

# Spatio-temporal changes in Great Grey Shrike *Lanius excubitor* impaling behaviour: from food caching to communication signs

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We studied temporal and spatial patterns of impaling behaviour in a resident population of the Great Grey Shrike *Lanius excubitor* throughout the year. The information was collected in western Poland during the years 2000–2003. The presented findings indicate several seasonal shifts in the pattern of impaling behaviour, expressed as changes in the taxonomic composition of larders, level of food consumption, concealment of impaling places, as well as the spatial distribution of larders. During the mating period, males impaled more prey before mating than afterwards, the majority of prey was located on borders of territories and in visible places, and a large part of the prey was left uneaten. The pattern described above indicates that during the mating period impaling behaviour has a signalling function. In contrast, during the breeding stages impaling was primarily used to store food – the distance from larders to nests decreased, more prey were stored in well hidden places, and a larger proportion of stored food was consumed.

Key words: impaling behaviour – spatial and temporal changes – displays – Great Grey Shrike – *Lanius excubitor*

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## INTRODUCTION

Shrikes, small to medium sized passerines, have some similarities to raptors both in morphology, for instance the presence of the tomial tooth on the beak, as well as in lifestyle, e.g. hunting techniques (Cade 1995). However shrikes, unlike raptors, do not have talons or strong feet, and they do not use legs during manipulation of prey, therefore impaling and wedging of prey is necessary for dismembering and portioning larger prey items. Shrikes also, in contrast to raptors, do not have

crops, thus they are forced to eat larger prey in several meals (Lefranc & Worfolk 1997, Harris & Franklin 2000). Moreover, food caching offers opportunities to access otherwise toxic prey (Yosef & Whitman 1992). Hence the impaling behaviour is considered to be an evolutionary feeding adaptation (Cade 1995). Food caching provides other benefits such as smoothing-out the short-term food shortages caused e.g. by harsh weather conditions (Lefranc & Worfolk 1997, Tryjanowski *et al.* 2003), or when energy requirements increase rapidly, for example during egg laying and during

rapid growth of nestlings (Carlson 1989). Moreover, impaled prey items may play an informative role in shrikes, as signals of quality of the territory or of the territory-owner. Such behaviour may improve mating and breeding success, as shown by Yosef & Pinshow (1989). Besides, impaled objects located in conspicuous places might serve as landmarks and therefore are useful for territory demarcation (Sloane 1991).

However, the majority of studies on impaling behaviour have traditionally focused on larders to determine diet composition or were restricted to only one of the potential functions or benefits in a short period of the shrike life-cycle (see citations above, but see also Karasawa 1976 and Kobayashi 1980 for the Bull-headed Shrike, *Lanius bucephalus*, in Japan). Only a handful of studies have examined seasonal and spatial aspects of caching behaviour (e.g. Hernández 1995) or made comparisons among closely related species (but see Valera *et al.* 2001).

The Great Grey Shrike *Lanius excubitor* represents one of the largest species of true shrikes (Lefranc & Worfolk 1997). Its diet consists mainly of insects, but also small vertebrates (rodents, birds, reptiles) which are regularly impaled or wedged (Lefranc & Worfolk 1997). We studied temporal and spatial patterns of impaling behaviour in a resident population of the Great Grey Shrike throughout the year. We hypothesized that the spatio-temporal pattern of impaling would change with season. If males used the larders for advertising territory occupation or for signalling the quality of the territory and/or of themselves, there should be a higher frequency of impaling before pairing than afterwards. Moreover, prey items should be located in visible places and on boundaries of territories. Also, we predicted that the proportion of uneaten prey items is higher during the mating phase than during the rest of the year. In contrast, during the breeding season, when the birds have the highest energetic requirements, we expected that the prey items are well hidden, that larders are located close to the nests, and that the level of consumption of the stored food is at its highest.

## STUDY AREA AND METHODS

The material was collected near the town of Odolanów (51°34'N, 17°40'E) in western Poland during the years 2000–2003. The study area (220 km<sup>2</sup>) is an agricultural landscape with arable fields, meadows, pastures and small woodlots of different ages, which are occasionally connected by rows of trees. This area supports one of the densest populations of the Great Grey Shrike in western Poland and in Europe (Tryjanowski *et al.* 1999, Antczak *et al.* 2004). This population is partially resident; some males occupy territories all year round (unpubl. data). In winter, birds arrive in the area, probably from the north-eastern parts of their breeding range (e.g. Ukraine, Russia). The breeding territories were regularly surveyed for breeding pairs and nests. Observations on foraging behaviour and breeding biology, including date of mating, laying date, clutch size, brood size (see Antczak *et al.* 2004), were recorded from late February until late July. During these observations territories were mapped. Winter territories were surveyed from late November to mid-February. Throughout the study period, we searched for impaled prey items along random transects dispersed throughout the territories; each searching session lasted 45 – 60 minutes. We collected data on: date, prey type and its state (fresh or dry), type of impaling substrate (e.g. bush, barbed wire, fences, exposed perches, top of trees), and distance from caches to the nest. The following periods were distinguished: wintering, mating, incubation, nestling and fledgling period. The last four periods formed the breeding season, and were used in comparison of distances between a larder and a nest. These periods were defined by direct observation in each territory. Mating period was defined from the start of territorial displays until gaining a female. Incubation was defined from egg laying to hatching date, nestling period as the presence of nestlings; fledgling period was defined as from fledging until two weeks after fledging. During the study period we surveyed 8 (year 2000) to 13–20 breeding territories (in 2001–2003).

Impaling sites were divided into two classes that express possibilities of concealment of stored food. 'Concealed larder' comprised the interior of large, dense bushes, such as willow (*Salix* sp.), elder (*Sambucus nigra*), thorn bushes (*Prunus spinosa*, *Crataegus* sp.) and pines (*Pinus sylvestris*) where stored food was well hidden. By contrast, 'conspicuous larders' were represented by places where impaled prey items were highly visible – mainly tops of trees, solitary upstanding sprigs, sparse parts of trees, and trees and bushes with wide sparse crowns like young specimens of *Betula* sp., *Padus* sp., *Alnus* sp., *Pyrus* sp. as well as artificial impaling places.

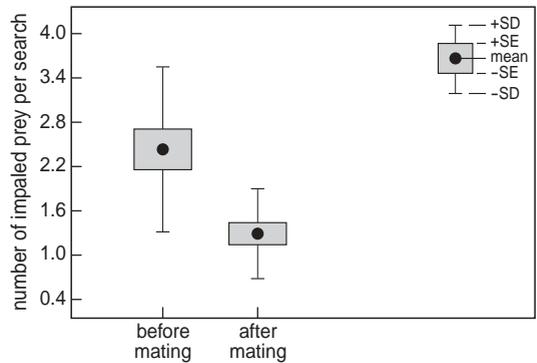
All basic statistics was performed using Statistica for Windows software. If variables met requirements of normality then parametric tests were used. If not, non-parametric methods were performed, or data were log transformed. Values are presented as means  $\pm$  1 SD. Because not all prey items were described completely, sample sizes differed slightly in particular analyses.

## RESULTS

### Seasonal changes in impaling frequency and composition of prey

During the study period 276 prey items cached by Great Grey Shrikes were found. Of these, 61 (22.1%) were impaled during winter, 70 (25.4%) in the mating period, 28 (10.1%) during incubation, 93 (33.7%) during the nestling period, and 24 (8.7%) during the fledgling period. The highest abundance of impaled prey per searching session was during the nestling period, fledgling period and in winter ( $2.00 \pm 0.96$ ,  $2.22 \pm 0.97$ ,  $2.14 \pm 1.97$ , respectively). However, considering all periods differences were not significant (One-way ANOVA:  $F_{4,271} = 0.62$ ,  $P = 0.64$ ). If the mating period is separated into two sub-periods, males impaled significantly more prey items before pairing with a female than after it ( $2.44 \pm 1.14$  vs.  $1.31 \pm 0.60$ ,  $n_1 = 18$  and  $n_2 = 16$ , respectively, Mann-Whitney test:  $Z = 2.98$ ,  $P = 0.002$ , Fig. 1).

Larder items ( $n = 276$ ) consisted of mammals



**Figure 1.** Comparison of mean number of impaled prey items by Great Grey Shrike males before and after mating, western Poland.

(20.6%), birds (30.7%), insects (23.8%), reptiles (20.6%) and amphibians (4.3%). Taxonomic composition of impaled prey items (considering number, not biomass) differed markedly throughout the season. During winter, rodents (mainly voles *Microtus* sp.), formed the bulk of larders, followed by insects; birds comprised 4.9% of all prey stored in this period. During mating and incubation periods there was dominance of lizards that composed almost half of all cached prey. Insects were the second most frequent prey, followed by mammals and birds. The nestling period was characterized by a strong dominance of birds (more than 60% of all impaled larders), whereas the proportions of mammals and reptiles were equally low. During the fledgling period, similar to the nestling period, birds were the main impaled prey (over 50%), followed by rodents.

### Changes in level of consumption of larders

Among the 236 prey items impaled by the Great Grey Shrike with information of consumption status, 149 (63.2%) had been consumed or had signs of partial consumption when initially found, 87 (36.8%) were left uneaten and consequently dried out. There were significant differences in the level of consumption of impaled prey through the season ( $\chi^2 = 66.24$ ,  $df = 4$ ,  $P < 0.01$ , Fig. 2). During winter more than half (53.9%) of impaled prey

were consumed though the proportion of uneaten prey was considerable (46.1%). In the mating period the majority (74.6%) of stored food was left uneaten. In contrast, during incubation more than 70% of all prey impaled was hoarded for consumption. Nestling and fledgling periods were characterized by even higher proportions of items consumed (90.4% and 84.2%, respectively).

**Seasonal changes in concealment of food and use of impaling places**

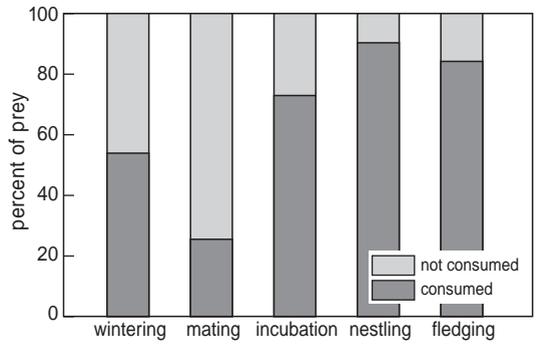
There were strong differences in the use of impaling substrates through the season ( $\chi^2 = 41.32$ ,  $df = 4$ ,  $P < 0.01$ , Fig. 3). During winter, prey items were stored in similar amounts in conspicuous and concealed places. During the mating period the use of ‘conspicuous larders’ increased steeply. At the beginning of incubation there was an increase of prey in hidden places, although an important part of the impaled prey was still located in visible places. Use of impaling places during the presence of young in the nests and just after fledgling showed a very similar pattern to one another by shrikes storing considerably more food in ‘concealed’ than in ‘conspicuous larders’.

**Scattering of stored resources**

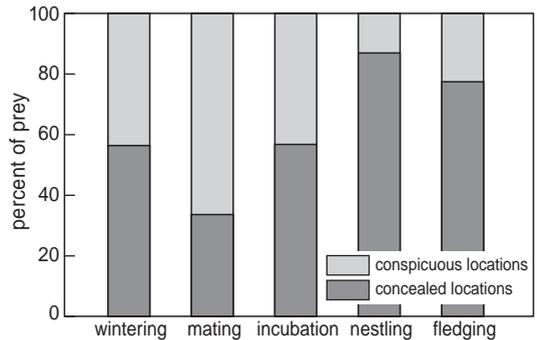
The Great Grey Shrikes cached on average  $1.06 \pm 0.25$  ( $n = 224$ ) items in the same impaling place and this pattern did not differ significantly through the year (Kruskal-Wallis test:  $H = 5.89$ ,  $P > 0.20$ ).

**Spatial distribution of larders during pre-breeding and breeding season**

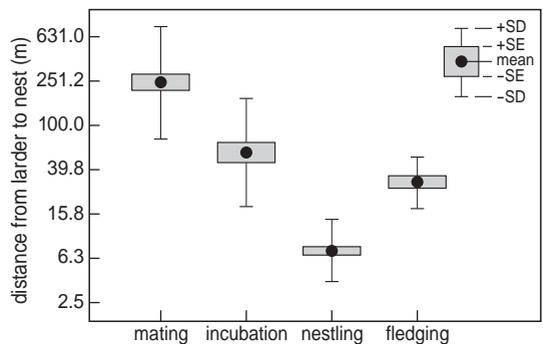
The distance from larder to nest differed significantly between periods (Kruskal-Wallis test:  $H = 108.09$ ,  $P < 0.0001$ , Fig. 4). Results of *post hoc* comparisons (Newman-Keuls test:  $P < 0.001$ ) showed significant differences between the mating period and all other stages of the nesting period. Shrikes impaled prey significantly further from future nest places, mainly on the borders of territories (mean  $389 \pm 310$  m,  $n = 42$ ) than in other periods of the year. The average distance from larder to the nest in the incubation period was



**Figure 2.** Seasonal changes in level of the consumption of impaled prey by Great Grey Shrike, western Poland.



**Figure 3.** Seasonal changes in concealment of stored food by Great Grey Shrike, western Poland.



**Figure 4.** Changes in spatial distribution of Great Grey Shrike larders expressed as distance from larder to nest in consecutive breeding stages.

112 ± 147 m ( $n = 27$ ) and was significantly closer than in the mating period but further than in nestling period. During the nestling stage, larders were located closer to the nests (mean 8.76 ± 4.38 m,  $n = 58$ ) than in other periods. During the fledgling period larders were again placed further from nests than in the nestling period (mean 34 ± 24 m,  $n = 17$ , Fig. 4).

## DISCUSSION

The presented findings indicate seasonal shifts in several aspects of impaling behaviour by Great Grey Shrikes: the taxonomic composition of larders, level of food consumption, concealment of impaling places, as well as the spatial distribution of larders. Regarding the taxonomic composition of impaled prey the most interesting finding is the great variation among periods. The data support, in general, the importance of small mammals for wintering Great Grey Shrikes (Olsson 1985, Starka 1991, Hromada & Krištin 1996). The marginal contribution of lizards and amphibians is understandable because of extremely low activity of these animals during winter. The dominance of birds in prey impaled during the period of rearing young is in agreement with other studies (Cade 1967, Lorek *et al.* 2000).

These findings confirm our predictions concerning the pattern of impaling throughout the year. Behaviour in the mating period showed a distinctive pattern. Firstly, males before mating impaled significantly more prey than afterwards. Indeed, the majority of prey was impaled in conspicuous places and more than 70% of stored food was left uneaten. Larders were located on the borders of breeding territories. During this period males use larders as an advertisement of territory occupation and the quality of the territory or themselves (Yosef & Pinshow 1989, Sloane 1991). The subsequent decrease in number of impaled prey items might be caused by changes in male behaviour e.g. mate guarding and intensive courtship feeding, indeed females might more directly judge male quality during precopulatory

displays (Lorek 1995, Tryjanowski & Hromada 2005). Larders on the borders of territories might represent information for neighbouring males and be a form of ownership advertisement. In contrast, the nesting period was characterised by a striking decrease of the distance from larders to nests, a high level of stored food consumption and concealment of larders that also fits our hypothesis well. As the breeding season progressed, the distance from larders to nests decreased. Such distribution of larders may be important for the incubating female who is completely dependent on the male and would thus increase nest attendance. At the time of nestling presence, the larders were located closest to the nests, serving probably as food buffers during the feeding of offspring. When fledglings left the nests and families dispersed, the larders were again located further from the nests. Breeding shrikes apparently adjust the distribution of stored resources to satisfy energy requirements, maximize delivery rate and minimize costs of food provisioning. The Great Grey Shrike larders in arctic Alaska were located further than 50 m from the nests during the breeding season. It was proposed that such a kind of scattered distribution of food caches might serve for confusion of potential predators, which are not able to locate the nest (Cade 1967). The same might be true for shrikes in western Poland. In this area the majority of shrikes breed in small woodlots or clumps of trees and larders widely scattered around the nest may also decrease the predation risk. The probability that a predator locates the nest may be reduced when breeding shrikes make short, seemingly indeterminate trips close to the nest, than when making long flights over open space directly to the nest site. Similar changes in the distribution of caches during nesting and fledging were recorded in other shrikes such as the migratory Loggerhead Shrike *Lanius ludovicianus migrans* (Esely & Bollinger 2003) and Red-backed Shrike *Lanius colurio* (Carlson 1985, Hernández 1995). At the time of rearing of nestlings, and just after fledging, the majority of food was stored in large, dense bushes such as willows or elders. These places offer good opportunities for concealing cached food. The

stages of nestling care were characterized by a high level of consumed food; more than 90% of impaled prey was used for consumption.

Interestingly, during winter, shrikes from the studied area left more than 46% of prey uneaten and larders were located in conspicuous places. These findings correspond well with results obtained by Sloane (1991) and Mizzel (1993) for resident populations of the Loggerhead Shrike where, in the non-reproductive period, a large part of prey was left uneaten and placed in visible places. During winter, western Poland supports Great Grey Shrikes from the northeastern parts of their range and in this period densities might be higher than in reproductive periods. The time of arrival of birds from the north-east might encourage resident birds to advertise their own territories. Mizzel (1993) recorded that resident Loggerhead Shrikes increased cache size prior to the arrival of migrant specimens. However it should be noted that Great Grey Shrikes have a prolonged mating period which sometimes might take place even at the end of the winter (Yosef 1992, Lefranc & Worfolk 1997).

The mean number of simultaneously impaled prey items in one place by shrikes in the study population was less than two and did not vary significantly through the year. This indicates that Great Grey Shrikes applied cache scattering in all periods, as recorded in other bird species including shrikes (e.g. Waite & Reeve 1992, Hernández 1995).

Our results, as well as those of other studies on shrikes, indicate that impaling behaviour might be very flexible. The impaling behaviour probably evolved as an evolutionary feeding adaptation to cope with manipulating and dismembering larger prey items (Cade 1995). However, how did impaled prey items become communication signals? Shrikes vocalize but, uncharacteristically for passerines, song does not play a territorial function (Harris & Franklin 2000). Despite this, shrikes display a strong territoriality not only during the breeding season, but exclusive territories might also be established during winter. It may be symptomatic that, so far, evidence for an information function of impaling behaviour has been obtained for year-round resident populations of the few

shrike species that occupy large territories in relation to body size (in the case of Great Grey Shrike over 100 ha, Tryjanowski *et al.* 1999, see also Yosef & Pinshow 1989). Perhaps the paucity of territorial song connected with year-round territoriality, long mating periods and large territory size led some populations to use alternatives to advertise territory holdings. Such alternatives might be impaled objects located in conspicuous places dispersed in territories. Impaled objects may survive several days as landmarks of occupancy, clearly providing information about the state of a particular territory. To sum up, the presented findings support our hypothesis that impaling behaviour serves both to convey information to conspecifics (signaling function during the mating period) and to store food (storage function during the breeding periods).

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## SAMENVATTING

Klauwieren zijn befaamd om het opspitsen van prooien op allerlei plaatsen. Waarom ze dat nu precies doen, is echter niet precies duidelijk. Zo eten ze vaak maar een klein deel op van de prooien die ze opspitsen, wat vreemd lijkt als het gewoon een vorm van bewaren is. In dit stuk proberen de auteurs meer te weten te komen over de functie van het opspitsen van prooien door Klapeksters *Lanius excubitor* in West-Polen. Ze hebben gedurende het gehele jaar onderzocht hoeveel prooien opgespiet werden, waar dit gebeurde, welke prooien dit waren en of ze ook daadwerkelijk werden opgegeten. Het blijkt dat de mannetjes tijdens de paarperiode vóór de paring meer prooien opspitsen dan erna. Dan gaat het aantal prooien dat wordt opgespiet (tijdelijk) drastisch omlaag. Dit wijst erop dat het opspitsen van prooien in de periode van paarvorming een functie heeft hij het aantrekken van een vrouwtje. In de winter en tijdens de paartijd werden de opgespietste prooien maar weinig opgegeten, terwijl in de nestfase de meeste prooien juist wel werden gegeten. De prooien werden in de winter en de paarperiode vooral op gemakkelijk zichtbare plekken aan de randen van de territoria opgespiet. In de nestperiode werden de prooien dichtbij het nest en vaak verborgen opgespiet. Dit wijst erop dat in de winter het opspitsen van prooien vooral een functie heeft om de vaak grote territoria af te bakenen. In het voorjaar heeft het vooral een functie om een partner aan te trekken, in de nestperiode om een voedselvoorraad aan te leggen voor het broedende vrouwtje en de nestjongen. (CB)

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