Food consumption and roosting behaviour of Great Grey Shrikes *Lanius excubitor* wintering in south-western Finland

Stefan Karlsson

Karlsson, S., Smedjevägen 29, FI-21610 Kirjala, Finland. stefan.karlsson@parnet.fi

For diurnal predators the short time of winter daylight may limit the possibilities to feed

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and hunt. In this field study, these aspects, as well as roosting behaviour, were evaluated in wild Great Grey Shrikes (*Lanius e. excubitor*). The main roost-sites were large junipers (*Juniperus communis*) and willows (*Salix* sp.). Daily mean amount of captured prey varied between 36.3-59.8 g and the daily mean food consumption was 44.1-62.6 g, both parameters being lowest in midwinter. In the diet, *Microtus*-voles dominated in the autumn and late winter whereas mice (mainly Harvest Mouse *Micromys minutus*) were most abundant in midwinter. Increased capture efficacy rather than increased hunting efforts enabled the shrikes to catch a fairly constant number of prey / day (2.1-3.1), independent on time available for hunting. With decreased amount of daylight the shrikes showed also signs of increased hunting activities in morning and evening twilight. The shrikes responded to shortened daylight time by decreasing the meal-to-meal interval and, as a result the portion of the daylight time used for feeding increased as the photoperiod shortened. Thus, the shrikes showed efforts to adjust their foraging and feeding behaviour in order to reach a stable prey capture rate and food consumption without increased energy costs.

1. Introduction

In winter, diurnal birds face an energetic dilemma in that the time available for foraging is short, simultaneously with the highest thermoregulatory costs. Principally, a bird may respond to thermal stress by increasing foraging (McKnight 1998, Boysen *et al.* 2001) or by decreasing time of activity with a concurrent increased use of fat reserves (Newton 1969). Since a substantial energy loss occurs during the long night a proper roost-site is important. Herein, wind protection is the main factor that saves energy (Walsberg 1986).

The Great Grey Shrike Lanius excubitor is a

thrush-size passerine bird with a raptor-like food composition. Compared to the body weight (65 g, Solonen 1994) and to small raptors and owls with a similar diet the daily food requirement (40–70 g) is remarkable high (Schön 1996). In SW Finland, near the northern boundary of the European winter range, the average diet of Great Grey Shrikes showed seasonal variations (Karlsson 2002). Surprisingly from an energetical point of view, the minute Harvest Mouse *Micromys minutus* was the most numerous prey in midwinter, whereas the considerable larger *Microtus*-voles dominated in autumn and late winter. A similar relationship was observed with respect to snow cover, Harvest Mouse being the more numerous prey in conditions with snow (Karlsson 2002).

The presence of a snow cover seems to decrease the hunting efforts for vertebrate prey but without any significant effect on the prey capture rate (Karlsson 2001). However, little is known how the Great Grey Shrike's foraging and feeding behaviour is affected by short daylight time or low temperatures. It is well-known that shrikes keep larders, i.e. impaled unused vertebrate prey or prey remains but these are apparently not used as longterm food stores (Olsson 1985a, Antczak et al. 2005). In addition, the feeding occurs in bouts separated with the period needed for pellet formation. Based on field observations a Great Grey Shrike feeding on vertebrates does not eat until the pellet from the previous meal has been released (Olsson 1985a). Consequently, the daily food consumption may be limited by physiological factors (time of pellet formation), external factors (eg. daylight time, adverse weather) and foraging behaviour (prey capture rate, prey size).

In the present field study, roost-sites, feeding behaviour, hunting activity, prey capture frequency and daily food consumption were evaluated among shrikes spending the non-breeding season in south-west Finland. To better understand their survival the observations were correlated to time of season (month), daylight length or air temperature.

2. Material and methods

2.1. General information

Shrikes were studied in SW Finland (about 60°20'N, 22°15'E) during October to March in the winter 1992/93 to winter 2005/06 (except in the winter 1993/94). The locations (1–2/season) were in Kaarina (1 location) and Parainen (5 locations). The main habitats at all locations were fields and different types of meadows typically located close to a reed-covered sea inlet (Karlsson 2001). Mean meteorological data are based on observations at Turku airport (Finnish Meteorological Institute), 10–20 km north from the study sites. Temperatures at study sites were used to compare shrike behaviour with prevailing conditions. If not otherwise specified in the text, autumn is referred to Octo-

ber-November, midwinter to December-January and late winter to February-March.

2.2. Field observations

All field data on shrike activities were done by following individual birds through binoculars from nearby forest edges. The exact number of birds studied is not known. Since shrikes are highly territorial during the non-breeding period (Olsson 1984a), only a few individuals were studied each season. Details recorded were time used for feeding, time between two subsequent bouts of feeding, hunting efforts and successful captures of vertebrates. Hunting efforts included all apparent efforts to catch a vertebrate prey, i.e. diving to the ground, pursuing of birds and hovering, with or without a subsequent diving. Hunting activity was assessed only in condition with no significant invertebrate availability (i.e. snow cover and/or air temperatures below 0°C, Karlsson 2001).

2.3. Meal and pellet analyses

The wet meal weight of one bout of feeding was assessed by weighing impaled prey or prey parts before and after the shrike visited the prey item. The total prey content has been reported previously (Karlsson 2002). The same material is here used for average vertebrate prey composition and analysed on a monthly basis (October–March). Pellets were collected beneath perches as well as in roost-sites and the width and length of intact pellets were measured to an accuracy of 0.1 cm. When determing pellet length, protruding pieces (tails, hair etc.) typical for Great Grey Shrike pellets were excluded as suggested by Olsson (1986).

The daily amount of prey (g, wet weight) captured and consumed was calculated for each month (October–March) to enable a comparison of these two parameters. The average daily amount of prey captured (P_c) was calculated on a monthly basis as

$$P_{c} = R (P_{M}m_{M} + P_{V}m_{V} + P_{S}m_{S} + P_{B}m_{B})t, \qquad (1)$$

where t is the time (in h) between sunrise and sunset at 15th of the corresponding month. R is the average capture rate (number of vertebrate prey / h) based on field observations. P is the mean portion of the particular prey type in the diet and m the mean wet weight (in g) of the prey according to Siivonen and Sulkava (1997) and Solonen (1994). Prey types were M (mice, *Micromys minutus*, mean weight 9.6 g), V (voles, *Microtus agrestis*, 35.9 g), S (shrews, *Sorex araneus*, 9.1 g) and B (birds *Parus major*, 19.0 g).

The average daily amount of prey (g, wet weight) consumed (P_{II}) was calculated as

$$P_{\rm U} = m n_{\rm meals} \,, \tag{2}$$

where m is the mean wet weight (in g) of one meal and n_{meals} the number of meals during the day time based on the average meal duration and meal interval. The latter was calculated as

$$n_{\text{meals}} = \frac{t}{d+i},$$
(3)

where t is the day time defined as in eq. 1, d the mean meal duration and i the mean meal interval.

2.4. Roosting behaviour

Roost-sites were found by following individual birds in the dusk and each bush and tree was verified as a roost-site based on the presence of a large amount of faeces and pellets, including very small ones typically seen in roost-sites (Olsson 1985b). In one winter territory, three frequently used roost sites were selected for wind shelter analyses. These were a juniper, a willow surrounded by reed and a willow on an open field. The wind speed was measured with an Xplorer 3 wind gauge (JDC Instruments, Switzerland, accuracy 0.1 m/s). The wind shelter is expressed as percentage of the maximum wind speed within the roosting site (measured during a period of 10 minutes) compared to that observed outside the roosting.

The end of active hunting from exposed perches was determined at dusk and regarded as the time the bird flew to the roost-site. Similarly, when the observation started at least one hour before sunrise, the first observation of the perching shrike was recorded.

3. Results

3.1. Weather conditions

Compared to long-term mean temperatures (1971–2000, Drebs *et al.* 2002), January–February were in average about 1°C milder whereas October–December and March were normal. Variation in monthly and daily mean temperatures are shown in Fig. 1. Maximum snow depth during the study period 1993–2006 was in average 37 cm \pm 13.1 per winter (Finnish Meteorological Institute, Turku).

3.2. Hunting behaviour

The diet showed seasonal differences. *Microtus*voles dominated in the autumn and late winter (March) whereas mice (mainly Harvest Mouse *Micromys minutus*) were most abundant in midwinter (Table 1; For more details on diet composition see Karlsson 2002). Hunting frequency decreased as the wintering season progressed (Fig. 2A). Nevertheless, the average number of daily captures of vertebrate prey (2.1–3.1 prey/day) remained stable throughout the season (Fig. 2B). In addition, the capture rate showed a peak in mid-

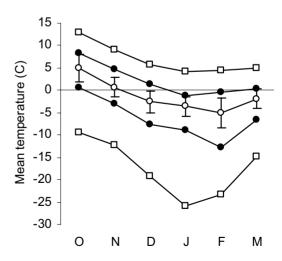


Fig. 1. Mean temperatures in 1992/93–2005/06 and in the period of shrike winter territory occupancy (October–March). \bigcirc = monthly mean temperature ± SD. Extreme mean temperatures are shown on a monthly basis (•) and on a daily (24-h) basis (□).

Table 1. The monthly (O-M) average diet composition. The diet is shown as percentage (%) of all vertebrate prey. Daylight corresponds to the time between sunrise and sunset at 15^{th} of each month. The observation time is the total time shrikes have been followed in the field.

Day light (h:min)	O 10:11	N 7:32	D 5:50	J 6:42	F 9:12	M 11:45
Voles	54.5	44.1	16.7	26.0	17.0	51.3
Mice	27.3	38.3	57.1	52.0	40.4	26.9
Shrews	12.0	14.7	9.5	16.0	19.1	17.4
Birds	6.2	3.0	16.7	6.0	23.5	4.4
Obs. time (h)	20.6	24.2	33.8	66.5	41.1	52.3

winter and the overall capture efficacy (captures/efforts) a tendency to increase as the wintering season progressed (Fig. 2C). Capture rate showed negative correlation with the daylight time ($r_p = -0.883$, d.f. = 4, P < 0.05) and positive correlation with the portion of mice in the diet ($r_p = 0.893$, d.f. = 4, P < 0.05).

ber, 16.7% of the daylight period was used for feeding whereas only 8.3% in October. However, if assessed on a 24-h basis the time portion used for feeding was unchanged throughout the wintering period (Fig. 2D). This was related to a positive relationship between meal-to-meal interval and the length of the daylight (Fig. 3A). Weak positive correlation was also observed with the air temperature (Fig. 3B).

3.3. Feeding behaviour

The portion of the daylight time used for feeding increased as the photoperiod shortened. In Decem-

The time used for feeding and prey handling during one meal showed no correlation with daylight length (Fig. 3C) but a weak negative trend with the air temperature was noted (Fig. 3D). The

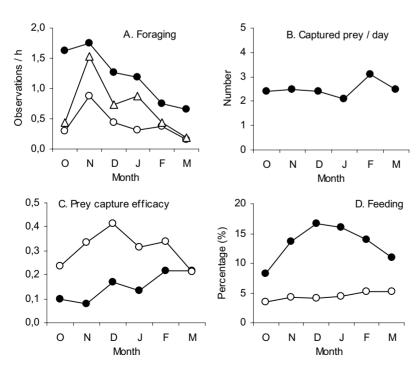
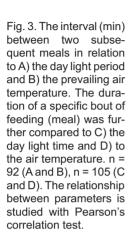
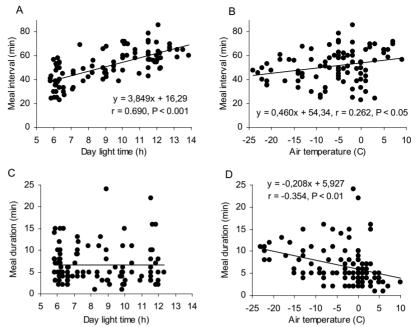


Fig. 2. The observed foraging and feeding behaviour on a monthly basis, October (O)-March (M). A) Different mode of hunting measured as observations / h. • = Divings to the ground, O = pursuing of birds, \triangle = hovering. B) Average number of captured vertebrate prey / day. C) Prey capture efficacy measured as captures / h (O) and captures / hunting efforts (\bullet) . D) Calculated portions (%) of the daylight time (•) or of the 24-h day (O) used for feeding.





mean (\pm SD) meal time (min) was 6.8 \pm 4.07. The mean (\pm SD) amount of a prey (*Microtus* sp. wet weight, g) consumed per meal was 6.1 \pm 1.05 (n = 10).

The pellet mean length was 23.8 mm \pm 6.29 and mean width 12.1 mm \pm 1.50 (n = 402). No difference in the pellets length was observed between

autumn, midwinter and late winter (ANOVA: $F_{2,128} = 1.99$, P = 0.14).

Based on capture rates, mean prey weights and monthly prey composition the daily average wet weight of captured prey was 50.4–59.8 g in the autumn and late winter. In midwinter, these values were considerable lower, 36.3–37.1 g (Table 3). If

Table 2. Description of roost-sites found in the shrike winter territories. The number corresponds to the number of seasons a shrike utilized the site for roosting.

Туре	Site specification / Number of seasons Free standing on an open field / 2				
Bird-cherry					
Juniper	Within a large bird-cherry in a small forest patch / 2				
Juniper	A stand of a few junipers on an open field / 4				
Juniper	A stand of a few junipers on an open field / 1				
Juniper	A stand of a few junipers and pines surrounded by a reed bed / 2				
Juniper	At a forest edge / 1				
Juniper	At a forest edge / 1				
Juniper	At a forest edge / 1				
Juniper	A small forest patch on an open field / 1				
Pine	A dense stand of small pines at a forest edge / 1				
Pine	Free standing pine on an open field / 1				
Willow	Edge of a small forest patch on an open field / 1				
Willow	Forest edge toward a reed bed / 1				
Willow	Forest edge toward an open field / 2				
Willow	Surrounded by a reed bed / 3				
Willow	Surrounded by a reed bed / 1				
Willow	Surrounded by a few small spruces on an open field / 2				

Table 3. Mean (± SD) meal duration and the meal interval observed in the field for each months of winter terri-
tory occupancy (O–M). The corresponding average wet weight (g) of daily captured prey (P _c) and consumed
prey ($P_{_{\mathrm{U}}}$) are calculated as described in Material and methods.

	0	Ν	D	J	F	М
Meal duration (min)	5.1 ± 2.50	6.9 ± 2.76	8.2 ± 3.32	7.4 ± 5.03	8.1 ± 3.78	7.3 ± 4.97
N	15	13	22	21	14	23
Meal interval (min)	56 ± 10.9	43 ± 11.2	40 ± 11.0	39 ± 10.3	50 ± 9.6	60 ± 9.8
N	10	11	18	18	15	20
$P_{c}^{}$, captured prey (g) $P_{u}^{}$, consumed prey (g)	59.8	53.2	37.1	36.3	50.4	57.8
	61.2	55.0	44.1	52.9	58.2	62.6

the amount of prey consumed was calculated from meal durations, meal intervals and meal wet weights the values were 55.0–62.6 g in autumn and late winter and 44.1–52.9 g in midwinter (Table 3).

3.4. Roosting behaviour

In total 17 different roost-sites were found. Among these two main types could be distinguished. Firstly, large thick junipers (*Juniperus communis*) and secondly, willows (*Salix* sp.) (Table 2). Seven (41%) roost-sites were utilized in two or more seasons. Each wintering shrike used at least 2–3 roosting sites. The wind shelter effect was highest in the juniper (36% of the outside wind speed was noted inside the roost-site), 44% in the willow within a reed bed and 64% in the willow on the open field. The relationship between wind speed outside and inside the roosting sites showed positive correlation (juniper: $r_p = 0.97$, willow surrounded by reed: $r_p = 0.99$, willow on open field: $r_p = 0.99$, all P < 0.01). Willows, including those used for roosting, were preferred for prey impaling and feeding (90% of all impaled prey were found in willows, n = 119) whereas no sign of feeding was observed in other roost-sites.

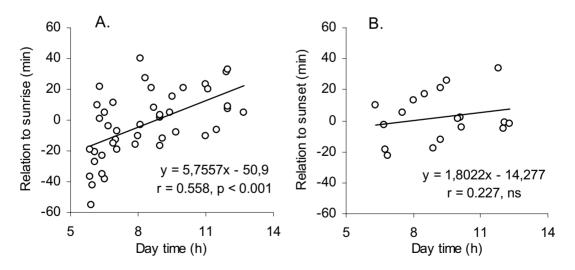


Fig. 4. The activity during morning (A) and evening twilight (B) in relation to daylight time. The morning activity (A) is measured as the first time when the shrike was observed on an exposed perch. Evening activity as the time the shrike flew to the roost site. 0 correspond to time of sunrise / sunset. Negative values correspond to time before sunrise (A) or after sunset (B). n = 42 observations (morning) and 18 (evening). The relationship between parameters is studied with Pearson's correlation test.

In the morning, the beginning of perching on exposed perches correlated positively with the daylight length (Fig. 4A). Especially in midwinter the birds tended to start this type of activity well before sunrise. The earliest observed hunting effort was 55 min before sunrise (a capture effort of a small tit *Parus* sp.). Similarly, the return to the roost-site appeared to occur later in midwinter, although this data did not correlate with the time of daylight (Fig. 4B). None of the data correlated with air temperature (at dawn: $r_p = -0.030$, d.f. = 41, at dusk: $r_p = -0.141$, d.f. = 18).

4. Discussion

Like other birds feeding on vertebrates, shrikes eject indigestible prey remains in the form of pellets. Normally a shrike does not eat until the pellet from the previous meal is released (Olsson 1985a). Consequently, not the prey availability but the time of pellet formation may determine the feeding interval which together with the short photoperiod may limit the energy intake in winter. Such digestive bottle-necks are rare in birds (Bednekoff & Houston 1994) and in the present study, shrikes appeared to avoid this by decreasing the meal-to-meal interval when the photoperiod shortened. The overall daily food consumption (44.1–62.6 g) was therefore within the same range as reported previously (40–70 g, Schön 1996).

If a concurrent reduction in the pellet formation time occurred was not possible to establish in the field since the actual release of the pellet was rarely recorded. Also other factors than the photoperiod may have influenced the meal-to-meal interval. According to Hilton et al. (1999) birds with rapid but inefficient digestion are restricted to high-quality food whereas species with slower digestion can exploit a wider range of prey types. The Great Grey Shrike consumes plenty of invertebrates in the summer and autumn but this food source is limited in winter (Huhtala et al. 1977, Karlsson 2002). Accordingly, the shrike's digestion may adapt to a more uniform diet consisting on vertebrates mainly by increasing digestion rate, enabling shorter meal-to-meal intervals. The reduced meal interval could also indicate a reduction in meal size. In many owls, the meal size correlates positively with pellet weight and meal-to-pellet interval (Duke *et al.* 1976, Duke & Rhoades 1977). Assuming a similar relationship in shrikes feeding on a similar diet, the lack of seasonal differences in pellet size indicates that the meal size is fairly stable.

In the midwinter period with the shortest daylight time, shrikes showed the highest prey capture rate. This was not due to an increase of hunting efforts but rather to an increased capture efficacy. Consequently, the average number of prey captured per day remained fairly constant during the entire wintering season without any obvious changes in the energy used for foraging. Similarly, Great Grey Shrikes decreased their hunting efforts in the presence of a snow cover but without any obvious effect on prey capture rate (Karlsson 2001). Also in that case the shrikes did not increase foraging-related energy costs (Karlsson 2001). Nevertheless, in midwinter the studied shrikes may face difficulties to catch enough prey to overcome energy costs, especially if dependent on small prey species. This was seen as a fairly low daily amount of captured prey in midwinter, i.e. 36-37 g/day which is slightly below previously reported food requirements (40-70 g, Schön 1996). During these short winter days the shrikes appeared to hunt often in twilight, although this behaviour is probably highly weather-dependent. The behaviour can be a direct effect of food shortage but may also be triggered by better prey availability due to higher activity of small mammals. Similarly, Olsson (1985b) noted that shrikes were frequently active in the evening twilight although other diurnal species (Tits Parus sp. and Magpies Pica pica) were already roosting. Great Grey Shrikes have also been seen to attack small birds at their roost-site (Clegg 1966, Pell & Hodson 1970).

The observed shrikes roosted in large junipers, as observed previously (Olsson 1984b). These bushes showed significant wind protection considered as a crucial factor to minimize thermoregulatory loss (Walsberg 1986). However, also leaf-less willows were used for roosting as observed in Indiana, US (Atkinson 1993) but not in Sweden (Olsson 1984). Typically most of these willows were located at forest edges or they were surrounded by dense reed beds. In general, it appeared that each shrike used a number of different roost-sites in their winter territory and some were likely never found. Although wind protection is a major factor in roost-site selection it appears that also other components may be of importance. Willows used for roosting were also used for prey handling and impaling whereas signs of such activities were not evident in junipers. When considering food consumption it is therefore not possible to exclude nocturnal feeding activity. Any direct evidence of such activity is, however, not available. During very cold, often calm nights, it may be energetically more beneficial to choose a roost-site with possibilities to feed (willows) rather than one providing optimal wind cover (junipers). In fact, nocturnal feeding is not an unknown phenomena for diurnal passerine birds visiting known food sources (Spencer 1982, Prescott 1985), as also a shrike's larders can be considered to present.

The presented considerations are based on average diet and shrike behaviour. In midwinter, the small Harvest Mouse dominated the average diet but the shrikes showed also higher prey capture efficacy and indications of increased hunting activities in morning and evening twilight. In addition, the shrikes responded to shortened daylight time by decreasing the meal-to-meal interval, enabling a fairly stable daily food consumption during the wintering season. Thus, the shrikes showed efforts to adjusted their foraging and feeding behaviour to enable a stable prey capture rate and food consumption without increased energy costs.

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Varfågelns *Lanius e. excubitor* vintertida födokonsumption och övernattningsbeteende i sydvästra Finland.

I norra Europa livnärar sig varfågeln *Lanius e. excubitor* vintertid på små ryggradsdjur och har ett stort födobehov jämfört med ugglor och rovfåglar med en liknande diet. I denna studie undersöks varfågelns jaktbeteende, födokonsumption och övernattningsbeteende för att få en uppfattning om artens överlevnadsstrategi under vinterhalvåret.

Varfågelns diet dominerades av dvärgmusen (*Micromys minutus*) under midvintern och av sorkar (*Microtus sp.*) under hösten och vårvintern (Tabell 1). Varfågelns fångsteffektivitet var högst under midvintern och detta skedde utan någon nämnvärd ökning i försöken att fånga byten (fig. 2A-C). Antalet byten var därför oförändrat 2.1-3.1 byte/day under hela perioden oktober-mars. Under midvintern använde varfåglarna också betydligt mera av den ljusa tiden för födointag än under hösten eller vårvintern (fig. 2D). Detta möjliggjordes av ett minskat intervall mellan två på varandra följande måltider (fig. 3A). En måltid (sork) bestod i medeltal av 6.1 g (SD = 1.05, n = 10) och det dagliga födointaget varierade på hösten och vårvintern mellan 55.0-62.6 g, medan detta var något lägre i december-januari (44.1-52.9 g). Motsvarande födotillgång beräknat ur fångstfrekvensen och bytessammansättningen var 50.4-59.8 g (höst och vårvinter) men endast 36.3-37.1 g under midvintern (tabell 3).

De studerade varfåglarna använde speciellt enrisbuskar och videbuskar som övernattningsbuskar (tabell 2). De senare var belägna på öppna fält, vid skogskanter eller inne i vassruggar. Vindskyddet var av samma storleksordning i enrisbusken och videbusken omgiven av vass. Spår av födointag noterades i videbuskar men inte i enrisbuskar. Därför kan man inte utesluta att varfåglarna emellanåt äter också nattetid. Speciellt under mycket kalla, ofta vindstilla nätter kan detta vara energetiskt mera lönande än att uppsöka vindskyddande enrisbuskar.

På basis av denna studie sker varfågelns födointag med kortare intervaller då dygnets ljusa tid blir kortare. För att maximera födotillgången under midvintern tenderar varfåglarna att öka jakteffektivitet utan att öka den energi som används för födosökning. Dessutom kunde samtidigt en ökad jaktaktivitet före soluppgången eller efter solnedgången noteras.

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