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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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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 ≤ 14 to ≥ 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 964km² 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 19th 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 ΔAIC 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 ≤ 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 ≤ 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 ≤ 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 ≤ 14 to ≥ 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 350m), 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 ≥ 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 ± 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 ± 0.24 chicks to 2.29 ± 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 ± 0.18 to 0.58 ± 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 $\Delta\text{AICc} = 0$ 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>	All raptors				Kestrel				Tawny owl				Sparrowhawk			
		Estimate	SE	ΔAICc	<i>W</i>	Estimate	SE	ΔAICc	<i>W</i>	Estimate	SE	ΔAICc	<i>W</i>	Estimate	SE	ΔAICc	<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	0.11	0.03	0	0.84	0.12	0.04	0	0.61
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	-0.87	0.68	0	0.92	-0.98	0.93	0	0.71	-0.72	1.62	6.94	0.03	-4.18	1.94	2.07	0.22
Altitude (above 355m)		2.57	1.01			3.18	1.26			-2.98	3.73			-1.22	3.97		
Goshawk abundance		0.03	0.03			0.01	0.04			0.08	0.06			0.01	0.06		
Altitude (226-354m) x GA		0.04	0.03			0.04	0.04			0.04	0.06			0.16	0.08		
Altitude (above 355m) x GA		-0.07	0.04			-0.09	0.05			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	ΔAICc	<i>W</i>	Estimate	SE	ΔAICc	<i>W</i>	Estimate	SE	ΔAICc	<i>W</i>	Estimate	SE	ΔAICc	<i>W</i>	Estimate	SE	ΔAICc	<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	0.04	0.01	0	0.8	-0.03	0.01	9.66	0.01	0.03	0.01	0	0.68	0.03	0.01	0	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	0.03	0.10	0	0.62	-0.09	0.12	3.55	0.14	0.29	0.21	0	0.64	-0.03	0.17	4.04	0.09	-0.04	0.13	3.20	0.16
Altitude (above 355m)		-0.40	0.15			-0.04	0.19			0.85	0.26			-0.06	0.26			0.12	0.20		
+ Goshawk abundance		-0.02	0.01			0.04	0.01			-0.04	0.01			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		

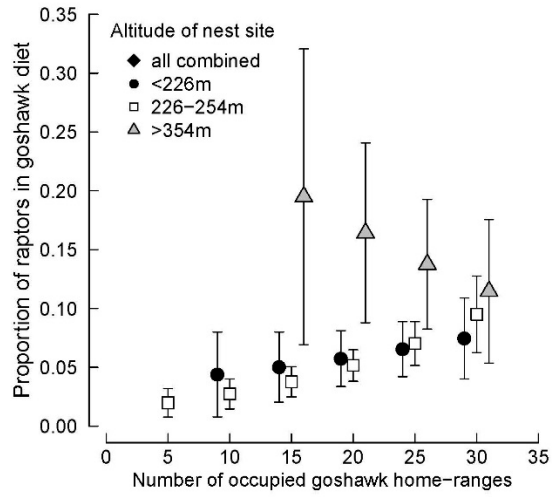
Figure Legends

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.

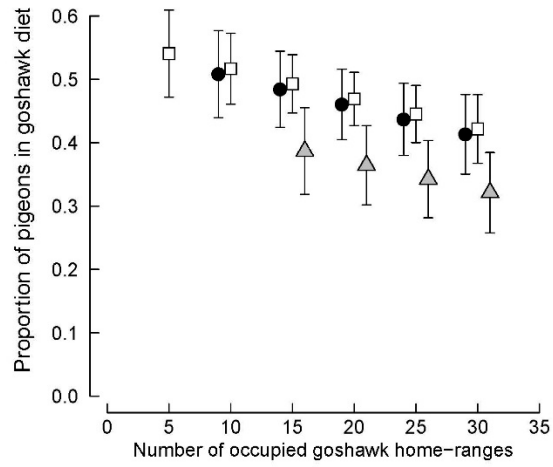
Figure 2. Changes in the proportion of northern goshawk breeding season diet comprised of: a) kestrels; b) tawny owls; c) sparrowhawks as the number of occupied goshawk home-ranges increased in Kielder Forest, UK. Error bars are the 95% confidence intervals.

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.

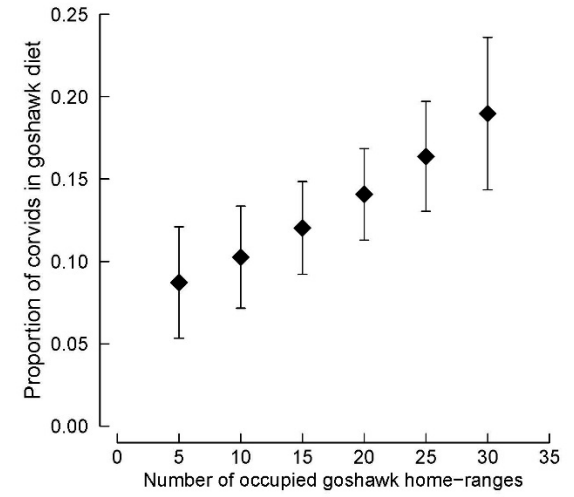
a)



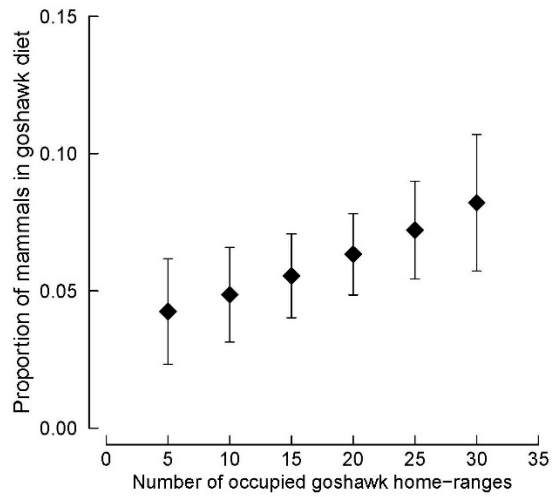
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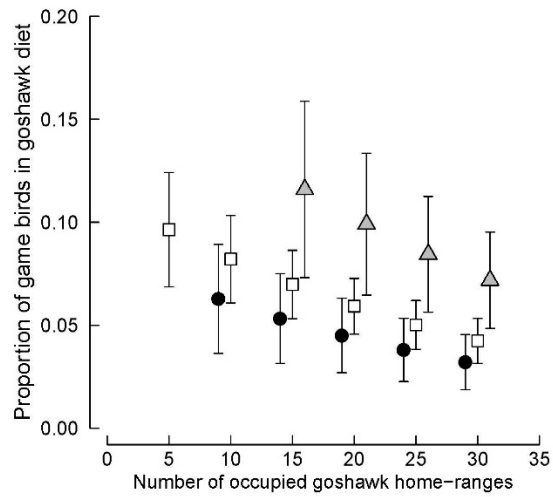
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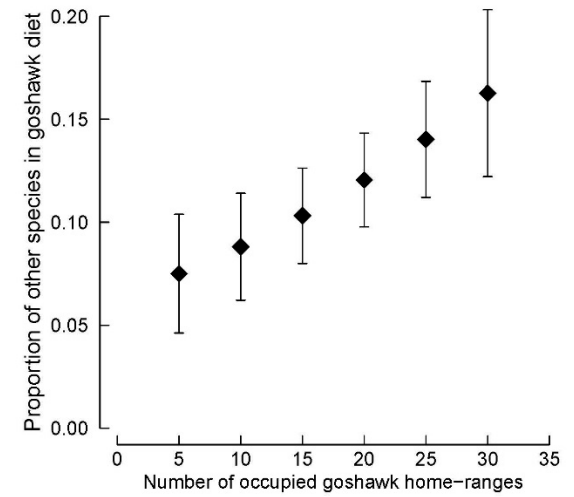
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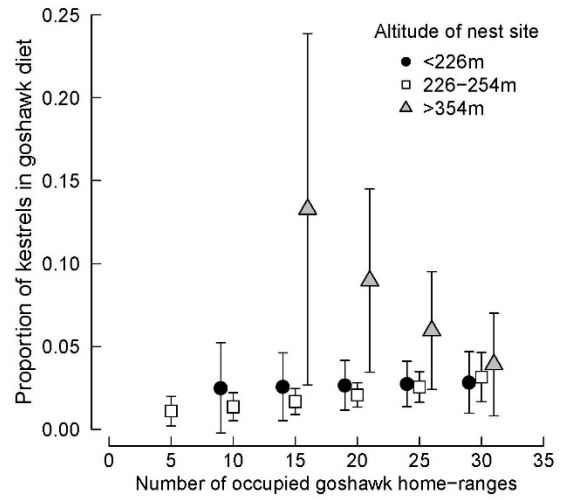
e)



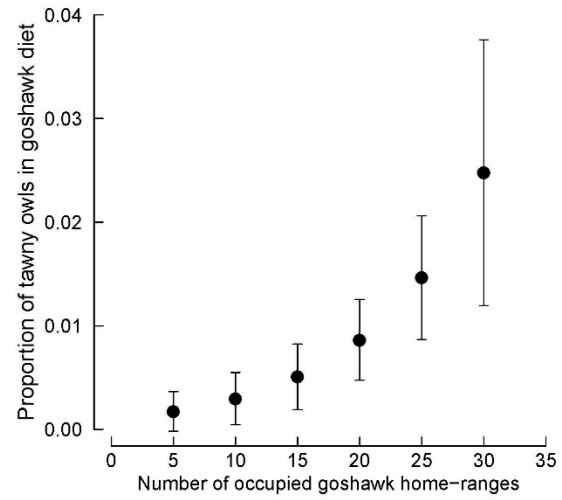
f)



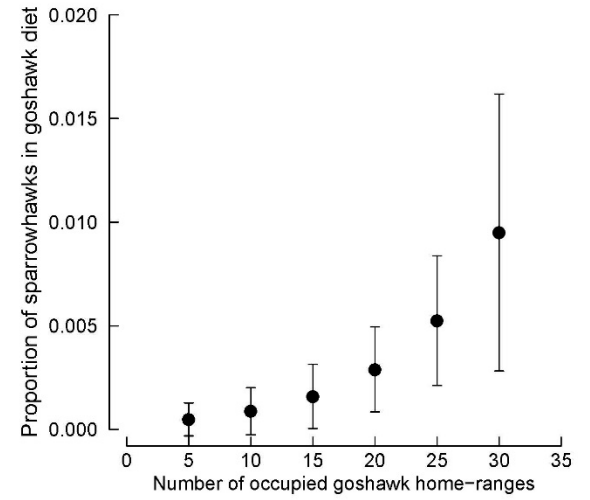
a)

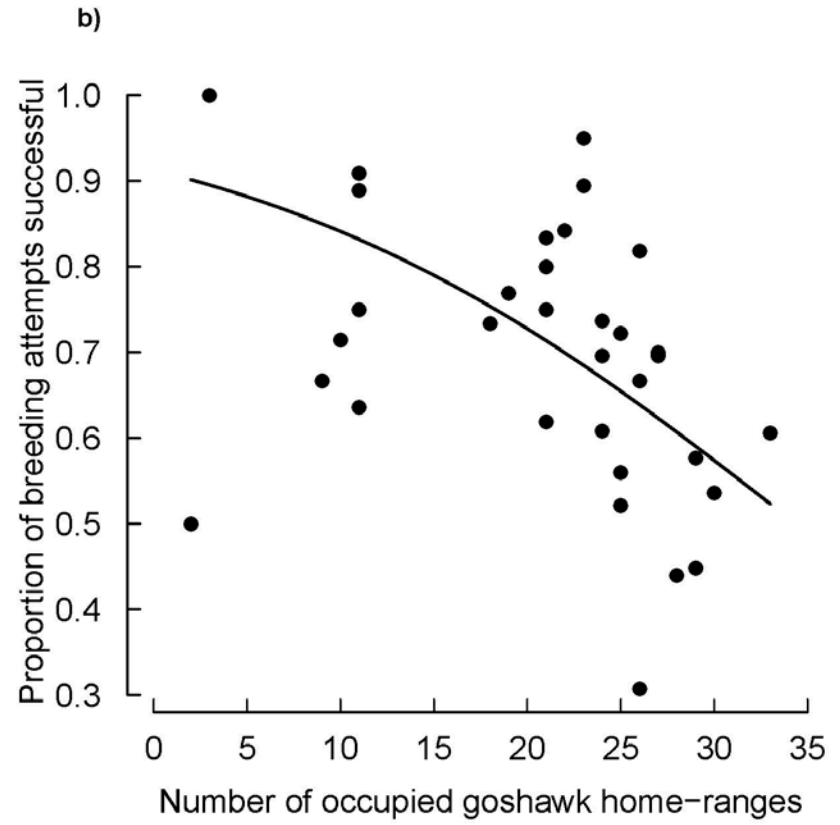
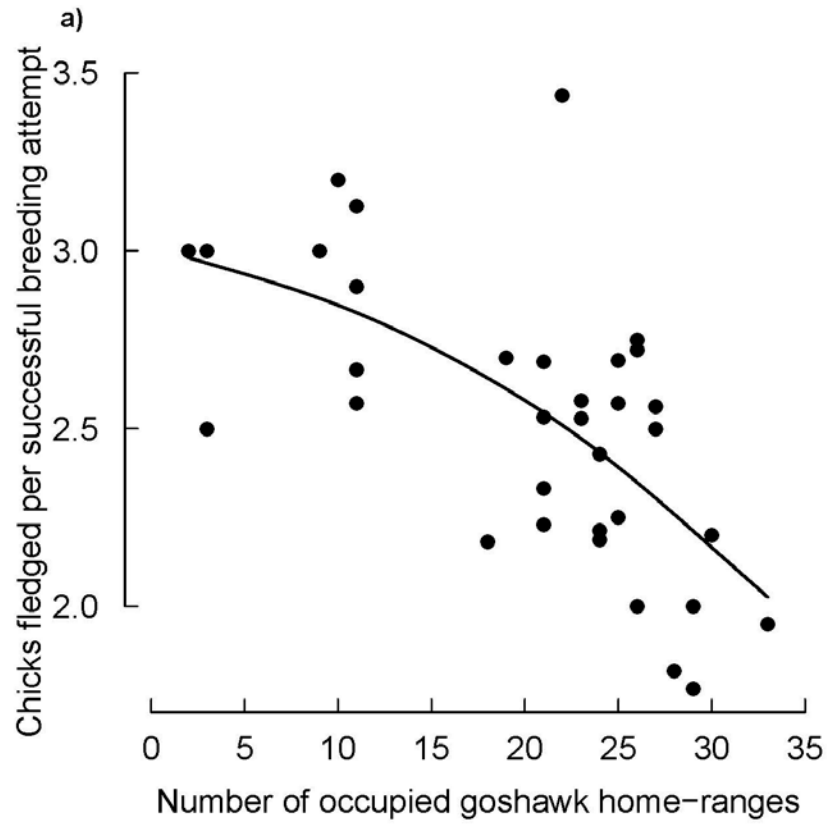


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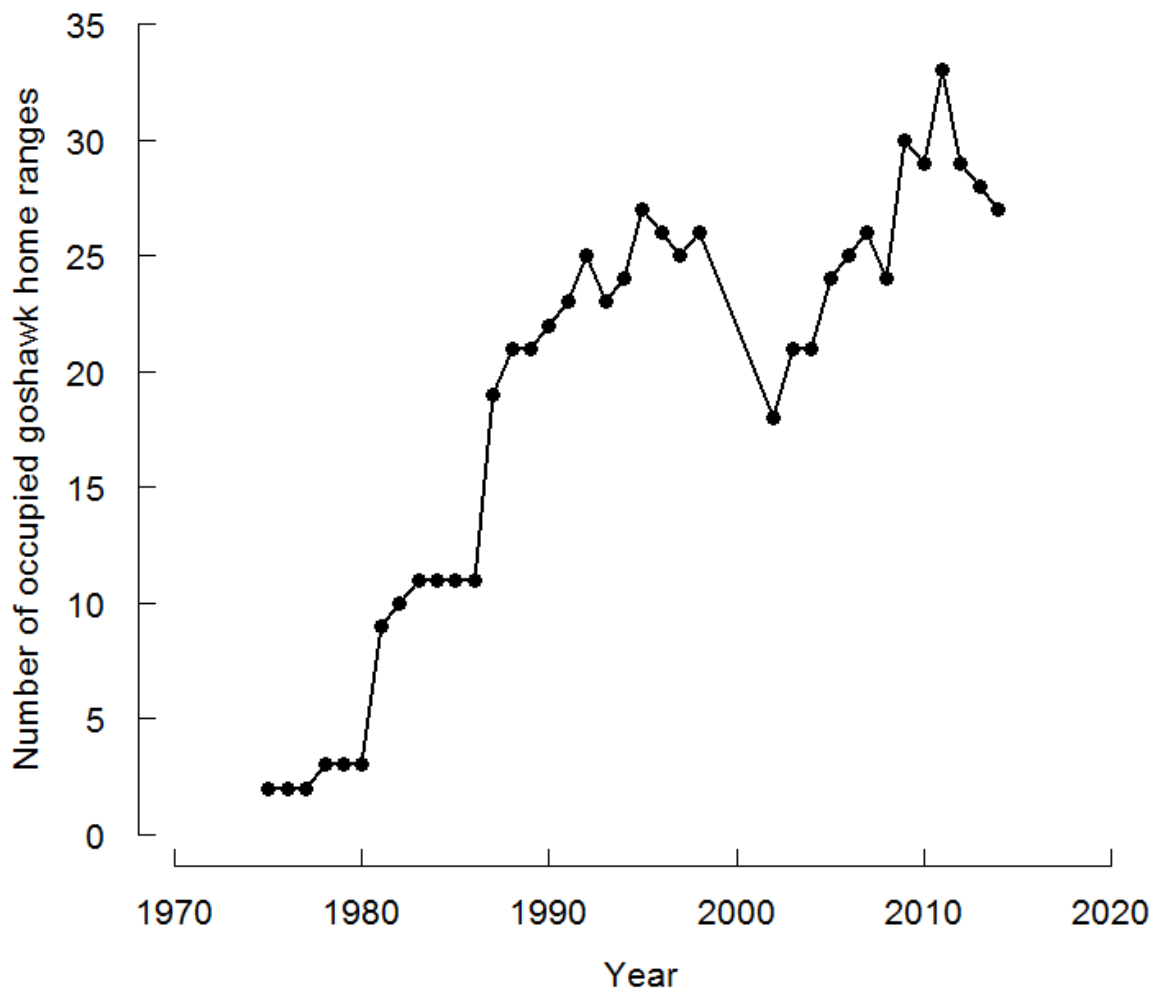


c)





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) 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		
	≤ 14	15-24	≥ 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)