



Females prefer extra-pair males that are older and better hunters

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ABSTRACT

Age of male is an important cue in mate selection, including extra-pair copulations; different phenotypic and behavioural traits are known to be age related. Paternity studies show that older males predominate as fathers of extra-pair young. It remains unclear if females actively choose older males because they possess high quality traits or because older males are more successful in coercing fertile females. We experimentally provided mounted males of different age (yearling vs. adult) of great grey shrike *Lanius excubitor* with nuptial gifts of different quality (vole vs. cricket) and observed reactions of females and their social partners. Females strongly preferred older males with energy-rich nuptial gifts. The reactions of females' social partner to the extra-pair male did not differ significantly amongst experimental groups. However, males responded to the reaction of their mates and male aggressive behaviour increased when their mate showed an interest in an intruder.

KEYWORDS

extra-pair copulations – *Lanius excubitor* – social status – birds

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INTRODUCTION

Many species of socially monogamous animals engage in extra-pair copulations (here after EPCs). The success in extra-pair fertilisations is skewed towards older males in many bird species (Weatherhead & Boag 1995; Dickinson 2001; Johnsen et al. 2001; Johnsen & Lifjeld 2003; Kleven et al. 2006; Bouwman et al. 2007; Schwarzová et al. 2008). To date, there have been basically proposed two non-excluding hypotheses to explain this pattern: (1) females prefer older males, because they – surviving longer – prove that they are carrying good genes for survival and (2) older males are more experienced in coercing females and able to better exploit opportunities for extra-pair matings, to perform sexual trips to neighbouring territories, etc. (Trivers 1972; Alatalo 1986; Weatherhead & Boag 1995; Kleven et al. 2006; Bouwman et al. 2007). Moreover, recent findings indicate age-related variation in testes size and quantity of sperm production, with older males having higher rate of

sperm production and as a consequence increased fertilisation success (Laskemoen et al. 2008).

Several phenotypic traits including behavioural traits are known to be age related and act as age indicators. For example, plumage quality (Siefferman et al. 2005; Budden & Dickinson 2009), song repertoire (Gil et al. 2001) and foraging efficiency (Bildstein 1983; Heise & Moore 2003) increase with age. Older males might be more successful in competition for territories, food resources and potential females; age of male may constitute a cue of male experience in nest defense investment and quality of parental care (Takagi 2003); and finally, it may provide information on survival perspective of an individual (Manning 1985).

If traits reflect the ability of a partner to contribute direct or indirect benefits to the offspring, choosy females are able to increase their fitness by mating with males displaying such traits (Andersson 1994; Alcock 2001). Moreover, the extra-pair young are mostly males (Schwarzová et al. 2008), thus

it is possible that sons will also be able to engage in EPCs in the future; this view is also important from the lifetime success of mothers.

Elaborate plumage and complex songs of males are two of the best known examples of sexually selected traits in birds in the context of EPCs (Hill 1991; Chiver et al. 2008). However, in species that do not possess distinct secondary sexual traits, males may use other means of signalling their quality to females. Often, males demonstrate key ecological skills that are crucial for survival and reproduction (Kingsolver & Huey 2003). Good example of such behaviour is display of hunting and/or provisioning skills (Yosef & Pinshow 1989) and providing food to females (Arnold & Bateson 1983; Tryjanowski & Hromada 2005).

The function of these two categories of traits – age of male and quality of gifts offered to female – is difficult to discriminate in the field because field studies mostly focused on the question concerning the role of a single trait in sexual selection (Wiley 2003). Therefore, manipulative experimental studies are useful for teasing apart the larger number of potentially correlated traits that may act as indicators of male quality and, hence, influence female choice.

Shrikes are passerine birds well known for their raptor-like mode of life, impaling of their prey and offering the prey as a nuptial gift prior copulation. They are, thus, good model organisms for such studies. To our knowledge, this is the first field study to test experimentally for effects of multiple traits in extra-pair mate choice in birds.

To discriminate between female preferences we used an experimental design, where females could choose from two independent traits – one reflecting the age represented by the adult plumage and the second demonstrating male hunting ability as reflected by the size of the nuptial gift (Tryjanowski & Hromada 2005). Hence, we addressed the following questions: (1) Do females choose extra-pair mates according to male age or size of nuptial gift? (2) Do males react according to rival's age or size of nuptial gift? Further, because a female's interest in EPCs endangers its partner's parental investment and fitness, therefore, we also tested (3) whether the reaction of males is positively correlated with female behaviour towards a potential EPC partner.

1. METHODS AND MATERIALS

Study species. The great grey shrike *Lanius excubitor* is a highly territorial, socially monogamous thrush-sized bird. There is no profound sexual dimorphism, and difference in coloration between the sexes is only marginal (Schön 1994; Probst 2001). Although the great grey shrike is a passerine, it does not possess intricate singing, as is typical for this group. However, males advertise their prowess to females by impaling corpses of prey on sharp twigs, on thorns and in forks or other suitable places (Yosef & Pinshow 1989; Yosef & Whitman 1992; Antczak et al. 2005). Impaling behaviour serves several functions including signalling territory boundaries, quality of male and temporal

food storage [see also review in (Yosef & Pinshow 2005)]. Furthermore, male shrikes routinely offer nuptial gifts to females prior to both intra- and extra-pair copulations (Lorek 1995; Tryjanowski & Hromada 2005). Males invest heavily in reproduction by providing food for females during egg laying, incubation and almost half of the nestling period. True Shrikes (Laniidae spp.), including the great grey shrike, start to breed in the second year of life and age of male has a significant effect on nestling production (Takagi 2003). Second year birds are able to breed but still attain part of immature plumage as brown buffs in great covers or delicate barring on the breast that disappears just after the first breeding (Lefranc & Norfolk 1997). Pairs produce a single brood each year, although replacement clutches can occur after nest failures. The size of the pre-copulatory gift affects female decisions whether to copulate or not (Tryjanowski & Hromada 2005). The species breeds mainly solitarily in pairs 300–1000 m from each other; however, polygyny has also been reported (Yosef 1992; Probst 2001; Tryjanowski & Hromada 2005). Males practice EPCs and offer larger, energetically richer prey items to their extra-pair females than to their own mates (Tryjanowski & Hromada 2005). Intra- and extra-pair copulations are preceded by pre-copulatory displays: the male faces the female, shivers and flutters his wings and utters a call or a quiet song and often offers a food gift (Carlson 1989; Lorek 1995; Tryjanowski & Hromada 2005).

Field Methods. We investigated the behaviour of great grey shrikes in a high-density population (Antczak et al. 2004) in western Poland during the breeding season from April to mid-May between 2003 and 2005. Individuals were distinguished by highly individual-specific wing patterns and eye-masks (Schön 1994; Probst 2001), and some (6–14 in different years) were individually marked with colour rings.

Females are thought to be fertile until the laying of the penultimate egg (Birkhead & Moller 1992; Lorek 1995). Female great grey shrikes, which lay up to eight eggs and start incubation from the third egg, are, therefore, potentially fertile until the fifth day of incubation (Lorek 1995). Experiments were performed at the start of breeding in the fertile period of individual females, covering the period from 14 April to 10 May. During the three breeding seasons, we tested a total of 56 pairs: 20 pairs in 2003, 18 in 2004 and 18 in 2005. Age of either males or females was not determined. Females were offered at random one of two different taxidermy models as follows: a fully grown male in its second year (there after yearling) representing the first year of sexual maturity in the great grey shrike (Lefranc & Norfolk 1997) or a male in adult plumage (at least three years old), both with two options of nuptial gift in the bill – either a field cricket (*Gryllus campestris*) or a common vole (*Microtus arvalis*). During the experiments, female and male behaviour was classified as qualitative measures of intensity of reaction to the mounted specimens and male reaction to the female's behaviour. Reactions of female shrikes to the mounted male were classified as follows: 0, no reaction; 1, female looks towards dummy; 2, female moves towards dummy; 3, female shows excitement and 4, female begs and

shivers wings. Reactions of male shrikes to the mounted male were classified as follows: 0, no interest in the dummy; 1, male looks toward decoy; 2, male moves towards decoy; 3, male starts to sing; 4, male shows nervousness, giving alarm calls; 5, males flies above decoy; 6, male attacks decoy and 7, male attempts to force copulation on female. Finally, male reactions to the reaction of their social partner were classified as follows: 0, male shows no reaction; 1, male shows nervousness and 2, male gives alarm calls, chases the female. All ordinal scales are based on our observations (mainly MA) of shrike's behavioural sequences.

Taxidermic mounts were obtained from The East Slovak Museum in Košice, Slovakia, and collections of the University of Life Sciences in Poznań, Poland. The prey items were attached to the mounts' bill. Thus, we obtained four experimental treatments – a two-year old yearling with a small or large gift and at least three years old adult bird with a small or large gift. Both prey items are frequently used by males during courtship and pre-copulatory display in the study population (Tryjanowski & Hromada 2005).

We performed 51 successful experimental presentations in total. All experiments have begun in the presence of both males and females; however, during the experiments, one or both birds sometimes left the territory; therefore, number of successful experiments differs from number of tested pairs and sample sizes differ amongst particular tests. The sizes of experimental groups were similar: adult male with cricket 14 presentations; adult male with vole 13; yearling with cricket 10; yearling with vole 14. The experiments were performed during the females' fertile period early in the morning (04:00 a.m. up to 10:00 a.m.) when copulation frequency of shrikes reaches a peak (Lorek 1995; Tryjanowski & Hromada 2005). Each experimental trial lasted 20 minutes with experimental presentation of the mounted specimen perched within 50 m of the fertile incubating female. During the experiment, five series of song were taped. In all trials, we used the same song recording as well as the same mounted males and vole. The birds were observed by a team of two or three observers; one person observed the female's reaction from the hide near the nest, the second person from a distance searched for the male and focused on male reaction. Each observer noted the exact reaction of birds. All experiments were performed under favourable weather conditions (no heavy rain, no strong wind).

Data Analysis and Statistics. To avoid pseudo-replication, we examined and used in the analyses only one observation per territory for each season. Because pairs are newly established for every breeding season, females were different in every year. Also, as individual birds can move from one territory to another in consecutive years and because we do not have marked all individuals in our population, we cannot discard some pseudo-replication by observing the same individual (male and/or female) in different years; however, we expect this source of pseudo-replication to be minimal. To improve the sample size and the power of the test, data from all years were pooled. Because the reaction of the two partners was not

always observed, tests differ slightly in sample size. All statistical tests were performed according to Zar (1999), and all tests were two tailed. Data are presented as mean \pm SE.

2. RESULTS

Our experimental design allowed us to discriminate between great grey shrike female preferences for two sexual male traits: age indicated by plumage and nuptial gifts. We found that neither male's age nor size of the nuptial gift alone offered to the female affected the female's decision significantly, whilst in combination, these two traits had a highly significant effect. Reactions of females to the dummy male intruder differed significantly amongst treatments. They reacted most strongly to the male in adult plumage with the larger nuptial gift, in contrast to the other three experimental groups (Kruskal–Wallis ANOVA, $\chi^2 = 11.238$, $df = 3$, $n = 48$, $P = 0.011$, Fig. 1). The reactions of males did not differ significantly amongst experimental groups (Kruskal–Wallis ANOVA, $\chi^2 = 4.141$, $df = 3$, $n = 48$, $P = 0.25$, Fig. 2).

However, the strongest response was the reaction of males to the reaction of their mates (Kruskal–Wallis ANOVA, $\chi^2 = 13.801$, $df = 3$, $n = 42$, $P = 0.003$, Fig. 3). The later result was also supported by a strong correlation between female reaction to the mounted specimen and male reaction to the female response within a single treatment (Kendall tau = 0.482, $n = 41$, $P = 0.0001$).

3. DISCUSSION

Our experimental design allowed us to discriminate between great grey shrike female preferences for two sexual male traits: age indicated by plumage and nuptial gifts. In most studies, different sexual cues were typically treated separately, ignoring their possible interactions and mainly focusing on how variation in sexual traits affects decisions of females (Lehtonen, Rintakoski & Lindström 2007). In many species, males exhibit

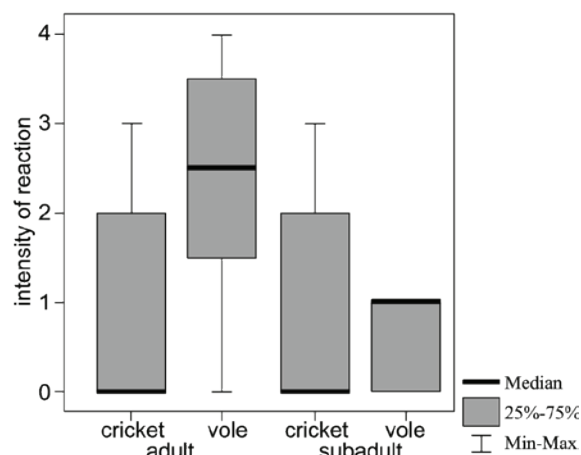


Figure 1. Reaction of female shrikes to a mounted extra-pair male, with respect to the colouration of the male (yearling vs. adult plumage) and the size of the nuptial gift (cricket vs. field vole).

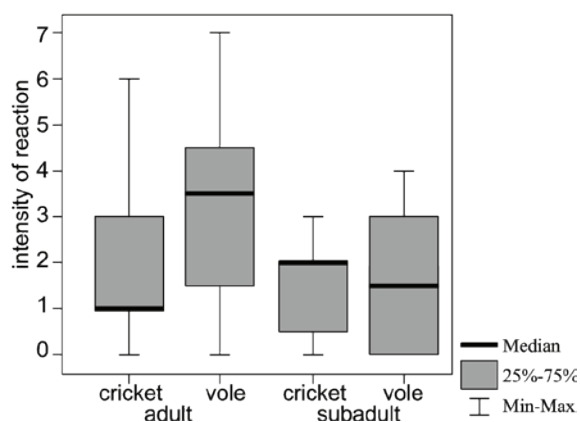


Figure 2. Reaction of the male to the mounted extra-pair male, regarding the colouration of male plumage (yearling vs. adult) and the size of the nuptial gift (cricket vs. field vole).

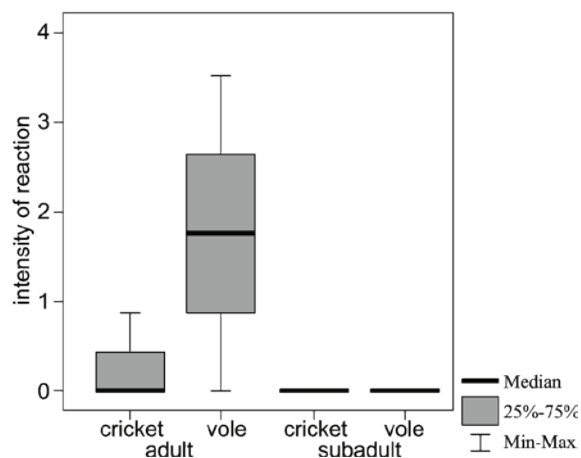


Figure 3. Reaction of the male shrikes to the reaction of their social mates

complex courtships involving feather ornaments, behavioural displays and extended phenotype traits, for example, quality of nest (Jennions & Petrie 1997; Candolin 2003; Loyau et al. 2005; Lehtonen et al. 2007; Vergara et al. 2011). It was suggested that mate choice is a multi-stage process, and multiple male display traits convey different information on the genetic and phenotypic quality of males (Borgia 1995; Keagy et al. 2011) and may provide redundant signals that improve mate assessment (Møller & Pomiankowski 1993; Freeman-Gallant et al. 2009; Keagy et al. 2011) and/or narrow down female choice (Robson et al. 2005). Moreover, some traits may reflect condition of male in the past (Sullivan 1994), others reflect his current condition (Scheuber et al. 2003) and some even in future (Boogert et al. 2011).

Our results correspond with a recent suggestion (Lehtonen et al. 2007) that female preferences can be based more on the combined effect of different cues than on each cue independently or additively, because they can interact mutually (Patricelli et al. 2003). Great grey shrike females preferred older males – potentially more experienced hunters – that delivered gifts of greater energetic value.

In the great grey shrike, the nuptial gift is necessary for successful within- and extra-pair copulations. Female shrikes are highly dependent on males for provisioning food during the copulation period, throughout incubation and up to the first eight days of the nestling period (Lefranc & Worfolk 1997; Tryjanowski & Hromada 2005). In the bull-headed shrike (*Lanius bucephalus*), females paired with older males laid more eggs per clutch than females paired with males in their second year, and in addition, age of the male was significantly correlated with the mass of nestlings (Takagi 2003). Therefore, from a female's perspective, mating with a skilled hunter is the best choice. As shown previously (Tryjanowski & Hromada 2005), males engaging in EPCs offered females more energy-rich nuptial gifts. The benefits of such energetically costly food items may exceed female costs of EPCs, and/or energy-rich gifts may

allow females to quickly assess the quality of an EPC partner. If male skills are heritable, females may acquire indirect fitness benefit. Alternatively, the quality of nuptial gifts may reflect male's hunting skills and current condition because prey capture is difficult and transport energetically costly especially for larger prey (Yosef 1993). Finally, approaching an extra-pair female with a large nuptial gift may be considered a handicap, because the male needs to cross the entire territory of a rival. In the great grey shrike, EPCs mostly take place near the female's nest (Lorek 1995; Tryjanowski et al. 2007), and the extra-pair male must behave surreptitiously (Tryjanowski et al. 2007), otherwise he can lose his investment and the opportunity to conclude the given sexual trip. The results presented here are consistent with this idea because female great grey shrikes showed more interest in (extra-pair) males with larger gifts, especially if the bird offering the nuptial gift was more than two years old. Unfortunately, our test cannot allow us to detect an effect of the age or gift per se.

If a female with a social partner engages in EPC simply to obtain a large food gift, then this reflects a short-term choice (immediate pay-off) – it is quite possible considering that EPC do not necessarily means fertilisation: level of offspring sired by extra-pair males in shrikes species with mixed reproductive strategies varies from 0% (*Lanius minor*), 10% (*L. bucephalus*) to 26.5% (*Lanius collurio*) (Yamagishi 1992; Krištín et al. 2008; Schwarzová et al. 2008). However, such dishonest behaviour would probably not be successful in a population in a long term. A male able to sneak in another territory burdened with a prey must be really a good male. Thus, a female should see him as a potential source of good genes, instead as a silly male with expensive gift. If males offering gifts would not fertilize extra-pair females, their fitness will not increase by EPC and thus, their genes for EPC search will not be spread in the population.

No doubt that experiment presented has some constraints such as the fact that in case of real extra-pair affairs,

birds should interact with each other. As shown in experiments with robotic females (Patricelli et al. 2003), the interactions that led to successful copulations are multi-stage processes, and males adjust their reaction according to female behaviour and vice versa.

Our experiments underlined the context dependence of female choice of extra-pair males, that is, the strong influence of her social mate's behaviour. In several cases of experimental presentation, guarding behaviour of the male mate modified the reaction of the female, when females noted the presence of their social partner, they immediately lost interest in the mounted male and they moved back to the nest. This finding suggests the possibility of high costs for females when engaging in EPC. Such costs might include physical punishment, as recorded in the lesser grey shrike (Valera et al. 2003). Indeed, we have observed in studied population that males chased their females after they exhibited interest in an extra-pair male (unpublished data). The hypothesis of high costs of EPCs was

also supported by a striking difference in the locations where copulations with social partners and extra-pair males took place: EPCs took place in more secluded locations (Tryjanowski et al. 2007). Our findings reveal the motivation of male behaviour: male mates reacted to an intruder and attempted to protect their paternity only if the female reacted to the intruder – a mounted male. Thus, our results underline the importance of social context of EPCs.

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