

## SEXUALLY DISTINCT DAILY ACTIVITY PATTERNS OF BLUE-EYED SHAGS IN ANTARCTICA

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**ABSTRACT.**—Sexually distinct rhythms of nest attendance were documented for Blue-eyed Shags (*Phalacrocorax atriceps*) in Antarctica. Males attended the nest from approximately 00:00–12:00 and foraged approximately from 12:00–24:00. Female activity patterns were the opposite. Timing of male courtship occurred around 12:00 during the prelaying and laying-incubation periods, and timing of chick feeding was also sexually distinct. Males fed chicks in the early morning and late evening while females fed chicks in the afternoon. The rhythms were colony-wide and, at least, partially influenced by times of sunrise and sunset. Although specific adaptive pressures influencing these patterns are unknown, intersexual foraging competition is presented as a possible explanation relative to other theories.

Field studies have documented diurnal activity rhythms in several species of colonial seabirds by measuring the timing and periodicity of certain behaviors (e.g., Palmgren 1949, Cullen 1954, Muller-Schwarze 1968, Delius 1970, Drent 1970, Burger 1976, Galusha and Am-laner 1978, and Conover and Miller 1980). Few studies, however, have found rhythms within breeding pairs. Additionally, synchronized, colony-wide, daily rhythms for each sex have seldom been reported (Snow 1963; Vestjens 1977; Gaston and Nettleship 1981; van Tets, pers. comm.; T. R. Birkhead, pers. comm.). During our studies at a colony of Blue-eyed Shags (*Phalacrocorax atriceps*), however, the existence of such behavioral rhythms became apparent. Although Murphy (1936) had noted "highly interesting" rhythms in this species, no further research had been conducted. Such rigid activity patterns would be of interest in measuring energy allocation between sexes (Bernstein and Maxson, unpubl. data) and also in answering questions concerning selection pressures on the Blue-eyed Shags and other colonial birds. Accordingly, we quantified timing of basic behavioral rhythms within breeding pairs to determine if the timing differed between sexes, and to determine how widespread individual rhythms were within the colony.

### STUDY AREA AND METHODS

We collected over 3,000 bird-hours of time budget data from 15 January 1979 to 1 April 1979 and from 23 September 1979 to 15 March 1980 at a colony of Blue-eyed Shags on Cormorant Island, 5 km southwest of Palmer Station, Anvers Island, Antarctica (64°46'S,

64°03'W). There were 485 nests on 31 December 1978 and 326 on 19 December 1979. Nests (2–10) were observed simultaneously every 30 s, at the tone of a metronome (see Wiens et al. 1970) either from dawn to dusk or for 24 h during periods of continuous daylight. Behaviors were categorized as: present at the nest (preening, resting, guarding chicks, etc.), incubating, brooding chicks, off the nest but gathering nest material (algae) nearby (Bernstein and Maxson 1982), and feeding chicks. Other behaviors that consumed little time, such as courtship or pair-bond maintenance, were considered as present at the nest if the shag was not simultaneously incubating or brooding. Shags were assumed to be foraging when absent from the nest or from the vicinity of the colony.

Data were grouped by sex for each of the following stages of the breeding cycle: prelaying, laying-incubation, brooding, and fledging periods. Laying and incubation were combined because incubation began during the interval between the laying of the first and second eggs (Williams and Burger 1979, Shaw 1981). The brooding period was further divided into three stages determined by size of the largest chick in a nest. Ulna length was the primary criterion (Dunn 1975b), and divisions were based on separations within the typical sigmoid growth curve. The early chick rearing stage was defined by chicks weighing less than 500 g and with ulnas less than 55 mm, the middle chick rearing stage by chicks of 500–1,000 g and ulnas of 55–120 mm, and the late rearing stage by larger chicks until they fledged. Early chick rearing ended approximately on day 12, the time also given by Dunn (1976)

for the beginning of thermoregulation in Double-crested Cormorant (*P. auritus*) chicks. Middle chick rearing ended near day 24, and chicks fledged between days 40 and 45. Technically, chicks were not brooded during late chick rearing, but a parent was always present (see Results). Fledged chicks were those whose molt and growth were near completion and those that were either beginning to fly or had recently been able to fly. Chicks that still returned to the nest to be fed were included in the fledging period; therefore, that period included post-fledglings until they abandoned the nest site.

Adult shags were sexed by body and bill size, and by vocalizations. Males were recognizably larger ( $3,022 \pm 170$  g SD,  $n = 16$ ) than females ( $2,576 \pm 138$  g SD,  $n = 21$ ), and were the only sex that called. Bills were seldom measured precisely, in order to minimize stress to the nesting birds, but males had visibly longer and deeper bills. Our bill data were supplemented by measurements by Parmelee (pers. comm.) and by observing birds that were displaying, copulating, and mated.

Adverse pack ice conditions limited travel to the island during early stages of the breeding cycle and during the early and middle chick rearing stages; we therefore have few data for these periods. However, to determine if rhythms of individual pairs under observation were colony-wide, we recorded the sex of the shag present at the nest at least every 4 h on 23 days at between 23 and 54 nests in one section of the colony; these data were supplemented by spot-checks.

Graphs of activity were based on averages of all nests observed, but only established nests that had been observed continuously from dawn to dusk were used in statistical analyses. To test for sexually distinct rhythms, each breeding period was examined for the behavior most definitive of the period: presence at the nest for the prelaying, late chick rearing, and fledging periods; incubation for the laying-incubation period; and brooding for the early and middle chick rearing periods. Changes in nest attendance were rapid, and, therefore, the hour of the day when definitive behaviors accounted for less than 50% of a shag's activity was tabulated for each pair. The differences of these times were analyzed by paired *t*-test to determine if timing of behaviors differed between sexes. Test sample sizes were 8, 7, 2, 3, 12, and 23 nests for the six stages, respectively. Timing of nest material collection by males during the prelaying and laying-incubation periods was analyzed in the same manner.

We could not examine chick-feeding rhythms

by a paired *t*-test because males fed chicks in the early morning (00:00–04:00) and late at night (20:00–24:00). The mean of these values would have falsely indicated that males fed chicks in the afternoon. Contingency tables were, therefore, used to analyze number of chick feedings at a given time between sexes and periods.

Times of sunrise and sunset were calculated from *The American Ephemeris and Nautical Almanacs* for 1979 and 1980 and converted to local time, 4 h behind Greenwich Mean Time. Linear regression was then used to determine correlations of these times with average daily timing of departure of females and return by males.

## RESULTS

Although darkness prohibited observation before 06:00 and after 20:00 during much of the prelaying period, we noted a sexually distinct rhythm during the hours of light (Fig. 1). Males were present on the nest more than females until 13:30 and the converse was true after 14:00 ( $P < 0.025$ ). Most courtship occurred between 13:00–14:00, as indicated by equal numbers of both sexes present during the gathering of nest material (Fig. 1).

The same patterns of behavior were noted during the laying-incubation period (Fig. 1). Both sexes were at the nest in the morning, but females began to leave after 02:00. Males most commonly incubated during the morning, and females began returning at about 11:00. Some pair-bond maintenance followed (see below), after which males departed. Males returned by 23:00, twilight on some days, and again began to incubate. The rhythms of incubation differed significantly between sexes ( $P < 0.001$ ).

After the females returned, males gathered nest material from nearby littoral waters between 10:00–15:00 and 12:00–14:00 during the prelaying and laying-incubation periods, respectively. Although gathering nest material lasted longer during prelaying, timing did not differ between the two periods ( $P > 0.1$ ). P. Shaw (British Antarctic Survey; pers. comm.) has observed a few females of this species gathering nest material, but we observed only males.

After the chicks hatched, males continued to attend the nest in the morning while females attended during the afternoon. Although we monitored only two nests during the early chick rearing period (Fig. 1), the brooding pattern between sexes approached statistical significance ( $P < 0.055$ ). The pattern of brooding for the middle chick rearing period and the pattern of presence on the nest during the late chick rearing period differed significantly between

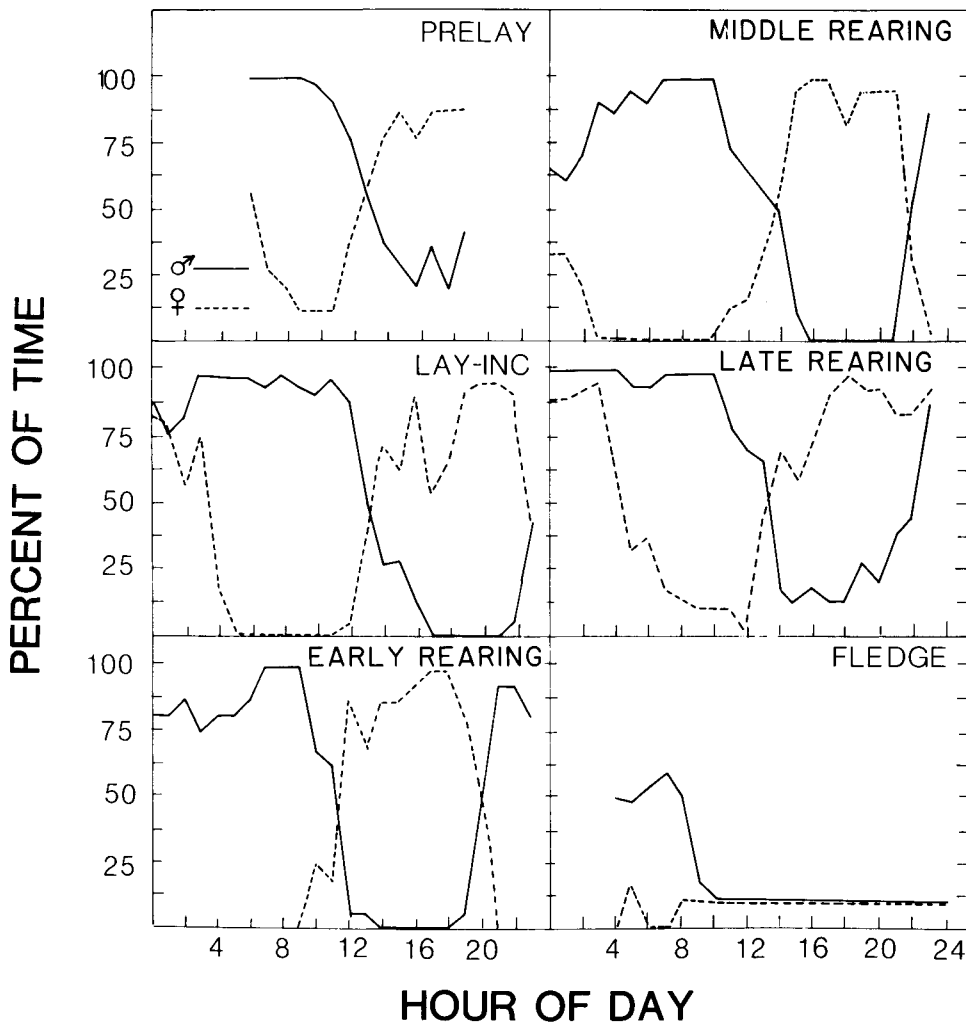


FIGURE 1. Patterns of definitive behaviors at study nests. Behaviors represented are presence at the nest for the prelaying, late chick rearing, and fledging periods; incubating for the laying-incubation period; and brooding for the early and middle chick rearing periods. Sample sizes are 13, 7, 2, 3, 27, and 47 nests, respectively.

sexes (Fig. 1) ( $P < 0.01$  and  $P < 0.001$ , respectively). Although both sexes spent most of their time away from the nest during the fledging period (Fig. 1), males attended significantly more than the females in the morning ( $P < 0.01$ ). During this period, most females and some males spent the evening on nearby rocky outcrops, possibly to escape the intense begging of chicks.

It appears, therefore, that males attended the nest in the morning while females foraged, and that they switched nest attendance around noon. Comparison with nests observed within a large area of the colony (Fig. 2) revealed that the patterns noted for the study nests were similar to those of the entire colony. Fluctuating numbers of males gathered nest material, a form of courtship and pair-bond maintenance, around midday during the prelaying and laying-incubation (Fig. 2).

Temporal separation of chick feedings between sexes was evident during all three brooding stages (Table 1) (all  $P < 0.005$ ). Although timing of chick feeding was more variable during the fledging period, sexual differences still were evident (Table 1) ( $P < 0.05$ ).

Day length influenced the rhythms; the timing of females' departure correlated with sunrise ( $r = 0.84$ ,  $n = 15$ ) while timing of the males' return to the colony correlated with sunset ( $r = 0.87$ ,  $n = 18$ ). Although shags often flew in windy stormy weather, departure time was delayed on days of strong winds (50–90 knots). For example, during a storm on 20 January 1979, about 30% of the nests had both adults present at 08:00. As shags attempted to take off, the wind forced them back into the colony. The only other factor notably influencing the rhythms was pack ice, which was highly variable during September–December

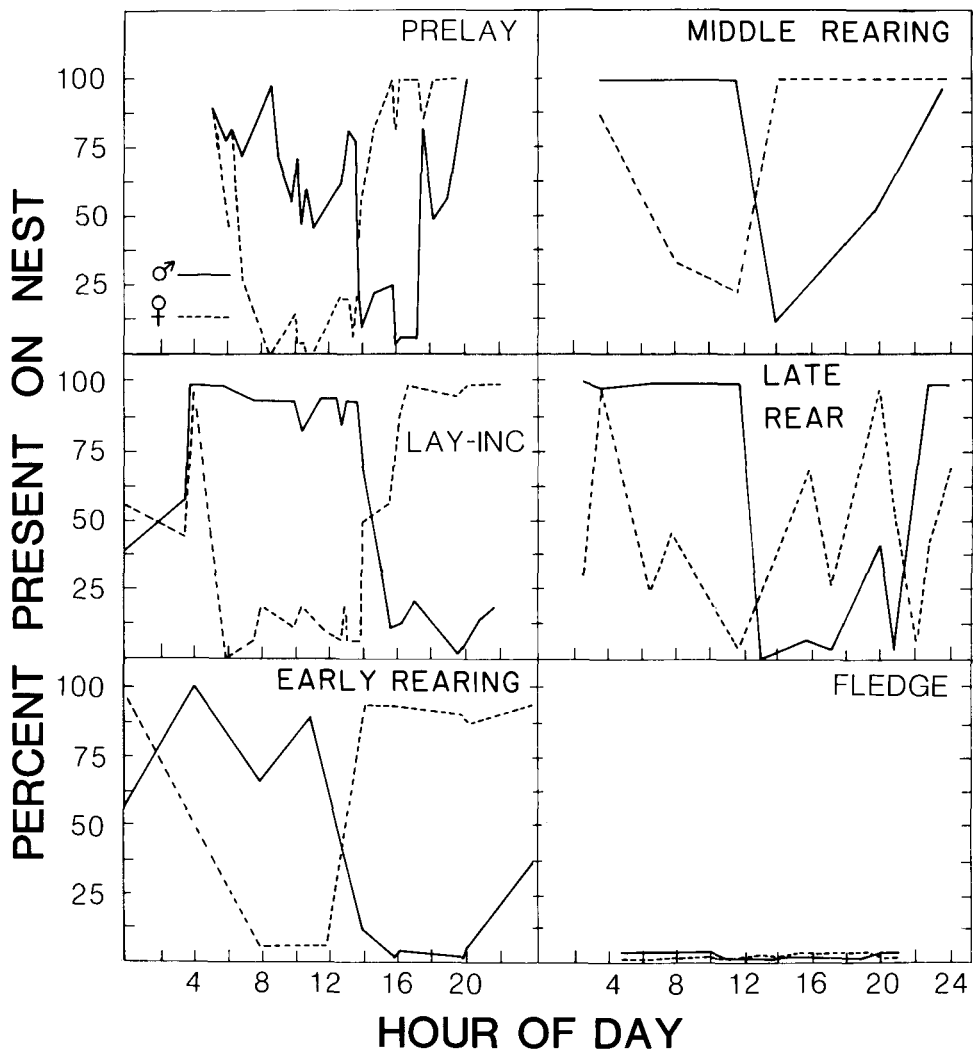


FIGURE 2. Patterns of presence at the nest for a section of the colony. Sample sizes are 50, 54, 42, 23, 23, and 23 nests, respectively.

and changed daily. With extensive ice cover, the birds had to fly farther to find open water in which to feed: for example, one day some females did not return until 17:30. Despite a reduced time for foraging, males still returned to the colony between 22:00–24:00.

Ice cover early in the breeding cycle also made shags vulnerable to piracy by South Polar Skuas (*Catharacta maccormicki*; Maxson

and Bernstein 1982). However, shags were not delayed for more than a few minutes by these attacks.

#### DISCUSSION

What selective pressures led to such rigid, sexually distinct rhythms of nest attendance? The question is even more intriguing because the activity patterns were maintained by all estab-

TABLE 1. Number and timing of chick feedings at study nests.

	Time	Early rearing	Middle rearing	Late rearing	Fledge	Total
Males	17:00–07:00	10	8	32	32	82
	08:00–16:00	0	0	21	6	27
Females	17:00–07:00	0	1	4	6	11
	08:00–16:00	7	5	30	15	57

Differences in timing of feeding between sexes,  $\chi^2 = 71.2$ ,  $P < 0.005$ .

lished pairs on nests, except in exceptionally severe weather and in spite of the fact that Blue-eyed Shags breed asynchronously within a colony, having up to a 5- to 6-week difference between laying dates (Murphy 1936; Shaw, pers. comm.; this study).

Feeding times correlated with return of the adult from foraging, and although chicks often begged for food during other times, they were rarely fed after the first few hours following return of the parent. This is probably related to the amount of time that food can be retained by an adult before it is too digested to feed to the chick. Lewis (1929), Mendall (1936), and Dunn (1975a) also noted peak feeding times in Double-crested Cormorants, as did Derenne et al. (1976) in the King Shag (*P. albiventer*) and Snow (1963) in the Common Shag (*P. aristotelis*).

One shag must always be at the nest from the prelaying period through the middle chick rearing period, either to guard the nest and territory from conspecifics or to guard and provide warmth to eggs and chicks. An unguarded nest was quickly dismantled or depredated. Chick protection may also be important during the late chick rearing period because a parent was always at the nest. However, protection from predation alone cannot account for the colony-wide, sexually distinct patterns observed.

Approximate sexually distinct rhythms of incubation have been found for several non-colonial birds (see Skutch 1976). In colonial pelecaniforms, Snow (1963) noted sexually distinct incubation rhythms in the Common Shag, and Vestjens (1977) noted rhythms similar to those of Blue-eyed Shags in the Australian Pelican (*Pelecanus conspicillatus*). In addition, van Tets (pers. comm.) has observed patterns of incubation similar to those reported by Vestjens (1977) in the Auckland Island Shag (*Phalacrocorax colensoi*) and the Bounty Island Shag (*P. ranfurlyi*), but not in the closely related Campbell Island Shag (*P. campbelli*). (See Mayr and Cottrell [1979], Walters [1980], and van Tets [1976] for differing views on the taxonomic status of these cormorants.) Derenne et al. (1976) also reported approximate 12-h incubation shifts in the King Shag on the Isles Crozet, but they did not distinguish sexes. As noted in van Tets (1976), Devillers and Terschuren (1978), and Bernstein and Maxson (1981) the southern hemisphere shags mentioned above form a circumpolar species complex in which the degree of relatedness is uncertain. Comparative studies might help to determine taxonomy, and, in this case, identify selective pressures influencing the rhythms that appear widespread among these birds.

Gaston and Nettleship (1981) observed that incubation shifts in the Thick-billed Murre (*Uria lomvia*) on Prince Leopold Island (74°N) changed from approximately 24 h during egg-laying to 12 h by the time of hatching. The 12-h rhythm was maintained until chicks fledged, with males present from late afternoon to early morning. These rhythms, sexually distinct and colony-wide, resulted in the male parent always being present at the time of fledging. Gaston and Nettleship (1981) argued that post-fledging survival is enhanced by the male's accompanying the chick, possibly because he is better than the female at guarding and feeding the chick (Nettleship, pers. comm.). The same 12-h pattern was noted in the Common Murre (*U. aalge*; T. R. Birkhead, pers. comm.).

Although Blue-eyed Shag fledglings typically first left the colony during the morning, when adult males would have been present, adult nest attendance had decreased by the fledging period, and chicks were usually alone. We never witnessed attacks on fledglings, but one chick died from a blow to the head, probably from a Brown (*Catharacta lonnbergi*) or a South Polar skua. Chicks were still fed at the nest site during the fledging period, but approximately equally by both parents. We do not know if chicks were fed away from the colony or the duration of post-fledging parental care.

Foraging efficiency, through the reduction of intersexual competition, might also have influenced the divergence of foraging times; several authors have noted sexual segregation of feeding niches (e.g., Selander 1966, Serventy 1967, Hogstad 1976, East 1980, Williams 1980, Saylor and Afton 1981). With regard to the shags, once the feeding times diverged, any male that did not follow the system and foraged with females would lose his territory, nest, eggs, or chicks. Even if the members of a mated pair were to switch times of foraging, the male's reproductive success would diminish because his mate would be forced to compete within foraging flocks of males. However, before this hypothesis can be tested, studies are needed to reveal if sexes of Blue-eyed Shags employ distinct foraging tactics, exploit different habitats, or capture different sizes of fish, as Nelson (1978) reported for the Blue-footed Booby (*Sula nebouxii*).

Our view of the adaptive pressures that influence sexually distinct, colony-wide activity patterns in Blue-eyed Shags remains speculative. Most seabird studies, including this one, focus attention upon activities at the colony. Such research provides information about factors influencing reproductive success and is easier to accomplish than following and ob-

serving individual foraging or fledgling birds. More attention must be focused, however, on activities away from the colony. Perhaps through comparative studies of many species of seabirds, the advantages conferred by their activity patterns can be learned.

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