PROMISCUITY IN THE CATTLE EGRET (*BUBULCUS IBIS*)

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ABSTRACT.—Among 19 pairs of individually marked Cattle Egrets (*Bubulcus ibis*) ca. 3 in 10 successful copulations were extrapair. Extrapair copulations potentially increased the reproductive success of five of the males by 18.6% on average. An anticuckoldry strategy was evident in the male's constant attendance at or near his nest when his female was fertile. The imperative to guard may have encouraged males to choose nest sites with nest materials and drinking water nearby. Males preferred extrapair copulations with fertile females and those on nests close to their own. Males successful in extrapair copulations generally nested higher and earlier than their neighbors. This behavior would serve a conditional promiscuous strategy well, but may have a different primary function. More certain evidence for such a strategy came from the timing of extrapair copulatory attempts, which peaked when females were laying and less closely guarded. *Received 24 January 1989, accepted 13 November 1989.*

THE MONOGAMOUS, colonially nesting male Cattle Egret (*Bubulcus ibis*) will sometimes copulate opportunistically with other females while guarding his own mate from other males. Such extrapair copulations (EPCs) have been reported in Cattle Egrets by Blaker (1969) and Lancaster (1970), but are described most fully by Fujioka and Yamagishi (1981). Fujioka and Yamagishi conclude that mate guarding by the male and aggression by the female minimize the occurrence of successful EPCs during the female's fertilizable period. It is not known if sperm from EPCs can fertilize eggs in the Cattle Egret, but this has been demonstrated for other bird species (Bray et al. 1975, Burns et al. 1980, Burke and Bruford 1987, Wetton et al. 1987).

Fujioka and Yamagishi (1981) and McKinney et al. (1984) propose the male Cattle Egret has a mixed mating strategy (*sensu* Trivers 1972). Dominey (1984: 385) defined "strategy" as "a set of rules stipulating which alternative behavioral pattern of several stated options [=tactics] will be adopted in any situation throughout life." In this, the "strategy" is a long-term objective whereas the "tactic" is a specific action which serves this objective. The existence of a strategy can only be inferred from the discovery of tactics whose primary function is to serve the strategy.

Although my study parallels that of Fujioka and Yamagishi (1981) to some extent, I used uniquely marked egrets and attempted a more complete analysis of the morphological and ecological correlates of EPCs than reported previously. My specific aims were to quantify the potential contribution of EPCs to the male's reproductive success and to identify breeding tactics which might subserve a promiscuous mating strategy.

METHODS

I studied a heronry near Gatton in southeast Queensland, Australia (27°31′S, 152°20′E) (McKilligan 1984). There were ca. 2,000 pairs of nesting Cattle Egrets at the heronry; most began to nest earlier than the 19 pairs under study. The study nests were in a group on the tops of 3.5-m-high young *Melaleuca* trees that formed a grove slightly apart from the main forest of *Melaleuca* used by most of the egrets. I observed copulatory behavior from a blind on a 3-m-high platform which was raised to 5.5 m after 2.5 days to view more nests. It was then 9 m from the most distant nest. I affixed a numbered tag to each nest and marked each nesting egret uniquely with an india-ink-soaked missile propelled from the blind through a blowpipe. Recognition was aided by the degree of development of the orange-buff breeding plumage characteristic of this species (McKilligan 1975). The terms "pale" and "orange" are used here to describe these different morphs. I determined each bird's sex from observations of intrapair copulations (IPCs). I assumed the male always mounted the female and not vice versa.

I recorded events at the study nests from 1400 to 1839 on 19 November 1984, and during all daylight

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[1] The Darling Downs Institute of Advanced Education has, as of 1 January 1990, changed its name to The University College of Southern Queensland. The address remains the same.

hours (0430–1830) every other day from 22 November to 10 December 1984 (10.5 days, 124.5 observation hours), when all had finished laying. At 10-min intervals the presence/absence of all marked birds was noted. I attempted to develop a complete record of copulation attempts, nest building, and fights. I termed a copulation *successful* if climaxed by a rapid lateral tail movement by the male against the female's upraised tail or, when foliage obscured my view, by the vigorous wing flapping males often gave with this tail movement. In much of the analyses, successful and unsuccessful EPC attempts are combined and collectively termed extrapair copulatory attempts (EPCAs). At the start and finish of each day, I recorded the number of eggs in each nest. On 23 December, 13 days after observations were finished, the nests were examined to map their heights and horizontal spacings, and to check on clutch survival.

Of the 19 nests, 8 were monitored through prelaying, laying, and early postlaying; 8 during one or two of these stages, and 3 were kept under observation but not monitored every ten min because of time constraints. Because it was impossible to concentrate on all 19 nests simultaneously, preliminary events (e.g. in copulations) were sometimes not observed, and the silent departure of an egret down through the tree canopy was sometimes overlooked until the next 10-min check.

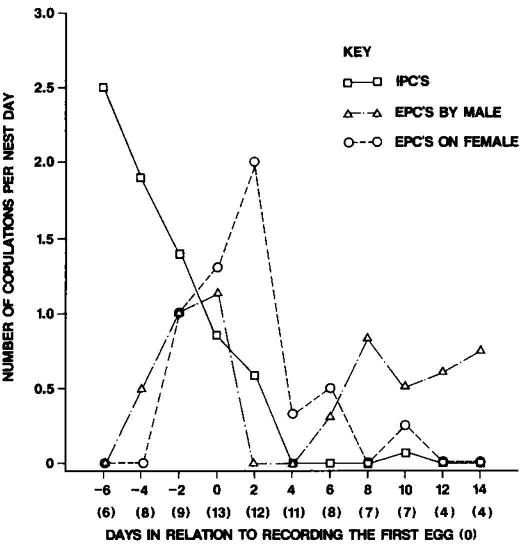

Fig. 1. Frequencies of successful intrapair and extrapair copulations per nest day in relation to day 0, when the first egg in each nest was recorded. Because observations were made every second day, this first egg could have been laid up to 36 hours before day 0. The number of nests under observation is in parentheses below day.

Results

Sixteen of the nests received eggs, three others were abandoned before egg laying. The clutch size (values are $\bar{x}$ ± SD, throughout) was 2.5 ± 0.73 (range: 1–4), which may be a slight underestimate as the eggs were not marked. Two eggs were lost during the observation period, and 6 of the 16 clutches were lost within 13 days of completing the observations. The most likely agents of egg loss were Torresian Crows (*Corvus orru*), which stole eggs from other nests in the heronry.

Copulation.—I observed 164 copulatory attempts among marked birds: 86 (52.4%) were intrapair and 78 (47.6%) extrapair. An additional 26 extrapair copulation attempts (EPCAs) were recorded between marked and unmarked birds. The durations of IPCs ($\bar{x}$ = 20.13 ± 4.37 s, n = 26) and EPCs ($\bar{x}$ = 18.8 ± 4.94 s, n = 10) were not significantly different. Among the 16 marked pairs with clutches, 10 males and 14 females engaged in EPCAs. All EPCAs took place on the female's nest. The intruding male came from his nest territory and returned immediately afterwards. The males attempted EPCs both when their mates were present (37% of EPCAs) and when they were absent (63%) (n = 51). These frequencies broadly correspond to the proportions of time they spent at the nest with and without their mates, respectively. When the male undertook an EPC in the presence of his female, she continued to incubate; and they exchanged a low-intensity greeting display on his return.

On 14 occasions when a male attempted an EPC, another immediately landed on his back; in some, a third or even a fourth added to the pile. Each male tried to maintain his position and dislodge the one on top of him. A number of unpaired males and females tried to establish themselves among the marked pairs, but no copulations were attempted by these males nor upon these females.

Among marked birds, the mean daily frequency of intrapair copulations (IPCs) was highest just after pairing. Intrapair copulations were reduced progressively, became infrequent after clutch completion, and ceased entirely by 12 days after the first egg was laid (Fig. 1). Extrapair copulations on marked females spanned the same period as the IPCs, but frequency peaked sharply during laying and exceeded IPC

TABLE 1. Percentage of extrapair copulation attempts (EPCAs) among marked birds by stage of breeding. Sample sizes are in parentheses.

	Stage of breeding		
	Prelaying	Laying	Postlaying
By males			
All EPCAs	24.4 (19)	17.9 (14)	57.7 (45)
Successful EPCAs	15.8 (3)	71.4 (11)	48.9 (23)
On females			
All EPCAs	33.3 (26)	43.6 (34)	23.1 (18)
Successful EPCAs	26.9 (7)	55.9 (19)	50.0 (9)

frequencies from then on. Marked males had EPCs that started a few days after pairing and continued through the observation period except for 2-4 days after their female laid her first egg. Overall, "postlaying" males (designated by their female's breeding stage) had the most EPCs (57.7%) and postlaying females the least (23.1%) (Table 1). Unmarked makes were not seen in EPCAs on marked females until 6 days into the observation period, when they chose postlaying females more often (18 of 21 EPCAs) than did marked males (17 of 46) ($\chi^2 = 11.9$, $P < 0.001$) when compared over the same period. These unmarked males mostly came from outside the group of marked nests.

There were no obvious diel patterns in the hourly frequencies of IPCAs or EPCAs except for a distinct peak in IPCAs in the late afternoon when the proportion of pairs at the nest was highest. The impression of an inverse correlation in the number of IPCAs and EPCAs per hour (noted also by Fujioka and Yamagishi 1981) was not substantiated ($r = -0.22$, $P > 0.05$).

Success of copulations.—Almost all (94.2%) IPCAs were successful in the sense that copulatory behavior was complete. Two failed when the females did not crouch as their mates attempted to mount them, and three failed because of attacks by neighbors. Only 47.4% of EPCAs between marked egrets were successful. Among 45 unsuccessful EPCAs (including some involving unmarked egrets), failures were caused by attack by the female's mate (42.8%), attack by another male attempting an EPC on the female (21.4%), resistance by the female (17.8%), interference by neighboring egrets (10.7%), or by unknown cause (7.1%).

If present, the male territory holder was always successful in driving away the intruding male. These "rescuing" males were all either prelaying- or laying-stage birds that had been stick collecting (10), standing near the nest—although possibly hidden from the intruder by foliage (6), or drinking (1). Only once did the male copulate with his mate within a few minutes of the "rescue."

All successful EPCs occurred after the female's mate had been absent at least 5 min, and usually considerably longer. When several males simultaneously attempted to copulate with the same female, only one was successful; but, of 30 such failures, 20 further attempts succeeded, 6 failed again, and 4 males made no further attempt on those females that day.

A proportion of females at each breeding stage were resistant to EPCAs. Prelaying females resisted 4 of 5 attempts, laying females 6 of 13, and postlaying 4 of 10. The indication here of more frequent resistance from prelayers was not significant. Although initially offering no resistance, the female involved pecked at the males retiring after 4 EPCs. Thus in 18 of these 28 fully documented EPCAs, the female manifested some aggression. No aggression occurred during IPCs.

Laying- and postlaying-stage males engaged in significantly more complete EPCAs than prelaying males ($\chi^2 = 7.8$, df $= 1$, $P < 0.01$) (Table 1). Usually, prelaying males had the well-guarded prelaying females available to their EPCAs, but even when only attempts on laying and postlaying females are considered, the success of prelaying males is relatively low (prelaying: 30%, $n = 10$; laying: 75%, $n = 8$; postlaying: 66%, $n = 33$). Males had significantly more success in EPCAs with laying and postlaying females than with prelaying birds ($\chi^2 = 5.1$, df $= 1$, $P < 0.01$).

Proportion of eggs fertilized by sperm from EPCs.—Seven marked males had 21 complete EPCs with five marked prelaying or laying females. During the same periods, these females participated in 51 IPCs and 2 EPCs with unmarked males; and they laid 11 eggs. The expected contribution of the EPCs by these marked males to the sperm that fertilized the 11 eggs can be estimated if it is assumed that the proportion of EPCs and IPCs on these females before egg laying is representative, and that EPCs had an equal chance with IPCs to contribute the fertilizing sperm. The probability of fertilization by an EPC was calculated separately for each egg. The

TABLE 2. Mean nest attendance and stick collecting rates for the 13 fully monitored nests with eggs. Attendance is not computed beyond 6 days nor stick collection beyond 18 days after the completion of the clutch.

	Prelaying	Laying	Postlaying
Nest attendance (%)			
Male	94.1	77.5	60.1
Female	43.8	41.3	46.7
Both	37.9	19.7	6.8
Sticks/nest collected each day ($\bar{x}$ ± SD)	24.8 ± 19.3	11.5 ± 12.2	4.6 ± 7.1
Nests (n)	10	12	11

mean of these probabilities was 0.27, indicating that 27% of the 11 eggs were likely to have been fertilized with sperm from EPCs.

Nest attendance, nest-material collection, and female guarding.—Normally, active nests were rarely left unattended, and unattended nests were soon pillaged for their sticks by other Cattle Egrets. Most males spent virtually all day at or near their nest during prelaying (average attendance 94.1%) and laying (77.5%) (Table 2). The lower mean figure for laying is mainly due to one male's absence for long periods. The females spent on average ca. 44% of their day at the nest during each breeding stage, but their visits during prelaying and laying were more frequent and shorter than during postlaying.

The fertile female was generally left alone at the nest only when the male went off to collect a nest stick or drink at the nearby lagoon. The average excursion to collect a stick took 104 s (range: 12-600 s, SD = 92, n = 132). All of the males and three females collected sticks (n = 1061; 96% collected by males). The bird which was not collecting did the nest building. The mean frequency of stick collecting reduced fivefold from prelaying to postlaying (Table 2). On average each prelaying male spent 41.7 min/day collecting sticks, the laying male 19.4 min/day, and the postlayer 7.7 min/day (to 18 days postlay).

Sticks were first collected from old nests and the ground within a radius of ca. 30 m of the nest tree. Once incubation started, however, birds flew as far as 400 m beyond the heronry to collect from a eucalypt woodland. I assumed that an egret that appeared through the canopy with a stick collected it nearby, whereas one that arrived above the canopy must have traveled a greater distance. Of 188 such recorded events, all the sticks brought to prelaying (n = 98) and laying (n = 14) egrets were apparently collected close to the nest tree, whereas 47% of the sticks carried by postlaying birds (n = 76) came from more distant sites.

On only 10 occasions, I saw male egrets leave their nests expressly to drink at a lagoon 80 m away. The birds returned within 30 s to 3 mins. Probably most drank when on feeding or stick-collecting excursions.

Factors associated with EPCAs.—The likelihood of a male or female Cattle Egret engaging in an EPCA might be related to the time of nesting, the spatial relationship of the two nests, the stage of breeding, or some indicator of female fertility (such as skin color).

I divided the 16 nests with eggs according to laying date into two equal groups, "early" and "late." All females received EPCAs except one early layer and one late one. Among the 8 males with early nests, all but one had EPCAs ($\bar{x}$ = 0.59 male/day) whereas only 3 of the 8 males with late nests did ($\bar{x}$ = 0.2 male/day). Among males that had EPCAs, the mean frequency was similar in early (0.66) and late (0.53) nesters. The early clutches (2.67) were larger than late clutches (2.4) (t = 2.7, df = 14, $P < 0.01$); and early clutches had a greater survival rate through incubation than later clutches (χ^2 = 4.2, df = 1, $P < 0.05$). The nests sat in the tree crowns. The farthest marked nests involved in an EPCA were ca. 3 m apart. From a comparison of EPCA frequencies for pairs of nests ranked as "close" with an equal number of pairs ranked "distant," it appeared EPCAs occurred more frequently between closer than more distant nests (t = 2.57, df = 14, $P < 0.05$). Males that completed EPCs had a higher mean nest height (299 cm; n = 7) than those with no complete attempts (283 cm; n = 9); and there was a significant correlation between the ranks of the heights of the male's nests and mean daily EPC score (Spearman rank correlation coefficient, r_s = 0.64, $P < 0.05$). As might be expected, most EPCs were directed at females in nests lower than those of the in-

TABLE 3. The number of extrapair copulation attempts (EPCAs) that occurred despite the birds of that breeding stage being outnumbered by other males (or unattended females) ($P < 0.5$) and those occurring with the odds in their favor ($P > 0.5$).

	Stage of breeding		
	Prelaying	Laying	Postlaying
By males			
$P < 0.5$	8	10	7
$P > 0.5$	2	0	23
On unattended females			
$P < 0.5$	7	17	1
$P > 0.5$	3	8	10

truding males (79%), and downward attempts appeared more often successful than upward ones (76% vs. 40%, $\chi^2 = 3.67$, df = 1, $P < 0.01$, NS).

Variations in EPC frequencies over breeding (Fig. 1) may not accurately reflect variations in either the strength of the male's tendency towards EPCs or the attractiveness of the females to males other than their mate. This is because no account is taken (Fig. 1) of the relative numbers of males, or unattended females, of each stage present at the onset of an EPCA. A fairer measure of strength of stage-related tendency or attractiveness may be calculated from the proportion of occasions when each stage was involved in an EPCA against the odds. Thus, if an EPCA involved the only laying-stage male among 6 males present, the odds were 5:1 ($P = 0.16$) against that stage of male engaging in an EPCA (all other things being equal). I grouped (Table 3) the EPCAs according to whether they were less likely in this sense ($P < 0.5$) or more likely ($P > 0.5$) (ignoring P-values of 0.5 and 1.0) separately for males and females.

The great majority of EPCAs by male prelayers (80%) and layers (100%) took place against the odds, but only 23% of those among postlayers did so. Similarly, 70% of prelaying and 68% of postlaying females received EPCAs when their stage was in the minority, but only 9% of postlayers did. The short duration of the laying stage would of course have ensured that this stage was usually in the minority.

Skin and plumage color.—The marked Cattle Egrets all initially had the red bill and iris, and magenta lores, characteristic of this species at the time of pair formation. These reverted to yellow from ca. 4–9 days after pairing, and 6–0 days before laying. Only one male engaged in EPCAs at the red-billed stage. Of 4 females whose bills turned yellow during the prelaying period, 3 received EPCAs at each bill color stage. Two males and 8 females had pale plumage and were therefore known to be one-year-olds. Neither of the pale males engaged in EPCAs, but 6 of the 8 pale females received EPCAs, as did 10 of the 11 orange females.

DISCUSSION

Among these marked Cattle Egrets, EPCs made up 31.4% of all complete copulations, similar to the 29.2% observed by Fujioka and Yamagishi (1981). I found that ca. 7.4% of all eggs laid in the marked nests could have been fertilized by EPCs. A similar value (6%) was obtained for the White Ibis (*Eudocimus albus*) by Frederick (1986). The Cattle Egrets I studied in Queensland were atypical compared with the adjacent colony. They nested later, had a lower clutch size, a lower clutch survival, and a higher proportion (26.3% vs. 4.7%) of recognizable (i.e. with pale plumage) one-year-olds. Therefore, the level of EPC activity observed may not be representative of the entire colony or the species. During extended studies of nesting Cattle Egrets, Blaker (1969) observed only 11 EPCAs and Lancaster (1970) recorded only 1 that was successful.

Contribution of EPCs to the cuckolding male's reproductive success.—My estimate of 27% of 11 eggs fertilized with sperm from EPCs would, if valid, mean that these 7 males collectively increased their egg production by almost 3 eggs through EPCs on marked females. Because their own females laid a total of 16 eggs, the males would on average have achieved an 18.6% increase in their fecundity by engaging in EPCs. For two of these males, there was a potential loss of fecundity from EPCs on their own females. The record of copulations was probably too incomplete to make assessment of individual gains and losses from EPCs worthwhile. Furthermore, the assumption on which these calculations are based, that sperm from IPCs and EPCs have an equal chance of fertilizing eggs, may not be valid. Sperm from EPCs have been shown to fertilize eggs in other species (Bray et al. 1975, Burns et al. 1980, Westneat 1987, Burke and Bruford 1987, Wetton et al. 1987), but whether their number and time of insemination allows them to compete equally with sperm from IPCs is unknown (see review by McKinney et al. 1984).

Despite these deficiencies and uncertainties, I believe that, through cuckoldry, some male Cattle Egrets can increase their reproductive success at the expense of other males. One would expect to find that each male pursued breeding tactics that helped guarantee his paternity of his mate's eggs, and some or all males used tactics which increased their chance of having EPCs.

The anticuckoldry strategy of the male.—Male Cattle Egrets guard against cuckoldry (and loss of nest sticks) by close attendance to the nest during their female's prelaying period. In most males, this includes her laying period also (see also Fujioka and Yamagishi 1981). This is effective because the resident male can always repel an intruder, and copulations have never been observed away from the nest site. By contrast, females left alone were often unable or unwilling to resist EPCAs, which emphasizes the need for the male's attendance. The male Little Blue Heron (*Egretta caerulea*) guards against cuckoldry in the same way (Werschkul 1982a). The energetic cost of guarding to the Cattle Egret is probably very high by analogy with the Little Blue Heron (Werschkul 1982b), and the males who leave their fertile females unguarded for long periods may be unable to sustain their fast.

The prelaying- and laying-stage male apparently accommodates his conflicting needs to collect nest sticks and guard his female by restricting his search to areas close to the nest. A measure of the strength of his guarding tendency comes from other observations of late nests built almost entirely of fresh *Melaleuca* sprigs instead of the preferred dry sticks. Apparently dry sticks were in short supply close to the nest trees, and the males chose to undertake the much more arduous task of breaking fresh material off the tree rather than fly 100 m to a eucalypt woodland where sticks were plentiful but from where they could not see their nests.

The fidelity of the Cattle Egret (and perhaps other colonial species) to their traditional nesting trees assumes a new significance in light of the requirement to have nesting materials nearby. Previously, the reuse of the same trees each year by the nesting Cattle Egret was puzzling as most trees were heavily infested with a tick (*Argas robertsi*) that attacked adult birds and caused the deaths of many young (McKilligan 1987); yet, close by, there were other groups of available trees with no ticks. Similarly, the need to be on guard constantly may explain this species' preference for nesting close to a drinking site (Sallee 1982, author's unpubl. obs.) without necessarily receiving the protection of being surrounded by water. Mock (pers. comm.) suggests the flimsy nests of Cattle Egrets may also be explained by the male's need to restrict his stick collection to the area near the nest site. An alternative tactic to guarding by the male is frequent copulation with his female (Birkhead et al. 1987). The Cattle Egret may in fact do both. The apparent anomaly here of the greatest frequency of IPCs occurring immediately after pairing may represent dual tactics. The initially frequent copulations would swamp any sperm received by the female in a previous, unsuccessful pairing (McKinney et al. 1984). Thereafter, the male relies mainly on guarding to ensure paternity.

Profile of the cuckolding male.—No EPCAs were undertaken by the two identifiable one-year-olds. The cuckolding males mostly nested earlier, had a higher breeding success than the other males, or both, suggesting that cuckolding males were the more experienced breeders (Coulson and White 1958).

The rates of EPCs by males were lowest just after pair formation. At this time, they may have been preoccupied with their own female. The rates were low also for a few days after their mates laid their first egg when their long stint of guarding was ending and the males were possibly at their lowest ebb physically. Frederick (1986) also said EPCs become more frequent, and IPCs less so, as breeding progresses in the White Ibis, but he did not mention a temporary reduction in EPCs by males. Unlike most male Cattle Egrets, the male White Ibises fed during the prelaying and laying periods.

To maximize his chance of a successful EPC, the male should choose a female who is fertile, receptive, and whose mate is occupied elsewhere. Postlaying females received relatively few EPCs, and those were mostly from unmarked males from more distant nests who may have been unaware that the females were infertile. Among prelaying females, the red-billed stage was most likely to be fertile but received fewer EPCAs than the yellow-billed stage, probably because the red-billed females were closely guarded. Extrapair copulation attempts on females peaked when they were laying. At this time they may still have been fertile but were less closely guarded. By contrast, Fujioka and Yamagishi (1981) showed approximately equal EPC frequencies on laying and postlaying females. From the vantage of a higher nest, the male might be better placed to choose the most opportune time for an EPCA on his neighbor by judging her stage of laying, and whether her mate was guarding her. Many EPCAs were foiled by the return of the female's mate, and it was probably tactical to delay the attempt for several minutes after the male's departure to distinguish between his short-term absences for stick collecting and longer absences. Such delays characterized all successful EPCAs.

The female's role in EPCAs.—Birkhead (1978) describes female Common Murres (*Uria aalge*) giving a mounting invitation to neighboring males, but only once in my study did a female Cattle Egret appear to solicit an EPC. Fujioka and Yamagishi (1981) saw no females initiate EPC attempts. The female Cattle Egret's signals of sexual acceptance of another male might be quite discreet because she could risk desertion if discovered by her mate (Gladstone 1979).

The aggressive response by some females to the intruding male could be a reaction to a perceived threat to her nest rather than resistance to copulation, and this might explain the lower EPCA success of prelaying males, with whom the female would be less familiar, than longer established males. On the other hand, the passivity of some females during EPCs may have been more to protect herself and her eggs (Mock 1983) than to demonstrate her cooperation. The females' varied responses to EPCAs make it difficult to guess their motivation.

Fujioka and Yamagishi (1981) say the male Cattle Egret has a mixed mating strategy. However, a "mixed" strategy is one where the alternatives are stochastically assigned (Dawkins 1980). The male Cattle Egret's action in guarding or not guarding his female or attempting an EPC seems more likely to depend on the prevailing circumstances than on chance and seems better described as a "conditional strategy" (Dawkins 1980, Dominey 1984). The existence of an anticuckoldry strategy in the Cattle Egret is amply demonstrated by a male that forgoes feeding opportunities and restricts his search to sticks close to the nest in order to guard his fertile female. By contrast, male behavior that could be construed as tactics to serve a promiscuous strategy may have a different primary benefit (e.g. higher nests to better avoid climbing predators). The effect may simply parallel IPC behavior, such as showing a preference for copulation with a fertile female. I identified only one tactic that seems unambiguously part of a promiscuous strategy: the tendency of many males to delay their EPC attempt until after the departure of the female's mate.

The close spacing of nests and the unequal opportunities among nesting male Cattle Egrets to select the most opportune circumstances for an EPCA apparently create what Emlin and Oring (1977) term the "environmental potential for polygamy." This nesting environment allows some males to increase their reproductive success through EPCs at the expense of other (possibly less experienced) males that nest later and lower, and guard their females less closely. There is a large variance in reproductive success among the males. This would promote female choice of a mate with promiscuous characteristics, because this would favor the reproductive success of her male offspring. The possible disadvantage of choosing such a male whose promiscuity might reduce his parental investment seems slight in a species where EPCs can be achieved with so little effort or risk to the male's own nest or female.

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