

# Decoy presentations as a means to manipulate the risk of extrapair copulation: an experimental study in a semicolonial raptor, the Montagu's harrier (*Circus pygargus*)

François Mougeot, Beatriz E. Arroyo, and Vincent Bretagnolle

Centre d'Etudes Biologiques de Chizé, Centre National de la Recherche Scientifique, F-79360 Beauvoir sur Niort, France

Mate guarding and frequent copulations are two alternative paternity assurance strategies found in birds. In species with intense courtship feeding, like raptors, the "frequent copulation" strategy is expected because male food provisioning conflicts with mate guarding. We evaluated experimentally the paternity assurance behavior of a semicolonial raptor, the Montagu's harrier *Circus pygargus*, using decoy presentations to simulate territorial intrusions. Breeding pairs were exposed to male and female decoys at different periods during the female's reproductive cycle. Agonistic responses to decoys were intra-sexual, and the timing and intensity of male attacks toward male decoys supported responses related to the risk of extrapair copulation (EPC): Male aggression peaked during the presumed fertile period and almost disappeared after clutch completion. During the fertile period, copulation rate was significantly higher, and copulations lasted longer, during male decoy presentations than during controls. Males also spent more time close to the female during male decoy presentations compared to controls, both during the early prelaying and fertile periods, but not during incubation. In the fertile period, males also increased presence time close to the female in the hour following the removal of the male decoy. Conversely, female decoy presentations had no significant effect on copulatory behavior or male presence time. These results showed that the risk of EPC can be experimentally manipulated by the means of decoy presentations, simulating male territorial intrusions, and that male Montagu's harriers increase their short-term copulation frequency and female surveillance when they perceive themselves at an increased EPC risk. *Key words:* *Circus pygargus*, copulation, experimental manipulation, mate guarding, sperm competition. [*Behav Ecol* 12:1–7 (2001)]

Cuckoldry has been documented in a wide range of bird species, and usually results from extrapair copulations (EPCs; Birkhead and Møller, 1992; Westneat and Sherman, 1997). As cuckoldry decreases fitness of putative parents, selection is expected to favor mechanisms that reduce its incidence (Birkhead and Møller, 1992). Two main alternative paternity assurance strategies have been so far described: mate guarding and frequent copulations. Mate guarding is the commonest strategy, consisting of a close monitoring of the female during the fertile period. The frequent copulations strategy ("Paternity Assurance" hypothesis; Birkhead et al., 1987; Møller and Birkhead, 1992; Simmons, 1990) is based on sperm competition mechanisms (see Birkhead and Parker, 1997), and is particularly expected in birds that cannot guard their mates due to ecological constraints (like in species with intense courtship feeding or in colonially breeding birds; Birkhead and Møller, 1992). However, high within-pair copulation frequencies, even in nonguarding species, may not always be an indication of sperm competition, as copulations may also serve functions other than fertilization, like pair bonding or mate assessment (e.g., Tortosa and Redondo, 1992; Villarroel et al., 1998). One way of testing whether copulation frequency in a given species is related to paternity assurance has been to look for differences in copulation rate in situations of varying EPC risk, like breeding density (e.g., Arroyo, 1999; Møller and Birkhead, 1993; Simmons, 1990; but see also Westneat

and Sherman, 1997). However, intraspecific studies of the relationship between copulation rate and density should control for potentially confounding variables. For instance, the risk of EPC may vary between years according to breeding density, but may also differ according to individual quality (e.g., Kempenaers et al., 1992; Møller, 1998; Smith, 1988; Wetton et al., 1995), and individuals may choose not to breed close to others, depending on their quality. For a given species, experimental manipulations may help to elucidate whether a given behavior, like increased copulation frequency or mate surveillance, appears as an individual response to a perceived EPC risk. Experimental manipulations of individual EPC risk are rare; this has been done only in passerines, by means of temporary male removals (e.g., Lifjeld et al., 1997) or manipulation of male phenotype (e.g., Johnsen et al., 1998), which is not feasible in all species. In this article, we investigated another method to experimentally increase the risk of EPC and assess the paternity assurance behaviors of a raptor species.

In raptors, males invest heavily in reproduction as they provide most of the food for the female and the nestlings (Newton, 1979). Cuckoldry therefore potentially represents a high cost. Most species perform prelaying courtship feeding, which conflicts with mate guarding, and copulate frequently. Raptors are territorial, but some species are colonial (Del Hoyo et al., 1994; Newton, 1979), a situation that may place males at a higher EPC risk (e.g., Arroyo, 1999; Simmons, 1990). The Montagu's harrier *Circus pygargus* is a semicolonial raptor with high male parental investment. The species is socially monogamous, but EPCs have been observed relatively frequently (ca. 6% of all copulations) and only in colonial situations (Arroyo, 1999). Moreover, within-pair copulation fre-

Address correspondence to François Mougeot. E-mail: frm@cch.ac.uk.

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quency during the laying period increased as the spacing between the nests used by breeding pairs decreased, suggesting that copulation frequency is related to EPC risk (Arroyo, 1999). In this study, we used decoy presentations to simulate territorial intrusions and manipulate experimentally the risk of EPC in Montagu's harriers. The sperm competition hypothesis predicts that male territorial intrusions should peak when the female is fertile, when EPCs can result in extra-pair fertilizations (EPFs; Møller, 1987a). We set up an experimental design according to this prediction: we presented pairs with male and female decoys at different periods during the female's reproductive cycle and expected male decoys presented during the fertile period to be perceived as an increased EPC risk. This prediction was confirmed by the timing and intensity of male agonistic responses. We then used this experimental manipulation to investigate how males responded to an increased EPC risk and precise the paternity assurance behaviors (mate guarding versus frequent copulations) exhibited by the species.

## METHODS

### Study species

The study was carried out in 1997–1998, in three 200–300 km<sup>2</sup> study areas located in western France: (1) Marais de Rochefort (45°57' N, 0°55' W); (2) south of Deux Sèvres Department (46°11' N, 0°28' W), and (3) Baie de l'Aiguillon (46°24' N, 1°24' W). The populations of Montagu's harriers in these three areas have been monitored for four to 10 years, and each year all nests were located, and their breeding parameters monitored (see Arroyo et al., 1998 for more details).

Female Montagu's harriers entirely rely on the food provisioned by the male from the early prelaying until at least half of the chick rearing period, and males contribute overall 80% of the food for the nestlings from hatching until independence (Arroyo, 1995). Male parental investment is thus high and EPF potentially represent an important fitness cost. Montagu's harriers nest solitary or in loose colonies (up to 27 pairs within 300 ha in our study areas; Krogulec and Leroux, 1993) and do not defend territories with fixed boundaries around the nest. Foraging usually takes place away from the nesting areas, up to 7 km or even more (Salamolard, 1997). For simplicity, we define as "breeding territory" the area around the nest site (ca. 50–150 m radius) where the female spends most of the time between pair formation and laying. Mate choice takes place at arrival from the winter quarters. The species is socially monogamous, but mate fidelity between seasons is very low (<14%: Leroux and Bretagnolle, unpublished data), and rare cases of polygyny and polyandry have been reported (Cramp and Simmons, 1980; Arroyo, 1996). Montagu's harriers copulate at a low rate compared to other raptors (28–45 copulations per clutch), but EPCs occur relatively frequently compared to other raptor species (6% of copulations,  $n = 141$ ) and in colonial situations (Arroyo, 1999). Given the high male parental investment, the semicolonial breeding and the occurrence of EPCs, the Montagu's harrier is potentially a good model to study paternity assurance behaviors.

### Experimental procedure

We used Montagu's harrier plastic decoys to simulate territorial intrusions. Pairs were presented with a male or a female decoy (the sexes are highly dichromatic; Cramp and Simmons, 1980). Three experimental situations were tested: Presentation of (1) female decoy; (2) male decoy with a prey (a dead mouse) at the feet, to simulate a male delivering a prey; or (3) male decoy without prey. Each test consisted of 2 h of

continuous focal sampling of behavior: 1 h with presentation of a decoy (experiment) preceded or followed, randomly, by 1 h without decoy (control). By comparing male behavior during controls preceding or following experiments, we may evaluate whether a perceived EPC risk still affects male behavior once the decoy is removed (for instance, if female surveillance persists after the territorial intrusion). The decoy was presented on a pole and was always placed when the male was absent. In order to minimize disturbance, the decoy was placed and removed quickly (in less than 1 min). The observer was covered with a camouflage net while placing the decoy if the female was present, and while removing the decoy. The birds never alarmed while the decoy was placed or removed, but did so during nest visits, so we believe that disturbance due to the observer was negligible. The distance between decoy and nest site (25 to 100 m) was noted for each test. Observations were then made from a hide or from a car. During experiments we recorded: (1) detection time by the male, recorded when the male flew within a 50 m radius from the decoy, and approached it (either to inspect it, by close circling, or to attack it); (2) male and female attack rate towards the decoy (in attacks h<sup>-1</sup>, time being counted from detection). During both controls and experiments, we also recorded (3) within-pair copulations, their duration (in s) and their success (i.e., whether the male succeeded or not in lowering its tail and achieving cloacal contact); (4) time spent by the male within the breeding territory, and thus close to the female; and (5) male display rate (display h<sup>-1</sup>, time being counted from detection).

A total of 93 tests were carried out on 45 different pairs. These were selected from the 50–80 nests found each year, based on the presence of recognizable individuals and the ease of conducting the experiments (visibility, access). Study pairs included 18 (39%) wing-tagged males and 13 (28.3%) wing-tagged females. Additionally, 15 males and 16 females had particular plumage features that allowed individual identification (double black bar on wing, melanistic or dark plumage, advanced moult, broken feathers, first-year birds). The remaining tests were conducted on isolated pairs (without neighboring pairs within 2 km). Nests were visited once during the incubation to check clutch size, and later in the season to measure and band the chicks. Some nests were visited during laying, providing exact laying dates: Eggs are laid on average each 2 days (1.5 to 3 days; Cramp and Simmons, 1980) and are blue, instead of white, for one day after laying (Balfour, 1962; Simmons, 1994). Otherwise, laying onset was determined backdating from hatching date (see Arroyo et al., 1998).

The onset of the female's fertile period depends on the length of time that viable sperm can be stored by females (Birkhead and Møller, 1992). Viable sperm storage duration is not known for Montagu's harrier, but usually last 6–10 days in birds (e.g., Birkhead and Møller, 1992). In Montagu's harrier, within-pair copulation rate peaks during the week preceding egg laying (Arroyo, 1999, unpublished data; Pandolfi et al., 1998), indicating a peak in female's receptivity to copulations. Moreover, EPC attempts and successful EPCs were observed only during the week before laying and during laying (Arroyo, 1999, unpublished data). These observations suggest that female Montagu's Harrier are fertile the week before laying. For the analyses, we therefore classified tests *a posteriori* into three periods relative to laying onset (day zero): (1) the days before -6 (from day -15 to -7), hereafter referred as to the early prelaying period; females might have been fertile during part of this period, but copulations occurring before day -6 probably had little chance to result in fertilization; (2) the days from day -6 until the day before the last egg was laid (clutch size of study pairs ranged from four to six eggs),

hereafter referred as to the fertile period; and (3) the incubation period (from the day the last egg was laid until hatching).

### Statistical analyses

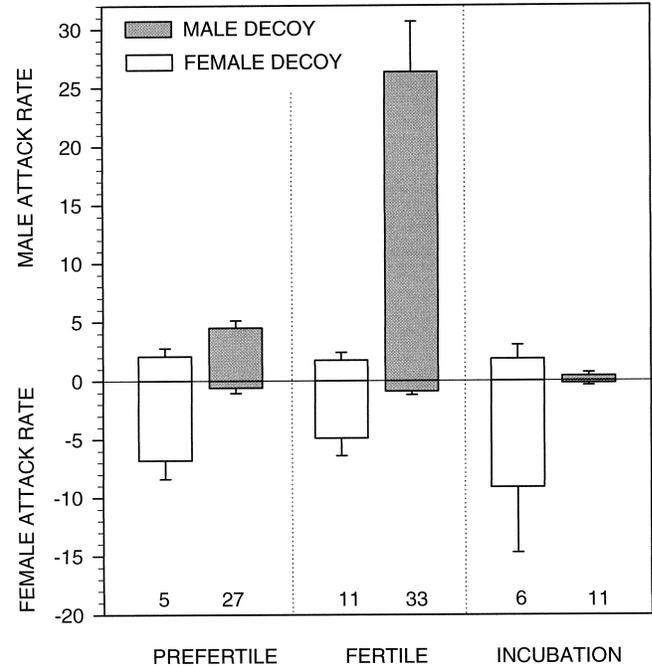
Statistical analyses were performed on SAS 6.03 (SAS, 1988). Data were checked for normality before performing parametric tests, transformed if necessary and, if still non-normally distributed, nonparametric statistics were used. We used ANCOVA analyses to assess the effects of period, distance from the nest and presence or not of prey on attack rate towards the decoys. For these analyses, attack rate was log-transformed, so that it fitted a normal distribution and its variance was homogeneous (Bartlett's test for homogeneity of variances,  $p > .05$ ). Male behavior (presence time, displaying rate) was investigated by comparing experiments and their corresponding control periods, using paired-sample tests. None or one copulation was usually observed per control or experiment, the only exception being three consecutive copulations (two unsuccessful followed by a successful one) during a male decoy presentation in the fertile period. We transformed copulation frequency into a binomial variable (occurrence versus absence), and used logistic regressions (Catmod procedure; SAS, 1988) to assess the effect of decoy presentations on copulation probability. Each pair was tested on average twice (range one to four), but only once with the same decoy for a given period. As the effects of decoy presentations on presence time, display rate and copulation probability were analyzed considering each period and decoy (male versus female) separately, there was no pseudoreplication effect. However, it could affect our analyses of detection time and attack rates, for which data from all periods were pooled. We then analyzed the data (1) using all tests (71 male and 22 female decoy presentations) and (2) using only the first test conducted on each pair with each decoy (42 male and 18 female decoy presentations). Both analyses gave the same results with regard to significance levels, so we present here the results with the complete data set ( $n = 93$ ).

## RESULTS

### Decoy detection and attacks

The sex of the decoy had no effect on detection time by males (One-way ANOVA,  $F_{1,91} = 1.43$ ,  $p = .24$ ), nor did the distance between decoy and nest site (Linear regression,  $F_{1,91} = 1.16$ ;  $p = .25$ ). However, time to detection by males depended on period ( $F_{2,90} = 4.01$ ,  $p = .021$ ): it did not significantly differ between the early prelaying and fertile periods ( $16.3 \pm 10.0$  min,  $n = 32$ ; and  $18.6 \pm 10.5$  min,  $n = 44$ , respectively), but was significantly longer during the incubation period ( $27.4 \pm 16.7$  min,  $n = 17$ ; Tukey tests,  $p < .05$ ) when males visits were less frequent. Once detected, the decoy was usually attacked (83% of tests) by either the male, the female, or both. Males overall attacked male decoys significantly more frequently than their mates (Paired-samples  $t$  test:  $t_{70} = 5.70$ ,  $p < .0001$ ); this difference was significant during the early prelaying (Paired  $t$  test:  $t_{26} = 4.83$ ,  $p < .001$ ) and fertile periods ( $t_{32} = 6.09$ ,  $p < .0001$ ), but not during incubation period ( $t_{10} = 0.73$ ,  $p = .48$ ; Figure 1). The female decoy was overall attacked by females significantly more than by their mates ( $t_{21} = 2.60$ ,  $p = .017$ ; Figure 1). Intersexual attacks were thus rare and agonistic behavior towards decoys was mainly intrasexual.

The average distance between decoy and nest site did not differ significantly between periods, whatever the decoy (One-way ANOVA: male decoy:  $F_{2,68} = 0.59$ ,  $p = .56$ ; female decoy:  $F_{2,19} = 0.11$ ,  $p = .89$ ). Male attack rate towards male decoys



**Figure 1**

Male and female attack rate (dives·h<sup>-1</sup>; mean  $\pm$  SE) towards male and female decoys in each of the study periods. Sample sizes (number of tests) are given below the histograms.

was significantly affected by the distance separating decoy and nest site, by the period the test was conducted and by their interaction, with no effect of adding a prey to the decoy (GLM; Period:  $F_{2,59} = 19.5$ ,  $p < .0001$ ; Distance, regressor:  $F_{1,59} = 3.69$ ,  $p = .06$ ; Prey:  $F_{1,59} = 0.62$ ,  $p = .43$ ; Period\*Distance:  $F_{2,59} = 10.13$ ,  $p < .001$ ; all other interactions not significant). Males attacked the male decoy significantly more during the fertile period than during the early prelaying period, whereas they seldom attacked during the incubation period (Figure 1). Attack rate increased with decreasing distance between decoy and nest-site, although only during the fertile period (Figure 2a).

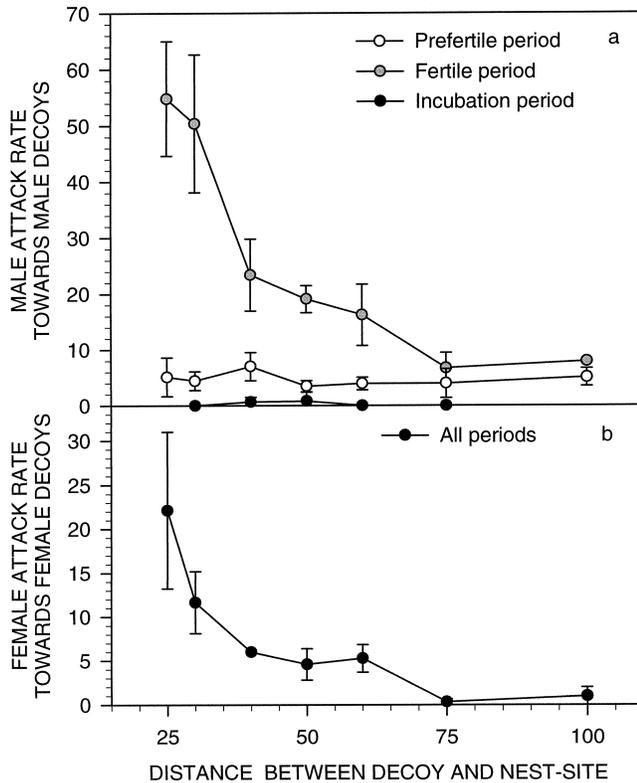
In females, attack rate towards the female decoy did not differ significantly between periods (ANCOVA;  $F_{2,16} = 0.88$ ,  $p = .43$ ; Figure 1), but was affected by distance ( $F_{1,16} = 11.00$ ,  $p = .004$ , Figure 2b), the interaction being not significant ( $F_{2,16} = 1.07$ ,  $p = .37$ ).

### Effects of decoy presentations on male display rate

During the early prelaying period, male aerial display rate was not significantly different during male decoy presentations ( $0.67 \pm 0.84$  display·h<sup>-1</sup>) and corresponding controls ( $0.41 \pm 1.21$  displays·h<sup>-1</sup>; Wilcox Matched-pairs Signed-rank test:  $|Z| = 1.19$ ,  $n = 27$ ,  $p = .23$ ). A significant difference was however found during the fertile period (experiments:  $1.22 \pm 1.51$ ; controls:  $0.27 \pm 0.84$  displays·h<sup>-1</sup>,  $n = 33$ ;  $|Z| = 3.50$ ,  $p < .001$ ). Male display rate during experiments was not significantly different when the male decoy was presented with or without a prey, whatever the period (Mann-Whitney U test; early prelaying period:  $U = 79.5$ ,  $p = .58$ ,  $n = 27$ ; fertile period:  $U = 132$ ,  $p = .93$ ,  $n = 33$ ). A female decoy presentation had no significant effect on male display rate, whatever the period considered (early prelaying period:  $|Z| = 0.80$ ,  $n = 5$ ,  $p = .43$ ; fertile period:  $|Z| = 1.34$ ,  $n = 11$ ,  $p = .18$ ).

### Effect of decoys on copulatory behavior

Copulation probability was not significantly different during controls and female decoy presentations, whatever the period,



**Figure 2**  
Attack rate (dives·h<sup>-1</sup>; mean  $\pm$  SE) of (a) males towards male decoys and (b) females towards female decoys according to distance between decoy and nest site.

nor was it during controls and male decoy presentations during the early prelaying period (Table 1). Conversely, copulation probability was significantly affected by the presence of a male decoy during the fertile period, being significantly higher during experiments than during controls (Table 1, Figure 3). Adding a prey to the male decoy had no significant effect (Table 1) and copulation probability was not different during the controls following or preceding male decoy presentations (Mann-Whitney  $U$  test: early prelaying period:  $U = 79.5$ ,  $p = .61$ ; fertile period:  $U = 120$ ,  $p = .60$ ).

The success of a copulation depended on its duration (Logistic regression:  $\chi^2 = 25.91$ ,  $df = 1$ ,  $p < .0001$ ): all copulations lasting  $\leq 2$  s were unsuccessful, and all copulations lasting  $\geq 5$  s were successful. During the early prelaying period, the mean duration of copulations was not significantly different between male decoy presentations ( $4.5 \pm 2.1$  s,  $n = 6$ ) and controls ( $4.0 \pm 1.0$  s,  $n = 5$ ; Mann-Whitney  $U$  test:  $U = 11$ ,  $p = .59$ ). Copulation success was also similar during controls and experiments (one out of five and one out of six unsuccessful copulations respectively; Fisher's exact test:  $p = .81$ ). During the fertile period, copulations lasted significantly longer during male decoy presentations ( $5.7 \pm 0.9$  s,  $n = 18$ ) than during controls ( $4.1 \pm 0.7$  s,  $n = 9$ ;  $U = 14$ ,  $p = .002$ ). However, similar proportions of unsuccessful versus successful copulations were observed during controls and male decoy presentations (one out of nine and two out of 18 respectively; Fisher's exact test:  $p = .75$ ). Mean copulation duration during experiments was not significantly different when the male decoy was presented with prey ( $5.5 \pm 1.1$  s,  $n = 10$ ) or without prey ( $6.0 \pm 0.8$  s,  $n = 8$ ;  $U = 29$ ,  $p = .36$ ).

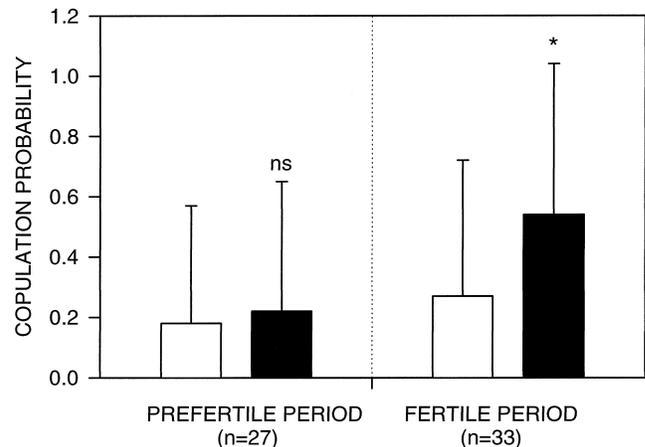
**Table 1**  
Results of logistic regressions conducted by period

Period	Decoy	Model	Source	df	$\chi^2$	$p$ -value
Early prelaying	Female	CE	CE	1	0.00	1.00
			Residuals	1	9.64	.0019
Early prelaying	Male	CE Prey	CE	1	0.14	.71
			Prey	1	1.19	.27
			CE*Prey	1	0.74	.39
			Residuals	1	19.97	.0001
Fertile	Female	CE	CE	1	0.39	.53
Fertile	Male	CE Prey	CE	1	6.08	.0137
			Prey	1	0.07	.79
Fertile	Female	CE	CE	1	8.46	.0036
			Residuals	1	1.23	.27
			Prey	1	1.83	.18
			Residuals	1	5.87	.0154
Fertile	Male	CE	CE	1	5.87	.0154
			Residuals	1	1.68	.19

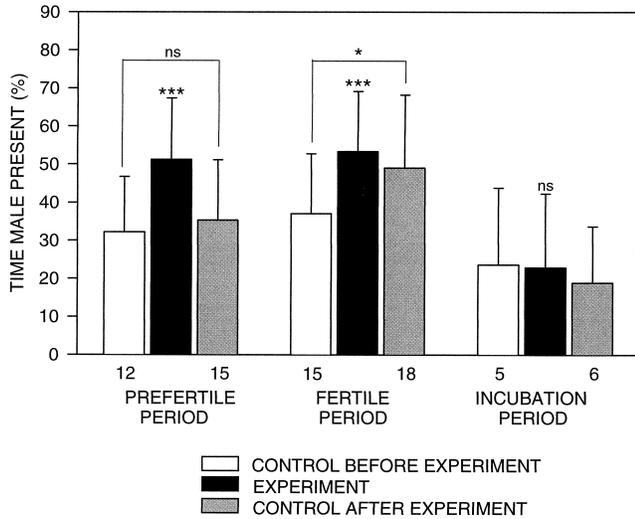
Logistic regressions were conducted by period using Catmod procedure, Weighted Least Squares option (SAS, 1988) to explain copulation probability (zero versus one per h) with the factors CE (control or experiment), Prey (presence or absence of a prey with the decoy), and their interaction in the case of male decoy presentations, and with the factor CE in the case of female decoy presentations.

#### Effect of decoys on male presence time

Males spent more time within the breeding territory during male decoy presentations than controls at the early prelaying (Wilcox Matched-pairs Signed-rank test:  $|Z| = 3.57$ ,  $p = .004$ ,  $n = 27$ ) and fertile periods ( $|Z| = 2.74$ ,  $p = .006$ ,  $n = 33$ ), but no significant difference was found during the incubation period ( $|Z| = 0.30$ ,  $p = .76$ ,  $n = 11$ ). During the fertile period, male presence time during controls was significantly longer when the control was carried out after the test (male decoy presentations) than when the control was before the test (Figure 4, Mann-Whitney  $U$  test:  $U = 79.5$ ,  $p < .041$ ,  $n = 33$ ). No such difference was found during the early prelaying period ( $U = 80$ ,  $p = .65$ ,  $n = 27$ ). The increase in male presence time was not significantly different when the male decoy was presented with or without a prey, whatever the period (early prelaying period: respectively  $+18.1 \pm 20.0\%$ ,  $n = 12$ , and  $+16.0 \pm 18.9\%$ ,  $n = 15$ , Mann-Whitney  $U$  test:  $U = 87.0$ ,  $p = .90$ ; fertile period: respectively  $+9.6 \pm 23.8\%$ ,  $n = 16$  and



**Figure 3**  
Copulation frequency (copulations·h<sup>-1</sup>; mean  $\pm$  SD) during controls (white bars) and male decoy experiments (black bars) during the early prelaying and fertile periods.



**Figure 4**

Time spent by male (in %; mean  $\pm$  SD) close to the female during controls and male decoy presentations in each of the study periods. Sample sizes are given below histograms. Note that controls following or preceding experiments have been grouped. Statistical tests refer to differences between experiments and their corresponding controls (see text).

+6.9  $\pm$  26.7%,  $n = 17$ ,  $U = 129.5$ ,  $p = .82$ ). A female decoy presentation had no significant effect on male presence time, whatever the period considered (early prelaying period:  $|Z| = 0.54$ ,  $p = .59$ ,  $n = 5$ ; fertile period:  $|Z| = 0.09$ ,  $p = .93$ ,  $n = 11$ ; incubation period:  $|Z| = 0.94$ ,  $p = .35$ ,  $n = 6$ ).

## DISCUSSION

### Use of decoys as a tool for manipulating EPC risk

Birds can be easily lured by the means of decoys or stuffed animals, a method already used to study territorial (e.g., Gowaty, 1981; Wiklund and Village, 1992) or anti-predator behavior (e.g., Dale et al., 1996; Wiklund, 1990). In this study, we used decoy presentations to simulate territorial intrusions and manipulate EPC risk. We first evaluate whether the decoy was perceived as a conspecific. This was likely because: (1) agonistic responses of Montagu's harriers towards decoys were intrasexual; (2) males increased displaying rate in the presence of the decoy; (3) some females solicited male decoys with prey; these three types of responses are unlikely in interspecific contexts; (4) the same decoy painted as a carrion crow *Corvus corone* (a local predator of harrier eggs), was attacked nine times more intensively during the incubation period than when painted as a conspecific and placed at the same distance from the nest (Arroyo, Mougeot and Bretagnolle, unpublished data). We therefore consider that Montagu's harrier perceived the decoys as conspecific intruders.

Second we evaluate whether male decoys were perceived as an increased EPC risk. Agonistic responses supported intrasexual competition (see also Wiklund and Village, 1992 for similar results in the Eurasian kestrel *Falco tinnunculus*). Intrasexual competition in males could result from either protection of nest sites or food resources, competition for mates or paternity assurance (Gowaty, 1981; Møller, 1987a; Wiklund and Village, 1992). The Montagu's harrier is semicolonial, and typically does not defend food resources associated with the nest site (Salamolard, 1997). If responses were related to nest site defense, the intensity of aggression would either vary little over periods or decrease throughout prelaying (Wiklund

and Village, 1992). Male agonistic responses related to competition for mates should peak early in the prelaying period, when mate choice takes place or mate changes may occur. Neither of these patterns was observed in male Montagu's harrier responses. Moreover, in response to competition for mates, we would have expected an effect of decoys on male displays in the early prelaying period rather than during the fertile period. Aerial displays probably have agonistic as well as sexual functions (Arroyo, 1995), and increased displaying rate during the fertile period may therefore be another agonistic response to male decoy presentations.

Overall, temporal variation in the intensity of male agonistic behavior (attacks, displays) best supported the hypothesis that male decoys were perceived by males as an increased EPC risk: Intrasexual aggression was low in the early prelaying period, peaked during the fertile period (when EPCs occurred and when the risk of EPF is probably the greatest, see below), and almost disappeared after laying was completed. The fact that a distance effect in male attack rate was only found during the fertile period also suggests that males responded to EPC risk, rather than territorially: The distance between decoy and nest site is then equivalent to the distance between decoy and female, which spends increasing time at nest. Similarly, in the Eurasian kestrel, the distance over which males responded with overt aggression in intrasexual contest decreased after clutch completion (Wiklund and Village, 1992). In other territorial birds, the size of the defended area also varies in relation to paternity defense (e.g., barn swallows *Hirundo rustica* and Yellowhammers *Emberiza citrinella*; Møller, 1990).

The lack of intersexual aggression also supported the hypothesis that intruding males represent an EPC risk: Most females (68%,  $n = 38$ ) never attacked and tolerated the presence of the male decoy. Furthermore, three females, in the absence of their mate, landed close to the male decoy presented with a prey and gave soliciting calls. These observations suggest that some females solicit extra-pair males for food or for EPCs. Similar observations were made in the Eurasian kestrel, in response to live decoys (see Wiklund and Village, 1992). In Montagu's harrier, successful EPCs were almost always solicited by the female (six out of seven EPCs), but were rarely traded against prey (Arroyo, 1999, unpublished data). The latter may explain why male aggression was not different towards male decoys presented with or without prey. In conclusion, agonistic responses supported the hypothesis that male decoy presentations during the female's fertile period were perceived by males as an increased EPC risk. We suggest that the use of decoys to manipulate EPC risk may also apply for other species.

Conversely to males, the intensity of female intrasexual aggression, although also depending on the distance between the female decoy and the nest site, did not differ between periods. However, given the small number of female decoy experiments conducted in this study, further investigations should be carried out to conclude on the possible causes of female intrasexual agonistic behavior (which may be related to competition for males, mate guarding of male, nest defense, and/or to the risk of intraspecific brood parasitism; Gowaty, 1981; Wiklund and Village, 1992).

### Paternity assurance behaviors in raptors

#### Frequent copulations

Most raptors copulate frequently and several authors have concluded that sperm competition is the most likely cause of such high copulation rates (e.g., Birkhead and Lessells, 1988; Koga and Shiraishi, 1994; Møller, 1987b; Negro et al., 1992; Simmons, 1990; Sodhi, 1991). However, this has rarely been tested (see below) and several species copulate frequently for

other reasons than sperm competition, like pair bonding and mate assessment (e.g., Negro et al. 1996; Villarroel et al., 1998). Given the fact that the exact duration of the fertile period is usually not known, it is hard to tell which proportion of the copulations may serve in pair bonding, mate assessment, fertilization or paternity assurance. Up to now, the best support for paternity assurance through frequent copulations in raptors came probably from empirical intraspecific comparisons: in several species, copulation frequency increases with breeding density, a situation of potentially increased EPC risk (Arroyo, 1999; Korpimäki et al., 1996; Simmons, 1990).

In this study, we showed that male Montagu's harriers increased their short term copulation frequency in response to a male decoy presentation and during the presumed female's fertile period, that is, when the risk of an EPC becoming an EPF was potentially the greatest. Simulated male intrusions had no significant effect on copulation frequency during the early prelaying period, when copulations probably had little chance to result in fertilization. In Montagu's harrier, EPCs attempts were observed only during the presumed fertile period, and successful EPCs mainly during the laying period (Arroyo, 1999, unpublished data). The peak in within-pair copulation frequency prior to egg laying (Arroyo, 1999, unpublished data) might be a way for females to control paternity: Females may have sufficient sperm from their partner to fertilize the clutch, and also retain the option of engaging in an EPC if they encounter a more preferred male, whose sperm will thus be favored (Birkhead and Møller, 1993; Birkhead and Parker, 1997). However, males may counteract this risk by adjusting their copulatory behavior during the female's fertile period and in situations where EPC risk is high; females may have more interest in accepting than in rejecting within-pair copulations, since they depend on their mate for food (see also Korpimäki et al., 1996). In birds, the last copulation before fertilization is usually more successful than earlier ones, and the success of an EPC increases with the interval between the previous pair copulation and the EPC (Birkhead and Parker, 1997). By copulating soon after discovering an extra-pair male near the female, male Montagu's harrier may thus benefit from the last male fertilization advantage (Birkhead and Møller, 1992; Birkhead and Parker, 1997) and reduce the risk that a possible EPC results in fertilization.

During the fertile period, copulations performed during male decoy presentations also lasted significantly longer than those performed during the corresponding controls. Longer copulations may ensure copulation success (i.e., the achievement of cloacal contact and sperm transfer) and may also reflect increased sperm transfer to the female. Copulation success is probably mainly under female control in the Montagu's harrier (Pandolfi et al., 1998), as well as in other raptor species (e.g., Birkhead and Lessells, 1988). In this study, copulation success was overall high (82%,  $n = 11$  and 89%,  $n = 27$  copulations for the early prelaying and fertile periods, respectively), and similar during controls and male decoy experiments. This suggests that longer copulations might be related to increased sperm transfer, which may be interesting for males in terms of sperm competition and fertilization probability (Birkhead and Møller, 1992; Birkhead and Parker, 1997).

These experimental results show that individual male Montagu's harriers adjust their short-term copulatory behavior when they perceive themselves at an increased EPC risk; the results thus support the "Paternity Assurance" hypothesis, and a frequent copulation paternity assurance strategy in Montagu's Harrier. They are also consistent with and complementary to empirical data, which showed that copulation rate during laying increased with increasing breeding density (Arroyo, 1999). Copulation frequency was then likely to be ad-

justed to an increased EPCs risk on colonies, which may be evaluated by the proximity of other males, as well as more frequent male territorial intrusions in such situations (Arroyo, 1995).

#### *Female surveillance*

We also found that male Montagu's harriers increased presence time within their breeding territory and close to their female in response to male decoy presentations, during both the early prelaying and fertile periods, but not during the incubation period. This may be a by-product of male agonistic behavior: males increased their presence time because they were occupied attacking the intruder. However, during the fertile period, males did not only increase presence time while the decoy was present, but also in the subsequent hr. Males may have stayed after the experiment because of the disturbance (due to the decoy or the observer). Such disturbance was, however, probably similar for female decoy presentations, which did have no significant effect on male presence time. Males may also have stayed if they needed to rest after attacking the decoy; such behavior was, however, not observed during the early prelaying period, nor after predator decoy presentations, which nevertheless elicited a much higher frequency of attacks (Arroyo, Mougeot, and Bretagnolle, unpublished data). Overall, female surveillance (mate guarding) was probably the most likely explanation for the increase in male presence time after a simulated male intrusion and during the fertile period.

Mate guarding is generally unexpected in birds with intense courtship feeding because it conflicts with foraging: With males looking for food and females staying near the nest site, the chances of maintaining an effective surveillance of the female are reduced (Birkhead and Møller, 1992; Møller, 1987b). However, male raptors may trade foraging and mate guarding under certain circumstances, as suggested in other species (see Birkhead and Lessells, 1988; Korpimäki et al., 1996; Simmons, 1990). Montagu's harriers breed and forage in open habitats, so female surveillance might be possible at long distances (see also Korpimäki et al., 1996). Furthermore, males may change their hunting behavior to increase surveillance, for instance foraging closer to their nest sites. This may explain why decoys were detected more rapidly during the early prelaying and fertile periods than during the incubation period. Nevertheless, male Montagu's harriers still spent considerable time (ca. 50%) far from the female during the critical fertile period, unlike mate guarding birds, which spend >90% of their time following their female. Moreover, in some species, males still loose paternity despite intense mate guarding (e.g., Johnsen et al., 1998; Kempnaers et al., 1995). Increased surveillance in Montagu's harrier therefore appears as the "best-of-a-bad-job" (Kempnaers et al., 1995): It may help to see and repel some intruders, but it is probably not sufficient to ensure paternity.

In conclusion, our experimental results support female surveillance during the fertile period, despite the male courtship feeding strategy, as well as a frequent copulation paternity assurance strategy in Montagu's Harriers. Mate guarding and frequent copulation may thus be complementary means to ensure paternity, as also suggested in some other courtship feeding raptors (Birkhead and Lessells, 1988; Korpimäki et al., 1996). The former may help to detect and repel at least some intruders, and reduce EPC opportunities, and the latter to minimize the risk of EPCs becoming EPFs. A low incidence of EPF has been found in most raptors so far studied, even in species with a high risk and occurrence of EPCs (e.g., Negro et al., 1996; Swatschek et al., 1993; Warkentin et al., 1994), suggesting efficient paternity guards. In Montagu's harrier, paternity analyzes have been performed in another popula-

tion (eastern Poland) and revealed no extra-pair fertilization (Wiacek and Koziol, 1997). Sample size was however small (eight pairs, 13 chicks; Wiacek and Koziol, 1997), and since EPF frequency may differ between populations of a given species (e.g., Petrie and Kempenaers, 1998), paternity analyses should also be conducted in our study population to assess whether male Montagu's harrier efficiently ensure paternity.

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