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Habitat selection and reproduction of red-backed shrikes *(Lanius collurio)* in relation to abundance of potential avian nest predators

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Zusammenfassung: Viele Untersuchungen zu Brutvogelarten in der Agrarlandschaft setzen die Abundanzen einzelner Arten in Beziehung zu bestimmten Eigenschaften (Parametern) der Landschaft. Nur wenige Studien berücksichtigen interspezifische Wechselwirkungen, wie etwa den Einfluss von Prädatoren auf die Habitatwahl. Im Allgemeinen wird angenommen, dass Beutetierarten ein Habitat mit geringem Prädationsrisiko bevorzugen, wobei allerdings die populationsbiologischen Konsequenzen für Beutetiere mit einem solchen Meidungsverhalten weitgehend unbekannt sind. Die Habitatwahl und Reproduktion des Neuntöters (*Lanius collurio)*, eines in buschreichem Grünland lebenden Singvogels (*Passeriformes)*, wurde über 7 Jahre hinweg untersucht. Dabei standen Einflüsse von potentiellen Gelegeräubern, insbesondere Corviden, im Mittelpunkt der Untersuchung. Verschiedene Experimente mit künstlichen „Neuntöternestern" ergaben, dass hauptsächlich Elstern (*Pica pica*) als Gelegeprädatoren auftreten. Daneben konnten aber auch mit geringerer Intensität Nebelkrähen (*Corvus corone cornix*) und Eichelhäher (*Garrulus glandarius*) als Nesträuber nachgewiesen werden. Die Ergebnisse der Experimente mit Kunstnestern bestätigten sich im Freiland dahingehend, dass Neuntöter bei der Brutplatzwahl die Nähe von Elstern und Nebelkrähen mieden. Darüber hinaus fand sich über die Jahre eine gegenläufige Beziehung zwischen den räumlichen Verteilungsmustern des Neuntöters und denen brütender Elstern und Nebelkrähen. Nahm etwa die Distanz zur nächsten brütenden Elster von einem zum nächsten Jahr hin ab, oder stieg die Brutdichte der Elster im Umkreis von einem km^2 an, so wurden selbst gut geeignete, traditionelle Bruthabitate verlassen. Dieses Meidungsverhalten gegenüber Rabenvögeln hat einen hohen adaptiven Wert: Neuntöter, die in größerer Entfernung zu besetzten Elstern- und Rabenkrähennestern brüten, tragen ein geringeres Prädationsrisiko als in Nachbarschaft brütende Individuen. Die vorliegenden Ergebnisse widersprechen teilweise anderen Studien, wonach die Habitatwahl von Vogelarten der Kulturlandschaft nicht von Prädatoren beeinflusst wird. Darüber hinaus legen die Ergebnisse der vorliegenden Arbeit nahe, dass interspezifische Interaktionen (z.B. Risiko der Gelegeprädation) Individuen durchaus dazu veranlassen können, in Bruthabitate minderer Qualität zu wechseln. Es ist daher möglich, dass die festgestellten Populationszunahmen bei zahlreichen generalistischen Prädatoren (z. B. Corviden) sowohl direkt (z.B. geringerer Bruterfolg durch Prädation) als auch indirekt (z.B. Produktion von Küken geringerer Qualität in suboptimalen Habitaten) zur Abnahme von Vogelarten der Agrarlandschaft beitragen. Allerdings sind hier weitere detaillierte Studien an anderen Populationen und Arten der Agrarlandschaft notwendig um genauere Angaben zu einer möglichen Populationsregulation durch Nestprädatoren machen zu können.

Summary: Many studies of farmland bird species have related abundance of species to different habitat variables, whereas few studies have incorporated the effects of predation on habitat selection. However, it is generally assumed that prey species select habitat with low risk of predation, but the consequences for prey population growth of this avoidance behaviour remain largely unknown. During seven years, I studied habitat selection and reproduction of red-backed shrikes (*Lanius collurio*), a passerine bird inhabiting shrub-rich grasslands, in relation to abundance of potential avian nest predators (i.e. corvids). Results from several experiments with artificial nests designed to mimic red-backed shrike nests suggest that magpies (*Pica pica*) are the most frequent nest predators on artificial nests. To a lesser extent also hooded crows (*Corvus corone cornix*) and jays (*Garrulus glandarius*) depredated artificial nests. The results from the artificial nest experiments were validated through the patterns of predation of real red-backed shrike nests, as these were depredated at faster rates close to nests of magpies and hooded crows than elsewhere in the landscape. Furthermore, red-backed shrikes avoided to breed in grasslands located close to magpie and hooded crow nests. In addition, at the landscape scale, between-year changes in the spatial distribution of breeding magpies and hooded crows were followed by inverse changes in the distribution of red-backed shrikes. For example, when the distance to closest magpie nest decreased, or when the number of magpie nests within 1 km^2 increased, red-backed shrikes avoided to breed in that area, despite a high abundance of suitable grasslands with a history of breeding red-backed shrikes. The behaviour of avoiding corvids was adaptive, as red-backed shrikes breeding far away from magpies and hooded crows experienced lower risk of nest predation than pairs breeding close to these corvids. My results partly contradict results of other studies, which have suggested that nest predators may not influence breeding habitat selection of farmland birds. Nevertheless, my results suggest that interspecific interactions such as nest predation may force individual birds to breed in habitats of lower quality. It is therefore possible that the observed population increases of many generalist predator species (e.g. corvids) may have contributed to the decline of farmland birds both in a direct way (i.e. low breeding success) and in an indirect way (i.e. successful nests produce fledglings of lower quality). Further studies on other populations and species are needed before the finer details of how nest predation may regulate populations of farmland birds may be fully understood.

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1 Introduction

The decline of farmland birds across western and northern Europe has received much attention during the last decade (Tucker & Heath 1994; Chamberlain et al. 2000; Donald et al. 2001). There is agreement that the population declines of farmland birds in western Europe have been caused by intensified agricultural practices, which have lead to loss and degradation of habitats (Chamberlain et al. 2000; Donald et al. 2001). In eastern and northern Europe, where some regions have experienced intensification of agricultural practices and others abandonment of agricultural land, one would expect that population trends of farmland birds should be different than in the western parts of Europe. However, the temporal pattern of the population declines of several farmland bird species in Sweden, a country with pronounced regional differences in land-use changes during the last 30 years, are similar to those observed in England (Wretenberg et al. 2006). The temporal similarities between England and Sweden suggest that other processes than changed agricultural practices may, at least partly, have contributed to the observed declines. Wretenberg et al. (2006) suggested that the similarities may be explained by farmland birds in England and Sweden sharing wintering grounds, where habitat changes may have contributed to the population declines.

Another hypothesis is that growing populations of predators have caused an increase in predation of adult and juvenile farmland birds, thereby contributing to the decline (Thomson et al. 1998; Stoate and Thomson 1999; Evans 2004). Several species of corvids, which are known to be important predators on eggs and nestlings of farmland birds, have increased in most parts of Europe at the same time as many farmland birds declined. However, few studies have tested whether the impact of corvid predation on eggs and nestlings of farmland birds could have contributed to the observed population declines. Two exceptions are the retro-perspective studies of how the increasing numbers and geographical distribution of magpies (*Pica pica*) in Great Britain have affected songbird populations (Gooch et al. 1991; Thomson et al. 1998). These studies suggested that increasing numbers of magpies did not affect numbers and reproduction of farmland birds (Gooch et al. 1991; Thomson et al. 1998). However, these studies were performed in Great Britain, where farmland birds already were suppressed by intensive agriculture. It is therefore likely that the potential negative impacts of increasing magpie numbers had relative small effect on already declining prey populations. Unfortunately, no study has investigated how increasing number of corvids affect prey species in areas with less intensified agricultural practices.

Here, I test whether increasing numbers of nest predators affect breeding habitat selection of a farmland bird, the red-backed shrike (*Lanius collurio*), in an area with relatively relaxed agricultural practices. I also investigate how the increasing populations of corvids affect reproductive success of red-backed shrikes.

2 Methods

The Study area

The study was conducted between 1997 and 2003 in a 94 km^2 area in south-central Sweden, just outside the city of Uppsala (59°48'N, 17°50'E). The study area is dominated by 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 Roos & Pärt 2004). No large changes in the land-use systems occurred over the course of this study.

The species

The magpie is an omnivorous, resident corvid. It builds a large, roofed nest in trees and shrubs, which is visible from a long distance. The breeding cycle starts early, between March and May. In most European countries the number of magpies has increased during the last 30 years. The ecology of magpies has been reviewed by Birkhead (1991).

The hooded crow (*Corvus corone cornix*) is also an omnivorous, resident corvid. It builds its open nest mainly in coniferous trees (Loman 1979). The breeding cycle starts early, between March and May. The number of hooded crows increased in most countries in the 1970s and 1980s, and thereafter levelled off. Recently, population declines have been observed in some countries (e.g. in Sweden; Svensson 2000).

The red-backed shrike is an insectivorous, long-distance migrant. Most red-backed shrikes arrive on the breeding grounds in Sweden in mid-May to early June from the wintering areas in Africa. Following arrival at the territory, a nest is built preferably in dense shrubs (mainly sloe; Söderström 2001) and the 4-6 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. Red-backed shrikes may lay a replacement clutch if the first clutch is depredated. The number of red-backed shrikes have declined dramatically in most countries, including Sweden, in recent decades (Tucker & Heath 1994; Lindström & Svensson 2002).Given the early start of the breeding cycle of the corvids, red-backed shrikes arriving from the wintering grounds have the potential to scan the landscape in order to avoid breeding corvids.

Breeding data of red-backed shrikes

Between 1997 and 2003 I visited all potential breeding sites (i.e. shrub-rich grasslands) in the study area at least every 10 days between mid-May and late July in order to find all breeding red-backed shrikes. When a red-backed shrike pair was found, I located the nest by following nest building behaviour and feeding trips. All located nests were re-visited every five days in order to record the date when the first egg was laid, the number of eggs laid, number of chicks hatched, and the breeding success of the nest (for further details, see Roos & Pärt 2004).

Artificial nest experiment

Between 1997 and 2002 I performed several experiments with artificial nests that were built in order to mimic real red-backed shrike nests. All nests were placed in thorny shrubs, that is, in nest sites used by red-backed shrike nests. Each nest was baited with two eggs of quail (*Coturnix coturnix*) and an egg made of a core of ceramic clay and a coating of plasticine. The plasticine eggs were used to identify the responsible predator by means of species-specific bill- and tooth imprints. Each plasticine egg was attached to the nest site shrub with a thin wire to prevent predators from flying away with the egg. (For more details about the artificial nest experiments, see Roos 2002; Roos & Pärt 2004).

3 Results

Artifical nest experiments

Results from several experiments with artificial nests suggest that magpies are the most frequent nest predators on artificial nests. For example, the artificial nests were depredated significantly faster when placed in territories of magpies than when placed in jackdaw territories, and almost significantly faster than when placed in hooded crow territories (Fig 1; see Roos & Pärt 2004 for more details). Furthermore, when pooling all data from the experiments between 1997 and 2002 (n = 1356 nests, of which 1020 were depredated),

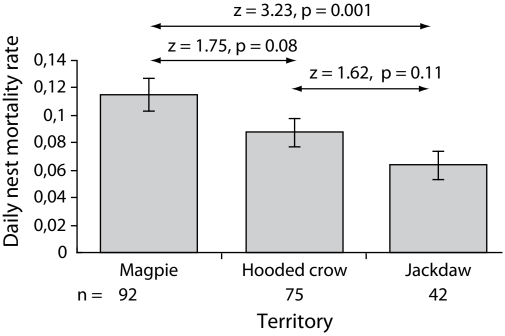

Fig. 1: Mean daily nest mortality rates (± S.E.) on artificial nests placed in magpie, hooded crow and jackdaw territories. Sample sizes are shown below S.E. bars and refer to the total number of nests. Z-values refer to tests among groups as indicated by arrows. (From Roos & Pärt 2004).

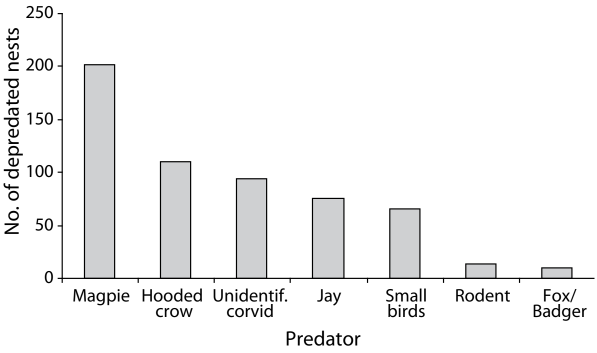

Fig. 2: Number of nests depredated by different species. In total, I used 1356 nests, of which 1020 were depredated. Of these, I was able to identify the responsible predator in 576 cases.

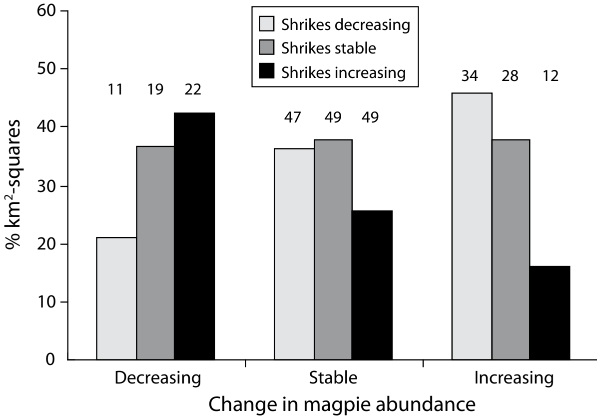

Fig. 3: The percentage of the between-year changes of red-backed shrike numbers (classified as either decreasing, stable, or increasing) in relation to between-year changes in magpie numbers (classified as either decreasing, stable, or increasing; n = 255 between-year changes). Sample size for each category is shown above each bar.

magpies were the most frequently identified predator of artificial nests (Fig. 2). To a lesser extent hooded crows and jays (*Garrulus glandarius*) also depredated artificial nests. Mammals were rarely identified as predators of artificial red-backed shrike nests (Fig. 2).

Breeding habitat selection of red-backed shrikes

At the landscape scale, red-backed shrikes were less likely to breed in km-squares with high abundance of breeding magpies. This was apparent in the reversed temporal changes of magpies and red-backed shrikes between 1997 and 2003. For example, when the number of magpies increased in a km-square, the number of red-backed shrikes most often declined in that km-square (Fig. 3). However, when the number of magpies declined in a km-square, the number of red-backed shrikes usually increased (Fig. 3).

At the scale of individual territories, territory occupancy frequency (0-3 years, monitored between 1997 and 1999) was positively related to mean distance to the closest magpie nest (ordinal logistic regression, $\chi^2 = 23.36$, df. = 1, $p < 0.0001$) (see also Roos and Pärt 2004). Furthermore, the between-year changes in magpie and hooded crow distribution were negatively correlated with the between-year changes in territory occupancy of red-backed shrikes. Thus, when magpies or hooded crows started to breed close to a previously occupied red-backed shrike territory, the red-backed shrike territory was often abandoned (Fig. 4). However, when the distance between a previously empty red-backed shrike territory and the closest magpie or hooded crow nest increased, the red-backed shrike territory was often re-colonised (Fig. 4).

Reproduction of red-backed shrikes in relation corvid abundance

The behaviour of avoiding corvids seems to be adaptive, as red-backed shrikes breeding far away from magpies and hooded crows experienced a lower risk of nest predation than pairs breeding close to these corvids (Fig. 5).

4 Discussion

Many studies of farmland bird species have related abundance of species to different habitat variables (Bradbury et al. 2000; Whittingham et al. 2005). Following this tradition, the decline of farmland birds has mainly been related to intensified agricultural practices, which have degraded the habitat (Chamberlain et al. 2000; Donald

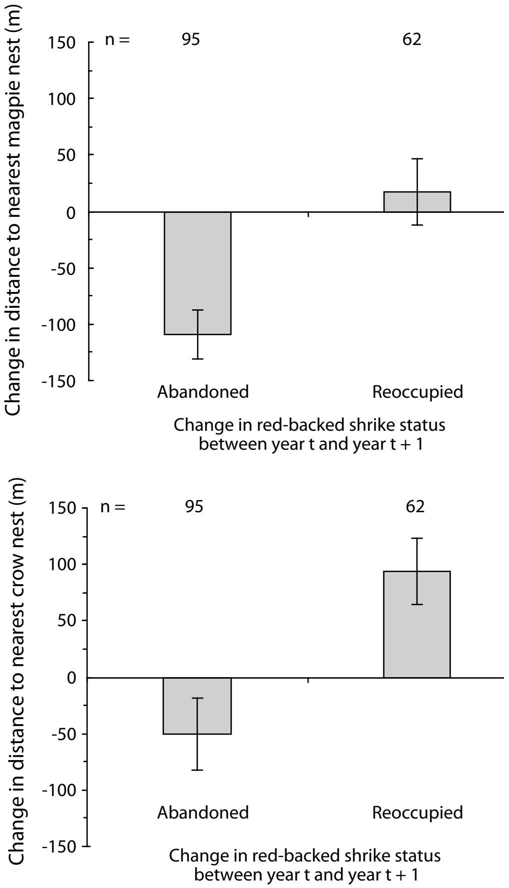

Fig. 4: Mean difference in distance (meters) between year t and year t + 1 between red-backed shrike territories and nearest nest of a) magpie and b) hooded crow, respectively, in relation to change in red-backed shrike territory occupancy between the years. Sample sizes are shown above each bar (± S.E.). 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. (From Roos & Pärt 2004).

et al. 2001). Few studies have integrated the effects of predation on habitat selection and population growth rates (but see Gooch et al. 1991; Suhonen et al. 1994; Thomson et al. 1998).

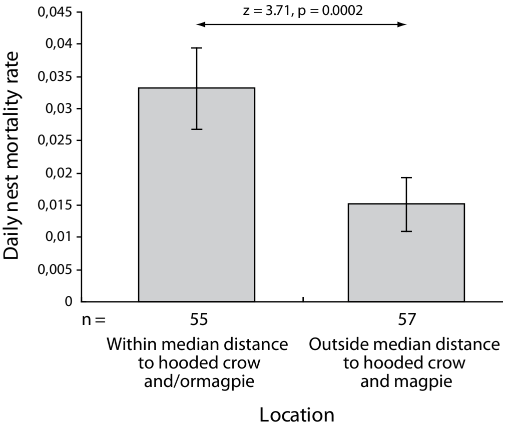

Fig. 5: Mean daily mortality rates (± S.E.) on red-backed shrike nests located within and outside, respectively, the yearly median distance between occupied red-backed shrike territories and closest hooded crow and magpie territories. Sample sizes are shown below S.E. bars and refer to the total number of nests pooled over the years 1997-1999. The z-value refers to test among groups as indicated by the arrow. (From Roos & Pärt 2004).

My results from the artificial nest experiment showed that magpies, and to a lesser extent hooded crows and jays, were the most frequently identified nest predators of artificial nests (Figs 1 and 2). Predation rates obtained from artificial nests should not be translated into actual predation rates of real nests for several reasons (e.g. Weidinger 2001; Pärt & Wretenberg 2002). For example, humans may not place the artificial nest in sites that birds would have chosen, there is no incubating bird in artificial nests, and quail eggs could be too large for small predators to open (Roper 1992). Despite these potential drawbacks, artificial nests are valuable tools for obtaining data on the identity of predators (but see Larivière 1999) and spatial variation in nest predation risk. My results showed that nest predation risk on artificial nests was higher close to magpie and hooded crow territories than elsewhere in the landscape (Fig. 1). This result was validated through the patterns of nest predation risk of real red-backed shrike nests (Fig. 5). In addition, the breeding habitat selection of red-backed shrikes suggested that I correctly identified the most important predators, because red-backed shrikes avoided breeding in grasslands located close to magpie and hooded crow nests.

Furthermore, my results suggested that the breeding habitat selection of red-backed shrikes was strongly influenced by the population dynamics of the two most important nest predators (i.e. magpies and hooded crows; Fig. 4). Thus, my findings partly contradict the results of other studies, which have suggested that nest predators do not influence the abundance or reproductive success of farmland birds (Gooch et al. 1991; Thomson et al. 1997). Yet, the behaviour of avoiding nest predators may be more common than previously thought, as both neotropical migrants and European raptors breed at higher densities at sites with a low abundance of their nest predators (Sergio et al. 2003; Fontaine & Martin 2006).

There are several non-exclusive explanations to why only some species seem to avoid their nest predators spatially. First, only species that experience a high risk of having their nests depredated should spend time and energy on searching for a breeding site with a lower predation risk. Second, single-brooded species or species with a low ability to lay a replacement clutch following depredation should be more selective, and avoid predators more efficiently than multi-brooded species (cf. Martin 1995). Third, in order to avoid a predator, the prey must be able to discriminate between sites with and without the predator. Thus, the predator must be conspicuous in order to be avoided. Alternatively, sites with the predator must be easily distinguishable through reliable cues, such as a conspicuous predator nest or the presence of another more conspicuous species with similar habitat requirements as the predator. Fourth, the prey species must start to breed later than the predator. This is because when the predator has started to breed it is restricted spatially through territorial behaviour, nest defence and caring of the chicks (i.e. similar to the theory of "central place foraging"; Carlson 1985). Thus, late-arriving migratory species may have an advantage over early-breeding resident species when it comes to selecting breeding sites with a low abundance of nest predators. Finally, for prey species to avoid nest predators efficiently, the most important nest predators should have small foraging territories with easily identified boundaries. The interspecific relationship between red-backed shrikes and magpies clearly fulfils several of these criteria. For example, red-backed shrikes have a high risk of nest predation (i.e. ca. 40-50% of all breeding attempts are being depredated) and it is a single-brooded species (albeit with high probability of laying a replacement clutch; personal observation). In addition, the magpie is a conspicuous bird, it builds a large nest, and it has a small territory (i.e. 3-9 ha; Birkhead 1991). Finally the red-backed shrike arrives after the magpies have started to breed.

To conclude, this study of red-backed shrikes and their nest predators suggests that perceived nest predation risk caused by increased number of corvids might force individual red-backed shrikes away from otherwise suitable habitats. In addition, the breeding success of red-backed shrikes was lower close to than away from breeding magpies and hooded crows (Roos 2002; Roos & Pärt 2004). Given that several other farmland bird species also have life-history traits that make them vulnerable to increased nest predation rates (i.e. single-brooded and/or have a low ability to lay a replacement clutch), increasing numbers of corvids may potentially affect the population dynamics of these farmland birds. It is therefore possible that the observed population increases of many generalist predator species (e.g. corvids) may have contributed to the decline of farmland birds both directly (i.e. low breeding success; Fig 5) and in an indirect way (i.e. successful nests produce fledglings of lower quality). Further studies on other populations and species are needed before the finer details of how nest predation may regulate populations of farmland birds can be revealed.

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