

MATE GUARDING IN THE MAGPIE-LARK

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Socially monogamous Magpie-larks *Grallina cyanoleuca* were studied to evaluate whether the potential for sperm competition was reduced by mate guarding or frequent copulation with the mate. Breeding among nearby pairs was sufficiently asynchronous to generate opportunities for extra-pair copulations, but frequent intra-pair copulation was not evident. The mean intra-pair and pair-to-nest distances were significantly smaller in the female's fertile period than at other times in the breeding cycle. Males were significantly more likely than females to both pursue and approach their mate, particularly during the fertile period, and thereby maintain or reduce the intra-pair distance. Males thus regulated the intra-pair distance. Eighty-three per cent of territorial intrusions by conspecifics elicited aggressive approaches by the paired, territorial male. Intrusions did not elicit male aggression significantly more often during the female's fertile period, but they did cause an immediate reduction in the intra-pair distance more frequently at this time. Collectively these observations suggest that male Magpie-larks exhibited mate guarding with the potential to reduce the chance of cuckoldry. Some alternative explanations for the behavioural trends observed are reviewed and considered less likely.

INTRODUCTION

Many female birds can store viable sperm in their reproductive tract for 6–10 days and some for much longer periods (Birkhead and Moller 1992). This facilitates sperm competition in which the sperm from more than one male compete to fertilize the egg(s) produced by a single female in one breeding attempt. Such competition places resident males at risk of cuckoldry. Recent DNA parentage studies show that in many apparently monogamous species this risk is considerable and apparent monogamy is thus often genetic polygamy (Sheldon and Burke 1994).

Various behavioural strategies may decrease this risk. One of the more common is mate guarding, in which a male stays close to his mate and aggressively repels other males that attempt to copulate with her, especially when she is fertile (i.e. shortly prior to egg laying, Birkhead 1979). Guarding may include singing and territory defence (Moller 1990, 1991). Mate guarding usually reduces the incidence of extra-pair paternity (Moller and Birkhead 1991), but is not entirely effective (Riley *et al.* 1995). When mate guarding is impossible or ineffective, the strategy of frequent copulation with the mate may be employed (Wagner 1992). This behaviour can displace or dilute a rival's sperm contribution and increase a male's chance of exploiting last male sperm precedence (Birkhead and Moller 1992). These two strategies may operate simultaneously in some bird populations (Sorenson 1994).

The Magpie-lark appears to be socially monogamous in that the usual breeding unit is a heterosexual pair, both members of which participate in all aspects of parenting (Tingay 1981). Where suitable breeding habitat is continuous over a substantial area, pairs characteristically occupy a mosaic of contiguous territories (Robinson 1947) and thus there is potential for extra-pair copulations. However, the openness of the habitat should facilitate detection of intruding conspecific males and so potentially make mate guarding an effective paternity guard.

The aim of this investigation was to evaluate whether the potential for sperm competition in Magpie-larks was reduced by mate guarding and/or frequent copulation with the mate. We predicted that the intensity of such behaviours would be greatest in the morning during the female's fertile period, because this is when fertilization can best be effected and hence when the risk of reduced paternity is maximal for a paired male. We particularly focused on (i) the proximity of pair members and how this was regulated, (ii) the calling rate of paired, territorial birds and (iii) the reactions of paired males to conspecific intruders on the territory.

STUDY SITE

The study was carried out on the 100 hectare Clayton campus of Monash University, 25 km east of Melbourne, Victoria (37°55'S, 145°08'E). The habitat comprises predominantly native, planted parklands and gardens, but includes a 3.2 hectare woodland reserve dominated by *Eucalyptus* and *Acacia* species.

Magpie-larks are markedly sexually dimorphic in the colour of their head and throat plumage (Simpson and Day 1989). At Clayton they typically built their mud nests high up on the outer branches of trees; consequently, direct inspection of contents was usually impossible and breeding stage was inferred from behaviour. During the breeding season from September to January all suitable habitat on the campus was occupied by a mosaic of adjoining territories. The clutch size of Magpie-larks is 2–5 and the eggs are laid on consecutive days. Incubation commences with the laying of the second egg. The incubation and nestling periods are 19 and 17–18 days, respectively; and young are dependent on their parents for about three months post-fledging (Robinson 1947; Tingay 1981).

METHODS

Behavioural observations

In the period July 1995 to January 1996, ten pairs of breeding Magpie-larks were observed, but particularly intensive observations were made on eight pairs throughout their breeding cycle. (Fig. 1). Two pairs failed to successfully incubate their clutch and two made a second breeding attempt. The various analyses presented here are based on six to eight pairs. Most observations were made on pairs involved in various activities, but particularly foraging, away from the immediate nest site. Magpie-larks are difficult to trap for banding purposes, but the birds we

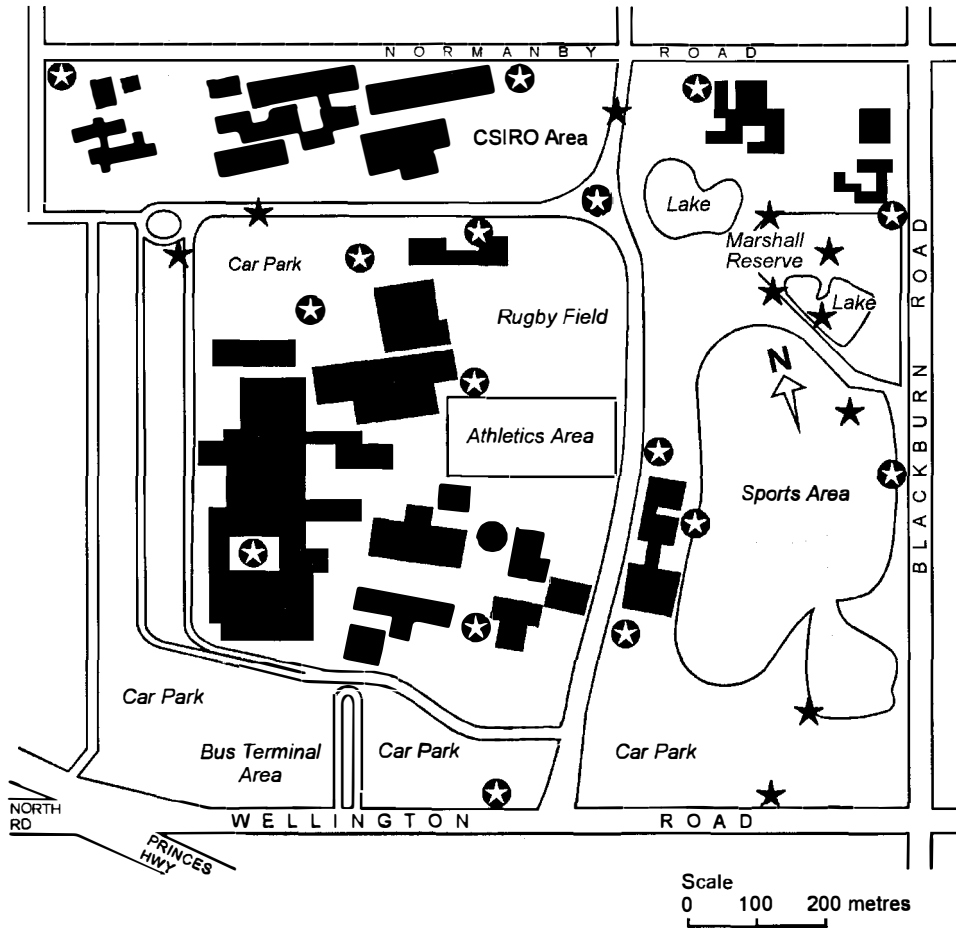


Figure 1. Distribution of Magpie-larks at the Clayton study site. The map shows the approximate centre of the territories of the ten pairs whose behaviour was studied (black stars) and the locations of active nests of pairs that were not studied intensively (white stars in black circles). A few nests probably escaped detection, particularly on the western boundary of the campus.

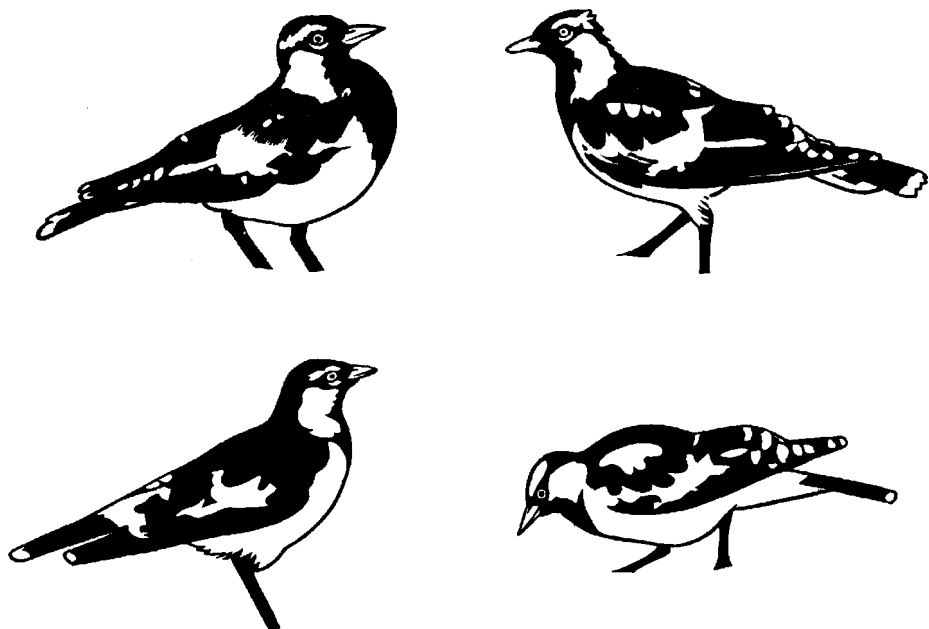


Figure 2. Plumage differences used to identify individual Magpie-larks. The four males illustrated display the variation in the number and shape of white plumage patches, particularly on the neck, wings and tail, that was used to identify individuals. The sketches were traced from photographs taken in the field.

studied could be reliably identified by their location and morphological characteristics. We used prominent individual plumage differences, particularly the number and shape of white patches on the neck, wings and tail (Fig. 2). These distinguishing marks were clearly visible and were routinely compared against a checklist by the observers. The pairs observed were in areas with limited human disturbance and good visibility for observers using 10 × 40 mm binoculars. Due to variation in daylength, each day was divided for analytical purposes into three equal diurnal intervals. To increase the independence of observations, a maximum of one 15 minute observation session was conducted on a given pair in any one diurnal interval on any particular day.

The behavioural variables recorded were:—

- (a) Intra-Pair Distance: the approximate distance between the members of a breeding pair was recorded at 1 minute intervals throughout the observation session on the following scale: 1 = <1 m; 2 = 1–5 m; 3 = 6–10 m; 4 = 11–25 m; and 5 = > 25 m. Sessional mean intra-pair distance scores were obtained from these records and then grand means (means of sessional means) for particular pair/stage/diurnal interval combinations were calculated.
- (b) Pair-to-nest distance: the approximate distance of a focal pair from its nest was recorded at the start of an observation session. The observer noted the precise location of the pair and later walked in a straight line between that point and the nest and counted the number of paces taken. One observer pace was roughly equal to 0.66 metres.
- (c) Flights: the number of flights of distances greater than 1 metre by one or both members of a pair was recorded for each one minute interval of an observation session. In particular, we recorded which bird flew; whether its mate followed within 30 seconds; the intra-pair distance at the start and finish of the flight if following occurred; whether 'unpursued' flights were away from or towards the mate. These measurements assessed whether one sex exerted a stronger influence than the other on maintaining a relatively small intra-pair distance. For analytical purposes, we grouped flights into two categories: (i) those which decreased the intra-pair distance or kept it constant through a pair member following its departing mate (pursuit flights) and (ii) those which decreased the intra-pair distance by movement towards a stationary mate (approach flights).
- (d) Calling Rate: we recorded the number of calls of any type given by each member of the pair for each one minute time interval of an observation session.
- (e) Reactions to conspecific intruders: during observations of a pair, we systematically recorded the presence of conspecific intruders on their territory and their reactions to the intruders. We particularly focused on: (i) the proportion of intrusions that elicited an aggressive approach by the resident male; and (ii) the proportion of intrusions that were followed by a decrease in the intra-pair distance of the pair under observation in the 2 minutes after intrusion commenced. A decrease was assessed relative to the mean intra-pair distance score in the 2 minute period preceding intrusion and only occasions when neither pair member flew away were analysed. To assess whether these decreases in intra-pair distance really resulted from intrusions, we also determined the extent of change in intra-pair distance in the 2 minutes before and after a randomly chosen set of non-intrusion times. These times were matched with the intrusion times with respect to the pair involved, the time of day and the stage of breeding.

Data analysis

If the variables measured act as paternity guards, they should show predictable differences across the different stages in the female's breeding cycle (pre-fertile, fertile and post-fertile) and/or with time of day (diurnal intervals 1–3) and/or sex. This variation was examined by two or three factor analysis of variance in which each pair of Magpie-larks was treated as a replicate. Data were transformed if they did not meet the assumptions of ANOVA. The intra-pair distance scale was treated as an interval scale because we were interested primarily in direction of change rather than absolute distances. Significant interaction terms were examined further with Tukey's HSD test; significant main effects were explored with one way ANOVAs and Tukey's tests. The use in some analyses of means of multiple measurements taken on one pair within

an observation session (e.g. for intra-pair distance) rather than repeated measures, was dictated by unavoidable variation in session duration. This variation also necessitated scaling some variables to a time interval less than the maximal session duration of 15 minutes (e.g. calling rate to calls/10 minutes). Some variables were necessarily derived by pooling data for a given pair for a particular stage across all diurnal intervals and/or sessions because of their low within-session frequencies. Stage differences in reaction rates to conspecific intrusion were analysed with a one-tailed non-parametric test for two related measures.

Calculating a female bird's fertile period requires knowledge of the period of viable sperm storage in the female reproductive tract (Birkhead and Moller 1992), but this is unknown for most wild birds, including Magpie-larks. However, using Tingay's (1981) data on the timing of copulation, laying and the onset of incubation, we estimated that the fertile period commenced about five days prior to the onset of incubation, a value similar to those derived for several other passerine species (Moller 1985; Ritchison *et al.* 1994; Kempenaers *et al.* 1995). The days of the breeding cycle were numbered relative to the start of incubation (Day 0), which was determined by direct observation. Days preceding Day 0 therefore had a negative sign. Thus the fertile period extended from Day –5 to the end of laying and the pre-fertile period from the start of nestbuilding (maximally Day –30) to Day –6. The behavioural variables could not be measured during the incubation period when one pair member was usually on the nest, so the post-fertile period effectively comprised the nestling and fledgling periods.

RESULTS

Synchrony of breeding

The onset of incubation was marked by the presence of one or the other pair member in the nest for most of the day. Eight pairs initiated incubation of their first clutch on 8, 15, 24, 25 September 17 and 19 (2) October and 23 November, respectively. Incubation of the second clutches of the two pairs which re-nested commenced on 5 and 22 December, respectively. Thus breeding appeared to be quite asynchronous in this population in the 1995–96 season.

Intra-pair and Pair-to-Nest Distances

The mean intra-pair distance score varied significantly with the stage of the breeding cycle. Mean scores for all stages differed significantly from one another, with the fertile stage having the smallest and the post-fertile the largest mean score (Table 1, Fig. 3a). On average, pair members were less than 5 metres apart when away from the nest during the fertile stage. Mean intra-pair distance score did not differ significantly with diurnal interval (diurnal intervals 1 and 3, 2.9 ± 0.6 ; diurnal interval 2, 3.1 ± 0.6 , $P > 0.05$, Table 1). Scores for all pairs for each day of the pre-fertile and fertile stages were therefore pooled, ignoring the diurnal interval in which they were obtained. A least squares linear regression analysis of these data showed a significant and gradual decrease in intra-pair distance score as the fertile stage was approached (Fig. 3b).

The mean Pair-to-Nest Distance varied significantly as a function of breeding stage ($P < 0.001$, Table 1), being 72.9 ± 3.4 and 24.5 ± 1.4 observer paces in the pre-fertile and fertile stages, respectively. Mean Pair-to-Nest distances did not vary significantly as a function of diurnal interval (diurnal interval 1, 53.1 ± 7.9 ; diurnal interval 2, 47.5 ± 7.3 and diurnal interval 3, 45.5 ± 7 observer paces, $P > 0.05$, Table 1).

Flights

The regulation of intra-pair distance was analysed by determining: (i) the probability that one member of a pair would pursue the other member when it flew away and (ii) the frequency at which one member of a pair flew towards the other member when it was stationary.

The percentage of flights away from the mate that elicited pursuit, and hence maintained or reduced the intra-pair distance, varied significantly with breeding stage and sex of the individual being followed. There was also a significant stage x sex interaction (Table 1, Fig. 4a). This pattern reflected the fact that males were significantly more likely to pursue their mate than were females (means: $49.3 \pm 15.6\%$ versus $22.6 \pm 2.3\%$ of occasions, $P < 0.001$). This was particularly the case in the fertile stage ($80.1 \pm 3.0\%$ versus $24.6 \pm 6.3\%$). Diurnal interval had no effect on the tendency to follow a departing mate (means: diurnal interval 1, $36.7 \pm 8.9\%$; diurnal interval 2, $35.8 \pm 8.9\%$; diurnal interval 3, $35.3 \pm 10.7\%$ of occasions, $P > 0.05$, Table 1).

The tendency to decrease the intra-pair distance by flying towards the mate when it was stationary varied significantly between the sexes (Table 1, Fig. 4b). Overall, males flew towards their mate more than did females (means: 1.38 ± 0.22 versus 0.62 ± 0.16 flights per 15 minutes, $P < 0.001$). There was also a significant breeding stage x sex interaction. This reflected a peak in the males' approach tendency during the fertile stage, when the approach tendency of females was at its minimum. Time of day did not influence the approach tendency significantly (mean flights per 15 minutes: diurnal interval 1, 1.05 ± 0.13 ; diurnal interval 2, 1.05 ± 0.62 ; diurnal interval 3, 0.91 ± 0.09 , $P > 0.05$, Table 1).

Calling rate

Calling rate varied significantly with diurnal interval, but not breeding stage or sex (Tables 1 and 2). Calling occurred at a greater frequency in diurnal interval 1 than in the other two diurnal intervals.

TABLE 1

Summary of Analyses of Variance in Measured Behaviours. Degrees of freedom for the Stage factor were 1 for Pair-Nest distance and 2 for all other variables. Sets of sample means differing significantly ($P < 0.05$) in Tukey's HSD tests are separated by an 'x'. IPD = intra-pair distance; S1, S2 and S3 = pre-fertile, fertile and post-fertile stages, respectively; DI = Diurnal Interval; F = female and M = male.

| Variable | F-Ratio | P-Value | Tukey outcome |
|-----------------------------|---------|---------|--|
| <i>IPD score:—</i> | | | |
| Stage | 260.222 | 0.000 | S1 x S2; S1 x S3; S2 x S3 |
| DI | 2.515 | 0.092 | |
| Stage x DI | 0.366 | 0.832 | |
| <i>Pair-Nest Distance:—</i> | | | |
| Stage | 165.116 | 0.000 | S1 x S2 |
| DI | 1.994 | 0.149 | |
| Stage x DI | 0.122 | 0.886 | |
| <i>Pursuit Flights:—</i> | | | |
| Stage | 14.730 | 0.000 | S2 x S1, S3 |
| DI | 0.024 | 0.977 | |
| Sex | 30.097 | 0.000 | M>F |
| Stage x DI | 1.061 | 0.381 | |
| Stage x Sex | 10.720 | 0.000 | FS2 x FS1, FS3, MS1, MS2, MS3 |
| DI x Sex | 1.012 | 0.368 | |
| Stage x DI x Sex | 1.123 | 0.351 | |
| <i>Approach Flights:—</i> | | | |
| Stage | 1.962 | 0.147 | |
| DI | 0.955 | 0.389 | |
| Sex | 73.104 | 0.000 | M>F |
| Stage x DI | 1.181 | 0.325 | |
| Stage x Sex | 23.955 | 0.000 | FS2 x FS1, FS3, MS1, MS2, MS3; MS2 x MS1, MS3, FS1, FS2, FS3 |
| DI x Sex | 0.253 | 0.777 | |
| Stage x DI x Sex | 0.078 | 0.989 | |
| <i>Calling Rate:—</i> | | | |
| Stage | 1.237 | 0.295 | |
| DI | 9.719 | 0.000 | DI1 x DI2, DI3 |
| Sex | 0.241 | 0.625 | |
| Stage x DI | 0.089 | 0.986 | |
| Stage x Sex | 0.361 | 0.698 | |
| DI x Sex | 0.099 | 0.906 | |
| Stage x DI x Sex | 0.055 | 0.994 | |

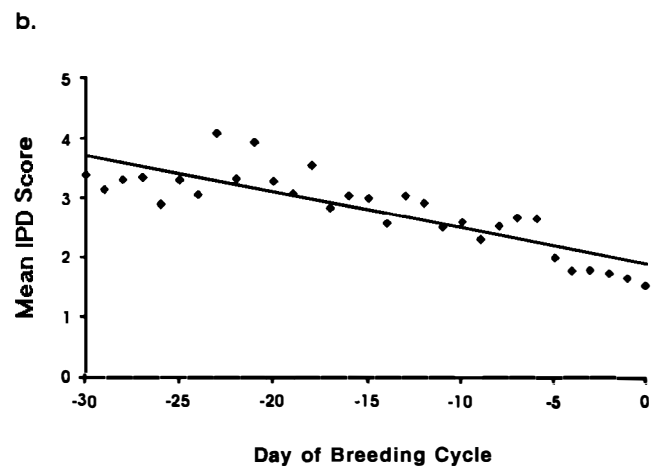
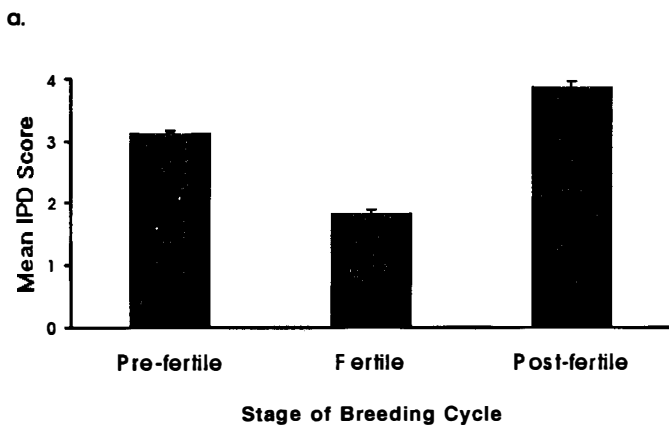


Figure 3. Variation in Intra-pair Distance (IPD) score as a function of stage (a) and day (b) of the breeding cycle in six pairs of Magpie-larks. a, One-sided error bars are shown for clarity. b, Day 0 is the onset of incubation. The fitted line is the least squares linear regression: $y = 0.06x + 1.901$, $t = -8.456$, $r^2 = 0.711$, $P < 0.001$.

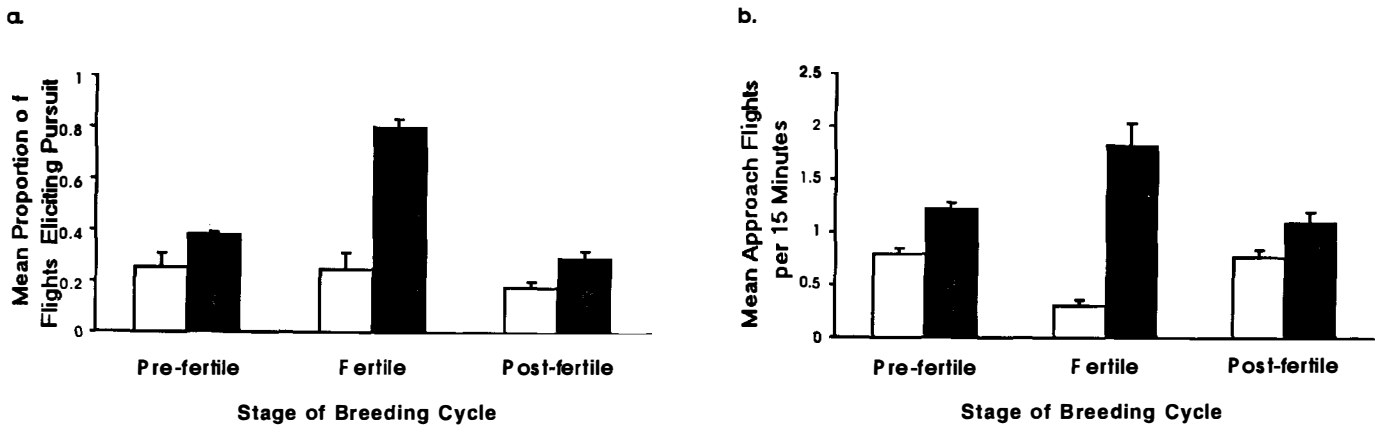


Figure 4. Variation in the tendencies to pursue (a) and approach (b) the mate in six pairs of Magpie-larks during the breeding cycle. One-sided standard errors are shown for clarity. a, unshaded and shaded columns indicate respectively the mean proportions of male and female flights eliciting pursuit by the mate. b, unshaded and shaded columns indicate respectively the frequency of approach flights towards the mate by females and males.

TABLE 2

Variation in calling rate of Magpie-larks with breeding stage and time of day. DI = Diurnal interval. Data are means (\pm SE) for six individuals of each sex. Calling rate was the number of calls of all types given per 10 minutes.

| Sex | Stage | Time of Day | | |
|--------|--------------|-------------|-----------|-----------|
| | | DI 1 | DI 2 | DI 3 |
| Male | Pre-fertile | 2.3 (0.6) | 1.3 (0.4) | 1.0 (0.2) |
| | Fertile | 2.3 (0.7) | 1.0 (0.3) | 0.9 (0.2) |
| | Post-fertile | 1.6 (0.5) | 0.7 (0.2) | 0.6 (0.2) |
| Female | Pre-fertile | 2.2 (0.5) | 1.6 (0.5) | 0.9 (0.2) |
| | Fertile | 2.0 (0.4) | 0.8 (0.2) | 0.6 (0.1) |
| | Post-fertile | 1.9 (1.1) | 1.2 (0.8) | 0.9 (0.4) |

Reactions to conspecific intruders

A male intruder featured in most of the conspecific intrusions recorded. Eighty-three per cent of the 206 observed intrusions elicited aggressive approaches by the paired, territorial male. However, for the seven pairs monitored, the mean percentage of intrusions that elicited aggression in the resident male did not increase significantly between the pre-fertile and fertile stages ($77 \pm 8\%$ versus $88 \pm 11\%$, $\chi = 2$, $P > 0.05$, Sign Test, Table 3). Paired females also approached conspecific intruders, but less frequently (10 times or 5% of intrusions).

TABLE 3

Proportion of conspecific intrusions that elicited approach by territorial males. (N) = total number of intrusions.

| Pair | Pre-fertile stage | | Fertile stage | |
|------|-------------------|------|---------------|------|
| | Proportion | (N) | Proportion | (N) |
| 1 | 0.83 | (12) | 1.00 | (4) |
| 2 | 0.75 | (28) | 1.00 | (20) |
| 3 | 0.65 | (20) | 0.96 | (26) |
| 4 | 0.71 | (14) | 0.75 | (8) |
| 5 | 0.88 | (32) | 0.82 | (11) |
| 6 | 0.85 | (13) | 0.80 | (5) |
| 7 | 0.75 | (8) | 0.80 | (5) |

An average of 39 per cent of intrusions and 45 per cent of 'matched times' (non-intrusion times) were followed by a reduction in the intra-pair distance in the pre-fertile stage ($n = 127$). Corresponding values for the fertile stage were 88 per cent and 54 per cent, respectively ($n = 79$) (Table 4). After scaling to take into account the reduction rate for the 'matched times', the tendency to reduce the intra-pair distance after an intrusion was found to be significantly greater in the fertile than in the pre-fertile stage ($N = 7$, $\chi = 0$, $P < 0.01$, Sign Test).

TABLE 4

Proportion of conspecific intrusions (I) and 'matched times' (MT) followed by a decrease in the Intra-Pair Distance. The sample sizes for intrusions and 'matched times' (see Methods for definition) are as in Table 3.

| Pair | Pre-fertile stage | | Fertile stage | |
|------|-------------------|------|---------------|------|
| | I | MT | I | MT |
| 1 | 0.42 | 0.50 | 1.00 | 0.50 |
| 2 | 0.32 | 0.50 | 0.95 | 0.55 |
| 3 | 0.40 | 0.45 | 0.81 | 0.62 |
| 4 | 0.43 | 0.36 | 0.88 | 0.38 |
| 5 | 0.31 | 0.50 | 0.91 | 0.55 |
| 6 | 0.38 | 0.46 | 0.80 | 0.60 |
| 7 | 0.50 | 0.38 | 0.80 | 0.60 |

DISCUSSION

Among the pairs of Magpie-larks studied, breeding was sufficiently asynchronous to provide both sexes with potential opportunities for extra-pair copulations. However, in 127 hours of observation of eight pairs in the pre-fertile and fertile stages, we saw no evidence of frequent intra-pair copulation. Although our observations were mostly made away from the nest site (but often in view of it), the characteristic scale and spatial distribution of the frequent copulation tactic in some species of birds (Birkhead and Lessells 1988; Sheldon and Burke 1994) make it unlikely that such behaviour went undetected. It seems likely that, as in many other socially monogamous passerines (Birkhead and Moller 1992), intra-pair

copulation in Magpie-larks at Clayton was infrequent and largely restricted to the immediate nest site. On the other hand, the close proximity of pair members, the way in which proximity varied during the breeding cycle and the manner in which it was regulated suggested that mate-guarding by males acted as a potential strategy for reducing promiscuity by their mates.

The intra-pair distance score was smallest during the fertile stage. Males also approached and pursued their mates proportionately more often at this stage. These observations are consistent with the prediction that mate guarding should be most intense at the time in the breeding cycle when the risk of cuckoldry is greatest (Kempnaers *et al.* 1995; Moller 1985; Riley *et al.* 1995). That males showed stronger tendencies than females to approach and pursue their mate suggested that they play the dominant role in maintaining the close proximity of the members of a pair. That the females' tendencies to approach or pursue their mate were weakest during their fertile period could indicate their interest in extra-pair copulations.

The absence of significant diurnal variation in most of the behaviours measured is not consistent with the prediction that guarding should be most intense in the morning when the ovum can be fertilized (Sheldon 1994). Even in species in which females store sperm, particularly intense mate guarding in the morning during the fertile period would be expected because it is usually the sperm of the last male to copulate with a female before ovulation that fertilize the ovum (Birkhead and Moller 1992). However, our observations may not have constituted a definitive test of the prediction that guarding should be most intense in the morning. Firstly, monitoring during the critical, but short, laying period was probably not sufficient to detect any such effect. Secondly, the arbitrary division of the photoperiod into just three diurnal intervals may be too coarse in this context.

Calling rate was constant during the breeding cycle, which may indicate that calling does not play an integral role in mate-guarding by males as has been suggested for some other species (Moller 1991). It has also been argued for some species that males may use singing to attract extra-pair mating opportunities (Eens *et al.* 1994). However, the absence of a sex difference in calling rate makes this a less likely possibility in Magpie-larks. Tingay (1974) suggested that the primary function of the antiphonal singing of Magpie-larks was pair bond maintenance, with territorial advertisement being secondary. The significantly higher calling rate of Magpie-larks in the morning is a characteristic shared with many other bird species (Birkhead and Moller 1992). This is the best time of day to effect fertilization and hence to attract extra-pair copulations (Smith 1988). However, it is also often the best time for sound signal transmission, due to favourable atmospheric conditions (Wiley and Richards 1978).

Magpie-larks are strongly territorial during the breeding season (Tingay 1974) and territorial behaviour itself has been proposed as a paternity-guarding strategy (Moller 1990). However, given the large size of Magpie-lark

territories, extensive territory defence and close mate-guarding during the fertile stage are likely to be incompatible. The male's tendency to approach conspecific intruders did not increase at this time, whereas the intra-pair distance score decreased both generally and in direct response to intrusion. Thus our observations suggest that close mate-guarding near the nest site during the fertile period was the prevalent paternity-guarding strategy employed by males.

Birkhead and Moller (1992) summarized several alternatives to male mate-guarding to explain the maintenance of close proximity by mates in socially monogamous bird species. Males may remain close to their mate because it maximizes intra-pair copulation opportunities, but male Magpie-larks followed their mate closely for much of the pre-fertile period and equally in all diurnal intervals, not just when the female was likely to be sexually receptive. In species with durable pair bonds, males may reduce their mate's risk of being captured by a predator by maintaining close proximity. Male Magpie-larks, however, relaxed the close following of their mate in the nestling and fledgling periods when, because of their contribution to parenting, females are perhaps more vulnerable to predation and also of greater gene replication value to their mate. Close proximity in some species may facilitate courtship feeding which is nutritionally beneficial to the female, but we never observed this behaviour in Magpie-larks. Females could benefit from close proximity of their mate through the reduction of harassment by other males (Lambrecht 1989). However, one would expect both sexes to be strongly involved in regulating the intra-pair distance were this the case, but males predominated in this respect in the Magpie-larks we studied. Finally, a small intra-pair distance might occur by default, because females occupy a relatively small range immediately before and during oviposition as a pre-breeding energy conservation strategy (Bjorklund and Westman 1986). Magpie-lark pairs did forage over a reduced area in the fertile period (as indicated by the reduced mean Pair-Nest Distance), but male and female did not influence the intra-pair distance score equally, as might be predicted by this hypothesis. Although we cannot entirely discount some of these alternatives on the present evidence, the pattern of maintenance and regulation of a small intra-pair distance in the Magpie-larks we studied seems best explained as a component of male mate-guarding behaviour.

Intense mate-guarding reduces the incidence of extra-pair paternity, but DNA parentage analysis shows that it does not always eliminate it (Freeland *et al.* 1995; Riley *et al.* 1995; Ritchison *et al.* 1994). Thus although the birds we studied showed strong mate guarding tendencies and provided no behavioural evidence of extra-pair copulations, the possibility that some degree of extra-pair paternity occurs in this species needs to be investigated through DNA paternity analysis. Intense mate guarding is probably facilitated in the Magpie-lark by a high level of visibility in its habitat and the ability of males and females to exploit the same, relatively static food items.

Some of the proximity regulating variables we measured (e.g. pursuit and approach flights) might be considered interrelated. However, the trends demonstrated for these measures were so robust statistically that most probability adjustment procedures (Sokal and Rohlf 1995) would not alter the outcome or interpretation of the analyses. We were only able to study a limited number of pairs, but the consistent behavioural trends observed suggest a more general applicability to the species. Nonetheless, it would be valuable to determine whether similar mate guarding occurs in subsequent breeding seasons and in other Magpie-lark populations and to further examine reactions to conspecific intruders.

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