



Do males of the great grey shrike, *Lanius excubitor*, trade food for extrapair copulations?

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In several animal species, males offer material gifts to females during a courtship or precopulatory display. The provision of nutrients is a male investment that can increase female reproductive success; therefore males can use such gifts to influence female choice. Clear examples of courtship feeding before extrapair copulations are scarce, however. We investigated courtship feeding in the great grey shrike. Males offered food both to their mate and to extrapair females. Food offered to extrapair females had a significantly higher energy value than that offered to the social mates. The size of prey offered may enable females to judge a male's quality. A larger gift resulted in a higher chance of copulation for males in both within- and extrapair events. We conclude that the energy value of nuptial gifts can explain why females of some species engage in extrapair copulations.

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Female animals often copulate with males that are not their social partners; however, their motivation is still a matter of discussion (Birkhead & Møller 1992; Griffith & Montgomerie 2003). Indirect genetic benefits are thought to be the most important reason for this behaviour (Petrie & Kempenaers 1998); however, direct, or nongenetic, reasons are most readily understood (Kondoh 2001; Møller & Jennions 2001). Direct fitness benefits have been equated with the material benefits acquired by females, and may derive from enhanced fertility, fecundity or parental care obtained from mating with preferred males, enhanced courtship feeding, higher quality of a breeding territory, antipredator behaviour of a mate, or simply the absence of directly transmitted diseases (Møller & Jennions 2001).

A male's reproductive success is limited by the number of females with which he copulates, whereas a female's reproductive success is limited by her investment in offspring (Trivers 1972). Thus, in general, males can be seen as the competing sex and females as the choosing sex (Atmar 1991; Kondoh 2001).

A female's choice of mate can be influenced by a male's investment of resources or time in courtship. Nongenetic

benefits are an integral feature of the mating systems of a variety of animals. Because the mating decision is controlled primarily by females, males try to persuade them by providing resources. Females prefer resources and paternal ability that have a direct effect on their reproductive success, and increase their fecundity (Møller & Jennions 2001). There are many possible direct benefits and they have been recorded in many animal taxa, including insects, fish, reptiles, birds and mammals. Such nongenetic benefits can comprise a territory with a crucial resource (Cronin & Sherman 1977) or parental care (Smith 1979). Vigilant males, watching for predators, can also allow females to spend more time foraging, collecting food resources that will be needed to produce a clutch of eggs (Artiss & Martin 1995).

The most common male investments in copulation are those of a nutritional value, in the form of either male secretions (Sakaluk 1984; Simmons 1990; Wedell 1993) or prey items (Thornhill 1976; Stanford 1995), sometimes even the male himself (Buskirk et al. 1984). None the less, evidence of direct benefits in extrapair copulations are surprisingly scarce.

One of the species offering food is the great grey shrike, a raptor-like passerine bird, in which the male gives prey (rodents, birds, lizards, or large insects) to females immediately before copulation (Yosef 1992; Lorek 1995). The species breeds mainly solitarily in pairs 500–1000 m from one another (Schön 1994a). However, cases of mixed reproductive strategy, polygamy and even extrapair

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copulations have been recorded (Yosef 1992; Lorek 1995; Probst 2001).

Shrikes are well known for impaling prey on thorns and sharp sprigs. Yosef & Pinshow (1989) have shown in an experimental study that great grey shrike females select a mate according to the size of prey impaled, with larders thus serving as an extended phenotype of a male. If the amount of food stored by the males can drive female mate choice, food provided before within and extrapair copulations by males may also influence the female's decision to copulate. Larger prey are likely to require a greater male investment in terms of hunting time and energy. Therefore, we hypothesized that the size of the nuptial gift should reflect a male's quality. We then predicted that females should choose those males that provide them with larger precopulatory food items because they would gain both direct and potentially indirect benefits. Consequently, a male's copulation success was predicted to be related to the size of the nuptial gift.

The overall fitness of a particular male can be elevated by extrapair copulations, with a single extrapair event representing a greater chance of fertilizing eggs than one of many within-pair copulations (Birkhead & Møller 1992). There is good evidence that female choice in extrapair copulations is based on male traits (Houtman 1992; Hasselquist et al. 1996). Therefore, assuming our first two hypotheses are correct, males should allocate their courtship gifts strategically. If they actively seek extrapair copulations, based on sexual selection theory, they should offer larger prey to extrapair females.

METHODS

Study Species

The great grey shrike is a territorial, socially monogamous bird. In the breeding season it defends large territories covering ca. 20–50 ha (Schön 1994b). Pairs produce a single brood each year, although replacement clutches can occur after nest failures (Schön 1994a). Only the female incubates, but young are fed and cared for by both parents (Schön 1994a, b). Copulations are preceded by precopulatory 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). The courtship-feeding intensity culminates several days before the first egg is laid, when copulations are most frequent (Lorek 1995).

Field Methods

We investigated the behaviour of the great grey shrike in a high-density population (up to 24 breeding pairs/100 km²) in western Poland, from the beginning of April to mid-May in 1999–2002. Individuals were distinguished by highly individual-specific wing patterns and eye-masks (Schön 1994c; Probst 2001), and some (6–14 in different years) were individually marked with colour rings under licence from the Ringing Center Department of Ornithology, Polish Academy of Sciences (for more details on study

sites and methods see Lorek 1995; Tryjanowski et al. 1999). Twenty-two males with both intra- and extrapair copulation attempts recorded were included in the study.

We considered a copulation attempt unsuccessful when courtship display (postures, wing shivering or courtship singing) by the male near the female (up to 0.5 m) was not followed by copulation itself. Because it was not possible to observe cloacal contact, we considered a copulation to have occurred when the mating event lasted for 3 s or more (Lorek 1995).

Data Analysis and Statistics

To determine whether nuptial gifts can indicate male quality, we correlated the value of food items (represented as energy content, see Table 1 and details below) delivered before copulation in within-pair attempts with the food value of items delivered in extrapair attempts, for particular males. To avoid pseudoreplication, we examined and used in the analyses only one observation of a male bringing food for each category.

To test whether males use larger prey items to solicit extrapair copulations, we compared the energy content (details below) of food items in within-pair and extra-pair gifts of all males, using the Wilcoxon matched-pairs signed-ranks test.

We calculated the usable energy content of prey items delivered as nuptial gifts from mean prey body size and published values of gross energy (kJ/g) and metabolizable energy coefficient (the proportion of overall energy content of the food item for a particular food item; Karasov 1990; Myrcha & Pinowski 1970; Table 1). Daily energy demand of the great grey shrike was estimated to be 113 kJ in the Negev Desert, Israel (Degen et al. 1992).

To establish the importance of food delivered before copulation, we compared the mean energy value of the nuptial gift with that of food delivered to a fertile female outside of copulation events. Female birds are thought to be fertile until the laying of the penultimate egg (Birkhead & Møller 1992). Female great grey shrikes, which lay up to eight eggs and start incubation from the third egg, are thus potentially fertile until the fifth day of incubation (Lorek 1995). Incubating females are fed almost exclusively by their mates (our unpublished data, based on data collected with digital cameras, from observations of 11 nests in the same study area), and thus males probably provide a significant part of the female's energy requirements during the fertile period.

To determine the male's investment in nuptial gifts, we investigated handling times (s) necessary for catching and processing the prey (including chasing, killing, transport and dismemberment of prey). We observed 47 cases of great grey shrikes hunting in the study area. Only observations where we saw the full spectrum of foraging behaviour (from resting time to hunt procedures) were included in the analysis.

Statistical tests were performed according to Zar (1999) and all tests are two tailed. Data are presented as mean \pm SD.

Table 1. Energy content of food items offered by great grey shrike males to females before copulation

Prey	DM/prey individual (g)	GE (kJ/g)	OE/prey individual (kJ)	MEC	ME/prey individual (kJ)	DE (%)	PR
<i>Passer montanus</i>	3.20	21.8	69.76	0.75	52.32	46.3	2.4
<i>Microtus arvalis</i>	4.20	23.5	98.77	0.75	74.08	65.6	1.5
<i>Lacerta</i> sp.	0.83	22.1	18.26	0.75	13.69	12.1	8.2
<i>Gryllus campestris</i>	0.25	23.2	5.87	0.77	4.52	4.0	25.0

DM: Dry mass (our data and Myrcha & Pinowski 1970 for *P. montanus*); GE: gross energy, kJ/g dry mass (Karasov 1990); OE: overall energy content (DM × GE); MEC: metabolizable energy coefficient (Karasov 1990; we used a coefficient of 0.75 for all vertebrates and the value for *G. domesticus* for *G. campestris*); ME: metabolizable energy (OE × MEC); DE: % of bird's daily energy requirement provided by one prey individual (Degen et al. 1992); PR: number of prey required for bird's daily energy requirement.

RESULTS

Males that offered courtship gifts of high energy value in within-pair copulations also did so in extrapair events (Spearman rank correlation: $r_s = 0.543$, $N = 17$, $P = 0.009$).

The energy content of the nuptial gift in unsuccessful copulation attempts (10.5 ± 15.1 kJ) was significantly lower than in successful attempts (76.8 ± 135.5 kJ) in within-pair events (Mann-Whitney U test: $U = 129.5$, $N_1 = 8$, $N_2 = 22$, $P = 0.029$) and in extrapair events (unsuccessful: 36.1 ± 45.2 kJ; successful: 277.1 ± 185.2 kJ; $U = 212.0$, $N_1 = 11$, $N_2 = 22$, $P = 0.002$).

Males offered different food items to extrapair females than to their mates (Fig. 1). The mean energy content of a gift offered to an extrapair female was nearly four times higher (75.3 ± 56.3 kJ) than that for a male's mate (19.0 ± 39.0 kJ; $N = 22$ males that delivered food to both an extrapair female and their mate; Wilcoxon matched-pairs signed-ranks test; $Z = 3.72$, $P < 0.001$). This represents 66.6 versus 16.8% of the female's daily energy requirement, respectively. The mean energy delivered by a male to an incubating fertile female was 19.0 ± 30.2 kJ/h (16.8% of the female's daily energy requirement, $N = 11$ nests) and comprised an average of one prey item/h.

The prey most frequently offered to extrapair females (vertebrates) was more costly for males in terms of time spent hunting. The handling time of hunting shrikes was significantly longer for vertebrate (33.0 ± 32.6 s) than for invertebrate prey (5.5 ± 2.6 s; Wilcoxon matched-pairs signed-ranks test: $Z = 3.41$, $N = 16$, $P < 0.001$).

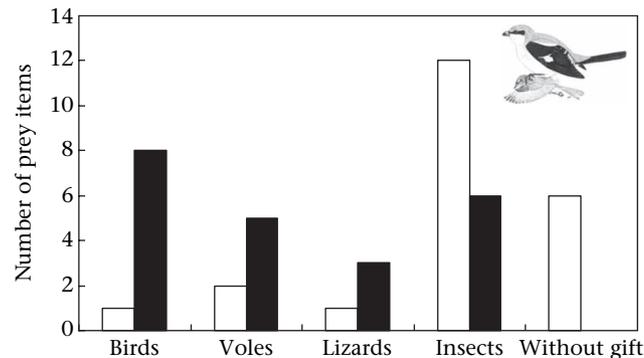


Fig. 1. Number of nuptial gifts offered by males to females in within-pair (□) and extrapair (■) copulations. Prey are shown by taxonomic group. G test: $G_{12} = 22.87$, $P = 0.029$.

DISCUSSION

We have shown that the value of the courtship gift could indicate a male's quality. Males that offered larger prey to their mate also did so when soliciting extrapair copulations. Courtship gifts signalling the quality or rank of the male have been recorded in a variety of animals, such as hanging flies, *Hylobittacus apicalis*, and chimpanzees, *Pan troglodytes* (Alcock 1998). Great grey shrike males that were able to offer larger (and more energy-rich) food items before copulation were more often selected as sexual partners. Female shrikes may choose the male before copulation, just after the gift is delivered.

Copulation success of the males was significantly higher if they offered larger and more energy-rich prey. This was true for both intrapair and extrapair copulations; no extrapair copulations were successful without a gift provided.

Male great grey shrikes contributed considerably to the nutrition of their mates during the fertile part of the incubation period by providing a substantial proportion of the female's daily food requirement. This means that males allocated their courtship gifts strategically to copulation attempts that could improve their overall fitness more dramatically. This finding corresponds with the predictions of sexual selection theory (Birkhead & Møller 1992).

Until recently, females were thought to gain only indirect, genetic, benefits from seeking extrapair copulations (Petrie & Kempenaers 1998). Other examples of direct benefits to females from extrapair matings are scarce in the literature. Female red-winged blackbirds, *Agelaius phoeniceus*, primarily a polygamous bird, may gain in terms of increased foraging opportunities on the territory of her extrapair mate and from additional defence against nest predators from this male if he is in a neighbouring territory (Gray 1997). In the purple-throated hummingbird, *Eulampis jugularis*, males provide cooperative females with access to food sources in their territories, exchanging food for copulation even during the nonbreeding season (Wolf 1975). The only known example of similar behaviour in a socially monogamous species is the Adélie penguin, *Pygoscelis adeliae*, in which males exchange nest material for copulations (Hunter & Davis 1998).

For males, seeking extrapair copulations is thought to be a trade-off between investing in mate guarding and parental care (Westneat et al. 1990). Nevertheless, in male great grey shrikes the fertilization benefits of precopulatory

gift giving must be weighed against the costs of acquiring such gifts. The capture of the larger vertebrate prey required higher energy expenditure because the shrikes had to chase them for longer than other prey. Furthermore, if a male invests more time in hunting to obtain a suitable nuptial gift for an extrapair copulation, he risks being cuckolded himself. Whatever the risks, the tendency of male shrikes to invest more in extrapair events suggests some potential benefits of this activity. We suggest that the behaviour observed in male great grey shrikes reflects the greater fitness benefits of a single successful extrapair event than multiple within-pair copulations. The investment of males in reproduction within a pair is high: they defend a territory, participate in nest building, and feed and guard their mates and offspring. By contrast, the only investment in an extrapair copulation is food.

Direct benefits for great grey shrike females were obvious in our study. Possible genetic advantages should be investigated further. If male ability to obtain valuable prey is somehow heritable, females may gain both direct and indirect benefits by choosing the male that provides them with the most valuable prey. However, mating with extrapair males could be costly. Females of the lesser grey shrike, *Lanius minor*, that engage in copulation with other males are sometimes punished by males (Valera et al. 2003). The female could also be risking divorce and a reduction in their partner's investment (Valera et al. 2003). This may be why females have higher standards in extrapair than within-pair copulations. Hence, the observed pattern may arise from a balance between the costs and benefits of extrapair copulations to a female.

We investigated the possible motivation of male shrikes for extrapair copulations. However, multiple mating by female birds is also interesting. There is evidence that mating with more than one partner is widespread in females of many animal taxa, from insects to mammals (Kondoh 2001). Material-benefit polyandry, or prostitution polyandry (Alcock 1988), is the most readily understood of several hypotheses for multiple mating by females. It states that both the females engaging in multiple mating and the males providing the direct benefit play essential roles in the evolution of polyandry. Therefore, the question arises: why has evidence for direct benefits in extrapair copulations been so scarce?

Future studies should investigate whether males that invest more really can increase their chances of reproductive success through extrapair offspring. If not (which is possible, see Valera et al. 2003), what exactly do both extrapair partners obtain from sexual contact with each other?

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