

Nest Predation Processes and Farmland Birds

Habitat Selection and Population Dynamics of Predators and Prey

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**Doctoral thesis
Swedish University of Agricultural Sciences
Uppsala 2004**

Acta Universitatis Agriculturae Sueciae
Silvestria 301

ISSN 1401-6230
ISBN 91-576-6535-4
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Tryck: SLU Service/Repro, Uppsala 2004

Abstract

Roos, S. 2004. *Nest predation processes and farmland birds: Habitat selection and population dynamics of predators and prey*. Doctor's dissertation.
ISSN 1401-6230, ISBN 91-576-6535-4

It is generally expected that predators affect the breeding biology of prey species, but most studies have had a prey-biased view of the predator-prey relationship. Without studying the predator, one may draw erroneous conclusions of how predators and prey interact and conservation strategies for prey species could therefore be misleading.

In this thesis, I investigated whether omnivorous avian generalists known to depredate nests of passerine birds, mainly the magpie (*Pica pica*) and the hooded crow (*Corvus corone cornix*), affected breeding habitat selection and population dynamics of one of their prey species, the red-backed shrike (*Lanius collurio*) in a Swedish farmland landscape (c. 94 km²). The studies were performed between 1997 and 2003.

My results showed that red-backed shrikes avoided to breed close to magpies and hooded crows, and that the spatial dynamics of red-backed shrikes between years were linked to corresponding spatial dynamics of the two corvid species. By avoiding corvids, red-backed shrikes increased their breeding success. The distribution and population dynamics of magpies were closely linked to human settlements. Thus, in areas with many houses and farms, magpies occurred in higher population densities and had higher reproductive success than in areas with few houses and farms. The studied magpie population increased in numbers by c. 86% between 1997 and 2003. At the same time did the red-backed shrike population decrease by c. 40% and this decline in numbers was closely linked to the increase of magpies both at a landscape and at a local scale (km²-squares). My results also suggest that corvid nest predators form a search-image for shrub nests and therefore display density-dependent nest predation. However, the density-dependent nest predation risk was nest-site and time specific. Thus, corvids formed a search-image for nests in junipers early in the season, while it was changed towards thorny deciduous shrubs late in the season, probably as a result of corresponding seasonal changes in shrub specific nest densities.

My results suggest that the effects of nest predation potentially could affect nest site choice, habitat patch choice and population dynamics of many song birds.

Key-words: Corvids, red-backed shrike, *Lanius collurio*, magpie, *Pica pica*, spatial avoidance, prey refuge, functional response, search image, density-dependent predation.

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Denna avhandling tillägnas min mor

Louise Roos (1944-2000),

som formade mitt naturintresse under oräkneliga bär- och svamputflykter.

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Ubi mens plurima, ibi minima fortuna
(Ordspråk)

Acti labores iusundi
(Cicero 106 - 43 B.C.)

Nunc est bibendum
(Horaz 65 - 8 B.C.)

Appendix

Papers I-V

The present thesis is based on the following papers, which will be referred to by their Roman numerals:

- I. Roos, S. and Pärt, T. 2004. Nest predators affect spatial dynamics of breeding red-backed shrikes (*Lanius collurio*).
Journal of Animal Ecology 73: 117-127.
- II. Roos, S., Siggstedt, J., and Pärt, T. Habitat selection and breeding success of magpies (*Pica pica*) in farmland: The relative importance of grasslands and human settlements.
Manuscript.
- III. Roos, S. An increasing magpie (*Pica pica*) population limit the distribution of red-backed shrikes (*Lanius collurio*).
Manuscript.
- IV. Roos, S. 2002. Functional response, seasonal decline and landscape differences in nest predation risk.
Oecologia 133: 608-615.
- V. Roos, S. and Pärt, T. When to expect density-dependent predation? An example with nest predators and shrub-nesting birds.
Submitted manuscript.

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Introduction

The most important cause of population declines of wild animals is habitat loss (Primack 1993; Meffe and Carroll 1994). The process of habitat loss involves at least four phenomena: Reduction in habitat area (Andrén 1994), habitat fragmentation (Andrén 1994; Noss and Csuti 1994) habitat degradation within patches (e.g. Knick and Rotenberry 2000), and habitat degradation in matrix (habitat between patches; Soulé et al. 1988; Noss and Csuti 1994). Another important factor causing population declines worldwide is alien species, that either have been deliberately introduced by humans or colonised areas following human-induced habitat alterations (Atkinson 1996; Godfray and Crawley 1998). Thus, the combination of habitat loss and invading species may act in concert, causing further negative effects on wild animals. Furthermore, as the species invading the disturbed environments often have low demands on specific habitat features (i.e. they are habitat generalists; Godfray and Crawley 1998), they may interact with populations of species with more precise demands on the environment (habitat specialists) through competition (Pimm 1991), parasitism (Donovan et al. 1997), and predation (Meffe et al. 1994; Robinson et al. 1995). Increased predation caused by invading generalist predators is probably the inter-specific interaction that historically has had the strongest negative impact on habitat specialists (Atkinson 1996).

In concordance with the assumption that habitat generalist thrive in landscapes being antropogenically modified, several species of generalists (such as many species in the *Corvidae* family) occur in higher abundance in farmlands than in forested landscapes (Bossemá et al. 1986; Andrén 1992). During the last decades, population increases of especially magpies (*Pica pica*) in farmlands have been reported from several European countries (Gregory and Marchant 1995; Svensson 1999; Jerzak 2001). This has occurred at the same time as several farmland birds have declined (Krebs et al. 1999; Chamberlain et al. 2000; Donald et al. 2001). As magpies are reported to frequently depredate eggs and nestlings of several farmland birds, it has been hypothesized that increasing magpie populations may have contributed to the observed population declines of farmland birds (Gooch et al. 1991). However, no study has so far found strong support for this hypothesis (Gooch et al. 1991; Gregory and Marchant 1995; Thomson et al. 1998; Stoate and Thomson 1999). Instead, it is widely believed that the population declines of farmland birds are caused by the major intensification of agricultural practices that has taken place during the last 50 years. The change in agricultural practices has undoubtedly caused loss of suitable breeding habitats (Benton et al. 2003) and reduced food abundance for farmland birds (Fuller et al. 1991). Unfortunately, the studies investigating the effects of magpies on potential prey species have all been conducted in countries where agricultural practices have been most pronounced (i.e. Denmark; Møller 1988; the UK; Gooch et al. 1991; the Netherlands; Dix et al. 1998). Thus, it may be difficult to observe the effects of predator-prey interactions when prey species already are suppressed by the intense agricultural practices (Stoate and Thomson 1999; Evans 2004). Furthermore, several of the studies have been conducted at a regional scale (see e.g. Gooch et al. 1991; Dix et al. 1998),

that is, at a scale that may be inappropriate when studying effects of predation, which normally is scale-dependent and most pronounced at smaller scales (Cantrell et al. 2001; Lima 2002).

Generally, predator-prey studies have mainly been investigating how predation risk affects foraging habitat selection (Sih 1982; Longland and Price 1991; Suhonen 1993; Utne et al. 1997). Both theoretical (e.g. Sih 1987; Holt 1996, 1997) and empirical studies (e.g. Mech 1977; Geer 1978; Meese and Fuller 1987; Suhonen et al. 1994) have tested whether predation risk may affect breeding habitat selection. However, these studies have primarily tested whether predation on adult individuals may affect choice of breeding habitat. Very few studies have examined how generalist predators depredate nest contents may affect breeding habitat selection (but see e.g. Schmidt 2001), although several theoretical (Donovan et al. 1995b; Cantrell et al. 2001) and empirical studies (Donovan et al. 1995a; Robinson et al. 1995) have investigated the effects of predation caused by generalist predators on population dynamics of prey populations. For farmland birds, who are confined to the decreasing areas of grassland habitats for breeding, the probability of spatially avoiding increasing numbers of generalist predators may have decreased during the last decades. Thus, the combined effects of habitat loss and increasing numbers of generalist predators could have the potential to further reduce the numbers of farmland birds (cf. Evans 2004). Currently, there is no study investigating population dynamics of both predators and prey in the farmland.

In order to study whether generalist predators (i.e. *Corvidae*) may affect breeding habitat selection of a potential prey species, one must first investigate whether predation risk is higher in territories of the predators than elsewhere in the landscape. Therefore, in the first study of this thesis (*paper I*), I investigated whether predation risk was higher in the territories of some potential avian nest predators (i.e. corvids). I also investigated whether red-backed shrikes (*Lanius collurio*), a farmland bird species with high nest failure rate due to nest predation caused by corvids (Cramp and Perrins 1993; Söderström 2001), avoided to breed close to the most important generalist predators.

Previous predator-prey studies have generally examined how individuals of prey species respond to situations with varying predation risk. However, the behaviour of the predators have received little attention, which may have influenced the interpretation of some results (Lima 2002). Clearly, one must also study the predator in order to fully understand the interaction between predators and prey. As the magpie has been suggested to be a major nest predator on farmland birds, I investigated the habitat preferences, reproduction, and territory fidelity of magpies in *paper II*.

An obvious next step (*paper III*) was to investigate how an increasing nest predator species (the magpie) may affect the distribution and local population numbers of a prey species (the red-backed shrikes) at the landscape scale. As no such studies exist today, we do not know whether all prey subpopulations are affected similarly by increasing numbers of generalist predators or whether some subpopulations remain unaffected. If differences between local populations exist, it may be of high conservation value to identify them and further explore why

these populations could remain stable. One possible scenario is that individuals of a prey species aggregate in areas with low numbers of predators, thereby increasing the local population density (i.e. the "refuge hypothesis"; Sih 1987). This scenario thus assumes that prey populations in areas with high numbers of generalist predators vanish due to either emigration or low fecundity (cf. Hames et al. 2001; Schmidt 2001; Schneider 2001). These issues were investigated in *paper III*.

As most predators display density-dependent predation (Sutherland 1996), predation could exert a selection against the aggregations of prey in refuges, as hypothesized above. However, it is not known whether generalist predators may display density-dependent predation towards increasing densities of nests, mainly because nest contents only make up a small proportion (< 5%; Cramp and Perrins 1994a, b, e) of most generalists' diet. Previous studies show no consensus, because some studies have found evidence for density-dependent predation (Göransson et al. 1975; Dunn 1977), while others have not (Blancher and Robertson 1985; Norment 1993). In *paper IV*, I therefore investigated whether the generalist predators may display density-dependent nest predation.

One possible explanation to the lack of consensus of previous studies regarding the occurrence of density-dependent nest predation may be that the predators have already formed a search image for the type of nest being studied. If this is the case, predation may become density-independent. However, for other nest types with low levels of background predation rates, density-dependent predation would be expected. I examined this hypothesis in *paper V*, by studying the predators search-image formation in relation to contrasting background levels of nest predation risk on two types of shrub nests (i.e. nests placed in either juniper or in deciduous shrubs).

Material and methods

Description of the study area

The studies in this thesis were conducted in a 93 km² large area south-east of Uppsala in south-central Sweden (approximately 59°48'N, 17°32'E). The study area is dominated by arable fields (59.5% of the total area). Semi-natural grasslands (12.2%) and mixed deciduous-coniferous forests (26.7%) cover relatively large areas, but these habitats are highly fragmented. Human settlements (0.6%), water (0.6%), and broad-leaved deciduous forests (0.4%) cover a small part of the study area. In total, 129 farms and 40 small villages with more than 10 households, and 3245 buildings are located in the study area. The study area is bordered by forests of the hemi-boreal type (Ahti et al. 1968).

Semi-natural grasslands is one of the most important habitat types for several farmland bird species (Söderström 1999), including red-backed shrikes (Söderström 2001; Vanhinsbergh and Evans 2002). The semi-natural grasslands in the study area have a long history of management (mainly grazing and to a lesser

extent mowing). Grazing by cattle, horses, and sheep was the most common form of management during the years of the studies. In the semi-natural grasslands, the most common shrubs (in order of decreasing abundance) were juniper (*Juniperus communis*), sloe (*Prunus spinosa*), and rose (*Rosa* spp.). Solitary trees and small groups of trees occur in most of the grasslands.

The complete study area was used in order to study habitat selection of magpies and for artificial nest experiments (see below). However, red-backed shrikes was only studied in the central part of the study area (approximately 75 km²; *papers I-IV*). By this approach, I was able to also account for corvids breeding outside the red-backed shrike study area.

During the years of study, a minor reduction in the area of grazed semi-natural grasslands has occurred. Approximately one per cent of the area grazed in 1997 was not grazed in 2003. About 40 houses have been built in the study area between 1997 and 2003. Other habitat variables have remained apparently the same over the years of the study.

The species

The members of the corvid family is well-known for their generalist foraging habits and omnivorous diet, which constitutes mainly of invertebrates and seeds, and to a lesser extent of eggs and nestlings (< 5%; Cramp and Perrins 1994a, b, e). In my study area, seven species of corvids occur regularly; raven (*Corvus corax*; approximately 4 pairs per year), hooded crow (*C. corone cornix*; > 75 pairs per year), rook (*C. frugilegus*; no pairs breeding in the study area, but foraging birds from colonies nearby were frequent), jackdaw (*C. monedula*; approximately 250 pairs per year), jay (*Garrulus glandarius*; approximately 50 pairs per year), nutcracker (*Nucifraga caryocatactes*; probably < 10 pairs per year), and magpie (>120 pairs per year). However, ravens, jays, and nutcrackers are mainly forest-dwelling corvids, rarely leaving the forested areas (e.g. Andrén 1990; Cramp and Perrins 1994f). Rooks and jackdaws rarely depredate nests (Cramp and Perrins 1994c, d). Thus, in farmland-dominated landscapes, magpies and hooded crows (and carrion crow (*C. corone corone*) in other parts of Europe) are the most common corvid nest predators on farmland birds (Møller 1989; Andrén 1992).

During the last decades, the number of magpies have increased in several European countries (Gregory and Marchant 1995; Svensson 1999; Jerzak 2001), while the number of the other corvids have remained relatively stable, at least in Sweden (Svensson 2000).

As increasing populations of magpies sometimes are blamed for the decline of many farmland birds (Birkhead 1991; Gooch et al. 1991), I studied habitat preferences and breeding ecology of magpies in more detail. Previous studies suggest that preferred magpie territories are associated with large area of grassland habitats and human settlements (Møller 1982; Birkhead 1991). Magpies breeding in these preferred territories defend their 3-9 ha territory all year around (Baeyens 1981a, b; Birkhead 1991). However, pairs breeding in low-quality territories may leave their breeding territory during winter, probably because such behaviour may

lead to the acquisition of better territories with higher food abundance (Baeyens 1981a, b). Magpies build large, conspicuous doomed nests in trees and shrubs. In Sweden, magpies start incubating the clutch (3-8 eggs) in April, and the clutch hatches after 22 days. Nestlings fledge at an age of about 27 days (Birkhead 1991). The main causes of breeding failure of magpies are nest predation (mainly caused by crows) and desertion (especially during egg laying and brooding; Birkhead 1991). If the first breeding attempt fails, a replacement clutch may be initiated (Birkhead 1991). Main mortality factors of adult magpies are predation caused by *Accipiter* hawks and hunting by humans (Birkhead 1991; Toyne 1998).

The red-backed shrike is an insectivorous, long-distant migrant breeding in grassland habitats in Europe and western Asia and wintering in southern Africa (Cramp and Perrins 1993). Red-backed shrikes are territorial, and defend their territory (size: 0.25-6 ha) from the time they arrive to the breeding areas (mid-May) until the brood leaves the nest (Cramp and Perrins 1993). Following arrival at the territory, an open nest is built, preferably in dense, thorny shrubs (mainly in sloe and junipers; Tryjanowski et al. 2000; Söderström 2001) and the 5-6 eggs are laid between late May and late June. The eggs are incubated for 14 days and nestlings stay in the nest for another 14 days.

As red-backed shrikes build open nests, predation on eggs and nestlings is the most important factor causing breeding failures (Jacobson and Stauber 1987; Tryjanowski et al. 2000; Söderström 2001). Replacement clutches are common if the first breeding attempt fails (Cramp and Perrins 1993; Söderström 2001). Main mortality factors for adult red-backed shrikes have not been studied explicitly, but predation caused by *Accipiter* hawks on the breeding grounds and Eleonora's falcons (*Falco eleonora*) during migration occur (Cramp and Perrins 1993). During the last decades, the numbers of red-backed shrikes have been reported to be declining, especially in western Europe (Tucker and Heath 1994).

Surveys of breeding corvids

Nests of hooded crows, magpies and jackdaws were surveyed each year between April 1 and May 25, that is, at the time of nest building and incubation. Nest sites were found by carefully censusing all parts of the study area at least twice. Nests were located at all sites where there were indications of 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 at an almost daily basis. Nests of other corvid species (see above) were not mapped, mainly because they breed in forests where the studied population of red-backed shrikes did not breed.

In 2001 and 2002, I studied breeding success of totally 128 magpie pairs (*paper II*). Generally, the status of the nest (failed or ongoing breeding) was checked at least two times during incubation and brooding, respectively. Active nests, easily recognised by frequent feeding trips to the nest by the parents, were revisited several times around the date when fledgling was expected to take place in order to determine whether the nest was successful or not. If one or more fledglings was seen, the breeding attempt was classified as successful.

The red-backed shrike population study

In order to find all breeding pairs of red-backed shrikes, all potential breeding habitat patches (i.e., open grass-dominated areas larger than 0.5 hectare with at least some shrubs) was visited every 10 days between May 20 and August 1. When a red-backed shrike pair was found, the territory was visited at least every five days 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. As the number of visits at the nest may increase nest predation rate (Tryjanowski 1999; but see Söderström 1999), my field assistants and I approached nests only when no potential nest predators were observed. In this thesis, mainly first breeding attempts have been analysed. However, in some analyses (e.g., total reproductive performance of red-backed shrikes in relation to distance to closest nest predator; *paper D*), I also included second breeding attempts.

Artificial nest experiments

In order to get estimates on relative nest predation risk in different sites, a common method is to use artificial nests baited with quail (*Coturnix spp.*) eggs (Roper 1992; Craig 1998) or eggs made of plasticine (Møller 1989). Ideally, these nests should mimic nests of the target prey species regarding nest location, general appearance, size, and conspicuousness (Major and Kendal 1995). An advantage of the use of artificial nests is that they are easily manipulated in time and space, which obviously is not true for natural nests (unless nest boxes are used). Furthermore, as high-quality individuals, in terms of breeding experience and competitive ability, are expected to breed in the best territories with high food abundance and low predation risk (e.g. Sutherland 1996), it is virtually impossible to separate the effects of territory quality and individual quality when studying nest predation risk using real nests (but see Goodburn 1991).

However, the use of artificial nests is beset with problems. First, there is obviously no adult bird incubating or protecting the artificial nest, and no parent bird is feeding the incubating adult and the chicks. These differences between artificial and real nests suggest that different predators using different cues for foraging, that is, visual-oriented (e.g. corvids) or smell-oriented (e.g. mammals), may depredate artificial and real nests (e.g. Willebrand and Marström 1988; Pärt and Wretenberg 2002). The effect of different predator faunas on real and artificial nests could be even more pronounced, because the common use of the relatively large quail eggs may prohibit small-mouthed predators, such as rodents (i.e. important nest predators on real eggs and nestlings in some parts of the worlds) to depredate artificial nests (Bayne et al. 1997; Maier and DeGraaf 2000; but see e.g. Craig 1998). On the other hand, plasticine eggs may, due to their smell, attract rodents (Pärt and Wretenberg 2002). Thus, it may be inappropriate to compare estimates of nest predation rates obtained from artificial and real nests (e.g. Major and Kendal 1995).

The most important difference between my studies using artificial nests (*paper I, IV, and V*) and most other published studies is that I placed the artificial nests in shrubs where the nest was invisible from outside the shrub. This means that predators must enter the shrub in order to find the nest, suggesting that estimates of predation rates on artificial nests presented in this thesis probably reflects foraging behaviour and search-image formation of the predators. Furthermore, in order to mimic real red-backed shrike nests, I made all artificial nests myself. I also used nest sites similar to the ones used by red-backed shrikes in terms of distance from the ground and top from the shrub (S. Roos and B. Söderström unpublished data). I baited the nests with two quail eggs and a plasticine egg for identification of the responsible predator (cf. Møller 1989). Previous studies in my study area suggested that rodents and larger mammals mainly depredated artificial ground nests, while corvids were the main predators on artificial shrub nests (Söderström et al. 1998; Pärt and Wretenberg 2002). As corvids easily break quail eggs, my choice of egg type should incur no bias in the estimates of predation rates. Furthermore, relative rates of nest predation on artificial nests were validated by corresponding relative estimates of predation on real red-backed shrike nests (*paper I, IV*). Thus, relative risk of artificial nest predation reflected predation risk on real red-backed shrike nests.

I used different experimental designs in the different studies. In *paper I*, I placed three artificial nests in thorny shrubs at approximately 50, 150, and 250 m from a corvid nest in 70 corvid territories. I used 31 magpie, 25 hooded crow, and 14 jackdaw territories that were located more than 400 m away from other corvid nests to minimise the effects of predation caused by neighbouring corvids. In *paper IV*, I placed artificial nests in junipers at either high (8 nests/ha), intermediate (4 nests/ha), or low (2 nests/ha) density in 39 semi-natural grasslands. I repeated the experiment three times during one season (May, June, and July). However, I changed nest densities in each grassland, so that each grassland only had a certain nest density once (i.e. using a Latin square design). In *paper V*, I placed artificial shrub nests at either high (8 nests/ha) or low (2 nests/ha) nest density in 39 semi-natural grasslands in June. For each grassland, I placed the nests in either sloe or juniper shrubs. I repeated the experiment in July, with the same treatment regarding density and nest site. In all studies, I used grasslands that were spatially separated (> 300 m), thereby decreasing the possibility that several experimental plots were located within the territory of a single pair of corvids.

Each study used different times that the nests were exposed to predators (*paper I* = 25 days; *paper IV* = 15 days; *paper V* = 10 days). However, for all studies, I revisited the artificial nests every five days in order to determine whether the nest was depredated or not. If it was depredated, the nest was removed and the imprints in the plasticine egg were compared with imprints made from stuffed animals known to depredate passerine nests.

I calculated daily nest mortality rates according to Mayfield (1961; 1975) and Johnson (1979). This method calculates an estimate based on the number of depredation events per days that the nests have been under observation. The method assumes that a nest was depredated exactly half-way between the last visit where the nest was active and the visit where it was found depredated.

The nest densities used in my studies were within the natural variation of shrub nests previously reported in this study area (range = 1.0-9.0 shrub nests per ha; Tomas Pärt & Bo Söderström, unpublished data).

In *paper V*, I used a modified technique to manufacture the plasticine eggs. Earlier experiments (*paper I, IV*) showed that predators were able to fly away with the plasticine egg, making it impossible to identify which species being responsible for a large proportion of the predation events. Therefore, I started to use eggs made of a core of ceramic clay that was covered by a layer of plasticine. These eggs were harder for predators to tear off from the artificial nests. Consequently, the percentage of unidentified predators was lower in *paper V* than in *paper I* and *IV*.

Results and Discussion

Spatial variation in nest predation risk (*Paper I, IV*)

Many ecological theories of habitat selection are based on the premise that individuals select habitats in order to minimise the risk of being killed by predators (e.g. Fretwell 1972; Sutherland 1996). However, it remains basically untested whether individuals of prey species avoid predators by selecting breeding habitats with low abundance of predators (but see Mech 1977; Møller 1988). For the avoidance behaviour to be adaptive, one would expect that there must exist predator refuges (Sih 1987) that individuals can identify and select with relatively low costs. Thus, to investigate whether potential prey species could avoid to breed in areas with high abundance of potential nest predators (i.e. corvids), I first investigated the spatial variation in nest predation risk by examining the relative importance of different corvid species as nest predators. Secondly, I tested whether nest predation risk varied between different sites in the farmland landscape.

By using artificial shrub nests (see Methods), I was able to obtain measurements on relative nest predation risk in different parts of the landscape. First, I found that there was a significant difference in nest predation rates on artificial nests placed in territories of magpies, hooded crows, and jackdaws, respectively (*paper D*). Highest nest predation rates were found in magpie territories, while hooded crow territories had intermediate and jackdaw territories had the lowest rates (for statistical details, see Fig. 1). This result is in agreement with data on diet of these corvids, because magpies and hooded crow are reported to consume eggs and nestlings, while jackdaws only rarely do so (Cramp and Perrins 1994b, c, e). Thus, estimates on nest predation risk from sites with jackdaws may be regarded as an average background level of nest predation risk caused by mammals and itinerant corvids.

Secondly, I showed that nest predation rates on artificial shrub nests were high in grasslands surrounded by farmland, intermediate in grasslands surrounded by

forested land, and low in grasslands surrounded by a mosaic of farmland and forested land (Fig. 2; *paper IV*).

The bill and bite marks in the plasticine eggs used in *paper I, IV, and V* revealed that magpies were the most frequently identified predator species (Table 1). However, the improved method of preparing the plasticine eggs used in *paper V* (i.e. using a hard core of ceramic clay covered by a thin layer of plasticine) suggest that depredation caused by hooded crows may have been underestimated in *paper I and IV*.

These results suggest that risk of nest predation differs depending on where in the landscape the nest is located. Nest predation risk is high within magpie and hooded crow territories and in grasslands with a farmland-dominated surrounding, while grasslands outside magpie and hooded crow territories and with relatively more forested land in the surroundings displayed a lower risk of nest predation. These results are in agreement with the findings of Andr en (1992), who found that there was a positive relationship between nest predation rates and the area of fields in the surrounding landscape.

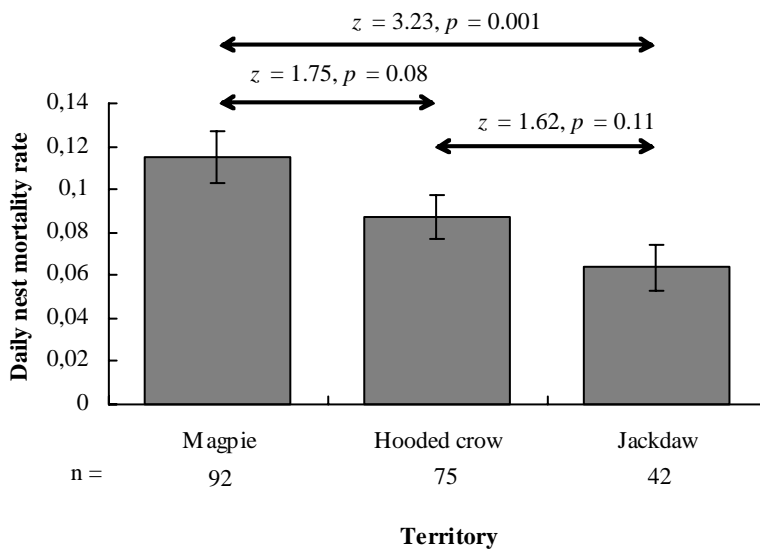


Figure 1. Mean daily nest mortality rates (\pm S.E.) on artificial nests placed in magpie, hooded crow and jackdaw territories. Sample sizes are shown below S.E. bars and refer to the total number of nests. Z-values refer to tests among groups as indicated by arrows.

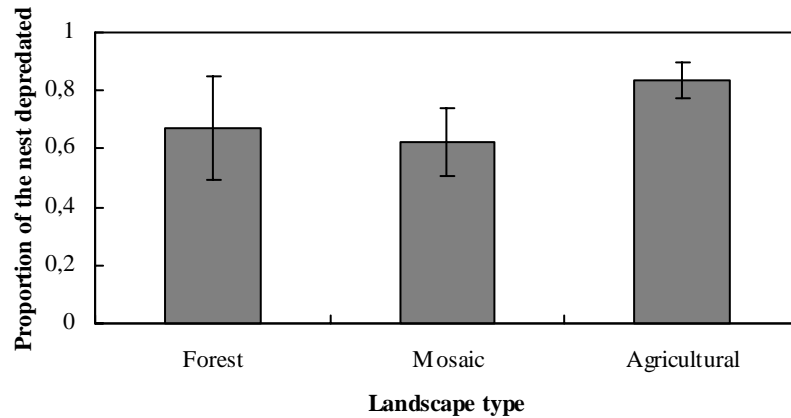


Figure 2. Proportion of the artificial nests being depredated in semi-natural grasslands surrounded by forest (n = 9 grasslands), mosaic between forest and farmland (n = 11 grasslands), and farmland (n = 19 grasslands). All grasslands received a total of 15 nests over the study period (*paper IV*).

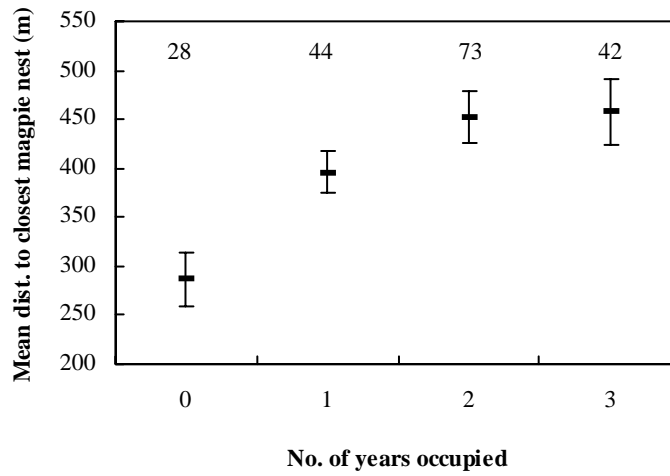
Table 1. Number of predation events on artificial shrub nests used in papers I, IV, and V caused by different species of predators

Species	Paper no.			Total
	I	IV	V	
Magpie	50	66	52	168
Hooded crow	11	17	42	70
Jay	19	37	14	70
Corvid	22	46	18	86
Small bird	0	9	24	33
Large mammal	0	0	4	4
Small mammal	0	4	8	12
Unknown	81	199	35	315
Total	183	378	197	758

Do potential prey avoid nest predators? (*Paper I*)

Based on the above results, I hypothesized that red-backed shrikes should avoid to breed close to breeding magpies and hooded crows, but that jackdaws should not be avoided (Table 1; *paper I*). Partly in line with this hypothesis, red-backed shrike territories located far away from magpie nests were occupied significantly more years than territories located close to magpie nests (ordinal logistic regression, $\chi^2 = 23.36$, $df = 1$, $p < 0.0001$; Fig. 3a; see also *paper IV*), while occupancy rate was not associated with distance to hooded crows and jackdaws ($p > 0.27$). In agreement with the general habitat preference of red-backed shrikes for grasslands with thorny shrubs (Söderström 2001; Vanhinsbergh and Evans 2002), amount of sloe shrubs within territories explained a residual part of the variation in territory occupancy rate (ordinal logistic regression, $\chi^2 = 20.58$, $df = 1$, $p < 0.0001$; Fig. 3b).

a)



b)

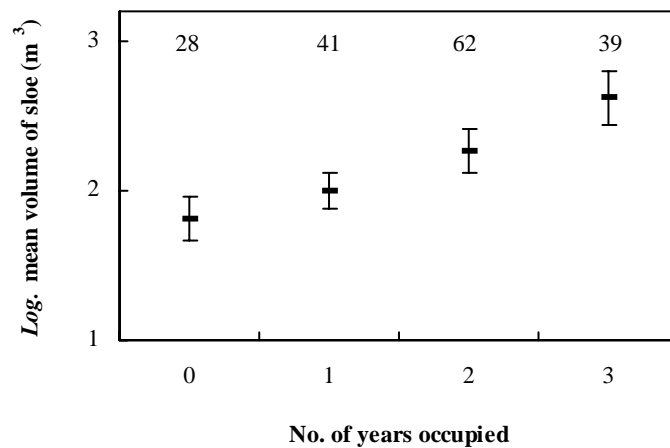
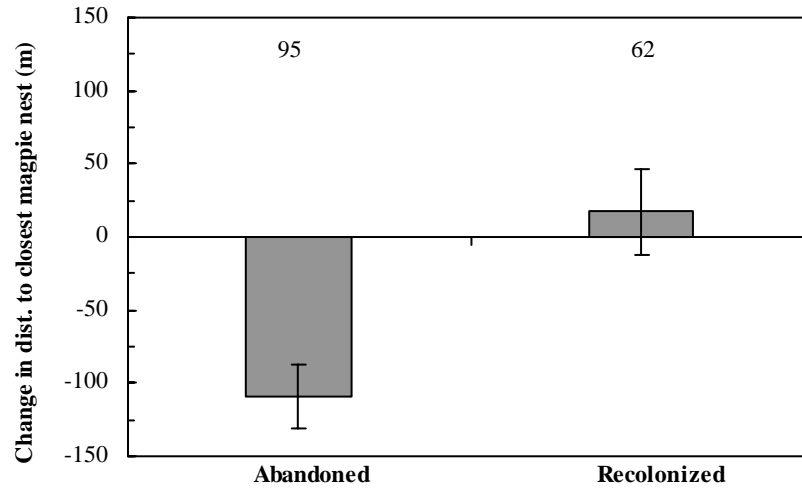


Figure 3. Relationships between a) mean distance to closest nest of magpie and frequency of territory site occupancy by red-backed shrikes, and b) *log.* mean volume of sloe within territory site, respectively. Sample sizes are shown above each point (\pm S.E.).

That red-backed shrikes actively avoided magpies and hooded crows was furthermore shown by the fact that between year-changes in spatial distribution of magpies and hooded crows were linked to reversed changes in the distribution of red-backed shrikes. When magpies or hooded crows established a new territory close to a previously occupied red-backed shrike territory, red-backed shrikes abandoned that territory. However, when magpie or hooded crows moved away from a previously unoccupied red-backed shrike territory site, red-backed shrikes re-colonised that territory (Fig. 4).

a)



b)

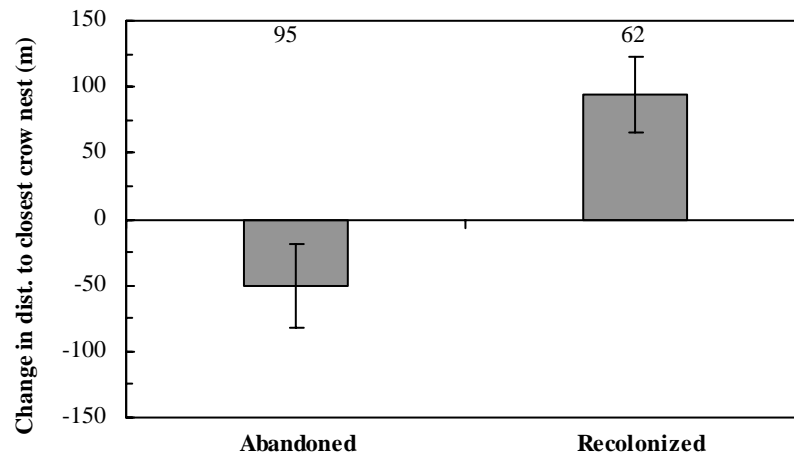


Figure 4. Mean difference in distance (meters) between year t and year $t + 1$ between red-backed shrike territories and nearest nest of a) magpie and b) hooded crow, respectively, in relation to change in red-backed shrike territory occupancy between the years. Sample sizes are shown above each bar (\pm S.E.). 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.

The behaviour of avoiding corvids seemed to be adaptive, because red-backed shrike breeding success was positively associated with distance to closest hooded crow nest (nominal logistic regression, $\chi^2 = 8.16$, d.f. = 1, $p = 0.0043$) and closest magpie nest (nominal logistic regression, $\chi^2 = 3.20$, d.f. = 1, $p = 0.074$; for mean \pm SE of daily nest mortality rates, see also Fig. 5). There was no association between nest outcome and distance to closest nest of jackdaw (nominal logistic regression, $\chi^2 = 0.09$, d.f. = 1, $p = 0.76$).

Thus, my results suggest that habitat selection of magpies and possibly hooded crow may affect patterns of habitat selection of red-backed shrikes.

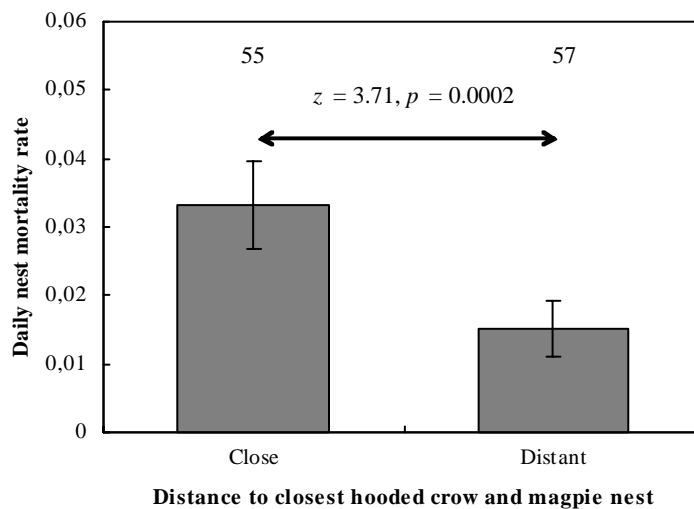


Figure 5. Mean daily mortality rates (\pm S.E.) on red-backed shrike nests located within and outside, respectively, the yearly median distance between occupied red-backed shrike territories and closest hooded crow and magpie territories. Sample sizes are shown above bars (\pm S.E.) and refer to the total number of nests pooled over the years 1997-1999. The z -value refers to test among groups as indicated by the arrow.

Habitat selection of an important nest predator, the magpie (Paper II)

In studies regarding predator-prey interactions, it is rarely appreciated that there are “two players on the field”. Instead, the main focus has historically been on how prey behave in situations with different apparent predation risk (Lima 2002). Predators have been treated like static features, with no reaction norms in behavioural decisions. This is obviously not true, because predators make decisions of where and when to hunt and use different foraging techniques in different situations (e.g. Crabtree et al. 1989; Lister and Garcia Aguayo 1992). Furthermore, small and medium-sized predators are often themselves prey of larger carnivores, which in turn may influence their spatio-temporal patterns of activity (Polis and Holt 1992; Holt and Polis 1997). All these factors highlight the

need to incorporate the behaviour of predators in studies of predator-prey interactions.

Because magpies are important predators on nests of passerine birds (*paper I and IV*), I investigated habitat preferences and spatial population dynamics of magpies using data from a seven-year study.

The results showed that magpie territories with high occupancy rates were located significantly closer to houses (multiple ordinal logistic regression, $\chi^2 = 23.57$, $df = 1$, $p < 0.0001$; Fig. 6) and farms (multiple ordinal logistic regression, $\chi^2 = 16.08$, $df = 1$, $p = 0.0001$), and at sites with longer total road length within 100 m from the territory centroid (multiple ordinal logistic regression, $\chi^2 = 6.29$, $df = 1$, $p = 0.012$) than territories with low occupancy rate. The probability that a magpie nest was successful followed the same spatial pattern as occupancy rate; Successful magpie nests were located significantly closer to houses (nominal logistic regression, $\chi^2 = 5.40$, $df = 1$, $p = 0.020$; Fig. 6) and farms (nominal logistic regression, $\chi^2 = 4.74$, $df = 1$, $p = 0.030$) than unsuccessful pairs. Finally, territories in which the magpie pair was breeding unsuccessfully were more likely to be abandoned the following year than territories where the pair raised young (χ^2 -test, $\chi^2 = 18.13$, $df = 1$, $p < 0.0001$).

These results suggests that the studied magpie population is partly limited by presence of high-quality breeding sites, that is, sites close to human settlements. The pre-emptive territoriality of the species (cf. Fretwell 1972) therefore suggest that the observed pattern of stable high-quality territories close to human settlements and ephemeral low-quality territories away from human settlements may contribute to a density-dependent population regulation, similar to a “buffer effect” (Brown 1969) or the “site-dependent population regulation hypothesis” (Rodenhouse et al. 1997). However, my results are in contrast to results from studies from the UK and continental Europe, which have shown that magpies prefer (Saino and Meriggi 1990; Birkhead 1991) and have higher breeding success in grasslands than elsewhere in the landscape (Goodburn 1987 cited in Birkhead 1991). The differences in relative importance of human settlements and grasslands may be due to climatological differences regarding winter temperature and snow cover. Harsher winter conditions make Swedish grasslands inaccessible as foraging habitats between November and March. The mild winters in southern and western Europe allow magpies to forage in grasslands during the whole year (Birkhead 1991). Thus, the relative importance of human settlements may be much more pronounced in areas with harsh winter conditions. This hypothesis is supported by studies from Denmark, which is a climatological intermediate between Sweden and continental Europe. Møller (1983) found that magpies in his Danish study area rarely foraged in farmyards during periods of warm weather, but when the ground was covered by snow or was frozen, magpies showed a strong preference for farmyards. Furthermore, Danish magpies showed a breeding habitat preference for both human settlements and grasslands (Møller 1982).

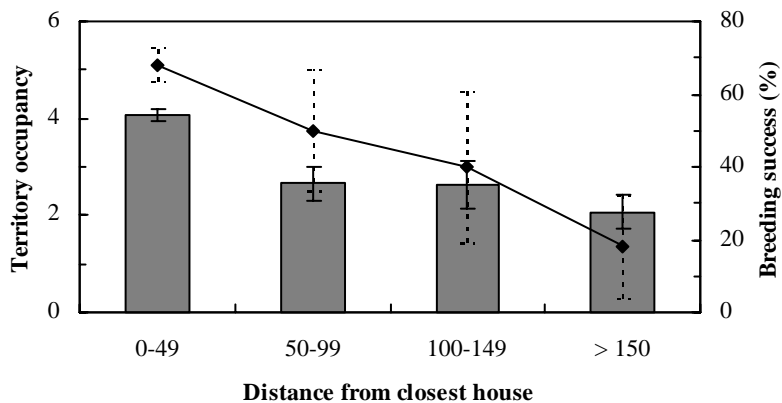


Figure 6. Relationship between the number of years the magpie territories were occupied (bars, mean \pm SE) and breeding success (line, mean \pm SE) in relation to distance to closest building.

The link between population dynamics of predators and prey (Paper I and III)

Studies exploring the link between population dynamics of prey and predators have generally examined how increasing population densities of a prey species trigger a numerical response of a specialist predator (Pimm 1991; Klemola et al. 2000). Furthermore, many studies have investigated how the increased numbers of predators may affect predation on main and alternative prey types (Pimm 1991; Bêty et al. 2002). Few studies have investigated how population dynamics of generalist predators may affect their prey species. In the case of the corvids and their possible effects on farmland birds, one would expect that there would be no numerical response of corvids, because the proportion of eggs and nestling in the diet of the corvids is small (< 5%; Cramp and Perrins 1994a, b, c, e). Instead, population dynamics of corvids may be affected by abiotic factors, such as weather (Birkhead 1991), but also by density-dependent factors such as density of invertebrate food abundance, competition, predation, and hunting (Loman 1980; Knight 1988; Birkhead 1991; Stone and Trost 1996).

In *paper I*, it was shown that the probability of territory occupancy of red-backed shrikes was affected by distance to closest magpie and hooded crow (Figs 3 and 4). In *paper III*, I worked at a landscape scale (using km²-squares) in order to examine whether an increasing magpie population limited the spatial distribution of a red-backed shrike population. A detailed analysis of changes in numbers within squares, in which I separated the magpie territories in high- and low-quality territories, clearly revealed that increasing numbers of magpies was associated with decreasing numbers of red-backed shrikes (Table 2, Fig. 7). My results furthermore showed that in km²-squares that never had breeding magpies (i.e. these km²-squares functioned as refuges; Sih 1987), the numbers of red-

backed shrikes remained at a relatively high and stable level, despite the total increase of magpie numbers in the total study area (*paper III*).

These result strongly contradicts with previous studies (Gooch et al. 1991; Thomson et al. 1998), which have shown that an increase of magpies is not followed by a decrease of their potential prey. There are at least two possible explanations for these different results. First, most other studies have used a regional scale when exploring potential negative effects of increasing magpie populations on farmland birds (Gooch et al. 1991; Dix et al. 1998), while my results suggest that a finer scale (i.e. km²-squares) may be more appropriate when investigating potential patterns of spatial predator avoidance. Secondly, other studies have been conducted in countries where the intensification of the agricultural practices has been most pronounced, while my study area is less affected by intense agriculture. As intensification of agricultural practices affect farmland birds negatively (Chamberlain et al. 2000; Donald et al. 2001), it may be hard to detect effects of increasing numbers of generalist predators on potential prey species when the latter already are suppressed by low food abundance.

Table 2. Ordinal logistic model showing the relationship between the number of breeding red-backed shrike pairs per 1 km² and the independent variables year, number of occupied high-quality magpie territories per 1 km² (# H-Q), number of occupied low-quality magpie territories per 1 km² (# L-Q) and the interaction between these two variables (# H-Q * # L-Q). I used the variable grid cell as a random factor in the analysis

Variable	Estimate ± S.E.	F	df	p
YEAR	-0.10 ± 0.027	15.26	1	0.0001
# H-Q	-0.22 ± 0.090	6.23	1	0.013
# L-Q	-0.34 ± 0.23	2.26	1	0.13
# H-Q * # L-Q	0.084 ± 0.046	3.27	1	0.072

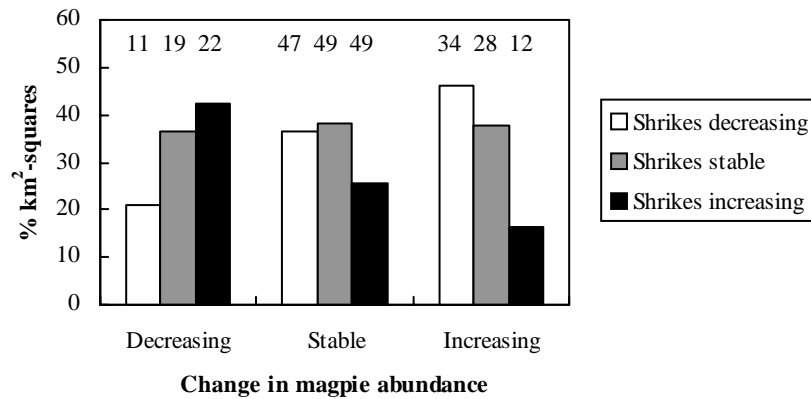


Figure 7. The percentage of the between-year changes of red-backed shrike numbers (classified as either decreasing, stable, or increasing) in relation to between-year changes in magpie numbers (classified as either decreasing, stable, or increasing; n = 255). Sample size for each category is shown above each bar.

Behavioural aspects of nest predation processes (*Paper IV and V*)

Generalist predators are expected to “switch” between different food types, depending on which of the food types are most available or rewarding (Takahashi 1968; Sutherland 1996). This change in diet is referred to as a functional response (cf. Takahashi 1968) and implies that many predator-prey interactions are density-dependent, that is, a predator consumes relatively more of a prey when the density of the prey is high than when it is low (Sutherland 1996). However, it may be questionable whether generalist predators, such as corvids, form and change search image for bird nests, as nest contents only constitute a minor part of their overall diet (Cramp and Perrins 1994a, b, e). One may instead expect predators to depredate nests in an “incidental” way (cf. Vickery et al. 1992), that is, nest predation is dependent on the time the predator spend in the patch. Also, previous studies examining the relationship between nest density and predation rates have reached different results. Some studies have found positively density-dependent predation rates (e.g. Göransson et al. 1975; Dunn 1977; Martin 1988b), while others did not find any relationship between density and predation (Norment 1993; Burke et al. 1998).

Because local bird community structure may be affected by density-dependent nest predation (Martin 1988b; Schmidt and Whelan 1999), it is important to know if and in which situations generalist predators display a functional response. For example, density-dependent nest predation may select for the coexistence of bird species that utilize different nest sites, thus decreasing the probability that nest predators form a search image for a certain nest site (Martin 1988b; Hoi and Winkler 1994).

In *paper IV*, I studied whether generalist predators (mainly corvids), displayed a functional response towards increasing densities of artificial nests. The result showed that the nests were depredated at a significantly higher rate when the density was high compared to when it was low or intermediate (Fig. 8).

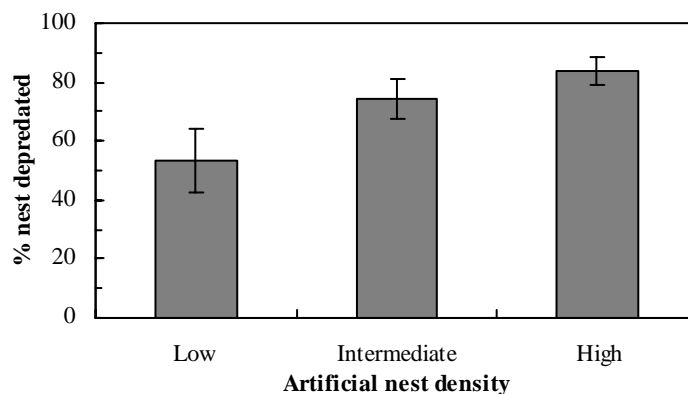


Figure 8. The proportion of the artificial nests being depredated after 15 days of exposure in relation to density of nests in the experimental 1 ha-square.

Several earlier studies testing this hypothesis with artificial nest experiments could be questioned, because they have used unnaturally high nest densities (i.e. up to 40 000 nests per ha) and too exposed nests (reviewed in Andrén 1991). Only few studies using natural nests have found a functional response of predators (Dunn 1977; Crabtree et al. 1989), which cast doubt on the generality of functional responses of generalist predators towards increasing nest densities. Furthermore, it is difficult to separate the effects of general productivity between sites that simultaneously affect nest density of prey species and densities of generalist predators, because the increased time predators spend in productive sites may increase the risk that nests are found and depredated incidentally (Vickery et al. 1992; Yanes and Suárez 1996). Thus, one has to show that predators do not respond to the same environmental factors (e.g. food abundance) as the prey species do. By using a balanced design in time and space (i.e. a Latin square design), I controlled for these spurious correlations between nest predator activity and food productivity. My results therefore suggest that generalist predators indeed may display a functional response towards increasing (artificial) nest densities placed in junipers.

In another experiment (*paper V*), I investigated in which situations one may expect to observe density-dependent nest predation. Previous studies suggested that natural nest densities of mainly finches are high in junipers early in the breeding season (Newton 1972). Later in the season, the number of natural nests initiated in deciduous shrubs increases (Newton 1972). Thus, nest densities should be low in deciduous shrubs early and high late in the season, while nest densities in junipers should display the opposite seasonal pattern (i.e. high density early and low density late in the breeding season). One may expect that the search-image of predators and the corresponding “background” predation level change in relation to changes in densities of natural nests. To test whether changing natural nest densities in the different types of shrubs affected the predators’ search-image formation and density-dependent predation, I placed artificial nests at two densities, either in junipers or in deciduous shrubs in semi-natural grasslands. I repeated the experiment one month later, with exactly the same treatment for each grassland, that is, grasslands that got high nest density in junipers in time period 1 received high density in time period 2 as well. This paired treatment allowed me to control for correlations between nest predator activity and food productivity.

The result showed that when background levels of predation risk were expected to be low (i.e., early for sloe nests and late for juniper nests; see above), predation risk on artificial nests was significantly increased by experimentally increasing the nest density (*t*-test, $t = 3.10$, $df = 37$, $p = 0.0037$; Fig. 9). This result shows that nest predation is density-dependent at low natural levels of nest densities. Interestingly, when background predation rates were expected to be high (i.e. early for juniper nests and late for sloe nests), an experimentally increased density reduced predation risk per artificial nest (*t*-test, $t = 3.10$, $df = 37$, $p = 0.043$; Fig. 9).

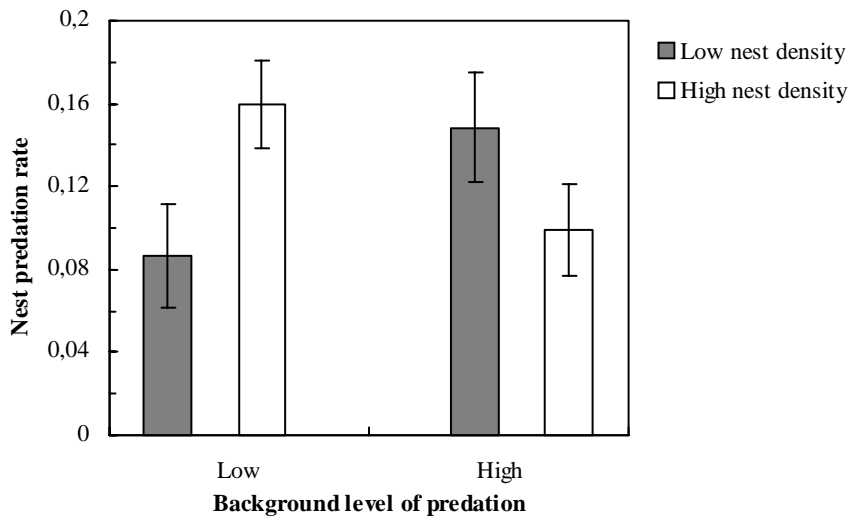


Figure 9. Nest predation rates for nests placed at low and high densities when the background level of predation was expected to be high and low, respectively, for the specific type of nest site shrub.

These results could be interpreted in terms of search-image formation of the predators. The temporal predation patterns on the artificial nests in combination with knowledge of density of natural nests in the two shrub types, suggest that the generalist corvids already had a search-image for nests in junipers early and for nests in deciduous shrubs late in the season. Consequently, most nests in junipers were depredated in the first time period, regardless of density. However, later in the season, the generalist predators had changed search-image towards nests in deciduous shrubs. Now, most nests in deciduous shrubs were depredated, regardless of density, while there was positive density-dependent predation for nests in junipers. The latter result probably reflects how the “incidentally” found juniper nest triggered a area-restricted search for more nests in the surrounding. As the probability of finding the first nest increases with nest density, my results suggest that predators may change search-image quickly in response towards increasing nest densities.

These results may explain why some previous studies did not find a relationship between nest density and predation rates. My results suggest that the existing search-image of the predators must be taken into account when density-dependent predation is investigated. Furthermore, these results support the hypothesis that density-dependent nest predation may select for the coexistence of bird species that utilize different nest sites (Martin 1988b; Hoi and Winkler 1994). Thus, local bird community structure may be affected by density-dependent nest predation caused by generalist predators (Martin 1988b; Marini 1997; Schmidt and Whelan 1999).

Conclusions

As nest predation has less serious effects on individual fitness as compared to predation on adults, it has generally been assumed that nest predation processes are of less importance than adult predation for the breeding biology of organisms. However, empirical evidence suggests that nest predation may strongly affect the ecology of short-lived passerines (and probably also other taxa). For example, studies have showed that nest predation risk may affect individual reproductive behaviours (Haskell 1994; Julliard et al. 1997; Roper and Goldstein 1997), nest site selection (Martin and Roper 1988; Götmark et al. 1995; Martin 1996), life-history evolution (Martin and Li 1992; Bosque and Bosque 1995; Martin 1995), population dynamics (Donovan et al. 1995a; Hames et al. 2001), and community structure (Martin 1988b; Marini 1997; Schmidt and Whelan 1998). Clearly, for short-lived passerine birds with high reproductive rate, the loss of clutches caused by nest predation may have large consequences for individual fitness and should thus not be underestimated as a factor affecting their ecology.

My thesis shows that irrespective of what kind of questions studied, one needs to understand both the predator and the prey perspective in order to be able to make realistic hypotheses, predictions, and tests of the effect of predation on the breeding biology of prey species. Unfortunately, this has rarely been done (e.g. Lima 2002). In the present thesis, however, the detailed knowledge of predator breeding habitat selection (i.e. magpies, *paper II, III*), and site- and density-dependent search image formation for prey (i.e. nests located in shrubs; *paper IV, V*), gave me unique opportunities to incorporate the perspective of both predators and prey. Thus, I was able to test specific hypotheses about the effect of nest predators on breeding habitat selection (*paper I, III*) and the nest site selection (*paper V*). Specifically, my results on how natural nest densities varies among deciduous and coniferous shrubs over the course of the breeding season and the corresponding changes in search-image formation of corvids (*paper IV, V*), made it possible to understand why a songbird species (i.e. the red-backed shrike) may display a seasonal change in nest site preferences (i.e. from sloe early in the season towards junipers late in the season; Söderström 2001). Furthermore, the spatial and temporal dynamics of red-backed shrikes (*paper I, III*) would have been enigmatic without knowledge about the high nest predation risk in magpie (and hooded crow) territories (*paper I*) and the habitat preferences of magpies (*paper II, III*). In addition, that breeding habitat preferences of magpies may change according to winter climate (i.e. the non-breeding period) may partly explain why my study and other studies conducted in countries with milder winters have reached different conclusions about the effects of increasing magpie populations on farmland bird population dynamics (Gooch et al. 1991; Thomson et al. 1998).

Conservation implications

Many farmland bird populations have undergone sharp population declines during the last decades. My studies suggest that nest predation may, at least in some situations, be a contributing factor to these declines. For example, the agricultural intensification, which is the single most important cause to the decline of many farmland birds (Chamberlain et al. 2000; Donald et al. 2001), have reduced and fragmented the area of suitable breeding habitats (Benton et al. 2003). This has probably increased local density of breeding birds in the few remaining patches. As my studies suggest that nest predators may form an area-restricted search-image for rewarding prey (i.e. nests of farmland birds; *paper IV, V*), higher density of nests in the remaining patches may have increased the risk of nest predation.

Furthermore, my studies (*paper IV, V*) in conjunction with other studies (e.g. Martin and Roper 1988) suggest that complex vegetation structure may reduce the risk of nest predation. Thus, in order to decrease the risk of nest predation for individual nests, conservation strategies in farmland habitats should aim at increasing vegetation heterogeneity, instead of, as today, reduce the number of potential shrubs suitable for nest sites for shrub-nesting birds (Jordbruksverket 2002). Definite rules are hard to give, but it may be important not to remove shrubs along forest-field ecotones and to leave shrubs of different species when semi-natural grasslands are restored (i.e. partly the opposite to present management recommendations given by the Swedish Board of Agriculture; Jordbruksverket 2002). Other studies suggest that several shrub-nesting farmland birds, including red-backed shrikes, occur in highest densities in grasslands when approximately 10 to 15% of the grassland area is covered by shrubs (Pärt and Söderström 1999a; Söderström 2001; Vanhinsbergh and Evans 2002).

My studies also suggest that magpies, an important predator on nests of open-nesting farmland birds, have small territories mainly located close to human settlements (*paper II*). At least red-backed shrikes, but possibly also other species, avoid to breed close to occupied magpie territories (*paper I, III*), and therefore also close to human settlements (*paper III*). An obvious strategy to decrease the probability of nest predation caused by magpies may therefore be to give higher conservation priority to grassland habitats located away from human settlements. Today, the decision of which grasslands that should receive financial aid rely only on within-grassland characteristics (i.e. mainly based on floristic and cultural heritage values; Jordbruksverket 2002). My results suggest that a landscape perspective may be beneficial for the conservation of farmland birds (see also e.g. Pärt and Söderström 1999a, b; Söderström and Pärt 2000).

Overall, my studies suggest that it is time to broaden the view on the conservation of habitats in general and of farmland semi-natural grasslands in specific. Species or habitat specific conservation strategies have so far been dominating, but my studies suggest that it may be important to also incorporate interspecies interactions (i.e. predation), because such interactions may affect breeding habitat selection patterns and population dynamics of species. For example, conservation strategies for forest birds in North America always take into account whether the

forest landscape is fragmented or not, because the degree of fragmentation may affect interspecific relationships such as nest predation and nest parasitism (Donovan et al. 1995a; Donovan et al. 1995b; Robinson et al. 1995).

Future questions and directions

Despite long days in the field and intelligent supervisors and colleagues, questions still remain to be answered (or at least explored) about the interactions between predators and prey in the farmland bird community. For example, my results have shown that red-backed shrikes may spatially avoid to breed close to breeding nest predators (*paper I, III*), but do also other species avoid nest predators or habitats associated with high risk of nest predation? As the potential breeding sites in the agricultural landscape are small and fragmented, such avoidance behaviour may be associated with a formation of breeding aggregations of con- and heterospecific birds. Thus, an obvious risk of such aggregations is that corvids may display nest site- and density-dependent nest predation (*paper IV, V*) and depredate most nests in such aggregations. This prediction give rise to several future questions to explore.

First, do bird species with similar nest sites avoid to breed in aggregations, or do they breed in aggregations but with species utilizing different nest sites (cf. Martin 1988b)? This question may be important to explore in order to understand the co-existence of prey species that share one or several predators (a relationship known as "apparent competition"; Martin 1988a; Hoi and Winkler 1994; Schmidt and Whelan 1998). Few studies have investigated whether such predator-prey interactions may affect population growth of prey, and more importantly, whether such interactions may change in relation to human alteration of habitats (e.g. Evans 2004).

Secondly, are farmland bird communities partly structured by nest-site specific search-image formation of corvids? If so, a prediction is that there is lower probability of density-dependent nest predation and thus lower potential risk of breeding in dense aggregations at sites where the vegetation complexity (i.e. number of potential nest sites in different shrub species) is high. Thus, it is possible that population growth rates of prey species are positively related to increasing vegetation complexity. Another important question may be to explore whether all predator species respond in the same way to increasing vegetation complexity regarding their search-image formation (cf. *paper IV*).

Thirdly, are the probabilities for co-existence of viable populations of both predators and prey higher in certain landscape types? A recent review of the effects of agricultural intensification on organisms inhabiting the farmland suggested that heterogeneity of landscapes (i.e. high variety of land-use categories per area) is the key to the conservation of farmland biodiversity (Benton et al. 2003). Another review suggested that the effects of predation may change depending on the degree of habitat alteration caused by humans (Evans 2004). To

explore this question, experiments must be replicated in several landscapes with different heterogeneity.

The best way to explore several of these question starts with detailed knowledge of both predator and prey and the relationship between species both within the predator guild (Polis and Holt 1992; Holt and Polis 1997) and between predators and prey (cf. Lima 2002). It also implies that ecologists working with behaviour should start to cooperate with ecologists working with populations at the landscape scale (and vice versa; cf. Sutherland 1996). Hopefully, this thesis may be a starting point for such interdisciplinary collaborations.

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Acknowledgements – Tack

Piiuh! Vilken pärs! Trots så många år som doktorand blev det stressigt på slutet. Jag antar att mina handledare tyckt att jag skulle ha börjat med skrivandet tidigare, haft kortare fältsånger, spelat mindre fotboll och ägnat mindre tid åt korridorsskvaller. Trots detta har de ställt upp helhjärtat för mig under samtliga år som doktorand på institutionen för naturvårdsbiologi. Framförallt har min huvudhandledare Tomas Pärt varit en sanslöst kunnig inspirationskälla som genom spridandet av litervis med bläck på mina försök till uppsatser förbättrat (och framförallt förkortat) lösryckta tankar till vetenskaplig text. Flera gånger har Du fått mig att växla personlighet från Pessimist-Staffan till Optimist-Staffan, genom att få mig att inse att projektet, trots svårigheter, har stor potential. På slutet, när jag jobbade i treskift för att få ihop allt, dök Du dessutom upp som en räddande ängel och bjöd på mat flera gånger. Tack Tomas! Utan Dina insatser hade det endast blivit en tumvante – eller möjligen en mycket, mycket lång halsduk med ojämna maskor! Jag hoppas verkligen att vi kan fortsätta att samarbeta i framtiden, även om det svider att en ”gammal gubbe” som Du kunde springa ifrån mig, en vältränad elitfotbollsspelare, i Oxford... (Vi hann i alla fall med bussen!)

Jag har haft förmånen att ha många biträdande handledare, vilket varit till stor hjälp eftersom de alla besitter kunskaper inom olika områden. Henrik André, biträdande handledare under mina två första år, vill jag tacka för flera goda råd rörande statistik. Pär Forslund, vad vore livet utan SAS? Massor med tack för olika råd under våra SAS-sessioner och för Dina konstruktiva kommentarer på uppsatserna! “Dozent” Åke Berg, mannen som är immun mot stress (?), har på rekordtid läst, kommenterat och gett konstruktiv kritik på alla manuskript i alla dess former, vilket verkligen förbättrat samtliga mina uppsatser. Slutligen har Bo Söderström varit ett senkommet, men efterlängtat, tillskott till handledargruppen. Bosse, stort Tack! för alla bra kommentarer på uppsatserna! Att Du dessutom är en sådan bra vän, reseledare (Tack för resorna i Uganda och Kenya!) och föredöme som forskare gör att det känns som att nu, äntligen! ska vi skriva något ihop om törnskatorna! Det var ju faktiskt Du som genom att driva törnskteprojektet mellan 1994 och 1997 satte grunden till allt! (... och jag vet att Du kommer att ta fram rödpennan och stryka ett par utropstecken, men Du är värd varenda ett!!!).

Trots mitt fanatiska intresse för fältarbete kunde jag inte göra allt själv. Utan mina fältassistenter och examensarbetsstudenter hade materialet varit väldigt tunt. Flera projekt återfinns inte i den här avhandlingen, men inget slit har varit förgäves, jag ska skriva om alla detaljer Ni noterat i fältprotokollen! Tack för Era ovärderliga insatser i fält: Niclas Backström, Alice Bjursell, Line Boberg, Pauline Englund, Sören Eriksson, Hanna och Fredrik Friberg, Henny Frid, Henrik Karlsson, Björn Nylander, Jennie Siggstedt, Ulf Svensson och Askia Wittern.

Tack också till “innepersonalen”: Göran Adelsköld, Sofia Gylje och Askia Wittern har bidragit till att GIS-kartorna fungerat. Sofia Gylje och Annika Rastén har sammanställt och datalagt mängder med fältinformation. De mer administrativa sysslorna har med stor flit tagits om hand av Jan Holmström, Sonja Jansson, Hans Jernelid, Katarina Perälä, Ulla-Britt Pettersson, Hillevi Saloniemi,

Roger Svensson och Margareta Waernulf. Tack för all Er hjälp med konton, undervisning, lokaler och anställningar! Och vad skulle jag ha kunnat göra utan hjälpen från datorkillarna? Tony Lindberg och Torbjörn Persson har klarat allt! Framförallt vill jag tacka Torbjörn, som varit med under i stort sett hela min doktorandtid, för alla handgripliga råd med trilskande program.

Jag vill också rikta ett stort tack till samtliga nuvarande och före detta doktorander vid institutionen för naturvårdsbiologi (både i Uppsala och på Grimsö). Utan Ert stöd, galna upptåg, hockeyspel, spex, innebandy, uggleturner och kamratskap hade livet varit betydligt fattigare. Tack till Er alla! Extra stort tack till Er som har stått ut med att dela rum med mig: Jonas Welander, Aina Pihlgren, Debora Arlt och Johan Wretenberg (i kronologisk ordning). Fågeldoktoranderna Debora Arlt, Ermias Azeria, Tomas Gustafson, Marcus Hedblom, Johan Samuelsson, Bo Söderström, Johan Wretenberg och Johan Åberg har hjälpt mig åtskilliga gånger i allehanda spörsmål – Tack! ”Predationsdoktoranderna” Anders Jarnemo har Bo Söderström har bidragit med många råd, diskussioner och ölkvällar – Tack!

Under en tvåmånaders vistelse på Nya Zeeland var Doug Armstrong en injektion som villigt diskuterade naturvårdsbiologi. Alla inom “Ecology Group” på Massey University förtjänar ett omnämnande för att de lät mig arbeta som “gästdoktorand” hos dem. Under Nya Zeeland-vistelsen upplät Åsa Berggren och Matt Low hela deras hus till mig. Ni lagade dessutom god mat och var villiga att diskutera skator, GIS och trevliga turistmål under många kvällar. Tack för allt, Åsa & Matt!

I huset Naturicum är det oftast en febril verksamhet. Vi har alla ett gemensamt intresse för naturvård, vilket underlättar och förgyller våra arbetsdagar. Tack till alla på NVB, CBM och ArtDatabanken för trevliga fikastunder och konstruktiva seminarier! Framförallt vill jag tacka Lennart Hansson, Lena Gustafsson och Marc-André Villard för att Ni varit villiga att diskutera allt mellan density-dependent predation och forskarutbildning.

Under min tid som doktorand har jag haft förmånen att få undervisa på många kurser på SLU. Det har varit både lärorikt och kul. Jag vill tacka mina lärarkollegor Peter Dalin, Torbjörn Ebenhard, Göran Hartman, Per Olof Hedgren, Mats Höggren, Lena Jonsell, Mattias Jonsson, Jan Lagerlöf, Bengt Olsson, Mats W. Pettersson, Tomas Pärt, Göran Thor och Olof Widenfalk för trevligt samarbete. Tack även till alla studenter som passerat revy på kurserna. Ni har bidragit med mycket inspiration och glädje!

Några vänner utanför institutionen finns fortfarande kvar, trots att arbetet tagit mycket tid under senare år. Tack för att Ni står ut med fältsånger och andra “konstigheter”! Framförallt vill jag tacka familjerna Törnqvist, Svärthagen, Grinnemo, Wittern, Norén, Grabbfestgänget, UIF-familjen och Gåvastbo jaktlag för att Ni påminner mig om att det finns ett annat liv än att titta in i en dator (eller en kikare) dagarna i ända!

Att jag blev biolog har många orsaker, men i mer vuxen ålder var det utan tvekan min entusiastiska biologilärare, Magnus Helldén på Katedralskolan i Lund, som återuppväckte min fascination för djur och natur. Tack Magnus!

Att bedriva forskning är verkligen inte billigt. Då jag inte varit fast anställd av Sveriges Lantbruksuniversitet för att bedriva studierna som ligger till grund för denna avhandling vill jag istället framhålla de stiftelser som generöst stöttat min forskning genom åren. Medel för lön har erhållits från Stiftelsen Oscar och Lili Lamms Minne (4 år) och från Centrala Studiestödsnämnden, CSN (2 år). Medel för datorinköp beviljades av Helge Ax:son Jonsons Stiftelse och institutionen för naturvårdsbiologi, SLU. Generösa resestipendier beviljades av Kungliga Skogs- och Lantbruksakademien, SLU (internationalisering av forskarutbildningen) och institutionen för naturvårdsbiologi, SLU. Ett flertal fonder stöttade fältdelen av projektet. Jag vill rikta mitt varma tack till Kungliga Skogs- och Lantbruksakademien, Verner von Heidenstams fond, Hierta-Retzius fond (bägge förvaltade av Kungliga Vetenskapsakademien), Stiftelsen Alvins fond (förvaltd av Sveriges Ornitologiska Förening och Naturvårdsverket), Elis Wides fond (förvaltd av Sveriges Ornitologiska Förening), Uddenberg-Nordingska stiftelsen, och inte minst Helge Ax:son Jonsons Stiftelse och Sven och Ebba Schwartz stiftelse.

Slutligen vill jag tacka mina närmaste. Pappa, utan Ditt stöd för min strävan att hela tiden utbilda mig hade det varit svårare att överleva exilen utanför Skåne. Inte minst ekonomiskt har det varit en stor lättnad att veta att Du finns som en "back-up"! Sorgligt nog får Mamma inte uppleva dagen då avhandlingen blir klar. Jag hoppas att Du på något sätt ändå kan känna den tacksamhet jag har för att också Du stöttade min utbildningsväg och inspirerat mig till att studera djur och natur. Desto roligare är det att Askia får vara med när avhandlingen går i hamn! Inte visste jag att en fältassistent kan vara så charmig ute på en vindpinad Laggaslätt! Tack för stödet under avhandlingsarbetet. Ich liebe Dich!