



Sex differences in impaling behaviour of Great Grey Shrike *Lanius excubitor*: Do males have better impaling skills than females?

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ABSTRACT

Prey impaling in shrikes *Laniidae* is considered to be a feeding adaptation to dismember and consume large prey and is unique among food-storing animals. However, other exaptations of this behaviour were recorded, including signals in mate choice, where cache size is a sign of male quality. Thus, due to a strong sexual selection, male and female birds might differ in their behavioural patterns of impaling behaviour. We examined sex differences in impaling behaviour of the Great Grey Shrike *Lanius excubitor* – one of the species where caches are known to be sexual signals. Data were collected in western Poland during breeding seasons in the years 2006–2010. In the studied population, we recorded several sex-specific differences in impaling behaviour. Males impaled prey, invertebrates as well as vertebrates, faster and with fewer attempts per impaling event than females. Sexes differed in the location of impaled prey; males selected more visible places, especially during the mating and courtship phase, whereas females impaled prey in concealed locations. Males also had slightly better impaling success compared to females. We suggest that sex differences in impaling behaviour may be due to different uses of impaled prey, and the better impaling skills of males may be the result of better experience in impaling which is forced by sexual selection in this species. We also discuss other factors which might trigger sex-specific differences in food caching by shrikes.

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1. Introduction

Sex-specific differences are widespread among animals and, since Darwin's studies, differences between males and females are a major focus of various fields in biology. One of the main reasons for sex differences is sexual selection; considered to be a major evolutionary force in the creation of sex-specific characters in living organisms.

True shrikes of the family *Laniidae*, small to medium size passerines with a lifestyle similar to raptors, exhibit the extraordinary behaviour of impaling prey on sharp objects, such as thorns, twigs or barbed wire, for later consumption. Today, this behaviour is considered as an evolutionary feeding adaptation to overcome the problems of dismembering and consuming large prey as well as exploiting toxic animals (Yosef and Whitman, 1992; Cade, 1995; Yosef and Pinshow, 2005; Antczak et al., 2005a,b). This behaviour also offers other benefits such as the storage of food

during inclement weather conditions and periods of food stress (e.g. nest building (Burton, 1999), rearing nestlings (Tryjanowski et al., 2003), signalling of territory quality, as landmarks of territory boundaries (Yosef and Pinshow, 1989; Sloane, 1991; Keynan and Yosef, 2010), and selection of suitable nesting places (Hromada et al., 2008)). However, according to the widely accepted idea of the evolutionary origin of impaling behaviour (Cade, 1995), communication purposes have a profound influence on behavioural patterns of impaling behaviour (Yosef and Pinshow, 2005). In an elegant experimental study, Yosef and Pinshow (1989) demonstrated that males of Southern Grey Shrikes *Lanius meridionalis* with larger caches attracted more females, achieved better breeding success and paired earlier. Thus, conspicuous larders act as signals in mate selection comparable to bower quality in bowerbirds (Yosef and Pinshow, 1989; Yosef, 1992; Borgia, 1995).

The communication role of impaling behaviour has been found in other species or populations of shrikes (Sloane, 1991; Mizzel, 1993; Antczak et al., 2005a,b; Hromada et al., 2008; Yosef and Pinshow, 2005; Keynan and Yosef, 2010). Impaling behaviour seems to be very flexible and changes substantially during the annual life cycle of shrikes; impaled prey may be used either for signalling purposes or as a temporary cache in the same population (Antczak et al., 2005a,b; Keynan and Yosef, 2010). Moreover,

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environmental conditions such as drought (Keynan and Yosef, 2010), weather conditions (Tryjanowski et al., 2003) or changes in food availability (Valera et al., 2001) affect patterns of food caching in shrikes. Although the impaling behaviour of shrikes has been studied in various contexts in the past, sex differences in food caching has received scant attention (but see Valera et al., 2003; Keynan and Yosef, 2010). Impaling of prey is performed by both sexes (Lefranc and Worfolk, 1997; Keynan and Yosef, 2010). However, because males use caches to attract potential females and impaled prey may be a sexual display, there should be profound differences in impaling behaviour between sexes. Such differences might be found, for example, in the location of larders, impaling experience and overall impaling success.

In this study we focus on sex differences in impaling behaviour in a Great Grey Shrike *Lanius excubitor* population in western Poland. In our previous study, we showed that impaling behaviour in the studied population changed significantly during the annual cycle, including males impaling prey during the mating period as signals of territory quality and of boundaries (Antczak et al., 2005a,b).

We tested the following predictions: male and female shrikes should differ in their patterns of impaling behaviour. We hypothesized that males should display better impaling skills expressed as a greater success in impaling prey in comparison to females. Moreover, because of the communication function of caches males should prefer more visible places for impaling prey.

2. Study area and methods

2.1. Study area

The material was collected near the town of Odolanów (51°34'N, 17°40'E) in western Poland during the years 2006–2010. The study area (220 km²) is an agricultural landscape with arable fields, meadows, pastures and small woodlots of different ages, which are in some cases connected by rows of trees. This area supports one of the densest populations of the Great Grey Shrike in western Poland or even in Europe (Tryjanowski et al., 1999; Antczak et al., 2004).

2.2. Field methods

2.2.1. General field procedures

Territories were regularly surveyed for breeding pairs and nests during the breeding season from late February to July. Observations on foraging behaviour and breeding biology including the date of mating, laying date, clutch size, and brood size were made using standard methods (see Antczak et al., 2004). During observations, the movements of birds were mapped.

2.2.2. Direct observations of impaling behaviour

During the study we observed male and female birds through high quality optics. After it was first spotted, a bird was followed and detailed notes made about its behaviour. The sex of birds was determined from behavioural observations (copulation, courtship feeding, incubation), some of the observed birds were individually ringed with colour rings. In a few cases, members of pair were distinguished by specific wing patterns (Schön, 1994). During observations of impaling the following data were recorded: type of prey (e.g. lizard, vole), place of impaling, total duration of impaling event in seconds, number of impaling places in one impaling event, impaling success (yes or no). The impaling event was defined from the start of searching the impaling place with prey in the beak until the prey was impaled on a thorn, branch or other substrate. The time devoted to consumption of the prey after successful impaling was not included. The number of impaling attempts in one event was defined as the number of places

where the particular bird tried to impale the prey until the prey was impaled successfully. The majority of direct observations of impaling behaviour were collected during mating and egg laying periods when birds of both sexes were observed together during mate guarding. During this period shrikes were highly visible due to sparse leaf cover. In general, due to strong differences in parental duties (only females incubate the clutch and brood chicks until their 8th day of life), males were much easier to observe (Lefranc and Worfolk, 1997). Only complete observations were included in analyses i.e. those including all information about impaling behaviour in a given impaling attempt (duration, number of attempts, impaling success). To avoid pseudoreplication, only one observation per bird was used in the analyses. We used only birds of well known origin, and however in mating periods territorial intrusions are not so rare in Great Grey Shrike and made almost exclusively by males, we never observed impaling behaviour during territorial intrusions (Tryjanowski et al., 2007)

Impaling sites were divided into two classes of concealment (Antczak et al., 2005a,b). “Concealed larders” 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. “Conspicuous larders” represented places where impaled prey were highly visible – mainly the tops of trees, solitary upright twigs, sparse parts of trees, and trees and bushes with wide sparse crowns, such as young *Betula* sp., *Padus* sp., *Alnus* sp., *Pyrus* sp., as well as artificial impaling places such as barbed wire and fences.

2.3. Data processing

Because the prey categories differ in size and weight which might affect impaling time; we used two statistical approaches to test differences in impaling behaviour between males and females. Firstly, we directly compared males and females using two sample tests where the dependent variables were impaling time and the number of impaling attempts per event. Due to non-normality of data, non-parametric tests were used. Analyses were performed separately for two categories of prey: invertebrates and vertebrates.

Frequencies were compared by Chi square tests with Yates correction. Values are presented as means \pm 1 standard deviation (SD). Analyses were performed using Statistica for Windows ver. 7 software.

3. Results

3.1. Taxonomic composition of impaled prey

In total, we observed 26 males and 15 females impaling prey. Both sexes impaled vertebrates and invertebrates with no significant difference in relative frequencies ($\chi^2 = 2.26$, $p = 0.13$).

3.2. Concealment of impaled prey

Males impaled prey significantly more often in conspicuous places than females (Chi-square test with Yates correction $\chi^2 = 9.87$, $df = 1$, $p = 0.002$). We noted gradual change in use of open impaling places by males; at the start of breeding season over 90% of prey was impaled in well visible locations, but in the nestling phase 55.5% were impaled in such places. Such changes in behaviour were not recorded for females which mostly impaled prey in concealed places in all analysed periods. Over 70% of impaled prey by females in mating phase were located in hidden places; in nesting phase this figure reached over 80% of prey.

Table 1
Comparison of male and female Great Grey Shrike in the time (in seconds) per impaling event and the number of impaling attempts per event. Results are presented separately for invertebrates and vertebrates. Sample sizes are given in parentheses. In all cases *U* Mann–Whitney tests were used.

Variable	Males	Females	Z	p
Time: invertebrates	6.6 ± 4.6 (5)	58.5 ± 83.1 (7)	1.38	0.16
Time: vertebrates	31.8 ± 33.4 (21)	201.7 ± 111.4 (8)	3.83	0.0001
No. of events: invertebrates	1.00 ± 0.00 (5)	2.28 ± 1.79 (7)	1.62	0.10
No. of events: vertebrates	1.2 ± 0.6 (21)	3.2 ± 1.5 (8)	2.83	0.0005

3.3. Impaling time and impaling success

Males impaled prey significantly faster than females, for both vertebrates as well as invertebrates (Table 1). In general, vertebrate impaling was more time-consuming than impaling of invertebrates for both sexes. Females performed significantly more attempts per impaling event than males for both invertebrate and vertebrate prey (Table 1). Females had lower impaling success overall (73.3%) than males (92.3%), but the difference was not significant ($\chi^2 = 1.957$ df=1, $p = 0.162$).

4. Discussion

Our findings indicate that, in the studied population of Great Grey Shrike, both males and females impaled prey, but they strongly differed in impaling performance. Firstly, males impaled prey faster than females for both vertebrates and invertebrates. Secondly, males were more proficient with impaling, since they displayed a lower number of impaling attempts per impaling event than females. The general picture is that, overall, males had better impaling skills, compared to females, for both vertebrate and invertebrate prey. Prey type also strongly affected impaling performance with major differences found between vertebrate and invertebrate prey. Such differences may be simply affected by prey body size and birds' ability to manipulate prey. The second major difference was the choice of impaling place. However, this difference might reflect contrasting functions of impaled prey: in males, prey have a role as a signal but in females prey serve only as a food cache. This was very obvious in males: at the start of breeding season, they impaled the majority of prey in conspicuous places, whereas during periods of incubation and nestling care, concealed and conspicuous places were used with similar frequency. This result supports previous findings about the communication role of impaled prey in the studied shrike population (Antczak et al., 2005a,b). Females from the studied population mostly impaled prey in hidden places. However, predation risk during impaling might strongly affect the choice of potential impaling places. As shown in this study; impaling is time consuming for females and their choice of concealed places might be beneficial to reduce predation risk. In contrast, males impaled prey in visible places as signals not only of cache size but also their ability to cope with the predation risk. Thus, impaling behaviour could be a manifestation of the handicap principle (Zahavi, 1975; Zahavi and Zahavi, 1997). Thus, impaling in visible places in mating period might be better individual strategy to signal the quality of territories and their owners.

Despite the fact that food caching in shrikes is well known, differences in impaling behaviour between sexes were previously poorly explored. In an experimental study of the Lesser Grey Shrike *Lanius minor*, which seldom impales prey, both males and females had similar impaling success and females preferred to eat food rather than store it (Valera et al., 2001). More recently, in Southern Grey Shrike *Lanius meridionalis*, Keynan and Yosef (2010) found that both sexes impaled prey and also that females used prey

to demarcate non-breeding territories. Unfortunately, we did not study impaling behaviour of females outside the breeding season.

Experimental studies in captivity showed that impaling behaviour in shrikes is innate and develops at an early stage of life. Indeed, early experience in sensitive periods may shape the selection of impaling substrates and impaling success. This behaviour is facilitated later in life and improved by increased experience with impaling substrates and prey types. This result was supported by experimental studies in free-living shrikes where impaling success increased with practice and experience (Valera et al., 2001). However, what might be responsible for such large differences in impaling behaviour between males and females in the studied population? We suggest that males have better experience with impaling prey due to strong sexual selection in creating caches. In the Great Grey Shrike, male mating success is related to cache size which is one of the signs of male quality. During the mating period, males frequently impale prey in visible places. Indeed, males are known to impale objects such as leaves or fruit (Yosef and Pinshow, 2005).

However, we suggest an additional factor which might cause sex differences in impaling behaviour in the Great Grey Shrike are the ecological conditions experienced by males and females during the non-breeding period. Firstly, males stay closer to breeding grounds; in fact, some males overwinter in breeding territories and females move further to the west and south. Thus, males might rely more on vertebrate prey, including voles and birds, during wintering (Hromada and Kristin, 1996; Antczak et al., 2005a,b; Karlsson, 2007) whereas females forage mainly on invertebrates. Since impaling is necessary for the consumption of large prey, males might impale vertebrates with a higher frequency during wintering or at the end of winter during their early return to breeding grounds. The proportion of vertebrate prey during wintering increases from south to north of their range (Nicolov et al., 2004). For example, in Bulgaria, wintering Great Grey Shrikes impale mostly crickets whereas in northern parts of their range voles and birds form the bulk of their diet (Olsson, 1985; Hromada and Kristin, 1996; Karlsson, 2007; Antczak et al., 2005a,b). Also, the fact that we performed this study in dense population might affect the signalling role of impaling behaviour, but this issue need additional study e.g. by comparing birds living in different social conditions.

To summaries our results we showed that male and female Great Grey Shrikes differ in behavioural patterns of impaling prey. Males from the studied population had better impaling skills and used impaled prey both as signals and as food caches. We suggest that sex-specific differences in impaling behaviour in Great Grey Shrike are affected by two drivers: sexual selection and different environmental conditions experienced by the sexes during wintering.

It will be especially worthwhile to study if these differences are present in the early stages of development of impaling behaviour. For example, young males might have better learning abilities than females. However, the primary function and evolutionary origin of impaling behaviour in true shrikes are linked to adaptations which help to cope with the consumption of larger prey but our study supports the view that sexual selection might be one of the

forces which strongly modifies the primary function of impaling behaviour.

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