

PAIR COPULATIONS, EXTRA-PAIR COPULATIONS, AND INTRASPECIFIC NEST INTRUSIONS IN MERLIN¹

NAVJOT S. SODHI

Department of Biology, University of Saskatchewan, Saskatoon, Saskatchewan S7N 0W0, Canada

Abstract. This paper reports three extra-pair copulations (EPCs) and two EPC attempts in Merlin (*Falco columbarius*). Three hypotheses of frequency of pair copulations were evaluated. The Merlins copulated both during fertile and non-fertile periods, providing support for the social bond hypothesis. Sixty copulations per pair were estimated for the whole breeding season. This copulation rate is high compared to other solo breeding non-raptorial birds and to that necessary to fertilize a clutch of four or five. As male Merlins cannot guard their mates continuously and there are possibilities of extra-pair copulations in the study area, this high copulation rate may be an insurance for genetic paternity, thus providing support for the sperm competition hypothesis. The majority of intraspecific nest intruders were chased from the vicinity of the nests during the fertile period.

Key words: *Merlin; Falco columbarius; copulations; extra-pair copulations; intraspecific nest intruders; sperm competition hypothesis.*

INTRODUCTION

Like most other birds (Birkhead et al. 1987, Birkhead 1988), little is known about the copulation behavior of the Merlin (*Falco columbarius*). Feldsine and Oliphant (1985), however, described displays associated with copulations in this primarily monogamous falcon and Laing (1985) noted 11 copulations at four nests at Denali National Park, Alaska. Virtually no data exist concerning behaviors of intraspecific nest intruders and response of resident Merlins towards them. Cramp and Simmons (1980: 313) stated that there is no record of aggressive encounters between conspecific Merlins during the breeding season. James and Oliphant (1986) also found that a resident pair generally tolerated an extra yearling male near the nest.

Here, I report three extra-pair copulations (EPCs), two EPC attempts, and examine the concordance of copulation behavior of the Merlin in relation to current hypotheses about copulation frequency in birds. Three main hypotheses have been proposed to explain the copulation behavior of birds (Birkhead et al. 1987). The social bond hypothesis states that copulation behavior is associated with formation and maintenance of the pair bond (Nelson 1965, Newton 1979), and a resulting prediction is that copulations occur outside the female's fertile period.

According to the copulation trading hypothesis, males decrease the risk of EPCs by feeding the females, thus limiting their need to visit other males for food (Birkhead and Lessells 1988) and the females, in turn, trade copulations for food to ensure a continuous food supply (Poole 1985). The prediction of this hypothesis is that the majority of copulations would be solicited by the females after prey deliveries by the males. The sperm competition hypothesis states that, if chances of EPCs are high, males should attempt to displace or devalue the sperm of possible competitors by copulating at a high rate (Birkhead et al. 1987). Because most male raptors are not known to guard their mates (Birkhead et al. 1987, Møller 1987a; but see Poole 1985), and are away from the nests (and females) foraging for varying amounts of time during the female's fertile period, this high copulation frequency would possibly dilute the possibility of fertilization by EPCs that may have occurred in their absence.

I also describe behavior of intraspecific nest intruders and the response of residents toward them. I tested two predictions of the sperm competition hypothesis, viz. majority of intraspecific nest intruders are males seeking EPCs and male nest intrusion rate should be higher during the fertile period than non-fertile period (Møller 1987b).

METHODS

I spent 679 hr watching 13 nests between May and July, 1988-1990. All observations were made

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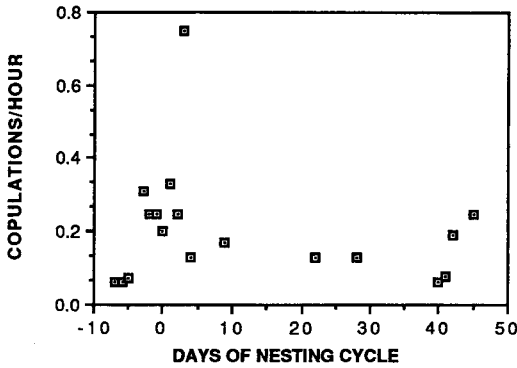


FIGURE 1. Seasonal variation in copulation rate in Merlin. Zero denotes start of egg-laying for a modal clutch of five. Note that initiation of egg-laying was determined (see Methods for details) for each observed female ($n = 13$). If more than one female was observed on a particular day of the breeding cycle an average of copulation rate was obtained to plot this figure.

at Saskatoon ($52^{\circ}07'N$, $106^{\circ}38'W$), Saskatchewan, Canada. The study area is described by Warkentin and James (1988). The breeding Merlin population was 20.5, 25.4 and 24.6 pairs/100 km² respectively during 1988, 1989, and 1990; which is the highest density for this species anywhere recorded (Sodhi et al., unpubl. data).

The falcons were observed from a car using $7\times$ binoculars, mostly during first and last four daylight hours. However, some dawn-to-dusk observations were also made (pre-laying period—4 days, incubation period—4 days, and nestling period—2 days). For some analyses, I divided the Merlin breeding season into the fertile (pre-laying and egg laying) and non-fertile (incubation, nestling, and fledging) periods. I determined these periods by behavior of the resident pair and/or backdating from estimated ages of young (assuming 32 days incubation, egg-laying interval 2 days; Palmer 1988). I assumed that the females became fertile 4 days prior to egg-laying (Berry 1972, Boyd et al. 1977). Resident falcons were either radio-marked, had a year-specific color band, or wore a U.S. Fish and Wildlife Service aluminum leg band.

RESULTS AND DISCUSSION

PAIR COPULATIONS

In all, I observed 41 pair copulations. The frequency of pair copulations peaked just prior to and during egg-laying (Fig. 1), when the chances

that introduced sperm will lead to fertilization are high (Møller 1987b).

As predicted by the social bond hypothesis, I recorded copulations during the fertile and non-fertile periods. Twenty-six copulations were observed during the fertile period in 130 hr (0.20 copulations/hr). The frequency of copulations recorded at Saskatoon during the fertile period of the females is lower than recorded elsewhere (0.67 copulations/hr; Laing 1985), but Laing's data were based on only 16 hr of sporadic observations.

Fifteen copulations were recorded in 549 hr during the non-fertile period (0.03 copulations/hr). I recorded copulations between seven days prior to and 35 days after egg-laying (Fig. 1). In other words, pair copulations were observed up to mid-nestling period and on 39 days out of 84 days of the non-fertile period. No copulations were observed during the fledging period, perhaps because males and females rarely come in contact with each other during this period.

Assuming the fertile period of 14 days and a daily activity of 15 hr, I estimate 42 copulations per clutch. For 39 days of the non-fertile period, when I observed pair copulations, with 15 hr of daily activity, I estimate 18 copulations per pair. In other words, a total of about 60 copulations/pair during the breeding season. Evidence from domestic birds suggests that a single insemination may fertilize an entire clutch (Lake 1975). Other studies have also recorded high copulation frequency in raptors, viz. the Peregrine Falcon, *F. peregrinus* (30 copulations/pair; Ratcliffe 1980); American Kestrel, *F. sparverius* (690 copulations; Balgooyen 1976); European Kestrel, *F. tinnunculus* (374 copulations; T. Meijer in Birkhead and Lessells 1988); Goshawk, *Accipiter gentilis* (>500 copulations; Møller 1987a); Osprey, *Pandion haliaetus* (160 copulations; Birkhead and Lessells 1988); and Prairie Falcon, *F. mexicanus* (194 during the pre-incubation period; Holthuijzen 1989). The high copulation rate in raptors compared with other monogamous birds is considered insurance against extra-pair fertilizations (Birkhead et al. 1987).

Of 41 copulations, only eight (19.5%) occurred within half an hour after the males gave food to the females and only three of these were initiated by solicitation by the females. It appears unlikely that female Merlins trade copulations for food.

In summary, the Merlins copulate in the fertile

as well as non-fertile period, which implies that copulations in Merlins have a role in maintenance of the pair bond. Other studies on raptors also reveal that the intrapair copulations occur both in fertile and non-fertile periods, e.g., the Cape Vulture, *Gyps coprotheres* (Robertson 1986), Goshawk (Møller 1987a), Osprey (Birkhead and Lessells 1988), and Prairie Falcon (Holthuijzen 1989). Males cannot remain with their mates continuously during the fertile period because of foraging needs and extra-pair copulations occurred in my study (see next section). Perhaps to increase the likelihood of genetic paternity, Merlins copulate at a higher frequency than is needed to fertilize a clutch of four or five eggs. My data provides indirect support for the sperm competition hypothesis. Very few (7.3%) copulations were solicited by the females after the males gave them food, providing no clear support for the copulation trading hypothesis.

EXTRA-PAIR COPULATIONS

On 3 May 1988, approximately at 09:00, I observed a non-resident adult male Merlin landing about 20 m from a resident female which was perched about 10 m from her nest. The male gave a copulation chatter (*Chrrr*; Feldsine and Oliphant 1985) while the female solicited copulation by bowing and fanning her tail. Then the male flew toward her and mounted her. After copulating, the male flew from the vicinity of the nest. On 5 May 1989, at 12:30, I observed a non-resident adult male copulating with the resident female about 25 m from her nest. After copulating, the male perched near the nest for about 10 min during which he frequently called *ki-ki-kee* (Feldsine and Oliphant 1985). In both instances, the resident females were egg-laying and thus potentially fertile. The resident males (radio-tagged) on both these occasions were hunting away from the nests. Because the copulations lasted about 5–10 sec, it seems likely that in both these EPCs the males had cloacal contact and ejaculation.

On 17 May 1990, at about 19:15, I observed an adult non-resident male flying near a resident female while the resident male was incubating. The female gave a copulation chatter and followed the intruder male and then both birds perched and copulated. The resident male came out of the nest but did not try to supplant the intruder male. The resident male then flew from

the nest tree and perched about 25 m from the female and the other male. After a few minutes, the intruder male flew toward and dived at him; the resident male crouched and gave weak *tic* calls (Feldsine and Oliphant 1985). The intruder male soared near the nest for approximately 5 min and then flew away. The lack of aggression by the resident male toward the intruder could possibly be due to two reasons: 1. the intruder male was stronger than him (Parker 1974), and 2. the female had laid a full clutch, so there was no possibility of cuckoldry. There was no apparent change in the behavior of the resident male after the EPC; he provided food for the female (and chicks; two young were successfully raised) and did not show any aggression toward her.

On 15 June 1988 (nestling period), at about 06:00, I observed a yearling male giving copulation chatters near a nest. He seemed to be ignored by the resident pair. On 7 June 1990, at 06:30, I saw a non-resident female near a nest in which the resident female was brooding. The resident male, perched nearby, gave copulation chatters and flew towards the intruder female, but no copulation occurred and she flew off from view.

As no intruder was individually color-marked, I could not determine their breeding status. Because two EPCs occurred when the females were potentially fertile, it appears that EPCs have some reproductive significance in Merlins (Cheng et al. 1982, Welsh and Sedinger 1990); EPC could serve as a secondary reproductive strategy (Mineau and Cooke 1979). The third EPC occurred after the female completed her clutch and was thus probably infertile. Extra-pair copulations and attempts at EPCs outside the female's fertile period probably occur because it is sometimes difficult for intruder males to accurately assess the fertility of the females (Mineau and Cooke 1979).

INTRASPECIFIC NEST INTRUDERS

I observed 28 nest intrusions, of which 19 (68%) were by males, four (14%) by females, and five (18%) by unknown sex ($\chi^2 = 14.2$, $df = 2$, $P < 0.01$). The frequency of male intruders during the fertile period was double (0.05/hr) than during the non-fertile period (0.02/hr).

Twelve intraspecific nest intrusions were recorded during the fertile period (0.09 intrusions/hr or an estimated 19 intrusions during the whole

period), seven (58%) were by males (three yearlings, four adults), two (17%) by females, and three (25%) by Merlins of unknown sex. Two intrusions by males resulted in EPCs (described above), four males were immediately chased by the resident males when the intruders landed near the nests. One intruder male called *ki-ki-kee* for about five min near a nest. He seemed to be ignored by the resident female; the resident male was away hunting. Both intruder females went into the nests (intraspecific brood parasitism attempts?) while the resident pair was sitting within 25 m from the nest, both these females were chased by the resident pair. Three Merlins of unidentified sex flew over the nests and did not elicit any response from the resident pair.

Sixteen nest intrusions occurred during the non-fertile period (0.03 intrusions/hr or estimated 38 intrusions, assuming 84 days of non-fertile period with 15 hr of daily activity). Twelve (75%) were by males (six yearlings, six adults), one resulted in EPC and an attack on the resident male and one was an attempted EPC (both described above). Three adult males attacked the resident males, one intruder tried to land on a resident male. As stated earlier, these males were possibly stronger than the residents. Five males stayed near the nests for a few minutes when present; all these males seemed to be ignored by the resident males. A yearling male brought a sparrow-sized bird and fed the nestlings and another male attacked a nest climber. Although extra birds near Merlin nests have been observed to defend nests and deliver prey to the resident female (James and Oliphant 1986), this is the first report of an extra bird feeding the chicks.

Two (12.5%) nest intruders were females. The resident male tried to copulate with one (described earlier) and the other extra female food-begged near the nest and was chased by the resident female. Two (12.5%) Merlins of unknown sex flew over the nest, one was chased by the resident male and the other did not elicit any apparent response behavior by the resident pair.

In summary, the majority of nest intruders were chased from the nests by the resident males during the fertile period, but intruders often were tolerated during the non-fertile period. This behavior is consistent in avoiding EPCs while minimizing risk of personal injury by avoiding fights when paternity is not at risk. As predicted by the sperm competition hypothesis, most of nest in-

truders were males and the frequency of male intruders was higher during the fertile period.

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