

EXTRAPAIR COPULATIONS IN THE MATING SYSTEM OF WHITE IBIS (*EUDOCIMUS ALBUS*)

by

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(With 5 Figures)
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Introduction

Studies of mating systems have generally used the social relationships between males and females to determine their mating relationships, and ultimately to categorize mating systems. For instance, durable pair bonding is frequently used as a criterion for defining monogamous mating systems (WITTENBERGER, 1981; WICKLER & SEIBT, 1983). However, a growing body of recent research shows that extrapair copulations (EPCs) are a frequent phenomenon in otherwise monogamous avian species (see reviews by FORD, 1983; MCKINNEY *et al.*, 1984). The wide interspecific distribution of EPC raises questions about the general patterns of gene flow and sexual selection in monogamous avian species. In most reports, however, extrapair matings have been poorly quantified, and no clear inference can be made as to their general importance or specific effects.

The goal of this paper is to clarify the mechanisms and importance of this type of mixed mating strategy in the white ibis (*Eudocimus albus*), specifically:

- 1) to determine the relative importance of EPCs as a reproductive mechanism;
- 2) to evaluate the costs and benefits of EPC behavior for both sexes;

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- 3) to identify the degree and sources of individual variation in EPC involvement and success; and
- 4) to describe the variables that influence the occurrence of EPCs among populations.

The importance of EPCs as a reproductive mechanism is almost unknown for any species. Several studies have now shown multiple parentage of clutches by using vasectomized males (Bray *et al.*, 1975), genetically based plumage markers (Burns *et al.*, 1980) or isozymes (Gowaty & Karlin, 1983; Mumme *et al.*, 1984; Gavin & Bollinger, 1985; Josse *et al.*, 1985; Westneat, 1987). With the notable exception of Westneat's study, these studies did not quantify the extent or importance of extrapair fertilizations.

Using extrapair copulations to measure fertilizations can be misleading for several reasons. Female cooperation, particularly in the form of cloacal eversion, is probably necessary for successful copulation in most birds (Lumpkin, 1981; van Tienhoven, 1983; PITCH & SHUGART, 1984), and the literature is full of reports of female protest during EPCs (McKinney *et al.*, 1984). In addition, EPCs often occur in some species long after females have completed clutches (McKinney *et al.*, 1984). These effects would mean that the frequency of EPCs would often overestimate the frequency of extrapair fertilizations. On the other hand, observation of EPCs can be very difficult in some species, and in one study EPC frequency was shown to grossly underestimate the frequency of extrapair fertilization (Westneat, 1987).

The evolutionary costs and benefits of engaging in EPC's are probably different for the two sexes. Males could increase their fitness in several ways by EPCs: by siring extrapair young in addition to those in their own nest; by insuring against infertility of their mates; or, for unpaired males, by fertilizing a paired female, especially if females are the rarer sex. Yet males might run important risks by engaging in EPC's, including injury from fights associated with EPCs (Rudegeair, 1975; Birkenhead, 1978; Fugoka & Yamagishi, 1981; Werschnkul, 1982; Birkenhead *et al.*, 1985) and loss of eggs, nesting material or paternity by leaving the nest or mate unattended to pursue EPCs (Kushlan, 1973; Mineau & Cooke, 1979; Werschnkul, 1982).

Similarly, it is unclear whether monogamous females gain or lose fitness by mating with extrapair males. Proposed benefits of EPC for females include additional parental care from males other than their nest mates (Trivers, 1972), increased genetic variability of the clutch (Williams, 1975; Gladstone, 1979), insurance against mate infertility (McKinney *et al.*, 1984), and increased fitness of offspring if the

extrapair male confers greater fitness than the pair-bonded male (MINEAU & COOKE, 1979; WEATHERHEAD & ROBERTSON, 1979; BUTTON, 1983).

Alternatively, a female might derive no benefit at all from EPC's (McKINNEY *et al.*, 1984; FITCH & SHUGART, 1984). By engaging in EPC's, females could be risking abandonment, decrease in parental care, physical attacks from her mate or extrapair males, damage to eggs, and possibly increased intrabrood competition if her clutch is sired by several males (HAMILTON, 1964; TRIVERS, 1972; BARASH, 1977; MAUNARD SMITH, 1977; BIRKHEAD, 1978; GLADSTONE, 1979; ROSKRAFT, 1983; FITCH & SHUGART, 1984).

Finally, if nesting is asynchronous, males might sacrifice any benefits from parental care in favor of pursuing EPCs (MAUNARD SMITH, 1977). Females might thus experience reduced paternal care for their young by pairing with males that were involved in EPCs.

It is clear, then, that the costs and benefits of EPCs for both sexes must be carefully measured before the evolutionary implications of EPC behavior can be fully understood.

In several studies, large variation has been found among individuals in EPC involvement and success. FУЛЮКА & YAMAQISHI (1981) suggested that dominance in male cattle egrets (*Bubulcus ibis*) was responsible for access to extrapair females. However, they investigated a dominance hierarchy of only four individuals. ROSKRAFT (1983) showed that EPC involvement in rooks (*Corvus frugilegus*) was dependent on age for both males and females, with older paired males copulating with younger extrapair females. However, the sources of individual variation in EPC remain poorly understood in most species.

EPC behavior has been found to vary considerably at the population and interspecific levels as well (see FREDERICK, 1985 for a review). To explain such variation, five hypotheses have so far been proposed.

1) Lack of female cooperation during EPCs can make EPCs impossible, and EPCs will not occur when they are disadvantageous to females (FITCH & SHUGART, 1985). FITCH & SHUGART specifically predict that EPCs will only involve unmated females, as paired females would risk male abandonment or punishment in response.

2) EPCs are more likely in densely nesting colonial species than in dispersed ones (BIRKHEAD, 1978). Though coloniality is neither necessary nor sufficient for EPC behavior (FORD, 1983; McKINNEY *et al.*, 1984) this hypothesis predicts that EPC frequency should increase with decreasing internest distances among colonial nesters.

3) Opportunities for EPC may increase if males are unable to guard their mates efficiently (BIRKHEAD, 1979; WERSCHNIG, 1982). In little blue herons (*Egretta caerulea*) frequency of EPC correlated with the distance males had to travel to get nesting material while leaving their mate unguarded (WERSCHNIG, 1982). Similarly, MINEAU & COOKE (1979) cite evidence that the distance to drinking water was responsible for a 10-fold difference in EPC rates among lesser snow geese (*Anser c. caerylesensis*).

4) A long fertile period can lead to more opportunities for extrapair fertilizations (BIRKHEAD *et al.*, 1985). According to this hypothesis, high frequency of EPC would be most likely in those species, populations, and individuals having lengthy fertile periods as a result of ecological conditions or nesting phenology.

5) Finally, high male-female sex ratios on the breeding site can lead directly to high frequency of EPC as a result of intensified male-male competition (BIRKHEAD *et al.*, 1985).

These five hypotheses offer predictions that are specific enough to be tested directly by analyzing variation in EPC frequency among individuals and study groups within a species, the white ibis. The results of a detailed study of EPCs in white ibis are probably applicable to a large number of species that show similar breeding characteristics such as dual parental care, strong pair bonding, colonial nesting, little or no polygyny or polyandry, and EPCs (McKINNEY *et al.*, 1984).

Methods

White ibis (*Eudocimus albus*) were studied over five nesting seasons (1979 through 1983) on Pumpkinseed Island, South Carolina (33°16'30"N 79°112'30"W). This multi-species estuarine rookery includes between 6,000 and 12,000 breeding pairs of white ibis annually. The island is flat and treeless, and nesting occurs primarily on a trampled mat of *Juncus roemerianus*. Nesting is dense, with the average distance between nearest neighbor nests equal to 0.69 m (N = 54 nests).

Ibis were observed from a portable burlap-and *Juncus*-covered blind (1 × 1 × 4 m tall) placed about 25 m from groups of ibis that had begun courtship 2-3 days earlier. Attempts to observe ibis from close range any earlier in courtship resulted in mass abandonment of courting sites. The entrance to the blind was oriented in such a way that ibis rarely reacted to the observer entering or leaving the blind. Nests in a given study group (20-50 pairs) were nearly synchronous (within 4 days of each other in onset), contiguous, and continuous with a much larger carpet of nests. Four different study groups were observed in two different seasons (see Table 1).

Low vegetation allowed a clear view of all individuals, and all nests in a study group could be observed in a single field of a pair of 9 × 35 binoculars. Nests were observed continuously for all daylight hours (12-14 h/day) except for a one-hour break (12:00-13:00 EST). All groups were observed from the morning after the blind was erected until clutches were completed in all nests (8-10 days). Daily nest inspections at 10:00 revealed the

date 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 (BENT, 1926; RUDGEAIR, 1975; SHIELDS, 1985).

I recognised individuals from distinctive facial features, primarily the outline of the border between facial skin and feathers (see Fig. 1). Individual characteristics were quickly memorized with the aid of drawings made on the first day of observations. Sexes were determined both by behavior and size; males are up to one-third larger than females (KUSHLAN, 1977a). To assist in identifying nest locations, I placed 6-15 numbered wooden stakes at random among the study nests at the time the blind was placed. Occasional observations were made on moonlit nights both with 9 x 35 binoculars and with a night vision scope (Apollo Lasers photomultiplier).

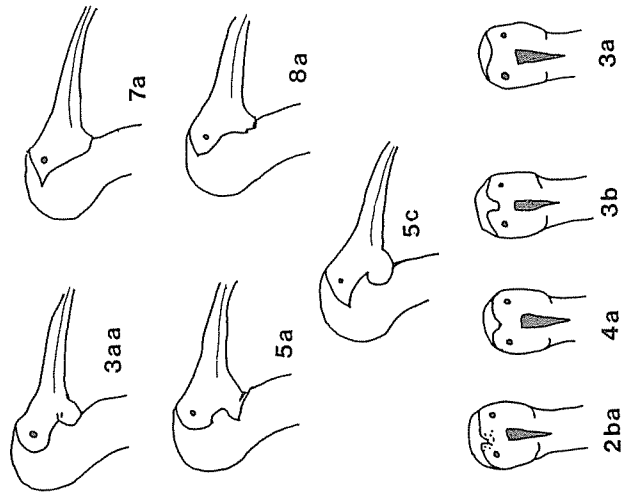


Fig. 1. Individual identification drawings of white ibis.

For all copulations observed, I recorded the time, outcome and identity of individuals involved by speaking into a tape recorder. One of several mutually exclusive outcomes was possible: (1) successful (cloacal contact appeared to have been made); (2) interrupted by other males; (3) interrupted by the female's nestmate; (4) unsuccessful as a result of female protest; or (5) unsuccessful for other reasons (male clumsiness, vegetation in the way, etc.). A protesting female usually refused to raise her tail and laid flat on the nest, or she actively attempted to dislodge the male, usually by giving a premature and violent billshake which often caused the male to lose balance and fall off.

Presence or absence of all individuals in a study group was noted once every ten minutes throughout each day. An individual was scored as present only if it was within one meter of its nest. Individuals usually remained within this distance when at the colony. The percentage of scan samples in which an individual was present provided a measure of nest attendance. Similarly, the number of successive scan samples in which

TABLE 1. Extrapair copulations in four different study groups*.)

Group	Starting date	Number of pairs	Pair-hours observed	Total copulations	Number of EPCs	Percent EPCs	EPCs per pair-hour
Central	4/26/82	16	1100.4	421	252	59.8	.229
West	6/6/82	14	986.2	234	120	51.2	.122
Central	4/5/83	23	1537.1	700	260	37.1	.169
West	4/27/83	30	2350.7	804	357	44.4	.152
West		83	5974.4	2159	989	45.8	.166

*All data shown here standardized for day of egg-laying -1 through +4 in each nest.

an individual was not present provided a measure of the time spent in a trip off the island. In male-male contests over unguarded females, losers were those males who were displaced. Using only those encounters in which neither male was the nest-mate of the female, I calculated an index of fighting ability for each male as the number of displacements of opponents divided by the total number of such encounters.

White ibis lay 2-4 eggs, laid every other day, and females were assumed to be fertile on any day up to and including the day the penultimate egg was laid. Based on evidence from several domestic species (SRURKKE, 1976; CHENG *et al.*, 1983), I assumed eggs were ovulated within 75 min of the laying of the previous egg and that they were fertilized at that time. Because the actual time of day of oviposition for white ibis is not accurately known, I included the entire day on which the penultimate egg was laid in a female's fertile period.

Potentially fertilizing copulations were only those that were both behaviorally successful and within the female's fertile period.

In order to eliminate any effects of variation among females in the timing of their nesting cycles, I standardized observations with respect to each female's egg-laying period by using only the data from days -1 (the day before the first egg was laid) through +4 (the fourth day after the day the first egg was laid). This period (6 days total) probably includes most of a female's fertile period.

After eliminating 51 pairs whose nests failed before completion of the clutch, or were not observed for part of the -1 to +4 regime, I had 83 pairs for use in intra- and intergroup analyses. Over 5,975 pair-hours were spent observing these 83 pairs during the standardized egg-laying days. Data from the 51 excluded pairs were used in compiling more general summaries of behavior. Overall, 15,580 pair-hours were spent observing mating behavior of the 134 pairs.

In comparisons of EPC frequency among study groups, I averaged the numbers of EPCs per pair-hour for each group. These rates are reported only for males, but since EPCs are performed quite close to the male's nest, this figure applies to females in the same study group as well. These rates were then compared with the average durations of male and female absences from the colony, the average percent of total time males spent on the colony, the average distance to nearest neighbors within each group, and the average clutch size for the group. All measures of behavior were averages calculated from observations during each female's standardized 6-day egg laying period.

Inter-nest distances were measured to the nearest cm in the two groups studied in 1982. In this report, EPC and WPC stand for extra-pair copulation and within-pair copulation, respectively.

Results

EPCs were so often behaviorally indistinguishable from normal within-pair copulations (WPC) that reliable behavioral differences between EPC and WPC were impossible to identify. The only criterion used to classify types of copulation was the identity of individuals.

All copulations of both types occurred on the nest of the female, and none were ever observed elsewhere on the island or in foraging or roosting areas. Owing to the length of observation periods and the excellent visibility of all individuals, I probably recorded nearly all of the copulations that occurred in daylight. EPC and WPC decreased sharply after dusk (Fig. 2), and observations on moonlit and starlit nights revealed almost no copulatory activity of any sort.

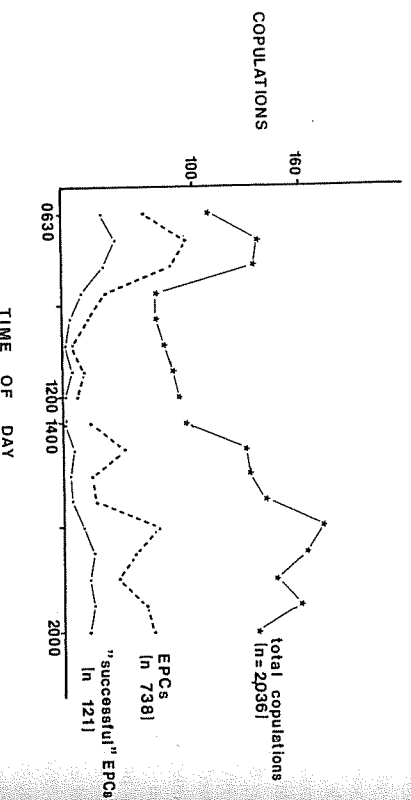


Fig. 2. Distribution of copulations during daylight hours. Data points represent number of copulations seen in the previous 40 mins. Data from South West Edge group, 30 pairs.

EPCs occurred in all study groups of ibis. Between one-third and one-half of all copulation attempts were between members of different pairs (see Table 1). 92.8% of all males and 96.4% of all females were involved in EPC attempts at least once. The majority of the EPCs (86.7%) were performed by individually identifiable males whose nests were within the boundaries of the study group. These known residents performed 84.6% of the potentially fertilizing EPCs. These estimates are conservative, since in the confusion of multimalle EPC episodes, some males that were actually residents were not clearly identified, and therefore classified as outsiders.

EPCs frequently occurred within the fertile period of the female and decreased after the end of the egg laying period (Fig. 3). Though copula-

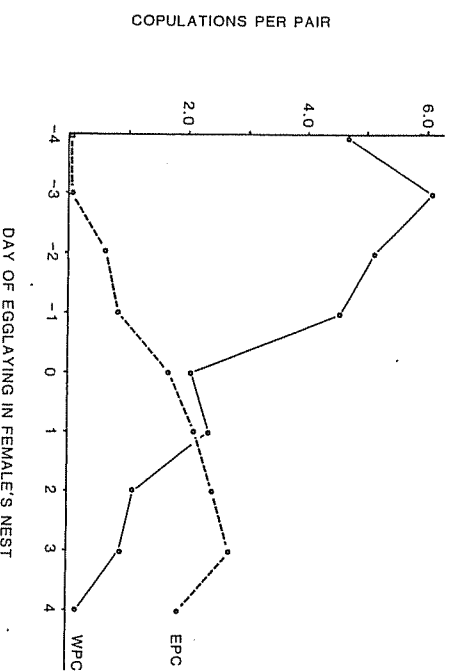


Fig. 3. Copulations in relation to egg-laying schedule. (4 study groups pooled, $N = 83$ pairs).

tions were not quantified in Fig. 3 after day +4, EPCs continued to drop off to practically nil by day +7. In all the rare instances in which the female's cloaca could be seen clearly with binoculars during copulation (16 times during WPCs and four times during EPCs), I saw that sperm was deposited and the cloaca was flared.

Both EPCs and WPCs occurred throughout the day (Fig. 2), but there were some subtle differences in timing. Statistical analysis of the timing of all copulations from the largest study group ($N = 2036$ copulations, S.W. Edge '83) showed that while EPCs reached peaks at the beginning and end of the day, WPCs did not have a similar early morning peak. The mean time of occurrence of both behaviorally successful EPCs and all types of EPCs combined occurred significantly earlier in the day than did the mean time of occurrence of WPCs (respectively, $t = 2.30$, $P < .05$; $t = 4.964$, $P < .001$). However, when copulations after 14:00 are compared, behaviorally successful EPCs occurred significantly later than WPCs ($t = 2.15$, $P < .05$).

EPCs did not usually involve physical force or attacks from the intruding male. 21.2% of all EPCs involved attacks by the intruding male, usually jabbing females on the head and back with their beaks before or immediately following an EPC attempt.

Females appeared to cooperate in the majority of EPCs. In 57.0% of all otherwise uninterrupted EPCs within the female's fertile period the female's behavior was not discernably different from that in response to WPCs. Females were significantly more likely to protest otherwise

uninterrupted EPCs during their fertile period than later ($\chi^2 = 4.116$, 1 df., $P < .05$, $n = 689$ EPC).

If present, males always attempted to interrupt EPC attempts involving their mates and almost invariably won those encounters. Only 3.2% of EPCs attempted when the female's mate was present ever resulted in a behaviorally successful copulation. These rare successes occurred only because the resident male was busy fighting off more than one intruder. Males spent 75.0% of the observed time during their mate's standardized egg-laying period on or within 1 m of the nest, whereas females spent only 48.0% of the same time present. One member of the pair was almost always on the nest during the observation periods. After the egg-laying period was over, males were present less than 60.0% of the time. Males were significantly more likely to initiate EPCs after their mate's fertile period was over rather than before (Table 2).

TABLE 2. Timing of EPCs by males in relation to their mates' fertile periods

	Observed	Expected ^{*)}
Number of male EPCs within mate's fertile period	744	937
Number of male EPCs outside mate's fertile period	716	522
	$\chi^2 = 111.46$, $P < .001$	

^{*)} Expected values = total of observed values times proportion of total observation time in that category.

EPC costs and benefits.

Fights.

EPCs frequently resulted in contests between an intruding male and the female's mate or between two intruding males. 53.4% of all EPC attempts involved contests between males. By contrast, only 4.0% of all WPCs involved male-male encounters. Life-threatening injury to males never occurred as a result of these fights, though in three cases, a returning male pulled large bunches of feathers from an intruder copulating with his mate, and in two other cases facial lesions resulted from fights. Facial scars were common among males, three of the focal males had crippled legs, and one had an injured eye. No females in any group had such wounds or disfigurement.

Loss of eggs.

Active nests on Pumpkinseed regularly suffered predation by fish crows (*Corvus ossifragus*), and probably laughing gulls (*Larus atricilla*). In 1984 a study of 468 marked eggs estimated a minimum of 8.6% lost to predation during the entire incubation period. Predation could only occur when a nest was unattended, because fish crows and laughing gulls were unable to displace white ibis from their nests. Male ibis left their nests unattended in only 14.8% of all EPCs. A male was significantly more likely to leave his nest to engage in EPC if his female was on the nest than if she were not present (Table 3).

TABLE 3. Male EPCs in relation to presence of the mate

	Observed	Expected ^{*)}
Number of male EPCs when mate is present	1244	701.5
Number of male EPCs when mate is absent	216	758.5
	$\chi^2 = 724.02$ ($P < .001$)	

^{*)} Expected Values = Total of observed values times proportion of total time spent observing in that category.

Nest parasitism.

Five cases of intraspecific nest parasitism were discovered in daily nest checks on Pumpkinseed (Frederick & Shields, 1986a). In three of the cases, new eggs appeared in a nest on two consecutive days, and in the others two eggs appeared in one day. White ibis normally lay eggs every other day (Bent, 1926; Rudgeair, 1975; Shields, 1985). Because parasitic eggs laid at the beginning and end of a host's laying period can be mistaken as normally laid eggs, daily nest checks underestimate the actual number of parasitic eggs. When this underestimation is corrected for (Frederick & Shields, 1986b), the actual number of parasitic eggs in the study groups is estimated to have been 7.58 (2.7% of all eggs, 44% of all nests).

The act of nest parasitism was never witnessed, and it is not known when egg dumping occurs. During egg-laying, both members of all pairs appeared to spend the night on or near the nest, and females almost never left the nest unguarded during incubation or nest building. Nest parasitism could presumably occur at times when the male leaves the nest unoccupied to perform EPCs. Nest parasitism is thus a potential cost for

males that leave their nests unattended while engaging in EPC, and for females who pair with promiscuous males.

Nesting material.

In three cases, males lost pieces of nesting material out of their nests while involved in EPCs when their female was not on the nest, and in 6 cases while she was there. No loss of eggs ever resulted from theft of nesting material in this study (but see KUSHMAN, 1973).

Males never contributed nesting material to their extrapair mates, and frequently stole nesting material from them. Of 164 cases of nesting material theft (NMT), 82.5% of them occurred in the 5 min before or after an EPC attempt and involved the male intruder stealing from the nest where the EPC occurred. 54% of all males stole nesting material, and 48% of the females in all groups had nesting material stolen from them. NMT was practiced routinely only by a few males in any group. Overall, 31% of the males performed over 56% of the NMTs seen. Similarly, these males concentrated their thefts on only a few females. Only 37% of the females were involved in over 63% of the NMTs.

Loss of paternity.

In 55 cases (3.77% of all EPC attempts), a female was approached or mounted by an extrapair male while her mate was involved in an EPC elsewhere. However, only 5 of these attempts were behaviorally successful, and none of these occurred during the female's fertile period. Therefore, none of these EPCs were likely to have been a risk to the resident male's paternity. Because males generally performed EPCs close to their own nests (mean = 1.26 m, N = 403), males were probably able to detect and interrupt EPCs at their own nest efficiently.

Male gain in fitness.

66 EPCs (6.7% of 989 EPCs) were both behaviorally successful and within the female's fertile period (Table 4). This means over 93% of all EPC attempts presumably failed to result in fertilization. It is very unlikely that all of these 66 EPCs fertilized eggs, because they had to compete with 610 behaviorally successful WPCs during the same period. Because behaviorally successful EPCs were never seen before day -1 for any pair (Fig. 3), first laid eggs could never have been fertilized by EPCs, and I assumed all were fertilized by the mate of the female that laid them. For second and third laid eggs, potentially fertile copulations had to

occur no more than 1 day before those eggs were fertilized (day 0, and +2, respectively), because of the large reduction in competitiveness of inseminations more than one day old (COMPTON *et al.*, 1978; CHENG *et al.*, 1982). If I assume that EPCs and WPCs occurring within this period had roughly equal chances of fertilization (MARTIN *et al.*, 1974; COMPTON *et al.*, 1978; CHENG *et al.*, 1982), EPCs would have accounted for 12.89 fertilizations, or 6.05% of all eggs laid (Table 4).

TABLE 4. Gametic contributions of EPCs and WPCs

Eggs laid	EPCs* observed	WPCs observed	% EPCs	Expected number extrapair fertilizations
First egg	83	??	0	0
2 and 3 egg clutches	0	??	0	0
Second egg egg clutches	34	11	5.07	1.72
Third egg egg clutches	49	6	2.51	1.23
Final egg clutches	49	171	22.27	10.91
Totals	215	66	9.76	12.89 (6.05% of 215 eggs)

*Potentially fertilizing copulations only, and occurring less than one day preceding the time of fertilization.

Physical attacks on females.

Before and after EPC, some males occasionally jabbed and beat females violently on the head and back with the tips of their bills. Often these attacks drew small amounts of blood, and sometimes feathers were removed. These attacks were only associated with EPCs. Of 152 such attacks, 96.2% occurred in the 5 min before or after an EPC at the attacked female's nest and involved the same individuals. However, only 16.3% of all EPC attempts were accompanied by attacks in the 5 min before or after the EPC. Attacks by intruding males did not seem to be a response to female lack of cooperation. Only 25.9% of 41 EPCs involving attacks had any lack of female cooperation, and 82.6% of 236 EPCs that had some lack of female cooperation had no attacks. In addition, females never protested any EPC attempt in 37.3% of 51 male-female dyads in which the male attempted an attack, and males never attacked in the EPC attempt in 65.2% of 118 dyads in which females protested.

Attacks seemed to influence the female's response to the same male in later EPC attempts. Among dyads that engaged in EPCs that involved male attacks, 55.0% of the next EPC attempts, and 57.2% of all ensuing EPCs included female protest or lack of cooperation. Among dyads that had no history of attacks associated with their EPCs, only 25.0% of the next, and 20.0% of all ensuing, EPCs showed any female protest or lack of cooperation. Thus, lack of female cooperation did not lead to attack by the male, but male abuse did lead to lack of female cooperation.

Attacks before or after copulation was regularly practiced only by certain males and directed at certain females. Overall, less than one quarter (23.0%) of all males accounted for over half (55.0%) of the attacks. Similarly, less than one third (31.0%) of the females were recipients of over half (55.0%) of the cases. Females that were chronically attacked, usually by particular males, would become wary and leave their nests at the approach of any males other than their mates. As a result, their nests were potentially more prone to predation, egg dumping, and nesting material theft than the nests of unabused females.

Breakage of eggs.

In the 1,460 cases of EPC observed, breakage of eggs never occurred. During a separate study of egg predation in more than 800 nests in 1984, six nests were seen in different parts of the colony that contained one or two crushed or partially flattened eggs. These nests were distant (>20 m) from one another. It is unknown whether these losses were a result of pesticide-induced thinning of the eggshell, clumsy parents, or commotion associated with EPC. Egg breakage from any cause seems to be very infrequent (less than 1% of nests).

Females engaging in EPCs never received food, nesting material, guarding or parental care of any sort from males that attempted EPC with them.

Individual correlates of EPCs.

Degree of involvement in all EPCs varied widely among individuals, as did involvement in potentially fertilizing EPCs. The number of potentially fertilizing EPCs attributable to individual males and females differed significantly from a Poisson distribution (Table 5).

In Spearman rank correlation tests (Table 6), the numbers of EPCs by individual males were significantly correlated with fighting ability, percent time present, and mean interval away. Numbers of EPCs by males

TABLE 5. Numbers of males and females performing potentially fertilizing EPC with different frequencies

	Number of EPCs				df	P		
	0	1	2	3			>4*	
Females	Observed 49	12	6	3	14	75.5	4	< .001
	Expected 18.5	27.8	20.8	10.4	5.4			
Males	Observed 35	27	7	3	11	46.3	4	< .001
	Expected 15.2	25.8	21.9	12.4	7.07			

* Expected values from Poisson distribution. Numbers of EPCs larger than four lumped owing to small sample sizes. Highest numbers for males were 16, and for females 15.

TABLE 6. Correlates of numbers of EPCs by individual males

Variable	S. Central N = 16	S. W. Edge '82 N = 14	E. Central N = 23	S. W. Edge '83 N = 30	Overall probability**)
Percent time present	.616***) P < .01	.190 P < .20	.244 P < .20	.289 P < .20	< .025
Fighting ability	.847 P < .001	.234 P < .20	.339 P < .05	.317 P < .05	< .001
Number of EPCs male's mate	-.430 P < .10	-.823 P < .05	-.387 P < .05	-.033 P < .20	< .025
Age interval away from nest	-.678 P < .001	-.032 P < .20	-.149 P < .30	-.277 P < .10	< .005
Percent time alone	-.594 P < .01	N.S.	N.S.	N.S.	N.S.
Number of WPCs	N.S.	N.S.	N.S.	N.S.	N.S.

** Obtained by combining results from the 4 study groups (Sokal & Rohlf, 1969).
*** Spearman Rank Correlation Coefficient. All data standardized for days of egg-laying -1 through +4 each nest.

were inversely correlated with the numbers of EPCs their own mate was involved in. Numbers of EPCs by males were not correlated with numbers of WPCs or with the amount of time their mates were alone on the nest.

Males whose mates laid three-egg clutches did not perform significantly more EPCs or spend any more time present than those males whose mates laid two-egg clutches, but the former males did take

TABLE 7. Characteristics of males with large and small clutches

Variable	Two-egg clutches*)	Three-egg clutches**)	t	P
Percent time present	\bar{x} = 76.89 S.D. = 8.406	\bar{x} = 76.53 S.D. = 8.461	0.529	.60
Number of EPC attempts	\bar{x} = 11.91 S.D. = 11.33	\bar{x} = 11.74 S.D. = 10.14	0.227	.85
Mean interval away from nest	\bar{x} = 4.27 S.D. = 1.167	\bar{x} = 3.18 S.D. = 2.386	3.65	.001

*) N = 35. **) N = 45.

significantly shorter intervals of leave (Table 7). This difference between males did not become significant until days +3 and +4 (Fig. 4). Females laying two eggs began taking significantly longer intervals of leave than the preceding day on day +2, and females laying 3 eggs on day +4 (Fig. 3).

The numbers of EPCs individual females were involved in were significantly correlated only with the percentage of time females were alone on the nest (Table 8). Numbers of EPCs by females were not correlated directly or inversely with number of WPCs, mean interval the female was away from the colony, mean interval her mate was away from

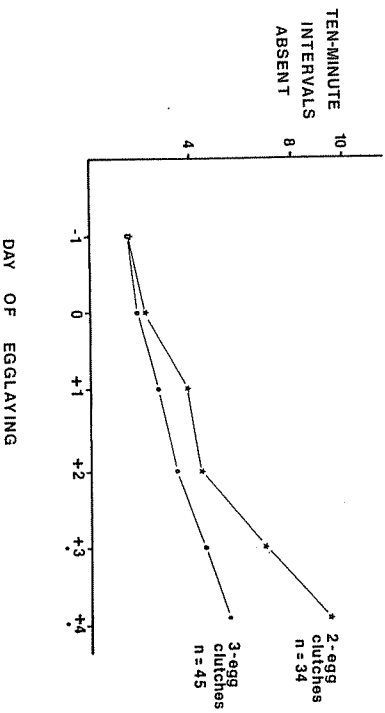


Fig. 4. Length of male absences from the nest in relation to the mate's egg-laying schedule. * indicates significant difference between the two groups (t-test, $P < .05$).

TABLE 8. Correlates of number of EPCs by individual females

Variable	S. Central N = 16	S. W. Edge '82 N = 14	E. Central N = 23	S. W. Edge '83 N = 30	Overall probability
Percent time male alone	.540**)	.220	.083	.355	< .05
Male mate's fighting ability	$P < .05$	$P < .20$	$P < .50$	$P < .05$	N.S.
Numbers of WPCs	N.S.	N.S.	N.S.	N.S.	N.S.
Average interval male mate away from nest	.521	N.S.	N.S.	N.S.	N.S.
Overall probability combining results from four separate study groups (Sokal & Rohlf, 1969).	$P < .05$				

*) Spearman Rank Correlation Coefficient. All parameters standardized for days of egg-laying through +4 in each nest.

TABLE 9. Extra-pair male's characteristics compared with female's mate

Characteristics of extra-pair male	Combined probability*)
Greater fighting ability	$P < .01$
Greater percent time present	$P < .02$
Smaller average continuous interval male off nest	$< .05 < P < .10$

*) Wilcoxon matched pairs tests, N = 90 EPCs, potentially fertilizing EPCs only. Test results from three study groups collapsed according to Sokal & Rohlf (1969).

the colony, or her mate's fighting ability. Large clutch size was an important correlate of numbers of female EPCs. Females laying 3 eggs experienced 1.36 times as many potentially fertilizing EPCs as females laying two eggs (Table 4).

Extrapair males had distinctly different qualities than the mates of their EPC partners (Table 9). Using only potentially fertilizing EPCs for analysis, extrapair males were of significantly greater rank in fighting ability than the female recipient's mate, and the extrapair male's ranked percent of time present was significantly higher. The former males were not significantly lower in rank than the latter males in average length of interval off the nest, but this difference approached significance ($.05 < P < .10$).

It was impossible to test whether female protests were evenly distributed among males, owing to the small number of EPCs for each male that were both within the female's fertile period and uninterrupted

by other males. However, some males seemed to be protested more often than others. One male was protested all 16 times he attempted a potentially fertilizing EPC, yet other males were never protested in 10, 14, and 16 similar attempts.

Females did not protest EPCs on the basis of male fighting ability. In 38 cases, females did not protest any more often when the male's fighting ability was less rather than greater than that of her mate (Wilcoxon matched-pairs test, $P > .20$).

Variance in estimated individual reproductive success from EPCs.

Only 32.5% of the 83 focal males and 24.1% of the females were involved in at least one EPC that could possibly have led to a fertilization. To estimate the expected number of extrapair fertilizations (EPFs) for an individual female, the number of potentially fertilizing EPCs preceding the laying of any egg by less than one day was divided by the total number of potentially fertilizing copulations (EPCs + WPCs) similarly preceding that oviposition. I then summed these figures over all eggs a female had laid. The number of EPFs by a male was the number of such EPFs any male had been responsible for. The mean number of EPFs for the 83 focal females was 0.123 (s.d. = 0.2680), and for the 83 focal males was 0.112 (s.d. = 0.2138). The total fertilizations for a male was equal to

TABLE 10. Individual numbers of EPCs and local nesting density

Correlates	Study group	
	South Central	S. W. Edge '82
Nearest neighbor distance		
^{vs}	.159*	.124
Number of male EPC attempts	(N.S.)	(N.S.)
Nearest neighbor distance		
^{vs}	.173	.243
Number of female EPC attempts	(N.S.)	(N.S.)
Mean distance to nearest four neighbors	.041	.030
^{vs}	(N.S.)	(N.S.)
Number of male EPC attempts		
Mean distance to nearest four neighbors	.067	.200
^{vs}	(N.S.)	(N.S.)
Number of female EPC attempts		

* Spearman rank correlation coefficient. All data standardized for day of egg-laying -1 through +4.

the number of EPFs the male was involved in plus the number of eggs in his nest minus the number of EPFs his mate was involved in. The mean number of male fertilizations was 2.63 (s.d. = 0.6408). The male with the highest number of expected EPFs in any group had 0.75 EPFs, representing a 25% increase in fertilizations over his 3 eggs, and a 28% increase over the mean number of male fertilizations. The female involved in the highest number EPFs had 1.083. Her mate, then, experienced a 54% decrease in fertilizations over his 2 eggs, and a 41% decrease relative to the mean number of male fertilizations. If males always sired all eggs in their nests, clutch size ($\bar{x} = 2.602$, s.d. = 0.5618) would be an accurate measure of male reproductive success. However, if EPCs are taken into account (as in the total male fertilizations measure above), EPC behaviour is theoretically responsible for increasing the variance in male reproductive success.

Sources of variation in EPC frequency among study groups.

Nesting density.

Numbers of EPCs by individual males were not correlated with the distance to the nest nearest that individual's, nor with the averaged distance to the nearest four nests (Table 10).

Comparing the two groups for which internest distances were available, there was a nearly two-fold difference in EPC rate, which approached significance ($t = 1.68$, $n = 16$, $.10 < p < .05$). However, there was only a slight and nonsignificant difference between the two groups in the averaged distance to the nearest nest ($t = 0.153$) or the nearest four nests ($t = 0.432$). Further, the direction of the association was contrary to the predictions of the nest density hypothesis. The higher EPC rate was associated with the lower of the nesting densities in both comparisons.

Length of fertile period.

Though clutch size seemed to be an important predictor of an individual female's involvement in EPCs, in comparisons between groups mean clutch size (and hence length of fertile period) was not correlated significantly with EPC rate ($r = 0.288$, 2 df), even though clutch size varied considerably between groups (range = 2.00-2.96).

Male attendance and EPC rates.

Average EPC rates were negatively correlated among groups with the time males spent on the nest ($r = -0.8066$) and positively correlated with

the durations of intervals males spent away from the colony ($r = 0.846$). While these correlations were not significant, they were very high considering the sample size ($n = 4$ groups).

The average length of time spent away from the colony varied considerably between groups but consistently between the sexes. Mean intervals away for males and females correlated significantly among groups ($r = 0.982$). Evidently, some seasonal variable had the same effect on the lengths of time both males and females spent away from the colony during egg-laying.

Sex ratio.

In the two largest study groups, daily EPC rates were compared with the daily sex ratio (total time all males present/total time all females present). Contrary to the predictions of the sex ratio hypothesis, daily EPC rates in both study groups were negatively correlated with sex ratios, both when EPC rate was measured as the number of EPCs/pair/hour ($r = -0.8318$, 7 df., $r = -.6330$, 5 df.), and when EPC rate was measured as the number of EPCs/female/female-hour ($r = -.7996$, $-.5770$, respectively). All these correlations approached significance ($.10 < P < .05$).

Discussion

The mating system of white ibis shows a striking and consistent departure from classical ideas of monogamy. EPCs were common in all seasons and study groups, and nearly all individual males and females were involved at least once in EPC. EPCs have also been reported in this species from two other geographically distant and ecologically different colonies in Florida (RUDENGAIR, 1975; KUSHMAN, 1973). The occurrence of EPCs in this species is therefore not restricted to certain nesting substrates or geographic locations.

Nearly all EPCs involved mated males seeking additional copulations, rather than unmated males unable to find mates or floaters specializing in EPCs. This situation is similar to that found for many other species that show EPC behaviour (FУЮКОА & УАМАЕИШИ, 1981; WЕRSCНКУ, 1982; ROSKRAFT, 1983; АFTON, 1985; MCKINNEY *et al.*, 1984; ВЯКНЕАД *et al.*, 1985).

Do EPCs fertilize eggs?

Both the form and timing of EPCs suggest that some are capable of fertilizing eggs. EPCs occurred most frequently during the egg-laying period

and decreased sharply afterwards. Only a minority of cases involved coercion by the male, and the majority of the potentially fertilizing EPCs involved complete cooperation on the part of the female. In all the cases where observation was possible, I could see that female cooperation involved cloacal flaring and that sperm transfer took place.

Both males and females acted as though EPCs carried a risk of insemination. By protesting, females seemed to be trying to avoid some risk of fertilization, because protestation of otherwise uninterrupted EPCs declined significantly after the fertile period was over. Guarding against cuckoldry seemed to be an important priority for males, both because males were so vigorous and efficient in defending their mates from EPCs, and because males left their mates unguarded in order to seek EPCs only after her fertile period had ended.

Finally, substantial costs are associated with EPC behavior for both sexes, and it is difficult to see why selection would not favor avoidance of these costs unless they were offset by a fitness benefit for one or both sexes.

Female or male control of EPC?

In many species, EPCs appear to be forced by physically dominant males, and females appear to have little choice but to submit to EPCs (MCKINNEY *et al.*, 1984). In contrast, this study found that EPCs were not physically forced by males, and females were in control of the outcome of most EPCs through some form of protestation. Females did not seem to risk physical injury as a result of protestation, even though male white ibis are larger than and physically dominant to females in most situations (KUSHMAN, 1977a).

In this light, the function of male attacks is unknown. Attacks were not a response to lack of female cooperation and only a minority of the males practiced it regularly. Attacks also led to a decrease in female cooperation in future EPC attempts with the same male. From a male's point of view, attacks would therefore seem maladaptive.

The function of female protest during EPC must be cautiously interpreted. Although female protest could serve to thwart extrapair fertilization, female protest could additionally or alternatively attract nestmates or other males to EPCs, thereby intensifying male-male competition (Cox & Le BOEUR, 1977). It thus cannot be concluded that female protest of EPC indicates a female's unwillingness to be fertilized by any, or even by that particular extrapair male, as MCKINNEY *et al.* (1984) and FITCH

& SHUGART (1984) have argued. The timing of protests in white ibis suggests that they could serve both functions.

Female cooperation during EPCs might also serve more than one function. LUMPKIN (1981) and POWER *et al.* (1981) have proposed that female responsiveness to EPC serves primarily to manipulate pair-bond mates into guarding the nest and female. If this were the primary explanation for female responsiveness in white ibis, females would not be expected to cooperate in EPCs when their mate was absent because they would suffer physical abuse and nesting material loss. Although female solicitations were never detected, females cooperated in over half of the potentially fertilizing EPCs when their mates were not present. Assuming such EPCs have some probability of fertilization, the consequences of this behavior have little to do with short-term mate manipulation. While manipulation of mate guarding could occur, the above evidence does not support this hypothesis as the *only* explanation for female cooperation during EPC.

Female cooperation might also protect eggs from damage during EPC (MINEAU & COOKE, 1979; MCKINNEY *et al.*, 1984). White ibis females do cooperate more when their fertile period is over and they are likely to be sitting on eggs. But females were also frequently sitting on partially completed clutches for a part of their fertile period and frequently protested EPCs in that situation. These protests never once resulted in egg breakage at those nests. Further, although a greater proportion of the protests occurred during the fertile period, females cooperated completely in most (57%) of the EPCs during this time. Thus the egg protection hypothesis cannot explain the pattern of female cooperation in EPCs in white ibis.

Because females were able to control the outcome of copulations without suffering physical abuse, female cooperation in EPCs during the fertile period suggests that females were attempting to enhance the chances of extrapair fertilization.

When fertile, female white ibis appeared to cooperate in some EPCs and protest others, a finding reported for several other species (BJORKLUND & WESTMAN, 1983; FITCH & SHUGART, 1984; BIRKHEAD *et al.*, 1985). One explanation for this variation is that females choose extrapair mates through protest. Though a rigorous statistical test of this hypothesis was not possible in this study, the qualitative evidence suggests certain males are consistently rejected as EPC mates by females, while others were not.

Costs and benefits of EPC behavior.

Several proposed costs of EPC for females were clearly of little importance. Egg breakage as a result of EPC activity never occurred, and apparent cuckoldry never elicited abandonment, reduction of parental care, or attacks by the female's mate (FREDERICK, 1985).

The clearest costs of EPC behavior for females were attacks by extrapair males and loss of nesting material during EPCs. Although the attacks never involved serious injury of females, frequent attacks might have led directly to higher risk of egg predation, egg dumping, and nesting material theft.

The consequences of losing nesting material are probably less severe at the Pumpkinseed colony than elsewhere, because the Pumpkinseed nests are made primarily of living rushes and are very difficult to disman- tle. In more characteristic colonies where fragile stick nests are constructed off the ground in trees and shrubs (RUDGEBAIR, 1975; ALLEN-GAMES, 1982; SHIELDS, 1985), loss of nesting material can lead directly to loss of eggs (KUSHLAN, 1973). Nesting material loss then, has probably been an important evolutionary cost for female ibises.

Females received no observable benefit from EPC partners other than their sperm. Unless females gained some fitness advantage from these genetic contributions, EPCs represented a net cost for females.

The most important costs of EPC behavior for males appeared to be egg predation, nest parasitism, and physical injury from fights. Though male wounds could result from activities not associated with reproduction, it is difficult to imagine why males would accumulate more wounds than females during nonbreeding activities. Although males also fought vigorously for nest sites during courtship, the frequency and intensity of male fights associated with EPCs suggest that these alternative mating attempts are an important source of injuries.

Egg predation is probably an important cost for males who leave their nests unattended. The low level of predation actually witnessed is probably an artifact, since crows are known to be extremely wary of blinds (MONTVEGGINI, 1976). Significant levels of predation were documented in parts of the colony where there was no blind. Egg predation is also well documented in other colonies of white ibis and has been found to be particularly severe during egg-laying (SHIELDS, 1985).

Male ibis definitely gained more nesting material than they lost by engaging in EPCs. The gain in nesting material almost certainly has effects on the quality of the nest structure and, more important, allows

the male to avoid spending time far away from the nest gathering it. Nesting material theft as a result of EPCs is probably a benefit for males and an important cost for the nesters that lose it. In this light, it is interesting that only a minority of males stole nesting material during EPCs.

The largest potential gain for males in EPC behavior was in increased direct fitness, as a result of fertilizing eggs for which they avoided the costs of parental care. Less than 7% of all EPCs had any chance of fertilizing eggs; these probably account for no more than 6% of all fertilizations.

This latter figure supposes that extrapair inseminations are just as likely to fertilize eggs as an equal number of within-pair inseminations occurring closely in time. Though sperm storage is known to vary across avian species (LAKE, 1975; HATCH, 1983), work with several domestic species shows that inseminations competing closely in time have roughly equal chances of inseminating the next egg (WARREN & GISH, 1943; MARTIN *et al.*, 1975; CHENG *et al.*, 1983).

Fertilization usually occurs within a short time of oviposition of the last egg, and inseminations closest in time to the ovulation are the most likely to fertilize the egg (STURKIE, 1976; CHENG *et al.*, 1983). By marking white ibis clutches at several times of night, I determined the time of oviposition of 30 eggs was between 0230 and 0400. Because few copulations of any sort occurred after nightfall, those most likely to fertilize eggs would be late in the day. By comparison with WPCs, behaviorally successful EPCs were concentrated at both the beginning and end of the day, and therefore appeared to be at least as well timed as WPCs to fertilize eggs.

In the absence of more accurate measurement of paternity, it seems reasonable to accept 6% as the best estimate of the proportion of eggs fertilized by EPCs. However, this figure almost certainly overestimates the proportion of surviving young resulting from EPCs. First, because most eggs are likely to be fertilized early in the day, the inclusion of the entire day the penultimate egg was laid on in the fertile period is a generous mistake. Second, it was assumed that copulations occurring more than one full day before a fertilization were uncompetitive. Though there is an enormous reduction in competitiveness of day-old sperm (CHENG *et al.*, 1983), this reduction is never complete. Because these carryover effects are poorly known, this is again, a generous error in the estimation of EPC fertilization rates. Finally, those young most likely to be the result of an EPC are those least likely to fledge. Third laid eggs in clutches of three were much more likely than others to be laid following an EPC, and

third hatching young are much more likely than others to die within the first week as a result of starvation (RUDEGAR, 1975; KUSHLAN, 1977b; FREDERICK, 1985). The degree of this differential mortality has not been accurately measured.

Individual correlates of EPC behavior.

Potentially fertile EPCs were nonrandomly distributed among both males and females. For males, avoidance of cuckoldry and extrapair mating success depended on their abilities to dominate other males, to remain near the nest, and to leave the colony for only short intervals. Fighting ability had obvious advantages: the winners of contests over unguarded females were very likely to copulate with those females. By remaining in the colony for long periods of time, males were able to defend their own mates more often from EPC attempts, and they were also able to copulate with unguarded females when their mates were absent. Thus the males that engaged in the most EPCs were cuckolded the least. Similar results have been reported for common murrelets (*Uria lomgia*) (BYRKHED *et al.*, 1985).

Certain males were unquestionably at greater risk of cuckoldry than others. All of the EPCs that could have led to fertilized eggs involved the mates of only 24% of the males. These presumably cuckolded males were those of low fighting ability and those that were not able to remain in the colony for long periods of time. These males were also able to perform the fewest EPCs.

Clutch size was not correlated with any set of male abilities. Thus clutch size was a good predictor of the chances of female extrapair fertilization, but not of her mate's involvement in EPC.

The ability of males to remain in the colony is apparently crucial for male reproductive success, and the evidence suggests that this ability is in part dependent upon foraging abilities. Because guarding the nest and mate seemed to be a high priority, males could be expected to spend the minimum time possible away from the colony. While away, foraging is likely to be the main activity of males because food seems to be the only resource males are unable to obtain from the colony. Therefore, the length of a male's absences from the colony is probably a good relative measure of his foraging time. Length of absences was a strong predictor of a male's total time on the colony. Thus a male's foraging abilities are evidently directly responsible for his total time in the colony and, therefore, for his degree of involvement in EPC.

There is some evidence that foraging abilities increase with age in white ibis. Both foraging efficiency and success increase with age among fledglings, first year, and adult white ibises (distinguishable by plumage) foraging at the same time and in the same location (Birdstern, 1984). It is impossible to age these birds after they have attained their adult plumage, and it is unknown whether feeding abilities improve with age after this time.

If feeding efficiency is correlated with age among adult white ibis, then older males would perform the majority of the EPCs and would be cuckolded the least, a finding reported for rooks (Roskrantz, 1983).

Possible fitness benefits of EPCs.

Through EPCs, males could increase their fitness by siring young for which they avoid the costs of parental care. Possible fitness benefits for females are not as obvious. As shown earlier, the only possible benefit females could gather from EPC behavior would be in multiple parentage of their clutch. If multiple parentage offers no compensating benefit, it is difficult to see why females should cooperate voluntarily in an otherwise costly behavior.

Multiple parentage of a clutch might increase a female's fitness in one of several ways. First, multiple matings might enhance a female's fertility. In domestic rabbits, mixtures of semen from several males has been shown to result in higher conception rates than ejaculates from single males (Beatty, 1960, Napier, 1961). However, if multiple matings were the only attribute of EPCs that enhanced the fitness of female ibis, the many females that were never involved in potentially fertilizing EPCs would have been expected to solicit EPCs when alone, and they did not. Further, females seemed to reject EPCs from some males and accept those from others. The latter result would be predicted only if males varied in their fertility, and females could recognize it. This might be possible if male fertility were age dependent (see review in Avery, 1983), and females could recognize age by some means. In any case, infertility would have to be a particularly chronic phenomenon in white ibis to explain the prevalence of female participation in EPCs at considerable potential cost.

Second, multiply sired clutches would have increased genetic variability compared to singly sired clutches, and this effect could lead to greater chances of some young surviving and breeding (Williams, 1975). However, Hamrton (1964) has also proposed that multiply sired

broods would suffer from increased intrabrood competition, and thus a lower overall fledging rate. It is not clear, then, whether or not the benefits of multiply sired clutches would outweigh the costs from a female parent's point of view. As above, female discrimination among extrapair mates, and females that never engage in EPCs are not predicted if all multiply sired clutches resulted in equal benefits.

Third, females might obtain better genes for their offspring by mating with certain extrapair males. If feeding and fighting abilities have any genetic basis, extrapair males would make better fathers on average than a female's present mate, for two possible reasons. If these traits were inherited by sons, the sons would also be superior at obtaining EPCs (Weatherhead & Robertson, 1979). In addition, both fighting and foraging abilities might give survival and breeding advantages to both male and female progeny.

Alternatively, if feeding and fighting abilities are related solely to age and have little genetic basis, the extrapair males most likely to inseminate females would in general be older than a female's mate. Females could theoretically increase their fitness by mating with an older male if age were a reliable indicator of superior genetically based survival traits (Trivers, 1972, Burtron, 1983).

None of the above hypotheses can be categorically excluded as genetic benefits for female white ibis, and all could occur to some extent. While the fertility enhancement and genetic variability arguments are the least complex, they do not explain the distribution of matings among individuals. Because EPCs in white ibis seemed to result in fertilization of females by males of predictably different qualities than the female's mate, it is possible that these alternative mates offer females desirable genes for their offspring.

Variables affecting EPC frequency.

Nesting density.

The predictions of the nesting density hypothesis were not confirmed in this study. Degree of local crowding could not account for large differences in individual involvement in EPC or in EPC rates between study groups. Nesting density was apparently not a primary determinant of EPC frequency within the Pumpkinseed colony.

Length of fertile period.

Length of fertile period was important in determining the chances of a female's having any eggs fertilized by extrapair males. However, clutch

size (a direct intraspecific measure of the length of the fertile period) did not account for variation in EPC rate among study groups, even though clutch size among study groups did vary significantly.

Male ibis are probably unable to predict the number of eggs a female will lay, and therefore cannot anticipate the actual number of chances for extrapair fertilizations. Because the potential gain in fitness through EPCs for males is large compared to their costs, a male's best strategy is probably to act as though the maximum number of eggs are available for fertilization in any given nesting season. Therefore, intraspecific EPC rates might not be expected to fluctuate with the average clutch size.

The best test of this hypothesis would be a comparison of fertile periods among species. However, clutch size is a poor measure of fertile period in many species (LAKE, 1975; HATCH, 1983; BIRKHEAD *et al.*, 1985), and this analysis awaits more precise information on the length of fertile period and the incidence of EPC in a variety of species.

Male guarding efficiency.

The time males spent near the nest and the lengths of their absences were reliable predictors of EPC frequency among both individuals and study groups. Food availability probably directly influenced both variables. The findings of WERSCHKUL (1982) and MINEAU & COOKE (1979) also demonstrate that local ecological conditions can influence EPC rates through mate guarding efficiency in other species.

Sex ratio.

Contrary to the predictions of the sex ratio hypothesis, EPC frequency was negatively correlated with sex ratio, though these correlations only approached significance. BIRKHEAD *et al.* (1985) found a significant positive correlation in their study of murrets, and it is unclear why these results disagree so completely. In white ibis, mate guarding seems to be effective, and high male-female ratios could suppress the chances of EPCs occurring. When the male-female ratio is low, however, many females are unguarded, and the remaining males are able to attempt EPCs without being interrupted. Although mate guarding had a clear effect in BIRKHEAD *et al.*'s study of murrets, it is possible that at high densities mate guarding is ineffective in that species. High male-female ratio cannot explain EPC frequency in white ibis, and its effects can apparently be variable, depending on the species.

Female cooperation.

Female cooperation was essential to successful EPC in white ibis, a result which supports the hypothesis that female cooperation was important in the evolution of EPC behavior (FRICH & SHUGART, 1984; MCKINNEY *et al.*, 1984). However, the sources of variation in female cooperation in this species and others remain poorly understood. One general explanation is that EPCs offer females no benefit unless they are without a mate; otherwise EPC involvement risks mate abandonment (FRICH & SHUGART, 1985; BIRKHEAD *et al.*, 1985). However, mate abandonment in response to cuckoldry has never been confirmed in any field study (FREDERICK, 1985). Furthermore, the prediction that only unpaired females will cooperate in EPC is directly contradicted by this study. Thus the reasons why females cooperate in EPCs might vary considerably between species. In this study, female cooperation was affected by the aggressiveness of the extrapair male, and by the female's reproductive status. Additionally, female lack of cooperation could be a mechanism of mate choice, either by direct rejection, or by incitation of male-male competition. A thorough understanding of female cooperation or lack of it will be an important new focus for research.

There seem to be a variety of conditions that are important to the evolution of EPC behavior in otherwise monogamous species. Female cooperation seems to be a general prerequisite for successful EPC in species where males lack an intromittent organ. However, female cooperation can be extremely difficult to identify, and it is unclear at this point exactly why females do cooperate in EPCs.

Assuming some female cooperation, any factor that reduces the efficiency of male mate guarding will create opportunities for EPC. These factors might include restricted availability of food, water, nesting material or other resources, or the necessity of patrolling a large territory, particularly where vegetation or landscape make visual contact between mates difficult (BURTON, 1983). Lengthy fertile periods can also be expected to reduce male guarding efficiency. However, clutch size, nesting density, and sex ratio are likely to be poor general predictors of EPC frequency among species.

Summary of mating system.

The mating system of white ibis is predominantly monogamous, as pair bonds are durable within breeding attempts, both sexes give substantial parental care, and at least 94% of all eggs are probably fertilized by the

male that later cares for them. However, EPCs are a prevalent mating strategy, pursued by almost all individuals to some extent. Although EPCs produce at most a small percentage of the young in each generation, this mating strategy probably allows some males to increase their reproductive success considerably, and if so, accounts for a great deal of the variance in estimated numbers of male fertilizations. However, if male EPC success varies with age, differences in lifetime reproductive success might be much smaller than the differences I have estimated from single seasons.

The correlates of male mating success in this system closely resemble those of males in classically polygynous species, in which large differences in mating success are based on fighting abilities and on the ability to remain on some central mating area in spite of starvation (WILEY, 1973; LE BOEUF, 1974; LEUTHOLD, 1977).

Summary

Mating behavior of white ibis was intensively observed in a large breeding colony in coastal South Carolina, U.S.A.

Extrapair copulations (EPCs) were found to be a frequent and regular feature of the mating system. EPCs appeared to be fully capable of fertilizing eggs, on the basis of their form, timing, and male and female behavior in response to them. Females appeared to cooperate fully in some EPCs; this cooperation included cloacal flaring, and sperm was clearly transferred during some EPCs. Females were able to reject EPCs, and EPCs were not forced by males. Based on the relative frequency of apparently successful extrapair and withinpair copulations, EPCs were estimated to fertilize 6.05% of all eggs.

EPC involvement among males was based on abilities to remain on the colony, to displace other males, and to take only short foraging trips. Female EPC involvement was based on the amount of time they were left unguarded. A male's EPC involvement was inversely correlated with that of his mate. Extrapair males were of distinctly different quality than the female's nestmate. Among study groups, EPC rate was not correlated with degree of local nesting density, sex ratio, clutch size. Female cooperation and the efficiency of male mate guarding were concluded to be important to the evolution of this mating strategy in white ibis.

It is concluded that EPC is an important strategy in this otherwise monogamous species. The exact costs and benefits of this strategy to both sexes are discussed.

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Zusammenfassung

Das Paarungsverhalten des weissen Ibis wurde in einer grossen Brutkolonie an der Küste South Carolinas, U.S.A. intensiv studiert.

Kopulationen mit anderen Kolonienmitgliedern als dem Brutpartner (extrapair copulations, EPCs) waren ein häufig und regelmässig beobachtetes Merkmal des Paarungssystems. Auf Grund ihrer Form, Wahl des Zeitpunkts, und des Verhaltens von Männchen und Weibchen in Reaktion darauf, scheinen EPCs völlig instande zu sein, Eier zu befruchten. Weibchen scheinen in manchen EPCs voll mitzuwirken, zum Beispiel durch Öffnen der Kloake, und in einigen EPCs wurde mit Sicherheit Sperma übertragen. Weibchen konnten EPCs ablehnen, und EPCs wurden von Männchen nicht erzwungen. Auf Grund der relativen Häufigkeit von offensichtlich erfolgreichen Kopulationen innerhalb und ausserhalb der Paare, wurde geschätzt, dass durch EPCs 6.05% aller Eier befruchtet werden.

Die Mitwirkung von Männchen an EPCs hing von ihren Fähigkeiten ab, in der Kolonie zu bleiben, andere Männchen zu verdrängen und nur kurze Ausflüge zur Nahrungsaufnahme zu machen. Die Mitwirkung von Weibchen an EPCs war davon abhängig, wie lange sie unbewacht waren. Die Häufigkeit der Teilnahme von Männchen an EPCs war umgekehrt korreliert mit der ihres Partners. Andere Männchen hatten eine deutlich andere Qualität als der Partner des Weibchens. Unter den Gruppen der beobachtet wurden, war die EPC-Rate nicht korreliert mit dem Grad der örtlichen Nestichte, dem Verhältnis der Geschlechter und der Gelegegrösse. Die Mitwirkung der Weibchen und die Wirksamkeit der Partnerbewachung der Männchen wurden als wichtige Faktoren in der Evolution dieser Paarungsstrategie des weissen Ibis angesehen.

Daraus wird geschlossen, dass EPCs eine wichtige Strategie für diese ansonsten monogame Art sind. Die Vor- und Nachteile dieser Strategie für beide Geschlechter werden diskutiert.