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Copulatory behaviour in a colony of lesser kestrels: sperm competition and mixed reproductive strategies

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Abstract. Copulation attempts were observed at a colony of lesser kestrels, *Falco naumanni*, in southern Spain in 1989 and 1990. Of 1397 observed copulation attempts, 6·7% were extra-pair copulations. Ten of the 13 focal pairs showed a seasonally bimodal pattern of daily copulatory rates. On average, the peaks occurred 65 and 5 days before the laying of the first egg. The mean number of copulations per female per clutch was 326·2. The three other pairs, formed by one yearling and an older individual, had a single maximum at an average of 15 days before laying. Frequent copulations in the lesser kestrel might have several functions: the early peak would be almost certainly outside the females' fertile period and would be related to pair bonding and sexual stimulation of the pair members. The peak closer to egg laying could be related to sperm competition since most extra-pair copulation attempts occurred close to the date of lay. Male lesser kestrels followed a mixed reproductive strategy, but the success of the extra-pair copulation attempts depended on the females (the larger sex) and their pairing status. Unpaired females tended to accept copulations with already paired males, whereas paired females rejected extra-pair copulations. Both sexes follow a strategy that tends to advance their respective laying dates and hence improve their breeding success.

Most bird species are considered to be monogamous (Lack 1968). Promiscuity is now known to be widespread, however, and the features of monogamous mating systems appear to be more complex than had previously been expected (Gladstone 1979; McKinney et al. 1984; Westneat et al. 1990). Trivers (1972) suggested that males should adopt a mixed reproductive strategy in those species in which males perform an important parental investment. In that way, males share parental care with their mates, but also exploit opportunities to fertilize other females, and thus parasitize the parental investment of other males (Møller 1991).

In the case of species showing reversed size dimorphism, it is likely that females must be willing to copulate in order for extra-pair copulation attempts to be successful. The female's interest in copulating with already paired males could vary depending on her pairing status. A mated female has little to gain from copulating with an intruder (Trivers 1972; Fitch & Shugart 1984; Birkhead et al. 1985; Westneat et al. 1990; but see Møller, in press), except having her eggs fertilized by a better quality male than her mate (Møller 1991). In addition, she risks being rejected, or receiving a lower level of investment from her mate. An unpaired female, however, probably has less to lose, and she would have the chance to mate, or even to reproduce with the help of a non-mate (Trivers 1972; Hunt & Hunt 1977).

When males adopt a mixed reproductive strategy, sperm competition (sensu Parker 1970) occurs. Consequently, males develop counter-strategies to ensure paternity. The most common adaptations seem to be mate guarding and devaluation of the competitors' sperm by copulating frequently (see Birkhead et al. 1987 for a review). For the vast majority of the birds of prey (Accipitriformes, Falconiformes and Strigiformes), these mechanisms are unlikely to co-occur, as males feed their mates during the copulatory period (see Newton 1979). Therefore, with males looking for food, and females staying in or near the nest site, the chances of maintaining effective mate guarding are reduced (Møller 1987). The high copulatory frequency shown by raptors has hence been related to the need for paternity assurance in situations of intense sperm competition (Møller 1987).

Many birds of prey have long copulatory periods (Cade 1960; Ellis & Powers 1982; Robertson 1986;

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Møller 1987; Bertran & Romero, in press). Thus, many copulations may be occurring outside the females' fertile period. According to Lumpkin (1983), Møller (1985) and Birkhead & Lessells (1988), extended copulatory periods could be a ploy by females to hide their fertile period, perhaps in order to obtain extra care from their mates. Males may also be uncertain about the exact timing of reproduction. They should therefore start to copulate early. Cade (1960) and Brown (1967) suggested that females would gain the necessary stimulation to become fertile by starting to copulate early. Finally, copulations could be used by the females to evaluate the aptitude of the males for parental care (Møller 1985; Aguilera & Alvarez 1989; Westneat et al. 1990).

The lesser kestrel, *Falco naumanni*, is a small colonial falcon that occurs in agricultural land in the southern Palearctic (Cramp & Simmons 1980). Although males and females do not show any significant differences for most body traits, females are up to 24% heavier than their mates (Cade 1982). Males perform an important role during the breeding season, feeding the females before laying (courtship feeding), sharing incubation, and delivering most of the nourishment for their offspring (Cramp & Simmons 1980; unpublished data).

We tried to establish the copulation patterns of lesser kestrels and to identify the factors that could be shaping those patterns. Additionally, we investigated whether males had a mixed reproductive strategy, and whether females' acceptance of extra-pair copulations was influenced by their pairing status.

METHODS

Observations were carried out in a lesser kestrel colony in Mairena del Alcor, Seville province (southern Spain), in 1989 and 1990. We counted 42 breeding pairs in 1989 and 40 in 1990, nesting in scattered holes in the walls of an old castle. A sample of nests in two consecutive walls of a tower was selected for systematic recording of behaviour. All the nests could be observed simultaneously from a point 70 m from the colony, without disturbing the birds. In 1989, nine pairs formed in that sector of the colony, and seven laid eggs. In 1990, seven pairs mated there and six subsequently laid eggs.

Each year, dawn to dusk surveys were carried out by one observer from early February to August, 2 or 3 days a week. Therefore, we were able to cover the entire reproductive season, from the arrival of the first migrants in February to the end of the fledgling period in August (see Negro et al. 1991). Our observations lasted 475 h in 1989 and 567 h in 1990. At the same time, one or two additional observers followed seven males and six females which had been equipped with radio-transmitters and were breeding in the sector of the colony under observation. These kestrels were selectively trapped and marked to see if pairs were copulating far from the colony in the hunting areas. Radio-tracking observations amounted to 952 h. In 1988 we started a ringing scheme in Mairena del Alcor and other neighbouring colonies. Many young and adult kestrels were marked with PVC bands for further individual recognition. As kestrels usually perch in exposed sites, our two-character rings proved to be easy to read at relatively large distances (up to 80 m) with a telescope (20–40 × 60). In 1989, 10 of the 14 individuals breeding in the nests under observation were ringed. In 1990, all 12 birds under close observation were ringed. Unmarked individuals established in the tower, as well as visiting lesser kestrels that stayed there for some days or weeks, were recognized by their particular plumage features (streak patterns in females, breast and belly spots in males). In the case of the males, regardless of whether or not they were ringed, we were able to distinguish between yearlings and full-plumage adults (2 or more years; see Cramp & Simmons 1980). Unringed females were considered to be more than 1 year old when they arrived at the colony in February (ringed yearling females, $N=20$, were never observed before mid-March).

Every time we observed a copulation, we noted the individuals involved and recorded the following. (1) Solar time: for analytical purposes, we divided daytime into three periods (from sunrise to 3 h later, the midday hours (of variable duration owing to photoperiodic increase throughout the copulatory period), from 3 h before sunset to sunset). Every copulation was assigned to one of these periods. (2) Success of the copulation attempt. We considered that copulation was successful, and transfer of sperm probable, when we observed apparent cloacal contact. (3) Length of the copulation attempt, measured to the nearest 0·1 s. We considered that the copulation attempt started when the male perched on the back of the

female. The attempt was considered finished when the male dismounted, or any of the mated individuals flew away. (4) Solicitation of copulations by females. Sometimes during the copulation season the females displayed a begging behaviour towards males, apparently to solicit copulations (see Cramp & Simmons 1980).

Additionally, we recorded the attendance times at the colony of every focal individual, registering their hour of arrival and departure. Courtship feedings by males to females (Cramp & Simmons 1980) were also recorded.

Dates were subsequently rearranged in relation to the beginning of laying, which was estimated by counting back 32 days from hatching date. The latter was estimated from the equation $Y = 10{\cdot}44 + 0{\cdot}14X$ ($r = 0{\cdot}94$, $N = 43$ nestlings, $P < 0{\cdot}001$), where Y is the age of the nestlings in days, and X the length of the eighth primary feather in mm (unpublished data). All statistical analyses were performed using the Biomedical Division Statistical Package (BMDP; Dixon & Brown 1983).

RESULTS

We observed 1397 copulation attempts (including successful and aborted ones), of which 99·9% took place in the colony, and 0·1% in the hunting areas. As observation hours were extensive both at the colony (1042 h) and outside it (952 h), we can conclude that practically all the copulations occurred at the colony. Nearly all copulation attempts occurred at the entrance of the nest holes or in their vicinity. Of all copulation attempts, 93·3% occurred within pairs; the rest (6·7%) were considered extra-pair copulations.

Pair Copulation Frequency

Daily frequency of copulations within pairs fluctuated greatly throughout the season (Fig. 1). We detected two patterns of variation in the copulatory frequency. Ten pairs, all of them formed by birds more than 1 year old, showed a clear bimodal seasonal pattern of daily copulation rates (copulations/h). On average, the peaks occurred 65 days (SD = 10·4, $N = 10$) and 5 days (SD = 3·3, $N = 10$) prior to the start of laying (day '0'). For six pairs, the first maximum was lower than the second; for three pairs the first was higher than the second one; and, finally, one pair showed similar copulation rates for both peaks (see Fig. 1). The second copulatory pattern comprised a single maximum, and was displayed by three mixed-pairs formed by one yearling (two males and one female) and one older individual. In these pairs, the peak of copulations occurred at an average of 15 days (SD = 8·9, $N = 3$) before the laying date. The second maximum exhibited by the first group of pairs tended to occur later than the single maximum displayed by the mixed-pairs. On the other hand, the maximum copulation rate tended to be higher for the three mixed-pairs than for the others (means 1·25, $N = 3$, versus 0·83, $N = 10$, copulations/h), although the difference was not significant (Mann–Whitney $U = 8{\cdot}00$, $P = 0{\cdot}256$). The mean rate of copulations per female per clutch for bimodal pairs was estimated to be 326·2 (SD = 67·2, $N = 10$, range 177·1–404·4) and for unimodal pairs 174·0 (SD = 132, $N = 3$; 59·3–318·3).

Of all within-pair copulation attempts 89·4% were successful. The mean duration of successful copulations was 6·7 s (SD = 0·07, $N = 998$). Copulations were apparently solicited by the females 91 times (7·0%). Solicited copulations tended to occur at the end of the copulation period in every pair, although the small sample sizes precluded statistical comparisons.

Diurnal Pattern of Pair Copulations

A three-way ANOVA showed that copulation frequency was affected by the hour ($F_{2,430} = 6{\cdot}33$, $P = 0{\cdot}002$), the date ($F_{2,430} = 14{\cdot}81$, $P < 0{\cdot}001$) and each individual pair ($F_{9,430} = 2{\cdot}69$, $P = 0{\cdot}004$). The interaction between the factors 'date' and 'pairs' was also significant ($F_{18,430} = 1{\cdot}74$, $P = 0{\cdot}02$). The copulations tended to peak in the early morning and late afternoon throughout the copulation period (Fig. 2).

Pair Copulation Rate and Colony Attendance

The time passing from when the pair rejoined to the first copulation decreased during the season, but not significantly so. Thus, in the 10 pairs showing extended copulatory periods, the average was 10·6 min ($N = 227$) before day −20, 6·7 min ($N = 257$) from day −20 to day −1, and 6·1 min ($N = 119$) beyond day −1 (Friedman's test, $\chi^2 = 5{\cdot}6$, $df = 9$, $P = 0{\cdot}061$).

Colony attendance of males was nearly constant during the copulation period, whereas females increased their presence at the colony as the laying

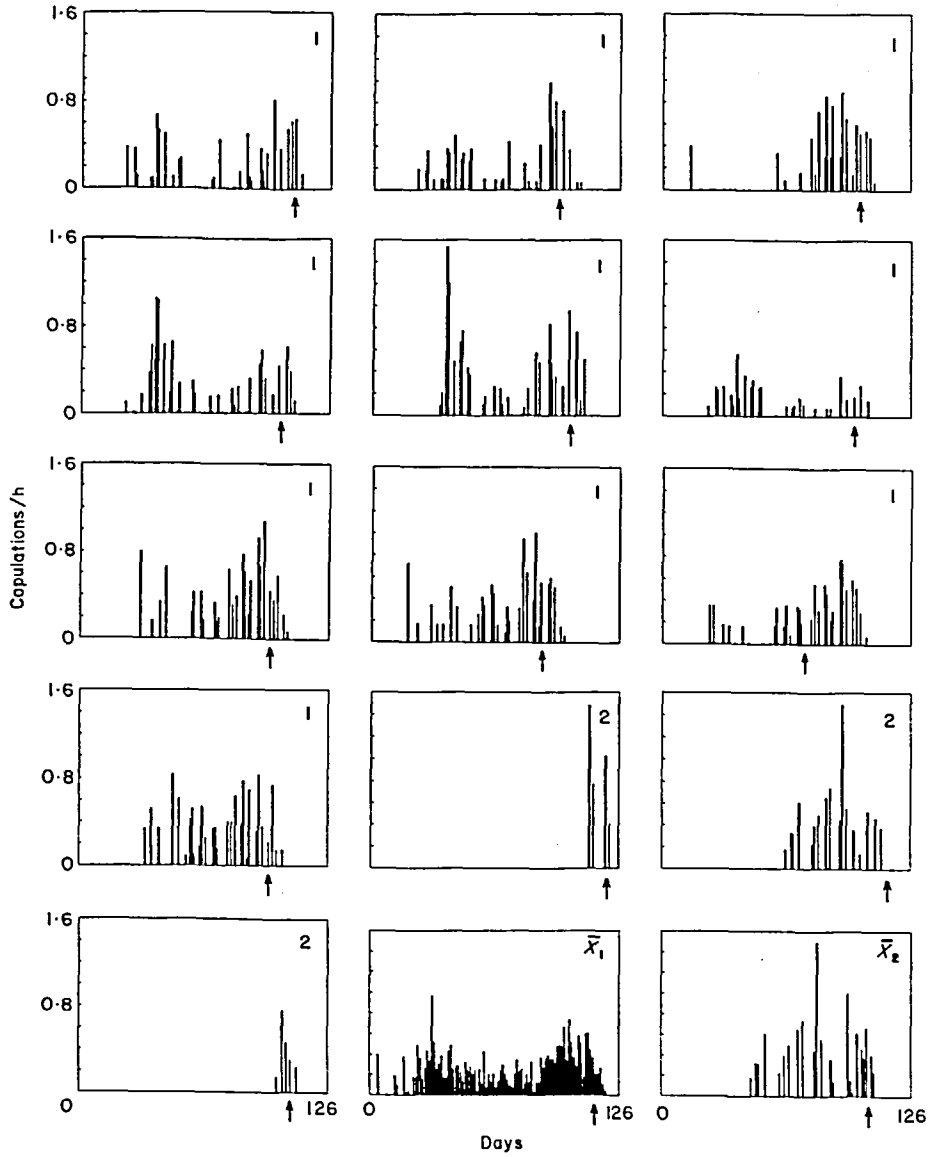

Figure 1. Daily frequency of copulation attempts by 13 pairs of lesser kestrels. Pairs labelled with number 1 were formed by birds more than 1 year old. Pairs labelled with number 2 had one yearling individual each. Mean values for each category of pairs have been included ($\bar{X}_1$ and $\bar{X}_2$). The start of laying is shown by arrows.

date approached (Fig. 3). As virtually all copulations occurred at the colony, the time from the pair rejoining to the first copulation could be influenced by the sex of the first member of the pair arriving. If the female were the first to arrive, the male might be expected to attempt a copulation immediately because the female might have been exposed to extra-pair copulations. Before day −20, copulations occurred 12·1 min after the arrival of the female if the male was already in the colony, and 9·1 min if the female was the first to arrive. From day −20 to day −1, the times were 6·3 min when the male was the first to arrive, and 8·1 for the opposite. After day −1 to the completion of the

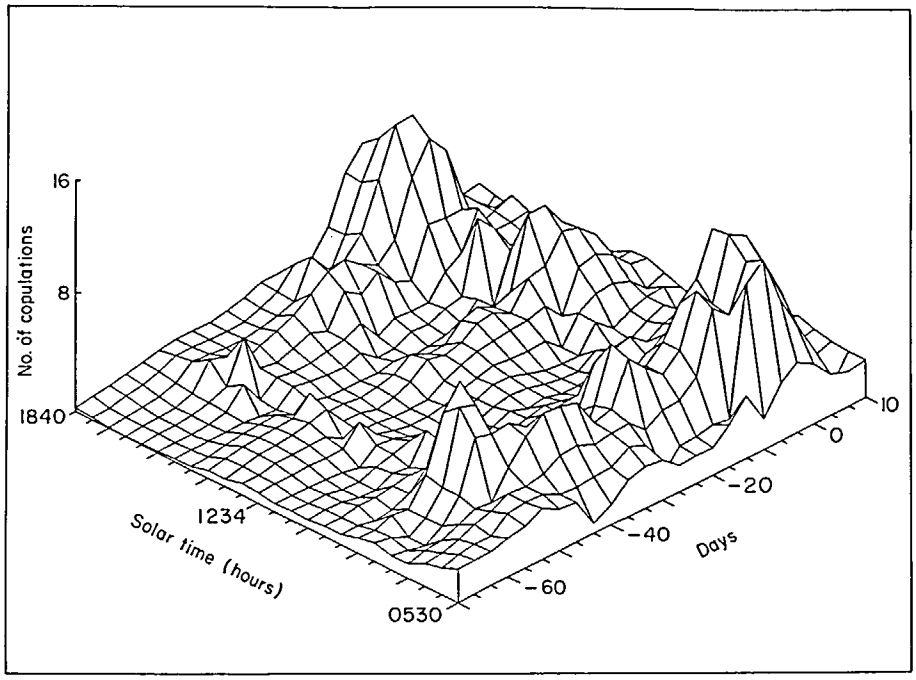

Figure 2. Frequency of copulations occurring at different hours of daytime during the copulatory period. Laying date = day '0'.

clutch (day +10, approximately), the times were 6·3 and 3·3 min, respectively. A three-way ANOVA showed that time from reunion to copulation was related to date ($F_{2,474}=10{\cdot}2$, $P<0{\cdot}001$) and to each individual pair ($F_{9,474}=4{\cdot}19$, $P<0{\cdot}001$) but not to the first sex to arrive ($F_{2,474}=0{\cdot}14$, $P=0{\cdot}86$). The interaction of factors 'date' and 'pairs' was also significant ($F_{18,474}=1{\cdot}71$, $P=0{\cdot}03$).

Pair Copulations, Laying Date and Mate Feeding

The females laying early in the season also started to copulate earlier ($r=-0{\cdot}855$, $df=11$, $P<0{\cdot}001$), and their copulation period was also longer ($r=-0{\cdot}783$, $df=11$, $P<0{\cdot}01$). However, the daily copulation rate was negatively correlated with the duration of the copulation period ($r=-0{\cdot}730$, $df=11$, $P<0{\cdot}01$).

The first males to start feeding their mates also fed them for a longer period ($r=0{\cdot}831$, $df=11$, $P<0{\cdot}001$) and started copulations comparatively earlier ($r=0{\cdot}560$, $df=11$, $P<0{\cdot}05$), although their copulation rate tended to be lower ($r=0{\cdot}560$, $df=11$, $P<0{\cdot}05$). There were no significant correlations ($P>0{\cdot}05$) between the daily mate-feeding rate and the date when copulations started ($r=0{\cdot}215$, $df=11$), the duration of the copulatory period ($r=-0{\cdot}263$, $df=11$), or the daily copulation rate ($r=-0{\cdot}175$, $df=11$).

Extra-pair Copulations

At least one member in 11 (85%) out of 13 monitored pairs engaged in extra-pair copulation episodes. Nine focal females (69%) and five males (38%) were involved in these episodes. A total of 64 extra-pair copulations (68·8%) were performed by paired males, 15 (16·1%) by unpaired males, and 14 (15·0%) by males of unknown pairing status. Of 30 (32·2%) extra-pair copulation attempts directed towards paired females none was successful. Sixty-three extra-pair copulation attempts were directed towards unpaired females; 58 (92%) were successful and five (8%) failed. The ratio of successful and unsuccessful copulations differed significantly for paired and unpaired females ($\chi^2=69{\cdot}52$, $df=1$, $P<0{\cdot}001$). Only two unpaired females that had copulated with already paired males finally mated

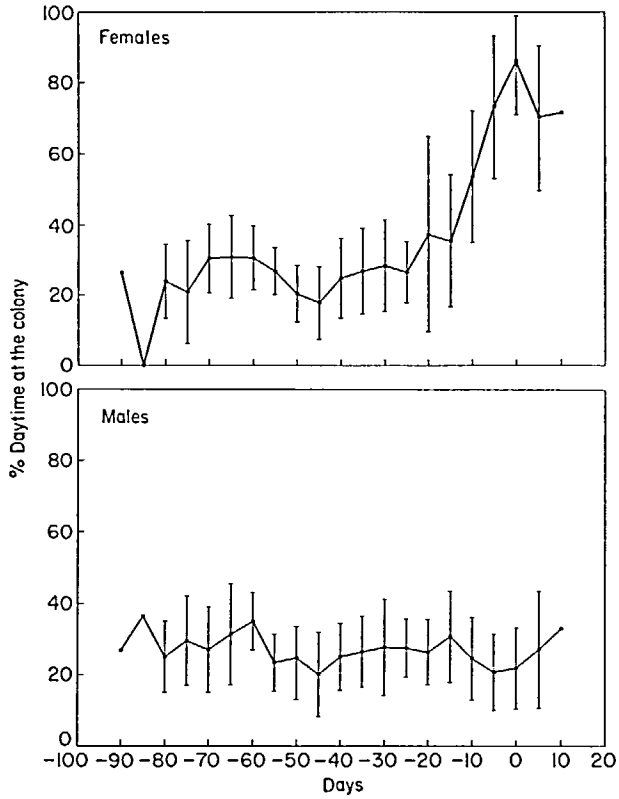

Figure 3. Colony attendance by male and female of 13 pairs of lesser kestrels during the copulatory period. $\bar{X} \pm$ SD are shown for 5-day intervals.

and stayed in the sector under observation. Neither of them received extra-pair copulations after pairing. One of them had copulated previously with six different paired males, although 90% ($N=58$) of copulations occurred with the same one. The other female copulated with at least one already paired male before establishing a pair-bond with another male.

Paired females received most of the extra-pair copulation attempts in the last few days before laying (Fig. 4). The frequency for unpaired females, however, reached a maximum between 30 and 40 days before laying. We could establish the cause for the failure of 33 extra-pair copulation attempts: (1) aggression directed at the intruder by the male paired with the female ($N=3$); (2) aggression by the female herself ($N=7$); (3) lack of cooperation by the female ($N=22$); and (4) the intruder male fell off the female ($N=1$). Paired males did not appear to spend much effort protecting their females, as they were close to their mates when many extra-pair copulation attempts took place ($N=18$), and attacked intruders only four times (22·2%).

DISCUSSION

Pair Copulation Pattern and Sperm Competition

Lesser kestrels showed two different copulation patterns. The more common pattern extended over a long period (up to 94 days). The daily copulatory rate under this pattern peaked twice with an average of 61 days between peaks. Long copulation periods do not seem to be exceptional in raptors: golden eagle, *Aquila chrysaetos*, more than 2 months (Ellis & Powers 1982); Cape vulture, *Gyps coprotheres*, more than 50 days (Robertson 1986); goshawk, *Accipiter gentilis*, 70 days (Møller 1987); Bonelli's eagle, *Hieraaetus fasciatus*, up to 10 weeks (Bertran & Romero, in press). Some copulations are probably therefore outside the female's fertile period, as the latter has been estimated to be about

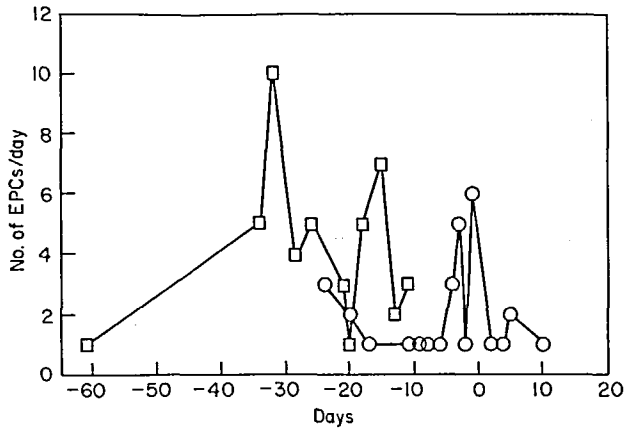

Figure 4. Number of extra-pair copulation (EPC) attempts involving paired (○) and unpaired females (□). Laying date = day '0'.

7 days in birds of prey (Grier et al. 1972, cited in Bird & Buckland 1976). The fertile period in the American kestrel, *Falco sparverius* (close morphologically and ecologically to the lesser kestrel), is about 11 days (Bird & Buckland 1976). Previous findings suggest that a long copulation period is not directly related to the insemination of females. Instead, it may be due to a reproductive synchronization between pair members (Brockway 1966; Brown 1967; Erickson & Zenone 1976).

In the lesser kestrel, the start of egg laying varies by up to 3 weeks from year to year and the duration of the laying season is about 1 month every year (unpublished data). In consequence, males might be uncertain about the start of reproduction. The females (see Møller 1985; Birkhead & Lessells 1988) could take advantage of an extended copulation time to disguise their fertile period and hence gain a longer period of care by their mates. Some observations on the lesser kestrel, however, permit us to reject these hypotheses: (1) females solicited copulations more frequently just before laying; (2) the highest extra-pair copulation rate directed towards paired females occurred the day before laying of the focal female; and (3) almost all extra-pair copulations occurred from day −10 to the completion of the clutch. Consequently, it would be difficult to explain how females disguise their fertile period from their mates and not other males. Females markedly changed their activity pattern as laying date approached, and stayed most of the daytime perching in front of their nests just before the start of laying (Fig. 3).

A second copulation pattern was shown by three pairs with at least one yearling, which formed late in the season and exhibited a single maximum of daily copulation rate about 15 days before laying. This pattern and the second half of the extended copulation pattern shown by the other 10 pairs may be influenced by sperm competition. However, the high number of copulations seems to outnumber that needed to fertilize the eggs of the female (Birkhead et al. 1987). In fact, captive lesser kestrels laid fertile clutches of four or five eggs after a single artificial insemination per egg (M. Pomarol, personal communication). Perhaps this high copulation rate could serve to dilute competitor's sperm, as has been suggested for other bird species (several species, Birkhead et al. 1987; goshawk, Møller 1987; spoonbill, *Platalea leucorodia*, Aguilera & Alvarez 1989). This interpretation is also supported by the fact that pairs that formed late in the season (thus involving females that had had the chance to copulate with different males) had higher copulation rates.

If the copulatory behaviour of the kestrels had evolved in a context of sperm competition, parallel adaptations to counteract its effects would be expected. Some of these presumed adaptations are: (1) the concentration of copulations in the first hours after the laying of the egg, when a 'fertilization window' occurs (Cheng et al. 1983; Birkhead et al. 1987; Møller 1987; Cheng & Burns 1988); and (2) a shorter time between the pair members rejoining after a separation and the first copulation in those periods when the likelihood of insemination

is higher (see review in Birkhead et al. 1987). In the lesser kestrel, which lays eggs during the night or at dawn (unpublished data), the daily pattern of copulations showed, as was expected, a peak in the early morning, but a similar peak occurred in the late afternoon. This bimodal pattern appeared throughout the copulatory period and, in our opinion, could be more related to the pattern of colony attendance by the birds than to fertilization pressures. In fact, the pattern of colony attendance is similar during the winter, before the start of the copulatory period (Negro et al. 1991).

The time between the mates rejoining after a separation and the first copulation did not decrease significantly as laying date approached. Moreover, we did not observe shorter delays before the first copulation when the female arrived at the colony before her mate. On the other hand, the increase in mate guarding during the females' fertile period (described in species with courtship feeding, see Birkhead et al. 1985, 1987) was not observed either. As laying date approached, males spent most of their time foraging far from the colony, and they returned there only to feed their mates and copulate (unpublished data). In consequence, lesser kestrels seemed to adopt some countermeasure to avoid sperm competition (high daily copulatory rates) but not others (concentration of copulations in the fertilization window, shorter delays before copulation as laying approached and when females arrived first at the colony). The reason could be the additional costs involved in adopting some of the strategies mentioned above. The adoption of strategies other than a high copulation rate to counteract competitor's sperm would result in less time for the males to hunt and to feed their mates. As the main function of mate feeding seems to be to fatten the female and hence achieve a larger clutch (Donázar et al., in press), the cost of countermeasures that lower the feeding rate might be too high.

Mixed Reproductive Strategies

Male lesser kestrels exhibited a mixed reproductive strategy and attempted to copulate both with their mates and with other females. Because most extra-pair copulation attempts occurred close to egg laying, female insemination seemed to be their function. The question remains why males have maintained the tendency to perform extra-pair copulations when most attempts appeared to be unsuccessful (at least those directed towards already paired females). It cannot be discounted, however, that such attempts could eventually be successful as was observed in the American kestrel (Towers 1990). High frequencies of nestlings genetically unrelated with their presumptive fathers have been reported in species with low levels of extra-pair copulations (Westneat 1987a, b). Furthermore, females could accept extra-pair copulations under certain circumstances, such as a long period of absence of the mate (see below). On the other hand, the cost/benefit ratio for males associated with extra-pair copulations might be so low that it could explain by itself the persistence of a male mixed reproductive strategy.

We have observed two strategies in female lesser kestrels depending on their pairing status. The adoption of one or the other is probably mediated by the different cost/benefit ratio in paired and unpaired females. Paired females involved in extra-pair copulation attempts were never fed by the non-mate males and risked being abandoned by their mates, or receiving less help from the male in raising their offspring (as documented by Møller 1988; Morton et al. 1990). The situation seems different for unpaired females. By accepting copulations by already paired males, unpaired females could gain access to a male and a nest site. After the death of a paired female, another female that had previously copulated with the paired male could gain a breeding opportunity by replacing the dead female. The annual adult mortality rate of lesser kestrels can be considered relatively high (about 30%; Negro 1991), so a strategy such as that described above might be adaptive. This suggestion is also supported by our observation after catching and releasing one paired female. That female was equipped with a tail-mounted radio-transmitter and, probably because of transitory stress, she deserted the colony for an entire day after being released. During the short period of absence, her mate admitted another female to the nest hole and copulated with the newcomer several times. The following day, the original female returned and regained her former mate and nest site.

A second reason for unpaired females to accept copulations by several males would be to obtain sexual stimulation. That way, females could pair later with an unpaired male and be in an advanced condition for an early laying. Females rearing offspring with the help of non-mates have been observed in other species (Trivers 1972; Hunt &

Hunt 1977), but we have not detected this in the lesser kestrel. Finally, and considering that some unpaired females copulated repeatedly over an extended period with the same already paired males, we cannot discount that some males pursue polygyny (Hiraldo et al. 1991) more than a mixed reproductive strategy with typical extra-pair copulations (see Westneat et al. 1990 for definitions). In that case, the main benefits for unpaired females would be to gain a good quality male and/or nest site (Møller, in press).

In conclusion, our results suggest that male lesser kestrels follow a mixed reproductive strategy, but the success of the extra-pair copulation attempts depends on the females and their pairing status. This pattern may have evolved as a result of the high parental investment of males in the breeding season. Both sexes follow a strategy that tends to advance their laying dates and hence to increase their breeding success. In that context, adaptations to avoid extra-pair fertilizations interfering with mate feeding would not be selectively advantageous for the males unless the frequency of extra-pair copulations was high. For females, fidelity would be selected in order to retain mate feeding, as suggested in species showing courtship feeding (Fitch & Shugart 1984; Poole 1985). Until now that strategy has never been observed in raptors, even though they appear to be good candidates, as parental investment is usually high in both sexes and reversed size dimorphism is widespread.

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