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Aborted Polygyny in the Lesser Kestrel *Falco naumanni* (Aves, Falconidae)

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Abstract

We observed three polygynous trios (one male and two females) in a colony of lesser kestrels in southern Spain. All these trios broke up before egg-laying because the secondary female deserted and paired with another male. The time spent by the bigamous males with the female at the colony, the copulation rates, and the mate-feedings, were always lower for the secondary females. Primary females received levels of investment similar to that obtained by females paired with monogamous males. Aggressions between the two females paired with the same male were frequent. Polygyny in the lesser kestrel might be favoured by a female biased sex-ratio, and maintained because bigamous males and secondary females can get some benefits, independently of the final success of the breeding attempt.

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Introduction

Polygyny is a frequent mating system in species that a) exploit exceptionally abundant resources, and b) show very low or non-existent male parental care (VERNER & WILSON 1966; ORIAN 1969; TRIVERS 1972). Nevertheless, in some birds of prey, males perform a very high parental investment and are occasionally polygynic in good trophic conditions (NEWTON 1979). In the present paper we describe bigamy attempts in the lesser kestrel (*Falco naumanni*), a colonial species belonging to a genus which rarely shows polygyny (CRAMP & SIMMONS 1980; VILLAGE 1990). In addition, we discuss the factors leading to this mating system in the species.

Methods

Observations were conducted 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, all nesting in the walls of an old castle. The sector of the colony under systematic observation consisted of two consecutive walls of a tower with 14 potential nest-holes. In 1989, 9 pairs formed in that sector of the

colony, and 7 finally laid eggs. In 1990, 7 pairs mated there and 6 subsequently laid eggs. There were additional holes temporarily occupied by unpaired individuals. All nest-holes could be observed simultaneously from a point 70 m in front of the walls.

The surveys were carried out by one observer, two or three days a week, and lasted from dawn to dusk. We covered the entire reproductive season, from the period of pairformation (Feb.—Mar.) to the fledging period (Jul.—Aug.). We totaled 475 h of observations in 1989 and 567 h in 1990. The observer used binoculars (8×30) and a telescope ($20\text{--}40\times$), and registered in a tape-recorder any behavioural interaction, such as copulations, mate-feedings or aggressions. We also recorded attendance times to the colony by registering arrivals and departures of any individual, which were identified by their PVC rings or by particular plumage features. 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. For the entire colony, the proportion of ringed adult birds was approx. $1/4$ in 1989 and $2/3$ in 1990. The age of some birds was known from their ringing dates, or their plumage in the case of the males (yearling vs. older, see CRAMP & SIMMONS 1980 for a description of plumages).

Results

Of 13 paired males under observation, 5 attempted extra-pair copulations with females other than their mate. Three of these already paired males established durable relationships with one unpaired female. We will consider onwards these males as bigamous and their two females will be called primary and secondary. One of the primary females was a yearling, whereas the other two were older (called adults). Two of the secondary females were adults, and the other one was of unknown age. All three bigamous males were adults. There was an apparent surplus of females in both years of study: in 1989, apart from the established pairs, there were 4 males (all yearlings) and 5 females (including two secondary females) which repeatedly visited the sector under observation; in 1990, one yearling male and three females (one of them became a secondary female) were frequent visitors.

We could not determine exactly when relationships began between bigamous males and their secondary females, but at least in two of the three cases males first paired with the primary female. The minimum duration of these trios was 20, 44 and 50 days, and began at least 74, 57 and 50 days, respectively, before primary females laid eggs. The ruptures between bigamous males and their secondary females were observed twice, and both occurred by the establishment of new relationships between those females and unpaired males. The day when the break up occurred, secondary females were attended by both the former and the new mate, and copulated with both of them. Afterward, previously secondary females only maintained relationships with their new mates.

The investment performed by bigamous males, in terms of time spent with every female at the colony, copulation rates and mate-feedings, was always lower in the case of the secondary females. Primary females, on the other hand, received levels of investment similar to that obtained by other females paired with monogamous males (Table 1).

Primary and secondary females of the same bigamous male showed a clear mutual incompatibility. Two secondary females occupied a different hole to that of the primary female, whereas one secondary female shared a nest-hole with the primary female. In the case of the two females sharing the same nest-hole, they

Table 1: Summary of data ($\bar{x} \pm \text{SD}$) concerning investment by three bigamous males in their primary and secondary females. Data on other females paired with monogamous males in the same periods have been included to enable comparisons. In parentheses, number of monogamous females

Females		% of daytime with male at the colony (n = d)	Copulations/d		Mate-feedings/d	
1	Primary	68.7 \pm 32	n = 5	2.0 \pm 0.7	n = 5	0*
	Secondary	33.6 \pm 19	n = 5	0.2 \pm 0.4	n = 5	0*
	Monogamous	90.2 \pm 20	n = 15	3.0 \pm 1.2	n = 15	0*
	(3)					
2	Primary	57.4 \pm 28	n = 16	5.8 \pm 4.0	n = 16	6.2 \pm 4.9 n = 6
	Secondary	26.5 \pm 24	n = 16	0.5 \pm 1.0	n = 16	0 n = 6
	Monogamous	57.6 \pm 31	n = 62	3.1 \pm 0.6	n = 49	7.1 \pm 1.8 n = 24
	(4)					
3	Primary	51.0 \pm 27	n = 24	5.1 \pm 3.9	n = 24	7.0 \pm 4.7 n = 11
	Secondary	26.5 \pm 23	n = 24	2.0 \pm 2.7	n = 22	1.4 \pm 1.4 n = 11
	Monogamous	55.1 \pm 26	n = 92	5.1 \pm 0.5	n = 74	6.9 \pm 1.1 n = 41
	(4)					

* This trio occurred outside the mate-feeding period.

never stayed there simultaneously. In fact, the secondary female only occupied the nest when the primary female was absent from the colony, and she was always expelled when the other came back to the nest. We also observed aggressions between two females of the same trio occupying nest-holes at the same wall (thus, they could see each other when at the colony). Most aggressions in this and the precedent case were started by the primary female (42 vs. 4). The only case where the females did not confront each other, they occupied nest-holes at different walls in the tower and could not see each other.

Discussion

The long duration of the described relationships led us to think that this behavior differed from promiscuity during or before the formation of pair bonds described in the closely related American kestrel (*Falco sparverius*) (BALGOOYEN 1976), and other bird species (WESTNEAT et al. 1990). Instead, our observations in the lesser kestrel seemed to be unsuccessful bigamy attempts. Bigamous males spent more time with their primary females, and fed them more. The copulation rate was also higher in the case of the primary females. This different pattern of care is similar in other species with occasional polygyny (MARTIN 1974; ASKENMO 1984; POOLE 1989). A certain incompatibility between first and secondary females has also been reported in polygynic species (LA PRADE & GRAVES 1982; YASUKAWA & SEARCY 1982; HURLY & ROBERTSON 1985). The failure of the bigamy attempts that we observed might be due to the scarcity of food during the breeding season in the years of study (authors unpubl.). It cannot be discarded, however, that

bigamous lesser kestrel could be successful under favourable conditions. The species' average clutch size is 4 (2—6) (CRAMP & SIMMONS 1980) but we have observed in 1991 a clutch of 7 composed by two clearly distinct sets (in colour and shape) of eggs (4 and 3), presumably laid by two different females. Additionally, I. SÁNCHEZ-GARCÍA (pers. comm.) observed 8 downy chicks in the same nest-hole in 1990 at Jerez (Southern Spain). BIJLSMA et al. (1988) and CADE (1982) also reported unusual clutches of 8 eggs, that could be due to two different females laying in the same place.

The tendency to try bigamy in the lesser kestrel could be favoured by the surplus of females, and maintained because bigamous males and secondary females can get additional advantages not necessarily related to a successful bigamy attempt. Secondary females can gain sexual stimulation through repeated copulations (BALGOOYEN 1976), as well as an adequate condition to lay eggs when fed by the bigamous male (NEGRO et al., in press). Therefore, they could be in an advanced condition to reproduce as soon as they pair with another male. On the other hand, the secondary female would gain precedence to substitute the primary one if the latter died. For the males, the advantages of pairing with a second female are obvious if the attempt is successful. But, even failing, they have the chance to fertilize the secondary female and get offspring raised by her and her new mate. This would be more likely if the secondary female leaves the bigamous male a few days before laying.

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Literature Cited

- ASKENMO, C. E. H. 1984: Polygyny and nest site selection in the pied flycatcher. *Anim. Behav.* **32**, 972—980.
- BALGOOYEN, T. G. 1976: Behavior and ecology of the American kestrel (*Falco sparverius* L.) in the Sierra Nevada of California. *Univ. Calif. Publ. Zool.* **103**, 1—83.
- BIJLSMA, S., HAGEMEIJER, E. J. M., VERKLEY, G. J. M. & ZOLLINGER, R. 1988: Ecological aspects of the lesser kestrel *Falco naumanni* in Estremadura (Spain). *Rapport* **285**. Katholieke Univ. Nijmegen.
- CADE, T. J. 1982: *The Falcons of the World*. Cornell Univ. Press, Ithaca.
- CRAMP, S. & SIMMONS, K. E. L. 1980: *The birds of the Western Palearctic* Vol. 2. Oxford Univ. Press, Oxford.
- HURLY, T. A. & ROBERTSON, R. J. 1985: Do female red-winged blackbirds limit harem size? I. A removal experiment. *Auk* **102**, 205—209.
- LAPRADE, H. R. & GRAVES, H. B. 1982: Polygyny and female-female aggression in red-winged blackbirds (*Agelaius phoeniceus*). *Am. Nat.* **120**, 135—138.
- MARTIN, S. G. 1974: Adaptations for polygynous breeding in the bobolink, *Dolichonyx oryzivorus*. *Amer. Zool.* **14**, 109—119.
- NEGRO, J. J., DONÁZAR, J. A. & 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, Berkhamstead.
- ORIANS, G. H. 1969: On the evolution of mating system in birds and mammals. *Am. Nat.* **103**, 589—603.

- POOLE, A. F. 1989: Ospreys. Cambridge Univ. Press, Cambridge.
- TRIVERS, R. L. 1972: Parental investment and sexual selection. In: Sexual Selection and the Descent of Man 1871—1971. (CAMPBELL, B. G., ed.) Aldine, Chicago, pp. 136—179.
- VERNER, J. & WILLSON, M. F. 1966: The influence of habitats on mating systems of North American passerine birds. Ecology 47, 143—147.
- VILLAGE, A. 1990: The Kestrel. T. & A. D. Poyser, London.
- WESTNEAT, D. F., SHERMAN, P. W. & MORTON, L. L. 1990: The ecology and evolution of extrapair copulations in birds. In: Current Ornithology. Vol. 7 (POWER, D. M., ed.) Plenum Press, New York, pp. 331—369.
- YASUKAWA, K. & SEARCY, W. A. 1982: Aggression in female red-winged blackbirds: a strategy to ensure male parental investment. Behav. Ecol. Sociobiol. 11, 13—17.

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