

Predation as a landscape effect: the trading off by prey species between predation risks and protection benefits

M. MÖNKKÖNEN, M. HUSBY*, R. TORNBERG†, P. HELLE‡ and
R. L. THOMSON§

Department of Biological and Environmental Science, POB 35, FI-40014 University of Jyväskylä, Finland; *Magne Husby, Nord-Trøndelag University College, Faculty of Education, Engineering and Nursing, Røstad, N-7600 Levanger, Norway; †Zoological Museum, POB 3000, FI-90014 University of Oulu, Finland; ‡Finnish Game and Fisheries Research Institute, Tutkijantie 2E, FI-90570 Oulu, Finland; and §Section of Ecology, Department of Biology, FI-20014 University of Turku, Finland

Summary

1. Predators impose costs on their prey but may also provide benefits such as protection against other (e.g. nest) predators. The optimal breeding location in relation to the distance from a nesting raptor varies so as to minimize the sum of costs of adult and nest predation. We provide a conceptual model to account for variation in the relative predation risks and derive qualitative predictions for how different prey species should respond to the distance from goshawk *Accipiter gentilis* nests.

2. We test the model predictions using a comprehensive collection of data from northern Finland and central Norway. First, we carried out a series of experiments with artificial bird nests to test if goshawks may provide protection against nest predation. Second, we conducted standard bird censuses and nest-box experiments to detect how the density or territory occupancy of several prey species varies with distance from the nearest goshawk nest.

3. Nest predation rate increased with distance from goshawk nest indicating that goshawks may provide protection for birds' nests against nest predation. Abundance (or probability of presence) of the main prey species of goshawks peaked at intermediate distances from goshawk nests, reflecting the trade-off. The abundance of small songbird species decreased with distance from goshawk nests. The goshawk poses little risk to small songbirds and they may benefit from goshawk proximity in protection against nest predation. Finally, no pattern with distance in pied flycatcher territory (nest box) occupation rate or the onset of egg-laying was detected. This is expected, as flycatchers neither suffer from marked nest predation risk nor are favoured goshawk prey.

4. Our results suggest that territory location in relation to the nest of a predator is a trade-off situation where adult birds weigh the risk of themselves being predated against the benefits accrued from increased nest survival. Prey species appear able to detect and measure alternative predation risks, and respond adaptively. From the prey perspective, the landscape is a mosaic of habitat patches the quality of which varies according to structural and floristic features, but also to the spatial distribution of predators.

Key-words: central-place foraging, meta-analysis, nest predation, raptors.

Journal of Animal Ecology (2007) **76**, 619–629
doi: 10.1111/j.1365-2656.2007.01233.x

Introduction

Traditionally, habitat selection concepts considered selection decisions as static processes focusing on

selecting sites based on certain structural or floristic features (Wiens 1989). However, recent evidence shows that there can be remarkable flexibility in habitat selection, and that decisions are often based on information gathered prior to decision-making to control the unpredictability in the environment (Reed *et al.* 1999; Doligez, Danchin & Clobert 2002; Forsman, Seppänen & Mönkkönen 2002). For a reproducing individual,

Correspondence: Mikko Mönkkönen, Department of Biological and Environmental Sciences, POB 35, FI-40014 University of Jyväskylä, Finland. E-mail: mikko.monkkonen@jyu.fi

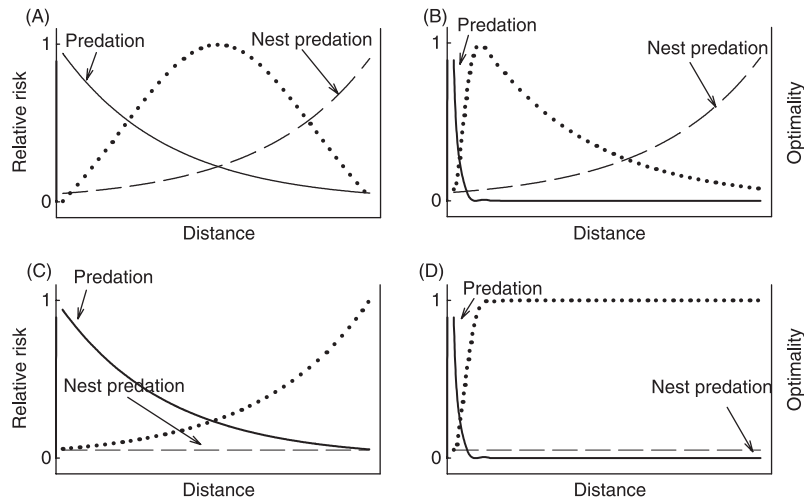


Fig. 1. Relative risk curves in relation to distance from a predator's nest for adult (solid line) and nest predation (dashed line). Dotted line refers to optimality of site selection when there is a trade-off between the two types of predation. Optimality is expressed as the inverse of the sum of the two types of predation. (A) True trade-off situation between the two predation types results in a predicted unimodal relationship between distance and relative optimality of nesting sites. (B) Under heavy nest predation but with little adult predation risk, optimal site for prey species is to settle relatively close to a predator to maximize the benefits from nest protection. (C) When nest predation is not important but there is heavy predation on adults, site optimality increases with distance to the predator. (D) Refers to a case when both adult and nest predation risks are low.

selecting a site that maximizes fitness is of crucial importance. Particularly for a short-lived organism the current breeding attempt may be the last, and the lifetime reproductive rate critically depends on the likelihood that the reproductive attempt succeeds.

Central-place foraging predators can have substantial effects on the survival, reproductive success and spatial distribution of their prey (Adriaensen *et al.* 1998; Dhondt, Kempenaers & Clobert 1998; Thomson *et al.* 2006a). It is known that central-place foragers, especially breeding avian predators, can affect prey spatial dynamics and community structure, resulting in diminished prey abundance around their nests (Meese & Fuller 1989; Sodhi, Didiuk & Oliphant 1990; Suhonen, Norrdahl & Korpimäki 1994; Norrdahl & Korpimäki 1998; Forsman, Mönkkönen & Hukkanen 2001; Thomson *et al.* 2006b). Owing to the nature of central-place foraging, the nest site of a predator anchors predation risk in the landscape creating a variable predation risk landscape (Thomson *et al.* 2006b). The idea of a predation risk landscape contends that, from the prey perspective, the landscape is a mosaic of habitat patches the quality of which varies, in addition to structural (vegetation and abiotic) features, according to the spatial dynamics of predators. The influence of a nesting predator depends strongly on the distance to the nest as the predation risk decreases with increasing distance, most likely attributed to a decrease in encounter rates with predators (Selås & Rafoss 1999).

The effect of predators on populations of their prey, however, is not always only negative. It has been suggested that avian predators can provide cover for birds' nests against nest predation (Norrdahl *et al.* 1995; Bogliani, Sergio & Tavecchia 1999; Quinn *et al.* 2003; Halme,

Häkikilä & Koskela 2004) by preying upon or evicting nest predators. Nest predation seems to be the main cause of variation in reproductive success among temperate and boreal birds (Martin 1995; Hanski, Fenske & Niemi 1996). Therefore, it is crucial to know the full effects, both negative and positive, that predators may have on their prey. Nest predation can indeed be very intense (Martin 1993) and is a potentially strong factor affecting breeding habitat selection (Forstmeier & Weiss 2004; Fontaine & Martin 2006). From the prey perspective, nest location in relation to the nest of a predator is a trade-off situation where adult birds weigh the direct and indirect costs of predation risk to themselves against the benefits accrued from increased nest survival.

The relative costs of adult and nest predation will vary among prey species depending on their perceived vulnerability to hawk predation and on life-history features such as the nest site and the value of current breeding attempt for inclusive fitness. Given the trade-off between the value of offspring and the risk on adult birds, the optimal location in relation to the distance from a bird of prey's nest varies so as to minimize the sum of risks of adult and nest predation (Fig. 1). When both adult and nest predation risks are relatively important, i.e. there is a true trade-off situation between adult and nest predation, a unimodal pattern of site occupancy should appear (Fig. 1A). When direct risk of predation is low (less preferred prey to a predator) and the risk of nest predation is high, then the optimal site to settle would be located relatively close to the predator's nest, because the benefits from protection against nest predation will then be maximized (Fig. 1B). Conversely, for a species with low risk of nest predation

(e.g. cavity nesters) but high risk of adult predation (preferred prey) optimality of the breeding site should increase with distance away from a predator's nest (Fig. 1C). Finally, if both risks are low there is little to optimize and site optimality should be relatively independent of distance (Fig. 1D).

In this paper, we study the effects of a central place foraging avian predator, the goshawk *Accipiter gentilis*, on nest predation and abundance of different groups of bird species using a comprehensive collection of data from northern Finland and central Norway. Goshawks prey upon medium-sized mammal and bird species (Tornberg 1997). The importance of forest grouse in the goshawks diet has dramatically diminished during the past decades following the long-term decline of grouse populations in Finland, and smaller prey such as corvids (Corvidae) and thrushes (*Turdus* spp.) have replaced grouse in goshawk diet (Tornberg, Mönkkönen & Pakkala 1999). Also in Norway, corvids and thrush-sized birds dominate the goshawk diet in the breeding season (Grønnesby & Nygård 2000). Corvids in particular are important nest predators of bird nests (Erikstad, Blom & Myrberget 1982; Storaas & Wegge 1987; Newton 1998). The shift in goshawk diet helped highlight the question whether goshawk actually can provide effective cover against nest predation and whether prey can adaptively respond to this cost–benefit situation.

We first studied, using artificial nests, how nest predation rate varied with distance from goshawk nests, and whether goshawk may provide cover against nest predation. Second, we addressed the question of optimal territory location relative to distance from goshawk nest. Because small passerine birds are not preferred prey, the goshawk entails only a slight direct risk and will mainly provide protection from nest predators. The optimal distance away from the goshawk nest will then depend on the risk of nest predation (cf. Fig. 1B and Fig. 1D). Open cup nesting passerines suffer from intensive nest predation, and consequently the model hypothesizes that open cup nesting small passerine birds should favour nesting close to goshawk (Fig. 1B), and their abundance would be a monotonic decreasing function of distance to goshawk nest. This prediction was tested with bird census data by examining densities of small songbirds at different distances from goshawk nests. Species that are relatively safe from nest predation (e.g. cavity nesters) and not favoured goshawk prey should show limited distance effect with respect to goshawk nest. To address this prediction we placed nest boxes for the pied flycatcher *Ficedula hypoleuca* at different distances from goshawk nests and monitored nest-box occupation and nest success rate. For larger, preferred prey species, a true trade-off applies, and we predict that they should favour intermediate distances away from goshawk to gain protection against nest predators but avoid areas of high direct or indirect predation risk (Fig. 1A). Consequently, the abundance of preferred prey should show a unimodal pattern against distance to goshawk nest. This prediction was tested

with bird census data and data on hazel grouse *Bonasa bonasia* territory occupation rate at different distances from goshawk nests.

Materials and methods

STUDY AREAS

The Finnish study area is located near Oulu in northern Finland (65°00'N, 25°30'E). The landscape lies in the mid-boreal forest zone, and is a mosaic of managed forests of different ages intermixed with peat-land, agricultural patches and human habitations. Forests comprise some 53% of total land area, peat-lands 17% and agricultural areas 16%. Forests are conifer dominated with few deciduous dominated stands. About 25% of forests are mature. The study area is close to the Bothnian Bay (Baltic Sea) coast, and is also characterized by small lakes and rivers. All goshawk nests were situated in mature conifer forest (> 80 years old).

The study area in central Norway is located 40–100 km north of Trondheim (63°45'N, 12°15'E). Like the Finnish study site, the area belongs to the boreal forest zone (western part), and is a mosaic of managed and natural forests, agriculture, human habitations, bogs, lakes and rivers. Forests, mainly conifer dominated, comprise some 33% of total land area and agricultural areas about 10%. More than half of the land area in the region is above the tree line. All of the goshawk nests were situated in mature conifer forest in the mosaic culture landscape, and only a few hundred metres away from the nearest farmland areas.

Goshawk home range size is smaller in the Finnish study area, where the average radius of the hunting range is about 2.5 km (95% convex polygon; Tornberg unpublished data), than in the Norwegian study area with about 4 km mean radius of a hunting range (Nygård *et al.* 2001). Sampling distances for prey abundance and predation on artificial nests in the Finnish and Norwegian study areas were adjusted accordingly so that maximum distances are longer in Norwegian than Finnish data (see, e.g. Table 1).

ARTIFICIAL NEST EXPERIMENTS

We carried out a set of experiments with artificial nests where the basic design was to distribute artificial nests at different distances away from goshawk nests. While the design details varied somewhat, the basic set-up was similar in all experiments (Table 1). In the first set of experiments in the Finnish study area, 50 artificial nests were distributed along two lines radiating out from a goshawk nest. An artificial nest was placed every 100 m in habitats similar to that of the goshawk nest and at the same altitude a.s.l. as the corresponding goshawk nest in all years. This experiment included two goshawk nests in both 2001 and 2002. A similar design was used in data sets II and III (Table 1) at eight and seven goshawk nests and at distances up to 2100

Table 1. Artificial nest experiment data. Five sets of experiments were carried out including a total of 34 goshawk nests (no. of GH nests; four to 10 per data set) and 1362 artificial nests (AN; 90–476 per data set and 18–63 nests per goshawk nest). Data set V is published (Mönkkönen, Väisänen & Tornberg 2000), others are unpublished. *D range* gives the variation in distances of artificial nests from the nearest goshawk nest. *Cat./cont.* tells whether artificial nests were distributed around goshawk nests at different distances more or less continuously (Cont.) or using distance categories (Cat.; number of categories is three in all cases). *Year* refers to year when data was collected and *Data source* to geographical origin of data (Finland/Norway)

Set	No. of GH nests	AN	D range (m)	Cont./cat.	Exp. (days)	% depredated	Year	Data source
I	4	200 (50)	0–1700	Cont.	25	30.5	2001–02	Finland
II	8	157 (20)	0–2100	Cont.	25	42.0	2004	Finland
III	7	439 (63)	0–4700	Cont.	25	45.2	2004	Norway
IV	10	476 (48)	250–5000	Cat.	10	23.6	2002–03	Norway
V	5	90 (18)	50–2500	Cat.	25	52.0	1996	Finland

and 4700 m, respectively. Data sets IV and V involved artificial nests distributed at three distance categories from goshawk nests with 10 goshawk nests in Norway and five goshawk nests in N Finland. Artificial nests were either near (≤ 250 m), at intermediate distance (750–1500 m) or very far away (≥ 2500 m) from a goshawk nest. All nests were in mature forest stands and not closer than 25 m to nearest forest edge. From the published data set V (Mönkkönen, Väisänen & Tornberg 2000) we excluded all other nests except those in mature forests to match with other data.

All artificial nests were open cup nests. Data sets I and II only included artificial nests placed on the ground, but III–V included nests placed on the ground and in trees (1–1.5 m in height). Nests on the ground were close to a tree, shrub or on a side of a tussock to mimic natural nest places. Nests in trees were made of wire baskets lined with dry grass and moss and were attached to limbs with iron wire. In each nest we put two fresh Japanese quail eggs (data set V) or one quail egg and one plasticine egg (other data sets). This egg size simulates thrushes, which nest in trees or on the ground, or small grouse such as the hazel grouse, which nest on the ground.

Experiments were commenced in late May–early June and completed by early July at the latest, corresponding to actual egg-laying and incubation period of birds. The nests were checked after 10, 15 and 25 days of exposure. A nest was considered depredated if either or both of the eggs had disappeared or been damaged. We used data after 25 days of exposure from experiments I–III and V, but data after 10 days of exposure from experiment IV. This was done in order to end up as close to 50% predation rate as possible and hence to maximize the power of the statistical tests.

Artificial nest experiments have been criticized because nest loss rate in such experiments may not reflect nest loss rates or patterns in natural nests (Storaas 1988; Major & Kendal 1996; Ortega *et al.* 1998; Mezquida & Marone 2003; Burke *et al.* 2004). Standardized sampling with dummy nests can nevertheless provide a reasonable estimate of relative nest predation pressure in different habitats even though extrapolation from artificial nests to real nests is problematic (Yahner 1996; Huhta, Jokimäki & Helle 1998; Sloan, Holmes & Sherry 1998).

A general pattern seems to be that the role of avian predators is emphasized with artificial nests whereas mammals may be more important with respect to real birds' nests (Willebrand & Marcström 1988). In this study the use of artificial nests is justified because we expected goshawk predation to result in spatial variation in corvid densities in particular.

Statistically, individual artificial nests cannot be considered independent data points because of spatial and ecological dependencies. All depredated nests within a set-up can result from one or few predator individuals, for example, and nests close to each other have alike fates. Therefore, we did not combine data from different set-ups but analysed data from each goshawk nest separately. Goshawk nests can be considered independent points because these were located far enough away from each other in space and/or time. For each goshawk nest separately ($n = 34$ in the analyses), we used logistic regression analysis to assess the role of distance in relation to the dependent variable, nest fate. Distance was either a continuous or categorical variable in the analyses. For data sets III–V, we also included into the models nest height as categorical variable (ground vs. tree/shrub), and tested for distance \times nest height interaction.

We used meta-analysis (Gurevitch & Hedges 1993; Cooper & Hedges 1994) to make a quantitative summary of the effects of distance on the survival of artificial nests. In other words, we used each goshawk nest as an independent replicate and assessed if nest survival is consistently and significantly associated with distance to goshawk nest. 'Effect size' in a meta-analysis is defined as the level of statistical relationship between two variables of interest. We opted for the Pearson product-moment correlation coefficient, r , as a measure of association between distance and nest survival. We transformed the results of logistic regression into correlation coefficients using the procedure outlined in Cooper & Hedges (1994). Fisher's z -transformed correlation coefficients were then used as the effect size in the meta-analysis. We fitted random-effects models with the data. In this way, we consider the correlation coefficient estimated for each experiment to be drawn from an underlying distribution of correlations rather than considering each experiment as providing an

estimate of a single common value (Cooper & Hedges 1994; Hedges 1994; Raudenbush 1994). Meta-analysis was run using MetaWin 2.0 (Rosenberg, Adams & Gurevitch 2000) to yield an estimate of mean effect size. Mean effect size can be considered significantly different from zero if its 95% confidence interval (derived by bootstrapping) does not include zero. Total heterogeneity, Q_T , measures if effects sizes are homogeneous. A significant Q_T indicates that the variance among effect sizes is greater than expected by sampling error.

BIRD CENSUSES

In Finland, we used the line transect method (Järvinen & Väisänen 1983) to estimate bird abundances at different distances from the goshawk nests. Transects were about 4 km long with the goshawk nest at the halfway point. Altogether nine treatment and four control transects were censused in June 2003 and 2004. Treatment transects included active goshawk nests, while control transects included an inactive goshawk nest that was active in the year prior to the census and was situated at least 4 km from the nearest active goshawk nest. Transects at inactive nests controls for the nonrandom location of goshawk nests. Goshawks breed in mature forests (Penteriani 2002; Nygård & Sørhuus 2004) and bird densities may change with distance due to habitat-related factors (see also statistical analysis for methods to control for habitat effects). Comparison of the effects of distance on prey abundance between treatment and control sites reveals the main effect of goshawk presence.

In Norway, line transects were not feasible due to a more fragmented landscape structure and a point count method with unlimited distance was used to estimate bird abundances. Censuses around seven active goshawk nests were carried out in June 2004 with 5-min stops at each of 9–11 point count stations per goshawk nest (total number of stations = 75), and in the same areas as the artificial nests were placed. Distance of point count stations to the nearest goshawk nest varied between 0 and 4700 m. In point count censuses, it was possible to control for habitat effects by locating the point count stations with care (all stations were in mature forests similar to goshawk nesting habitats) and no control was needed.

All censuses were conducted in early to mid-June between 04.00 and 10.00 h in fair weather (no rain or hard wind and temperatures well above zero), and the area close to the goshawk nest was censused in the middle of each census period.

Bird species in the census data were divided into two categories according to their body size. Species weighing less than 60 g were small birds, all others were large birds. This body mass limit was used because goshawk only occasionally prey upon birds smaller than the smallest thrush (the redwing *Turdus iliacus*) that weighs about 60 g. Small and large birds were analysed separately because the hypotheses differ accordingly (see Introduction and Fig. 1).

For point count data we calculated the total number of individuals (small and large birds separately) per point count station. These data were analysed using linear regression with distance as an independent variable assuming that point counts stations are statistically independent units. This is a reasonable assumption because the distance between stations was, in nearly all cases, more than 300 m (a few exceptions of distances of 200 m due to the terrain) and no stimulus to attract birds was used that would result in overlap of individuals. For large birds we fitted a quadratic model including the squared distance term to test the predicted unimodal density pattern in relation to distance from goshawk nest (see Fig. 1). We tested for the normality of the model residuals to justify the use of linear modelling. Both for small and large birds residual distributions did not deviate from normality (Kolmogorov–Smirnov statistics, 0.064 and 0.094, d.f. = 75, P -values 0.20 and 0.095, respectively).

In Finnish line transect data we only considered bird individuals observed on the 50 m wide main belt. The main belt was divided into 100-m long sections yielding a total of 492 plots of 0.5 ha. We counted the number of observations per plot from the original field notes. The supplementary belt (> 25 m from the census line) observations were not used because their distance to goshawk nest cannot be accurately assessed. Only 200 (41%) plots were observed occupied by one or more small bird species, with low bird densities resulting in most 0.5 ha plots being observed empty. Therefore, we used logistic regression to test for the effects of distance on the probability of a plot being occupied by a small bird species. In addition to distance we included habitat class as an independent variable to control for the effects of habitat structure on bird presence. Each 0.5 ha plot was assigned to one of three habitat classes: mature mesic (spruce dominated or mixed spruce–deciduous) forests; mature xeric (pine dominated) forests; all other habitat types (e.g. sapling stands, clear-cuts, pine bogs). We also tested if the main effect of year, year \times distance interaction or habitat \times distance interactions were necessary in the model. Interaction terms assess if the effect of distance on the probability of observing a small bird on a plot was similar across years and habitats. We started with a full model and removed nonsignificant terms step by step to end up with as parsimonious model as possible. For large birds, only 32 plots (27 on goshawk and five on control lines) were occupied (319 vs. 141 empty) and it was not reasonable to fit any model with such scanty data.

Spatial autocorrelation potentially causes a problem in analysing the line transect data as the plots within a transect are not necessarily independent observations. Spatial autocorrelation results in unduly inflated degrees of freedom in statistical tests and therefore increases the risk of type I error (Legendre & Legendre 1998). To see if spatial autocorrelation leads to a bias in our case we summarized the results from all line transects censuses by considering each treatment or control goshawk nest

(not individual line transect plot) as an independent observation and submitted transect specific effect sizes to meta-analysis. We ran logistic regression for each line transect separately and transformed model parameters into z -transformed correlation coefficients (Cooper & Hedges 1994) to yield an effect size for each treatment and control transect. We added the Norwegian data points into the meta-analysis after transforming the parameters of linear regression into z -transformed correlation coefficients. This was done to test if Finnish and Norwegian data combined provided support for the hypothesis that abundance of small birds should monotonically decrease with increasing distance from goshawk nests. Meta-analysis procedures are similar to those described above for artificial nest experiments.

PIED FLYCATCHER DATA

Nest boxes were placed at distances between 20 and 800 m from three active goshawk nests in our Finnish study area. Altogether 68 nest boxes were provided (16, 20 and 32 nest boxes per territory). Nest boxes were at least 70 m away from each other in lines radiating out in two to four directions from goshawk nests, depending on the landscape structure. They were placed in comparable habitats suitable for the pied flycatcher, i.e. mature spruce or mixed spruce–deciduous forests. We monitored the occupation of the nest boxes and also determined whether nesting attempts failed (were depredated) vs. succeeded (produced at least one fledgling). Because only three of 56 nesting attempts failed, nest survival was not analysed. We also checked the date of first egg in each nest to see if distance to goshawk nest affected the timing of nesting in the pied flycatcher.

As with the artificial nest experiment with a rather similar design we assumed that the nest-box occupation is not independent of the occupation of neighbouring nest boxes but the patterns among different goshawk territories are independent. Therefore, we ran logistic regression for occupation (not occupied vs. occupied) against distance for the three territories separately. We used meta-analysis to assess quantitatively whether occupation depends on distance (see analysis of artificial nest experiment). Likewise, the date of first egg data was initially analysed against distance separately for the three goshawk territories, and subsequently summarized with meta-analysis.

HAZEL GROUSE DATA

In the Finnish study area we also estimated hazel grouse abundance using plot censuses. We established 150×150 m² squares at distances between 100 and 2850 m from the nearest goshawk nest and with a minimum distance of 400 m between squares. Hazel grouse presence was determined by a whistle specifically designed to attract hazel grouse. The field work was carried out between 1 and 15 May in 2001, 2002 and 2003 before the onset of egg-laying. We whistled at each corner of

the square for 6 min with 30 s interval (altogether 12 times). Swenson (1991) has shown that this method is efficient in assessing the presence of hazel grouse throughout the year, and particularly in spring, when both males and females defend territories against conspecifics of the same sex.

The squares were divided into three habitat categories according to hazel grouse preference (Åberg, Swenson & Angelstam 2003): 1 = preferred habitats including mixed dense forests ($n = 31$); 2 = habitats of intermediate quality, e.g. mature spruce forests, drained peat bogs, etc. ($n = 29$); 3 = suitable but not preferred habitats, typically open pine dominated forests ($n = 14$). On 24 of the 74 squares visited, one or more hazel grouse were observed. We used logistic regression to reveal if distance was related to hazel grouse presence as predicted (unimodal pattern). The occupancy status of squares were assumed independent of each other as they were located more than 400 m apart and not likely occupied by the very same grouse individuals. In the model we included distance, distance squared, habitat class, year, as well as year \times distance and habitat class \times distance interaction terms. Terms were removed from the model starting with interaction terms if not significant. Because of a larger number of nested models we also calculated Akaike information criterion (AIC) and AIC differences (Δ AIC) to assist model comparison. The model with the smallest AIC value can be considered the best but as a rule thumb any model with Δ AIC less than 2 relative to minimum AIC also receives substantial support (Burnham & Anderson 2002).

Results

ARTIFICIAL NEST EXPERIMENTS

According to logistic regression models, of 34 independent effects of distance on nest survival, 25 were negative (eight significant) and nine positive (two significant). In cases where distance was treated as a continuous variable, 16 slopes were negative and three positive. Meta-analysis showed that cumulative effect size was significantly different from zero (mean effect size = -0.174 ; 95% confidence interval -0.318 to -0.030) indicating that distance from goshawk nests has a significant negative overall effect on nest survival. Total heterogeneity was not significant ($Q_T = 45.10$, d.f. = 33, $P = 0.078$) suggesting that the results from the 34 independent experiments are consistent. In summary, nest survival decreases significantly and consistently with distance from active goshawk nests.

There was no case of a significant interaction between distance and nest height. Nests placed on the ground survived better than nests placed in trees/shrubs (74% vs. 54% survival, respectively). According to meta-analysis, 22 independent experiments that also included nests in trees/shrubs provided consistent results ($Q_T = 20.63$, d.f. = 21, $P = 0.482$) that nests on the ground had a higher survival rate than nests in trees (mean effect size = 0.209 ; 95% confidence interval 0.125 – 0.296).

Table 2. Regression models for variation in bird presence-absence (logistic regression; Finnish data) or numbers (linear regression; Norwegian data)

	χ^2	d.f.	<i>P</i>	<i>B</i>
Finland, line transect data, small birds				
Goshawk sites				
Total model	11.91	3	0.008	
Habitat	6.97	2	0.031	
Distance	4.54	1	0.033	-0.041
Control sites				
Total model	17.80	3	< 0.001	
Habitat	16.21	2	< 0.001	
Distance	1.42	1	0.234	0.041
Finland, hazel grouse data				
Total model	15.30	4	0.004	
Habitat category	9.20	2	0.010	
Distance	1.81	1	0.179	1.80
Distance ²	3.04	1	0.081	-0.86
	<i>F</i>	d.f.	<i>P</i>	
Norway, small birds				
Distance	2.05	1, 73	0.683	-0.077
Norway, large birds				
Total model	2.69	2, 72	0.075	
Distance	5.30	1, 72	0.024	1.18
Distance ²	5.10	1, 72	0.027	-0.30

χ^2 and *F*, fit of the model and each parameter included; d.f., degrees of freedom; *P*, significance level; *B*, regression slope for distance.

BIRD CENSUS RESULTS

In line transect data, the probability of a 0.5-ha plot possessing a small bird decreased significantly with distance from goshawk nest. The slope indicates that this decrease within the 2 km range of this study is about 20% (Table 2). For control transects (inactive goshawk nests) the model is significant but the effect of distance was not (Table 2). Despite the small sample size and low power to detect a significant distance effect in control transects, the trend in how distance affected the probability of a 0.5-ha plot possessing a small bird was the opposite to that found in treatment transects. Habitat types clearly differed in their percentage of occupied plots being 52%, 30% and 38% in mesic forests, xeric forests and other habitat types, respectively. This indicates a higher density of small birds in mesic forests than in all other habitats. Year effect and all interaction terms could be removed from the model suggesting a consistent effect of distance on small bird abundance among years and habitats. In the Norwegian point count data there was a weak decline in abundance with distance away from the goshawk nest (Table 2).

In combined Finnish and Norwegian data on small birds, 11 out of 16 goshawk sites showed a negative trend between distance to goshawk nest and the probability of presence (Finnish data) or abundance (Norwegian data). One negative and one positive trend were statistically significant (Table 3). Meta-analysis revealed that the

Table 3. Summary of the regression analyses of small bird census data for each goshawk nest separately

SiteID	<i>n</i>	<i>B</i>	<i>P</i>	<i>r</i>
GF1	40	-0.016	0.815	-0.037
GF2	33	-0.032	0.703	-0.066
GF3	33	-0.012	0.881	-0.026
GF4	40	-0.056	0.335	-0.152
GF5	40	-0.035	0.575	-0.089
GF6	40	-0.173	0.024	-0.357
GF7	40	0.007	0.916	0.017
GF8	40	-0.063	0.269	-0.175
GF9	40	-0.013	0.853	-0.035
GN1	11	1.007	0.017	0.925
GN2	9	0.162	0.584	0.483
GN3	11	-0.452	0.266	-0.747
GN4	11	0.016	0.956	0.055
GN5	11	-0.432	0.299	-0.723
GN6	11	-0.161	0.538	-0.526
GN7	11	-0.568	0.110	-0.851
CF1	33	0.007	0.936	0.053
CF2	33	-0.063	0.433	-0.137
CF3	40	0.052	0.410	0.130
CF4	40	0.095	0.217	0.195

SiteID, indicates whether a site is a goshawk nest (G) or control site (C), and country (Finland vs. Norway); *n*, sample size: number of 100 × 50 m² squares in Finland, number of point count stations in Norway; *B*, regression slope based on logistic regression (Finnish sites) or linear regression (Norway); *P*, significance level of the slope; *r*, correlation coefficient derived from model statistics for meta-analysis.

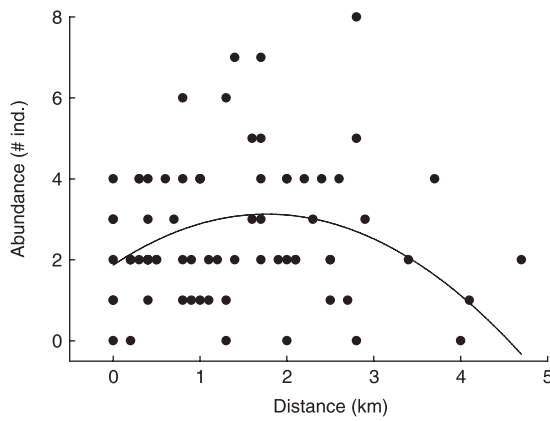


Fig. 2. Abundance (no. of individuals observed) of large birds against distance to goshawk nest in the Norwegian data. For regression parameters see Table 2.

overall effect of distance on small birds was negative and significant (mean effect size = -0.12 ; 95% confidence interval -0.19 to -0.05). Total heterogeneity was not significant ($Q_T = 4.37$, d.f. = 9, $P = 0.89$) suggesting that the results from the censuses provide consistent information. Three of four control sites showed positive but nonsignificant effect of distance (Table 3). In control transects the overall effect was positive but not significantly different from zero (mean effect size = 0.07 ; 95% confidence interval -0.06 – 0.17).

Regression model for large bird numbers in the point count data from Norway included significant linear and quadratic terms of distance to goshawk nest (Table 2). This means that the abundance of large birds peaked at the intermediate distances (about 2 km) away from the goshawk nest (Fig. 2).

PIED FLYCATCHER

Fifty-six of 68 nest boxes became occupied by nesting pied flycatchers. On all three goshawk territories the relationship between the probability of a nest box being occupied and distance to the nearest goshawk nest was positive but not significant. Meta-analysis showed that nest-box occupancy was not related to distance (mean effect size = 0.15 , 95% confidence interval -0.33 – 0.78). Total heterogeneity was not significant ($Q_T = 0.19$, d.f. = 2, $P = 0.91$) suggesting consistent pattern among territories. Data on the date of first egg were available for 53 flycatcher nests. The onset of flycatcher egg laying was not related to distance to goshawk nest on any of the three goshawk territories (one positive and two negative linear trends). Mean effect size was slightly negative (-0.05) but not significantly different from zero (95% confidence interval -0.70 – 0.60 ; $Q_T = 0.19$, d.f. = 2, $P = 0.91$).

HAZEL GROUSE

The best fit model for the hazel grouse data includes the effect of habitat and the second order (quadratic) effect

of distance to goshawk nest (Table 2). According to the best fit model the probability of detecting hazel grouse was about 0.5 at the distance of 1.1 km from the goshawk nest, and decreased both towards the goshawk nest and away from this optimum point. This model is able to predict correctly the presence vs. absence of hazel grouse on squares in 73% of the 74 cases. The model also includes the effect of habitat class reflecting the fact that the probability of observing hazel grouse differs between habitat types. Even though the distance effect is not statistically significant using traditional P -level criteria, Akaike's information criterion suggested that the model with distance effects (AIC = 87.96) was better than the model without them (i.e. including only habitat effect; AIC = 90.31; Δ AIC = 2.35) or with linear distance effect only (AIC = 89.74; Δ AIC = 1.78). Because Δ AIC-value for the model with linear distance effect only was less than 2, this model must be considered equally well supported by the data. According to this model, probability of detecting hazel grouse decreases with distance (slope = -0.057). No year or interaction effect was statistically significant, and these more complicated models received considerably less support (Δ AIC varied from 2.39 to 7.72).

Discussion

Our results suggest that goshawks may provide cover against nest predation, and that potential prey species appear to take this into account in their habitat selection. First, the survival of artificial nests significantly decreased with distance from goshawk nests. Lower rates of nest predation near goshawk nests were found despite the density of artificial nests being higher at closer distances. Higher nest density should result in higher rates of predation as predator search efficiency increases (e.g. Roos 2002). Therefore, our suggestion that goshawks may decrease the rate of nest predation in closer proximity seems quite robust. Our results further suggested that nests on the ground survived better than those in trees and shrubs, which implies that avian predators and/or the red squirrel *Sciurus vulgaris* have mainly been responsible for the patterns we observed.

Secondly, combined Finnish and Norwegian census data (meta-analysis) showed that the abundance of small songbird species decreased with distance from goshawk nests (e.g. Fig. 1, panel B). This pattern was particularly true for the Finnish data and did not stem from changes in habitat quality with distance as this pattern was absent in control transects and was consistent among different habitat types. For small songbirds, goshawk predation risk entails little cost; however, acquiring protection against potentially destructive nest predation may entail large benefits. Nevertheless, songbird densities do vary with forest age (see, e.g. Helle & Mönkkönen 1990), and our habitat categorization only partially accounted for this variation. However, as the interaction term between distance and habitat was not significant, the decreasing pattern also applies to

mature mesic forests where most goshawk nests were located. Therefore, it appears that this result is not due to among-habitat variation in song bird densities.

Thirdly, and consistent with our predictions, the abundance (or probability of presence) of larger birds, the favoured goshawk prey, showed a unimodal pattern with distance from goshawk nest. This suggests an avoidance of the immediate vicinity of goshawk nests but a preference for some intermediate distance where potential protective benefits may still be accrued (e.g. a true trade-off in Fig. 1, panel A). Finally, no pattern with distance in territory (nest box) occupation rate or in the timing of nesting was detected for the pied flycatcher (Fig. 1, panel D). Flycatchers suffer low nest predation risk and are not favoured goshawk prey. Therefore, these results support the conceptual model presented in the introduction. However, while support for the model is strong for small vs. large passerines, it is somewhat weaker for the hazel grouse. The pied flycatcher results must also be interpreted with caution because only three goshawk territories were included.

The abundance of larger species peaked between 1.1 km (hazel grouse in Finland) and 2 km (large birds in Norway) from goshawk nests. Radio-tracking data on four male and three female hawks (Tornberg, unpublished) suggest that goshawk hunting spans about 2.5 km around the nest in the Finnish study area with a mean home range (95% convex polygon) of 20 km². In a radio-telemetry study on four nesting goshawk pairs within and near our Norwegian study area, Nygård *et al.* (2001) found that home range sizes vary from 20 to 94 km² with a mean of 49 km², giving a mean range of 4 km. Therefore, the peak abundance of main prey is approximately half way through the goshawk hunting range. The costs (both direct and indirect) of predation risk on prey is presumably not a linear function of distance but a function of area (distance squared) over which predation risk is diluted (Selås & Rafoss 1999; Forsman *et al.* 2001; but see Thomson *et al.* 2006b). Thus, distances of 1–1.5 km represent relatively low-risk areas of predation by the goshawk compared with close vicinity of goshawk nest. Because nest predation risk at the respective distances to goshawk nest can be high, e.g. < 50% survived in Mönkkönen *et al.* (2000) experiment, it certainly pays for the prey to settle at some intermediate distance to optimize between the costs and benefits (cover against nest predation).

Earlier studies have shown that prey species abundance can vary with distance to predator nests, and that the effects of distance differ according to predation risk to parent birds. For example, curlews *Numenius arquata* prefer to nest closer to kestrel *Falco tinnunculus* nests than expected from random distribution to gain protection against nest predation (Norrdahl *et al.* 1995). In contrast, in the very same area, densities of small birds, which are potential prey of kestrels, are lower near the predator nests (Suhonen *et al.* 1994). Several other studies have shown the preference by bird species to settle close to

a predator if the predator poses only a small risk of predation to adults (Meese & Fuller 1989; Sodhi *et al.* 1990; Ueta 1994; Sergio *et al.* 2004). Our results on abundance of small birds are in line with these earlier findings.

In addition, our results indicate a trade-off between the variation in the predation risk and nest protection benefits with distance from goshawk nests, and that prey species adaptively respond to this. Quinn & Kokorev (2002) suggested similar trade-off for red-breasted geese *Branta ruficollis* nesting in association with peregrine falcons *Falco peregrinus* in arctic Siberia, and the optimal distance was found to be 46 m from hawk eyries. In our case, the response by prey to trade-off was clearly a landscape-level effect extending few kilometres from goshawk nests. Earlier studies have largely focused on species on open habitats (e.g. tundra, agricultural areas) where responses to visual cues such as predator presence are readily detectable. Our results suggest that detailed information gathering on relative predation risks and protection benefits takes place also in structurally more complex forest landscapes (see also Thomson *et al.* 2006b).

The observed prey distribution pattern may also result from increased adult predation rates near to, and increased nest predation rates further away, from the goshawk nests despite an initially even distribution early in the spring. However, we observed the unimodal pattern for the hazel grouse in early May, before the onset of nesting. Likewise, bird census data particularly in the Finnish study area were collected in the early phase of songbird nesting activities shortly after their arrival from spring migration. These patterns are therefore unlikely to reflect factors other than a response to the presence of a goshawk nest. In addition, the decreasing abundance of small songbirds with distance at active goshawk nests, but the absence of this pattern at inactive goshawk nests (see Methods) suggests a purposeful aggregation of individuals around goshawk nests. It seems that active hawk nests may serve as cues to settling prey individuals, and involves information gathering and trading-off between alternative risks to optimize habitat quality.

The numerical responses to predation risk and protection benefits are adaptive and results in fitness effects have been shown in some earlier studies (Norrdahl *et al.* 1995; Quinn & Kokorev 2002). Thomson *et al.* (2006b) showed that pied flycatchers avoided nest boxes in close proximity to sparrowhawk *Accipiter nisus* nests and settled later in these boxes. Flycatchers breeding close to sparrowhawks produced 4–17% smaller nestlings relative to those further away. In our study, pied flycatcher nest-box occupancy did not reflect distance from goshawk nest. Clearly, pied flycatchers, and probably also other bird species, are able to recognize and discern relative predation risks and protection benefits by different, yet closely related predators such as the two *Accipiter* hawks. Birds are also able to correctly assess levels of nest predation risk and adjust habitat

selection decisions accordingly (Forstmeier & Weiss 2004; Fontaine & Martin 2006). Breeding corvids, important nest predators, have been shown to affect the spatial distribution of their avian prey (Tryjanowski 2001; Roos & Pärt 2004).

As the goshawk has a Holarctic distribution we suggest that the relationships we observed between goshawk, songbirds and grouse may apply throughout its distribution. The ability of prey individuals to respond to spatial variation in predation risk, however, depends on how saturated bird populations and communities are. If breeding habitat is saturated, competition for limited breeding territories is the primary determinant of settlement patterns, and the predation risk landscape is not expected to have a major influence. Therefore, even though the predation risk landscape may be a general and important concept in understanding the variation in habitat selection of prey populations at larger spatial scales, the consequences of the spatial variation in predation risk are more likely to get manifested in environments where predation, disturbances or temporal variation in resource levels, for example, keep prey populations well below the carrying capacity of the environment. Nevertheless, even in saturated communities, the spatial variation in predation risk, which stems from the nests of breeding predator, will influence habitat quality as perceived by prey individuals. We anticipate that this may be expressed in other large-scale patterns, such as individual quality, for example. Future research will confirm or dispute this idea.

Our results support recent views that breeding raptors have positive consequences, even for potential prey, in the context of natural systems containing an entire suite of predators (e.g. Sergio *et al.* 2006). We further emphasize the importance of the actual presence of breeding raptors as a vital cue in the habitat selection process. In a recent paper Pakkala, Kouki & Tiainen (2006) found that goshawk presence had a positive effect on the abundance and breeding success of a number of species associated with a similar habitat type. The strongest positive effect was found in the three-toed woodpecker *Picoides tridactylus*, which has considerably declined in Fennoscandia during the past few decades due to forestry. Pakkala *et al.* (2006) found that the positive effect of goshawk on the woodpecker was particularly strong in fragmented landscapes and they suggested that goshawk could reduce edge-induced nest predation on woodpecker nests. Thus, predators may help the conservation of species benefiting from the proximity of predators by reducing nest predation risk and potentially also negative effects from more abundant competitor species.

Acknowledgements

We are grateful to S. Junttunen, H. Uusitalo and A. Paasivaara for assisting in field work. J. Forsman and three anonymous referees provided fruitful comments on an earlier version of this paper.

References

- Åberg, J., Swenson, J.E. & Angelstam, P. (2003) The habitat requirements of hazel grouse (*Bonasa bonasia*) in managed boreal forest and applicability of forest stand descriptions as a tool to identify suitable patches. *Forest Ecology and Management*, **175**, 437–444.
- Adriaenssen, F., Dhondt, A.A., Van Dongen, S., Lens, L. & Matthysen, E. (1998) Stabilizing selection on blue tit fledgling mass in presence of sparrowhawks. *Proceedings of the Royal Society, London, Series B*, **265**, 1011–1016.
- Bogliani, G., Sergio, F. & Tavecchia, G. (1999) Woodpigeons nesting in association with hobby falcons: advantages and choice rules. *Animal Behaviour*, **57**, 125–131.
- Burke, D.M., Elliott, K., Moore, L., Dunford, W., Nol, E., Phillips, J., Holmes, S. & Freemark, K. (2004) Patterns of nest predation on artificial and natural nests in forests. *Conservation Biology*, **18**, 381–388.
- Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Inference: a Practical Information-Theoretic Approach*. Springer-Verlag, New York.
- Cooper, H. & Hedges, L.V. (1994) *The Handbook of Research Synthesis*. Russel Sage Foundation, New York.
- Dhondt, A.A., Kempenaers, B. & Clobert, J. (1998) Sparrowhawk predation and Blue Tit adult annual survival rate. *Ibis*, **140**, 580–584.
- Doligez, B., Danchin, E. & Clobert, J. (2002) Public information and breeding habitat selection in a wild bird population. *Science*, **297**, 1168–1170.
- Erikstad, K.E., Blom, R. & Myrberget, S. (1982) Territorial hooded crows as predators on willow ptarmigan nests. *Journal of Wildlife Management*, **46**, 114–119.
- Fontaine, J.J. & Martin, T.E. (2006) Habitat selection responses of parents to offspring predation risk: an experimental test. *American Naturalist*, **168**, 811–818.
- Forsman, J.T., Mönkkönen, M. & Hukkanen, M. (2001) Effects of predation on community assembly and spatial dispersion of breeding forest birds. *Ecology*, **82**, 232–244.
- Forsman, J.T., Seppänen, J.-T. & Mönkkönen, M. (2002) Positive fitness consequences of interspecific interaction with a potential competitor. *Proceedings of the Royal Society of London, Series B*, **269**, 1619–1623.
- Forstmeier, W. & Weiss, I. (2004) Adaptive plasticity in nest-site selection in response to changing predation risk. *Oikos*, **104**, 487–499.
- Grønnesby, S. & Nygård, T. (2000) Using time-lapse video monitoring to study prey selection by breeding Goshawk *Accipiter gentilis* in Central Norway. *Ornis Fennica*, **77**, 117–129.
- Gurevitch, J. & Hedges, L.V. (1993) Meta-analysis: combining the results of independent experiments. *Design and Analysis of Ecological Experiments* (eds S. Scheiner & J. Gurevitch), pp. 378–398. Chapman & Hall, London.
- Halme, P., Häkkinen, M. & Koskela, E. (2004) Do breeding Ural owls *Strix uralensis* protect ground nests of birds?: An experiment using dummy nests. *Wildlife Biology*, **10**, 145–148.
- Hanski, I.K., Fenske, T.J. & Niemi, G.J. (1996) Lack of edge effect in nesting success of breeding birds in managed forest landscapes. *Auk*, **113**, 578–585.
- Hedges, L.V. (1994) Statistical considerations. *The Handbook of Research Synthesis* (eds H. Cooper & L.V. Hedges), pp. 29–38. Russell Sage Foundation, New York.
- Helle, P. & Mönkkönen, M. (1990) Forest succession and bird communities: theoretical aspects and practical implications. *Biogeography and Ecology of Forest Bird Communities* (ed. A. Keast), pp. 299–318. SPB Academic Publishing bv, The Hague.
- Huhta, E., Jokimäki, J. & Helle, P. (1998) Predation on artificial nests in a forest dominated landscape – the effects of nest type, patch size and edge structure. *Ecography*, **21**, 464–471.

- Järvinen, O. & Väisänen, R.A. (1983) Correction coefficients for line transect censuses of breeding birds. *Ornis Scandinavica*, **60**, 97–104.
- Legendre, P. & Legendre, L. (1998) *Numerical Ecology*, 2nd English edn. Elsevier, Amsterdam.
- Major, R.E. & Kendal, C.E. (1996) The contribution of artificial nest experiments to understanding avian reproductive success: a review of methods and conclusions. *Ibis*, **138**, 298–307.
- Martin, T.E. (1993) Nest predation among vegetation layers and habitat types: revising the dogmas. *American Naturalist*, **141**, 897–913.
- Martin, T.E. (1995) Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs*, **65**, 101–127.
- Meese, R.J. & Fuller, M. (1989) Distribution and behaviour of passerines around Peregrine (*Falco peregrinus*) eyries of western Greenland. *Ibis*, **131**, 27–32.
- Mezquida, E.T. & Marone, L. (2003) Are results of artificial nest experiments a valid indicator of success of natural nests? *Wilson Bulletin*, **115**, 270–276.
- Mönkkönen, M., Väisänen, P. & Tornberg, R. (2000) Goshawks may reduce predation rates on birds' nests. *Wildlife in Finland*, **46**, 27–36. (In Finnish with English summary).
- Newton, I. (1998) *Population Limitation in Birds*. Academic Press, London.
- Norrdahl, K. & Korpimäki, E. (1998) Fear in farmlands: how much does predator avoidance affect bird community structure? *Journal of Avian Biology*, **29**, 79–85.
- Norrdahl, K., Suhonen, J., Hemminki, O. & Korpimäki, E. (1995) Predator presence may benefit: kestrels protect curlew nests against nest predators. *Oecologia*, **101**, 105–109.
- Nygård, T. & Sørhuus, H. (2004) Nord-Trøndelag. *Hønehauken I Norge. Bestandens Status Og Utvikling Siste 150 Ar* (ed. H. Grønlien), pp. 21–22. Norsk Ornitologisk Forening (NOF) Rapportserie 5–2004.
- Nygård, T., Wiseth, B., Halley, D., Grønnesby, S. & Grønlien, P.M. (2001) Hønehauken i skogbrukslandskapet. NINAs strategiske instituttprogrammer 1996–2000. Virkninger av fysiske naturinngrep – systemøkologisk innretting. *Sluttrapport* (eds T.M. Heggberget & B. Jonsson, B.), pp. 78–88. Norsk institutt for naturforskning, Trondheim (In Norwegian with English figure and table captions).
- Ortega, C.P., Ortega, J.C., Rapp, C.A. & Backensto, S.A. (1998) Validating the use of artificial nests in predation experiments. *Journal of Wildlife Management*, **63**, 925–932.
- Pakkala, T., Kouki, J. & Tiainen, J. (2006) Top predator and interference competition modify the occurrence and breeding success of a specialist species in a structurally complex forest environment. *Annales Zoologici Fennici*, **43**, 137–164.
- Penteriani, V. (2002) Goshawk nesting habitat in Europe and North America: a review. *Ornis Fennica*, **79**, 149–163.
- Quinn, J.L. & Kokorev, Y. (2002) Trading-off risks from predators and from aggressive hosts. *Behavioral Ecology and Sociobiology*, **51**, 455–460.
- Quinn, J.L., Prop, J., Kokorev, Y. & Black, J.M. (2003) Predator protection or similar habitat selection in red-breasted goose nesting associations: extremes along a continuum. *Animal Behaviour*, **65**, 297–230.
- Raudenbush, S.W. (1994) Random effects models. *The Handbook of Research Synthesis* (eds H. Cooper & L.V. Hedges), pp. 301–322. Russell Sage Foundation, New York.
- Reed, J.M., Boulinier, T., Danchin, E. & Oring, L.W. (1999) Informed dispersal: prospecting by birds for breeding sites. *Current Ornithology*, **15**, 189–259.
- Roos, S. (2002) Functional response, seasonal decline and landscape differences in nest predation risk. *Oecologia*, **133**, 608–615.
- Roos, S. & Pärt, T. (2004) Nest predators affect the spatial dynamics of breeding red-backed shrikes (*Lanius collurio*). *Journal of Animal Ecology*, **73**, 117–127.
- Rosenberg, M.S., Adams, D.C. & Gurevitch, J. (2000) *Metawin. Statistical Software for Meta-Analysis with Resampling Tests*, Version 2.0. Sinauer Associates, Sunderland, MA.
- Selås, V. & Rafoss, T. (1999) Ranging behaviour and foraging habitats of breeding Sparrowhawks *Accipiter nisus* in a continuous forested area in Norway. *Ibis*, **141**, 269–276.
- Sergio, F., Rizzoli, F., Marchesi, L. & Pedrini, P. (2004) The importance of interspecific interactions for breeding-site selection: peregrine falcons seek proximity to ravens nests. *Ecography*, **27**, 818–826.
- Sergio, F., Newton, I., Marchesi, L. & Pedrini, P. (2006) Ecologically justified charisma: preservation of top predators delivers biodiversity conservation. *Journal of Applied Ecology*, **43**, 1049–1055.
- Sloan, S.S., Holmes, R.T. & Sherry, T.W. (1998) Depredation rates and predators at artificial bird nests in an unfragmented northern hardwoods forest. *Journal of Wildlife Management*, **62**, 529–539.
- Sodhi, N.S., Didiuk, A. & Oliphant, L.W. (1990) Differences in bird abundance in relation to proximity of Merlin nests. *Canadian Journal of Zoology*, **68**, 852–854.
- Storaas, T. (1988) A comparison of losses in artificial and naturally occurring capercaillie nests. *Journal of Wildlife Management*, **52**, 123–126.
- Storaas, T. & Wegge, P. (1987) Nesting habits and nest predation in sympatric populations of capercaillie and black grouse. *Journal of Wildlife Management*, **51**, 167–172.
- Suhonen, J., Norrdahl, K. & Korpimäki, E. (1994) Avian predation risk modifies breeding bird community on a farmland area. *Ecology*, **75**, 1626–1634.
- Swenson, J.E. (1991) Evaluation of a density index for territorial male hazel grouse *Bonasa bonasia* in spring and autumn. *Ornis Fennica*, **68**, 57–65.
- Thomson, R.L., Forsman, J.T., Mönkkönen, M., Hukkanen, M., Koivula, K., Rytönen, S. & Orell, M. (2006a) Predation risk effects on fitness related measures in a resident bird. *Oikos*, **113**, 325–333.
- Thomson, R.L., Forsman, J.T., Sardà-Palomera, F. & Mönkkönen, M. (2006b) Fear factor: prey habitat selection and its consequences in a predation risk landscape. *Ecography*, **29**, 507–514.
- Tornberg, R. (1997) Prey selection of the goshawk *Accipiter gentilis* during the breeding season: the role of prey profitability and vulnerability. *Ornis Fennica*, **74**, 15–28.
- Tornberg, R., Mönkkönen, M. & Pakkala, M. (1999) Changes in diet and morphology of Finnish goshawks from 1960s to 1990s. *Oecologia*, **121**, 369–376.
- Tryjanowski, P. (2001) Proximity of raven (*Corvus corax*) nest modifies breeding bird community in an intensively used farmland. *Annales Zoologici Fennici*, **38**, 131–138.
- Ueta, M. (1994) Azure-winged magpies, *Cyanopica cyana*, 'parasitize' nest defense provided by Japanese lesser sparrowhawks, *Accipiter gularis*. *Animal Behaviour*, **48**, 871–874.
- Wiens, J.A. (1989) *The Ecology of Bird Communities*, Vol. 1. Cambridge University Press, Cambridge.
- Willebrand, T. & Marcström, V. (1988) On the danger of using dummy nests to study predation. *Auk*, **105**, 378–379.
- Yahner, R.H. (1996) Forest fragmentation, artificial nest studies, and predator abundance. *Conservation Biology*, **10**, 672–673.

Received 9 August 2006; accepted 6 February 2007