

# EXTRAMARITAL AND PAIR COPULATIONS IN THE CATTLE EGRET

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**ABSTRACT.**—The copulatory behavior of the Cattle Egret (*Bubulcus ibis*) was observed in a heronry in central Japan. In 38 of 147 extramarital copulation (EC) attempts with seven females, the males seemed to succeed in ejaculation. There were relatively few complete ECs prior to egg laying, because females responded aggressively to approaching males and because the mates of the females stayed in the territories for 78.8% of the time and protected the females. After egg laying, the aggressiveness of females against approaching males decreased and their mates spent more time outside the territories, resulting in an increase in the occurrence of complete ECs. Fighting males that were approaching a female exhibited a dominance hierarchy. The most dominant male stayed in the territory for the longest time and copulated most intensively with his mate and other neighboring females.

Extramarital copulations are likely to occur in colonial herons, but mate-guarding by the male and aggression by the female mate enhance the probability that copulations will be performed only between members of the pair during the fertilizable period of the female. Thus, the monogamous pair bond is maintained. *Received 24 April 1980, accepted 3 September 1980.*

IN recent years there has been a growing interest in extramarital or promiscuous copulations ("rape"; McKinney 1965, MacRoberts 1973, Barash 1977, Bailey 1978, Wishart 1978, Beecher and Beecher 1979, Gladstone 1979, Mineau and Cooke 1979). In herons, there is little quantitative information on the frequency of extramarital copulations (ECs), although qualitative observations note its occurrence (Meanley 1955, Blaker 1969, Lancaster 1970, Wiese 1976, Gladstone 1979). Inoue (in prep.) found that ECs comprised 23% of 121 complete copulations in the Little Egret (*Egretta garzetta*).

We observed many ECs during a breeding study of the Cattle Egret (*Bubulcus ibis*). Here we describe the behavior accompanying both pair copulations and ECs, analyze quantitative data on the temporal variation in the frequency of ECs, and consider underlying causal factors.

## STUDY AREA AND METHODS

Our study was conducted in a heronry located 15 km north of Tsu City, Mie Prefecture, central Japan (34°50'N, 136°35'E). The altitude is 20 m above sea level. The heronry has been established for many years on a small island (50 × 300 m) in the Ishigaki Pond (ca. 400 m in diameter), which is mostly surrounded by rice fields. The island is mainly covered with a thick forest of the Japanese black pine (*Pinus thunbergii*), the crowns and branches of which furnish suitable nesting sites for herons. During our study, the heronry consisted of more than 1,000 birds of five ardeid species: Little Egrets, Black-crowned Night Herons (*Nycticorax nycticorax*), Intermediate Egrets (*Egretta intermedia*), Cattle Egrets, and Great Egrets (*Casmerodius albus*), in order of decreasing abundance.

All of our observations were made from a blind on a 3.6-m-high scaffold at the southern edge of the heronry. Copulatory behavior was observed with the unaided eye or with a binocular telescope (9 × 35) as necessary. Observations were carried out for 34 days, from 10 May to 20 June 1978, amounting to a total of 455.5 h; the longest observation period was from 0330 to 2000.

Because *B. ibis* lacks sexual dimorphism, the individuals that laid eggs or were repeatedly mounted by their mates were considered females. No "reverse mounts" were observed in two pairs (369.1 observation-h) in which the sexes were determined by egg laying. All members of the 10 pairs that we observed were individually recognizable by idiosyncracies in the bill, leg, lore, plume, and so on. Seven pairs

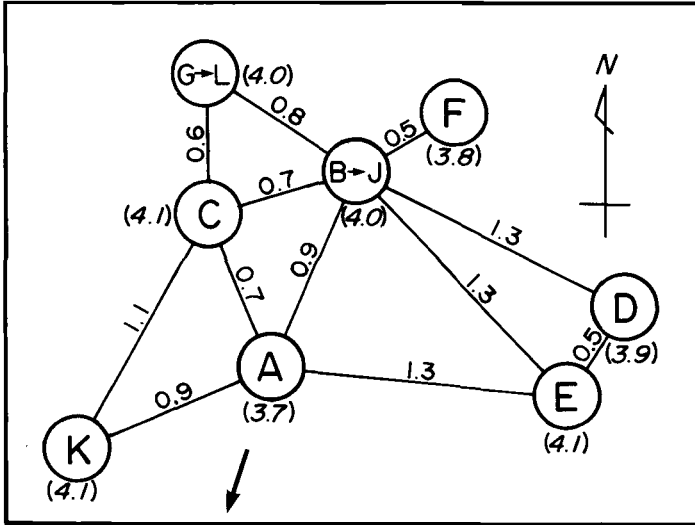


Fig. 1. Distribution of the observed nests. Nests abandoned by pairs of B and G were later used by pairs J and L. Figures denote the distance (m) between nests. Nest height (m) is expressed in parentheses. The blind was 7.6 m distant from A's nest in the direction of the arrow.

(Male A-Female a, B-b, C-c, E-e, J-j, K-k, L-l) were regularly observed. The neighboring three pairs (D-d, F-f, G-g) were observed when they interacted with members of the seven focal pairs. The distribution of the nests of these pairs is shown in Fig. 1. All of the nests could be seen clearly from the blind, allowing us to record in detail the movements of up to five pairs simultaneously.

The breeding cycle was divided into three stages for each pair (Fig. 2). (1) *The nest-building stage* followed pair formation and continued until the day on which the first egg was laid. (2) *The egg-laying stage* was the interval between the laying of the first egg and the last egg. (3) *The incubation stage* lasted from the day following the laying of the last egg until the hatching of the first chick. Three pairs (A-a, B-b, C-c) were observed during all three stages, but the observations of the remaining four pairs were discontinued at some point during the breeding cycle. Only Pair L-l was successful. In four of the six unsuccessful pairs, whole clutches were probably preyed upon by snakes (*Elaphe climacophora*). The other two nests were destroyed by other herons stealing nest material.

In this paper, a "pair copulation" means a complete copulation between members of a mated pair. The 15 observations of mere mounting (i.e. incomplete copulations) are not considered here. The term

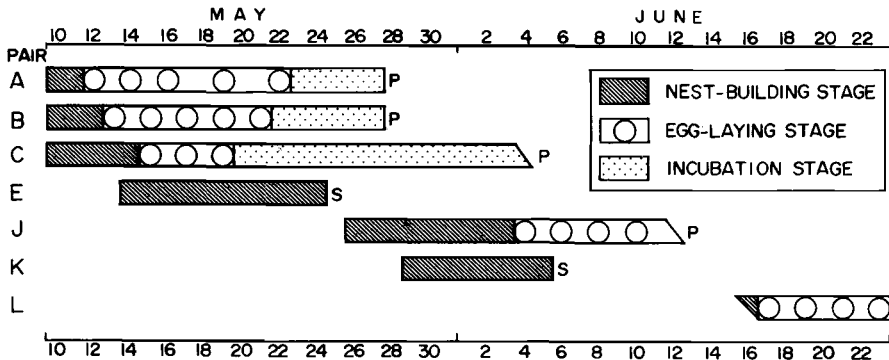


Fig. 2. Breeding progression of the seven pairs regularly observed. In the egg-laying stage, circles indicate egg-laying dates. P = abandonment owing to predation. S = abandonment owing to stealing of nest material by other herons.

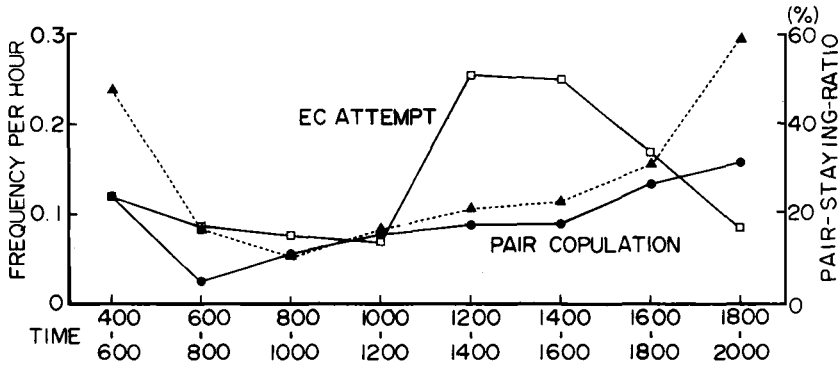


Fig. 3. Diurnal variation in the frequency of pair copulations (solid circle), EC attempts (open square), and pair-staying-ratio (solid triangle).

“extramarital copulation (EC) attempt” is used to designate any incident in which a male attempts to copulate with a female of another pair, without regard to its presumed success in transferring sperm. When many males attempted ECs with one female simultaneously or successively, the EC attempt by each male was counted as one EC attempt incident, and the series of the EC attempts was recorded as a “multiple EC attempt.” EC attempts were divided into complete ECs and incomplete ECs. A complete EC was defined as one in which the male succeeded in mounting the female’s back and in apparently establishing cloacal contact. Incomplete ECs included failure to mount or mounting in which male-female cloacal contact appeared to be impossible. We assume that males succeeded in transferring sperm in complete ECs and failed to do so in incomplete ECs.

## RESULTS

### PAIR COPULATIONS

All 92 pair copulations that we observed (Table 1) occurred in the territory of the pair (defined operationally as the area within about 1 m of each nest). Pair copulation behavior occurred in the following sequence. (1) *Approach*: a male perched inactively 0.5–3 m from his mate (92.4% of the 92 observations) or had just arrived with nest material (7.6%). The male walked toward his mate, usually with his scapular plumes raised, and sometimes gave a few “rick rack” calls (Blaker 1969). In 13 of 37 observations, the Stretch Display, which functions as a sexual and distance-reducing display (Blaker 1969), was performed by the female prior to the male’s approach. (2) *Mounting*: the male mounted the back of his mate, who usually crouched with her wings slightly spread and with her neck extended. The male then gradually crouched on her, while alternately resting his weight on one foot and the other and spreading his wings for balance. (3) *Cloacal contact*: after the male had crouched,

TABLE 1. The numbers of observations of pair copulations and extramarital copulation (EC) attempts on each female.

	Female							Total
	a	b	c	e	j	k	l	
Observation hours	181.6	187.5	258.1	93.8	186.6	56.8	67.0	1,031.4
Pair copulations	4	22	11	18	21	6	10	92
Complete EC attempts	4	6	21	3	0	0	4	38
Incomplete EC attempts	14	19	28	30	4	4	10	109

TABLE 2. Comparison of behaviors occurring during pair copulations and extramarital copulation (EC) attempts.

Sequence: Behavior (performer):	Approach				Post-copulation	
	Stretch display (♀)		"Rick rack" call (♂)		Tremble-shoving (♀)	
	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>
Pair copulations	35.1	37	34.6	52	49.3	71
EC attempts	0.0	147	76.7	73	48.5	33 <sup>a</sup>

<sup>a</sup> Only complete EC attempts.

he rubbed his cloaca on his mate's cloaca by moving his tail laterally. The female held her tail up and continued crouching until the male dismounted. (4) *Post-copulation*: the male moved away from his mate immediately after dismounting. The entire mounting lasted from 11 to 35 s ( $\bar{x} = 22.7 \text{ s} \pm 3.84 \text{ SD}$ ,  $n = 78$ ). Afterwards, the female frequently performed Tremble-shoving, a component of nest-building behavior (Lorenz 1955, cited in Blaker 1969; original not available).

The diurnal variation in the frequency of pair copulations is shown in Fig. 3, together with the pair-staying-ratio (the proportion of the total observation time that both members of a pair were in the territory). Because pair members spent nights together in the territory, the pair-staying-ratio tended to be high in early morning and late afternoon. Pair copulations, which tended to occur in early morning and late afternoon, clearly corresponded with the pair-staying-ratio. Four pairs (A-a, B-b, C-c, E-e) were observed throughout one night in the dim light of mercury-vapor lamps in a nearby stadium (2000 on 18 May to 0400 on 19 May), but they did not attempt pair copulations or ECs.

#### EXTRAMARITAL COPULATIONS

The numbers of EC attempts directed toward each female are given in Table 1. Of the 147 observations of EC attempts, 38 (25.9%) were apparently complete ECs. All the ECs occurred in the females' territories, mostly on their nests.

ECs proceeded in the following sequence. (1) *Approach*: a male walked rapidly (57.1% of the 147 EC attempts) or jumped directly (42.9%) from his territory toward a female. The male uttered "rick rack" calls more frequently than in pair copulations ( $\chi^2 = 22.3$ ,  $P < 0.001$ ) (Table 2). Contrary to the behavior of females in pair copulations, the female did not give the Stretch Display (Table 2). (2) *Mounting*: the male rapidly mounted the female whether she crouched or not. He then crouched gradually on her as in pair copulations. The behavior proceeded to the next sequence only in complete ECs. (3) *Cloacal contact*: this was similar to that observed in pair copulations. The female held her tail up, not refusing cloacal contact. (4) *Post-copulation*: the male dismounted quickly after the ejaculation and returned rapidly to his territory. The mounting ranged in duration from 12 to 32 s ( $\bar{x} = 20.1 \text{ s} \pm 4.10 \text{ SD}$ ,  $n = 32$ ). The mean duration of mountings in pair copulations was 2.6 s longer than that in ECs ( $t = 3.16$ ,  $P < 0.005$ ). The female displayed Tremble-shoving at a similar rate to that observed in pair copulations ( $\chi^2 = 0.006$ ,  $P > 0.05$ ) (Table 2).

Incomplete ECs were caused by active interference by the male mate (38.5%), by other males (37.6%), or by the refusal of the female (23.9%). The males did not succeed in mounting (74 cases, 67.9%) or in ejaculation (35 cases, 32.1%) in the 109

incomplete ECs. Failed males returned immediately to their own territories. After failures, the females who suffered ECs performed Tremble-shoving less frequently (20.7% of 87 cases) than in apparently complete ECs ( $\chi^2 = 9.10$ ,  $P < 0.01$ ).

The diurnal distribution of the occurrence of ECs is shown in Fig. 3. The frequency of ECs seems to relate inversely to that of pair copulations, but the cause of this is not clear.

In the presence of their own mate, males attempted ECs 0.218 times per hour, while in their mate's absence, ECs were attempted 0.115 times per hour. The difference between these frequencies was significant ( $\chi^2 = 10.09$ ,  $P < 0.01$ ). Thus, EC attempts appear to be stimulated by the presence of the male's primary mate.

#### RESPONSES TO MALES WHO ATTEMPT ECs

Males attempting ECs elicited several sorts of responses, which may be categorized as follows.

*Response of male whose mate suffered EC.*—If a female suffered EC in the presence of her mate, that mate chased the male away without exception (42 observations). The male mate ran up to the invading male rapidly, in most cases in apparent response to the calls of the female. Usually the invading male rapidly flew from the female, avoiding the attacks of the male mate. Otherwise, the male mate vigorously pecked or bit the invading male, scattering its feathers, until the latter departed.

*Response of neighboring males.*—When a male was attempting EC with a female in the absence of her mate, the neighboring male(s) occasionally participated in the EC. Such multiple EC attempts were observed 17 times (43 times in terms of single EC attempts). In each multiple EC attempt, the participants ranged in number from 2 to 4 ( $\bar{x} = 2.24 \pm 0.55$  SD), and they attempted ECs from 2 to 10 times ( $\bar{x} = 2.53 \pm 0.78$  SD). Neighboring males also occasionally disturbed the male who attempted EC without themselves attempting EC (7 observations). In either case, fighting among males occurred around the female who suffered EC. Defeated males gave up EC attempts and returned to their territories (38 observations). On three occasions, a male stopped his own EC attempt and returned to his territory because his own mate was in danger of suffering EC by another male. In all, 41 EC attempts were disturbed by neighboring males.

*Response of female who suffered EC.*—The responses of females in the 64 EC attempts that were undisturbed by a male mate or neighboring males were divided into three categories. (1) Aggressive responses ( $n = 23$ ), during which the female grasped at the male and fell down with him ( $n = 2$ ), jumped aside and pecked the male ( $n = 4$ ), or pecked or bit the male while facing him ( $n = 17$ ). (2) Vocal responses ( $n = 9$ ), in which females uttered weak cries, presumably identical to the "Chatter Call" (Blaker 1969); these cries might have had the function of attracting the mate's attention when he was nearby. (3) Nonresisting responses ( $n = 24$ ), in which the female did not move and usually continued incubating but seemed to hold her tail up to facilitate the cloacal contact. In 8 of the 64 cases, the response of the female was not known.

Females dislodged males who attempted ECs in 20 (87.0%) of the 23 cases of aggressive response, in only 1 (11.1%) of the 9 cases of vocal response, and in 5 (62.5%) of the 8 unknown cases. Overall, 26 EC attempts (40.6% of the 64 EC attempts) were repulsed by females.

*Response of female whose mate attempted EC.*—The mates of males attempting

TABLE 3. Wins and losses by males involved in extramarital copulatory attempts. Two cases in which it was not determined which male was defeated are omitted.

	Male name	Loser					Total		Winning ratio	Relative dominance rank
		B	D	G	C	A	Wins	Losses		
Winner	B	—	1	3	4	10	18	3	0.857	1
	D	3	—	0	5	0	8	3	0.727	2
	G	0	1	—	0	0	1	3	0.250	3
	C	0	1	0	—	1	2	10	0.167	4
	A	0	0	0	1	—	1	11	0.077	5

EC usually ignored the EC attempts without showing any particular posture or movement. In 1 of 50 instances, the female merely looked back at the EC attempt by her mate.

**DOMINANCE RELATIONSHIP AMONG MALES**

Males attempting ECs occasionally fought among themselves, and these encounters were expressed as dominance relationships (Table 3). Relative dominance rank seemed to affect the ratio of complete ECs to all EC attempts, the number of EC attempts, and the number of pair copulations of a male (Table 4). It should be noted that the most dominant male (B) had the highest male-staying-ratio (see Fig. 6).

Homosexual copulations between males were observed eight times. The most dominant male (B) did not participate in these copulations. The suffering males were Male C (5 times), Male A (2), and Male E (1). It is noteworthy that the dominance ranks of C and A were low (Table 3). The males who attempted homosexual copulations (C, D, J, and K) always ranked higher than or equal to the respective suffering males.

**FREQUENCY OF COPULATORY BEHAVIOR**

The frequency of pair copulations and EC attempts with respect to the breeding stage of each female are shown in Fig. 4. Among the seven females, the frequency of pair copulations was similar in the nest-building stage but varied in the later stages. The frequency of pair copulations for each female decreased as the stages advanced. On the other hand, variation in the frequency of ECs among females was marked. The mean frequency of EC attempts was similar in the first two stages but was much lower in the incubation stage.

The ratio of pair copulations to all complete copulations (pair copulations plus complete ECs) for each female is here called the "pair copulation ratio" (PCR). The

TABLE 4. Correlation between a male's dominance rank and his copulatory behavior.

Male name <sup>a</sup>	B	C	A
Relative dominance rank	1	4	5
Number of EC attempts <sup>b</sup>	43 (0.229)	30 (0.116)	24 (0.132)
Complete ECs (%) <sup>c</sup>	32.6	10.0	8.3
Number of pair copulations <sup>b</sup>	22 (0.117)	11 (0.043)	4 (0.022)

<sup>a</sup> Males D and G in Table 3 are omitted because of a lack of quantitative observations of their copulatory behavior.

<sup>b</sup> Frequency per hour in parentheses.

<sup>c</sup> The proportion of complete ECs to total EC attempts.

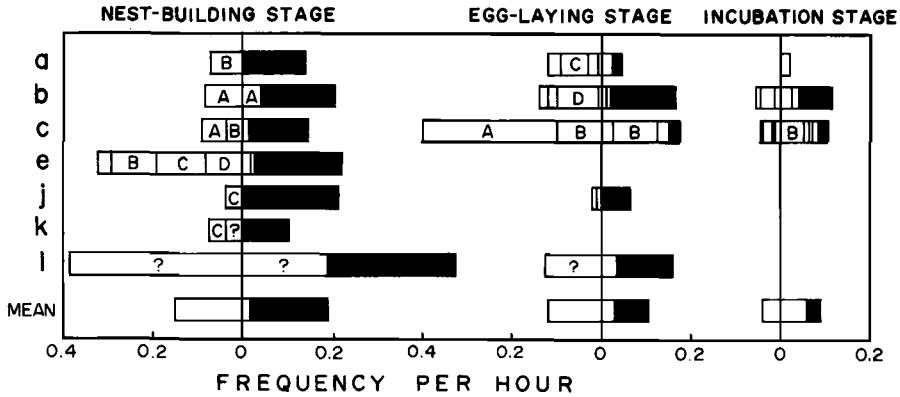


Fig. 4. Frequencies of pair copulations and EC attempts received by each female during three breeding stages. Pair copulations (black bar) and complete ECs (white bar) are shown on the right and incomplete ECs on left. Names of males (capital letters) with EC frequencies of  $\geq 0.03/h$  are shown. ? was an unidentified male from beyond the study area.

PCRs of the seven females for the three stages are shown in Fig. 5. In the nest-building stage, the PCRs of all the females except Female l were greater than 80%. In the later stages, the PCRs generally decreased. There was considerable variation of PCRs among the females. In the two later stages, the ratios of Females a and c were low, while that of b was still high. Female j had a high PCR because of the absence of surrounding pairs at the time of breeding. Pair E-e established a nest in the area in which Pairs A-a, B-b, C-c, and D-d had started their nesting about 1 week earlier (see Fig. 2). Female e, therefore, suffered many EC attempts but main-

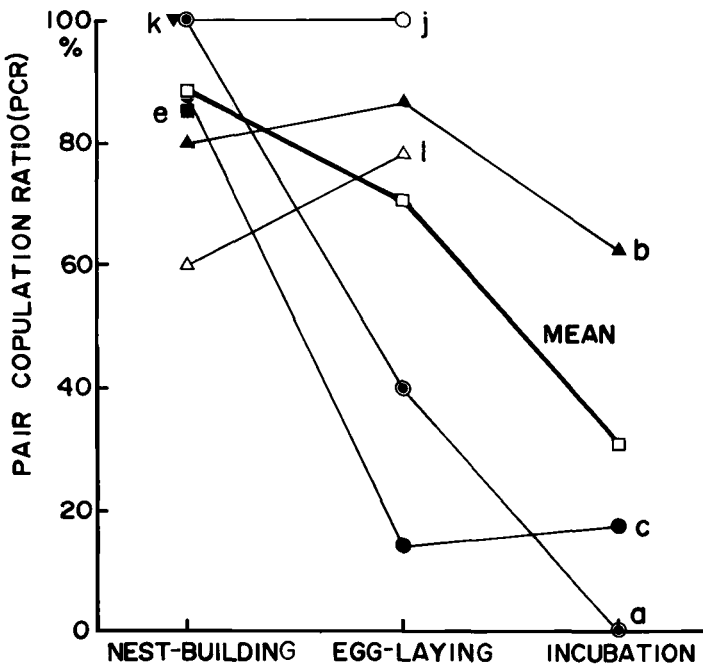


Fig. 5. Variations of pair copulation ratios of seven females during three breeding stages.

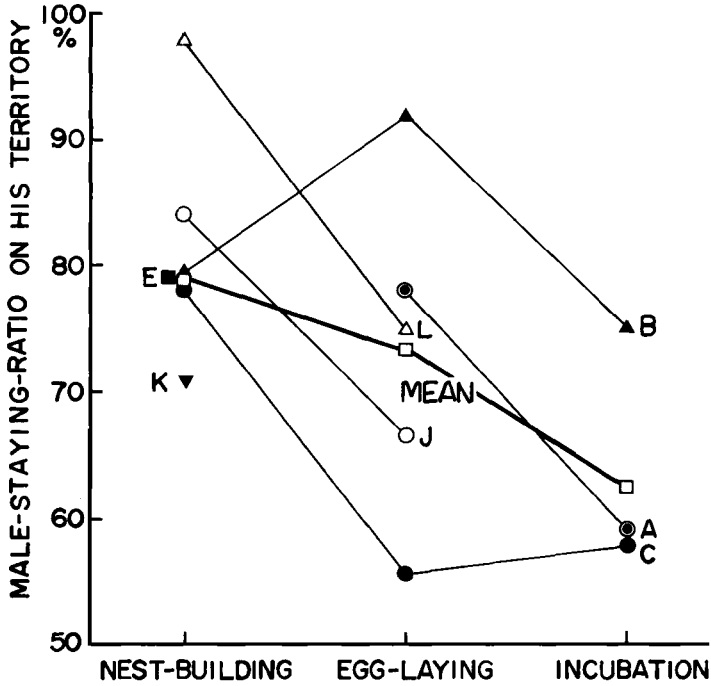


Fig. 6. Variations of staying ratios of seven males on their territories during three breeding stages.

tained a high PCR due to the disturbance of EC attempts by neighboring males. The major cause of the low PCR of Females a and c in the egg-laying stage might be the low amount male-staying-time.

The presence of a male in his territory allows him to thwart EC attempts upon his mate. All of the 38 complete ECs occurred while male mates were outside of their territories. As shown in Fig. 6, the staying-time of males in their own territories generally decreased as the breeding stages advanced. The staying-time of Males B and C increased, however, in the egg-laying and incubation stages, respectively. The similar change during the three stages between PCRs (Fig. 5) and the male-staying-times (Fig. 6) might be due to the guard effect of male mates.

The proportions of the three categories of female responses to males attempting ECs in the three breeding stages are shown in Fig. 7. The proportion of aggressive response decreased and that of nonresisting increased as the stages progressed. The

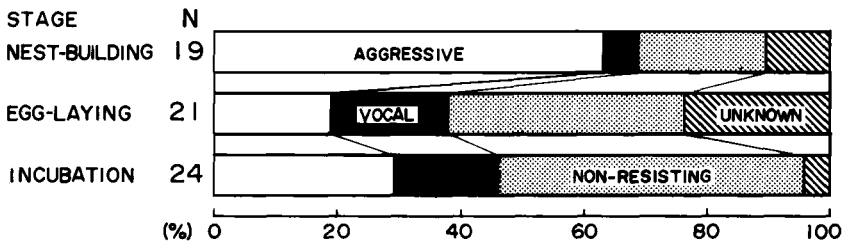


Fig. 7. Responses of females to males in EC attempts in which there was no disturbance from other males.



difference in the proportions of the responses is not significant between the egg-laying and incubation stages ( $\chi^2 = 0.14$ ,  $P > 0.05$ ) but is significant between the nest-building and egg-laying stages ( $\chi^2 = 8.72$ ,  $P < 0.01$ ). The reduction in aggressiveness toward males who attempted ECs probably contributed to the decrease in PCRs shown in Fig. 5.

#### DISCUSSION

In this study, 29.2% of 130 complete copulations observed were complete ECs. In colonial herons, the following factors underlie the occurrence of EC attempts: (1) at least one member of a pair must always be in the territory to defend the nest from the stealing of nest-material by other herons (Blaker 1969, Tomlinson 1976, Rodgers 1978), and (2) each member of a pair usually leaves the nest for at least a few hours each day for foraging. These conditions often provide a situation in which the female is left alone on the small territory. Colonial nesting in herons may therefore promote the occurrence of EC attempts. Mock (1976, 1978), however, never witnessed any kind of forced or extramarital copulations in the Great Blue Heron (*Ardea herodias*) or the Great Egret, both of which normally nest in tightly packed colonies.

The incidence of ECs for each female appears to be related to the density of pairs surrounding the female and to the synchrony of their breeding cycles. EC attempts occur frequently in an area where sexually active birds are congregating. Mock (1976, 1978) did not report the densities of birds in his breeding colonies, but the apparent absence of EC attempts suggests that it may have been low. In our study, the extent to which a female avoided ECs successfully depended upon the staying-ratio of her mate and her aggressiveness against males who attempted ECs. The decline in PCRs during the incubation stage is presumably a result of the decline in male-staying-ratio and female aggressiveness, although the dominance rank of the male may affect the PCR of the female mate; more information is required, however, before any real assessment can be made. Although many EC attempts occur in the area in which sexually active birds are congregating, these EC attempts are vulnerable to disturbance by neighboring males because multiple EC attempts are likely to occur there. There are thus few complete ECs in spite of many EC attempts, as shown in the case of EC attempts toward Female e.

EC attempts were always initiated by males. Thus, it seems that ECs are advantageous only to males, or more advantageous to males than to females. A male Cattle Egret forms a monogamous pair bond with a female with whom he will share parental duties, while he also routinely seeks opportunities to attempt ECs with other mated females whom he will not aid. Such a strategy by males represents a "mixed reproductive strategy" (Trivers 1972). ECs, in this case, may benefit mated males only to the extent that the stolen copulations increase the likelihood of the eggs of EC-suffering females being successfully fertilized.

Indeed, male Cattle Egrets preferentially attempted ECs with fertilizable mated females (Figs. 4 and 5), as do male Bank Swallows (*Riparia riparia*) (Beecher and Beecher 1979). The breeding stage of Cattle Egrets is indicated by the degree of redness of the beak and iris (Blaker 1969, pers. obs.). It is therefore possible that the degree of color changes of beak and iris provides a cue whereby a potential EC-attempting male can recognize whether a female is fertilizable or not.

In Cattle Egrets it is a significant waste of a male's parental investment when his

mate's eggs are fertilized by other males, because the male contributes substantially to the rearing of the chicks. Males remain in the territories for a considerable time after the relief of nest-guarding, in contrast to females, who depart from the territories immediately after the relief. Males stay in their territories for a longer time during the fertilizable periods of their mates than during the sterile periods (Fig. 6). These facts support the suggestion that a long stay of male herons in their territories may serve not only as prevention against stealing nest material but also against "cuckoldry." This presumption is also supported by observations of Little Blue Herons (*Florida caerulea*), in which males fast to protect their mates from ECs (Werschkul 1979; Werschkul MS).

It is not clear why females respond aggressively to males until egg-laying and respond passively thereafter (Fig. 7). Gladstone (1979) suggested that, in colonial monogamous birds, females defend themselves against EC attempts and maintain the pair bond in order to protect the investment of the male. This suggestion may be applied to the present study. Male parental care is as great as that of the female in many colonial herons (Meanley 1955, Blaker 1969, Tomlinson 1976). Nevertheless, young herons frequently starve to death (Meanley 1955, Siegfried 1972, Rodgers 1978, Werschkul 1979). A monogamous mating system therefore seems obligatory for colonial herons. In Cattle Egrets, males show mate guarding behavior against males who attempt ECs, as has been documented in many birds (Dwyer 1974, Hoogland and Sherman 1976, Barash 1977, Bailey 1978, Wishert 1978, Beecher and Beecher 1979), and females respond aggressively to males who attempt ECs until the eggs are laid. As a result, in this species copulations that are likely to result in fertilization are performed mostly between members of a pair, and the monogamous pair bond is maintained.

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