ORNIS SVECICA 11:7–18, 2001 https://doi.org/10.34080/os.v11.22858

Selection of habitat and perches by the Great Grey Shrike *Lanius excubitor* and the effects of snow layer and prey type

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Abstract

Field observations on Great Grey Shrikes *Lanius excubitor* were performed in four study areas in SW Finland (60°N, 22°E). The relation between habitat use, perch selection, prey type and the presence of a snow layer was evaluated. The mean yearly (± SE) territory size was 144 ha ± 14.3. The habitat selection depended on if snow cover was present, reflecting the favouring of vegetation-scarce arable fields when hunting invertebrates and vegetation-rich habitats when mainly vertebrates were available. Consistent with theories on optimal perch height, the shrikes chose higher perches when mainly vertebrates were hunted and also increased the time/perch, probably reflecting that vertebrate prey occur less frequently than invertebrate prey. The selection of lower perches when hunting invertebrates was evident in mild winter periods but not in the autumn; the reasons for this is discussed. The appearance of snow increased the distance to mammalian prey but the average capture frequency of mammals remained unchanged. In accordance with optimal foraging theory the shrikes preferred to hunt invertebrates when these were available rather than to adopt a hunting strategy that would optimise the encounter rate with vertebrates. However, the average hunting rate of ground-living prey decreased as the snow depth increased whereas energetically costly types of hunting behaviour, like rate of movements, hovering and hunting of birds remained unchanged.

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Received 24 November 2000, Accepted 25 February 2001, Editor: A. Brodin

Introduction

The Great Grey Shrike *Lanius e. excubitor* is a raptor-like passerine, hunting mainly from perches in semi-open habitats (Olsson 1984a, Schön 1994, 1996). When available, invertebrates are the favoured prey but the species is also capable to capture a sufficient amount of small mammals or passerine birds to survive even severe winter conditions (Kauppi & Rajala 1975, Huhtala et al. 1977, Olsson 1986). In winter, each individual maintains a hunting territory, usually without any contacts with other individuals (Olsson 1984b).

The density of perches of suitable type and height in habitats with sufficient prey availability is crucial for successful foraging (Schön 1994). Theoretically, the optimal perch height for a ground-hunting bird is a function of visible area, prey size, prey density and wind (Mills 1979). The visibility may also affect the habitat selection since shrikes usually prefer habitats with scarce vegetation unless a surrounding vegetation-rich area exhibits a higher prey abundance that outweighs the low visibility (Mills 1979). Olsson (1984a) mentioned that the shrikes choose higher perches when hunting vertebrates. By using optimal foraging theory, Mills (1979) predicted that a switch from small but abundant prey to larger prey with lower abundance should increase the perch height, distance to prey, distance between perches and the time spent perching. He confirmed these predictions, which I refer to as "optimal perch height theory", in a study of Loggerhead Shrikes *Lanius ludovicianus* in Arizona, despite some difficulties in determining prey size (Mills 1979). In the present study the switch from hunting both invertebrates and vertebrates to mainly vertebrates, may provide a good opportunity to test the predictions outlined above.

Optimal foraging models also predict a maximisation of the energy intake by selection of hunting habitat, patches within the habitat, foraging method and prey type (Stephens & Krebs 1986). Winter-time Great Grey Shrikes prefer to hunt ground-living invertebrates when available (Olsson 1986) indicating that these are of energetic importance despite their small size compared to vertebrates. Therefore, invertebrate availability may determine the choice of hunting habitat.

The aim with this study is to describe habitat use, perch selection and prey types with respect to optimal foraging theory (Stephens & Krebs 1986, Mills 1979), especially by investigating how behaviour is affected by differences in prey availability that can be attributed to different snow conditions.

Material and methods

Territory, size and habitat use

Shrikes were studied in the field from late September to early April in 1992–2000 (total of 198 days), with exception of the winter 1993/1994. Observations were collected from four different study areas (1–2 areas per season) in the coastal, boreo-nemoral region of SW Finland (Figure 1). The specific locations were:

Study area 1: Kaarina, Rauvolanlahti, 60°25´N, 22°17´E
Study area 2: Pargas, Nilsby, 60°20´N, 22°25´E
Study area 3: Pargas, Sydmo, 60°17´N, 22°08´E
Study area 4: Pargas, Hoggais, 60°19´N, 22°15´E

The yearly territory size was determined from a map and calculated from number of one ha squares exhibiting one or more used perches (Olsson 1984b, Schön 1994). At each visit to a territory the hunting habitats were recorded. A shrike was counted to have used a specific habitat for hunting if the bird performed at least one hunting effort there.

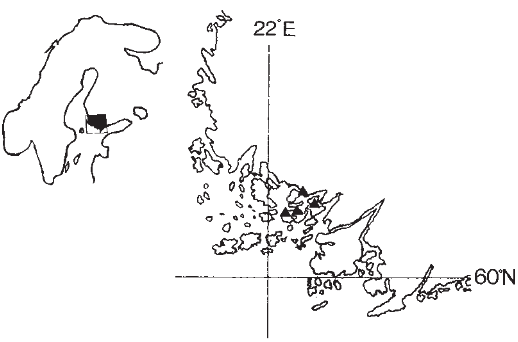

Figure 1. The location of the study areas (▲).
Studielokalerna (▲).

Perch selection and hunting behaviour

To calculate the number of available perches I counted isolated trees, bushes and small groups of trees (approx. <0.1 ha) in all territories. When the birds perched on telephone wires, the line between two poles was considered as one perch. In addition, available perches were grouped into two height categories, <10m and >10m.

Shrike behaviour was studied by observation with binoculars (0.5–11 h/day, total 171h, 105 days). All hunting efforts and successful captures of vertebrates were recorded. The type of perch was recorded and perch heights were estimated into the categories <2 m, 2–5 m, 5–10 m or >10 m using a selection of known standards in the territory. In the analyses I only included perching bouts if the shrike moved to a new perch for reasons other than to visit an impaled prey, to transport prey to an impaling site, or because of disturbance.

The moved distance between perches during a period of continuous observation (>1 h) was used to measure the mobility. The distance from the perch to a point where a mammal prey was caught was estimated using known distances in the territory.

Habitat structure

The relative frequency of the open habitats is presented in Table 1. At the time of shrike arrival to the study areas (late September/early October) the arable fields were harvested or autumn-sown, thus they were either bare or covered by very low vegetation. The dry meadows were covered chiefly by grass (*Poaceae*) and scattered stands of umbelliferous plant (*Apiaceae*) and *Cirsium*-thistles. The wet meadows consisted of occasionally flooded areas, mainly with vegetation of rushes (*Juncaceae*) and sedges (*Cyperaceae*). The habitats were mostly well demarcated except for wet meadows and reedbed areas, which changed more gradually into each other. In this work reedbeds stand for areas covered entirely by dense stands of reed *Phragmites communis*.

Snow conditions

At each visit to a study area the snow depth was measured at 2–4 standard sites. The sites were located on sections of open arable fields that were not shaded by forest edges. Of the 95 observation days that I considered snow free, 77% were days when the ground was completely free from snow cover, whereas 23% were days with scattered areas of

Table 1. The relative (%) distribution of the main open habitats in the studied Great Grey Shrike winter-territories calculated from the largest yearly territory observed.
Relativa (%) förekomsten av de öppna biotoperna i de studerade vinterreviren beräknat från det största observerade årliga reviret.

Study area *Lokal*	1	2	3*	4*
Arable fields *Odlad mark*	67	69	61	53
Dry meadows *Torra ängar*	21	14	25	31
Wet meadows *Våtängar*	4	5	5	7
Reed beds *Vassvikar*	8	12	9	10
Total size (ha) *Totala ytan (ha)*	200	160	75	80
Yearly mean (ha) ± SE *Årligt medeltal (ha) ± SE*	170 ± 11.4		110 ± 12.2	
	n =4	n=3		

*) Not monitored for the whole season. *Ingen fullständig period (september–april) studerad.*

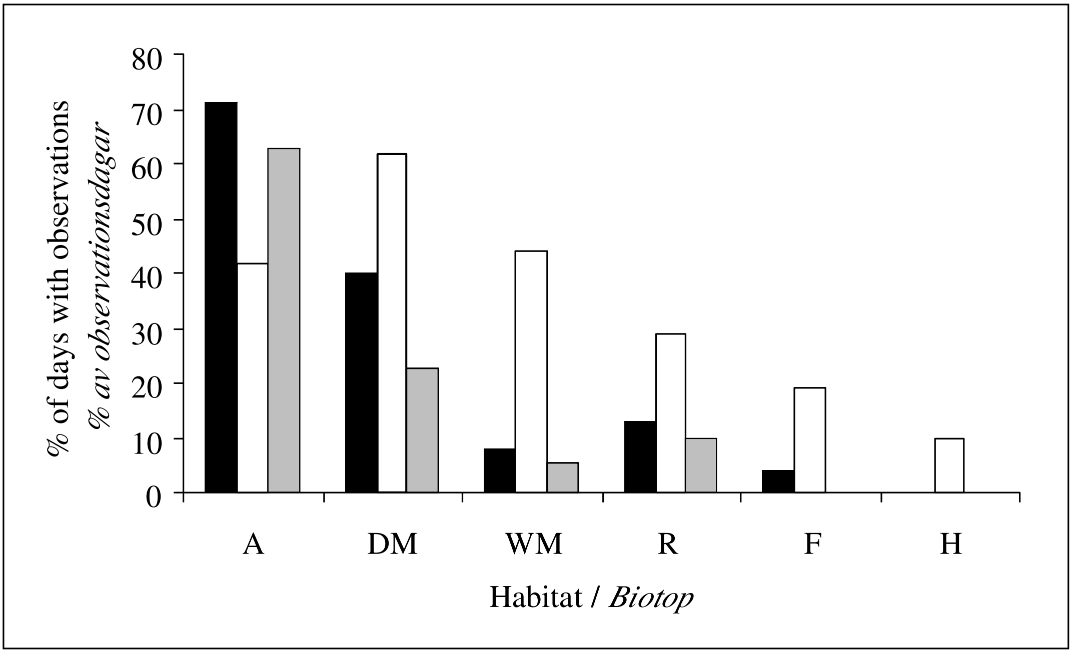

Figure 2. Habitat use of the studied Great Grey Shrikes. Days with at least one hunting effort in a habitat as percentage of total number of observation days, together with the mean relative (%) abundance of the open habitats. White columns = days with snow (103 days), black columns = snow free days (95 days), grey columns = relative abundance of the habitat. A = arable fields, DM = dry meadows, WM = wet meadows, R = reeds, F = forest, H = human habitation.
Varfågelns utnyttjandet av olika biotoper. Antal dagar då jaktförsök noterats i en biotop som % av samtliga observationsdagar. Som jämförelse är den relativa (%) förekomsten av de öppna biotoperna inkluderade. Vita staplar = dagar med snötäcke (103 dagar), svarta staplar = snöfria dagar (95 dagar), gråa staplar = den relativa förekomsten av biotoptypen. A = odlad mark, DM = torra ängar, WM = våtängar, R = vassvikar, F = skog, H = bosatta områden.

snow. The latter condition occurred mainly during snow melting when snow remained in ditches and along forest edges. Days with snow (103 days of observation) describe conditions with a continuous snow cover. Yearly maximum snow depth varied from 20 cm (1992/1993) to 60 cm (1998/1999), with intervening snow-free periods in most winters.

Statistics

All statistical analyses were performed using a single observation or a combined series of observations of a single individual as sample unit. Possible individual preferences may represent a source of error since it is not known if the same individual has been sampled repeatedly. The reference used for statistical analyses was Mäkinen (1978).

Results

Territory and hunting habitats

In the two study areas (1 and 2) studied during a complete season, the yearly territory size varied between 88 and 200 ha (mean ± SE = 144 ha ± 14.3, n=7; Table 1). The shrikes preferred different habitats under conditions with snow cover compared to snow free periods (χ^2=48.80, df=5, p<0.001, Chi-square test; Figure 2). Meadows and reedbed areas were more frequently used in periods with snow whereas arable fields were more frequently used in snow free periods. Compared to their relative abundance dry meadows were used more frequently than expected, independently on snow conditions. In the presence of snow cover arable fields were used less and wet meadows and reedbeds more than expected. Under severe winter conditions the shrikes hunted also in forests and among human habitations.

Under snow free conditions most mammalian prey was taken on arable fields while they were taken in all habitats during periods with snow cover (Table 2). In periods with snow, significantly more mammals were taken in vegetation-rich (meadows and reeds) than in vegetation-scarce (arable fields) open habitats, (p<0.01, Fisher´s Exact Test). In arable fields, ditches with dense vegetation were of special importance in autumn and in snow free periods whereas more prey was caught from the open parts when snow was present (p<0.05, Fisher´s Exact Test).

Hunting frequency

The average frequencies of the different modes of hunting together with the successful captures of vertebrates are presented in Table 3. Under snow depths below 30 cm there was only a tendency that the average capture rate of mammals should decrease although a clear decrease of the encounter rate with ground-living prey was evident (Figure 3). A total of 4 successfully captured birds has been observed and the average rate of bird-hunting efforts (n=57) did not increase with increased snow depth. Also hunting by hovering remained independent of snow conditions.

Perch selection and effect of snow layer

Deciduous trees and telephone wires were the most available and most frequently used perches. In deciduous trees the shrikes favoured high perches

Table 2. Successful hunting of small mammals in different habitats in the presence or absence of a snow cover.
Lyckade fångster av små däggdjur i de olika biotoperna i förhållanden med eller utan snötäcke.

	No snow *Snöfritt*	Snow *Snö*
Arable fields *Odlad mark*		
Total *Totalt*	15	13
Arable parts *Odlad del*	3	8
Ditches *Diken*	12	5
Dry Meadows *Torra ängar*	2	9
Wet meadows *Våtängar*	0	5
Reedbeds *Vassvikar*	1	7
Forest and forest edges *Skog samt skogskanter*	0	2
Human habitations *Bosatta områden*	0	1

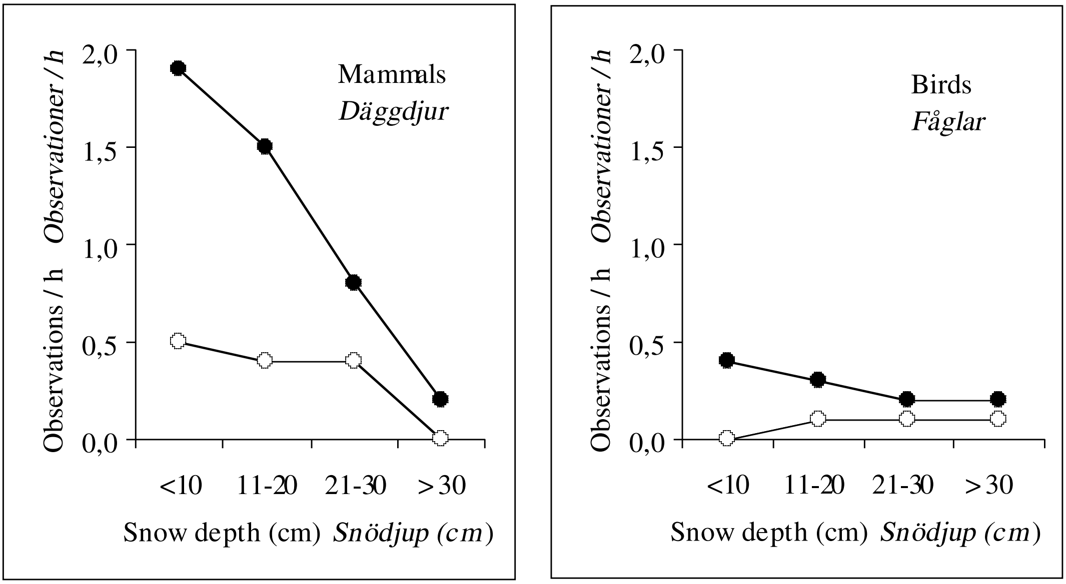

Figure 3. The effect of snow depth on the average hunting (•) and capture (o) frequency of ground-living prey (mainly mammals) and birds. In the case of ground-living prey the hunting includes drop-hunting and hovering. Number of observation days and hours were: <10: 23 days, 61h, 11–20: 14 days, 26.5h, 21–30: 8 days, 14h and >30: 8 days, 8.4h.
Snödjupets inverkan på jaktintensiteten (•) och fångstfrekvensen (o) på marklevande byten (troligen mestadels däggdjur) och fåglar. Beträffande marklevande byten inbegriper jaktintensiteten droppjakter samt ryttlingar. Antal observationsdagar samt timmar var: <10: 23 dagar, 61h, 11–20: 14 dagar, 26.5h, 21–30: 8 dagar, 14h och >30: 8 dagar, 8.4h.

when compared to the availability (χ^2=263.7, df=1, p<0.001, Table 4). This was especially evident when the ground was snow-covered (χ^2=14.76, df=1, p<0.001, Table 5). In the Loggerhead Shrike, wind speed affected the selection of perches (Mills 1979). In the present study no wind measurements were performed but in strong wind with snowfall, the shrikes preferred perches along wind-sheltered forest edges rather than in trees or on telephone wires in open country.

Activity of invertebrate foraging and perch selection

Under snow free conditions, the frequency of drop hunting strikes increased when the temperature was above 0°C but in the presence of a snow cover the

Table 3. The total frequency (observations / h) of different hunting techniques of the Great Grey Shrike and successful hunting of vertebrates.
Frekvensen (observationer / h) av olika mönster i varfågelns jaktbeteende samt lyckade jakter av ryggradsdjur.

	No snow *Snöfritt*	Snow *Snö*
Days of observation (n) *Observationsdagar (n)*	52	53
Observation time (h) *Observationstid (h)*	61	110
Drop hunting *Droppjakt*	8.39	0.93
Hovering *Ryttling*	0.44	0.54
Areal chase of insects *Jakt av flygande insekter*	0.23	0
Bird-hunting *Jakt på fågel*	0.33	0.34
Captured mammals *Tagna däggdjur*	0.30	0.36
Captured birds *Tagna fåglar*	0	0.04

Table 4. Percentage of observed and available perches. Deciduous and coniferuous trees include single trees and small groups of trees in open habitat.
Observerade utsiktsplatser (%) samt tillgängliga (%). Löv- och barrträd inkluderar enskilda träd samt små grupper av träd.

		Observed *Observerad*	Available *Tillgänglig*
Observations *Observationer* (n)		1192	
Available perches *Tillgängliga* (n)			1136
Deciduous tree	>10m	31	7.0
Lövträd	<10m	30	56
Coniferuous tree	>10m	1.2	4.4
Barrträd	<10m	1.1	8.8
Telephone wire *Ledning*		22	18
High plant *Växt*	<2.0m	4.9	–
Roof of a barn *Lada*		0.2	0.7
Pole *Stolpe*	>10m	1.7	0.3
	<10m	1.2	4.8
Tree in forest *Träd i skog*		3.8	–
Ground *Marken*		3.2	–

hunting activity for ground-living prey remained independent of temperature (Figure 4). Judged from these observations active foraging on invertebrates occurred when the drop-hunting frequency exceeded 10 strikes/h.

During active hunting of invertebrates the shrikes favoured lower perches in winter but not in the autumn (September–October) (Figure 5). In periods with snow higher perches were used and the time/perch increased with increased perch height (Figure 5 and 6). Sometimes the shrikes refrained from hunting invertebrates also during snow free conditions, probably depending on lack of invertebrates. Under such conditions the time on each perch in-

Table 5. Percentage of observed perches and height selection in deciduous trees with and without snow layer.
Observerade utsiktsplatser (%) samt höjd i lövträd med och utan snötäcke.

		Snow *Snö*	No snow *Snöfritt*
Observations *Observationer* (n)		501	691
Deciduous tree	>10m	40	24
Lövträd	<10m	29	31
Telephone wire *Ledning*		16	26
Others *Övriga*		15	19

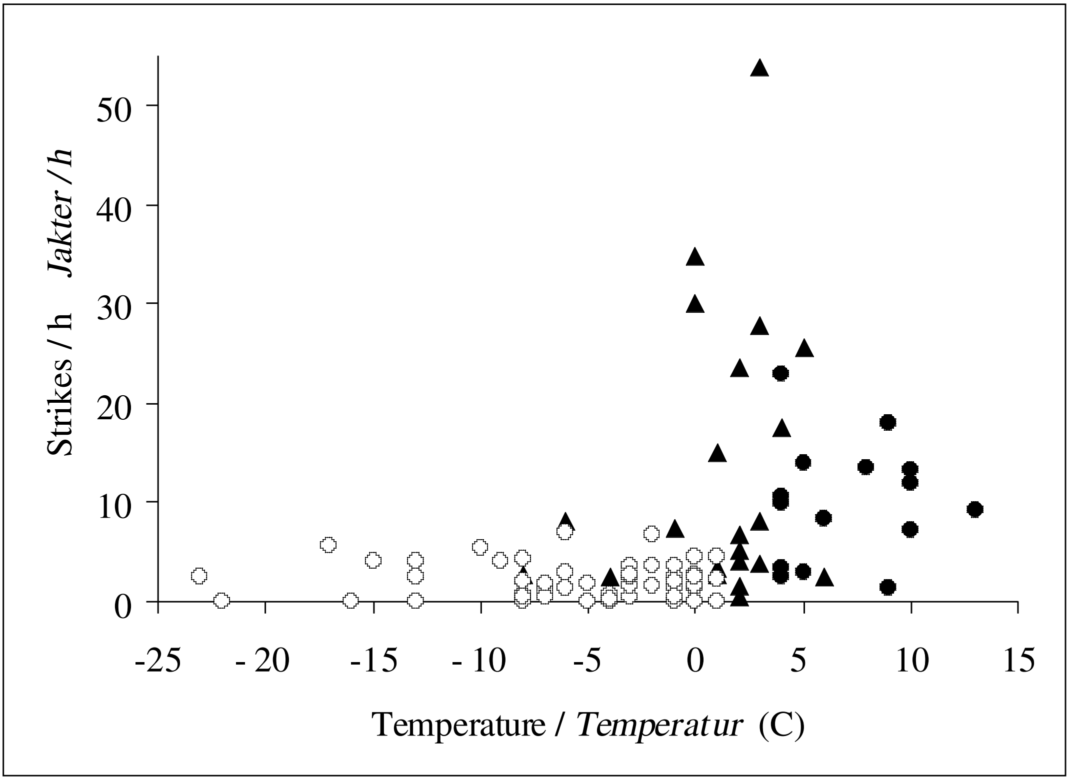

Figure 4. Drop hunting activity (strikes/h) plotted as a function of air temperature (C°). o = snow cover present, October–March, • = no snow cover, autumn, September–October and m = no snow cover, November–February. Only days with >1 h of continuous observation included.
Intensiteten av droppjakt (jakter/h) vid olika temperaturer (C°). o *= snötäcke, oktober–april,* • *= snöfritt, september–oktober och* m *= snöfritt, november–februari. Enbart dagar med >1 h av kontinuerliga observationer är inkluderade.*

creased together with perch height (F=2.82, df1=3, df_2=77, p<0.05, one-way ANOVA). This did not occur under conditions with active foraging on invertebrates (autumn: F=1.21, df1=3, df_2=37, not significant, and snow-free winter days: F=1.46, df1=3, df_2=96, not significant). Nevertheless, the overall time/perch was longer when mainly vertebrates were hunted, independent on the snow condition (mean ± SE = 12.8 min ± 0.68, n=294 vs. 8.1 min ± 1.82, n=160, p<0.001, t-test).

Movement between perches

Mobility did not change with snow depth (F=0.599, df1=4, df_2=70, one-way ANOVA) even though this presumably decreased the availability of small mammals (Figure 7). The total mean (±SE) rate of mobility was 650 m/h ± 54.1 (n=75 days of observation).

Distance to mammalian prey

The mean distance (±SE) from the perch to the point where a small mammal was captured was considerably longer when snow cover was present (65 m ± 6.8, n=36) than when the ground was snow free (30 m ± 4.0, n=18, p<0.001, t-test).

Discussion

Territory size and habitat selection

Compared to previous studies, the mean yearly territory size, 144 ha, in my study area was slightly larger than in south-eastern Sweden (110 ha, Olsson 1984b) and considerably larger than in central Europe (52–68 ha, Schön 1994). This is consistent with previous calculations showing that territory size increases with latitude (Schön 1994). However, the territory size may be very different between years

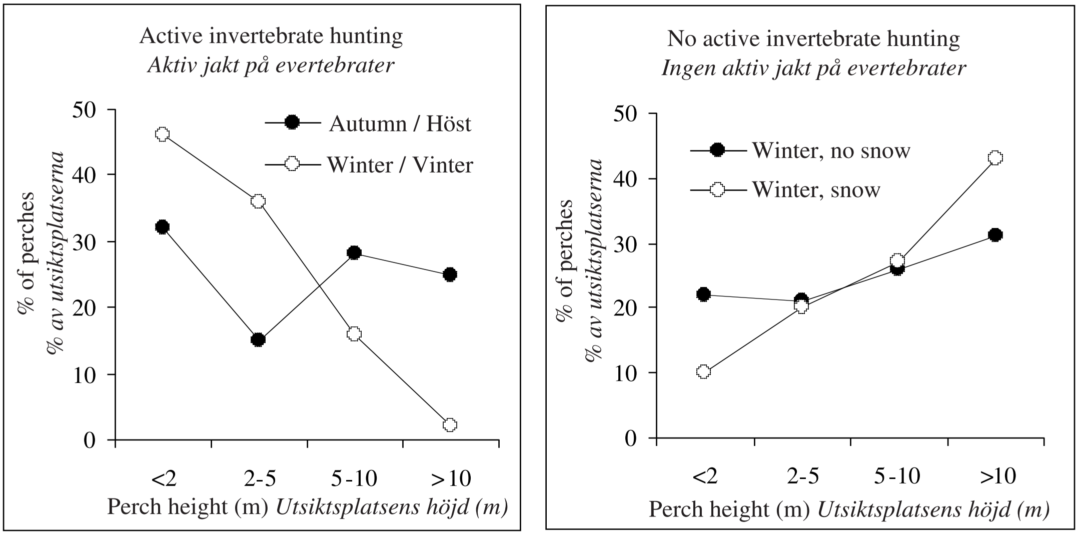

Figure 5. Percentage of selected perches together with the activity of invertebrate hunting. Autumn (September–October) data was collected on 7 days (382 min on perches). Active invertebrate foraging in winter was observed on 8 days (733 min). Periods without active hunting for invertebrates occurred during all days (41 days) with snow (2945 min) and some snow free winter days (11 days, 820 min).

Valda utsiktsplatser (%) och jaktaktiviteten på evertebrater. Data från hösten (september–oktober) representerar 7 dagar och 382 min på utsiktsplatser. Aktiv jakt på evertebrater (>10 droppjakter/h) noterades under vintern (8 dagar, 733min) medan perioder utan jakt på evertebrater observerades alla dagar med snö (41 dagar, 2945 min) och några snöfria vinterdagar (11 dagar, 820 min).

(Olsson 1984b) due to differences in prey abundance and availability. Also the perch density may affect the territory size (Yosef & Grubb 1994) making it difficult to compare territories in different regions.

As in south-eastern Sweden (Olsson 1984a) vegetation-rich meadows were essential hunting habitats in winter but in my study also dense reedbeds were important. In the present study area, the main vertebrate prey was the Harvest Mouse *Micromys minutus* and *Microtus*-voles (Karlsson 1998). In winter, meadows are important habitats for these rodents and the Harvest Mouse is also common in reedbeds (Siivonen & Sulkava 1994). The fact that shrikes preferred reedbeds in my study but not in Olsson's probably depend on that the Harvest Mouse does not occur in south-eastern Sweden. According to Mills (1979) shrikes use areas with high vegetation only if a high prey density compensates the low visibility. Apparently this was the case in my study.

The habitat use was different depending on snow conditions. The use of vegetation-scarce arable fields in periods without snow indicates that these areas are especially used for foraging on invertebrates. This is consistent with previous studies on shrike behaviour and vegetation structure (Mills 1979, Brandl et al. 1986, Yosef & Grubb 1993, Schaub 1996). Thus, the shrikes chose the habitat that maximised the number of invertebrates and not the vegetation rich habitats where the density of small mammals appeared to be highest. According to optimal foraging theories it may thus be more energetically rewarding to hunt invertebrates than vertebrates.

Perch selection and activity of invertebrate hunting

When hunting vertebrates only, the shrikes selected higher perches and increased the time/perch. This is consistent with theories of optimal perch height under conditions of increased prey size in combination with decreased prey availability (Mills 1979). The shrikes favoured lower perches when hunting invertebrates in winter, but not in autumn. This could depend on the presence of foliage on the deciduous trees, which may be avoided by the shrikes (Huhtala et al. 1977). Instead especially telephone wires were frequently used. Also, the type of invertebrate prey is different in the autumn than during mild winter days. Large insects are favoured

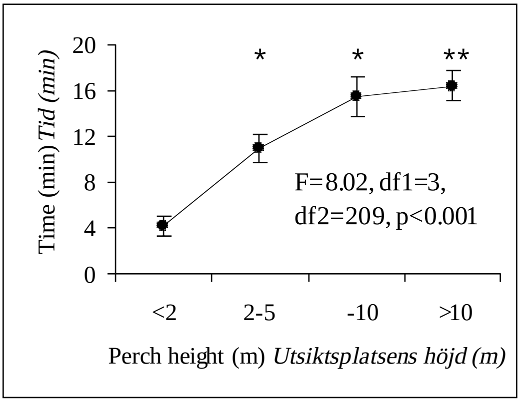

Figure 6. The time minutes/perch ± SE under conditions with snow when there was no obvious foraging on invertebrates. One-way ANOVA was used to test the differences. *) different to <2 m group and **) different to <2 m and 2–5 m groups (A posteriori comparison with Newman-Keul´s test, p<0.05 level).
*Tiden (min)/utsiktsplats ± SE i förhållanden med snö och då ingen jakt på evertebrater iakttogs. Envägs-ANOVA användes för att jämföra tiden/utsiktsplats. *) signifikant jämfört med <2 m gruppen och **) jämfört med <2 m samt 2–5 m gruppen (Newman-Keul´s test, p<0.05).*

in the autumn but these are not available in winter when spiders are more important (Olsson 1986). Also the Woodchat Shrike *Lanius senator* uses lower perches when hunting smaller invertebrates (Schaub 1996). In addition, territorial advertisement and territory occupation may cause the use of higher perches (Mills 1979). However, these factors should not affect perch selection decisions during the winter since the territories are already occupied and the shrikes usually have no contact with conspecifics (Olsson 1984b).

An increased frequency of perch-changes and thus an increased mobility may reflect an increase in prey searching rate (Schaub 1996). In the present study the mean mobility between perches remained independent of snow depth. This probably illustrates the habit of the species to hunt in an energy-saving way from a few favourable perches in a known territory. Together with the observed increase of time/perch when hunting vertebrates only, it indicates that the distance between two perches increases when hunting from higher perches, as suggested by the theory of optimal perch height (Mills 1979).

Considerations on optimal foraging theory

Snow is probably the most important external factor affecting the availability of different prey types. In northern wintering areas invertebrates are available only during periods of mild weather, and vertebrates, mainly shrews, voles and mice, are the prey that the Great Grey Shrike depends on for survival in cold weather (Huhtala et al. 1977, Olsson 1986).

According to the zero-one rule of the prey model (Stephens & Krebs 1986) a predator should always ignore less profitable prey if the encounter rate with more profitable prey is sufficiently high. Likewise, the predator should always take less profitable prey if the contacts with more profitable prey are sufficiently infrequent. The Great Grey Shrike confirms the predictions in the sense that the optimal strategy for hunting invertebrates always is adopted if these are available (Olsson 1986). In the present study this was evident as an increased drop hunting activity when the temperature was above 0°C and the ground snow-free. Shorter distance to prey, short handling time and higher rates of encounters and successful captures may make the hunting of invertebrates energetically rewarding despite their small size.

The average rate of successfully captured mammals remained similar in conditions without or with snow

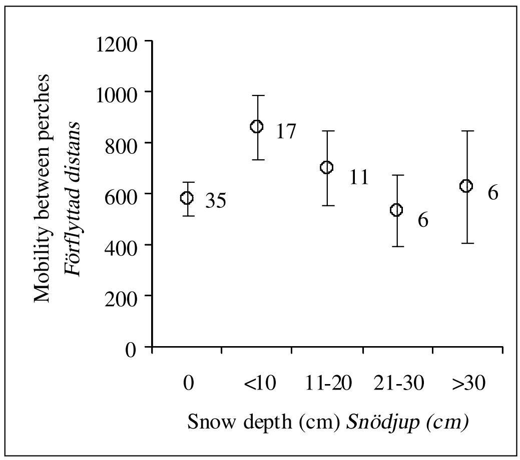

Figure 7. The mobility of Great Grey Shrikes measured as distance between perches in metres moved per hour (± SE) during a period of continuous observation (1h or more) at different snow depths. Data labels = number of observation days.
Varfåglarnas rörlighet mätt som tillrygalagd sträcka mellan utsiktsplatser (m) per timme (± SE) under en tid av kontinuerlig observation (>1h) samt olika snödjup). Antal observationsdagar visas invid varje data.

cover indicating that an adaptation to hunting for invertebrates did not affect the energy received from large prey. This may depend on that also vertebrates became easier to capture or more common under snow free conditions. Thus the switch of habitat and preference for lower perches when hunting invertebrates maximised the total energy in accordance with optimal foraging theory. Invertebrates were hunted from lower posts and probably as a consequence of this the distance to captured mammals decreased under snow free conditions. Thus, the energy used per successfully taken mammal may also be lower under such conditions compared to when there was snow cover.

An increase in snow depth decreases the availability of ground-living mammals to avian predators. In this study the average number of encounters with ground-living prey decreased with increased snow depth, but only under conditions with a snow cover deeper than 30 cm was there a negative trend on the capture rate of mammals. The Great Grey Shrike is generally not considered to be an effective predator on birds. Still an increased snow depth have been associated with an increase of birds in the diet (Leivo 1942, Olsson 1984b), possibly as a result of an increased number of weak and more easily captured individuals (Olsson 1984b). My study supports this suggestion since the rate of bird-hunting did not seem to increase with snow depth.

Conclusions

With the exception of a frequent use of reedbeds in periods with snow, the habitats were similar as observed previously (Olsson 1984a). The habitat selection probably depended on the availability of invertebrates and was therefore different depending on snow cover. In winter, perch selection followed predictions from theories on optimal perch height (Mills 1979), i.e. increased perch height and an increased time/perch in conditions with decreased prey availability but increased prey size. In accordance with optimal foraging theory the shrikes appeared to be able to maximise the energy intake by changing habitat and perch height to utilise invertebrates when available.

Acknowledgements

During the preparation of the manuscript Viking Olsson, Remo Probst, Martin Schön, Anders Brodin and an anonymous reviewer provided me with valuable comments and suggestions.

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Sammanfattning

Valet av jaktbiotop och utsiktsplatser hos varfågeln Lanius excubitor *samt effekten av snötäcke och bytestyp*

Inledning

Varfågeln är en rovfågellik tätting som i motsats till övriga törnskatearter kan övergå till jakt på enbart ryggradsdjur. Detta möjliggör att arten kan övervintra regelbundet också i Norden (Huhtala et al. 1977, Olsson 1986). Ett villkor för effektiv jakt är lämpliga utsiktsplatser i öppna landskap (Olsson 1984a, Schön 1994). I denna uppsats beskrivs fältobservationer av varfågelns val av biotop samt utsiktsplatser i några vinterlokaler i sydvästra Finland (Figur 1) med en tyngdpunkt på anpassningar till olika snöförhållanden samt jagad bytestyp.

Metoder

Undersökningen utfördes 1992–2000, varje vinterhalvår (slutet av september t.o.m. början av april) förutom 1993/94. Vid varje besök (n=198 dagar) till någon av lokalerna noterades jaktbiotopen. Revirens storlek beräknades enligt Olsson (1984b) och Schön (1994). Varfågeln ansågs utnyttja en biotop ifall den observerades göra åtminstone ett jaktförsök där. Fåglarna observerades med kikare (0.5–11h/dag, totalt 171 h, 105 dagar). Samtliga jaktbeteenden och lyckade jakter av ryggradsdjur noterades. Utsiktsplatsernas höjd samt avståndet till taget byte (däggdjur) uppskattades på basen av kända avstånd i reviret. Beräkningarna av varfåglarnas rörlighet baserades på hur lång sträcka de tillryggalade per tidsenhet mellan utsiktsplatserna.

Resultat

Genomsnittsstorleken på reviren var 144 ha (SE=14.3) (Tabell 1). Typiska jaktbiotoper var åkermarker, torra gräsängar, våtängar samt vassvikar och under strängare vinterperioder också skogsmark samt miljöer nära mänskliga bosättningar. Varfåglarna utnyttjade fler olika biotoper under perioder med snötäcke än under hösten eller snöfria vinterperioder. Under perioder med snö användes vassvikar och ängar mera än väntat medan åkermarkerna mindre än väntat jämfört med förekomsten av dessa biotoper (Figur 2). Under snöfria förhållanden fångades däggdjursbyten i diken mellan plöjda eller skördade åkerfält medan de vegetationsrika biotoperna hade större betydelse i snötäckta marker (Tabell 2).

Intensiteten av olika jaktformer samt fångstfrekvensen av ryggradsdjur presenteras i Tabell 3. Jaktintensiteten på marklevande djur minskade med ökat snödjup, vilket inte var fallet beträffande jakt på småfågel (Figur 3). Lövträd var den vanligaste typen av utsiktsplats och träd högre än 10m föredrogs då marken var snötäckt (Tabell 4 och 5). Valet av höjd för utsiktsplatserna var också beroende av bytestypen. I snöfria marker tilltog ”droppjakt”-intensiteten med temperaturen när denna var över 0 °C som en följd av ökad jakt på ryggradslösa djur (Figur 4). Varfåglarna föredrog låga utsiktsplatser under snöfria vinterperioder då evertebrater jagades medan förhållandet var det motsatta då dessa inte var tillgängliga (Figur 5). Under förhållanden med snö ökade tiden/utsiktsplats med utsiktsplatsens höjd (Figur 6) och överlag var tiden/utsiktsplats längre då enbart vertebrater jagades (12.8 min, SE=0.68 vs. 8.1 min, SE= 1.82, $p<0.001$, t-test). Varfåglarnas rörlighet visade inget beroende av snödjup (Figur 7) men avståndet från sittplats till taget byte var betydligt längre (65 ± 41 m) när marken var snötäckt än när den var snöfri (30 ± 17 m, $p<0.001$, t-test).

Diskussion

För varfågeln betyder ett snötäcke ett färre antal tillgängliga byten p.g.a. den ringa åtkomligheten av ryggradslösa djur. Som en följd av detta utnyttjade varfåglarna då i större utsträckning alla tillgängliga biotoper och speciellt de vegetationsrika biotoperna var då av stor betydelse. Dessutom noterades en övergång till högre utsiktsplatser. Utnyttjandet av högre utsiktsplatser samt längre tid/utsiktsplats överensstämmer med teorierna om val av utsiktsplats under förhållanden med färre men större byten (Mills 1979). Under jakt på evertebrater valde varfåglarna lägre utsiktsplatser under vintern men inte under hösten. Detta kunde orsakas av att: 1) lövträden fortfarande har löv, vilket innebär att varfågeln undviker dessa p.g.a. sämre sikt (Huhtala et al. 1977), 2) skillnader i bytesval, på hösten jagas större, och även flygande insekter medan dessa ej är tillgängliga under vintern då spindlar är av större betydelse (Huhtala et al. 1977, Olsson 1986), 3) på hösten då reviren etableras har varfågeln ett större behov att framhäva sin närvaro för övriga varfåglar. Detta torde ha mindre betydelse vintertid då enskilda varfåglar har mycket liten kontakt med varandra (Olsson 1984b).

Liksom i en tidigare studie (Olsson 1984a) var ängsmarker betydligt mera utnyttjade än vad som kunde väntas av deras relativa förekomst i reviren. I

min studie gällde detta även vassvikar under förhållanden med snö. Detta är troligen ett resultat av rikligare bytesförekomst och då speciellt av *Microtus*-sorkar på ängsmarkerna och dvärgmusen *Micromys minutus* i bägge biotoperna (Siivonen & Sulkava 1994, Karlsson 1998). Den högre preferensen för vassvikar i min studie jämfört med Olssons beror troligen på att dvärgmusen inte förekommer i hans undersökningsområde. Om evertebrater är tillgängliga föredrar varfågeln dessa (Olsson 1984b) och detta torde vara den primära orsaken till att varfågeln jagade huvudsakligen på odlad mark under hösten och under snöfria milda vinterperioder. Skördade eller plöjda fält saknar sikthinder i form av vegetation och torde därför vara utmärkta marker för jakt på marklevande ryggradslösa djur. Sålunda verkar tillgången på evertebrater styra varfågelns val av jaktbiotop och dess val av höjd på utsiktsplatsen. Frekvensen av fångade däggdjur var dock densamma i snöfria som i snötäckta marker. Att detta skedde trots att varfågeln föredrar evertebrater kan bero på att också vertebrater blev vanligare eller att de blev lättare att fånga. Varfågelns sätt att anpassa jaktsättet verkar medföra en maximering av energiintaget helt enligt teorierna om optimal furagering (Stephens & Krebs 1986).