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► **To cite this version:**

Bo Söderström, Henrik Karlsson. Increased reproductive performance of Red-backed Shrikes in forest clear-cuts. *Journal für Ornithologie = Journal of Ornithology*, 2010, 152 (2), pp.313-318. 10.1007/s10336-010-0587-8 . hal-00629470

HAL Id: hal-00629470

<https://hal.science/hal-00629470>

Submitted on 6 Oct 2011

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SHORT NOTE

Increased reproductive performance of red-backed shrikes *Lanius collurio* in forest clear-cuts

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Word count: 3200 (excluding references), 1 table, 1 figure

Abstract In Sweden, the centre of distribution of the nationally red-listed red-backed shrike *Lanius collurio* has shifted from farmland landscapes to forest landscapes from the 1960s until today. In this study, reproductive performance of red-backed shrikes breeding in grasslands in a 75-km² farmland landscape and clear-cuts in a 75-km² forest landscape were compared during 1994–1995. During 2003, order of settlement and reproductive performance as well as food abundance and nest predator abundance were assessed in a 3-km² area in each landscape type. The average number of fledglings was significantly higher in clear-cuts than in grasslands. Furthermore, post-fledgling survival and the probability of replacement clutches following nest failure were likely to be higher in clear-cuts than in grasslands due to the significantly earlier arrival date to clear-cuts. These differences are likely explained by a lower nest predation in clear-cuts compared to grasslands. Today, forest clear-cuts represent the primary habitat of the red-backed shrike in Sweden, and likely also elsewhere in the boreal parts of northern Europe.

Keywords Breeding biology, Red-backed Shrike, Grasslands, Clear-cuts, Sources, Sinks

Zusammenfassung

Erhöhte Fortpflanzungsleistung von Neuntöttern *Lanius collurio* in Wald-Kahlschlagsflächen

In Schweden hat sich das Verbreitungszentrum des in der nationalen Roten Liste geführten Neuntötters *Lanius collurio* von den 1960er Jahren bis heute von Ackerlandschaften zu Waldlandschaften hin verschoben. In dieser Studie haben wir die Fortpflanzungsleistung von Neuntöttern, die in Grasflächen in einer 75 km² großen Ackerlandschaft brüteten, und Neuntöttern, die in Kahlschlagsflächen in einer 75 km² großen Waldlandschaft brüteten, in den Jahren 1994 und 1995 verglichen. Im Jahre 2003 wurden die Reihenfolge der Ansiedlung und die Fortpflanzungsleistung sowie die Nahrungs- und Nesträuberabundanz in einer 3 km² großen Fläche in beiden Landschaftstypen abgeschätzt. Die durchschnittliche Anzahl

ausgeflogener Jungvögel war in Kahlschlagsflächen signifikant höher als in Grasflächen. Außerdem waren das Überleben nach dem Ausfliegen und die Wahrscheinlichkeit von Ersatzgelegen nach Nestverlust in Kahlschlagsflächen aufgrund des signifikant früheren Ankunftsdatums wahrscheinlich höher als in Grasflächen. Diese Unterschiede können wahrscheinlich mit einer niedrigeren Nestprädationsrate in Kahlschlagsflächen verglichen mit Grasflächen erklärt werden. Heutzutage stellen Kahlschlagsflächen das Primärhabitat des Neuntöters in Schweden und vermutlich auch anderswo in den Borealregionen Nordeuropas dar.

Introduction

The environmental prerequisites for breeding red-backed shrikes *Lanius collurio* have been extensively studied (e.g., Durango 1954; Olsson 1995a; Söderström 2001; Titeux et al. 2007; Brambilla et al. 2009). They require open, sun-exposed areas for hunting, free-standing foraging perches and thick shrubs for nesting. These features occur in semi-natural grasslands, fallow land, field-forest edges and roadside verges in farmland landscapes, but also in recent clear-cuts, young spruce plantations and along forest edges in forest landscapes, which may act as a suitable breeding habitat for early-successional bird species, otherwise traditionally found in farmland grasslands (Pärt and Söderström 1999; Söderström 2009). Today, several farmland bird species in Sweden have a substantial part of their population in open habitats in forest landscapes, for example, yellowhammer *Emberiza citrinella*, whinchat *Saxicola rubetra* and wryneck *Jynx torquilla* (Ottvall et al. 2007; Söderström 2004, 2009).

The first records of breeding red-backed shrikes in clear-cuts in Sweden are from the 1960s (Svensson et al. 1999). Today, 69% of all red-backed shrikes in Sweden occur on land classified as forest or clear-cut, while only 28% occur on farmland or grassland (Ottvall et al. 2009). The Swedish population of red-backed shrikes has decreased by 30–49% since 1975 (Ottvall et al. 2008), and the population trend since 1998 declined slightly more in farmland than in non-farmland landscapes (Ottvall et al. 2007, 2008).

Agricultural practices have changed rapidly since 1900 and once important traditional farmland habitats have declined in area while arable fields and coniferous plantations have become prevalent in large-scale, monotonous farmland landscapes (Robertson et al. 1990). The area of semi-natural grasslands in Sweden has decreased from about 15 000 km² in the early 1900s to 4 630 km² one hundred years later (Statistics Sweden 2008). Forest clear-cutting is a relatively new practice in Sweden. In the early 1900s, most of the logging was selective and stands were naturally regenerated (Axelsson 2001). In 1950, selective logging

was forbidden on state forests and the use of clear-cut harvesting and regeneration through planting of seedlings increased dramatically in Sweden (Ebeling 1959). Today, roughly half of Sweden is covered by productive forest land (226 520 km²) and clear-cut harvesting is annually practiced on about 1% of all productive forest land (Statistics Sweden 2008). Thus, clear-cut harvesting is *annually* practised on a forest area that roughly equals the *total* amount of grasslands of high biological value in Sweden.

Here, the reproductive performance of red-backed shrikes breeding in forest clear-cuts and farmland grasslands were compared during three years. Causal factors affecting reproductive output were estimated using surveys of food abundance and potential nest predators. The main hypothesis was that the reproductive performance was higher in forest clear-cuts than in farmland grasslands. If red-backed shrikes are able to assess differences in nest predation risk, as suggested by Roos and Pärt (2004), it was anticipated that red-backed shrikes should settle earlier in forest clear-cuts than in farmland grasslands.

Materials and Methods

The study area is situated east of the city of Uppsala (59° 52'N, 17° 38'E) in the eastern part of south-central Sweden. The landscape is a mosaic of forest and farmland within the hemiboreal vegetation zone (Ahti et al. 1968). The forest area was about 75 km² and mainly composed of mixed coniferous-deciduous forests with numerous clear-cuts and forest stands of varying age. Recently cut and older clear-cuts (<3 and >20 years since harvest, respectively) are unsuitable as breeding habitat for red-backed shrikes (Hoflin 1994). We therefore only surveyed clear-cuts between 3 and 20 years of age (n = 67, min–max area = 1–47 ha). Clear-cuts were selected using recent aerial photographs (1:10 000) and information from the stand database of Holmen Skog. The majority of the clear-cuts were planted with spruce. The farmland area was about 75 km² and consisted of 80% arable fields interspersed

with small woods (11%) and semi-natural grasslands (9%) such as grazed pastures, leys and small grass strips between forest and arable fields. All grasslands within the farmland area were surveyed for breeding red-backed shrikes ($n = 131$, min–max area = 1–25 ha).

In 1994 and 1995, all 67 forest clear-cuts and 131 farmland grasslands within the 150 km² area were surveyed once a week – between 15 May and 15 July – for breeding Red-backed Shrikes. In 2003, we performed daily surveys between 13 May and 15 July and, since time was a restraining factor, a smaller 3-km² area in each landscape was used. The selected sub-areas hosted the highest breeding densities (15 to 30 pairs each year) within each landscape in 1994–95. Seventeen grasslands of a total area of 110 ha were surveyed in the farmland area, and seven clear-cuts of a total area of 50 ha in the forest area. The survey route was changed every day in order to visit all sites at different times. In addition to visually searching (using binoculars) and listening for calls, we used a portable CD-player with song, contact and warning calls from a male shrike. The majority of newly arrived males responded immediately to the recorded song by either singing or flying up to the nearest look-out (females responded by flying up to a look-out). To minimize disturbance, we immediately stopped playing if we recorded a male and/or a female.

The search for nests was initiated when the male started to deliver food to the incubating female. Searching for nests was only performed when no potential nest predators were in sight and during fair weather. No search attempt lasted longer than 8 minutes and at least 1 day between each attempt was required to minimize disturbance. Red-backed shrikes are especially sensitive to disturbance during nest building, egg-laying and early incubation (Jakober and Stauber 1987; Olsson 1995a; Tryjanowski and Kuzniak 1999). Therefore, as soon as we located the nest site and determined clutch size, we did not re-visit the nest until the calculated hatching date. Throughout the study, we found all active red-backed shrike nests in territories.

The date of clutch initiation was recorded by direct observation or estimated by back-calculation assuming that one egg was laid per day and that incubation lasted 14 days from the penultimate egg (Söderström 2001). The age of nestlings was based on known hatching date or by estimating the skin colour and degree of feather development of nestlings (Olsson 1995a). Pairs that succeeded to produce at least one fledgling were recorded as successful. When complete clutches or broods prematurely disappeared, they were recorded as depredated. Nestlings vacate the nest when 14–16 days old, but they are able to jump out of the nest and hide a few days earlier to avoid potential nest predators. Therefore, we carefully counted nestlings 10–12 days after hatching. We made a final visit to check the nest site and the breeding territory for fledglings and feeding parents a few days after calculated the fledging date, carefully listening for the characteristic sounds from begging chicks.

Large insects such as bees (family Apidae), grasshoppers and crickets (family Acrididae) and beetles (order Coleoptera) comprise the main food of red-backed shrikes (Cramp and Perrins 1993). We used two techniques to compare the numbers of insects available to shrikes. Pitfall traps were used to collect ground-living insects, especially carabids (Koivula et al. 2002). The traps were made of yellow plastic and with steep sloping sides (depth 4 cm, sides 18 cm). The reflection of the yellow colour is known to attract pollinators (Calabuig 2000), particularly hoverflies (family Syrphidae) and bees (family Apidae). Forty traps in each habitat were used in insect surveys between 28 May and 9 June 2003. Traps were divided into ten sets of traps with four in each set. The following criteria had to be met for the placement of traps: (1) no cattle should have access to traps in grasslands, (2) location in an active or potential red-backed shrike breeding habitat, (3) open area with grass height 10–30 cm and at least one potential hunting perch 1.5–3 m high < 15 m from the closest trap, (4) > 200 m between sets to achieve independence. The four traps were located in the corners of a 5 x 5 m square, where the first trap was located at random. Traps were dug into the ground so that the edge was level with the ground, and filled to 70% with

water. A small amount of synthetic, non-aromatic washing-up liquid was added to reduce surface tension. Traps were emptied every second day and all captures were identified to the taxonomic level of order.

Line transect surveys of bees and bumble-bees were used as a complement to pitfall traps. Transects started in the centre of the set of trap sets and were 100 m long. We slowly walked (1 km per hour) the transects and recorded specimens within 2 m on each side of the transect. Each transect was surveyed three times from the end of June to mid-July. All transects were visited the same day and surveys were only conducted in fair weather. In statistical analyses we used the total number of specimens collected using both methods. Analyses were thus based on 40 pitfall traps emptied 6 times and 10 line transects surveyed 3 times in each habitat. Only arthropod orders, which were important as food for adults or nestlings, were included in the analyses.

Potential avian nest predators seen or heard within 50 m from an active red-backed shrike territory were recorded together with the time spent in each site from mid-May to mid-July 2003. Nest predator species included magpie *Pica pica*, hooded crow *Corvus corone cornix*, and jay *Garrulus glandarius* (Söderström 2001; Roos and Pärt 2004). Mammalian nest predators are not major predators on red-backed shrike nests in the study area (Söderström et al. 1998).

Statistical analyses were performed using SPSS 11.5 and JMP 3.2.6 statistical packages. We tested all data for normality and homogeneity of variances. Dependent variables were transformed using the natural logarithm prior to analyses, but the resulting figures of ANOVAs are shown using non-transformed data. When the assumptions of parametric tests not were met we used non-parametric tests (i.e. Mann-Whitney tests of arrival date, predator and food abundance in 2003). *P*-values refer to two-tailed probabilities.

Results

The arrival date of males did not differ significantly between habitat types. However, females arrived almost five days earlier in clear-cuts than in grasslands (Table 1). Male and female red-backed shrikes in clear-cuts spent four days less between pair formation and the initiation of egg-laying. Consequently, females in clear-cuts laid the first egg in clutches significantly earlier than in grasslands (Table 1), and this pattern was consistent across years (Fig. 1a).

There was no significant difference in clutch size between habitat types (Fig. 1b), nor did the number of fledglings from successful nesting attempts differ between habitat types, when accounting for the effect of laying date on reproductive performance (i.e. statistically removing the effect using residual analyses). Both clutch size and number of successful fledglings from first breeding attempts decreased significantly as the breeding season progressed (linear regression; clutch size, $y = 6.62 - 0.04x$; $r^2 = 0.14$, $P < 0.001$; number of fledglings, $y = 5.93 - 0.03x$; $r^2 = 0.05$, $P < 0.017$ when excluding depredated nests).

Predation events on nest contents were twice as common in grasslands (28 of 103 nests depredated, 27%) compared to clear-cuts (7 of 52 nests depredated, 13%), which constituted a marginally significant difference between habitats ($\chi^2 = 3.72$, $P = 0.046$). When including both successful and predated nests in the analyses, clear-cut nesting attempts produced significantly more fledglings than in grasslands (Fig. 1c).

A total of over 13 000 arthropods were collected using the two census techniques. The most abundant arthropod orders were spiders *Araneae* (41 % of total abundance), ants *Formicidae* (22%), flies *Diptera* (14%) and beetles *Coleoptera* (11%). Among prey normally consumed by adult shrikes, only Orthopterans were significantly more abundant on clear-cuts than in grasslands (Mann Whitney test, $Z = 2.38$, $P = 0.017$; *Coleoptera* and *Hymenoptera* $P > 0.25$). Soft-bodied insects – which red-backed shrike parents hunt for nestling food – were in contrast significantly more common in grasslands than on clear-cuts (*Araneae* $Z = -2.80$, $P = 0.005$, *Lepidoptera* larvae $Z = -2.21$, $P = 0.027$, *Diptera* $Z = -3.78$, $P < 0.001$).

During the breeding season of 2003, a total of 111 and 90 hours were spent in territories of red-backed shrikes in clear-cuts and in grasslands, respectively. The dominant predators on eggs and nestlings of red-backed shrikes – magpie, hooded crow and jay – were observed three times more often in grasslands than in clear-cuts (0.42 ± 0.18 vs. 0.13 ± 0.05 observations hour⁻¹; MannWhitney test, $Z = 2.15$, $P = 0.031$).

Discussion

This study showed that females arrived five days earlier to clear-cuts, and spent four days less between arrival and commencement of egg laying, than in grasslands. Males probably also arrived earlier to clear-cuts since six males were observed already on the first survey date compared to only one male in grasslands. No female was observed on the first survey date, and females typically arrive a few days later than males to the breeding grounds (Carlson 1989). Tryjanowski and Sparks (2001) suggested a strong negative link between first arrival date and population size, given that observation probability and song activity are increased in high-density populations. Population density in clear-cuts was three times higher than in grasslands (in 2003: 0.28 versus 0.09 pairs/ha), but observation probability was likely to be very high in both habitats (daily surveys using playback). Furthermore, there was a strong correlation between the date of first egg and arrival date of females ($r = 0.62$, $P = 0.002$), which indicates that there was no detection bias.

The earlier settlement of females, and probably also males, in clear-cuts may suggest a preference for this habitat over grasslands. Birds returning first to breeding areas are expected to settle in preferred habitats, while less preferred habitats will be occupied later or not at all (Fretwell and Lucas 1970). If there were no differences in habitat quality, red-backed shrikes arriving from their winter quarters would be expected to settle earlier in the grassland area located 15 km south of the clear-cut area. An alternative explanation to the observed

settlement patterns is a scarcity of alternative habitats in the forest landscape, which may have caused a higher degree of site fidelity in clear-cuts (cp. Tryjanowski et al. 2007). The total amount of potential breeding habitats in the forest landscape was less than half than that in the farmland landscape. Unfortunately, no assessments of breeding dispersal have been possible to make due to very low return rates of colour-ringed individuals (Söderström and Roos, unpublished).

The average number of fledglings was higher in clear-cuts than in grasslands; furthermore, post-fledgling survival and the probability of a second – or even a third – replacement clutch following nest failure is likely to be higher in clear-cuts due to earlier breeding (Söderström 2001, Müller et al. 2005). Females initiated egg-laying 4 (1994), 2.5 (1995) and 7.5 (2003) days earlier in clear-cuts than in grasslands. This habitat-specific difference was to a large part explained by the fact that red-backed shrikes spent four days less between pair formation and clutch initiation on clear-cuts than in grasslands (Table 1).

Food limitation may explain why shrikes in clear-cuts spent less time between arrival and clutch initiation. This study found no significant differences between habitat types in the abundance of invertebrate prey important for foraging adult red-backed shrikes during May (i.e. beetles and bees; Olsson 1995b). Similarly, Carlson (1989) showed that the experimental provision of impaled mealworms to male red-backed shrikes, which in turn were courtship fed their mates, did not affect the number of days before commencing laying eggs.

An alternative explanation is that older more experienced and/or higher-quality individuals arrive first, and might preferentially settle in forest clear-cuts. Higher-quality males are more attractive to females and will form pairs earlier than lower-quality males. Furthermore, the red-backed shrike is an aggressive species (Tryjanowski and Golawski 2004), and more experienced and/or higher-quality individuals may easier deter a potential nest predator from attempting to eat eggs or nestlings.

Nest predation has repeatedly been shown to be the major cause of reproductive failure in the red-backed shrike (e.g. Söderström 2001, Müller et al. 2005, Titeux et al. 2007). Earlier studies have demonstrated that the spatial distribution of two major nest predators – magpie and hooded crow – influenced habitat selection of the red-backed shrike (Roos and Pärt 2004, see also Söderström et al. 1998, Söderström 2001, Müller et al. 2005). Our results showed that significantly more individuals of these two corvid species and European jays were encountered in grasslands than in clear-cuts, and significantly more nests were depredated in the former habitat. Similarly, Roos (2002) found higher predation levels on shrub nests in grasslands than in clearcuts in the same general area as this study was conducted. Red-backed shrike may have used visual cues for an increased nest predation risk prior to breeding (Roos and Pärt 2004), although another study found no evidence that red-backed shrikes were able to correctly assess predation risk when they settle after migration (Pasinelli et al. 2007). Increasing vegetative cover, and hence nest concealment, in clear-cuts where spruce saplings are evenly spread across the regeneration area, likely contributed to the significantly lower predation risk in clear-cuts. Grassland pairs nested in spatially aggregated sloe or juniper shrubs that typically covered less than 10 % of the grassland area. Thus, for visually-searching bird predators, red-backed shrike nests were likely more conspicuous in grasslands. Roos (1997) showed that the predation risk of red-backed shrike nests in grasslands was significantly lower with a high abundance of potential nest site shrubs within a 10 m radius from the nest site. In conclusion, habitat-specific differences in reproductive performance are likely explained by a combination of safer nest sites and depressed predator abundances in clear-cuts compared to grasslands.

The centre of red-backed shrike distribution in Sweden has gradually shifted from farmland to forest landscapes from the 1960s until today. During this period, the practice of clear-cut harvesting has increased dramatically, whereas a 30% decrease in the area of semi-

natural pastures has occurred by conversion of pastures to conifer plantations or arable fields (Pärt and Söderström 1999). Today, breeding habitats are at least four times as common in forest than in farmland landscapes. Data on a national scale imply steeper population declines in farmland, than in non-farmland, landscapes (Ottvall et al. 2008), which suggests that farmland habitats may act as population sinks. Forest clear-cuts represent the primary habitat of the red-backed shrike in Sweden, and likely also elsewhere in the boreal parts of northern Europe where a similar change in land-use has occurred after the Second World War (e.g. Finland and the Baltic states).

Acknowledgements

We wish to express thanks to the Master of Science students Maria Hoflin, Sören Eriksson and Pär Karlsson who performed much of the field work. The Royal Academy of Swedish Sciences and SLU financed this study.

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Exceptionally high breeding-site fidelity in the Red-backed Shrike *Lanius collurio*.

Ardea 95:316–320

Table 1. Phenology of red-backed shrike breeding activities in forest clear-cuts and farmland grasslands in 2003.

	Forest	Farmland	Z^2	P
	clear-cuts ¹ (n)	grasslands ¹ (n)		
Male arrival	16.3 ± 1.0 (16)	18.9 ± 1.6 (14)	1.32	0.18
Female arrival (pair formation)	17.5 ± 0.8 (15)	22.3 ± 1.7 (12)	2.21	0.027
No. days from female arrival to first egg	8.6 ± 0.6 (14)	12.6 ± 1.6 (7)	2.30	0.021
Date of first egg	26.1 ± 1.1 (14)	33.6 ± 1.1 (10)	3.48	<0.001

¹ Julian dates are presented (1 = 1 May, 31 = 31 May etc).

² Z-values refer to Mann-Whitney U-tests.

Figure legends

Fig. 1. Average (a) date of clutch initiation, (b) clutch size and (c) number of fledglings of red-backed shrikes breeding in farmland grasslands and forest clear-cuts. The interaction “habitat type x year” was non-significant in all ANOVAs ($P > 0.083$). Sample sizes are shown on top of bars and error bars denote 95% confidence intervals.

(a) clutch initiation: habitat type ($F_{1, 149} = 14.61, P < 0.001$), year ($F_{2, 149} = 15.73, P < 0.001$).

(b) clutch size: habitat type ($F_{1, 148} = 0.13, P = 0.91$), year ($F_{2, 148} = 0.33, P = 0.77$).

(c) number of fledglings: habitat type ($F_{1, 148} = 4.51, P = 0.035$), year ($F_{2, 149} = 2.20, P = 0.11$).

