

NESTING ECOLOGY OF THE LITTLE BLUE HERON: PROMISCUOUS BEHAVIOR

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ABSTRACT.—Sixty-four extramarital copulations were observed from 1976–1978 in a nesting colony of Little Blue Herons (*Florida caerulea*). In almost all cases the male and female involved had paired and the female had not completed egg-laying. Extramarital copulations occurred at the female's nest site; the intruding male nested nearby. All but one of the extramarital copulations occurred when the paired male was away from the nest site. The paired male, when present, and the female supplanted intruding males. However, once mounted, the female's extramarital copulatory behavior was passive, similar to that with her mate. This apparent lack of resistance may not have been cooperative but rather a way to reduce reproductive failure due to the egg loss that sometimes occurred during extramarital copulations. Overall, extramarital copulations occurred relatively infrequently, owing to: (1) the nest-guarding behavior of the pair male, and (2) the uncooperative behavior of the female.

The selective pressures favoring colonial nesting must be strong because such behavior has disadvantages (Hoogland and Sherman 1976). One such drawback for males is the competition for females caused by the accessibility of females to other males besides their mates during the copulatory period. A male must not only attract a mate but also avoid wasting time and effort raising offspring not his own (Trivers 1972, Beecher and Beecher 1979). Furthermore, when extramarital or promiscuous copulations are frequent it may not be advantageous for males to participate in the rearing of young. For this reason, when care by both parents is necessary for nestling survival, selection is thought to favor those females who are monogamous (rather than promiscuous) and resist extramarital copulations (Gladstone 1979). Thus, colonial nesting contains conflicting selective pressures. Male promiscuity, which should be favored, will weaken selective pressures for males to participate in brood rearing. The resolution of this conflict will, in part, determine the structure of the mating system.

Little Blue Herons (*Florida caerulea*) nest in colonies and synchronize their breeding activities within a colony. This habit renders females subject to mounting by males other than their mates (Rodgers 1980). Indeed, this species was among the first reported to have extramarital copulations (EC; Meanley 1955), although this phenomenon has now been reported for other species with similar reproductive habits (Gladstone 1979). Meanley (1955) observed females to copulate with neighboring males more than with their mates, suggesting a promiscuous mating system. However, Rodgers (1980) noted little promiscuity among Little Blue Herons.

Males participate equally with females in rearing the young (Meanley 1955, Werschkul 1979, Rodgers 1980) suggesting monogamy. In this paper I expand on these observations by reporting my findings on the mixed reproductive habits of the Little Blue Heron. In particular I examine to what extent the mating system of this colonial nester is monogamous by analyzing observations on the frequency, form, and proximate factors promoting EC.

STUDY AREA AND METHODS

I studied the reproductive ecology of Little Blue Herons in a mixed-species upland heronry located near Cliftonville, Mississippi (33°10'N, 87°45'W) from 1976 through 1978. The four nesting species were Little Blue Herons (ca. 2,000 pairs), Cattle Egrets (*Bubulcus ibis*; ca. 1,200 pairs), Great Egrets (*Casmerodius albus*; ca. 8 pairs), and Snowy Egrets (*Egretta thula*; ca. 3 pairs). The heronry site, an old stand of osage orange (*Maclura pomifera*) and other hardwoods with low overstory resulting from previous cutting for fence posts, had been used continuously by nesting herons and egrets since 1947 (Werschkul 1977). All observations reported herein were made in areas of the heronry where Little Blue Herons were the only nesting waders.

Blinds, constructed atop scaffolding (ca. 5 m), allowed me to view nests at close range (3 to 15 m). During 1976 and 1977 I entered the blinds between 06:00 and 08:00 and remained 4 to 12 h. I spent an estimated 600 h observing during these visits. During the 1978 breeding season I entered the blind at 06:00 on 3 April and remained until 18:00 on 16 April, a two-week period, except from 18:00 on 8 April until 06:00 on 9 April and from 18:00 on 13

April until 06:00 on 14 April. Data from these latter observations are the basis for most of this report. I watched 20 nests and recorded behavioral activities associated with pairing, nest construction, and egg-laying. I estimated distances from each of the monitored nests to reference poles placed among the nests and in view from the blind. Of these 20 nests, I watched 10 nests more closely, recording interactions between the pair and neighboring birds, all of whom were identifiable.

Aided by binoculars and a spotting scope, I was able to recognize individuals by their unique characteristics in body markings. I continually updated my sketches of these features because some of the features, particularly those on the bill, were ephemeral. I was able to distinguish only those individuals with territories near the blind: outsiders could not be individually recognized. Sex was determined by position during copulation. Terminology of displays follows that of Rodgers (1980).

Data were analyzed with the SPSS Statistical Package (Nie et al. 1975) for descriptive statistics and comparison of population parameters. Means presented herein are given with one standard deviation (SD).

RESULTS

EXTRAMARITAL COPULATIONS

I observed 64 ECs during the three-year study. Nearly all (96.9%) ECs were by males on females although twice (3.1%) one male mounted another.

Three conditions almost always existed during an EC: (1) both male and female were paired, (2) the female had not completed egg-laying, and (3) copulation occurred at the female's nest site. ECs were usually observed early in the nesting season, but they were also seen later among late-nesting or re-nesting females and neighboring males.

Males generally nested close to the female whom they intruded upon. The mean distance among the 20 nests monitored in 1978 was 8.5 m (SD = 4.5, $n = 190$). The mean distance between the intruding male's nest and the female's nest was 3.5 m (SD = 2.5, $n = 27$) a significantly shorter distance ($t = 9.03$, $df = 215$, $P < 0.01$). In 59% of the ECs the intruder nested in the nearest occupied nest site to the female.

I observed 33 ECs in 1978 over a period of 14 days. I did not quantify the frequency of copulations within a pair. I suspect that within-pair copulations were more frequent than ECs. For example, the highest number of ECs seen at any one nest over a period of 14 days was nine. Nine within-pair copulations were not

uncommon in one day. Still, ECs were more frequent at some nests than others—14 nests with 0–1 EC, 3 nests with 2–3 ECs, 4 nests with 4–5 ECs, and 1 nest with 9 ECs—and it is possible that some females were mounted by promiscuous males more than by their mates (see also Meanley 1955).

Multiple males were involved in eight (12.5%) ECs (range = 2–4). Twice I observed a late-arriving male mount a male that was mounting the female.

BEHAVIOR OF THE PAIRED MALE

The frequency of ECs depended on the presence or absence of the paired male. Of 33 ECs, only one occurred when the paired male was present. Nesting material was gathered exclusively by males and was given to the female who placed the sticks in the nest. Most of the ECs were seen when the paired male departed to collect nesting material.

If a male returned to the nest site during an EC he supplanted the intruding male. The duration of mounting was significantly less ($t = 7.3$, $df = 22$, $P < 0.01$) when the paired male returned ($\bar{x} = 3$ s, $SD = 1$, $n = 14$) than when he did not return ($\bar{x} = 8$ s, $SD = 2$, $n = 10$). Paired birds did not copulate after the male had interrupted an EC; instead they engaged in ritualized appeasement behavior, Bill Nibbling and allopreening.

Those paired males who intruded upon other females left their nests exposed and liable to stick piracy, brood parasitism, and, if the female was present, EC, although I did not witness this. The intruding male quickly returned to his own nest after attempting an EC.

BEHAVIOR OF THE UNPAIRED MALE

I did not see unpaired males mount, or attempt to mount, paired or unpaired females (but see Rodgers 1980). In general, unpaired males selected a potential nesting territory and advertised for a mate. Pairing was usually rapid, within 48 h; otherwise the advertising male moved elsewhere. Most unpaired males defended areas with an existing nest, which was not improved until after pairing. Once an advertising male started building a nest where none had existed. I did not see advertising males attempt EC. I could not determine the identity of the male in 6 of 33 copulations in 1978; these six unidentified males were from outside the observation area and might have been unpaired.

BEHAVIOR OF THE PAIRED FEMALE

From pairing until the end of egg-laying, females left the nesting colony to forage during

part of each day whereas males remained in the colony. Females were alone at the nest when males gathered nesting material, and it was at this time that most ECs were seen.

Pair copulation was usually preceded by a Greeting response by the female to the approaching male. The females' responses to intruding males were varied although some sort of resistance (=escape) behavior was generally evident (78.6%, $n = 33$). If a female did not detect an approaching male she was usually mounted. If she detected an intruder, she gave alarm calls and Forward displays: this usually prevented mounting; most attempts at mounting by intruders failed. If a female was mounted, she ceased resisting. After being dismounted, the female did not pursue the intruder but remained at the nest.

Female Little Blue Herons change the position of their tail during copulation in order to aid sperm transfer, as do other herons (Mock 1976). I looked for but did not note any differences in female position during pair copulation and EC. Mounting times, however, were on the average shorter ($t = 3.06$, $df = 18$, $P < 0.01$) for ECs ($\bar{x} = 8$ s, $SD = 2$, $n = 10$) than for within-pair copulations ($\bar{x} = 12$ s, $SD = 4$, $n = 10$). In addition, appeasement behavior (Bill Nibbling and allopreening) preceded and followed within-pair copulations while defensive behavior preceded and followed ECs.

NESTING SUCCESS

Nests where ECs occurred were less successful than those where they did not. Of 27 nests with one or more observed EC, 16 (43%) were abandoned. This was significantly more ($\chi^2 = 7.89$, $df = 1$, $P < 0.01$) than the proportion of nests where no ECs were observed (15%, $n = 20$). In five cases of EC, disruption of the nest and the loss of some eggs resulted in the abandonment of the nest. I saw no significant loss of nesting material at the other 11 nests and, in these cases, active nests one day were inactive the next.

DISCUSSION

ECs have been reported for Little Blue Herons (Meanley 1955, Rodgers 1980) and other colonial nesting species (Kushlan 1973, Burger et al. 1978, Beecher and Beecher 1979, Gladstone 1979, Fujioka and Yamagishi 1981). Mounting does not necessarily mean fertilization because copulation may not result (Fisher 1971) and the behavior may be motivated by non-sexual reasons (Hailman 1978). ECs do, however, sometimes result in fertilization (Bray et al. 1975). Although my observations are not conclusive, they suggest that among Little Blue Herons ECs are motivated by sexual reasons

because (1) when mounting occurs the behavior of males and females during EC is similar to copulation between paired birds (see also Meanley 1955, Kushlan 1973), and (2) females were mounted by intruding males only just before and during the egg-laying period (see Beecher and Beecher 1979), and (3) males would mount later nesting females after the period of frequent within-pair copulations.

ADAPTIVENESS OF MALE BEHAVIOR

Unpaired males did not participate in EC, which suggests a higher reproductive success for paired birds with mixed reproductive habits than for unpaired males that copulate promiscuously without pairing. Selection may ultimately favor acquiring nesting territories and mates early in the nesting season because synchronized nesting will limit the quality and the number of nest sites and females (Maynard-Smith 1977) available to late-nesting males. In addition, the timing and frequency of EC by neighboring birds suggest that recognition of individuals and reproductive status are important in promoting EC. Therefore, the proximate cause of the lack of EC by unpaired males may be that this type of information is not readily available except to neighboring birds.

The behavior of paired males shows conflicting demands: they feed, pair, construct a nest, guard the nest and mate, and attempt to mount other females. To feed and gather nesting material, males must leave the nest. If a paired male leaves the female alone at the nest, however, the chances of EC increase. If he leaves the nest when the female is absent, stick piracy or brood parasitism may result. The resolution of these conflicting demands appears to be that males rarely leave the colony to feed and quickly return to the nest when gathering nesting material (Werschkul 1982). In this way, males are able to pursue all their activities. Finally, paired males rarely, if ever, attempt EC with distantly nesting females. However, to gather information on sex and reproductive condition for distantly nesting females, males would have to leave their nests and mates unguarded. Only when gathering nesting material does a paired male regularly travel so far as to leave his mate vulnerable to EC, thereby jeopardizing his reproductive investment of establishing a territory.

Among Cattle Egrets, male-male mountings are thought to be an expression of a dominance relationship (Fujioka and Yamagishi 1981). For Little Blue Herons, these mountings may be bonafide attempts at EC where the mounting male has misidentified the sex of the recipient bird. I observed only four mountings between

males during this study, two of which occurred during multiple mountings of a female. Paired male Little Blue Herons were always able to prevent EC or supplant intruding males. Thus dominance relationships among male Little Blue Herons do not include access to females.

FEMALE FIDELITY

Extensive parental care by male and female Little Blue Herons is essential for nestling survival, and selection should favor female fidelity (Orians 1969, Gladstone 1979). Females did not solicit ECs and resisted intruding males. Only when mounted did the paired female not resist EC. It is unclear, however, whether or not this is a sign of cooperation, since ECs always took place on the female's nest and resistance could disrupt the nest. Even without female resistance, nesting failures sometimes resulted in this way, suggesting that once mounted, the benefits to females for resisting are outweighed by the costs.

MATING SYSTEM

Overall the mating system of the Little Blue Heron is monogamous (Wittenberg and Tilson 1980). Although males pursue promiscuous copulations, because females are uncooperative and paired males guard their mates, they are rarely successful. Still, the frequency of ECs varies among nests as well as among colonies (Meanley 1955, Rodgers 1980). I suspect that the variation in ECs among nests during this study, and perhaps among colonies as reported in the literature, depends partly on the males' behavior in gathering nest material. I observed ECs to occur when males left the nest to gather nesting material, so any decrease in the number of trips, or the distance traveled, would lessen the opportunity for neighboring males to pursue ECs. Meanley (1955), who saw numerous ECs, observed that nests were newly constructed and males sometimes would collect nesting material away from the colony. Rodgers (1980, pers. comm.), who saw few ECs, observed that males collected nesting material from below the nest site and did not leave the colony. Seemingly, the opportunity for males to pursue ECs will determine its frequency. One proximate factor identified by my study is the availability of nesting material although reproductive experience, colony structure, and nest location may also be important and warrant further study.

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