More secluded places for extra-pair copulations in the great grey shrike *Lanius excubitor*

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Summary

Extra-pair copulations (EPCs) are prominent features of avian mating systems. EPCs can be costly for both sexes, especially if extra-pair encounters are discovered by a social partner. The threat of extra-pair fertilization of the social partner could potentially result in physical punishment, reduced parental investment or divorce. In order to reduce the costs of EPCs, natural selection may favour behaviour that reduces the likelihood of detection of EPC by a social partner. Moreover, habitat structure may influence the efficiency of male paternity guards and, therefore, the possibilities of seeking and obtaining EPCs. We tested this hypothesis with the great grey shrike *Lanius excubitor*, a socially monogamous passerine bird, living in semi-open landscapes. We have found that 1) extra-pair and within-pair copulations (WPCs) occurred in different places, and 2) individuals of both sexes chose more secret places for extra-pair than for within-pair copulations.

Keywords: copulation, costs of mating, sexual conflict, shrikes.

Introduction

Extra-pair copulations (EPCs) create a potential for sexual conflict in pair-bonding animals (Johnsen et al., 1998; Westneat & Stewart, 2003; Low, 2005). There is specific gender asymmetry in extra-pair copulations – males can improve their fitness more substantially, whereas females are more at

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risk (Trivers, 1972; Birkhead & Møller, 1992). This is because, in most cases, females invest more in reproduction and exercise mate choice, and males compete with other males for mates. Therefore, a greater variance in extra-pair mating success is found in males compared to females – most EPCs occur for only a handful of males in the population, but, in females, successful EPCs are more evenly distributed (Birkhead & Møller, 1992).

Both sexes can benefit from EPCs, such as in increased fitness, insurance against mate infertility, possible future mate acquisition and genetically diverse and, therefore, high quality young (Birkhead & Møller, 1992; Kempenaers & Dhondt, 1993; Jennions & Petrie, 2000). Females can also obtain material benefits via EPCs, such as access to resources (Wolf, 1975; Kempenaers & Dhondt, 1993; Gray, 1997; Hunter & Davis, 1998; Tryjanowski & Hromada, 2005). However, infidelity also bears specific costs – males risk sperm depletion, cuckoldry, reduction in parental care and increased likelihood of divorce; females risk reduced partner's investment, divorce, retaliation, violence and injury from mates (Birkhead & Møller, 1992), as well as harassment from extra-pair males (Valera et al., 2003).

Males have several paternity assurance behaviours: frequent copulation to reduce the chance that an EPC will result in paternity, guarding by closely following females, and finally punishing them (Birkhead & Møller, 1992; Tryjanowski & Hromada, 2005). Therefore, females seeking extra-pair affairs adopt a behaviour that allows them to avoid the constraining effect of male guarding (Johnsen et al., 1998; Mays & Ritchison, 2004). Also, unfaithful males, when foraying in neighbouring territories for fertile females, often approach females secretively by moving quietly and stealthily, and using vegetation as cover (Mays & Ritchison, 2004). This increases the likelihood of a successful extra-pair copulation, which can end in extra-pair offspring (Lorek, 1995; Mays & Ritchison, 2004). Thus, the behaviour of both sexes, seeking extra-pair affairs and at the same time defending themselves against partner's faithlessness, is best viewed as a co-evolutionary arms race between them (Westneat & Stewart, 2003). There is substantial variation in extra-pair paternity, even in the same species in different nests and years, but little is known concerning the ecological factors affecting such differences (Johnsen & Lifjeld, 2003). For instance, habitat complexity has been proposed as an important determinant of an animal's extra-pair activity (Westneat & Sherman, 1997; Mays & Ritchison, 2004).

It is reasonable to assume that sites of EPCs and WPCs differ. However, testing where animals copulate is difficult because many species live in habitats that are exposed and offer little cover (open water bodies, open landscapes, etc.) or, by contrast, are densely covered (e.g., forest and scrub vegetation). Therefore, testing the copulation place hypothesis could only be done effectively in a habitat that potentially offers both kinds of places, such as semi-open landscapes. This requirement is satisfied in the great grey shrike, a raptor-like passerine bird of open farmland, which was chosen for our research. The way an animal selects the location of copulation might be part of an arms race between partners. There are many players in EPCs and strategies adopted may differ between them (Valera et al., 2003). We have therefore hypothesized that both sexes should chose more secluded places for EPCs, than those for WPCs.

Methods

Study species

The great grey shrike *Lanius excubitor* is a territorial, socially monogamous bird; however, extra-pair copulations are an integral part of its reproductive strategy. In the breeding season it defends large territories covering ca. 20-50 ha (Schön, 1994a). The species nests in a tree or thorny bush in semi-open farmland with lot of meadows and arable fields with scattered woodlots, single trees and bushes. Pairs produce a single brood each year, although replacement clutches can occur after nest failures (Schön, 1995; Antczak et al., 2004). 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 nuptial gift consisting of some food item (Lorek, 1995). Precopulatory gifts differ regarding the status of female – the energetic value of gifts before EPCs is about fourfold of those before WPCs (Tryjanowski & Hromada, 2005). Copulations are most frequent in the early morning, until 09.00. In the population studied, pair copulations occur about 30 times per clutch, peaking 2 days before the first egg is laid (Lorek, 1995; our unpubl. data). 79% of male intrusions from neighbouring territories occurred during the fertile period of the resident female. Only in 8.7% of cases did the intruder leave without approaching either the resident female or the nest.

Extra-pair copulations occur in 33.3% of the territorial intrusions by neighbouring males. The females are permissive toward EPCs during their receptive period. In 81.3% of the cases when a male detected an intruder male attempting to copulate with his mate, a within pair copulation followed within 30 min (Lorek, 1995). Females choose the males following their display and nuptial gift (Tryjanowski & Hromada, 2005).

Field procedures

The study was carried out in the Wielkopolska region (52°28′N; 16°48′E), western Poland, in a high-density population (up to 24 breeding pairs/100 km²), during the breeding seasons of 2001-2005. In total we surveyed 184 territories, and we visited each territory for at least five hours per breeding season during the female fertile period. However, because the mating period of the species is relatively short and limited to 3-4 weeks (Lorek, 1995; Tryjanowski & Hromada, 2005; our unpubl. data), only the data from 28 well surveyed territories were used for analysis. We included only fertile females in our study. The fertile period of the female was designated as beginning 3 days prior to the laying of the first egg and ending with the laying of the penultimate egg (Lorek, 1995).

As unhidden copulation places, we considered open, exposed barbed wire, electrical lines and poles, and tops of trees. As hidden, or secluded, sites we considered places inside shrubs and on internal branches of trees, mainly Scots pine *Pinus silvestris* and European alder *Alnus glutinosa*. All territories included both open and hidden sites. There was no difference among the territories studied, regarding the distribution and occurrence of secluded/open habitats. We conducted intensive behavioural observations during the mating and egg laying periods with special attention to copulation behaviour and territory intrusions. In some cases territories were monitored by a team of three observers. The shrikes under observation were individually marked with coloured rings. Individuals were distinguished on the basis of wing patterns and eye-masks, which are highly individual-specific (Schön, 1994b; Probst, 2001). These individual marks are relatively easy to identify for experienced observers, especially as the birds were bold and conspicuous (Probst, 2001). For more details on study sites and methods see: Antczak et al. (2004); Tryjanowski & Hromada (2005).

Data analysis and statistics

For each female, a maximum of three copulations was observed. To avoid pseudoreplication, i.e., including two similar copulation events with the same female, we analysed only the first within pair copulation and first extra pair copulation per female. Not all females were observed in both categories. All statistical tests are two-tailed. We used the SPSS software ver. 12.0 PL for statistic computing.

Results

All 26 within-pair copulations occurred at open places such as electrical lines, fences or tops of trees, but only two of 13 (15.4%) extra-pair copulations occurred in such open places and the rest took place at more secretive locations (inside tree crowns and bushes) (Table 1). The difference in different copulation locations (open vs. secretive) according to copulation status (EPC vs. WPC) was very statistically significant ($\chi^2 = 6.43$, d.f. $= 1$, $p = 0.011$). Among 13 EPC copulations, nine males were identified as neighbours but we were unable to identify the territorial status of the remaining four extra-pair males.

Males more regularly engaged in extra territorial forays, therefore extra-pair copulations often took place in the territory of the female. Extra-pair events occurred closer to the nest of the resident female (mean $\pm$ S.D. $= 67 \pm 133$ m, $N = 13$), than in WPCs (mean $\pm$ S.D. $= 153 \pm 118$ m, $N = 26$) (t-test, $t = 2.07$, $p = 0.046$). Only in two EPC cases did the female leave the nest and travel to the neighbouring territories (binomial test, $N = 13$, $p = 0.022$).

Table 1. Sites used by great-grey shrikes as copulatory places.

Site type	Copulation		Total
	Within-pair	Extra-pair	
Open	26	2	28
Secluded	0	11	11
Total	26	13	39

Discussion

Although the active role of choosy females during EPCs is often stressed, a more useful view would probably be to emphasize the game among multiple players – females, their social partner and extra-pair males (Lifjeld et al., 1994; Petrie & Kempenaers, 1998; Westneat & Stewart, 2003). These conflicts of interests can lead to arms races among participants and influence behaviour of both females and males. We have found that, in great grey shrikes, both sexes behave surreptitiously during EPCs.

Our findings provides support for a rather old, but rarely tested idea: that habitat structure, in particular whether the breeding habitat is open or visually secluded, may influence the efficiency of male paternity guards and, therefore, the possibilities of seeking and obtaining EPCs. This idea was firstly proposed by Westneat et al. (1990), then reiterated by Westneat & Sherman (1997), but, to date, tested only by Mays & Ritchison (2004).

Surreptitious behaviour close to the nest of the resident female during EPCs is in sharp contrast to behaviour of great grey shrikes during WPCs. This behaviour can be an adaptive response to the diverging functions of within-pair and extra-pair copulations. WPCs, beside their reproductive role, can also signal the female's fertility and readiness for extra-pair affairs to a third party, the neighbouring males (Durango, 1956; Jakober & Stauber, 1994). When females of an allied species, the red-backed shrike *Lanius collurio*, give copulation calls, males from neighbouring territories rapidly approach and attempt to interfere with copulation (Durango, 1956). Frequent copulation as territorial signalling was also recorded in raptorial birds (Negro & Grande, 2001). Female great grey shrikes seem to control copulation (Lorek, 1995; Tryjanowski & Hromada, 2005). It is therefore possible that they are manipulating the copulation places to achieve specific goals – within-pair copulations can serve as an advertisement to inform neighbouring males about their fertility. Moreover, females of pairs nesting in clusters more often initiated movements during intensive mate guarding; this behaviour might be part of a strategy, informing neighbouring males about their presence and fertility (Lorek, 1995; our unpubl. data). Such behaviour was not observed in solitary nesting pairs (Lorek, 1995). The findings presented in this paper show that females of the great grey shrike rarely performed extraterritorial forays – in fact we noted only two cases, but this result might be biased since females might be extremely hidden and difficult to detect.

Other studies have also indicated that females rarely actively seek extra-pair copulations (review in Westneat & Stewart, 2003). However, the behavioural options of females and their tendency to engage in extra pair affairs might also be influenced by other factors such as the experience of a social mate in mate guarding, density, age and quality of potential extra-pair males, habitat structure of territories as well as the individual experience of the female.

In all cases, when we were able to determine male identity during EPC (69% of all EPCs recorded), males were from neighbouring territories, which is in agreement with data presented by Lorek (1995) and Schön (1995). That is plausible since the majority of the great grey shrike in our study area breed in clusters from two up to four pairs, where nests are between 300 m to 1500 m from each other, as well as solitary pairs.

In contrast to WPCs, both sexes behave surreptitiously and select secluded places for extra-pair copulations in the great grey shrike. The place of extra-pair copulation is important for females for at least two reasons: firstly, the success of the females' extra-pair affairs depends on their ability to stay hidden, and secondly, the high costs of EPC such as male punishment or the reduction of male investment in parental care.

However, males can also be forced to behave surreptitiously during extra-pair copulations. Birkhead and Møller (1992) suggested that extra-pair copulation can improve their fitness more than within-pair copulation. Males' extra-pair affairs are more expensive than WPCs (Birkhead & Møller, 1992) and success depends on their ability to stay unnoticed by the resident male during intrusion. There is an increasing body of evidence that males during extraterritorial forays try to behave surreptitiously (Kleven et al., 2006). It is very interesting that extra-pair copulations in the studied population of the great grey shrike on average took place closer to the nests of the resident females, sometimes even at the nest. This finding indicates that males had direct information about the nest location of neighbouring pairs.

Females obtain more valuable gifts from extra-pair than within-pair copulations – great grey shrike males invest several times more in extra-pair than in within-pair copulations (Tryjanowski & Hromada, 2005). Thus, males of the great grey shrike not only risk interruption of copulation but also the loss of the expensive precopulatory gift during EPCs. Moreover, the ability of the male to stay undetected during extra-pair forays and copulation can indicate their condition and overall quality for the choosy female. Kleven et al. (2006) proposed an interesting idea that females might benefit from EPC

with intruding males, if the exploratory behaviour of males is heritable – the sons from extra-pair affairs might have similar behavioural traits.

We conclude that EPCs and WPCs in the studied population of great grey shrike differ in their place of occurrence. This may be explained by avoiding the costs of EPCs by both partners, and by the different function of EP and WP copulations, explanations that are not mutually exclusive. We have shown that individuals are not always free to seek EPCs. Many recent studies have focused on the potential benefits of EPCs for females, but we also need to consider to what extent various costs (e.g., physical punishment) and ecological constraints influence extra-pair behaviour of animals of both sexes.

References

Antczak, M., Hromada, M., Grzybek, J. & Tryjanowski, P. (2004). Breeding biology of the Great Grey Shrike *Lanius excubitor* in W Poland. — Acta Ornitol. 39: 9-14.

Birkhead, T.R. & Møller, A.P. (1992). Sperm Competition in Birds: Evolutionary Causes and Consequences. — Academic Press, London.

Durango, S. (1956). Territory in the Red-backed Shrike *Lanius collurio* L. — Ibis 98: 476-484.

Gray, E.M. (1997). Female red-winged blackbirds accrue material benefits from copulating with extra-pair males. — Anim. Behav. 53: 625-639.

Hunter, M. & Davis, L.S. (1998). Female Adélie penguins acquire nest material from extra-pair males after engaging in extrapair copulations. — Auk 115: 526-528.

Jakober, H. & Stauber, W. (1994). Copulations and mate-guarding in the Red-backed Shrike (*Lanius collurio*). — J. Ornitol. 135: 535-547.

Jennions, M.D. & Petrie, M. (2000). Why do females mate multiply? A review of the genetic benefits. — Biol. Rev. 75: 21-64.

Johnsen, A., Litfjeld, J.T., Rohde, P.A., Primmer, C.R. & Ellegren, H. (1998). Sexual conflict over fertilizations: female bluethroats escape male paternity guards. — Behav. Ecol. Sociobiol. 43: 401-408.

Johnsen, A. & Lifjeld, J.T. (2003). Ecological constraints on extra-pair paternity in the bluethroat. — Oecologia 136: 476-483.

Kempenaers, B. & Dhondt, A.A. (1993). Why do females engage in extra-pair copulations? A review of hypotheses and their predictions. — Belg. J. Zool. 123: 93-103.

Kleven, O., Marthinsen, G. & Lifjeld, J.T. (2006). Male extraterritorial forays, age and paternity in the socially monogamous reed bunting (*Emberiza schoeniclus*) — J. Ornithol. 147: 468-473.

Lifjeld, J.T., Dunn, P.O. & Westneat, D.F. (1994). Sexual selection by sperm competition in birds: male-male competition or female choice? — J. Avian Biol. 25: 244-250.

Lorek, G. (1995). Copulation behavior, mixed reproductive strategy, and mate guarding in the Great Grey Shrike. — Proc. West. Found. Vert. Zool. 6: 218-227.

Low, M. (2005). Female resistance and male force: context and patterns of copulation in the New Zealand stitchbird *Notiomystis cincta*. — J. Avian Biol. 36: 436-448.

Mays, H.L. & Ritchison, G. (2004). The effect of vegetation density on male mate guarding and extra-territorial forays in the yellow-breasted chat (*Icteria virens*). — Naturwissenschaften 91: 195-198.

Negro, J.J. & Grande, J.M. (2001). Territorial signaling: a new hypothesis to explain frequent copulation in raptorial birds. — Anim. Behav. 62: 803-809.

Petrie, M. & Kempenaers, B. (1998). Extra-pair paternity in birds: explaining variation between species and populations. — Trends Ecol. Evol. 13, 52-58.

Probst, R. (2001). Successful bigamy in the Great Grey Shrike *Lanius e. excubitor*. — Ornis Fenn. 78: 93-96.

Schön, M. (1994a). Characteristics of the habitats of the Great Grey Shrike *Lanius e. excubitor* in the region of the southwestern Schwäbische Alb, Southwestern Germany: seasonal utilization and territory size, structural characteristics and their changes, microstructures and cultivation. — Őkol. Vőgel 16: 253-496.

Schön, M. (1994b). Sex-, age- and individual characters in the plumage pattern of the Great Grey Shrike *Lanius e.excubitor* in comparison with other Shrikes: on the effectiveness of optical signals. — Őkol. Vőgel 16: 11-80.

Schön, M. (1995). Breeding behavior of the Great Grey Shrike in Southwestern Germany. — Proc. West. Found. Vert. Zool. 6: 235-241.

Trivers, R.L. (1972). Parental investment and sexual selection. — In: Sexual Selection and the Descent of Man, 1871-1971 (Campbell, B., ed.). Aldine, Chicago, p. 136-179.

Tryjanowski, P. & Hromada, M. (2005). Do males of the great grey shrike, *Lanius excubitor*, trade food for extrapair copulations? — Anim. Behav. 69: 529-533.

Valera, F., Hoi, H. & Krištín, A. (2003). Male shrikes punish unfaithful females. — Behav. Ecol. 14: 403-408.

Westneat, D.F., Sherman, P.W. & Morton, M.L. (1990). The ecology and evolution of extrapair copulations in birds. — Curr. Ornithol. 7: 331-369.

Westneat, D.F. & Sherman, P.W. (1997). Density and extra-pair fertilization in birds: a comparative analysis. — Behav. Ecol. Sociobiol. 41: 205-215.

Westneat, D.F. & Stewart, I.R.K. (2003). Extra-pair paternity in birds: Causes, correlates, and conflict. — Annu. Rev. Ecol. System. 34: 365-396.

Wolf, L.L. (1975). Prostitution behaviour in a tropical hummingbird. — Condor 77: 140-144.