

Nest predators affect spatial dynamics of breeding red-backed shrikes (*Lanius collurio*)

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Summary

1. Predation may be a strong selective factor affecting individual behaviour and life histories. However, few studies have investigated whether predators affect breeding habitat selection of prey species.
2. We tested whether breeding habitat selection and reproduction of a tropical migrant, the red-backed shrike (*Lanius collurio* L.), was related to the presence of breeding pairs of its potential nest predators, magpie (*Pica pica* L.), hooded crow (*Corvus corone cornix* L.) and jackdaw (*C. monedula* L.).
3. Only magpie and hooded crow territories were associated with an elevated risk of predation based on an artificial nest experiment with nests mimicking red-backed shrike nests. Predation risk on real red-backed shrike nests was also higher close to nests of hooded crow and magpie than elsewhere in the landscape.
4. Occupation frequency of known red-backed shrike territory sites during 3 years of study increased with increasing mean distance to the nearest magpie nest.
5. Changes in spatial distribution of corvids affected the spatial distribution of red-backed shrikes. Vacant red-backed shrike territory sites were more likely to become occupied in the next year when magpie and hooded crows had moved away from the site, while occupied sites were more likely to be abandoned in the next year when at least hooded crows had moved closer.
6. Our results suggest that breeding territories of nest predators may affect breeding habitat selection of prey species. Thus, a large part of an observed spatial dynamics of prey species may be caused by a corresponding spatial dynamics of predators. Because sink territories are occupied more irregularly than source territories, we suggest that the dynamics in predator sinks may be the driving force of the spatial dynamics of prey species.

Key-words: artificial nest, habitat selection, nest predation, predator avoidance, territory occupancy.

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Introduction

Several recent studies on a variety of organisms have shown that predation can be a strong selective factor affecting individual behaviour, such as foraging decisions (Lima 1992; Utne, Brännäs & Magnhagen 1997), mate choice (Forsgren & Magnhagen 1993; Endler 1995) and life history patterns (Rodd & Reznick 1997). That predation also affects breeding habitat selection patterns and the resulting spatial distribution of species is less well studied (but see Peterson, Bull & Wheeler 1992). However, it is often assumed that prey species actively avoid

territories of predators or habitat patches associated with high predator activities when choosing breeding habitat.

Although predation itself may affect the dynamics of populations (e.g. Rodd & Reznick 1997; Klemola *et al.* 2000), the spatial avoidance of predators may potentially have consequences for population dynamics of prey species. For example, increasing populations of predators may force prey species to choose habitats of otherwise lower quality (e.g. in terms of food), thus increasing the proportion of the prey population that is breeding in poor habitats (cf. Pulliam & Danielson 1991). As a result, population growth rates will be affected negatively and extinction risks of populations may increase (Pulliam & Danielson 1991). Furthermore, the identification of source habitats may be ambiguous

when predators affect the quality of the habitat, especially when the predators are cryptic. However, whether prey species actively avoid breeding in patches with predators (e.g. predator territories) and whether short-term spatial dynamics of predators affect the spatial dynamics of prey species is almost unknown.

We studied the shrub-nesting red-backed shrike (*Lanius collurio* L.) and its potential nest predators, the corvids (Söderström, Pärt & Rydén 1998; Söderström 2001; Roos 2002). Although individual fitness is affected less by nest predation (i.e. predation on eggs or nestlings) than by predation on adults, nest predation is a potentially strong selective factor shaping breeding habitat selection patterns (Martin 1988; Roos 2002). The constraints of restricted dispersal on habitat selection patterns and patch occupancy dynamics (see e.g. Lima & Zollner 1996) are negligible, as both the prey and predator species are good dispersers at the scale of the study (i.e. an 80-km² study area).

First, we investigated the assumption that the predation risk on nests is higher close to nests of potential predators than elsewhere in the landscape by means of an artificial nest experiment. Secondly, given that this assumption was fulfilled, we hypothesized that red-backed shrikes should avoid breeding close to the most important predator species as judged from predation risk on artificial nests in territories of different predator species and identification of predator species at depredated nests. Thirdly, given that red-backed shrikes are less likely to breed close to predators, we hypothesized that the spatial dynamics of red-backed shrikes should be affected by the spatial dynamics of its most important nest predator species.

Estimates of nest predation risk and relative importance of nest predators that are independent of prey species behaviour were obtained by means of an experiment using artificial red-backed shrike nests within the territories of three corvid species, namely magpie (*Pica pica* L.), hooded crow (*Corvus corone cornix* L.) and jackdaw (*Corvus monedula* L.). Jackdaw territories were used as a conservative control for background levels of nest predation in the landscape, because they only rarely depredate nests (Cramp & Perrins 1994b: 120–140). We interpreted relative rates of nest predation because absolute rates are generally unreliable (Major & Kendal 1995). The relative rates were validated by observational data on habitat selection of red-backed shrikes and the fate of their nests. Longitudinal data on changes in spatial distribution of breeding red-backed shrikes in relation to changes in spatial distribution of breeding corvids were used to investigate predator avoidance and patterns of spatial dynamics.

Materials and methods

STUDY AREA AND STUDY SPECIES

The study was conducted between 1997 and 1999 in an 80-km² agricultural dominated landscape with its

surrounding forest edges south-east of Uppsala, south-central Sweden (59°48' N, 17°50' E). The study area consisted of arable fields (60%), pastures (10%), mixed deciduous–coniferous forests (20%) and broad-leaved deciduous forests (10%). The shrub-rich grasslands suitable for red-backed shrikes were scattered all over the study area, many of which were located in the vicinity of forest edges (for a detailed description of grassland habitats, see Pärt & Söderström 1999). In the grasslands, the most common shrubs (in order of decreasing abundance) were juniper (*Juniperus communis* L.), sloe (*Prunus spinosa* L.) and rose (*Rosa* spp.).

In the study area, approximately 70–100 pairs of red-backed shrikes have been breeding annually between 1994 and 1999 (for details, see Söderström 2001). A total of 207 spatially separated territories were occupied at least once during these 7 years. Hereafter, we refer to these sites as 'territory sites'. In the analyses we used both occupied and unoccupied territories.

Most red-backed shrikes arrive in mid-May to early June from the wintering areas in Africa, which is when corvids are incubating or feeding their nestlings. Following arrival at the territory, a nest is built preferably in dense shrubs (mainly sloe; Söderström 2001) and the four to six eggs are laid at the beginning of June. The eggs are incubated for 14 days and nestlings stay in the nest for another 14 days.

During 1997, 1998 and 1999 we visited all potential breeding habitat patches (i.e. open grass-dominated areas larger than 0.5 hectare with some shrubs) at least every 10 days between 20 May and 1 August in order to find all breeding attempts. Given five visits per territory (i.e. the minimum number of visits) the probability of missing a breeding pair was calculated to 0.08% ($n = 95$ pairs). Therefore, we are confident that we found all breeding pairs. When a red-backed shrike pair was found, the territory was visited in at least 5-day intervals to obtain data on nest site, date of egg-laying and hatching, clutch size and number of fledged young (for details, see Söderström 2001). Nest predation was evident when all eggs or nestlings disappeared, whereas cold eggs or dead nestlings were defined as desertion of a nest. Although the number of visits at the nest has been shown not to affect nesting success (Söderström 2001), we approached nests only when no potential nest predators were observed. In this paper we analysed mainly first breeding attempts, because they coincide in time with the breeding of corvids and with the timing of the artificial nest experiment (see below). However, in some analyses (e.g. total reproductive performance of red-backed shrikes in relation to distance to closest nest predator) we included second breeding attempts.

Nest sites of all breeding hooded crows, magpies and jackdaws were mapped between 1 April and 25 May (i.e. at the time of nest-building and incubation) in 1997, 1998 and 1999. Nest sites were found by carefully censusing all parts of the study area at least twice. Nests were located at all sites indicating a territory of magpie,

hooded crow or jackdaw. During these censuses more than 95% of the corvid nests were found, to judge from the few new corvid nests found later in the field season when the whole study area was covered on an almost daily basis. Nests of other corvids (see below) were not mapped, mainly because they breed in forests where red-backed shrikes do not breed (Cramp & Perrins 1993; own observation), but all observations of these less common species were mapped. Each year, about 200 pairs of jackdaws, 130 pairs of magpies, 80 pairs of hooded crows, 40 pairs of European jays (*Garrulus glandarius* L.), 10 pairs of nutcrackers (*Nucifraga caryocatactes* L.) and four pairs of ravens (*Corvus corax* L.) nested in the study area. Here, we analysed only the spatial distribution of nests of magpies, hooded crows and jackdaws, because we have comparable data (i.e. nest locations) for only these three species.

ARTIFICIAL NEST EXPERIMENT

In 1997, we placed three artificial nests in random directions at approximately 50-, 150- and 250-m distances from a corvid nest in 70 corvid territories. Our choice of corvid territory was based on two criteria. First, the corvid nest had to be located within 100 m from a grassland with thorny shrubs (i.e. a potential breeding habitat of red-backed shrikes). Secondly, the corvid nest had to be located more than 400 m from other nests of hooded crows, magpies or jackdaws to minimize the effects of predation caused by neighbouring pairs. In total, 31 magpie, 25 hooded crow and 14 jackdaw territories met these criteria. Because jackdaws often bred in colonies (range 2–13 pairs, mean \pm SE = 4.86 ± 1.12), several pairs of jackdaws frequently occupied a 'jackdaw territory'. However, there was no correlation between colony size of jackdaws and nest predation risk (Spearman's rank correlation, $r_s = 0.20$, $P = 0.46$).

Each nest was placed on average at the same height from ground (mean \pm SE = 1.00 ± 0.023 m), the same distance from the top (mean \pm S.E. = 0.92 ± 0.029 m) and edge (mean \pm SE = 0.90 ± 0.29 m) of the shrub as did red-backed shrikes, on average, in 1997–99 (Staffan Roos, unpublished data). The artificial nests were made of chicken wire lined with dry grass and moss and placed in sloe ($n = 108$) or rose ($n = 101$). There was no difference in nest predation risk among artificial nests placed in these two shrub species (G -test, $G = 0.03$, d.f. = 1, $P = 0.86$). Two small quail (*Coturnix coturnix* L.) eggs (size = 30×24 mm) and one plasticine egg (of the same size as a red-backed shrike egg, i.e. 22×16 mm) were placed in each nest. Because red-backed shrikes lay an average clutch of 5.26 eggs (mean numbers for the years 1997–99; Staffan Roos, unpublished data), the volume of egg contents was similar in artificial (≈ 21 cm³ egg content) and real nests (≈ 19 cm³ egg content). The plasticine egg was tied to the chicken wire in the artificial nest with a thin wire, which was hidden thoroughly in the nest material. Thus, our arti-

ficial nests mimicked closely real red-backed shrike nests concerning nest habitat, nest site, concealment and location within shrubs.

The nests were placed between 4 June and 14 June and each nest was checked during daytime at 5-day intervals for a period of 25 days, that is a time-span similar to the incubation and nestling period of the red-backed shrike. Results from another artificial nest experiment in the same area showed that there is no difference in nest predation risk between artificial nests visited at daylight and nests visited at night (i.e. when corvids are inactive; Roos 2002). A nest was considered depredated when at least one of the quail eggs was missing, broken or when there were bite or bill marks on the plasticine egg. When a nest was depredated it was removed from the shrub, and the imprints in the plasticine egg were used to identify the predator species by comparing the imprints with those made from stuffed corvids. If the plasticine egg was missing, the surroundings within a radius of 10 m were searched thoroughly. In cases when no plasticine egg was found, or when it had no imprints, the predator was regarded as 'unknown'. There was no difference in the mode of depredation (i.e. all eggs gone, quail eggs gone but no imprints, nest gone, etc.) of nests with unknown predators among territories of the three corvid species (G -test, $G = 0.64$, d.f. = 4, $P = 0.96$).

GEOGRAPHIC ANALYSES

All artificial and real red-backed shrike nests, corvid nests, farms and forest edges were mapped and distances between artificial and real red-backed shrike nests, respectively, and nests of each corvid species and habitat element were measured. Habitat features of red-backed shrike territories were mapped within a 1-hectare circle centred on the nesting shrub (for details, see Söderström 2001), as red-backed shrike territories are on average 1–3 hectares. We included only the amount of sloe shrubs within this circle in the analyses, because a previous study based on the same territories showed that this habitat variable was the only one associated significantly with territory preferences and occupation patterns for first breeding attempts (Söderström 2001). Between 1997 and 1999 there were no visual changes in the vegetation structure and composition within grasslands that had been inhabited by red-backed shrikes, as management regimes did not change over these years.

STATISTICAL ANALYSES

Daily nest mortality rates (\pm SE) for both artificial and real red-backed shrike nests were calculated according to Mayfield (1961, 1975) and Johnson (1979). We used two-tailed tests when investigating whether artificial nests located in magpie, hooded crow and jackdaw territories, respectively, differed in daily nest mortality rates. We then obtained a Z -value, which we tested

against a *Z*-distribution (Zar 1996). When we analysed daily nest mortality rates on real red-backed shrike nests, we pooled all 3 years because of the low sample size for nests located inside corvid territories (see Results). Nest predation risk on real red-backed shrike nests (depredated vs. successful) was analysed with nominal logistic regression including year (1997, 1998 and 1999) as a factor in the models.

G-tests were used in contingency table analyses with Williamson's correction (G_{adj}) when sample sizes were small (Sokal & Rohlf 1995). In analyses investigating relationships between predation risk on artificial nests and distance to nearest corvid nest, each territory plot was treated as a replicate and an estimate of daily nest predation rate was thus based on the fate of the three artificial nests in each territory. This pooling was conducted because there was no difference in nest predation risk between nests placed at 50, 150 and 250 m, respectively (see Results). Because the obtained estimate of nest predation varied along an ordinal scale, we used ordinal logistic regression (McCullagh 1980; see also Thomson, Furnes & Monaghan 1998). Ordinal logistic regression was also used to analyse frequency of territory occupancy between 1997 and 1999, because frequency of occupancy varied between 0, 1, 2 or 3 years. Relationships between spatial dynamics of red-backed shrikes and spatial dynamics of corvids were analysed by nominal logistic regressions. First, we tested whether the probability of occupation of a previously unoccupied territory site was related to changes in distance to nearest corvids the following year (i.e. only territory sites unoccupied in the first year were analysed). Secondly, we analysed whether the probability of abandonment of a previously occupied territory site was related to a spatial change in corvid distribution. To control for the direct effects of distance to corvids in the neighbourhood of red-backed shrike territories, we always included distance to nearest nest of the three corvid species in the first year as covariates in the models. To avoid pseudo-replication we used a territory site only once when it was empty or occupied, respectively, during all 3 years.

In general, we always included variables regarding distances to nearest nest of each corvid species in multiple regression models. However, we also tested models including amount of sloe to investigate whether this environmental variable explained an additional significant proportion of the observed variation of the models. Previous studies (e.g. Angelstam 1986; Andrén 1992) have shown that nest predation risk in a patch may be associated with the number of corvids observed around that patch. However, in no case did a model with the numbers of corvid nests within 1000 m from the red-backed shrike territory sites deviate significantly from those based on only distance to closest nests (e.g. Sokal & Rohlf 1995). We therefore present only tests on distances to nearest corvid nests.

To validate the results of the artificial nest experiment, we compared daily nest mortality rates of real

red-backed shrike nests located close to and far away from corvid nests. However, we could not use the same spatial scale as in the artificial nest experiment (i.e. within 250 m from a corvid nest), because red-backed shrike generally avoided breeding close to hooded crows and magpies (see Results). Instead, we used the yearly median distance between occupied red-backed shrike territories and closest nest of hooded crow and magpie, respectively, to obtain daily nest mortality rates of real nests in the presence and absence of magpies and hooded crows in the neighbourhood. Distance to jackdaw nests was ignored in this test, as we found no indication of jackdaws depredating shrub nests.

Data on distances that were not normally distributed were log-transformed to obtain normality. All logistic regression analyses were performed with the JMP statistical package on Macintosh (version 3.2.6; SAS 1999). Values reported are mean \pm 1 SE, unless stated otherwise. All multivariate models presented here were significant ($P < 0.025$ in all cases).

Results

ARTIFICIAL NESTS: PREDATOR IDENTIFICATION AND PREDATION RISK

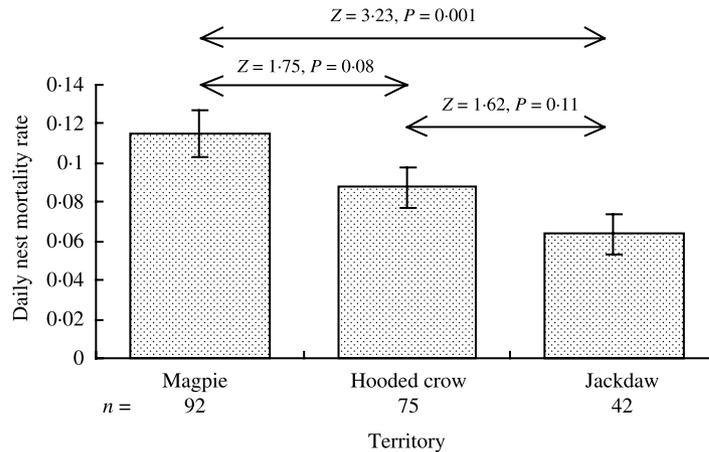
Overall, 87.6% of the artificial nests ($n = 209$, one nest was destroyed by a human and thus deleted from further analyses) were depredated after 25 days of exposure. Mean daily nest mortality rate was 0.091 ± 0.006 . Magpie was the most frequently identified nest predator, followed by European jay and hooded crow (Table 1). In no case did we identify jackdaw as a predator on artificial red-backed shrike nests (Table 1). Although the relative frequencies of identified nest predators differed among corvid territories (*G*-test, $G = 13.49$, d.f. = 4, $P = 0.009$), magpie was the most frequently identified nest predator in territories of all three corvid species (Table 1).

A large fraction of nest predators were not identified to species (56% when including 'unknown corvid' and 'unknown'). Our data, however, suggest that most unknown predators were corvids, because we found no imprints on plasticine eggs of small mammals (e.g. red squirrel (*Sciurus vulgaris* L.), weasel (*Mustela nivalis* L.) or mice (*Apodemus* spp.)). Previous studies in our study area show that these mammals frequently leave imprints on plasticine eggs when depredating artificial nests (Söderström *et al.* 1998; Roos 2002). The percentage of depredation cases classified as unknown corvids was slightly higher in magpie (14.5%) than in hooded crow territories (6.1%), while pattern was the opposite concerning those classified as 'unknown' (42.2% and 51.5% for magpie and crow territories, respectively). However, these differences were not statistically significant (identified pooled vs. unknown corvid vs. unknown: $G = 3.26$, d.f. = 2, $P = 0.20$).

Daily nest mortality rate on artificial nests differed significantly between corvid territories, with highest

Table 1. Observed (Obs.) and expected (*Exp.*) numbers of predation cases on artificial nests caused by different nest predator species within territories of three species of corvids

Nest predator	Territory						Total Obs.
	Magpie		Crow		Jackdaw		
	Obs.	<i>Exp.</i>	Obs.	<i>Exp.</i>	Obs.	<i>Exp.</i>	
Magpie	29	23	13	18	8	9	50
Hooded crow	1	5	8	4	2	2	11
European jay	6	9	7	7	6	3	19
Unknown corvid	12	10	4	8	6	4	22
Unknown	35	37	34	29	12	15	81
Total	83		66		34		183

**Fig. 1.** Mean daily nest mortality rates (\pm SE) on artificial nests placed in magpie, hooded crow and jackdaw territories. Sample sizes are shown below SE bars and refer to the total number of nests. Z-values refer to tests among groups as indicated by arrows.

rates in magpie, intermediate rates in hooded crow and lowest rates in jackdaw territories (Fig. 1). Mean daily nest mortality rate (mean across species \pm SE) did not differ between nests located 50 (0.092 ± 0.011), 150 (0.082 ± 0.010) and 250 m (0.099 ± 0.012) from the nest of corvids ($Z < 1.06$, $P > 0.28$, for all species). Thus, our data on artificial nests are in line with the assumption that nest predation risk is higher in magpie and hooded crow territories than elsewhere in the landscape (e.g. jackdaw territories).

TERRITORY OCCUPANCY AND DISTANCE TO CORVIDS

In the years 1997, 1998 and 1999, the numbers of red-backed shrike first breeding attempts were 97, 95 and 80, respectively. Frequency of territory site occupancy (i.e. 0–3 years) increased significantly with increasing mean distance to nearest magpie nest ($\chi^2 = 23.36$, d.f. = 1, $P < 0.0001$; Fig. 2a). As shown previously (Söderström 2001), the amount of sloe shrubs within territories explained a residual part of the variation in territory occupancy ($\chi^2 = 20.58$, d.f. = 1, $P < 0.0001$; Fig. 2b). There was no association with mean distance to nearest nest of hooded crow and jackdaw ($P > 0.27$ in both cases).

DO SPATIAL DYNAMICS OF CORVIDS AFFECT THE SPATIAL DYNAMICS OF SHRIKES?

Red-backed shrikes, magpies and hooded crows displayed a high degree of spatial territory dynamics between years. Red-backed shrike territory sites that were occupied in year t were often abandoned in year $t + 1$ (49.5% in 1997–98 and 33.33% in 1998–99). Each year, 20–25% of previously unoccupied territory sites became occupied. Turnover rate in corvid territories was also high. Approximately 20% of the occupied magpie territories were abandoned between subsequent years, while 25% of the population were breeding in new territories. Thirty-eight per cent of the occupied hooded crow territories were abandoned between years, while about 35% of the population were breeding in new territories.

The changes in territory occupancy of red-backed shrikes between years was linked at least partly to the changes in territory occupancy of magpies and hooded crows, but not to jackdaws. The probability that an occupied red-backed shrike territory site in year t became unoccupied in year $t + 1$ was related significantly to crows having moved closer to the territory (Table 2, Fig. 3), while the same trend for magpies was not statistically significant. However, occupied territory sites

Table 2. Probability that a red-backed shrike territory site that was occupied in year t was abandoned in year $t + 1$ in relation to change in distance to closest nest of three corvid species, between year t and year $t + 1$, respectively, and distance to closest nest of corvids in year t (nominal logistic regression, model: $n = 164$, $\chi^2 = 17.46$, d.f. = 6, $P = 0.0077$)

Probability of abandonment	Parameter estimate \pm SE	d.f.	χ^2	P
Change in distance to magpie between years	0.0014 \pm 0.0010	1	2.02	0.17
Distance magpie first year	-0.0027 \pm 0.0011	1	6.33	0.012
Change in distance to crow between years	0.0016 \pm 0.0007	1	5.04	0.029
Distance crow first year	-0.0008 \pm 0.0006	1	1.92	0.17
Change in distance to jackdaw between years	0.0000 \pm 0.0010	1	0.03	0.96
Distance jackdaw first year	0.0002 \pm 0.0005	1	0.16	0.69

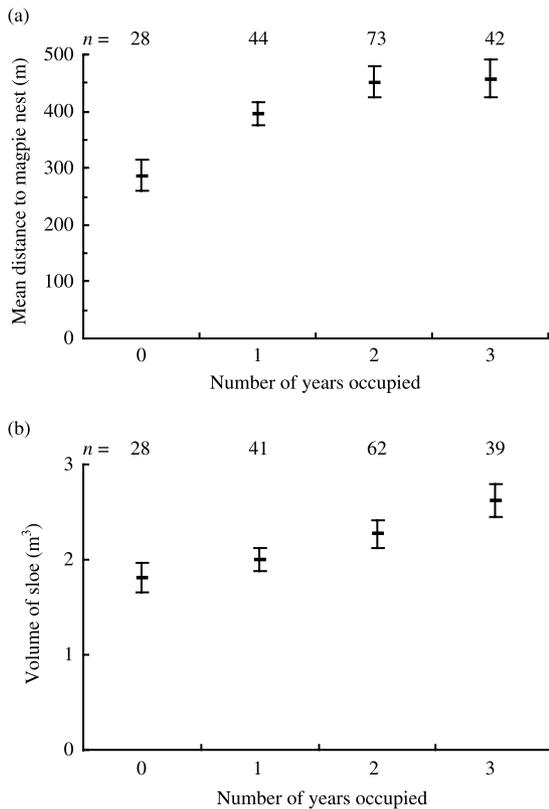


Fig. 2. Relationships between (a) mean distance to closest nest of magpie and (b) log mean volume of sloe within territory site and frequency of territory site occupancy by red-backed shrikes, respectively. Sample sizes are shown above each point (\pm SE).

were more likely to be abandoned when magpies were breeding close to the site than when they were breeding far away from the site in year t . The probability that an unoccupied territory site in year t became occupied in year $t + 1$ increased significantly when hooded crows and magpies had moved away from the red-backed shrike territory (Table 3, Fig. 3). Similarly, probability of occupation was related positively to distance to closest magpie nest in year t . In both subsets analysed, there was no significant correlation between a change in closest distance to magpie and hooded crow nests ($r < 0.14$, $P > 0.07$).

Previous studies suggest that individuals may abandon a breeding site following a reproductive failure

(e.g. Switzer 1997). However, when we included breeding success ('successful' if first or replacement clutch produced fledglings, otherwise 'unsuccessful') in the model predicting abandonment, the final model did not improve significantly ($\chi^2 = 2.43$, d.f. = 1, $P = 0.12$). However, when we included the amount of sloe in territory sites, the model predicting abandonment improved almost significantly ($\chi^2 = 3.81$, d.f. = 1, $P = 0.051$), indicating that sloe-poor territory sites were abandoned at a higher rate than sloe-rich territories. When we included the amount of sloe in territory sites, the model predicting occupation of previously unoccupied territory sites did not improve significantly ($\chi^2 = 0.71$, d.f. = 1, $P = 0.40$).

NEST PREDATION ON REAL RED-BACKED SHRIKE NESTS

Most red-backed shrikes avoided breeding close to magpie and hooded crow territories (see above). Each year, only few red-backed shrike pairs occupied territory sites that were located within the territories of corvids. However, the variation in distance between red-backed shrike and corvid territories allowed us to test whether nest predation risk differed between red-backed shrike nests located close to compared to far away from corvid territories. We tested whether outcome (i.e. predated vs. successful) of red-backed shrike nests was associated with distance to closest corvid territory. We found that successful outcome of red-backed shrike nests was associated significantly with long distance to nearest crow nest (nominal logistic regression, $\chi^2 = 8.16$, d.f. = 1, $P = 0.0043$) and tended to be related to long distance to nearest magpie nest (nominal logistic regression, $\chi^2 = 3.20$, d.f. = 1, $P = 0.074$). There was no association between nest predation risk and distance to nearest jackdaw nest (nominal logistic regression, $\chi^2 = 0.09$, d.f. = 1, $P = 0.76$). Analyses of mean daily nest mortality rates (according to Mayfield 1961, 1975; Johnson 1979) of red-backed shrike nests located close to (i.e. within the yearly median distance; see Methods) or far away from (i.e. outside the yearly median distance) nests of the different corvid species also showed that daily nest mortality rates were higher close to hooded crows and magpies than elsewhere in the landscape ($z = 3.71$, $P = 0.0002$; Fig. 4).

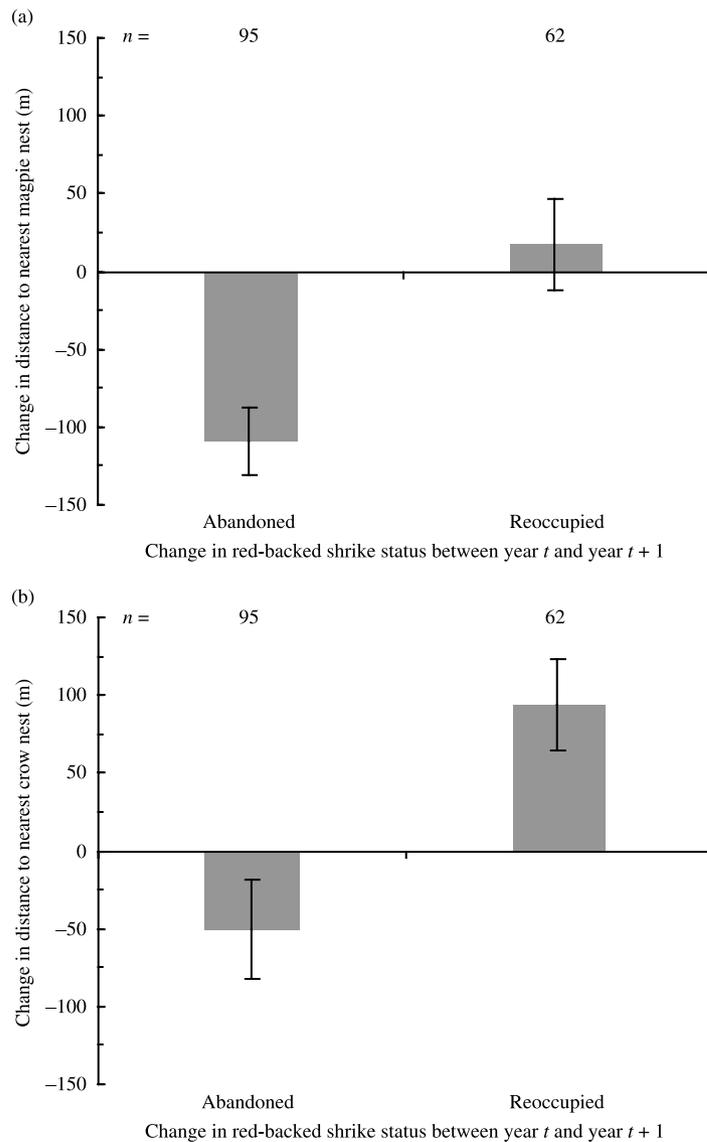


Fig. 3. Mean difference in distance (meters) between year t and year $t+1$ between red-backed shrike territories and nearest nest of (a) magpie and (b) hooded crow, respectively, in relation to change in red-backed shrike territory occupancy between the years. Sample sizes are shown above each bar (\pm SE). Positive values of bar indicate that the distance between the territory site and closest corvid nest has increased between years, while negative values indicate that the distance between the territory site and closest corvid nest has decreased between years.

Table 3. Probability that a red-backed shrike territory site that was unoccupied in year t was occupied in year $t+1$ in relation to change in distance to nearest nest of three corvid species between year t and year $t+1$, respectively, and distance to closest nest of corvids in year t (nominal logistic regression, model: $n = 159$, $\chi^2 = 32.11$, d.f. = 6, $P < 0.0001$)

Probability of occupation	Parameter estimate \pm SE	d.f.	χ^2	P
Change in distance to magpie between years	0.0034 \pm 0.0012	1	10.00	0.0016
Distance to magpie nest first year	-0.0033 \pm 0.0010	1	11.78	0.0006
Change in distance to crow between years	0.0018 \pm 0.0008	1	4.75	0.029
Distance to crow nest first year	-0.0009 \pm 0.0007	1	1.95	0.16
Change in distance to jackdaw between years	0.0005 \pm 0.0008	1	0.43	0.51
Distance to jackdaw nest first year	0.0001 \pm 0.0005	1	0.64	0.80

Discussion

Predation risk on artificial nests mimicking red-backed shrike nests was elevated in the close neighbourhood of magpie and hooded crow nests (Fig. 1). This result was

validated by predation rates on natural nests of red-backed shrikes, which also suggested that predation rate was higher close to breeding hooded crows and magpies, compared to elsewhere in the landscape (Fig. 4). Thus, we expected red-backed shrikes to spatially avoid

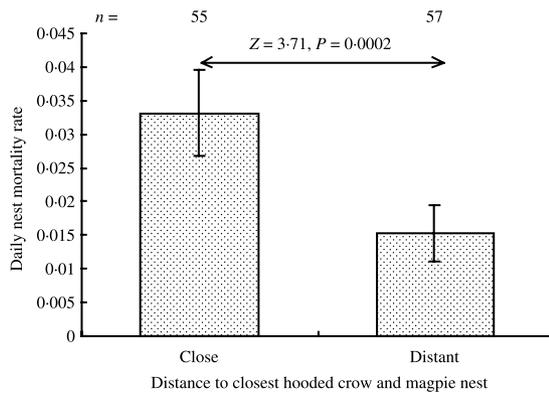


Fig. 4. Mean daily mortality rates (\pm SE) on red-backed shrike nests located within and outside, respectively, the yearly median distance between occupied red-backed shrike territories and closest hooded crow and magpie territories. Sample sizes are shown above SE bars and refer to the total number of nests pooled over the years 1997–99. The Z-value refers to test among groups as indicated by the arrow.

breeding pairs of these two corvid species. In line with this expectation, we found that red-backed shrike territory sites were occupied less frequently when magpies were breeding close to that site (Fig. 2). Furthermore, the spatial dynamics in territory occupancy of red-backed shrikes was associated with the spatial dynamics of breeding magpies and hooded crows (Tables 2 and 3; Fig. 3). For example, red-backed shrikes were more likely to occupy a previously unoccupied territory site when magpies and hooded crows had moved away from that territory site. Thus, our results suggest that the spatial distribution and dynamics of nest predator territories may affect habitat selection patterns and territory dynamics of prey species.

The realism and use of artificial nests when investigating relative rates of nest predation and relative importance of nest predator species could be questioned, mainly because our artificial nests did not have attending parents (e.g. Willebrand & Marcström 1988; Major & Kendal 1995). Our results suggest, however, that the experiment broadly captured relative rates of nest predation within territories of the three corvid species and the true nest predators on real red-backed shrike nests. First, predation rate on artificial nests was highest in territories of magpie, intermediate in crow and lowest in jackdaw territories (Fig. 1) and predator identifications suggested that jackdaws did not depredate artificial red-backed shrike nests. Data on natural nests of red-backed shrikes indicated a similar relationship between predation risk and presence of different corvid species (e.g. Fig. 4). Thus, the patterns of predation of real red-backed shrike nests validated the results obtained from the artificial nest experiment. Secondly, red-backed shrikes were also found to avoid mainly magpies and hooded crows (Tables 2 and 3, Fig. 3), but not jackdaws.

A large fraction of the predators on artificial nests were unknown (Table 1), but our data suggest that the

majority of these were corvids (see Methods and Results). The relative importance of magpie, hooded crow and European jay as judged from predator identifications could, however, be questioned. In fact, it seems likely that hooded crow depredations were underestimated, because hooded crow is the largest corvid species and is probably most able to tear off the plasticine egg (i.e. being classified as ‘unknown’). Accordingly, the percentage of ‘unknown’ was slightly higher in crow as compared to magpie territories. However, uncertainties in the data on predator identification does not affect our general interpretations because they are based on nest predation rates within different corvid territories, and patterns of predator avoidance and predation of real bird nests.

A between-year change in distance to nearest nests of hooded crows and magpies significantly predicted an occupation of previously vacant red-backed shrike territory sites, while only a change in distance to hooded crows predicted abandonment (Tables 2 and 3). Generally, the effects of nearest nesting corvids on the probability of abandonment of red-backed shrike territory sites were weaker than for the probability of occupation. Site fidelity of red-backed shrikes and declining population size of shrikes, however, could partly explain the above-mentioned inconsistencies. In other populations of red-backed shrikes individuals may display a high degree of site fidelity, especially when breeding successfully (Jacobson & Stauber 1987). Thus, some individuals may have returned to the same site despite corvids having moved closer to the site. Similarly, because the population numbers dropped from 97 to 80 pairs (probably reflecting a general decline of the species; Lindström & Svensson 2002), several territory sites may have been abandoned independently of the spatial distribution of corvid nests.

Several studies have shown prey species to avoid habitat patches associated with high risk of nest predation: for example, forest edges and small forest patches (e.g. Møller 1988; Andrén 1990). Furthermore, studies on different organisms have shown that predators may affect their prey species’ microhabitat use when foraging (Longland & Price 1991; Watts 1991; Suhonen 1993; Suhonen, Halonen & Mappes 1993). However, few studies have investigated the direct spatial relationships between predators and their prey species concerning breeding habitat selection. Møller (1988) tested whether blackbirds (*Turdus merula* L.) breeding in farmland avoided magpie territories, but found no evidence for a direct avoidance of magpies. Blackbirds, however, seemed to avoid small woodland patches that were associated with high risk of nest predation. Other studies (Suhonen, Norrdahl & Korpimäki 1994; Norrdahl *et al.* 1995) have shown that European kestrels (*Falco tinnunculus* L.) may modify breeding bird communities in farmland areas. They suggested that small birds, preferred prey by the kestrels, avoided breeding in the vicinity of kestrel nests (Suhonen *et al.* 1994). They also showed that curlews (*Numenius arquata* L.) preferred

to breed close to breeding kestrels, probably because kestrels deterred corvids, and as a consequence nest predation risk in the neighbourhood of kestrel nests was reduced. Finally, peregrine falcons (*Falco peregrinus* Tunstall) are reported to alter the distribution of breeding passerines around their nests, so that fewer passerines breed close to the falcon nests (Meese & Fuller 1987). However, most of these results are based on cross-sectional observational data, and could therefore be explained by predator–prey differences in food preferences, which affect their habitat preferences and their respective spatial distribution among habitats.

We used longitudinal data on between-year spatial shifts of predators and prey in habitats that at least superficially did not change over this time period (see Methods) to avoid the shortcomings of the cross-sectional data mentioned above. Red-backed shrikes responded to between-year spatial shifts in magpie and hooded crow distribution (Tables 2 and 3; Fig. 3), which strongly suggests a direct avoidance of breeding territories of these two corvid species. Although red-backed shrikes prefer sloe-rich grasslands (Söderström 2001; this study), amount of sloe only improved significantly the model predicting abandonment, and not the model predicting occupation. Our results, therefore, suggest that red-backed shrikes may change their choice of breeding habitats when nest predators breed close to an otherwise preferred habitat (i.e. sloe-rich grassland). It seems unlikely that these results would reflect species differences in habitat requirements of predators and prey, because the habitat did not change between years. Furthermore, magpies and red-backed shrikes broadly prefer the same habitat when foraging, which is sun-exposed semi-open grasslands with shrubs and single trees (Birkhead 1991; Cramp & Perrins 1993, 1994a; Olsson 1995). Also, hooded crows prefer grasslands for foraging in spring and summer, although to a lesser extent than magpies (Cramp & Perrins 1994c). All three species mainly consume large ground-living invertebrates (Högstedt 1980; Tatner 1983; Cramp & Perrins 1994a,c; Olsson 1995), although in addition red-backed shrikes commonly feed on flying *Hymenoptera* (Cramp & Perrins 1993; Olsson 1995). An alternative explanation to our results on spatial avoidance may therefore be that red-backed shrikes avoid the corvid species in order to decrease the competition for food. However, this competition-based hypothesis is less likely, as red-backed shrikes and corvids have different morphological measurements of bills (Cramp & Perrins 1993, 1994a,c), and therefore forage on different species of invertebrates (e.g. Högstedt 1980; Cramp & Perrins 1993, 1994a,c). Finally, different habitat preferences regarding proximity to houses and opposite population trends of red-backed shrikes and magpies could, potentially, contribute to the observed patterns of avoidance. However, contrary to the expectations of this idea, the most robust result of spatial shifts was when red-backed shrike colonized territory sites that were abandoned by corvids (Table 3), while the results were less clear con-

cerning red-backed shrikes abandoning territory sites when corvids moved closer to that site (Table 2). Furthermore, a previous study showed that there was no relationship between habitat preferences and reproductive success of red-backed shrikes, respectively, and distance to closest house (Söderström 2001).

A large part of the changes in territory occupation of magpies and hooded crows between years was caused probably by human persecution (crows and magpies are hunted regularly in the study area) and by a significantly higher proportion of corvid pairs abandoning territories of lower quality (cf. Pulliam & Danielson 1991). Other studies suggest that the best magpie territories in terms of reproduction and survival ('sources') are located close to human settlements, because of a reduced nest predation by crows and ravens (Baeyens 1981; Birkhead 1991) and because magpies find food easily all year round near human settlements (Baeyens 1981; Birkhead 1991). In our study area, magpie territories located far away from human settlements (i.e. mainly farms) are more likely to experience nest predation (87.5%) than those located near human settlements (25.9%; Staffan Roos & Jennie Siggstedt, unpublished data). Furthermore, as the magpie population has increased recently (both in the study area and on a nationwide scale; Svensson 1999), the number of occupied magpie 'sink' habitats has probably increased. Thus, magpies have increasingly colonized shrub-rich grasslands far away from human settlements. Therefore, we suggest that the dynamics of 'sink' habitats of corvids may be the major driving force in the observed patterns of red-backed shrike territory dynamics.

To conclude, our results show that prey species may avoid breeding sites of predators when selecting breeding habitat. The degree of avoidance of territories of predators may, however, vary depending on the costs and benefits of spatial avoidance. Generally, one may expect risky patches being avoided more efficiently by avoiding habitat structures related with a high risk (e.g. common foraging areas of predators) rather than avoiding territories of predators. Clearly, this is also what has been observed in many studies where the major nest predators are characterized by large area requirements (e.g. mammals: Storaas & Wegge 1987; Crabtree, Broome & Wolfe 1989; Vickery, Hunter & Wells 1992; hooded crows: Berg 1996). Concerning generalist predators on bird nests, we suggest spatial avoidance of predator territories to be most marked when the predator and prey species habitat requirements overlap and when the territory of the predator species is small. This is because territory boundaries are assessed more easily when territories are small compared to when they are large. Because sink habitats are expected to display more marked dynamics in occupancy than sources (Pulliam & Danielson 1991), we suggest sink habitats of predators to be relatively more important as a driving force for the spatial dynamics of prey species than are source habitats. Although only few studies have shown predators to affect habitat

preferences and spatial dynamics of prey species, we expect it to be more common than shown so far.

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