NEST ATTENDANCE OF PARENT BIRDS IN THE PAINTED SNIPE (*ROSTRATULA BENGHALENSIS*)

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ABSTRACT.—I observed 15 pairs of Painted Snipes (*Rostratula benghalensis*) in Japan for 24-h periods in order to compare the nest attendance behavior of males and females and to document changes in their behavior during the laying period. From a few days before the laying of the first egg until the day the second egg was laid, the male and female consorted with each other (stayed within 5 m of each other) more than 90% of the observation time. They visited the nest repeatedly on the first and second days of laying. On the third day, the consorting ratio decreased to 58.5%, and the male typically started to incubate. He continued to incubate that night. After laying the third egg, the female usually did not visit the nest except to lay the fourth and last egg. The male continued incubation, and the female met her mate only when she laid the last egg. The absence of female incubation and the early termination of consorting behavior are consistent with the possibility that Painted Snipe females are polyandrous. *Received 12 January 1982, accepted 4 October 1982.*

AMONG the polyandrous charadriiform species, comprehensive studies of pair-bond maintenance have been conducted on only four species, the Northern Jacana (*Jacana spinosa*; Jenni and Collier 1972, Jenni and Betts 1978), the Spotted Sandpiper (*Actitis macularia*; Hays 1972, Oring and Knudson 1972, Maxson and Oring 1980), the Red-necked Phalarope (*Phalaropus lobatus*; Hildén and Vuolanto 1972), and the Red Phalarope (*Phalaropus fulicaria*; Schamel and Tracy 1977). Although a detailed study of the Painted Snipe (*Rostratula benghalensis*) has not been conducted, sex role reversal and an apparently unbalanced sex ratio suggest the possibility of polyandry in this species (Beven 1913, Baker 1935, Lack 1968, Hays 1972, Oring and Knudson 1972, Jenni 1974). The objectives of this study were (1) to compare the nest attendance of male and female Painted Snipes, (2) to measure the amount of time the members of the pair spend together (consorting ratio) during laying and incubation periods, and (3) to consider the evidence for polyandry.

STUDY AREAS AND METHODS

Field observations were made in two areas. The preliminary study was done in Chuzu Town, southeast of Lake Biwa, central Japan (136°02'E, 35°08'N), from May to June 1978 (Biwa area). Nest observations were conducted in 20-ha abandoned fields among paddy fields at an elevation of about 85 m. Marshy plants, mainly buttercup (*Ranunculus quelpaertensis*), bitter cress (*Cardamine lyrata*), foxtail (*Alopecurus aequalis*), and cudweed (*Gnaphalium affine*), grew sparsely in these abandoned fields. The water depth in this area varied from 0 to 15 cm.

The main study was conducted in Toyo City, northwestern Shikoku Island, Japan (133°03'E, 33°57'N), from March to August 1979 (excluding May) and from June to July 1980 (Toyo area). This 40-ha study area of reclaimed land faces the Japanese Inland Sea. A quarter of the area was used as paddy fields, and the rest was marshy grassland that was plowed once or twice a year, usually in June and July. The study area was traversed by six parallel roads 200 m apart and by another road that intersected them at right angles. This poorly drained area was always covered with water. Until it was plowed, dense reed (*Phragmites communis*) or bulrush (*Scirpus planiculmis*) grew there every year. After it was plowed, the grasses grew only patchily or sparsely before September. The Toyo area is about 300 km west of the Biwa area.

Most data for the field study were obtained by continuous observations. Observations that started after 1800 are identified as "nocturnal observations" and were made with the aid of a flashlight. Behavior was observed with binoculars (9×) and a spotting scope (15×). Behavioral acts were recorded in seconds, and the data were later converted to minutes for calculations. Of 27 birds observed, 4 males and 2 females were marked with neck bands. Because no other birds of the same sexes as the banded individuals were observed entering their nests, any male or female who entered a nest was considered the progenitor of the eggs in the nest.

All observations reported here were made at nests with four eggs. The four eggs were laid on consecutive days, and the days of laying were identified as

TABLE 1. The length of visits to the nest during the laying period (minutes ± SD). Numbers in parentheses indicate nocturnal visits.

	Day 1	Day 2	Day 3	Day 4
Female				
Length of egg-laying visits	35.5 ± 17.5	62.3 ± 33.4	32.8 ± 7.4	15.9 ± 1.9
Number of egg-laying visits	2	4	5	6
Length of other visits	3.6 ± 3.7	6.1 ± 5.2	5.7 ± 5.3	1 —
Number of other visits	43	50	36	1
Male				
Length of visits	3.6 ± 8.0	8.0 ± 12.8	22.6 ± 31.7 (21.6 ± 15.1)	43.4 ± 52.8 (36.1 ± 10.2)
Percentage of stays longer than 30 min	2.0	6.8	26.2 (35.3)	46.8 (76.9)
Number of visits	99	85	92 (17)	47 (13)
Number of nests	4	7	9 (1)	8 (1)

day 1, day 2, and so on. These four days comprise the laying period. A span of a few days before day 1 is referred to as the prelaying period. The incubation period extends from the day after day 4 until hatching.

The percentage of time during which the two members of a pair stayed within 5 m of each other was termed the consorting ratio. Consorting behavior was studied at the Toyo area for a total of 17 days (162.0 h). Other observations were made at both the Toyo and Biwa areas.

Nest-related behavior in the Biwa area was observed from blinds about 10 m from the nests. Four nests were observed for a total of 17 days (190.8 h). Observations were made at the Biwa area during two nights (22.6 h) of the incubation period. All diurnal observations at the Toyo area were made from a blind on a car roof 1.5 m above the ground. By driving the car along the roads, I was able to follow the birds when they left their nests. Nine pairs were observed at the Toyo area for a total of 36 days (368.7 h) Two of these nine pairs abandoned their nests during the laying period, so the data from these nests were excluded from the results (total 7 days). Two nests were observed a total of four nights (47.0 h) during the laying period. Activity at night at the Toyo area was observed at intervals of 1 min from about 20 m when a flashlight was switched on for about 5 s and off for about 55 s.

RESULTS

Clutch size and time of laying.—Of 33 nests found, 2 had 3-egg clutches, 30 held 4 eggs, and only 1 held 5 eggs. Accordingly, the normal clutch size in this species is considered to be four.

The time of laying was recorded 17 times. During the laying period, a female laid an egg every morning between 0700 and 1100 (Fig. 1). She stayed on the nest far longer when coming to lay an egg than at other times (Table 1). The female was on the nest for a much shorter duration when she laid the fourth egg ($\bar{x}$ = 15.7 min) than when she laid the earlier eggs ($\bar{x}$ = 44.0 min). All other visits to the nest by the female during the laying period were much shorter ($\bar{x}$ = 5.1 min); 88.5% of these visits were less than 10 min.

On four additional days when the 1st, 2nd, or 3rd eggs were laid but egg laying was not observed, females stayed on the nest for 39, 42, 46, and 47 min between 0800 and 1210 (Fig. 1; 22 June 1979, 21 June 1978, 3 June 1978, and 12 June 1979, respectively). These four stays were the only long stay on those days. It is assumed that egg laying occurred during these long visits. Egg laying was not seen at two nests on day 4, but the females entered the nests only once, and it is assumed that they laid during these visits (Fig. 1; 30 March 1979 and 21 July 1979).

Nest visitation on each laying day.—On day 1, both sexes entered the nest frequently during the morning (Fig. 1), but they often left it for a long time during the afternoon. They returned to the nest in the evening. The male stayed about the same length of time (Table 1) and entered the nest about as frequently as the female did. No observations were made on the night of day 1.

On day 2, the duration of diurnal visits increased but the number of visits decreased

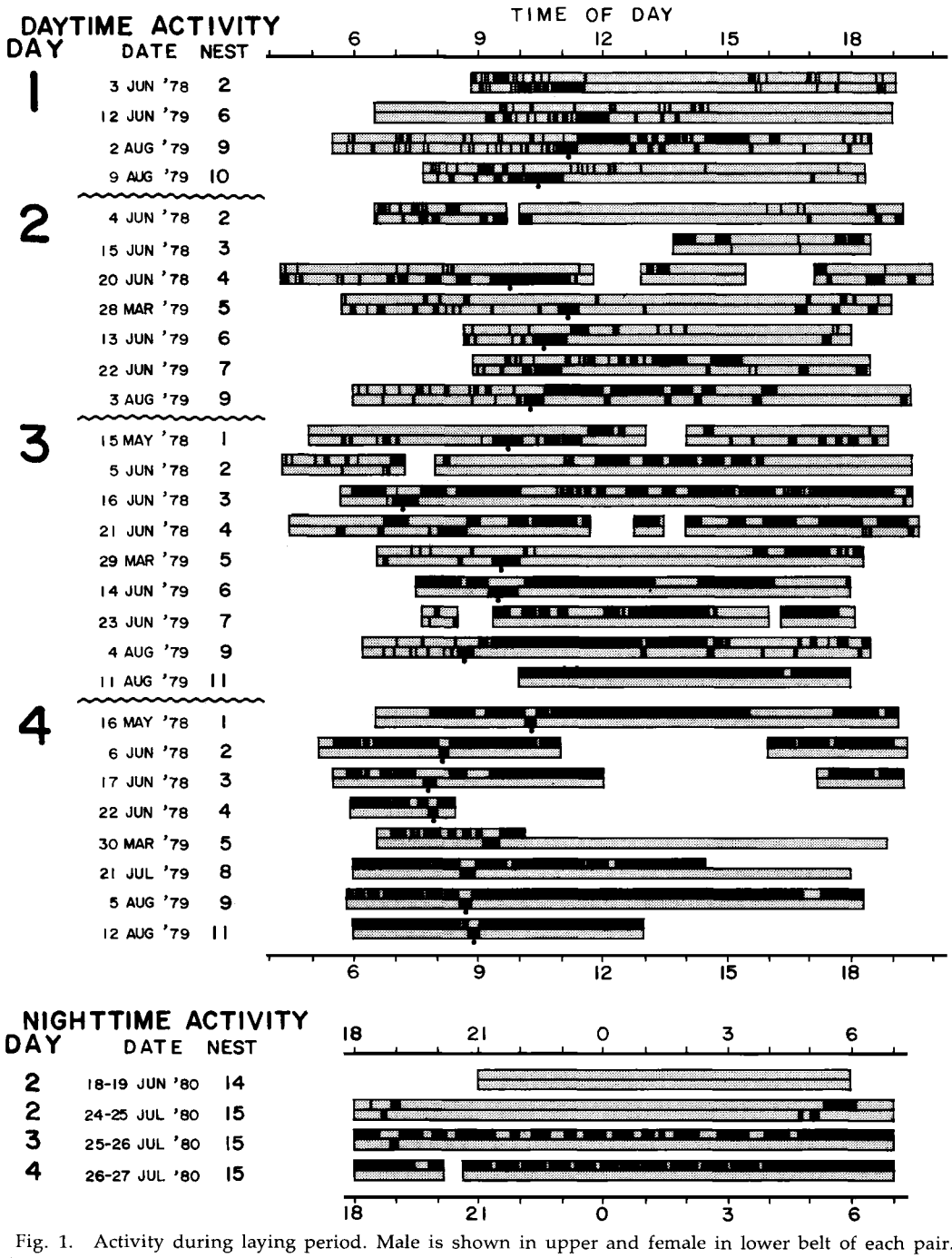

Fig. 1. Activity during laying period. Male is shown in upper and female in lower belt of each pair. Black band shows time spent on nest and shaded band out of nest. Small dot shows the time of egg laying. Day 1 is the first day of egg laying and day 4 the last day.

slightly in both sexes. In two nests watched at night, both sexes left the nest site just after dark and returned just before light. At Nest 15 the male and female left the nest at 1907 and returned at 0443. At Nest 14 the male and female were gone when observations started at 2100 and returned to the vicinity (within 5 m) of the nest at 0426.

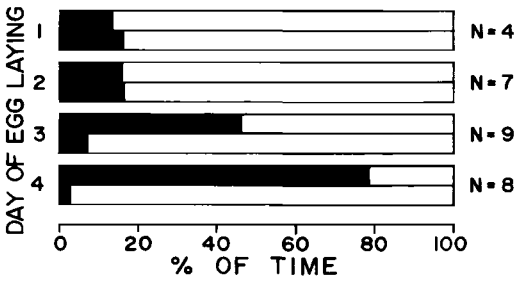

Fig. 2. Average percentage of daylight time on nest. Upper belt shows male stays and lower belt female stays. Black band shows percentage of time spent on nest and white band out of nest. Number of nests observed is shown.

TABLE 2. The percentage of daylight hours during which the male and female of a pair stayed within 5 m of each other.

	Average (range)	Number of hours observed	Number of pairs
Prelaying period	99.6 (98.5–100.0)	23.6	4
Laying period			
Day 1	99.0 (97.5–100.0)	34.0	3
Day 2	92.8 (89.3–95.9)	42.6	4
Day 3	58.8 (38.4–81.0)	29.7	3
Day 4	7.9 (3.3–16.7)	32.1	3

On day 3, both sexes changed their patterns of nest visitations, but in different ways. Females entered the nest repeatedly before laying the third egg but after that did not return to the nest until 1800 in all but two nests. Females entered three of four nests between 1800 and 1930. At Nest 15 the female entered the nest at 1851, left at 1903, and did not return that night, but her mate spent the night on the nest. During the day males visited the nest about as often as the previous day, but the average visit was much longer (Table 1).

On day 4, all but one of the females entered the nest only once and laid the last egg at that time. After leaving the nest, they were never seen near it again. At Nest 9 the female left the nest 1 min after entering it, but she returned 30 s later and laid the fourth egg. Males entered the nest less often than previously but stayed much longer during each visit. The males stayed on the nest at night, but females did not return to the nest.

Two males in the Toyo area abandoned their nests after their females laid the third egg, but the females still laid the fourth egg in the nests. Pair 12 visited their nest in typical fashion through day 3. On day 4, the female exhibited typical behavior. She entered the nest, laid the fourth egg, left the nest, and never returned. The male on day 4, however, never visited the nest, nor was he seen around the nest. I began observing Nest 13 on day 2. The male did not enter the nest between 0744 and 1157 on day 2, nor at any time on day 3, and he did not even visit the vicinity of the nest on day 4. His female stayed on the nest more than 40% of the total observation time on both days. On day 4 she stayed on the nest much longer than the other females. On her first visit she stayed for 27 min and laid the fourth egg. She then flew off and returned 80 min later and stayed on the nest for 5.5 h. Neither the male nor the female returned after day 4.

Total time spent on nest in laying period.— During the whole laying period of daylight hours, males stayed on the nest four times as much as females (39.8% vs. 9.9%). As egg laying advanced, males increased and females decreased the amount of time they spent on the nest (Fig. 2). On days 1 and 2, females spent slightly more time on the nest than males did (16.4% vs. 13.2% and 16.7% vs. 16.2%, respectively). On day 3 some males spent a longer time on the nest than previously, and it was on this day that the greatest range was seen in the percentages of time spent on the nest for different males. The males on five of the nine nests spent more than 50% of the day on the nest (46.2% on average, range 16.3%–71.3%). The females on day 3 reduced their time on the nest to only 7.3%. On day 4 the males spent 78.7% of the day on the nest, and females spent only 3.0%.

Females did not visit their nests at all at night during the laying period, and males did not visit at night until after the third egg was laid. A male spent 68.6% of the night following the laying of the third egg and 86.7% of the night following the laying of the fourth egg on the nest.

Male nest attendance in the Painted Snipe reached mid-incubation levels on day 3, and the incubation started on day 4. In the Red-necked Phalarope (Hildén and Vuolanto 1972),

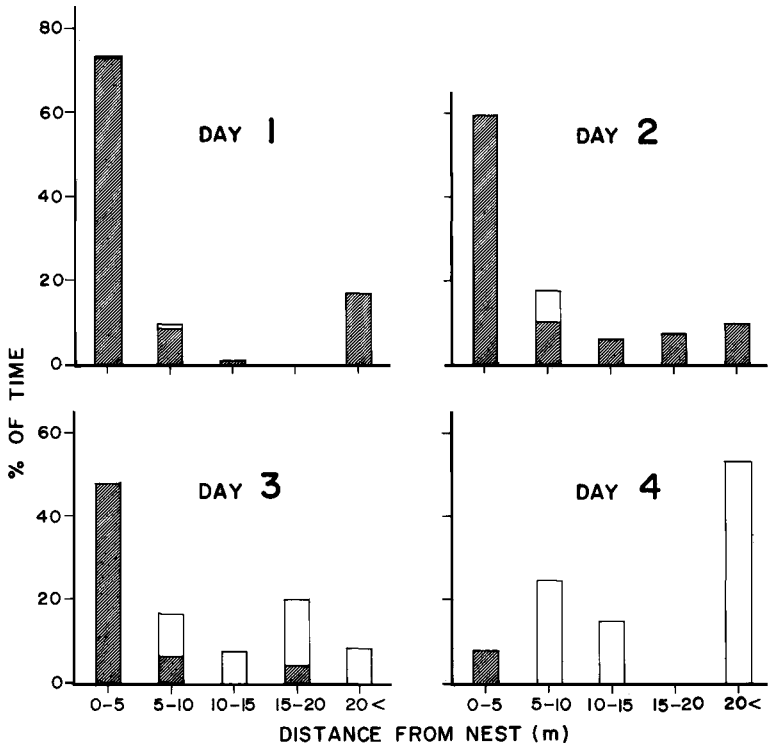

Fig. 3. Average distance of female from nest. Shaded bar shows time female spent with male and white bar shows time female spent alone.

male visits to the nest become gradually more frequent and longer as the laying period progresses. The Spotted Sandpiper male incubates sporadically before day 3 (Maxson and Oring 1980). In the Red Phalarope (Schamel and Tracy 1977, Mayfield 1979), the Wilson's Phalarope (*Phalaropus tricolor*; Howe 1975), and the Wattled Jacana (*Jacana jacana*; Osbone and Bourne 1977), males appear to begin incubating on day 3.

Consorting ratio.—A male usually followed a female for three or four days during the prelaying period. The consorting ratio was 99% in the Toyo area during the prelaying period. Although the consorting ratio for the whole laying period was 68%, it decreased from 99% on day 1 and 93% on day 2 to only 8% on the last day (Table 2). The consorting ratios varied widely among individual pairs on day 3. In two of the three pairs the female consorted with the male on day 4 only when she came to lay. One female (Nest 9), however, returned to the vicinity of the nest after laying the fourth egg and stayed within 5 m of the incubating male.

Because the male and female arrived at the nest together early in the morning before the laying of the third egg, it is possible that they had consorted during the preceding night. The female probably left her mate on the nest at night after the third egg was laid, however, because the male began spending considerable time on the nest and the female did not stay in the vicinity of the nest.

As egg laying advanced, the amount of daylight time females stayed within 5 m of the nest decreased in the Toyo area (Fig. 3). On days 1 and 2, females stayed within 5 m of the nest most of the time and consorted with the males almost all day. Within 10 m of the nest, females were occasionally separated from the males, who stayed on the nest, but when females went more than 15 m from the nest, the males always followed. On day 3 females spent less time within 5 m of the nest and often went away from the nest alone. After laying the fourth egg, females left the nest and moved solitarily, while the males stayed on the nest.

Behavior during the incubation period.—Dur-

TABLE 3. Nest attendance of male during the incubation period. (Females did not visit the nest during the incubation period.)

	Daytime	Nighttime
Average percentage time on nest (range)	80.4 (64.9–94.7)	89.6 (88.2–91.1)
Average duration of nest visits in minutes (range)	39.8 (23.9–110.4)	92.9 (77.7–111.2)
Percentage of visits exceeding 30 min	53.4	100.0
Number of days	14	2
Number of hours observed	156.0	22.6

ing the incubation period males typically left the nest 1.3 times per hour for about 10 min. Males sometimes remained on the nest for several hours, especially during the morning. At other times, they stayed away from the nest for as long as 40 min. Males were on the nest 80% of the time during the day and 89% during the night (Table 3). At night the males left the nest less frequently and spent longer periods on the nest.

When males left the nest, they usually walked or flew away immediately. In 61 of 85 observations made during the incubation period, males left the vicinity of the nest within 1 min of leaving the nest. This behavior differed markedly from behavior during the laying period, because the male spent much time in the vicinity of the nest during the laying period. A male typically flew back to a place about 20 m from the nest and then walked to the nest, where he preened for a time before entering the nest.

The incubation period averaged 16.8 days (range 16–18 days, $n = 6$). During the incubation period, the female was never seen at the nest and apparently never came anywhere near the nest (confirmed by banded females for 7 days). When the male interrupted incubation to forage, he did not consort with any females (confirmed for 6 days). The male and his chicks left the nest within a half-day after all the eggs hatched, and they never returned to their nest ($n = 4$).

DISCUSSION

In species such as the Mountain Plover (*Charadrius montanus*; Graul 1973) and the Sanderling (*Calidris alba*; Parmelee and Payne 1973), which have double clutches, females incubate the last clutch with or without males. In the polyandrous Spotted Sandpiper, females help with incubation unless they obtain a new mate (Hays 1972, Maxson and Oring 1980). On the other hand, only the males incubate in the Northern Jacana (Jenni and Betts 1978), the Red-necked Phalarope (Hildén and Vuolanto 1972), and the Red Phalarope (Mayfield 1979), all of which have proved to be polyandrous. In the Wilson's Phalarope (Howe 1975), which is probably polyandrous, only males incubate. The Painted Snipe female decreased the time she spent on the nest as egg laying advanced, and almost all her nest visits occurred before the third egg was laid and were less than 10 min long, except for the four egg-laying visits. After a male started to incubate, the female did not visit the nest again except to lay the fourth egg, nor was she ever seen in the vicinity of the nest. Therefore, incubation is performed only by a male. A female neither helps her mate nor incubates alone. This suggests that the degree of sex-role reversal in incubation is more complete in the Painted Snipe than in the Mountain Plover, the Sanderling, or the Spotted Sandpiper and is similar to that in the Northern Jacana and the three species of phalaropes. One Painted Snipe female began incubating when her mate abandoned their nest but ceased after about a half-day. This fact may suggest that ancestral Painted Snipe females incubated.

In the species in which females do not incubate, females may desert their mates during incubation, as in the Red Phalarope (Schamel and Tracy 1977, Ridley 1980); they may help their mates, as in the Northern Jacana, the females of which visit the nest, shade the eggs (Jenni and Betts 1978), and help defend the territory against other birds, even during the incubation and rearing periods (Jenni and Collier 1972, Jenni 1974); or they may desert their mates as soon as or before the clutch is completed, as in the Red-necked Phalarope (Hildén and Vuolanto 1972) and the Wilson's Phalarope (Howe 1975). In the Painted Snipe, males did not follow their mates on or after day 4, and females

did not visit their nests after the fourth egg was laid. The pair bond of the Painted Snipe appeared to break down after the laying of the last egg in the same way as the pair bonds of Red-necked and Wilson's phalaropes do. It is advantageous to a sequentially polyandrous female that she desert the first mate as soon as possible and gather energy reserves sufficient to obtain the next mate and to lay his clutch. In the simultaneously polyandrous American Jacana, a female stays with her mate and prepares to lay the replacement clutch for him (Jenni and Collier 1972).

Painted Snipe females are unlikely to mate with another male during the prelaying period or on the first and second days of laying, because they consort with their current mates most of the time on these days. Females also consort with their mates during the night after the second egg has been laid. During day 3, females begin spending less time with their mates, but by this time it is likely that their fourth egg has already been fertilized. It is extremely unlikely that even the last egg could be fertilized by some other male. After laying the last egg and abandoning their mates, the females could begin to consort with other males. The abandonment of the mate and emancipation from incubation make it possible for females to mate with other males, thus enabling this species to have a sequentially polyandrous mating system.

A simultaneously polyandrous female copulates with several males in a short time. In contrast, a sequentially polyandrous female mates with only one male during a set period. The probability of a male rearing his own offspring is different in these two polyandrous sytems. In the sequentially polyandrous species, a male has only to keep his mate for a few days before and during the laying period to ensure that he will rear his own offspring (Schamel and Tracy 1977). A simultaneously polyandrous female lays the first set of eggs on one nest for the first mate and the second set of eggs on another nest for the second mate, successively (Jenni and Collier 1972, Maxson and Oring 1980), but she copulates with several males during that period. Northern Jacana females copulated with three or four different males in a single afternoon (Jenni and Collier 1972). One Spotted Sandpiper female copulated with two different males for two days, and she laid for the earlier mate on the next day. She copulated only with the later mate during the laying period of the earlier mate (Oring and Maxon 1978). In these cases, the earlier male does not always rear his own offspring, although Northern Jacana females spend a greater amount of time in the earlier male's territory just before and during the laying period and simultaneous mating is exceptional in the Spotted Sandpiper. Other mechanisms may explain fertilization in species with a simultaneously polyandrous mating system. Physiological and genetic research on these species will be necessary to identify these mechanisms.

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