



# Copulatory behaviour and paternity in the American kestrel: the adaptive significance of frequent copulations

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## ABSTRACT

The adaptive significance of repeated withinpair copulations is not well understood. We analysed the copulatory behaviour of 16 pairs of solitary-nesting American kestrels, *Falco sparverius*, in southern Quebec (Canada), and the achieved reproductive success (paternity) of 21 kestrel families determined by DNA fingerprinting, in terms of four hypotheses. (1) The paternity assurance hypothesis, which suggests that males copulate frequently to avoid being cuckolded, was rejected because there were few extrapair copulation attempts (<1% of all copulations observed), withinpair copulations were not timed during the fertile period and mate attendance did not increase as the fertile period approached. (2) The immediate material benefits hypothesis, which suggests that females trade copulations for food, was refuted because copulations most often occurred without food transfers, especially outside the fertile period. (3) The female mate guarding of males hypothesis, which suggests that females distract their mates from other mating opportunities by copulating frequently, was rejected because extrapair copulation attempts were infrequent, male and female solicitation frequencies were similar and females did not differ in the timing or frequency of solicitations. (4) The mate assessment hypothesis, which suggests that assessment of mate quality is mediated via copulation, most closely predicted the behaviour observed since withinpair copulations were frequent outside the fertile period and at pair formation, males and females solicited similar numbers of copulations and pairs did not differ significantly in solicitation or copulation frequency. In line with this hypothesis we found that only one brood was extrapair, probably the result of mate replacement.

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The majority of vertebrates copulate a few times each breeding season shortly before fertilization but many species, from dolphins (Würsig 1989) to birds (Birkhead & Møller 1992), copulate hundreds of times more than is necessary for fertilization, both during and outside the fertile period. This enormous variation suggests that copulation frequency is under complex selection pressures but these pressures are poorly understood.

Most detailed investigations of copulatory behaviour appeared only after it was recognized that postcopulatory competition among sperm from different males (sperm competition) has a significant impact on mating system evolution (Parker 1970; Smith 1984; Birkhead & Møller

1992; Keller 1994). Consequently, almost all analyses of copulatory behaviour in the past two decades describe frequent withinpair copulations (WPCs) as a paternity guard (see the paternity assurance hypothesis: Møller 1987; Simmons 1990), for example lions, *Panthera leo* (Packer & Pusey 1983), sheep, *Ovis aries* (Hogg 1984), primates (Møller 1988) and birds (Birkhead & Møller 1992). However, the paternity assurance hypothesis (Simmons 1990), also known as the sperm competition hypothesis (Birkhead et al. 1987) and the paternity confidence hypothesis (Eens & Pinxten 1995), seems inadequate for at least some frequently copulating species that have (1) low frequencies of extrapair copulations (EPC; Tortosa & Redondo 1992), (2) copulations before the fertile period (Negro et al. 1992) and (3) a decrease in frequency of WPCs during the fertile period (Birkhead & Møller 1993). Very few studies consider alternative hypotheses to the paternity assurance hypothesis and many lack data on genetic paternity which provides essential information on reproductive success and has

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**Table 1.** Predictions of four hypotheses that explain the adaptive significance of frequent withinpair copulations (WPCs) during the prefertile and fertile periods for birds that do not guard their mates

Hypothesis	Predictions
Paternity assurance	(1) WPCs increase in fertile period (2) Mate attendance increases in fertile period (3) Female solicitation increases when paternity confidence is low
Immediate material benefits	(1) Females exchange food for WPCs
Female mate guarding of male	(1) WPCs occur from pair formation until egg laying (2) Females control copulations via solicitation (3) Females differ in soliciting behaviour
Mate assessment	(1) WPCs occur from pair formation until egg laying (2) Both sexes solicit WPCs (3) Pairs do not differ in solicitation frequency

proven a much more reliable index of cuckoldry than behavioural observations.

We investigated the adaptive significance of frequent WPCs in relation to paternity assurance, food-bringing behaviour and withinpair communication. We tested four hypotheses (Table 1) that explain why frequent WPCs occur both outside and during the fertile period in birds that do not guard their mates: (1) the paternity assurance hypothesis (Simmons 1990), which suggests that males copulate at a high frequency to dilute ejaculates from EPCs; (2) the immediate material benefits hypothesis (Tasker & Mills 1981; Hunter et al. 1992), which suggests that females trade copulations (assurances of paternity) with males for benefits such as food, nest materials or protection from other males; (3) the female mate guarding of males hypothesis (Petrie 1992), which suggests that females dissuade their males from EPCs by copulating frequently with them, to reduce the male's ejaculate reserves and energy to remate, during, and pre-emptively before, other females intrude on to the territory; and (4) the mate assessment hypothesis, which suggests that individuals may acquire information about mate quality via frequent copulation. We suggest this last hypothesis as a revised version of the mate assessment hypothesis proposed by Tortosa & Redondo (1992). In this way we consider both the male and female perspective.

We tested these four hypotheses by analysing the copulatory behaviour of the American kestrel, *Falco sparverius*, the most frequently copulating bird (>600 copulations/clutch, Balgooyen 1976; also see Birkhead & Møller 1992). The relevance and predictions of each hypothesis vary with time and sex since selection pressures may change during the breeding season and between males and females. Therefore, we concentrated our analysis on the timing, success and solicitation of WPCs from pair formation until incubation. We also described the frequency of food transfers, EPCs and territorial intrusions and the incidence of extrapair paternity (EPP). We then compared our results with previously published reports on the copulatory behaviour of other kestrels and birds of prey.

## METHODS

### Study Species

The socially monogamous American kestrel is a small falcon with pronounced sexual size and colour dimorphism (Bird 1988). It is migratory in Canada and defends a breeding territory of approximately 0.24 km<sup>2</sup> (Bowman 1985). Both sexes incubate and feed offspring, but hunting during courtship, laying and incubation is done almost exclusively by the male (Balgooyen 1976). The American kestrel is thought to practise a mixed reproductive strategy (sensu Trivers 1972). Extrapair copulations (Childs & Mossman 1952; Cade 1955; Willoughby & Cade 1964; Balgooyen 1976; Bird 1988), territorial intrusions (Balgooyen 1976), mate switching (Bortolotti & Iko 1992), polygynous trios (Towers 1990; De Lucca 1993) and helpers at the nest (Wegner 1975) have all been observed, although these behaviours may not be widespread (Bird 1988). Female kestrels can also store sperm in sperm storage tubules (Bird & Buckland 1976; Bakst & Bird 1987) which allows different males to compete for paternity of the four or five eggs that normally make up a clutch (Bird 1988).

### Study Areas

We observed wild American kestrels nesting in nestboxes during 1992–1993 in southwestern Quebec (Canada; 45°25'N, 75°05'W). All boxes were erected on dead hardwood trees in hedgerows bordering fallow fields or telephone poles along secondary roads. The distance between observed nestboxes ranged from 500 to 1500 m. Kestrels did not appear to be philopatric (<2% band returns in 1993).

American kestrels in our area have been extensively studied in the past decade. They show little or no inter-year pair or site fidelity and a high incidence of interyear divorce and death (Bowman et al. 1987). Lifjeld & Robertson (1992) suggested that temporary mate removal studies are important in order to test the paternity assurance hypothesis. Bowman & Bird (1987) established the

existence of a floating population of unmated birds in our study area and performed a mate replacement study on 16 pairs during incubation. They found that 50% of males were replaced after an average of 36 h and that no replacement pair successfully reared any young.

### Focal Observations

Beginning in mid-March, we visited nestboxes every other day until the kestrels arrived (usually in late March), which allowed us to observe early courtship. We chose seven pairs in 1992 and nine in 1993 for systematic recording of behaviour from pair arrival until the end of laying, while we visited the remaining occupied nestboxes once a week. We selected focal pairs according to arrival time and ease of observation. In 1992, we chose three pairs that arrived early on the breeding territory (late March) and four pairs that arrived with most migrants (April). In 1993, we chose two early pairs, four pairs that arrived with the majority and three late pairs. In 1992, the average arrival date of focal pairs was 7 April, in 1993, 9 April (no significant difference between years, Wilcoxon two-sample test:  $Z=0.25$ ,  $N_1=7$ ,  $N_2=9$ ,  $P=0.80$ ). Average laying dates were 30 April in 1992 and 29 April in 1993 (no significant difference between years, Wilcoxon two-sample test:  $Z=0.23$ ,  $N_1=7$ ,  $N_2=9$ ,  $P=0.80$ ).

A hidden observer observed focal individuals using binoculars and a  $\times 20$ –60 telescope, positioned 100–150 m from the nest. Each pair was observed once every 2 days during a 1-h (1992) or 2-h (1993) period. These observation periods were evenly distributed throughout the daylight hours following a rotational schedule from dawn to dusk. In 1992 each observation bout lasted a mean  $\pm$  SD of  $86 \pm 34$  min ( $N=59$ ) and in 1993  $107 \pm 46$  min ( $N=196$ ; for description of pair identification see Blood sampling below).

### Analysis of Copulatory Behaviour

For each copulation observed we noted solicitation, success and individuals involved. Copulations involved few preliminaries except solicitation (also see Balgooyen 1976). We considered a copulation solicited when, before the male mounted the female, the female moved towards him and lifted her tail to expose her cloaca (see Roest 1957). Copulation was classified as male initiated if the male moved towards the female and mounted her with no apparent solicitation. Copulation was considered successful when cloacal contact was believed to have occurred (male lowered tail to join cloacas). We timed copulations to the nearest 0.1 s using a chronometer. We observed only two aerial displays (for description see Village 1990) and they were not analysed.

Copulatory behaviour was analysed relative to the female's fertile period. We synchronized the observation dates of each pair about day 0, the day the first egg was laid. The copulation period of each pair was divided into two periods: prefertile and fertile. The prefertile period was from the first observation of the pair (usually the day the pair arrived on the territory) until the onset of the

fertile period (day  $-12$ , Bird & Buckland 1976). The fertile period was from day  $-12$  until the end of egg laying (day  $+8$ ). The two periods together comprised approximately 34 days. To estimate day 0, we checked the nest when it appeared the female was brooding and, thereafter, every 4–5 days. For each egg observed, we counted back 2 days (since eggs are typically laid every 48 h in the American kestrel, Bird 1988) to estimate the day the first egg was laid. Finally, we estimated the number of copulations per pair in the breeding season using the following equation: (copulations observed  $\div$  hours observed)  $\times$  days observed  $\times$  hours of daylight.

### Associated Behaviours

Several hypotheses that explain repeated copulations in birds predict that food transfers, intrusions and mate attendance are associated with copulation (Table 1). Food is transferred (from male to female) from pair formation until the end of incubation. In our area, meadow voles, *Microtus pennsylvanicus*, were the main food transferred (62% of all transfers). Intrusions were defined as the entry of nonpair kestrels into the breeding territory of the nesting pair (an area of ca.  $0.24 \pm 0.04$  km<sup>2</sup> ( $\bar{X} \pm$  SE) in our kestrel population; Bowman 1985). We recorded mate attendance as the time the observer estimated that the male and female of a pair could see one another and/or the time both individuals were within 100 m of each another. In addition, for each pair we recorded arrival date, laying date, breeding success (number of nestlings) and incidence of EPFs by DNA fingerprinting.

### Statistical Analysis of Behaviour

We analysed data on bird behaviour and pair characteristics using SAS (SAS Institute 1987). Although variance in most behaviours was homogeneous, most data were not normally distributed (except where noted). Frequency values of behaviour were usually ranked into groups and ranges of values were low. For all these reasons we used nonparametric statistics. For correlations we used Kendall's tau-b correlation coefficients, where  $Z = \text{tau-b} / (\text{asymptotic standard error})$  was a test of significance of tau in terms of a normal distribution (Freeman 1987).

### Blood Sampling

From March to July in 1992 and 1993 we took blood samples from 65 adults and 122 nestlings and we used 21 whole families, 21 putative fathers, 21 putative mothers and 89 nestlings ( $\bar{X}=4.3$  nestlings per pair, range 2–5) in the DNA analysis. Five of the 21 families were focal pairs we had observed closely. The other 16 nests were each visited at least five times during the breeding season. We attempted to catch the adults as early in the breeding season and as close to the nestbox as possible to colour-band individuals and confirm that they occupied the nest where caught. However, individuals captured within the first 2 weeks of arrival often abandoned their nest sites.

Some focal individuals (five of 32) were trapped and colour-banded before observations began but we left most individuals (20 of 32) unbanded. They were identified by plumage characteristics (highly variable in American kestrels, Parkes 1955) and behavioural habits during each observation bout. Although quite reliable, this approach diminished the probability of observing mate switching. To limit the probability of capturing 'floaters' we attempted to capture adults at the nest. Of the 21 families analysed, 18 females (86%) and 13 males (62%) were caught inside the nestbox during the incubation period.

## DNA Fingerprinting

DNA fingerprinting methodology was as described in Negro et al. (1996). Briefly, we took 0.3 ml of blood from the jugular vein of each captured American kestrel using an EDTA-coated 1 cc syringe and a 28 gauge needle. DNA was later extracted from blood cells using a protocol modified from Jeffreys & Morton (1987). Aliquots of 5 µg of DNA were digested with restriction enzyme *Hinf* I (Wolfes et al. 1991) and samples were run (15 per gel) on 0.7% agarose gels at 30 V for 36 h in a 1 × TPE buffer (pH=8.0). Gel hybridizations were carried out according to Zishler et al. (1989) using <sup>32</sup>P-labelled simple sequence oligonucleotide probe (GGAT)<sub>4</sub>. Autoradiography was at room temperature without intensifying screens for an average of 3–4 days of exposure. Banding patterns were only compared between individuals on the same gel and the lanes of nestlings were flanked by those of their putative mother and father. The position of the most intensive bands were scored for each lane (band-sharing analysis followed Negro et al. 1996). We assumed that bands assorted independently since a previous study of six families of captive birds originating from our wild population of kestrels found no sex-linked bands (Cunningham 1995).

## RESULTS

### Copulatory Behaviour

#### Timing

Kestrel pairs copulated frequently during the prefertile and fertile periods (Table 2). The highest frequency was at pair formation (peaking on day -18; Fig. 1) after which WPC frequency decreased to zero by day +8.9 ± 2.68 ( $\bar{X} \pm SD$ ; the end of egg laying). Of 385 copulations observed, 45.1% occurred before the fertile period began (before day -12). Copulation frequency decreased as the breeding season progressed and was significantly lower during the fertile period than the prefertile period (Wilcoxon signed-ranks test:  $Z=4.3$ ,  $N=16$  pairs,  $P<0.001$ ). Thus, copulation frequency was highest when the female was not fertile.

#### Success and duration of copulations

The majority (81%) of all copulations observed were considered successful, 13% unsuccessful and 6% were not

Table 2. Average copulation frequencies (per h) of 16 American kestrel pairs observed in Quebec (Canada) in 1992 and 1993

Pair	Hours observed	Prefertile period (cop/h)	Fertile period (cop/h)	Copulations observed
<b>1992</b>				
MA	25	1.36	0.43	21
92F	17	1.00	0.63	13
W25	16	0.50	1.00	14
DV20	13	0.83	0.50	7
92L	12	0.38	0.25	4
92R	19	1.40	0.86	17
W14	12	1.00	0.20	3
<b>1993</b>				
C2	18	0.00	0.89	16
DV20	40	3.85	0.71	49
93I	36	3.23	0.74	52
W9	41	0.00	0.38	18
92L	31	0.00	0.61	19
C8	53	1.99	0.88	56
D1	45	0.96	0.50	34
92N	29	0.00	0.77	26
93D	40	1.18	0.78	36

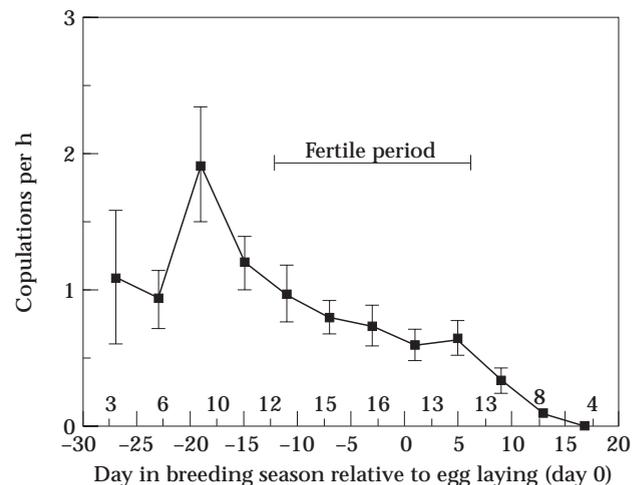
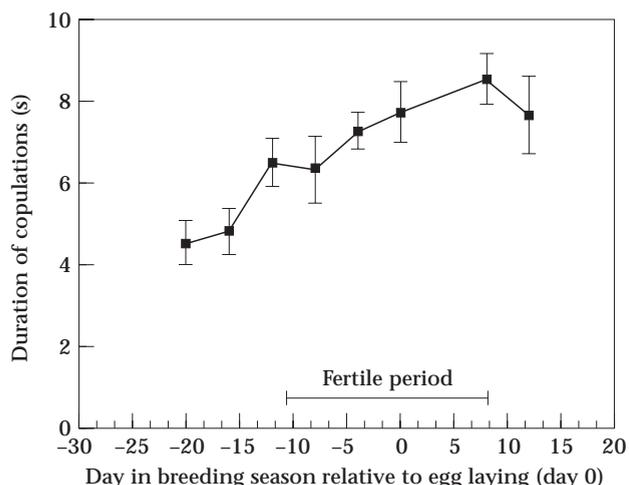


Figure 1. Average copulation rates of wild American kestrels in Quebec (Canada) during the prefertile and fertile periods. Numbers above the X-axis are the numbers of pairs observed during each time interval. Error bars are the standard error of the mean, 0=date first egg in clutch was laid, and the fertile period, day -12 to day +8, includes maximum sperm storage duration of 12 days before the first egg is laid (see text).

classified. Only one copulation (0.3% of all copulations observed) was an EPC. The duration of copulations increased significantly during the fertile period (paired  $t$  test:  $t_{109}=2.84$ ,  $N=9$  nests,  $P<0.05$ ; Fig. 2, Table 3). The frequency of WPCs was negatively correlated with the duration of copulation (Kendall's  $\tau=-0.123$ ,  $N=111$ ,  $P<0.05$ ) and the frequency of unsuccessful WPCs was higher in the prefertile period (Wilcoxon signed-ranks test:  $Z=2.0$ ,  $N=9$  pairs,  $P<0.05$ ).



**Figure 2.** Average duration of copulations among wild American kestrels during the prefertile and fertile periods. Error bars are the standard error of the mean and 0=date first egg in clutch was laid.

**Table 3.** Average frequencies of analysed behaviours (per h $\pm$ SD, except duration) associated with withinpair copulation (WPC) frequency in the American kestrel in Canada

Behaviour	Prefertile period	Fertile period
Unsuccessful WPCs	0.23 $\pm$ 0.37	0.10 $\pm$ 0.27
Duration of WPCs (s)	5 $\pm$ 2.1	7 $\pm$ 3
Solicitation by female	1.05 $\pm$ 1.23	0.42 $\pm$ 0.68
Initiation by male	0.92 $\pm$ 0.65	0.27 $\pm$ 0.40
Mate attendance	0.56 $\pm$ 0.37	0.47 $\pm$ 0.32

### Extrapair copulations

We observed only one EPC which took place on day - 11 at a nest site where the nearest nest was 500 m away. The intruding female, a recent arrival in the study area, approached the resident male at his perch by his nestbox and attempted to enter the nestbox. The resident female, perched close by, attacked the intruder and then went into the nestbox. Then the intruder perched on top of the nestbox and was mounted by the resident male for 3 s. The resident female exited the box and drove the intruder away. The resident pair then copulated. They copulated again 20 min later, at which time the same intruder female returned and attacked the pair, stopping the copulation. The resident female chased the intruder female again and then entered her nestbox.

### Solicitation

Males and females initiated copulations at similar frequencies. Of all copulations observed, 50% were solicited by the female, 40% by the male and 10% were not categorized. Solicitation by the female did not differ significantly between the prefertile and fertile periods (Wilcoxon signed-ranks test:  $Z=1.76$ ,  $N=9$  females, NS) nor between females (Kruskal-Wallis test:  $\chi^2_8=10.9$ , NS; Table 3). Initiations by the male were higher in the prefertile period (Wilcoxon signed-ranks test:  $Z=4.5$ ,  $N=9$

males,  $P<0.001$ ) although the frequency did not differ between males (Kruskal-Wallis test:  $\chi^2_8=9.94$ , NS).

Of the copulations that failed ( $N=39$ ), 64% were initiated by males, 30% by females and 6% were unclassified. There was no significant difference in the rate of unsuccessful copulations when solicited by females or initiated by males (Wilcoxon signed-ranks test:  $Z=0.216$ ,  $N=9$  pairs, NS). Males were occasionally observed to reject female solicitations ( $N=11$ ), either by flying away or remaining motionless. Finally, we noticed that females could end copulations by turning their head back towards the mounted male and sometimes biting (<4% of copulations).

## Associated Behaviour

### Food transfers

We observed 68 food transfers ( $N=10$  pairs,  $\bar{X}\pm SD=7.4\pm 1.8$  food transfers each). The frequency of food transfers per h was not significantly correlated with copulation frequency (Kendall's  $\tau=0.07$ ,  $N=255$ , NS). Nests where food transfers were observed did not differ significantly in their copulatory frequency compared to nests where no food transfers were seen (Wilcoxon signed-ranks test:  $Z=-1.20$ ,  $N=16$  pairs, NS).

### Territorial intrusions

We observed 30 intrusions, 87% female and only 13% male. Intrusions were brief ( $\bar{X}\pm SD=3.5\pm 2.64$  min,  $N=30$ ). Male and female intrusions occurred throughout the breeding season although not for all pairs. However, pairs that suffered intrusions did not copulate more than those where no intrusions were observed (Wilcoxon signed-ranks test: female intrusions:  $Z=-1.54$ ,  $N=16$  nests, NS; male intrusions:  $Z=1.5$ ,  $N=16$  nests, NS). The occurrence of female intrusions was not significantly correlated with female solicitations (Kendall's  $\tau=0.04$ ,  $N=111$ , NS) nor were male intrusions correlated with male initiations (Kendall's  $\tau=0.07$ ,  $N=111$ , NS). At two nests we observed a 'floater' female staying within 500 m of the pair for up to a week and repeatedly intruding to solicit copulations from the paired male.

Female intruders always approached the resident male and often called to the male and assumed a soliciting stance. When present, resident females attacked and chased the intruding female off the territory. The majority of female intrusions (53%) were followed by a WPC either during or after the intrusion ( $\bar{X}=7.25$  min after the intruder's departure). Of 16 copulations that followed female intrusions, 31.3% were solicited by the female, 18.7% were initiated by the male and 50% were not categorized.

Of the four male intrusions observed, two were at one nest on different days (-19 and day +3) and two at different nests on days -19 and -2. Male intrusions lasted, on average  $\pm SD$ ,  $2.75\pm 2.06$  min ( $N=4$ ). In all cases, the resident male was on the territory. Once we observed an intruding male approach a resident female (day +3), after which the female immediately joined her mate at their nestbox where they copulated.

### Mate attendance

Mate attendance (for definition see Methods) averaged 49.5% and did not vary significantly between the preferential and fertile periods (Wilcoxon signed-ranks test:  $Z=1.68$ ,  $N=16$  pairs, NS; Table 3). Pairs differed significantly in their mate attendance (Kruskal-Wallis test:  $\chi^2_{15}=47.7$ ,  $P<0.001$ ) and males that spent more time with their mates copulated more frequently (Kendall's  $\tau=0.36$ ,  $N=255$ ,  $P<0.001$ ). Mate attendance was not significantly lower in the pairs that incurred male intrusions (Wilcoxon signed-ranks test:  $Z=0.7$ ,  $N=16$  pairs, NS), indicating that male presence did not seem to have an effect on intrusions by extrapair males.

### Interpair Comparisons

#### Copulation

To calculate the average copulation rate per season per pair and to take into account variances in copulation frequency throughout the breeding season, we averaged copulation frequencies across the prefertile (arrival to day -13), prelaying (day -12 to day -1) and laying periods (day 0 to day +10) for all pairs. For the prefertile period, we calculated an average  $\pm$  SD of  $230 \pm 145$  copulations ( $N=12$ , range 43-440), for the prelaying period  $151 \pm 65$  copulations ( $N=16$ , range 45-275) and for the laying period,  $73 \pm 25$  copulations ( $N=12$ , range 26-109). Averaging these frequencies we obtained  $454 \pm 78$  copulations per pair per clutch ( $N=16$ ) or approximately 13.6 copulations per day. See Table 2 for differences between pairs in copulatory behaviour. Pairs did not differ significantly in their copulatory frequency (Kruskal-Wallis test:  $\chi^2_{15}=24.1$ , NS).

#### Arrival and laying dates

Copulation frequency was not significantly correlated with arrival or laying date (Kendall's  $\tau=-0.05$ ,  $N=255$ , NS and  $\tau=-0.07$ ,  $N=255$ , NS, respectively). Thus, pairs did not differ significantly in copulation frequency even though the difference in arrival and laying dates between pairs was sometimes 3-4 weeks (see Fig. 3).

#### Breeding success

Breeding success was either zero, four or five nestlings per nest. Copulation frequency of pairs did not vary significantly with brood size (Kruskal-Wallis test:  $\chi^2_2=4.1$ , NS).

### Extrapair Fertilizations

We obtained the genetic fingerprints of 21 families (42 parents and 89 offspring) (Fig. 4). The oligonucleotide (GGAT)<sub>4</sub> probe revealed a mean  $\pm$  SD of  $12.2 \pm 2.99$  bands ( $N=131$ ) and few unique bands (Fig. 5). A comparison of the bands of eight unrelated individuals revealed a low background band-sharing coefficient ( $0.131 \pm 0.114$ , range 0-0.33). Thus, the probability of making a false claim of band sharing was  $0.131^{5.80} = 7.58 \times 10^{-6}$  following Bruford et al. (1994). The sexes did not differ substantially in the number of bands scored (males:  $5.48 \pm 2.04$ ,  $N=21$ ; females:  $5.67 \pm 1.49$ ,  $N=21$ ). All nestlings were

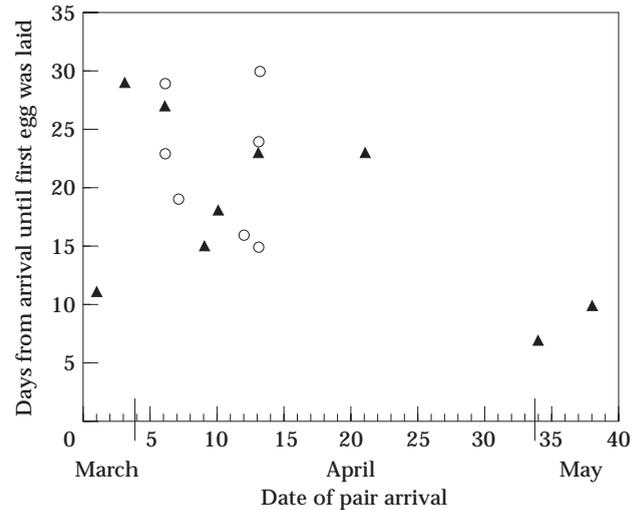


Figure 3. Dates of arrival and laying for 16 pairs of solitary-nesting American kestrels in 1992 (○) and 1993 (▲).

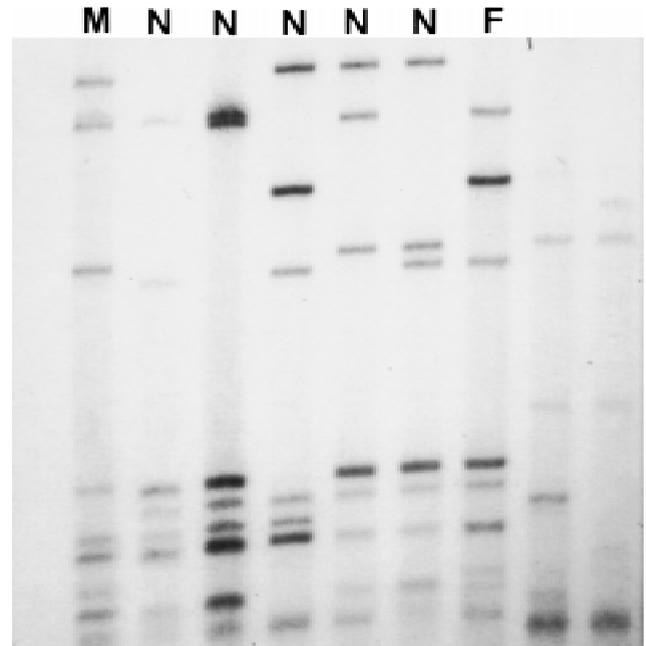


Figure 4. DNA fingerprints of one American kestrel family with no extrapair paternity. Each vertical lane corresponds to one individual. F=female, M=male, N=nestling.

offspring from their putative mother. We found two broods (10% of families, 11.2% of nestlings) in which none of the nestlings was related to the putative father. All neighbouring males were checked by DNA fingerprinting as possible fathers but none was implicated.

## DISCUSSION

### Paternity Assurance

American kestrels copulate more frequently than is needed to fertilize a clutch. Although WPC frequency is

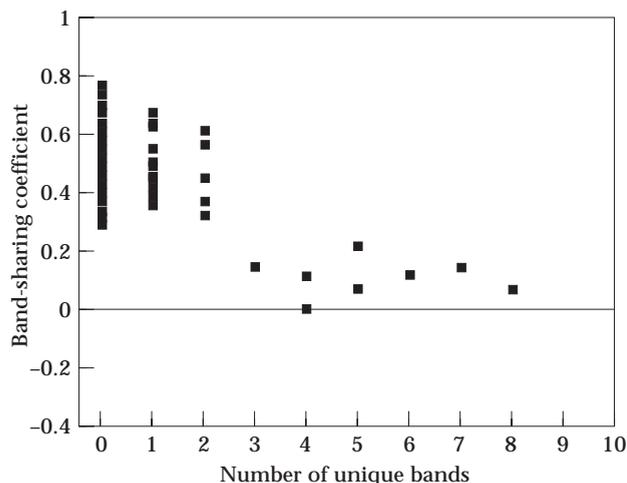


Figure 5. The proportion of shared bands (band-sharing coefficient) versus the number of unique bands found in American kestrel nestlings but not in either parent.

probably the highest of all birds, EPCs were rare (<1%) compared with most birds (5.9%, Birkhead & Møller 1992) which suggests a low intensity of sperm competition. Approximately half of all copulations observed were outside the fertile period which also suggests a secondary role for copulations besides that of paternity assurance. An important assumption of the paternity assurance hypothesis is that 'extra-pair copulations and thus sperm competition are sufficiently frequent to cause a high copulation rate' (Møller 1987). Our data do not appear to support this hypothesis since we found EPC attempts were very low and presumably not frequent enough to lead to a high WPC frequency.

From our results it appears that the low number of EPFs observed is the result of a lack of EPCs and not of a sophisticated anticuckoldry defence system, as concluded by Warkentin et al. (1994) for merlins, *Falco columbarius*. Our results contradict previous studies on other raptors (Robertson 1986; Møller 1987; Birkhead & Lessells 1988; Simmons 1990; Sodhi 1991; Holthuijzen 1992; Koga & Shiraishi 1994) which conclude that sperm competition is high and is the main cause of a high copulation frequency.

Despite our findings, we cannot completely reject the idea that frequent copulations during the fertile period may act to dilute sperm from the few males that gain EPCs. Although EPFs occur infrequently in kestrels (also see Negro et al. 1996), these falcons maintain a very high WPC frequency throughout the laying period compared with other birds. This behaviour may have evolved to enhance the probability of fertilization. However, EPC attempts should occur if high copulation rates are to be explained by sperm competition (Tortosa & Redondo 1992).

Even if we assume that our rate of EPCs is a low estimate, that is, we missed observing some EPCs or more intensive observations would have revealed a higher incidence, three major predictions of the paternity assurance hypothesis were not supported. First, female solicitation

did not increase as the fertile period approached nor did females solicit more copulations in pairs that incurred intrusions. Second, although intrusions occurred, male kestrels did not protect their parental investment more by increasing mate attendance during the fertile period. In addition, males initiated more copulations in the prefertile period. Third, even considering the maximum sperm storage interval of 12 days (Bird & Buckland 1976), withinpair copulations were common outside the fertile period and decreased in frequency during the fertile period. We did not test the insemination window hypothesis (a secondary hypothesis of the paternity assurance hypothesis; Birkhead & Møller 1992), that males preferentially copulate with females immediately after each egg is laid, because it is confusing and has recently been criticized by its former proponents (Birkhead et al. 1996).

Since we knew the maximum length of sperm storage of female kestrels we could distinguish between copulations that could have a role in fertilization and those that could not (Bird & Buckland 1976). We were thus in a good position to test the paternity assurance hypothesis. Previous studies of raptor copulatory behaviour did not make this important distinction. Many species of raptors show unexplained prolonged copulatory periods with an early peak of copulations probably outside the fertile period: lesser kestrel, *Falco naumanni*, 65 days before laying (Negro et al. 1992), European kestrel, *Falco tinnunculus* 20 (Meijer & Schwabl 1989), goshawk, *Accipiter gentilis*, 30–40 (Møller 1987), osprey, *Pandion haliaetus*, 16–20 (Birkhead & Lessells 1988), prairie falcon, *Falco mexicanus*, 27 (Holthuijzen 1992). The paternity assurance hypothesis may not fully explain the copulatory behaviour of these raptors either.

### Extrapair Paternity in Kestrels

The results of our paternity study are similar to four recent reports of low paternity in Eleonora's falcon *F. eleonora* (0%, Swatschek et al. 1993) the merlin (0%, Warkentin et al. 1994), the colonial lesser kestrel (3.4%, Negro et al. 1996) and the European kestrel (5%, Korpimäki et al. 1996). However, our percentage of EPFs is not directly comparable to other birds since the extrapair male achieved exclusive paternity. We found no term to describe a completely cuckolded nest and suggest 'extramale take-over' as opposed to EPF. The one we observed may be due to a mate replacement that we did not observe or we might have caught the wrong male and not identified him correctly. Depending on the time between pair formation and egg laying, females could conceivably arrive on the breeding territory already inseminated (Quay 1989), although this has not yet been documented in raptors. We suspect a mate replacement occurred since, in most cases of EPF in birds, extrapair young represent either a minority or majority of the brood and hardly ever all the young (also see Birkhead 1996). Completely cuckolded nests have also been observed in the European kestrel (Korpimäki et al. 1996) and the lesser kestrel (Negro et al. 1996) as well as other birds (Westneat 1988; Oring et al. 1992; Pinxten

et al. 1993) and are most probably due to rapid mate replacement. More inseminations involve greater sperm precedence and assurance of paternity (Hatch 1987; Birkhead & Møller 1992). Although it is currently unknown if one or several EPCs can fertilize all the eggs in a clutch, physiological evidence suggests not (Birkhead 1996) and for kestrels it is difficult to explain how one EPC may take precedence over more than 10 WPC per day.

### Immediate Material Benefits

The immediate material benefits hypothesis (Tasker & Mills 1981) suggests that females trade copulations (assurances of paternity) with males for benefits such as food, nest materials or protection from other males. Most copulations we observed occurred without food transfers. Several authors have suggested that food transfers are related to copulation in raptors (for review see Carlier & Gallo 1995), but other studies have found no statistically significant relationship between the two (Birkhead & Lessells 1988; Simmons 1990; Negro et al. 1992; Koga & Shiraishi 1994; Green & Krebs 1995). Since many falconiforms differ in the synchrony of food transfers and copulations this discrepancy is understandable. Food transfers may sometimes be associated with copulations and 'feeding of females by males appears to be part of the system of mutual sexual arousal' (Kostina & Panov 1979). Females, however, did not solicit more after food transfers, suggesting that they do not trade food for copulations.

### Female Mate Guarding of Males

The female mate guarding of males hypothesis (Petrie 1992) suggests that females dissuade their males from EPCs by copulating frequently with them. Unlike the paternity assurance hypothesis, the female mate guarding of males hypothesis suggests that females with low-quality males will solicit fewer WPCs. The first two predictions of this hypothesis were upheld, namely, females solicited copulations from pair bonding until egg laying and solicited more copulations than males when there was a risk that their male could mate with other females (i.e. during female intrusions). In general, however, females did not solicit more copulations than males. It appears that the copulatory act is initiated by both sexes and not controlled exclusively by the soliciting female. In addition, all pairs copulated at similar frequencies and all females solicited at a similar rate. Thus, the third prediction, that females with high-quality males will copulate and solicit more copulations than other females, was not upheld, although some paired males may be more attractive than others (i.e. some males incurred more female intrusions and participated in more EPCs).

We did not test a fourth hypothesis of the female mate guarding of males hypothesis, that 'within-pair copulation frequency will be negatively correlated with the male's investment in extra-pair copulations or polygyny'

(Whittingham et al. 1994), since it is tautological (Eens et al. 1995; Whittingham et al. 1995). For example, although males do not appear to need guarding in our population because they hardly ever partake in EPCs this could mean that (1) females guard their males well and therefore suffer low mate loss, or (2) females need not solicit so many copulations to guard their males because males do not need guarding.

Instead, one important result allows us to reject this hypothesis definitively. Namely, females did not solicit most or all copulations, as seen in other birds where this hypothesis may apply (Eens & Pinxten 1995). In our population the female tactic of soliciting copulations to guard their mates may not always work. Even if females would like to guard males and are following a best-of-a-bad-job strategy (Eens et al. 1995), female-female aggression seems a less expensive method to combat female-female competition for mates (Slagsvold & Lifjeld 1994; Whittingham et al. 1995). This is what we observed. The majority of female intruders were physically expelled from the territory by the resident female. Females were often battling for possession of the male or territory (also observed by Bortolotti & Iko 1992). This suggests that extrapair, female-solicited copulations are prevented by female-female aggression, as seen in other birds (Wittenberger & Tilson 1980).

Although we did not quantify the relative roles of males and females in reproduction, it appeared that primary male investment was high enough for females to fight over males. In addition, females were not receptive to EPCs, effectively increasing the male's net gain of behaving parentally and decreasing the possibility of the male deserting (for discussion of these points see Westneat et al. 1990 and Fitch & Shugart 1984). This makes sense since the male provides essential food resources during laying and incubation (Bird 1988) and the female cannot rear nestlings alone in the wild (Village 1990; personal observation). Our observations demonstrate that females fight to obtain this limiting resource. Consequently, male choice may be more important in kestrels at pair bonding than female choice, which has proven difficult to quantify in kestrels (Duncan & Bird 1989; Bortolotti & Iko 1992; Palokangas et al. 1992).

### Mate Assessment

Finally, the mate assessment hypothesis states that individuals may acquire information about mate quality via copulation. There have been few analyses of copulations as courtship communication in birds but much research has been done on mammals (e.g. Bastock 1967) where intromission may be 'courtship communication in the tactile modality' (Dewsbury 1988). Many authors have proposed that copulation may be used to assess the quality of an individual (Fitch & Shugart 1984; Westneat et al. 1990; Hunter et al. 1992; Tortosa & Redondo 1992). Specifically, it has often been suggested that males honestly advertise their aptitude for parental care or fitness by performing energetically costly copulations (see the mate assessment hypothesis, Tortosa & Redondo 1992). In birds where parental care appears equal for both

sexes (as in raptors, Newton 1979), male choice may be just as important as female choice (Gladstone 1979; Andersson 1994). Thus, it is in the interests of both males and females to choose the fittest mate. Therefore we amplified the male assessment hypothesis to include assessment of females by males. The male assessment hypothesis suggests that males honestly advertise their body condition by performing energetically costly copulations and females choose males according to quality. Although this hypothesis, like the paternity assurance hypothesis, suggests that withinpair copulations should be higher in species with extensive male care, it predicts that they should peak at the time of pair formation and decrease 'as early as the male is confident of the female's commitment to lay eggs in his nest' (Tortosa & Redondo 1992).

Four predictions of the mate assessment hypothesis were upheld, namely; withinpair copulations were frequent both outside and within the fertile period, and were initiated equally by both sexes, pairs did not differ significantly in solicitation or copulation frequency, and individuals (intruders) moved away from territories where potential mates did not attend to their solicitations.

Of the four hypotheses we considered, the mate assessment hypothesis best explains our observations. In addition, this hypothesis helps us to evaluate the increase in copulation duration between the prefertile and fertile periods.

According to the paternity assurance hypothesis, the immediate material benefits hypothesis and the female mate guarding of males hypothesis, copulations are equally potent during and outside the fertile period since the male is unaware of the female's fertility status. However, copulations outside and during the fertile period seem to be different. Prefertile period copulations may be called 'courtship copulations' since they are not involved in fertilization. We suggest that early copulations in kestrels may be used as courtship communication of mate quality. As the fertile period approaches, the character of the copulatory act changes to adapt to its primary role as a conduit for fertilization without necessarily losing its secondary role of mate assessment, since an individual's quality may change over time (Hunter et al. 1992). This change in the character of copulation is displayed in the American kestrel by copulations becoming longer as the fertile period approaches, which is also seen in other raptors, for example, bald eagle, *Haliaeetus leucocephalus* (Laszlo & Retfalvi 1965), gyrfalcon, *Falco rusticolus* (Wrege & Cade 1977), peregrine falcon, *Falco peregrinus* (Ratcliffe 1980), and may be a generalized form of courtship communication, similar to that seen in mammals (Dewsbury 1988). In addition, we observed that female kestrels could end copulations (control their duration). This has been observed previously in kestrels (Bishop 1925), peregrine falcons (Gallo et al. 1991) and black kites, *Milvus migrans* (Koga & Shiraishi 1994). We suggest that the female allows copulations to last longer just as the fertile period approaches.

As with previous studies, we assumed that all WPCs and EPCs, in or outside the fertile period, involved the trans-

fer of sperm. We do not know if early copulations involve sperm transfer but, in the American kestrel, sperm is produced 72 days before laying (although early sperm appears more abnormal in shape, Bird & Lagüe 1977). The mate assessment hypothesis does not make assumptions about the cost of WPCs. Theoretically, the cost of one copulation should decrease as the number of copulations increases (Parker 1984). Although no physiological studies have been made, the cost of one copulation/insemination in frequently copulating birds may be very small.

How information is transmitted between mates by copulating is yet to be revealed. In mammals, multiple copulations, with or without ejaculation, affect sperm numbers, facilitate sperm transport, mediate female receptivity and produce neuroendocrine reflexes (Dewsbury 1988). This may occur in birds as well. For example, the copulation patterns in our population are quite similar to changes in androgen levels in captive American kestrels that originated from our study area (Rehder et al. 1988).

## Conclusions

We conclude that sperm competition is low in the American kestrel and that copulatory behaviour is not significantly related to food transfers or female mate guarding of males. Intrasexual competition among males for fertilizations seems low and both sexes avoid extrapair interactions. We suggest that copulations are frequent because they may serve two distinct and important purposes: (1) fertilization (during the fertile period); and (2) mate assessment during the prefertile and fertile periods. We suggest that further research on copulatory behaviour in raptors should consider the reproductive physiology of courtship communication via copulation.

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