Territorial intrusions and copulation patterns in red kites, *Milvus milvus,* in relation to breeding density

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Two main paternity assurance strategies are generally found in birds: mate guarding and frequent copulations. The latter is expected particularly in species such as raptors that cannot guard their mates efficiently because of ecological constraints, such as frequent courtship feeding. I investigated the prelaying behaviour of red kites, in which the males courtship feed. I compared pair behaviour in situations of varying breeding density and simulated male territorial intrusions by presenting decoys. Males' certainty of paternity was likely to decrease with increasing breeding density, because of the proximity of other males and more frequent male territorial intrusions during the presumed fertile period. The percentage of time spent by males within their breeding territory during the prelaying period was positively related to the number of close breeding neighbours, suggesting territory surveillance and mate guarding. The kites copulated frequently and over a long period. Copulation frequency prior to and during laying increased with breeding density, and in isolated pairs in response to simulated male territorial intrusions. The results support the idea of paternity assurance through frequent copulations during the presumed fertile period of the female, and suggest that early copulation activity is related to functions other than fertilization, such as pair bonding or mate assessment.

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Extrapair paternity has been documented in a wide range of bird species, and usually results from extrapair copulations (EPCs; Birkhead & Møller 1992a; Westneat & Sherman 1997). Because it decreases the fitness of the putative parents, selection is expected to favour behaviours that reduce its incidence. Two main paternity guards are generally found in birds: mate guarding and frequent copulations (Birkhead et al. 1987; Møller & Birkhead 1992; Birkhead 1998). The mate-guarding strategy, in which males closely follow their mate during the fertile period, is the commonest and probably the most effective paternity guard (Birkhead & Møller 1992a). The frequent copulation strategy is based on sperm competition (i.e. competition between the ejaculates of different males for the fertilization of a given set of ova; Birkhead & Parker 1997). Males may copulate frequently to try to secure their paternity, as the probability of fertilization by a male is closely proportional to the relative amount of sperm he delivers to the female. Additionally, frequent copulations increase his chance of being the last male to copulate before fertilization, which also gives him a fertilization advantage (Birkhead & Parker 1997; Birkhead 1998). The frequent copulation

strategy is expected particularly in birds that cannot guard their mate efficiently, because of ecological constraints. This is the case in colonially breeding birds, in which at least one partner has to guard the nest site from conspecifics, and in birds with intense courtship feeding, in which the male has to hunt for food for the female, while she stays by the nest (Birkhead et al. 1987; Møller & Birkhead 1992).

Food provisioning by males is found in many raptor species (Newton 1979) and conflicts with mate guarding. Raptors usually have high copulation frequencies and several studies of copulatory behaviour have concluded that sperm competition is the most likely cause (e.g. Robertson 1986; Møller 1987a; Birkhead & Lessells 1988; Simmons 1990; Sodhi 1991; Holthuijzen 1992; Koga & Shiraishi 1994; Korpimäki et al. 1996; Arroyo 1999). However, this has rarely been tested, and some species are known to copulate frequently probably for reasons other than sperm competition, such as pair bonding or mate assessment (see Negro et al. 1992, 1996; Villarroel et al. 1998).

The majority of raptors are territorial and strongly defend their breeding territory, but some species show various degrees of coloniality, or may breed at different densities, depending on food abundance (e.g. Newton 1979; Cramp & Simmons 1980; Korpimäki et al. 1996). A

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high breeding density potentially increases EPC risk (Simmons 1990; Møller & Birkhead 1993; but see Westneat & Sherman 1997). If frequent copulations are related to paternity assurance, males should copulate more frequently when the risk of EPC is greater. This has been investigated empirically by comparing copulation patterns at different densities and looking for an increase in within-pair copulation frequency with local density (Simmons 1990; Korpimäki et al. 1996; Arroyo 1999). Variables other than nest spacing as indicators of EPC risk have rarely been used, and the effects of potentially confounding variables are difficult to evaluate in such comparisons. Territorial intrusions, which usually increase with breeding density, may be a relevant cue for males to evaluate EPC risk and adjust their behaviour. Male territorial intrusions can be simulated with decoy presentations and used to test the paternity assurance behaviour of a given species (Gowaty 1981; Mougeot et al., in press).

In the red kite, prelaying courtship feeding is intense. This species nests both solitarily and in loose assemblages when the food supply is abundant (Cramp & Simmons 1980). I first studied the prelaying behaviour of the red kite, with particular emphasis on territorial intrusions and EPCs in order to evaluate the degree of risk experienced at different breeding densities. My second aim was to assess the paternity assurance strategies of this species, by comparing the behaviour of pairs breeding at different densities. I expected within-pair copulation rate and/or mate guarding to increase with the number of close breeding neighbours and when the female was fertile (prior to and during egg laying). I also tested whether the different patterns arise from individual adjustments of behaviour according to the EPC risk experienced. To do this, I used decoy presentations to simulate territorial intrusions in some isolated pairs. I expected these pairs to adjust their short-term behaviour during the experiments to the level of pairs breeding with close neighbours and experiencing more frequent territorial intrusions. Finally, I also discuss whether frequent copulations serve functions other than fertilization in red kites.

METHODS

Study Area and Species

I studied red kites in the Regino valley (47°30′N, 7°40′E), in northwestern Corsica. This coastal valley, characterized by extensive cattle rearing and a locally abundant rabbit, *Oryctolagus cuniculus*, population, is highly suitable for kites, and holds the main breeding population of the island (Patrimonio 1989; Thibault & Bonaccorsi 1999). The rabbit, introduced at the end of the 1970s, greatly increased in numbers between 1989 and 1998, in concert with the red kite population, which was estimated at 30–35 breeding pairs in 1989 (Patrimonio 1989) and 60–80 breeding pairs in 1996–1998, when I conducted this study. The overall breeding density was high (1.5–2 pairs/km^2 on average) but nest dispersion ranged from dispersed to clumped nests (clumps of 3–12 pairs/km^2), the highest breeding densities usually being

found where rabbits, the main prey of kites, were more numerous (see Viñuela & Veiga 1992 for similar observations on the black kite, *Milvus migrans*). In the study area, pairs usually defend a small breeding territory (an area of ca. 200 m around the nest site). Males regularly leave this territory to forage within the valley, or in the surrounding mountains. The species is socially monogamous, and females are fed almost exclusively by the male from early prelaying until half-way through the chick-rearing period (Cramp & Simmons 1980). Red kites are sedentary in Corsica (Patrimonio 1989; Thibault & Bonaccorsi 1999). The first pairs return and settle on breeding sites in January. Laying occurs between early March and late April (Patrimonio 1989) and fledging from June to late August.

Behavioural Observations

I studied preincubation behaviour of red kites from early February to mid-April in 1996 and 1997, and in March–April 1998. I observed 26 different pairs (eight in 1996, 13 in 1997 and five in 1998) out of the ca. 50 breeding pairs found each year. The pairs chosen had a distinctive plumage feature that allowed me to identify both members. These features were broken flight feathers, advanced moult of primaries or rectrices and unusual colour markings. I regularly drew the plumages of all study birds, as well as those of their close neighbours, to map broken and moulted feathers; constancy in individual plumage characteristics was high throughout the study (from pair settlement until the beginning of incubation). The sexes are identical in plumage, and although females are ca. 5% larger than males (Cramp & Simmons 1980), sexing in the field is not possible from morphology or plumage. However, only females have a solicitation call (personal observation). I therefore first assessed the sex of study kites during copulations.

Observations were made with binoculars and a 20–60 × telescope, from a high point 200–300 m from the nest site, which allowed a good overview of the whole breeding territory. The birds always seemed unconcerned by my presence. During focal observations, I recorded continuously all the following behaviours. (1) Intrusions and interactions with conspecifics: I recorded as an 'intrusion' the entry of a conspecific within the breeding territory, when it was flying up to 50 m high (individuals crossing the territory above this height, for example to forage far from their nest, were not recorded as intruders). All intrusions elicited at least a low-intensity agonistic response from a pair member (territorial calling, agonistic display from a perched pair member, or escorting flights). Additionally, I recorded whether intrusions resulted in 'interactions', that is, in flight aggression by a pair member (chase, dive bombing, talon grasping or mutual cartwheeling; see Cramp & Simmons 1980 for descriptions of behaviours). (2) Copulations: I recorded their occurrence, their duration(s) and their success (i.e. whether cloacal contact was achieved). I am confident that all copulations were recorded during observation periods because (a) the red kite is a large species, and usually copulates on conspicuous perching sites, (b)

copulations were often preceded by a solicitation display and by the female calling, and (c) females spent almost all their time close to the nest, particularly during the critical fertile period. I also recorded (3) prey deliveries by the male; and (4) the time the male and female spent within the breeding territory. I used the number of neighbouring breeding pairs within a 500-m radius around the nest site (corresponding to the average internest distance) as a measure of breeding density; this ranged from 0 to 4 for study pairs.

I made 244 focal observations (385.5 h). Each observation period lasted on average 1.6 h (range 1–2 h), and each study pair was observed for 15 h on average (8.5–36.5 h), with a rotational schedule from dawn to dusk (each pair was sampled once between 0700 and 1100, once between 1100 and 1500, and once between 1600 and 2000 hours on 3 consecutive days, and so on). Pair behaviour was studied until laying was completed. I visited nests at least twice (during incubation and the nestling period). I analysed data from focal observations on the basis of relative date (i.e. day number, relative to day 0, the first egg date). I determined laying onset during observations when the nest contents (eggs) could be checked at a distance, or by backdating from hatching date, which I calculated from chick measurements (I studied the growth of 15 chicks of known hatching date in 1996; unpublished data). I assumed that eggs are laid every 2 days (personal observation). The mean laying date of study pairs did not differ significantly between years (Kruskal–Wallis test: $\chi^2_2 = 4.53$, $P = 0.10$).

The length of the fertile period (i.e. the period when a copulation can lead to the fertilization of the eggs) is poorly known in raptors. It depends on the maximum duration of viable sperm storage, the time between fertilization of an egg and its subsequent deposition and the number of days in which the clutch is completed (Birkhead & Møller 1992b; Birkhead 1998). In most birds, the fertile period starts ca. 10 days before the first egg is fertilized and ends when the final egg of the clutch is fertilized (Birkhead & Møller 1992b). Among raptors, the fertile period duration is precisely known only for the American kestrel, *Falco sparverius,* and it averages 8 days, with a maximum viable sperm storage of 12 days (Bird & Buckland 1976). The exact duration of the female's fertile period is not known for the red kite. However, I considered two prelaying periods on the basis of the study birds' bimodal pattern of copulation rate (see Results): the early prelaying period (days prior to day −12, day 0=laying of the first egg), which included the first peak in copulation frequency, and the late prelaying period (from day −12 until the day before the last egg was laid), which included the second peak. Although determination of laying onset may be imprecise, the fertile period was likely to be included in the late prelaying period, whereas copulations occurring in the early prelaying period (from day −40 to −12) had little chance of fertilization.

Experimental Procedure

I used a red kite decoy to simulate the presence of an intruder within a breeding territory. The plastic decoy was in a resting position, painted as an adult (more than 2 years old; see Cramp & Simmons 1980 for a full plumage description), and was the size of a small kite, to simulate a male rather than a female. I presented the decoy either with a prey (half of a dead rabbit) at its feet, to simulate a male delivering prey, or without prey. The decoy was placed at a controlled distance from the nest site (50–100 m, i.e. within the breeding territory) during the male's absence. Each test included 2 h of focal sampling of behaviour: 1 h without decoy presentation (control) and 1 h with decoy presentation (experiment). I recorded continuously the behaviour of study pairs during controls and experiments, as for focal sampling of behaviour. Once detected, the decoy was often inspected (by close circling) and sometimes attacked. All decoy attacks consisted of a dive that ended ca. 50 cm above the decoy, with the legs extended towards it (the birds never touched the decoy). I thus considered only attack rate (which was calculated as the number of dives after detection; attacks/h) as a measure of the intensity of agonistic response towards the decoy. I conducted 64 experiments on 16 different pairs in 1997 and 1998. Each pair was tested on average four (three to five) times, with at least a 3-day interval between two consecutive tests on a given pair. I had no evidence that habituation or sensitization had occurred from a previous exposure to the decoy.

Statistical Analyses

For statistical analyses, I used SAS 6.11 (SAS 1988). I checked the data for normality before performing parametric tests, and transformed them if necessary. Otherwise, nonparametric procedures were used. All data are expressed as mean ± SD and all statistical tests are two tailed. To determine whether certain behaviours were associated, I looked for correlations between the frequencies of behaviours, taking each focal observation as a unit (see Villarroel et al. 1998 for similar analyses). The range of variation in most behaviour was usually low (for example, none, one or two copulations or prey deliveries were seen per focal observation), so nonparametric correlations were used (Kendall tau correlations). I investigated the effects of nest spacing on the behaviour of study pairs by prelaying period, looking for correlations between the mean behavioural parameters of each pair and the number of close breeding neighbours. I also analysed the effects of decoy presentations on male behaviour by type of experiment (decoy presented with or without prey) and by prelaying period. Some pairs were tested twice with the same type of experiment for a given period. To avoid pseudoreplication, I considered only one test per study pair for the analyses (the first one conducted with a given type of experiment and during a given period). Sample sizes thus included nine different pairs in the early prelaying period (all tested both with the decoy without prey and the decoy with prey) and 13 pairs in the late prelaying period (11 pairs tested both with the decoy alone and the decoy with prey). The average timing of these tests, relative to laying onset was −18.5 ± 5.3 days, $N = 18$, and −4.3 ± 4.4 days, $N = 24$ for the early and late prelaying periods, respectively. This

timing was similar for both types of experiment (decoy with or without prey), for both periods (*t* tests: $t_{16}=0.3$, $P=0.77$ and $t_{22}=1.2$, $P=0.25$ for the early and late prelaying periods, respectively). I used paired-sample tests (Wilcoxon signed-ranks tests) to investigate (1) between-period differences in individual male attack rate (by type of experiment), (2) within-period differences in individual male attack rate towards the decoy presented with or without prey, and (3) differences in territorial intrusion rate and male presence within the territory during experiments and corresponding controls, for each period and each type of experiment separately. Since only one or no copulation was observed during controls or experiments of a given test, I used logistic regressions (CATMOD procedure, maximum likelihood option; SAS 1988) to test for differences in copulation probability between controls and experiments.

RESULTS

Copulations and Associated Behaviours

Timing and frequency of within-pair copulations

Pairs started to copulate ca. 40 days before laying, once established on breeding territories. The mean copulatory pattern, relative to laying onset, was bimodal (Fig. 1a), with a first peak in copulation rate ca. 25 days before laying, and a second, more marked, 3–6 days before laying. The average copulation rate was 0.37 ± 0.10 copulations/h (range 0.24–0.67, $N=16$ pairs) during the early prelaying period and 0.47 ± 0.13 copulations/h (range 0.31–0.75, $N=26$ pairs) during the late prelaying period. For the 16 pairs for which there were estimates for both the early and the late prelaying periods, the mean within-pair copulation rate was significantly higher in the latter period (paired-samples *t* test: $t_{15}=2.15$, $P<0.05$). Assuming 12 h of daylight (the activity period of red kites in February–March), I estimated a mean of 234 ± 30 copulations (range 188–307, $N=16$ pairs) per clutch, from pair settlement until laying completion. Copulation duration averaged 5.4 ± 1.6 s (range 1–9, $N=137$), and did not differ between the early and late prelaying periods (paired-samples *t* test: $t_{15}=0.24$, $P=0.80$). The success of a copulation (i.e. the achievement of cloacal contact) depended on its duration (logistic regression: -2 log likelihood ratio$=17.14$, $\chi^2_1=81.6$, $P<0.0001$) and most copulations (88.8%, $N=137$) were successful.

Extrapair copulations

I observed five extrapair copulations, all in the late prelaying period (days -8, -6, -1, 1 and 3) and while the legitimate male was absent. All but one were successful, and three of them were preceded by an extrapair prey delivery. Two EPCs were by a 'satellite' male, which attended a breeding territory, already occupied by a pair, for ca. 8 days. This male brought nest material several times, and prey twice (traded against EPCs), and was often vigorously attacked by the original male. Two other EPCs involved a female that copulated first with her mate and a few minutes after with a neighbouring male, whose
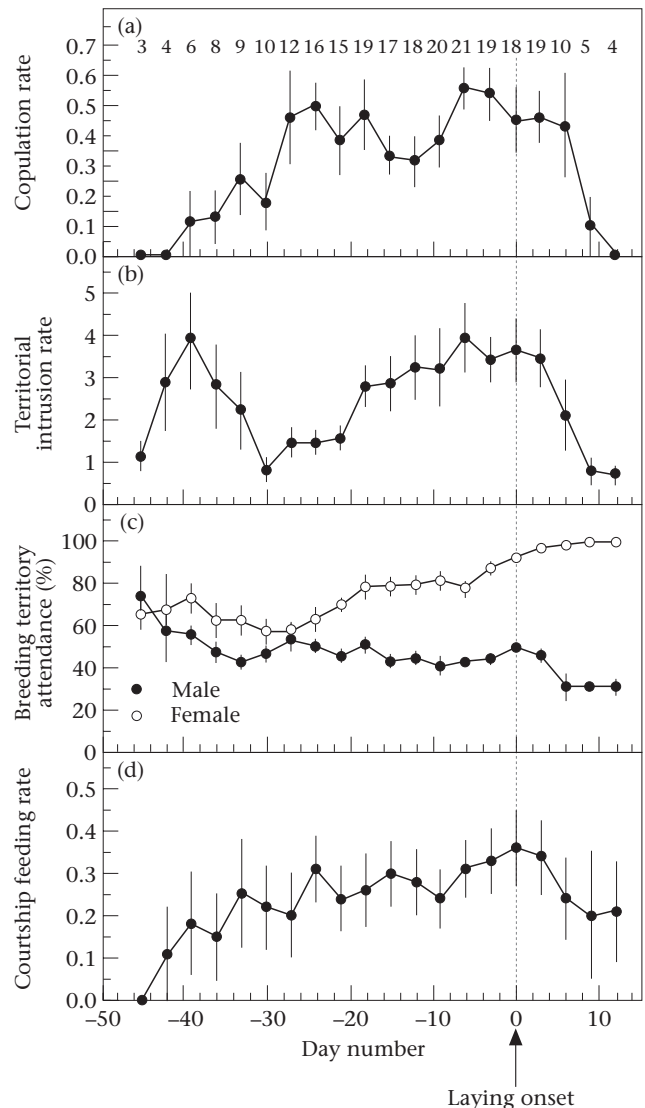

Figure 1. Mean±SE frequency of (a) copulations/h, (b) territorial intrusions/h, (c) male and female breeding territory attendance (percentage of time) and (d) male prey deliveries/h in relation to laying onset. Sample sizes (number of focal observations) are given in (a).

breeding territory overlapped with that of her mate. The other EPC was by a male of unknown origin. Overall, EPCs accounted for 3.5% of all copulations ($N=142$) and concerned four out of the 26 study females (15%), all breeding with close neighbours (more than two breeding pairs within a 500-m radius around the nest site).

Territorial intrusions, territory attendance and courtship feeding

The pattern of territorial intrusion frequency was also bimodal, with a first peak when pairs settled on breeding territories (day -40) and a second in the late prelaying period, around laying time (Fig. 1b). The frequency of territorial intrusions rapidly decreased after laying and remained low during incubation. Territorial intrusions frequently resulted in agonistic interactions (the

Table 1. Associations between the main behaviours of study pairs

	Early prelaying period		Late prelaying period	
Associated behaviours	tau	P	tau	P
Intrusion rate–interaction rate	0.63	0.0001	0.65	0.0001
Intrusion rate–copulation rate	0.02	0.75	0.27	0.001
Intrusion rate–time male present	0.18	0.005	0.19	0.002
Courtship feeding rate–copulation rate	0.21	0.007	0.06	0.41
Time male present–courtship feeding rate	−0.04	0.54	−0.02	0.74

Kendall tau correlations; $N=119$ and 125 focal samplings of behaviour for the early and late prelaying periods, respectively.

frequency of interactions was strongly related to the frequency of territorial intrusions during both the early and the late prelaying periods; Table 1). Most intruders were chased by the male: 59% of territorial contests involved only the male, 16% only the female and 25% the pair ($N=470$ interactions). The sex of the intruder could be assessed in the case of two neighbouring study pairs. In the early prelaying period, intrusions by neighbouring males and females were equally frequent (65% by males, $N=26$; $\chi^2_1=1.9$, NS), but in the late prelaying period, intrusions were more frequently by neighbouring males (83%, $N=59$; $\chi^2_1=21.9$, $P<0.001$) than females.

The time spent by the male within the breeding territory decreased regularly throughout the prelaying period (Fig. 1c; linear regression: $F_{1,242}=9.2$, $P<0.003$). Conversely, females spent increasingly more time within the territory as laying approached (Fig. 1c; $F_{1,242}=86.6$, $P<0.0001$). As male presence decreased, the frequency of prey deliveries to the female regularly increased throughout the prelaying period (Fig. 1d; $F_{1,242}=4.6$, $P=0.033$). However, the time spent by the male within the breeding territory was not related to courtship feeding rate, in either period (Table 1).

Within-pair copulation frequency was positively related to male courtship feeding rate in the early prelaying, but not during the late prelaying period (Table 1). During the early prelaying period, 68% ($N=37$) of the prey deliveries by the male were followed, in the subsequent 30 min, by a successful copulation, against 43% ($N=49$) during the late prelaying period ($\chi^2_1=4.23$, $P<0.05$).

Behavioural Correlates of Nest Spacing

The average frequency of territorial intrusions in each breeding territory increased significantly with the number of neighbours during both the early and late prelaying periods (Fig. 2a, Table 2). Males breeding within groups thus had to face the proximity of other males and more frequent territorial intrusions. Within-pair copulation frequency was not affected by breeding density in the early prelaying period, but increased significantly with the number of close neighbours in the late prelaying period (Fig. 2b, Table 2). Time spent by the male within the breeding territory increased significantly with the number of neighbours during both the early and the late

prelaying periods (Fig. 2c, Table 2). Considering focal observations as units, copulation rate was also positively related to the frequency of territorial intrusions, during the late prelaying period only (Table 1). Similarly, male attendance was positively related to intrusion rates during both periods (Table 1). Nest spacing, because of differences in the number of neighbouring males and in the frequency of territorial intrusions, thus affected male territory attendance and copulation frequency prior to and during egg laying.
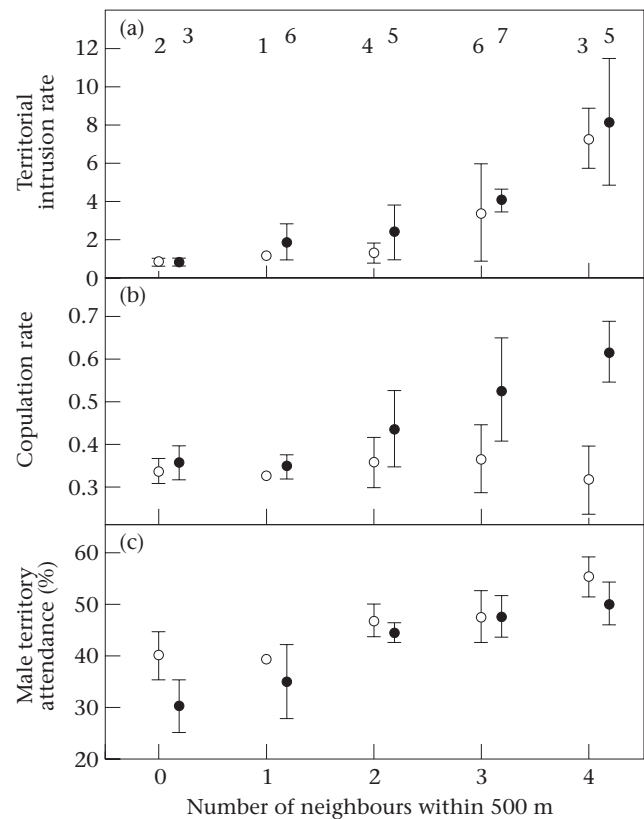

Figure 2. Mean±SE frequency of (a) territorial intrusions/h, (b) copulations/h and (c) male breeding territory attendance (percentage of time), during the early prelaying (○) and late prelaying (●) periods in relation to the number of breeding neighbours within 500 m. The number of pairs sampled in each period is given in (a).

Table 2. Spearman correlations between mean pair behaviour and breeding density (number of breeding neighbours within 500 m of the nest), according to period

	Early prelaying period		Late prelaying period	
	r_S	P	r_S	P
Territorial intrusions/h	0.73	0.0001	0.81	0.0001
Within-pair copulations/h	−0.01	0.96	0.78	0.001
Time male present (%)	0.78	0.0001	0.84	0.0001

$N=16$ and 26 study pairs for the early and late prelaying periods, respectively.

Responses to Simulated Intrusions

The decoy was detected by the male in all experiments. Time to detection was similar during the early (18.9 ± 7.3 min, $N=22$ tests) and late prelaying periods (18.7 ± 9.0 min, $N=34$), but was significantly longer during the incubation period (26.8 ± 5.8 min, $N=8$; one-way ANOVA: $F_{2,61}=3.36$, $P<0.05$). Females never attacked the decoy, in either period. The decoy was attacked by the male more often in the late prelaying period (in 23 of 34 tests) than in the early prelaying period (five of 22 tests; G test: $G_1=9.4$, $P=0.002$), and males never attacked after laying was complete ($N=8$ tests). Individual male attack rate towards the decoys was significantly higher during the late prelaying than during the early prelaying period, in both types of experiment (Fig. 3a; Wilcoxon signed-ranks test: decoy without prey: $|Z|=2.20$, $N=9$ males, $P<0.03$; decoy with prey: $|Z|=2.66$, $N=9$, $P<0.008$). In the early prelaying period, males attacked the decoy presented without or with prey at similar rates (Fig. 3a; $|Z|=0.53$, $N=9$, $P=0.59$), whereas in the late prelaying period, male attack rate was significantly higher when the decoy was presented with prey (Fig. 3a; $|Z|=2.49$, $N=11$, $P<0.02$). The frequency of territorial intrusions, which affected pair behaviour, was not different during controls and experiments, in either period (Table 3). Males spent significantly more time within the breeding territory during decoy presentations than during controls during both prelaying periods (Fig. 3b, Table 3), but not during the incubation period ($|Z|=0.43$, $N=7$, $P=0.67$). Within-pair copulation probability did not differ between controls and experiments in the early prelaying period, in both types of experiment (decoy with or without prey; Fig. 3c, Table 4). In the late prelaying period, copulation probability was significantly higher during decoy presentations than during controls (Fig. 3c), this difference being significant only when the decoy was presented with prey (Table 4).

DISCUSSION

Territorial Intrusions, Breeding Density and EPC Risk

In the red kite, territorial intrusions were frequent and their timing, relative to laying onset, was bimodal: a first
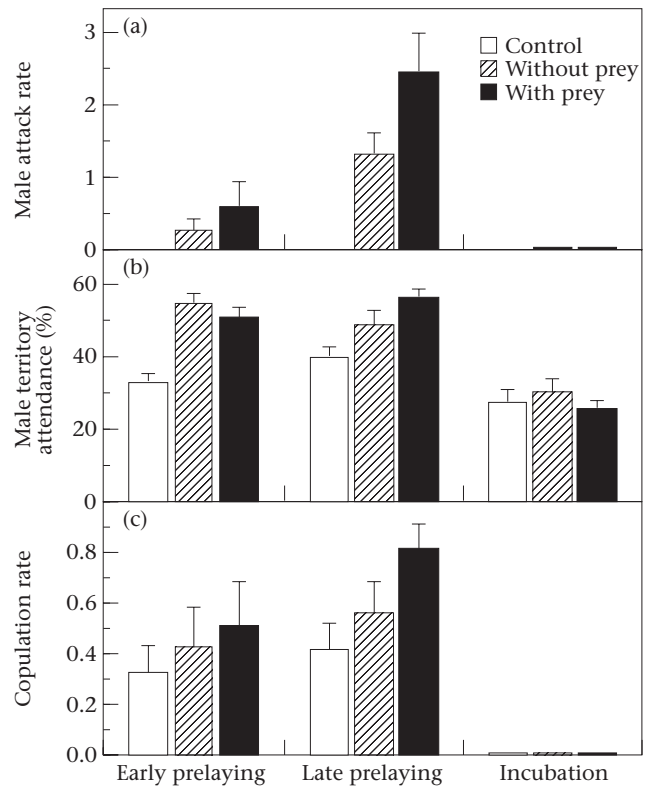

Figure 3. Mean±SE frequency of (a) male attacks/h towards the decoy, (b) male territory attendance (percentage of time) and (c) copulations/h in relation to period. Sample sizes are given in Table 3.

peak occurred early in the prelaying period and a second prior to and during laying. Intrusions by neighbouring breeding birds were by individuals of both sexes early in the prelaying period, but mainly by males in the late prelaying period. This probably also holds true for breeding intruders other than close neighbours, since breeding females spent most of their time at the nest or on a nearby perch prior to and during laying (Fig. 1c). However, I could not tell the sex of nonbreeding intruders, nor the proportion of nonbreeders among the intruders. A high degree of intrasexual competition in males during the prelaying period has been described in the closely related black kite (Koga & Shiraishi 1994), as well as in other raptor species (e.g. Sodhi 1991; Arroyo 1995; Mougeot et al., in press). In my study, the majority of intruders were attacked and chased by the male territory owner rather than by the female, suggesting that territorial intrusions resulting in agonistic interactions were mainly by males (intrasexual competition). Intruders may visit breeding territories for several reasons (establishment of territory boundaries, prospecting for potential vacancies, extrapair copulations), which are expected to produce different seasonal patterns and depend on the sex of intruders (see Møller 1987b). Following these predictions, the first peak in red kite territorial intrusions would be best explained by the 'territory establishment' hypothesis (establishment of territory boundaries by breeding males and females early in the breeding season), and the second, which was probably mainly by males (at

Table 3. Tests for differences in pair behaviour during decoy presentations and controls according to period and experiment (decoy presented with or without prey)

Period	Experiment	Behaviour	Difference control/experiment		
			$\|Z\|$*	P	N
Early prelaying	Decoy	Intrusion rate	0.52	0.60	9
		Time male present	2.67	<0.008	
	Decoy+prey	Intrusion rate	0.63	0.53	9
		Time male present	2.67	<0.008	
Late prelaying	Decoy	Intrusion rate	0.96	0.33	13
		Time male present	3.04	<0.003	
	Decoy+prey	Intrusion rate	0.28	0.78	11
		Time male present	2.93	<0.004	

*Wilcoxon signed-ranks tests; sample size refers to the number of pairs tested.

Table 4. Results of the logistic regressions (CATMOD procedure, maximum likelihood option; SAS 1988) performed by period and by type of experiment (decoy with or without prey) to test for differences in copulation probability between controls and experiments

Period	Experiment	Source	χ^2_1	P
Early prelaying	Decoy	Control/experiment	0.22	0.64
		Likelihood ratio	0.00	1.00
	Decoy+prey	Control/experiment	0.24	0.61
		Likelihood ratio	3.74	0.06
Late prelaying	Decoy	Control/experiment	0.61	0.43
		Likelihood ratio	0.16	0.69
	Decoy+prey	Control/experiment	4.81	<0.03
		Likelihood ratio	1.17	0.28

For sample sizes see Table 3.

least in the case of breeding intruders) and coincided with the female's presumed fertile period, by the 'sperm competition' hypothesis (breeding neighbours or nonbreeders seeking EPCs). The 'nonterritory holder' hypothesis, which predicts an increasing frequency of intrusions until territories are filled, followed by a stable level of intrusions (see Møller 1987b), was not supported by the observations: intrusion frequency decreased rapidly after laying, and was very low during the incubation period. The frequency of red kite intrusions also increased with local breeding density, during both the early and the late prelaying periods, as predicted by both the territory establishment and sperm competition hypotheses (Møller 1987b). Frequent intrusions by males during the fertile period, and particularly by close neighbours, have been documented in a number of bird species (reviewed in Møller 1987b) and support the hypothesis that intruders sought EPCs.

I observed EPCs only during the second peak in copulation frequency (the presumed fertile period), which also corresponded to the second peak in territorial intrusions. All EPCs occurred when the legitimate male was absent and were observed in pairs breeding with three or four close neighbouring pairs, facing frequent territorial intrusions (33% of females, $N=12$, breeding in such situations engaged in an EPC). Since females spent almost all of their time (ca. 90%; Fig. 1c) close to their nest prior to and during laying, opportunities for them to achieve successful EPCs far from their breeding territory

during the fertile period were probably scarce, and in any case were similar for females breeding at different densities. These observations of EPCs, although few, thus supported the idea of an increased EPC risk for red kites breeding at high density compared with solitary pairs, because of the proximity of other males (some EPCs involved neighbouring breeding males) and because of more frequent male territorial intrusions. Similarly, the frequency of EPCs increased with local density in two semicolonial harrier species (Simmons 1990; Arroyo 1999). Opportunities for EPCs are likely to increase with density (Westneat et al. 1990), and EPCs are usually more frequent in colonial than in solitary bird species (Møller & Birkhead 1993; but see also Westneat & Sherman 1997). This may not hold true for all raptor species, however. For instance, similar EPC rates were found in solitary and colonially breeding lesser kestrels, *Falco naumanni* (Tella 1996). In the Eurasian kestrel, *Falco tinnunculus*, EPCs and EPC attempts were observed only in years of high breeding density (and food abundance), but were not markedly more frequent than in a lower-density year (Korpimäki et al. 1996). Such differences between species might depend not only on opportunities, but also on the relative costs and benefits of EPCs for females (Westneat et al. 1990; Petrie & Kempenaers 1998).

In red kites, uncertainty of parentage was thus likely to increase with breeding density because of the proximity and behaviour of other males during the presumed fertile period, and because some females engaged in

EPCs. Frequent male territorial intrusions during the late prelaying period also appeared to be a relevant cue for males to assess EPC risk, and adjust their behaviour accordingly.

Breeding Territory Surveillance

In raptors with intense courtship feeding, mate guarding is usually not expected since it conflicts with providing food for the female, and therefore cannot be efficient: with males looking for food and females staying near the nest site, the chances of maintaining effective mate guarding are reduced (Møller 1987a; Birkhead & Møller 1992a). In the red kite, male presence within the breeding territory was positively related to the frequency of territorial intrusions, and increased with the number of close breeding neighbours, both before and during the presumed fertile period. During the prelaying periods, males regularly visited their territory, and spent considerable time flying over its boundaries. Their behaviour changed markedly during incubation, when they usually left the nest vicinity for longer times. Similarly, males increased their presence in response to simulated territorial intrusions (decoy with or without prey) during the prelaying periods, but not during incubation. They also detected the decoy more quickly in the prelaying periods than in the incubation period. These results thus suggest that males may nevertheless try to survey their breeding territory and mate as much as possible, despite the ecological constraints, in order to detect and repel intruders. Male presence appeared directly related to the frequency of territorial intrusions, and thus probably to territory defence, early in the prelaying period, and to female surveillance when she is fertile. Mate guarding has also been suggested in some other raptor species, despite the courtship feeding strategy (see Birkhead & Lessells 1988; Simmons 1990; Korpimäki et al. 1996).

The lack of relationship between feeding rates and male presence within the territory suggests that red kites managed to mate-guard without compromising their foraging efficiency. Males may survey their territory at a distance, while foraging (see also Simmons 1990; Korpimäki et al. 1996), and I saw male red kites returning from great distances to chase intruders. The highest breeding densities were usually found where their main prey, rabbits, were more abundant. A high prey abundance may allow males to forage closer to their nest sites and increase surveillance. Similarly, in the Eurasian kestrel, the time spent by males in mate guarding increases in years of abundant food and high breeding density (Korpimäki et al. 1996). Nevertheless, male raptors still leave their female unattended for considerable periods. Therefore, increased surveillance appears to be the best of a bad job: it may help to reduce EPC opportunities and evaluate EPC risk, but does not prevent a male from being cuckolded (Kempenaers et al. 1995). Males that cannot guard their mate efficiently should shift their behaviour from guarding to copulating frequently (Birkhead & Møller 1992a).

Paternity Assurance Through Frequent Copulations

In the red kite, mean within-pair copulation frequency during the presumed fertile period increased significantly with the number of close breeding neighbours. Copulation frequency was then also directly related to the frequency of territorial intrusions. These empirical results are consistent with the idea that red kites copulated frequently prior to and during laying (when the risk of extrapair fertilization is greatest) to ensure paternity, because certainty of paternity was likely to decrease with the proximity of other males. Similarly, a positive relationship between copulation frequency and breeding density has been found in three other raptor species: the African marsh harrier, *Circus ranivorus* (Simmons 1990), the Montagu's harrier, *Circus pygargus* (Arroyo 1999), and the Eurasian kestrel (Korpimäki et al. 1996). Such correlations may be affected by potentially confounding variables, such as differences in the quality of individuals breeding at different densities. However, my results suggest that the positive relationship between density and within-pair copulation frequency resulted from individual adjustments to perceived EPC risks, as males of isolated pairs responded to simulated intrusions by copulating more frequently.

As the sexes are not dimorphic in plumage (Cramp & Simmons 1980), the decoy might have been perceived as a male or female intruder. Several factors, however, indicated that it was perceived as an extrapair male, particularly when presented with prey, and as an increased EPC risk during the late prelaying period. First, the temporal variation in the frequency of attacks towards the decoy was best explained by protection of parentage rather than other causes (see Gowaty 1981; Møller 1987b; Wiklund & Village 1992; Mougeot et al., in press): males attacked more frequently during the presumed fertile period than before and never attacked during the incubation period. A response related to offspring protection was therefore unlikely. Agonistic responses related to protection of the breeding territory should either vary little or decrease between the early prelaying and incubation periods (Wiklund & Village 1992), while those related to competition for mates should peak early in the prelaying period, during pair formation, and decrease thereafter. Both territory defence and competition for mates may explain male responses towards the decoy during the early prelaying period, but were unlikely explanations for the higher male attack rate observed during the presumed fertile period. Second, males were more aggressive towards the decoy presented with prey than the one without prey only during the late prelaying period. The decoy with prey was likely to be perceived as a male because females are fed by males, and stay within their breeding territory to eat the prey delivered by males (Cramp & Simmons 1980). Males might have been more aggressive to try to steal the prey. This seems unlikely, however, as the decoy with prey was attacked at a similar rate as the decoy without prey during the early prelaying period, and was never attacked during the incubation period. Moreover, kleptoparasitism was rarely observed on the study area (in

three out of 86 observed prey deliveries; unpublished data). A higher attack rate on the decoy with prey also supported a response related to protection of parentage: a male attending a territory with prey potentially represents a high EPC risk, since EPCs may be traded by females against prey in this species (the decoy with prey was likely to mimic a male adopting a 'sneaker' strategy; Møller 1987b). Finally, males also copulated more frequently in response to decoy presentations when the risk of cuckoldry was greatest: when the decoy was presented with prey and prior to and during laying, when an EPC may result in fertilization.

My observations are thus consistent with and complementary to my empirical results: males breeding solitarily faced few territorial intrusions overall, and accordingly copulated less frequently than those breeding with close neighbours. However, they were able to increase their short-term copulation frequency when they perceived themselves at an increased EPC risk. Similar experimental results have been obtained in the Montagu's harrier (Mougeot et al., in press). The high copulation frequencies prior to and during laying observed in pairs breeding with close neighbours were thus likely to be adjusted to a higher EPC risk in those circumstances. My results thus support the hypothesis that red kites copulate frequently prior to and during laying to secure their genetic paternity ('paternity assurance' hypothesis; Birkhead et al. 1987; Simmons 1990; Birkhead & Møller 1992a).

Other Functions of Frequent Copulations

During the fertile period, females may trade frequent copulations for benefits such as food as an assurance of paternity for their partner ('female immediate benefit' hypothesis; Tasker & Mills 1981), or solicit them to prevent their mate from engaging in EPCs ('female mate guarding of male' hypothesis; Petrie 1992). In my study, mean copulation rate was positively related to the male's feeding rate, but only during the early prelaying period. In some raptor species, the male's prelaying courtship feeding rate may indicate his quality and future investment (e.g. Simmons 1988; Donazar et al. 1992; Green & Krebs 1995). There was, however, no evidence that female red kites traded copulations for prey, or that females mated with good-quality males (with high courtship feeding rates) solicited more copulations than others while they were fertile, as predicted by the female immediate benefits or female mate guarding of male hypotheses. Moreover, my experimental results suggest that frequent copulations during the fertile period were initiated by males, when they perceived themselves at an increased EPC risk. Females may then have more interest in accepting than in rejecting these copulations, since they depend on their mate for food (Korpimäki et al. 1996; Mougeot et al., in press).

Frequent copulations may serve functions other than fertilization, such as pair bonding (Newton 1979) or mate assessment (males may advertise their quality by performing energetically costly copulations; see Tortosa & Redondo 1992; Negro et al. 1996; Villarroel et al. 1998). Many raptor species show prolonged copulatory periods, with an early peak in copulation activity (20–65 days before laying, depending on the species; e.g. Møller 1987a; Negro et al. 1992; Pandolfi et al. 1998; Villarroel et al. 1998; this study), which probably occurs before the female is fertile. Early copulation activity of red kites (between day −40 and −12) was not related to breeding density, nor adjusted during simulated intrusions, and was thus unlikely to be related to fertilization and paternity assurance. These early copulations were probably related to mate assessment (as males with high provisioning rates then copulated more frequently than others) or to pair bond maintenance and reinforcement. Similar results were also found in the Montagu's harrier, in which copulation rate was positively related to the male's feeding rate only during the prefertile period, and was adjusted to breeding density and EPC risk during the fertile period (see Pandolfi et al. 1998; Arroyo 1999; Mougeot et al., in press). These observations suggest that the function of frequent copulations in red kites changed from mate assessment/pair bonding early in the prelaying period, to fertilization/paternity assurance when the female was fertile.

Conclusions

Red kites copulated frequently (234 copulations per clutch on average) and over a long period. My study showed that copulations may have different functions depending on their timing (see also Villarroel et al. 1998). Frequent copulations prior to and during laying appeared to be related to paternity assurance and to be adjusted to the male's uncertainty of paternity, which may be evaluated by the proximity of other males and the frequency of male territorial intrusions. However, an important proportion of prelaying copulations appeared to be related to pair bonding or mate assessment rather than fertilization. The variable 'copulations per clutch' may thus be an indicator of the intensity of sperm competition (e.g. Birkhead & Møller 1992a), mate assessment (e.g. Tortosa & Redondo 1992; Villarroel et al. 1998), or both. This study thus emphasizes the need to test predictions associated with the expected functions of copulations, and I suggest that male decoy presentations provide a useful tool for testing paternity assurance behaviour in other bird species.

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