COPULATIONS AND MATE GUARDING OF THE SPOONBILL
(PLATALEA LEUCORODIA)

by

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(With 7 Figures)

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; Möller, 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 (Möller, 1985); increased

1) We are grateful to J. A. Amat, T. R. Birkhead, F. McKinney, A. P. Möller and an anonymous referee for their comments on an earlier draft of this paper. We thank also J. López Rojas and F. Campos for drawing the figures. Financial support was provided by ADENA-WWF, Junta de Andalucía and Consejo Superior de Investigaciones Científicas.
genetic variability of the offspring (Gladstone, 1979); obtaining protection from her mate (Lumpkin, 1983); being fertilized by the more competitive 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 competition 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; Möller, 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 & Simmons, 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 through EPCs and by paternity 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