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Sperm Competition and Copulation Intervals of the White Spoonbill (*Platalea leucorodia*, Aves, Threskiornithidae)

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Abstract

Some aspects of sperm competition were studied in the white spoonbill (*Platalea leucorodia*) breeding in Doñana National Park (SW Spain). Shorter pair copulation intervals occurred during the prelaying period, when females were subjected to a relatively high frequency of extra-pair copulations. Pair copulation intervals with an intermediate extra-pair copulation by the male mate were longer than those without extra-pair copulation. This result indicates that males need a time of recovery between copulations before they can perform another. Extra-pair copulations by the females did not affect the length of intervals between pair copulations. There were no differences between the lengths of the intervals between an extra-pair copulation by the female and the following pair copulation for cases in which the male mate detected an intruder male attempting copulation with his mate and those in which the intruder remained undetected. However, the correlations obtained between copulatory intervals for detected and undetected cases suggest a copulatory response by their mates, although affected by the required recovery time between copulations by the males. Finally, since extra-pair copulations mainly occurred while male mates were collecting nest material, they engaged in this activity shortly after pair copulations, probably to avoid a last-male advantage under the sperm competition pressure.

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Introduction

When males are uncertain of their paternity, there should be strong selection favouring adaptations ensuring paternity (PARKER 1970, 1984). Male birds avoid the effect of cuckoldry by means of two tactics: mate guarding (e.g. BEECHER & BEECHER 1979; BIRKHEAD 1979, 1982) and sperm devaluation (MCKINNEY et al.

1983, 1984). The evidence presented by BIRKHEAD et al. (1987) indicates that copulation frequency of birds increases in relation to the risk of sperm competition. Males ensure in this way a numerical surplus of their own sperm over competitors' sperm and thus increase their probability of fertilizing the eggs (PARKER 1984).

Other components of the copulatory behaviour of birds may also have evolved in a context of sperm competition. Individual male swallows (*Hirundo rustica*) reacted by increasing pair copulation rate when their mates were chased by other males and, besides, by shortening time intervals between chases and copulations (MØLLER 1987). Furthermore, it has been observed in some bird species that pair copulations (forced or unforced) follow immediately after a female mate has been subjected to an extra-pair copulation (e.g. BARASH 1977; MCKINNEY & STOLEN 1982; AFTON 1985; BIRKHEAD et al. 1988) or following an intrusion by a strange male (references in BIRKHEAD et al. 1987). However, sperm production is limited (DEWSBURY 1982), and, therefore, males may need a period of recovery after a copulation before they can perform another. Since an extra-pair copulation may occur at any time after a pair copulation, the time interval between an extra-pair copulation by a female and the following pair copulation might be a crude measure of the copulatory response by male mates.

Alternative evidence for a paternity insurance copulatory response by males might appear from a comparison of the intervals between two consecutive pair copulations separated by an extra-pair copulation by the female and the intervals between two pair copulations without an intermediate extra-pair copulation. Since intervals between pair copulations may be affected by other factors, I first examined the effects of nesting cycle, inter-pair differences and extra-pair copulations by male mates on pair-copulation intervals of white spoonbills (*Platalea leucorodia*). I then explored evidence for copulatory responses of male mates to extra-pair copulation by their mates.

On the other hand, since extra-pair copulations mainly occurred while male mates were collecting nest material (AGUILERA & ALVAREZ 1989), I examined whether males employed copulatory tactics in connection with this activity to improve their success under the pressure of sperm competition.

White spoonbills are colonial birds in which males and females share nest building, defence, incubation and nestling feeding (AGUILERA 1988). In another paper, AGUILERA & ALVAREZ (1989) have shown that extra-pair copulation attempts account for 19 % of all copulation attempts, and a minimum of 60 % of mated males and 75 % of mated females were involved in extra-pair copulations at least once. These results suggest a strong selection pressure due to sperm competition in this population.

Methods

Mating behaviour of white spoonbills was studied at the mixed species heronry of Doñana National Park (SW Spain) during the breeding seasons 1985–1986. The nests of spoonbills were placed on cork oaks (*Quercus suber*) in the border of a brackish marsh (for a general description of the study area see VALVERDE 1958). Behavioural observations were done with 10 × 40 binoculars and 20–60 telescope from two blinds placed 60 m from the spoonbills' nests. Each year, 8 to 12 pairs

occupying contiguous nests were simultaneously observed from dawn to sunset 3 or 4 days a week from the onset of breeding until nestlings left the nest. Overall, 4700.9 pair-h from 28 different pairs were recorded. Individuals were recognized by distinctive features of the light spot on the upper tip of the bill (AGUILERA & ALVAREZ 1989), and sexes were distinguished by the larger body size of males and checked by positions during copulation. I recorded the time of each copulation attempt involving individuals of the study pairs, the identity of the birds and the outcome of attempts. I also registered the time of each trip to obtain nest material and the identity of the birds.

The breeding cycle of each pair was classified in four periods according to the day when the first egg was laid (day 0): early prelaying (from the day that the pair occupied the nest site until day -6), prelaying (from day -5 to day -1), laying (from day 0 to day +6) and incubation (from day +7 until the day prior to the hatching of the first egg).

Statistics were used following SIEGEL (1956). For most statistical analysis I assumed copulations and copulation intervals to be independent observations.

Results

The nesting cycle significantly affected the time interval between two consecutive pair copulations (Fig. 1, Kruskal-Wallis one-way analysis of variance, $H = 9.16$, $df = 3$, $p < 0.05$). Shorter copulation intervals occurred during prelaying. No significant differences of copulation intervals among pairs were observed during prelaying, when a sufficient sample size was available ($H = 19.7$, $df = 8$, $p > 0.05$).

Pair copulation intervals separated by an extra-pair copulation by the male were significantly longer than pair copulation intervals without an intermediate extra-pair copulation during the prelaying period (pair copulation intervals with

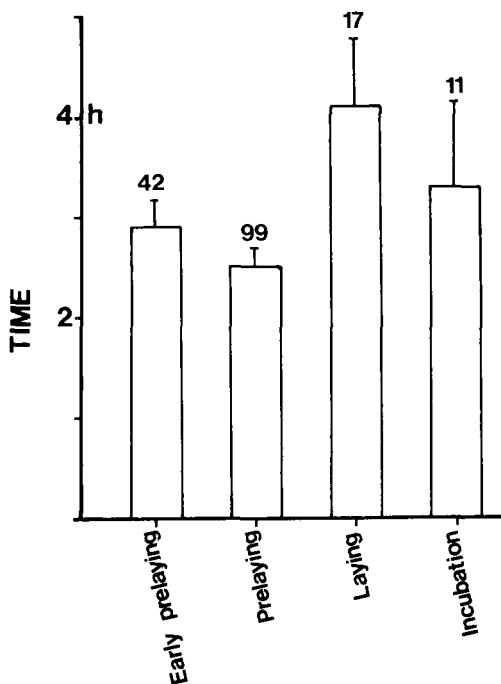


Fig. 1. Nest cycle variation in the mean time interval between pair copulations. Bars are 1SE. Numbers represent sample sizes

an intermediate extra-pair copulation by the male: $\bar{x} = 3.95$ h, $SE = 0.81$ h, $n = 7$; pair copulation intervals without extra-pair copulation: $\bar{x} = 2.36$ h, $SE = 0.22$, $n = 92$; Mann-Whitney U-test, two tailed, $U = 136$, $p = 0.011$). This result indicates that males need a recovery time between two consecutive copulations.

Intervals between two consecutive pair copulations with an intermediate extra-pair copulation by the female were shorter ($\bar{x} = 1.79$ h, $SE = 0.17$ h, $n = 9$) than those without an extra-pair copulation ($\bar{x} = 2.54$ h, $SE = 0.22$ h, $n = 88$), although the difference was not significant ($U = 433.5$, $p > 0.05$).

Only in two out of 12 cases when the male mate detected an intruder male attempting copulation with his mate, a pair copulation followed before a 10 min period elapsed. I analysed differences between all cases in which male mates detected the presence of an intruder male attempting copulation on their nest ($n = 12$) with cases in which intruder males were not detected ($n = 12$). Because

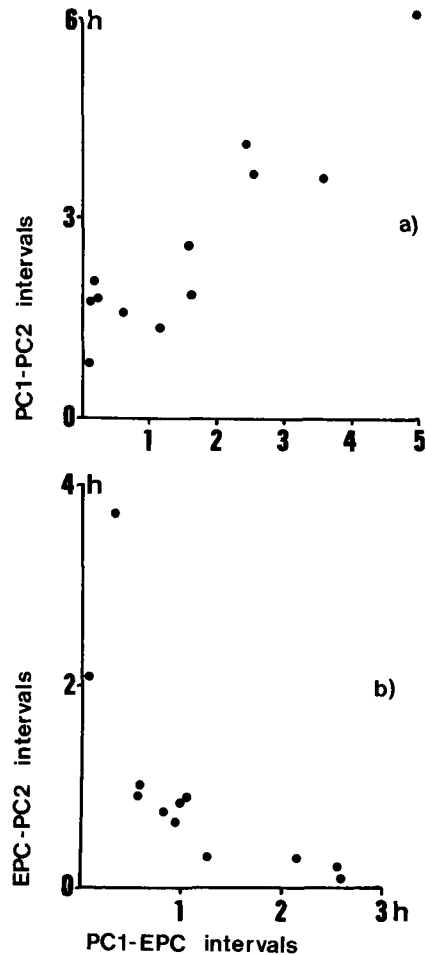


Fig. 2: Relationship between some copulatory intervals for a) cases when male mate detected the intruder male attempting copulation with his mate and b) cases when the intruder remained undetected. EPC = extra-pair copulation by the female mate; PC1 = pair copulation before an EPC; and PC2 = pair copulation after an EPC

all these extra-pair copulation attempts occurred during the short intervals in which females' mates were collecting nest material and since time differences between the moment in which an extra-pair copulation attempt occurred and the arrival at the nest by male mates were null when intruders were detected, and shorter than 2 min when they were undetected, I used, for comparative purposes, the moment in which the extra-pair copulation attempt occurred as "point zero" in both cases. No differences were found between the mean length of the intervals between an extra-pair copulation attempt and the next pair copulation for these two sets (intruder detected: $\bar{x} = 1.02$ h, SE = 0.18 h; intruder undetected: $\bar{x} = 1.00$ h, SE = 0.33; U = 84, $p > 0.05$). If males detected an intruder male and responded by copulating with their mates after a relatively short period, this

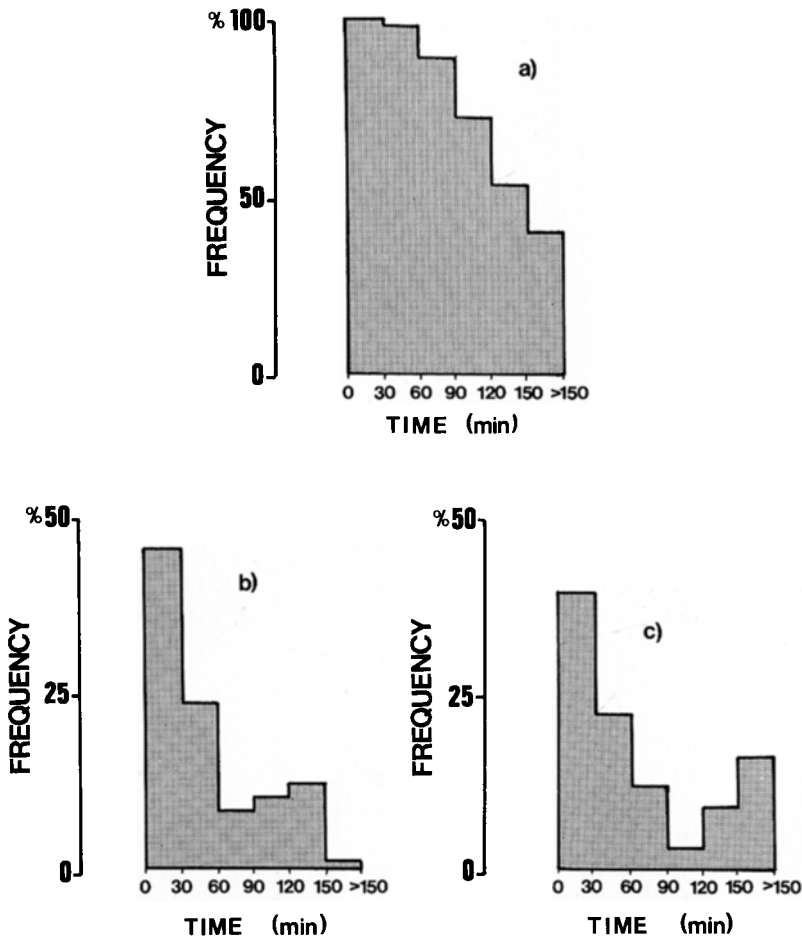


Fig. 3: a) Cumulative reverse distribution of time intervals between two consecutive pair copulations ($n = 171$); b) distribution of the intervals between pair copulation and nest material trips by males ($n = 203$); and c) distribution of the intervals between a pair copulation and the next extra-pair copulation by the female mate ($n = 32$)

period being affected by the length of the interval since the last copulation, then one should expect a positive correlation between this interval and the interval between the two pair copulations with this intermediate extra-pair copulation. In cases where male mates did not detect intruder males, the former interval should be irrelevant and this should not show any correlation with pair copulation intervals. As predicted, the correlation between these two intervals was high and significant when a male intruder was detected ($r_s = 0.81$, $p < 0.01$, Fig. 2) and low and not significant when an intruder remained undetected ($r_s = 0.18$, $p > 0.05$).

The intervals elapsed since and to the previous and the next pair copulation with respect to an extra-pair copulation were strongly negatively correlated when male mates did not detect any intruder male ($r_s = -0.93$, $p < 0.01$; Fig. 2), while this correlation was non-significant when an intruder was detected ($r_s = 0.27$, $p > 0.05$).

The distribution of the intervals between a pair copulation and the next extra-pair copulation by the female did not depart significantly from the pair copulation-nest material trip time interval distribution (Fig. 3; Kolmogorov-Smirnov, two sample test, $D = 0.13$, $n_1 = 203$, $n_2 = 32$, $p > 0.05$). On the other hand, male mates collected nest material shortly after a pair copulation in a proportion greater than expected according to the distribution of time intervals between pair copulations (Fig. 3; $D = 0.58$; $n_1 = 171$, $n_2 = 203$, $p < 0.01$).

Discussion

Some male birds copulate with their mates immediately after they have been subjected to an extra-pair copulation. In this study no significant differences were observed among an extra-pair copulation by the female and the following pair copulation interval for cases when intruders were detected and cases when they were undetected. These results do not necessarily reflect a lack of copulatory response by males to extra-pair copulations by their mates but an imposition of the required recovery time between copulations by males. This is supported by various correlations between copulation intervals. An extra-pair copulation by the female occurring shortly after a pair copulation may not elicit an immediate copulatory response by her mate because his recovery time between copulations has not been reached yet. However, if the copulation response is actually presented by the male mates, a positive correlation between the interval elapsed since the last pair copulation until the extra-pair copulation and the interval since that copulation and the next pair copulation should be expected. This relationship was observed only in cases when male intruders were detected, whereas in those cases in which intruders remained undetected, the former interval should be meaningless and thus this correlation should not be expected. For constant interval lengths, if they are randomly divided in two periods, the longer is one the less is the other and, therefore, a negative correlation between them should be expected. This is the situation observed in this study for the relationship between the intervals since the previous and the next pair copulation in relation to an extra-

pair copulation by the female when male intruders were not detected, i.e. intervals between two consecutive pair copulations were randomly divided; whereas when the intruders were detected, the correlation was not found, probably due to an "a posteriori" change in the length of the intervals between pair copulations as a consequence of the copulatory response by male mates.

An important question in connection with the sperm competition is the effect of the order in time of the inseminations on the fecundation of the eggs. There are few studies as yet on this topic in birds (see however, COMPTON et al. 1978; CHENG et al. 1983; SIMS et al. 1987; BIRKHEAD et al. 1988) although all of them indicate an advantage to the last male copulating, but only when inseminations were separated more than three hours. MØLLER (1988) showed that monogamous bird species with a high intensity of sperm competition copulate frequently, but each ejaculate contains a smaller number of sperm than species with both low rate of copulations and low intensity of sperm competition. He suggests that this situation has evolved to avoid the last male advantage. The results of this study support this hypothesis. Shorter copulation intervals in spoonbills occurred during prelaying, when female mates experience the maximum frequency of extra-pair copulations (AGUILERA & ALVAREZ 1989). By maintaining short intervals between pair copulations, male mates may avoid the priority in egg fecundation by extra-pair copulations of their mates occurring after that critical time period. In this respect, it is also interesting that males collected nest material shortly after a pair copulation. In doing so, males minimize the intervals between a pair copulation and the moments when an extra-pair copulation might occur and thus avoid a possible last male advantage. On the other hand, the similarity between the interval distributions of pair copulation-nest material trips and pair copulation-next extra-pair copulation indicates opportunism by males when attempting extra-pair copulations.

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Literature Cited

- AFTON, A. D. 1985: Forced copulation as a reproductive strategy of male lesser scaup: A field test of some predictions. *Behaviour* **92**, 146—167.
- AGUILERA, E. 1988: Compartimento reproductivo de la espátula (*Platalea leucorodia*). Unpubl. Doct. Thesis. Univ. de Sevilla.
- & ALVAREZ, F. 1989: Copulations and mate guarding of the spoonbills (*Platalea leucorodia*). *Behaviour*, in press.
- BARASH, D. P. 1977: Sociobiology of rape in mallards (*Anas platyrhynchos*): Responses of the mated male. *Science* **197**, 788—789.
- BEECHER, M. D. & BEECHER, I. M. 1979: Sociobiology of bank swallows: Reproductive strategy of the male. *Science* **205**, 1282—1285.
- BIRKHEAD, T. R. 1979: Mate guarding in the magpie (*Pica pica*). *Anim. Behav.* **27**, 866—874.
- 1982: Timing and duration of mate guarding in magpies (*Pica pica*). *Anim. Behav.* **30**, 277—283.

- , ATKIN, L. & MØLLER, A. P. 1987: Copulation behaviour of birds. *Behaviour* **101**, 101—138.
- , PELLAT, J. & HUNTER, F. M. 1988: Extra-pair copulation and sperm competition in the zebra finch. *Nature* **334**, 60—62.
- CHENG, M., BURNS, S. T. & MCKINNEY, F. 1983: Forced copulations in captive mallards. III. Sperm competition. *Auk* **100**, 302—310.
- COMPTON, M. M., VAN KREY, H. P. & SIEGEL, P. B. 1978: The filling and emptying of the uterovaginal sperm-host glands in the domestic hens. *Poult. Sci.* **57**, 1696—1700.
- DEWSBURY, D. A. 1982: Ejaculate cost and male choice. *Am. Nat.* **119**, 601—610.
- MCKINNEY, F. & STOLEN, P. 1982: Extra-pair-bond courtship and forced copulation among captive green-winged teal (*Anas crecca carolinensis*). *Anim. Behav.* **30**, 461—474.
- , DERRICKSON, R. & MINEAU, P. 1983: Forced copulation in waterfowl. *Behaviour* **86**, 280—291.
- , CHENG, K. M. & BRUGGERS, J. 1984: Sperm competition in apparently monogamous birds. In: *Sperm Competition and the Evolution of Animal Mating Systems*. (SMITH, R. L., ed.) Acad. Press, New York, pp. 523—545.
- MØLLER, A. P. 1987: Behavioural aspects of sperm competition in swallows (*Hirundo rustica*). *Behaviour* **100**, 92—104.
- 1988: Testes size, ejaculate quality and sperm competition in birds. *Biol. J. Linn. Soc.* **33**, 273—283.
- PARKER, G. A. 1970: Sperm competition and its evolutionary consequences in the insects. *Biol. Rev.* **45**, 525—567.
- 1984: Sperm competition and the evolution of animal mating strategies. In: *Sperm Competition and the Evolution of Animal Mating Systems*. (SMITH, R. L., ed.) Acad. Press, New York, pp. 1—60.
- SIEGEL, S. 1956: *Nonparametric Statistics for the Behavioral Sciences*. McGraw-Hill, New York.
- SIMS, M. E., BALL, G. F. & CHENG, K. M. 1987: Sperm competition after sequential mating in the ringed turtle-dove. *Condor* **89**, 112—116.
- VALVERDE, J. A. 1958: An ecological sketch of the Coto Doñana. *Brit. Birds* **51**, 1—23.

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