

NEST ATTENDANCE BY MALE AND FEMALE GRAY HERONS

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Reproductive success in birds is assumed to be limited by the rate at which food is delivered to the nest, and in many species success increases when both parents feed their chicks (e.g., Drent and Daan 1980, Krebs and Davies 1981). However, Krebs and Davies (1981) argued that each sex might be expected to exploit the other by reducing its own investment in parental care. Some authors have assumed that females spend more energy than males before incubation starts (in producing eggs), as a consequence of which they are expected to contribute more to subsequent breeding activities (Alexander 1974, Trivers 1972). Males, on the other hand, may have been engaged proportionally more in territorial defense and courtship behavior, which also require serious energetic investments (Burger 1981, Gladstone 1979, Montevocchi and Porter 1980). However, such acts may be considered mating effort rather than parental behavior (Butler and Janes-Butler 1983).

In this contribution we discuss nest attendance by both sexes of the Gray Heron (*Ardea cinerea*). This species does not show distinct sex-related variation in size or color that could be adaptive in the division of parental tasks between partners of a pair as in many other species. We have only considered stages after pair formation. During incubation and the period of care for small chicks, one member of a pair generally does not leave the nest until its mate relieves it. When chicks are older, Gray Herons visit their nest only for short periods to feed the chicks. We have used the mean number of nest visits and the mean time away from the nest as variables. Our main questions were (1) do the sexes behave differently as far as parental care during the course of the reproductive cycle, as predicted by the hypotheses mentioned above, and (2) do sexually-distinct activity patterns exist in the course of the breeding cycle and during the course of the day?

METHODS

Gray Herons were observed from blinds in three heronries in northern Belgium. Two observers were usually present. In 1 heronry a 20 m tower was built to reach the level of the nests. Two heronries near Antwerp were studied in 1981 and 1 in the province of Limbourg in 1983. In each of the first 2 heronries 11 occupied nests were observed, in the latter 14 were observed. Visibility decreased gradually in the latter heronry as a consequence of growing leaves, causing difficulties in identifying birds on the nest. No such problem occurred at the other study sites. In each heronry all nests studied were watched simultaneously during each observation session.

One observation session usually covered a complete 24-h cycle, and the time of arrival and departure at nests of each individual were recorded. No observations were obtained for birds away from the nests. All nests were marked, and the birds were usually watched with the naked eye, or, at night, with an image-intensifier and infrared-binoculars. As herons arriving at the colony always call before landing, we assume that no arrivals were missed, even at night. The field work started as soon as the first nests were occupied, and finished when most chicks had fledged. Observations were made more than once a week in each heronry.

Gray Herons do not show distinct sexual size dimorphism (e.g., Baker 1982), so size cannot be used to identify sexes. However, many birds show individual variability in the pattern of black, gray, and white feathers on forehead and crown, and this pattern was recorded on a card for individuals at each nest. At some nests partners could be distinguished easily, but at others binoculars had to be used to check for small differences. Whenever we observed 2 birds copulate, we could determine each individual's sex. Of the 36 nests studied, 22 pairs could be sexed and identified with certainty. Only the data relating to these pairs were used in this study.

The reproductive cycle was divided into 5 sections: (1) the pre-incubation period, in which both partners are present on the nest, but not yet incubating (this does not include the period before the pair had been formed), (2) the incubation period (approximately 4 weeks), (3) the period of brooding and guarding small chicks (of up to 4 weeks old), (4) the period of feeding large chicks, and (5) the period in which chicks attempt to fledge, but still return to the nest to be fed. The course of the day was divided into 4 periods of 6 h each: night (2200–0400), morning (0400–1000), daylight (1000–1600) and evening (1600–2200). Data were analyzed using SAS (Statistical Analysis System 1982). Only non-parametric tests were used.

RESULTS

Frequency of nest attendance.—Males attended the nest on average 1.8 ± 0.4 (SD) times daily, females 1.9 ± 0.5 times (number of nest days = 389 in both sexes). The difference is not significant (2-tailed Mann-Whitney *U*-test; $U = 234.5$; $P > 0.8$). Data were similar even when considered separately for the 3 heronries studied (Table 1). The sexes visited the nest at similar frequencies throughout the reproductive cycle and throughout the day (Table 2). There was a very slight tendency

TABLE 1. Frequency of nest attendance by Gray Herons in three heronries (values are means \pm SD; values in parentheses give sample size).

	Berendrecht	Wilrijk	Zonhoven
Males	1.9 ± 0.4 (13)	1.8 ± 0.35 (6)	1.6 ± 0.5 (3)
Females	1.9 ± 0.5 (13)	2 ± 0.5 (6)	1.6 ± 0.5 (3)

TABLE 2. Frequency of nest attendance by Gray Herons during several stages of the reproductive cycle and during the course of the day (values are means \pm SD; values in parentheses give sample size).

	Pre-laying period	Incubation	Feeding and guarding small chicks	Feeding old chicks	Feeding chicks attempting to fledge
Males	2.6 \pm 0.9 (15)	1.6 \pm 0.4 (22)	2.4 \pm 0.6 (16)	1.6 \pm 0.6 (12)	0.6 \pm 0.6 (6)
Females	2.4 \pm 1.0 (15)	1.7 \pm 0.6 (22)	2.5 \pm 0.7 (16)	1.7 \pm 0.8 (12)	0.4 \pm 0.6 (6)
Difference ^a	127.5	272	143	73.5	/
	2200-0400	0400-1000	1000-1600	1600-2200	
Males	0.65 \pm 0.4 (20)	1.2 \pm 0.3 (22)	0.8 \pm 0.4 (22)	0.9 \pm 0.94 (22)	
Females	0.5 \pm 0.4 (20)	1.2 \pm 0.3 (22)	0.8 \pm 0.3 (22)	0.8 \pm 0.3 (22)	
Difference ^a	155	234.5	205.5	196.5	

^a Values are results from Mann-Whitney's *U*-test; *P* always > 0.1 (two-tailed test).

TABLE 3. Relationships between the frequency of nest attendances of both partners of a pair of Gray Herons in the course of the reproductive cycle and in the course of the day (values are Spearman-rank correlation coefficients; values in parentheses give sample size).

Pre-laying period	Incubation	Feeding and guarding small chicks	Feeding old chicks	Feeding chicks attempting to fledge
0.2 (15)	0.17 (22)	0.83** (16)	0.07 (12)	0.55 (6)
2200-0400	0400-1000	1000-1600	1600-2200	
-0.31 (20)	0.43* (20)	0.4* (22)		-0.2 (22)

* $P < 0.05$; ** $P < 0.001$.

for male birds to be present on their nests more often during the pre-incubation period and at the moment of chick fledging, as compared to females, and also at night and during the evening. However, these differences were never significant. Consequently, we conclude that males and females attended their nests at similar rates.

Rates of nest attendance of both partners within a pair were strongly correlated, when the data for the different nests were considered separately (Spearman-rank correlation; $r_s = 0.59$; $n = 22$; $P < 0.005$). This suggests that similarity in parental care is greater within than between pairs. Brood size cannot be held responsible for this observation as neither males nor females significantly increased nest attendance when more chicks had to be cared for ($r_s = 0.12$ and 0.34 for males and females respectively; $n = 22$; $P > 0.05$). A similar comparison between rates of nest attendance by members of a pair, but applied to different stages of the reproductive cycle and different periods of the day, showed highly significant correlations for periods of care for small chicks and for the morning hours (Table 3), when the rate of nest attendance is maximal (van Vessem and Draulans 1986, see also Table 2). All calculated trends were positive, apart from the observations at night and during the evening, when birds were absent from the nest for proportionally long periods (see below).

Males engaged in the gathering of nest material in 73.6% of all nest-building sessions recorded ($n = 69$), and usually collected more sticks per session than females (5.8 ± 5.2 and 2.2 ± 3.0 sticks for males and females respectively). Females also seemed to pick up proportionally more sticks from surrounding nests than males. We did not consider several short-time returns with sticks to the nest as separate visits. However, sexual variability in stick-gathering between nests and partners was high: in 8 pairs the male did all the work and in 1 pair the female, but in the other pairs both sexes shared the building behavior. Consequently, performance of this behavior cannot be used to discriminate between sexes, as the error could be substantial.

Time away from the nest.—Mean time absent from the nest was con-

TABLE 4. Mean time absent from the nest by Gray Herons in the course of the reproductive cycle (values are mean number of hours \pm SD; values in parentheses give sample size).

	Pre-laying period	Incubation	Feeding and guarding small chicks	Feeding old chicks
Males	3 \pm 1.7 (11)	5.85 \pm 4.9 (18)	5.1 \pm 3.4 (57)	7.8 \pm 5.3 (25)
Females	2.3 \pm 2.5 (14)	6.4 \pm 5.1 (24)	5.2 \pm 3.7 (62)	6.25 \pm 4.5 (33)
Difference ^a	37.5*	192	1403.5	301.5*

^a Values are results from Mann-Whitney's *U*-test; * *P* < 0.05 (two-tailed test).

sidered separately for all stages of the reproductive cycle, as the progress of breeding activities seemed to affect the mean time spent away from the nest vicinity in a distinct way (van Vessem and Draulans 1986, see also Table 4). Both sexes showed similar variability in mean time spent away from the nest during the course of the reproductive cycle (Table 4). Males spent significantly more time away from the nest during the pre-incubation period (Table 4) when a lot of nest building is done. This difference does not include records of birds that remained at their nests throughout the entire observation period. Females remained absent from the nest longer than males during incubation, but less long when chicks no longer had to be guarded. However, only the latter difference was significant. Attendance rates in the presence of small chicks were very similar. During the fledging stage nest visits were too irregular to provide reliable data for both sexes.

Overall nest attendance.—When the data on frequency of nest attendance and time absent from the nest were combined, we found that, before incubation starts, males were absent approximately 7 h 48 min and females 5 h 30 min. However, males spent more time collecting sticks for the construction of the nest (which can take many hours per session), while females actually arranged sticks on the nest. Absence from the nest in this period does not necessarily imply less investment.

Our calculations indicated that males incubated approximately 1 h 30 min per day more than females (\pm 14 h 36 min and 13 h 6 min respectively). This covers more than 24 h, because birds occasionally stood together at the nest. In fact, some birds (mainly males) remained present at the nest after being relieved (mainly to preen), especially at the beginning of the incubation period. Also stick-gathering sessions usually occurred after nest relief. When small chicks were present, males again spent more time on the nest than females, but the difference was reduced to approximately 45 min (11 h 48 min and 11 h for males and females respectively). However, males fed small chicks less frequently/visit than females (1.62 ± 1.1 ($n = 48$) and 1.9 ± 1.2 ($n = 44$) times), but the difference was not significant (2-tailed Mann-Whitney *U*-test; $U = 1015$; $P > 0.6$). The sum of both periods is less than 24 h as a consequence of some nests being unguarded after the chicks were a few weeks old.

When chicks grew older, both parents spent almost all of their time on the foraging grounds, and usually remained at the nest for only short periods. Males seemed to perform fewer feeding sessions, as their mean time away from the nest was significantly longer than that of females (Table 4). Our data also indicate that males gave up parental behavior earlier than females did, which was suggested by the fact that, when chicks attempted to fledge, females returned to feed fledgings more often than males. Three out of 19 nests where chicks reached the fledging stage were no longer visited by any of the parents during this period (15.8%), and 7 were visited at least once by both parents (36.8%). Nine nests (47.4%) were visited by only 1 parent, of which 5 were females (55.6%), 2 males (22.2%), and 2 unidentified individuals.

DISCUSSION

Our data do not confirm the suggestions of Lowe (1954), who assumed female Gray Herons incubate only at night, nor the conclusion of Creutz (1981) who wrote that females incubate more than males, nor the statement of Milstein et al. (1970) that males do more than 95% of the nest building. We did not find any sexually different daily activity patterns in the Gray Heron, such as has been described for some shag-species which, however, show sexual dimorphism in size (Bernstein and Maxson 1984).

Our data suggest that male and female Gray Herons attend their nest at similar rates. Males seem to engage in proportionally more guarding of nests with eggs and small chicks than females. Only before incubation started did males spend longer periods away from the nest than females, including sessions of gathering sticks for the construction or repair of the nest. Bernstein and Maxson (1984) found that during the pre-laying period male Blue-eyed Shags (*Phalacrocorax atriceps*) spend up to 5 h daily carrying sticks to the female. Female Great Black-backed Gulls (*Larus marinus*) were also present on the nesting territory more than males before incubation started, although both sexes invested equally in nest building (Butler and Janes-Butler 1983). Mock (1979) argued that during the pre-laying period male herons may be engaged in extra-marital courtship, but by leaving his partner, a male provides opportunities for his partner to be mated by other males. We do not have clear observations on the presence and behavior of extra-pair birds. When nest attendance was no longer critical (when chicks had grown old enough to make guarding senseless), female Gray Herons seemed to spend less time on the foraging grounds between food turns than males did, and when chicks approached fledging, females more than males continued to provide regular care.

Our data suggest that male Gray Herons invest a little more in guarding their nesting territory and its contents (and in activities that include nest guarding, such as incubation), but less in feeding chicks than females. Even during brooding and guarding very small chicks immediately

after hatching males fed chicks less frequently than females. Male Black Skimmers (*Rhynchops niger*) and Western Gulls (*Larus occidentalis*) appeared to defend nesting territories more intensely than females, as the latter tended to defend chicks only (Burger 1981, Pierotti 1981). Female Black Skimmers fed chicks more often than males (as the latter did not leave the nesting territory as frequently), but this was not the case in the Western Gull, in which males are much larger than females and forage relatively more successfully. This certainly does not apply to the Gray Heron, where sex dimorphism is absent.

Our data also show that less variability exists in frequency of nest attendance between partners within a pair than between pairs, and that, especially in those periods in which maximal nest attendance was required, both sexes contributed about equally to parental activities. As such, we cannot confirm the prediction of Trivers (1972), that females invest more than males in reproductive behavior, nor the idea of Krebs and Davies (1981) in sexes exploiting each other. However, our results do suggest that the sexes may direct their parental investment differently (e.g., nest selection, construction and defense in the case of the male, and egg formation in the case of the female). This does not prevent both sexes of a pair of Gray Herons from attending their nest at comparable rates, although small differences may become apparent.

SUMMARY

Male and female Gray Herons (*Ardea cinerea*) attended their nests at comparable rates throughout the entire reproductive period. Males engaged more than females in carrying sticks to the nest, which may explain longer times away from the nest during the pre-incubation period. However, males incubated 1 h 30 min more per day than females, and brooded and guarded small chicks approximately 45 min longer. Male herons, on the other hand, spent less effort than females in feeding chicks, resulting in longer times between food turns, when guarding of the nest is no longer critical. Our data also indicated that variability in nest attendance between partners within a pair was much less than variability between pairs. Both partners of a pair seemed to attend their nest at similar rates during those periods of both the reproductive cycle and the day, in which the nest was visited most frequently. There was no evidence of consistent differences in reproductive behavior in the course of the day between sexes.

ACKNOWLEDGMENTS

We are most grateful to Count D. Legrelle for the opportunity to study the heronry on his property at Berendrecht, to Mr. J. Fleur, who allowed access at the heronry at Wilrijk, and to the Bijnens family, who helped with the field work in the heronry at Zonhoven. The observation tower was provided and mounted by the Travhydro company through the efforts of Mr. De Vos and Mr. Fichtelberger. The companies ACS

and Mourik provided hides. Night-vision material was borrowed from the army thanks to Captain Gilboux. This work was made possible through grants of the Institute for the Stimulation of Scientific Research in Industry and Agriculture (I.W.O.N.L.), and was supervised by Prof. Dr. A. F. De Bont.

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