



# Territorial signalling: a new hypothesis to explain frequent copulation in raptorial birds

J. J. NEGRO & J. M. GRANDE

Department of Applied Biology, Estación Biológica de Doñana, Spanish Council for Research (CSIC)

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Copulation patterns have been reported for numerous species of diurnal raptors (Order Falconiformes), possibly because their copulations are typically conspicuous and frequent. The majority of raptorial birds for which precise estimates are available copulate more than 100 times per clutch (see Table 1), with the American kestrel, *Falco sparverius*, copulating up to 690 times per season (Balgooyen 1976). Since only one successful copulation seems to be enough to fertilize a full clutch (Lake 1975; Birkhead et al. 1989), and there are costs associated with copulation (Birkhead & Møller 1992), an explanation for the high frequency of intrapair copulations in raptors and other birds is needed (e.g. Catry & Furness 1997).

Birkhead et al. (1987) and Møller & Birkhead (1992a) suggested several hypotheses to explain frequent copulation: (1) to increase the chances of fertilizing all the eggs; (2) to strengthen or maintain the pair bond; (3) to take advantage of a low predation risk; or (4) to dilute the sperm of competitors. Simmons (2000) has recently reported that polygynous harriers (*Circus* spp.) may suffer from sperm depletion, as they have lower hatching rates than monogamous pairs; this would support hypothesis 1 above. The pair bond maintenance and predation risk hypotheses have never been adequately tested in birds. Animals are generally assumed to be at greater risk when copulating, but there are also suggestions that mating individuals could gain from an 'alliance' of defensive mechanisms (Gwynne 1989), and this could be true for raptors. The sperm competition hypothesis has gained more attention and support (Birkhead & Møller 1992), and the current paradigm is that frequent intrapair copulations are used as a paternity guard, as an alternative to mate guarding in species where males are unable to guard their mates efficiently.

Other hypotheses have been proposed, such as females soliciting copulations to prevent their mates from engaging in extrapair copulations (Petrie 1992), or to assess the quality of their mates (Tortosa & Redondo 1992; Negro et al. 1996; Catry & Furness 1997; Lens et al. 1997;

Villarroel et al. 1998). Recently, some authors specifically studying raptors have advocated a compromise: frequent copulation outside the fertile period would have functions unrelated to fertilization, such as mate assessment, whereas those taking place during the presumed fertile period of the female would be related to paternity assurance (Negro et al. 1996; Villarroel 1998; Mougeot 2000). This idea is not entirely new: Newton (1979) and Village (1990) suggested that, given the occurrence of copulations after egg laying in raptors, the function of copulations was not restricted to fertilization.

## Raptor Copulation Patterns and Sperm Competition

The study of raptor copulation behaviour has revealed several common features (see also Table 1): (1) daily copulation rates often follow a bimodal distribution, with an early peak 18–65 days before laying, and a second peak coinciding with the onset of laying (Mougeot 2000); (2) copulation often continues during incubation or the chick-rearing period (Robertson 1986; Sodhi 1991; Holthuijzen 1992; Watson 1997; Bertran & Margalida 1999); and (3) the incidence of extrapair copulations (EPCs) and extrapair fertilizations is very low, for both solitary and colonial species (Simmons 2000). These patterns are not predicted by the sperm competition hypothesis. First, the early peak of copulations may lie outside the female's fertile period, which starts about 1 week before laying in the American kestrel, the only raptor for which the length of the fertile period has been determined (Bird & Buckland 1976). Second, under sperm competition, copulations should drop to zero after the clutch is completed and the female is no longer fertile. Third, if frequent copulations were used to ensure paternity, individuals seeking EPCs should be a common sight, and this is not the case for raptors.

## Copulations as Signals of Territory Ownership

It has been suggested that copulation could be some kind of advertisement (Ellis & Powers 1982; Simmons

Correspondence: J. J. Negro, Department of Applied Biology, Estación Biológica de Doñana (CSIC), Avda María Luisa s/n 41013 Sevilla, Spain (email: negro@ebd.csic.es).

Table 1. Summary of information about copulation behaviour of 47 diurnal raptors (Order Falconiformes)

Species	Copulation rate	Copulation period	Site of copulation	Conspicuousness	Breeding dispersion	Copulation pattern	EPC frequency (%)	EPF frequency (%)	Source
Oxprey, <i>Pandion haliaetus</i>	160	Start around 20 days prior to egg laying, immediately after arriving. End 7–8 days after first egg is laid	Most at the nest, but also some in breeding area	Yes	Solitary or in loose colonies	Bimodal	1		Birkhead & Lessells 1988; Green 1976
Honey buzzard, <i>Pernis apivorus</i>	High	Start some weeks before egg laying to mid nestling period	At nest or close by	Yes?	Solitary				Cramp & Simmons 1980
Black-shouldered kite, <i>Elanus caeruleus</i>	High	laying to mid nestling period	Breeding area	Yes	Solitary				Cramp & Simmons 1980; J. Ferrero, personal communication
Red kite, <i>Milvus milvus</i>	234	–40 to +10	Breeding area	Yes	Solitary	Bimodal	3.5		Mougeot 2000
Black kite, <i>Milvus migrans</i>	196	–40 to +30	Breeding area	Yes	Solitary or in loose colonies	Bimodal	3.2		Koga & Shiraishi 1994; unpublished data
African fish eagle, <i>Haliaeetus vocifer</i>	High	Some outside the breeding season	Breeding area	Yes	Solitary				Brown 1980
White-tailed eagle, <i>Haliaeetus albicilla</i>	High?		Breeding area	Yes?	Solitary				Cramp & Simmons 1980
Palmnut vulture, <i>Cypohierax angolensis</i>	High	–90 to +87	At nest	Yes?	Solitary?				Del Hoyo et al. 1994; Mundy et al. 1992
Bearded vulture, <i>Gypaetus barbatus</i>	55	–25, some after clutch is ended	Breeding area	Yes	Solitary	Bimodal	0.52		Bertran & Margalida 1999
Egyptian vulture, <i>Neophron percnopterus</i>	High	Some after clutch is ended	Breeding area	Yes	Solitary	Unimodal	2.6		Donazar et al. 1994
African white-backed vulture, <i>Gyps africanus</i>	High		At nest or close by	Yes	Colonial				Mundy et al. 1992
Indian white-backed vulture, <i>Gyps bengalensis</i>	High				Colonial				Birkhead et al. 1987
Ruppell's vulture, <i>Gyps ruepelli</i>	High	Until end of laying	At nest or close by	Yes	Colonial				Mundy et al. 1992
Griffon vulture, <i>Gyps fulvus</i>	High?		At nest or close by	Yes	Colonial				J. A. Donazar, personal communication
Cape griffon, <i>Gyps coprotheres</i>	100/female/clutch	–90 to +140	At nest	Yes	Colonial		0.5		Mundy et al. 1992
Snake eagle, <i>Circus galliscus</i>	High	At least 120 days, some after clutch is ended	Close to nest	Yes	Solitary				Cramp & Simmons 1980
African marsh harrier, <i>Circus ranivorus</i>	135	Start well before egg laying to +14	Breeding area	Yes	Solitary or in loose colonies		2.1		Simmons 1990, 2000
Hen harrier, <i>Circus cyaneus</i>	105	Start well before egg laying to –30 to +21	Breeding area	Yes	Solitary or in loose colonies				Cramp & Simmons 1980
Montagu's harrier, <i>Circus pygargus</i>	High	Start well before egg laying to well after clutch is ended	Breeding area	Yes	Solitary or in loose colonies	Bimodal	3.5–3.4		Arroyo 1999; Pandolfi et al. 1998
Dark chanting-goshawk, <i>Melierax metabates</i>	High	Start well before egg laying to well after clutch is ended			Solitary				Cramp & Simmons 1980
Shikra, <i>Accipiter badius</i>	High	2 weeks before egg laying, but some after clutch is ended	At nest or close by	Yes?	Solitary				Cramp & Simmons 1980
African little sparrowhawk, <i>Accipiter minullus</i>	High	–21 to the end of laying		Yes	Solitary			5.4	Liversidge 1962
Sparrowhawk, <i>Accipiter nisus</i>	372	At least from –30	Breeding area	Yes	Solitary	Constant	0		Birkhead & Möller 1992; Newton 1986
Cooper's hawk, <i>Accipiter cooperii</i>				Yes	Solitary				Rosenfield et al. 1991

Table 1. Continued

Species	Copulation rate	Copulation period	Site of copulation	Conspicuousness	Breeding dispersion	Copulation pattern	EPC frequency (%)	EPF frequency (%)	Source
Black sparrowhawk, <i>Accipiter melanoleucus</i>	Low?		Close to nest	Yes?	Solitary				Brown & Brown 1979
Goshawk, <i>Accipiter gentilis</i>	518	–52 to +20	Close to nest	Yes	Solitary	Bimodal	1.3		Gavin et al. 1998; Möller 1987
Ridgway's hawk, <i>Buteo ridgwayi</i>	High?	Not clear, but seen through 2 months	Breeding area?	Yes	Solitary				Wiley & Wiley 1981
Common buzzard, <i>Buteo buteo</i>	High		Breeding area	Yes	Solitary				Cramp & Simmons 1980
Guiana crested eagle, <i>Morphnus guianensis</i>			Close to nest	Yes	Solitary				Bierregaard 1984
Harpy eagle, <i>Harpia harpyja</i>	9	–17 to 0	At nest or close by	No?	Solitary				Rettig 1978
Lesser spotted eagle, <i>Aquila pomarina</i>		From at least –21, and some during incubation period	Breeding area	Yes	Solitary				Cramp & Simmons 1980
Spanish imperial eagle, <i>Aquila adalberti</i>		Some after clutch is ended	Breeding area	Yes?	Solitary				Meyburg 1987
Golden eagle, <i>Aquila chrysaetos</i>	High?	–46 to +55	Breeding area	Yes?	Solitary				Watson 1997
Black eagle, <i>Aquila verreauxii</i>	High?	–30 to postfledging period	Breeding area	Yes?	Solitary				Gargett 1990
Bonelli's eagle, <i>Hieraetus fasciatus</i>	High?	–43 to +15	Breeding area	No?	Solitary	Bimodal			Bertran & Romero 1992
Booted eagle, <i>Hieraetus pennatus</i>	Low?		Breeding area	No?	Solitary				F. G. Vilches & E. Casado, personal communication
Black-and-white hawk-eagle, <i>Spizastur melanoleucus</i>			Close to nest	Yes?	Solitary				Strauch 1975
Lesser kestrel, <i>Falco naumanni</i>	362	–65 to +10	At nest or close by	Yes	Colonial	Bimodal	6.7	3.4	Negro et al. 1992, 1996
Common kestrel, <i>Falco tinnunculus</i>	218	At least from 3 weeks before laying, some after clutch is ended and some in winter	Breeding area	Yes	Solitary	Bimodal	1	5.3 –1.9	Korpiimäki et al. 1996; Village 1990; Villarroel et al. 1998; unpublished data
American kestrel, <i>Falco sparverius</i>	690	–30 to +17	Breeding area	Yes	Solitary	Bimodal	0.3	10	Villarroel et al. 1998; unpublished data
Eleanor's falcon, <i>Falco eleonorae</i>	High	At least from –90	Breeding area		Colonial		<1	0	Burns 1996; Möller & Birkhead 1992b; Villarroel et al. 1998; Walter 1979
Hobby, <i>Falco subbuteo</i>									Möller & Birkhead 1992b
Merlin, <i>Falco columbarius</i>	60	–7 to +35	Breeding area	Yes	Solitary		0	0	Sodhi 1991; Sodhi et al. 1993
Saker falcon, <i>Falco cherrug</i>	High		Breeding area	Yes	Solitary				Cramp & Simmons 1980
Gyr falcon, <i>Falco rusticolus</i>	47		Breeding area	Yes	Solitary				Cramp & Simmons 1980
Prairie falcon, <i>Falco mexicanus</i>	194	–50 to +50	Breeding area		Solitary	Constant	0		Holthuijzen 1992
Peregrine falcon, <i>Falco peregrinus</i>	High	–21, some after clutch is ended	Breeding area	Yes	Solitary				Ratcliffe 1981
Taita falcon, <i>Falco fasciinucha</i>	High		Breeding area	Yes?	Solitary				Hartley et al. 1993

Copulation rate: number of copulations by female and clutch; if precise data were not available, we considered the copulation frequency as high if copulation was described as frequent; copulation period: laying of the first egg day 0; site of copulation: we considered the breeding area as the defended territory around the nest site; conspicuousness: we considered a species to have conspicuous copulations when individuals vocalized while copulating and if copulations were performed on exposed and prominent places; nonconspicuous were silent copulations in secluded places; breeding dispersion refers to solitary versus colonial breeders; copulation pattern: bimodal if there were two peaks in copulation activity prior to laying, and unimodal or constant when there was just one peak or none was evident, respectively; extrapair copulation (EPC) frequency: percentage of extrapair copulations in relation to the total number of observed copulations; extrapair fertilization (EPF) frequency: percentage of chicks genetically unrelated to their putative father.

1990; Village 1992). Several studies mention that raptors give copulation calls which make it easy to infer when a pair is copulating, even when the human observer is far away (Ellis & Powers 1982; Møller 1987; Simmons 1990, 2000; Mougeot 2000). In addition, raptor copulations usually take place in prominent or conspicuous places (e.g. Bertran & Margalida 1999; Mougeot 2000). In the case of the Cape vulture, *Gyps coprotheres*, Robertson (1986) stated that copulations may indicate nest site occupancy.

To explain the high daily copulation rates of raptors over extended periods of time, we propose a new hypothesis, namely that mating pairs are signalling territory ownership to conspecifics and possibly to other avian species. We have arrived at this conclusion after reviewing the available information and directly asking raptor biologists (Table 1) about two aspects almost neglected in previous analyses: (1) the conspicuousness of the copulation; and (2) location of the pair during mating in relation to the nest site. If repeated copulations have a function related to territoriality or the signalling of breeding status one would expect raptors to copulate preferentially in the defended breeding area, and copulations to be conspicuous, so as to convey information to potential signal receptors.

Raptors indeed mate on exposed sites, such as treetops, fenceposts, or cliff edges, and mating individuals often give copulation calls. Both males and females may call while copulating (e.g. goshawk, *Accipiter gentilis*: Møller 1987; Cooper's hawk: *Accipiter cooperii*: Rosenfield et al. 1991; black-and-white hawk-eagle, *Spizastur melanoleucus*, Strauch 1975), although it seems that only females call in harriers (Simmons 2000), and perhaps only males in other species (e.g. Cape vulture, Robertson 1986).

Regarding the location of mating within the pair's home range, raptors tend to copulate in the area where intruders (i.e. conspecifics and other birds) are not tolerated (Table 1). Colonial species (see Table 1), such as the lesser kestrel, *Falco naumanni* (Negro et al. 1992), or the Cape vulture (Robertson 1986) copulate almost exclusively at the nest site. In the case of the lesser kestrel, which one of us (J.J.N.) has studied extensively, no copulations have ever been observed on the foraging grounds, even though members of a pair often occur together in the same foraging flock. Territorial species, on the other hand, copulate close to the nest site and on the borders of the defended breeding territory, which may have a radius of several hundred metres. This is the case for the American kestrel, also studied by J.J.N. (unpublished data), or the harriers, which typically copulate less than 150 m from the nest site (but only 3% of copulations occur on the nest itself, Simmons 2000). As with colonial raptors, copulations outside the territory are rare.

Copulations conveying information to third parties would not be exclusive to raptors. A secondary social function of copulations has already been recognized in monkeys (Hall & DeVore 1965; Jolly 1972). Alvarez & Cónsul (1978) observed, for instance, a pair of geladas, *Theropithecus gelada*, copulating in response to an intruding male. In this case, the mating individuals threatened the intruder while copulating.

## Copulations Outside the Female's Fertile Period

The first peak of copulations in raptors, soon after pair reunion, is readily explained by the territory-signalling hypothesis, as it would inform conspecifics of the establishment of a breeding pair. However, we cannot reject the hypothesis that raptors copulate outside the fertile period to strengthen pair bonds (Newton 1979). This hypothesis is difficult to test, but a clear prediction is that pair members should copulate at a high rate when the pair reunites or establishes the territory. The mate assessment hypothesis does not require a fertilization context (see above) and it also predicts early copulations in raptors. None the less it is a less satisfactory explanation. Given that raptors are long-lived birds that typically keep pair bonds for many years (Newton 1979), why would an individual evaluate its partner year after year, especially when there is little evidence of divorce during the breeding season (Newton & Wyllie 1996)?

## Can Copulations Become Communication Signals?

The primary function of copulations is certainly the fertilization of eggs, and initially evolved for this function. Lotem et al. (1999), however, have suggested that selection on behaviours to be performed differently when observed by other animals can lead to significant quantitative changes in behaviour. Thus copulations may not have evolved as communication signals, but may still have signalling functions. If for example, breeding raptors reduce intrusion rates of conspecifics by copulating conspicuously in their territories, the signalling component of copulations may have caused their frequency to increase.

Raptors do show other territorial displays performed chiefly by males in flight (see review for several raptor species in Simmons 2000, pp. 69–70). According to Simmons, undulating flights, or skydancing, are mainly territorial but may also attract females because they are visible for several kilometres in some species. Displays by male raptors diving from high above the territory and terminating on the nest site (called skyspiralling in harriers) seem to be aimed at prospecting females. These aerial advertisements would mainly take place early in the breeding season, while copulations may continue as a territory-holding signal as soon as individuals establish the pair bond.

Raptors often vocalize, but their repertoire of distinct calls is generally limited. In American kestrels, only three basic vocalizations have been identified in all intra- or interspecific interactions (Willoughby & Cade 1964), whereas, for example, Canada geese, *Branta canadensis*, have eight (Collias & Jahn 1959) and many passerines have 12 or more (Thorpe 1961). In the Eurasian kestrel, *Falco tinnunculus*, Village (1990) reported that the calls of mating pairs were the same as those expressing a mild alert state.

Perhaps the paucity of vocalizations has led the majority of raptors to use alternatives to advertise territory holding, and conspicuous copulations may be such an alternative. Displays performed by a single individual

may convey only incomplete information about its pairing status (i.e. the receiver is not sure that the territory is filled). However, when two birds copulate potential intruders clearly see that there is a pair in the territory.

### Benefits from Signalling Territory Ownership by Copulating

Raptors tend to have few or no predators and can copulate frequently without risk. We thus return to one of the original hypotheses for frequent copulations proposed by Møller & Birkhead (1992a): that repeated intrapair copulations may occur when the risk of predation is low. However, we prefer to consider the lowered predation risk as a prerequisite for copulations to be performed at high frequency and in exposed places, rather than the main reason for frequent copulations.

Raptors are generally limited by availability of nest sites (Newton 1979), and nesting territories are vigorously defended against intruders of the same or different species (Newton 1979; Simmons 2000). Raptors are well armed and encounters can be injurious or lethal. Physical contact, with the birds locking talons and falling earthward, is often observed if the intruder enters the exclusion area of an established pair (see e.g. Simmons 2000, page 72). To avoid this extreme aggression it would pay raptors to advertise territory holding efficiently. Conspicuous and frequent intrapair copulations performed on the boundaries of the territory or at the nest site may sometimes serve this purpose. The action of the mating birds would clearly inform potential intruders or neighbours about their breeding status and where they are trying to reproduce. In turn, receivers of the signal may also benefit because they may learn that the territory is occupied without engaging in costly fights with the owners (both male and female raptors participate in territorial defence, Newton 1979).

The fact that the majority of unsuccessful copulations, without cloacal contact, occur during the first peak of copulations (Negro et al. 1992; Pandolfi et al. 1998; Bertran & Margalida 1999) provides additional support for our hypothesis: any sperm transferred would be wasted if the main purpose of the mating pair were to inform neighbours or potential intruders of their territory boundaries.

Finally, copulations must to be performed during the fertile period to fertilize the eggs but raptors may have chosen to prolong the copulatory period (before and after the fertilization window) because the cost of copulations may be lower than that of chasing intruders away, or engaging in dangerous fights.

### Predictions of the Territorial Signalling Hypothesis

We predict that colonial raptors will have higher copulation rates than solitary ones because the number of potential signal receivers is higher. For the same reason, within species, breeders are expected to copulate at higher rates in denser populations. These predictions, however, are also made by the sperm competition

hypothesis (Birkhead & Møller 1992). Using data from 12 species, Simmons (2000) reported that colonial raptors showed lower rates than semicolonial or territorial species. Unfortunately, good estimates of copulation frequency are not available for the majority of species, and further research is needed before new comparisons are attempted.

If the signalling component of copulations were mainly visual, we predict that nocturnal raptors (i.e. owls) would tend not to use copulations as a territorial display. Owls usually advertise their presence during the breeding season by repeatedly giving easily audible calls along the boundaries of their territories (Cramp 1985; McGregor & Dabelsteen 1996). Unfortunately, we have been unable to find a single study of copulations in a truly nocturnal owl. However, according to the descriptions of copulatory behaviour of some owl species (i.e. eagle owl, *Bubo bubo*, little owl, *Athene noctua*, tawny owl, *Strix aluco*, or the long-eared owl, *Asio otus*; Cramp 1985), copulations are performed close to the laying date and therefore in a fertilization context.

An exception among diurnal raptors could be the harriers, whose auditory capabilities exceed those of other raptors (Simmons 2000). Harriers tend to copulate on the ground but their copulations are noisy and this could be the signal to other harriers that the territory is filled (R. Simmons, personal communication). In fact, another prediction is that copulations should be more frequent in diurnal raptors with smaller vocal repertoires. Copulations should be more audible (i.e. noisier or with both males and females calling) in species living in closed than in open habitats. In addition, copulation calls should be more frequent during territory establishment.

We also predict that bird species that are territorial but cannot defend their territories against larger birds and predators will have low copulation rates and would copulate both near the nest site and on the foraging grounds (wherever they can). Again, there are few published examples, but a description for purple sandpipers, *Calidris maritima*, fits these predictions perfectly (Pierce & Lifjeld 1998): only nine copulations were observed after several years of observation, seven taking place on the territory and two on the foraging grounds.

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