Responses of male white ibises
to their mate's extra-pair copulations

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Summary. I intensively observed the mating behavior of 134 pairs of white ibises for over 15000 pair hours to examine the responses of males to extra-pair copulations (EPC) involving their mates. Females often cooperated completely in apparently fertile EPCs. Male mate-guarding was vigorous and effective. Males did not respond to apparent sperm competition with forced-pair copulation, physical punishment, or abandonment of their mates. I found no negative correlation between degree of female promiscuity and the amount of parental care her mate gave to the entire brood. Males also did not reduce paternal care given to the young most likely to be the result of an EPC. I hypothesize that males are constrained in the behaviors they can use to avoid misplaced paternity in this species. While male mate-guarding reduces the opportunities for female involvement in EPC, the behaviors used by males to protect paternity apparently have not prevented the evolution of female receptiveness during EPC attempts.

Introduction

Among monogamous avian species, copulation between members of different pair-bonds is a relatively widespread phenomenon (Gladstone 1979; Ford 1983; McKinney et al. 1984). It is not surprising that monogamous males should take advantage of every opportunity to inseminate extrapair females (Bateman 1948; Trivers 1972). But where males give parental care to offspring at the cost of other fitness benefits, they should be selected to avoid giving parental care to unrelated young (Trivers 1972; Maynard Smith 1977; Werram et al. 1980). Male behavior which leads to avoidance of this cost is predicted to be strongly developed in monogamous species that exhibit extra-pair copulations (EPCs).

Males might avoid misplacing parental care by ensuring the exclusive paternity of the broods they give care to. Males could delay reproduction to ensure that their mates are not laying eggs fertilized by previous copulations with other males (Power et al. 1981), or simply guard their mates intensively from EPC attempts (Birkhead 1978, 1979; Beecher and Beecher 1979; Mineau and Cooke 1979; Werschkul 1982a, b; Buitron 1983; Bjorklund and Westman 1983; Afton 1985; Birkhead et al. 1985). A male also may forcibly copulate with his own mate immediately following her involvement in an EPC, presumably to dilute the sperm of extra-pair males (Barash 1977; McKinney et al. 1984; Afton 1985). Additionally, males have been predicted to physically attack female mates that consort or copulate with extrapair males, making female involvement in EPCs so costly that females do not engage in it even in the absence of their mates (Trivers 1972; Barash 1976; Maynard Smith 1977; Fitch and Shugart 1984).

Males also might avoid the cost of misplaced parental care by giving parental care only in relation to their certainty of paternity (Trivers 1972; Joste et al. 1985; Craig and Jamieson 1985). This response might be graded, or all-or-none. The latter case would result in abandonment (Trivers 1972; Maynard Smith 1977; Craig and Jamieson 1985).

Of these possible male strategies, the occurrence of physical attacks, abandonment and reduced parental care are the most controversial. These male responses would have direct conse-

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quences for a female's fitness and consequently could lead to the evolution of female resistance to EPC attempts (Trivers 1972; Barash 1976; Birkhead 1978, 1979; Gladstone 1979; Fitch and Shugart 1984; Birkhead et al. 1985).

Evidence of abandonment, physical attack, and reduction of parental care by males is scarce. Although abandonment and punishment of females in response to evidence of extra-pair consortship have been demonstrated in ring doves (*Streptopelia risoria*) in laboratory settings (Erickson and Zenone 1976; Zenone et al. 1979), these responses have never been unambiguously documented in the field, despite considerable efforts (Fisher 1971; Barash 1976; Birkhead 1978; Power and Doner 1980; Fujioka and Yamagishi 1981; Werschkul 1982a, Birkhead et al. 1985).

Here, I analyse the responses of male white ibises (*Eudocimus albus*) to extrapair copulations involving their pair-bonded mates. Although pair bonds in this species last at least one breeding season, and both sexes contribute roughly equal proportions of parental care (Frederick 1985), frequent EPCs have been observed (Kushlan 1973; Rudegeair 1975). These EPCs probably result in fertilizations, since they often involve sperm transfer and complete female cooperation during the fertile period (Frederick 1987a). I have estimated that EPCs fertilize at least 6% of the eggs laid by white ibises. Male white ibises contribute substantial amounts of paternal care in favor of mating with other females and are never polygynous. Paternity assurance behavior should therefore be under strong positive selection in this species (Trivers 1972).

Methods

Mating behavior of white ibises was studied over five nesting seasons (1980–1984) on Pumpkinseed Island, an estuarine breeding colony in coastal South Carolina (Georgetown Co., 33 16′30″ N, 79 12′30″ W), a rookery described in detail in Frederick (1985).

Ibises were observed from a blind (1 m × 1 m × 4 m tall) placed 25 m from groups of birds that had begun courtship less than two days before. All nests in a given study group (20–50 pairs) were contiguous, and the study group itself was part of a much larger area of nests. All nests in a study group could be viewed in a single field of 9 × 35 binoculars, and low vegetation (trampled *Juncus roemarianus*) allowed unimpaired visibility of all individuals at any time. Observations were recorded by speaking directly into a tape recorder microphone. Five study groups were observed, one in 1981, and two each in 1982 and 1983.

Nests were observed continuously for all daylight hours (12–14 h/day) except for a one-hour midday break, from the morning after blind placement until clutches were completed in all nests (8–10 days). Overall, more than 15 580 pair-hours were spent observing the mating behavior of 134 pairs. Daily nest inspections at 10:00 showed the date that each egg was laid in each nest. Clutches were considered complete when no eggs were laid in a nest for more than two consecutive days; white ibises normally lay from two to four eggs, one egg every other day (Bent 1926; Rudegeair 1975; Shields 1985). Females were considered fertile on any day up to and including the day the penultimate egg was laid (Sturkie 1976).

Individuals were recognised by distinctive facial features (Frederick 1987a), primarily the outline of the border between facial skin and feathers. Individual identities were memorized from drawings made on the first day of observations. Sexes were determined both by behavior and size; males are about one third larger than females (Kushlan 1977a).

For all copulations observed, the time, identity of individuals involved, and outcome were recorded. An EPC was considered behaviorally successful if cloacal contact appeared to have been made, and potentially fertile if it also occurred within the female's fertile period.

To compare the behavior of individuals, involvement in EPCs was standardized for the day of egglaying in the home nest. I used data only from days −1 (the day before the first egg was laid) through +4 (the fourth day after the first egg was laid). This period (6 days total) includes the majority of the fertile period for nearly all females. Though pairs were often observed earlier than day −1, mate guarding by males before day −1 was nearly continuous, and no behaviorally successful EPCs were seen prior to this time. By standardizing, I controlled both the amount of time spent observing and the timing of observations in relation to the egglaying period.

Parental care was measured in two study groups. In 1981, I compared the number of EPCs in which a female was involved (standardized as above) with her mate's later contribution of parental care. I used data from 11 pairs that were observed for a total of 2100 pair-hours during courtship and egglaying, 1541 pair-hours during incubation, and 1004 pair-hours during feeding of nestlings. During incubation, all individuals were watched for 12 consecutive hours for at least 2 consecutive days at a time, in order to determine when the daily nest exchanges occurred. During feedings of young, I recorded the number of feeding bouts and the number of regurgitations each individual performed. Regurgitations began when a parent gaped widely with a nestling's bill inside the gape and ended when the nestling's bill was withdrawn from the parent's gape. No attempt was made to quantify the amount or type of food that was exchanged. All 11 nests were within 4 days of each other in clutch initiation (incubation begins with the laying of the first egg), so feeding observations were made on young of similar ages.

In a second investigation of paternal care, I measured relative contributions of males and females to the care of each young in the hatching sequence. I have estimated that the last egg to be laid in a clutch is more than nine times as likely as the others to be fertilized by an EPC (Frederick 1987a), and thus the last young to hatch is predicted to be least likely to be sired by the male providing parental care. In 1984, I made observations of the feeding behavior of 7 pairs whose mating histories were unknown. Feeding behavior was quantified as above, except that regurgitation rates were determined separately for each nestling. Nests with three young were selected at random. All three young were marked on the head with a patch of paint for identification from the blind (Testors Enamel; color of paint was randomized with respect to age of young in different nests). The relative age of young was easily determined by size while at the nest, as a result of asynchronous hatching. Oldest members of different broods were within 5 days of each other in hatching. All together, I watched six nests over 4 days for a total of 187.5 pair-hours.

Results

Mate guarding

Males always attempted to interrupt EPC attempts involving their pair-bonded female and were usually successful at thwarting EPCs at their own nest. Males spent much longer on the nest during nest-building and egglaying than did females, and males were significantly more likely to leave their female unattended to attempt EPCs when she was infertile than when she was fertile (Frederick 1987a).

Males had ample evidence of the possibility of extrapair insemination of their mate. Combining observations from the 1982 and 1983 study groups, males interrupted EPC attempts involving their pair-bonded mates a total of 370 times. Of these, 221 were within the female's fertile period. In seven cases, the male clearly witnessed a potentially fertilizing EPC involving his own mate but was unable to thwart it, either because he was already involved in chasing off another intruding male, or because he was only just returning to the colony as the EPC was completed. In the 1981 study group in which parental care was measured, two males witnessed potentially fertilizing EPCs involving their own mates.

Forced copulations

Males never attempted to use force to copulate with their mate immediately following an apparently successful EPC attempt or at any other time ($n = 1170$ within-pair copulations).

Physical attacks

Males were never seen attacking their own mates, though females were seen pecking and stabbing at their own mates on three occasions. Males were quite capable of attacks, however, as they are larger and socially dominant to females in most situations. During courtship and egglaying males are extremely aggressive; intra- and inter-sexual fights between non-pair bonded individuals are common at this time, during EPC, within-pair copulation, and nest-building (Kushlan 1973; Rudegeair 1975; Frederick 1986, 1987a). Considering the amount of time spent observing, both forced-pair copulations and physical punishment can be said to occur rarely, if at all in response to female involvement in EPC.

Abandonment

In two of the four study groups, a total of fourteen nests were abandoned during egglaying, but none

Table 1. Parental feedings to young in relation to order of hatching ($n = 6$ pairs)

		Percent of all feedings		
		1st hatching	2nd hatching	3rd hatching
Female	Mean	37.35	32.01	28.53
	S.D.	4.499	5.272	6.230
Male	Mean	34.29	27.84	37.18
	S.D.	9.513	2.523	13.100

t-test for differences between feedings of 1st and 3rd young: females: $t = 0.517$, N.S. 5df; males: $t = 0.0038$, N.S. 5df

Table 2. Male and female feedings to third-hatching young in broods of three ($n = 6$ pairs)

	Male	Female	t
Total number of feedings	$\bar{X} = 48.83$ S.D. $= 17.27$	$\bar{X} = 47.17$ S.D. $= 17.54$	0.238 (N.S.)
Percentage of all feedings to third young	$\bar{X} = 51.30$ S.D. $= 4.94$	$\bar{X} = 48.39$ S.D. $= 4.94$	0.844 (N.S.)
Third-young feedings as a percentage of feedings to entire brood	$\bar{X} = 37.18$ S.D. $= 13.10$	$\bar{X} = 28.53$ S.D. $= 6.23$	1.46 (N.S.)

of these abandonments could be associated directly with female involvement in EPC. In all cases it was impossible to determine which member of the pair initiated the abandonment. Eight occurred during or immediately following inundation of nests and eggs by high tides, two immediately following predation of the clutch, and one following severe aggressive interactions with neighbors (Frederick 1986). At another abandoned nest, the male had a crippled leg and was unable to copulate. No probable cause could be associated with the abandonment of the two remaining nests. In those two cases, the female of the pair had not been involved in more than the study group's average number of EPCs, and the males at those nests had not been observed witnessing any potentially fertilizing EPCs involving their mate. Thus there is little evidence for abandonment in response to female EPC. Even if both unexplained abandonments were a response to female EPC, the behavior is rarely used by males. Over 94% of all females were involved in EPCs at least once during egglaying (Frederick 1987a); of these, the two unexplained abandonments constitute less than 2%.

Reduction of male parental care

For the 15 pairs studied in 1981, Spearman rank correlation tests showed no significant relationship between the number of EPC attempts a female had been involved in (range = 1–23, $\bar{X}$ = 9.63) and her mate's subsequent degree of paternal care, measured either as his contribution to incubation time (range = 37.7–68.1%, $\bar{X}$ = 54.6%, rs = −0.0091, N.S.) or his regurgitations to young (range = 38.2–72.3%, $\bar{X}$ = 56.6%, rs = −0.3180, N.S.). Two of the males in this group had witnessed a behaviorally successful EPC involving their female during her fertile period. Both of these males later contributed more than the mean percentage of incubation time and feedings.

For the 6 pairs studied in 1984 with 3 young each, neither males nor females showed significant differences in percent of regurgitations to oldest and youngest (third-hatching) young (Table 1). Most importantly, no differences were found between males and females in their numbers of regurgitations to the youngest nestling (Table 2).

Discussion

Although male white ibises frequently witnessed the involvement of their mates in EPCs, I found no evidence that males responded to such apparent inseminations with forced-pair copulation, abandonment, or physical attacks of the female, despite large sample sizes.

The two tests concerning parental care and certainty of paternity are less straightforward. Since both tests accept rather than disprove the null hypothesis, and do so with relatively small sample sizes, their results should be treated as inconclusive. It can be concluded that reduction of paternal care in response to female EPCs, if it occurs at all, is not dramatic in this species. The possibility remains that parental birds manipulate food distribution within their broods through the size of the bolus (a parameter not measured), rather than by the number of regurgitations.

While mate defense was vigorous in response to EPC, it should be noted that mate defense may not serve solely to protect against extrapair inseminations. Female involvement in EPCs often resulted in time spent off the nest, and led to increased nest parasitism, egg predation, and nesting material theft (Frederick 1987a). All these could have direct effects on the fitness of the pair-bonded male, and would lead to selection for increased mate guarding during the egglaying period.

Male white ibises, then, did not respond to

EPCs involving their mates in any of the predicted ways, other than defense of mate. Several interpretations of this result are possible. First, EPCs might never result in fertilized eggs and thus not represent a threat to paternity. There is no genetic evidence that EPCs have a reproductive function in this species, though there is abundant circumstantial evidence that they do. EPCs occurred most often during the female's fertile period and frequently involved cloacal contact, female cloacal eversion, apparent transfer of sperm, and complete female behavioral cooperation (Frederick 1987a). Further, males always defended their mate vigorously from EPC attempts and females thwarted EPCs more often when fertile than when infertile. While this evidence is not proof of the reproductive function of EPCs, it is difficult to explain these features in other ways. However, the relative effectiveness of EPCs is strongly dependent upon their timing in relation to female fertility. The timing of fertility in white ibis is an assumption derived from experiments with domestic fowl and ducks (Warren and Gish 1943; Martin et al. 1974; Cheng et al. 1980), which might not be applicable to Ciconiforms. Further, sperm storage is known to vary considerably across species (Lake 1975; Hatch 1983), and nothing is known about this variable in Ciconiforms. Thus while EPCs probably result in some fertilized eggs, it is crucial to measure their relative effectiveness (Westneat 1987a, b) before attaching any evolutionary importance to the behavior.

Second, it is possible that young resulting from EPCs do not usually survive and therefore male paternity assurance behaviors are never under strong selection. Eggs laid last (third and fourth) are much more likely than others to have been fertilized by an EPC, and the resultant young rarely survive (Rudegeair 1975; Kushlan 1977b). At least 4% of second-laid eggs, however, are estimated to be fertilized by EPCs (Frederick 1985), and broods of two frequently survive to fledging (Rudegeair 1975, pers. obs.). It is probable then, that male ibises can suffer some reduction in fitness as a result of misplaced parental care.

A third hypothesis is that males occasionally do raise young they did not sire, and that most suggested male paternity assurance strategies are ineffective. For instance, forced copulation (FC) of the female following EPCs may not be possible in most birds. The majority of the reported cases of FC have so far been within the Anseriformes, in which, unlike most other birds, the male has an intromittent organ (Barash 1977; McKinney et al. 1984; Afton 1985). In avian species lacking

an intromittent organ, there is some evidence that female cooperation is necessary for successful insemination (Fisher 1971; Van Tienhoven 1983; Fitch and Shugart 1984; McKinney et al. 1984; Frederick 1987a; but see Westneat 1987a, b). Thus FC may be a paternity assurance behavior that is mechanically difficult to pursue in many avian species.

Physical attacks on the female by her mate also may be inneffective. Physical attacks in other contexts seem to have little coercive effect on the behavior of female white ibises. Even violent physical attacks on females by extrapair males during EPCs reduced rather than increased the female's cooperation in ensuing EPC attempts (Frederick 1987a). It also is possible that attacks on the female by her mate lead to a reduction in any benefits of long-term pair bonding, such as cooperation, synchrony or an increase in re-pairing (Coulson 1966). Though white ibises are long-lived (Bent 1926; one record of a 15 year-old male breeding on Pumpkinseed Island), little is known about the duration of their pair bonds.

Reduction of parental care in response to cuckoldry would only benefit a male if it caused the female to assume more of the parental care (Trivers 1972) or if the male could be certain he were only reducing parental care to young he did not sire. Because biparental care seems ecologically mandatory in this species (Kushlan 1977b), a reduction in male parental care would be strongly selected against, unless males were able to determine paternity. It is considered unlikely that males have any way of directly recognising the parentage of young in their nest.

Abandonment by male White Ibises in response to cuckoldry might also incur more costs than benefits (Maynard Smith 1977). Important factors include the probability that the male can find a new mate and nesting territory, the probability of the future mate being fertilized by other males, and the number of young raised by the abandoned mate.

For male white ibises on Pumpkinseed Island, the availability of mates and nests is probably not an important constraint on abandonment. Large courting groups of ibises form from late March through late June; unpaired courting females appear to be available throughout this time. During this study, nesting space was probably not limiting, since the colony supported 39% more nests in 1975 without apparent crowding (Frederick 1987b).

The probability of a male ibis misplacing parental care depends not on his mate's behavior, but on the relative guarding and fighting abilities

of neighboring males (Frederick 1987a). Unless the surrounding males in a future nesting situation are substantially less successful in EPC than in the present situation, a male can expect no reduction in misplaced paternity by abandoning the present mate to pair with another.

By abandoning their mates, males can expect none of their young to fledge. Predation, exposure, and distance to food sources make biparental care mandatory in this species. Brood reduction is common even when both sexes contribute full-time parental care (Rudegeair 1975; Kushlan 1977b; Allen-Grimes 1982; Frederick 1985; Shields 1985). In this study, no individuals of either sex ever attempted to continue parental care if the other member of the pair disappeared.

Thus by abandoning his mate, a male stands little chance of having the female raise any of the young, and has no assurance that misplaced paternity will be reduced with a future mate.

In the past, it has often been assumed that male abandonment, physical attacks of the female and reduction of paternal care were important in limiting EPCs in monogamous species because these male behaviors forced the evolution of female resistance to EPCs (Barash 1976; Gladstone 1979; Fitch and Shugart 1984). While there is much evidence that male mate-guarding can constrain females' opportunities for alternative matings (Werschkul 1982a, b; Bjorklund and Westman 1983), there is no field documentation of physical attacks, abandonment or reduction of paternal care in response to the mate's involvement in EPCs or in extrapair consortship. In this study, I could find no evidence of these responses, even under the circumstances considered most likely to produce them. Male guarding behavior may constrain opportunities for female involvement in EPCs, but the evolution of female behavior during EPCs has probably not been influenced by male "sanctions".

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