

Functional analysis of mate-feeding in the Lesser Kestrel *Falco naumanni*

José Antonio Donázar, Juan José Negro and Fernando Hiraldo

Donázar, J. A., Negro, J. J. and Hiraldo, F. 1992. Functional analysis of mate-feeding in the Lesser Kestrel *Falco naumanni*. – Ornis Scand. 23: 190–194.

Mate-feeding was studied at 13 nests in a colony of Lesser Kestrels *Falco naumanni*. Additionally, the seasonal variation in body mass of males and females was investigated throughout the breeding cycle. On average, mate-feedings ($n = 783$) began 54 d after the pair's first copulation and 16.5 d before the laying of the first egg, and lasted 23.7 d. Body mass of females increased from the beginning of the mate-feeding period and peaked at egg-laying. Males' body masses were less variable and tended to decrease from the mate-feeding period to the end of the breeding cycle. Our results suggest that mate-feeding is not relevant to pair formation, although it cannot be discounted that this behaviour may be important in tightening the pair-bond. The most evident function of mate-feeding in the Lesser Kestrel seems to be to increase the female's body mass, possibly to allow the laying of earlier and larger clutches. In fact, the start of the mate-feedings was correlated with laying date, and the earlier the laying, the larger the clutch.

J. A. Donázar, J. J. Negro and F. Hiraldo, Estación Biológica de Doñana. CSIC. Apdo. 1056. 41080 Sevilla. Spain.

Introduction

Mate-feeding, or courtship-feeding (see Nuechterlein and Storer 1989 for definitions), is widespread in birds (Smith 1980). Different functions have been proposed for this behaviour. It has been suggested that mate-feeding is important in the process of pair formation and to maintain pair-bonds (Lack 1940, Kluijver 1950, Brown 1967, Stokes and Williams 1971, Niebuhr 1981, Tasker and Mills 1981). A temporal relationship between mate-feedings and copulations has been reported in a number of species, suggesting that mate-feedings act to induce copulations (Brown 1967, Calder 1968, Stokes and Williams 1971, Tasker and Mills 1981, but see Kilham 1981, Niebuhr 1981, Wiggins and Morris 1988). In addition, mate-feedings could be used by the females to evaluate the males' parental ability (Nisbet 1983, Simmons 1988, Carlson 1989, Korpimäki 1989). But a more common explanation for mate-feedings is

that they improve the females' nutritional status to meet the energy requirements of egg laying (Krebs 1970, Taylor 1979, Lundberg 1980, Lifjeld and Slagsvold 1986, Avery et al. 1988, Palokangas et al. 1991). It has been demonstrated in different species that high mate-feeding rates improve clutch quality, either by advancing the laying date (Royama 1966, Tasker and Mills 1981, Daan et al. 1990), or by increasing the number and/or volume of the eggs (Nisbet 1973, Morris 1986, Salzer and Laskin 1990, Palokangas et al. 1991).

Mate-feeding is common in birds of prey and its main function in that group would be to improve the female's body condition (Newton 1979, but see Poole 1985). The energy stored by the female would be needed for egg laying and incubation. Additionally, Newton (1979) noted that in those raptorial species in which incubation is exclusively carried out by females (European Kestrel *Falco tinnunculus*, Sparrowhawk *Accipiter nisus*, Tawny Owl *Strix aluco*) only the females increase in weight,

Received 11 July 1991

Revised 16 October 1991

Accepted 28 October 1991

© ORNIS SCANDINAVICA

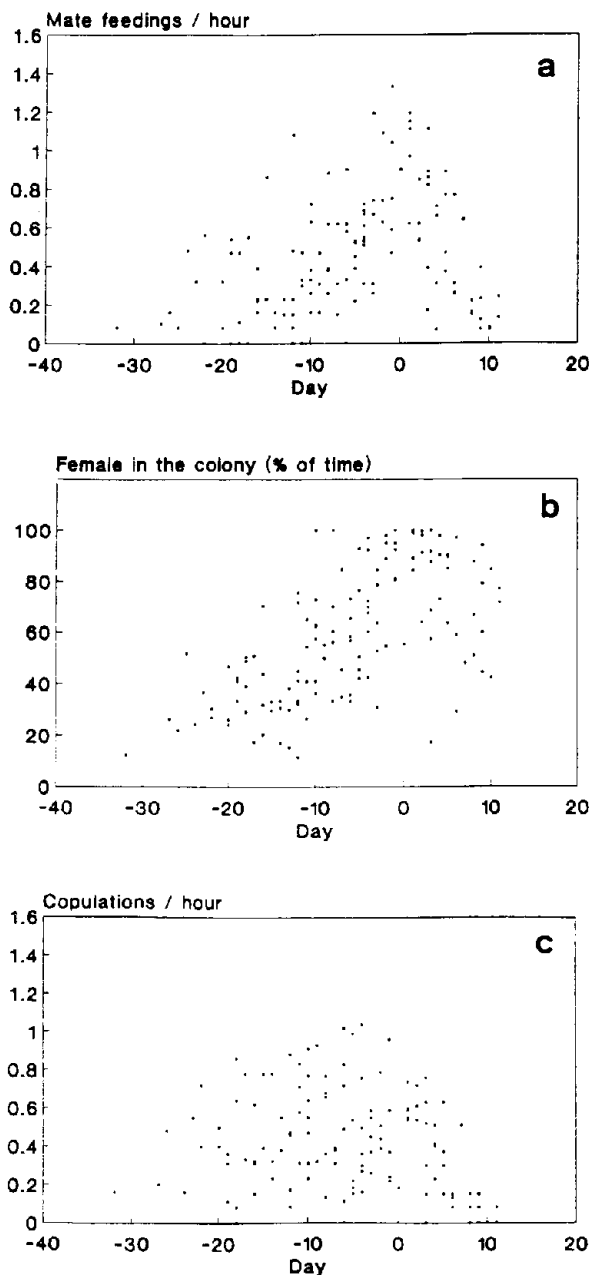


Fig. 1. Seasonal variation of (a) mate-feeding frequency, (b) percent of time spent by the females at the colony and (c) copulation frequency, of 13 pairs of Lesser Kestrel. Data plotted in relation to each pair's start of laying (day "0").

whereas in vultures (*Gyps* spp.) in which both sexes share this task, both males and females put on weight before incubation.

The Lesser Kestrel *Falco naumanni* is a small colonial bird of prey. Males feed their females from before to a few days after egg laying and both sexes incubate (Cramp and Simmons 1980). In this paper we analyse

the function of mate-feeding in the Lesser Kestrel in relation to the hypotheses mentioned above.

Study area and methods

The study was conducted in a Lesser Kestrel colony at Mairena del Alcor, Seville province (southern Spain) in 1989 and 1990. Lesser Kestrels nested in an old castle where we counted 42 pairs in 1989 and 40 in 1990. For behavioural observations, we selected a sector of the colony containing seven breeding pairs in 1989 and six in 1990. These nests were observed simultaneously from a point 70 m from the colony.

Observations were carried out two or three days a week, and lasted from dawn to dusk. The dates for the start and end of the mate-feeding period for each pair were considered to be those of the first and last observed feeding. We covered the entire reproductive season, from February to August, amounting to 475 hours of observation in 1989 and 567 in 1990. On a tape-recorder, the observer registered copulations, mate and chick feedings, as well as arrivals and departures of any individual to or from the nests under observation. Prey size was not considered because most deliveries were of large insects and there was no apparent difference between pairs in the size of prey taken. Because every observation was timed, we were able to determine whether mate-feedings were immediately followed by copulations, and to measure the time from the food-transfer to the first copulation. Incubation shifts were recorded to estimate the contribution of each sex. Individuals were identified by colour rings, or by particular plumage features. In 1989, 10 of the 14 individuals breeding in the monitored sector of the colony were ringed. In 1990, all 12 monitored birds were ringed.

All the nests were visited at least twice during the breeding season. Laying dates were estimated by counting back 32 days from hatching dates, which were calculated from the length of the 8th primary feather of the young (see Negro et al. in press). In 1988–1990 we captured and weighed 111 female and 62 male adult Lesser Kestrels at different breeding stages in Mairena and five other neighbouring colonies.

Results

Frequency and distribution of mate-feedings

We observed mate-feedings ($n = 783$) from the second week of April to the first week of June. In the 13 monitored pairs, mate-feedings started, on average, 16.5 d (range day -32 to day -7) before the laying of the first egg (day "0") and ceased 6.5 d after this day (range day -2 to day 11). The average duration of the mate-feeding period was 23.7 d (10–38, $n = 13$). The

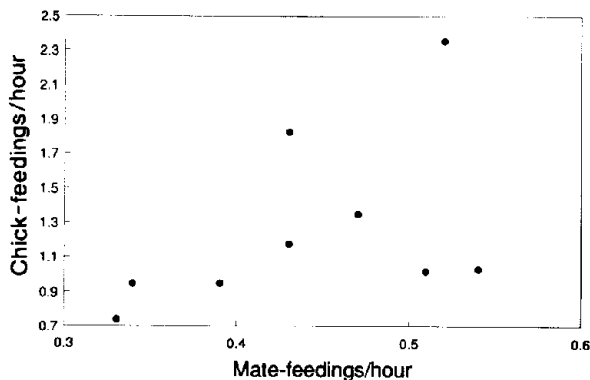


Fig. 2. Relationship between mate-feeding and chick feeding rates of nine male Lesser Kestrels.

peak in mate-feeding (more than one feeding per hour) occurred at the beginning of egg laying (Fig. 1a). Females spent more and more time in the colony as laying approached, and from a few days before laying (mean = 4 d, range 0–12, $n = 13$ pairs) they spent more than 90% of the daytime in the colony (Fig. 1b). During this period they got almost all their nourishment from the males.

Relationship between mate-feedings and copulations

Copulations started on average 54 d (range 77–0, $n = 13$) before mate-feedings. The peaks of copulation and mate-feeding coincided (Fig. 1c), their daily frequencies showing a significant, although weak, correlation ($r = 0.21$, $df = 131$, $p < 0.05$). Considering the five 10-d periods from day –24 to day 25 (first egg date = “0”), we detected significant correlations between the daily frequencies of mate-feeding and copulation only in the interval from day –24 to day –15 ($r = 0.54$, $df = 20$, $p < 0.01$), when both frequencies increased, and between days 6 to 15 ($r = 0.75$, $df = 12$, $p < 0.01$), when both frequencies decreased. Copulations occurred more frequently when males returned to the colony without prey (52%, $n = 329$) than when they returned to the females with food (35%, $n = 618$) ($\chi^2 = 17.15$, $df = 2$, $p < 0.001$).

Relationship between mate-feeding and chick-feeding rates

To find out whether mate-feedings can be used by the females to evaluate male quality, we correlated the frequencies of mate and chick feeding for every male using those pairs which successfully raised chicks ($n = 9$). The correlation coefficient was high and significant ($r_s = 0.65$, $df = 7$, one-tailed $p < 0.05$) (Fig. 2).

Changes in body mass of males and females

The females' body masses varied markedly during the reproductive season (Fig. 3), from about 140 g 45 d before laying to about 200 g at the time of laying. Body mass began to rise during the mate-feeding period. Additionally, the correlation between the average mate-feeding frequency and female body mass in the above mentioned five 10-d periods was significant ($r_s = 0.90$, $df = 3$, $p < 0.05$). The males' body masses showed less variation, ranging from about 125 to 150 g during the entire reproductive season.

Relationship between mate-feeding and breeding parameters

The quality of the clutches seemed to be related to mate-feeding rates as well as to laying date. Clutch size in the Lesser Kestrel decreases throughout the breeding season (Negro 1991). Additionally, the earlier mate-feeding started, the earlier egg laying occurred (Fig. 4a), and the largest clutches were usually laid by the first females receiving mate-feeding (Fig. 4b).

The role of males and females during incubation

During daytime both members of the pair took turns at incubating the eggs. In the 10 pairs that we observed, males incubated on average 56.2% of the time (461 h and 9 min) (range = 46.4%–86.0%), and females 43.8% (range = 14.0%–54.6%). Nocturnal incubation seemed to be carried out by the females exclusively. Thus, in seven days of observation, only females incubated at dusk and they were also incubating at dawn. Eight radio-tagged individuals (4 males and 4 females) followed during the incubation period (unpubl. data) also

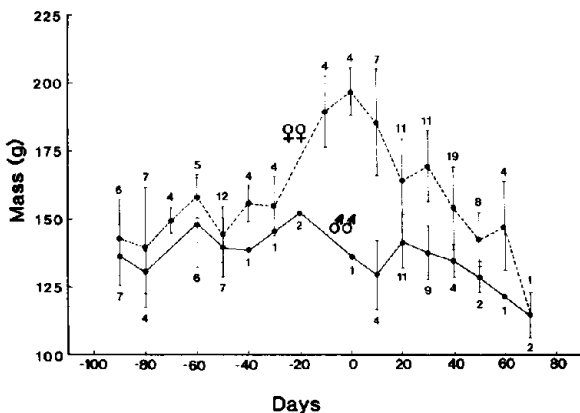


Fig. 3. Body mass of male ($n = 62$) and female ($n = 111$) Lesser Kestrels in relation to stage of breeding (day “0” = start of laying). Bars show standard deviations and numbers above and below bars are sample sizes.

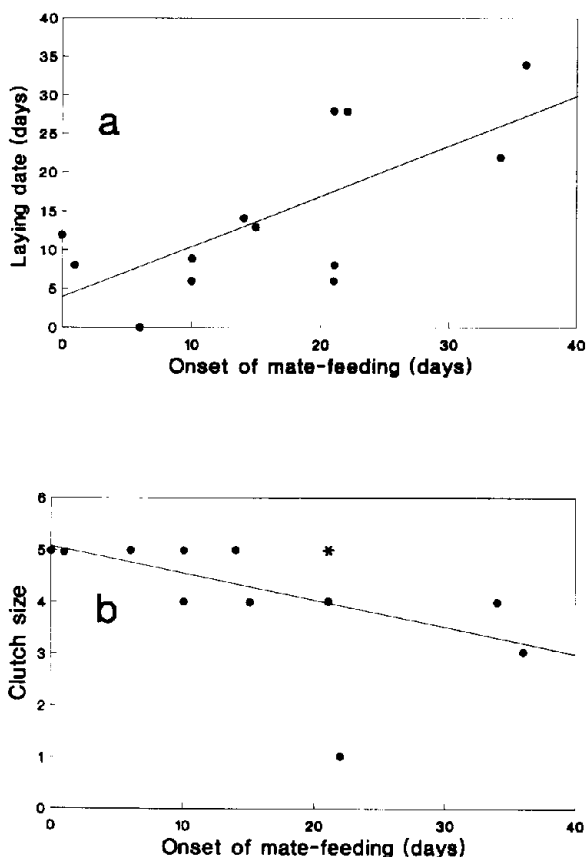


Fig. 4. (a) The relationship between laying date and the onset of mate-feeding ($n = 13$ pairs). The line indicates the regression equation ($r = 0.73$, $y = 2.5 + 0.6x$, $p < 0.05$, $df = 11$). (b) The relationship between clutch size and onset of mating feeding ($r = -0.49$, $y = 5.07 - 0.05x$, $p = 0.08$, $df = 11$; *two records).

behaved in the same manner – the males roosted in the hunting areas while the females stayed on their nests at night.

Discussion

In the Lesser Kestrel, mate-feeding began approximately eight weeks after pair copulations started, i.e. when the pairs were already formed, and at a time when paired females rejected extra-pair copulation attempts (Negro et al. in press). This fact suggests that mate-feeding has no function in the Lesser Kestrel's pair formation. On the other hand, the correlation between mate-feeding and chick-feeding rates was significant, hence females might test male parental ability through mate-feeding rates. However, if a female decided to abandon a poorly provisioning male during the mate-feeding period, she would hardly have any opportunity

to pair with a better male in that season. During the periods when feedings occurred, the only males apparently available seemed to be 1-yr olds without their own nest-hole (Hiraldo et al. 1991, Negro et al. in press).

We cannot reject the hypothesis that mate-feeding plays a role in strengthening pair-bonds. In the Lesser Kestrel, already paired females usually reject EPCs, but poorly-fed females could be prone to accept EPCs if they are fed in exchange, as suggested for the Osprey *Pandion haliaetus* (Poole 1985). The increase in feeding rates before laying that we observed in Lesser Kestrels could therefore be explained as an attempt by the males to assure paternity.

The relationship between mate-feedings and copulations was not clear in the Lesser Kestrel. But the fact that pairs usually copulated more often when the males returned to the nest without prey suggests that the two activities are unrelated. In fact, significant correlations between the two parameters only occurred when both increased or decreased, but not when their maximum values were reached. The weak general correlation found between mate-feeding and copulation rates probably means that both parameters tend to change in a similar way as the laying date approaches, but for different reasons. In the Lesser Kestrel, as in other bird species, the peak in copulation frequency around the laying date probably is a male countermeasure to avoid the effects of EPCs during the female's fertile period, when sperm competition is intense (Negro et al. in press). A similar increase in mate-feeding rates would be expected if the function of mate feeding was to improve the female's body condition prior to laying. The female's body mass rose markedly before laying and reached a maximum just as laying started, decreasing afterwards until the end of the breeding season. This suggests that a significant part of the female's body reserves is used to form the eggs, as in other bird species (see Introduction). Several facts also suggest that mate-feeding contributes to the increase in female body mass prior to laying. First, body mass variations were significantly correlated with mate-feeding frequency. Second, because from a few days before laying the females stayed much of the time in the colony without hunting, they were dependent on the prey delivered by the males. Third, the first females to receive mate-feedings were the first to lay eggs, and were those which laid the largest clutches. Other parameters, such as the onset and duration of the copulatory period, and male quality, may also affect laying date and breeding success (Meijer et al. 1990, Negro et al. in press). This suggests that an important selective pressure could be operating to advance laying date. In fact, the first pairs to start breeding usually achieve a higher breeding success (unpubl. data), as is also the case in populations of the European Kestrel (Cavé 1968, Daan et al. 1990, Meijer et al. 1990, Village 1990, Palokangas et al. 1991).

The incubation of the clutch constitutes an important energy expenditure, and for some hole-nesting passer-

rinc birds this expenditure can equal that of the last period of the nestling stage (see Moreno et al. 1991, and references therein). The present results do not permit us to determine whether any part of the energy accumulated by the females is utilized for incubation. However, we can reject the hypothesis that the prelaying variations in mass shown by both sexes in some raptors are related to their roles in incubation. Male Lesser Kestrels, although sharing incubation with their mates, did not increase in mass before the incubation period as suggested by Newton (1979). Probably, the high energy expenditure involved in mate-feeding does not allow male Lesser Kestrels to store fat reserves (Moreno 1989). Similarly, male Sparrowhawks, European Kestrels, Tawny Owls (see Newton 1979 and references therein), and Tengmalm's Owls (Korpimäki 1990), all performing mate-feedings, do not put on weight before incubation. Male vultures, on the other hand, do not feed their females (Brown and Amadon 1968) and increase in weight, perhaps because they suffer a lower level of stress than the males of the above-mentioned species.

Acknowledgements – We thank M. de la Riva for his help in the field work. Funding was provided by the CSIC-CICYT project Pb87-0405 and a Predoctoral Fellowship for JJN.

References

- Avery, M. I., Krebs, J. R. and Houston, A. I. 1988. Economics of courtship-feeding in the European bee-eater (*Merops apiaster*). – *Behav. Ecol. Sociobiol.* 23: 61–67.
- Brown, L. and Amadon, D. 1968. *Eagles, Hawks and Falcons of the World*. – Country Life Books, London.
- Brown, R. G. B. 1967. Courtship behaviour in the lesser black-backed gull, *Larus fuscus*. – *Behaviour* 29: 122–153.
- Calder, W. A. 1968. Breeding behavior of the roadrunner *Geococcyx californianus*. – *Auk* 84: 597–598.
- Carlson, A. 1989. Courtship feeding and clutch size in red-backed shrikes (*Lanius collurio*). – *Am. Nat.* 133: 454–457.
- Cramp, S. and Simmons, K. E. L. 1980. *The Birds of the Western Palearctic*. Vol 2. – Oxford University Press, Oxford.
- Daan, S., Dijkstra, C. and Tinbergen, M. 1990. Family planning in the Kestrel (*Falco tinnunculus*): the ultimate control of covariation of laying date and clutch size. – *Behaviour* 114: 83–116.
- Hiraldo, F., Negro, J. J. and Donazar, J. A. 1991. Aborted polygyny in the Lesser Kestrel *Falco naumanni* (Aves, Falconidae). – *Ethology* 89: 253–257.
- Kilham, L. 1981. Courtship feeding and copulation of Royal Terns. – *Wilson Bull.* 93: 390–391.
- Kluijver, H. N. 1950. Daily routines of the great tit, *Parus m. major* L. – *Ardea* 38: 99–135.
- Korpimäki, E. 1989. Mating system and mate-choice of Tengmalm's Owls. – *Ibis* 131: 41–50.
- 1990. Body mass of breeding Tengmalm's *Aegolius funereus*: seasonal, between-year, site and age-related variation. – *Ornis Scand.* 21: 169–178.
- Krebs, J. R. 1970. The efficiency of courtship feeding in the blue tit *Parus caeruleus*. – *Ibis* 112: 108–110.
- Lack, D. 1940. Courtship feeding in birds. – *Auk* 57: 169–178.
- Lifjeld, J. T. and Slagsvold, T. 1986. The function of courtship feeding during incubation in the pied flycatcher *Ficedula hypoleuca*. – *Anim. Behav.* 34: 1441–1453.
- Lundberg, A. 1980. Vocalizations and courtship feeding of the Ural Owl *Strix uralensis*. – *Ornis Scand.* 11: 65–70.
- Meijer, T., Daan, S. and Hall, M. 1990. Family planning in the Kestrel (*Falco tinnunculus*): the proximate control of covariation of laying date and clutch size. – *Behaviour* 114: 117–136.
- Moreno, J. 1989. Strategies of mass change in breeding birds. – *Biol. J. Linn. Soc.* 37: 297–310.
- , Gustafsson, L., Carlson, A. and Pärt, T. 1991. The cost of incubation in relation to clutch-size in the Collared Flycatcher *Ficedula albicollis*. – *Ibis* 133: 186–193.
- Morris, R. D. 1986. Seasonal differences in courtship feeding rates of male common terns. – *Can. J. Zool.* 64: 501–507.
- Negro, J. J. 1991. *Ecología de poblaciones del cernícalo primilla Falco naumanni*. – Unpubl. Doctoral Thesis, University of Seville.
- and Hiraldo, F. in press. Nest site selection and breeding success in the Lesser Kestrel (*Falco naumanni*). – *Bird Study*.
- , Donazar, J. A. and Hiraldo, F. in press. Copulatory behaviour in a colony of Lesser Kestrels: sperm competition and mixed reproductive strategies. – *Anim. Behav.*
- Newton, I. 1979. *Population Ecology of Raptors*. – T. & A. D. Poyser, Berkhamsted.
- Niebuhr, V. 1981. An investigation of courtship feeding in Herring Gulls *Larus argentatus*. – *Ibis* 123: 218–223.
- Nisbet, I. C. T. 1973. Courtship feeding, egg size and breeding success in common terns. – *Nature (London)* 241: 141–142.
- Nuechterlein, G. L. and Storer, R. W. 1989. Mate feeding by Western and Clark's Grebes. – *Condor* 91: 37–42.
- Palokangas, P., Alatalo, R. V. and Korpimäki, E. 1991. Female choice in the Kestrel under different availability of mating options. – *Anim. Behav.*
- Poole, A. 1985. Courtship feeding and Osprey reproduction. – *Auk* 102: 479–492.
- Royama, T. 1966. A re-interpretation of courtship feeding. – *Bird Study* 13: 116–129.
- Salcer, D. W. and Larkin, G. J. 1990. Impact of courtship feeding on clutch and third-egg size in glaucous-winged gulls. – *Anim. Behav.* 39: 1149–1162.
- Simmons, R. E. 1988. Food and the deceptive acquisition of mates by polygynous male harriers. – *Behav. Ecol. Sociobiol.* 23: 83–92.
- Smith, S. N. 1980. Demand behaviour: a new interpretation of courtship feeding. – *Condor* 82: 291–295.
- Stokes, A. W. and Williams, H. W. 1971. Courtship feeding in gallinaceous birds. – *Auk* 88: 543–559.
- Tasker, C. R. and Mills, J. A. 1981. A functional analysis of courtship feeding in the Red-billed Gull, *Larus novaehollandiae scopulinus*. – *Behaviour* 77: 221–241.
- Taylor, I. R. 1979. Prey selection during courtship feeding in the Common Tern. – *Ornis Scand.* 10: 142–144.
- Wiggins, D. A. and Morris, R. D. 1988. Courtship and copulatory behaviour in the Common Tern *Sterna hirundo*. – *Ornis Scand.* 19: 163–165.