COPULATORY BEHAVIOR OF SEMI-COLONIAL MONTAGU'S HARRIERS[1]

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Abstract. The copulatory behavior of the monogamous Montagu's Harrier (*Circus pygargus*) was studied between 1992 and 1995 near Madrid, Spain. Copulations started around 20 days before laying, and typically stopped at the end of the laying period. Copulation frequency peaked just before the start of the laying period, averaging 2.2 copulations day^{-1}. Females copulated on average 39 times per brood. Copulation rates apparently were not related to food provisioning by males except in the early pre-laying period. At least 5 and up to 11 (4–8%) of the copulations observed were extra-pair copulations (EPCs), and all occurred within the fertile period. Montagu's Harriers increased their copulation rate in situations of increased EPC risk: solitary pairs copulated for a shorter period of time and at an overall lower frequency, whereas pairs nesting in clumps showed higher copulation rates with increasing number of neighboring pairs. This increase was most marked during the laying period, when there is a higher risk of EPCs producing extra-pair fertilizations.

Key words: Circus pygargus, *coloniality, copulation, extra-pair copulations, Montagu's Harrier.*

INTRODUCTION

Two main methods of paternity assurance occur in birds. In many species, males attempt to prevent their mate from engaging in extra-pair copulations (EPCs) by closely following and guarding her from the advances of other males (Birkhead 1979). When mate-guarding is prevented by ecological constraints, paternity assurance might be achieved by means of frequent within-pair copulations (Birkhead et al. 1987). By copulating frequently, a male may be able to dilute sperm from rival males and thereby decrease the risk of cuckoldry.

Close mate-guarding is prevented in species where males provide food for the female, who stays by the nest prior to laying (Møller and Birkhead 1992). Birds of prey (Accipitridae) belong to this category. Thus it is assumed that paternity in raptors is assured by means of frequent copulation (Birkhead and Møller 1992). Close mate-guarding also is prevented in colonial contexts, when one member of the pair must remain at the breeding site to defend it against intruders (Møller and Birkhead 1992). Colonial birds may have higher copulation rates than solitary species because the risks of EPCs are higher in colonial situations (Birkhead and Lessells 1988). Indeed, a comparative interspecific study

with mainly non-raptorial species found that EPCs were significantly more frequent among colonial than in solitary mate-guarding species, and that birds that experience a high rate of EPCs performed intra-pair copulations more often than other species (Møller and Birkhead 1993). However, Simmons (1990) and subsequently Korpimäki et al. (1996) showed that this prediction is weakly supported in interspecific comparisons of raptors, because some solitary species copulate much more frequently than colonial ones, and because the frequency of EPCs is relatively low among raptors and is not related to the species' copulation frequency. Simmons (1990) further suggested that, in raptors, intraspecific comparisons in species with varying degrees of EPC risks are better to test the paternity assurance hypothesis: his study on the African Marsh-Harriers (*Circus ranivorus*) indicated that clumped pairs copulated more frequently than solitary ones. In another intraspecific comparative study, European Kestrels (*Falco tinnunculus*) copulated more frequently in the year when extra-pair paternity was highest (Korpimäki et al. 1996), indicating that birds behaved differently in circumstances when EPC risk varied. No other study has assessed the effect of EPC risk on copulation behavior in a large population of raptors, nor has any study analyzed temporal variation in copulation behavior in relation to the risk of EPCs in raptors.

The Montagu's Harrier (*Circus pygargus*) is a medium-sized ground-nesting raptor, with a clumped or semi-colonial nest dispersion (Cramp and Simmons 1980, Arroyo 1995). The degree of clumping varies between years and between areas, with pairs nesting either solitarily or in loose colonies from 2 to over 30 pairs (Martelli 1987, Arroyo 1995). Montagu's Harriers are mainly monogamous, although bigamy has occasionally been described (Cramp and Simmons 1980). Bigamy was not recorded in this study, and males provided most of the parental investment in terms of food supply and nest defense (Arroyo 1995). Thus, cuckoldry could have a high cost for males. The risk of cuckoldry potentially increases with increasing number of neighboring pairs, and I hypothesized that male Montagu's Harriers adjust their paternity assurance behavior accordingly.

In this paper I describe the copulatory behavior of Montagu's Harrier in relation to onset of laying and courtship feeding, the occurrence of EPCs in the population, and their distribution in relation to onset of laying and nest dispersion. I also evaluate the pattern of copulation frequency in relation to differences in breeding density.

METHODS

A population of Montagu's Harriers was monitored between 1992 and 1995 in an agricultural area (195 km²) located 20–40 km northeast of Madrid, Spain, where they breed in cereal crops (mainly wheat). All nests were found in the study area each year, and their locations were plotted on 1:10,000 maps of the study area. Population size varied among years between 39 and 51 pairs (mean ± SD = 46.2 ± 6.2). Nests were distributed either solitary or in loose colonies of 2–16 nests. For each nest, I calculated from map locations the number of neighbors as the number of other nests within a radius of 600 m; the latter was chosen because the frequency distribution of nearest neighbor distances in the study area was bimodal (Arroyo 1995), and 600 m was the longest distance between nearest neighbors recorded within the "clumped" category of nests.

Birds were monitored from arrival (late March–early April). Copulation rates were calculated from focal observations, which were carried out for pairs that could be easily and accurately observed (24, 26, 19, and 24 pairs each year, respectively). Each focal observation lasted 1–4 hr (2.3 ± 1.2 hr), and each focal pair was observed on average every three days. Observations were made from vantage points (small hills), which were located 300–2,000 m from the nests. Because the study area is generally very flat except for these vantage points, visibility of copulation behavior, aerial activity, and food passes was very good, even when distances from the birds were relatively large. I am thus confident that most copulations were recorded during the observation periods. Additionally, these vantage points allowed me to monitor up to 3–5 pairs at the same time. Copulation rates per female were estimated from the total number of attempted matings (successful plus unsuccessful) observed. For copulations observed outside focal observations, the date, the female involved, and whether copulations followed a food pass or not also were noted. Breeding individuals were unmarked, except for eight breeding females in 1994 and 1995. However, females could be identified individually through plumage differences and their consistent use of defended perching sites once nest locations had been settled. Copulation rates refer to copulation rates per female, not per pair. Males were generally more difficult to identify individually. Copulations were considered to be within-pair copulations unless proved otherwise. Thus the frequency of extra-pair copulation is a minimum figure, as some copulations considered as within-pair copulations could have been misclassified.

Laying date was calculated by backdating from hatching date, which was estimated from the length of the eighth primary of nestlings (Arroyo 1995) except for a few nests in which it was recorded directly by nest visits. Copulations were very rarely seen before 20 days prior to the onset of laying (Fig. 1). To standardize observation effort among pairs for which focal observations started at different times in relation to their laying date, only observations made from 20 days before laying until the end of the laying period were considered for frequency analyses. Each focal pair was observed an average of 9.8 ± 4.5 hr during this period. To analyze the variation in copulation frequency with time, I divided this period into three intervals: (1) early pre-laying (20 to 11 days before laying), (2) late pre-laying (10 to 1 day before laying), and (3) laying period (day of first egg to day of last egg). Females observed for less than 1 hr in any given period were excluded from the analyses. For some females, no laying date could be as-
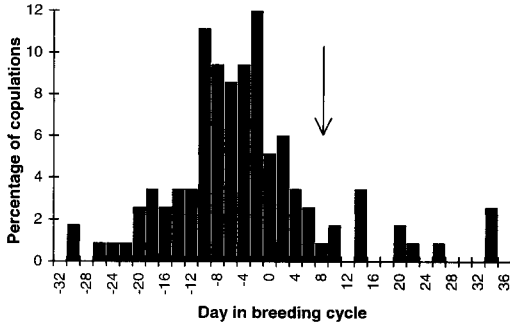
FIGURE 1.   Frequency of observed copulations in relation to onset of laying (0 = day of first egg), all years combined (*n* = 117 copulations). The arrow indicates the end of the average laying period.
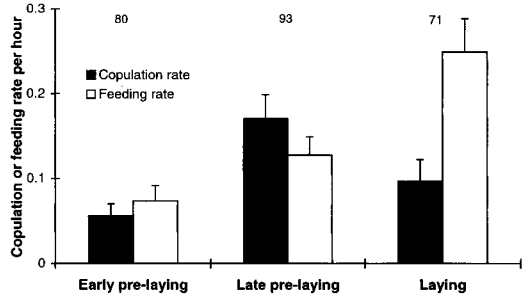

FIGURE 2.   Mean (± SE) copulation and feeding rates in the pre-laying and laying periods. Sample sizes (number of nests observed) are given above each bar.

signed, either because they did not lay eggs or because the clutch failed before hatching; therefore, these females were excluded from date analyses.

Analyses of behavior were made with nonparametric statistics (Kruskal-Wallis, Kendall's tau (τ) correlations, chi-square tests), given the low ranges of values observed, and that most nontransformed data were not normally distributed. All analyses were performed with SPSS 6.1 (Norusis 1989). All data are presented as mean ± SE.

RESULTS

COPULATION FREQUENCY

A total of 141 copulations from 93 females were observed over the four years of the study. Of these, 117 could be related to the female's laying date (Fig. 1). Copulations started as early as 30 days before the start of clutch initiation and typically stopped at the end of the laying period. However, some copulations (12%) were observed after the end of laying, either during the incubation period or even, as at one nest in 1994, a few days after hatching. Copulations were most frequently observed prior to the onset of laying (Fig. 1). Indeed, copulation rate peaked in the 10 days before the laying of the first egg (late pre-laying), when it averaged 0.17 ± 0.23 hr^{-1} (or 2.2 copulations day^{-1}), nearly twice the rate in any of the other two periods (Fig. 2). Copulation rate per hour was significantly higher in the late pre-laying period than in the early pre-laying or laying periods (Kruskal-Wallis, χ^2_2 = 12.8, P < 0.001). Taking account of this temporal difference in copulation frequency, assum-

ing 13 hours of daylight (approximately the activity period for the harriers in the pre-laying period), two-day intervals between the laying of consecutive eggs and an average clutch of four eggs, the mean total number of copulations per clutch was estimated to be 39 ± 5 (*n* = 93 females).

Eight (4%) paired females in the study area did not lay eggs after building nests. Seven were seen copulating at least once (10% of all observed copulations involved nonlaying females). These females copulated early in the season in relation to the mean annual laying date, and at a relatively high rate (0.13 ± 0.11 copulations hr^{-1}, *n* = 4 females).

Copulations occurred throughout the day, except very early in the morning, when Montagu's Harriers generally showed little activity at that time of the year. Peak copulation frequency was observed between mid-morning and noon, with another smaller peak in the early evening (Fig. 3).
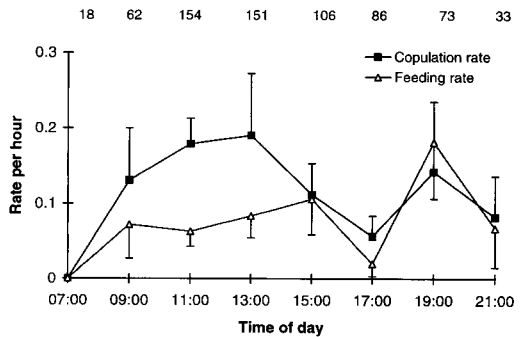

FIGURE 3.   Daily pattern of copulation frequency and prey deliveries (mean ± SE). Number of hours of observation in each period (all nests and years combined) above the graph.

COPULATIONS AND COURTSHIP FEEDING

Females were fed by males as soon as pair bonds were established, and females were never observed hunting for themselves. In the pre-laying or laying period, only 27 of 98 copulations were preceded by a food pass. However, the daily pattern of copulations during the pre-laying period matched the daily pattern of prey deliveries calculated for the same period (Fig. 3, $r = 0.687$, $n = 9$, $P < 0.05$), although prey delivery rates in the morning, when copulations were most frequent, were relatively low. Furthermore, copulation rate per female was related to feeding rate during the early pre-laying period (Kendall's $\tau = 0.23$, $n = 80$, $P < 0.018$): females that were fed more frequently copulated more often. In contrast, no such relationship was found during the late pre-laying or laying periods (Kendall's $\tau = 0.09$ and 0.11, $n = 93$ and 71 females, respectively, $P > 0.1$). During the laying period, food delivery rate was significantly higher than in the previous periods (Kruskal-Wallis, $\chi^2_2 = 8.4$, $P < 0.01$), and it was similar to the rate of feeding maintained throughout the incubation period (Arroyo 1995).

In contrast to laying females, 10 out of 13 copulations of nonlaying females followed a food pass. Feeding rates of nonlaying females also were high (0.24 ± 0.14, $n = 5$) compared to the feeding rates of other females in the pre-laying period (Fig. 2). Similarly, eight out of nine copulations observed after the laying period occurred after a food pass. Finally, copulations sometimes occurred in episodes, with a pair copulating two or three times only a few minutes apart. Copulation bouts occurred more commonly after a food pass than without food ($\chi^2_1 = 8.5$, $P < 0.005$).

EXTRA-PAIR COPULATIONS

Over the four years of the study, at least five EPCs were observed in the study area. In two instances, after receiving food from one male, a female flew towards another male and solicited a copulation; the second male had previously brought food to a different female. While the second male was mounting the female, the first male flew towards them, and chased the extra-pair male away. A third case involved a female that copulated with two different males in succession. In a fourth case, a male, after copulating with the female he had presented food to, went towards another female who was eating prey given to her by another male and copulated with her. Lastly, a female paired to an adult male was seen copulating with a first-year male. Additionally, four copulations, two of them involving wing-tagged females, were seen far from nesting areas, which might have been EPCs, because pair copulations usually occur near the nest (Simmons 1990). On two other occasions, a male interrupted a copulating pair and chased the copulating male, a behavior similar to that observed during the known EPCs. This gives a total of 11 definite or possible EPCs.

Overall, these EPC observations accounted for 3.6–7.8% of all observed copulations, and involved 5.3–9.6% of the monitored females (lower figures in the ranges refer to known EPCs, and higher figures to known plus suspected EPCs). Because males were not individually identifiable, some of the copulations considered as within-pair copulations might have been EPCs, so the frequency presented is a minimum figure.

Four of the known EPCs occurred during the female's laying period, and one of them in the week prior to laying. All the suspected EPCs occurred in the 10-day period prior to laying. Eight of these 11 observations occurred in the largest and/or densest colonies each year (with 7–14 pairs each), the other 3 took place in middle-sized colonies (3–4 pairs). Four of the five females involved in known EPCs had five or more neighbors, the other one had two. Of the suspected EPCs, one female had one neighbor, another one two neighbors, a third one three, and three females had five neighbors or more. Thus, EPCs were particularly frequent in big colonies, for females with a high number of neighbors, and during the laying or late pre-laying periods.

COPULATION RATES AND NEST DISPERSION

Considering the entire copulation period (-20 days until the end of the fertile period), copulation rate per female increased with the number of neighbors but not significantly so (Kendall's $\tau = 0.13$, $n = 93$ females, $P = 0.11$). A different pattern was apparent when the three periods were considered separately. Solitary pairs seemed to copulate only over a short period: copulations were observed only in the late pre-laying period (Fig. 4). Clumped pairs copulated over a longer period. Before laying, copulation rates were similar regardless of the number of neighbors (Fig. 4); however, during the laying
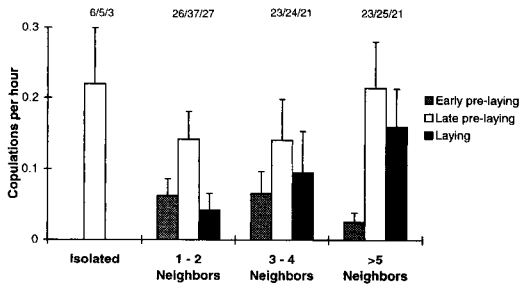
FIGURE 4. Mean copulation rate per female in isolated nests, small colonies, and bigger colonies in the pre-laying and laying periods. Sample size (number of females observed) above the histograms.

period, copulation frequency was significantly higher with increasing numbers of neighbors (Kendall's $\tau = 0.22$, $n = 67$, $P = 0.03$). The estimated total number of copulations per clutch increased from 28 in isolated pairs, to 30 in small, 35 in medium, and 45 in large colonies.

DISCUSSION

COPULATION FREQUENCY AND FOOD PRESENTATION

Copulation rates in the Montagu's Harrier were related to food presentation in the early pre-laying period, when mate choice takes place. Repeated copulations also were more frequent after a food pass than in the absence of food. Females, who ultimately control copulations, may trade copulations for food to test the male's ability or motivation to provide food later in the season. This is further supported by data indicating a relationship between food and copulation in two other species of harriers: Hen Harrier (*Circus cyaneus*) and Swamp Harriers (*C. approximans*). Male Hen Harriers, being highly polygynous, vary widely in their provisioning rate to females (Simmons et al. 1986), and females use courtship food as a cue for future parental investment (Simmons 1988). In this species, food preceded 73% of 59 copulations (Picozzi 1984). Bigamy also has been described for the Swamp Harriers (Baker-Gabb 1981), and female Swamp Harriers solicited copulations more frequently after males had made a kill (Baker-Gabb 1981). In contrast, most pairs of African Marsh-Harriers remained faithful between years (Simmons 1990), so mate assessment prior to laying is not necessary. Copulations in African Marsh-Harriers were not related to food (Simmons 1990), and only 50% of 125 copulations

observed were preceded by food delivery. In the Montagu's Harrier, the lack of relationship between food provisioning and copulations in the late pre-laying and laying period may be related to the fact that mate choice is already made at this stage.

The association between copulation and food in nonlaying females also supports the hypothesis that females that have a lot to loose from poor male provisioning trade copulations for food. Nonlaying females are usually those in poorer physical condition (Newton 1979), and were more reluctant to copulate without food presentation. In contrast, the relationship between copulations outside the fertile period and food presentation was probably a chance effect: on most occasions when males visited the nesting areas in the incubation or nestling period, they were carrying food.

COPULATION FREQUENCY AND EPC RISK

Female Montagu's Harriers copulated about 40 times for each clutch of eggs. Birkhead and Møller (1992) defined copulations as frequent when they occurred more than 20 times per brood, or more than 2 copulations day^{-1}. This suggests that Montagu's Harriers experience some degree of sperm competition (Birkhead and Møller 1992), or male awareness of the risk of it. In this population at least 4–8% of all observed copulations were EPCs, which could have resulted in extra-pair fertilizations, because they frequently occurred within the laying period when copulations have the highest probability of fertilizing the eggs (Møller 1987). The risk of EPC was related to nest dispersion, because EPCs were most frequent in large colonies. The hypothesis that Montagu's Harriers used sperm competition as a paternity assurance strategy was supported by the observation that copulation frequency increased with the number of neighbors, with females nesting in big colonies almost doubling the total number of copulations per clutch relative to solitary females. The fact that the increased copulation rates in colonial situations occurred in the laying period, when most observed EPCs occurred, suggests that males were responding to cuckoldry risk at the appropriate times. DNA studies are needed to ascertain the real risk in terms of extra-pair paternity.

EPC frequency in the semi-colonial Montagu's Harrier was relatively high as compared

TABLE 1.   Copulation frequency and EPC rate in raptors. Total = total number of copulations female^{-1} clutch^{-1} in the pre-laying period. Max. = maximum number of copulations female^{-1} day^{-1}. EPC = observed percentage of extra-pair copulations.

Species	Total	Max.	EPC	References
Osprey (*Pandion haliaetus*)	160	12	0.3	Birkhead and Lessels 1988
White-backed Vulture (*Gyps africanus*)	—	—	<1	Mundy 1982
Cape Griffon Vulture (*Gyps coprotheres*)	69	6	0.7	Robertson 1986
Egyptian Vulture (*Neophron percnopterus*)	55	9	4.6	Donázar et al. 1994
Red-shouldered Hawk (*Buteo lineatus*)	—	—	<1	McCrary and Bloom 1984
Goshawk (*Accipiter gentilis*)	518	29	—	Møller 1987a
Black Kite (*Milvus migrans*)	196	11	2.7	Koga and Shiraisi 1994
African Marsh-Harrier (*Circus ranivorus*)	69	7	2	Simmons 1990
Montagu's Harrier (*Circus pygargus*)	39	5	3.6–7.8	This study
Merlin (*Falco columbarius*)	42	8	7.3	Sodhi 1991
European Kestrel (*Falco tinnunculus*)	374	—	—	Birkhead and Lessels 1988
	218	—	1	Korpimäki et al. 1996
Lesser Kestrel (*Falco naumanni*)	174	16	6.7	Negro et al. 1992
American Kestrel (*Falco sparverius*)	690	18	>5	Balgooyen 1976
Prairie Falcon (*Falco mexicanus*)	194	4	0	Holthuijzen 1991
Mean ± SE	215 ± 55	11 ± 2	2.7 ± 0.7	

with other raptor species: 67% of the other 12 species for which EPC data were available showed values lower than that found in the Montagu's Harrier (Table 1). Furthermore, if considering also probable EPCs, the value found in this study lays within the highest found in other species (Table 1). Nevertheless, copulation rate of Montagu's Harriers was low when compared with that of other raptor species (Table 1): average total copulations in the pre-laying period for the other studied species was 215, and average maximum copulations per day was 11, figures much higher than those found in this study. This leads to the conclusion, in agreement with Simmons (1990) and Korpimäki et al. (1996), that interspecific comparisons do not support predictions from the sperm competition hypothesis, such as that colonial raptors should copulate more often than territorial ones. There is large variation in the copulation frequency of raptor species (Table 1), and phylogenetic effects should be evaluated in interspecific comparisons. In contrast, intraspecific or intrageneric pairwise comparisons may help overcome the potential effect of phylogenetic components (Møller and Birkhead 1992). It would thus be interesting to assess copulation frequency in strictly territorial and solitary harriers such as the Swamp Harrier or the Spotted Harrier (*C. assimilis*).

ACKNOWLEDGMENTS

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