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Intraguild predation and competition impacts on a subordinate predator

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Abstract

Intraguild (IG) predation and interspecific competition may affect the settlement and success of species in their habitats. Using data on forest-dwelling hawks from Finland, we addressed the impact of an IG predator, the northern goshawk *Accipiter gentilis* (goshawk), on the breeding of an IG prey, the common buzzard *Buteo buteo*. We hypothesized that the subordinate common buzzard avoids breeding in proximity of goshawks and that interspecific competitors, mainly *Strix* owls, may also disturb common buzzards by competing for nests and food. Our results show that common buzzards more frequently occupy territories with low IG predation threat, and with no interspecific competitors. Furthermore, common buzzards avoided territories with high levels of grouse, the main food of goshawks, possibly due to a risk of IG predation since grouse can attract goshawks. High levels of small rodents attracted interspecific competitors to common buzzard territories and created a situation where the food was abundant for the common buzzard but so were the competitors. These results suggest interplay between top-down and bottom-up processes influencing interactions between avian predator species. In conclusion, the common buzzard needs to balance the risks of IG predation and interference competition with the availability of its own resources. Presence of other predators associated with high food levels may impede a subordinate predator taking full advantage of the available food. Interspecific interactions with dominant predators have thus the potential to influence the distribution pattern of subordinate predators.

Key-words: bird-of-prey; predator avoidance; interference competition; dominance; food conflict

58 **Introduction**

59 Predation and competition are two major types of interspecific interactions that modify the
60 structure of biological communities (Schoener 1983; Sih et al. 1985; Gurevitch et al. 2000).
61 Predation is a well-known asymmetric interaction because predators gain benefit from their
62 prey (Begon et al. 2005). Similarly, it is common for one species to be affected more than the
63 other in interspecific competition over shared resources (Schoener 1983). The combination of
64 competition and predation, known as intraguild predation (IGP; predation and consumption of
65 competitors of the same guild), has complex impacts on the interacting species, since both
66 species use the same resource(s) while one or both species can also predate the other (Polis et
67 al. 1989).

68 Predators regulate or limit the abundance and distribution of their prey both directly, by killing
69 them, and indirectly, through non-lethal fear effects, which affect the behaviour and
70 distribution of prey (Sih et al. 1985; Preisser et al. 2005; Cresswell 2008; Ritchie and Johnson
71 2009). Non-lethal fear effects can cause a prey to avoid areas where the probability to encounter
72 predators is high (Pearson and Livezey 2003; Sergio et al. 2003, 2007; Morosinotto et al. 2010).
73 Prey may also reduce their activities (vocalization, movements) to avoid detection (Crozier et
74 al. 2006; Sergio and Hiraldo 2008), or even move to other areas due to predation threats
75 (Kostrzewa 1991; Chakarov and Krüger 2010). Because of fear effects, prey have less time for
76 foraging and reproduction, which implies that predators impact directly and indirectly the
77 fitness of their prey (Sih et al. 1985; Polis et al. 1989; Ritchie and Johnson 2009). IGP
78 potentially has more complex consequences for the interacting parties than competition or
79 predation alone (Polis et al. 1989; Polis and Holt 1992), because despite the IGP fear, IG prey
80 are often attracted to the same resources as the IG predator.

IGP is a widespread, size-mediated phenomenon (Arim and Marquet 2004), often associated with periods when the principal food of the IG predator is scarce (Polis et al. 1989; Palomares and Caro 1999; Rutz and Bijlsma 2006; Sergio and Hiraldo 2008; Ritchie and Johnson 2009; Greenville et al. 2014). IGP is widely documented among birds-of-prey (Sergio and Hiraldo 2008), many of which are opportunistic feeders and have a broad diet that also includes other raptors, especially during shortage of food (Rutz and Bijlsma 2006; Sergio and Hiraldo 2008). Birds-of-prey involved in IGP need to have a shared resource such as a nesting site (Kostrzewa 1991; Zuberogoitia et al. 2005), breeding territory, i.e. a defended area around a nesting site in a suitable habitat (Krüger 2002a, 2004), diet (Hakkarainen and Korpimäki 1996; Sergio et al. 2007), or a combination of these factors (Poole and Bromley 1988; Fielding et al. 2003). The amount of species-specific resources regulates both species separately, which in turn influences their interaction (Daugherty et al. 2007; Ritchie and Johnson 2009). IGP is most evident among raptor species with similar resource requirements (Korpimäki 1986; Fielding et al. 2003; Martínez et al. 2008). The intensity of IGP can also vary with environmental conditions, such as fragmentation, influencing both species (Møller et al. 2012). Thus, as predator–prey systems, IGP systems are influenced by top-down (effects of IG predator on IG prey) and bottom-up processes (e.g. effects of resources; Ritchie and Johnson 2009; Chakarov and Krüger 2010).

The occurrence of IGP in birds-of-prey is most often determined from observed IGP events or prey items collected from nesting sites (e.g. Mikkola 1976; Pokrovsky and Lecomte 2010). However, a detailed understanding of IGP and its effects on IG prey often requires long-term datasets or field experiments (as e.g. in Kostrzewa 1991; Krüger 2002a; Zuberogoitia et al. 2008). Few raptor studies have focused on how IGP and resource levels simultaneously affect IG prey (Krüger 2004; Møller et al. 2012).

Here, we address the impact of an IG predator on an IG prey with two similar-sized forest hawks, the northern goshawk *Accipiter gentilis* (hereafter goshawk) and the common buzzard *Buteo buteo*. These species coexist in Eurasia (Cramp and Simmons 1980) where they can compete for nesting sites and territories (Kostrzewa 1991; Krüger 2002a). The dominant goshawk can take over common buzzard nests and may exclude it from high quality forests suitable for both species (Krüger 2002a, 2002b; Hakkarainen et al. 2004). Goshawks can also predate both adult and juvenile common buzzards (eight verified or suspected events recorded in Finland 1981–2009; unpublished common buzzard nest card data of the Finnish Museum of Natural History Luomus), while the common buzzard is not known to predate goshawks (Kostrzewa 1991; Krüger et al. 2001). Both species have declined in Northern Europe, probably due to intensive forestry (Widén 1997). The common buzzard, whose population decline has been steeper than that of the goshawk, is currently listed as threatened in Finland (Mikkola-Roos et al. 2010; Valkama et al. 2011). Additionally, other birds-of-prey breed in hawk nests. Among these, the Ural owl *Strix uralensis* and the great grey owl *S. nebulosa* also eat voles, a shared food resource with common buzzards (Korpimäki 1986; Reif et al. 2001), and can compete for nests and food with the common buzzard. Such interspecific competitors were recently called “parallel impacts” that, unlike top-down and bottom-up processes, influence species of the same trophic level (Laundré et al. 2014).

We studied the impact of the goshawk IGP threat on common buzzard reproduction in a novel way, by also accounting for other potential factors that can affect their interaction. Our aim was to elucidate how IGP threat posed by the goshawk (top-down factor), interspecific competitors (parallel), and climatic factors as well as food availability (bottom-up factors) affect the occurrence and breeding of the subordinate IG prey, the common buzzard. We used a unique dataset, consisting of comprehensive long-term spatial data on hawk nests, food abundances and climate from North Karelia, Finland. Based on previous evidence, we hypothesized that

(1) due to high risk of IGP, the common buzzard avoids settling close to the goshawk, and this effect can be stronger when the availability of food for the goshawk is low; and (2) the presence of other nest and food competitor species interfere with common buzzard reproduction.

Materials and methods

Study area

This study was carried out in North Karelia, a region of 21 584 km² in eastern Finland (Fig. 1a, b). Land area is dominated by forestry land (89%) in this region (Ylitalo 2013; Tike 2014). Forests are dominated by Scots pine *Pinus sylvestris* and Norwegian spruce *Picea abies* (Ylitalo 2013).

Study species

The goshawk and common buzzard are middle-sized forest-dwelling hawks. Throughout Europe, mature forests and food availability are important for the goshawk (Penteriani 2002; Tornberg et al. 2006; Selås et al. 2008), while food, climate and interspecific interactions regulate common buzzard populations (Sidorovich et al. 2008; Lehikoinen et al. 2009; Chakarov and Krüger 2010; Jonker et al. 2014). Both the goshawk and common buzzard construct their stick nests under the tree crown layer (Penteriani 2002; Lõhmus 2006), and they can breed in each other's nests or in nests built by the European honey-buzzard *Pernis apivorus* (hereafter honey-buzzard; Online Resource 1). On the other hand, nests of these three hawks

150 are also used by other species such as the great grey owl, the Ural owl and the common raven
151 *Corvus corax*.

152 In Finland, adult goshawks are sedentary while common buzzards are short- or long-distance
153 migrants arriving in Finland in March or April (Saurola et al. 2013). The goshawk feeds mainly
154 on forest grouse, especially the Eurasian black grouse *Lyrurus tetrix*, and the hazel grouse
155 *Bonasa bonasia* (Tornberg 2001; Sulkava et al. 2006). Goshawks switch to prey on grouse
156 when they are abundant, and grouse availability affects the population size and dispersal of
157 goshawks (Lindén and Wikman 1983; Byholm et al. 2003; Sulkava et al. 2006). Goshawks
158 predate also corvids *Corvidae*, trushes *Turdus* sp., common woodpigeons *Columba palumbus*,
159 European red squirrels *Sciurus vulgaris* and occasionally other raptors, including common
160 buzzards (Kostrzewa 1991; Sulkava et al. 2006; Luomus, unpublished raptor nest card data).

161 Common buzzards feed mainly on small mammals (voles of the genus *Microtus*, water voles
162 *Arvicola amphibius* and shrews, e.g. *Sorex araneus*) while grouse chicks and juveniles, other
163 birds, adders *Vipera berus*, and juveniles of the mountain *Lepus timidus* and brown hare *L.*
164 *europaeus* are important alternative food (Reif et al. 2001).

165

166 Hawk territory data

167 The North Karelian Ornithological Society has recorded a history of known hawk territories
168 since the 1980s. For this study, we used this hawk-territory data from 1997–2009. Here, we
169 defined a territory as an ensemble of alternative nests that are assumed to belong to the same
170 hawk pair due to their proximity. Overall, 539 hawk territories were considered, which
171 included between one and seven alternative nests (mean 1.9 nests). For details on territory
172 visits, see Online Resource 2 and Santangeli et al. (2012).

173 The coordinates of a territory were acquired, separately for each year, from that nest in which
174 preparations for breeding had advanced furthest (typically the nest with a breeding attempt).
175 Each year, common buzzards could choose an alternative nest within their territory that was
176 most distant from the closest occupied goshawk nest (goshawks can also switch between
177 alternative nests in their territory). Thus, year-specific coordinates are better at capturing the
178 potential effect of the goshawk on the common buzzard compared to static coordinates (i.e.
179 fixed territory coordinates for all years), because the goshawk threat (see ‘goshawk threat
180 index’ section) is distance-based and can change yearly. If several alternative nests within a
181 common buzzard territory had the same status (equally decorated or all unoccupied), the
182 average coordinates of these were used as territory coordinates.

183 In a particular year, a species (common buzzard, goshawk, nest competitor species, see
184 ‘competitor in territory’) was considered to *occupy* a territory if the species had decorated or
185 was breeding in one of the alternative nests, or if full-grown bird(s) or a fledged brood were
186 observed. A territory was considered *unoccupied* by a species in a particular year, if the species
187 was not observed in the territory, but had occupied the territory in the past. Two species could
188 co-occupy a common buzzard territory in the same year in different alternative nests (Online
189 Resource 1), but usually different species occupied a common buzzard territory in different
190 years. Thus, a territory could be unoccupied by one species, but occupied by another within a
191 year. Our data included 943 events of territory unoccupancy and 682 events of territory
192 occupancy by common buzzards (events when a territory was unoccupied or occupied by
193 common buzzards in a year) in a total of 378 territories (Fig. 1b).

194 A common buzzard breeding attempt was accounted for in a territory if one of the alternative
195 nests had eggs or chicks (or their remains), or if a fledged brood was observed. Breeding
196 success was defined for those territories that had a breeding attempt with a verified breeding
197 result. A breeding attempt was considered *successful* if at least one chick was raised at

minimum to ringing age (14–28 days old), otherwise it was deemed *unsuccessful*. In our study, the common buzzard had 315 successful and 61 unsuccessful breeding attempts for 207 territories.

The search effort for new hawk territories increased in the 2000s in North Karelia. This led to an increase in the number of hawk territories reported and occupied (Online Resource 3 Fig. 1a). This also led to an increased proportion of occupied territories (Online Resource 3 Fig. 1b), which was partly due to the fact that occupied territories are more easily found (the occupancy rate of newly found territories was on average 80%). The yearly occupancy rate in old territories (on average 34%) increased as well. These changes were therefore taken into account when analysing the data (see below). There were no trends in the proportion of successful breeding attempts (Online Resource 3 Fig. 1b).

Goshawk threat index

Data were gathered on 551 events of goshawk occupancy from 192 territories during 1997–2009. Goshawk threat surfaces were constructed across the study region for each year based on the location of occupied goshawk territories. The goshawk threat index ranged from 0 to 1 and was highest in occupied goshawk territories. Goshawk threat was assumed to follow a flat-top bivariate Gaussian kernel around a goshawk territory. We used a flat-top kernel because real threat sensed by common buzzards in the proximity of goshawks is not known and therefore, we assumed it constant and maximal within a certain range around occupied goshawk territories (see Online Resource 2). Since the behaviour of breeding goshawks is not well known, nine different goshawk threat surfaces were constructed using all combinations of three flat-top ranges (1, 2 and 3 km) and standard deviations ($SD = 1, 3$ and 4 km) as explained

in Online Resource 2. The goshawk threat surfaces differed based on how far the maximum threat (= 1) was assumed to extend around an occupied goshawk territory (controlled with the flat-top range distance), and how fast the threat decreased towards zero beyond that distance (regulated with SD). Each common buzzard territory then received the associated nine different goshawk threat indices from the nine goshawk threat surfaces based on the goshawk threat value on the surface at the common buzzard territory coordinates. The threat indices varied annually among common buzzard territories because they depended on how far the common buzzard and goshawk territories were from each other in each year.

An increase in search effort had a positive impact on the goshawk threat index (Online Resource 3 Fig. 2) because new goshawk and common buzzard territories were found between previously known territories. This was shown by decreases in inter- and intraspecific nearest-neighbour distances (Online Resource 3 Figs. 3a–c). Therefore, nine residual goshawk threat indices were calculated from which the impact of increased search effort was removed. These were obtained by fitting linear models with one of the nine goshawk threat indices in a common buzzard territory as a response, and a measure of effort (total number of reported goshawk, common buzzard and honey-buzzard territories in each year) as an explanatory variable (Online Resource 3 Fig. 1a). All three hawk species were considered, because they frequently use each other's nests and new common buzzard territories could have been previously occupied by the goshawk or the honey-buzzard. The residuals of the nine models were then used as an effort-corrected goshawk threat in the analyses (hereafter goshawk threat).

Competitor in territory

The great grey owl, Ural owl and common raven also occupied alternative nests in common buzzard territories during the study years (in 49, 10 and one occasion, respectively) and were

considered as interspecific competitors in common buzzard territories. These species occupied a nest before the common buzzards arrived from migration, making those nests unavailable to common buzzards. The great grey owl and Ural owl are vole specialists (Korpimäki 1986; Voous 1988) and may compete for food, or hunting patches, with common buzzards. Of the other nest users, the honey-buzzard was not considered a competitor for the common buzzard because honey-buzzards generally migrate 3–4 weeks after the common buzzards. The goshawk's influence on the common buzzard was measured using goshawk threat as defined in the previous section. For further details on interspecific occupiers of common buzzard territories, see Online Resource 1.

To examine if the presence of a competitor species in a territory affected the occupancy or reproduction of the common buzzard, a 'competitor in territory' variable was defined as 1, if the owls or the common raven occupied the territory, and 0, if no competitors were reported to occupy the territory within a year. Competitors at least in one year were found in 48 territories, whereas competitors were absent from 330 territories throughout the study period.

Vole index

The Finnish Forest Research Institute (currently Natural Resources Institute Finland) gathered data on vole abundance (the main food of common buzzards) from four trapping sites (black squares in Fig. 1b). In the spring of each year, voles were trapped in forest and open grassland habitats within the trapping sites (Korpela et al. 2013). The abundance of the two most common vole species, the field vole *Microtus agrestis* and the bank vole *Myodes glareolus*, were pooled annually from the two habitats at each trapping site. Populations of these species are geographically synchronous (Korpela et al. 2013). A vole abundance index was calculated for

each trapping site using the formula: $\log_e((\text{pooled number of voles} + 1) \text{ trap nights}^{-1}) \times 100$. The vole index was standardized to mean = 0 and SD = 1 for each trapping site; this standardization corrects for variation in habitat quality between trapping sites. A yearly average of the standardized vole indices across the different trapping sites was then calculated. Vole abundance fluctuated widely in eastern Finland (Online Resource 3 Fig. 4).

Grouse data

Grouse abundance was used as a measure of food levels for goshawks (main food) and common buzzards (alternative food). Grouse abundance (individuals forest-km⁻² of the black grouse, hazel grouse, capercaillie *Tetrao urogallus* and willow grouse *Lagopus lagopus*) was estimated using wildlife triangle surveys from 1996 to 2009 (Lindén et al. 1996; details in Online Resource 2). Data were gathered yearly from an average of 133 (range = 121–150) wildlife triangles. All individuals regardless of the species were pooled to create a grouse_{all}-index, and all juveniles were used to create a grouse_{juv}-index for each wildlife triangle (Online Resource 2).

To generalise grouse abundances from wildlife triangles to the whole study area, an interpolation map was constructed for the grouse_{all}- and grouse_{juv}-indices for each year using the inverse distance weight method (IDW; see Online Resource 2) in ArcGIS 10 (Esri, USA). An interpolated value of grouse_{all}- and grouse_{juv}-index was then extracted at each common buzzard territory location for each year (Online Resource 2).

The previous year's grouse_{all}-index in the common buzzard territories was used as a measure of food abundance for local overwintering goshawks because it was assumed that goshawks potentially prefer and overwinter successfully in areas with abundant grouse. The current year's

grouse_{all}-index in the common buzzard territories was used as an estimate of food availability for the goshawk during the breeding season, and the current year's grouse_{juv}-index was used as a measure of alternative food for the common buzzard.

Weather data

Spring and early summer temperatures, as well as early summer precipitation affect the onset of breeding and breeding performance of the common buzzard in Finland (Lehikoinen et al. 2009). Therefore, March, April and June mean temperatures and June precipitation were included in our analyses.

Weather data included daily precipitation and averages of daily temperatures within each 10 × 10-km grid-cell of the study region (Venäläinen et al. 2005). Monthly mean temperatures and total precipitation were then calculated and used for the common buzzard territories in the respective grid-cells.

Statistical analyses

Generalized linear mixed models (GLMMs; Zuur et al. 2009) were used to independently model the territory occupancy (1 = occupied, 0 = unoccupied) and breeding success in a territory (1 = successful, 0 = unsuccessful) of the common buzzard. Both models assumed a binomial distribution and were modelled using a logit-link function. Because our data was partly gathered from the same territories but for different years, the territory identity was used as a random effect on the intercept in all models to avoid pseudoreplication (Hurlbert 1984). Because the inference made from territories visited more often was considered more reliable,

territories which were visited multiple times were given double the weights of the territories visited only once. Model variables were standardized to mean = 0 and SD = 0.5 to render the variables (including binomial variables) comparable with each other (Gelman 2008). The residuals of the models were tested using a Moran's *I* test to verify the absence of spatial autocorrelation (Bivand 2014). All GLMM-analyses were conducted using the package lme4 (Bates et al. 2014) within the R statistical language (R Core Team 2013).

Territory occupancy

The nine different goshawk threats were first fitted to nine GLMMs to test how each goshawk threat influence common buzzard occupancy or breeding success. Akaike information criterion (AIC) was used to select the GLMM, and thus goshawk threat, that most parsimoniously explained the occupancy or breeding success of the common buzzard (Zuur et al. 2009). If different alternative models yielded an AIC within ≤ 2 of the best model (Burnham and Anderson 2002; Grueber et al. 2011), the subsequent occupancy or breeding success analyses were also conducted with these goshawk threats to see whether their information was congruent with the model including the best threat index.

For common buzzard territory occupancy, the influences of the vole index, the goshawk threat, the previous year's grouse_{a11}-index, competitor in territory, and March and April temperatures were considered. Also the interaction between the goshawk threat and the previous year's grouse_{a11}-index was examined to test whether the influence of goshawk threat on common buzzard occupancy depended on the main food level of the goshawk.

Since the search effort and consequently the proportion of occupied common buzzard territories increased during the studied years, the effects on occupancy of newly found territories and the sampling year were tested. The best occupancy model was thus refined by (i) excluding the first-year data from new territories (which are often occupied when found),

or (ii) excluding the first-year data from new territories and including a continuous variable ‘year’ to the model. These refinements accounted for the impact of an increase in sampling effort on occupancy (i) due to new territories only, and (ii) in old territories. Additionally, common buzzard territory occupancy in the previous year may partly explain the occupancy probability in the next year because territories can tend to be re-occupied in succeeding years. This was tested by (iii) adding to the final occupancy model a binomial variable ‘previous occupancy’, which defined whether a territory was occupied or not by the common buzzard in the previous year. The first-year data was excluded from new territories before this refinement because no information on the previous occupancy was available for the first year.

Additionally, since most of the interspecific competitors were vole-eating owls, the effect of vole abundance on occupancy of competitors in common buzzard territories was studied using only the 48 territories where a competitor was found at least once during the sampling period. Data were included from all years from these territories, and a binomial-GLMM was then fitted where the presence or absence of competitors in these territories was explained by the vole index.

Breeding success

The influences of the following variables on common buzzard breeding success were considered: the vole index, the goshawk threat, the current year’s grouse_{all}-index, the current year’s grouse_{juv}-index, April and June temperatures, and June precipitation. However, the two grouse indices were highly correlated ($|r| > 0.7$; Dormann et al. 2013). Therefore, their influences on breeding success were studied independently with GLMMs whose AICs were then compared. The GLMM with the grouse_{all}-index had a lower AIC than the GLMM with the grouse_{juv}-index, and the current year’s grouse_{all}-index was selected for the breeding success analysis. An interaction between the goshawk threat and the current year’s grouse_{all}-

index was included to examine the impact of the goshawk threat on breeding success when the main food level of the goshawk varied. The variable ‘competitor in territory’ was excluded from the breeding success analyses because common buzzards rarely bred in territories where competitors were present (only five breeding attempts in territories with competitors, as opposed to 371 breeding attempts without a competitor in the territory).

Results

Territory occupancy

The occupancy of common buzzard territories was most influenced by goshawk threat with a 1-km range and SD 1 (Online Resource 4). The probability of common buzzard occupancy increased with decreasing goshawk threat (Fig. 2), lower grouse_{all}-levels in the previous year, lower March temperatures and when a competitor was not found in the territory (Table 1). The vole index, April temperatures and the interaction of the goshawk threat and previous-year’s grouse_{all}-levels had no significant associations with the probability of common buzzard occupancy, and the interaction was removed from the final model presented in Table 1.

When we run the final occupancy model (i) without the first-year data of new territories, or (ii) as in (i) but with year as a continuous explanatory variable, or (iii) as in (i) but with a ‘previous occupancy’ as an explanatory variable, the results were consistent with those presented in Table 1. The ‘year’ variable (ii) was not significantly associated with territory occupancy in the old territories. However, ‘previous occupancy’ (iii) had a significant and positive association with

territory occupancy (estimate: 0.53, SE: 0.11, z : 4.64, $P < 0.001$). Thus, common buzzards occupied more likely territories than the species had occupied in the previous year.

The probability of presence of a ‘competitor in territory’ was significantly higher with a higher vole index in those common buzzard territories from which a competitor species had been reported at least in one year (estimate: 1.52, SE: 0.32, z : 4.72, $P < 0.001$; Online Resource 3 Fig. 5). This means that the presence of vole-eating competitors, mainly *Strix* owls, in common buzzard territories was dependent on vole-levels.

Despite the overall avoidance of the IG predator goshawk, some common buzzards settled in goshawk territories and shared a territory with goshawks during the same year in 27 occasions. Moreover, common buzzards usually occupied abandoned goshawk territories when vacant (Online Resource 1). Instead, presence of interspecific competitors interfered with the common buzzards. Only in a few occasions did the common buzzard re-occupy their territory where a competitor had settled (Online Resource 1).

Breeding success

The probability of successful breeding of the common buzzard was higher with increasing April temperatures, the only significant variable in the model (Table 2). The interaction of the selected goshawk threat (with a 1-km range and SD 1, Online Resource 4) and the current year’s grouse_{all}-index was not significantly associated with breeding success, and we removed it from the final model. Models with the eight other goshawk threats yielded almost similar AIC values with the model containing the selected threat index (Online Resource 4), and the subsequent breeding success analyses with these alternative goshawk threats gave congruent

results with those in Table 2. The goshawk threat was not significantly associated with common buzzard breeding success in any of the models.

Of the 61 breeding failures, 47 occurred during the egg-laying or incubation period in April–May, while 14 occurred at the nestling period.

Common buzzards managed to breed successfully in the same territory with the IG predator goshawk in 15 occasions, but rarely with owl-competitors (only twice with the great grey owl, Online Resource 1).

Discussion

Our results indicate that avoidance of both intraguild predators and interspecific competitors affect the settlement of common buzzards in a territory. Both higher goshawk threat and presence of interspecific competitors in the territory decreased the probability of common buzzard occupancy. This suggests that presence of IG predators or competitors are important clues for common buzzards arriving from migration, when they decide whether to settle in a territory to breed. After common buzzards minimized the levels of these interferences and chose to occupy a safe territory (often with low goshawk threat and no interspecific competitors), the remaining level of goshawk threat had no significant impact on common buzzard breeding success. Thus, factors determining the settling decision of common buzzards no longer seem to affect their breeding performance.

Additionally, late-winter temperatures affected common buzzard territory occupancy because the occupancy probability increased with low March temperatures. Cold and snowy winters have sometimes been associated with better vole survival (Aars and Ims 2002). However,

because vole levels had no significant impact on common buzzard occupancy, there is no clear evidence of the underlying mechanism that made March temperatures influence occupancy.

Common buzzard breeding success increased with higher April temperatures. Egg-laying normally occurs in late April, but common buzzards breed earlier in warm springs (Kontkanen and Nevalainen 2002; Lehikoinen et al. 2009). Warm spring temperatures seem beneficial during the sensitive early stage of common buzzard breeding, when breeding attempts can be vulnerable for adverse cold spells. Most breeding failures occurred during the egg-laying and incubation periods, although some late failures may have been missed because nests were not always visited after ringing.

We found no significant impact of vole levels on common buzzard occupancy or breeding success. These results seem to contradict the idea that voles are important prey for common buzzards. However, it is possible that our vole index captured only coarse scale patterns and as such did not reveal an association with common buzzard territory occupancy and breeding success. Due to few vole trapping sites, vole data were year-specific and not territory-specific within a year. Thus, if locally high vole numbers increased occupancy or breeding success in some territories, this effect was missed. Another possibility is that voles had no significant effect on common buzzard occupancy or breeding success, because common buzzards can predate other prey, such as birds, when voles are scarce (Reif et al. 2001). Also appearance of interspecific competitors, associated with vole peak years, could reduce the significance of vole abundance to common buzzards by suppressing common buzzard occupancy in those years. It is also possible that avoidance of the IG predator (goshawk) is more important for the common buzzard, and it could thus mask the importance of vole abundance.

449 Intraguild predator avoidance

450 We found no support for the hypothesis that the effect of IGP threat on common buzzard
451 occupancy would be higher when the main food level of the IG predator is low. Instead, the
452 overall negative effect of goshawk threat on common buzzard occupancy indicated that
453 subordinate common buzzards generally avoid territories with a high risk of IGP, irrespective
454 of levels of the main food of the IG predator. This fear of IGP is probably adaptive, since the
455 offspring of subordinate predators are occasionally predated by goshawks (Petty et al. 2003;
456 Bijlsma 2004). Common buzzard chicks are vulnerable in their open nest and opportunistically
457 hunting goshawks can attack common buzzard nests irrespective of grouse abundance. The
458 goshawk threat that most affected common buzzard occupancy had a range of 1-km and SD 1.
459 This range corresponds to the average foraging distance of goshawks in a Scandinavian prey-
460 rich environment (Penteriani et al. 2013).

461 It is plausible that the frequent activity of foraging goshawks would overly stress the common
462 buzzards and therefore, the territories with a high goshawk threat often remained unoccupied
463 by buzzards. However, it is important to recall that the goshawk threat index does not translate
464 into a direct IGP risk, in the sense that common buzzards would always be predated from
465 territories with a high risk, as discussed below. Nevertheless, Sergio and Hiraldo (2008)
466 concluded that even rare IGP-events are enough to sustain IGP-fear in the IG prey population,
467 and the fear of IGP triggers behavioural changes, such as predator avoidance. The presence of
468 IG predators can lead to territory abandonments and decreasing occupancy rates of the IG prey
469 (Sergio and Hiraldo 2008). IG predators can even impact the diversity of the whole raptor
470 assemblage by their control over lower-level predators (Sergio et al. 2007). In line with these
471 previous findings, we found that common buzzard occupancy was lower with increasing threat
472 of the IG predator.

Despite the potential IGP threat, some common buzzards settled and bred in goshawk territories. This reflects the contradiction in IGP when the IG prey is attracted to the same resources shared with its IG predator. Common buzzards and goshawks use similar forests for nesting (Lõhmus 2006), although their forest habitat use may differ otherwise, and both can benefit from already existing nests (Kostrzewa 1991; Jiménez-Franco et al. 2014). Common buzzards that are bold, or oblivious, enough to breed in the same territory with goshawks may even benefit from protection from the latter against other nest predators, such as corvids, and interspecific competitors, such as Ural owls, that avoid goshawks (Krüger 2002a; Pakkala et al. 2006; Rebollo et al. 2011). Subordinate species may also show individual plasticity by being bolder or becoming more experienced in defending their nesting sites (Krüger 2002a; van Lanen et al. 2011).

Interference competition

Common buzzard occupancy was lower in territories where competitors were present. In addition, common buzzards rarely bred successfully with competitors in the same territory (Online Resource 1). Great grey owls and Ural owls eat mainly small rodents and they are not known to predate common buzzards (Korpimäki 1986; Voous 1988). However, since these owls compete for both nests and food with the common buzzard, such an intensive interspecific competition likely affects common buzzards. Ural owls and great grey owls are also known to aggressively defend their nests (Voous 1988), which can result in frequent conflicts with interspecific competitors and unsuccessful breeding of both competitors (Kostrzewa 1991). While some common buzzard individuals succeed in defending their territories against interspecifics (Kostrzewa 1991), it would be overall more advantageous for the common buzzards to avoid breeding near competitors.

497

498 Food conflict

499 Common buzzard occupancy probability decreased with increasing levels of grouse in the
500 previous year. High levels of grouse in the landscape may translate into a higher risk of IGP
501 for the common buzzard because grouse can attract goshawks. Similarly, an abundance of voles
502 could enhance interference with interspecific raptors since the presence of vole-eating
503 predators in common buzzard territories was associated with high vole levels. Common
504 buzzards arriving from migration have to make a rapid decision on occupancy based on all
505 information from surroundings since the time between the arrival, territory establishment and
506 the onset of breeding is short (Kontkanen and Nevalainen 2002). This stage is crucial because
507 a breeding failure due to bad occupancy decision would entail a waste of reproductive
508 investment. Therefore, although abundant food would appear to be beneficial for the common
509 buzzards, they might in reality prefer to avoid areas with high levels of grouse or voles, due to
510 increased risk of IGP or interspecific competition.

511 Thus, although voles are the main food and grouse are an alternative food for the common
512 buzzards, interspecific competitors or IG predators can prevent common buzzards from fully
513 exploiting the peak phases of these food resources. Such a trade-off between exploitation of
514 food abundance and avoidance of IG predators or food competitors was previously suggested
515 for birds-of-prey by Potapov (1997). In his study area, rough-legged buzzards *Buteo lagopus*
516 were not the most abundant during a lemming peak year. The likely reason was that a bigger
517 predator, the nomadic snowy owl *Bubo scandiacus*, bred then in larger numbers than usually.
518 A similar trade-off between food availability and predation risk was also suggested by Heithaus
519 and Dill (2002) for marine ecosystem, where bottlenose dolphins (*Tursiops aduncus*) avoided

foraging in food-rich shallow waters due to high predation risk by tiger sharks (*Galeocerdo cuvier*).

Top-down, bottom-up and parallel effects

The relative importance and interplay of top-down and bottom-up processes in regulating populations is a focal but controversial issue for terrestrial, freshwater and marine ecosystems (Jeppesen et al. 1997; Pace et al. 1999; Baum and Worm 2009; Greenville et al. 2014; Laundré et al. 2014). Predation and competition can have large effects on communities, and predation effects may partly depend on the intensity of intra- and interspecific competition (Sih et al. 1985). In our study, we found evidence of top-down control (goshawk threat influenced common buzzard occupancy) that was unrelated to main food levels (grouse) of the IG predator. We also detected bottom-up effects on the common buzzard, because grouse levels negatively affected occupancy. These findings are in line with those of Thompson and Gese (2007) based on an IGP system of coyotes (*Canis latrans*, the IG predator) and swift foxes (*Vulpes velox*, the IG prey), whereby swift foxes select sites based on safety from IG predators rather than resource availability.

We also found parallel impacts (i.e. presence of interspecific competitors that reduce common buzzard occupancy) and indirect bottom-up effects whereby high resource levels (voles) attracted interspecific competitors that in turn interfered (as parallel effects) with the common buzzard. This corresponds to a theoretical situation where a dominant interspecific competitor confounds bottom-up effects on a subordinate competitor (Laundré et al. 2014).

Overall it seems that both IG predators and interspecific competitors can impact the behaviour (occupancy) of subordinate species in a “landscape of fear”, restricting areas of suitable safe

habitat for subordinate species (Chakarov and Krüger 2010; Laundré et al. 2014). In our study area, interspecific competitors were rather rare (appearing in 48 out of 330 common buzzard territories) and may not have a major impact on the threatened common buzzard. However, in areas where interspecific predators and competitors are abundant, they can have implications on conservation of subordinate predators (Buchanan et al. 2007).

Conclusions

We have shown that interspecific interactions with an intraguild predator and other competitors appear to be important in determining the occupancy decisions of a subordinate predator early in the breeding season, before a substantial investment in reproduction is made. Common buzzard occupancy was driven by the avoidance of an IG predator (goshawk) and interspecific competitors (*Strix* owls). Interspecific interactions may even prevent the subordinate predator from fully exploiting the optimal periods of its food resources.

Our study shows that interspecific interactions have the potential to shape the distribution patterns of subordinate predators. This can have important implications for species management in changing environments. Specifically, a subordinate species could be excluded owing to predation threat and competition from areas otherwise apparently suitable for breeding.

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804

805 **Electronic Supplementary Material**

806 The following Supporting Information is available for this article online:

807 Online Resource 1: Hawk territory dynamics

808 Online Resource 2: Additional information on materials and methods

809 Online Resource 3 Figures 1–5: Figures on the data

810 Online Resource 4: The AICs of the occupancy and breeding success GLMMs with different
811 goshawk threats

812

813 **Fig. 1** a) The study area North Karelia in eastern Finland. b) Territories of the common
814 buzzard (light grey dots, n = 378) and occupied territories of the goshawk (dark grey dots, n =
815 192) in 1997–2009. Four black squares indicate the vole trapping sites. Exact within-site
816 trapping locations have varied during the study years, but this variation occurred within the
817 range of spatial synchrony of the vole cycle

818

819 **Fig. 2** The probability of common buzzard territory occupancy along the goshawk threat,
820 based on the final occupancy-GLMM. Other variables were standardized in their means. The
821 line presents the predicted values and dots are the data points: 0 = unoccupied, 1 = occupied
822 common buzzard territories

823

Figure 1.

829 **Figure 2.**

830

831

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833

834 **Table 1** The logit-estimates of the final GLMM best explaining common buzzard territory occupancy. Model variables were standardized (mean
835 0, SD 0.5). Territory identity was used as a random effect (SE 2.17)

Variable	Estimate	SE	z-value	$P(> z)$ ^a
Intercept	-0.22	0.13	-1.67	0.096
Vole index ^b	-0.07	0.10	-0.65	0.513
Goshawk threat ^c	-0.71	0.14	-5.02	< 0.001 ***
Grouse _{all} -index ^d	-0.32	0.11	-2.99	0.003 **
Competitor in territory ^e	-2.86	0.41	-6.94	< 0.001 ***
Temperature, March (°C)	-0.24	0.09	-2.50	0.013 *
Temperature, April (°C)	-0.06	0.11	-0.52	0.603

836 ^a Significance levels: *** < 0.001, ** < 0.01, * < 0.05, n.s. ≥ 0.05

837 ^b $\log_e((\text{number of voles} + 1) \text{ trap nights}^{-1}) \times 100$

838 ^c Goshawk threat with a 1-km range and SD = 1 (values 0–1)

839 ^d Grouse_{all}-index of the previous year: adults and juveniles of all grouse species (individuals forest-km⁻²)

840 ^e Estimate for the case that a territory has a competitor

841 **Table 2** The logit-estimates of the final GLMM best explaining the breeding success of the common buzzard. Model variables were standardized
842 (mean 0, SD 0.5). Territory identity was used as a random effect (SE 0.67)

843

Variable	Estimate	SE	z-value	$P(> z)^a$
Intercept	1.91	0.17	10.98	< 0.001 ***
Vole index ^b	-0.15	0.37	-0.40	0.689
Goshawk threat ^c	0.27	0.35	0.78	0.436
Grouse _{all} -index ^d	0.50	0.36	1.37	0.171
Temperature, April (°C)	0.68	0.32	2.15	0.032 *
Temperature, June (°C)	0.22	0.38	0.58	0.561
Precipitation, June (mm)	-0.45	0.31	-1.44	0.150

844 ^a Significance levels as in Table 1

845 ^b $\log_e((\text{number of voles} + 1) \text{ trap nights}^{-1}) \times 100$

846 ^c Goshawk threat with a 1-km range and SD = 1 (values 0–1)

847 ^d Grouse_{all}-index of the current year: adults and juveniles of all grouse species (individuals forest-km⁻²)

848

Electronic Supplementary Material ESM 1 to:

Intraguild predation and competition impacts on a subordinate predator

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Hawk territory dynamics

Hawk nests are important resources for many raptors (McInville and Keith 1974; Pakkala et al. 2006; Jiménez-Franco et al. 2014). Nest construction demands time and energy (Jamieson and Seymour 1983; Margalida and García 1999) that can be saved when raptors re-use old stick nests. Moreover, some raptors (e.g. owls) do not construct nests themselves and they can be dependent on nest providers (McInville and Keith 1974; Springer and Kirkley 1978; Zhou et al. 2009).

In North Karelia, common buzzard nests were also occupied by the great grey owl, goshawk, honey-buzzard, Ural owl or common raven during the study period. However, the common buzzard territories were mostly occupied by the common buzzard only. The following numbers indicate how many other species have occupied the 378 common buzzard territories during the study period:

Common buzzard only: 225 territories

Common buzzard + 1 species: 112 territories

Common buzzard + 2 species: 33 territories

Common buzzard + 3 species: 8 territories

Thus, 153 (40.5%) of the common buzzard territories have also hosted other species.

Although even three other species have occupied the common buzzard territories, at most two species occupied a territory during the same breeding season. In the 153 territories, the territory occupancy has been dynamic, since a total of 220 changes in the territory occupier species were detected during the study period. These changes include that another species could enter in the territory (two species occupying the territory simultaneously), or occupancy alternated between the common buzzard and the other species in different years,

or between the other species (e.g. from the great grey owl to the goshawk), possibly including years of unoccupancies in-between.

Perhaps the most interesting events are the changes of the occupier species in consecutive years. In a total of 27 occasions, the common buzzard had occupied a territory in the previous year, but *not in the next year*, when the great grey owl (13 occasions), goshawk (4), Ural owl (4), honey-buzzard (2), common raven (1), goshawk and great grey owl together (2) or honey-buzzard and great grey owl together (1) occupied the territory. Of these species, all except the honey-buzzard can occupy the territory before the common buzzard arrives from spring migration. Only four times, the common buzzard had occupied a territory in the previous year and *continued to co-occupy* the territory with another species in the next year. The co-occupier was then the goshawk (one occasion), great grey owl (1), Ural owl (1), or honey-buzzard (1). In all the four occasions, the common buzzard had no breeding attempt. There were more occasions when the common buzzard had not occupied the territory in the previous year but *co-occupied* it with another species *in the next year*. The common buzzard shared a territory this way with the goshawk 26 times (common buzzard then succeeded / failed / had no breeding attempt in 15 / 2 / 9 occasions, respectively), with the great grey owl five times (2 / 2 / 1), with the Ural owl once (0 / 1 / 0) and with the honey-buzzard once (1 / 0 / 0).

To compare with, we present the respective numbers for the goshawk territories. In 17 occasions, the goshawk had occupied a territory in the previous year, but the territory occupier changed in the next year. Then the territory occupier was the common buzzard in 12 occasions, great grey owl in four occasions, and honey-buzzard once. These species were probably not causing the disappearance of the goshawk, because the common buzzard and honey-buzzard arrive from migration after the goshawk has established its territory, and the great grey owl is presumably subdominant compared to the goshawk. In 13 occasions, the goshawk had occupied a territory in the previous year and continued to occupy it with

another species in the next year. Then the co-occupier was the common buzzard eight times (common buzzard then succeeded / failed / had no breeding attempt in 6 / 1 / 1 occasions, respectively) and great grey owl five times. Of these 13 occasions, the goshawk succeeded / failed / had no breeding attempt in 10 / 2 / 1 occasions.

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Electronic Supplementary Material ESM 2 to:

Intraguild predation and competition impacts on a subordinate predator

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Titles below correspond to those in the article

Haw territory data

During a territory visit, bird-of-prey ringers and trained volunteers recorded the status of each of the alternative nests (i.e. whether the nest was decorated or unoccupied, the breeding result of a breeding attempt, the number of chicks, and the species occupying the nest). They also recorded information on the nest condition (e.g. good, fallen). The nests were frequently unoccupied for some years, leading to nest deterioration and even falling. Despite this, ringers continued their territory visits because after vacant periods, the same nests were refurbished or new alternative nests were built. However, alternative nests were sometimes lost (i.e. fallen definitely or nest tree cut), since they had been unoccupied for extensively long periods of time or were still unoccupied after a break of couple of years in territory inspection. In this case, we excluded the history of an alternative nest one year after the nest was proved fallen, or if the alternative nest was not found (presumably fallen) after a break in territory inspection.

Goshawk threat index

Nine goshawk threat surfaces were created across the study region for each year based on the location of occupied goshawk territories. The threat ranged from 0 to 1 on the surface, being highest at occupied goshawk territories. It was considered constant (threat = 1) within a range of 1 km, 2 km or 3 km around an occupied goshawk nest. Of these ranges, 1 km corresponds to an average foraging distance of goshawks in a prey-rich environment (Penteriani et al. 2013) or “close” breeding distance between goshawks and common buzzards (Hakkarainen et al. 2004); 2 km is a half of the distance between neighbouring goshawks (Tornberg 2001); and 3 km is an average foraging distance of goshawks in prey-poor environment (Penteriani et al. 2013) or “distant” breeding distance between goshawks and common buzzards

(Hakkarainen et al. 2004). Beyond the range, the threat decreased towards zero with increasing distance from the occupied goshawk nest. More specifically, flat-top (due to assumed constant threat within the range) bivariate Gaussian kernels were built with standard deviations (SD) = 1, 3 or 4 around each goshawk territories to measure the threat influence of goshawks. Different SDs regulated how deeply the threat decreased beyond the range (1 = deep, 4 = more gentle decrease). These distances were assumed, because we had no data on how far a threat effect of goshawks on common buzzards could reach. Gaussian distribution was assumed to represent the decrease whose exact shape is unknown, and bivariate kernels were used to create a landscape of threat (threat contours around goshawk territories). Each common buzzard territory then received nine different goshawk threat indices from the nine threat surfaces (constructed with combinations of three ranges and three SDs) based on the threat value on the surface at the common buzzard territory coordinates.

Grouse data

In July and August of each year, volunteers counted all grouse species along a 12-km-long equilateral triangle route (Lindén et al. 1996). In this time of the year females are still with their broods. Females with a brood were counted separately from adults without a brood. Grouse abundances were converted into species-specific grouse indices (individuals forest- km^{-2}). The most abundant grouse species in North Karelia were the black grouse and hazel grouse (Online Resource 2 Fig. 1). The capercaillie *Tetrao urogallus* was less abundant and the willow grouse *Lagopus lagopus* was rare. Populations of different grouse species were synchronous in North Karelia (Online Resource 2 Fig. 1; see also Lindström et al. 1996). For each wildlife triangle, an index of all adult and juvenile grouse (grouse_{all}) and an index of all juvenile grouse (grouse_{juv}) were created by pooling the grouse_{all}-indices and grouse_{juv}-indices of all four grouse species, respectively (Online Resource 2 Fig. 1 & Fig. 2). Pooling grouse indices of different species has been criticized, since the populations of different

grouse can have separate impacts on predators (Tornberg et al. 2013). However, the aim of using the grouse indices was to measure the levels and distribution of grouse food in the hawk territories, and not species-specific functional effects of different grouse species on the predators.

Figure 1

Fig. 1 The yearly averages of pooled grouse_{all} (adults + juveniles) indices (individuals forest-km⁻²) of all grouse species in the wildlife triangle surveys in North Karelia, and the yearly averages of species-specific grouse_{all} indices. On average, grouse were surveyed on 68 (range 60–79) wildlife triangles in each year 1996–2009

Figure 2

Fig. 2 The yearly averages of grouse_{all} and grouse_{juv} (juveniles) indices (individuals forest-km⁻²) in 1997–2009 in the wildlife triangle surveys in North Karelia

The capercaillie and the goshawk are sexually size-dimorphic (Cramp and Simmons 1980; Lindén 1981), and the capercaillie has also a biased sex ratio (males 40%, females 60%; Helle et al. 1999). The large capercaillie cocks are in general too big as a prey for the male goshawks (which are smaller than the females), and the predation rates of female goshawks on the capercaillie are also rather low (Tornberg 1997, 2001; Tornberg et al. 2006). We assumed that female goshawks (50% of the breeding goshawks) can predate the capercaillie hen only (60% of adult capercaillies), and therefore, the adult capercaillie index (included in the grouse_{all}-index) was multiplied by 0.3 ($= 0.5 \times 0.6$; the proportions of female breeding goshawks and adult capercaillie hen, respectively). The corrected grouse_{all}-index was then used in the analyses.

Wildlife triangles from North Karelia and within a 50-km buffer-zone outside the North Karelia (except beyond the country border) were included. Data were thus gathered yearly from an average of 133 (range = 121–150) wildlife triangles. An inverse distance weight method (IDW) was used to generalize the grouse indices from the wildlife triangles to non-sampled areas (areas without triangles) in ArcGIS 10 (Esri, USA). First a raster was created with a grid-cell size of 100×100 m over the study area. Wildlife triangles were then searched for with a radius of 50 km from each grid-cell in each year, and interpolation for each grid-cell was based on grouse indices of at minimum four wildlife triangles. The IDW gives less weight for grouse indices from more distant wildlife triangles, and a power of two was used as a value regulating the decrease of grouse index values with an increasing distance. Interpolations produced for each year a grouse_{all}- and a grouse_{juv}-layer (Online Resource 2 Fig. 3), where each grid-cell had an interpolated grouse_{all}- or grouse_{juv}-index value. Finally, the interpolated grouse-indices were extracted into hawk territories situating in the respective grid-cells.

Fig. 3 The interpolation of grouse_{all}-indices (individuals forest-km⁻²) in 1999. The IDW-interpolation was based on grouse_{all}-indices of 143 wildlife triangles situating in North Karelia (delineated with the black outline; the red line represents the border between Finland and Russia) and within 50 kilometres around North Karelia. Triangles: wildlife triangles, where a darker green colour indicated a higher grouse_{all}-index. Yellow dots: common buzzard territories (occupied and unoccupied, n = 84). Red dots: goshawk territories (occupied, n = 20) in 1999. Map: National Land Survey of Finland, 2010

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Electronic Supplementary Material ESM 3 to:

Intraguild predation and competition impacts on a subordinate predator

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Figure 1

Fig. 1 a) The number of reported territories of the common buzzard, goshawk and honey-buzzard, and numbers of occupied territories of the common buzzard and goshawk in North Karelia in 1997–2009. Search effort increased in early 2000s and as a consequence, the numbers of occupied common buzzard and goshawk territories increased. b) The proportions of occupied common buzzard and goshawk territories increased in 1997–2009, partly because newly found territories were often occupied. The proportion of successful breeding attempts of the common buzzard was not increasing

Figure 2

Fig. 2 The average goshawk threat indices in the common buzzard territories in 1997–2009. The goshawk threat ranged from 0 to 1, being highest (threat = 1) at occupied goshawk nests and constant within a specified range. Beyond the range, the threat decreased towards zero with increasing distance from the occupied goshawk nest. Different standard deviations (SD) regulated how deeply the threat decreased beyond the range. Nine different goshawk threat indices were created by using combinations of three range distances (1 km, 2 km, 3 km) and three standard deviations (1, 3, 4)

Figure 3

Fig. 3 a–c) Average nearest-neighbour distances $\pm$ standard errors of occupied territories during the study period. a) Interspecific nearest-neighbour distances (NNDs) of the common buzzard and goshawk. Interspecific pairs were not included if they were occupying the same territory during the same year. The minimum distance between the occupied common buzzard and goshawk territories was 398 m. b) Intraspecific NNDs of the common buzzard territories. The minimum distance between occupied common buzzard territories was 712 m. c) Intraspecific NNDs of the goshawk territories, with a minimum distance of 1524 m between occupied goshawk territories. Note the different scale at the y-axis. Minimum NNDs are often longer for intraspecific than interspecific territories since intraspecific competition is usually stronger than interspecific (Schmutz et al. 1980; Connell 1983; Katzner et al. 2003). Nearest-neighbour distances, calculated with R-package spatstat (Baddeley and Turner 2013), decreased during the years because new territories were found between the known territories

Figure 4

Fig. 4 The average of standardized vole abundance indices ($\log((\text{number of voles} + 1) \text{ trap nights}^{-1}) \times 100$) of the four trapping sites (see Fig. 1b in the article) in 1997–2009

Figure 5

Fig. 5 The average vole index ($\log((\text{number of voles} + 1) \text{ trap nights}^{-1}) \times 100$) when common buzzard territories had a competitor (1) or had no competitor (0). The figure includes only territories that had a competitor at least in one year (48 territories). Presence–absence data of competitors was included from all years from these territories. Possible competitors were the great grey owl, Ural owl or common raven (in 49, 10 and one occasion, respectively)

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Table 1 The AICs of the GLMMs where common buzzard occupancy or breeding success was modelled using one of the nine goshawk threats as an explanatory variable. The goshawk threat of the GLMM with the lowest AIC (marked with bold) was selected for further occupancy and breeding success analyses. Since AICs of all breeding success GLMMs were within ≤ 2 of the best model, the subsequent breeding success analyses were also conducted with these goshawk threats

Goshawk threat	AIC	
	Occupancy	Breeding success
range 1 km, SD 1	3423.83	337.27
range 2 km, SD 1	3440.00	337.78
range 3 km, SD 1	3447.81	337.55
range 1 km, SD 3	3438.71	337.78
range 2 km, SD 3	3447.17	337.75
range 3 km, SD 3	3447.08	337.78
range 1 km, SD 4	3443.31	337.77
range 2 km, SD 4	3447.01	337.79
range 3 km, SD 4	3446.81	337.77