



Breeding density, cuckoldry risk and copulation behaviour during the fertile period in raptors: a comparative analysis

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Extrapair copulations (EPCs) and fertilizations (EPFs) occur in many socially monogamous bird species, including raptors. In this group of species, males invest heavily in reproduction through the feeding of female and young, so the cost of cuckoldry is particularly high. The feeding of females by males, characteristic of most species, conflicts with mate guarding, so raptors are expected to use frequent within-pair copulations (WPCs) for paternity assurance. In this study, I reviewed information on copulation behaviour of diurnal raptors, and used regression analyses and phylogenetic comparative analyses to investigate relations between density, EPC frequency and WPC behaviour. EPCs occurred in most raptor species studied (68%, $N = 19$), mostly during the presumed fertile period of females. EPC frequency, measured as the percentage of females engaging in EPC but not the percentage of extrapair copulations, was positively related to breeding density. The rate and relative duration of WPCs were also positively related to breeding density, but only WPC rate was positively related to EPC frequency (percentage of females). Frequently copulating species had relatively larger testes, underlying higher sperm production capacities. The results support the hypotheses that sperm competition intensity increases with breeding density, and that male raptors rely on frequent copulations to ensure paternity. Despite the risk, EPFs rarely occurred in raptors, suggesting efficient paternity guards.

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In many socially monogamous birds, females engage in extrapair copulations (EPCs), which might result in extrapair paternity (EPP; Birkhead & Møller 1992, 1998). Given the potentially high costs of cuckoldry, males are expected to use behaviours aimed at reducing the incidence of EPCs and the likelihood of EPPs. Two main alternative paternity assurance behaviours are generally found in birds: mate guarding, which consists of close following of the female while she is fertile to prevent EPCs, and frequent copulations (increased sperm transfer) to reduce the chance that EPCs result in EPPs (Birkhead & Møller 1992). Mate guarding cannot be effective in some species because of ecological constraints. This is the case, for instance, in colonially breeding birds, in which one partner guards the nest while the other forages, or in species in which males provide food for the female. Males are then predicted to use frequent copulations (increased sperm transfer) to reduce the chance that EPCs result in

fertilizations (Birkhead et al. 1987; Birkhead & Møller 1992; Hunter et al. 1993).

Among birds, raptors are of particular interest for studying cuckoldry risk and paternity assurance behaviours. In this group of species, males invest heavily in reproduction by feeding their female and providing most of the food to their young (Newton 1979; Simmons 2000). Given this high male parental investment, the costs as well as the benefits of cuckoldry are particularly high, and selection is expected to have favoured intense paternity assurance behaviours (Birkhead & Møller 1992). The feeding of the female by the male during the prelaying and egg-laying periods implies that males cannot mate-guard efficiently, because they have to leave their female unattended while hunting. Although some raptor species perform some mate guarding (e.g. Simmons 2000; Mougeot et al. 2001, 2002), the chances of maintaining effective surveillance and preventing females from engaging in EPCs are greatly reduced, and so a paternity assurance strategy of frequent copulation is predicted.

Birds of prey are large and perform conspicuous copulations, which are well documented. Most raptors

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copulate at very high rates (up to several hundred times for a clutch) and many studies of raptor copulation behaviour have suggested that paternity assurance (sperm competition) is the most likely reason for these high copulation rates (e.g. Robertson 1986; Møller 1987; Simmons 1990; Sodhi 1991; Negro et al. 1992; Arroyo 1999; Mougeot 2000; Vidén & Richardson 2000; Mougeot et al. 2001). Raptors also copulate over particularly extended periods (e.g. Møller 1987; Negro et al. 1992; Villarroel et al. 1998; Mougeot 2000): frequent copulations outside the fertile period probably have functions other than fertilization, such as pair bonding, mate assessment (Villarroel et al. 1998; Mougeot 2000; Mougeot et al. 2002) or territorial signalling (Negro & Grande 2001).

The paternity assurance hypothesis predicts that the rate of within-pair copulations (WPCs) during the fertile period should increase in situations of increased EPC risk, for example, at high breeding density (Møller & Birkhead 1993). So far, the hypothesis that raptors copulate frequently as a means of ensuring paternity has been tested mostly at the intraspecific level, focusing on semicolonial species, in which individuals breed either solitarily or in loose or dense colonies. Consistent with the hypothesis, some studies found that both EPC and WPC frequencies increased with local breeding density (e.g. Simmons 1990; Korpimäki et al. 1996; Arroyo 1999; Mougeot 2000; Vidén & Richardson 2000). However, other studies found no support for these predictions (Tella 1996; Mougeot et al. 2002). Comparisons across raptor species might therefore provide useful insights into the effect of sperm competition on the high copulation rates of raptors. Interspecific comparisons of copulation behaviour have been attempted, but the results have been inconclusive (Møller 1987; Simmons 2000; Negro & Grande 2001), possibly because these comparisons did not consider the phylogenetic relations between raptor species or appropriate measures of cuckoldry risk.

In this paper, I have reviewed published information on raptor copulation behaviour to investigate the relations between breeding density, EPC frequency and WPC behaviour during the fertile period across raptor species. I considered two measures of EPC frequency: the percentage of observed copulations that were extrapair, and the percentage of study females that were observed engaging in EPCs. Percentage of extrapair copulations, used in previous interspecific comparisons (e.g. Simmons 2000; Negro & Grande 2001), might not be an appropriate measure of cuckoldry risk if the species uses frequent copulations to reduce the relative incidence of EPCs, because it would include both a measure of the risk and of the behaviour to reduce it. I used both regression analyses and phylogenetic comparative analyses to test the following three main predictions of the 'paternity assurance' hypothesis: (1) cuckoldry risk (EPC frequency) should increase with the breeding density of the species; (2) WPC frequency and duration (as potential measures of sperm transfer rate to the female) should increase with cuckoldry risk and thus with breeding density and EPC frequency; (3) WPC frequency and duration should be positively related to the testes mass of the species (as an indirect measure of sperm production capacities; Møller

1991). Finally, I have reviewed published information on extrapair paternity to evaluate the outcome of sperm competition in raptors.

METHODS

Comparative Data

Within-pair and extrapair copulation behaviour

Most raptor species copulate over extended periods, and probably well before the females are fertile. Based on the paternity assurance hypothesis, I predicted that WPC rate would be adjusted to EPC risk when females are fertile (i.e. when copulations and possible EPCs can result in fertilizations). The duration of the fertile period varies across bird species, averaging about 10 days, but lasting as long as 40–60 days in some species (Birkhead & Møller 1992). In raptors, the duration of the fertile period is known only for the American kestrel, *Falco sparverius*, with an average duration of viable sperm storage of 8 days (Bird & Buckland 1976). I predicted that female raptors would be fertile at least during the week preceding laying and during laying, and that the risk of an EPC resulting in EPF would be greatest during this period. As a measure of mean WPC frequency I gathered data from published information on the average number of copulations per female and per day during the week before laying and the laying period. I also gathered information on the average duration (s) of copulations involving cloacal contact (behaviourally successful copulations) as another potential indicator of sperm transfer rate to the female.

Information on the frequency and timing of EPCs was obtained from studies that involved individually recognizable individuals (either marked with colour rings, wing tags, radiotags or identified from individual features, such as plumage or head-marking patterns). Two measures of EPC frequency were extracted: the percentage of observed copulations that were extrapair, and the percentage of observed females that engaged in EPCs. A measure of the percentage of males engaging in EPC would probably not be reliable (male raptors usually seek EPCs away from their breeding territory) and was not considered. I also reviewed information on the timing of EPCs, that is, whether they occurred early in the prelaying (more than 7 days before laying, when females might not have been fertile), during the week before laying and laying (when females are fertile) or after laying was completed (nonfertile period).

Copulation data may be subject to observational biases, for instance if copulations, and EPCs in particular, are more easily detected in some species than in others (Westneat & Sherman 1997). Raptors are large birds that can be easily observed, and they perform conspicuous copulations, often associated with solicitation displays and calls, and in which EPCs are as conspicuous as WPCs. Before and during laying, females spend almost all their time at or close to the nest site, which means that opportunities to seek and achieve copulations elsewhere are greatly reduced. In fact, females engage in copulations (within-pair or extrapair) almost exclusively at the nest or nearby, within the breeding territory. Thus, by considering copulation data for individual females, measures of WPC rate and EPC frequency are likely to be accurate and comparable across raptor species.

Breeding density

I used average nearest-neighbour distance (NND, m) as a measure of breeding density (the lower the NND, the greater the density), which was the information available for most species. When available, I always used NND from the population where the copulation behaviour was studied. Otherwise, I used information from other, more general sources (Cramp & Simmons 1980; Brown et al. 1982; Palmer 1988; Marchant & Higgins 1993).

Body mass and testis mass

Information on body mass of raptor species was obtained from various general sources (Cramp & Simmons 1980; Brown et al. 1982; Palmer 1988; Marchant & Higgins 1993). Most raptors have high degrees of sexual dimorphism, with females larger and heavier than males (Newton 1979). I used male body mass during the breeding season for allometric corrections. Data on testis mass of raptors are from Møller (1991), except for one species (Montagu's harrier, *Circus pygargus*; F. Mougeot, unpublished data), where it was based on dissections of dead breeding birds.

Statistical Analyses

Dependent variables were transformed for normalization. I used arcsine transformations for both measures of EPC frequency (percentage of copulations and percentage of females) and natural logarithmic transformations for body mass, NND, mean WPC rate and WPC duration. I first looked for allometric relations between study parameters and body mass (Calder 1984), using General Linear Model (SAS 2001). Whenever I found a significant relation, I used the residuals from the regression to remove the variation of the trait caused by body mass.

A potential problem associated with interspecific comparisons is the nonindependence between species that share common ancestry (Harvey & Pagel 1991). To take into account this potential problem, I used comparative analyses by independent contrasts (Felsenstein 1985; Harvey & Pagel 1991). I used a derivative of the CAIC software (CAPRI, CNRS-UMR 5558, Lyon, France) to calculate contrasts in the data that are independent of phylogenetic associations. In these analyses, the statistical units are the nodes of the phylogeny, and the variables are contrasts calculated as a weighted difference in a given parameter between species or groups of species either side of each node. For the relations across raptor species, I used a molecular phylogeny based on the sequencing of about 1500 bp of cytochrome *b* (Wink et al. 1998). However, the usefulness of phylogenetic comparative methods has been challenged (Ricklefs & Stark 1996; Bjorklund 1997; Price 1997), and most authors nowadays perform two types of analyses, one accounting for phylogenetic inertia (phylogenetic method) and another using raw data (conventional method). Thus, I tested for associations between study variables using both conventional and phylogenetic methods. The data set was unbalanced, because information on certain parameters was missing for some species. Furthermore, phylogenetic information was not available for all raptor species (Table 1), so sample size differed

between analyses and according to the method (conventional or phylogenetic) used.

I used regression analyses (GLM procedure, SAS 2001) to test for associations between study variables or between standardized independent contrasts, using *t* tests for the null hypothesis of no relation between two sets of variables or contrasts. All tests are two tailed. Overall, the results of the regression analyses using the phylogenetic or conventional method were similar in terms of the direction of relations, their significance level and the percentage of variance explained (although for the latter, R^2 values were often greater for association between contrasts than for study parameters).

RESULTS

The information gathered on raptor copulation behaviour is summarized in Tables 1 and 2. I first looked for relations between study parameters and body mass. NND (GLM: $t_{1,46} = -0.04$; $P = 0.96$), both measures of EPC frequency (percentage of copulations: $t_{1,18} = -1.66$, $P = 0.14$; percentage of females: $t_{1,18} = -1.44$, $P = 0.17$) and mean WPC rate ($t_{1,37} = -0.66$; $P = 0.51$) were not significantly related to body mass. However, copulation duration ($t_{1,45} = 4.80$, $P < 0.001$) and testis mass ($t_{1,14} = 4.39$, $P < 0.001$) were both significantly positively related to body mass. For subsequent analyses, I considered the residuals from the relations with body mass for copulation duration and testis mass, hereafter referred to as relative copulation duration and relative testis mass.

EPC Frequency

EPCs have been reported in 68% of raptor species studied ($N = 19$). They occurred mostly during the presumed fertile period of females (week preceding and during laying; 13 of 13 species), as well as earlier in the prelaying period (5 of 11 species) and, more rarely, after clutch completion (3 of 13 species; Table 2). The percentage of copulations that were EPCs was low overall (range 0–13% of observed copulations; Table 2), and the percentage of females engaging in EPCs was more variable across species (range 0–69% of observed females; Table 2). The percentage of copulations that were extrapair was significantly positively related to the percentage of females engaging in EPCs (Table 3). The percentage of copulations that were EPCs was not related to NND (Table 3), but the percentage of females engaging in EPC was (Table 3, Fig. 1a, b). Analyses correcting or not for phylogeny gave similar results (Fig. 1a, b; Table 3). Thus, more females engaged in EPCs in species breeding at higher density, although the relative percentage of extrapair copulations did not increase with density.

WPC Frequency

WPC rate (average number of copulations per day and pair) was significantly negatively related to NND (Table 3, Fig. 1c, d), indicating that WPCs were more frequent in species breeding at higher density. WPC rate was also positively related to the percentage of females engaging in

Table 1. Raptor species characteristics and within-pair copulation behaviour

| Species* | Species characteristics | | | Copulation behaviour | | Source |
|---------------------------------|-------------------------|-------|--------------|----------------------|-----------------|---|
| | Body mass† | NND‡ | Testis mass§ | Mean rate** | Mean duration†† | |
| <i>Haliaeetus albicilla</i> | 4015 | 1500 | | 3.0 | 12.0 | Cramp & Simmons 1990 |
| <i>Haliaeetus vocifer</i> | 2210 | 1000 | | 3.5 | 10.0 | Brown 1980 |
| <i>Milvus migrans</i> | 810 | 80 | 6.43 | 10.8 | 6.0 | Koga & Shiraishi 1994 |
| <i>Milvus milvus</i> | 950 | 500 | | 5.6 | 5.4 | Mougeot 2000 |
| <i>Buteo buteo</i> | 750 | 1000 | 2.53 | 4.5 | 9.0 | Hubert 1994 |
| <i>Buteo jamaicensis</i> | 945 | | 1.33 | 3.0 | 8.5 | Palmer 1988 |
| <i>Buteo lagopus</i> | 810 | 3000 | | 1.9 | 9.0 | Palmer 1988; Cramp & Simmons 1980 |
| <i>Parabuteo unicinctus</i> | 690 | 500 | | 3.5 | 15.5 | Palmer 1988 |
| <i>Accipiter cirrhocephalus</i> | 126 | 1500 | | 6.0 | 11.5 | Marchant & Higgins 1993 |
| <i>Accipiter cooperii</i> | 350 | 1600 | | 6.7 | 4.5 | Rosenfield et al. 1991 |
| <i>Accipiter gentilis</i> | 700 | 2000 | 7.29 | 5.1 | 9.3 | Møller 1987 |
| <i>Accipiter nisus</i> | 145 | 950 | 0.53 | 4.3 | 9.0 | McGrady 1991 |
| <i>Circus cyaneus</i> | 345 | 1700 | | 1.0 | 4.0 | Picozzi 1984; J. T. Garcia & B. E. Arroyo, unpublished data |
| <i>Circus pygargus</i> | 260 | 600 | 3.10 | 2.2 | 4.5 | Arroyo 1999 |
| <i>Circus ranivorus</i> | 425 | 250 | | 3.5 | 5.6 | Simmons 1990 |
| <i>Circus aeruginosus</i> | 500 | 900 | 3.04 | 2.2 | 5.0 | G. Burnoleau & C. Bavoux, unpublished data |
| <i>Aquila audax</i> | 1030 | 5500 | | | 7.5 | Marchant & Higgins 1993 |
| <i>Aquila chrysaetos</i> | 3570 | 5000 | 7.36 | 3.3 | 11.0 | Ellis 1979; Ellis & Powers 1982 |
| <i>Aquila heliaca</i> | 2625 | 2000 | | 3.5 | 8.0 | Meyburg 1975; Cramp & Simmons 1980 |
| <i>Aquila pomarina</i> | 1325 | 1500 | | | 8.0 | Cramp & Simmons 1980 |
| <i>Aquila verreauxi</i> | 3600 | 2300 | | 4.0 | 7.5 | Garget 1990; Brown et al. 1982 |
| <i>Hieraetus fasciatus</i> | 1720 | 8000 | 2.30 | 3.0 | 5.5 | Cheyland 1972; Cramp & Simmons 1980 |
| <i>Harpia harpyja</i> | 4500 | 10000 | | 0.5 | | Rettig 1978 |
| <i>Aegypius monachus</i> | 9250 | 250 | | | 45.0 | Cramp & Simmons 1980 |
| <i>Gyps africanus</i> | 7400 | 500 | | | 30.0 | Houston 1976; Mundy et al. 1992 |
| <i>Gyps coprotheres</i> | 7900 | 10 | | 8.0 | 42.0 | Mundy et al. 1992 |
| <i>Gyps fulvus</i> | 7900 | 25 | | 10 | 35.0 | Cramp & Simmons 1980 |
| <i>Gyps ruppelli</i> | 6800 | 100 | | | 25.0 | Houston 1976; Mundy et al. 1992 |
| <i>Circus gallicus</i> | 1665 | 6000 | | 3.5 | 3.5 | Cramp & Simmons 1980 |
| <i>Gypaetus barbatus</i> | 5495 | 12400 | 33.80 | 4.7 | 10.2 | Bertran & Margalida 1999 |
| <i>Neophron percnopterus</i> | 2025 | 2500 | | 5.2 | 13.7 | Donazar et al. 1994 |
| <i>Pernis apivorus</i> | 630 | 3000 | | | 7.5 | Cramp & Simmons 1980 |
| <i>Elanus axillaris</i> | 250 | 530 | | | 10.0 | Marchant & Higgins 1993 |
| <i>Elanus caeruleus</i> | 230 | 3000 | | 5.4 | 11.0 | Ferrero et al. 2003 |
| <i>Cathartes aura</i> | 1425 | 5000 | | 2.25 | 38.9 | Palmer 1988 |
| <i>Coragyps atratus</i> | 1990 | 1860 | | | | Palmer 1988 |
| <i>Pandion haliaetus</i> | 1430 | 2500 | 17.65 | 9.8 | 9.0 | Vidén & Richardson 2000; Birkhead & Lessells 1988 |
| <i>Polyboroides typus</i> | 712 | 5500 | | | 12.5 | Brown et al. 1982 |
| <i>Falco berigora</i> | 412 | 4000 | | | 5.0 | Marchant & Higgins 1993 |
| <i>Falco longipennis</i> | 210 | 420 | | 1.5 | 4.5 | Marchant & Higgins 1993 |
| <i>Falco tinnunculus</i> | 155 | 700 | 0.72 | 9.4 | 6.0 | Korpimäki et al. 1996 |
| <i>Falco naumanni</i> | 150 | 5 | | 12.1 | 6.7 | Negro et al. 1992 |
| <i>Falco mexicanus</i> | 555 | 2500 | 3.95 | 3.8 | 3.8 | Holthuijzen 1992 |
| <i>Falco peregrinus</i> | 735 | 4800 | | 8.0 | 8.0 | Cramp & Simmons 1980 |
| <i>Falco columbarius</i> | 160 | 1200 | 0.19 | 3.0 | 7.5 | Sodhi 1991 |
| <i>Falco sparverius</i> | 110 | 900 | 2.11 | 8.3 | 6.0 | Villarroel et al. 1998 |
| <i>Falco subbuteo</i> | 180 | 4000 | | 2.0 | 5.0 | Cramp & Simmons 1980 |
| <i>Falco eleonorae</i> | 350 | 10 | | 5.5 | 10.0 | Walter 1979 |

*Species that are underlined were not included in the phylogenetic comparative analyses because of the lack of phylogenetic information.

†Average male body mass (g).

‡Average distance to nearest breeding neighbour (m).

§Average testis mass (g). All data are from Møller 1991, except for *Circus pygargus* (F. Mougeot, unpublished data).

**Average within-pair copulation rate (number of copulations per female and per day during the weeks preceding laying and laying).

††Average duration of behaviourally successful copulations (s).

EPC (Table 3, Fig. 2), but was not related to the percentage of copulations that were extrapair (Table 3). WPC rate was positively related to relative testis mass; this relation was not significant ($P = 0.06$) without correcting for phylogeny, but was significant ($P < 0.01$) when correcting for phylogeny (Table 3, Fig. 3).

Relative WPC Duration

Relative WPC duration was significantly positively related to WPC rate: species copulating frequently also copulated for relatively longer (Table 3). Relative WPC duration was significantly negatively related to NND (Table 3, Fig. 1e, f),

Table 2. Frequency and timing of extrapair copulations in diurnal raptors

| Species | Frequency | | Timing‡ | | | Source |
|------------------------------|----------------|------------|---------|---|----|---------------------------------|
| | % Copulations* | % Females† | EPL | F | PF | |
| <i>Milvus migrans</i> | 2.7 (246) | 50.0 (4) | 0 | + | 0 | Koga & Shirishai 1994 |
| <i>Milvus milvus</i> | 2.5 (142) | 15.0 (26) | 0 | + | 0 | Mougeot 2000 |
| <i>Buteo buteo</i> | 0 (55) | 0 (9) | | | | Hubert 1994 |
| <i>Accipiter nisus</i> | 13 (150) | 39.1 (23) | + | + | 0 | McGrady 1991 |
| <i>Aquila chrysaetos</i> | 0 (21) | 0 (5) | | | | Ellis 1979; Ellis & Powers 1982 |
| <i>Circus pygargus</i> | 3.5 (141) | 12.0 (93) | 0 | + | 0 | Arroyo 1999 |
| <i>Circus ranivorus</i> | 2.1 (196) | 16.7 (12) | 0 | + | + | Simmons 1990 |
| <i>Gyps coprotheres</i> | 0.7 (670) | 12.5 (16) | + | + | + | Robertson 1986 |
| <i>Neophron percnopterus</i> | 4.6 (43) | 5.6 (18) | 0 | + | 0 | Donázar et al. 1994 |
| <i>Gypaetus barbatus</i> | 0 (189) | 0 (8) | | | | Bertran & Margalida 1999 |
| <i>Pandion haliaetus</i> | 1.9 (166) | 23.1 (13) | + | + | 0 | Vidén & Richardson 2000 |
| <i>Coragyps atratus</i> | 0 – | 0 – | | | | Decker et al. 1993 |
| <i>Falco tinnunculus</i> | 1 – | 4.0 (54) | ? | + | 0 | Korpimäki et al. 1996 |
| <i>Falco naumanni</i> | 6.7 (1397) | 69 (13) | + | + | 0 | Negro et al. 1992 |
| <i>Falco subbuteo</i> | 0 – | 0 – | | | | Møller & Birkhead 1993 |
| <i>Falco eleonorae</i> | 1.7 (60) | 9.1 (11) | ? | + | 0 | Walter 1979 |
| <i>Falco columbarius</i> | 7.3 (41) | 15.4 (13) | 0 | + | + | Sodhi 1991 |
| <i>Falco sparverius</i> | 0.3 (385) | 4.0 (16) | + | + | 0 | Villarreal et al. 1998 |
| <i>Falco mexicanus</i> | 0 (553) | 0 (52) | | | | Holthuijzen 1992 |

*Extrapair copulation (EPC) frequency measured as the percentage of copulations that were EPCs (sample size, in parentheses, refers to the number of observed copulations).

†EPC frequency measured as the percentage of females that engaged in EPC (sample size, in parentheses, refers to the number of observed females).

‡Timing of EPCs: whether EPCs have been observed (+) or not (0) in the following periods: early prelaying (EPL, >1 week before laying), fertile (F, week preceding laying and laying) and postfertile (PF, after clutch completion).

indicating that species breeding at higher densities copulated for relatively longer. However, relative WPC duration was not significantly related to EPC frequency (percentage of females engaging in EPCs or percentage of extrapair copulations) or relative testis mass (Table 3).

DISCUSSION

Regardless of the method used (phylogenetic or conventional), interspecific comparisons of raptor copulation behaviour showed that EPC frequency (percentage of females engaging in EPCs), WPC rate and relative WPC duration were all negatively related to NND and thus increased with the breeding density of the species. WPC rate was positively related to both the percentage of females engaging in EPC and relative testis mass. Below I discuss these findings in line with predictions from the paternity assurance hypothesis for frequent copulations.

Cuckoldry Risk and Breeding Density

EPCs occurred in 68% of studied raptor species, and EPC frequency was predicted to increase with breeding density. Accordingly, I found that the percentage of females engaging in EPC was negatively related to NND indicating an increased risk of cuckoldry in species breeding at higher density. However, the other measure of raptor EPC frequency (the percentage of extrapair copulations) was positively related to the percentage of females engaging in EPC but was not significantly related to density. This result could be explained by the finding that WPCs were also

positively related to breeding density. The percentage of extrapair copulations might thus be a poor indicator of cuckoldry risk in raptors, and possibly in other species copulating frequently for paternity assurance, because it includes a measure of both the risk and the intensity of the counterstrategy (WPC frequency). This result in turn explains why previous comparative studies in raptors failed to find relations between breeding density and EPC risk (Simmons 2000; Negro & Grande 2001). It also highlights the importance of gathering information on the percentage of females engaged in extrapair behaviour in studies of EPC risk.

An increased cuckoldry risk at higher density was supported in a number of intraspecific studies of raptor copulation behaviour. In several species, EPCs occurred more frequently in pairs breeding with close neighbours than in isolated situations (e.g. Simmons 1990; Korpimäki et al. 1996; Arroyo 1999; Mougeot 2000; Vidén & Richardson 2000). However, other studies found no evidence for EPC frequency to increase with local density (e.g. Tella 1996; Mougeot et al. 2002). Such differences between species might result from differences in the relative costs and benefits of EPCs for females (Westneat et al. 1990; Petrie & Kempnaers 1998). My results nevertheless indicate that cuckoldry risk covaries positively with density in raptors. The finding is also consistent with that of another comparative analysis conducted across bird species, showing a positive association between EPC frequency and density (Møller & Birkhead 1993).

The positive association between EPC risk and density might reflect that opportunities for females to engage in EPCs increase with density, because of an increased

Table 3. Regression analyses of study parameters and of independent contrasts of parameters

| Regression of Y on X | Regression of study parameters | | | | | Regression of independent contrasts | | | |
|--------------------------------|--------------------------------|-------|--------|--------------|----------------|-------------------------------------|-------|--------|----------------|
| | df | t | P‡ | Slope ± SD | R ² | df | t | P‡ | R ² |
| EPC frequency (% copulations)* | | | | | | | | | |
| EPC frequency (% females)* | 1,18 | 6.15 | <0.001 | 0.32 ± 0.05 | 0.67 | 1,17 | 4.72 | <0.001 | 0.55 |
| EPC frequency (% copulations)* | | | | | | | | | |
| NND† | 1,18 | -1.52 | 0.15 | -0.02 ± 0.02 | 0.11 | 1,17 | -1.67 | 0.16 | 0.15 |
| EPC frequency (% females)* | | | | | | | | | |
| NND† | 1,18 | -3.70 | <0.01 | -0.09 ± 0.02 | 0.43 | 1,17 | -5.10 | <0.001 | 0.62 |
| Mean WPC rate† | | | | | | | | | |
| NND† | 1,36 | -3.53 | <0.01 | -0.12 ± 0.04 | 0.26 | 1,28 | -3.26 | <0.01 | 0.26 |
| EPC frequency (% copulations)* | 1,18 | 1.15 | 0.29 | 1.05 ± 0.95 | 0.07 | 1,17 | 1.70 | 0.16 | 0.08 |
| EPC frequency (% females)* | 1,18 | 3.03 | <0.01 | 0.86 ± 0.32 | 0.35 | 1,17 | 3.37 | <0.01 | 0.42 |
| Relative testis mass | 1,14 | 2.07 | 0.06 | 0.38 ± 0.18 | 0.25 | 1,12 | 4.17 | <0.01 | 0.59 |
| Relative WPC duration | | | | | | | | | |
| NND† | 1,44 | -4.52 | <0.001 | -0.14 ± 0.03 | 0.32 | 1,32 | -3.60 | <0.05 | 0.32 |
| EPC frequency (% copulations)* | 1,18 | 1.67 | 0.10 | 1.32 ± 0.74 | 0.16 | 1,17 | 1.07 | 0.35 | 0.14 |
| EPC frequency (% females)* | 1,18 | 1.34 | 0.20 | 0.40 ± 0.30 | 0.10 | 1,17 | 1.75 | 0.15 | 0.17 |
| Mean WPC rate† | 1,36 | 2.22 | <0.05 | 0.35 ± 0.16 | 0.12 | 1,28 | 2.10 | <0.05 | 0.10 |
| Relative testis mass | 1,14 | -0.11 | 0.91 | -0.02 ± 0.15 | 0.01 | 1,12 | 0.67 | 0.62 | 0.04 |

EPC: extrapair copulations; NND: nearest-neighbour distance; WPC: within-pair copulation.

*Arcsine-transformed variable.

†Log-transformed variable.

‡Two-tailed probability significance level.

number of neighbouring males and frequency of male territorial intrusions, and also because of mate-guarding constraints associated with courtship feeding by the male (Møller 1987; Birkhead & Møller 1992; Simmons 2000). An alternative explanation is that the EPC behaviour of females contributes to the clustering of breeding territories and to increasing breeding density ('hidden lek' hypothesis; Wagner 1993). In monogamous species, a female associates with one male but can seek EPCs with other males, and in particular with a more attractive and better-quality neighbouring male than her mate. To do so, females could select for aggregated males while discarding isolated males, thereby favouring the clustering of breeding territories and the formation of colonies (Wagner 1993). In raptors, breeding density appears to be driven mainly by food abundance (Newton 1979), but this hypothesis might be worth testing in some semicolonial species, such as harriers, in which individuals can choose whether to breed in isolated situations or in colonies of varying density.

Frequent Within-pair Copulations

According to the paternity assurance, or sperm competition, hypothesis, frequent copulations during the fertile period function primarily to ensure paternity (Birkhead & Møller 1992, 1998). The hypothesis predicts that WPC

frequency should increase in situations of increased EPC risk, such as high breeding densities. For instance, many colonial bird species copulate frequently, which might be related to a higher cuckoldry risk in colonial situations (Birkhead & Møller 1992, 1998; Møller & Birkhead 1993). I found that EPC frequency was negatively related to NND. Thus, if species use frequent copulation for paternity assurance, WPC rate should also be negatively related to NND and I found this to be the case as well. Furthermore, WPC rate was also positively related to the percentage of females engaging in EPC in a given raptor species. The results were thus consistent with the hypothesis that male raptors rely on frequent copulation to ensure paternity.

The best support for paternity assurance through frequent copulations in raptors has come from intraspecific comparisons showing an increase in WPC rate with local breeding density, a situation of potentially increased EPC risk (Simmons 1990; Korpimäki et al. 1996; Arroyo 1999; Mougeot 2000; Vidén & Richardson 2000). In two species, males also increased their short-term copulation frequency in response to simulated male territorial intrusions during the fertile period (Mougeot 2000; Mougeot et al. 2001). However, other studies found little or no support for the same predictions, and contrasting results were also found in different populations of the same species (e.g. Vidén & Richardson 2000; Mougeot et al. 2002). The results from the interspecific comparisons help clarify the overall situation, and suggest that sperm

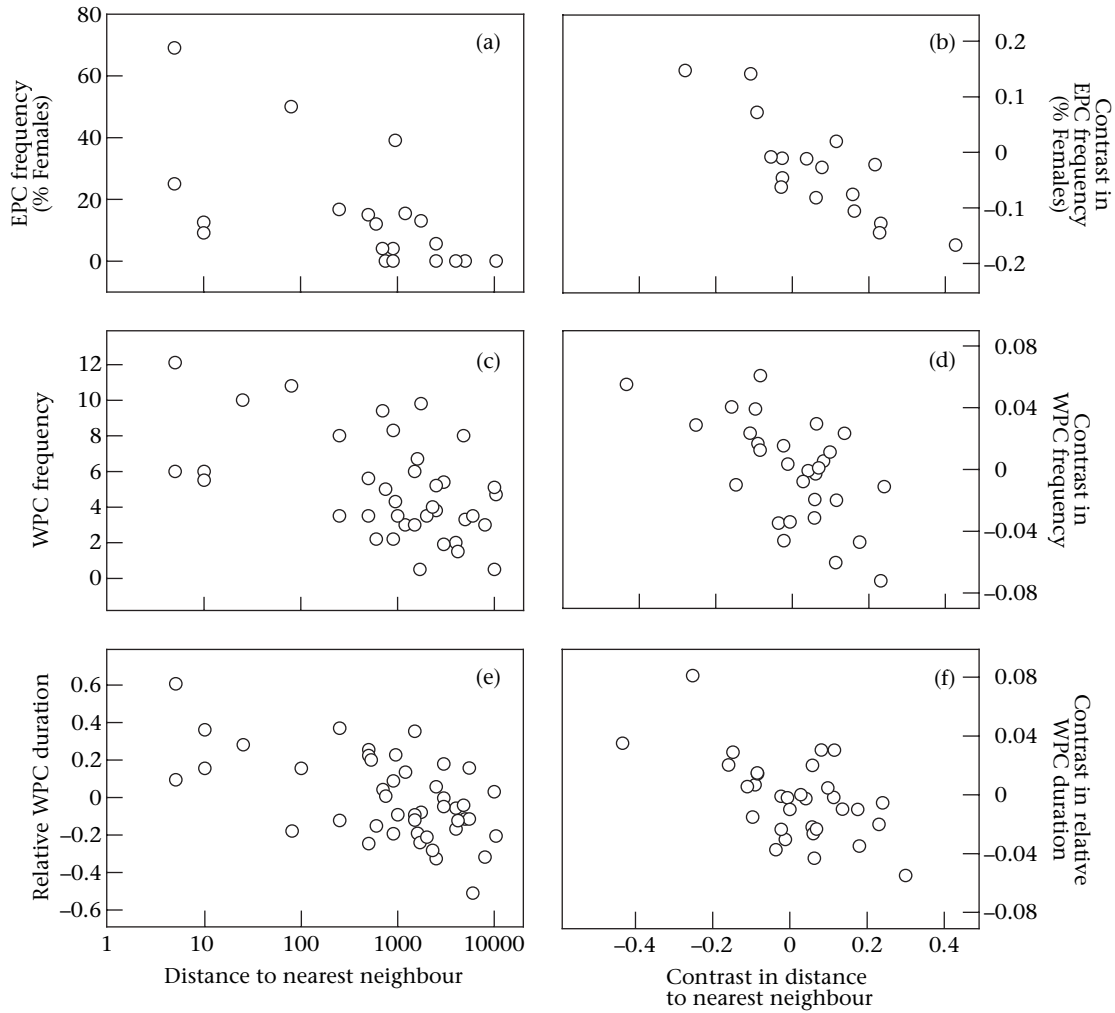


Figure 1. Relations between distance to nearest neighbour (NND; log scale) and (a) extrapair copulation (EPC) frequency (% females engaging in EPC), (c) within-pair copulation (WPC) frequency and (e) relative WPC duration. Relations between contrasts in NND and contrasts in (b) EPC frequency (% females), (d) WPC frequency and (f) relative WPC duration.

competition and paternity assurance are likely causes for the high copulation rates by raptors when females are fertile. In this study, I considered WPC rate only during the week before and during laying and therefore conclude only that WPC rate covaries with cuckoldry risk when the

females are fertile, and when the risk of an EPC resulting in EPP is greatest. Raptors copulate over extended periods, and copulations early in the prelaying period are likely to have functions other than paternity assurance, including nonfertilization functions. This possibility has already

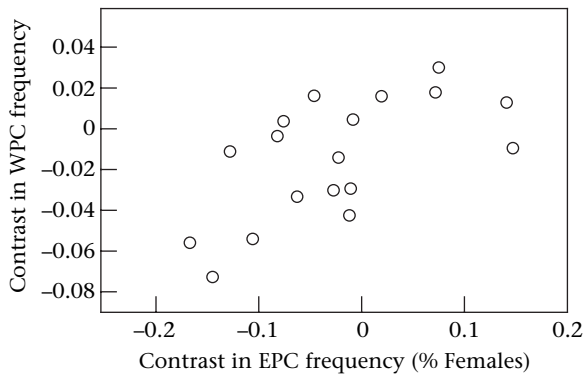


Figure 2. Relation between contrasts in within-pair copulation frequency and contrasts in extrapair copulation (EPC) frequency (% of females engaging in EPC).

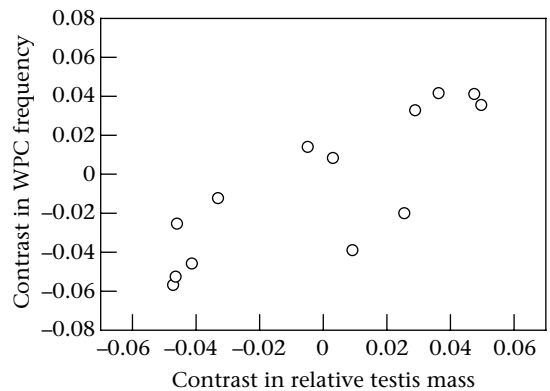


Figure 3. Relation between contrasts in within-pair copulation (WPC) frequency and contrasts in relative testis mass.

been highlighted in a number of raptor species, in which WPC rate early in the prelaying period was not related to density or adjusted to EPC risk, but WPC rate before and during laying increased with density (e.g. Arroyo 1999; Mougeot 2000; Mougeot et al. 2001). Because frequent copulations are likely to have nonfertilization functions in raptors, it is also important to establish whether frequently copulating species might have higher sperm production capacities. I found that WPC rate was positively related to relative testis mass, suggesting that raptor species might be adapted to sperm competition both behaviourally (frequent WPCs) and physiologically (larger testes; see also Møller 1991).

According to the sperm competition hypothesis, males increase sperm transfer to their females to reduce the chances that an EPC will result in EPF. This is because the probability of fertilization is proportional to the relative contribution by each male (Birkhead & Møller 1998). Copulating frequently also increases the chance of being the last male to copulate before fertilization, which also gives a fertilization advantage (Birkhead & Møller 1998). Increasing the duration of WPCs could also enhance sperm transfer. In Montagu's harrier, males increased not only WPC rate but also copulation duration in response to an experimentally increased EPC risk (Mougeot et al. 2001). In raptors, copulation duration was positively related to body mass, possibly because larger species need more time to ensure behaviourally successful copulations (with cloacal contact and sperm transfer). After correcting for body mass, I found that the relative duration of WPCs was positively related to the breeding density of the species. This result suggested that copulations might be relatively longer in species facing an increased EPC risk. However, relative copulation duration was not significantly related to either measure of EPC frequency, nor to relative testis mass. It is thus not clear whether WPC duration relates to paternity assurance or other functions. Longer copulations might ensure that cloacal contact and sperm transfer are achieved, but might not be associated with increased sperm transfer. Information on the duration of cloacal contact during copulations might be a better indicator of sperm transfer, but these data were too scarce for raptors.

Extrapair Paternity in Raptors

When EPCs were observed, most occurred during the week before and during laying, when females were fertile (Table 2) and could have resulted in extrapair fertilization (EPF). To assess the possible outcome of sperm competition in raptors, I reviewed published information on extrapair paternity (Table 4). EPFs have been reported in 40% of raptor species studied ($N = 10$) and their incidence is always relatively low (1–5% of young or broods). The costs and benefits of cuckoldry are nevertheless relatively high, given the high investment in reproduction by male raptors. The data on extrapair paternity suggest that, despite the risk, the counterstrategies to ensure paternity might be efficient in reducing the likelihood of EPCs resulting in EPFs. Although the percentage of females engaging in EPC increased with density, the percentage of copulations that were extrapair did not. This result

Table 4. Frequency of extrapair fertilizations in diurnal raptors

| Species* | % Young† | % Broods‡ | Source |
|----------------------------|-----------|-----------|------------------------|
| <i>Buteo galapagoensis</i> | 0 (66) | 0 (10) | Faaborg et al. 1995 |
| <i>Accipiter gentilis</i> | 1.3 (77) | 2.6 (39) | Gavin et al. 1998 |
| <i>Accipiter nisus</i> | 5 – | 5.4 – | Møller & Birkhead 1993 |
| <i>Circus pygargus</i> | 0 (13) | 0 (8) | Wiacek & Koziol 1997 |
| <i>Coragyps atratus</i> | 0 (36) | 0 (16) | Decker et al. 1993 |
| <i>Falco tinnunculus</i> | 1.9 (319) | 2.7 (75) | Korpimäki et al. 1996 |
| <i>Falco naumanni</i> | 3.4 (87) | 3.8 (26) | Negro et al. 1996 |
| <i>Falco eleonorae</i> | 0 (60) | 0 (17) | Swatschek et al. 1994 |
| <i>Falco columbarius</i> | 0 – | 0 – | Warkentin et al. 1994 |
| <i>Falco sparverius</i> | 0 (89) | 0 (42) | Villarroel et al. 1998 |

*Species that are underlined are colonial or semicolonial; other species are territorial.

†Extrapair fertilization (EPF) frequency measured as the percentage of young that are extrapair (sample size, in parentheses, refers to number of young).

‡EPF frequency measured as the percentage of broods containing extrapair young (sample size, in parentheses, refers to number of broods).

suggests that the relative risk of EPF might not be higher in species breeding at higher density, probably because WPC rate also increased with density. In birds in general, there is no obvious association between EPP frequency and density (Westneat & Sherman 1997) despite a positive association between density and EPC frequency (Møller & Birkhead 1993). EPPs do not appear to be more frequent in colonial or semicolonial raptors ($\bar{X} \pm \text{SD} = 1.1 \pm 1.5\%$ of extrapair young, $N = 5$ species) than in territorial ones ($1.3 \pm 2.2\%$, $N = 5$; Table 4). However, more information is needed on EPFs in raptors to assess how EPF frequency varies according to density, EPC risk or the intensity of paternity assurance strategies. Future studies could also investigate why female raptors engage in EPCs, including the possibility that EPCs function as a strategy for improving mate choice (Westneat et al. 1990; Birkhead & Møller 1998). In some species, EPCs occurred after clutch completion or early in the prelaying period (Table 2), suggesting functions other than fertilization, such as mate assessment (e.g. Colwell & Oring 1989; Wagner 1991). During the fertile period, females might use EPCs as a means to ensure that all the eggs are fertilized, in case of low fertility of their mate, or as an attempt to have their eggs fertilized by a male of higher quality than the current mate (Birkhead & Møller 1992, 1998). Both detailed intraspecific studies and interspecific comparisons would be helpful for clarifying the functions of EPC behaviour in this group of species.

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