

Season-dependent diet composition and habitat use of Red-backed Shrikes *Lanius collurio* in SW Finland

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The local habitat use and diet of Red-backed Shrikes were studied in a main study area of 1.4 km² in SW Finland. Based on pellets (n = 688), *Carabidae* beetles constituted 29.1% of the prey (n = 3,388) and *Apidae* (especially bumble bees), 18.3%. The rest was mainly representative of other beetle families (21.6%), other hymenopterons (12.6%) and *Orthoptera* (8.3%). In the diet, beetles decreased whereas *Apidae* and *Orthoptera* increased as the season progressed, reflecting alterations in abundance and vegetation-dependent availability of these prey. Breeding shrikes were found in natural unmowed meadows (n = 14 pairs) and in areas created by forestry (n = 11). The start of incubation (average June 9th), territory size, breeding success (3.4–3.7 large nestlings/pair) and the abundance and percentage of diet of the main prey were similar in both habitats. However, in the post-breeding season, shrikes avoided habitats created by forestry but showed a particular preference for meadows. This was, in part, related to a high abundance of *Orthoptera* insects in this habitat type, which was supported by diet analyses. In addition, factors minimizing the risk of predation, i.e. the openness of meadows, may have contributed to the observed habitat selection. The role of suitable post-breeding habitats is discussed based on the observed population decline of Red-backed Shrikes.



1. Introduction

The Red-backed Shrike (*Lanius collurio*) is a long-distance migratory passerine breeding in most parts of Europe. The majority of the population breeds in semi-open habitats created or maintained by human activities (Lefranc & Worfolk 1997). In common with many other shrike species, the Red-backed Shrike population has declined due to reasons not fully established (Lefranc & Worfolk 1997, Väisänen *et al.* 1998). Possible causes are reduced insect abundance due to wetter climate or use of pesticides, adverse changes in non-breeding areas, as well as habitat loss (reviewed in Lefranc & Worfolk 1997).

However, it is clear that the species has suffered from the gradual change of agricultural landscapes toward larger monocultures (Lefranc & Worfolk 1997). Red-backed Shrikes forage mainly on large insects of the orders *Coleoptera*, *Hymenoptera* and *Orthoptera* (Cramp & Perrins 1993), and the habitat selection is strongly influenced by the availability of these prey species. Traditionally, the species has favoured shrubby cattle-grazed pastures or other habitats with sustained low vegetation allowing good visibility of ground-living beetles (Brandl *et al.* 1986, Olsson 1995a). Pastures have declined dramatically in northern Europe (Pitkänen & Tiainen 2000), but this habitat loss has been compensated for by cleared or

thinned forests created by modern forestry (Olsson 1995a, Väisänen *et al.* 1998). These habitats resemble forests severely affected by storms or fires, i.e. the likely breeding grounds for shrikes in Neolithic times (Lefranc & Worfolk 1997).

In Finland, the Red-backed Shrike breeding season is short, spring migration culminates in the last third of May and autumn migration in the second third of August (Lehikoinen *et al.* 2003). The highest breeding density (5.8 pairs/km²) is found in forest clear cuts in the southern part of the country (Väisänen *et al.* 1998). In the present study area (SW Finland), the quality of forestry-created habitats (thinned pine forests) and natural meadows were compared based on breeding parameters. However, avian habitat use is often dependent on seasonal preferences. The breeding habitat is selected based on nesting requirements, whereas the non-breeding habitat use is strongly associated with food abundance (Block & Brennan 1993). Hence, breeding and post-breeding habitat preferences of Red-backed Shrikes were analysed with respect to diet composition, foraging behaviour and prey abundance. The role of post-breeding habitat is discussed with respect to recent population decline.

2. Material and methods

The study was conducted on Ålö island in Parainen, coastal SW Finland (60°17'N, 22°10'E), in 1993 and 1997–2002. Shrikes were studied intensively during the breeding season (defined as May–July) and post-breeding season (defined as the first half of August) in a main area of 1.4 km². Areas affected by forestry were extensively thinned old pine (*Pinus sylvestris*) forests (in total 0.12 km²). The surface vegetation in these areas varied from rocks covered only by moss or lichen to high (up to 1.2 m) dense vegetation of various species but especially raspberry (*Rubus idaeus*). The remaining forests (0.83 km²) were intact coniferous-dominating forests unsuitable for shrikes. The open fields were mainly used for agricultural production (wheat, oats, potatoes or sugar beet, in total, 0.4 km²), but a few intact natural meadows (0.05 km²) with patches of small trees or shrubs were also present during all seasons studied. The meadows were covered by uniform vege-

tation, consisting mainly of grass (*Poaceae* sp.). The grass height increased steadily during the season, from 10–30 cm at the end of May to 80–120 cm in August.

I used data on breeding success, time of incubation commencement, territory size, prey abundance, diet and foraging behaviour to assess selection and quality of suitable habitats. Red-backed Shrike pairs of which at least one of the sexes was observed collecting nest material were considered as commenced breedings. In 1997–2001, the breeding success was determined at the stage of large nestlings (age about 10 days) (n = 25 started breedings). Since visits to the nest may affect breeding success (Tryjanowski & Kuźniak 1999), no nests were controlled before evidence of nestlings was observed (female bringing food to the nest). The date of incubation start was estimated from the nestling age (determined with the aid of photographs in Olsson 1995b) and the average incubation time (15 days, Lefranc & Worfolk 1997).

Based on the highly territorial behaviour characteristic of the species (Olsson 1995a, Lefranc & Worfolk 1997), the territory size was determined as the area covered by the perches used by the male during the incubation and nestling phase. The foraging behaviour was studied visually with binoculars. Three types of hunting performances, drop hunting, aerial pursuits or catching of prey from tree branches or bushes were recorded. Drop hunting included diving from perches onto prey within the vegetation or on the ground. Hunting activity was calculated as performances/hour.

To assess the abundance of the main prey, surface-dwelling beetles were counted by pitfall traps and the number of bumble bees and grasshoppers/crickets (Order *Orthoptera*) by visual observation. The prey abundance was determined in one meadow-type territory (in 1999 and 2001) and in one forest-type territory (in 2000 and 2001). In principal, the pitfall traps were constructed according to Cooper and Whitmore (1990), with the exception that no preservative was added. The trap surface area was 88 cm²/trap. The traps (n = 2–4/territory) were placed within the territory close to the most frequently used perches but not closer than 10 m to each other. Collection was performed during periods of 15–36 hours (mean 24.4, SD = 7.14). Captured beetles were determined to the taxonomic level of family (according to Douwes *et*



Fig. 1. A typical Red-backed Shrike territory in a thinned old pine forest located close to an arable field (upper photograph) and a meadow used by Red-backed Shrikes during the breeding and post-breeding phase.

al. 1997). Since the prey size of nestlings are chiefly below 10 mm and adult individuals prefer larger prey (Hernandez 1993), the captured beetles were classified into two size groups, < 10 mm and \geq 10 mm. An abundance index was calculated as number of beetles/24 h per trap. Visual observation was used to determine the abundance of bumble bees and adult *Orthoptera*. Counting was performed along a fixed 200 m route through each territory, in total 5–8 times/month (May–August). The counting was done between 10 am and 12 am. At each occasion the actual number counted was used as an abundance index.

The diet was determined from pellets, collected mainly beneath perches and to a minor degree under nests. Accordingly, the observed diet

corresponds mainly to male individuals at the beginning of the season. Pellets were dissected and fragmented invertebrates were analyzed under a magnifier glass (6x) or a microscope. Arthropod prey was determined to the taxonomic level of family or (sub)order and vertebrates to species. The number of prey was determined based on the number of heads or jaws (vertebrates, most insects), cephalothoracics (*Arachnoidea*), legs (*Odonata*), intact/partly fragmented specimens (*Diplopoda*, *Isopoda*) or shell fragments (*Gastropoda*). Pellets were collected in total from 15 locations, but in 1999–2001, predominantly in territories selected for evaluation of field prey abundance. Since breeding Red-backed Shrikes have a strict territorial behaviour (Lefranc & Worfolk

1997), pellets collected in each territory were considered to originate from the pair breeding and foraging in the specific territory.

Statistical analyses followed general methods (Campbell 1989). All t-tests were independent and two-tailed.

3. Results

3.1. Breeding data

In the main study area, breeding was observed in the meadows ($n = 14$ started breedings/4 locations) and in thinned pine forests ($n = 11/4$) (Table 1, Fig. 1). No breeding was observed in arable fields despite potential sites, i.e. ditches with scattered bushes. The breeding territory size was similar in forest and meadow habitats (total mean = $1.4 \text{ ha} \pm 0.31$).

In both habitats, the mean date of incubation start was June 9 (range May 30–June 21) and the number of large nestlings per nest (total mean = 3.6 ± 1.44) was similar (Table 1). In both breeding habitats, one started breeding failed and the shrikes disappeared from the territories. Second broods were not observed. In the post-breeding season, shrikes were almost exclusively observed in meadows and along ditches in arable fields and only once in forest habitats (Table 1). Data on foraging behaviour, diet and prey abundance were used to investigate possible reasons for this seasonal difference in habitat use.

3.2. Hunting behaviour

Foraging occurred most frequently by drop hunting (70.1% of all hunting attempts, $n = 405$), but aerial catches (25.2%) and foraging in tree or bush branches (4.7%) were also observed. The hunting behaviour was studied in the breeding territories to assess possible habitat differences in foraging behaviour. No significant differences in total hunting activity were evident in the two breeding habitats (Table 2). However, toward the end of the breeding season drop hunting was more frequently employed in the forest-type habitat than in meadows (Table 2). Nevertheless, compared to the nestling period shrikes foraging in meadows during the post-breeding season engaged in drop hunting significantly more often than any other mode of hunting (Table 2, $\chi^2 = 22.62$, $P < 0.001$, $df = 1$, 2×2 contingency table).

Most territories were located nearby arable fields; hence, these fields were used to some extent as foraging habitats. In forest-type territories with borders along arable fields, hunting efforts occurred more frequently within the forest (87.7% of all efforts, $n = 196$) than in the arable field (12.3%). Among shrikes breeding in meadows, the corresponding use of arable fields was 7.7% ($n = 209$). Thus, compared to an even distribution, arable fields were significantly less important as foraging habitats as the main breeding habitat (forest-type territories: $\chi^2 = 65.17$, $P < 0.001$, meadow-type territories: $\chi^2 = 91.32$, $P < 0.001$, 2×2 contingency table $df = 1$).

Table 1. The open habitats in the main study area and the occurrence of Red-backed Shrikes during the breeding and the post-breeding season in 1997–2001. ME = meadows, TF = thinned old pine forests and AF = arable fields. The mean number of large nestlings is based on all started breeding. The post-breeding occurrence is defined as percentage (%) of visits ($n = 20$) to the study area when at least one shrike has been observed foraging in the habitat. *) No significant difference, $P = 0.618$, $df = 1$, Student's *t* test.

	ME	TF	AF
Area (km ²)	0.05	0.12	0.4
Started breedings (n)	14	11	0
Territory size (ha)	1.4 ± 0.30	1.4 ± 0.37	–
Incubation started (mean)	June 9	June 9	–
Failed breedings, n (%)	1 (7)	1 (9)	–
Nestlings (mean \pm SD)*	3.4 ± 1.41	3.7 ± 1.49	–
Post-breeding (%)	100	5	60

Table 2. The overall hunting activity (attempts/hour) and the proportion (%) of drop hunting among all hunting efforts in the two types of breeding habitats. The seasons are: I = before incubation, II = incubation, III = nestlings, IV = post-breeding period. ns = not significant.

Season	Total activity		Drop hunting (%)	
	Meadows	Forests	Meadows	Forests
I	15.5 (4.9 ¹) $\chi^2 = 0.022$, ns ³	15.7 (1.4)	77.6 (76 ²) $\chi^2 = 1.924$, ns ⁴	90.9 (22)
II	7.2 (7.2) $\chi^2 = 1.952$, ns	21.3 (2.3)	69.2 (52) $\chi^2 = 0.892$, ns	77.6 (49)
III	12.8 (2.9) $\chi^2 = 0.271$, ns	18.7 (6.7)	35.1 (37) $\chi^2 = 9.728$, P < 0.01	64.0 (125)
IV	8.8 (5.0)	–	86.4 (44)	–

1 Time (h) used for observation.

2 Total number of observed hunting attempts.

3 2 × 2 contingency table (df = 1) to test for differences in the distribution of number of hunting efforts and time used for observation.

4 2 × 2 contingency table (df = 1) to test for differences in the distribution of number of drop hunting and other hunting methods.

3.3. Diet composition

Based on the total pellet material, the diet was composed of 53.0% of beetles, 30.9% of hymenopterans and 8.3% of *Orthoptera* by number of prey (Appendix). Among beetles, the most

important prey was ground beetles (Fam. *Carabidae*, 29.0% of all prey) and among hymenopterans, bumble bees (*Bombus* sp., Fam. *Apidae*, 17.6%). Vertebrates (1.5% of all prey) were dominated by lizards (*Lacerta vivipara*) and shrews (*Sorex araneus* and *Sorex* sp.). The main

Table 3. The mean percentage (%) ± SD of the main prey found in the pellets of Red-backed Shrikes. The sample unit is number of locations. During breeding, pellets were collected in meadow-type and forest-type territories, but in the post-breeding season, shrikes occurred almost exclusively in meadows or in arable fields (no pellets were collected in this habitat). P-values were obtained by Student's *t* tests. Habitat differences (df = 14) correspond to comparisons between meadow-type and forest-type breeding sites. The seasonal differences (df = 11) correspond to comparisons between the breeding and post-breeding season in meadow-type locations.

	Breeding			Post-breeding	
	Meadows	Forests	Habitat (P)	Meadows	Season (P)
<i>Coleoptera</i> tot.	59.0 ± 4.58	53.7 ± 7.70	0.132	36.6 ± 12.91	0.016
<i>Carabidae</i>	32.8 ± 5.17	26.8 ± 7.74	0.101	21.4 ± 11.07	0.082
<i>Scaraebidae</i>	4.9 ± 3.12	6.4 ± 3.93	0.440	2.6 ± 1.01	0.103
<i>Curculionidae</i>	8.5 ± 3.24	7.9 ± 4.26	0.785	2.7 ± 2.49	0.006
<i>Elateridae</i>	2.7 ± 1.89	3.1 ± 2.81	0.761	1.4 ± 0.71	0.153
<i>Silphidae</i>	5.1 ± 2.37	3.9 ± 1.83	0.280	3.6 ± 3.48	0.428
<i>Hymenoptera</i> tot.	29.0 ± 4.43	34.1 ± 10.22	0.231	39.6 ± 5.38	0.007
<i>Apidae</i>	17.5 ± 3.07	16.7 ± 6.78	0.768	20.6 ± 6.99	0.390
<i>Vespidae</i>	4.8 ± 2.71	5.4 ± 4.29	0.738	4.4 ± 3.76	0.839
<i>Formicidae</i>	4.1 ± 3.07	3.6 ± 3.41	0.747	7.3 ± 6.20	0.331
<i>Heteroptera</i> tot.	2.2 ± 0.72	4.1 ± 2.18	0.048	0.2 ± 0.39	< 0.001
<i>Orthoptera</i> tot.	5.9 ± 3.41	0.6 ± 0.74	0.006	23.5 ± 6.68	0.002
Vertebrates tot.	1.4 ± 1.25	1.6 ± 1.31	0.794	0.2 ± 0.31	0.047
Prey total (n)	1,630	1,111		639	
Locations (n)	7	8		5	

Table 4. Field abundance indices (mean \pm SD) of pitfall-trapped beetles (number of beetles/24h per trap), bumble bees (*Bombus* sp.) and *Orthoptera* sp. Data on pitfall-trapping were: total time (h) used for trapping, mean number of traps/trapping period (range 2–4) and total number of trapping periods. Abundance of bumble bees and *Orthoptera* sp. was studied by visual counting in the field (abundance index = total number of individuals counted along the fixed route).

	Breeding		Post-breeding	
	Meadows	Forests	Meadows	Forests
<i>Coleoptera</i> total				
< 10 mm	3.6 \pm 4.96	1.6 \pm 2.51	5.9 \pm 7.94	4.5 \pm 2.09
\geq 10 mm	2.2 \pm 1.47	2.3 \pm 1.44	4.7 \pm 2.61	3.4 \pm 1.77
<i>Carabidae</i> sp.				
< 10 mm	0.2 \pm 0.29	0.1 \pm 0.25	0.7 \pm 1.24	1.8 \pm 1.41
\geq 10 mm	1.5 \pm 1.15	1.8 \pm 1.12	4.1 \pm 2.74	2.3 \pm 1.07
Time (h)	214	214	85	65
Traps (mean)	2.6	3.4	2.7	3.0
Periods (n)	8	9	3	4
<i>Bombus</i> sp.	5.3 \pm 5.85	3.9 \pm 4.28	3.6 \pm 2.07	3.8 \pm 2.48
<i>Orthoptera</i> sp.	29.4 \pm 30.89	26.6 \pm 26.64	106.6 \pm 36.09	63.7 \pm 17.42
Observations (n)	18	17	11	8

diet composition in the two breeding habitats is shown in Table 3. During the breeding season, the breeding habitats showed no differences in the diet composition of ground beetles and bumble bees. However, during breeding, *Orthoptera* species were significantly more frequent prey in meadows, whereas land bugs (sub-order *Heteroptera*) occurred slightly more frequently in the diet of shrikes breeding in the forest habitats. In the post-

breeding period, Red-backed Shrikes were seldom seen in the forest habitats (Section 3.1.); thus, a habitat comparison could not be performed. At this stage of the season, particularly *Orthoptera* and *Hymenoptera* were more frequent prey than during breeding, whereas the shrikes foraged significantly less on beetles, land bugs and vertebrates (Table 3).

Table 5. P-values (df) obtained by Student's *t* test analyses of prey abundance indices. Habitat differences correspond to comparisons between the meadow-type and the forest-type territory. The seasonal differences correspond to comparisons between the breeding and post-breeding season in the particular type of territory. B = Breeding season, PB = Post-breeding season.

	Habitat differences		Seasonal differences	
	B	PB	Meadows	Forests
<i>Coleoptera</i> total				
< 10 mm	0.313 (15)	0.747 (5)	0.561 (9)	0.067 (11)
\geq 10 mm	0.906 (15)	0.465 (5)	0.066 (9)	0.239 (11)
<i>Carabidae</i> sp.				
< 10 mm	0.651 (15)	0.338 (5)	0.259 (9)	0.004 (11)
\geq 10 mm	0.660 (15)	0.269 (5)	0.046 (9)	0.464 (11)
<i>Bombus</i> sp.	0.397 (33)	0.842 (18)	0.385 (27)	0.976 (23)
<i>Orthoptera</i> sp.	0.769 (33)	0.011 (18)	< 0.001 (27)	0.004 (23)

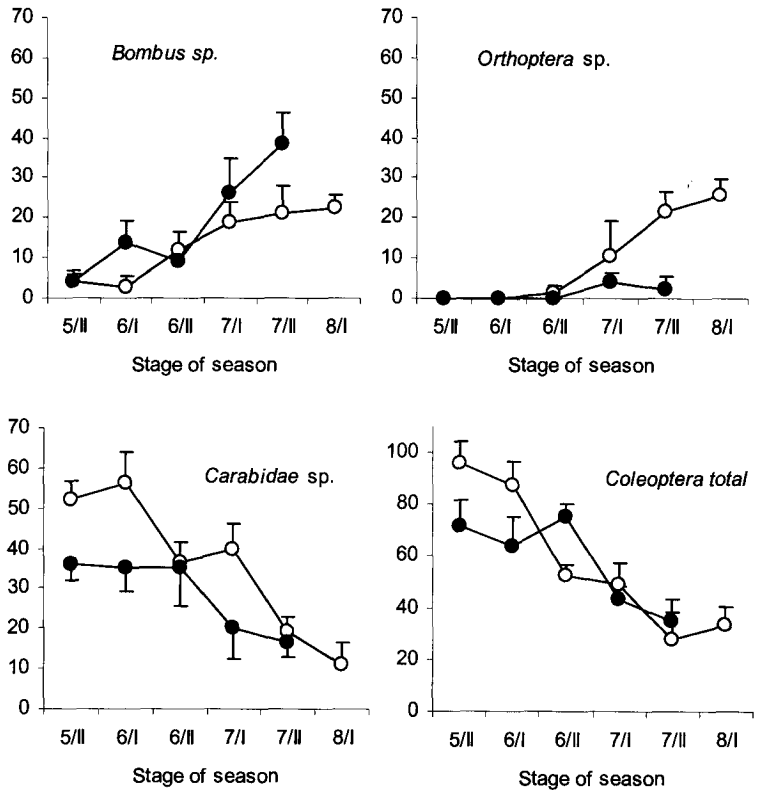


Fig. 2. Seasonal changes of bumble bees (*Bombus* sp.), *Orthoptera*, ground beetles (*Carabidae* sp.) and beetles in total as prey (mean% ± SD) in the Red-backed Shrike diet. The figures are based on the complete pellet material. O = meadows (n = 5–7 locations/stage of season), ● = forests (n = 5–8 locations/stage of season). The stage of season is defined as month/half of month.

3.4. Field abundance of the main prey

The observed mean abundance indices of ground-living beetles, bumble bees and *Orthoptera* in the studied meadow-type and forest-type territory are shown in Table 4. No differences were observed in the bumble bee and beetle abundance but in the post-breeding season *Orthoptera* species were significantly more abundant in the meadow compared to the forest-type territory (Table 5). Both territories showed increased abundance of potential prey in the post-breeding season. These were especially *Orthoptera* (both habitats) and small (<10 mm) carabids (forest habitat) (Table 5).

3.5. Role of season and prey abundance in prey selection

The use of the main prey (beetles, *Bombus* and *Orthoptera*) throughout the season is shown in Fig. 2. Generally, the use of bumble bees and *Orthoptera* increased whereas the use of beetles

decreased as the season progressed. To evaluate the role of prey abundance in the seasonal changes of prey selection, contingency tables were em-

Table 6. Comparison of the seasonal distribution of field abundance indices (expected distribution) and the seasonal changes of the particular prey in the diet of Red-backed Shrikes. Contingency tables were used to test differences in distribution. The diet data were obtained from pellets collected in the same territory as where abundance studies were performed. Statistically insignificant results indicate an abundance-dependent utilisation of the prey type. The material was collected during two seasons in one meadow-type territory and in one forest-type territory. The season was divided into stages as in Fig. 2. ns = not significant.

	Meadow, χ^2 (df)	Forest, χ^2 (df)
<i>Bombus</i> sp.	6.57 (5), ns	2.66 (4), ns
<i>Orthoptera</i> sp.	2.14 (4), ns	2.18 (2), ns
<i>Carabidae</i> sp.	15.57 (5), P < 0.01	4.06 (4), ns

ployed (Table 6). The decreased use of *Carabidae* beetles in the meadow-type territory differed significantly from the field abundance, whereas *Orthoptera*, bumble bees and *Carabidae* beetles (forest habitat) were preyed upon in an abundance-related manner.

4. Discussion

The main finding in this local study was the clear difference in habitat preference during the breeding and post-breeding season. Forest habitats (thinned old pine forests) were equally used as breeding habitat as natural meadows but, during the post-breeding phase, shrikes showed a high preference for meadows and arable fields whereas forests were avoided. The start of incubation, territory size and the mean number of large nestlings/started breeding were similar, suggesting no differences in reproduction quality between the two breeding habitats. Furthermore, the abundance and diet composition of the main prey showed no substantial differences during the breeding season. The high preference for meadows in the post-breeding phase coincided with the significantly higher abundance of grasshoppers and crickets (*Orthoptera*) in this habitat. A similar pattern of post-breeding switch in habitat preference was observed among Reed Warblers (*Acrocephalus scirpaceus*) and Sedge Warblers (*A. schoenobaenus*) on the Baltic Sea coast (Chernetsov 1998). These warblers nested in both dry and wet reedbeds, but during the post-breeding periods they were much more common in the wet areas where suitable food was more abundant. The author suggested that the purpose of post-breeding movement between habitats is to find suitable sites for moult and pre-migratory fattening (Chernetsov 1998).

In general, *Orthoptera* species are active insects that occur frequently in high numbers in late summer. At this stage of the season, juvenile shrikes forage independently and especially large and fairly slow crickets may be a profitable prey for inexperienced shrikes. It is well known that shrikes choose foraging habitats where especially large insects are abundant (Brandl *et al.* 1986, Hernandez 1993, Wagner 1993, Lefranc & Worfolk 1997). However, in a previous diet versus

prey abundance study in Spain (Hernandez *et al.* 1993), Red-backed Shrikes showed negative selection of *Orthoptera* whereas *Coleoptera* and *Hymenoptera* were selected positively. This may reflect the lack of a simple division between main and alternative prey where the prey abundance is of higher importance, supported in the present study by the comparison of seasonal prey abundance and percentage of diet. However, individuals breeding in northern Europe are slightly larger than shrikes of the southern population (Cramp & Perrins 1993), which could also explain regional differences in prey preferences.

Since *Orthoptera* insects occurred also in the forest habitats, prey abundance is unlikely to solely explain the observed post-breeding habitat preferences. In addition, the meadows may be more attractive to Red-backed Shrikes because of their openness as compared to the thinned pine forests in the study. Schön (1994) defined the surveyability as a common characteristic of preferred habitats among shrikes, allowing, e.g. detection of prey and predators. Predation, especially by raptors, is probably the main cause of death among shrikes (Lefranc & Worfolk 1997), because the preferred hunting behaviour of shrikes is sitting-and-waiting on exposed perches. Especially corvids are important nest predators of shrikes (Roos 2002). In the study area, no records of predation were obtained but potential predators were frequently observed. These were especially Sparrowhawk (*Accipiter nisus*), Goshawk (*A. gentilis*), Hobby (*Falco subbuteo*), Jay (*Garrulus glandarius*), Hooded Crow (*Corvus corone cornix*) and Raven (*Corvus corax*). The thinned pine forests probably provided sufficient protection against nest predators (corvids), but the variable terrain could give good hunting opportunities for *Accipiter* raptors. Hence, following the disruption of breeding territories the selection of meadows as foraging habitats might also be influenced by an anti-predator behaviour, as predicted by theories of optimal habitat selection (Huoston & McNamara 1999).

Block and Brennan (1993) defined a habitat as suitable if the number of produced offspring ensures population continuity. For the Red-backed Shrike a reproduction rate of 2.9–3.0 fledglings/year per pair has been calculated to balance mortality (Jacobson & Stauber 1987, Rytman

1996), thus the breeding success observed in the present study (3.4–3.7 large nestlings/all started breedings) should be sufficient for population stability. Because of the concealed behaviour of fledglings, the counting of offspring is usually done at the ringing age (8–10 days) (Olsson 1995b, Tryjanowski *et al.* 2000). However, the determination of breeding success at this stage may be hampered by loss during later nestling days. In Poland, the number of fledglings was about 75% of the number of ringing-aged nestlings (Tryjanowski *et al.* 2000). Applying a similar degree of loss would reveal 2.6–2.8 fledglings/ started breeding in the present study. Although this number is slightly below the calculated limit needed for population continuity, the number is higher than, e.g. in Poland (Tryjanowski *et al.* 2000) with a stable population of Red-backed Shrikes (Dombrowski *et al.* 2000). As the focus of the present study was a local population, no conclusions may be drawn for a larger population. However, this study does not suggest low reproductive rate as the primary cause for the negative population trend, which is similar to findings obtained in Sweden (Olsson 1995b).

In line with previous diet studies of adult Red-backed Shrikes (reviewed in Cramp & Perrins 1993), bumble bees, beetles and *Orthoptera* were of special importance. The seasonal changes in the use of these prey species were similar to those observed by Wagner (1993) and attributed to the gradual increase in *Orthoptera* insects and bees, simultaneously with a vegetation-dependent reduced availability of ground-living beetles. The role of vegetation cover in the mode of hunting is well known among shrikes (Brandl *et al.* 1986, Wagner 1993, Yosef & Grubb 1993) and thus these changes in prey abundance and availability may apply also to the seasonal changes observed in the use of drop hunting. However, weather-dependent insect activity may also strongly influence the foraging behaviour (Solari & Schudel 1988, Olsson 1995a). In the present study, it is therefore difficult to draw any significant conclusions from the fairly low number of observations, but the data did not reveal any sign of differences between the breeding habitats. Furthermore, Red-backed Shrikes breeding in meadows showed the most obvi-

ous decrease in drop hunting frequency in line with the role of vegetation. In addition, the seasonal increase in vegetation height in meadows probably contributed to the significant difference between *Carabidae* abundance and the role of these beetles in the diet, in contrast to *Bombus* and *Orthoptera*. Nevertheless, in this habitat, post-breeding shrikes foraged mainly by drop hunting, probably reflecting the increased use of *Orthoptera* prey and/or the presence of inexperienced juvenile birds.

Taken together, the selection of the studied meadows as post-breeding foraging habitat appears obvious from an optimal foraging point of view. A high abundance of prey (of which some (*Tettigoniidae*, order *Orthoptera*) are among the heaviest insects in Finland), allowing a fairly low foraging activity per unit obtained energy, together with the habitat openness minimizing the risk of predation are fully in accordance with theories of optimal habitat selection (Huoston & McNamara 1999). From a conservation point of view, the results of this local study indicated that a habitat suitable for breeding (thinned old pine forests) is not always a favourable foraging habitat for Red-backed Shrikes preparing for autumn migration. If this finding is a general phenomenon, the switch of available habitats in northern Europe from those associated with traditional agriculture to forest-type habitats could in fact have contributed to the negative population trend, despite an unchanged rate of fledglings/pair. Further studies are necessary to clarify this issue on a larger scale. In addition, although shrikes did not breed along ditches in arable fields and seldom foraged in this habitat during breeding, this habitat was frequently used in the post-breeding season. With the availability of meadows, pastures and grasslands declining, this points to the importance of conserving ditches in agricultural practices, not only for breeding farmland birds (Piha *et al.* 2003) but also for species, like the Red-backed Shrike, that use this microhabitat for post-breeding foraging.

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Törnskatans *Lanius collurio* födoval och utnyttjande av olika biotoper i SW Finland

Biotop- och födovallet hos törnskatan undersöktes på Ålön (Pargas) i sydvästra Finland under åren 1993 och 1997–2002. Majoriteten av materialet insamlades inom ett 1,4 km² stort område, där törnskator häckade på ångar (n = 14 häckningsförsök) eller i gallrade torra tallskogar (n = 11) (Fig. 1). Ingen väsentlig kvalitetsskillnad kunde noteras mellan dessa häckningsbiotoper på basis av revirstorleken, datum för påbörjad ruvning och antalet stora boungar (Tabell 1).

Under häckningssäsongen (perioden maj–juli) var också förekomsten av de viktigaste bytena (jordlöpare, humlor) och utnyttjandet av dessa likartade i de båda biotoperna (Tabell 3). Däremot favoriserade törnskator ångar under perioden efter häckning (definierad här som första hälften av augusti), då tallskogar undveks så gott som fullständigt (Tabell 1). Detta kan förklaras utifrån en rikligare tillgång på gräshoppor och syrsor (*Orthoptera*) i ångsmarkerna (Tabell 4 & 5), men ångarnas större öppenhet kan också maximera möjligheterna att upptäcka predatorer. Sålunda föreföll biotopvalet efter häckningssäsongen stämma överens med teorier gällande optimal furagering. Vidare undersöktes törnskatornas jaktbeteende i de två biotoperna. Energisnåla dykningar mot marklevande byten var den dominerande jaktmetoden (Tabell 2). Också dessa resultat antydde att ångarna energetiskt sett var den fördelaktigare biotopen – den rikliga förekomsten av stora byten såsom gräshoppor och speciellt vårtbitare möjliggjorde en optimering av energiintaget.

På basis av spybollar (n = 688) insamlade under hela säsongen (maj–augusti) bestod födan till 29,1 % av jordlöpare (n = 3 388 byten) och till 18,3 % av *Apidae* (speciellt humlor). De övriga bytena var närmast representanter för övriga skalbaggefamiljer (21,6 %), övriga steklar (12,6 %) och *Orthoptera* (8,3 %) (Appendix). Födösammansättningen förändrades under säsongen som ett resultat av en ökad tillgång på humlor och gräshoppor samt en vegetationsberoende minskad tillgång på marklevande skalbaggar (Fig. 2, Tabell 6).

Törnskatans populationsutveckling har varit negativ i stora delar av utbredningsområdet. En bidragande faktor är förändringar i jordbruksmar-

kerna, särskilt den drastiska minskningen av buskrika ångar och betesmarker. I norra Europa har arten däremot rikligt med häckningsbiotoper i form av avvercade eller gallrade skogar. Denna lokala studie visade dock att en biotop som lämpar sig för häckning (gallrad tallskog) inte nödvändigtvis är optimal inför höstflyttningen. Är mönstret allmänt giltigt kan förskjutningen när det gäller tillgängliga biotoper – d.v.s. från sådana förknippade med traditionellt jordbruk till sådana som uppkommer inom modernt skogsbruk – ha en negativ inverkan på populationsutvecklingen i ett längre perspektiv.

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Appendix. The diet composition (number of prey and%) of the Red-backed Shrike in the study area based on pellets (n = 688 pellets) collected from the end of May to mid-August.

Prey taxon	n	%
Invertebrates total	3,338	98.5
<i>Insecta</i> total	3,298	97.3
Order <i>Coleoptera</i> total (incl. sp.)	1,797	53.0
Fam. <i>Carabidae</i>	985	29.1
Fam. <i>Curculionidae</i>	196	5.8
Fam. <i>Scarabaeidae</i>	159	4.7
Fam. <i>Silphidae</i>	150	4.4
Fam. <i>Elateridae</i>	105	3.1
Fam. <i>Staphylinidae</i>	36	1.1
Fam. <i>Chrysomelidae</i>	26	0.8
Fam. <i>Cerambycidae</i>	18	0.5
Fam. <i>Cantharidae</i>	16	0.5
Fam. <i>Dytiscidae</i>	10	0.3
Fam. <i>Coccinellidae</i>	3	0.1
Fam. <i>Hydrophilidae</i>	3	0.1
Fam. <i>Cleridae</i>	2	0.1
Fam. <i>Buprestidae</i>	1	0.0
Fam. <i>Anobiidae</i>	1	0.0
Fam. <i>Histeridae</i>	1	0.0
Order <i>Hymenoptera</i> total (incl. sp.)	1,046	30.9
Fam. <i>Apidae</i>	620	18.3
Fam. <i>Formicidae</i>	167	4.9
Fam. <i>Vespidae</i>	158	4.7
Fam. <i>Ichneumonidae</i>	27	0.8
Fam. <i>Pompiloidae</i>	17	0.5
Fam. <i>Sphecidae</i>	8	0.2
Fam. <i>Tiphiidae</i>	6	0.2
Fam. <i>Cimbicidae</i>	4	0.1
Fam. <i>Siricidae</i>	1	0.0
Order <i>Orthoptera</i> total (incl. sp.)	281	8.3
Fam. <i>Tettigoniidae</i>	24	0.7
Suborder <i>Heteroptera</i> total (incl. sp.)	86	2.5
Fam. <i>Pentatomidae</i>	76	2.2
Fam. <i>Nepidae</i>	2	0.1
Order <i>Odonata</i> total	48	1.4
Order <i>Diptera</i> total	25	0.7
Fam. <i>Tipulidae</i>	22	0.6
Fam. <i>Tabaridae</i>	1	0.0
Fam. <i>Syrphidae</i>	1	0.0
Fam. <i>Asilidae</i>	1	0.0
Order <i>Lepidoptera</i> total	10	0.3
Order <i>Ephemeroptera</i> total	3	0.1
Order <i>Mecoptera</i> total	2	0.1
<i>Arachnoidea</i> total	23	0.7
<i>Diplopoda</i> total	13	0.4
<i>Gastropoda</i> total	2	0.1
<i>Isopoda</i> total	2	0.1
Vertebrates total (incl. sp.)	50	1.5
<i>Lacerta vivipara</i>	26	0.8
<i>Sorex araneus</i> (+ <i>Sorex</i> sp.)	12	0.4
<i>Micromys minutus</i>	5	0.1
<i>Clethrionomys glareolus</i>	3	0.1
Aves sp.	3	0.1