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## MONOGAMY AND POLYANDRY IN THE SPOTTED SANDPIPER

LEWIS W. ORING AND MERLE L. KNUDSON

Photographs by the authors

In the preceding article, Hays (1972) convincingly demonstrated the existence of polyandry in an individually marked population of Spotted Sandpipers (*Actitis macularia*) on Great Gull Island, off the eastern tip of Long Island, New York. She found six of 11 females to be polyandrous in a population that averaged 1.9 males per female over a two-year period. The purpose of our paper is to compare Spotted Sandpiper polyandry in two Minnesota populations — one on the mainland in Itasca State Park and the other on a small island in Leech Lake, Cass County; to describe the nature of polyandrous mating systems in other shorebirds; and to theorize as to the evolution of polyandry in the Spotted Sandpiper.

The Spotted Sandpiper is one of a number of shorebird species for which polyandry has long been suspected. Female Spotted Sandpipers are larger, more heavily spotted, and more aggressive than males, which do most of the incubating and rearing of the brood. Similar sexual dimorphism and distribution of behavioral roles within the pair are found in the Common Sandpiper (*A. hypoleucos*), indicating that polyandry may be equally well developed in the Spotted Sandpiper's Old World counterpart (Oring, pers. observ.).

In the American Jacana (*Jacana spinosa*), Jenni and Collier (1972) demonstrated classical polyandry — females averaging 2.2 males per territory and the much smaller males setting up their own territories within areas defended by females. Hoffman (1949) described serial polyandry in the Pheasant-tailed Jacana (*Hydrophasianus chirurgus*) — females forming brief pair-bonds one at a time, with 7 to 10 males per season.

Nethersole-Thompson (1951; in Bannerman, 1961) reported that the Dotterel (*Eudromias morinellus*) was sometimes polyandrous, the larger females laying two clutches, each incubated by a different male. Walter Graul (pers. commun.) found that, in the Mountain Plover (*Eupoda montana*), pair-bonds were short-lived with males sometimes fertilizing second clutches for their original mates or for other females, and females sometimes laying second clutches with their first mate or a new mate. Both sexes incubated, but only one member of a pair incubated each nest.

In both Temminck's Stint (*Calidris temminckii*) and Sanderling (*C. alba*), females probably often lay two clutches — one incubated by each member of the pair (Hilden, 1965; Parmelee, 1970; Parmelee and Payne, in press). Parmelee (pers. commun.) believes that the Sanderling is sometimes serially polyandrous. A similar situation may occur in Temminck's Stint.

In the phalaropes (Phalaropodidae) and painted snipes (Rostratulidae), females are larger and more aggressive than males, and only males incubate and brood the young. These phenomena, along with disparate sex ratios, led to the idea that these groups exhibit polyandry (Beven, 1913; Nethersole-Thompson and T. E. Randall in Bannerman, 1961). Recently, Raner (1972) showed that in an individually marked population of four female and six male Northern Phalaropes (*Phalaropus lobatus*), two of the females laid two clutches for each of two males. In addition, Raner (1972) observed a possible incident of polyandry in the Spotted Redshank (*Tringa erythropus*). It appears that polyandry is a more common phenomenon than we previously supposed, its existence perhaps being masked by the fact that while the potential for polyandry may be genetically present, its expression may be dependent upon a particular set of environmental conditions which often are not present.

### Study Areas

The work reported here represents one aspect of a comprehensive study of Spotted Sandpiper behavior, conducted at Itasca State Park sewage lagoon, or LaSalle Lagoon, from 1969 to 1972. The lagoon, including the cleared area around it, is an isolated patch of Spotted Sandpiper habitat 6.8 hectares in size and surrounded by virgin forest for four or more kilometers in all directions (Figure 1). We have never known a breeding bird to leave the lagoon temporarily; other sandpipers rarely visit it except in migration. The cleared area around the lagoon is practically devoid of woody vegetation, and there are large areas where vegetative cover is scattered (Figure 2). On each of the more than 100 mornings spent at the lagoon, we recorded one or more potential predators, including red-sided garter snakes (*Thamnophis sirtalis*), six species of birds, and ten mammals.

Early in 1972, we began a study of Spotted Sandpiper behavior on Pelican Island in Leech Lake, a small island of 1.6 hectares within 0.5 km of three other islands, where Spotted Sandpipers do not breed, and 8 km from the mainland (Figures 3 and 4). The breeding sandpipers sometimes visited the other islands, but we never saw a bird flying to or from the mainland. The only evidence of predators observed in nine visits to the island were two garter snakes seen on each of two days, and feces, believed to be those of mink (*Mustela vison*), on one day. Ring-billed Gulls (*Larus delawarensis*) were always on or near the island, but we never saw them in areas where sandpipers bred.

### Methods

In 1969, four pairs of Spotted Sandpipers bred at the lagoon. We marked two males. In 1970, there were 11 breeding birds, five females and six males, and all but one female and one male were marked with colored plastic leg bands and enamel paint. In 1971, there were eight breeding birds, four females and four males, and seven were marked with colored plastic leg bands and Sanford's magic marker pens. In 1972, there were seven breeding birds, three females and four males, and all were marked with color bands and magic marker pens.

We caught birds by a variety of methods, the most efficient of which were funnel traps, placed along the shore in favorite feeding spots, and a 0.75-meter diameter spring-loaded nest trap. When properly used, the spring trap was 100 per cent effective.

In 1970, 1971, and 1972, we made observations from 05:00 to 10:00 and 18:30 to 20:30 hours every day from the time the birds arrived until hatching. During periods of peak activity, we watched almost continuously throughout the day. Additional observations, on a less regular basis, continued throughout the season until all birds fledged. From a number of high spots around the lagoon we could observe several pairs at once, and, with the help of various students

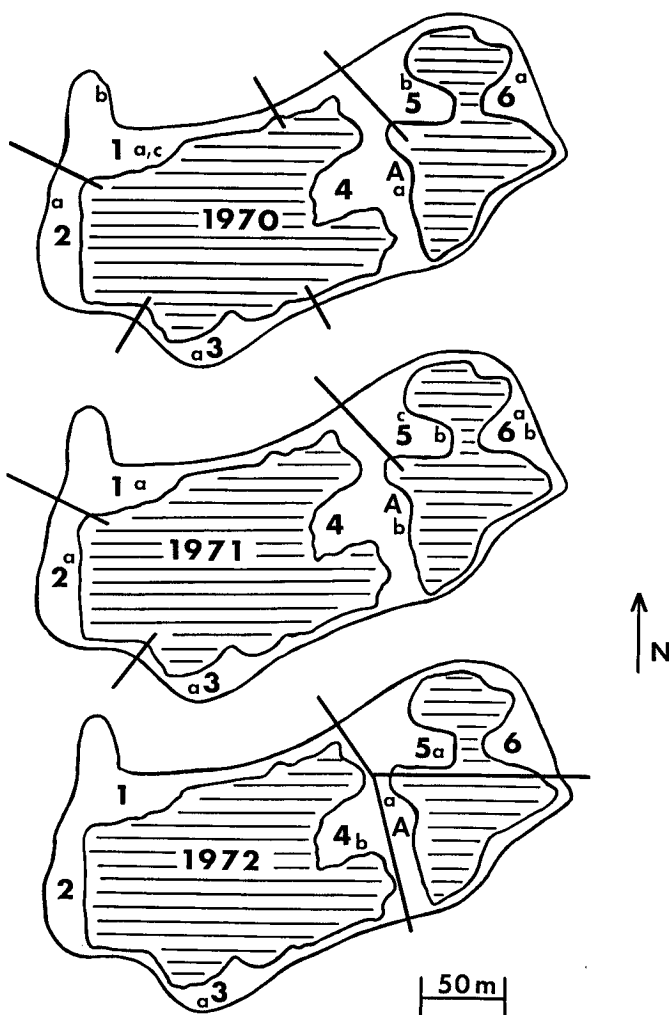


Figure 1. Lagoon maps showing territorial boundaries and nest locations for 1970-1972. Numbers one through six and large A indicate principal nesting areas; small letters indicate positions of nests in chronological order, a through c.

and staff at the University of Minnesota Biological Station, it was possible to monitor the nest-building, egg-laying, copulation, and incubation behavior of virtually every pair. We mapped territories by noting zones of conflict between adjacent pairs. Individual markers, as well as sexually dimorphic features, allowed us to identify accurately each individual and its sex.

We visited Pelican Island several times in 1969, 1970, and 1971, and on 24 May and 6, 13, 14, 21, and 27 June 1972. Two observers were present on 13 and 21 June, three on 14 June, and 13 on 27 June. Although we did not color band the birds, we were able to keep track of virtually every bird because three females had unmistakable plumage features and the island was very small. We ascertained the number of males as follows: on 21 June there were two newly hatched broods accompanied by males; seven nests where males were incubating; and one male prospecting for a nest site with his mate. On that same day, six females were simultaneously observed. We had collected a seventh female the week before. We estimated the total breeding population, therefore, as seven females and 10 males.

The vocalization terminology follows that of Knudson (1972). Epigamic vocalizations are those that tend to occur in reproductively motivated situations — e.g., in mate attraction.



## Results

In 1970, five females at Itasca State Park laid eight clutches while paired to six males. Four hatched and four were depredated (Table 1). Three females laid one clutch, one laid two, and one three. The females laid all replacement clutches in the same general area of the lagoon as their initial nests, but there was a tendency for these females to build their second nests at opposite ends of territories from original ones (Figure 1).

In 1971, four females laid seven clutches for four males. Two laid single clutches, one laid two, the other three. Three clutches hatched, two were destroyed, and two deserted (Table 1). No females were polyandrous. Female 74, which laid three clutches, alternated successive nests from one side of her original territory to the other. Female 5 laid her second clutch in a newly acquired territory more than 200 meters from her original nest and only 15 meters from where Female 74 had searched for a nest site at the start of the season.

In 1972, three females laid four clutches for four males. Two laid one clutch each; the third, Female 96, laid two, one for each of two males (Table 1). In order to form her second pair-bond, with Male 75, Female 96 moved over 200 meters to an area so close to the territory of Female 72 that fighting occupied most of three days. The two nests were 43 meters apart. Of four clutches laid, one was completed 21 May and another 23 May. The female, which laid the clutch on 21 May, completed another for her second mate on 29 May. The fourth clutch, completed on 5 June, was laid by a female which did not arrive until 29 May and which probably bred elsewhere before coming to the lagoon.

None of the 1972 clutches hatched; three were depredated and one was deserted in a severe thunderstorm. Immediately following each catastrophe, the birds involved disappeared. After 26 June, no sandpipers were present at the lagoon, whereas in years when four or five females bred, renesting persisted into early June.



Figure 2. Breeding Area 1 at the lagoon at the time of hatching. When nest sites were being chosen, this sandy area had scattered herbaceous and grassy cover less than 10 centimeters high.

TABLE 1  
Mating Histories of Spotted Sandpipers at Lake Itasca, Minnesota,  
1970-1972

<i>Female number</i>	<i>Year</i>	<i>Male</i>	<i>Area number</i>	<i>Clutches hatched</i>	<i>Clutches depredated</i>	<i>Clutches deserted</i>
72	1970	70	1, 1, 1	1	2	—
72	1971	70	1	1	—	—
72	1972	20	4a	—	—	1
73	1970	75	3	1	—	—
74	1970	78	6	—	1	—
74	1970	UnM*	5	—	1	—
74	1971	UnM*	6, 5-6**, 5	—	1.5	1.5
YG†	1970	71	2	1	—	—
UnM*	1970	B1†	4a	1	—	—
96	1971	71	2	1	—	—
96	1972	71	3	—	1	—
96	1972	75	5	—	1	—
5	1971	75	3, 4a	1	—	1
19	1972	21	5	—	1	—

\*Unmarked.

\*\*First two eggs destroyed in Area 5, the second two laid, then deserted, in Area 6. Tabulated in totals as a depredated clutch.

†Color marked only.

In 1970, two surplus males visited the lagoon — one, which was expelled during the initiation of pair-bonds, and another, which arrived just as Female 74 was completing her first clutch. This latter male became Female 74's second mate. In 1971, we banded four surplus males early in the season and there may have been additional ones, but none remained to form pair-bonds with resident females. In 1972, one or two extra males visited the lagoon briefly at the start of the season, but the residents chased them off. Another surplus male arrived late in the season — the morning of the day when one female was to lay her third egg and another female her first. This late arrival paired with the female which laid her fourth egg the day he arrived, and she moved more than 200 meters to join him. The following account of this incident of polyandry illustrates the intensity of aggression directed toward surplus males, as well as the site tenacity which some males exhibit.

On 20 May, Female 72 laid her first egg early in the morning on the dike separating Areas 4 and 5, and Female 96 laid her third egg late in the morning in Area 2. The total number of songs between 05:30 and 08:30 on the previous two days had been 45 and 33, respectively, with the females doing most of the vocalizing. At daybreak, a male had arrived, which had incubated two clutches

in 1971, one in Area 3 and the other between Areas 4 and 5. When he came directly to the dike where he had incubated last in 1971, there was a great amount of vocalizing — 67 songs and 27 epigamic calls from 05:30 to 08:30 — with most of the singing by the males. On the previous morning, the resident male had been relatively silent. Chasing followed, and, as is usually the case during egg-laying, the resident male did most of the chasing. The newcomer, Male 75, persistently returned to the area following chases.

The next day, song rates remained high — 69 songs and 10 epigamic calls in three hours — and so many chases took place, the majority of which erupted into prolonged aerial chases high above the lagoon, that a count was impossible. The birds spent 27 minutes of one 30-minute period chasing, mostly in the air. However, by 10:00 the chasing had subsided and Male 75 was appeasing Male 20 on the dike and chasing him from Area 4. Late that afternoon, Female 96 laid her fourth egg for Male 71 and immediately took up residence with Male 75. She fought intensely with Female 72 that evening along the dike.

Female 96 spent 22 May in Area 4 with her new mate. Much of the time she spent fighting with Female 72 which laid her third egg that day. Both females were again sexually active and they dominated the aggression between the two pairs. Between 05:30 and 08:30 there were 98 songs and 42 epigamic calls — a large increase over previous days in both aggressive and reproductively motivated vocalizations.

The next day, 23 May, fighting was brief and sporadic, and vocalizations dropped to 85 songs and 17 epigamic calls from 05:30–08:30. Nest site prospecting and nest-building occupied most of the new pair's time. The female laid her first egg early on 26 May in Area 4. By that time, vocalizations had decreased to six songs and no epigamic calls from 05:30–08:30.

Seven of the 10 breeding males, marked during the course of this study, returned the next year to breed at the lagoon; and one of the three, which did not return to breed, nested at a small pond 4 km away. Four of seven females returned in subsequent years, and an additional banded female, without a color band, bred 4 km north of the lagoon. This female may have been a lagoon-breeding bird, which lost her color band, or a young female hatched at the lagoon. However, of 16 chicks banded at the lagoon in 1970 and 11 banded in 1971, none have yet returned.

Of the seven marked males that bred at the lagoon in successive years, only one had his first nest in the second year outside the territory where his last nest of the preceding year had been. One male moved approximately 150 meters to breed in an adjacent but unoccupied territory. Another, which left the lagoon in 1970 after his nest was destroyed and while his mate was paired with a new male, bred 4 km north of the lagoon in 1971.

Of the four marked females that returned to breed, two nested with the same males and in the same territories as their last nests of the previous year and two bred in areas more than 150 meters away. One of the two females that moved was paired to a new male; the other arrived with her previous mate and they moved together 100 meters to a new territory.

In three cases, both members of a marked breeding pair returned to breed at the lagoon, and their first pair-bonds were with their former mates. In one case, Female 72 in 1971, was already paired to, and copulating with, a new male when her former mate arrived. She tolerated her former mate which then drove off the new male. This female laid her first egg the second day after her



old mate arrived — in the very scrape in which the pair hatched a clutch the previous year. We have never known a female to lay an egg in less than three days from the time her pair-bond was formed or her nest lost, indicating that in this case one male was responsible for the female's initial ovarian development, and another male for fertilizing her eggs.

#### Pair-bond Formation

Little time is required for the formation of a pair-bond. When the males first arrived in spring, there was usually a surplus of females, and aggression around the males was so intense and chases so frequent and prolonged, that it was difficult to determine when a bond was or was not formed. However, it appears that even the first pair-bonds of the season are formed within a few minutes of the male's arrival—when he leaves the shoreline and enters nesting cover with a female. From that point on, we have observed no changes in pair relationships until after laying, except when one member of a pair was killed or caught in a trap. We observed pair-bonding of late arriving males more easily because they returned to the spots where they had incubated the previous year or, in the case of new males, to areas of high activity. Several minutes after encountering an unpaired female, the male and female formed a pair-bond though, in some cases, a day passed before they were able to approach each other closely enough to allow copulation. The following resumé of the arrival of Male 20 illustrates the rapidity of pair-formation.

Two unmarked males arrived at the lagoon at daybreak on 15 May 1972. About 10:10, after unsuccessfully attempting to settle in an area already holding an established pair, they entered the territory of an unpaired female, Female 72, which had arrived five days earlier and established herself in Areas 4 and 5, some 200 meters from where she had bred in 1970 and 1971. Within 15 minutes of their arrival in the territory of Female 72, there were two male-male fights, three chases, 31 songs, 18 epigamic vocalizations, and six slow songs.

One hour and seven minutes after they entered Female 72's territory, one male had established his superiority over the other and was running into nesting cover with tail down, followed by the female in tail-up posture and the second male. The female intermittently turned and chased the second male. After a few initial runs into nesting cover, the pair flew to the shore and fed. Throughout the day both male and female sang frequently, averaging about one song per minute. At one point, the male flew to the female in an apparent copulation attempt, but the female threatened him and then immediately assumed the reproductively motivated tail-up posture. At 16:08, the female walked into the nesting cover, the male followed, and nest site prospecting began. The next morning the pair began copulating; the female laid the first egg on 20 May, just five days after the arrival of the male.

#### Incubation

Following the laying of the third egg, there is an increase in female sexual and aggressive activity, which is manifested by higher singing rates and either an increase in territorial defense or in the number of intrusions into other territories where sexual or aggressive activity is going on, or both. There is, however, a good deal of individual variation in the nature of female behavior after laying, perhaps mediated by the amount of activity nearby. Some females begin incubating with, or before, the laying of the fourth egg, whereas others show a sudden surge in sexual activity and only begin incubating after several



Figure 3. Aerial photograph of Pelican Island. Seven of nine original nests were on that part of the island shown in the lower left, one-fourth of the picture. Four of these nests were on or near the main beach and three were beneath dense shrubs and trees. The other two nests were at the tips of the island at the extreme top and lower right of the photograph.

days of extensive singing and aerial advertisement. Presumably, females which show the greatest increase in post-laying sexual activity and the weakest incubation tendencies are those most likely to form bonds with second males, should surplus males be available.

In 1972, Female 19 proved to be the most frequently incubating female we studied. She began incubating a few hours before she laid the fourth egg, and, near the end of the incubation period, she sat from early morning until late afternoon. Still, her singing rate, which had decreased sharply during the early part of the egg-laying period, increased greatly after she laid the third egg (Figure 5). She sang over other territories too and, on several occasions, was expelled from them. She did not, however, move to any unoccupied areas to establish a new territory although one-half of the lagoon was vacant.

Female 5, in 1971, did not incubate during the first four days of incubation. Not only did her singing rate increase after laying the third egg, but she began visiting all areas of sandpiper activity, displaying sexually to males, attempting to expel females, and centering her activity largely around a male whose mate had left the lagoon and which was being coveted at the time by a newly arrived female. Female 5 attempted for three days to form a pair-bond with this male and, after being expelled 10 times in four days by two other females in the vicinity, established a territory in an unoccupied area at the other end of the lagoon. She spent an entire day singing over and around this new area prior to the time we trapped her original mate which promptly deserted his nest and rejoined her. They renested, this time in a new area which she had claimed, 200 meters from the first nest. This male was the only one to desert following nest-trapping.



During the time of post-laying sexual resurgence, females incubated briefly, usually sometime between 06:30–09:00 and 19:30–21:00, or both periods. There was a good deal of individual variation in the amount of time females spent incubating independent of weather and stage of cycle, but all of the eight females, whose incubation patterns we studied, showed a general tendency to incubate more in the later part of the incubation period and in cold, rainy, or windy weather. Females that had been sitting on the nest regularly sometimes skipped incubation completely on warm days.

### Replacement Clutches

The initiation of replacement clutches or clutches for second mates averaged 5.3 days after predation or desertion. In two cases, in which the female was sexually active but not yet incubating, the first eggs of the new clutches were laid 3.5 and 5 days after loss of the nest or desertion of mate. In three nests with incubating females, the first eggs of the replacement clutches were laid four, four, and six days after predation. Another female waited 10 days after deserting an unincubated, but partially destroyed, second clutch before laying the first egg of her third clutch.

### Instability of Pair-bonds

Pair-bonds break as rapidly as they form. As mentioned above, Female 72 had formed a pair-bond and was copulating with a new male in 1971 when her mate of 1969 and 1970 arrived. It was only a matter of minutes before she paired with her former mate. We observed another equally rapid pair-bond switch earlier in 1971, involving this same female. Female 96 had been paired to, and copulating with, Male 71 for eight days. Their nest was already lined on the morning of 22 May when we caught Female 96 in a trap. Less than



Figure 4. Area of Pelican Island where seven nests were located, showing herbaceous vegetation which harbored four nests (foreground) and woody vegetation which surrounded three (background). All vegetation was growing on sand. Herbaceous plant cover was approximately 0.5 meter high and extended 30 meters from the beach toward the island's center. The mixed deciduous woods was 20 to 50 meters from the beach and had a canopy 8 to 13 meters high.

15 minutes later we saw Male 71 copulating with Female 72 which had been unpaired previously. In addition, he defended her territory against an intruding male and followed his new mate into nesting cover. We released Female 96 from the trap 15 minutes after Male 71 and Female 72 had copulated. She flew directly to her nest. Observations of the birds concerned were discontinued after this time. However, Female 96 and Male 71 were again nest-building together the following morning, and their first egg was laid early 25 May. Female 72 thus copulated with three different males between 22 and 24 May when her old mate finally arrived.

### Pelican Island Population

The 1972 breeding population included an estimated 1.43 males per female. The seven females laid a minimum of 13 clutches including two replacement clutches — after we had removed the first clutch — and one following the single incident of predation. Back-dating 21 days from the date of first hatching on the island, the three earliest clutches were completed on 28 or 29 May. Single eggs were taken from all nests being incubated on 27 June. They hatched in an incubator at various times up to 18 July. On 27 June, a pair, whose eggs were removed, immediately began prospecting for another nest site. If they had laid a new clutch, the eggs would not have hatched until the end of July.

In 1972, we kept track of eight clutches for a total of 127 clutch days; in 1971, we observed a single nest for over 14 additional days. Only one nest was depredated during this time — a garter snake destroyed it while we were on the island on 21 June 1972. Assuming a 21-day incubation period, 141 clutch days are equal to approximately 6.7 incubation periods; and one case of predation in 6.7 incubation periods provides an estimated predation rate of 15 per cent.

Nine original clutches on Pelican Island in 1972 averaged 3.4 eggs. Five of the nine nests were on the island's main beach, the site of daily visits by fishermen between 11:30 and 13:30. As a result of the almost certain disturbance, four of five beach nests had reduced clutch sizes — 3, 3, 3, 2 — while a fifth on the beach and four nests elsewhere on the island had normal clutches of four eggs.

### Comparison of LaSalle Lagoon and Pelican Island

The breeding density of Pelican Island in 1972 was 7 to 10 times that at the lagoon in various years despite the fact that nest sites and food appeared to be more readily available at the lagoon. In addition, the number of available males was greater on the island than at the lagoon — 1.43 versus 1.17 males per female. Disparities in breeding density and the ratios of males to females are attributed to the differences in predation rates — 47 per cent at the lagoon and 15 per cent on the island. Since males are far more susceptible to predation because of their predominant role in incubation, the greater number of males on the island is easy to account for. Differences in predation rates between the two study areas may have been even higher in past years. This was the first year that we noted garter snakes on the island.

Sandpipers used all the sparsely vegetated areas on the island as nest sites. Seven nests, simultaneously active on one quarter of the island, were so close together that the greatest distance separating any two nests — 37 meters — was less than the distance between the closest two nests at the lagoon — 43 meters. We found no nests in the densely wooded area surrounding the lagoon,

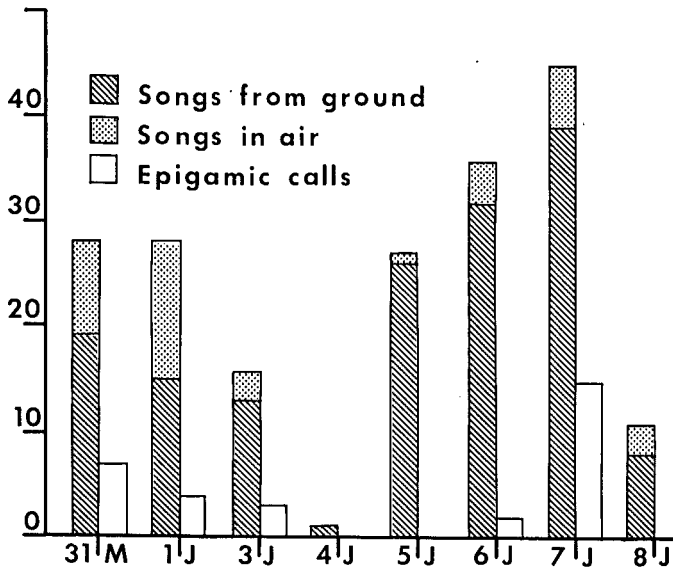


Figure 5. Total number of songs and epigamic calls at the lagoon from 05:30-08:30, 31 May to 8 June 1972. Female 19 laid her first egg 05:40, 2 June; her third 10:00, 4 June. Six birds, three males and three females, were present. Virtually all vocalizations were uttered by Female 19 and an adjacent female.

whereas on the island we found three of the nine original nests, in 1972, beneath dense shrubs or trees. Aggressive behavior was much more frequent and intense on the island than at the lagoon. Furthermore, it continued much longer each day and extended farther into the season. Aggressive responses to song playbacks were three times greater on the island than at the lagoon (Knudson, 1972).

Because of the high degree of overt aggression on the island, the sandpipers began their nests about a week later than at the lagoon. Also, with a few exceptions, sandpipers never firmly established territorial boundaries on the island, and intense aggression continued throughout the season. However, at the lagoon, birds always established firm boundaries within a couple of days of arrival, after which overt aggression was rare unless new birds arrived. Disturbances by fishermen not only brought about reduced clutch sizes on the island, but probably, in conjunction with intense aggression, caused the birds to nest in marginal habitats.

## Discussion

Those individuals making the greatest contribution to the gene pool of future generations are, biologically speaking, the most successful. However, as the number of offspring increases, counter selective forces, such as limited food supply for young, decreased parental care, and increased stress on the female, come into play. In shorebird species where predation rates are high and food supplies great and seasonally prolonged, one would expect that there might be selection for multiple clutches — either in conjunction with monogamy or polyandry. Various environmental factors bringing about instability — for example, relatively frequent storms for shoreline breeding species, or unpredictable food supplies due to drought for species in arid environments —



might act in much the same manner as a high rate of predation. Where multiple clutches have evolved, it is likely that it has come about with certain compromises which minimize female stress, such as advanced age at first breeding, assumption by the male of certain stressful behaviors such as incubation and brood rearing, or a reduction in the size of the clutch or egg.

The Spotted Sandpiper is one of a few scolopacids that successfully colonized the south temperate parts of North America. In doing so, it occupied areas with longer periods of high food supply and longer summers in which to rear young, thus increasing the potential for multiple clutches. At the same time, the southern colonization brought the species into contact with a number of new ground predators, including snakes, and a whole host of southern mammals.

The fact that Spotted Sandpipers breeding on the mainland are subjected to high predation is indicated by the 47 per cent rate of egg predation at the lagoon. The sparsely vegetated areas where Spotted Sandpipers nest are not only frequented by mammals hunting around the water's edge, but also by snakes seeking sunning spots or hunting frogs. The highly ritualized distraction display and unique squealing vocalization associated with it indicate that a high rate of predation has long been a part of the pressures facing Spotted Sandpipers.

Spotted Sandpipers in Minnesota certainly are capable of laying multiple clutches because food supplies remain high throughout most of the summer, pair-bonds are rapidly formed and broken, and the period between clutches is brief. Two females at the lagoon each laid three clutches in a single year (Table 1). Young from only one of these clutches hatched, and they fledged successfully. Likewise, we know that one parent alone can successfully incubate because, of four clutches incubated solely by the male, three hatched; the fourth was destroyed by a predator.

The Spotted Sandpiper thus has evolved the potential for serial polyandry in conjunction with increased length of the breeding season and high predation rates encountered during its southern colonization. In the face of the instability caused by predation, natural selection probably favored a mating system that increased the total number of offspring, in spite of the concomitant increase in stress to the female. At the same time, natural selection favored the evolution of greater participation by the male in incubation and brood-rearing, a slight increase in the female to egg-weight ratio, and possibly a delay in the age at which females first breed. Orians (1969) pointed out that unless females are able to recover sufficiently between successive clutches, there is no advantage in increasing the production of offspring.

On islands, where instability due to predation is minimal, serial polyandry is more common than on the mainland where the predation pressures that gave rise to the system are manifested. What seems to be a paradox is due to the large number of surplus males available in the absence of predation; for during the course of the species' evolution, females developed behavioral and physiological mechanisms that allowed them to breed repeatedly whenever surplus males were available.

Similar characteristics, indicative of compromises selected for during the evolution of Spotted Sandpiper polyandry, are exhibited to a greater or lesser extent by phalaropes, painted snipes, jacanas, Dotterels, and Common Sandpipers (Table 2). Among the shorebird species for which polyandry has been suggested and multiple clutching demonstrated, only the Mountain Plover

and Sanderling deviate with regard to these characters. In the case of the Mountain Plover, Graul (pers. commun.) showed that the mating system is complex and variable, and he attributes its evolution largely to the lack of stability in their short-grass prairie environment. Considering the extreme conditions under which Sanderlings nest in the high arctic, there is little doubt but that whatever their system eventually proves to be, it will show adaptations for highly unpredictable food supplies, short seasons, and rigorous climatic conditions in contrast to polyandrous systems which have evolved in areas with high predation rates, long seasons, and abundant food.

It appears that various types of polygamous mating systems, including polyandrous ones, are more common among shorebirds than we previously supposed. Within the suborder Charadrii, certain species occupy some of the harshest arctic and arid environments, others the temperate forests and grasslands, and still others various tropical habitats. These species are exposed to the diversity of food supplies, season lengths, and predation pressures typical of their environments. In response to this great array of selective pressures, a large variety of social systems has evolved. Where a system of multiple clutches of various types has evolved, we find various compromises reducing female stress. Studies of those species exhibiting these compromise characteristics will undoubtedly reveal new and interesting cases of polyandry.

TABLE 2  
Characteristics of Some Shorebirds for Which Polyandry  
Has Been Demonstrated or Suggested\*

	Female 3 per cent larger than male	Egg or clutch size reduced	Female dominant in courtship	Male does most incubating
American Jacana ( <i>Jacana spinosa</i> )	++	++	+	++
Pheasant-tailed Jacana ( <i>Hydrophasianus chirurgus</i> )	++	++	+	++
Spotted Sandpiper ( <i>Actitis macularia</i> )	+	+	+	+
Common Sandpiper ( <i>A. hypoleucos</i> )	+	+	+	+
phalaropes (three species)	++	++	+	++
painted snipes (two species)	++	+	+	++
Dotterel ( <i>Eudromias morinellus</i> )	+	+	+	++
Mountain Plover ( <i>Eupoda montana</i> )	—	+	—	—
Sanderling ( <i>Calidris alba</i> )	—	+	—	—

\*Compiled from Dement'ev *et al.*, 1969; Mackworth-Praed and Grant, 1962; Parmelee, pers. commun.; Ridgway, 1919; Witherby *et al.*, 1940; and personal observations. Plus marks indicate relative expression of the various characteristics; dashes indicate the lack of the characters mentioned.

### Summary

We studied the mating patterns of an individually marked population of Spotted Sandpipers (*Actitis macularia*) from 1970 to 1972 at a 6.8-hectare sewage lagoon in Itasca State Park, Minnesota, and an unmarked population in 1972 on a 1.6-hectare island in Leech Lake, Minnesota.

At Itasca, 12 females laid 19 clutches for 14 males. Only two females bred with a second male in a single year, yielding an average of 1.17 males per female. Seven clutches, 37 per cent, hatched; nine, 47 per cent, were destroyed by predators; and three, 16 per cent, were deserted. Surplus males were rare and were chased intensely by resident males.

Seven of 10 marked breeding males and four of seven marked females returned to breed the following year. Six of seven returning males and two of four returning females bred in the same territories where they last bred the preceding year. In three cases, both members of a pair returned and each time the old pairs were formed again.

Pair-bonds were formed in a matter of minutes, but once birds paired, there was no evidence of promiscuity. Following the laying of the third egg, we saw a marked sexual resurgence in females, whether they commenced incubation or not. Female incubation was highly variable depending on the stage of cycle, the individual concerned, and the weather. Replacement clutches were initiated an average of 5.3 days after predation or desertion.

Seven females bred with 10 males on Pelican Island in 1972, yielding an average of 1.43 males per female. The rate of predation was approximately 15 per cent, and clutch size was reduced by disturbance from fishermen during egg-laying. The high breeding density on the island led to late nesting, intense aggression, territorial instability, and the use of marginal nesting habitat.

The fact that Spotted Sandpipers have had a long association with heavy predation is indicated by their highly ritualized distraction display. Their colonization of temperate areas, however, increased the length of their breeding season. These factors, and food availability over a longer season, have led to the evolution of serial polyandry. During the evolution of serial polyandry, counter selection brought about certain compromises in the form of a slight increase in the ratio of the weight of the female to the weight of the egg, increased role of males in such stressful behaviors as incubation and brood-rearing, and possibly a delayed age at which females first breed.

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