

# Male shrikes punish unfaithful females

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The costs to females of participating in extrapair copulations is an interesting but hitherto neglected topic in behavioral ecology. An obvious potential cost to females is male physical sanctions. However, although retaliation and punishment by male partners has been proposed as a basic cost for female extrapair behavior in theory, it has not been experimentally demonstrated. We studied the breeding biology of the lesser gray shrike (*Lanius minor*) and combined field observations and a field experiment to show that (1) there is a high intrusion rate during the female's fertile period, and extrapair copulations occur in this population; (2) by detaining females during the fertile phase, males were induced to retaliate physically against their partners, thereby increasing costs related to female extrapair behavior; and (3) there were no obvious costs to males of punishing their mates. DNA fingerprinting reveals that extrapair paternity is rare or absent in this population. Although we cannot conclude that monogamy at the genetic level is the result of male retaliation, we do show that male physical sanction is a cost that deceptive females have to assume. Males' strategies based on coercion should be considered when explaining variation in extrapair paternity across species. *Key words*: extrapair paternity, genetic monogamy, male coercion, male control, punishment, sexual conflict. [*Behav Ecol* 14: 403–408 (2003)]

Sexual conflict over reproduction occurs when the evolutionary interests of males and females do not coincide. Females of many animal species often mate with more than one male, and they can obtain a variety of benefits by doing so (Petrie and Kempenaers, 1998; Westneat and Sargent, 1996). In passerine birds, for example, extrapair paternity ranges from 0–70% (Petrie and Kempenaers, 1998), and 75% of all genetic studies of socially monogamous species have detected extrapair young (Birkhead, 1998; Birkhead and Møller, 1992; Gowaty, 1996). From the male perspective, extrapair copulations are profitable for those males that sire extra offspring and are prejudicial for the cuckolded males. Male mates thus develop counterstrategies to avoid or at least make extrapair behavior more difficult for females (Trivers, 1972), and consequently, a conflict between the sexes arises. One of these tactics may be physical coercion (Clutton-Brock and Parker, 1995). Retaliation and punishment by male partners has been proposed as a basic cost for female extrapair behavior in theory (Clutton-Brock and Parker, 1995; Westneat et al. 1990). Certain kinds of male aggression against females have been described in mammals (Clutton-Brock and Parker, 1995; Smuts and Smuts, 1993) and birds (Gowaty and Buschhaus, 1998; McKinney et al. 1983; McKinney and Evarts, 1997), in which most cases involve intimidation of females to accept copulations (Clutton-Brock and Parker, 1995; Gowaty, 1996; Gowaty and Buschhaus, 1998). There is also some evidence that males may reduce their parental care as a form of punishment (Dixon et al. 1994; but for a review of the lack of relationship between paternal contribution and genetic paternity, see Gowaty, 1999). Recent evidence suggests that aggressive retaliatory tactics, such as physical attacks, may serve as a general means by which males can induce females to avoid extrapair

copulations (Johnstone and Keller, 2000). To date, however, there is no experimental evidence for male aggression toward females serving to deter females from extrapair copulations, and it has been 25 years since the first anecdotal evidence (Barash, 1976) of male retaliation was reported. One explanation for the lack of evidence for frequent male physical sanctions might be that, if there is a threat of male aggression, females will rarely pursue extrapair copulations.

The conventional approach to explaining the phenomenon of extrapair behavior by females is to search for benefits of copulating with more than one male, and relatively little attention has been paid to the costs of engaging in extrapair behavior (Petrie and Kempenaers, 1998). Moreover, there is nearly no information on the occurrence of costs of harassment and intimidation in relation to female extrapair behavior. In the present study, we focus on such costs by exploring males' strategies based in coercion. Specifically, we experimentally test the occurrence of costs to females resulting from male physical coercion after manipulating paternity uncertainty.

## METHODS

### Study area and species

The lesser gray shrike (*Lanius minor*) is a socially monogamous long-distance migratory passerine, declining and highly endangered all over Europe. Pairs produce a single brood per season, although replacement clutches can occur after nest failures. Incubation is performed by the female, but young are fed and cared for by both parents (Cramp and Perrins, 1993).

The study was conducted from the end of April–July in 1996–1999 in a 20-km<sup>2</sup> plot in Central Slovakia (40°35'–38' N, 19°18'–22' E; 450–850 m above sea level) on the southern slopes of the Polana Mountains Biosphere Reserve. This area supports one of the last stable and dense populations of the lesser gray shrike in Central Europe (Krištín et al., 2000).

### Fieldwork

Starting at the end of April, we systematically searched the study site for nests, which were mapped and regularly

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monitored. For each nest, we recorded the onset of laying, clutch size, hatching and fledging success, and failure causes.

Adult birds were clap-netted and individually color-ringed. Blood samples were taken, and the birds were monitored over the rest of the breeding season. We provided nestlings with an aluminum ring and took blood samples from 6-day-old to 10-day-old nestlings. We measured several morphological variables in both adults and chicks, including weight, tarsus length, and wing length.

Behavioral observations were performed for 20-min observation periods using time sampling in 30-s intervals. We recorded the number of intruders, copulation attempts, and mate guarding behavior. As a measure of mate guarding intensity, we recorded the time both partners stayed together within a radius of 50 m (a distance in which a male could probably reach and defend the female or at least interfere an extrapair copulation attempt by an intruder). As a more strict measurement in this regard, we also recorded the time male and female were within 10 m. We began recording the proximity of partners to each other on the arrival from migration of the female, which occurred approximately 5 to 8 days before egg laying. Hence, average partner proximity was calculated for the fertile period (prelaying phase, day -5 to day -1; laying phase, from day 0 to the penultimate day of egg laying, where day 0 is when the first egg is laid) and during incubation and chick feeding (32 days). Observations were performed throughout the day between 0500–2000 h.

## Experimental approach

### Short term removal experiment

To investigate male reaction to female absence during the fertile phase, we experimentally retained some females for an extra time after ringing, blood sampling, and measurements. We retained 15 females during the fertile phase, and as a control, 10 males were retained during egg laying and 52 males and 41 females during other phases of the breeding cycle (mainly feeding).

Shrikes were captured and detained in cloth bags for approximately 1 h ( $\pm 5$  min SE), mainly during the morning hours (0800–1200 h), and were then released from an adjacent territory to simulate a visit to neighboring shrikes. Birds always returned directly to their own territory. In the 20 min after the return of the detained bird, behavioral interactions with the partner were categorized as nonaggressive or aggressive, the latter including at least chases but also physical aggressions and forced copulation attempts.

### Fitness consequences for the males of punishing the mate

To examine whether coercion to the partner had costs to males, we looked for differences in basic breeding parameters between experimental nests in which female retention resulted in males punishing the female and control nests (in which male aggressive behavior was never observed). We recorded clutch size, hatching success, and fledging success (number of chicks at least 10 days old in nests in which at least one chick fledged), and we compared each nest in a pair design with at least another nest (or with the mean value if we had several possible control nests) with the same breeding status (the nearest nests with the same day of start of laying). Furthermore, we analyzed differences in chick development (i.e., body weight corrected for size, in our case wing length; correlation between body weight and wing length:  $r = .85$ ,  $p < .001$ ,  $N = 195$  chicks) between experimental and control nests. We did not correct for differences in brood size because residual body weight/nest was not correlated with brood size

( $r = -.19$ ,  $p > .2$ ,  $N = 38$ ), and brood size did not differ between the experimental and the control group ( $5.12 \pm 0.51$  versus  $5.64 \pm 0.35$ , respectively; Wilcoxon matched-pairs test:  $z = 0.50$ ,  $N = 8$  nests,  $p = .61$ ). Finally, we compared whether a breeding attempt was successful (at least one chick fledging) or not (no chick fledging) for the two groups, ignoring nest losses owing to heavy rainfall, because such losses should not be owing to individual variation in parental investment.

Sample size should be 11 (the number of experimental nests in which male coercion was recorded), but predation and desertion reduced the sample size.

## DNA fingerprinting

Blood samples, drawn from the brachial vein, were suspended in 98% ethanol and stored at 4°C. Except for minor modifications, our fingerprinting procedures followed standard techniques described in Epplen and Zischler (1990). For DNA extraction, ethanol was removed, blood was added to 5 ml of buffer B (25 mM EDTA, 75 mM NaCl, 10 mM Tris at pH 7.0) and incubated overnight with 3 mg proteinase K and 0.5 ml 10% SDS at 37°C. DNA was purified by salting out with saturated NaCl and, after ethanol precipitation and washing with 70% ethanol, was dissolved overnight in TE buffer (10 mM Tris, 1 mM EDTA at pH 8.0) at 37°C. For each fingerprint, about 10  $\mu$ g DNA was digested overnight with 10  $\mu$ l *Hae*III enzyme. DNA was then repurified by phenol-chloroform-isoamyl extraction, precipitated by isopropanol at -20°C for 2 h, air-dried, and dissolved overnight in 10  $\mu$ l TE and 10  $\mu$ l stop-buffer (0.25% Brom-phenol blue, 0.25% xylancyanol, 30% glycerol in water) at 37°C. DNA was separated by agarose gel electrophoresis at 42 V for 32 h and transferred to a nylon membrane by Southern Blotting. DNA hybridization was based on a dig-11-UTP labeled oligonucleotide [(GATA)<sub>4</sub>] probe.

For parentage assignment, we included data on 2 years comprising 26 complete families with 136 offspring (1996,  $N = 4$  nests; 1997,  $N = 22$  nests) and 14 families with a single adult (in 10 cases, the adult was the male; only in 4 cases, female; 1996,  $N = 5$  nests; 1997,  $N = 9$  nests). We mainly followed the method described by Westneat (1990) and Hunter et al. (1992). We scored an average  $\pm$  SD of  $21 \pm 4.2$  bands ( $n = 328$  individuals trapped in the population during both years) in the approximate size range of 3.0–23 kb. We assessed the proportion of band sharing ( $D = 2Fab/[Fa + Fb]$ , where  $D$  is band sharing coefficient;  $Fab$ , the number of bands present both in individual  $a$  and  $b$ ; and  $Fa$  and  $Fb$ , the total number of bands present in individual  $a$  and  $b$ ; see Wetton et al. 1987) between adults and putative father-young and putative mother-young, respectively, for each family. Parentage assignment was made by comparison of DNA similarities, with the 99% confidence ranges of band sharing values for known relatives and nonrelatives.

For each young (of complete families), we measured the number of novel bands (bands found in the nestlings DNA profile but not found in the DNA profile of putative parents). If only one or two novel fragments were present and all other bands could be assigned to one or both parents, novel fragments were considered to result from mutations or scoring errors. We used the method of Westneat (1993) to set a statistical limit to the number of these bands and to set 99% confidence limits to band sharing between parents and young.

We used parametric tests when assumptions for normality were met. Otherwise data were transformed or nonparametric tests were used.

## RESULTS

### Social mating patterns

Monogamy appears to be the mating system of this species on the social level, because almost all pairs we could monitor through the whole breeding cycle (53 pairs with both pair members ringed) had no indication for mate switching. Only in one case did we observe mate switching during egg laying. In this case, two females were competing for one male, and the male was watching this conflict without interfering. A switch occurred after the first female already laid three eggs. The second female went on laying in the same nest just 1 day later.

Pair stability between successive breeding attempts is also high. In nine cases in which we could identify both partners for the first and second breeding attempt (initial nesting attempt with failure and replacement nest), all remained together. Thirty one of 77 (40.2%) adult males, 17 of 69 (24.6%) adult females, and 51 of 790 nestlings were recovered. However, we found no pair stability at all between seasons, and no nestling ever mated with a parent.

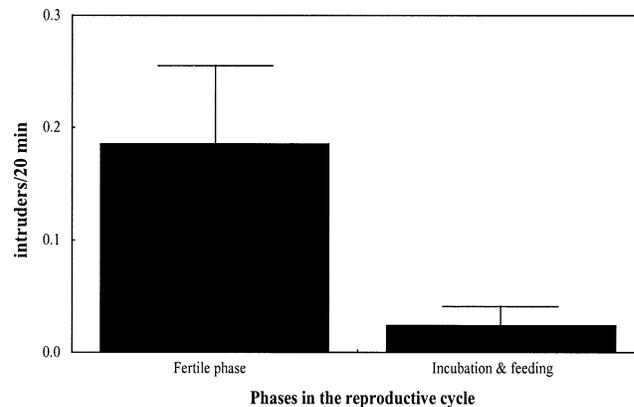
In all cases (37, 35, 32, and 30 breeding pairs for 1996–1999, respectively), both partners provided parental care. Therefore, the mating system is seasonal monogamy with biparental care.

### Intrusions and mate guarding behavior

Intrusions, mainly by neighboring males, frequently occur throughout the female fertile period. We witnessed 116 intrusions during 1996–1999, and in all 51 cases in which we identified the sex of the intruder, it was a male (binomial test,  $p < .000001$ ). Intruders were mostly close neighbors; only in two out of 28 (7.1%) cases in which we could identify the intruder, it belonged to nests other than the two nearest ones to the focal nest. The intrusion rate during the focal female's fertile period was 7.7 times higher than during the incubation and feeding phase (Wilcoxon matched-pairs test:  $z = 2.1$ ,  $N = 15$  nests,  $p = .03$ ) (Figure 1). All 51 male intrusions ended with the resident male chasing away the intruder, suggesting that male-male aggression is a form of paternity defense.

We observed seven extrapair copulation attempts during four observation years. Three of them occurred when the female was on the border of the territory, the rest as a consequence of a neighboring male's intrusion.

Male shrikes respond to the evident risk of losing paternity. We found that males spent 79% (SE = 2.5,  $N = 28$  nests) of the time within 50 m of their partner and 46% (SE = 2.74,  $N = 28$  nests) within 10 m. Four lines of evidence suggest that the male's maintenance of close proximity to his partner is a paternity assurance tactic: (1) in 88.3% ( $\pm 5.9$  SE) of cases, the male approached the female after an intrusion, whereas only in 11.7% ( $\pm 4.6$  SE) did the female approach the male (Wilcoxon matched-pairs test:  $z = 3.11$ ,  $N = 14$  nests,  $p = .002$ ). (2) Partner proximity is significantly higher during the female fertile period, which comprises the prelaying (day –5 to day –1) and the laying phases (day 0 to the day the penultimate egg was laid), than after the fertile period (incubation plus nestling feeding; overall ANOVA model:  $F = 7.1$ ,  $df = 2, 43$ ,  $p = .0021$ ). Post hoc comparisons revealed significant differences between the prelaying and the incubation-feeding phase (Newman-Keuls test,  $p < .0008$ ) and the laying and the incubation-feeding phase (Newman-Keuls test,  $p < .006$ ) (Figure 2a). (3) Partner proximity was almost similar throughout the fertile period (prelaying versus laying phase; Newman-Keuls test,  $p > 0.2$ ) and throughout the day (repeated-measures ANOVA:  $F = 0.36$ ,  $df = 2, 14$ ,



**Figure 1**

Intruder rate during and after (incubation and nestling feeding) the female fertile period (day –5 to the day when the penultimate egg was laid; day numbers are relative to the day when the first egg was laid which is day 0). Given is the mean intruder frequency  $\pm$  SE for 15 breeding pairs during 20-min observation periods.

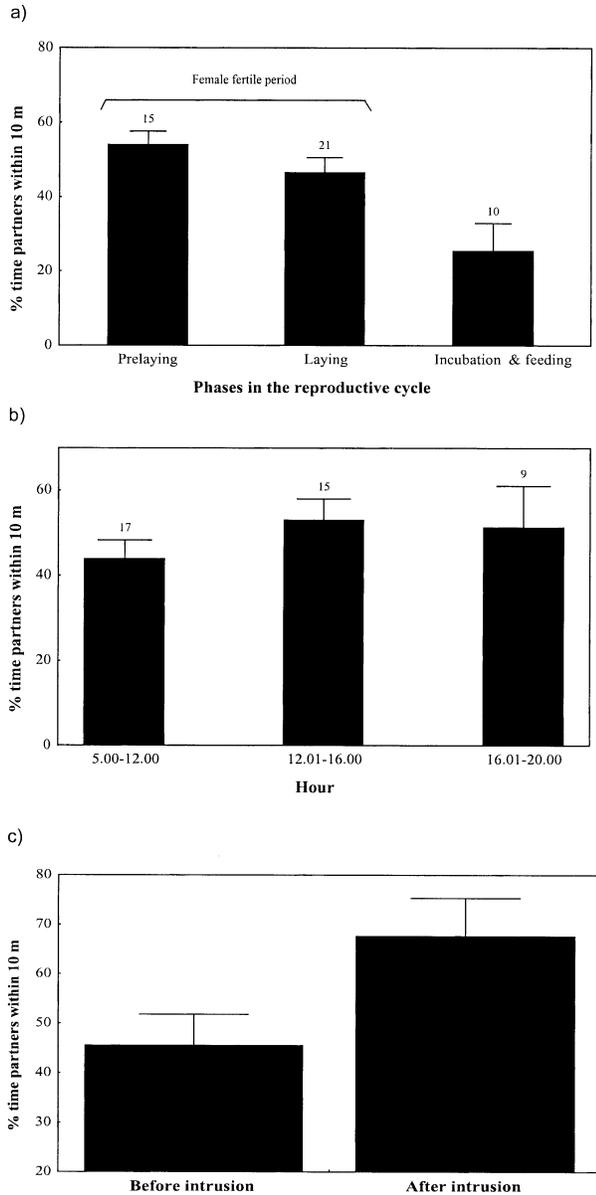
$p > .6$ ) (Figure 2b). (4) The percentage of time that pair members were within 10 m was significantly higher after than before an intrusion (Wilcoxon matched-pairs test,  $z = 2.04$ ,  $N = 12$  nests,  $p = .04$ ) (Figure 2c).

### Male retaliatory attempts

Our short-term female removal experiments during the fertile period, aimed to increase paternity uncertainty, induced strong reactions in males. During female absence, 13 (86.7%) of 15 males sang and called loudly from the nest tree, and at least six males (40%) were observed intruding into neighboring territories. Moreover, 11 (73.3%) of 15 female removals during the fertile period resulted in clear cases of male physical aggression toward the female immediately after releasing her back to the territory (Figure 3). These aggressive attacks ranged from chases and close following in the less aggressive cases to chases, pecking, and several successive forced copulations and copulation attempts in the most aggressive ones (Table 1). Male aggressive behavior lasted, in most cases, some minutes (enough to peck on the female and copulate with her). Just in one case, male punishment lasted some hours, as the male even chased the female out of the territory. She returned during the night and laid an egg the following morning. In most cases, released females came back directly to the nest tree, but some of them were obviously reluctant to meet the partner (Table 1).

In contrast, female removals during chick feeding did not have such effects either on male behavior (both during retention and after female release) or on female behavior after releasing ( $N = 41$ ). Likewise, male removal revealed no similar reactions by the female during the fertile period ( $N = 10$ ) or during chick feeding ( $N = 52$ ) (Figure 3).

Male aggressions to their partners were also recorded in nature though infrequently. In fact, despite intense observation in 53 nests, we only observed male aggressions (chasing, forced copulation attempts, and physical attacks) against their partners during the female fertile period in nine cases (observed in nine nests) as a result of female absence or female behavior (approaches, staying far from the nest) in presence of intruders (Table 2). Therefore, occurrence of male aggressive behavior toward the partner was significantly more frequent in pairs in which the female was detained



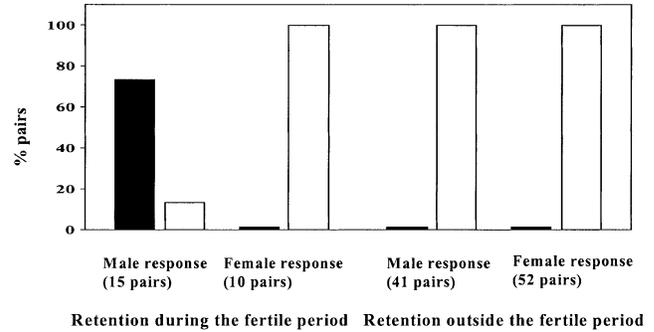
**Figure 2**  
Mate guarding as paternity assurance strategy. The time both partners spent within 10 m of each other during and after the female fertile period (a), throughout the day during the female fertile period (b), and before and after an intrusion by an outside male (c) ( $n = 12$  pairs).

(73.3%) than in pairs in which she was not (16.9%) (Proportion test,  $p = .0001$ ).

In summary, both experimental and field observations support the cause-effect relationship between male punishment and paternity uncertainty.

#### Costs to males of punishing the mate

We did not record any fitness consequences to males of punishing the mate. Egg laying was not delayed in any case, and experimental nests did not differ from control ones in clutch size ( $5.87 \pm 0.35$  versus  $6.13 \pm 0.23$ , respectively; Wilcoxon matched-pairs test:  $z = 0.98$ ,  $N = 8$  nests,  $p = .32$ ), hatching success ( $88.09\% \pm 8.14$  versus  $90.61\% \pm 3.80$ , respectively, Wilcoxon matched-pairs test:  $z = 0.10$ ,  $N = 8$  nests,



**Figure 3**

Sexual coercion (aggressive attacks) by resident individuals toward their partners in relation to the fertile and chick feeding period and the sex retained. Behavioral interactions with the partner were categorized as nonaggressive (empty bars) or aggressive (filled bars).

$p = .91$ ), fledgling success in successful nests ( $4.85 \pm 0.55$  versus  $5.50 \pm 0.34$ , respectively; Wilcoxon matched-pairs test:  $z = 0.67$ ,  $N = 7$  nests,  $p = .50$ ), and chick body condition (Wilcoxon matched-pairs test:  $z = 0.52$ ,  $N = 6$  nests,  $p = .60$ ). The proportion of successful nests (at least one chick fledged) was similar for the experimental (seven out of 11, 46.7%) and the control group (eight out of 11, 72.7%; proportion test,  $p = .65$ ). Nest desertion occurred in only two nests, and in the remaining nine cases, male and female attended the nest.

#### Genetic mating pattern

The band sharing coefficient of assumed unrelated adults averaged 0.39 ( $SD = 0.05$ ,  $n = 27$ ), and the calculated 99% upper confidence limit was 0.42. The band sharing coefficient of offspring and related parents averaged 0.67 ( $SD = 0.08$ ,  $N = 307$ ), the lower 99% confidence limit being 0.51. The probability of finding one novel band per individual was 0.10294 (14 out of 136 individuals). Thus, the probability of finding two novel bands is 0.010597; three novel bands, 0.000112; and four novel bands, 0.00000001. Hence, for 136 nestlings, the expected number of individuals with two, three, or four novel bands is 1.44, 0.015, and 0.000002. These values are similar to what we found (two individuals with two novel bands and zero with three or more novel bands).

Fingerprinting analyses thus revealed that females are faithful because none of the investigated nests contained chicks fathered by an extrapair male ( $N = 36$  broods from two breeding seasons).

#### DISCUSSION

Our results show that there is a potential for extrapair behavior in the lesser gray shrike. This species is less territorial than are other shrike species (Jakober and Stauber, 1994; Schön, 1994), and frequently breeds in dense aggregations (Krištín, 1995; Krištín et al. 2000). As a result, territorial intrusions are frequent and rate high during the female fertile phase. Consequently, males try to guard their females. Male lesser gray shrikes performed mate guarding. Such a paternity assurance tactic seems to be a rather low-priced strategy in this species, as the open habitat structure facilitates female visual control. In addition males frequently copulate with their females during the fertile period and especially after intrusions by other males (Valera F, Hoi H, Krištín A, in preparation).

Although certain ecological conditions can facilitate male vigilance to the partner (e.g., in our case, high visibility in the breeding area probably enables males to keep visual contact

**Table 1**  
Male and female behavior in female retention experiments

Answer	Cases
Male answer	
No aggression	4
Chases and close following or attraction	2
Chases and forced copulation attempts (no.)	2 (>1, >1)
Chases, punishment, and forced copulation attempts (no.)	7 (1, >1, 2, >2, 4, 6, 6)
Female answer	
Returning to the nest tree (two females engaged in non forced copulations)	9
Returning to the territory but further from the male	3
Hiding and reluctant to meet the male	3

with their partners almost 100% of the time), there is increasing evidence that females can control paternity under a variety of circumstances (Eberhard, 1996; Gowaty, 1999; Hoi-Leitner et al. 1999; Petrie and Kempenaers, 1998; Wagner et al. 1996). Therefore, we would expect some other factors involved. Our results suggest that female lesser gray shrikes avoided pursuing extrapair copulations, even when they had the rare opportunity to do so in the absence of their partner as (1) they usually seldom leave their territory during their fertile period, and during 10 male removals in the female's fertile period the female never left the territory; and (2) the five observed intrusions by neighboring males when the male partner was detained did not result in a copulation attempt.

There are two possible explanations for this female behavior. First, extrapair copulations are not a part of female's mating strategy in this species. However, this would be unusual in a passerine bird (Birkhead, 1998), and in fact, extrapair copulations do occur. Second, females could benefit from extrapair copulations but avoid them because the cost of male retaliation outweighs any possible benefits. We observed spontaneous cases of male retaliation when the females behaved in a way that might decrease the male's certainty of paternity (Table 2). In addition, we were able to induce male punishment at a much higher rate than the one observed in nature by experimentally increasing paternity uncertainty. Physical punishment occurred only during the fertile period of the female and is only shown by males toward their females. Moreover, when we presented female models in the males' territories, we did not observe aggressive attacks but three of 13 males performed extrapair copulation attempts (Valera F, Hoi H, Krištin A, in preparation). These observations indicate that (1) males attempt extrapair copulations when given the opportunity (see also Results), and (2) males are not aggressive to extrapair females, but only to their partners.

In summary, the important result of this study is that we were able to experimentally establish a cause-effect relationship between male punishment and paternity uncertainty.

Retaliation and punishment by male partners has been proposed as a basic cost for female extrapair behavior in theory (Clutton-Brock and Parker, 1995; Westneat et al., 1990). Recently, Johnstone and Keller (2000) suggested that aggressive retaliatory tactics, such as physical attacks, may serve as a general means by which males can induce females to avoid extrapair copulations. In contrast, few reports indicate

**Table 2**  
Observational evidences for male control of female behavior

Male behavior	Cases (nests)	Day in female fertile cycle	Cause (no. cases)
Attraction to the nest	4 (3)	-4, -4, -4, -3	Female far from nest (2) Intruder nearby (2)
Chases	5 (5)	Prefertile (<-5), +1, +3, +5, +6	Intruder nearby (4) Female leaves the territory (1)
Chases and copulation attempt	2 (2)	+1, +3	Female approaches a neighbor (1) Intruder nearby (1)
Chases and physical punishment (one case with copulation attempt)	2 (2)	Prefertile (<-5), -2	Prolonged absence (1) After repeated chases to an intruder and the female (1)

that males of a bird species try to directly control female extrapair behavior by making it too costly for females to perform this behavior (for review, see Gowaty and Buschhaus, 1998), and to our knowledge, male retaliation as a response to female extrapair behavior has been reported only once (Barash, 1976).

However, when the benefits of sexual coercion to males are high, males can develop such strategy to a point at which they have substantial costs to females (Clutton-Brock and Parker, 1995). Selection would favor males who inflict such costs on their partners if, by doing so, they discourage remating.

This study demonstrates that if paternity certainty is decreased males become more aggressive to their mates. One question then is as follows: Does this cause the genetic monogamy found in this species? From our data, we cannot conclude that genetic monogamy is the result of male retaliatory tactics. Other factors, such as the essential role of paternal care (Henderson et al., 2000), insufficient genetic heterogeneity between males (Birkhead and Møller, 1996), or nesting synchrony (Birkhead and Møller, 1992), may account for monogamy at the genetic level. However, theory predicts that if punishment follows detection of a deceptive behavior, it may reduce or even negate the benefits of acting deceptively (Clutton-Brock and Parker, 1995). Therefore, male retaliatory strategies have the potential to prevent female extrapair behavior. Our finding of absence of extrapair paternity during two breeding seasons agrees with such prediction and suggests that the threat of physical sanctions together with constant visual surveillance may provide successful paternity assurance strategy for male lesser gray shrikes. To reach such conclusion, it would be necessary to manipulate the degree of male control. For instance, one could ask whether more extrapair copulations, and perhaps even extrapair paternity, will take place if males somehow are prevented from being aggressive. Similarly, a male removal experiment would theoretically leave the females free to make a mate choice without a mate-guarding male to prevent her. Evidence of male control would be increased female extrapair copulation activity when the male is unable to mate guard. Unfortunately, the first approach seems

unfeasible, and a simple male removal would not distinguish a widowing effect from a lack of guarding.

We did not aim to explain why no extrapair paternity exists in this species. Our aim was to explore the costs of extrapair behavior for females, and we found that males impose direct costs to their partners. Physical punishment can be severe, but it seems to be limited to a short period after female absence. Therefore, it may have a primarily intimidating function. Clutton-Brock and Parker (1995) suggested that attacks on females are likely to have some cost to the males themselves. We were unable to detect fitness consequences for the male on the subsequent breeding, as breeding parameters were similar in experimental and control nests. This suggests that male lesser gray shrikes exert an optimal level of punishment in the sense that it is effective in intimidating the female while keeping the costs to males small.

One could ask if male coercion is also important in other passerines. Although there is little evidence for frequent male physical sanctions, this could be the result of females avoiding circumstances in which they are exposed to harassment (Clutton-Brock and Parker, 1995). Experimental manipulations of paternity certainty, like the one reported here, could prove useful to answer the former question. Only few studies have experimentally widowed males temporarily to determine their response to female absence, and none of the studies aimed to explore male-female conflict as a result of an increased paternity uncertainty (see review in Pinxten et al. 1995). We suggest that short-term removal experiments can contribute to understand the importance of damaging mating tactics, such as physical aggression, as a significant factor in explaining the wide variation in extrapair paternity across species.

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