COPULATIONS AND MATE GUARDING OF THE SPOONBILL (PLATALEA LEUCORODIA)

by

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Introduction

Now that has been established that extra-pair copulations (EPCs) can fertilize eggs in monogamous bird species (*e.g.* BRAY *et al.*, 1975; BURNS *et al.*, 1980; ALATALO *et al.*, 1984; GAVIN & BOLLINGER, 1985; MØLLER, 1987; QUINN *et al.*, 1987; EVARTS & WILLIAMS, 1987; WESTNEAT, 1987), attention can be given to the costs and benefits of these activities for both sexes, as well as the behavioural mechanisms involved.

Compared to strictly monogamous males, those practicing a Mixed Reproductive Strategy (MRS: TRIVERS, 1972; BEECHER & BEECHER, 1979; FITCH & SHUGART, 1984) would increase their reproductive success. On the other hand, if female cooperation is essential for successful EPCs in many bird species (TIENHOVEN, 1983; LUMPKIN, 1983; FITCH & SHUGART, 1984; FREDERICK, 1987; see for exceptions MCKINNEY *et al.*, 1983 and BIRKHEAD *et al.*, 1985), the control that females have on the outcome of EPC attempts may open new opportunities for females to benefit from EPCs.

Proposed benefits of such behaviour to the female are: avoidance of infanticide (CROOK & SHIELD, 1985); provision of resources by approaching males, such as food, nest material, *etc.* (THORNHILL, 1984); additional parental care to her offspring (DAVIES, 1985); better genetic quality of offspring (GLADSTONE, 1979); transmission to their sons of the tendency to practice extra-pair copulations (MØLLER, 1985); increased

genetic variability of the offspring (GLADSTONE, 1979); obtaining protec-
tion from her mate (LUMPKIN, 1983); being fertilized by the more com-
petitive sperm (KNOWLTON & GREENWELL, 1984) and, finally, assuring
fertilization of her eggs (McKINNEY et al., 1984).

Among the potential costs to females of accepting EPCs, probably the
most important would derive from desert by her mate (TRIVERS, 1972;
GLADSTONE, 1979). Other proposed costs include an increase of competi-
tion among nestlings as a consequence of a lesser degree of relatedness
among them (HAMILTON, 1964), attacks on her by her mate as a response
to EPCs (BARASH, 1976), reduced paternal care (DAVIES, 1985), stealing
of nest material and/or injury inflicted by the approaching male
(FREDERICK, 1987), or injury that in some cases may even cause the death
of the female (McKINNEY et al., 1983; AMAT, 1987).

Once sperm competition (sensu PARKER, 1970) has been established,
paired males developing a counter-strategy in defence of their paternity
would be at a selection advantage. Mate guarding is probably the most
widespread paternity defence behaviour among male birds (e.g. BEECHER
& BEECHER, 1979; BIRKHEAD, 1979, 1982; BJORKLUND & WESTMAN, 1983,
1986; BUITRON, 1983; CARLSON et al., 1985; MØLLER, 1985; BIRKHEAD et
al., 1987). Other tactics are aggression by the male toward his mate after
she has been exposed to an EPC opportunity, producing a delaying
ovulation, as described for the ringed dove (Streptopelia risoria) by
HUTCHINSON & LOVARI (1976) and devaluation of the competitors' sperm
by a high copulatory frequency (McKINNEY et al., 1983; BIRKHEAD et al.,
1987). The most sophisticated tactic, employed by male dunnocks
(Prunella modularis), involves pecking at the female's cloaca to induce her
to expell previously inseminated sperm (DAVIES, 1983).

This paper is concerned with the behavioural mechanisms developed
by male and female spoonbills (Platalea leucorodia) under the pressure of
sperm competition. Breeding colonies of spoonbills contain tightly
clumped nests and are located in low shrubs and trees (CRAMP & SIM-
MONS, 1977). Since males of this species make a large contribution to
parental investment by sharing incubation, nest building and defence,
and chick feeding with their mates (AGUILERA, 1988), we should expect
males to attempt to increase their fitness both though EPCs and by pater-
nity defence tactics.

Methods

The study was carried out at the mixed species heronry at Doñana National Park (SW
Spain) during the breeding seasons of 1985 and 1986. This heronry included 374
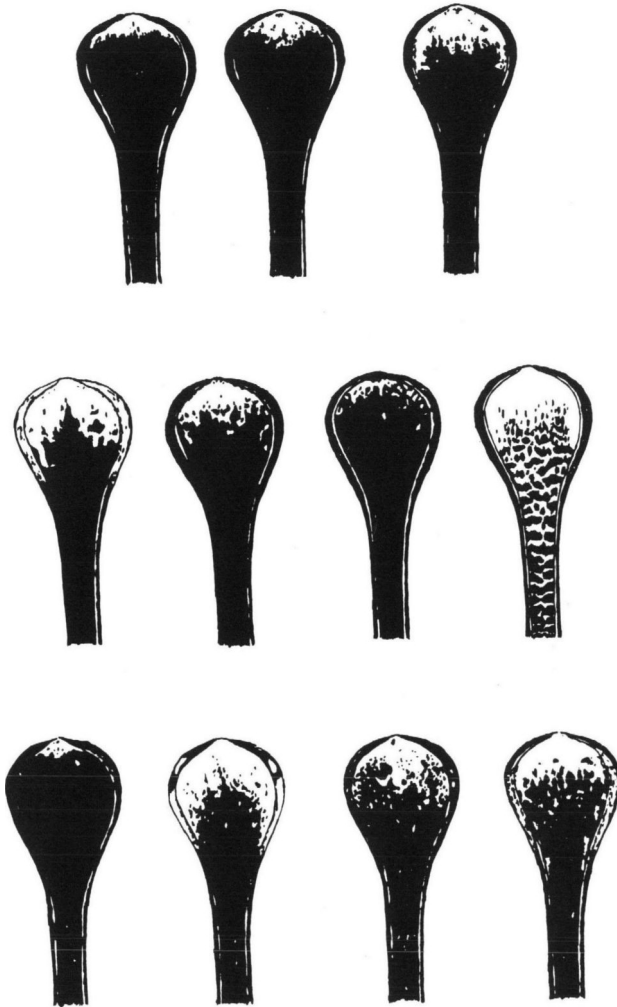
Fig. 1. Some examples of the upper bill spot pattern of spoonbills (drawings from specimens in bird skin collection at Doñana Biological Station).

breeding pairs of spoonbills in 1985 and 237 pairs in 1986 and was composed of the following species: grey heron (*Ardea cinerea*), cattle egret (*Bubulcus ibis*), little egret (*Egretta garzetta*), night heron (*Nycticorax nycticorax*) and white stork (*Ciconia ciconia*) as well as spoonbills. Also nesting at the heronry were jackdaws (*Corvus monedula*), magpies (*Pica pica*) and black kites (*Milvus migrans*), which were seen preying upon eggs or chicks (AGUILERA, 1988).

All the spoonbills' nests were located on trees, mostly cork oaks (*Quercus suber*), in the ecotone between the marsh and the low shrub. For a description of the ecosystems and

vertebrate communities of Doñana, see VALVERDE (1958, 1967), ALLIER *et al.* (1974) and AMAT *et al.* (1979).

Behavioural observations were done with the help of 10 × 40 binoculars and 20-60 telescope from two blinds on top of towers 6.5 m and 4.5 m high at about 60 m distance from the spoonbill nests. The birds were observed three or four days a week, without interruption from dawn to sunset (13 to 15 hours), usually from the time that the pair was formed and occupied a nest site until the young fledged. Observations of behaviour were also made throughout four moonlight nights in 1986.

The study birds could be recognized as individuals mainly by the colour and pattern of the light spot on the upper tip of the black bill (Fig. 1) or by plumage features. Sexes were distinguished easily by the larger body and bill size of males, and sexing was checked by the positions during copulation (males always mounting females).

The following phases in the reproductive cycle of each pair were distinguished: (1) Prelaying: from the moment that pair is formed until the day before the first egg is laid; (2) Laying: from the day the first egg is laid (day 0) until the day of the last egg (day +6 for a clutch of four); (3) Incubation: from day +7 until the day prior to the hatching of the first egg; (4) Nestlings: from the day of hatching of the first egg until the young leave the nests.

No studies are available neither for the spoonbill, nor for any other species of Ciconiiformes, on the length of the female's fertile period (the maximum time-span between insemination and the laying of a fertile egg). Our observations on pairs of spoonbills showed that the average period between the first copulation and the day when the clutch was started was 6.7 days (N = 9). This is within the known range of variation in sperm viability studies on other species, from seven days in the ringed dove (ZENONE *et al.*, 1979) to 60 days in the grey-faced petrel (*Pterodroma macroptera*, IMBER, 1976). Therefore we consider the fertile period from the day when the pair was seen to copulate for the first time to the day when the penultimate egg in the clutch was laid.

While collecting data, eight to 12 pairs occupying contiguous nests were observed simultaneously. Each individual's presence was noted during scan samples at 15 min intervals and all occurrences of copulation, carrying of nest material, and aggression were recorded. An individual was considered as present on the nest when it was either at its nest site or collecting nest material nearby.

Whenever a copulation involving any individual of the study pairs was attempted, we recorded the time, the bird's identity and the outcome. The outcomes were classified according the following mutually exclusive categories: (1) "Successful", when cloacal contact appeared to occur, (2) "Interrupted" by the male mate, in cases of extra-pair copulation attempts, (3) "Failed" as a result of the female's aggressive or evasive behaviour, (4) "Unsuccessful" due to other causes (male slips down from the female's back, a kite approaches, *etc.*).

In the statistical analysis of the data SIEGEL (1956) and SOKAL & ROHLF (1969) were followed. If not specified mean values ± S.D. are given.

Results

Pair copulations.

Copulatory behaviour was always watched on the nest sites. Pair copulations (PCs) lasted 9.7 ± 2.3s (N = 18), and they were always preceded by the precopulatory display "Rubbing back" by the male (AGUILERA, 1988). All PCs and PC attempts (PCAs) occurred on the nest site of the pair, and were observed from the first day on which the pair-bond was
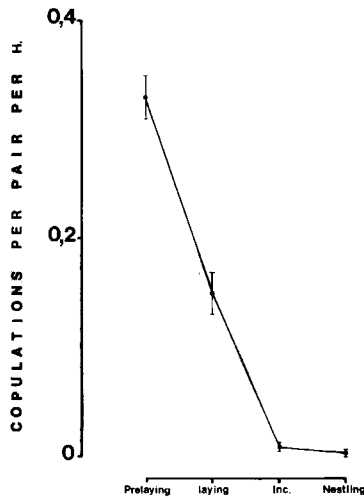
Fig. 2. Nest cycle variation in pair copulations frequency. Sample sizes (no. pairs) are: Prelaying, 22; Laying, 21; Incubation, 27 and Nestling, 21.

established (see Methods) until, exceptionally, the nestling period. The frequency of PCs was highest during the prelaying and laying periods (Fig. 2).

Copulations were recorded in all 22 pairs observed during the prelaying phase, 19 of 21 pairs during the laying period, 6 of 27 pairs during the incubation period and 2 of 21 pairs during the nestling period.

Assigning 12 days for the female's fertile period (seven days during prelaying plus five days from the day the first egg is laid to that of the penultimate egg in a clutch of four) and assuming 14 hours of daylight, we can estimate that a female is inseminated by her mate 42 times, on average, during that period.

When daily variation of PC frequency is examined from the first day that a pair takes possession of the nest site to the last day of the laying period, a peak is observed on day -1 (Fig. 3).

The success of PCAs estimated as the proportion of copulation attempts resulting in cloacal contact (and presumably sperm transference) was 94.7% (N = 362).

Extra-pair copulations.

In contrast to pair copulations, no precopulatory display was recorded preceding extra-pair copulation attempts (EPCAs). The EPCAs directed
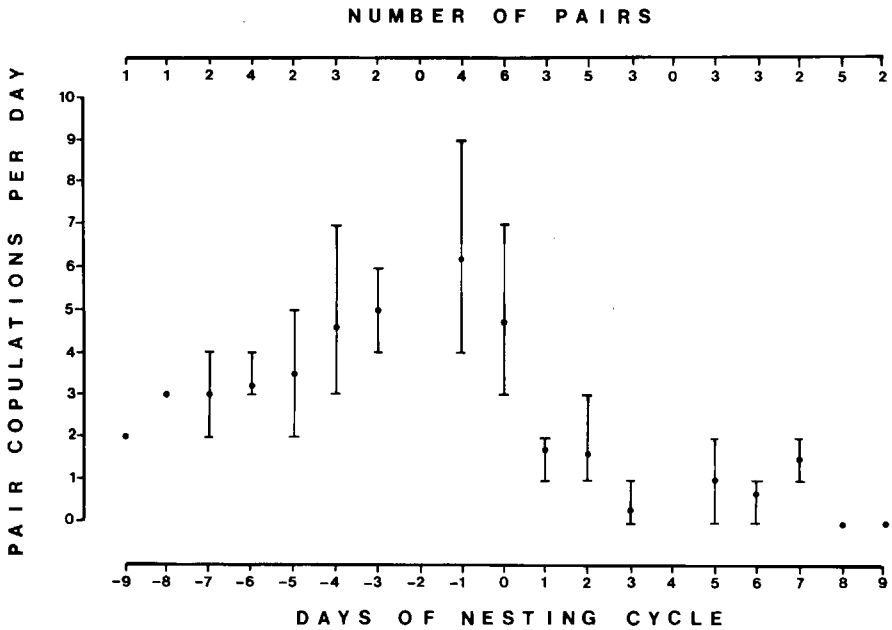
Fig. 3. Mean frequency of pair copulation in relation to time of egg-laying (day 0 = day when the first egg is laid). Only included pairs watched from dawn to sunset. Bars are range.

to paired females always occurred in the females' nests, while in the few cases when EPCAs were directed to unpaired females, they all occurred near or over the nest of the performer male (see below).

Nineteen percent of 447 copulation attempts (CAs) were EPCAs and involved some member of the 25 study pairs. Of the 25 study females that we saw copulating with their mates, 19 (76%) were involved in EPCAs. These females were the objects of 75 EPCAs (17.2% of all CAs in which they were seen participating). Of these attempts, in 66 cases (88%), we were certain that the males involved were paired (63 cases included study males).

Fifteen males (60% of the 25 study males) participated in some EPCA, besides three other males that we started to watch when they were already incubating or attending nestlings. These 18 males performed 74 EPCAs (17% of the total number of CAs), 68 of which (91.9%) were directed towards paired females (64 of them to study females). Five EPCAs were directed at unpaired females standing on unoccupied egret and

heron nests in the vicinity of the performer male nests, and one EPCA was directed at an unpaired female standing on the nest of a study male. On the arrival of this female at the male's nest, she was first attacked by him, but a few minutes later he copulated with her, then attacked her again, and finally chased her away from the nest.

In addition, in 1986, four CAs were directed by two different males towards an individual male of another study pair, although due to the aggressive response by the target male, mounting was never completed.

Contrary to various other bird species (*e.g.* FUJIOKA & YAMAGISHI, 1981; BEECHER & BEECHER, 1979; MØLLER, 1985; EMLEN & WREGE, 1986; BIRKHEAD *et al.*, 1985; FREDERICK, 1987; MCKINNEY *et al.*, 1983), EPCAs involving more than one individual male were never recorded.

Distance between nests and its relation to EPCAs.

The mean distance between nests occupied by males and females involved in some EPCA was shorter than that between the nests of all study pairs in the two nesting seasons.

The mean distance between 13 nests of study pairs was 4.9 ± 3.7 m (Range: 0.4-11 m, $N = 78$) in 1985, while that between nests of some of the owners involved in EPCAs was 1.3 ± 0.7 m (Range: 0.4-3 m, $N = 16$), the difference between the two means being statistically significant ($t = 3.98$, $P < 0.01$). The corresponding values in 1986 were 5.2 ± 2.8 (Range: 0.5-14 m, $N = 98$) and 2.7 ± 1.2 m (Range: 1.5-5 m, $N = 10$), respectively, the difference also being significant ($t = 2.74$, $P < 0.01$).

Males directed EPCAs mainly at females occupying the nearest neighbouring nests (60% of the cases) or to females being second nearest neighbours (32.6%) (Fig. 4, Kolmogorov-Smirnov one sample test for independence of distances, $N = 50$, $D = 0.43$, $P < 0.01$).

Reproductive status and EPCAs.

Two parameters have been examined in order to assess the influence of the reproductive status of individuals on the tendency to show EPC behaviour.

Firstly, the proportion of males and females participating in EPCAs may be a useful estimate of the extent of this behaviour among the individuals of our population. However, since the duration of the various reproductive stages differs and our sample effort varied between states, this measurement will be valid only for comparative purposes between sexes.

Across all the reproductive phases, the greatest proportion of females involved in EPCAs occurred during the prelaying period, while the males participated more in EPCAs when their female mates were laying (Fig. 5a), but those differences were not significant (χ^2 tests) for any reproductive period.

The second measurement used, rate of EPCAs over time, showed a similar pattern, with maxima during the prelaying period for females and during the laying period for males (Fig. 5b).
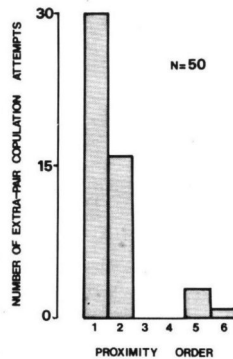

Fig. 4. Relationship between proximity of nests (1 = nearest, 2 = 2nd nearest, n = nnd nearest) and occurrence of extra-pair copulation attempts.

Extra-pair copulations and female fertility.

The frequency of EPCAs for females was almost eightfold during their presumed fertile period as compared to their nonfertile period (Table 1), indicating that males attempt extra-pair copulations mostly with females that can be fertilized.

EPCAs were significantly more successful during than outside the female fertile period (Table 2). All EPCs occurred while the females were alone on their nests. In 22 of 29 EPCs the female's mate was collecting nest material in the colony and in the other seven cases he was away from the colony (incubation: 3 cases; laying: 3 cases; prelaying: 1 case).

An EPCA might fail because of interference by the female's mate before cloacal contact occurred or as a consequence of evasive behaviour of the female. During the fertile period the principal cause of failure was interference by the mate (Table 3). On arriving at his nest, the male would attack the intruder, throwing him away from the nest without any resistence on the part of the attacked male.
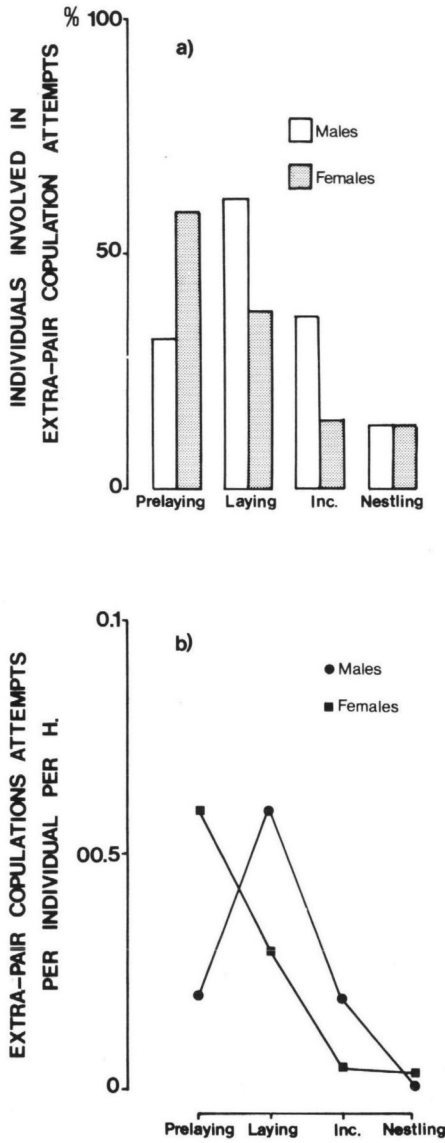
Fig. 5. Seasonal variation in (a) the proportion of individuals involved in extra-pair copulation attempts and (b) the frequency of extra-pair copulation attempts. In both cases sample sizes (no. pairs) are the same as those in Figure 2.

TABLE 1. Frequency of extra-pair copulations attempts (ECAs) in relation to the female fertility period

Female status	Number of females	Female-hours of observation	Number of ECAs	ECAs per female-hour
Fertile	26	1179.3	55	.047
Nonfertile	28	3521.6	20	.006

TABLE 2. Female fertility and success of the extra-pair copulation attempts (ECAs)[1])

Female status	Successful ECAs	Unsuccessful ECAs	Percent of success
Fertile	26	29	47.3
Nonfertile	3	17	15.0

[1]) $\chi^2 = 5.15$, $p < 0.05$.

TABLE 3. Causes of failure of extra-pair copulation attempts in relation to the fertility status of the females[1])

Female status	Male-mate interrupted	Avoided by the female	Percent avoided by the female
Fertile	24	5	17.2
Nonfertile	6	11	64.7

[1]) $\chi^2 = 8.65$, $p < 0.01$.

TABLE 4. Success of the extra-pair copulation attempts (ECAs) not interrupted by the male mate in relation to the reproductive status of the females[1])

Female status	Number of successful ECAs	Number of unsuccessful ECAs	Percent of success
Fertile	26	5	83.9
Nonfertile	3	11	21.4

[1]) $\chi^2 = 13.8$, $p < 0.001$.

An effect of the female's reproductive status on the way she avoids copulation was apparent. Females avoiding copulation during their fertile period more frequently did so by jabbing at the intruder male (5 out of 5 cases), causing him to lose balance while trying to mount. On the contrary, during their nonfertile period females avoided copulation by not raising their tails (10 out of 11 cases, Fisher exact test, P = 0.0014).

As a whole, females were more effective rejecting EPCAs during than outside their nonfertile period (Table 4).

Daily rhythms of copulatory activity.

Pair copulations as well as EPCs were observed throughout the daylight hours, but none were recorded taking place during the night. Both PC and PCA frequencies showed a peak in the early morning and another in the afternoon. However, this pattern did not depart significantly from the null hypothesis of equal occurrence for every hour of the daylight period (Fig. 6a, Kolmogorov-Smirnov one sample test, N = 304, D = 0.04, NS, and N = 283, D = 0.06, NS, for PCAs and PCs respectively), although there was a slight tendency for PCs and PCAs to occur at times just before expected. When daily variation in PC frequencies between the prelaying and laying periods were compared, no significant difference was found (Fig. 6b, Kolmogorov-Smirnov two sample test, N1 = 195, N2 = 55, D = 0.07, NŜ).

On the other hand, a significant difference was detected between the observed frequencies of EPCAs and the expected values on the null hypothesis, the former occurring later than expected (N = 195, D = 0.19, P < 0.05). Two peaks in EPCAs frequencies were apparent, one between 8:00 h and 9:00 h and another around 18:30 h (Fig. 7). This pattern was also significantly different from that for pair copulations (EPCAs *vs* PCAs: D = 0.19, P < 0.05; EPCAs *vs* PCs: D = 0.2, P < 0.05).

Mate guarding.

During the prelaying period, females were left alone in their nests, on average, 1.2% ± 7.8% of daylight hours (Range: 0-6.8%; N = 19) and 3.3% ± 46.3% during the laying period (Range: 0-46.9%; N = 21). The difference between the two periods was not significant (Wilcoxon matched-pairs test z = 36; P > 0.8). The slight difference between the two means was even less important when we consider that it was mainly the effect of one individual male being away from his nest 46.9% of the
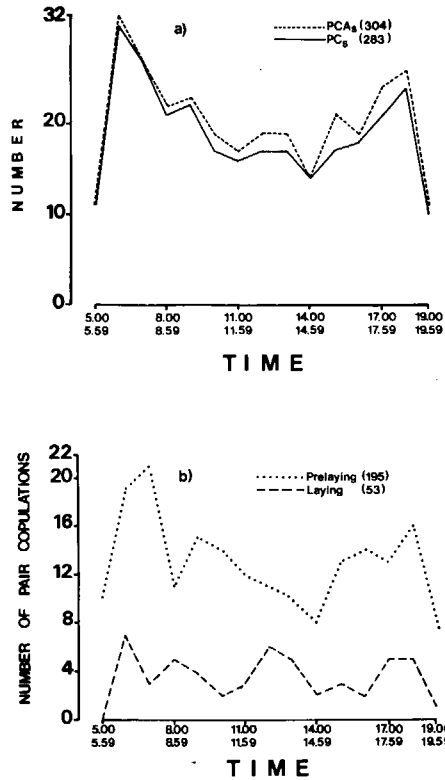
Fig. 6. Daily variation in (a) pair copulations and pair copulation attempts (all reproductive periods combined) and (b) pair copulations separated on prelaying and laying periods. Sample sizes in parentheses.

daylight time. When this individual was excluded from the sample, the average proportion of time that females stayed alone in their nest is almost equal for the two reproductive periods (Laying: mean = 1.1%, S.D. = 1.7%; Range: 0-3%; N = 20).

During the incubation period, females were alone in their nests 6.9% ± 4.6% of daylight hours (Range: 0.4-20.4%; N = 21), a proportion significantly greater than that during the two preceding periods (z = 30; P < 0.001; and z = 19.0, P < 0.01, compared with prelaying and laying periods, respectively).

As already explained in Methods, males were considered to be absent from their nest when they were away from the colony and not when collecting materials in the vicinity of the nests. As a great proportion of
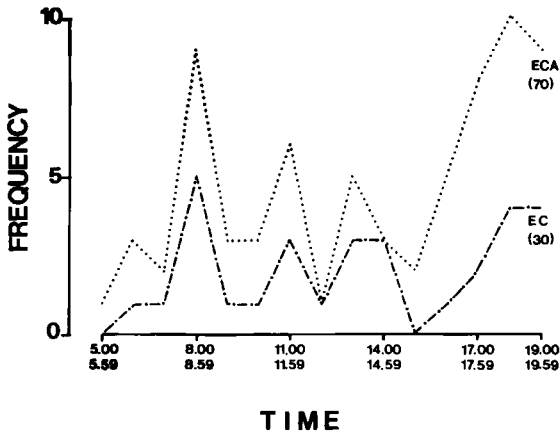
Fig. 7. Daily distribution of extra-pair copulation attempts (ECAs) and extra-pair copulations (ECs). Sample sizes in parentheses.

EPCA occurred while the male consort was collecting nest material, we should expect the latter to reduce the risk of cuckoldry while involved in that activity. This is probably why males collected material nearer to the nest than females did (Table 5). Also, during the fertile period of the females, their consorts tended to collect materials more often from or under the tree where the nest was located than during their females' nonfertile period (78.9%, N = 260; and 68.3%, N = 183, respectively; $\chi^2 = 6.26$; d.f. = 1, P<0.02).

Discussion

Mixed reproductive strategy of the males.

As implied in TRIVERS' (1972) definition, one of the predictions of the Mixed Reproductive Strategy hypothesis is that the male involved in an extra-pair copulation should be paired. This is precisely the case for the spoonbills in the present study, where most of the EPCAs directed to focal females came from paired rather than unpaired males. The situation is much the same in other bird species in which EPCAs occur (e.g. MINEAU & COOKE, 1979; FUJIOKA & YAMAGISHI, 1981; WERSCHKUL, 1982; RØSKAFT, 1983; MØLLER, 1985; BIRKHEAD et al., 1985; FREDERICK, 1987; HATCH, 1987).

The extent of MRS among paired males is apparently great, as reflected by the finding that 60% of them were recorded at some time in

TABLE 5. Distance from the sites where nest material is collected to the nest-tree periphery. Percentages in parentheses[1])

| | Distances (m) | | | | | |
	0	1-20	21-40	41-60	61-80	>80
Males	330	38	19	2	2	52
	(74.5)	(8.6)	(4.3)	(0.5)	(0.5)	(11.7)
Females	30	5	26	9	1	14
	(35.3)	(5.9)	(30.6)	(10.6)	(1.8)	(16.5)

[1]) $\chi^2 = 111.7$, d.f. $= 5$, $p < 0.001$.

an EPCA. Furthermore, this figure should be considered an underestimation, since the study males were not observed continuously.

If paired males were trying to maximize their reproductive success by practising a MRS, they would direct their EPCAs mainly towards already mated females. There are two possible explanations for the rejection of unpaired females that approached paired males on their nest site. Firstly, if sperm is limited (DEWSBURY, 1982), males should optimize sperm use by copulating with their mates, in order to secure paternity, and with other paired females if these are the only ones able to rear offspring successfully. Secondly, by rejecting an unpaired female approaching his nest, a male would avoid the risk of egg parasitism or egg destruction by that female (four cases of females destroying other spoonbills' eggs were recorded).

Males directed EPCAs preferentially to paired females in their fertile phase. The ability of males to discriminate between fertile and nonfertile females may have evolved (a) by a process of optimization of sperm allocation while attempting copulation preferentially with those females with high probability of being fertilized or/and (b) by the high benefit derived from approaching fertile females, as opposed to the risk resulting from leaving mate or nest unattended.

The way that male birds recognize the reproductive status of females is poorly known, although JONES (1986) demonstrated the detection of fertile females by male bank swallows (*Riparia riparia*) on the basis of the former's heavy flight, as consequence of their higher weight during prelaying and laying. FUJIOKA & YAMAGISHI (1981) suggested that cattle egret (*Bubulcus ibis*) males might detect the females reproductive status by the more bright coloration of bill and facial skin during their fertile period. For the spoonbill there are several features varying seasonally,

such as the condition of the crest feathers and the intensity of the yellow collar patch, which could be used by males. Besides, the continuous visual contact with neighbouring spoonbills might allow detection of the female's reproductive status by behavioural correlates such as the frequency of pair-copulations or her nest attendance. Detection based on behavioural traits is suggested by the fact that most EPCAs directed to females came from neighbouring males.

Tactics of paternity defence.

BIRKHEAD et al. (1987) showed how the frequency of copulations in birds can be determined by the risk of sperm competition. As pointed out by these authors, a high copulatory frequency can be explained in two ways: Firstly, it may help to conceal the fertile period of the females (BIRKHEAD, 1979). The most important prediction of this hypothesis would be that the seasonal pattern of copulatory frequency would either be random or constant and should extend over a period longer than the female fertile period. Our results do not support this hypothesis since the first copulations of mated pairs occurred when the female was very likely already fertile. In addition, the nesting cycle pattern of copulatory frequency was not constant, but increased progressively until laying started. In this way copulation frequency would reveal rather than conceal the fertile period.

Secondly, a high frequency of copulations may act to devaluate the sperm of possible competitors (McKINNEY et al., 1983, 1984). If, as demonstrated for domestic bird species, the probability of fertilization is directly related to the number of inseminations (MARTIN et al., 1974), we would expect that males of those species (or populations) with intense sperm competition would copulate very frequently with their mates during their fertile period (BIRKHEAD et al., 1987). Our results appear to support this hypothesis since pair-copulation frequency in spoonbills increased progressively until egg laying started and, in addition, mated males performed less EPCAs during the prelaying than during the laying and incubation periods. This could result from sperm competition of high intensity during prelaying (the time when females experience the maximum frequency of EPCAs) and/or from a decrease in the probability of fertilization derived from inseminations occurring during the laying period.

The seasonal pattern of copulatory frequency observed in spoonbills is probably the most common pattern in birds (see BIRKHEAD et al., 1987 for review). The question remains why a higher copulation frequency

does not occur at laying, precisely the time when most eggs are fertilized (STURKIE & OPEL, 1976)? The existence of sperm-storage glands in females (UV glands; HATCH, 1983; BAKST & BIRD, 1987; SHUGART, 1988 and references there) is probably the most important factor controlling that copulatory pattern. Unfortunately, the mechanism by which these glands function is still poorly known (COMPTON et al., 1978; CHENG et al., 1983; SIMS et al., 1987; BIRKHEAD et al., 1988). If UV glands were overflowed by sperm in the prelaying period, sperm then inseminated would be less successful attaining egg fertilization, either because its viability decreases in the reproductive tract of female or because it is expelled by an egg passing through the oviduct (BAKST, 1981). The proposed overflow of UV glands during prelaying and its negative effect over the fertilization success of the sperm inseminated after that overflow could explain the observed seasonal pattern of copulations in spoonbills and other bird species, as well as the different allocations that males give to their sperm production. Males attempt to fill the UV gland of their mates and then maintain a low copulatory frequency which provides just sufficient sperm to replace that already used by the mate and at the same time enables males to allocate most of their sperm production to extra-pair copulations.

It has also been proposed that males would increase their reproductive success by copulating mostly at the time of highest probability of fertilization (CHENG et al., 1983; AFTON, 1985; MØLLER, 1987). In connection with this, CHENG et al. (1983) showed the existence of fertilization windows, i.e. a short interval after every oviposition when an insemination may fertilize the next egg. Consequently, males practicing this tactic should preferentially copulate immediately after egg laying. Since the temporal pattern of PCs does not depart significantly from the null hypothesis of equal copulatory frequency throughout the day, male spoonbills do not appear to maximize their reproductive success by arranging the PCs in time. Nevertheless it may be of interest that the temporal pattern of EPCAs does depart significantly from the null hypothesis, most occurring in the late evening. Although the usual time of egg laying is not yet known for spoonbills, the only two cases observed during this study were at 17:05 h and 18:25 h which would support the hypothesis of a temporal optimization tactic in EPCAs occurrence, as showed in swallows (*Hirundo rustica*) by MØLLER (1985).

Mate guarding by males during their mates' fertile period is the most commonly described tactic for noncolonial birds to prevent sperm competition (*e.g.* BIRKHEAD, 1979, 1982; POWER et al., 1981; CARLSON et al.,

1985; BJÖRKLUND & WESTMAN, 1986). For colonial species, the use of this term is frequently misleading when considered in its strict sense, since the need of an almost continuous nest protection by at least one member of the pair prevents males from carrying out both nest protection and mate guarding simultaneously.

For this reason, BIRKHEAD et al. (1987) classified colonial bird species as "nonguarders". However, when mate guarding is applied in a functional sense (BIRKHEAD, 1979), this behaviour should be observed more often in sites where copulations are more likely to occur, i.e. at the nest site. Consequently, paired males should spend, as they actually do, more time in the nest when their mates are fertile rather than nonfertile, in this way presumably increasing their certainty of paternity (e.g. FUJIOKA & YAMAGISHI, 1981; WERSCHKUL, 1982; BIRKHEAD et al., 1985; FREDERICK, 1987; HATCH, 1987). In this regard, colonial bird species should be reclassified as guarders. In our study, all EPCs directed to paired females occurred on the female's nest site, while their mates were absent. Females were left alone in the nest by their mates more frequently in their nonfertile period than during their fertile period, suggesting that mate guarding is used by paired males as a behavioural tactic to prevent extra-pair copulations. In addition, as most EPCAs occurred while the females mates were collecting nest material, males resorted to do most collecting from short distances during the fertile period, in this way probably reducing the risk of cuckoldry.

Costs and benefits of EPCs for females.

Most of the proposed costs of EPCs for females are of little or no importance for female spoonbills. We never observed mate desertion, nor attacks on or injury to females, as responses to EPCs. Besides, males attempting EPCs did not steal nest material not did they attack the females, as has been observed in white ibis (Eudocimus albus, FREDERICK, 1987). On the other hand, no increase in competition among the nestlings as a consequence of reduced relatedness was apparent, since no aggressive behaviour among them has been regularly observed.

Some of the hypotheses regarding benefits for females from EPCs can be evaluated with field data like ours. A possible male strategy to increase their reproductive success may consist of infanticide directed selectively towards the young of females not fertilized by them. Females may respond by laying a replacement clutch which would increase the male's reproductive opportunities (CROOK & SHIELDS, 1985). As a counter-

strategy females may accept copulations from such males, offering them some probability of paternity (DAVIES, 1985) or rather concealing their fertility period by accepting copulations from them at any stage in the reproductive cycle. The last hypothesis is not supported by behaviour of female spoonbills, since their acceptance of EPCAs depended in great part on the reproductive phase.

Since apparently no resources were provided by males attempting EPCs, the benefits obtained could be fertilization by males of higher genetic quality than her mate or transmission of the tendency to perform EPC behaviour to male offspring. The second hypothesis would imply that females would accept EPCAs by any paired male, since all of the males attempting them would transmit the tendency. Since, according to our data, females accepted EPCAs only by some males, rejecting others, we can discard this hypothesis in favour of the choice of high quality males. In general, males attempting EPCs were in a more advanced stage than the female's mate and if this would imply better qualities on the part of EPCAs initiators, females would benefit by being fertilized by them. In the same context, and since most of the females' EPCs occur with the nearest neighbouring males, a female should choose not only its partner but should also take into account the quality of the nearest neighbour males as possible EPC partners.

Female spoonbills might also benefit by being receptive towards strange males by forcing their mates to constant vigilance of the nest, the site where copulations take place. By so doing, females could dedicate more time to feeding while males are on the nests. This hypothesis would imply similar benefits to the females as suggested by LUMPKIN (1983) as an effect of extending the receptive time of the female over her actual fertility period.

A likely consequence derived from the permissive behaviour of the paired females towards EPCAs and the tendency by their mates to stay guarding at the nest would be the increased paternity of those males staying for longer time at the nest site. If, as showed for the white ibis by FREDERICK (1987), the males spending a long time vigilant at the nest site are particularly skillful in obtaining food, female spoonbills would obtain the benefit derived by sharing descendants with those males.

Summary

Copulatory behaviour and mate guarding of spoonbills (*Platalea leucorodia*) nesting at Doñana National Park (SW Spain) were studied during two breeding seasons. Pair copulations were most frequent during the prelaying phase of the female, with a peak on the day before the first egg was laid. Most of the paired males (60%, N = 25) and females

(76%, N = 25) were involved in extra-pair copulation attempts (EPCA) and, overall, 19 per cent of the copulation attempts recorded were EPCAs, the targets being primarily paired females. A hypothesis about the optimization of the use of sperm production by paired males is proposed: males give most of their copulatory attention to their mates during the prelaying phase, the latters' uterovaginal sperm storage glands being in this way filled, and, once this is achieved, males turn their attention towards other females in prelaying phase.

Devaluation of the sperm of competitors by means of high copulation frequency, optimization of the seasonal pattern of pair copulations, and intense mate guarding were the primary tactics employed by males in defence of their paternity.

Considered that copulations are not completed without collaboration on the part of the female, their permissiveness towards EPCAs during the fertile period suggests advantages to females. Among the hypotheses on benefits of extra-pair copulations to female spoonbills, genetic quality of the offspring may be improved by this behaviour, and females may also benefit from the effects of intense nest vigilance by their mates.

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Resumen

Se ha estudiado durante 1985-1986 la custodia a la hembra y el comportamiento copulatorio de la espátula (*Platalea leucorodia*) anidando en el Parque Nacional de Doñana (SW de España). Las cópulas de la pareja fueron más frecuentes durante la fase de prepuesta, con un máximo el día antes de la puesta del primer huevo. Una gran parte de los machos (60%, N = 25) y de las hembras (76%, N = 25) emparejados estuvieron implicados en intentos de cópulas extra-maritales (ICEs). El 19% del total de los intentos de cópulas registrados fueron ICEs, dirigidos principalmente a hembras emparejadas. Se propone una hipótesis sobre la optimización del uso de la producción espermática por los machos emparejados: éstos dirigirían principalmente su atención copulatoria a sus parejas durante la fase de prepuesta, llenando de este modo las glándulas uterovaginales con su esperma y, una vez que esto ocurre, redirigirían su atención hacia otras hembras en estado de prepuesta.

Las principales tácticas de defensa de la paternidad empleadas por los machos fueron la devaluación del esperma de los competidores, por medio de una alta frecuencia copulatoria, así como una intensa custodia a la hembra.

Puesto que las cópulas no llegan a completarse sin la colaboración de la hembra, su permisividad hacia los ICEs durante el período fértil sugiere ventajas para ellas. Entre las hipótesis sobre los beneficios para las hembras derivados de las cópulas extramaritales, el aumento de la calidad genética de la descendencia así como los efectos de la intensa vigilancia del nido por su pareja, encontraron apoyo en nuestro estudio.