshawk abundance, and the influence that the number of years elapsed since the individual first started breeding had on breeding propensity depended on whether the individual had bred successfully the year before (Table 9, see also Appendix 6c). The model including an interaction between spring vole densities and total goshawk abundance plus the interaction between breeding success the previous year and the number of years elapsed since they started breeding performed similarly to the best model (ΔAICc = 1.92; see appendix 6c). Breeding propensity increased strongly, to near 100 % as vole density increased above 150 vole ha^{-1}. At low vole densities (below 50 vole ha^{-1}), breeding propensity was predicted to increase by up to 34% in years when local goshawk local abundance was relatively high (above the 75th percentile) compared to when local goshawk abundance was lower (below the 25th percentile; Figure 17a). Breeding propensity increased with the number of years elapsed since the individual starting breeding (by up to 15 %, from 0.73 one year after starting breeding to 0.88 12 years after starting to breed), but only for those owls who had sucessfully bred the previous year (Figure 17b).

Clutch size

Owl clutch size averaged 2.85 ± SD 0.82 eggs, with 43.8% of clutches containing 3 eggs (range 1-6). The largest clutches were laid in years of high spring vole densities and clutch size was predicted to increase by 45%, from 2.42 ± SD 0.07 when vole densities were below 50 voles ha^{-1} to 3.49 ± SD 0.13 when vole densities were above 150 voles ha^{-1} (Figure 18). There was weak evidence supporting the hypothesis that spatial variation in vole densities also affected clutch size, as the model including an interaction between spatial variation in vole densities and the categorical spring vole density covariate was ranked 2nd and performed considerably better than most other models, although it performed less well than the best model (ΔAICc = 6.52, Table 10 and Appendix 6d).

Completing a breeding attempt

On average 95% of breeding attempts were completed. The probability of a breeding attempt being completed was dependent on the number of eggs that had been laid and on how well connected that breeding territory was to goshawk nest sites (Table 11). There was weak evidence of an non-additive effect between these two covariates as the model with an interaction performed similarly to the best model which only included an additive effect (ΔAICc = 1.67; Table 11). The probability of breeding attempts being completed was lower when owls were breeding in territories well connected to goshawk nest sites, 0.93 ± SD 0.07 for owls breeding in territories above the 75th percentile of goshawk connectivity compared to territories poorly connected to goshawk nest sites 0.97 ± SD 0.03 for owls breeding in territories below the 25th percentile of goshawk connectivity.

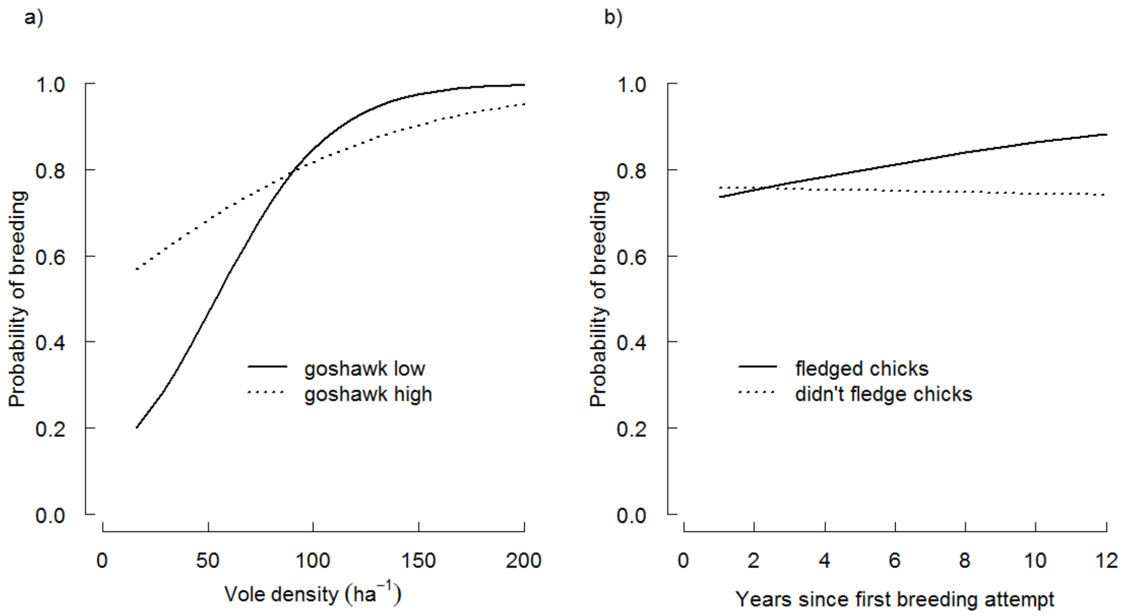

Figure 17. The predicted probability of adult female tawny owls breeding in relation to (a) the density of their main prey, (field voles), when the abundance of their main predators (Northern goshawks) was low, at the 25th percentile of the recorded range (solid line) and high, at the 75th percentile (dotted line). (b) the length of time (years) since their first reproductive attempt for individuals who had successfully bred the previous year (solid line) and individuals who did not successfully breed the previous year (dotted line).

The probability of a breeding attempt being completed increased by 11%, from 0.88 ± SD 0.04 when only one egg had been laid to 0.99 ± SD 0.004 when four eggs were laid (Figure 19). There was no evidence to suggest that the decision to complete a breeding attempt was related to annual or spatial fluctuations in vole densities, the number of years elasped since the individual became reproductively active or whether the individual had successfully bred the previous year, as models including these covariates all performed worse than the null model (Table 11 and Appendix 6e).

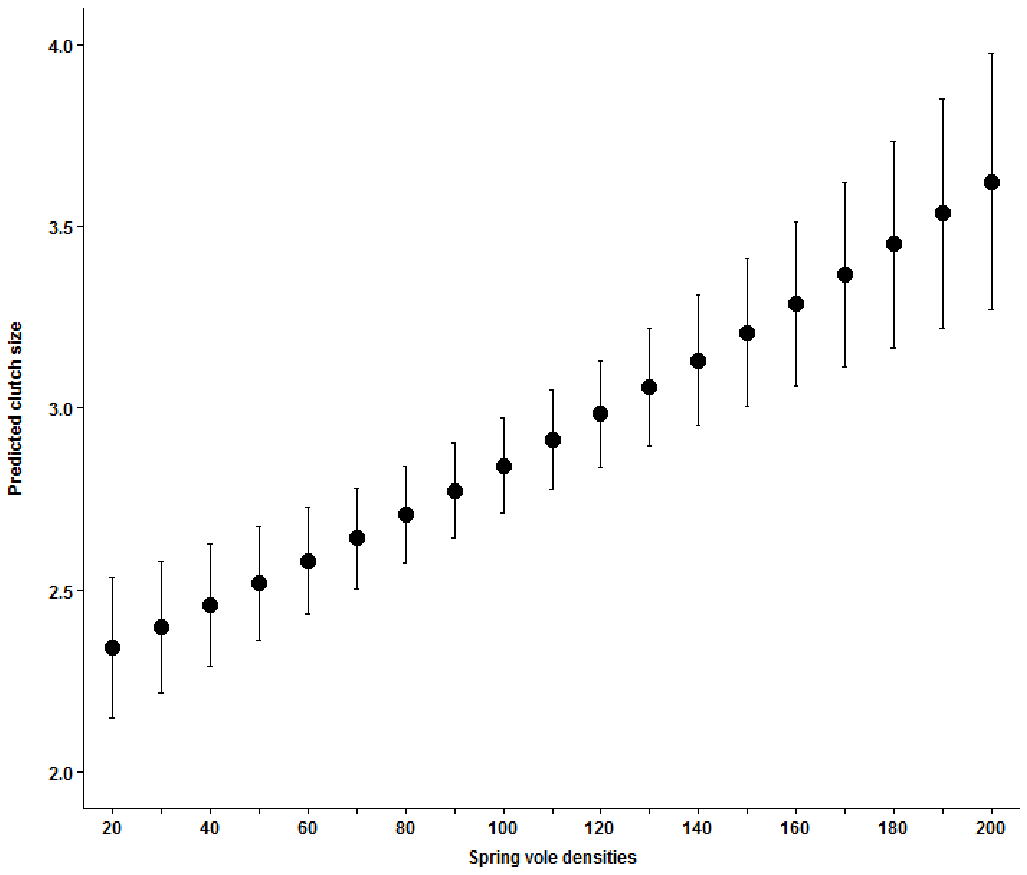

Figure 18. Tawny owl clutch size estimated in relation to the densities of their main prey, field voles in the spring, just prior to laying.

Table 9. Model estimates and selection of tawny owl breeding propensity in relation to variation in predation risk (total goshawk abundance; local goshawk abundance; connectivity of the owls territory to all goshawk nest sites; distance to the nearest goshawk nest site), Food availability (spring vole densities; spatial variation in vole densities across the study site). Breeding propensity was also examined in relation to whether the individual had successfully bred the previous year and the number of years elapsed since the owl first started breeding. The most parsimonious model is emboldened.

	Model	*np*	Estimate	SE	ΔAICc
1.	Null	3			37.24
2.	Total goshawk	4	0.41	0.24	36.52
3.	Local goshawk	4	0.45	0.25	36.26
4.	Connectivity to goshawks	4	-0.01	0.12	39.26
5.	Nearest goshawk	4	0.05	0.10	39.06
6.	Spring voles density	4	1.09	0.26	25.69
7.	Categorical spring vole density (CSV)	6	-0.83	0.56	33.12
	Spatial variation in vole densities (SVVD)		-0.62	0.44	
	CSV x SVVD		0.02	0.61	
8.	Breeding success previous year (BS)	4	0.34	0.22	27.81
9.	Years since 1st reproduction (Y1st)	4	0.08	0.03	32.42
10.	Spring voles	5	1.13	0.23	20.25
	+ Local goshawk		0.52	0.18	
11.	Spring voles (SV)	6	1.15	0.23	15.79
	Local goshawk (LG)		0.15	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.	**Breeding success previous year**	**9**	**-0.34**	**0.35**	**0.00**
	Years since 1st reproduction		**-0.01**	**0.05**	
	BS x Y1st		**0.13**	**0.05**	
	Spring voles		**1.17**	**0.23**	
	Local goshawk		**0.13**	**0.22**	
	SV x LG		**-0.69**	**0.26**	

Table 10. Model estimates and selection to determine whether the extent to which tawny owl invested in reproduction (clutch size) was related to proxies of predation risk (total goshawk abundance; local goshawk abundance; connectivity of the owls territory to all goshawk nest sites; distance to the nearest goshawk nest site), Food availability (spring vole densities; spatial variation in vole densities across the study site) and intrinsic attributes (whether the individual had successfully bred the previous year and the number of years since the individuals first breeding attempt). In all below analysis the identity of the breeder and year were fitted as a random effects.

	Model	*np*	Estimate	SE	ΔAICc
1.	Null	3			17.11
2.	Total goshawk	4	-0.035	0.032	17.99
3.	Local goshawk	4	-0.017	0.033	18.88
4.	Connectivity to goshawk	4	0.007	0.024	19.04
5.	Nearest goshawk	4	-0.007	0.022	19.02
6.	**Spring vole density**	**4**	**0.125**	**0.023**	**0.00**
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

Discussion

Food availability in spring and goshawk abundance (implying predation risk), interacted to alter the reproductive decisions of female tawny owls. Breeding propensity was highest when field voles were abundant in spring and goshawk abundance was relatively low. In addition, breeding propensity also increased with the number of years elapsed since becoming reproductively active, a measure related to the age of owls but only for those owls that had successfully bred the previous year, which indicates that owl reproductive decisions alter with age. Clutch size increased with the density of vole prey. Ninety-five percent of breeding attempts were completed and modelling of variation therein suggested a trade-off between intrinsic and extrinsic factors, with individuals having laid small clutches (which mainly occurred in the later years of the study period) and those breeding in territories more connected to goshawk nest sites being less likely to complete their breeding attempt. Taken together, these changes imply a change in strategy coinciding with changes in extrinsic conditions.

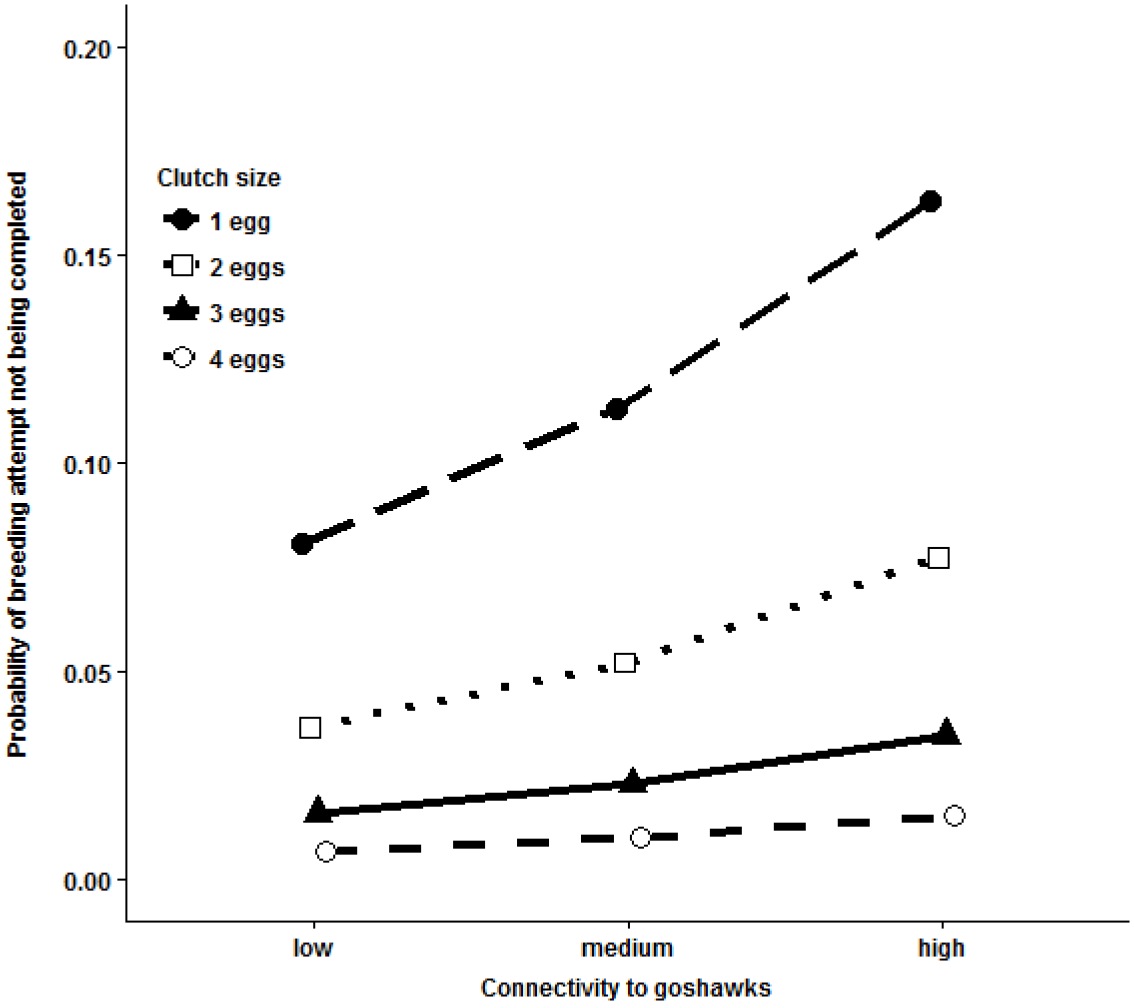

Figure 19. The predicted probability that tawny owl abandoning a nesting attempt in relation to the reproductive value of the current breeding attempt (clutch size) and how well their breeding territory was connected to the surrounding goshawk nest sites.

Table 11. Model estimates and selection for analyses investigating the relationship between the probability that tawny owl breeding attempts were completed and proxies of predation risk (total goshawk abundance; local goshawk abundance; connectivity of the owls territory to all goshawk nest sites; the distance to the nearest goshawk nest site), Food availability (spring vole densities; spatial variation in vole densities across the study site) and attributes intrinsic to the breeder (whether they had successfully bred the previous year and the number of years since their first breeding attempt) and the breeding attempt (clutch size) and the age of the breeding female. The identity of individuals and year were fitted as random effects in all models.

	Model	*np*	Estimate	SE	ΔAICc
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 all 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
11.	**Connectivity to all goshawks**	**5**	**0.84**	**0.28**	**0.00**
	+ Clutch size		**-0.60**	**0.17**	
12.	Connectivity to all goshawks (CG)	6	-0.35	0.59	1.85
	Clutch size (CS)		0.89	0.31	
	CG x CS		-0.10	0.23	

Breeding propensity

Whilst previous studies have shown that a greater proportion of individuals breed when food is abundant (Pietiäinen 1989; Petty 1992a; Mills *et al.* 2008), and when predation risk is relatively low (Sih 1988; Candolin 1998; Spaans *et al.* 1998), here we found that predation risk and food availability interacted to have a combined effect on breeding propensity. For a given amount of food, breeding propensity differed according to predation risk (Figure 17). This suggests that: 1) breeding propensity is not purely constrained by the amount of food available prior to the breeding season and 2) owls are capable of assessing changes in environmental conditions and make facultative decisions about whether to breed.

If owls were responding to increasing predation risk by not breeding then for a given amount of food, breeding propensity should be lower when predation risk is high; however this was not the case. It has been suggested that individuals should increase their reproductive effort, as their probability of surviving and producing offspring in the future declines (i.e. individuals should terminally invest as they near the end of their lives; Williams 1966; Clutton-Brock 1984). In Chapter 4 we showed that adult tawny owl survival is predicted to be lowest when goshawk abundance is relatively high and food is scarce. Consequently, here we argue that one plausible explanation for the higher breeding propensity observed in years when goshawks were abundant and food scarce is that owls are responding to having a relatively low probability of surviving and reproducing in the future (due to these environmental conditions) by terminally investing in reproduction. Reproductive value declines with age for tawny owls as they senesce both in terms of survival and reproduction (Millon *et al.* 2011). In addition, reproduction is generally accepted to reduce parental survival (Nur 1984; Cox & Calsbeek 2010; see also Chapter 4). Therefore, if older owls and those who bred the previous year have a lower survival probability compared to younger individuals and those which did not breed, they should have more incentive to terminally invest. Consequently, we posit that the observed increase in breeding propensity with age (number of years elapsed since becoming reproductively active) for individuals who had bred the previous year may be a case of aged owls terminally investing.

Clutch size

The strong positive effect of food availability on investment in reproduction (clutch size), is concordant with the results of several other studies investigating the impact of food availability on clutch size (Ballinger 1977; Crawford *et al.* 2006; Lehikoinen *et al.* 2011). However, in contrast to the findings of studies on other avian species (Eggers *et al.* 2006; Thomson *et al.* 2006) and indeed with the results of a study investigating the impact of a predation on tawny owl reproductive success (Sergio *et al.* 2007), we found no evidence of an association between owl cutch size and any proxy of predation risk. We therefore posit that goshawks were not eliciting any anti-predatory behaviours in owls over the winter, when owls are acquiring the food resources needed to build up body condition prior to breeding, which have reduced owl foraging efficiency prior to the breeding season. Female goshawks are thought to leave Kielder Forest in winter, returning in February, just prior to owls laying (Petty, S.J. personal communication), such that predation risk for owls is presumably lower in Kielder Forest during the winter. Furthermore, nights are relatively long prior to the breeding season, at the time when they are acquiring the food resources they use for breeding, hence there is likely to be little overlap in the time-periods where both nocturnal tawny owls and diurnal goshawks are active, compared to the summer months when nights are relatively short. Both of which are likely to mean that owls have a low risk of being killed by goshawks over the winter prior to the breeding season. This temporal segregation could explain why our results conflict with those of the aforementioned studies, where the predator and prey species are active at the same time.

Completing a breeding attempt

As predicted by life-history theory, individuals who had invested more in reproduction, in terms of laying more eggs and therefore had broods with a high reproductive value, were more likely to complete their breeding attempt, a finding also consistent with previous studies (Delehanty & Oring 1993). However, there was no evidence to suggest that older individuals (i.e. those with a lower reproductive value) were more prone to completing a breeding attempt. Thus the decision to complete a breeding attempt varied according to the reproductive value of the breeding attempt, but not with the reproductive value of the breeder.

Predation risk was the main extrinsic process influencing whether breeding attempts were completed, as the probability of nests failing increased for owls breeding in territories well connected to goshawk nest sites (i.e. those which were breeding in relatively close proximity to several goshawk nest sites). Predation risk for both adults and fledglings increases throughout the breeding season (Petty *et al.* 2003; Hoy *et al.* 2014). Therefore, the increased tendency of owl not to complete breeding attempts as predation risk increased is consistent with female owls, having already commenced breeding (when predation on owls is relatively infrequent), deciding to reduce their vulnerability to predation by not continuing with the breeding attempt as predation risk increases.

Reproductive strategies

Here we define a reproductive strategy as the set of reproductive decisions which influence reproductive output. Owl breeding strategies appeared to change in response to environmental conditions, as the extent to which individuals invested in reproduction (in terms of breeding propensity and clutch size) was strongly influenced by food availability (Figure 17 & Figure 18). Owls also responded to increasing predation risk by making facultative decisions about whether to complete the breeding attempt. Although there was no year-year colinearity between our temporal covariates of predation risk and food availability, these covariates were correlated when averaged over a larger time scale (5 years), hence both these environmental conditions (predation risk and food availability) changed simultaneously in different ways. Therefore, we cannot fully disentangle the effects of food availability and predation risk on owl breeding decisions. Overall the effect of changes in food availability on breeding propensity was greater than the effect of changing predation risk (Figure 17, Table 9). Given the overall percentage of breeding attempts not completed was very low (5%), the main reproductive decisions influencing reproductive output were whether to breed and how much to invest (clutch size), both of which were largely driven by food availability. Indeed, the proportion of the population breeding and average clutch size explained 82.86% and 15.9% of the total variation in the annual reproductive success of the tawny owl population respectively (when reproductive success was measured as the average number of chicks which fledged per occupied owl territory), whereas whether or not breeding attempts were completed only explained 0.08% of the total variation in reproductive success (see Appendix 7). Therefore, the bottom-up effect of food availability appeared to be the main extrinsic process shaping reproductive decisions and output, hence the main factor shaping reproductive strategies in tawny owls.

During the study period food availability declined whilst predation risk increased, and tawny owls began to breed more frequently, but invested less per breeding attempt. This could be indicative of owls switching from an ‘all your eggs in one basket’ reproductive strategy, of saving resources to invest more in one or a few reproductive attempts in the future, to a ‘bet-hedging’ reproductive strategy of spreading reproductive effort more evenly across years. Although a bet-hedging strategy decreases the average reproductive output of an individual, by minimising variation in their reproductive success, it can increase an individual’s fitness in certain situations (Slatkin 1974; Starrfelt & Kokko

2012). For example, whilst it may be beneficial to forgo breeding when environmental conditions are poor for a short period of time, if environmental conditions remain the same for an extended time period, it will become less advantageous, even inauspicious to forgo breeding, as the possibility of reproducing in the future under better conditions is low. In the latter part of the study period goshawk abundance has been consistently high, whilst vole densities have been relatively low though still varying cyclically in Kielder Forest. We therefore posit that the changes in owl reproductive decisions we observed are the result of declining food availability, and to a lesser extent increasing predation risk selecting against the eggs in one basket reproductive strategy, in favour of a bet-hedging strategy.

Overall our results suggest that both bottom-up (food availability) and top-down (predation risk) mediated processes can interact to have a combined effect on reproductive strategies and that the reproductive response of individuals to variation in environmental conditions depends on intrinsic factors. However, the extent to which each process influenced reproductive decisions depended on the reproductive decision in question. Although many of our results were in line with previous studies and theoretical predictions, our comprehensive approach highlights the complex nature of how intrinsic and extrinsic trade-offs act in combination to shape tawny owl reproductive decisions. We also provide empirical evidence supporting the terminal investment hypothesis and the hypothesis that top-down and bottom-up processes interact to drive selection on life-history strategies.

Acknowledgements

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CHAPTER 6

GENERAL DISCUSSION

Brood of goshawk chicks which have just been ringed

Thesis summary

The overarching aim of this PhD was to examine the extent to which both top-down (predation) and bottom-up (food) processes shape the population dynamics and demography of a long-lived species, the tawny owl. In Chapter 2, I quantified goshawk predation on tawny owls and examined the extent to which it had changed over the study period. In Chapter 3, I sought to establish what impact changes in food availability and predation risk had on owl population dynamics (including recruitment and immigration). In Chapter 4, I examined the impact of goshawk predation on owl survival, senescence and the strength of life-history trade-offs. Lastly, in Chapter 5, I investigated the impact of variation in food availability and predation risk on owl breeding decisions and reproductive strategies. Before discussing the salient findings of this thesis and their implications, I first address in detail the validity of a key assumption of many analyses, namely that the proxies of predation risk used throughout this thesis were reliable indicators of predation risk. Then I give my interpretation of what the combination of all my results suggest the impact of food availability and predation risk is on: population dynamics, recruitment, immigration, survival, senescence, the strength of life-history trade-offs, breeding decisions and reproductive strategies.

Validation of proxies

Using proxies to test hypotheses is not ideal, however it is often the only option because it is difficult to directly measure how much food is available, the amount of predation occurring and the level of predation risk to which individuals/populations are exposed to in natural systems. Thus one of my first aims was to find suitable proxies for variation in predation/predation risk. Several different proxies of predation risk were used to take into account the fact that both the abundance and location of predator home ranges are likely to influence encounter rates between predators and their prey, hence influence the probability of owls being predated by goshawks. In this thesis I used two temporal proxies for predation risk, total and local goshawk abundance, a spatial proxy of predation risk, distance to the nearest goshawk nest site and connectivity to all goshawk nest sites, this last proxy takes into account both the abundance and location of predators. I found that the per capita predation rate on tawny owls increased over the study period as goshawk abundance increased. Therefore, the assumption that, as goshawks colonised the forest and increased in abundance, predation risk for owls would increase, seemed reasonable. In addition, the tawny owl ring recovery data suggested that the average distance between the nestbox an owl was last seen using and the goshawk nest the ring and carcass of the owl was recovered in was 2.6 km. Furthermore, 72% of owl ring recoveries were found in goshawk nest sites less than 2.6km away from their own territory. This suggests that goshawk predation on owls is fairly localised, hence predation risk is higher for individuals living in relatively close proximity to goshawks. Therefore, using spatial proxies of predation risk such as distance to the nearest predator and connectivity to predators as spatial proxies of predation risk also seemed justifiable.

Overall, in terms of model performance both distance to the nearest goshawk nest site and connectivity to all goshawk nest sites performed less well than temporal proxies of predation risk (local and total goshawk abundance) in the majority of analyses. The relatively poor performance of these spatial proxies of predation risk could plausibly be due to them being based on Euclidean distances which do not take into account the influence of habitat structure on species movements and interactions. Goshawk movement is likely influenced by the location of forest edges, as this is where the majority of hunting takes place (Kenward 1982). Additionally, habitat structure can influence the amount of predation occurring, with smaller predators living in more structured habitat suffering less from predation by larger predators (Finke & Denno 2002; Janssen *et al.* 2007). Consequently, owl predation risk may not only depend on the distance to the nearest goshawk nest site, but also on how close the owls nest site is to the forest edge and whether the habitat is structured in such a way that it might reduce predator-prey encounter rates and consequently predation risk. I posit that although, the movement of avian predators, such as goshawks is seemingly unrestricted by habitat barriers, the relatively poor performance of these spatial proxies of predation risk could be due to Euclidean distances being a poor approximation of ecological distances as highlighted by Sutherland *et al.* (2015).

Alternatively, tawny owls may alter their behaviour to minimise their chance of being predated if they are able to perceive differences in predation risk. Indeed, there is evidence to suggest that raptors can assess predation risk and that they alter their behaviour accordingly. For, example, little owls *Athene noctua* were observed to cease foraging and either stayed still or fled to a nearby safe refuge upon detection of their predators

(Zuberogoitia *et al.* 2008). Additionally, merlins reduced the length of time spent actively hunting and altered their spatial usage of habitat (preferring to hunt close to cover) to reduce their vulnerability to predation by peregrine falcons (Buchanan 2012). Owls are also thought to reduce vocal activity in an attempt to decrease the probability that they will be detected by predators (Rudolph 1978; Crozier *et al.* 2006; Zuberogoitia *et al.* 2008). Therefore, a better understanding of the anti-predator behavioural response of tawny owls to goshawk predation risk and estimates of the ecological distances travelled by both species and their habitat usage would help to clarify this and perhaps identify better proxies of predation risk and improve future studies examining the impact of goshawks on tawny owls.

The impact of food availability and predation risk on population dynamics, recruitment and immigration

The results of a finely parameterised simulation study indicated that changes in vole population cycles would drive the owl population towards extinction (Millon *et al.* 2014). However, my analyses in Chapter 3 suggested that owl population size was unrelated to temporal variation in food availability and predator abundance, at least in the short term. Additional analysis revealed that the apparent stability of the owl population was largely due to an increase in immigration into the study area, a result consistent with the findings of Millon *et al.* (2014) and goshawk predation being selective on owls with a low reproductive value. Although many studies have reported that predation is selective, few have attempted to link such predation biases with their demographic impact. The importance of age-selective predation in determining the overall impact of predators on populations has been raised previously; however, it has hitherto only been examined with respect to differences in predation rates on adult and juvenile age classes (Gervasi *et al.* 2012). Indeed no studies that I are aware of have actually investigated the role that age-selective predation on adults has in determining the overall impact of predation on prey population dynamics under natural conditions. In Chapter 3 I attempted to address this knowledge gap and demonstrated that selective predation on adult age classes does have a strong influence on population dynamics, hence highlighting the importance of selective predation in determining the overall impact of predators on populations. Consequently, the results of this chapter have important implications for conservation management, particularly in North America and Europe, where populations of several large predator species are currently increasing in abundance (Maehr *et al.* 2001; Deinet *et al.* 2013).

In Chapter 3, I found that predation risk interacted with owl food availability to have a combined effect on recruitment of new breeders into the population the following year. Recruitment of new breeders into the population was higher following years when food availability was low and predator abundance high. I hypothesised that the higher proportion of new recruits entering the breeding population was due to fewer breeders surviving to the following year; hence more territories became available for new breeders following years when food was scarce and predator abundance high. The results of my analysis in Chapter 4 provide support for this hypothesis, as the survival of older breeding female owls was estimated to be lower in years when goshawk abundance was high and food availability was low. Therefore the combined effect of declining food availability and increasing predation risk on older owl survival appears to be affecting the recruitment of new breeders into the population the following year, by influencing breeding owl survival, hence the number of territories becoming available.

I also found a positive correlation between owl food availability and the proportion of local recruits entering the population after a 2- and 3-year lag and that the proportion of local recruits entering the breeding population each year declined over the study period; hence, there appeared to be a shortage of local recruits. I hypothesised this was most likely caused by a reduction in owl productivity and juvenile survival due to declining food availability, as juvenile owl survival is positively associated with vole densities (Millon *et al.* 2010, 2014) and owl productivity increases along with food availability in spring (Petty 1987; Millon *et al.* 2010). However, given that: i) I found goshawk predation was selective on juvenile owls (Chapter 3) and ii) predation on owls increased along with goshawk abundance (Chapter 2), I also suspected that goshawk predation on juvenile owls could in part be contributing to the decline in local recruits. Furthermore, if predation risk influences owl breeding decisions it should also impact the number of local recruits available. However, when I analysed juvenile owl survival my results suggested that goshawk predation was not an additive cause of mortality for juvenile owls (Appendix 2). In addition, although I found evidence to suggest that increasing predation risk influenced owl breeding decisions, the impact of predation was relatively small, when compared with the strong positive impact of food availability on owl reproduction. Consequently, the results of my analyses on juvenile survival and owl breeding decisions support the hypothesis that the decline in local recruits entering the population is largely due to the negative impact of declining food availability on juvenile owl survival and reproductive success.

One limitation of the work reported in this thesis is that I only examined the short term effect of fluctuations in food availability and predation risk on owl population size. However, now that the impact of predation and food availability on owl recruitment, survival and breeding decisions/strategies has been quantified, an obvious next step would be to incorporate the functional responses of owls to these extrinsic factors into a stochastic population model, in a manner similar to that done in Millon *et al.* (2014). In addition, given Kielder Forest appears to be a ‘sink’ habitat for tawny owls, it would also be interesting to establish how the dynamics of tawny owl populations in the surrounding area are changing, as this may also affect the stability and persistence of the Kielder Forest owl population, if such populations are acting as source populations.

The impact of variation in predation risk and food availability on survival, senescence and the strength of life-history trade-offs

Despite the common belief that older individuals are more vulnerable to predation, only a handful of studies have actually examined this prediction in wild populations of long-lived species (such as Kunkel & Pletscher 2001; Wright *et al.* 2006). Furthermore, I am unaware of any studies which have investigated whether the observed pattern of age-selective predation could be shaping actuarial senescence in wild populations, despite the fact that the role of predation in shaping senescence has been theoretically debated for several decades (Williams 1957; Abrams 1993; Williams & Day 2003; Williams *et al.* 2006; Caswell 2007). In Chapter 3 I showed that goshawk predation was selective on older owls and in Chapter 4 I found a negative relationship between older owl survival and goshawk abundance. Furthermore, the pattern of senescence in owl survival was inversely related to the age-dependent pattern of predation risk. Together these results provide some of the first empirical evidence supporting the theoretical prediction that age-dependent predation is an extrinsic mechanism that ultimately influences actuarial senescence (Abrams 1993; Caswell 2007). Consequently, the work reported in Chapter 4 has made a valuable contribution towards filling this knowledge gap. Lastly, as far as I am aware this is the only study which has examined whether predation on adult mesopredators occurs with sufficient frequency to impact on adult survival at the population level.

In contrast to the strong impact that increasing predator abundance had on older owl survival, changes in food availability had a relatively small additive effect. This result implies that the proximate change in individuals which makes older owls more vulnerable to predators has a much smaller impact on their foraging ability. There is a large volume of evidence demonstrating that as birds of prey age, they become increasing proficient hunters (Lack 1968; Marchetti & Price 1989; Wunderle 1991; Rutz *et al.* 2006). Given that older individuals have more experience and superior hunting technique, it may compensate for any impact that a decline in physiological condition has on their foraging ability. I can only speculate as to what mechanism makes tawny owls more vulnerable to predation by goshawks as they age, as the probability of observing the capture of tawny owls is very low, due to the elusive behaviour of goshawks. Senescence is thought to occur due to the accumulation of somatic damage (Von Zglinicki 2002; Cawthon *et al.* 2003; Hofer *et al.* 2005 and references therein). Consequently, as individuals age and their physical condition deteriorates, individuals who fall below a certain threshold of condition may be less able to either avoid being detected or physically evade being captured by predators (Mesa *et al.* 1994). Tawny owls do not moult all their flight feathers each year, thus flight feather condition can deteriorate with age, particularly for individuals which breed in consecutive years, as fewer feathers are replaced in years when breeding takes place (Figure 20; Petty 1994). Poor flight feather condition has been linked with an increased risk of being predated (Slagsvold & Dale 1996; Swaddle *et al.* 1996; Lind 2001). Thus, a decrease in feather condition with age could be the proximate mechanism that causes older owls to have a higher risk of being predated. Interestingly, unlike other forms of somatic damage, wear and tear to feather condition can be optionally reversed by moulting, a process linked to whether the individual breeds or not, therefore owls could potentially alter their breeding strategies to improve their feather condition, hence reduce their vulnerability to predation. There is some data available on the number of feather moulted by each individual between consecutive recaptures, as primary flight feathers were permanently marked with picric acid. Consequently, it may be possible to the used this moult data in combination with survival analysis to proximately test the prediction that poor feather condition increases vulnerability to predation. However, I put it forward that the reason for the relatively large impact of predator abundance on older owl survival and the comparatively small impact of food availability is that the decline in physiological condition with age is not sufficient enough to reduce an owls foraging ability, but does impair their ability to escape being captured by agile predators, such as goshawks.

Alternatively, if owl behaviour changes with age it could also be responsible for the increased vulnerability to predation with age. Individuals in poor condition are known to take greater risks and suffer high predation rates (McNamara & Houston 1987, 1994; Sinclair & Arcese 1995; Hays, Kennedy & Frost 2001; Heithaus *et al.* 2007). Consequently, if the decline in condition with age alters the extent to which individuals engage in ‘risky behaviour’ the individual’s survival probability should decrease with age. Several species of owl, including tawny owls, are known to aggressively defend their broods against potential predators (Mikkola 1983; Kontiainen *et al.* 2009). Such defensive behaviour could in theory make these individuals more vulnerable to predation. Thus, if brood defence behaviour intensifies with age, as an individual’s condition and probability of survival declines (i.e. a form of terminal investment), it could explain why the survival of older owls was affected by increasing predator abundance, but not by changes in food availability.

In Chapter 4, I reported evidence to suggest that the full extent of the trade-off between reproduction and survival in later life only becomes apparent when examined in combination with increasing predation risk. Furthermore, the strength of the trade-off between survival and reproduction becomes altered as predation risk increases. In addition, I also found evidence suggesting that owl reproductive strategies varied according to both intrinsic and extrinsic conditions (Chapter 5). Together, these results highlight the importance of considering the role of extrinsic conditions when examining senescence, breeding strategies and life-history trade-offs in future studies.

Figure 20. The extent of wear on tawny owl primary flight feathers when they have not been replaced for more than 2 years. When adults were caught during the breeding season their primary and secondary flight feathers were permanently marked with picric acid (yellow stains), so that we could ascertain which feathers had been moulted and replaced in between subsequent recaptures.

However, the majority of studies investigating senescence and life-history trade-offs in long-lived species have done so in systems, where predators are largely absent or have not examined the role that extrinsic factors play in shaping such life-history trade-offs (for example see Boonekamp *et al.* (2014). Furthermore, studies which have examined how changes in extrinsic conditions, such as increased predation risk affect the trade-off between reproduction and survival, have only examined the short-term effects (i.e. the effect of reproductive decisions on survival within the same or following year). Consequently, the work done during this PhD provides some of the first empirical evidence linking the strength of life-history trade-offs accumulated over a life-time to extrinsic conditions. These results also have important implications for how the results of previous studies examining life-history trades-offs should be interpreted, particularly if they have been conducted under laboratory conditions or in relatively predator-free systems.

Unfortunately, unbiased data on age- and cause-specific owl mortality was not available in sufficient quantity to enable us to estimate age- and cause-specific survival probabilities, hence I was unable to test the hypothesis that extrinsic conditions influence senescence and life-history trade-offs in a more direct way. However, future research could use multi-state, capture-mark-recapture memory models (where states reflect breeding effort) to directly estimate the age-specific survival cost of reproduction and more directly assess how changes in predation risk and food availability influence the cost of reproduction.

The impact of top-down and bottom-up processes on owl breeding decisions and reproductive strategies.

Overall my results suggest that both bottom-up (food availability) and top-down (predation risk) mediated processes interact to have a combined effect on reproductive strategies. However, the extent to which each process influenced reproductive decisions depended on the reproductive decision in question. Unexpectedly, I found that when food availability was scarce, owl breeding propensity was higher when goshawk abundance was relatively high, compared to when it was low. Given that older owls have a low probability of survival when predation risk is high and food scarce (Chapter 4), I posit that the relatively high breeding propensity observed when goshawk are abundant is due to tawny owls responding to having a low probability of surviving (due to these poor environmental conditions) by terminally investing. In further support of the hypothesis that owls terminally invest, older individuals were more likely to breed. A bet-hedging approach can theoretically increase an lifetime reproductive success, under such circumstances (Starrfelt & Kokko 2012). Consequently, I suggest that the overall changes in owl reproduction reported in Chapter 5 are the result of owls switching to a bet-hedging strategy of reproducing more frequently, rather than saving resources to invest in future reproductive attempts, as the probability of them surviving and reproducing in the future is decreased.

A simulation study used to predict how the dynamics of the Kielder Forest owl population would change in response to variation in winter climatic conditions and vole population cycles, suggested that the population was heading for extinction and ascribed the collapse of the owl population to a reduction in breeding propensity (Millon *et al.* 2014). However, this study did not consider that owls could adaptively respond to changes in extrinsic conditions and did not use data collected after 2009, unlike in this thesis. The results of

Chapter 5 suggest that owls are adjusting their reproductive strategies in response to changes in environmental conditions, such that in more recent years, when vole densities have been relatively low, breeding propensity was higher than it was in the past, at comparable vole densities. Consequently, such a change in owl breeding strategies may help to buffer the negative impact of declining vole densities on owl population dynamics. This hypothesis could be further examined using a simulation approach to include the impact that predators have on owl demographic rates, and determine what the optimum breeding strategy is for the current predator/food/climate regime. Additionally, given that my results suggest that breeding propensity is not purely constrained by the amount of food available prior to the breeding season, it would also be interesting to assess whether the benefit of not breeding in a given year has changed over the study period, as this is likely to play a key role in natural selection on owl reproductive strategies.

Final remarks

Owing to the richness of the multi-species data collected in the study site, the work undertaken during this thesis has attempted to untangle the roles that both top-down (predation) and bottom-up (food) processes play in shaping the population dynamics (population size recruitment, immigration) and demography (survival, life-history trade-offs and breeding strategies) of a long-lived species. I show that top-down and bottom-up processes interact to have a combined effect on the population dynamics and demographic rates of individuals of species occupying middle tropic levels. Furthermore, I also demonstrate that the impact that extrinsic factors have on demography depends on attributes intrinsic to the individuals. The work done in this thesis provides empirical support for several long-standing theoretical predictions which have hitherto largely been lacking, most notably the increased vulnerability of old individuals being an extrinsic factor shaping senescence and influencing the strength of life-history trade-offs. Much of the research focusing on senescence and life-history trade-offs has been done in systems where predators were largely absent. Although researchers might have a better understanding of how bottom-up processes affect life-history trade-offs and strategies in predator free systems, I feel that such studies are missing a vital piece of the puzzle, as the work done in this thesis suggests that the full impact of the trade-off between survival and reproduction only became apparent when predation was also considered. Furthermore, my results also provide evidence to suggest that age-selective predation was shaping the pattern of actuarial senescence. As species in natural systems are often subject to one or several main causes of extrinsic mortality, I think that this failure to link the intrinsic trade-off between survival and reproduction with extrinsic causes of mortality, such as predation is potentially a major weakness of this field. Lastly, my results highlight the importance of considering the top-down impact of superpredation on mesopredators, which is particularly important for conservation and wildlife management in both North America and Europe, as several large predator populations are currently increasing in abundance and recolonising their former ranges.

APPENDIX 1

GENETIC MARKERS VALIDATE USING THE NATURAL PHENOTYPIC CHARACTERISTICS OF SHED FEATHERS TO IDENTIFY INDIVIDUAL NORTHERN GOSHAWKS, *ACCIPITER GENTILIS*

Primary feathers moulted by the same female goshawk in subsequent years

Abstract

The recognition of individual animals is essential for many types of ecological research, as it enables estimates of demographic parameters such as population size, survival and reproductive rates. A popular method of visually identifying individuals uses natural variations in spot, stripe or scar markings. Although several studies have assessed the accuracy of these methods in mammals, crustaceans and fish, there have been no attempts to determine whether phenotypic characteristics are accurate when used for birds. Furthermore, few studies have attempted to assess whether shed or moulted body parts are reliable when used to visually identify individuals. Here we assessed the accuracy of using phenotypic characteristics to identify avian individuals using a double-marking experiment, whereby nine microsatellite genetic markers and natural markings on shed feathers were used to independently identify northern goshawks (*Accipiter gentilis*). Phenotypic and genetic identification of individuals was consistent in 94.4% (51/54) comparisons. Our results suggest that the phenotypic characteristics of shed feathers can be reliably used as a non-invasive and inexpensive technique to monitor populations of an elusive species, the northern goshawk, without having to physically re-capture or re-sight individuals. We posit that using natural markings on shed feathers will also be a reliable method of identifying individuals in avian species with similar phenotypic characteristics, such as other *Accipiter*s.

Introduction

Many areas of ecological and conservation research require individuals to be uniquely identifiable so that population sizes, dispersal, survival, reproduction and immigration rates can be estimated (Goodall 1986; Nichols 1992) and also for behavioural studies (Grellier *et al.* 2003; Weir 2009). Individuals can be made recognisable by applying various types of artificial marks or tags. However, the process of capturing individuals and applying such marks can be invasive, expensive, risky, time consuming and can affect the behaviour of the marked individual and its survival probability (Walker *et al.* 2012). A less invasive method uses natural variation in phenotypic characteristics, such as stripe, spot or scar patterns to identify individuals (Pennycuick 1978; Goodall 1986; Friday & Smith 2000). Photographs of natural markings taken by camera traps is a particularly important method of identifying individuals in studies on large predators, whose wide-ranging and elusive behaviour makes it difficult to gather re-capture data or re-sighting data by eye (Trolle &

Kéry 2003; Karanth *et al.* 2006; Ariefiandy *et al.* 2013). Although the use of natural markings and camera traps to collect photo-ID re-sighting data works well for some species, for several practical reasons the use of camera traps is rarely used in avian studies requiring the identification of individuals.

The phenotypic characteristics of moulted feathers has been used to identify individuals of elusive birds, without having to physically recapture or re-sight them by eye, or using camera traps. Natural markings on feathers moulted by several *Accipiter* species are thought to be stable (i.e. do not change over an individual's lifespan after the first moult) and vary enough between individuals to enable individuals to be identified, once in adult plumage (Opdam & Muskens 1976). However, none of the 19 studies using this method of natural markings on shed feathers to identify individuals in *Accipiter* populations attempted to validate the method independently (for example see Rutz 2012, Saga and Selås 2012). It is important to assess the accuracy of phenotypic methods used to identify individuals because of the wide range of studies, across several disciplines that rely on accurate identification of individuals. For example, individual identities are used to develop and evaluate conservation management strategies for tigers (*Panthera tigris*; Karanth *et al.* 2006). The probability of incorrectly identifying two individuals as the same (a false positive error) or of classifying two individuals as different, when in fact they are the same (a false negative error) has been long recognised (Bateson 1977). Yet, compared to the number of studies which used natural markings to identify individuals, there have been relatively few attempts to validate this method or to calculate the associated error rates (Stevick *et al.* 2001; Gosselin, Sainte-Marie & Sevigny 2007; Gubili *et al.* 2009; Waye 2013). Error rates can vary dramatically. For example, natural variation in pigmentation and scars correctly identified individual humpback whales (*Megaptera novaeangliae*; Stevick *et al.* 2001) in 96.6% of cases; however the method of using colour and spot patterns to identify tiger salamanders (*Ambystoma tigrinum*) was only accurate 67% of the time (Waye 2013). This 10-fold variation in error rates, from excellent to effectively useless suggests a strong need to validate the different types of phenotypic characteristics used to identify individuals, for each taxonomic group, before they are used to estimate demographic parameters.

‘Double marking’, the use of two independent methods of identifying individuals, is one way to test the reliability of phenotypic characteristics as individual identifiers (Stevick *et al.* 2001; Gosselin *et al.* 2007; Gubili *et al.* 2009). Microsatellites are neutral genetic markers used to identify individuals (Chistiakov, Hellemans & Volckaert 2006) and have been used as an independent, unbiased and individually-fixed arbiter of the accuracy of phenotypic characteristics in double marking studies on cetaceans, crustaceans and fish (Stevick *et al.* 2001; Gosselin *et al.* 2007; Gubili *et al.* 2009). However, we are not aware of any double marking studies validating the use of phenotypic characteristics in avian species to identify individuals. Furthermore, there have been few studies which have used double marking to validate the use of shed body parts for individual identification (Gosselin *et al.* 2007).

Northern goshawk *Accipiter gentilis* (hereafter goshawk) is an elusive avian predator, difficult to observe in its wooded habitat and adults are difficult and time-consuming to physically capture. Although 13 studies have used natural markings on shed feathers to identify individual goshawks (e.g. Rutz 2012), none have attempted to validate the method independently. Five microsatellite markers have already been shown to uniquely identify individuals using blood samples taken from known individuals (Bayard de Volo *et al.* 2005). Here we use nine microsatellite markers to genetically characterise, and if possible, identify individual goshawks from a population in north east Scotland, UK and use this method to assess the accuracy of using phenotypic characteristics of shed feathers as an identification tool.

Methods

Feather collection & phenotypic identification

Female goshawks start moulting their flight feathers during the egg laying period, and males soon after. During the incubation period (April-May) many of the inner primary feathers shed by females (and a few from males) can be found by searching below occupied nests and nearby perches. Shed feathers were collected from a goshawk population in north east Scotland, centred on 57° 3’N, 2° 30’W (map p.138 in Marquiss 2011) and stored at room temperature in paper envelopes filed according to locality, year and date of collection.

The present study used only the inner primary feathers moulted by adult breeding female goshawks. The shape of each feather was used to determine which particular part of the wing sequence it was from (i.e. P1 to P5). We used the total feather length and width of calamus to sex the individual it came from, as comparable wing feathers moulted by male and female goshawks differ in size, the females being larger (Cieslak & Dul 2006). Only feathers shed by mature individuals were included because the colour changes during the transition from immature (1 year old) to mature (over 2 years old) plumage (Opdam & Muskens 1976). The feathers of immatures are those grown simultaneously in the nest and are brown, fringed with buff, whilst those of mature birds (produced in sequence from the first moult) are plain grey, some with pale fringes; clearly different from those of yearlings (Cieslak & Dul 2006). To visually identify adult individuals we compared feathers from the same wing and position within the primary sequence, from year to year (e.g. P2 illustrated in Figures 21, 22) using three phenotypic characteristics; length, colour and pattern of pigmentation as described in Opdam & Muskens (1976).

Genetic identification

DNA was extracted from a 3-5mm clipping from the tip of the lower calamus, using a standard salt extraction protocol with a 100% ethanol precipitation following the methods in Hogan *et al.* (2008). All samples were genotyped at nine microsatellite loci (seven of which, Age2; Age4; Age5; Age7; Age9; Age10 and Age11 are described in Dawnay *et al.* (2009), and the remaining two, AgCA224 and AgCA365, in Takaki *et al.* (2008). These particular loci were chosen to maximise power for individual identity, as they were the most polymorphic microsatellite markers. PCR amplifications were performed in a 10µl total reaction volume containing: 2µl of extracted DNA, 1 x reaction Buffer (Bioline), 0.2mM of each dNTP, 0.25 U *Taq* DNA polymerase (Bioline), 1.5 mM $MgCl_2$ and 1 µM primer using a G-Storm thermal cycler. Genotypes were resolved on an automatic ABI 3730 Capillary DNA sequencer (DNA Sequencing and Services, MRCPPU, College of Life Sciences, University of Dundee, Scotland, http://www.dnaseq.co.uk). Allele size was determined by eye using Genemarker 1.4 (Soft Genetics).

We checked all genotyping scores for errors resulting from the presence of null alleles (one or more alleles failing to amplify), stuttering (changes to allele sizes during PCR) and large allele drop out (large alleles not amplifying as efficiently as smaller alleles) using

Microchecker 2.2.1, (Van Oosterhout, Hutchinson, Wills & Shipley 2004). The rate of genotyping error was estimated by re-genotyping eight samples (9% of the data) at all loci and error rates were calculated from the number allelic mismatches.

We calculated the probability of individual identity, *P*(ID) as the probability that two individuals, drawn at random from a population will share the same genotypic profile, according to Waits, Luikart, & Taberlet, (2001) for all nine loci using Genalex 6.501 (Peakall & Smouse 2006). $P(\mathrm{ID})_{\mathrm{sib}}$ represents the upper boundary of *P*(ID) (where siblings are found and included; Waits, Luikart, & Taberlet 2001) and $P(\mathrm{ID})_{\mathrm{unbiased}}$ represents the lower boundary of a theoretical *P*(ID), after sample size corrections (Paetkau *et al.* 1998). We included both boundaries as the true *P*(ID) has been demonstrated to fall somewhere between these two, with $P(\mathrm{ID})_{\mathrm{sib}}$ providing a reliable conservative estimate of the upper boundary, assuming that the population studied does not deviate from Hardy-Weinberg expectations (Waits *et al.* 2001). Departures from Hardy–Weinberg equilibrium (HWE) were tested for using a Markov Chain Monte Carlo approach (1000 de-memorisations, 100 batches, 1000 iterations) in GENEPOP 4.0.10 (Raymond & Rousset 1995; Rousset 2008) incorporating a Bonferroni correction ($\alpha = 0.005$).

Validation of phenotypic method

We used 83 feathers collected over a 15 year period, from 26 nesting territories occupied by goshawks. We compared feathers collected at the same location, but in different years, as goshawks in the UK are resident, persistently use the same nesting woods and only breed once a year, hence are unlikely to be represented at multiple sites in the same year (Kenward 2006). Phenotypic identification was carried out by MM using the measures described by Opdam & Muskens (1976) and preceded genetic identification, carried out by RB. Both methods were applied independently and as a double blind test to reduce any potential bias. No results were exchanged until after the genetic analysis was complete.

Results & discussion

We were able to genotype 98.8% (82/83) of our feather samples. Aside from a failed amplification, there were no genotyping errors and we did not detect any null alleles or large allelic dropout at any locus. Between 2 and 13 alleles were scored per locus, with $P(\mathrm{ID})_{\mathrm{unbiased}}$ for all loci estimated as 5.8×10^{-8} and $P(\mathrm{ID})_{\mathrm{sib}}$ as 1.1×10^{-3} (Table 12), meaning that the probability of two individuals sharing the same multilocus profile was less than 0.0001. Genetic markers suggested that these 82 samples came from 37 unique individuals. Of the 54 comparisons made between pairs of samples collected at the same goshawk nest territory, 36 were phenotypically identified as being samples from the same individual (see Figure 21 for an example); the remaining 18 comparisons were phenotypically identified as being samples from different individuals (see Figure 22 for an example). Phenotype-based and genetic assignments of individuals matched in 51 (94.4%) comparisons. Of the three discrepancies found, one was a false positive (i.e. two samples were thought to have come from the same individual based on phenotypic characteristics, but were genetically assigned as different individuals); the other two discrepancies were false negatives (i.e. where two samples were phenotypically identified as coming from different individuals, yet were from genetically identical individuals). The false positive and false negative error rates were therefore 97.2% and 88.9% respectively. The phenotypic method of identifying individual goshawks from shed feathers described by Opdam & Muskens (1976) therefore appears to be reliable. Consequently, despite goshawks being elusive, changes in the individuals occupying nest sites can be reasonably accurately monitored using this inexpensive phenotypic technique, without further recourse to genotyping.

Overall our results suggest that phenotypic characteristics of shed feathers are a reliable method of identifying individual goshawks, and may be similarly accurate for other species, such as Eurasian sparrowhawks *Accipiter nisus*, thought to show a similar level of variation in feather characteristics (Opdam & Muskens 1976). Furthermore, now that the error rate of using the phenotypic method has been quantified, it can be accounted for in future studies that use this phenotypic method and when evaluating the status of populations and planning management strategies. These error rates may also be used to calculate the degree of confidence one can have when interpreting the results of previous studies using this phenotypic method.

Author contributions

S. Hoy & M. Marquiss designed the research. M. Marquiss collected all field samples. R. Ball carried out all genetic analysis. S. Hoy and R. Ball wrote the first draft and X. Lambin, D. Whitfield and M. Marquiss contributed to revisions.

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Table 12. Probability of identity estimates for nine microsatellite markers for *A. gentilis*. N_A number of alleles, * cumulative values for P(ID).

Locus	N_A	P (ID)$_{unbiased}$	P (ID)$_{sib}$	P (ID)$_{unbiased}$*	P (ID)$_{sib}$ *
Age 2	10	5.8×10^{-2}	3.6×10^{-1}	5.8×10^{-2}	3.6×10^{-1}
Age 4	13	4.2×10^{-2}	3.4×10^{-1}	2.4×10^{-3}	1.2×10^{-1}
Age 5	5	3.3×10^{-1}	6.0×10^{-1}	8.0×10^{-4}	7.1×10^{-2}
Age 7	5	1.3×10^{-1}	4.2×10^{-1}	1.0×10^{-4}	3.0×10^{-2}
Age 9	2	3.9×10^{-1}	6.1×10^{-1}	4.2×10^{-5}	1.8×10^{-2}
Age 10	8	1.0×10^{-1}	4.2×10^{-1}	4.5×10^{-6}	7.8×10^{-3}
Age 11	4	2.4×10^{-1}	5.3×10^{-1}	1.1×10^{-6}	4.2×10^{-3}
AG CA224	4	2.7×10^{-1}	5.5×10^{-1}	3.1×10^{-7}	2.3×10^{-3}
AG CA365	5	1.8×10^{-1}	4.8×10^{-1}	5.8×10^{-8}	1.1×10^{-3}

Figure 21. Moulted female *Accipiter gentilis* inner primary feathers collected at the same nest site location, in subsequent years, assigned as belonging to the same individual based on their phenotypic characteristics (length, shape, colour and pattern of pigmentation).

Figure 22. Four female *Accipiter gentilis* inner primary feathers collected at the same nest site in different years, thought to have been moulted by different individuals based on their phenotypic characteristics (length, shape, colour and pattern of pigmentation).

APPENDIX 2

Effect of predators and food availability on juvenile tawny owl survival

Background information & Methods

Understanding the many factors which influence juvenile survival is important as they will also impact recruitment and ultimately population dynamics. Predation is a major cause of natural mortality in wild populations (Sullivan 1989; Sandercock *et al.* 2011) and therefore one extrinsic factor likely to influence juvenile survival. Starvation is also a major cause of natural mortality; hence the availability of food is also likely to influence juvenile survival. Here we quantify the impact that temporal variation in food availability and predator abundance has on juvenile survival in a population of tawny owls in Kielder Forest, northern England.

Goshawks are the main predator for tawny owls in our study site and previous work has shown that goshawk predation was selective on newly fledged owls (Chapter 3; Coles and Petty 1992, Koning *et al*. 2009). The extent of goshawk predation on tawny owls was found to increase as the Kielder Forest goshawk population increased in abundance (Chapter 2). Therefore we used goshawk abundance as one temporal proxy for predation risk, and included it as a yearly covariate (i.e. with the same value for all owls in a given year) in the analysis. We used two additional spatial proxies for goshawk predation risk: distance from an owl's nest to the nearest occupied goshawk nest site and connectivity of an owl's nest to all occupied goshawk nest sites, as the probability of being predated is also likely to depend on how predator and prey species are distributed spatially relative to one another. Distance to the nearest goshawk nest site and connectivity of an owls natal territory to all goshawk nest sites were calculated for every individual, and modelled as an individual covariate, in the same way as done in (Chapter 4 and Chapter 5). As proxies of predation risk are not independent of each other, the effect of each was examined in separate models to avoid any issues caused by any multi-collinearity.

Variation in autumn densities of field voles has previously been shown to impact juvenile tawny owl survival (Millon, Petty & Lambin 2010; Millon *et al.* 2011, 2014). Consequently, in order to assess the impact of goshawk predation on juvenile survival, we compared models which included proxies for goshawk predation risk with one which only included a measure of food availability, autumn vole densities. Vole densities were averaged across the whole study area and fitted as an annual temporal covariate as done by (Millon *et al.* 2010, 2011, 2014). As recapture data was not available for males throughout the study period, our analysis of juvenile owl survival was based on data from female owls only, ringed as chicks between 1980 and 2012 (N=1,241), with the last recapture of individuals in 2013. Thus, the exact age of all individuals was known. Juvenile owls cannot be accurately sexed without molecular analyses. Consequently, the sex of individuals never recaptured as adults or sexed as chicks using DNA was unknown. As the sex ratio of chicks born in our study site was even 1:1 (N =312, over 4 years; Appleby *et al.* 1997), half the number of chicks born each year minus the number known to be female, were randomly assigned as females, as done in previous analyses (Nichols *et al.* 2004; Millon *et al.* 2010). The rest of these chicks were assumed to be males and excluded from the analysis. Owls are only recaptured when breeding and the probability of owls starting to breeding varies between ages 1-4 (Millon *et al.* 2010). Recapture probabilities were therefore modelled as time-dependent and age-specific [(1, 2–3, 4+)] as done in Millon, Petty & Lambin (2010). This analysis was carried out in E-SURGE version 1.9.0 (Choquet *et al.* 2009). Goodness-of-fit tests were carried out in U-CARE 2.3.2 (Choquet *et al.* 2005) and over-dispersion was accounted for by adjusting the *c-hat* to 2.01. Model selection was based on Quasi-Akaike's information criterion corrected for small sample size (QAICc; Burnham & Anderson 2002).

Results & discussion

On average 1st year survival was estimated to be 0.19. Autumn vole densities explained the most variation in juvenile survival (slope on logit scale: $\beta = 0.5 \pm 0.16$, %Dev = 39) and the model including only autumn vole densities as a temporal covariate was the most parsimonious, performing better than all other models, including those testing for either an additive or interactive effect of autumn vole densities and goshawk abundance (see Table 13; QAICc = 1.06 and 2.09 respectively). Therefore, juvenile owl survival appeared to be unrelated to increasing predation risk, which suggests that predation is not an additive cause of mortality for owls in their first year of life.

Table 13. Model selection for annual survival of female tawny owls in their first year of life. Recapture probability was modelled as [a(1,2-3,4+)+t]. The most parsimonious model is indicted by bold text.

Models	Deviance	*np*	ΔQAIC
Constant	2730.43	38	15.23
Food	**2695.61**	**39**	**0.00**
Goshawk abundance	2726.31	39	15.27
Distance to nearest goshawk	2729.52	39	16.87
Connectivity to goshawks	2730.35	39	17.28
Food + goshawk abundance	2693.53	40	1.06
Food + distance to nearest goshawk	2694.86	40	1.72
Food + connectivity to goshawks	2694.88	40	1.72
Food x goshawk abundance	2691.39	41	2.09
Food x distance to nearest goshawk	2694.48	41	3.62
Food x connectivity to goshawks	2694.79	41	3.78

APPENDIX 3

Appendix 3a

List of the species recorded as being killed by northern goshawks and the number of each species killed in the early (1975-1996) and the late (1997-2014) part of the study period, along with the body mass used to estimate their % biomass contribution to goshawk diet and the taxonomic prey group each species was assigned to.

Common name	Mass (g)	Prey group	Total early period	Total late period
Barn owl (*Tyto alba*)	300	Raptor	0	14
Black grouse (*Tetrao tetrix*)	1065	Game	5	0
Blackbird *(Turdus merula)*	100	Other	40	36
Black-headed gull (*Chroicocephalus ridibundus*)	290	Other	7	0
Blue tit (*Parus caeruleus*)	10.5	Other	1	0
Budgerigar (Melopsittacus undulatus)	35	Other	1	0
Carrion crow/rook (*Corvus corone/Corvus*	510	Corvid	915	214
Chaffinch (*Fringilla coelebs*)	24	Other	47	25
Coal tit (*Periparus ater*)	9	Other	11	1
Collared dove (*Streptopelia decaocto*)	200	Pigeon	0	1
Common buzzard (*Buteo buteo*)	890	Raptor	0	2
Common frog (*Rana temporaria*)	22.7	Other	1	1
Common gull (*Larus canus*)	400	Other	1	0
Common kestrel (*Falco tinnunculus*)	208	Raptor	151	77
Common lizard (*Zootoca vivipara*)	4	Other	4	0
Common shrew (*Sorex araneus*)	9.5	Mammal	1	0
Common toad (*Bufo bufo*)	55	Other	2	0
Crossbill (*Loxia curvirostra*)	43	Other	25	16
Cuckoo (*Cuculus canorus*)	120	Other	2	2
Curlew (*Numenius arquata*)	985	Other	10	0
Domestic chicken (*Gallus gallus domesticus*)	1900	Other	0	1
Eurasian jay (*Garrulus glandarius*)	170	Corvid	93	81
Eurasian bullfinch (*Pyrrhula pyrrhula*)	21	Other	1	0
European hare (*Lepus europaeus*)	3500	Mammal	3	0
European rabbit (*Oryctolagus cuniculus*)	1600	Mammal	172	80
Feral pigeon (*Columba livia*)	300	Pigeon	1522	240
Field vole (*Microtus agrestis*)	30	Mammal	62	5
Fieldfare (*Turdus pilaris*)	100	Other	6	20
Red-legged partridge (*Alectoris rufa*)	490	Game	14	2
Goldcrest (*Regulus regulus*)	6	Other	1	3
Great spotted woodpecker (*Dendrocopos major*)	85	Other	1	19
Great tit (*Parus major*)	18.5	Other	2	0

Common name	Mass (g)	Prey group	Total early period	Total late period
Green woodpecker (*Picus viridis*)	190	Other	0	1
Grey squirrel (*Sciurus carolinensis*)	552.5	Mammal	0	1
Jackdaw (*Corvus monedula*)	220	Corvid	50	12
Kittiwake (*Rissa tridactyla*)	410	Other	0	2
Lapwing (*Vanellus vanellus*)	230	Other	4	1
Lesser black-backed gull (*Larus fuscus*)	830	Other	2	0
Lesser redpoll (*Acanthis cabaret*)	11	Other	1	1
Long-eared owl *(Asio otus*)	290	Raptor	6	11
Magpie (*Pica pica)*	220	Corvid	3	10
Mallard (*Anas platyrhynchos*)	1090	Other	7	6
Meadow pipit/tree pipit	19	Other	47	12
Merlin (*Falco columbarius*)	205	Raptor	13	1
Mistle thrush (*Turdus viscivorus*)	130	Other	115	85
Mole (*Talpa europaea*)	100	Mammal	0	1
Moorhen (*Gallinula chloropus*)	320	Other	0	1
Newt (*Triturus vulgaris*)	30	Other	0	1
Northern goshawk (*Accipiter gentilis*)	1000	Raptor	5	8
Oyster catcher (*Haematopus ostralegus*)	540	Other	1	0
Pheasant (*Phasianus colchicus*)	1190	Game	62	34
Pied wagtail (*Motacilla alba*)	21	Other	1	0
Pygmy shrew (*Sorex minutus*)	4	Mammal	1	0
Rat (*Rattus norvegicu*s)	360	Mammal	0	2
Raven (*Corvus corax*)	1200	Corvid	1	0
Red grouse (*Lagopus lagopus scotica*)	600	Game	561	70
Red squirrel (*Sciurus vulgaris*)	200	Mammal	108	87
Redshank (*Tringa totanus*)	120	Other	1	1
Robin (*Erithacus rubecula*)	18	Other	13	3
Short-eared owl (*Asio flammeus*)	330	Raptor	22	1
Siskin (*Carduelis spinus*)	15	Other	15	5
Skylark (*Alauda arvensis*)	38.5	Other	1	1
Snipe (*Gallinago gallinago*)	110	Other	5	5
Song thrush (*Turdus philomelos*)	83	Other	105	68
Sparrowhawk (*Accipiter nisus*)	205	Raptor	26	22
Starling (*Sturnus vulgaris*)	78	Other	28	8
Stoat (*Mustela erminea*)	266.25	Mammal	2	0
Swallow (*Hirundo rustica*)	18.5	Other	2	0
Tawny owl (*Strix aluco*)	470	Raptor	39	67
Teal (Anas crecca)	330	Other	1	0
Tree creeper (*Certhia familiari*s)	10	Other	0	1
Weasel (*Mustela ni*valis)	90.25	Mammal	16	0
Whinchat (*Saxicola rubetra*)	17	Other	1	0
Willow warbler (*Phylloscopus trochilus*)	10	Other	1	2
Wood pigeon (*Columba palumbus*)	450	Pigeon	1431	530
Woodcock (*Scolopax rusticola*)	280	Other	37	23

Appendix 3b

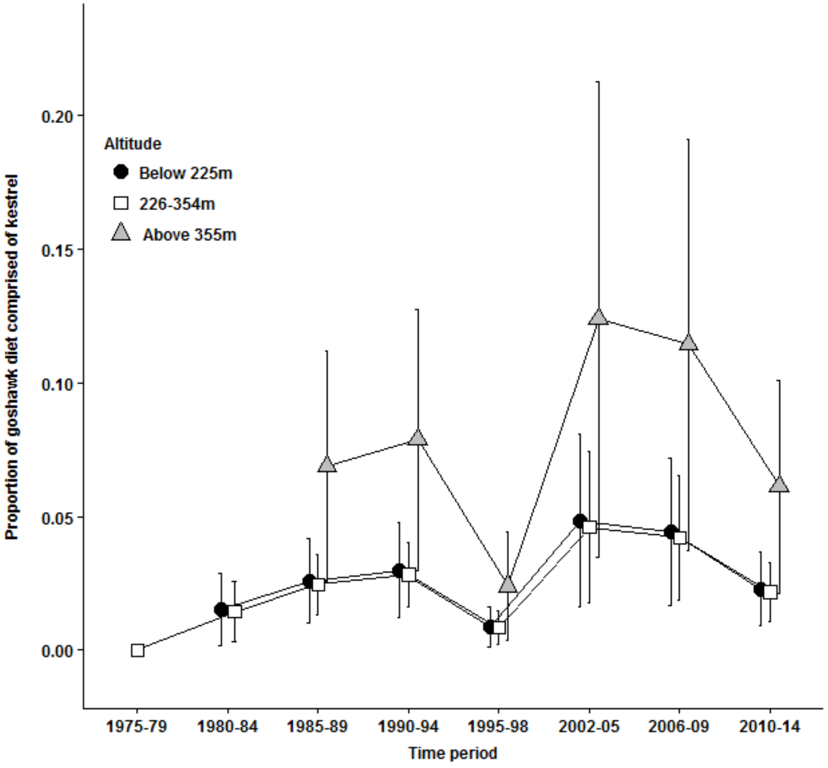
Difference in the occurrence each prey group and each raptor species in goshawk diet between the spring (March to May) and summer (June-August).

Prey group	March-May *n*	June-August *n*	March-May % frequency	June-August % frequency	March-May % biomass	June-August % biomass
Pigeon	630	3094	41.89	49.43	35.91	45.22
Corvid	105	1274	6.98	20.35	7.16	22.11
Game	233	515	15.49	8.23	24.83	13.26
Mammal	163	378	10.84	6.04	22.68	11.96
Raptor	94	371	6.25	5.93	4.11	4.41
Other	279	627	18.55	10.02	5.3	3.05
Total	1504	6259	100	100	100	100

Species	March-May *n*	June-August *n*	March-May % frequency all species	June-August % frequency all species	March-May % biomass all species	June-August % biomass all species	March-May % of all raptors	June-August % of all raptors
Common kestrel	41	186	0.66	12.37	0.33	6.01	43.62	52.1
Tawny owl	16	90	0.26	5.98	0.29	6.57	17.02	25.21
Sparrowhawk	13	35	0.21	2.33	0.1	1.11	13.83	9.8
Short-eared owl	10	13	0.16	0.86	0.13	0.67	10.64	3.64
Barn owl	5	9	0.08	0.6	0.06	0.42	5.32	2.52
Long-eared owl	5	12	0.08	0.8	0.06	0.54	5.32	3.36
Merlin	3	11	0.05	0.73	0.02	0.35	3.19	3.08
Common buzzard	1	1	0.02	0.07	0.03	0.14	1.06	0.28
Total	94	357	1.52	23.74	1.02	15.81	100	100

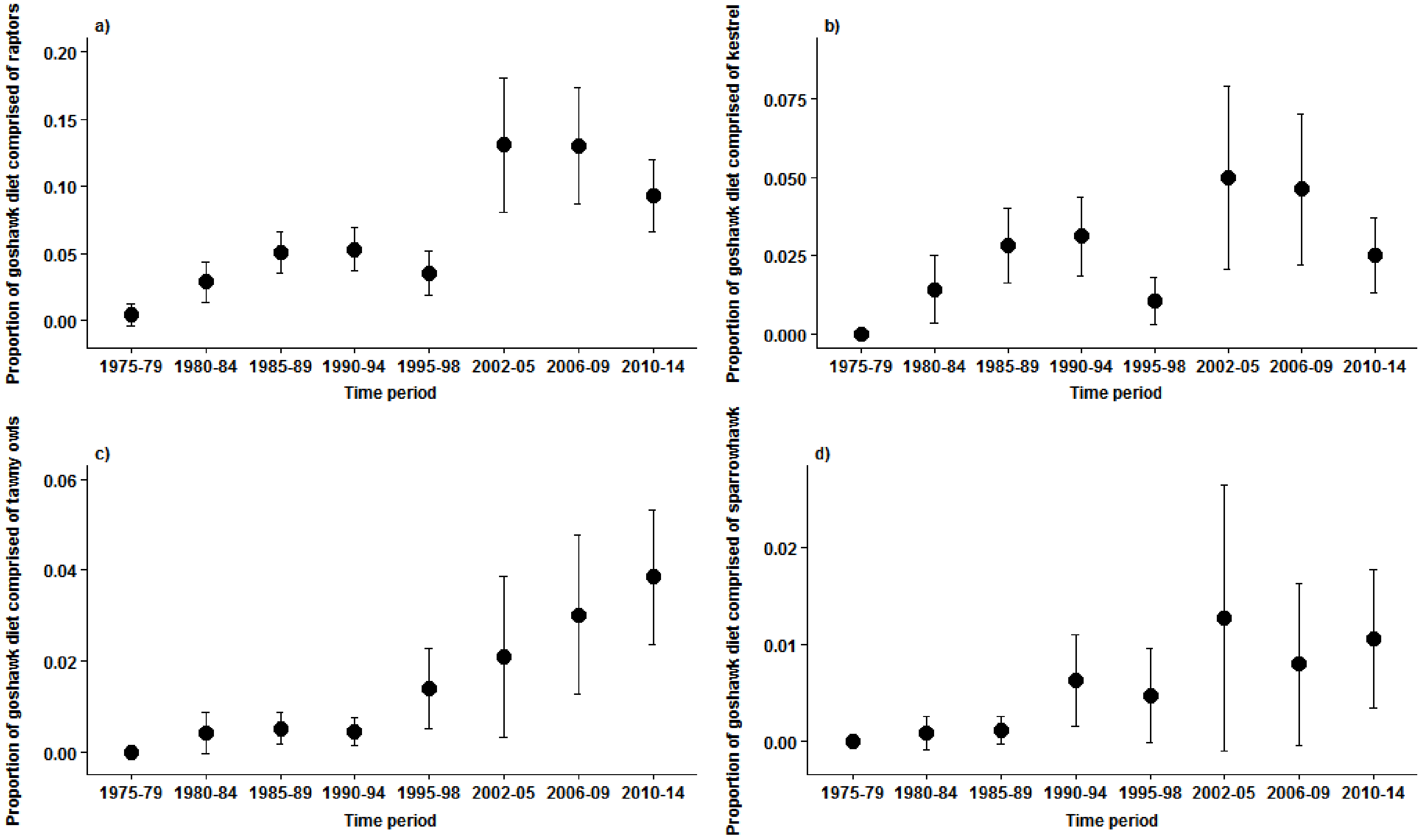
Appendix 3c

Variation in the proportion of goshawk diet comprised of kestrels during in the breeding season, for goshawks with home-ranges at different altitudes and averaged over 4-5 year periods.



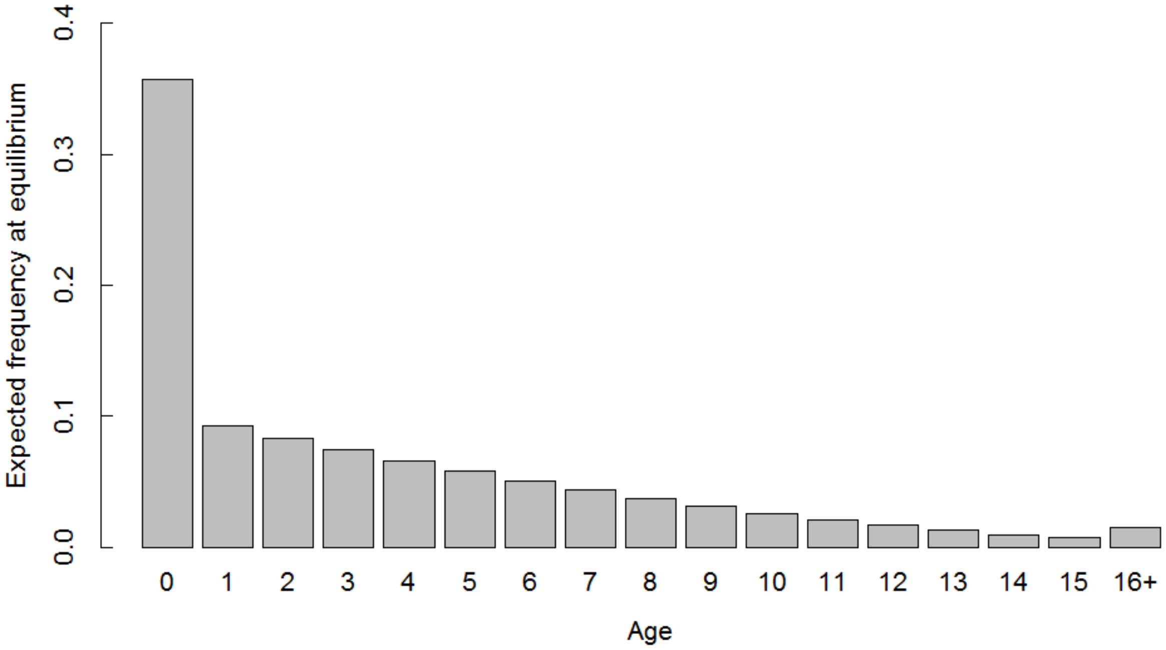
Appendix 3d

Changes in the proportion of goshawk diet comprised of a) all raptor species; b) kestrel; c) tawny owl and d) sparrowhawk during the breeding season, averaged over 4-5 year periods.



APPENDIX 4

Appendix 4a



The expected age distribution of the tawny owl population at equilibrium predicted by the population matrix model in Appendix 4b.

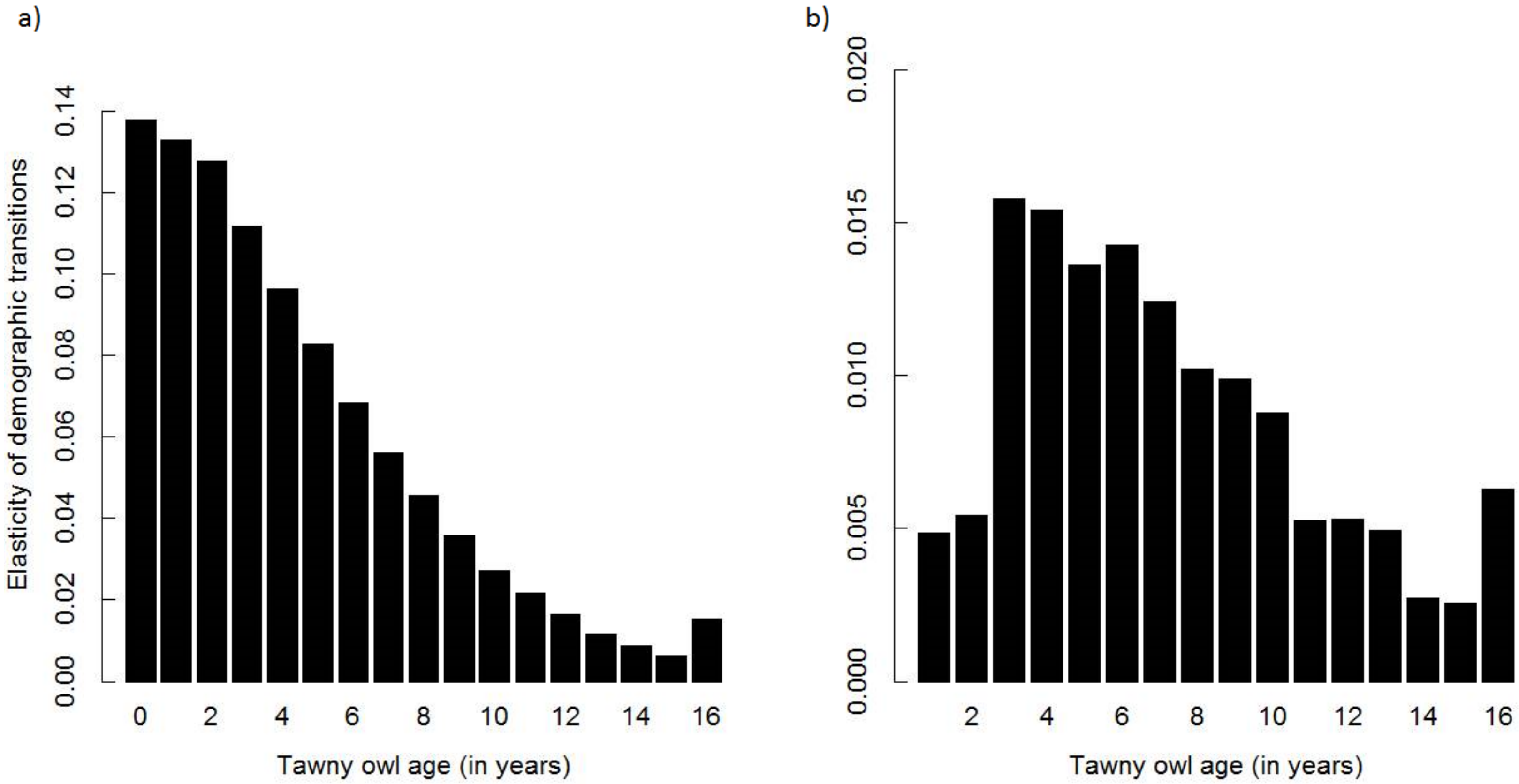
Appendix 4b

$$\begin{pmatrix} Nj \\ Na1 \\ Na2 \\ Na3 \\ Na4 \\ Na5 \\ Na6 \\ Na7 \\ Na8 \\ Na9 \\ Na10 \\ Na11 \\ Na12 \\ Na13 \\ Na14 \\ Na15 \\ Na16 \end{pmatrix} t+1 = \begin{pmatrix} S0.pb.psb1.f1 & S1.pb.psb2.f2 & S2.pb.psb3.f3 & S3.pb.psb4.f4 & S4.pb.f5 & S5.pb.f6 & \dots & S15.pb.f16 & S16.pb.f16 \\ S0 & 0 & 0 & 0 & 0 & 0 & \dots & 0 & 0 \\ 0 & S1 & 0 & 0 & 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & S2 & 0 & 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & 0 & S3 & 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & 0 & 0 & S4 & 0 & \dots & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & S5 & \dots & 0 & 0 \\ . & . & . & . & . & . & \dots & . & . \\ . & . & . & . & . & . & \dots & . & . \\ . & . & . & . & . & . & \dots & . & . \\ . & . & . & . & . & . & \dots & . & . \\ . & . & . & . & . & . & \dots & . & . \\ . & . & . & . & . & . & \dots & . & . \\ . & . & . & . & . & . & \dots & . & . \\ . & . & . & . & . & . & \dots & . & . \\ 0 & 0 & 0 & 0 & 0 & 0 & \dots & S16 & S16 \end{pmatrix} = \begin{pmatrix} Nj \\ Na1 \\ Na2 \\ Na3 \\ Na4 \\ Na5 \\ Na6 \\ Na7 \\ Na8 \\ Na9 \\ Na10 \\ Na11 \\ Na12 \\ Na13 \\ Na14 \\ Na15 \\ Na16 \end{pmatrix} t$$

A post-breeding population matrix model with 17 age classes (juvenile and ages 1-16 years old) representing the tawny owl population of Kielder Forest. S0-S16 denotes age-specific survival probability, where S0 = 0.26 and is the probability of juvenile survival, adult survival estimates (S1-16) are the age-specific survival of females averaged over years of high and low vole densities calculated by Millon, Petty and Lambin (2010). Age specific fecundities were calculated based on several parameters. *f*1-16 (*f*1 = 0.975; *f*2 = 0.99, *f*3 = 1.23, *f*4 = 1.12, *f*5 = 0.95; *f*6 = 1.15; *f*7 = 1.11; *f*8 = 1.03; *f*9 = 1.13; *f*10 = 1.16; *f*11 = 0.83; *f*12 = 1; *f*13 = 1.15; *f*14 = 0.82; *f*15 = 1; *f*16 = 0.98) are the age-specific average number of daughters produced per female. pb is the probability of breeding (which was constant for all ages). It was estimated as 0.68, the average probability of breeding between 1987 and 1998. Fecundity estimates for owls aged 1-4 years old also included an age specific probability of starting breeding (psb) estimated as (psb1 = 0.14, psb2 = 0.32, psb3 = 0.8, psb4 = 0.94) calculated by Millon, Petty and Lambin (2010).

Appendix 4c

Estimates of age-dependent elasticities of an age structure matrix model representing demographic transitions for (a) survival and (b) fecundity for the Kielder Forest tawny owl population between 1987 and 1998.



APPENDIX 5

Appendix 5a

Method for calculating individual proxies of predation risk

Encounter rates between predators and prey species can be influenced by how both species are distributed spatially, relative to one another. For example, some individuals may be living in relatively close proximity to, and have a high risk of being preyed upon by many predators, whilst others may have fewer predators living nearby and hence a much lower overall risk of being preyed upon. Therefore in our analysis we used two spatial proxies of predation risk, distance from an owls nest site to the nearest predator and connectivity of an owls nest site to all predators, both fitted as individual covariates.

Distance to the nearest predator

The distance between every occupied owl nestbox and all goshawk nest sites occupied in the same year was calculated in metres, using ArcMap 10 (ESRI 2011). Nest locations were used as a proxy for the centre of activity for owls and goshawks during the breeding season. For each individual, the distance to the nearest goshawk nest site was calculated for each year that an owl was known to be alive. These values were then averaged over the years each individual spent in each age/breeding-class to give an average estimate of the age-specific distance to the nearest goshawk.

Connectivity to predators

The connectivity index *S* as described by Hanski (1994) was used to calculate how well each owl territory was connected to all goshawk nest sites, using the below formula proposed,

$$S_i = \sum \exp(-\alpha d_{ij})$$

where S_i is the connectivity of a tawny owl territory to all the surrounding goshawk nest sites. d_{ij} is a matrix of the distances in km *d*, between owl nestbox *i* and goshawk nest site *j*, this is then weighted by α following a negative exponential. In this study, we fixed the value of α to reflect the distances goshawks travelled to predate owls. During the study period, 50 tawny owl rings have been recovered in goshawk nest sites (Chapter 3). These tawny owl ring recoveries were used to estimate the distances goshawks travelled to predate owls, i.e. the distance between the nestbox an owl was last observed using and the goshawk nest site the ring was recovered in. The distance between the nestbox an owl was last observed using and the goshawk nest site the ring was recovered in was estimated for 46 of the owl rings recovered. 29 (63 %) of recoveries were predated by goshawks nesting less than 2 km away from their nest boxes, and 42 (91 %) were predated by birds less than 4km away. The average distance a goshawk travelled to predate an owl was 2.6 km (± SE 0.32 km). Based on the distribution of these 46 owl ring recovery distances, we estimated that the influence each goshawk nest site had on the probability of an owl being predated halved at a 1.4 km (α =0.49). These spatial covariates of predation risk assumed nest locations were the activity centre for owls and goshawks during the breeding season and were calculated separately for each owl territory, every year. For each owl, S_i was calculated for each year that the owl was known to be alive. These values were then averaged over the years each individual spent in each age/breeding-class to give an average estimate of S_i.

Appendix 5b

Model selection for analyses characterising the age-dependent pattern of adult female tawny owl survival using data from both locally born individuals and immigrant female owls**.**

Model	Deviance	*np*	*ΔAICc*
Constant	2062.34	34	5.44
estimate for each age	2040.51	48	14.12
threshold after 1 year	2061.95	35	7.20
threshold after 2 years	2058.85	35	4.09
threshold after 3 years	2058.19	35	3.44
threshold after 4 years	2058.92	35	4.17
threshold after 5 years	2057.57	35	2.81
threshold after 6 years	**2054.75**	**35**	**0**
threshold after 7 years	2057.75	35	3.00

APPENDIX 6

Appendix 6a

Correlation between covariates of predation risk and food availability.

Local vs total goshawk abundance (*r* = 0.83, *N* = 27, *P* < 0.001).

Spring vole density vs spatial variation in vole densities (*r* = -0.66, *N* = 27, *P* < 0.001).

Total goshawk abundance vs spring vole densities (*r* = -0.36, *N* =27, *P* = 0.053).

Total goshawk abundance vs spatial variation in vole densities (*r* = 0.12, *N* = 27, *P* = 0.54).

Local goshawk abundance vs spring vole densities (*r* = -0.18, *N* = 27, *P* = 0.35).

Local goshawk abundance vs spatial variation in vole densities (*r* = -0.11, *N* = 27, *P* = 0.56).

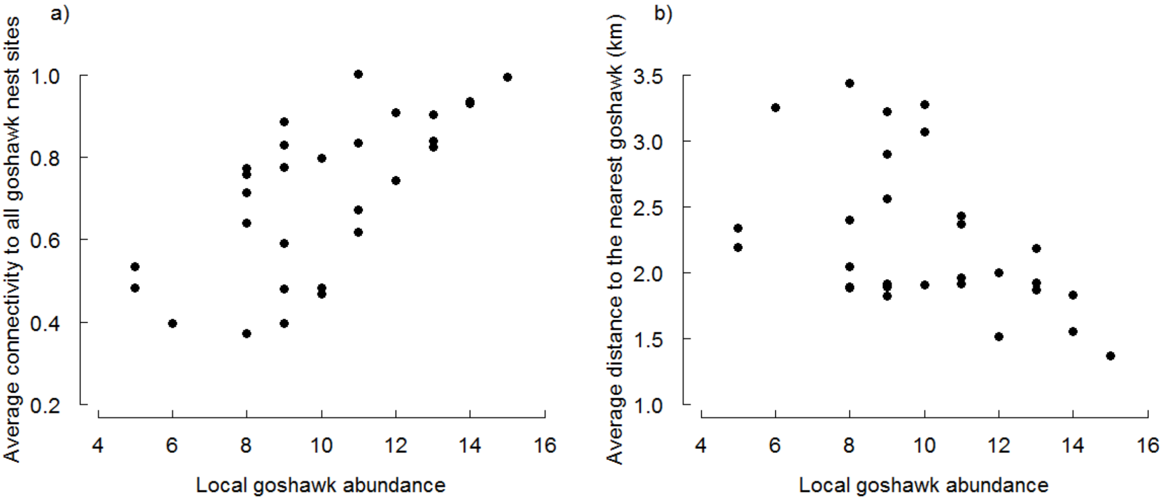


Figure 23. The correlation between local goshawk abundance and a) connectivity from an owls nest site to all goshawk nest sites averaged across the owl population each year b) the distance from an owls nest site to the nearest goshawk nest site, averaged across owls population each year.

Appendix 6b

The age specific reproductive value estimated for female tawny owls.

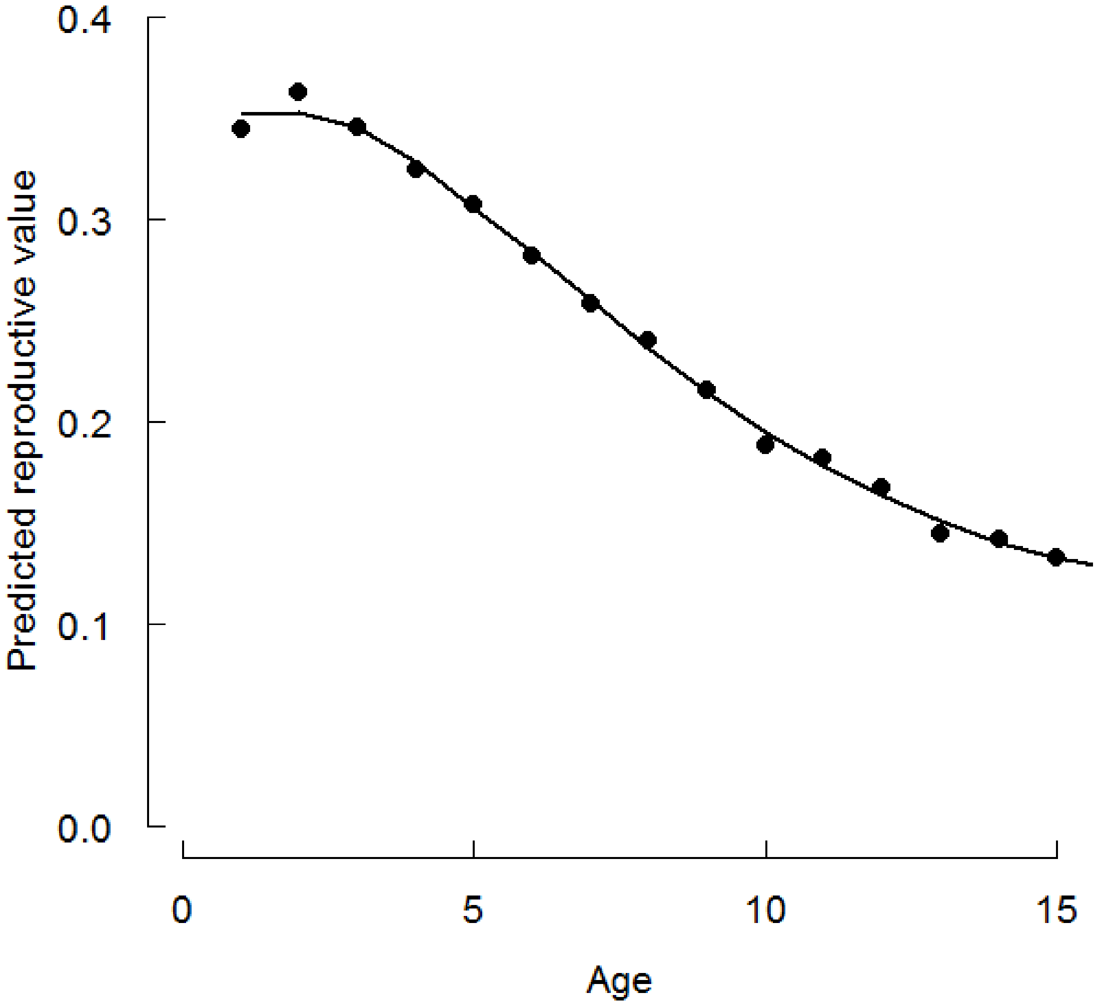


Figure 24. The age specific value was calculated using the left eigenvector of a Leslie matrix model as described in (Caswell 2001). We used the matrix model and parameterisation used to project population dynamics for this same tawny owl population Chapter 3.

Appendix 6c

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

	Model	*np*	Estimate	SE	ΔAICc
1.	Null	3			37.24
2.	Total goshawk	4	0.41	0.24	36.52
3.	Local goshawk	4	0.45	0.25	36.26
4.	Connectivity to goshawk	4	-0.01	0.12	39.26
5.	Nearest goshawk	4	0.05	0.10	39.06
6.	Spring voles	4	1.09	0.26	25.69
7.	Categorical spring vole density (CSV)	6	-0.83	0.56	33.12
	Spatial variation in vole densities (SVVD)		-0.62	0.44	
	CSV x SVVD		0.02	0.61	
8.	Breeding success previous year	4	0.34	0.22	27.81
9.	Years since 1st reproduction	4	0.08	0.03	32.42
10.	Spring voles	5	1.18	0.23	18.61
	+ Total goshawk		0.54	0.17	
11.	Categorical spring vole density (CSV)	7	-0.99	0.52	30.80
	Spatial variation in vole densities (SVVD)		-0.69	0.41	
	CSV x SVVD		0.36	0.58	
	+ Total goshawk		0.45	0.21	
12.	Total goshawk	5	0.39	0.24	27.35
	+ Breeding success previous year		0.33	0.22	
13.	Total goshawk	5	0.41	0.24	31.86
	+ Years since 1st reproduction		0.08	0.03	
14.	Spring voles	5	1.13	0.23	20.25
	+ Local goshawk		0.52	0.18	
15.	Categorical spring vole density (CSV)	7	-0.88	0.54	32.80
	Spatial variation in vole densities (SVVD)		-0.58	0.43	
	CSV x SVVD		0.14	0.59	
	+ Local goshawk		0.34	0.22	
16.	Local goshawk	5	0.43	0.25	27.10
	+ Breeding success previous year		0.32	0.22	
17.	Local goshawk	5	0.46	0.26	31.46
	+ Years since 1st reproduction		0.08	0.03	
18.	Spring voles	5	1.09	0.26	27.71
	+ Connectivity to goshawk		0.003	0.12	
19.	Categorical spring vole density (CSV)	7	-0.82	0.56	35.15
	Spatial variation in vole densities (SVVD)		-0.62	0.44	
	CSV x SVVD		0.02	0.61	
	Connectivity to goshawk		0.01	0.12	
20.	Connectivity to goshawk	5	-0.03	0.12	29.77
	+ Breeding success previous year		0.34	0.22	
21.	Connectivity to goshawk	5	-0.01	0.13	34.45
	+ Years since 1st reproduction		0.08	0.03	

	Model	*np*	Estimate	SE	ΔAICc
22.	Spring voles	5	1.09	0.26	27.52
	+ Nearest goshawk		0.05	0.10	
23.	Categorical spring vole density (CSV)	7	-0.84	0.57	35.03
	Spatial variation in vole densities (SVVD)		-0.63	0.45	
	CSV x SVVD		0.03	0.61	
	+ Nearest goshawk		0.04	0.10	
24.	Nearest goshawk	5	0.05	0.10	29.55
	+ Breeding success previous year		0.34	0.22	
25.	Nearest goshawk	5	0.02	0.11	34.41
	+Years since 1st reproduction		0.08	0.03	
26.	Spring voles	5	1.09	0.26	16.20
	+ Breeding success previous year		0.32	0.22	
27.	Spring voles	5	1.11	0.26	20.53
	+ Years since 1st reproduction		0.08	0.03	
28.	Categorical spring vole density (CSV)	7	-0.83	0.57	24.09
	Spatial variation in vole densities (SVVD)		-0.60	0.45	
	CSV x SVVD		0.02	0.61	
	+ Breeding success previous year		0.31	0.22	
29.	Categorical spring vole density (CSV)	7	-0.86	0.57	28.22
	Spatial variation in vole densities (SVVD)		-0.65	0.45	
	CSV x SVVD		0.07	0.61	
	+ Years since 1st reproduction		0.08	0.03	
30.	Breeding success previous year	5	0.34	0.23	24.33
	+ Years since 1st reproduction		0.07	0.03	
31.	Spring voles (SV)	6	1.14	0.23	17.68
	Total goshawk (TG)		0.24	0.25	
	SV x TG		-0.48	0.28	
32.	Total goshawk	6	0.42	0.30	29.36
	Breeding success previous year (BS)		0.33	0.22	
	TG x BS		-0.04	0.24	
33.	Total goshawk	6	0.50	0.27	33.35
	Years since 1st reproduction (Y1st)		0.08	0.03	
	TG x Y1st		-0.02	0.03	
34.	Spring voles	6	1.15	0.23	15.79
	Local goshawk (LG)		0.15	0.21	
	SV x LG		-0.68	0.26	
35.	Local goshawk	6	0.60	0.30	28.12
	Breeding success previous year		0.32	0.23	
	LG x BS		-0.23	0.23	
36.	Local goshawk	6	0.56	0.28	32.80
	Years since 1st reproduction		0.08	0.03	
	LG x Y1st		-0.03	0.03	
37.	Spring voles	6	1.09	0.27	29.71
	Connectivity to goshawk (CG)		-0.01	0.13	
	SV x CG		-0.03	0.16	

	Model	*np*	Estimate	SE	ΔAICc
38.	Connectivity to goshawk	6	-0.04	0.17	31.79
	Breeding success previous year		0.35	0.23	
	CG x BS		0.02	0.19	
39.	Connectivity to goshawk	6	-0.09	0.17	35.99
	Years since 1st reproduction		0.08	0.03	
	CG x Y1st		0.02	0.03	
40.	Spring voles	6	1.13	0.27	29.00
	Nearest goshawk (NG)		0.10	0.12	
	SV x NG		0.12	0.16	
41.	Nearest goshawk	6	0.14	0.14	30.72
	Breeding success previous year		0.37	0.23	
	NG x BS		-0.17	0.18	
42.	Nearest goshawk	6	0.11	0.17	35.99
	Years since 1st reproduction		0.08	0.03	
	NG x Y1st		-0.02	0.03	
43.	Spring voles	6	0.85	0.32	16.83
	Breeding success previous year		0.45	0.25	
	SV x BS		0.37	0.31	
44.	Spring voles	6	1.56	0.34	17.05
	Years since 1st reproduction		0.05	0.03	
	SV x Y1st		-0.10	0.04	
45.	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	
46.	**Breeding success previous year**	**9**	**-0.34**	**0.35**	**0.00**
	Years since 1st reproduction		**-0.01**	**0.05**	
	BS x Y1st		**0.13**	**0.06**	
	+ Spring voles		**1.17**	**0.23**	
	Local goshawk		**0.14**	**0.22**	
	SV x LG		**-0.69**	**0.26**	
47.	Breeding success previous year	9	-0.32	0.35	1.92
	Years since 1st reproduction		-0.01	0.04	
	BS x Y1st		0.13	0.06	
	Spring voles		1.16	0.23	
	Total goshawk		0.21	0.25	
	SV x TG		-0.51	0.29	
48.	Breeding success previous year	9	-0.29	0.35	13.56
	Years since 1st reproduction		-0.01	0.05	
	BS x Y1st		0.13	0.06	
	+ Spring voles		1.11	0.27	
	Connectivity to goshawk		-0.02	0.13	
	SV x CG		-0.02	0.16	

	Model	*np*	Estimate	SE	ΔAICc
49.	Breeding success previous year	9	-0.29	0.35	12.90
	Years since 1st reproduction		-0.01	0.05	
	BS x Y1st		0.13	0.06	
	+ Spring voles		1.15	0.27	
	Nearest goshawk		0.08	0.12	
	SV x NG		0.13	0.16	
50.	Categorical spring vole density (CSV)	12	0.55	0.64	4.89
	Spatial variation in vole densities (SVVD)		0.32	0.40	
	CSV x SVVD		-0.45	0.48	
	+ Breeding success previous year		-0.33	0.35	
	Years since 1st reproduction		-0.01	0.05	
	BS x Y1st		0.13	0.06	
	+ Spring voles		1.52	0.45	
	Local goshawk		0.20	0.24	
	SV x LG		-0.63	0.27	

Appendix 6d

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

	Model	*np*	Estimate	SE	ΔAICc
1.	Null	3			17.11
2.	Total goshawk	4	-0.035	0.032	17.99
3.	Local goshawk	4	-0.017	0.033	18.88
4.	Connectivity to goshawk	4	0.007	0.024	19.04
5.	Nearest goshawk	4	-0.007	0.022	19.02
6.	**Spring voles**	**4**	**0.125**	**0.023**	**0.00**
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.	Successfully bred previous year	4	0.028	0.046	18.75
9.	Years since 1st reproduction	4	0.002	0.006	18.97
11.	Spring voles	5	0.126	0.024	2.02
	+ Total goshawk		0.001	0.024	
12.	Categorical spring vole density (CSV)	7	-0.126	0.063	8.51
	Spatial variation in vole densities (SVVD)		-0.067	0.036	
	CSV x SVVD		-0.005	0.027	
	+ Total goshawk		-0.023	0.062	
13.	Total goshawk	5	-0.035	0.032	19.63
	+ Breeding success previous year		0.028	0.045	
14.	Total goshawk	5	-0.035	0.032	19.81
	+ Years since 1st reproduction		0.003	0.006	
16.	Spring voles	5	0.130	0.023	1.50
	+ Local goshawk		0.017	0.024	
17.	Categorical spring vole density (CSV)	7	-0.126	0.062	8.50
	Spatial variation in vole densities (SVVD)		-0.068	0.036	
	CSV x SVVD		-0.022	0.061	
	+ Local goshawk		-0.006	0.026	
18.	Local goshawk	5	-0.016	0.033	20.53
	+ Breeding success previous year		0.028	0.046	
19.	Local goshawk	5	-0.017	0.033	20.74
	+ Years since 1st reproduction		0.002	0.006	
21.	Spring voles	5	0.126	0.023	1.98
	+ Connectivity to goshawk		-0.005	0.022	
22.	Categorical spring vole density (CSV)	7	-0.129	0.059	8.49
	Spatial variation in vole densities (SVVD)		-0.068	0.036	
	CSV x SVVD		-0.021	0.061	
	+ Connectivity to goshawk		0.005	0.022	
23.	Connectivity to goshawk	5	0.007	0.024	20.68
	+ Breeding success previous year		0.028	0.046	
24.	Connectivity to goshawk	5	0.007	0.024	20.90
	+ Years since 1st reproduction		0.002	0.006	

	Model	*np*	Estimate	SE	ΔAICc
25.	Spring voles	5	0.125	0.023	2.02
	+ Nearest goshawk		0.0002	0.022	
26.	Categorical spring vole density (CSV)	7	-0.128	0.059	8.47
	Spatial variation in vole densities (SVVD)		-0.067	0.036	
	CSV x SVVD		-0.006	0.022	
	+ Nearest goshawk		-0.022	0.061	
27.	Nearest goshawk	5	-0.007	0.022	20.67
	+ Breeding success previous year		0.028	0.046	
28.	Nearest goshawk	5	-0.008	0.022	20.85
	+ Years since 1st reproduction		0.003	0.006	
39.	**Spring voles**	**5**	0.125	0.023	1.88
	+ Breeding success previous year		0.016	0.043	
30.	Spring voles	5	0.126	0.023	1.93
	+ Years since 1st reproduction		0.002	0.006	
31.	Categorical spring vole density (CSV)	7	-0.130	0.059	8.43
	Spatial variation in vole densities (SVVD)		-0.067	0.036	
	CSV x SVVD		-0.022	0.061	
	+ Breeding success previous year		0.015	0.044	
32.	Categorical spring vole density (CSV)	7	-0.132	0.059	8.31
	Spatial variation in vole densities (SVVD)		-0.068	0.036	
	CSV x SVVD		-0.021	0.061	
	+ Years since 1st reproduction		0.003	0.006	
33.	Breeding success previous year	5	0.025	0.047	20.70
	+ Years since 1st reproduction		0.002	0.006	
34.	Spring voles (SV)	6	0.122	0.022	1.57
	Total goshawk (TG)		-0.014	0.024	
	SV x TG		-0.049	0.030	
35.	Total goshawk	6	-0.038	0.042	21.65
	Breeding success previous year (BS)		0.028	0.045	
	TG x BS		0.005	0.045	
36.	Total goshawk	6	-0.017	0.040	21.20
	Years since 1st reproduction (Y1st)		0.004	0.006	
	TG x Y1st		-0.006	0.007	
37.	Spring voles	6	0.124	0.024	2.46
	Local goshawk (LG)		0.007	0.026	
	SV x LG		-0.030	0.029	
38.	Local goshawk	6	-0.020	0.042	22.54
	Breeding success previous year		0.028	0.046	
	LG x BS		0.006	0.045	
39.	Local goshawk	6	-0.006	0.040	22.52
	Years since 1st reproduction		0.003	0.006	
	LG x Y1st		-0.003	0.006	
40.	Spring voles	6	0.131	0.022	2.73
	Connectivity to goshawk (CG)		-0.008	0.022	
	SV x CG		-0.028	0.024	

	Model	*np*	Estimate	SE	ΔAICc
41.	Connectivity to goshawk	6	0.003	0.031	22.67
	Breeding success previous year		0.028	0.046	
	CG x BS		0.009	0.043	
42.	Connectivity to goshawk	6	-0.007	0.029	22.70
	Years since 1st reproduction		0.028	0.046	
	CG x Y1st		0.000	0.043	
43.	Spring voles	6	0.129	0.023	3.38
	Nearest goshawk (NG)		0.002	0.022	
	SV x NG		0.019	0.023	
44.	Nearest goshawk	6	-0.007	0.029	22.70
	Breeding success previous year		0.028	0.046	
	NG x BS		-0.0004	0.043	
45.	Nearest goshawk	6	-0.013	0.031	22.84
	Years since 1st reproduction		0.003	0.006	
	NG x Y1st		0.001	0.006	
46.	Spring voles	6	0.120	0.033	3.87
	Breeding success previous year		0.015	0.043	
	SV x BS		0.009	0.042	
47.	Spring voles	6	0.119	0.031	3.86
	Years since 1st reproduction		0.002	0.006	
	SV x Y1st		0.002	0.006	
58.	Breeding success previous year	6	0.074	0.065	21.57
	Years since 1st reproduction		0.008	0.008	
	BS x Y1st		-0.013	0.012	

Appendix 6e

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

	Model	*np*	Estimate	SE	ΔAICc
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 goshawk	4	-0.58	0.16	8.74
5.	Nearest goshawk	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	0.004	20.68
10.	Clutch size	4	0.89	0.29	9.54
11.	Spring voles	5	-0.36	0.19	18.28
	+ Total goshawk		-0.38	0.23	
12.	Categorical spring vole density (CSV)	7	0.88	0.51	22.26
	Spatial variation in vole densities (SVVD)		0.05	0.23	
	CSV x SVVD		-0.26	0.47	
	+ Total goshawk		-0.39	0.23	
13.	Total goshawk	5	-0.21	0.21	21.71
	+ Breeding success previous year		0.06	0.37	
14.	Total goshawk	5	-0.22	0.21	21.60
	+ Years since 1st reproduction		0.02	0.05	
15.	Total goshawk	5	0.86	0.30	11.27
	+ Clutch size		-0.13	0.24	
16.	Spring voles	5	-0.39	0.19	16.86
	+ Local goshawk		-0.43	0.21	
17.	Categorical spring vole density (CSV)	7	-0.39	0.20	21.56
	Spatial variation in vole densities (SVVD)		0.86	0.50	
	CSV x SVVD		-0.02	0.24	
	+ Local goshawk		-0.24	0.48	
18.	Local goshawk	5	-0.26	0.19	20.97
	+ Breeding success previous year		0.03	0.37	
19.	Local goshawk	5	-0.26	0.19	20.88
	+ Years since 1st reproduction		0.02	0.05	
20.	Local goshawk	5	0.86	0.29	10.52
	+ Clutch size		-0.24	0.23	
21.	Spring voles	5	-0.18	0.17	9.61
	+ Connectivity to goshawk		-0.57	0.16	

	Model	*np*	Estimate	SE	ΔAICc
22.	Categorical spring vole density (CSV)	7	0.54	0.47	13.18
	Spatial variation in vole densities (SVVD)		-0.05	0.23	
	CSV x SVVD		-0.05	0.47	
	+ Connectivity to goshawk		-0.59	0.16	
23.	Connectivity to goshawk	5	-0.58	0.16	10.77
	+ Breeding success previous year		0.003	0.35	
24.	Connectivity to goshawk	5	-0.58	0.16	10.68
	+ Years since 1st reproduction		0.01	0.05	
25.	**Connectivity to goshawk**	**5**	**0.84**	**0.28**	**0.00**
	+ Clutch size		**-0.60**	**0.17**	
26.	Spring voles	5	-0.19	0.19	15.90
	+ Nearest goshawk		0.46	0.21	
27.	Categorical spring vole density (CSV)	7	0.42	0.47	19.94
	Spatial variation in vole densities (SVVD)		-0.05	0.23	
	CSV x SVVD		0.03	0.46	
	+ Nearest goshawk		0.47	0.21	
28.	Nearest goshawk	5	0.48	0.20	16.93
	+ Breeding success previous year		0.06	0.37	
29.	Nearest goshawk	5	0.48	0.21	16.95
	+ Years since 1st reproduction		0.004	0.05	
30.	Nearest goshawk	5	0.87	0.28	5.47
	+ Clutch size		0.50	0.21	
31.	Spring voles	5	-0.27	0.21	20.97
	+ Breeding success previous year		0.10	0.38	
32.	Spring voles	5	-0.26	0.20	20.98
	+ Years since 1st reproduction		0.01	0.05	
33.	Categorical spring vole density (CSV)	7	0.56	0.49	25.33
	Spatial variation in vole densities (SVVD)		-0.01	0.26	
	CSV x SVVD		-0.09	0.49	
	+ Breeding success previous year		0.08	0.38	
34.	Categorical spring vole density (CSV)	7	0.55	0.49	25.34
	Spatial variation in vole densities (SVVD)		-0.02	0.26	
	CSV x SVVD		-0.08	0.48	
	Years since 1st reproduction		0.01	0.05	
35.	Breeding success previous year	5	0.05	0.39	22.68
	+ Years since 1st reproduction		0.01	0.05	
36.	Clutch size	5	0.86	0.28	11.67
	+ Breeding success previous year		0.06	0.38	
37.	Clutch size	5	0.88	0.29	11.49
	+ Years since 1st reproduction		0.01	0.05	
38.	Spring voles (SV)	6	-0.35	0.18	17.02
	Total goshawk		-0.55	0.27	
	SV x TG		-0.51	0.30	

	Model	*np*	Estimate	SE	ΔAICc
39.	Total goshawk	6	-0.16	0.30	23.70
	Breeding success previous year (BS)		0.08	0.38	
	TG x BS		-0.09	0.40	
40.	Total goshawk	6	0.01	0.27	22.10
	Years since 1st reproduction (Y1st)		0.05	0.06	
	TG x Y1st		-0.08	0.06	
41.	Total goshawk	6	0.74	0.85	12.13
	Clutch size (CS)		0.93	0.31	
	TG x CS		-0.35	0.34	
42.	Spring voles	6	-0.42	0.19	16.62
	Local goshawk (LG)		-0.49	0.21	
	SV x LG		-0.33	0.23	
43	Local goshawk	6	-0.36	0.27	22.73
	Breeding success previous year		-0.02	0.38	
	LG x BS		0.19	0.36	
44.	Local goshawk	6	-0.15	0.26	22.50
	Years since 1st reproduction		0.03	0.06	
	LG x Y1st		-0.03	0.05	
45.	Local goshawk	6	0.19	0.74	12.18
	Clutch size		0.90	0.30	
	LG x CS		-0.17	0.28	
46.	Spring voles	6	-0.16	0.20	11.58
	Connectivity to goshawk (CG)		-0.58	0.16	
	SV x CG		-0.04	0.17	
47.	Connectivity to goshawk	6	-0.73	0.22	11.68
	Breeding success previous year		-0.19	0.40	
	CG x BS		0.34	0.32	
48.	Connectivity to goshawk	6	-0.34	0.23	10.73
	Years since 1st reproduction		0.06	0.06	
	CG x Y1st		-0.06	0.05	
49.	Connectivity to goshawk	6	-0.35	0.59	1.85
	Clutch size		0.89	0.31	
	CG x CS		-0.10	0.23	
50.	Spring voles	6	-0.16	0.21	17.88
	Nearest goshawk (NG)		0.45	0.21	
	SV x NG		0.04	0.21	
51.	Nearest goshawk	6	0.59	0.29	18.64
	Breeding success previous year		-0.03	0.40	
	NG x BS		-0.23	0.41	
52.	Nearest goshawk	6	0.34	0.29	18.54
	Years since 1st reproduction		0.02	0.06	
	NG x Y1st		0.04	0.06	
53.	Nearest goshawk	6	0.23	0.76	7.37
	Clutch size		0.91	0.30	
	NG x CS		0.11	0.31	

	Model	*np*	Estimate	SE	ΔAICc
54.	Spring voles	6	-0.23	0.29	22.98
	Breeding success previous year		0.11	0.38	
	SV x BS		-0.06	0.36	
55.	Spring voles	6	-0.49	0.28	21.34
	Years since 1st reproduction		0.01	0.05	
	SV x Y1st		0.07	0.05	
56.	Breeding success previous year	6	0.22	0.53	24.51
	Years since 1st reproduction		0.04	0.08	
	BS x Y1st		-0.05	0.11	
57.	Clutch size	6	1.46	0.46	9.85
	Breeding success previous year		2.56	1.38	
	CS x BS		-1.04	0.55	
58.	Clutch size	6	0.91	0.40	13.51
	Years since 1st reproduction		0.03	0.20	
	CS x Y1st		-0.01	0.08	

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