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COPULATION BEHAVIOR IN THE OSPREY IN RELATION TO BREEDING DENSITY[1]

PER WIDÉN
Department of Nature and Environment, Karlstad University, S-651 88 Karlstad, Sweden, e-mail: per.widen@kau.se

MALENA RICHARDSON
Arabygatan 22, S-35236 Växjö, Sweden

Abstract. We studied Osprey (*Pandion haliaetus*) copulation behavior in two geographically separated subpopulations with different breeding densities. In the low density area, the nearest neighbor distance between nests was 7 km, and in the high density area 1.4 km. The frequency of successful copulations was significantly higher in the high density area, 0.65 hr^{-1} as compared to 0.30 hr^{-1}. Extra-pair copulations were recorded only in the high density area, and extra-pair visits by intruding Ospreys also were more frequent there. There was no relation between copulations and delivery of food or nest material. Our results support the idea that copulation behavior is related to breeding density, but whether or not this is a result of sperm competition or some other social factor remains undetermined.

Key words: copulation, Osprey, Pandion haliaetus, *sperm competition.*

INTRODUCTION

It has long been recognized that the function of copulation behavior in raptors is more than just fertilization (Newton 1979). Birkhead et al. (1987) examined possible explanations for interspecific differences in copulation frequency in birds. They found that most evidence supported the sperm competition hypothesis, which states that high copulation frequency is a strategy for paternity assurance in species such as raptors, that cannot guard their mates during the fertile period, and therefore are susceptible to extra-pair copulations. Møller (1987) showed that among raptors, copulation frequencies were in fact highest in species where the male provides the female with all her food prior to laying, spending much time away from her in the fertile period.

In many socially monogamous birds, copulations between non-mates, i.e., extra-pair copulations (EPC), are frequent (Westneat et al. 1990, Birkhead and Møller 1992) and can result in extra-pair paternity (Westneat 1987, 1990, Birkhead and Møller 1992). Consequently, selection should strongly favor behavior that reduces the risk of being cuckolded. On the other hand, at least some raptor species copulate well outside of the fertile period (Holthuijzen 1992), a behavior that can not be explained by sperm competition.

The Osprey (*Pandion haliaetus*) is a fish-eating raptor that is found throughout the forested parts of Fennoscandia. Males are unable to guard their mates because they provide them with nearly all their food during the fertile period, ranging over large areas. While the male is away, the female remains at the nest site (Poole 1989), leaving her susceptible to extra-pair copulations. Birkhead and Lessells (1988) report that Ospreys copulate on average 59 times per clutch, far more frequent than would be needed to fertilize the clutch. The Osprey is unusual in that it breeds in extremely varying densities in different areas, from very dispersed to colonial, but with little variation in density between years within each area. Thus, it is an ideal species for comparisons of copulation behavior between subpopulations with different population densities. In this paper we investigate how dispersion affects copulation behavior in the Osprey by comparing two geographically separate subpopulations, with different breeding densities.

In some bird species, males trade food for copulations (Tasker and Mills 1981), and this could be one function of courtship feeding found in most raptors during the fertile period (Poole 1985, Møller 1987). Therefore, we also investigate whether copulations are related to delivery of food or nest material.

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METHODS

This study was performed during the breeding seasons of 1996 and 1997 in two areas where breeding densities of Ospreys differed substantially. The low density area is situated in the boreal forest zone (Sjörs 1965) of Värmland in central Sweden (59°40'N, 12°15'E). In this area, Ospreys nested with a mean (± SD) nearest neighbor distance between occupied nests of 7.8 ± 5.8 km (range 1.5–16.5, $n = 9$) in 1996, and 6.2 ± 4.9 km (range 1.5–18.0, $n = 10$) in 1997.

The high density area was situated in Småland, southern Sweden, about 350 km SSE of the low density study area, in the boreo-nemoral zone (Sjörs 1965). In 1996, the study was performed at Lake Åsnen (56°35'N, 14°45'E), and in 1997 at Lake Helgasjön (56°58'N, 14°45'E). These, and other large lakes in the area, hold very dense Osprey populations, about 40–50 pairs at Lake Åsnen, and about 15 pairs at Lake Helgasjön (Hallberg and Hallberg 1993). The Osprey population at Lakes Åsnen and Helgasjön was not censused in 1996 or 1997, but in 1993 the average nearest neighbor distance between occupied nests was 1.2 ± 0.8 km (range 0.3–4.1, $n = 48$) at Lake Åsnen (Lars-Olof Hallberg, pers. comm.) and 1.6 ± 0.4 km (range 1.1–2.6, $n = 14$) at Lake Helgasjön (estimated from Hallberg and Hallberg, unpubl. data). The breeding density does not fluctuate much between years, and it can be assumed that the densities were about the same when this study was performed (Lars-Olof Hallberg, pers. comm.).

The high density area has been surveyed for many years (Hallberg and Hallberg 1993), and it is unlikely that there existed unknown occupied nest sites. The low density area was less well known, and nest sites may have been missed. However, the density we found there is typical for much of forested Fennoscandia, and we are confident that few, if any, nests were missed. In southwestern Sweden, Eriksson (1985) reported an average distance to the nearest occupied nest of 7.9 km (range 2.5–25.4, $n = 19$), which is similar to our low density area.

Observations started when the pair had returned from migration in early April, and terminated when incubation started.

The nests were all built in the tops of pine trees (*Pinus sylvestris*) and hence they were conspicuous and easily observed from a distance. With few exceptions, all copulation activity takes place on the nest (Poole 1989).

In 1996, we observed three nest sites in the low density area and four in the high density area. In 1997, we moved to other nest sites, and observed three in the low density area and three in the high density area. Thus, our data comes from a total of 13 nest sites. Because the birds were not marked, individual recognition was difficult, especially between years. However, we assume that the different nest sites also represent different pairs, and hence they are treated as independent samples.

Some raptors show a marked diurnal pattern of copulation with a peak in the early morning (Birkhead and Lessells 1988, Simmons 1990). In order to record as many copulations as possible, we therefore observed the nests for 6 hr day^{-1}, starting 30 min before sunrise. With a few exceptions in the low density area in 1996, only one nest per area could be observed at a time, and hence we moved between nest sites, observing one nest per area and day.

Observations were made from positions where it was possible to see the nest without disturbing the birds. Topography made it possible to choose sites with good view into the nest. Not all copulation attempts were successful, and a copulation was recorded as successful when the male mounted the female who tilted forward, and they appeared to achieve cloacal contact, otherwise it was recorded as an unsuccessful copulation attempt (Birkhead and Lessells 1988). Because the birds were not marked, we could not with absolute certainty determine when extra-pair copulations occurred. We used behavior and individual differences in the plumage as cues to determine when a copulation was in fact extra-pair.

Total observation time was 172 hr in the low density area, and 96 hr in the high density area. The temporal distribution of the observation time, in relation to start of incubation, is shown in Figure 1.

Statistical tests follow methods described in Sokal and Rohlf (1995). Means are presented ± SD. Statistical tests are two-tailed when possible.

RESULTS

COPULATION FREQUENCY

A total of 166 copulations was observed, 75 in the low density and 91 in the high density area.

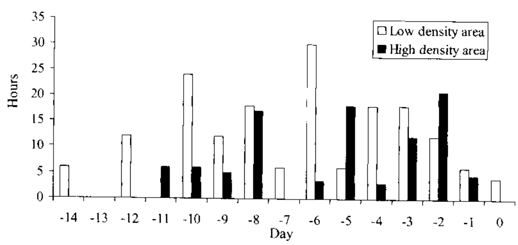

FIGURE 1. Temporal distribution of duration of total observation time of Ospreys in low and high density areas, in relation to start of incubation (= day 0).

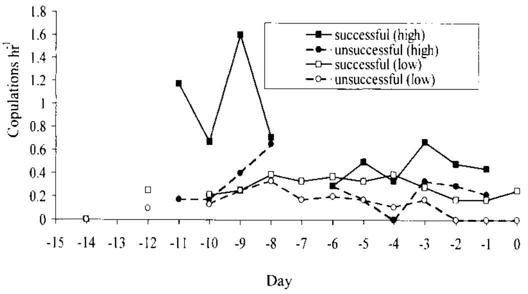

FIGURE 2. Temporal pattern of successful and unsuccessful copulations of Ospreys, relative to start of incubation (= day 0). In the high density area, observations started on day −11, and no observations were made on days −7 and 0. In the low density area, observations started on day −14, and no observations were made on day −13.

The proportion of copulation attempts that were successful was about the same in the two areas; on average 64% per pair in the low density and 69% per pair in the high density area. All copulations except four were performed on the nest.

Mean frequency of successful copulations in the low density area was 0.25 ± 0.16 hr^{-1} in 1996, and 0.35 ± 0.16 hr^{-1} in 1997, and in the high density area 0.65 hr^{-1} in both years, ± 0.18 in 1996 and ± 0.19 in 1997. There was no significant difference between years (Mann-Whitney *U*-test, $z = 0.89$ and $z = 0.18$, in the low and high density areas, respectively). Average frequency of unsuccessful copulations in the low density area was 0.17 ± 0.08 hr^{-1} in 1996 and 0.13 ± 0.04 hr^{-1} in 1997, and in the high density area 0.27 ± 0.26 hr^{-1} in 1996 and 0.33 ± 0.01 hr^{-1} in 1997. There was no significant difference between years (Mann-Whitney *U*-test, $z = 0.44$ and 1.07, in the low and high density areas, respectively).

To compare copulation frequency, we pooled the results of 1996 and 1997. Mean frequency of successful copulations per pair was significantly higher in the high density area, 0.65 ± 0.17 hr^{-1}, than in the low density area, 0.30 ± 0.15 hr^{-1} ($z = 2.80$, $P < 0.01$, two-tailed). Unsuccessful copulations were also more frequent in the high density area, 0.30 ± 0.19 hr^{-1} versus 0.15 ± 0.06 hr^{-1}, although not statistically significant ($z = 1.72$, two-tailed).

Temporal variation in copulation frequency is shown in Figure 2. It is difficult to discern any clear pattern.

TIMING OF COPULATIONS

Of all successful copulations in the low density area (1996 and 1997 pooled), 13 (27.1%) occurred within 30 sec of male arrival at the nest, and 20 (41.6%) within 30 sec of when he left. This difference was not significantly different from an expected equal distribution of copulations after arrival—before departure ($\chi^2_1 = 2.0$, $P > 0.10$). Corresponding figures for unsuccessful copulations were 7 (26.9%) after arrival and 10 (38.5%) before departure ($\chi^2_1 = 0.5$).

In the high density area, 30 (49.2%) of the successful copulations occurred after arrival, and 23 (37.7%) before departure ($\chi^2_1 = 0.9$). Corresponding figures for unsuccessful copulations were 16 (53.3%) after arrival and 11 (36.7%) before departure ($\chi^2_1 = 0.9$).

COPULATIONS IN RELATION TO DELIVERY OF PREY AND NEST MATERIAL

We found no evidence that a male's return with fish or nest material was immediately associated with copulation. In the low density area, males were observed arriving with fish on 21 occasions, and in none of these cases did he copulate immediately after arrival. We recorded one successful and one unsuccessful copulation before departure, during the same visit as when a fish was delivered. On 137 occasions, males were observed arriving with nest material, and in none of these cases did he copulate immediately at arrival, but on one occasion before departure.

In the high density area, males were observed arriving with fish on 16 occasions, and in none of these cases did he copulate immediately after arrival. One unsuccessful copulation occurred during the same nest visit after a fish delivery, before the male's departure. On 97 occasions, a male was observed arriving with nest material, and in none of these cases did he copulate immediately after arrival. However, nine successful and three unsuccessful copulations occurred before departure, after delivering nest material.

EPCs AND EXTRA-PAIR VISITS

Copulations that were judged to be EPC were recorded only in the high density area; two successful in 1996 at two different nest sites, and one successful and one unsuccessful at one nest site in 1997, and one unsuccessful at a different nest site. The difference in occurrence of EPCs between low- and high-density areas was not statistically significant (Mann-Whitney U-test, $z = 2.10$).

The successful EPCs all occurred in the same way; while the regular male was away an intruding male rapidly approached the nest, landed directly on the female's back, copulated, and flew straight away. The female cooperated, and the whole incident passed in a few seconds. One of the EPC attempts was unsuccessful because the female actively resisted the male. The EPCs were not associated with delivery of food or nest material.

Two of the successful EPCs occurred 5 days before, and one 2 days before, incubation started. The unsuccessful EPCs occurred at 8 and 3 days before incubation, respectively. Other Ospreys sometimes came close to the nest site while the resident pair was there. In the low density area this was observed four times; once a visiting male circled low over the nest while the resident pair was there, once the resident male and female both engaged in chasing the intruder away, and on two occasions the resident male engaged in a short aerial fight with a male intruder. In the high density area, intruding Ospreys were observed 35 times. Usually when an intruding Osprey appeared close to the nest, the female laid down flat in the nest, while the resident male watched the intruder. Sometimes the intruder was chased off, mostly by the resident male alone, sometimes assisted by the female. On four occasions an intruder actually landed in the nest, and stayed there for a short time together with the resident pair; on three of these occasions the intruder brought a fish. No aggression was observed in these cases. In one case when the resident pair was sitting in the nest, an intruding male tried to land on the back of the female, but she did not cooperate.

The difference in occurrence of extra-pair visits between the areas was significantly different from an even distribution ($\chi^2_1 = 49$, $P < 0.001$).

DISCUSSION

COPULATION FREQUENCY AND EPCs

Our main finding was that Ospreys copulated more than twice as frequently in a very high density population, as compared to a low density population. Furthermore, extra-pair copulations were recorded only in the high density area, and the occurrence of intruding Ospreys was significantly higher there. This is consistent with the idea that the higher the density, the greater the risk of EPC.

Simmons (1990) studied copulation behavior in a colony of the African Marsh Harrier (*Circus ranivorus*), comparing copulation frequency in one colony in different years. He found that copulation frequency was higher in years when pairs in the colony bred closer together. Our populations were stable, and as expected we did not find any difference in copulation frequency between years. Korpimäki et al. (1996) studied a population of European Kestrel (*Falco tinnunculus*) over a 3-year vole cycle when both food abundance and breeding density fluctuated strongly. They found that pair copulation frequency was highest in the year of maximum breeding density, and only then was extra-pair fertilization recorded.

Birkhead and Lessells (1988) reported that Osprey copulation frequency followed a temporal pattern, peaking 4–7 days before laying. Our results (Fig. 2) show no such pattern, although this might be due to limited data. If there was in fact such a temporal variation in copulation frequency in our Osprey populations, a difference between areas might appear if there was a systematic difference in the distribution of observation times between the areas, biasing the results. However, the observation times did in fact cover the whole period from arrival until incubation started (Fig. 1). Thus, the observed difference in copulation frequency between the areas can not be explained by any difference in observation pattern.

Birkhead and Lessells (1988) recorded an average of 59 successful copulations per Osprey clutch, in an area in Scotland where average distance between nests was 8 km. Their density was similar to our low density area, but the copulation frequencies can not be immediately compared, because we did not measure the total number of copulations. However, total number of copulations can be approximately estimated, using the average frequency of successful copulations in our low density area, 0.30 hr^{-1}, multiplied by the average daylength, 15 hours, and the duration of the study, 14 days, which gives 63 copulations per clutch. This is an over-estimate, as our data come only from the morning-hour observations, when copulation frequency is highest. Nevertheless, it appears that the copulation frequency found in our low density area was similar to that found by Birkhead and Lessells (1988).

The proportion of successful copulations was higher in our study than reported by Birkhead and Lessells (1988), who found that only 39% of copulations were successful. They showed that newly established pairs had a higher proportion of unsuccessful copulation attempts than old pairs. It is possible that the difference is due to our pairs being older, especially given that the population in Scotland was increasing at the time of study, whereas our populations were stable. Simmons (1990) reported that the proportion of successful copulations in the African Marsh Harrier was 73%, which is similar to our results.

TIMING OF COPULATIONS

If last sperm precedence is an important factor, as suggested by Birkhead and Møller (1992), males could counteract the risk of being cuckolded during their absence by immediate copulation when they return. However, we found no preference for copulating immediately after arrival, nor for copulation immediately before departure. This is in accordance with recent studies of the mechanisms of sperm competition, indicating that number and quality of sperm may be more important than last sperm precedence (Birkhead et al. 1995a, 1995b).

A relation between copulation and courtship feeding has been suggested (Poole 1985, Møller 1987), but was not supported by our data. Neither in Goshawk (*Accipiter gentilis*) (Møller 1987), Osprey (Birkhead and Lessells 1988), or the African Marsh Harrier (Simmons 1990) has any relation between prey delivery and copulation been found. However, in Montagu's Harrier (*Circus pygargus*), copulation rates were related to food presentation in the early pre-laying period (Arroyo 1999), and in Hen Harrier (*C. cyaneus*; Picozzi 1984, Simmons 1988) and Swamp Harrier (*C. approximans*; Baker-Gabb 1981), the females solicited copulations more frequently after males had presented food.

EXPLANATIONS OF COPULATORY PATTERN IN RAPTORS

Birkhead et al. (1987) examined possible explanations for interspecific differences in copulation frequency in birds, and in addition to sperm competition they discussed three other main hypotheses: the fertilization hypothesis states that copulation occurs only as often as necessary to fertilize the eggs; the social bond hypothesis states that frequent copulation is associated with the formation and maintenance of pair bonds; and the predation hypothesis states that copulation frequency and form is related to the risk of predation.

The fertilization and the predation hypotheses cannot explain the differences in copulation frequency between the high and low density Osprey populations. The social bond hypothesis is difficult to test because it makes no clear predictions (Birkhead et al. 1987). However, as pointed out by Westneat et al. (1997), density is likely to affect behavior because as spatial proximity increases, so does the likelihood of direct interaction. Thus, a higher copulation frequency in an area with higher density, as we found, may be consistent with both the sperm competition and the social bond hypothesis.

We did not continue our observations after incubation started, but Birkhead and Lessells (1988) studied Osprey copulation behavior throughout the entire breeding season, and found that copulation frequency dropped to zero within a couple of days after the first egg was laid. There are raptor species that copulate outside the presumed fertile period. Brown (1966) reported that Crowned Eagle (*Stephanoaetus coronatus*) started copulating more than three months before egg-laying, and on one occasion copulated almost a year before egg-laying (the Crowned Eagles bred only every second year). Cape Vultures (*Gyps coprotheres*) copulate long after egg-laying, and in fact over the whole year (Robertson 1986). Similarly, Merlins (*Falco columbarius*) copulate well after the fertile period (Sodhi 1991). Holthuijzen (1992) reported that the Prairie Falcon (*Falco mexicanus*) copulated at least 51 days before clutch completion, and continued copulating well into the brood-rearing period, about 60 days after incubation started. In Montagu's Harrier, 12% of the observed copulations occurred after laying (Arroyo 1999). Neither the sperm competition hypothesis, the fertilization hypothesis, or the predation hypothesis can explain copulations outside the fertile period. The only possible explanation is that such copulations have some kind of social function, e.g., to maintain social bonds.

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