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**FREQUENT COPULATIONS DESPITE LOW SPERM
COMPETITION IN WHITE STORKS
(*CICONIA CICONIA*)**

by

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(With 6 Figures)

(Acc. 1-VI-1992)

Summary

White Storks *Ciconia ciconia* paired for ca. 30 days before laying a clutch. During this period, mates copulated frequently (160 copulations/pair; 0.4 copulations/daylight h), but copulation rate was drastically reduced a week before laying of the eggs. Both fewer copulation attempts by males and lower female receptivity accounted for this reduction. This pattern was the same regardless of whether pairs nested solitarily or in colonies. Colonial as well as solitary males spent more time at the nest before egg-laying while the opposite trend was found for females. Consequently, females were more likely to remain alone at their nests while ovulating. Colonial birds had ample opportunities for engaging in extra-pair copulations (EPC) during the female fertile period, but these were very infrequent (0.4% of all successful copulations) and involved recently-paired birds exclusively. This suggests that sperm competition in this species is of little relevance for explaining patterns of pair copulations. Accordingly, males did not guard their female mate and the timing of copulation was poorly tuned to chances of fertilizing the female's eggs. However, it remains to be explained why storks copulated so much and for a prolonged period when the risk of EPC was so low. It is suggested that copulations may be part of a signalling system by which males advertise and females assess the physical condition of the male, which is likely to correlate with the ability of males to forage efficiently for them and their offspring. In support of this possibility, males who copulated frequently fed chicks at a higher rate during the nestling period.

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Introduction

Many birds and mammals copulate far more frequently than is needed for successfully inseminating females. Copulations probably entail costs, making partners vulnerable to predation (BIRKHEAD *et al.*, 1987), and consume time and energy that otherwise could be spent for other purposes (PARKER, 1974; DALY, 1978; DEWSBURY, 1982), thus copulation patterns are expected to evolve under directional selection favouring low copulation rates (EATON, 1978). However, monogamous birds show a remarkable interspecific variation in the extent and duration of copulation periods, which suggests that copulation behaviour is under more complex selection pressures than merely fertilizing the female's eggs (BIRKHEAD *et al.*, 1987; DEWSBURY, 1988).

BIRKHEAD *et al.* (1987) looked for an adaptive explanation for this variation and found that neither fertilization constraints nor predation pressures could satisfactorily explain it. Instead, they concluded that the extent to which the female is likely to be fertilized by nonmate males (*i.e.* the intensity of sperm competition (PARKER, 1970) among ejaculates) determines how frequently a male should copulate with his female mate in order to be certain of his paternity (BIRKHEAD *et al.*, 1987; BIRKHEAD, 1988; MØLLER & BIRKHEAD, 1992). Extra-pair copulations (EPC) are widespread in birds (see reviews by GLADSTONE, 1979; FORD, 1983; MCKINNEY *et al.*, 1983, 1984; MOCK & FUJIOKA, 1990; WESTNEAT *et al.*, 1990; BIRKHEAD & MØLLER, 1992), and recent methodological advances in techniques for detecting multiple paternity in broods of apparently monogamous species have demonstrated that EPC sometimes lead to a high incidence of extra-pair fertilizations (MOCK & FUJIOKA, 1990; WESTNEAT *et al.*, 1990; MØLLER, 1991; WEATHERHEAD & MONTGOMERIE, 1991).

When males make a substantial investment in offspring care, as in most monogamous birds, they will obviously benefit from fertilizing the eggs of nonmate females, thus parasitizing the paternal expenditure of cuckolded males. Females could also benefit from copulating with several males in a given breeding season (WESTNEAT *et al.*, 1990; BIRKHEAD & MØLLER, 1992). Consequently, males will be expected to actively seek copulations with nonmate females, trying simultaneously to protect their own paternity (*e.g.* by guarding their female mate while she is fertile), and restrict their parental expenditure to the offspring of their mate. On the other hand, the female should try to maintain a stable pair bond with her mate in order to benefit from his paternal expenditure while occasionally allowing nonmate males to fertilize her eggs. This rather complex sce-

nario in which both members of a pair practise a mixture of monogamy and promiscuity was termed by TRIVERS (1972) a Mixed Reproductive Strategy, and both theoretical and empirical evidence suggest that it may be common, rather than an exception, among birds traditionally considered to be exclusively monogamous (FORD, 1983; MCKINNEY *et al.*, 1984; BIRKHEAD *et al.*, 1987; MOCK & FUJIOKA, 1990; WESTNEAT *et al.*, 1990).

EPC rates vary both across populations of a species (McROBERTS, 1973; MINEAU & COOKE, 1979; WERSCHKUL, 1982; FREDERICK, 1987; SMITH, 1988; MCKILLIGAN, 1990) and among related species (BIRKHEAD, 1978; MCKINNEY *et al.*, 1983; LEFELAAR & ROBERTSON, 1984), but the causes underlying such variation remain poorly understood. However, two factors are thought to facilitate the occurrence of EPC:

- 1) A high density of breeding pairs, like colonial nesting (FORD, 1983; WESTNEAT *et al.*, 1990). Although coloniality is neither necessary nor sufficient for an EPC strategy to occur (WESTNEAT, 1987), some studies (BIRKHEAD, 1978; MØLLER, 1985, 1987a) have reported EPC to be more prevalent among colonial than among dispersed or solitary breeders.

- 2) The lack of effective mate guarding by males (BIRKHEAD *et al.*, 1987; MØLLER & BIRKHEAD, 1992). Many birds of prey (including owls and shrikes) cannot effectively guard their female mate during her fertile period, because males have to hunt to provision the female, and this would render females especially susceptible to EPC attempts by other males. Similarly, males of colonial herons, egrets, and ibises also cannot guard their female mate because they can only leave the nest to forage when it is guarded by his mate, in order to prevent nest destruction by conspecifics (FUJIOKA & YAMAGISHI, 1981). These species are actually among the best known examples of the existence of a Mixed Reproductive Strategy (GLADSTONE, 1979; FUJIOKA & YAMAGISHI, 1981; WERSCHKUL, 1982; FREDERICK, 1987; AGUILERA & ALVAREZ, 1989; MCKILLIGAN, 1990).

Some colonial storks (*Ciconiidae*) fall within category 2) above. Nests are often highly clumped (HAVERSCHMIDT, 1949; KAHL, 1966a, b, 1972; CRAMP & SIMMONS, 1977; CREUTZ, 1985) and stealing of nest material is frequent. Detailed information on mating behaviour and copulation rates is lacking for virtually all species but preliminary observations suggest that white storks *Ciconia ciconia* have high copulation rates (CREUTZ, 1985), hence a high degree of sperm competition was assumed for this species (BIRKHEAD *et al.*, 1987; MØLLER & BIRKHEAD, 1992). This paper reports the results of a study originally aimed at recording variation in intra- and extra-pair copulation patterns of white storks nesting at

different densities. We also found extremely high pair-copulation rates. However, contrary to expectations, we found EPC to be rare and unlikely to result in extra-pair fertilizations, so we consider copulation patterns in this species to arise from selection pressures other than sperm competition.

Methods

Breeding data were collected during November 1989 to July 1990 and November 1990 to July 1991, covering the whole breeding cycle from pair settlement at breeding sites to fledgling independence. Observations were performed at four different breeding sites in southwestern Spain. Information concerning the year when data were collected, observation hours and sample sizes is presented in Table 1. Some birds were marked with numbered PVC rings (see below). Among unmarked birds, some could be recognized by distinctive features: abnormal bill colouration (1 bird), large permanent callosities at the tibio-tarsal joint (3 birds), and the unique pattern of distribution of black outer tail-feathers (27 birds) (for details of the identification method see CHOZAS, 1983). The remaining birds were marked with permanent non-toxic dye.

1. La Dehesa Colony. The largest breeding colony in Western Europe, comprising more than 100 pairs nesting on a white olive tree *Olea europaea* woodland near rice fields. A regular banding program with numbered PVC rings has been routinely performed since 1985, hence most birds younger than 6 years old were marked. We selected 23 pairs nesting in the densest part of the colony as a sample for recording behavioural observations. 25 birds were ringed, 4 were dyed and 17 showed distinctive features.

TABLE 1. The number of white stork pairs observed, observation hours per nest, nest dispersion and the type of data collected for each breeding site during 1990 and 1991

| | Breeding site ¹⁾ | | | | | |
|--|-----------------------------|------|------|------|--------|------|
| | 1 | 2 | | 3 | | 4 |
| Study year | 1990 | 1990 | 1991 | 1991 | 1990 | 1991 |
| Number of focal pairs | 23 | 12 | 12 | 8 | 5 | 3 |
| Number of marked birds | 25 | 0 | 0 | 11 | 0 | 0 |
| Observation nest-hours | 897 | 867 | 450 | 450 | 270 | 210 |
| Average distance between nearest nests (m) | 6.5 | 5.5 | | 5.0 | >5,000 | |
| Type of data collected: | | | | | | |
| Copulation behaviour | + | + | + | + | + | + |
| Time of birds at the nest | + | + | + | + | + | + |
| Chick provisioning | + | + | | | | |
| Date of pair settlement and formation | + | | + | | + | + |
| Laying date | | | + | + | + | + |
| Clutch size | + | + | | | | |
| Fledging success | + | + | | | | |
| Nest piracy | + | + | | + | | |
| Male body mass | | | + | | | |
| Nest volume | | | + | | | |

¹⁾ 1: La Dehesa; 2: Pedroche; 3: Jerez; 4: solitary nests near urban Córdoba.

2. Pedroche Colony. A small colony of 12 pairs nesting on buildings. No bird was ringed, 10 were dyed and 9 showed distinctive features. All birds abandoned the colony area after breeding.
3. Jerez Colony. An 8-pair colony of sedentary wild birds nesting at Jerez Zoological Gardens, where they live year round. 11 birds were ringed and 5 showed distinctive features.
4. Solitary nests. Eight unmarked pairs nesting dispersed over a wide area of cultures surrounding urban Córdoba were observed. Nests were abandoned after breeding.

The information recorded at each breeding site during a given breeding season is summarized in Table 1.

Continuous observations from dawn to dusk were performed during the earliest (pre-nestling) phase of the breeding cycle at all focal nests, and continued throughout the nestling period at La Dehesa and Pedroche. Observations took place from hidden places at 10-70 m from the nests with the aid of 20-45×60 zoom telescopes. Due to the general slow movements of adult storks, it was possible to obtain a continuous sampling of behavioural variables by keeping under observation all focal colonial pairs simultaneously. Continuous sampling was employed for measuring the percentage of time spent at the nest by males and females and the rate of occurrence of the following behaviours: copulations (see below), food provisioning to nestlings, gathering and stealing nest materials, aggression and visits to a different nest.

Copulations between members of the same pair (Pair Copulations, PC) were considered successful if they ended in cloacal contact. Copulations in which the male mounted the female but no cloacal contact followed were regarded as copulation attempts, in addition to mounting attempts by the male mate. The duration of copulations was measured with a stopwatch and included mounting movements. Male storks were easily dislodged from the female's back in very windy days, so we did not include in the sample those copulations occurring when birds had obvious difficulties for maintaining the equilibrium due to heavy wind.

Since female birds can store viable sperm for several days following copulation, the duration of the fertile period (*i.e.* the period over which copulations can result in fertilization) spans from some days before laying of the first egg to ca. 24 h before laying of the last egg in the clutch (BIRKHEAD, 1988). The duration of sperm storage in birds is dependent upon several factors. Species in which males and females spend relatively little time together during the laying period (*e.g.* many seabirds), and species in which copulations are infrequent (*e.g.* some lek-breeding galliforms) have the longest durations of sperm storage recorded (BIRKHEAD & MØLLER, 1992). For the remaining birds, the average duration of sperm storage ranges between 6 and 11 days (average 8.6) and shows a positive correlation with the spread of laying, *i.e.* the product of clutch size and the mean interval between eggs (BIRKHEAD & MØLLER, 1992). We lack information about the duration of sperm storage in any living species of stork. Consequently, we estimated it as the predicted value for a laying spread of 6 days (4×1.5) calculated from BIRKHEAD & MØLLER's survey (1992, table 3.3), which renders an estimated duration of 8 days. The viability of stored sperm may be highly reduced at storage durations longer than the average duration of sperm storage (BIRKHEAD & MØLLER, 1992). Consequently, we will assume that the period of maximum fertilizability of the female (MF) lasts from 7 days before laying of the first eggs (day 0) to the day before the last egg in the clutch is laid. Accordingly, the period preceding maximum fertilizability (pre-MF) will then referred to as the period between pair formation and day -8. In some analyses, we also considered the period of pair formation (the 10 days following pair formation), and consequently those days were not included in the pre-MF period whenever such distinction is made.

We also recorded the calendar dates of settlement at the nest (migrating birds only), pair formation (the date when a pair started to copulate), and laying of the first egg. In addition, we determined clutch size and fledging success as the number of chicks reaching nutritional

independence. When analyzing the relationship between brood size and fledging success with rates of copulation and food provisioning, we only took into account those broods with no partial mortality due to causes other than starvation.

During 1991, we recorded the body mass of 9 out of the 12 breeding males at Pedroche Colony during the female pre-MF period. Males were attracted to a portable balance provided with a baited platform placed close to the nest, allowing the male to land on it, while an observer remained in a hide a few metres from the balance. The value closest to the onset of laying for each male was selected. In addition, we measured the cylindrical volume (height \times cup area) of nests before the arriving of the breeding birds.

Observations at Jerez Colony during 1991 were intended to determine the effect of supplementary feeding upon copulation and nest attendance patterns. Birds were continuously provisioned with *ad libitum* amounts of horse meat from at least a month before egg laying. Supplementary feeding at La Dehesa and Pedroche colonies was precluded because of the disturbing effects of daily provisioning. We compared the behaviour of males at Jerez (food-supplemented pairs in the text) with that of males at Pedroche (non-supplemented pairs). It is unlikely that any difference between the two sites (except for the treatment) could account for the differences observed because birds breeding at such different sites as La Dehesa, Pedroche and Cordoba (solitary pairs) showed a very high uniform pattern of copulations and nest attendance (see Results).

Statistical analyses were performed according to ZAR (1984). Behaviour rates were compared by mean of two-way ANOVAs accounting for the effects of breeding site and time in the female breeding cycle. Since the same pairs were observed throughout the nesting cycle, we used a repeated measures design (SAS Institute 1987) to guarantee statistical independence between data points. All simple linear correlation coefficients appearing in the text are nonparametric (Spearman).

Results

1. Pair settlement and formation.

Colonial males (N=32) arrived at breeding sites and settled at nests between 15 November and 17 March (median 17 January). Dates of settlement at Pedroche colony were inversely correlated with male body mass (Spearman $r=-0.75$, $p<0.05$, N=9). Females arrived on average 9 days (± 10.3 SD, N=32) later. Out of 35 pairs with known settlement dates, males occupied first a vacant nest in 28 cases, and females in the remaining 7 cases. Those males (N=28) who settled at nests prior to their female mate accepted and paired with the first incoming female, but 3 out of 7 unpaired females occupying vacant nests repelled the first arriving male, and paired with the second one.

At Pedroche, larger nests were occupied first ($r=-0.83$, $p<0.01$, N=11). Males who obtained nests earlier in the season attracted mates sooner, so that male settlement dates were highly correlated with female pairing dates (Pedroche: $r=0.99$, $p<0.001$, N=11; Solitary pairs, $r=0.97$, $p<0.01$, N=8). Pairs formed earlier in the season tended to lay eggs earlier (Pedroche: $r=0.49$, N=11, ns; Solitary pairs: $r=0.84$, $p<0.05$, N=8). In turn, clutch size decreased as the season advanced (La Dehesa: $r=-0.46$,

$p < 0.05$, $N=23$; Pedroche: $r=-0.83$, $p < 0.01$, $N=12$), as did the number of young that fledged (La Dehesa: $r=-0.70$, $p < 0.01$, $N=23$; Pedroche: $r=-0.75$, $p < 0.05$, $N=10$).

Both members of a pair remained together for ca. 30 days before the start of laying (La Dehesa: 29 days \pm 14 SD, $N=19$; Pedroche: 25 days \pm 17 SD, $N=12$; Jerez: 37 days \pm 15 SD, $N=8$). Some birds failed to attract a mate (Small colonies only, 1990: 4 out of 48; 1991: 5 out of 45). Virtually all unmated birds behaved as males, displaying at females, aggressively defending the nest and actively gathering nest materials, which could indicate that sex ratios at breeding sites were slightly male-biased.

2. Timing of pair copulations.

We recorded 5,850 PC attempts at colonial nests, of which 4,230 were successful (72.3%). The same figures for solitary pairs were 1,065 and 805 (75.6%), respectively. Copulations always took place on the nest, and no bird was observed to attempt copulating out of a nest. Males solicited copulations by stroking the female's back with their necks. Females were never observed to display behaviours which could be interpreted as a solicitation. A female showed her lack of receptivity toward male copulation attempts by slightly moving away when the male attempted to mount her. Female unreceptivity was the cause of most copulation failures. A complete mounting sequence ending in cloacal contact lasted on average 12.2 s (\pm 1.3 SE, $N=51$). No differences in mounting durations were detected according to breeding site or time in the female cycle.

During the pre-MF and the MF periods, white stork pairs copulated 160 times on average (SE=7.6, $N=51$, all pairs). Some copulations took place during the incubation period, yielding a mean number of 206 (\pm 8.5 SE) copulations per breeding season. Both at colonial and solitary nests, PC rates declined during the breeding cycle but not steadily, reaching a peak shortly after pair formation and showing a two-fold decrease around a week before clutch initiation (Fig. 1). Such a seasonal decrease was due to the combined effects of males soliciting fewer copulations and a lower successful/attempted PC ratio during the MF period (Table 2). Colonial pairs copulated at similar rates than solitary pairs, but colonial males attempted more copulations (Fig. 2, Table 2). This difference is probably due to the higher proportion of time that colonial birds spent at the nest (Fig. 2), since copulation rates per h the pair spent together were slightly higher for solitary pairs (Table 2).

Colonial pairs showed a bimodal daily rhythm of PC, with peaks in

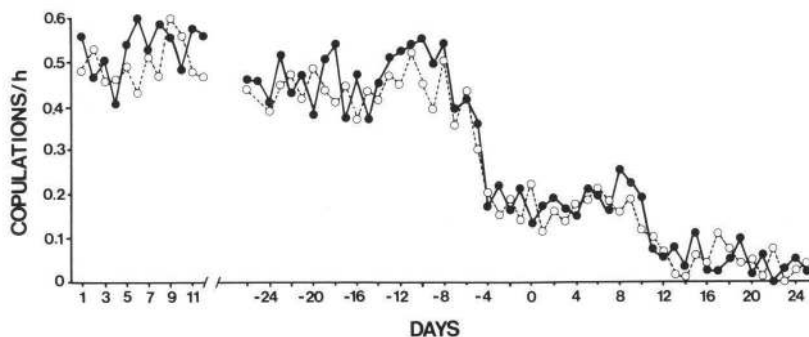


Fig. 1. Variations in the average frequency of pair copulations per daylight h of colonial (open dots) and solitary pairs (black dots) during the female breeding cycle divided into two periods: the 10 days following pair formation (left side, day 0 = day of pair formation), and the period preceding and following egg laying (right side, day 0 = day of laying of the first egg in the clutch). All pairs were incubating beyond day +6.

TABLE 2. Mean values (SE in brackets) of pair copulation rates, male copulation attempts, and the copulatory success (the percentage of total male copulation attempts ending in cloacal contact) of colonial (La Dehesa, Pedroche) and solitary White Storks during the 10 days following pair formation (PF), and the female pre- MF (P) and MF (F) periods

| | Colonial (N=35) | | | Solitary (N=8) | | | Effects ¹⁾ | | |
|--|-----------------|-----------------|----------------|----------------|-----------------|----------------|-----------------------|--------|-----|
| | PF | P | F | PF | P | F | C | F | CxF |
| Copulations/daylight h | 0.50 (0.07) | 0.48 (0.07) | 0.23 (0.09) | 0.46 (0.05) | 0.42 (0.06) | 0.20 (0.07) | 1.8 | 442*** | 2.2 |
| Copulations/h the pair stayed together | 1.01 (0.01) | 0.99 (0.07) | 0.50 (0.01) | 1.01 (0.02) | 1.04 (0.03) | 0.51 (0.06) | 2.9* | 473*** | 1.3 |
| Male copulation attempts/daylight h | 0.60 (0.10) | 0.58 (0.09) | 0.38 (0.09) | 0.55 (0.06) | 0.51 (0.07) | 0.35 (0.07) | 3.9* | 40*** | 0.5 |
| Copulatory success | 82.7 (2.6) | 82.4 (5.0) | 58.2 (1.6) | 83.7 (1.6) | 83.3 (3.1) | 57.4 (2.8) | 1.8 | 125*** | 1.3 |
| Copulations/clutch (pre-incubation period) | | 155.5 (6.01) | | | 152.6 (11.6) | | | | |
| Copulations/clutch (Total) | | 210.0 (9.2) | | | 189.1 (11.3) | | | | |

¹⁾ F values from a two-way repeated measures ANOVA assessing the effects of Coloniality C (df = 1,123), time in the female breeding cycle F (df = 2,123), and their interaction CxF (df = 1,123).

* p<0.05; ** p<0.01; *** p<0.001.

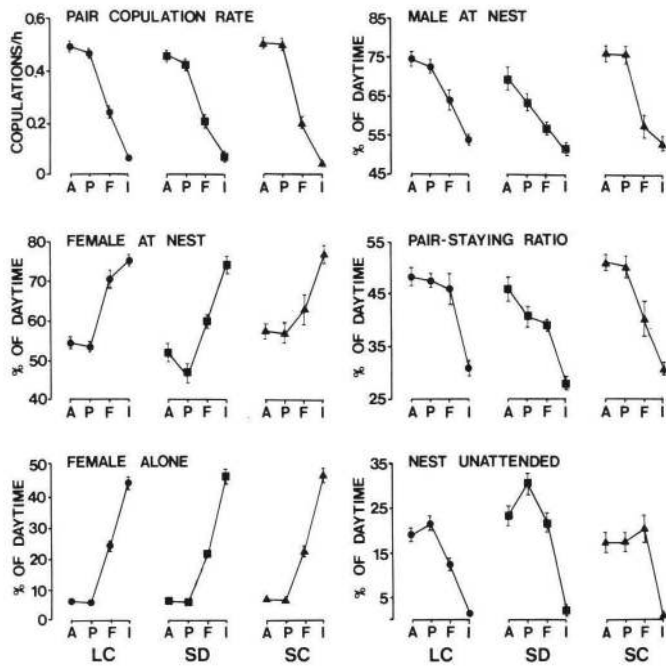


Fig. 2. Mean (\pm SE) frequency of pair copulations, the percentage of daytime spent at the nest by both members of a pair, and the percentage of time that the female mate and the nest were left alone, according to female reproductive stage for colonial and solitary pairs: A: ten days after pair formation; P: pre-MF period; F: MF period; I: incubation; LC: large colony; SC: small colony; SD: solitary, dispersed nests. See text for definitions.

early morning (0700-0800) and late afternoon (1700-1800). The afternoon peak was especially marked during the female MF phase (Fig. 3). Daily variations in PC rates could be the result of both males and females actively seeking more copulations during peaks of PC activity or, alternatively, be a side-effect of diel variations in the time both members of a pair spent together. White storks had little opportunity to copulate during the central daylight hours, because the pair-staying ratio also showed a bimodal daily pattern. Calculation of PC frequencies per h the pair stayed together showed that birds actually sought more copulations during the dusk hours of the female MF period (Fig. 3).

Those pairs copulating more frequently during the female pre-MF phase also did so during the female MF phase ($r=0.33$, $p<0.05$, $N=43$, all pairs), but daily PC rates during the incubation period were not corre-

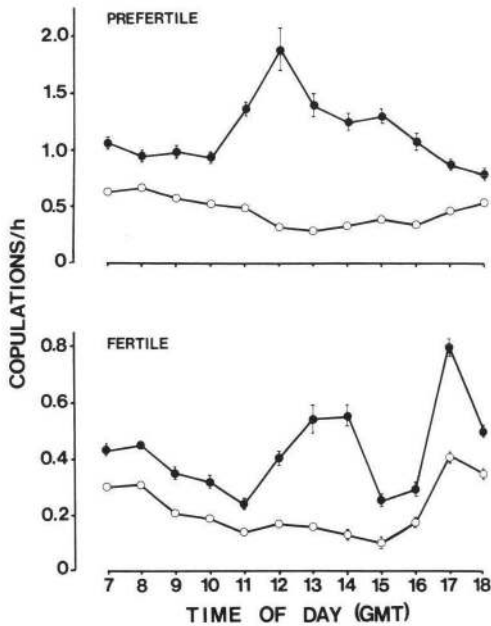


Fig. 3. Daily variation in the pair copulation rate per daylight h (open dots) and per h the pair stayed together (black dots) during the female pre-MF and MF periods. Differences between hours are significant in all four cases (repeated measures ANOVA). Bars around mean values are SE.

lated with PC rates during the female pre-MF ($r=0.02$, ns, $N=43$), or MF phase ($r=0.09$, ns, $N=43$).

There was a strong tendency for males to copulate immediately on returning to the nest site more frequently than expected according to the distribution of time that both members of a pair spent together. Males copulated at a higher rate within the 10 min of arrival than during the rest of the time both members of a pair spent together. This differed (male by male) from the expected values in Table 3 (Chi-square test, $p<0.05$). Virtually all colonial and solitary males deviated significantly from expected (Binomial test, $p<0.001$).

3. Patterns of nest attendance.

Both at colonial and solitary nests males and females differed in the proportion of daylight hours spent attending the nest in relation to the female breeding stage (Fig. 2). Results from “*a posteriori*” multiple compar-

TABLE 3. Observed pair copulation rates of colonial (La Dehesa, Pedroche) and solitary males during the female pre-MF and MF periods during the 10 min following arrival of the male at the nest and during the rest of the time that both members of a pair remained together

| | Colonial | | Solitary | |
|--------------|----------------|----------------|----------------|----------------|
| | Pre-MF | MF | Pre-MF | MF |
| 10 min | 4.82 (0.55) | 3.09 (0.37) | 4.26 (0.78) | 3.13 (0.41) |
| Rest of time | 0.56 (0.04) | 0.22 (0.02) | 0.59 (0.06) | 0.27 (0.02) |
| Expected | 0.98 (0.04) | 0.51 (0.16) | 1.04 (0.08) | 0.50 (0.06) |

Expected values are those estimated under the hypothesis that copulations occur uniformly in time. Values are the mean number of copulations per h the pair stayed together and SD (in brackets) (N=51).

isons (Scheefe test) in repeated measures ANOVAs assessing the effects of female breeding stage and coloniality upon percentages of time spent at the nest for males and females revealed the following significant trends. Both colonial and solitary males spent less time at the nest after the end of the female pre-MF period. Colonial males spent more time at the nest than solitary ones at any period. Females spent a significantly higher proportion of daytime at the nest once they entered the MF period. Females at solitary nests spent less time at the nest than colonial ones.

At Pedroche, heavier males spent a higher proportion of daytime at their nests than lighter males during the female pre-MF period ($r=0.71$, $p<0.05$, $N=9$). Females paired to heavier males spent less time alone at the nest ($r=-0.66$, $p<0.05$, $N=9$). In addition, fledging success was positively correlated with the percentage of time a male spent at his nest during the pre-incubation period ($r=0.48$, $p<0.05$, $N=23$ colonial pairs).

Variations in the pair-staying ratio for colonial and solitary pairs during the breeding cycle are shown in Fig. 2. A significant decrease occurred at the onset of incubation. In addition, solitary pairs spent a lower proportion of time together at the nest than colonial ones. Since males remained at the nest for longer than females during the pre-MF period, females were much more likely to be alone at the nest during their MF period, and such a trend was the same for colonial and dispersed nesters (Fig. 2). The percentage of daytime that nests remained unattended was higher for solitary than for colonial breeders and reached a minimum during the incubation period (Fig. 2).

4. Stealing of nest material.

A likely reason why at least one member of a pair should remain at the nest during most of the breeding cycle is that, at colonies, unattended nests were soon pillaged by neighbouring birds. In 38 focal pairs, 32 males (84.2%) and 19 females (50%) were observed to steal material from neighbouring nests. Out of 1,250 episodes of nest robbing, 78.7% were performed by males and 21.3% by females. In virtually all cases where a thief attempting to steal material if it was discovered by some member of the resident pair, it was attacked ($N=275$), 18% of such encounters ending in physical combat. Bleeding injuries were apparent in 2% of cases. Most robbing attempts were successful, however, and resident pairs only managed to prevent theft in 22% of cases. When both members of a resident pair were present, males aborted robbing in 69% (± 2.0 SE) and females in 31% (± 1.4 SE) of cases ($N=43$ pairs). Despite intense aggressive defense by resident pairs, robbing attempts were directed at active, occupied nests more frequently than expected by chance according to the availability of occupied and unoccupied nests. Of 20 males at La Dehesa and Jerez colonies (where unoccupied nests were available), 13 directed a significantly higher proportion of robbing attempts towards occupied (but unattended) neighbour nests (Chi-square, $p<0.05$), 2 showed a significantly lower proportion and 5 did not differ from expected (Binomial test, $p<0.01$, $N=15$).

5. The effect of supplementary feeding upon PC rates and nest attendance patterns.

No differences in hourly PC rates were found between non-supplemented ($N=12$) and food-supplemented ($N=8$) colonial pairs, but a significant interaction appeared between treatment and phase in the breeding cycle (Fig. 4). Food-supplemented pairs copulated less frequently during the female pre-MF period and more frequently during the incubation period than non-supplemented pairs. The total number of copulations per clutch was higher for food-supplemented pairs (186 ± 40 SE *vs.* 156 ± 10 SE) but the difference was non significant. Males at food-supplemented nests spent a higher percentage of daytime at their nests at any breeding stage and did not decrease attentiveness once their female mate entered the MF period. Females at food-supplemented nests also spent higher time amounts at their nests than females in non-supplemented nests (Fig. 4).

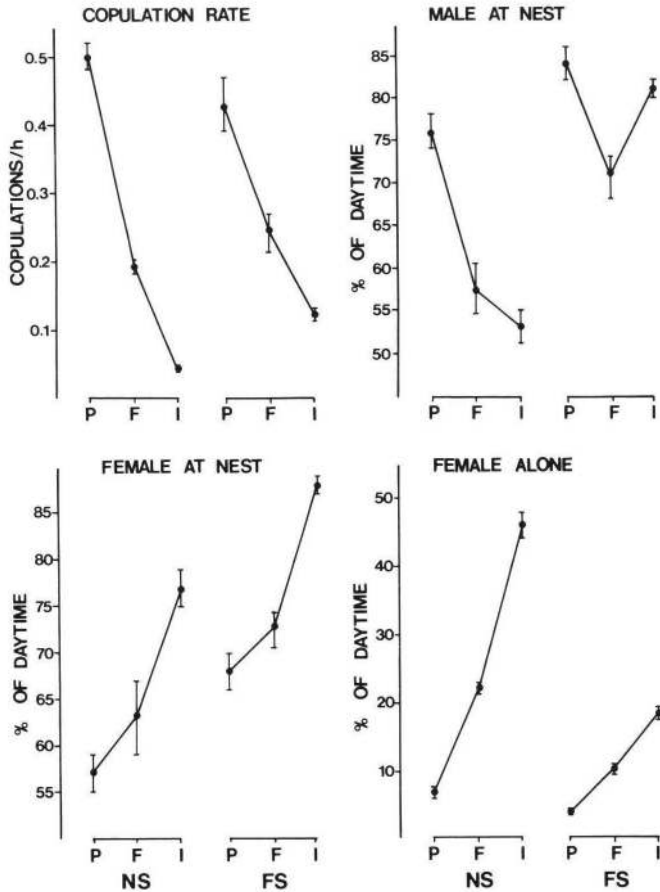


Fig. 4. Mean (\pm SE) frequency of pair copulations, the percentage of daytime spent at the nest by both members of a pair, and the percentage of time that the female mate remained alone, according to female reproductive stage for food-supplemented pairs (FS, right side) and non-supplemented pairs (NS, left side). Explanations as in Fig. 2.

6. Correlates of PC behaviour.

There was an association between the occurrence of PC and the apportionment of nest material by male mates. Male storks contributed more (67%) than females to the collection of nest materials. Like PC rates (Fig. 1), hourly frequencies of apportionment trips by the male decreased around the onset of laying (Fig. 5). The success of copulation attempts by the male during the 10 min following arrival at the nest largely depended on whether it carried nest materials. Females were more likely to be

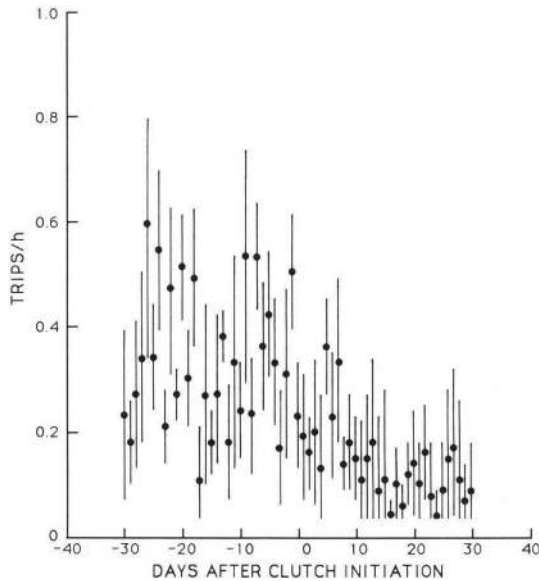


Fig. 5. Daily rates of male trips to the nest transporting nest materials plotted against time in the female breeding cycle (day 0 is the day of laying of the first egg in the clutch). Bars around means are SE.

receptive to copulation attempts by their male mate immediately after his arrival at the nest if he brought nest materials ($83.6\% \pm 8.5$ SE of copulation success) than if not ($68.7\% \pm 9.2$ SE) (Wilcoxon test, $Z=5.2$, $N=43$, $p<0.001$). In addition, previous male experience with female receptivity seemed to affect subsequent nest-building activity of the male. Males were more likely to bring nest material during the trip following a successful copulation ($26.7\% \pm 10$ SE) than a failed copulation ($23.0\% \pm 7$ SE) (Wilcoxon test, $Z=2.2$, $p<0.05$). Rates of apportionment of nest materials by individual males were correlated with PC rates during the female pre-MF and MF periods (Table 4).

The effect of male settlement dates upon PC rates was obscure. At Pedroche, we obtained contradictory results during 1990 and 1991. The high correlation showed by these two variables during the pre-MF period in 1991 could in turn explain the relationship between PC rates and nest volume during the same year. When the effect of settlement date was controlled for, nest volume and PC rates failed to show a significant correlation (partial $r=0.52$, $df=8$, ns). Male body mass seemed not to affect PC rates to a great extent (Table 4) but, like with nest volume, sample sizes were too small to be conclusive.

TABLE 4. Correlates of pair copulation rates per daylight h obtained for colonial and solitary pairs during the female pre-MF and MF periods

| | Colonial | | | Solitary | | |
|---|----------|---------|-------------------|----------|-------|---|
| | Pre-MF | MF | N | Pre-MF | MF | N |
| Clutch size | 0.07 | 0.08 | 33 ^{1,2} | 0.62 | -0.39 | 8 |
| Date of male settlement | | | | | | |
| 1990 | 0.16 | -0.20 | 12 ² | 0.00 | 0.20 | 8 |
| 1991 | -0.89** | 0.10 | 12 ² | — | — | |
| Date of pair formation | | | | | | |
| 1990 | 0.05 | -0.19 | 11 ² | -0.09 | 0.19 | 8 |
| Nest volume | 0.79* | -0.13 | 11 ² | — | — | |
| Male body mass | 0.36 | -0.13 | 9 ² | — | — | |
| Male rate of apportionment of nest materials | 0.55*** | 0.67*** | 35 ^{1,2} | | | |
| % of time male at the nest | 0.59** | 0.38 | 23 ¹ | 0.71 | 0.67 | 8 |
| Male rate of chick provisioning | 0.56** | 0.43* | 23 ¹ | — | — | |
| Fledging success | 0.61** | 0.12 | 23 ¹ | — | — | |

Values are Spearman rank correlation coefficients and sample sizes.

1) La Dehesa; 2) Pedroche.

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Copulation rates showed a significant positive correlation with male chick-feeding rates and the percentage of time males stayed at the nest (Table 4). The correlation between copulation rate and chick-feeding rate disappeared after controlling for brood size effects but the percentage of time that males remained at the nest during the pre-MF period still showed a significant partial correlation with chick-feeding rates when brood size was kept constant (partial $r = 0.56$, $df = 20$, $p < 0.01$). Fledging success was correlated with copulation rates during the female pre-MF period. The relationship between copulation frequency and male feeding rates was more clear when the total number of copulations per clutch was considered. Frequently copulating males fed chicks at higher rates ($r = 0.59$, $N = 23$, $p < 0.01$) even after controlling for the effect of brood size (partial $r = 0.56$, $df = 20$, $p < 0.01$). The number of copulations per clutch also was correlated with the percentage of time spent by males at the nest during the pre-MF period ($r = 0.41$, $N = 35$, $p < 0.05$). Rates of chick provisioning by females were also significantly correlated with PC rates, after controlling for brood size (partial $r = 0.46$, $df = 20$, $p < 0.05$). In fact, chick provisioning rates by both members of a pair were highly correlated each other (partial $r = 0.91$, $df = 20$, $p < 0.001$).

7. Extra-pair copulations at colonial nests.

Despite that both males and females had ample opportunities for engaging in EPC behaviour with neighbouring birds of the opposite sex during the female MF period (Table 5), the occurrence of EPC was extremely rare. The number of successful EPC was 19 (13 at La Dehesa, 6 at Pedroche), which renders a proportion of 0.45% of total successful copulations. On 55 occasions (see below), already paired storks were observed to fly to a nest in which a member of the opposite sex stayed alone but, except in the 9 cases reported, males never attempted to mount females. This means that the proportion of EPC attempts as a percentage of total copulation attempts (5,850) would lie between 0.32 and 0.94%, the former figure being probably more realistic.

TABLE 5. Opportunities for EPC for colonial males and females

| | Breeding Colony | | | Average |
|-------------------------|-----------------|---------------|--------------|---------|
| | La Dehesa | Pedroche | Jerez | |
| Opportunity for Females | 10.1 (3.8) | 8.5 (1.8) | 2.0 (0.9) | 6.9 |
| Males | 27.2 (3.9) | 18.9 (2.3) | 8.3 (1.2) | 18.1 |
| Number of focal pairs | 23 | 12 | 8 | |

Mean values and SD (in brackets) are given for the percentage of daytime a fertile female was alone at her nest while a neighbouring male was present (opportunity for females) and the percentage of daytime a male was present while a neighbouring fertile female was alone at her own nest (opportunity for males).

Nine females belonging to 43 study pairs participated in successful EPC. Two ringed females were 5 and 3 years old. Six females flew to, and copulated on the nest of a neighbouring (< 20 m) male, while the remaining 3 received the visit of a nonmate male with whom they copulated on her own nest. None of the 9 females involved in EPC was paired for more than five days when EPC occurred and 5 deserted their mate after engaging in EPC, pairing with another male afterwards. On each occasion a female participated in an EPC, her male mate was absent from the colony. All females engaging in EPC laid eggs at least 12 days after EPC occurred (mean = 20.3 d ± 7.5 SD) (Fig. 6). Females were observed flying to a nest other than their own while the resident male was present in

another 23 cases. Eight females participated in such visits, of which 5 had previously engaged in successful EPC. The visiting female was repelled in 16 cases by the male alone and by both members of the resident pair in 7 cases.

Seven males were observed to participate in successful EPC. Two ringed males were 5 years old. Five paired focal males were visited by a female and copulated on his own nest, and two flew to a different nest and copulated with recently paired females. These two males came from a distant part of the colony and were not included in the focal sample, hence their pairing status was unknown. Males who participated in EPC did so between 54 and 15 days before their female mate laid eggs. This is most surprising because males were more free to spend time away from the nest after the onset of incubation. Focal males were observed to visit others' nests in another 48 cases when resident birds were present: 23 the

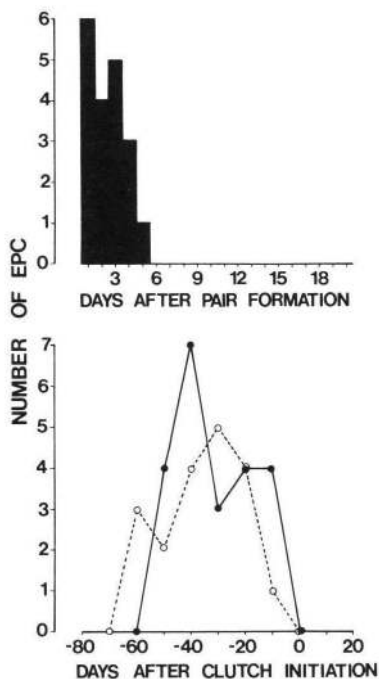


Fig. 6. Upper: the number of EPC performed by female white storks at different times after pair formation. Lower: the number of EPC performed by female white storks at different times of her breeding cycle (open dots) and the number of visits by male white storks to non-mate females while they remained alone at her nest, at different times of the breeding cycle of the visited female (black dots). Day 0 is the day of laying of the first egg in the clutch.

female alone, 16 the male alone and 9 both members of the resident pair. Fig. 6 shows that most alone females who were visited by males were not in their MF period. Females attacked and repelled the approaching male in all these cases.

When both members of a pair, while present on their nest, were approached by another bird, the male attacked the intruder more frequently than the female (Wilcoxon test, $Z=4.13$, $p<0.001$, $N=43$). Males attacked intruding males and females equally often ($Z=1.78$, ns) but females preferred to attack intruding females over males ($Z=2.09$, $p<0.05$).

8. Female desertions.

Out of 43 paired females at colonies, 9 (21%) deserted their mate prior to egg laying. Desertion took place 6 days on average after pair formation (range 2-14 days, $N=7$). Three ringed females were 4, 6, and 6 years old (mean 5.3), while five deserted males were 2.4 years old on average (± 1.14 SD). Females who deserted mates spent significantly longer amounts of time alone at the nest during the pair-formation period (12.3%, ± 2.2 SD, $N=7$) than females who remained with her first male mate (6.47%, ± 1.5 SD, $N=35$) (Mann-Whitney test, $Z=2.04$, $p<0.05$). In addition, deserting females had lower PC rates (0.39 copulations/h, ± 0.09 SD) than females who did not desert their mates during the same period (0.49 copulations/h, ± 0.06 SD) (Mann-Whitney test, $Z=4.87$, $p<0.001$).

Discussion

Both female and male white storks breeding at colonies had ample opportunities for engaging in EPC, but they did not. First, EPC in this study occurred at a frequency much lower (0.4%) than it has been reported for related colonial species (cattle egret *Bubulcus ibis*: 29-31%, FUJIOKA & YAMAGISHI, 1981; MCKILLIGAN, 1990; spoonbill *Platalea leucorodia*: 19%, AGUILERA & ALVAREZ, 1989; white ibis *Eudocimus albus*: 36%, FREDERICK, 1987). Second, EPC were poorly tuned with the female MF period and, consequently, any sperm deposited by a nonmate male would have to compete with many further pair-copulations extended over a period of several (>10) days. Studies with domesticated birds have revealed that the last insemination before fertilization has priority (BIRKHEAD, 1988). Since the intensity of sperm competition should be directly related to the ratio EPC/(PC+EPC) at the time of ovulation, this means that sperm competition must be necessarily weak or absent in this species. Both males and

females participated more in extra-pair interactions early in the breeding cycle, when pairs had just recently formed. This, together with the more active role played by females in both EPC behaviour and pair formation (see also HAVERSCHMIDT, 1949; COLLIN, 1973; BROWN *et al.*, 1982), strongly suggests that EPC were part of a "mate sampling" strategy (ENS, 1992) rather than of a mixed reproductive strategy (WESTNEAT *et al.*, 1990).

We feel unable to advance an explanation for the lack of EPC in white storks. However, our results raise the question of how copulation patterns are to be explained in the absence of sperm competition. Consistent with the apparent lack of sperm competition, white storks lacked some behaviours which have been generally assumed to have evolved as male countermeasures to EPC in the context of a Mixed Reproductive Strategy.

a) The coincidence of PC and EPC or male intrusion pressure with the female fertile period (FITCH & SHUGART, 1984; MCKINNEY *et al.*, 1984; BIRKHEAD, 1988; MOCK & FUJIOKA, 1990; WESTNEAT *et al.*, 1990). White storks lacked tuning of maximum daily EPC and PC rates with the female MF phase. Many monogamous species in which EPC are common show a peak in PC (and also EPC) near or at the onset of the female laying period (AGUILERA & ALVAREZ, 1989), which is a likely adaptation for minimizing the risk of extra-pair fertilizations. White storks, on the contrary, drastically reduced PC rates around a week before egg laying, and this effect was due to both a lower receptivity by females and a lower rate of copulation attempts by males.

b) The existence of mate guarding (BIRKHEAD, 1979; FORD, 1983; FITCH & SHUGART, 1984; MCKINNEY *et al.*, 1984; MOCK & FUJIOKA, 1990). White stork males spent less time at the nest during the female MF than pre-MF period, while the opposite pattern has been observed in cattle egrets (FUJIOKA & YAMAGISHI, 1981) and spoonbills (AGUILERA & ALVAREZ, 1989). Since, in all these species, females only copulate at the nest, the extent of nest guarding directly reflects effective mate guarding, thus females paired to males with a lower attentiveness at the nest during his female fertile periods experienced higher EPC rates (FREDERICK, 1987; WESTNEAT *et al.*, 1990). Male absence caused females to spend a much higher proportion of daytime alone at the nest during their MF period than before, which is also at variance with the expected pattern under conditions of sperm competition (*e.g.* FREDERICK, 1987; AGUILERA & ALVAREZ, 1989; BIRKHEAD & MØLLER, 1992).

c) The occurrence of a daily pattern of copulations which parallels the chance of fertilization. In many birds studied, ovulation takes place

within a few (<100) minutes after laying of the preceding egg (CHENG *et al.*, 1987; BIRKHEAD, 1988; CHENG & BURNS, 1988), and any copulation occurring during such a "fertilization window" would maximize the probability of fertilizing the ova. White storks showed a peak of copulations in late afternoon which was especially marked during the female MF period. Most (74%) eggs were laid during the morning (0700-1200) (48 eggs, 21 pairs), hence a "fertilization window" would be expected on late morning and not at dusk, when most copulations took place.

d) The higher prevalence of behaviour related to sperm competition (*e.g.* copulation rates or mate guarding) among colonial than among solitary-nesting species or populations (BIRKHEAD, 1978; MØLLER, 1985; BIRKHEAD *et al.*, 1987). Colonial storks did not copulate more than solitary ones, and the lower fraction of time spent at the nest by solitary birds can be easily explained by the higher risk of nest robbery at colonies.

On the other hand, white stork copulation rates are among the highest ever recorded for birds: only 4 out of 57 species copulate 160 times per clutch or more (BIRKHEAD & MØLLER, 1992). In addition, copulations extended over a prolonged period (often several weeks) prior to fertilization the eggs. The evolution of high copulation rates and extended copulatory periods in birds have been explained by invoking selective pressures related to sperm competition (BIRKHEAD *et al.*, 1987; MØLLER, 1991; BIRKHEAD & MØLLER, 1992). The two proposed advantages of extended copulation periods are:

- a) The result of females concealing ovulation in order to prevent sexual harassment by non-mate males or to obtain benefits provided by their mates during the pre-laying period (THORNHILL, 1984; LUMPKIN, 1981, 1983; BIRKHEAD & LESSELLS, 1988; MØLLER, 1985, 1987b).
- b) A way of males for swamping any sperm stored by their female mate resulting from previous matings (McKINNEY *et al.*, 1984; AGUILERA & ALVAREZ, 1989; McKILLIGAN, 1990).

The main problem with these hypotheses in the case of the white stork is that they all assume that sperm competition is an important selective force favouring sperm swamping or concealing ovulation to nonmate males. However, it is still possible that female storks gained a benefit from male care during the pre-MF period (mechanism a above), hence they were selected to retard ovulation as much as possible (THORNHILL, 1984; LUMPKIN, 1983). Male white storks neither protected females from sexual harassment by other males (LUMPKIN, 1983) nor provisioned mates with food (TASKER & MILLS, 1981; MØLLER, 1987a), but gathered and appor- tioned nest materials. The close association between copulation and nest

construction behaviour by males would mean that females were trading copulations for nest materials. A weakness of this hypothesis is that, by retarding ovulation in order to obtain a large nest, females would also delay egg-laying, and later clutches were less productive. In addition, it fails to explain why females should not solicit copulations and why males should attempt to copulate at such high rate. However, the association between nest building and copulation could explain why males tended to copulate immediately on returning to their nest, presumably after collecting nest material. This pattern is commonly explained as a tactic of paternity assurance when the risk of EPC is high (BIRKHEAD & MØLLER, 1992).

If high copulation rates in the white stork can neither be explained by constraints imposed by egg fertilization or predation pressures, nor as an adaptation to sperm competition, we must consider the possibility that copulations are part of a process of mate assessment involved in the acquisition and maintenance of the pair bond (BIRKHEAD *et al.*, 1987; BIRKHEAD & MØLLER, 1992). This hypothesis assumes that mating is costly both in terms of sperm production (DALY, 1978; DEWSBURY, 1982) and copulating effort, hence females may choose good-quality males by choosing vigorously courting (*i.e.* copulating) males (DEWSBURY, 1988; GRAFEN, 1990). That males need a recovery time between copulations is suggested by the fact that intervals between PC by male spoonbills with an intermediate EPC by the male mate were longer than those without an EPC (AGUILERA, 1989). Copulations often occur at times when they have nothing to do with fertilization (ELLIS & POWERS, 1982; MCKINNEY *et al.*, 1984; ROBERTSON, 1986; JAMIESON & CRAIG, 1987; NUECHTERLEIN & STORER, 1989; SODHI, 1991; BIRKHEAD & MØLLER, 1992) but which could be potentially involved in mate assessment by females.

Our results on female desertion (also HASS, 1966) support the idea that females preferred to mate with males that copulated frequently and were less likely to leave them alone at the nest, or beared any trait which correlated with copulation rate and nest attendance. Such a preference could have evolved by two possible mechanisms (KIRKPATRICK & RYAN, 1991): (i) indirect selection of preferences for males carrying good genes for general vigour, and or (ii) direct selection of preferences for males who provide resources to offspring.

A prediction arising from the mechanism of indirect selection for male vigour is that males copulating more frequently during the period of assessment (pre-MF) should be heavier and better at obtaining the larger nests. This prediction was not supported by the available data but sample sizes were quite small.

The possibility that females could employ PC as a cue for male aptitude for parental care has been repeatedly suggested, but supporting evidence is still lacking (FITCH & SHUGART, 1984; MØLLER, 1985; WESTNEAT *et al.*, 1990). We found that PC rates during the female pre-MF period were highly correlated with rates of chick feeding by males, because males who spent more time at the nest copulated more frequently. It is likely that the percentage of time a male can remain at the nest without feeding is positively related to foraging efficiency (FREDERICK, 1987), which in turn must be related to the rate of chick provisioning. That time spent at the nest was dependent upon the nutritional condition of the male, is suggested by the fact that heavier males and males artificially supplied with food attended the nest for longer. Nest and mate guarding competes temporally with male feeding activity (BIRKHEAD & MØLLER, 1992). In species (*e.g.* swallows) in which mate guarding lasts for a few days, a large body mass may allow males to keep on guarding for longer (MØLLER, 1987c), but male reserves may be insufficient when guarding extends over a much longer period. Females could then be able to assess the foraging efficiency of males prior to laying by monitoring the percentage of day-time they spend at the nest and, simultaneously, imposing them a sensible energetic cost in the form of frequent copulations and, perhaps, the apportionment of nest materials. This hypothesis states that spending time at the nest and copulating frequently may be costly forms of mate investment. Accordingly, males should reduce their attentiveness once the female has committed herself to lay eggs. Male white storks did in fact this, and the effect was less important when males were provided with food. On the other hand, food-supplemented males copulated less during the pre-MF period, which seems not to be in agreement with this hypothesis.

As it stands, the hypothesis does not state that females can assess the foraging efficiency of males by monitoring their rate of PC. Instead, copulations are viewed as part of a complex communicative system by which males advertise their good body condition *in spite of* guarding the nest. Monitoring the duration of male nest guarding is open to cheating because males could stay at the nest for long periods at the expense of their own energetic reserves. Unless males spend energy at a high rate during the period of female assessment, females monitoring the extent of male nest guarding will be assessing the quality of male energy reserves, instead of their current feeding efficiency. However, the amount of male energetic reserves may be decoupled from his current foraging efficiency (*e.g.* in migrating species, or when adults and nestlings require different food items). The use of energetically costly signals is required for the

reliability of this communicative system to remain stable over time (ZAHAVI, 1977; GRAFEN, 1990). Since the assessment process takes place in the context of mating, copulations are good candidates to become incorporated as major components of a costly signalling system. Unlike white storks, herons, egrets and ibises are mostly sedentary, and this difference could perhaps be related to the lack of a costly signalling system in these species.

BIRKHEAD *et al.* (1987) argued that copulations were unlikely to be used by females as a form of male assessment because in most species are males, rather than females, who solicit copulations. But as more evidence is accumulated, the opposite turns to be true: females solicit copulations in 88% of species studied (BIRKHEAD & MØLLER, 1992). However, once copulations are regarded as courtship signals, they could evolve as a form of male advertisement in which the male takes the initiative for copulation. Females paired with males able to feed chicks at a high rate may be selected in turn to increase feeding rates if this improves the number or quality of fledged chicks (WINKLER, 1987). Consequently, males advertising their quality might benefit both from securing a mate and from increased rates of chick provisioning by females. In agreement with this idea, rates of chick provisioning by females also showed a significant correlation with copulation rates, and chick feeding rates by males and females were also strongly correlated each other. The "Male Assessment" hypothesis could also explain why males should reduce PC attempts as early as they are confident of the female's commitment to lay eggs in his nest. Many monogamous species (*e.g.* BIRKHEAD *et al.*, 1987) show a dramatic drop in PC rates at the onset of laying. This is problematic to the "Sperm Competition" hypothesis because daily PC rates decrease when females still have fertilizable ova, but it makes sense as a reduction in advertising effort once females no longer need to be persuaded to lay eggs by means of costly signals. In a modified version, the "Male Assessment" hypothesis has also been invoked to explain the high copulation rates and associated female adaptations (low conception rates, anovulatory oestrus, and synchrony of oestrus) of feline mammals (EATON, 1978).

Comparative studies have proved to be very useful at elucidating the mechanisms underlying the variation in copulation patterns among birds (BIRKHEAD *et al.*, 1987; MØLLER, 1991; BIRKHEAD & MØLLER, 1992). It is unfortunate, however, that "Male Assessment" hypotheses fail to provide a simple variable (like the $EPC/(PC+EPC)$ ratio in the "Sperm Competition" hypothesis) with which PC patterns are expected to covary in a predictable way. This is so because female interests are likely to vary from

species to species and also because the extent to which males advertise by copulating (*i.e.* the contribution of copulations to the whole signalling system) may also vary. Two predictions of the "Male Assessment" hypothesis are virtually the same as those of the "Sperm Competition" hypothesis: (i) higher PC rates among monogamous-polyandrous (having extensive male parental care) than among polygynous birds (lacking much paternal care) (MØLLER, 1991), and (ii) higher PC rates among non guarders (*e.g.* raptors, which may also have female-feeding, see below) than among guarders (BIRKHEAD *et al.*, 1987; & MØLLER, 1991).

On the other hand, the first hypothesis does not predict a direct relationship between PC rates and the extent of sperm competition *within monogamous* species, a prediction that awaits to be tested. Our results suggest, however, that this should be measured directly (*e.g.* as the EPC/(PC+EPC) ratio), and not inferred from another variable like the extent of guarding or the degree of breeding sociality. Otherwise, we may be losing substantial residual variance in copulation rates which is useful for identifying selective pressures (other than sperm competition) favouring high copulation rates.

For example, copulation patterns in raptors have been extensively explained as male counteradaptations to sperm competition in the absence of effective mate guarding (BIRKHEAD *et al.*, 1987; BIRKHEAD & LESSELLS, 1988; MØLLER, 1987a, 1991; BIRKHEAD & MØLLER, 1992; NEGRO *et al.*, in press). In support of this hypothesis, MØLLER (1987a) found that (i) male goshawks *Accipiter gentilis* copulated more frequently than usual after returning from a hunt; (ii) males spent a lower fraction of daytime at the nest site after eggs laying than before; and (iii), across species, copulation frequency showed a strong positive correlation with the extent of male provisioning during the pre-laying and the egg-laying periods. Such patterns, however, also make sense under the hypothesis that males advertise and females assess male quality by copulation frequently during the period of male nutritional stress. MØLLER (1987a) actually did not find evidence of sperm competition in goshawks. EPC are usually characterised by a very low (often less than 50%) success (FUJIOKA & YAMAGISHI, 1981; FREDERICK, 1987; WESTNEAT, 1987; BIRKHEAD & LESSELLS, 1988; NEGRO *et al.*, in press), which lowers the average success of total copulation attempts. However, more than 99% of all copulations analyzed by MØLLER were successful (see also ROSENFELD *et al.*, 1991, for another putative example). In fact, when the extent of mate guarding and breeding density, instead of female provisioning is considered, many raptorial species are found which do not fit the expected pattern (SIMMONS, 1990).

All this claims for the necessity of detailed field studies of the copulation behaviour of birds as the only way to distinguish among several plausible (and not exclusive) hypotheses. In this context, the search for species with a low degree of sperm competition will be especially helpful for identifying additional factors accounting for the variation in copulation patterns.

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Zusammenfassung

Weißstörche *Ciconia ciconia* verpaaren sich ca. 30 Tage vor der Eiablage. In dieser Zeit kopulierten die Partner häufig (160 Kopulationen/Paar; 04 Kopulationsrate eine Woche vor der Eiablage drastisch absank. Dem liegen sowohl eine verringerte Anzahl von Kopulationsversuchen seitens des Männchens als auch eine geringere Empfängnisbereitschaft des Weibchens zugrunde. Dieses Verhaltensmuster war unabhängig davon ob die Paare solitär oder in Kolonien brüteten. Kolonie- und solitärbrütende Männchen verbrachten mehr Zeit