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Short communication

Landscape and season effects on the diet of the Goshawk

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There are two general effects of habitat loss and fragmentation of mature boreal forests (Schmiegelow & Mönkkönen 2002). First, fragmentation by farmland creates stable structures such as permanent edge zones with enrichment of species diversity and density (Andrén 1992, Berg & Pärt 1994). Secondly, modern forestry with clear-cuts creates sharp, unstable boundaries between forest and open areas, usually with less pronounced edge effects (Helle 1983, Schmiegelow & Mönkkönen 2002). Considering the vast array of studies on the effects of habitat loss and fragmentation on bird populations, relatively little attention has been paid to the role of predators, other than nest predators, across different landscapes (Lampila *et al.* 2005). Predators' searching efficiency may improve due to a diminished area where prey live (Storaas *et al.* 1999). By killing smaller predators and nest predators, top predators may contribute positively to prey species populations (Petty *et al.* 2003, Mönkkönen *et al.* 2007). Increased availability of alternative prey as a result of landscape change may deflect predation from the main prey species (Angelstam *et al.* 1984). The final outcome of these landscape-related predator–prey interactions is likely to depend on direct functional and numerical responses of predators to the variation in the abundance and vulnerability of the main and alternative prey, as well as on the indirect controlling effect of top predators on smaller predators and nest predators.

In northern latitudes the Northern Goshawk *Accipiter gentilis* relies mainly on grouse as a staple food during most of the year (Tornberg 1997, 2001, Tornberg & Colpaert 2001). Breeding season diet, however, contains a large spectrum of alternative prey species, mainly birds (Tornberg 1997). The proportion of grouse in the diet is at the lowest during late nestling phase when fledglings of alternative prey such as larger passerines and waterfowl are readily available (Lindén & Wikman 1983, Tornberg 1997). Goshawks mainly use mature forests for nesting (Penteriani 2002), but they are more flexible in their choice of hunting habitats (Kenward & Widén 1989, Tornberg & Colpaert 2001). Even though the diet and habitat associations of the Goshawk are relatively well known, we do not have a clear picture of how these vary with landscape structure.

In this study, we examined Goshawk predation on grouse (Willow Grouse *Lagopus lagopus*, Black Grouse *Tetrao tetrix*, Capercaillie *Tetrao urogallus*, Hazel Grouse *Bonasa bonasia*) along a landscape gradient. We also examined whether predation on alternative prey was dependent on the same landscape gradient.

METHODS

Study area

The study area comprised roughly 1700 km^2 of coastal lowland situated near the city of Oulu in northern Finland (25°30′E, 65°00′N). Almost one third of the area is covered by peat-lands, natural and drained bogs. There are few lakes, but many rivers in the area forested mainly by Scots Pine *Pinus sylvestris* and Norwegian Spruce *Picea abies* mixed with Birch *Betula pendula* and Aspen *Populus tremula*.

Collection of food remains

Food remains were collected in active Goshawk territories between 1989 and 2003, during the nest building and incubation period from the beginning of April to the end of May (hereafter spring), and the nestling period from the beginning of June until mid-July (hereafter summer); at least once during both periods in each year the territory was occupied by a breeding pair. In spring, collection was done searching the surroundings of the nest where feeding takes place. In summer, collection was made from the nest, because food remains accumulate there, especially during the last week before fledging. Identification of food remains to species level was carried out with reference to collections of the Zoological Museum of University of Oulu. Collection years per territory varied from 1 to 10. Prey weights were taken from Wikman and Tarsa (1980) and specimens from the Zoological Museum of University of Oulu.

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Grouse data

Grouse density was obtained from annual wildlife triangle counts, organized by the Game Research Institute since 1988, where a three-person chain, each person 20 m apart, counts the numbers of four species of grouse encountered when walking sides of the triangle, each side 4 km long, during the first part of August. Counters (local hunters) register the number of adult birds and chicks (Lindén *et al.* 1989, Kurki *et al.* 2000). We used data from 22 triangles for 1989–2003. Mean annual density of adult grouse varied between 5 and 15 ind/km^2 and that of juvenile grouse between 2 and 13 ind/km^2.

We estimated grouse density for each territory from annual data of at least five nearest triangles, weighting the value with distance according to the equation:

$$D_j = \frac{\sum n_{ij}/(1+d_{ij})}{\sum 1/(1+d_{ij})}$$

where n_{ij} is density of grouse of ith wildlife triangle and d_{ij} is distance of ith wildlife triangle to jth nesting site.

Grouse data were used only for those years when the nesting site was active and prey remains were collected. Grouse abundance estimates for the spring season were obtained from grouse counts of the previous year using the pooled number of adults and chicks for each species, which may give a better index of grouse density during spring than using grouse count data of the current year. For the summer season we used the number of adult grouse in the current year, thereby minimizing the time interval between collection of prey remains and grouse censuses. In both cases, grouse abundance estimates do not incorporate mortality. We assumed that mortality is consistent among Goshawk territories and therefore does not bias analyses.

Landscape structure

Landscape analysis of the Goshawk nesting territories was based on digitized base maps (1 : 50 000) and digitized aerial black and white photographs (with scales 1 : 10 000 and 1 : 20 000, provided by National Land Survey of Finland) within a 3-km radius of the nests. Aerial photographs were from the latter part of the 1990s, i.e. around the middle of the collection period of the prey remains. Maps and photographs were imported to MAPINFO (7.0). We estimated the area of fields, open bogs, drained bogs, mature forests (more than 60 years old), and clear-cuts (< 10 years old). These landscape elements constitute on average about 60% of the landscape area (Table 1). The rest of the landscape is mainly composed of differently aged young forests but also includes small areas of sand pits, settled areas, lakes and ponds (Table 1).

Table 1. Mean area of different habitat types in 22 Goshawk territories within 3 km radius around the nest, and corresponding correlations for principal components.

Habitat element	Area (km^2)	se	% of area	PC1	PC2
Fields	1.4	0.4	4.8	−0.805	0.397
Bogs	2.8	0.4	10.0	0.704	−0.498
Drained bogs	5.9	0.5	20.8	0.310	0.763
Old forest	4.0	0.2	14.0	0.458	0.663
Clear-cut	1.6	0.1	5.7	0.731	0.179
% Explained				39.7	29.2

Statistical analysis

We used the proportions of particular prey categories in Goshawk diet as response variables in our statistical models. Proportions were calculated as means for each territory over the years for spring and summer separately. Because proportions are interdependent, we analysed log-ratios: we divided prey proportions of interest (grouse, corvids and ducks) by the proportion of all other prey species pooled and took natural logarithm of the ratio (Aebischer *et al.* 1993).

For landscape data, we used principal component analysis on square-root transformed areas of fields, bogs, ditched areas, old forests and clear-cut areas within the territory. To explain the variation in the proportion of a particular prey (grouse, corvids or ducks) in Goshawk diet in spring and summer we used linear mixed-effects models as implemented in the package nlme (Pinheiro *et al.* 2006) in R 2.4.1 statistical software (R Development Core Team 2006). Landscape variable (PC1 from principal component analysis), density of grouse and period (spring/summer) were set as fixed factors, and territory as a random factor. We constructed all possible models including main effects and two-way interactions of fixed factors, and selected the 'best' model using Akaike information criteria (Burnham & Anderson 2002). There was heteroscedasticity that was linked to the number of cases when a territory was active, and hence occurred within models explaining the proportions of corvids and ducks in Goshawk diet. Thus, in these models, we used the exponential variance function varExp (Pinheiro *et al.* 2006), defining the number of collections of food remains as a variance covariate. A goodness-of-fit model was assessed by visual investigation of residual plots.

RESULTS

We extracted two principal components from the area-based landscape features that explained 69% of the variation of the original data (Table 1). The first principal component (PC1) described a habitat gradient from

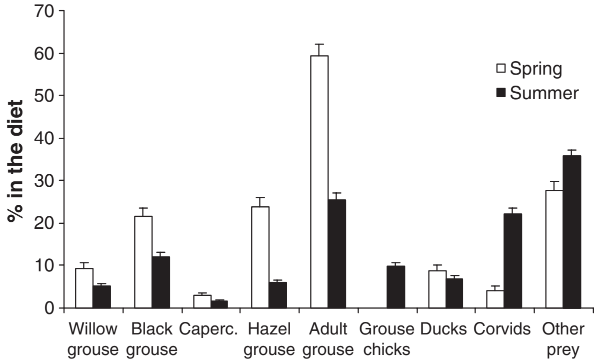

Figure 1. Spring and summer diet of the Goshawk identified from prey remains collected from 22 Goshawk territories near Oulu during 1989–2003. Bars are means calculated from percentages of 99 samples containing 1016 prey items in spring and 102 and 1580 in summer, respectively. Standard errors of the means are denoted by thin bars.

cultivated fields to open bogs and clear-cuts, i.e. from forest fragmentation by agriculture to forest fragmentation by bogs, but also by forestry. The second principal component (PC2) represented a landscape gradient from open, bog-dominated landscapes to more forested (closed) landscapes.

Grouse were the most important prey in spring, but their relative contribution to Goshawk diet was considerably less in summer (Fig. 1). The most important alternative prey were ducks (mainly Teal *Anas crecca* and Mallard *Anas platyrhynchos*) in spring, and corvids (Hooded Crow *Corvus corone*, Magpie *Pica pica* and Jay *Garrulus glandarius*) in summer (Fig. 1).

Surprisingly, the proportion of grouse in Goshawk diet showed no relationship with their density, particularly in spring ($F_{1,18} = 0.004$, $P = 0.951$). In summer, there was a slight positive trend, but it was not significant ($F_{1,20} = 2.761$, $P = 0.112$). Grouse appeared to distribute fairly evenly over the landscape gradient and the density of grouse was not dependent on landscape structure in the vicinity of Goshawk nests (spring $F_{1,18} = 1.654$, $P = 0.227$; summer $F_{1,20} = 0.317$, $P = 0.580$).

Goshawks killed proportionally more grouse during spring than during summer ($F_{1,18} = 7.029$, $P = 0.0162$). During spring, the proportion of grouse in the Goshawk diet did not vary with PC1, but during summer, it increased with decreasing agricultural impact on the landscape (Fig. 2a). This caused a significant period in relation to PC1 interaction ($F_{1,18} = 17.093$, $P < 0.001$). We found no significant models in relation to PC2.

The proportion of corvids in the Goshawk diet decreased with decreasing agricultural impact on landscape both in spring and in summer ($F_{1,19} = 59.340$, $P < 0.001$; Fig. 2b). A significant main effect was found for period indicating a seasonal shift in corvid predation; more corvids were killed in summer than in spring ($F_{1,20} = 6.327$, $P = 0.021$). Ducks were taken relatively

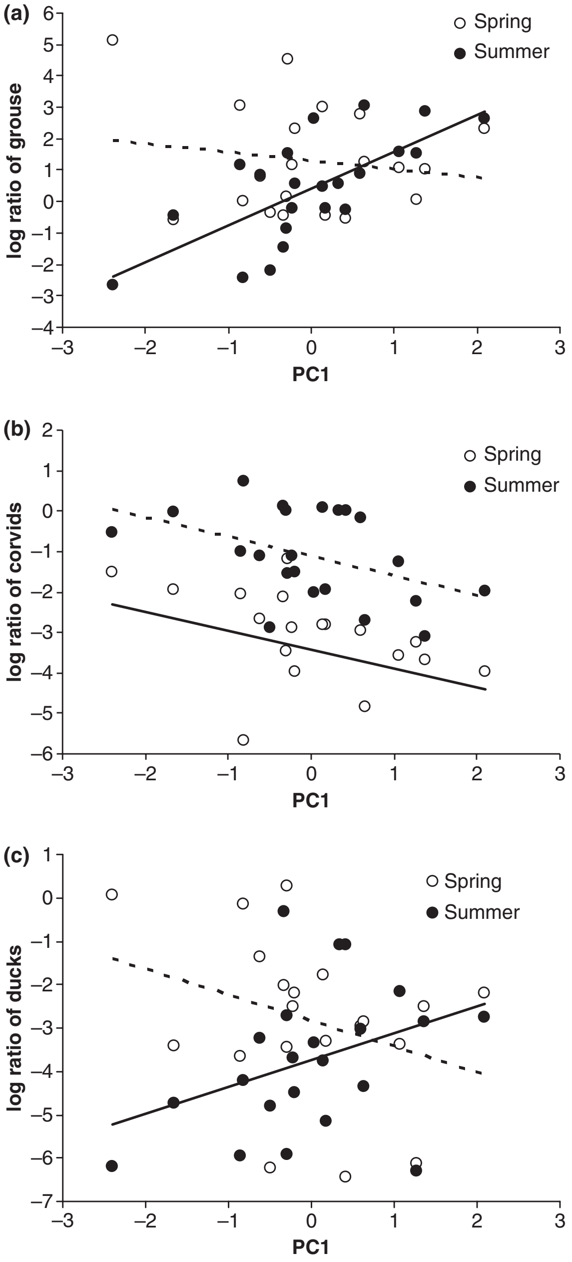

Figure 2. Mean proportions (log-ratios) of grouse (a), corvids (b) and ducks (c) in Goshawk diet in spring and summer in relation to PC1 scores extracted from landscape variables (Table 1). Regression lines for spring (dashed line) (a) $Y = 1.35 - 0.266X$, (b) $Y = -3.16 - 0.490X$, (c) $Y = -2.54 - 0.675X$, and for summer (continuous line) (a) $Y = 0.431 + 1.17X$, (b) $Y = -1.10–0.490X$, (c) $Y = -3.64 + 0.445X$ are shown.

more in landscapes characterized by agriculture than in forest and peat-land dominated landscapes in spring, but the pattern was reversed in summer, showing a strong PC1 by period interaction ($F_{1,18} = 6.651$, $P = 0.019$; Fig. 2c). Also in this case, period had a marginally significant main effect, indicating that ducks formed a smaller proportion of prey in summer than in spring ($F_{1,20} = 4.158$, $P = 0.056$). The density of grouse had no impact on the use of alternative prey, as density of grouse around the territories did not explain any of the variation in the use of alternative prey. Hence, density of grouse was excluded from all of the statistical models.

DISCUSSION

Our results showed that Goshawk predation on grouse was not related to grouse density but, in common with alternative prey including corvids and ducks, was significantly linked to landscape structure and phase of breeding. One reason for the lack of density-dependence could be a poor ability of our grouse census to reflect territory-based densities correctly because of a relatively scarce network of wildlife triangles (1 per 80 km^2) in the study area. However, the long duration of the study (15 years) might approximate real densities in most cases. On the other hand, predation on the main alternative prey, corvids (see Tornberg 1997), may have been related to their density. Although we did not have count data on corvids, their density is probably many times higher near cultivated areas than in the hinterlands (Andrén 1992, Smedshaug *et al.* 2002). Predation on ducks may also have been related to their availability, because the proportion of ducks in Goshawk diet was highest during the migration period of ducks.

The pattern of Goshawk predation observed on its main prey, grouse, and two alternative prey types, corvids and ducks, may have resulted from changes in vulnerabilities among these prey types. Juvenile corvids are naïve and easy prey for hunting raptors (e.g. Newton 1986). Besides, they are a suitably sized prey for Goshawks and being locally abundant they might displace more difficult prey, such as adult grouse and ducks, in the diet (grouse chicks are generally too small to be hunted when Goshawk chicks are small; Tornberg 1997, Reif *et al.* 2004). This raises the interesting possibility that corvids may buffer grouse against Goshawk predation (Kenward 1986, Pech *et al.* 1995). Because Goshawks limit the numbers of corvids (Rutz *et al.* 2006), serious nest predators of grouse (Angelstam 1986), the net effect of Goshawk on grouse near settlements in some instances may remain fairly low or even positive (Milonoff 1994, Mönkkönen *et al.* 2000, 2007).

We conclude that predator – main prey – alternative prey interactions are complicated by landscape and season effects and provide a challenge for further theoretical and empirical research. Thus the functional response of predators to variation in prey abundance, as well as any strong net effect of predators on prey populations, can be mediated or even removed by changing landscape structure. For example, Goshawks may pose a relatively small negative (or even positive) net effect on grouse populations in landscapes that sustain high densities of corvids and other nest predators, but may have a much more detrimental effect elsewhere. This could result in higher productivity of grouse in the former case, which would be interesting for game management and make it important to understand the critical densities and times when switching between main prey and alternative prey might take place.

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