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# Density-dependent increase in superpredation linked to food limitation in a recovering population of northern goshawks *Accipiter gentilis*

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1       **Density-dependent increase in superpredation linked to food**  
2       **limitation in a recovering population of northern goshawks,**  
3                                   *Accipiter gentilis*

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14  
15       **Keywords:** food-stress hypothesis, intraguild predation, mesopredator suppression

16 **ABSTRACT**

17 A better understanding of the mechanisms driving superpredation, the killing of smaller  
18 mesopredators by larger apex predators, is important because of the crucial role superpredation  
19 can play in structuring communities and because it often involves species of conservation  
20 concern. Here we document how the extent of superpredation changed over time, and assessed  
21 the impact of such temporal variation on local mesopredator populations using 40 years of  
22 dietary data collected from a recovering population of northern goshawks (*Accipiter gentilis*),  
23 an archetypical avian superpredator. We then assessed which mechanisms were driving  
24 variation in superpredation, e.g., was it opportunistic, a response to food becoming limited (due  
25 to declines in preferred prey) or to reduce competition. Raptors comprised 8% of goshawk diet  
26 on average in years when goshawk abundance was high, which is higher than reported  
27 elsewhere. Additionally, there was a per capita increase in superpredation as goshawks  
28 recovered, with the proportion of goshawk diet comprising raptors increasing from 2% to 8%  
29 as the number of goshawk home-ranges increased from  $\leq 14$  to  $\geq 25$ . This increase in  
30 superpredation coincided with a population decline in the most commonly killed mesopredator,  
31 the Eurasian kestrel (*Falco tinnunculus*), which may represent the reversal of the  
32 “mesopredator release” process (i.e., mesopredator suppression) which occurred after  
33 goshawks and other large raptors declined or were extirpated. Food limitation was the most  
34 likely driver of superpredation in this system given: 1) the substantial decline of two main prey  
35 groups in goshawk diet, the increase in diet diversity and decrease in goshawk reproductive  
36 success are all consistent with the goshawk population becoming food-limited; 2) it’s unlikely  
37 to be purely opportunistic as the increase in superpredation did not reflect changes in the  
38 availability of mesopredator species; and 3) the majority of mesopredators killed by goshawks  
39 do not compete with goshawks for food or nest sites.

40

## 41 INTRODUCTION

42 Understanding the mechanisms driving variation in superpredation, the killing of smaller  
43 mesopredators by larger apex predators, is an important issue in ecology. This is partly because  
44 superpredation can directly impact mesopredator population dynamics which may then cascade  
45 to affect lower trophic levels (Paine 1980), but also because many of the superpredator and  
46 mesopredator species involved are of conservation concern (Palomares and Caro 1999, Caro  
47 and Stoner 2003, Ripple and Beschta 2004, Ritchie and Johnson 2009). However, despite this,  
48 and the crucial role superpredation can play in structuring communities, it is still not clear what  
49 mechanism (or combination of mechanisms) drives one predator to kill another.

50

51 Optimal foraging theory suggests that predators should attempt to kill prey when the energy  
52 gained outweighs the energetic cost and potential risk of injury involved (Berger-Tal et al.  
53 2009). However, mesopredators are unlikely to represent a profitable prey source, even when  
54 they fall within the preferred size range of the superpredator, because their densities are often  
55 relatively low compared to that of other prey species. Furthermore, the risk of injury associated  
56 with attacking mesopredators is presumably higher than for other prey types, because  
57 mesopredators have evolved to kill other species (Lourenço et al. 2011a). Consequently,  
58 several alternative (but not mutually exclusive) hypotheses have been put forward to explain  
59 superpredation. The competitor-removal hypothesis suggests that superpredators kill  
60 mesopredators to free up shared resources (Serrano 2000). This leads to the prediction that  
61 superpredation will largely involve mesopredator species which compete with the  
62 superpredator for food or other resources, such as nest sites (e.g. intraguild predation). In  
63 contrast, the predator-removal hypothesis suggests that superpredation is a pre-emptive tactic  
64 to decrease the probability of the superpredator or their offspring being killed (Lourenço et al.

65 2011b). Under this scenario, the mesopredator species expected to be killed the most frequently  
66 are those which pose a threat to the superpredator or their offspring.

67

68 Alternatively, rather than being a response to the presence of other predators, the food-  
69 limitation hypothesis, also known as the food-stress hypothesis, suggests that mesopredators  
70 are killed to make up the shortfall in the superpredators diet when preferred prey species decline  
71 (Polis et al. 1989, Serrano 2000, Rutz and Bijlsma 2006, Lourenço et al. 2011a, b). Food  
72 limitation may also occur if there is an increase in the number of individuals (conspecifics or  
73 other species) exploiting preferred prey species, particularly if increasing predator densities  
74 elicit anti-predator behaviours in their prey (such as spatial or temporal avoidance of risky  
75 areas) which make prey more difficult to find and/or catch. Many populations of large predator  
76 species are currently increasing in abundance and recovering their former ranges across both  
77 North America and Europe (Maehr et al. 2001, Deinet et al. 2013, Chapron et al. 2014).  
78 Consequently, if superpredation is a response to density dependent food limitation, then the  
79 extent of superpredation occurring might be expected to increase during the recolonisation  
80 process, even if mesopredators are not a preferred prey species. However, whether such a per  
81 capita increase in superpredation has actually occurred or whether it coincides with or follows  
82 the colonisation process is as yet unknown.

83

84 Here we evaluate support for the food-limitation hypothesis, and other proposed determinants  
85 of superpredation in a recovering population of northern goshawks (*Accipiter gentilis*), using  
86 data collected between 1973 and 2014, over a 964km<sup>2</sup> area of Kielder Forest, United Kingdom  
87 (55°13'N, 2°33'W). The northern goshawk (hereafter goshawk) is an archetypical avian  
88 superpredator known to prey upon a large diversity of both avian and mammalian prey,  
89 including other raptors (Rutz et al. 2006, Sergio and Hiraldo 2008, Lourenço et al. 2011a).

90 Goshawks are the apex predator in this study system as Kielder Forest lacks other predator  
91 species known to prey on goshawks, such as Eurasian eagle owls (*Bubo bubo*) (Chakarov and  
92 Krüger 2010).

93

94 Goshawks were extirpated from the UK in the late 19<sup>th</sup> century. However, scattered populations  
95 were subsequently re-established in the 1960s and 70s after birds escaped or were released by  
96 falconers (Marquiss and Newton 1982, Petty and Anderson 1995, Petty 1996). In Kielder  
97 Forest the goshawk population recovered rapidly after the first recorded breeding attempt in  
98 1973, and 25-33 goshawk home-ranges are now occupied (see Appendix S1; Petty & Anderson  
99 1995). Such a large increase in goshawk abundance, was presumably concomitant with an  
100 increase in intraspecific competition for food and nest sites. However, goshawks may also have  
101 become food-limited because of a long-term decline in the abundance of red grouse (*Lagopus*  
102 *lagopus*) and a substantial decline of feral pigeon (*Columba livia*) in recent years in England  
103 (Robinson et al. 2015), as both species are important prey for goshawks in our study area (Petty  
104 et al. 2003a). The term feral pigeon includes both racing and homing pigeons.

105

106 The first aim of this study was to quantify the extent of superpredation and then to test the  
107 prediction that there has been a per capita increase in superpredation during the colonisation  
108 process by examining goshawk dietary data. Our second aim was to determine whether  
109 superpredation was impacting local populations of the most commonly preyed upon  
110 mesopredator species, for which local population trends are well characterised. We then  
111 assessed whether the goshawk population had become food-limited as the population  
112 recovered. It is difficult to directly assess food limitation for generalist predators, such as  
113 goshawks, without comprehensive prey abundance surveys (Rutz and Bijlsma 2006).  
114 Consequently, we examined two different lines of evidence to proximately assess food

115 limitation. First, we examined temporal variation in goshawk diet to determine whether there  
116 had been any decline in the contribution of certain prey species/groups known to be important  
117 for goshawks. We then examined changes in the reproductive success of the goshawk  
118 population, because reproductive success is closely associated with food availability in  
119 goshawks and other raptor species (Newton 1979, 1998, Rutz and Bijlsma 2006, Millon et al.  
120 2008). Lastly, we evaluated evidence supporting the alternative hypotheses of superpredation  
121 by examining which mesopredator species were being killed by goshawks (e.g. were they  
122 known to compete with goshawks for food or nesting sites).

123

## 124 **METHODS**

125 Kielder Forest is situated in Northumberland, in the north of England, adjacent to the border  
126 with Scotland. For a map of the study area see (Petty et al. 2003b). Each year active goshawk  
127 home-ranges were located by searching suitable nesting habitat within the forest (between the  
128 end of February and end of the breeding season). The locations of active nests were recorded  
129 and these sites were then visited at least four times to establish whether a breeding attempt took  
130 place, to record the number of chicks that fledged and collect dietary data.

131

### 132 **Quantifying superpredation**

133 To quantify superpredation and to determine whether there had been a per capita increase in  
134 superpredation as the goshawk population expanded, we used goshawk dietary data.  
135 Specifically, we quantified the proportion of goshawk diet comprised of other raptor species  
136 each year. Here we use the term raptor to refer to all diurnal and nocturnal birds of prey.  
137 Goshawk diet was characterised by searching for the remains of prey (feathers, bones and fur)  
138 in the area surrounding active nest sites during nest visits between March-August, 1975-2014  
139 (except between 1999-2001), in the same way as described in Petty *et al.* (2003). When possible,

140 at the end of the breeding season the top layer of nesting material was removed from active  
141 nests and searched for additional prey remains. Prey remains were removed or buried to avoid  
142 double counting in subsequent searches. We were able to identify 7763 prey items to species  
143 level by comparison with reference collections. It was not always possible to differentiate  
144 carrion crow (*Corvus corone*) from rook (*C. frugilegus*) remains. Therefore crow/rook refers  
145 to the abundance of both species in the diet, although rooks were scarce in the study area. We  
146 identified and quantified the minimum number of individuals of medium to large prey species  
147 by counting skeletal remains, whereas small avian prey (less than 100g) were identified and  
148 quantified by plucked feathers. Collecting and quantifying dietary data in this way is likely to  
149 underestimate the contribution of small prey items (Ziesemer 1983). However, this should not  
150 influence the results of our analyses as such items are relatively unimportant to goshawk diet  
151 in terms of biomass.

152

153 Once the proportion of goshawk diet comprising raptors had been calculated for each nest  
154 site/year, we examined how it varied in relation to the number of occupied goshawk home-  
155 ranges (measured as a continuous variable) using generalised linear mixed effect models  
156 (GLMM) with a binomial error structure fitted using the *lme4* package (Bates et al. 2015).  
157 Goshawk diet has previously been shown to change with altitude, presumably reflecting  
158 changes in abundance and diversity of prey species at different altitudes (Marquiss and Newton  
159 1982, Toyne 1998). Consequently, we also examined whether the contribution of raptors to  
160 diet varied with the altitude of the goshawks nest site. Goshawk home-ranges were grouped  
161 into three altitudinal bands as follows: low, if the nest site was 225m or below, medium if  
162 between 226-354m, and high if 355m or above. We used these cut-offs because goshawk home-  
163 ranges above 355m were generally surrounded by open moorland habitat, whereas home-  
164 ranges below 225m were surrounded by forest, pasture and water (streams, rivers and a large

165 reservoir). The identity of home-ranges and year were both fitted as random effects to account  
166 for variation in diet between years and between home-ranges. Model selection was based on  
167 Akaike's information criterion corrected for small sample size (AICc) and AICc weights ( $W$ ;  
168 Burnham and Anderson 2002). The best performing model will have a  $\Delta AIC$  of zero, because  
169  $\Delta AICc$  is the AICc for the model of interest minus the smallest AICc for the set of models  
170 being considered. Models are generally considered inferior if they have a  $\Delta AICc > 2$  units.  
171 AICc weights ( $w$ ) are an estimate of the relative likelihood of a particular model for the set of  
172 models being considered. Model assumptions were validated by visually inspecting residual  
173 plots; but they did not reveal any obvious nonlinear relationships, unless otherwise mentioned.  
174 Correlograms (with a lag distance up to 10km) were used to check for spatial-autocorrelation  
175 in the residuals of the best performing model. However, we found no evidence of spatial-  
176 autocorrelation in this, nor any other analyses of goshawk diet.

177

### 178 **Impact on local mesopredator populations**

179 To assess the impact of changes in goshawk predation on local populations of the three most  
180 frequently preyed upon raptor species Eurasian kestrels (*Falco tinnunculus*), tawny owls (*Strix*  
181 *aluco*) and Eurasian sparrowhawks (*Accipiter nisus*; Petty *et al.* 2003), we first examined  
182 whether the proportion of goshawk diet comprising these three raptor species changed with  
183 goshawk abundance (measured as a continuous variable) using the same GLMM approach  
184 described above. We then used dietary data to estimate the minimum number of each  
185 mesopredator species killed each year by goshawks when  $\leq 14$ , 15-24 and 25+ goshawk home-  
186 ranges were occupied (for methods see Appendix 2). We used these three goshawk abundance  
187 categories to keep broadly similar sample sizes despite large variation in the number of prey  
188 remains recovered each year (range 10- 678). Temporal variation in predation rates on kestrel,  
189 tawny owl and sparrowhawk were then compared to changes in the local population dynamics

190 of these species. Annual counts of territorial kestrel pairs in and around the forest have been  
191 recorded since 1975 as part of a larger study on merlins (*Falco columbarius*; Newton, Meek &  
192 Little 1986; Little, Davison & Jardine 1995). Breeding tawny owls have been monitored  
193 continuously in a subsection of the forest since 1979 (Petty 1992, Petty et al. 1994, Hoy et al.  
194 2015). The number of occupied sparrowhawk territories in a subsection of the study area has  
195 been recorded since 1974 (Petty 1979; Petty *et al.* 1995).

196

### 197 **Assessing food limitation**

#### 198 *Declines in important prey*

199 To indirectly infer if the goshawk population had become food-limited we assessed whether  
200 there had been any decline in the contribution of important prey species/groups in the diet. We  
201 first examined how the dominance of main prey species in the diet changed as the goshawk  
202 population expanded. This was done by ranking species from most to least important, firstly in  
203 terms of their frequency contribution to diet and then in terms of their biomass when the number  
204 of occupied goshawk home-ranges was  $\leq 14$ , 15-24 and 25+. A full list of species killed by  
205 goshawk and their mean body mass values used in biomass calculations can be found in  
206 Appendix 3. Certain taxonomic groups are known to be important to goshawk diet. For  
207 example, *Columbiformes* are an important prey for goshawks across most of Europe,  
208 comprising up to 69% of all prey items (reviewed in Rutz *et al.* 2006). Whereas, *Tetraonidae*  
209 comprised almost 80% of goshawk diet in some years at northerly latitudes, and in southern  
210 Europe *Lagomorphs* were an important prey source (reviewed in Kenward 2006). We therefore  
211 categorised prey into taxonomic groups as follows: raptors, pigeons (*Columbiformes*), corvids  
212 (*Corvidae*), game birds (*Tetraonidae* and *Phasianidae*) mammals (mainly *Lagomorpha*, and  
213 *Sciuridae*), and 'other'. This 'other' group largely consists of passerines but also includes other  
214 prey species, which are only occasionally taken. We then estimated both the frequency and

215 biomass contribution of these groups to goshawk diet and examined how the frequency  
216 contribution varied in relation to goshawk abundance (measured as a continuous variable)  
217 using the same GLMM approach. We were unable to assess whether variation in the proportion  
218 of goshawk diet comprised of these different prey species/groups were related to changes in  
219 the abundance of these prey species/groups as local population trends were not available.  
220 Lastly, because diet diversity had generally been observed to increase in other raptor  
221 populations as they became food-limited (Rutz and Bijlsma 2006, Lourenço et al. 2011a), we  
222 also examined how prey diversity changed with goshawk abundance using estimates of the  
223 Shannon-Wiener diversity index when  $\leq 14$ ; 15-24; 25+ goshawk home-ranges were occupied.

224

#### 225 *Goshawk reproductive success*

226 We also indirectly assessed whether the goshawk population had become food-limited by  
227 examining how goshawk reproductive success varied in relation to the number of occupied  
228 home-ranges (measured as a continuous variable). In this analysis, we used two different  
229 measures of reproductive success: the average number of chicks fledged per successful  
230 breeding attempt and the proportion of breeding attempts which failed. We did not analysed  
231 variation in goshawk reproductive success prior to 1977 because goshawks did not reproduce  
232 successfully until a few years after the first home-ranges became established. Because the  
233 relationship between goshawk abundance and the number of chicks fledged per successful  
234 breeding attempt appeared to be non-linear we used generalised additive models (GAM) to  
235 characterise this relationship, fitted using the *mgcv* package (Wood 2015). In contrast, the  
236 relationship between the proportion of failed goshawk breeding attempts and goshawk  
237 abundance could be adequately characterised by generalised linear models (GLM) with a  
238 binomial error structure. All analyses were carried out in R version 3.0.3 (R Core Development  
239 Team 2015). Descriptive statistics are presented as the mean  $\pm$  1SD.

240

## 241 **RESULTS**

### 242 **Superpredation increased during the colonisation process**

243 Overall, raptors comprised 6% of all identifiable prey killed by goshawks ( $N= 7763$ ) and  
244 represented 4% of goshawk prey in terms of biomass (Appendix 4). There was a per capita  
245 increase in superpredation as goshawks recovered, with the proportion of goshawk diet  
246 comprised of raptors increasing from 2% to 8% as the number of goshawk home-ranges  
247 increased from  $\leq 14$  to  $\geq 25$ . However, the proportion of raptors in goshawk diet was best  
248 modelled by an interaction between goshawk abundance and the altitude of the goshawk home-  
249 range (Table 1). The contribution of raptors to goshawk diet increased with goshawk  
250 abundance in home-ranges at the two lower elevations bands ( $\leq 225\text{m}$  and  $226\text{-}354\text{m}$ ). However,  
251 there was no significant change in the proportion of raptors in the diet at higher altitudes (e.g.,  
252 above  $350\text{m}$ ), where the contribution of raptors to goshawk diet was highest (Fig. 1a).

253

### 254 **Impact on local mesopredator populations**

255 Kestrels and tawny owls were both ranked within the 10 most important prey species, both in  
256 terms of their frequency and biomass contribution to diet (Table 2). Kestrels were the most  
257 commonly preyed raptor species, representing almost half (49%) of all raptors killed by  
258 goshawks ( $N = 465$ ; Appendix 5). However, this proportion declined from 55% to 39% as the  
259 number of occupied goshawk home-ranges increased from  $<15$  to  $>24$  (Appendix 5). Kestrels  
260 contributed most to goshawk diet in high altitude home-ranges (Fig. 2a). The number of  
261 kestrels estimated to be killed each year by the goshawk population initially increased with  
262 goshawk abundance, from 14 [11-18 95% CI] when fewer than 15 goshawk home-ranges were  
263 occupied to 223 [197-248 95% CI] when 15-24 home-ranges were occupied. However, it then  
264 declined to 176 [154-198 95% CI] when more than 24 goshawk home-ranges were occupied

265 (Table 3). At the same time, there has been a substantial decline in the number of kestrel pairs  
266 recorded breeding in the study site. For example, there were 29 breeding pairs in 1981  
267 compared to only five pairs in 2014.

268

269 Tawny owls then sparrowhawks were the next most commonly preyed upon raptor species,  
270 representing 23% and 10% respectively of all raptors killed by goshawks (Appendix 5). The  
271 contribution of both tawny owls and sparrowhawks in goshawk diet increased as the number  
272 of goshawk home-ranges increased; however, there was no evidence to suggest that it varied  
273 with altitude (Table 1; Fig.2b-c). The rank order importance of tawny owls to goshawk diet  
274 also increased from 9 to 7 as the number of occupied goshawk home-ranges increased from  
275 15-24 to  $\geq 25$  (Table 2). Our estimates suggested there was huge increase in the number of  
276 tawny owls killed by goshawks each year, from an average of 5 [3-8 95% CI] to 159 owls [141-  
277 176 95% CI] as the number of occupied goshawk home-ranges increased from <15 to >24  
278 (Table 3). The number of sparrowhawks killed by goshawks was also estimated to increase,  
279 from 1 [1-2 95% CI] to 53 [44-61 95% CI] as the number of occupied goshawk home-ranges  
280 increased from <15 to >24 (Table 3). Despite the estimated increase in predation on both tawny  
281 owls and sparrowhawks, there was no evidence to suggest that local populations had declined.  
282 That is, there was little interannual variation in the number of occupied tawny owl territories,  
283 which averaged  $56 \pm 4.07$  between 1985-2014 (Hoy et al. 2015), and sparrowhawks were  
284 known to occupy 7-14 home-ranges between 1974-1979 (Petty 1979) and 7-16 home-ranges  
285 between 2002-2014 (unpublished data).

286

## 287 **Assessing food limitation**

288 *Declines in important prey species/groups*

289 Almost half (48%) of all identifiable prey items were pigeons (Appendix 4). Wood pigeon  
290 (*Columba palumbus*) then feral pigeon were the two commonest prey species, irrespective of  
291 the number of goshawk home-ranges occupied (Table 2). The proportion of pigeons in  
292 goshawk diet declined over the study period as goshawk abundance increased, irrespective of  
293 home-range altitude (Fig. 1b; Table 4). For example, the biomass contribution of pigeons to  
294 diet declined from 52% to 40% as the number of home-ranges increased from <15 to >24. This  
295 decline in pigeon in goshawk diet appeared to be driven by a decrease in feral rather than wood  
296 pigeons. The contribution of pigeons to goshawk diet was lowest in higher altitude home-  
297 ranges, where moorland habitat predominated (Fig 1b; Table 4).

298

299 Crow/rook, red grouse and rabbit consistently ranked within the top-5 most important prey  
300 species, both in terms of biomass and frequency contribution to diet, irrespective of the number  
301 of goshawk home-ranges occupied (Table 2). The proportion of corvids and mammals in the  
302 diet increased with goshawk abundance (Fig 2c-d). For example, corvids and mammals  
303 comprised 11% and 4% respectively of diet (in terms of frequency) when <15 home-ranges  
304 were occupied, but 19% and 8% of diet respectively when >24 home-ranges were occupied  
305 (Appendix 4). In contrast, the contribution of game birds (including red grouse) declined as  
306 goshawk abundance increased, in all three altitudinal categories (Table 4; Fig. 2e). Although  
307 the dietary contribution of corvids and mammals did not vary with altitude, the proportion of  
308 game birds (especially red grouse) was noticeably higher for high altitude home-ranges (e.g.,  
309 above 350m; where moorland habitat is more common). Goshawk diet also became more  
310 diverse as goshawk abundance increased, with the Shannon-Wiener diversity index increasing  
311 by 24% from 2.1 to 2.6 when the number of occupied goshawk territories increased from being  
312 <15 to >24.

313

### 314 *Declines in reproductive success*

315 Overall the reproductive success of goshawks declined as the number of occupied home-ranges  
316 increased. This decline appeared to be driven by both a decline in the average number of chicks  
317 fledging per successful breeding attempt and an increase in the number of nesting attempts  
318 failing (Fig. 3). The number of chicks fledging per successful breeding attempt decreased from  
319 an average of  $2.90 \pm 0.24$  chicks to  $2.29 \pm 0.36$  chicks as the number of occupied goshawk  
320 home-ranges increased from  $<15$  to  $>24$  (Fig. 3a). The proportion of successful breeding  
321 attempts declined from an average of  $0.81 \pm 0.18$  to  $0.58 \pm 0.14$  when the number of occupied  
322 home-ranges increased from  $< 15$  to  $> 24$  (Fig. 3b).

323

## 324 **DISCUSSION**

### 325 **Superpredation has increased during the recolonization process**

326 The amount of superpredation in our study site, particularly in recent years, is noticeably higher  
327 than recorded elsewhere. For example, raptors comprised up to 8% of goshawk diet in Kielder  
328 Forest when goshawk abundance was high (Appendix 4) which is higher than the average of  
329 2% estimated in a review of goshawk diet in Europe (Rutz et al. 2006, Lourenço et al. 2011a).  
330 Whilst many other studies provide a snapshot indication of the frequency of superpredation in  
331 a given system, relatively few have documented temporal variation in the frequency of  
332 superpredators killing other predators (but see Serrano 2000, Rutz and Bijlsma 2006),  
333 particularly in a recovering superpredator population. That there was a per capita increase in  
334 superpredation as the goshawk population recovered (Fig. 1a) has potentially important  
335 implications for conservation and management, because similar increases in superpredation  
336 may be expected in other superpredator populations currently recolonising former ranges in  
337 both North America and Europe (Maehr et al. 2001, Deinet et al. 2013, Chapron et al. 2014).  
338 For example, if increases in superpredation negatively affect the dynamics of mesopredator

339 species which are also of conservation concern it could lead to management conundrums for  
340 conservation projects aimed at restoring apex predator populations. However, it is important to  
341 note that when apex predator populations were reduced or extirpated, many previously  
342 suppressed mesopredator populations increase dramatically (Soulé et al. 1988, Crooks and  
343 Soulé 1999, Ritchie and Johnson 2009). Consequently, any declines in mesopredator  
344 populations which accompany the restoration of large predators may represent the reversal of  
345 this “mesopredator release” process (i.e., mesopredator suppression), rather than a shift to a  
346 new state.

347

### 348 **Impact on local mesopredator populations**

349 It’s important to note that our calculations of how many kestrels, tawny owls and sparrowhawks  
350 were killed by goshawks each year is not only likely to include breeding birds (i.e. the ones on  
351 which local population counts were based) but also non-breeders (e.g., “floaters”), individuals  
352 migrating through the study site (in the case of kestrels) and immigrants from neighbouring  
353 populations. Nevertheless, the large increase in the number of kestrels being killed each year  
354 (from an estimated 14 to 176; Table 3) coincided with a decline in the local kestrel population,  
355 which is consistent with an increase in goshawk predation having a negative impact upon the  
356 local kestrel population. However, the decline in kestrels could also be partly related to other  
357 factors, such as habitat changes or a decline in the amplitude of field vole (*Microtus agrestis*)  
358 population cycles in the study area (Cornulier et al. 2013), as they are the main prey for kestrels  
359 in our study site. Nevertheless, our results suggest that goshawks were killing a progressively  
360 greater proportion of a declining kestrel population, which may have contributed to the study  
361 area becoming a sink habitat, as previously suggested by Petty et al. (2003a).

362

363 In contrast, local breeding population of tawny owls and sparrowhawks did not decline over  
364 the study period, despite the substantial increase in the number killed each year by goshawks  
365 (Table 3; Fig. 2). This suggests that goshawk predation on tawny owls and sparrowhawks is  
366 compensatory rather than additive. Indeed, the impact of goshawk predation on the local tawny  
367 owl population is likely to be mitigated by goshawks selectively killing individuals with low  
368 reproductive values (e.g. juveniles and old owls, which have a lower probability of surviving  
369 and reproducing than prime-aged adults Millon et al. 2010, 2011), thus reducing the overall  
370 impact of predation at the population level (Hoy et al. 2015). Another factor which may be  
371 compensating for the increase in goshawk predation on tawny owls is the increase in  
372 immigrants entering the local population in recent years (Millon et al. 2014). Hence, goshawk  
373 predation may also have led to Kielder becoming a sink habitat for tawny owls. Unfortunately,  
374 we do not have equivalent data for sparrowhawks to be able to evaluate whether changes in  
375 immigration and/or selective predation of individuals with low reproductive values was also  
376 mitigating the impact of increased goshawk predation.

377

### 378 **Goshawks have become food-limited**

379 The substantial decline of two main prey groups (pigeon and game birds) in goshawk diet, the  
380 increase in diet diversity and decrease in goshawk reproductive success are all consistent with  
381 the goshawk population becoming increasingly food-limited as the population increased. The  
382 decline of pigeon and game birds in goshawk diet over the study period (Figs. 2b and 2c),  
383 presumably reflected a decline in the availability of two important prey species, namely feral  
384 pigeon and red grouse. Although, we cannot directly compare observed changes in the  
385 prevalence of feral pigeon and red grouse in diet to changes in their abundance (because  
386 regional population trends are not available), there is indirect evidence to suggest that the  
387 availability of these two prey species has declined. At a national level there has been a long-

388 term decline in red grouse populations in England, and feral pigeon populations are also  
389 thought to have declined by 26% since 1995 (Robinson et al. 2015). The decline in feral pigeons  
390 in goshawk diet may also be related to a decline in the number of stray racing pigeons entering  
391 the forest, because of a sustained decrease in the number of people participating in pigeon  
392 racing since the late 1980's (RPRA 2012). Furthermore, there is also anecdotal evidence of a  
393 local decrease in the abundance of red grouse and their main habitat over the study period  
394 (M.D., personal observation).

395

396 The increase in diet diversity we observed also indirectly supports the notion that there has  
397 been a decline in the availability of important prey, because when such food become scarce,  
398 predators are forced to switch to alternative species to make up the shortfall. Indeed, diet  
399 diversity was found to be negatively related to the abundance of important prey species for  
400 both goshawks (Rutz and Bijlsma 2006), sparrowhawks (Millon et al. 2009) and Eagle owls  
401 (*Bubo bubo*; Serrano 2000). Thus, together our results are consistent with goshawks switching  
402 to alternative prey species (raptors, corvids and mammals) as the availability of preferred prey  
403 species (e.g. feral pigeons and grouse) declined and they become food limited.

404

405 The decline in goshawk reproductive success as goshawk numbers increased (Fig. 3) provided  
406 additional and independent evidence that goshawks became food-limited given that goshawk  
407 reproductive success is known to be positively related to food availability (Rutz and Bijlsma  
408 2006). A decline in reproductive success could also arise if goshawks had smaller home-ranges  
409 in high density years. However, this seems unlikely given that the average distance between  
410 goshawk nest sites has varied little since the mid-80's (mean distance between nest sites = 3.97  
411 km  $\pm$  0.43; coefficient of variation = 0.11). A decline in reproductive success with increasing  
412 density could also arise if individuals establishing home-ranges in later years were forced to

413 settle in “poor-quality sites” because all the “good-quality sites” were already occupied  
414 (Rodenhuse et al. 1997). Although the biggest decline in reproductive success was observed  
415 in territories established towards the end of the study period, reproductive success also declined  
416 in territories established in the early and mid-part of the study period (Appendix 6). One likely  
417 reason for the decline in reproductive success, hence food availability being population wide  
418 (rather than restricted to certain home-ranges), may be because goshawk hunting ranges  
419 overlap (Kenward 2006), such that individuals nesting in the later established “poor-quality  
420 sites” may still forage and deplete prey in areas used for hunting by birds nesting in “good-  
421 quality site”.

422

### 423 **Mechanisms underlying superpredation**

424 The increase in the proportion of raptors in the diet as goshawk abundance increased (Fig. 1),  
425 viewed in combination with the results of other analyses is consistent with predictions for the  
426 food-limitation hypothesis of superpredation. That is, as the availability of preferred prey  
427 (pigeon and grouse) declined goshawks appear to have switched to alternative, less profitable  
428 prey species, such as raptors. Furthermore, predictions of alternative hypotheses were not  
429 supported by our data. For example, if superpredation was purely opportunistic then changes  
430 in the frequency of mesopredator species in the diet are expected to reflect changes in  
431 mesopredator abundance (Polis et al. 1989). However, the contribution of kestrels to goshawk  
432 diet was higher in the later part of the study, despite kestrels declining. Furthermore, only two  
433 buzzards were known to have been killed by goshawks, despite a substantial increase in the  
434 abundance of buzzards in the forest since 1995 (over 80+ home-ranges now occupied). Our  
435 results also do not provide support for the predator-removal hypothesis given that the raptor  
436 species killed by goshawks were of no or little threat either to adult or juvenile goshawks  
437 (Appendix 5). Support for the competitor removal-hypothesis is also lacking because the

438 majority (83%) of raptors killed by goshawks are unlikely to compete with goshawks for food  
439 as they are largely dependent on field voles (e.g., kestrels and tawny owls; Appendix 5), yet  
440 voles only make up 0.06% of goshawk diet in terms of biomass. Furthermore, buzzards were  
441 seldom preyed upon by goshawks, yet they are known to compete with goshawks for nest sites  
442 and kill some of the same species as goshawks (Bijlsma 1994, Krüger 2002a, b). We therefore  
443 conclude that food limitation is the most likely driver of superpredation in this system given:  
444 1) the decline in two main prey groups, the increase in diet diversity and the decrease in  
445 goshawk reproductive success suggest that the goshawk population has become food-limited;  
446 2) superpredation does not appear to be purely opportunistic, given that variation in goshawk  
447 predation on different raptor species did not mirror local mesopredator population trends; and  
448 3) the species of mesopredator killed offer little support for either the predator- or competitor-  
449 removal hypotheses of superpredation.

450

## 451 **CONCLUSIONS**

452 Here we have provided evidence to show how superpredation varied over time in a recovering  
453 population of an apex predator, the northern goshawk. Our results suggest that increasing rates  
454 of superpredation were a response to declining food availability (pigeon and grouse) linked to  
455 increasing goshawk numbers. Thus, this study offers insights into the mechanisms driving  
456 variation in superpredation. We found evidence suggesting that an increase in goshawk  
457 predation may be contributing to a decline in the most frequently preyed mesopredator,  
458 Eurasian kestrels, a species which is also of conservation concern nationally. Thus, our results  
459 indicate that superpredation is likely to be an important factor to consider when developing  
460 conservation and management strategies for mesopredator species in the future. However,  
461 rather than a shift to a new alternative state, we suggest that the decline in kestrel numbers (and  
462 their likely persistence in refuges/areas with lower superpredator abundance) possibly

463 represents a reversal of a mesopredator release process (i.e. mesopredator suppression)  
464 following the extirpation of goshawks, and decline in other larger raptor species in the UK.  
465 Thus the results presented here may also offer insights into how other raptor communities will  
466 change in areas where goshawks are starting to recover. Lastly, in addition to the direct effect  
467 that an increase in predation can have on mesopredator population dynamics by increasing  
468 mortality rates, it is also important to consider that recovering superpredator populations may  
469 also be influencing mesopredator dynamics by negatively affecting mesopredator reproduction  
470 success. For example, mesopredators are more likely to abandon breeding attempts when  
471 superpredator densities are high (Mueller et al. 2016, Hoy et al. 2016).

472

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625

Table 1. Model selection and parameters for the analysis of variation in the proportion of goshawk diet comprised of all raptor species and also kestrels, tawny owls and sparrowhawks separately. We examined whether diet varied in relation to goshawk abundance (number of home-ranges occupied) and the altitude of the goshawk home-range (e.g., below 225m, between 226-354m and above 355m). The most parsimonious model will have a  $\Delta AICc = 0$  and is highlighted in bold. The number of parameters estimated in each model is designated in the *np* column. *AICc* weights (*W*) are an estimate of the relative likelihood of a model.

Model	<i>np</i>	All raptors				Kestrel				Tawny owl				Sparrowhawk			
		Estimate	SE	$\Delta AICc$	<i>W</i>	Estimate	SE	$\Delta AICc$	<i>W</i>	Estimate	SE	$\Delta AICc$	<i>W</i>	Estimate	SE	$\Delta AICc$	<i>W</i>
1. Null	2			26.74	<0.01			11.87	<0.01			13.51	<0.01			9.36	0.01
2. Goshawk abundance (GA)	4	0.06	0.02	14.46	<0.01	0.02	0.02	12.53	<0.01	<b>0.11</b>	<b>0.03</b>	<b>0</b>	<b>0.84</b>	<b>0.12</b>	<b>0.04</b>	<b>0</b>	<b>0.61</b>
3. Altitude (226-354m)	5	-0.01	0.19	13.2	<0.01	-0.18	0.26	2.7	0.18	0.15	0.35	17.09	<0.01	-0.2	0.49	9.89	<0.01
Altitude (above 355m)		0.95	0.28			0.96	0.38			0.36	0.52			0.92	0.76		
4. Altitude (226-354m)	6	0.03	0.18	4.89	0.08	-0.15	0.25	3.94	0.1	0.22	0.34	3.66	0.13	-0.12	0.47	2.66	0.16
Altitude (above 355m)		0.84	0.27			0.95	0.38			0.14	0.5			0.58	0.72		
+ Goshawk abundance		0.05	0.02			0.02	0.02			0.11	0.03			0.11	0.04		
5. Altitude (226-354m)	8	<b>-0.87</b>	<b>0.68</b>	<b>0</b>	<b>0.92</b>	<b>-0.98</b>	<b>0.93</b>	<b>0</b>	<b>0.71</b>	-0.72	1.62	6.94	0.03	-4.18	1.94	2.07	0.22
Altitude (above 355m)		<b>2.57</b>	<b>1.01</b>			<b>3.18</b>	<b>1.26</b>			-2.98	3.73			-1.22	3.97		
Goshawk abundance		<b>0.03</b>	<b>0.03</b>			<b>0.01</b>	<b>0.04</b>			0.08	0.06			0.01	0.06		
Altitude (226-354m) x GA		<b>0.04</b>	<b>0.03</b>			<b>0.04</b>	<b>0.04</b>			0.04	0.06			0.16	0.08		
Altitude (above 355m) x GA		<b>-0.07</b>	<b>0.04</b>			<b>-0.09</b>	<b>0.05</b>			0.11	0.13			0.07	0.15		

Table 2. The 10 most important prey species in northern goshawk breeding season diet, ranked in order of decreasing importance in terms of both their frequency in the diet and biomass contribution to diet when the number of occupied goshawk home-ranges was estimated to be less than 14, between 15-24 and 25 or more.

Species rank	Frequency						Species rank	Biomass		
	<14 occupied goshawk home-ranges	<i>n</i>	15-24 occupied goshawk home-ranges	<i>n</i>	>25 occupied goshawk home-ranges	<i>n</i>		<14 occupied goshawk home-ranges	15-24 occupied goshawk home-ranges	>25 occupied goshawk home-ranges
1.	Feral pigeon	531	Wood pigeon	848	Wood pigeon	625	1.	Wood pigeon	Wood pigeon	Wood pigeon
2.	Wood pigeon	488	Feral pigeon	752	Feral pigeon	479	2.	Red grouse	Crow/rook	Crow/rook
3.	Red grouse	277	Crow/rook	597	Crow/rook	383	3.	Feral pigeon	Feral pigeon	Rabbit
4.	Crow/rook	149	Red grouse	221	Red grouse	133	4.	Crow/rook	Rabbit	Feral pigeon
5.	Jay	35	Kestrel	128	Rabbit	108	5.	Rabbit	Red grouse	Red grouse
6.	Song thrush	30	Rabbit	126	Red squirrel	89	6.	Pheasant	Pheasant	Pheasant
7.	Mistle thrush	27	Mistle thrush	85	Mistle thrush	88	7.	European hare	Kestrel	Tawny owl
8.	Field vole	25	Red squirrel	84	Jay	78	8.	Jay	Red squirrel	Red squirrel
9.	Kestrel	24	Song thrush	78	Kestrel	76	9.	Mallard	Tawny owl	Kestrel
10.	Red squirrel	22	Jay	61	Tawny owl	69	10.	Kestrel	Mistle thrush	Jay

Table 3. Estimated number of kestrels, tawny owls and sparrowhawks killed during the breeding season (March-August) each year by the Kielder Forest goshawk population when the number of occupied goshawk home-ranges was estimated to be less than 14, between 15-24 and 25 or more.

Species	Occupied goshawk home-ranges	Estimated % biomass of goshawk diet	Average number killed per pair	Mean number killed each year the by entire goshawk population	95% CI lower bound	95% CI upper bound
Kestrel	< 14	0.47	2.20	14	11	18
	15-24	2.29	10.23	223	197	248
	> 25	1.63	6.44	176	154	198
Tawny owl	< 14	0.34	0.70	5	3	6
	15-24	1.69	3.33	72	62	83
	> 25	3.32	5.79	159	141	176
Sparrowhawk	< 14	0.04	0.21	1	1	2
	15-24	0.37	1.66	36	28	45
	> 25	0.48	1.92	53	44	61

Table 4. Model selection and parameters for the analysis of variation in the proportion of goshawk diet comprised of different prey groups (pigeons, corvids, game birds, mammals and other). We examined whether diet varied in relation to goshawk abundance (number of home-ranges occupied) and the altitude of the goshawk home-range (e.g., below 225m, between 226-354m and above 355m). The most parsimonious model will have a  $\Delta\text{AICc} = 0$  and is highlighted in bold. The number of parameters estimated in each model is designated in the *np* column. AICc weights (*W*) are an estimate of the relative likelihood of a model.

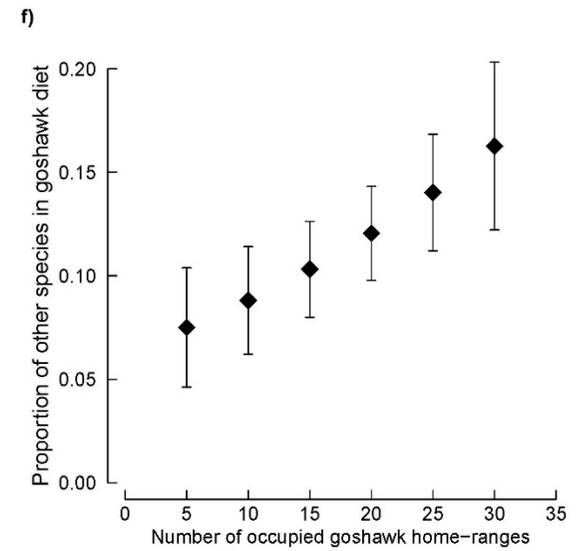
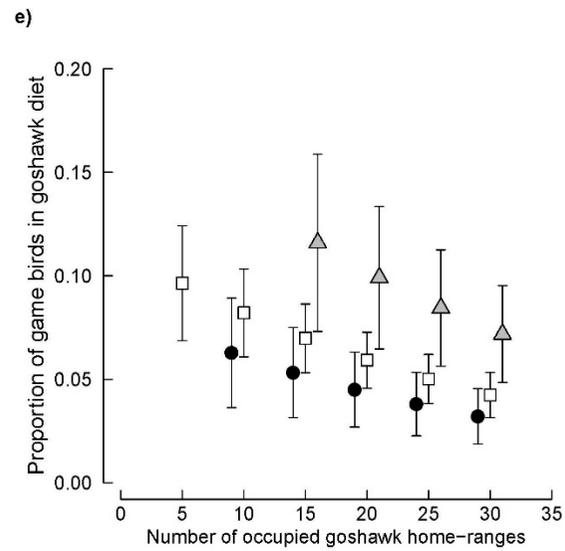
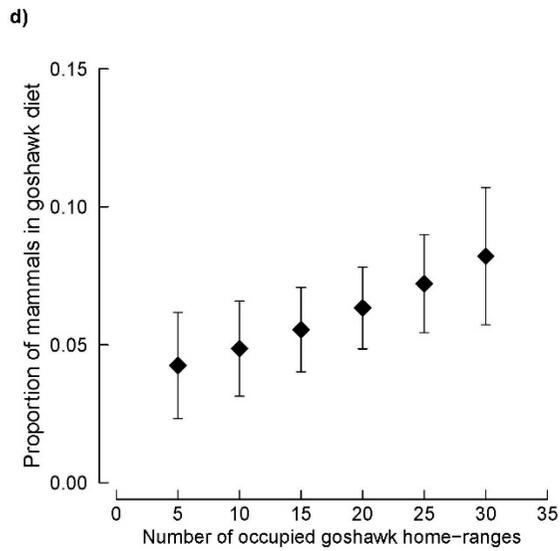
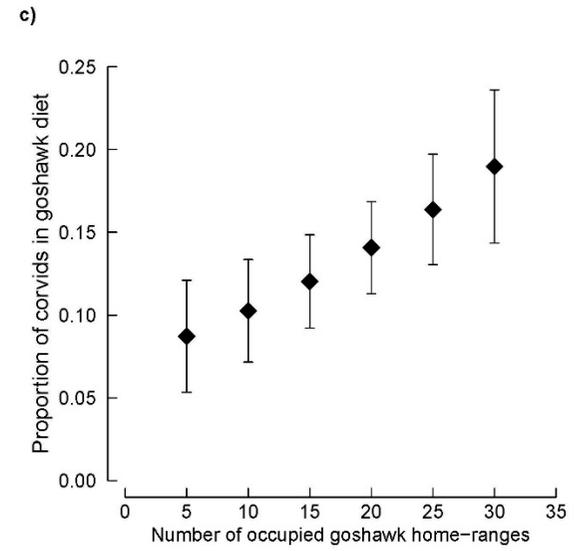
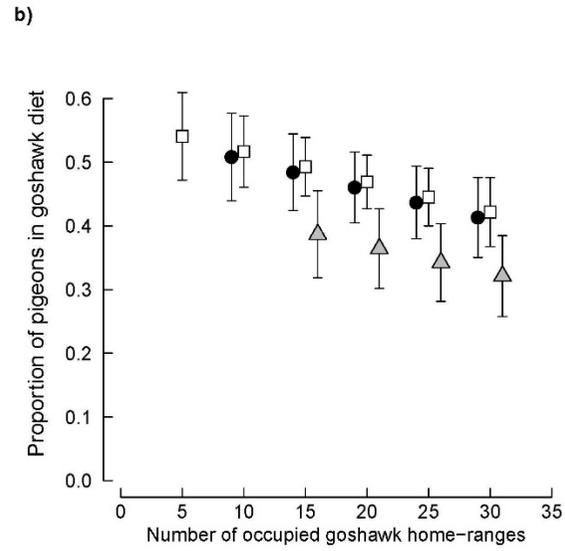
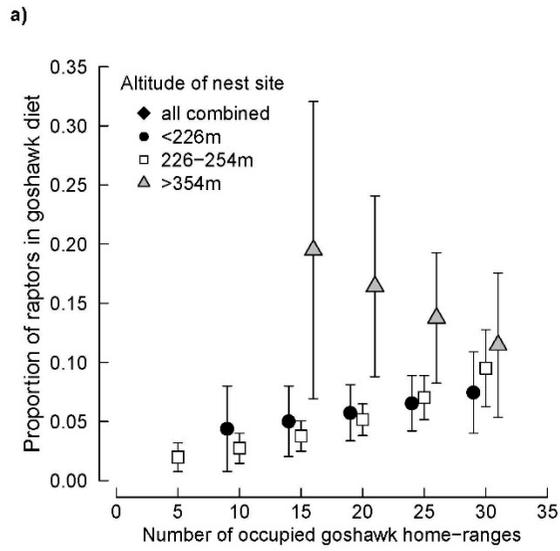
Model	<i>np</i>	Pigeons				Corvids				Game birds				Mammals				Other			
		Estimate	SE	$\Delta\text{AICc}$	<i>W</i>	Estimate	SE	$\Delta\text{AICc}$	<i>W</i>	Estimate	SE	$\Delta\text{AICc}$	<i>W</i>	Estimate	SE	$\Delta\text{AICc}$	<i>W</i>	Estimate	SE	$\Delta\text{AICc}$	<i>W</i>
Null	2			16.82	<0.01			7.94	0.02			23.01	<0.01			2.60	0.19			6.77	0.03
Goshawk abundance (GA)	4	-0.02	0.01	10.49	<0.01	<b>0.04</b>	<b>0.01</b>	<b>0</b>	<b>0.8</b>	-0.03	0.01	9.66	0.01	<b>0.03</b>	<b>0.01</b>	<b>0</b>	<b>0.68</b>	<b>0.03</b>	<b>0.01</b>	<b>0</b>	0.77
Altitude (226-354m)	5	0.04	0.10	4.04	0.08	-0.11	0.12	10.96	<0.01	0.32	0.22	22.75	<0.01	-0.05	0.17	6.55	0.03	-0.05	0.13	9.21	0.01
Altitude (above 355m)		-0.42	0.15			-0.02	0.19			0.55	0.26			0.001	0.26			0.16	0.20		
Altitude (226-354m)	6	<b>0.03</b>	<b>0.10</b>	<b>0</b>	<b>0.62</b>	-0.09	0.12	3.55	0.14	<b>0.29</b>	<b>0.21</b>	<b>0</b>	<b>0.64</b>	-0.03	0.17	4.04	0.09	-0.04	0.13	3.20	0.16
Altitude (above 355m)		<b>-0.40</b>	<b>0.15</b>			-0.04	0.19			<b>0.85</b>	<b>0.26</b>			-0.06	0.26			0.12	0.20		
+ Goshawk abundance		<b>-0.02</b>	<b>0.01</b>			0.04	0.01			<b>-0.04</b>	<b>0.01</b>			0.03	0.01			0.03	0.01		
Altitude (226-354m)	8	-0.29	0.34	1.54	0.29	-0.12	0.42	5.96	0.04	0.30	0.60	1.15	0.36	0.01	0.64	7.76	0.01	0.32	0.49	6.10	0.04
Altitude (above 355m)		-1.29	0.60			0.77	0.71			-0.78	1.15			-0.83	1.39			1.03	0.89		
Goshawk abundance		-0.03	0.01			0.04	0.02			-0.04	0.02			0.03	0.03			0.05	0.02		
Altitude (226-354m) x GA		0.01	0.01			0.002	0.02			-0.001	0.03			-0.002	0.03			-0.01	0.02		
Altitude (above 355m) x GA		0.04	0.02			-0.03	0.03			0.06	0.04			0.03	0.05			-0.04	0.03		

## Figure Legends

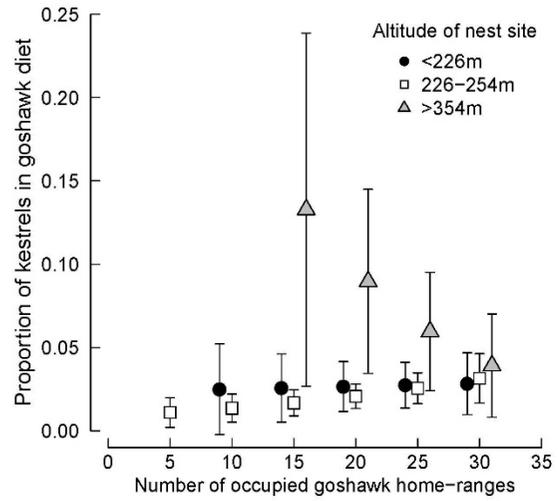
Figure 1. Changes in the proportion of northern goshawk breeding season diet comprised of: a) raptors; b) pigeons; c) corvids; d) mammals; e) game birds and f) other species as the number of occupied goshawk home-ranges increased in Kielder Forest, UK. Error bars are the 95% confidence intervals.

Figure 2. Changes in the proportion of northern goshawk breeding season diet comprised of: a) kestrels; b) tawny owls; c) sparrowhawks as the number of occupied goshawk home-ranges increased in Kielder Forest, UK. Error bars are the 95% confidence intervals.

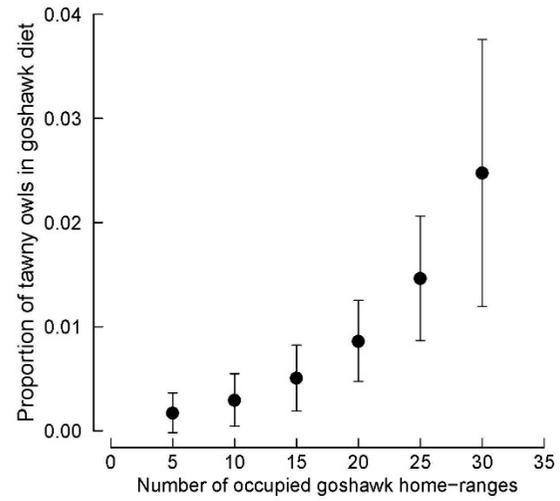
Figure 3. Inter-annual variation in goshawk reproductive success measured as: a) the number of chicks fledged per successful breeding attempt (line represents predicted values generated from a GAM) and b) the proportion of breeding attempts which were successful (line represents predicted values generated from a GLM) as the number of occupied goshawk home-ranges increased in Kielder Forest, UK.



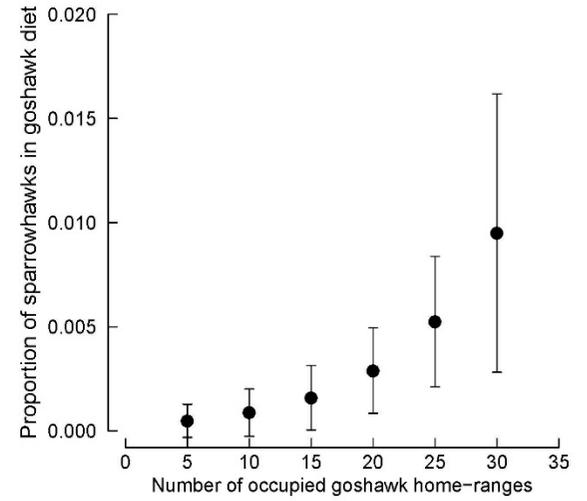
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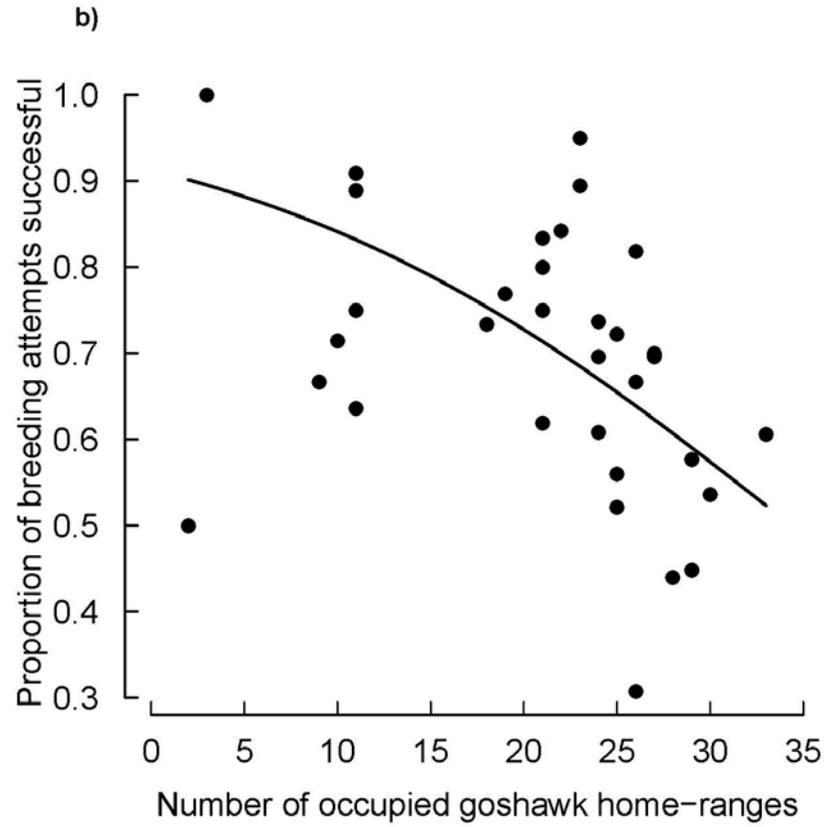
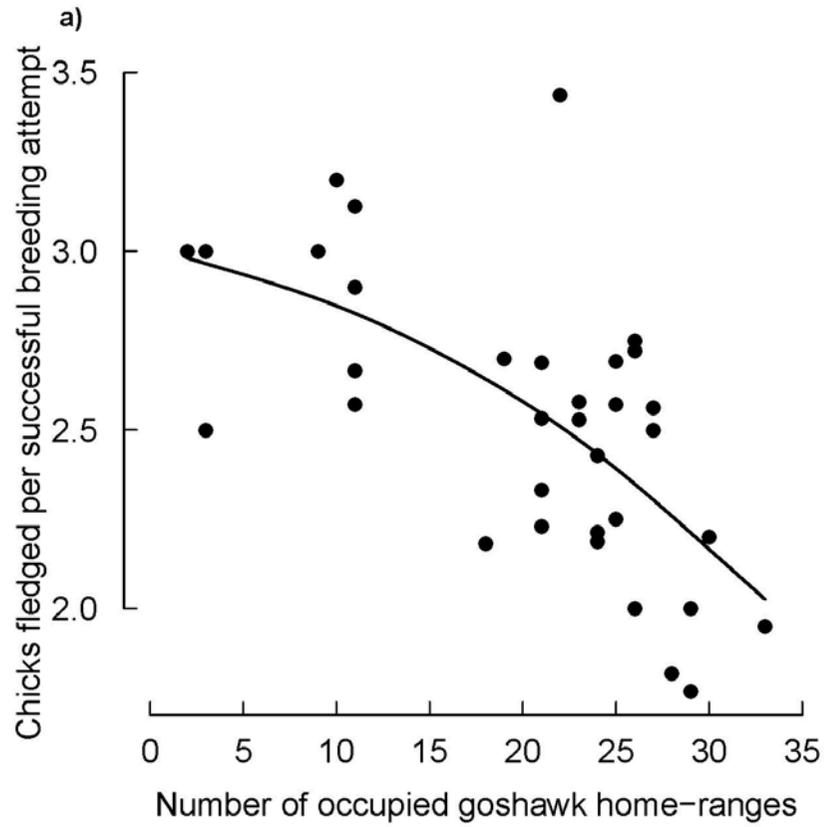


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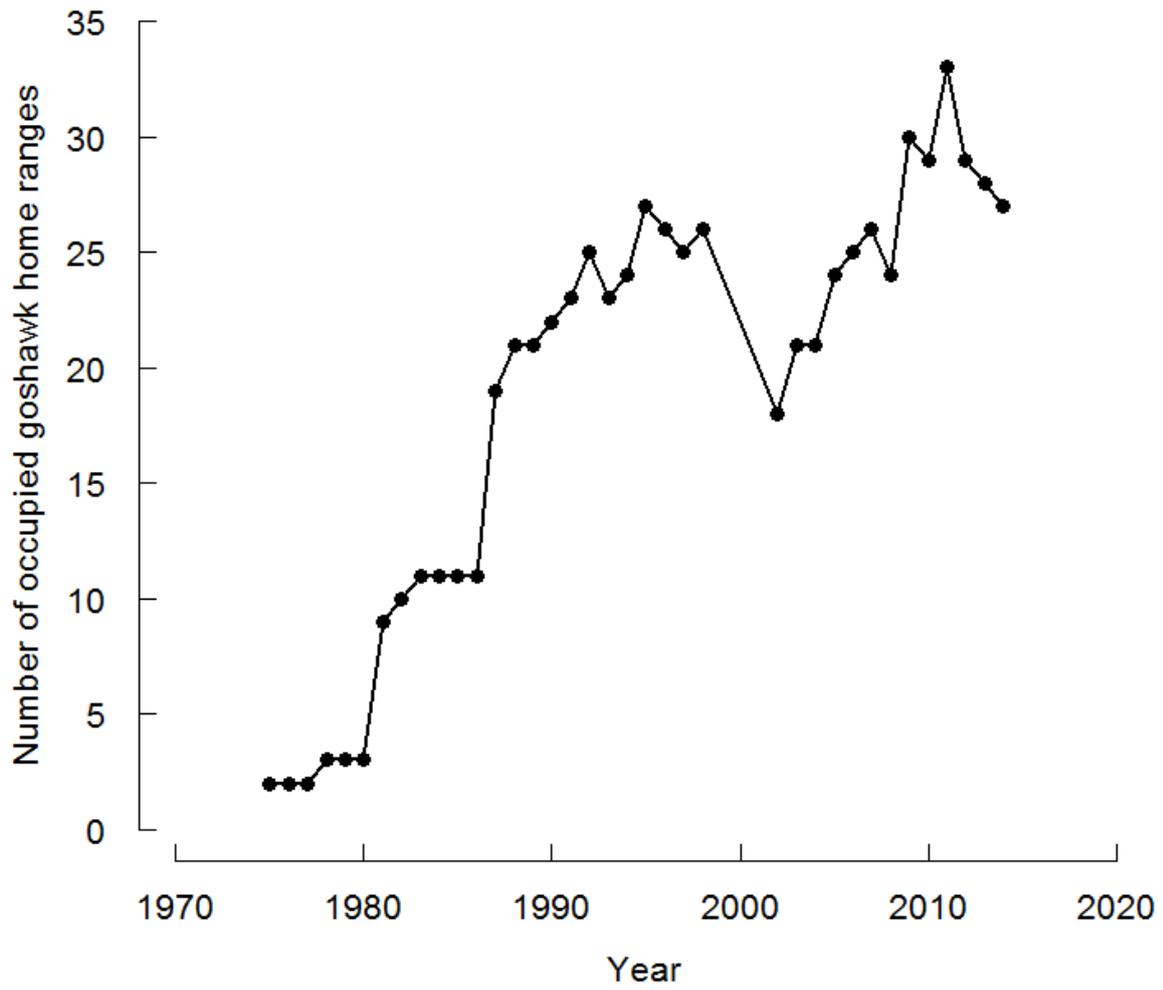


c)





**Appendix 1:** The number of occupied northern goshawk home-ranges in Kielder Forest, UK



**Appendix 2:** The average number of kestrels, tawny owls and sparrowhawks killed by the goshawk population each year

To estimate the average number of each species killed by the goshawk population each year, we first calculated the average number of each species killed per pair of goshawks, each year when 1-14, 15-24 and 25+ goshawk home-ranges were occupied, using the following equation taken from 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 (i.e. offspring) during the breeding season (161g of food per day (CF+CM/2) \* 108 days \* mean fledged brood size of breeding pairs). The mean fledged brood size of goshawks was 2.19 in years when fewer than 15 home-ranges were occupied, 1.93 when 15-24 home-ranges were occupied and 1.31 when 25 or more home-ranges were occupied. The CY estimate assumes that young goshawks: 1) hatch around mid-May; 2) do not leave their natal territory until August; and 3) that juveniles have the same overall food intake as adults. Although young nestlings require less food than adults, older nestlings require more, such that when averaged over the entire period nestling food intake can be assumed to be equivalent to that of 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. We used the dietary data to estimate of the proportion biomass of each of the three mesopredator species in goshawk diet for each of the three goshawk abundance categories (i.e. using pooled annual diet data collected when the number of occupied goshawk home-ranges was 1-14, 15-24 and 25+). This average proportion was then used in the above equation to calculate the number of individuals of each species killed 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 and how that has changed as the goshawk population increased in abundance, 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 for each of the goshawk abundance categories. The average number of home-ranges occupied in each goshawk abundance category was estimated to be 6.5, 21.75 and 27.38 when 1-14, 15-24 and 25+ goshawk home-ranges were occupied respectively.

**Appendix 3:** List of the species killed by northern goshawks in Kielder Forest, and the taxonomic prey group they were assigned to, along with the body mass used for each species to estimate their percentage biomass contribution to goshawk diet. We were not always able to differentiate between male and female prey remains, consequently we used the midpoint between the average mass for males and females in our biomass estimates. Body mass estimates for birds were obtained from the British Trust for Ornithology's website ([www.bto.org/birdfacts](http://www.bto.org/birdfacts)) and mass estimates for mammals were obtained from the British Mammal Societies website (<http://www.mammal.org.uk>).

Prey group	Common name	Mass (g)
Corvid	Carrion crow/rook ( <i>Corvus corone/C. frugilegus</i> )	510
Corvid	Eurasian jay ( <i>Garrulus glandarius</i> )	170
Corvid	Jackdaw ( <i>Corvus monedula</i> )	220
Corvid	Magpie ( <i>Pica pica</i> )	220
Corvid	Raven ( <i>Corvus corax</i> )	1200
Game	Black grouse ( <i>Tetrao tetrix</i> )	1065
Game	Pheasant ( <i>Phasianus colchicus</i> )	1190
Game	Red grouse ( <i>Lagopus lagopus scotica</i> )	600
Game	Red-legged partridge ( <i>Alectoris rufa</i> )	490
Mammal	Common shrew ( <i>Sorex araneus</i> )	9.5
Mammal	European hare ( <i>Lepus europaeus</i> )	3500
Mammal	European rabbit ( <i>Oryctolagus cuniculus</i> )	1600
Mammal	Field vole ( <i>Microtus agrestis</i> )	30
Mammal	Grey squirrel ( <i>Sciurus carolinensis</i> )	552.5
Mammal	Mole ( <i>Talpa europaea</i> )	100
Mammal	Pygmy shrew ( <i>Sorex minutus</i> )	4
Mammal	Rat ( <i>Rattus norvegicus</i> )	360
Mammal	Red squirrel ( <i>Sciurus vulgaris</i> )	200
Mammal	Stoat ( <i>Mustela erminea</i> )	266.25
Mammal	Weasel ( <i>Mustela nivalis</i> )	90.25
Other	Blackbird ( <i>Turdus merula</i> )	100
Other	Black-headed gull ( <i>Chroicocephalus ridibundus</i> )	290
Other	Blue tit ( <i>Cyanistes caeruleus</i> )	10.5
Other	Budgerigar ( <i>Melopsittacus undulatus</i> )	35
Other	Chaffinch ( <i>Fringilla coelebs</i> )	24
Other	Coal tit ( <i>Periparus ater</i> )	9
Other	Common frog ( <i>Rana temporaria</i> )	22.7
Other	Common gull ( <i>Larus canus</i> )	400
Other	Common lizard ( <i>Zootoca vivipara</i> )	4
Other	Common toad ( <i>Bufo bufo</i> )	55
Other	Crossbill ( <i>Loxia curvirostra</i> )	43
Other	Cuckoo ( <i>Cuculus canorus</i> )	120
Other	Curlew ( <i>Numenius arquata</i> )	985
Other	Domestic chicken ( <i>Gallus gallus domesticus</i> )	1900
Other	Eurasian bullfinch ( <i>Pyrrhula pyrrhula</i> )	21
Other	Fieldfare ( <i>Turdus pilaris</i> )	100

Prey group	Common name	Mass (g)
Other	Goldcrest ( <i>Regulus regulus</i> )	6
Other	Great spotted woodpecker ( <i>Dendrocopos major</i> )	85
Other	Great tit ( <i>Parus major</i> )	18.5
Other	Green woodpecker ( <i>Picus viridis</i> )	190
Other	Kittiwake ( <i>Rissa tridactyla</i> )	410
Other	Lapwing ( <i>Vanellus vanellus</i> )	230
Other	Lesser black-backed gull ( <i>Larus fuscus</i> )	830
Other	Lesser redpoll ( <i>Acanthis cabaret</i> )	11
Other	Mallard ( <i>Anas platyrhynchos</i> )	1090
Other	Meadow pipit/tree pipit ( <i>Anthus pratensis/A. trivialis</i> )	19
Other	Mistle thrush ( <i>Turdus viscivorus</i> )	130
Other	Moorhen ( <i>Gallinula chloropus</i> )	320
Other	Newt ( <i>Triturus vulgaris</i> )	30
Other	Oyster catcher ( <i>Haematopus ostralegus</i> )	540
Other	Pied wagtail ( <i>Motacilla alba</i> )	21
Other	Redshank ( <i>Tringa totanus</i> )	120
Other	Robin ( <i>Erithacus rubecula</i> )	18
Other	Siskin ( <i>Spinus spinus</i> )	15
Other	Skylark ( <i>Alauda arvensis</i> )	38.5
Other	Snipe ( <i>Gallinago gallinago</i> )	110
Other	Song thrush ( <i>Turdus philomelos</i> )	83
Other	Starling ( <i>Sturnus vulgaris</i> )	78
Other	Swallow ( <i>Hirundo rustica</i> )	18.5
Other	Teal ( <i>Anas crecca</i> )	330
Other	Tree creeper ( <i>Certhia familiaris</i> )	10
Other	Whinchat ( <i>Saxicola rubetra</i> )	17
Other	Willow warbler ( <i>Phylloscopus trochilus</i> )	10
Other	Woodcock ( <i>Scolopax rusticola</i> )	280
Pigeon	Collared dove ( <i>Streptopelia decaocto</i> )	200
Pigeon	Feral pigeon ( <i>Columba livia</i> )	300
Pigeon	Wood pigeon ( <i>Columba palumbus</i> )	450
Raptor	Barn owl ( <i>Tyto alba</i> )	300
Raptor	Common buzzard ( <i>Buteo buteo</i> )	890
Raptor	Common kestrel ( <i>Falco tinnunculus</i> )	208
Raptor	Long-eared owl ( <i>Asio otus</i> )	290
Raptor	Merlin ( <i>Falco columbarius</i> )	205
Raptor	Northern goshawk ( <i>Accipiter gentilis</i> )†	1000
Raptor	Short-eared owl ( <i>Asio flammeus</i> )	330
Raptor	Sparrowhawk ( <i>Accipiter nisus</i> )	205
Raptor	Tawny owl ( <i>Strix aluco</i> )	470

† Goshawk chicks were only included in the diet if there was evidence to suggest that it was a case of cannibalism rather than fledglings dying in the nest.

**Appendix 4:** Variation in the proportion of northern goshawk diet made up different prey groups as goshawk abundance increased. Total refers to all dietary data collected during the breeding season between 1973 and 2014, the other columns show estimates from dietary data collected in years when 1-14, 15-24 and 25 or more goshawk home-ranges were occupied.

Prey group	<i>n</i>				% Biomass				% Frequency			
	Total	1-14	15-24	25+	Total	1-14	15-24	25+	Total	1-14	15-24	25+
Pigeon (Columbidae)	3724	1019	1601	1104	43.37	51.80	41.75	39.82	47.97	57.18	46.61	43.36
Corvid (Corvidae)	1379	190	694	495	19.15	11.52	22.18	20.25	17.76	10.66	20.20	19.44
Game (Phasianidae, Tetraonidae)	748	296	287	165	15.55	25.46	13.97	10.91	9.64	16.61	8.36	6.48
Mammal	541	74	255	212	14.08	6.13	15.16	18.05	6.97	4.15	7.42	8.33
Raptor (Accipitridae, Falconidae, Strigidae)	465	44	225	196	4.35	2.05	4.16	6.17	5.99	2.47	6.55	7.70
Other	906	159	373	374	3.50	3.04	2.77	4.80	11.67	8.92	10.86	14.69
Total	7763	1782	3435	2546	100	100	100	100	100	100	100	100

**Appendix 5:** Occurrence of raptor species in the breeding season diet of a northern goshawk population in Kielder Forest, UK when the number of goshawk home-ranges occupied each year was estimated to be 1-14, 15-24 and 25 or more.

Species	<i>n</i>				% Biomass				% Frequency				% of raptors			
	Total	1-14	15-24	25+	Total	1-14	15-24	25+	Total	1-14	15-24	25+	Total	1-14	15-24	>25
Common kestrel *	228	24	128	76	1.46	0.68	1.83	1.48	2.94	1.35	3.73	2.99	49.03	54.55	56.89	38.78
Tawny owl *	106	7	30	69	1.53	0.45	0.97	3.04	1.37	0.39	0.87	2.71	22.80	15.91	13.33	35.20
Sparrowhawk	48	2	22	24	0.30	0.06	0.31	0.46	0.62	0.11	0.64	0.94	10.32	4.55	9.78	12.24
Short-eared owl *	23	7	14	2	0.23	0.32	0.32	0.06	0.30	0.39	0.41	0.08	4.95	15.91	6.22	1.02
Barn owl *	14	0	3	11	0.13	0	0.06	0.31	0.18	0	0.09	0.43	3.01	0	1.33	5.61
Long-eared owl *	17	0	12	5	0.15	0	0.24	0.14	0.22	0	0.35	0.20	3.66	0	5.33	2.55
Merlin	14	0	12	2	0.09	0	0.17	0.04	0.18	0	0.35	0.08	3.01	0	5.33	1.02
Northern goshawk	13	4	3	6	0.40	0.55	0.21	0.56	0.17	0.22	0.09	0.24	2.80	9.09	1.33	3.06
Common buzzard	2	0	1	1	0.05	0	0.06	0.08	0.03	0	0.03	0.04	0.43	0	0.44	0.51

\* Denotes raptor species which are dependent on field voles.

**Appendix 6:** The proportion of goshawk breeding attempts which were successful (i.e. fledged at least one chick) shown in relation to goshawk abundance (number of occupied goshawk territories) and according to when the goshawk home-range first became established. Numbers in parentheses are the total number of breeding attempts for each category.

Home-ranges established	Number of occupied goshawk home ranges		
	$\leq 14$	15-24	$\geq 25$
Early (1973-1986)	0.73 (60)	0.76 (114)	0.51 (112)
Middle (1987-2001)	-	0.77 (96)	0.61 (125)
Late (2002-2014)	-	0.75 (20)	0.25 (44)