The importance of breeding density and breeding synchrony for paternity assurance strategies in the lesser grey shrike

Dedicated to Professor Karel Hudec in honour of his 80th birthday

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A b s t r a c t . Breeding density and breeding synchrony have been reported to influence the intensity of sperm competition although results obtained so far are not conclusive. In this study we examine the investment of male lesser grey shrike (*Lanius minor*) into paternity guards in relation to breeding synchrony and breeding density. Male shrikes perform a double strategy to ensure paternity. They copulate frequently, mainly after territorial intrusions by other males, and guard their mates throughout the whole fertile phase. Our results indicate that, the two socio-ecological factors investigated, indirectly affect extra-pair behaviour in LGS's. Males seem to be constrained by the frequency of intrusions by neighbouring males and this risk is associated with laying synchrony. The risk of intrusions depends on the timing and overlap of breeding attempts and males adjust their investment to paternity assurance accordingly. Furthermore, females seem to alter their egg laying patterns to minimise synchrony in situations where they find themselves in dense breeding situations. This is indicated by the negative correlation between breeding density and breeding synchronization. Extra-pair paternity, however, was not detected in our population. Thus the rate of extra-pair paternity is not necessarily an adequate measure to identify the influence of socio-ecological factors on male and female mating strategies.

Introduction

One way males, especially of monogamous species, can increase their reproductive success is to seek copulations outside the pair bond (T r i v e r s 1972). However, a male's extra-pair behaviour is constrained. Important constraints in this respect could be a limited sperm supply or a limitation in time to perform extra pair copulations since males have to fertilise and guard their own females during their fertile period (B i r k h e a d & M ø l l e r 1992, 1998). The necessity for guarding the own female partner decreases as it moves out of the fertile period, e.g. when the female proceeds from the pre-laying to the early incubation period. From this moment onwards there is more time free for extra-pair behaviour. Consequently the risk of cuckoldry as well as the time available for extra-pair behaviour is associated with synchronisation of egg-laying in females (S t u t c h b u r y & M o r t o n 1995) and the number of available extra-pair partners (W e s t n e a t & S h e r m a n 1997). The importance of synchrony is supported by the fact that the degree of synchronization in start of breeding is related to the rate of extra-pair paternity (S t u t c h b u r y & M o r t o n 1995, K e m p e n a e r s 1997, W e a t h e r h e a d 1997, W e s t n e a t & S h e r m a n

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1997, W e s t n e a t & G r a y 1998, T h u s i u s et al. 2001, W e s t n e a t & S t e w a r t 2003, S p o t t i s w o o d e & M ø l l e r 2004, F i s h m a n & S t o n e 2005). In terms of availability of extra-pair partners the distance to the nearest neighbouring breeding pairs, or the number of breeding pairs in the proximity seems to be important as there is evidence that density of breeding pairs affects extra-pair paternity in some species (W e s t n e a t & S h e r m a n 1997, W e s t n e a t & S t e w a r t 2003). Thus to better understand constraints on male behaviour related to extra-pair copulations and paternity assurance it may be important to simultaneously examine breeding synchrony and density since these two factors very likely interact. There is scarce information on whether males adjust, or are able to adjust their investment in paternity assurance tactics to varying risk of cuckoldry. One indication comes from bluethroats (*Luscinia svecica*). In this species, e.g. quality differences between pair members and possible extra-pair partners seem to influence whether females cooperate with their mate or not (J o h n s e n & L i f j e l d 1995). To minimize the chances for being cuckolded, less attractive males consequently invested more in mate guarding or other paternity guards (L i f j e l d et al. 1994, J o h n s e n & L i f j e l d 1995, J o h n s e n et al. 2001).

This furthermore means that, to properly understand the influence of socio-ecological factors like density or breeding synchrony on extra-pair paternity, the role of paternity assurance has also to be considered.

The aim of this study is to identify the (i) behavioural tactics male lesser grey shrikes (*Lanius minor*) use to protect their paternity and, (ii) whether male lesser grey shrikes (henceforth LGS) adjust their investment in paternity assurance to the risk for cuckoldry. In birds mate guarding and frequent within-pair copulations have been shown to be the two most common paternity guards (B i r k h e a d & M ø l l e r 1992). Therefore we investigate a possible role of these two paternity assurance tactics in our species. During the fertile period we have never seen a female LGS leaving the territory, but territory intrusions by other males are quite frequent (see Results, and V a l e r a et al. 2003). Thus paternity assurance in LGS is not to stop their females sneaking off, but rather preventing extra-pair males from harassing and copulating with the female.

To examine the risk of cuckoldry on male investment in paternity assurance we particularly focus on the importance of the timing of breeding, including synchronisation of breeding attempts and the breeding order (who starts first) of neighbouring pairs and, the number of potential extra-pair males in terms of breeding density (e.g. distance of the nearest neighbours, number of active breeding pairs in the proximity).

Methods

Study area and species

The study was conducted during the 1996, 1997 and 2003 breeding season in central Slovakia (40º35´-38´N, 19º18´-22´E, 450–850 m a.s.l.). The study area comprises 20 km^2 of traditionally farmed plot on the southern slopes of Poľana Mts Biosphere Reserve and it houses one of the last stable and dense populations of the LGS in central Europe (75–85 breeding pairs/20 km^2) (K r i s t i n et al. 2000).

In the migratory lesser grey shrike incubation starts with 3rd–5th egg and is performed mainly by the female. Start of egg-laying for first clutches lasts for about two weeks. In 1996 from 11 to 23 May (median = 17 May), 1997 from 9 to 25 May (median = 18 May) and

2003: from 6 to 26 May (median = 15 May). Both sexes feed and care for the young (own unpublished data). In this study area all birds were single-brooded even though there were replacement clutches after early nest failures (K r i s t i n et al. 2000). This replacement clutches start usually more than seven days later. One explanation of this delay is that males need some time to fully recover their gonads. There is indication that male gonads regress shortly after the fertile period of their own mate (see Discussion). Breeding density was highly variable with a distance between nearest nests ranging from 25 to 1125 m (mean distance $\pm$ SE = 167.1 $\pm$ 34.7, N = 22). 39.7 % (23/58) of all first clutches had two or more nests within a radius of 200 m.

F i e l d w o r k

We started trapping birds shortly after territory establishment by means of clap-nets. Shrikes were individually colour ringed (N = 102) and followed up over the rest of the season. Prior to incubation nests were monitored every third day and later on every seventh day. Start of egg-laying, clutch size, hatching and fledgling success as well as causes of nest failures were recorded.

For the three years (1996, 1997 and 2003) we have behavioural data of 9, 7 and 6 pairs, respectively. We pooled the data for the three years because (i) no pair was used twice and (ii) we found no year effect on copulation frequency, % time mates spent within 10 m and intruder frequency (Anova, for all P > 0.4). The time between the arrival of the female in a territory and the start of nest building is usually not more than five days. Copulations have not been detected earlier than 5 days before start of laying (unpublished data). Therefore we define the fertile period as the period between day -5, where day 0 is the day when the first egg is laid, to day +3 (three days after laying the first egg and when incubation usually starts). During the fertile phase we made behavioural observations using time sampling (30 s intervals) during 20 min periods (N = 132 protocols) throughout the morning (0500–1100 hrs). We filled in only one protocol per nest/day. For each nest we did six protocols during the fertile period. Three observers tried to monitor all fertile nests on the same day. We recorded the number of intruders, copulation activity (copulation attempts and number of successful copulations) and mate guarding behaviour. As a measure of mate guarding intensity we took the time both partners stayed together within a radius of 10 m (a distance where a male could easily reach and defend the female or at least stop a copulation attempt of an intruder).

We investigated the risk of female extra-pair behaviour in relation to different socio-ecological parameters. It is difficult to predict how male LGS may perceive the risk of cuckoldry in terms of potential competitors. Therefore we used different parameters and measured breeding density in terms of (i) distance to the nearest nest, (ii) number of nests within a radius of 200 m (this is usually the diameter of a LGS territory, see Wirtitsch et al. 2001) and, (iii) mean distance to the two nearest nests. As an index of breeding synchrony we used the percentage of overlapping fertile days between the fertile periods of the focal female and the nearest neighbouring female. In an earlier study (V a l e r a et al. 2003) we could already show that all intruding birds where males (females have never been observed to leave the territory) and that in about 93% of the cases the intruder was the nearest neighbour. During the fertile period of a female we observed in average 0.61 $\pm$ 0.15 territorial intrusions per hour, which is about 7.7 times higher than during the incubation or feeding period (V a l e r a et al. 2003). Our observations suggest that laying stage is also important. We observed that

males, whose females are in later fertile stages than the focal one, are more likely to become intruders (see Results). Thus, the risk of getting intruders does not only depend on the length of the overlap but also on how and when two neighbour females overlap. To better express the risk of cuckoldry we calculated a risk index (RI) based on intruder frequency which includes breeding order, synchrony and density. The RI considers the fertility stage of the neighbouring female in relation to that of the focal female. The RI ranges from 0 (when the neighbouring female is not yet in her fertile phase during the main fertile period of the focal female – no intrusions observed) to 3 (the neighbouring female is incubating during the main fertile period of the focal female – most intrusions observed, see Results, Table 1 and V a l e r a et al. 2003). No risk seems contradictory when the neighbouring female is not yet in her fertile phase. One might think that at times when the male should already produce sperm and the risk of loosing his own paternity is low, he should engage in extra-pair copulations and try to intrude into other territories at little risk to himself and a male should more likely intrude when his female is pre-fertile than when she is at the peak of her fertility. Thus the RI should be high in the pre-fertile period. Males very likely know in which reproductive state their females are (see also L o w 2004). There are, however, obvious behavioural/biological reasons why males do not tend to leave their female in the week prior to start of her fertile period (until day -5). First of all, there is only one week between arrival at a territory and start of nest building which can be called pre-fertile period since we did not observe any copulations in 50 protocols of 12 pairs. Furthermore this is the time when the pair bond is still weak and the male has to persuade a female to stay with him. During that period males constantly sing, follow the female and try to attract her to possible nest sites. During that period courtship is very intense and this is also the period when females have been observed to switch mates. Thus leaving the own female unattended during that period would lead to a high risk of loosing the partner and this probably explains why males do not seek extra-pair copulations in this early mating period.

In cases where a neighbouring female overlaps the fertile phase of the focal female with several periods (e.g. one day in category 0 to +3 and several days in category +4 to +7) we consider the rank of the period overlapping most (in our example category +4 to +7), and if both periods overlap for the same time (same number of days) with the focal female we use the higher value (in our example, the one corresponding to the period +4 to +7, that is rank 3, see Table 1). This procedure is based on the assumption that males do not have exact information on neighbouring nests and thus will most likely adjust their effort in paternity guards to the maximum risk. We calculated the RI for the two nearest active nests and used the sum of both values for analyses.

Only first clutches were considered for investigating the relationships between paternity assurance strategies, intruder rate, breeding density and breeding synchrony.

Table 1. Risk index values related to different fertility phases of focal and neighbouring female. 0 = no risk, 3 = highest risk for extra male intruders. For details see Methods.

Phase of neighbouring female	Phase of focal female	Risk index value
Pre-fertile		0
day -5 to -1		1
day 0 to +3	main fertile phase (day -5 to +3)	2
day +4 to +7 (start and full incubation)		3

Parametric tests were used when data were normal or could be transformed to approximate a normal distribution, otherwise non-parametric tests were applied. Tests are two-tailed and data are presented as means ± SE, unless otherwise stated.

Results

The role of within–pair copulation frequency and mate guarding as paternity assurance strategies

The role of copulation frequency as a paternity guard is indicated by the positive correlation between male copulation attempts and the mean number of intrusions ($r = 0.53$, $P = 0.03$, $N = 22$). More importantly we found that (i) within-pair copulation attempts were significantly more frequent within five minutes after an intrusion than within five minutes before (paired t-test: $t = 2.59$, $P = 0.017$, $N = 22$ nests) (Fig. 1) and, (ii) copulations after an intrusion were not evenly distributed but in most cases occurred shortly afterwards (median duration: 97 sec, lower and upper quartile: 42 and 320 sec respectively).

Mate guarding is indicated by the fact that the time males spend within 10 m of their female is positively correlated to the mean number of territorial intrusion by other males ($r = 0.50$, $P = 0.034$, $N = 22$) but mate guarding and within-pair copulation frequency seem to be independently used from each other. There was no relationship between the time male and female spent together within a radius of 10 m and within-pair copulation activity (successful copulations/20 min and copulation attempts/20 min) (Pearson correlations, in all cases, $P > 0.1$, $N = 22$ nests). Furthermore, no relationship was found between these two behaviours with respect to the day of the fertile period (Spearman correlations, in all cases, $P > 0.1$, $N = 12$ days).

Are paternity guards related to breeding density?

Neither the time a pair spent within 10 m of each other, frequency of copulation attempts nor the rate of successful copulations correlated with any measure describing breeding density (in
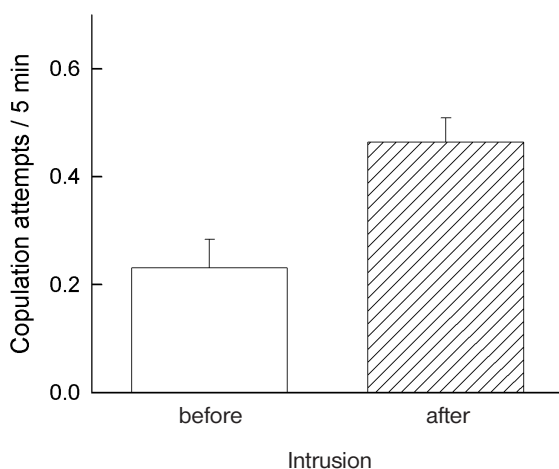

Fig. 1. Male copulation attempts within 5 min before and after an intrusion. Given are means ± SE ($N = 22$ nests).

Table 2. Relationship among different paternity guards, intruder rate and variables describing breeding density and breeding synchrony (for details see methods). Given are Pearson *r* coefficients

	Copulation attempts/20 min	Successful copulations/20min	% time pair < 10 m	Intrusion/20 min
Breeding density				
Distance to nearest nest	0.07	0.21	-0.11	-0.22
N° nests < 200 m	-0.14	-0.05	-0.09	-0.21
Mean distance to two nearest nests	0.15	0.24	0.01	-0.12
Breeding synchrony				
% overlapping days with most synchronous neighbouring nest	0.31	-0.05	0.26	0.59*

$N = 22$, $P > 0.1$, * $P = 0.023$

all cases, $P > 0.2$, $N = 22$ nests) (Table 2). We also found no significant correlation between the mean number of intrusions and breeding density (Pearson correlations, in all cases, $P > 0.1$, $N = 22$ nests) (Table 2).

Are paternity guards related to breeding synchrony?

Neither copulation attempts, the frequency of successful copulations nor the time a pair spent together within a radius of 10 m were correlated with the percentage of overlapping fertile days between the focal female and the nearest most synchronous neighbouring female (Pearson correlations, $P > 0.1$ in all cases, $N = 22$ nests) (Table 2). However, we found a positive correlation (Pearson correlations, $r = 0.71$, $P = 0.0012$, $N = 22$ nests) between the mean intruder rate and the percentage of overlapping fertile days between the focal female and the nearest most synchronous neighbouring female.

Are paternity guards related to intruder risk and the risk of cuckoldry?

In 22 nests we observed 23 cases of territorial intrusion in which we could identify 23 different intruders (for one nest we found two different intruders). All intruders were neighbouring males. The nests of 96 % (22 out of 23) of all intruders were in the laying or early incubation phase but only one in the prefertile/fertile phase, which is significantly more than one would expect by chance (binomial test: $z = 4.4$, $P < 0.001$). Moreover, 73 % (16 out of 22) of all these intrusions occurred when the intruder's nest was in a more advanced stage than the victim's nest (in 5 cases nests with complete clutches) and in only two cases we found the contrary ($z = 3.3$, $P < 0.001$). This suggests an order effect. Thus breeding order and synchrony between neighbours seems to be important in determining the risk of intrusions.

Partner proximity (<10 m) correlated significantly with the "intruder risk index", reflecting the likelihood of the two nearest neighbours to become intruders (for details see methods) ($r = 0.67$, $P = 0.0006$, $N = 22$ nests) (Fig. 2a). The frequency of copulation attempts increased with the "risk index" of the two nearest neighbours ($r = 0.66$, $P = 0.0009$, $N = 22$ nests) (Fig. 2b).

Examining the relationship between breeding synchrony and breeding density we found that the number of nests within a radius of 200 m was negatively correlated with

the percentage of overlapping fertile days between the focal female and the nearest most synchronous neighbouring female ($r = -0.64$, $P = 0.004$, $N = 22$).
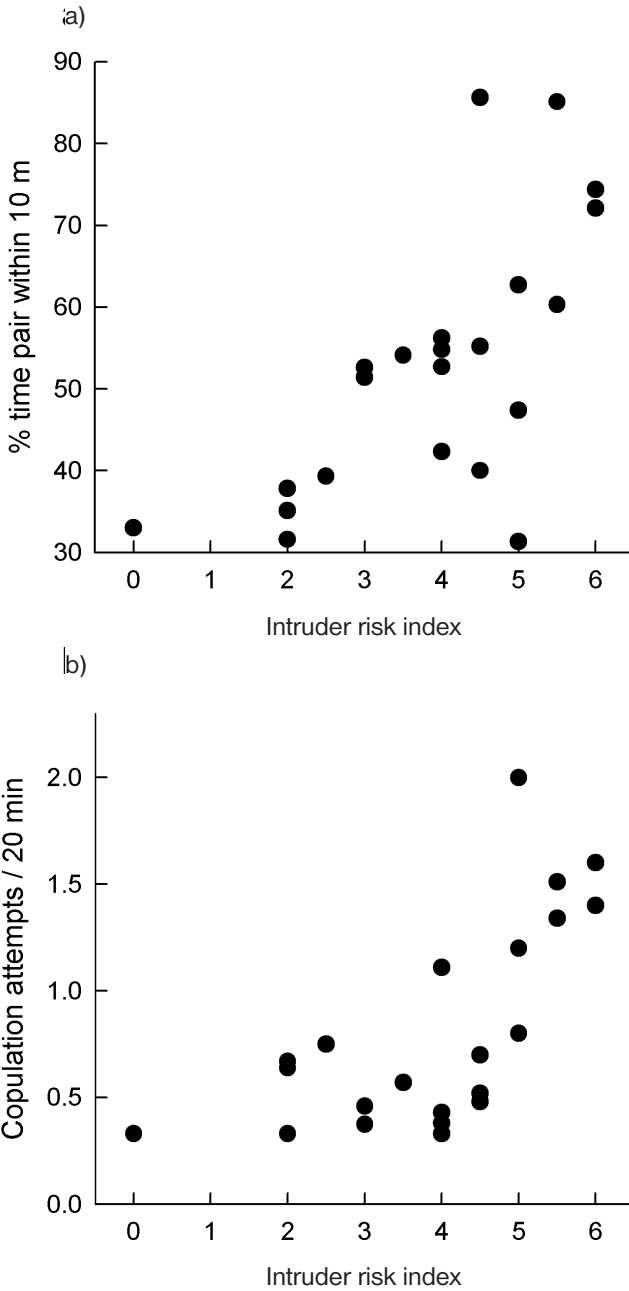

Fig. 2. Relationship between the intruder risk index (likelihood of the two nearest neighbours to become an intruder, for details see Methods) and a) % time pairs within a radius of 10 m and b) male copulation attempts/20 min.

Discussion

Our results show that territorial intrusions of mainly neighbouring males and extra-pair copulation attempts by intruding males occur (V a l e r a et al. 2003, own unpublished data). Male removal experiments revealed in fact that, even a short absence of the territory owner is immediately detected by neighbouring males and results in intrusions (unpublished results). Faced with this risk, we found that male shrikes use different strategies to reduce this risk and to assure paternity. The fact that within-pair copulations are frequent and copulation attempts increased after territorial intrusions suggests that they are likely to be used as a post copulatory paternity guard. We found that within-pair copulation attempts are non-randomly distributed and occur more frequently just after chasing an intruder. Such a behaviour has been also described for other shrike species (see J a k o b e r & S t a u b e r 1994, L o r e k 1995). We could further show that male shrikes adjust their mate guarding behaviour to the occurrence of intrusions. Therefore, in contrast to many other species (see B i r k h e a d & M ø l l e r 1992), LGSs perform a double paternity assurance strategy that seems to be very successful since an earlier study revealed no evidence for extra-pair paternity in this species (V a l e r a et al. 2003). Females seem to be faithful and cooperate with their males since during the whole study we never saw a female leaving the own territory (V a l e r a et al. 2003). Such a double paternity assurance strategy is rare and reported for male chaffinches *Fringilla coelebs* (S h e l d o n 1994). S h e l d o n (1994) also identified intruder frequency as the important factor but female chaffinches seemed to be less cooperative with their social mates resulting in extra-pair offspring.

Our results further show that male extra-pair behaviour is constrained by the time available for intrusions and this constraint seems to become less important when the own female moves from the pre-laying to the early incubation period. Our observations have shown that most male intruders are neighbouring males (V a l e r a et al. 2003) and they start to intrude to other territories when their own female is in a more advanced breeding stage, mostly in the late laying or early incubation phase (see Results). The question is why males do not intrude at other times, e.g. when the male should already produce sperm but the risk of loosing paternity is still low. A male could seek extra-pair copulations with no or lower risk for cuckoldry already when his own female is in the pre-fertile period. Males very likely know in which state their female partners are (see also L o w 2004). One reason why males do not tend to leave their female in the pre-fertile period (which is about one week after she arrived in the territory) is that, this time is mainly used for courtship behaviour. Males constantly display, sing, follow the female and try to attract her to possible nest sites. Furthermore, this is also the time when females switch mates (own unpublished data). Thus leaving the own female unattended, at the time when the pair bond is not very strong, would significantly increase the risk of loosing the partner and this very likely explains why males do not seek extra-pair copulations during the early mating period. On the other hand, the reason why males do not continue intruding into other territories and searching for extra-pair copulations much after female started incubating, may be due to the fact that LGSs are single-brooded and it is likely that the gonads regress shortly after the end of the fertile period of a male's mate. This is partly supported by our experiments with dummy female birds which have shown that males do not respond to dummy birds at all when they are offered during late incubation or a later phase, whereas males try to copulate with the dummy when offered in an earlier stage (unpublished results). Hence, studying the role of breeding synchrony in relation to reproductive strategies of a species one should consider the

physiological differences of the reproductive organs which may occur between single and multi-brooded species. Thus, as a result of these constraints in extra-pair behaviour, resident males seem to adjust their paternity assurance tactics to the risk of cuckoldry.

Breeding density as an indicator for sperm competition has been reported to have a strong effect on extra-pair paternity and paternity guards in some species (G i b b s et al. 1990, G o w a t y & B r i d g e s 1991, M ø l l e r 1991, H o i & H o i - L e i t n e r 1997, W e s t n e a t & S h e r m a n 1997) but not in others (W e s t n e a t & S h e r m a n 1997). If sperm competition increases with breeding density one would expect that males adjust their investment in paternity guards to breeding density. However, we found no effect of our density measures neither on mate guarding nor on within-pair copulation rate. This could be explained by the fact that intruder rate did not increase with density. But then the question is why intruder frequency is not directly related to the number of neighbouring males? In fact, several studies suggest that extra-pair males are usually close neighbours (M ø l l e r 1987, W e t t o n et al. 1995, L o w 2005) and this is also the case in our study species (see Results). One explanation could be that higher density results in smaller territories which are easier to control and may facilitate a more efficient territory (mate) defence, e.g. already at the boundary of a territory. This may somehow outweigh an increased intruder pressure (W e s t n e a t & S h e r m a n 1997). Alternatively, the distance to a neighbour may be negligible from the perspective of a male looking for an extra-pair mate even when breeding in a more isolated situation (D u n n et al. 1994). Furthermore, our results show that breeding synchrony may also play a role. We found that breeding density is negatively correlated with breeding synchronization which suggests that LGSs breeding in dense clusters are less synchronous. Thus, paternity uncertainty as a consequence of intruders is not necessarily a result of the mere distance between or number of nests per given area, but it is also influenced by the timing of breeding of neighbouring males. The positive relationship between breeding synchrony and intruder rate and the negative one between breeding synchronization and density suggests that both factors have to be considered together to estimate the risk of loosing paternity.

Limited sperm supply in the pre-fertile period could be another limiting factor in relation to extra-pair behaviour. Males probably synchronise their gonadal development with their female fertile period (A l l e n 1934) and therefore some males may be unable to afford, or still be incapable to seek extra-pair copulations at the time when the first female breeding in the population is fertile. Indeed, there is some evidence that males start seeking extra-pair copulations only after completion of their own brood in house sparrows (W e t t o n et al. 1995) and house wrens *Troglodytes aedon* (J o h n s o n et al. 2002). In this study we show that intruder frequency depends on the timing of breeding in relation to the neighbouring male. Therefore, it is not enough to look for breeding synchronization but it is necessary to consider at what moment of the breeding cycle the fertile phases of the females overlap. Female LGSs start incubating after laying their third egg and, therefore, it seems unlikely that they engage in extra-pair copulations after this time. Males, however, have more time to intrude into other territories to seek extra-pair copulations without the risk of being cuckolded meanwhile.

When examining male anti-cuckoldry tactics we found no effect of breeding synchrony in terms of overlapping fertile phases of neighbouring females. However, when we included the phase of the intruder's female, males increased mate guarding and copulation attempts. Thus, males seem to become aware of this situation and react to the increasing risk of a neighbouring pair with a female in the late laying phase. The best option for a male to avoid

a high investment in paternity guards would therefore be to breed as early as possible or, at least, not to nest near a pair whose nesting cycle has started a few days earlier. There is evidence for such a settlement strategy since we found that breeding density of a cluster was negatively related to breeding synchrony which means that pairs in a similar phase of the breeding cycle do not nest near each other. It is very likely that females decide when to lay and are able to alter the start of egg-laying depending on breeding density. This would further mean that the system is driven by females and that females try to avoid harassment and the costs associated with extra-pair copulations. Males, however, may play some role because they are responsible for territory establishment and defence, it seems likely that when choosing a nesting site, males also incorporate factors influencing paternity assurance in territory choice. In this species territories are close to each other and the habitat is very open. Males and females therefore might have little difficulties assessing activities of neighbouring birds and thus their timing relative to other individuals (W e s t n e a t & G r a y 1998).

In summary, the two socio-ecological factors investigated indirectly affect extra-pair behaviour in LGS's. Namely males seem to be constrained by the frequency of intrusions by neighbouring males and this risk is associated with laying synchrony. The risk of intrusions depends on the timing and overlap of breeding attempts and males adjust their investment to paternity assurance accordingly. Females seem to alter their egg laying patterns to minimise synchrony in situations where they find themselves in dense aggregates. Extra-pair paternity, however, has not been detected in our population (V a l e r a et al. 2003). Thus the rate of extra-pair paternity is not necessarily an adequate measure to identify the influence of socio-ecological factors on male and female mating strategies.

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