



Effects of territorial intrusions, courtship feedings and mate fidelity on the copulation behaviour of the osprey

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We studied copulation behaviour of the osprey, *Pandion haliaetus*, a semicolonial, fish-eating raptor, in Corsica (Mediterranean). Pairs copulated over a long period (45 days) and at a high rate, with, on average, 288 within-pair copulations (WPCs) for a clutch. Pairs breeding at higher density faced more frequent territorial intrusions than others and were potentially at an increased cuckoldry risk. However, and contrary to predictions of the 'paternity assurance' hypothesis for frequent copulations, we found that WPC rate decreased with increasing frequency of territorial intrusions. Male territory attendance increased with territorial intrusion frequency, to the detriment of the food provisioning of the female. Both attempted and successful WPC rates were positively related to the amount of food delivered by the male. Thus, the more frequent the territorial intrusions, the more time the male spent within his territory, the less he courtship fed and the smaller the fish he delivered, and the less the pair copulated successfully. WPC rate was also higher in newly formed pairs than in established pairs, and decreased with increasing pair bond length. The results suggest that males rely on mate guarding rather than frequent copulations to ensure paternity, and do not support the idea that sperm competition is the main cause of frequent WPCs. Nonfertilization functions of frequent copulations, such as pair bonding, mate assessment and mate retention, were likely early in the prelaying period. The findings that WPC rate decreased with mate fidelity and that females traded copulations for food suggest that mate retention was a possible function of frequent copulations in this species.

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While most vertebrates copulate only a few times shortly before fertilization, some species copulate frequently and over extended periods (e.g. Birkhead et al. 1987; Birkhead & Møller 1992, 1998). The reasons for these repeated matings are still poorly understood (Hunter et al. 1993). Several copulations might be needed to ensure that all the ova are fertilized ('fertility assurance' hypothesis; Birkhead et al. 1987), but many species copulate far more frequently than would be needed for fertilization (see Hunter et al. 1993).

High copulation rates are found in many bird species, with copulations occurring frequently both in fertilization and nonfertilization contexts. Extrapair copulations (EPCs) have been recorded in many bird species, and frequent within-pair copulations (WPCs) may be used to

reduce their chance of resulting in extrapair fertilizations ('paternity assurance' or 'sperm competition' hypothesis; e.g. Birkhead et al. 1987; Birkhead & Møller 1992, 1998). Pair copulations may further be traded by females for direct benefits such as food, nest material or protection ('immediate material benefits' hypothesis; Tasker & Mills 1981; Hunter et al. 1993). Females may also use frequent copulations to dissuade their mate from engaging in EPCs or changing mate ('female mate guarding of male' hypothesis; Petrie 1992), or to assure their mate of their paternity and ensure their future investment in reproduction ('future material benefits in the form of parental care'; see Hunter et al. 1993). Finally, frequent WPCs may also function in pair bond maintenance and reinforcement (Newton 1979; Birkhead et al. 1987) or in mate assessment (individuals may acquire information about mate quality via copulations; Tortosa & Redondo 1992; Villarroel et al. 1998).

Among birds, raptors copulate at very high rates (several hundred times for a clutch) and over particularly extended periods (e.g. Møller 1987a; Negro et al. 1992;

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Villarroel et al. 1998; Mougeot 2000). In most species, females are fed exclusively by their mate from pair formation until halfway through the chick-rearing period (Newton 1979): males thus have to leave their female unattended while hunting, and cannot therefore guard their mates efficiently. Extrapair copulations have been observed in most raptors, and several studies have concluded that paternity assurance (sperm competition) is the most likely reason for their high copulation rates (e.g. Møller 1987a; Simmons 1990; Negro et al. 1992; Arroyo 1999; Mougeot 2000). Other possible functions of frequent copulations, and particularly nonfertilization functions, are also likely (e.g. Negro et al. 1996; Villarroel et al. 1998) but have rarely been considered.

We investigated the effects of breeding density, territorial intrusions and male–female relationships (courtship feeding and mate fidelity) on the WPC behaviour of ospreys, *Pandion haliaetus*. Our predictions were as follows. First, cuckoldry risk potentially increases with breeding density, because of the proximity of other males and more frequent territorial intrusions (Møller & Birkhead 1993; but see also Westneat & Sherman 1997). This prediction has been validated in several raptor species (e.g. Simmons 1990; Arroyo 1999; Mougeot 2000), including the osprey (Vidén & Richardson 2000). If frequent copulations function in paternity assurance, WPC rate should increase with territorial intrusion frequency. Second, we tested for an association between copulations and food delivery rate by the male. In the osprey, courtship feeding rate reliably indicates male quality and future investment in reproduction (Green & Krebs 1995). Females may thus trade copulations for food as a direct benefit, or copulate frequently with good-quality males (good food providers) to ensure mate fidelity (female mate guarding of male hypothesis) and future investment in reproduction (future material benefits hypothesis). Finally, we tested for differences in copulation behaviour according to mate fidelity. If frequent WPCs function in mate assessment, pair bonding and/or as a means to ensure mate fidelity, newly formed pairs, in which partners have to assess each other and improve pair bonds, should copulate more frequently early in the prelaying period than those that had already bred together in previous years.

METHODS

Study Species and Population

The osprey is a widespread fish-eating raptor with intense courtship feeding (Cramp & Simmons 1980; Poole 1985, 1989). The species is socially monogamous, although both polygyny and polyandry have been reported (Cramp & Simmons 1980; Poole 1989). Ospreys are semicolonial (individuals do not defend feeding territories) and breeding dispersion ranges from solitary nesting (nest sites well apart and regularly spaced) to loosely colonial (aggregated nest sites, with internest distances of a few hundred metres) or colonial (aggregated nests a few metres apart) in different populations (e.g. Cramp & Simmons 1980; Palmer 1988).

Corsica (42°N, 9°E), western Mediterranean, has a resident population of ospreys, whose breeding range is restricted to the sea coasts on the northwest of the island (Thibault & Patrimonio 1991; Thibault et al. 1995). This sedentary population has been intensively monitored from 1977 to 1998, and has increased gradually, from six breeding pairs in 1977 to 30 in the late 1990s (Thibault et al. 1995). The breeding density was high when this study was conducted (average internest distances of 1.5–2 km). Breeding lasts more than 6 months, from February to July (Thibault & Patrimonio 1991). Birds nest on pinnacles along the rocky sea coast. We observed nests from land at less than 300 m with a telescope, looking down upon the nest, so we had a good view of the nest contents. General monitoring included one visit each month, from March to August, to check the nests and identify breeding birds. As the number of pairs was relatively small, we could obtain breeding data for the total population.

Behavioural Observations

We studied preincubation behaviour of ospreys in February–May 1991, 1993, 1996 and 1997. Study pairs were selected for ease of observation (good viewing conditions of the nest contents and the cliffs around the nest site) and access to the viewpoint. Birds were observed with a $\times 20$ –60 telescope 100–300 m from the study nests (or from a hide when the observer was less than 200 m from the nest); the birds always seemed unconcerned by the presence of the observer. All study birds were individually identified, either from their Darvic colour band (30% of individual-years, $N=46$) or from their individual head-marking pattern (see Bretagnolle et al. 1994). Birds were colour ringed at the nest as fledglings when 3–4 weeks old (no adult bird was caught). We had a licence for ringing and tagging ospreys from the Centre de Recherche sur la Biologie des Populations d'Oiseaux.

Ospreys have stereotyped behavioural displays (see Bretagnolle & Thibault 1993 for a thorough description), which helped us record and quantify the behaviour of study birds. During focal observations, we recorded all copulations, their duration (s) and success (i.e. whether cloacal contact was achieved); cloacal contact does not necessarily imply sperm transfer (e.g. Birkhead et al. 1989), and copulation success hereafter refers to behavioural success of copulations. We also recorded all fish deliveries by the male, and an estimate of fish size (four classes of fish size, relative to feet size: if the visible part of the fish was as large as the feet, it was scored as 1, if twice as large, it was scored 2, etc.). We quantified the percentage of time spent by the male and female within the breeding territory (i.e. at the nest or perched within ca. 300 m of the nest site, which corresponds to the defended area), and the percentage of time spent by the female in solicitation displays (either for food or copulations; it was not possible to differentiate between these two). Female solicitation calls can be heard at a great distance from the nest, and could always be recorded from the viewpoint. Finally, we recorded all territorial intrusions (i.e. the entry of an osprey other than the focal

pair into the breeding territory, which usually resulted in defence or protection displays by pair members; see Bretagnolle & Thibault 1993). Intruders could sometimes be sexed, when they landed at the nest or nearby (the perched displays being sexually dimorphic; see Bretagnolle & Thibault 1993), but could not be individually identified.

Behavioural observations lasted 3–5 h, and each pair was observed every 3–5 days, with a rotational schedule from dawn to dusk (pairs were sampled once between 0700 and 1100 hours, once between 1100 and 1500 hours and once between 1600 and 2000 hours, and so on). We conducted 129 observations (totalling 575.5 h) on 23 pair-years between 1991 and 1997. Each pair-year was observed for 25 h on average (range 10–57 h). Behavioural observations were conducted until laying of the last egg, and continued during the incubation for nine pair-years. Study pairs ranged from solitary to loosely colonial. The number of neighbouring breeding pairs within a 5-km radius of the nest (range 0–6) was used as a measure of local density. Laying onset was determined during focal observations, when we checked the nest content from the viewpoint. Laying date and breeding density of study pairs did not differ significantly between years (Kruskal–Wallis test: $\chi^2_3=2.3$ and 2.2, respectively, NS). General monitoring (see above) allowed us to detect between-year mate changes during the study period. Mate change (i.e. whether mates had bred together the previous year) was assessed for 18 study pair-years, pair bond length (i.e. the number of consecutive years mates bred together) for 17 pair-years (for which individual identification was available for all years since first breeding or since a mate change), and prelaying duration was known for 15 of these pairs.

Data from focal observations were analysed on a relative date basis (with day 0 being the day the first egg was laid for a given pair). We investigated seasonal patterns of behaviours by considering the average frequency of pair behaviours calculated over 5-day periods relative to day 0. The length of the fertile period (i.e. the period when a copulation can lead to fertilization) depends on the maximum duration of viable sperm storage (7–42 days, depending on bird species), the time interval between fertilization of an egg and its subsequent deposition, and the number of days in which the clutch is completed (Birkhead & Møller 1992; Birkhead 1998). Eggs are laid every 2–3 days in the osprey (Cramp & Simmons 1980; Birkhead & Lessells 1988; personal observation), so we considered that the fertile period ended on day 3 or 5 for clutches of two or three eggs, respectively. The onset of the fertile period, however, was not known. The earliest observations were conducted 41 days prior to laying, so females might have been fertile during the whole study period. When looking for associations between behaviours, we thus considered the average frequency of pair behaviour calculated over the whole study period, until the end of the fertile period. When testing predictions related to a fertilization function (paternity assurance) of frequent copulations, we also considered the average frequency of behaviours over a shorter, subjective, period, from day –10 to the end of the fertile period (hereafter

referred as to the late prelaying period) when females were fertile, and when the risk of an EPC resulting in fertilization was potentially the greatest.

Statistical Analyses

For statistical analyses we used SAS 8.00 (SAS 1999). Data were first checked for normality and transformed (with a log transformation) when necessary; if the data were still not normally distributed we used nonparametric statistics. *P* values are two tailed. All data are expressed as mean \pm SD. The sample size for behavioural observations included at least 18 females and 17 males, and 20 pairs, three of which were sampled in 2 different years. Because of the latter, and to deal with potential pseudoreplication problems and year effects, we used Generalized Linear Mixed models (SAS 1999), including pair and year as random effects, to analyse behavioural data. We tested for associations between frequencies of behaviours, or between frequency of a particular behaviour and pair bond length, using univariate linear mixed models. The mean frequency of behaviours was calculated over the whole prelaying period, or over the late prelaying period only (see above). Similarly, we used mixed models with pair and year included as random effects to test for associations between copulation duration, success and courtship feeding or fish size. Copulation duration was fitted with a normal distribution and a log link function (mixed procedure, SAS 1999) and copulation success was fitted with a binomial distribution for the response variable and a logit link function (Glimmix procedure, SAS 1999).

RESULTS

Timing and Frequency of Copulations

Within-pair copulations

The prelaying period (from pair settlement until laying onset) lasted on average 39 ± 12 days (range 26–70, $N=19$ pair-years). WPC frequency increased early in the prelaying period, was overall high from day –30 until laying began, with a slight peak during the 5 days before laying, and rapidly decreased during laying (Fig. 1a). Overall, 57.9% of WPCs were successful. The success of a copulation was related to its duration (Glimmix model: $F_{1,244}=64.75$, $P<0.0001$): all copulations lasting >10 s resulted in cloacal contact while all those lasting <6 s were unsuccessful.

Taking into account the duration of the prelaying period, the average copulation rate of study pairs, and given the 13 h of daylight (the activity period of Corsican ospreys in March–April), we estimated a mean \pm SD of 288 ± 111 copulations/clutch (range 139–578, $N=16$ pair-years) and 167 ± 81 successful copulations/clutch (range 51–341, $N=16$).

Extrapair copulations

We observed four EPC attempts. Three of these were rejected by the female, and were thus unsuccessful. These

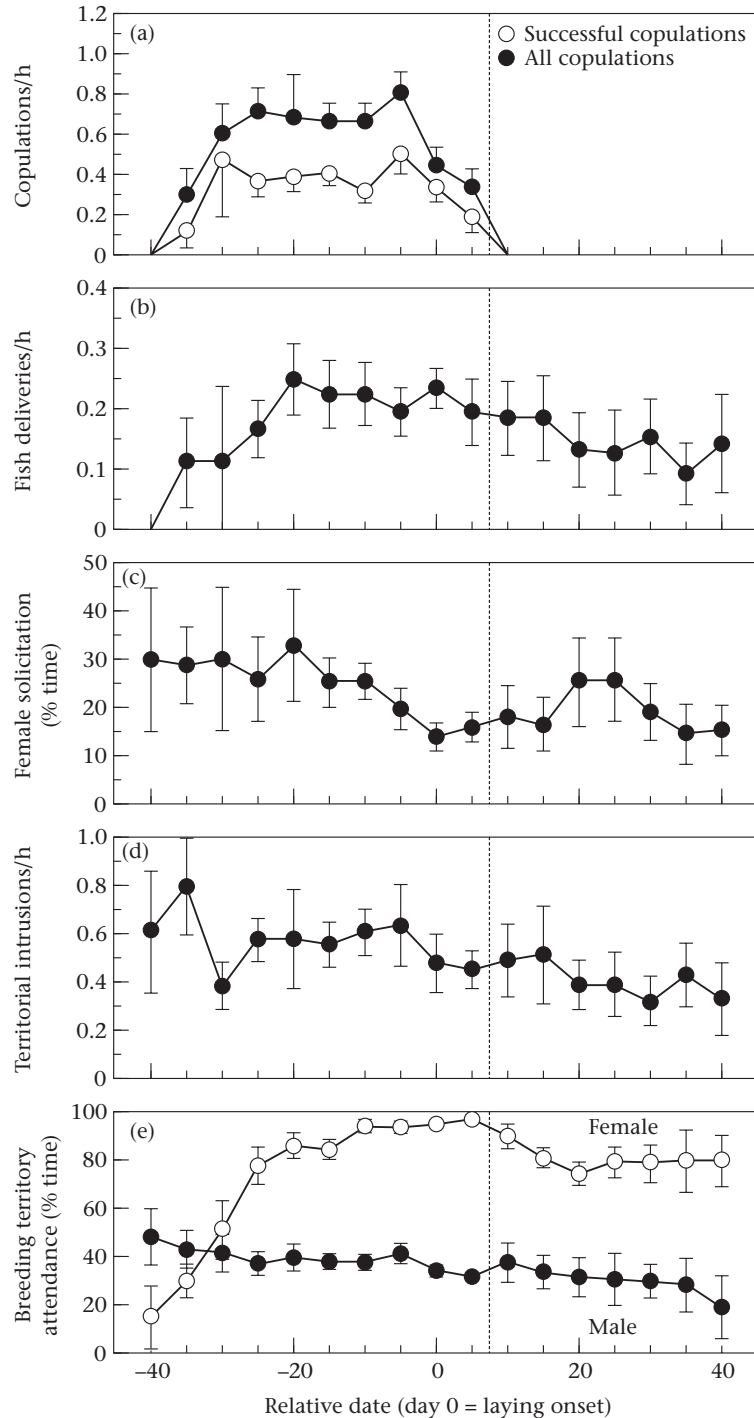


Figure 1. Frequency of behaviours ($\bar{X} \pm \text{SE}$) relative to laying onset (day 0). (a) Within-pair copulations and successful copulations; (b) male fish deliveries; (c) female solicitations; (d) territorial intrusions; and (e) male and female attendance (% time within the breeding territory). Based on 575.5 h of observation conducted on 23 pair-years. The vertical line sets the limit between the end of the fertile period and the incubation period.

failed EPC attempts occurred early in the prelaying period (between day -41 and -21) and involved two females, which were in protection display when the male tried to copulate. The successful EPC was observed on day -25 and was not forced. It occurred during an absence of the legitimate male, and was by a neighbouring breeding

male whose nest was 500 m from, and in sight of, that of the cuckolded male. Successful EPCs accounted for 0.4% of 248 observed copulations. Mate changes during the prelaying period were also observed in four (17%) of the 23 study pair-years; they occurred 35–20 days before laying and were likely to be divorces since both the

Table 1. Results of the univariate mixed models testing for associations between the frequencies of pair behaviours

Dependent variable	Explanatory variable	df	F	P	Parameter estimate±SE
Copulation rate	Courtship feeding rate	1,19	8.36	0.009*	1.01±0.35
	Fish size	1,19	5.04	0.037	0.37±0.16
	Female solicitation rate	1,19	9.90	0.005*	-0.13±0.04
	Intrusion rate	1,19	15.81	0.001*	-0.58±0.15
Successful copulation rate	Courtship feeding rate	1,19	27.52	<0.0001*	1.41±0.27
	Fish size	1,19	6.78	0.018	0.41±0.16
	Female solicitation rate	1,19	14.94	0.001*	-0.15±0.04
	Intrusion rate	1,19	11.14	0.004*	-0.52±0.16
Time male present	Intrusion rate	1,19	19.06	<0.001*	0.88±0.20
Courtship feeding rate	Time male present	1,19	15.87	<0.001*	-0.23±0.06
Fish size	Time male present	1,19	9.78	0.006*	-0.45±0.14
Solicitation rate	Courtship feeding rate	1,19	9.60	0.007*	-4.12±1.49
	Fish size	1,19	24.82	<0.0001*	-2.59±0.52
	Time male present	1,19	26.87	<0.0001*	2.13±0.41

Variables were log transformed for normalization. All models included pair and year as random effects.

* $P < 0.05$, after sequential Bonferroni adjustment.

previous year's mate and the new mate were seen at the nest. One was a male change and the other three female changes.

Courtship Feedings and Within-pair Copulations

Courtship feeding (male fish delivery) rate increased early in the prelaying period, (from settlement to day -20), and tended to decrease throughout the incubation period (Fig. 1b). Females solicited particularly frequently early in the prelaying period, when pairs settled on breeding sites, and the frequency decreased thereafter (Fig. 1c). Mean female solicitation rate was significantly negatively related to the average male courtship feeding rate and to the average size of fish delivered by the male (Table 1). Mean WPC rate and successful copulation rate were both significantly positively related to male fish delivery rate (Table 1, Fig. 2), tended to increase with the average size of fish delivered, and were significantly negatively related to female solicitation rate (Table 1). Copulation rate and successful copulation rate were thus overall positively associated with the amount of food provisioned to the female.

We further analysed, for each copulation, whether the male had brought a fish during the previous 60 min. This could be assessed for 210 copulations. Only 70 (33.3%) of these copulations were preceded by a fish delivery. Copulations were, however about three times more frequent than fish deliveries. Of 67 fish deliveries 68.7% were followed, during the next 60 min, by at least one copulation. Copulations lasted significantly longer after a courtship feeding (8.4 ± 3.3 s, $N=70$) than after a return without fish (6.6 ± 3.7 s, $N=140$; mixed model: $F_{1,206}=11.7$, $P < 0.001$). The probability of copulating successfully was also significantly higher after a fish delivery (0.71) than after a return without fish (0.46; Glimmix model: $F_{1,206}=10.3$, $P < 0.002$). Furthermore, the mean duration of copulations following a fish delivery increased signifi-

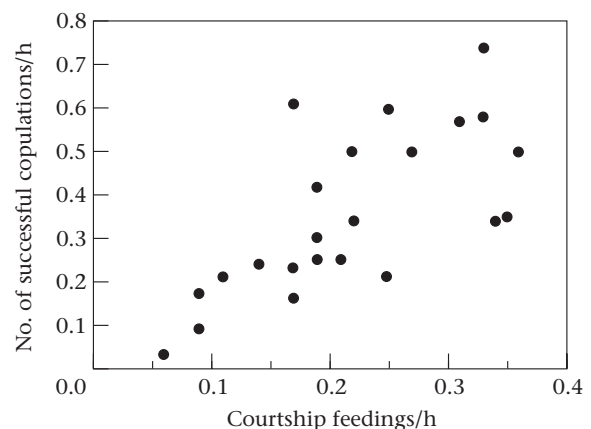


Figure 2. Relation between mean male fish delivery rate to his mate and mean within-pair successful copulation rate (calculated over the whole prelaying period, until the end of the fertile period).

cantly with the size of the fish (mixed model: $F_{1,66}=7.5$, $P < 0.001$; Fig. 3). The probability of copulating successfully after courtship feeding also increased significantly with fish size (Glimmix model: $F_{1,61}=6.52$, $P < 0.013$; Fig. 3).

Territorial Intrusions and Pair Behaviour

Territorial intrusions were frequent throughout the prelaying and incubation periods, with no obvious seasonal peak in territorial intrusion frequency, in particular prior to and during laying (Fig. 1d). The sex of intruders was assessed for 46 prelaying territorial intrusions. These observations suggested that male and female territorial intrusions were overall equally frequent (54% of intruders were males, $N=46$). This proportion was not significantly different during the late prelaying period (from day -10 until the end of fertile period), when 56% of intruders ($N=27$) were males ($\chi^2_1=0.01$, NS). Overall, territorial

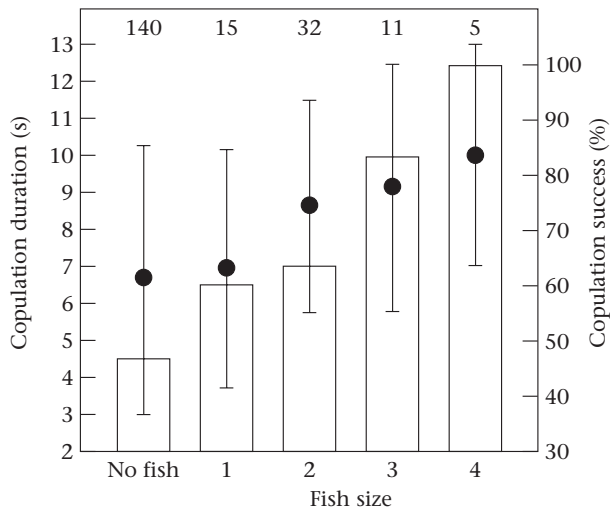


Figure 3. Duration (●) and success (□; with cloacal contact) of copulations ($\bar{X} \pm SE$) following male fish deliveries according to fish size index. The duration and success of copulations not preceded by a courtship feeding are also illustrated for comparison. Sample size (above histograms) refers to the number of copulations.

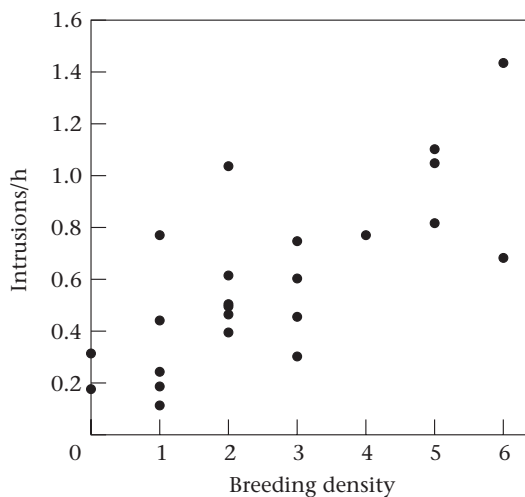


Figure 4. Mean territorial intrusion frequency according to breeding density (number of breeding neighbours within 5 km). $N=23$ pair-years.

intrusion frequency increased significantly with local breeding density (mixed model: $F_{1,19}=20.0$, $P<0.001$; Fig. 4). A similar relationship was found for mean territorial intrusion rate during the late prelaying period only (mixed model: $F_{1,19}=19.4$, $P<0.001$).

Contrary to predictions of the paternity assurance hypothesis, we found that pairs facing frequent territorial intrusions copulated less frequently than others. Both mean WPC rate and successful WPC rate were significantly negatively related to mean territorial intrusion rate (Table 1). For the late prelaying period only, there was also a tendency for WPC rate and successful WPC rate to decrease with increasing territorial intrusion frequency (mixed models: $F_{1,19}=4.08$ and 5.07 , $P=0.06$ and 0.04 , respectively).

Male territory attendance varied little throughout the prelaying and incubation periods (Fig. 1e) but was significantly positively related to territorial intrusion frequency (Table 1). Mean courtship feeding rate and mean fish size were significantly negatively related, and mean female solicitation rate was significantly positively related, to male territory attendance (Table 1). Thus, the more frequent the territorial intrusions, the more time the male spent within his breeding territory, the less food he delivered to the female and the more she solicited. The latter might explain why pairs facing frequent territorial intrusions copulated less than others (see above).

Mate Fidelity and Copulation Behaviour

Neither laying date nor prelaying duration differed significantly between newly formed and older pairs, or varied significantly according to pair bond length (Table 2). WPC rate and success, however, did vary with mate fidelity. First, copulation frequency relative to laying onset differed between new and old pairs (Kolmogorov–Smirnov test: $D=0.44$, $N=15$, $P<0.05$; Fig. 5): new pairs copulated more frequently than old pairs early in the prelaying period, with a peak in WPC frequency 20–25 days before laying (whereas in old pairs, WPC rate increased from pair settlement, and peaked only on day 5 prior to egg laying; Fig. 5). Second, new pairs copulated more times per clutch than old pairs (Table 2) and the number of copulations per clutch decreased significantly with increasing pair bond length (Table 2, Fig. 6). In contrast, mean WPC success was significantly lower in new than in old pairs, and increased significantly with pair bond length (Table 2, Fig. 6). Overall, the number of successful copulations per clutch did not differ significantly between new and old pairs, or according to pair bond length (Table 2, Fig. 6).

DISCUSSION

Corsican ospreys copulated over a long period (45 days) and at a high rate, with on average 288 copulations and 167 successful copulations per clutch. Many copulations were unsuccessful (cloacal contact, and thus sperm transfer, was not achieved in 42% of the copulations) as found in other studies (Poole 1985; Birkhead & Lessells 1988). We discuss below the effects of territorial intrusions, courtship feeding by the male and mate fidelity on the rate and behavioural success of WP copulations, and the possible fertilization and non-fertilization functions of frequent WPCs in Corsican ospreys.

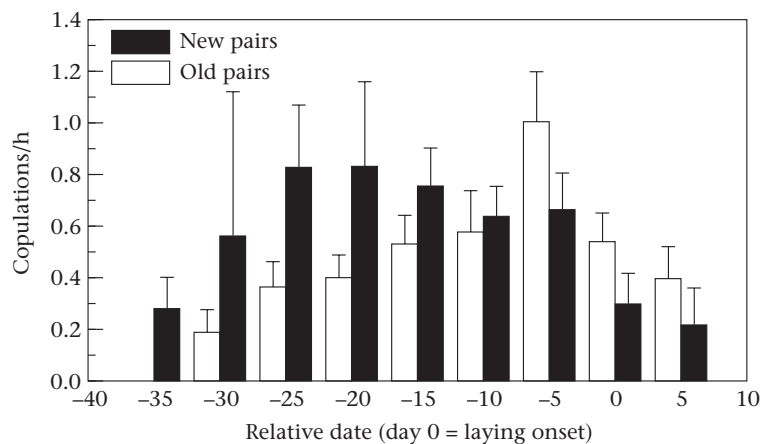
Territorial Intrusions and Paternity Assurance

Many bird species copulate frequently, probably as a means to ensure paternity (Birkhead & Møller 1992, 1998). High copulation rates are found particularly in colonial bird species, and in courtship-feeding bird species, such as raptors (Birkhead et al. 1987; Birkhead & Møller 1992). These might be related to an increased EPC

Table 2. Behavioural differences between pairs with or without mate change, relative to the previous breeding season, and according to pair bond length (number of successive years that a pair had bred together)

	Mate fidelity				Pair bond length		
	No change	Mate change	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	
Laying date	2 April±8 (8)	3 April±13 (10)	0.09	NS	0.07	NS	(17)
Prelying duration (days)	37.8±10.2 (7)	42.1±14.3 (9)	1.23	NS	0.39	NS	(15)
Number of copulations per clutch	235±84 (7)	329±116 (9)	5.12	<0.05	10.11	<0.01	(15)
Number of successful copulations per clutch	166±64 (7)	168±97 (9)	0.01	NS	0.12	NS	(15)
Copulation success (%)	72.1±9.9 (8)	49.0±14.6 (10)	13.72	<0.01	13.14	<0.01	(17)

Sample sizes (number of pair-years) are given in parentheses. Mixed models testing for differences between pairs with or without mate changes, or according to pair bond length included pair and year as random effects. $df=1,11$ except for laying date (1,14) and copulation success (1,15).

**Figure 5.** Frequency of within-pair copulations ($\bar{x} \pm SE$) relative to laying onset (day 0) in pairs that changed or kept the mate of the previous breeding season.

risk at high breeding density, and to mate-guarding constraints associated with courtship feeding (Møller 1987a; Birkhead & Møller 1992). Comparisons across bird species showed that EPC frequency, but not the frequency of extrapair paternity, the outcome of sperm competition, was positively related to breeding density (Møller & Birkhead 1993; Westneat & Sherman 1997). The idea of an increased cuckoldry risk at high density is poorly supported by comparisons across raptor species (Simmons 2000) but was supported by intraspecific comparisons in several semicolonial raptors: pairs breeding at high density face more frequent territorial intrusions, a greater EPC risk, and also copulate more frequently than others (e.g. Simmons 1990; Korpimäki et al. 1996; Arroyo 1999; Mougeot 2000; Vidén & Richardson 2000). If Corsican ospreys copulate frequently to ensure paternity, we expected males facing frequent territorial intrusions, and potentially a greater EPC risk, to copulate more frequently than others. We found that osprey pairs breeding at higher density (with more neighbouring breeding pairs) faced more frequent territorial intrusions but, in contrast to predictions, copulated less frequently than others. WPC rate was significantly negatively related to territorial intrusion frequency, and tended to be negatively related to territorial intrusion frequency during the most critical late prelying period, when the risk of an

EPC resulting in fertilization is greatest. These results thus contrast with those from other raptor species, and also with those from another osprey population, in which both EPCs and territorial intrusions were more frequent, and ospreys copulated more than twice as frequently in a high-density than a low-density area (Vidén & Richardson 2000).

Although we observed extrapair copulations, their incidence was low (0.4% of copulations, $N=248$), despite a high breeding density (average internest distances of 1.5–2 km) and frequent territorial intrusions. A similar incidence was found in Scotland (0.3%), at a much lower breeding density, with territorial intrusions ca. 15 times less frequent than in Corsica (Birkhead & Lessells 1988). In Sweden, EPCs were 10 times more frequent (3.3% of copulations, $N=91$) in a high-density area (average internest distances of 1.2–1.6 km; Vidén & Richardson 2000). Observations suggest that females reject most EPC attempts, are aggressive and do not cooperate with strange males (see also Poole 1985, 1989; Birkhead & Lessells 1988; Vidén & Richardson 2000). Mate changes during the prelying period were observed during this study and may have resulted in sperm competition if females copulated with different males before re-pairing. However, as well as the EPCs, mate changes occurred early in the prelying period (>20 days before laying), and

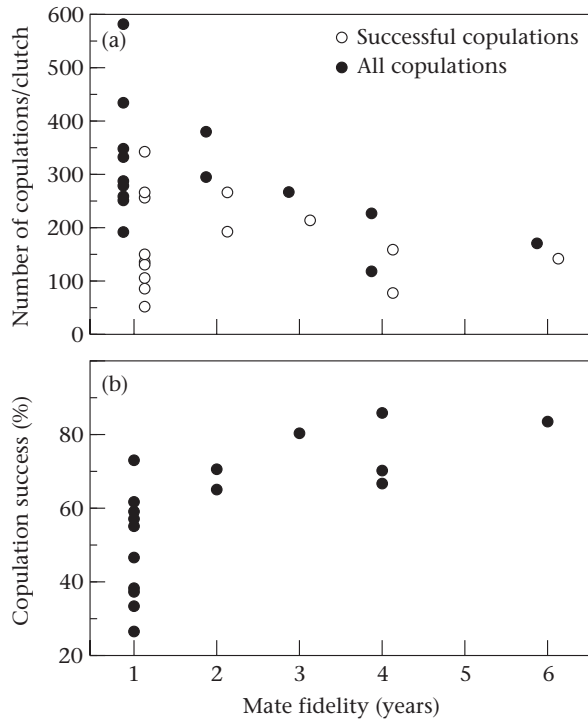


Figure 6. (a) Number of within-pair copulations and successful copulations per clutch and (b) mean copulation success (% of copulations with cloacal contact) according to mate fidelity (number of successive years a pair bred together).

copulations might then have had little chance of fertilization. Several bird species probably use EPCs for appraisal and future acquisition of mates (e.g. Colwell & Oring 1989; Wagner 1991). The EPC and EPC attempts observed in this study (early in the prelaying period) might thus have been used for mate assessment rather than for fertilization.

Given the high parental investment by male raptors, intense paternity guards are likely to have been selected, even when the risk is small (Møller 1987a). We found that male attendance increased significantly with territorial intrusion frequency, suggesting that males' response to intruders was to spend more time near the nest site and the female. Males might thus rely on mate guarding (increased nest attendance) rather than frequent copulations when facing frequent territorial intrusions and a potentially increased cuckoldry risk. Their behaviour might be aimed primarily at preventing EPCs, by deterring male intruders and dissuading their female from engaging in extrapair matings. This could explain the overall low incidence of EPC. Because of increased surveillance the risk of paternity loss and the need to copulate frequently might not have been higher in pairs facing frequent territorial intrusions. Mate guarding by following is not usually expected in raptors, because it conflicts with the food provisioning of the female (Birkhead & Møller 1992). Several studies have nevertheless shown that male raptors perform some mate guarding while maintaining their food-provisioning rate (Birkhead & Lessells 1988; Simmons 1990; Korpimäki et al. 1996;

Mougeot 2000; Mougeot et al. 2001). Our results suggest that males increased attendance to the detriment of the food provisioning of the female: the more time the male spent within his breeding territory, the less frequently he delivered fish, and the smaller the fish he brought back. Reduced provisioning rates might also explain why pairs facing frequent intrusions copulated less frequently than others, since both attempted and successful WPC rates were positively associated with the amount of food the female received (see below).

Intruders may visit nests for several reasons, which are expected to produce different seasonal patterns (see Møller 1987b). In Corsica, intruders were as often males as females, and territorial intrusion rate did not peak prior to and during laying, as predicted by the sperm competition hypothesis (Møller 1987b; e.g. Mougeot 2000). The observed seasonal pattern (Fig. 1d) would be best explained by the nonterritory holder hypothesis (intruders prospecting for a vacancy) rather than by the sperm competition (males seeking EPCs prior to and during laying) or by the territory establishment hypotheses (frequent intrusions early in the breeding season to establish territory boundaries; see Møller 1987b). The nonterritory holder hypothesis rests upon the assumption that territories are in short supply and/or that some territories are of a higher quality than others. Shortage of breeding territories and intense competition for nest sites were likely in Corsica, where the population has gradually increased and almost stabilized in the late 1990s (Thibault et al. 1995), and new breeding pairs used artificial nests almost immediately. Although some males may have visited nests seeking EPCs, most intruders might have been individuals looking for a breeding site or a mate.

Courtship Feeding and Copulations

The female immediate benefits, future material benefits and female mate guarding of male hypotheses have predictions related to the association between copulations and courtship feedings, either as a direct benefit, or as an indicator of male quality (Hunter et al. 1993). We found a positive association between WPC rate and success and male food-provisioning rate: the more frequently the male delivered fish, the more often the pair copulated and did so successfully. There was also a tendency for attempted and successful WPC rates to be positively related to the average size of fish provisioned to the female. We also found short-term associations between courtship feeding and copulations: the duration and success of WPCs were significantly higher after a fish delivery than after a return without fish, and increased significantly with the size of the fish. Altogether, the results suggest that the frequency of successful copulations increased with the amount of food the female received. Copulations may be initiated by males or females, but their duration and success are probably mainly under female control (Poole 1985; Birkhead & Lessells 1988). Our results showed that poorly fed females (those receiving fish less frequently and smaller fish) were

giving more solicitation calls, and were also probably more reluctant to copulate and to do so successfully.

Associations between copulations and courtship feedings have been found in other raptors (e.g. Arroyo 1999; Mougeot 2000), as well as in other courtship-feeding birds, such as seabirds (e.g. Tasker & Mills 1981; Neuman et al. 1998), with courtship feeding enhancing the behavioural success of copulations. The courtship feeding rate of males influences the female's choice of mate (e.g. Newton 1986; Simmons 1988) and is a reliable indicator of future investment in reproduction, that is future provisioning rate, in several bird species (e.g. Nisbet 1973; Wiggins & Morris 1986), including the osprey (Green & Krebs 1995). Observations from Corsican ospreys also showed that male provisioning rates in the incubation and chick-rearing periods were positively correlated with prelaying courtship feeding rate (unpublished data). Courtship feeding by the male may also be a means of maintaining mate fidelity (e.g. Tasker & Mills 1981; Fitch & Shugart 1984; Poole 1985). Frequent copulations associated with courtship feeding might thus function for mate retention, as a means to ensure mate fidelity and future male investment in reproduction. In the osprey, poorly fed females have been observed begging for food, and eventually EPCs, from passing males (Poole 1985; Birkhead & Lessells 1988), and are more likely to change mate (Poole 1985). In Corsica, prelaying mate changes were also associated with low provisioning rates by the male (<0.15 fish delivery/h). Females might thus benefit from soliciting and accepting frequent copulations from a good provisioning male by dissuading him from engaging in EPCs or from changing mate (female mate guarding of male hypothesis; Petrie 1992) and by ensuring future paternal care (future material benefits hypothesis; Hunter et al. 1993).

Mate Fidelity and Copulation Behaviour

The pair bonding and mate assessment hypotheses have predictions related to seasonal patterns in within-pair copulation frequency and mate fidelity. Several species show a bimodal seasonal pattern in copulation rate, with a first peak early in the prelaying period and a second before and during laying. The first peak might be related to nonfertilization functions of copulations, such as mate assessment and pair bonding, and the second to paternity assurance (e.g. Negro et al. 1992; Mougeot 2000). New pairs, in which mates have to assess each other and improve their pair bond, are also expected to copulate more frequently than experienced pairs. We found that newly formed osprey pairs copulated more frequently than experienced pairs, but with a lower success (see also Poole 1985; Birkhead & Lessells 1988 for similar findings on copulation success). Copulation success increased with pair bond duration, suggesting that cooperation between mates ensuring successful copulations increases with mate fidelity. New pairs copulated more frequently than experienced pairs particularly early in the prelaying period, supporting the idea that frequent copulations, even if not successful, might then be part of a pair-bonding and mate assessment process. Newly

formed pairs were also more likely to change mate than others; the fact that they copulated more frequently than others was also consistent with a mate retention function of frequent WPCs.

Overall, we thus found little support for sperm competition to be the main cause of high copulation rates in Corsican ospreys. Although we cannot reject the idea that frequent copulations might function in paternity assurance, the results suggest that males rely on mate guarding rather than copulations to prevent paternity loss. Other functions, and particularly nonfertilization functions, were more likely to explain frequent copulations. The results are consistent with several nonexclusive functions: mate assessment, pair bonding and mate retention. New pairs copulated more frequently than others early in the prelaying period probably for mate assessment and pair bond improvement, and females traded frequent and successful within-pair copulations for food possibly to ensure mate fidelity and future investment in reproduction from good food-providing males.

Differences from Other Osprey Populations

Information on osprey copulation behaviour is available for several populations, from Massachusetts, U.S.A. (Poole 1985), Scotland, U.K. (Birkhead & Lessells 1988), British Columbia, Canada (Green & Krebs 1995) and Sweden (Vidén & Richardson 2000). Our results contrast with those from other osprey populations, in which a paternity assurance function of copulations was supported (Birkhead & Lessells 1988; Vidén & Richardson 2000) and no clear association between food transfer and copulation rate or success was found (Birkhead & Lessells 1988; Green & Krebs 1995; Vidén & Richardson 2000). In one study, however, poorly fed females were less willing to copulate and less faithful to their mates than well-fed females (Poole 1985). These different findings suggest that the functions of frequent WPCs, or their relative importance, differ between osprey populations.

One of the main differences between populations was that the Corsican population is sedentary, whereas all the other study populations are migratory. Sedentary Corsican ospreys have a long prelaying period (ca. 40 days), whereas in migratory populations the prelaying period was much shorter (ca. 14 days in Scotland and Sweden, 20 days in Massachusetts and British Columbia; Poole 1985; Birkhead & Lessells 1988; Green & Krebs 1995; Vidén & Richardson 2000). Although copulation rates and provisioning rates were similar across populations, Corsican ospreys copulated more per clutch overall (ca. 290) than those from other populations (160 in Scotland, Birkhead & Lessells 1988; ca. 150 in Sweden, Vidén & Richardson 2000). In several raptors with an extended copulation period, seasonal variation of copulation rates shows a bimodal pattern, with a first peak early in the prelaying period, and a second peak prior to egg laying, when the female is fertile (e.g. Møller 1987a; Negro et al. 1992; Mougeot 2000). In two raptor species, copulation rate correlated positively with courtship feeding rate early in the prelaying period (first peak), but not during the fertile period (second peak), when it was then

adjusted to breeding density and EPC risk (e.g. Arroyo 1999; Mougeot 2000). Copulations might thus have non-fertilization functions early in the prelaying period and a fertilization/paternity assurance function before and during laying (Negro et al. 1992; Villarroel et al. 1998; Mougeot 2000). A long prelaying period might allow more time to evaluate different partners and favour mate changes rather than EPCs; this could favour non-fertilization functions of copulations, such as mate assessment, pair bonding and mate retention, rather than a paternity assurance function, as our results suggest for Corsican ospreys. In migratory populations, time constraints might give fewer opportunities for prelaying mate changes, favour an EPC strategy in females and fertilization (paternity assurance) functions of frequent WPCs.

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