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Sexual Differences in Nest Attendance and Chick-Feeding Rhythms of White Spoonbills

EDUARDO AGUILERA

Estación Biológica de Doñana, Apartado 1056, E-41080 Sevilla, Spain

Sexual separation of activity rhythms may be favored if each sex can forage either at night or during the day. This should be especially advantageous during reproduction, when breeding activities (pair formation, mate guarding, nest defense, incubation, etc.) compete with time for foraging, and overall energy demands are higher. Although there is extensive literature on feeding habits of wading birds, few studies focus on daily rhythms of foraging (reviewed in Kushlan 1978). Some typical night-herons, including

the Yellow-crowned Night-Heron (*Nyctanassa violaceus*) and the Black-crowned Night-Heron (*Nycticorax nycticorax*), also forage during the day (Mock 1975; Fasola 1982, 1984). On the other hand, Wood Storks (*Mycteria americana*), Great Blue Herons (*Ardea herodias*), Reef Herons (*Egretta sacra*), and Gray Herons (*Ardea cinerea*), mainly diurnal foragers, are reported to forage at night (Kahl 1964, Krebs 1974, Black and Collopy 1982, Draulans and van Vesseem 1985, van Vesseem and Draulans 1986). Knowledge of daily

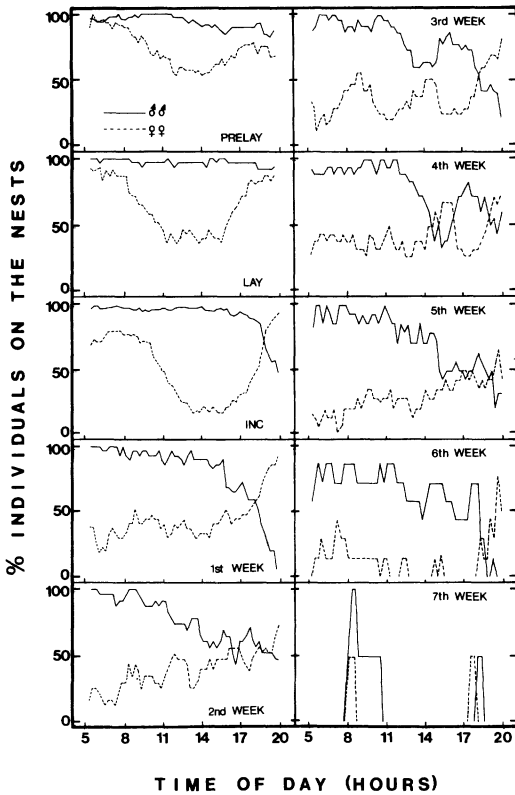


Fig. 1. Daytime patterns of nest attendance by males and females throughout the reproductive cycle. The chick-rearing stage is divided into seven 1-week periods. Sample sizes in Table 1.

rhythms of parental activities is even more limited (Whitelaw 1968, Milstein et al. 1970, Urban 1974, Kushlan 1976, Ramo and Busto 1985, van Vessem and Draulans 1986), and the only detailed study on sexual differences in daily activity rhythms (van Vessem and Draulans 1986) found none.

In southern Spain, White Spoonbills (*Platalea leucorodia*) forage during the day and night. I found sexual differences in daily rhythms of nest attendance and chick-feeding of this species throughout the reproductive cycle. From these differences, I suggest paternity defense and extrapair fertilizations are advantages for males.

I studied a mixed-species heronry in Doñana Na-

tional Park (southwestern Spain) during the breeding seasons of 1985–1986. This heronry included 374 pairs of White Spoonbills in 1985, and 237 pairs in 1986. Gray Herons, Cattle Egrets (*Bubulcus ibis*), Little Egrets (*Egretta garzetta*), Black-crowned Night-Herons, and White Storks (*Ciconia ciconia*) also bred in the colony in both years. Common Jackdaws (*Corvus monedula*), Black-billed Magpies (*Pica pica*) and Black Kites (*Milvus migrans*) frequently took eggs or chicks (Aguilera 1988). Spoonbills nested in cork oaks (*Quercus suber*) on the border of a brackish marsh. A general description of the study area may be found in Valverde (1958).

Observations were conducted from two blinds on towers 6.5 m and 4.5 m high, located at the periphery of the colony ca. 60 m from the nests. Birds were observed without interruption from dawn to sunset (13–15 h), 3–4 days a week, usually from the first settlement of the birds at the nesting sites until young were fledged.

Eight to 12 pairs that occupied contiguous nests were observed simultaneously with 10 × 40 binoculars and 20 × 60 telescope. Individuals were recognized by distinctive features of the light spot on the upper tip of the bill (Aguilera and Alvarez 1989), and sexes were distinguished by the larger body size of males and verified by position during copulations. Every 15 min, scan samples of individuals present at the study nests were made. An individual was considered present when it was either at its nest site or collecting nest material nearby. During intervals between scans, I recorded the time of each chick-feeding that involved individuals of study pairs, and I recorded the identity of birds that provisioned chicks. Because parents intermittently fed chicks for several hours after arrival at the nest (length of interval depending on chick age), I included only the initial feeding after arrival.

The behavior of some pairs in different breeding stages was observed on four nights with good moonlight conditions in 1986. These observations started before sunset and ended ca. 0600, when all off-duty individuals of the study pairs had returned to the colony. In this way I determined the hour of departure and arrival of each individual during a nocturnal absence. The white plumage of birds allowed easy detection of arrival or departure of individuals. In addition, every 30 min I shone a flashlight on study nests to check attending individuals. There was no apparent effect on the birds.

I divided the breeding cycle of each pair into stages

TABLE 1. Sampling effort during the daytime in different reproductive stages.

	Prelay	Lay	Incubate	Chick-rearing (age in weeks)						
				1	2	3	4	5	6	7
Pairs (n)	22	21	26	20	16	14	12	10	5	2
Scans (n)	2,692	1,767	6,807	1,684	1,345	1,350	1,058	817	407	114

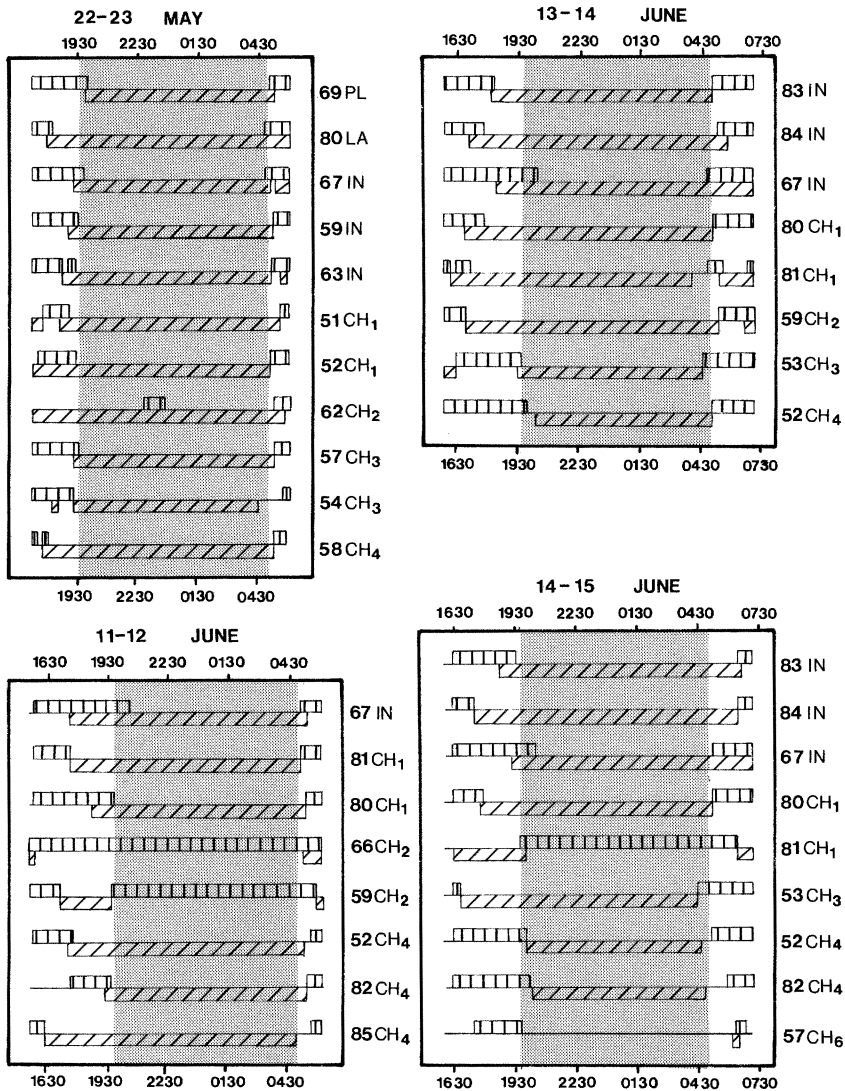


Fig. 2. Nest attendance during four nights (shaded areas) in 1986. Numbers and letters at right of each box represent pair identification and reproductive stage, respectively (PL = prelaying, LA = laying, IN = incubation, CH_n = chicks in the *n*th week after hatching). For each pair, bars with vertical lines denote presence of the male on the nest, and bars with slanted lines indicate presence of the female.

of prelaying, laying, incubation, and chick rearing. To examine differences in nest-attendance pattern relative to chick age, I subdivided chick rearing into seven 1-week periods, starting when the first egg hatched (Table 1). All male and female nest-attendance patterns (Fig. 1) differed significantly from those expected under the null hypothesis of equal probability of attendance at any hour of daytime (Chi-square tests, $P < 0.01$). Differences between male and female patterns were significant (Chi-square tests, $P < 0.001$) for every reproductive stage, except the seventh week

after hatch when sample size was too small to test statistically.

From prelaying to incubation stages, most females attended nests in the early morning and afternoon. The probability of a female on the nest at midday decreased as nesting season progressed (values ranged from 54.2% of females on the nest at 1400 during prelaying to 23.5% during incubation, Fig. 1). During prelaying and laying, more than 90% of males were on the nest at any time during the day. During incubation, males also stayed on the nests throughout

the morning and afternoon, but they began to leave the colony earlier in the evening (ca. 1830).

During the first two weeks post-hatch, male nest-attendance pattern was similar to the pattern during incubation, but they left the colony earlier (Fig. 1). In contrast to pre-hatch stages, ca. 30% of females were present just before sunrise (ca. 0500), and some returned ca. 0900. Between 0900–1700, no marked rhythm of attendance was found among females (ca. 50% on the nests), but after 1700, the proportion of females present on the nest increased, and by 1945 most of them were attending (Fig. 1). During week 3, some males left the colony ca. 1400 but returned ca. 1700, and they left again at sunset. This pattern was accentuated during week 4 (Fig. 1). The pattern of female nest-attendance during week 3 peaked ca. 0800, 1400, and 2000, but during week 4 only two peaks (ca. 1600 and 2000) were observed. Week 5 after hatch was marked by a notable reduction in the time that females spent on nests. Only a few females were present on the colony in the morning (none were present at 0700). Another feature of week 5 was the decrease in the number of females in the evening, as nestlings began to be left unattended (see below). The rhythm of nest attendance by males during week 5 was not very different than week 4. During the last two weeks that nestlings remained at the nests (weeks 6 and 7), females were rarely present on the nests; however, males remained an additional week (week 6), in a diurnal pattern similar to that of week 5 (Fig. 1).

Overnight, males generally were absent from the colony (presumably foraging), while females attended the nests (Fig. 2). I observed only three exceptions; all occurred when chicks were less than 2 weeks old. When nestlings were more than 4 weeks old, they were left alone on 8 of 9 occasions. Males left the colony between 1600 and 2030 ($\bar{x} = 1900 \pm 1.25$ [SD], $n = 32$) with a peak at 1945. Males returned between 0400 and 0630 ($\bar{x} = 0445 \pm 0.5$, $n = 34$) with a peak at 0430.

Diurnal rhythms of chick-feeding by males and females were significantly different (Kolmogorov-Smirnov, two-sample tests, $D = 0.44$, $n_1 = 188$, $n_2 = 323$, $P < 0.001$). Males fed in the early morning and again ca. 1800, with almost no activity at midday (Fig. 3). This pattern departed significantly from the null hypothesis of equal frequency of chick provisioning throughout daylight hours (Kolmogorov-Smirnov, one-sample test, $D = 0.38$, $n = 188$, $P < 0.01$). Females fed chicks throughout the day ($D = 0.07$, $n = 323$, $0.05 < P < 0.1$), although two peaks, one ca. 0830 and the other ca. 1830, were noted (Fig. 3). There were no significant differences between years in chick-feeding rhythms of either males ($D = 0.14$, $n_1 = 122$, $n_2 = 56$, $P > 0.1$) or females ($D = 0.17$, $n_1 = 233$, $n_2 = 84$, $P > 0.1$).

During overnight observations, of ca. 40 nests/night, I observed chicks being fed only once (at 2300). There

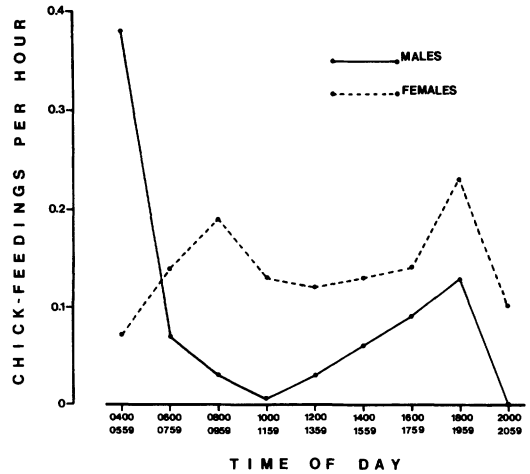


Fig. 3. Chick-feeding patterns by males and females during the daytime. Sample size: males = 188, females = 323; all chick ages combined.

were no differences between pair members in being the last to feed chicks in the evening ($n = 19$ females, 11 males; $\chi^2 = 2.1$, $df = 1$, $P > 0.1$), but a significant difference was found for being the first to feed in the morning ($n = 5$ females, 25 males; $\chi^2 = 8.33$, $df = 1$, $P < 0.01$). On 7 of 11 occasions that males gave the last feeding in the evening, the same birds fed chicks first the next morning. Females fed chicks first the next morning on only 1 of 19 occasions that they gave the last evening feeding (Fisher test of exact probability, $P = 0.005$). These results support the view that males are specialized to forage at night whereas females forage during the day. By foraging overnight, males can attend the nests throughout the daylight hours.

To my knowledge, this is the first avian example of such a marked day-night separation between sexes in terms of their feeding/nest-attendance patterns. Blue-eyed Shags (*Phalacrocorax atriceps*) exhibit 12-h rhythms of alternating nest attendance (Bernstein and Maxson 1984). During breeding, the Antarctica night is very short or nonexistent, and both members of the pair forage during daylight hours. Bernstein and Maxson (1984) suggested that intersexual foraging competition may explain the observed differences. By separating timing of foraging, males and females avoid competition in foraging areas and keep one individual at the nest. Avoidance of competition in spoonbills may lead to the observed sexual differences, but it does not explain why males attend the nests during the day and females at night.

I regularly observed extrapair copulation attempts during this study. Indeed, 19% of all copulation attempts, which involved at least 60% of study males and 75% of females, were extrapair copulations (Aguilera and Alvarez 1989). Most extrapair copula-

tions were directed to paired females at nests, and all occurred during the day; but males made successful cloacal contact only when the female's mate was absent (mainly collecting nest material). Male spoonbills employ a variety of behaviors both to avoid being cuckolded and to increase their reproductive success through extrapair fertilizations (Aguilera 1989, Aguilera and Alvarez 1989). In relation to the seasonal pattern of nest attendance, males spent more time on nests during their mates' fertile period. Also, paired females were more frequently alone at nests during the postfertile period (Aguilera and Alvarez 1989). Copulations do not occur at the foraging sites, and defense of genetic paternity is an advantage for males that remain at nests during the day. In addition, paired males can increase their reproductive success by obtaining extrapair fertilizations at the nest sites. Breeding in spoonbills is highly asynchronous, with a 3-month interval between the dates of the first and the last clutch in the colony (Aguilera 1988). This may be an advantage for a male during the postfertile period of his primary mate (44.6% of 74 extrapair copulation attempts were performed by males during their mates' postfertile periods). There is evidence to support defense of paternity and seasonal patterns of male nest attendance in other colonial birds (Fujioka and Yamagishi 1981; Werschkul 1982a, b; Birkhead et al. 1985; Frederick 1987; Hatch 1987). Contrary to those species, male spoonbills probably do not need to fast or reduce opportunities to feed, as a cost of remaining in the breeding area, because they can forage at night.

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