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POLYANDRY IN THE SPOTTED SANDPIPER

HELEN HAYS

Polyandry, as it appears in ornithological literature, is one of those anthropomorphic misnomers which necessitates defining whenever it is used. In humans it literally means that a woman has many husbands at the same time, any one of which could be the father of her children. In birds, a polyandrous female may have many mates, all of which could contribute genes to each clutch of eggs. Until recently there have been no reports in birds of anything approximating this definition. However, Ridpath (1972) discusses breeding trios consisting of a female and two males in the Tasmanian Native Hen (*Tribonyx mortierii*). He recorded both males copulating at least once with the female in most trios.

Jenni and Collier (1972) described polyandry in a population of the American Jacana (*Jacana spinosa*) on a seven-acre pond in Costa Rica. They observed that one female copulated with three different males in a twenty-minute period, and another copulated with four different males in a single afternoon. Molnar (1950) reported more than one male cuckoo copulating with a female.

If the copulations reported in the above instances function in transferring active sperm to the oviduct of the female with ova ready to be fertilized, then several males could copulate successfully with a single female in a matter of minutes, hours, or even days, and the resulting clutch of eggs could be the combined effort of a kind of copulatory roulette. If, on the other hand, the observed copulations do not function in the above sense, the act itself could serve in establishing a bond between individuals, and could or could not help to coordinate their reproductive efforts for a later period when the copula-

Junior Editor's Note. Many ornithologists have focused in recent years on avian social systems, relating the disciplines of behavior and ecology in their field work. Two such studies appear here. I was excited to learn, when conversing with Helen Hays in November 1971, that in her study of Spotted Sandpipers on Great Gull Island, she had discovered serial polyandry. And I was elated when she consented to submit her work to *The Living Bird*, which she did in March 1972.

Early in the summer of 1972, while teaching at the University of Minnesota's Biological Station at Lake Itasca, I learned of Lewis Oring's work there on the same species — and that he, too, had found serial polyandry among his marked birds. He was acquainted with Miss Hays' study through an abstract she had submitted for a symposium to be given at the forthcoming meeting of the American Ornithologists' Union. I solicited Lewis Oring's paper in July. It seemed appropriate for *The Living Bird* to publish two papers on the mating system of the same species by two ornithologists carrying on independent studies in regions as far apart as Minnesota and New York.

tions would be functional. Although difficult to determine whether or not the copulations are functional, this seems to me a critical point in establishing that these species are polyandrous in the strict definition of the term.

Authors have also used the term polyandry when referring to females of a few families of birds which copulate and pair with a male for a matter of days, lay eggs, and then repeat this pattern with a number of males successively. This is often called serial polyandry.

Finally, the term is also applied in describing behavior of a normally monogamous species in which a female in one season has been noted to nest with two different males.

In rheas (*Rheidae*) observed in captivity, Steinbacher (1951) mentioned that a number of females mate with one male and all deposit eggs in one nest. The male then incubates; the females move on to another male. In certain species of tinamous (*Tinamidae*), as in the rheas, groups of females deposit in one nest eggs that only the male incubates. The females then disappear, presumably moving on to another male (Lancaster, 1964). In other tinamous, a single female may mate with a male and then move on to mate with another (Beebe, 1925; Schäfer, 1954). Seth-Smith (1905) noted that his captive tinamou females mated with more than one male. Hauth (1890) and Hoesch (1959), observing captive buttonquail (*Turnicidae*), noted that females laid eggs for a number of males successively. Hoffman (1949) found that a female Pheasant-tailed Jacana (*Hydrophasianus chirurgus*) might nest with as many as six males in one season. A female paired for a short period with each male, then left him to incubate the eggs while she moved on to the next male. Vernon (1971) mentioned polyandry in the Black Coucal (*Centropus grillii*). Rada-baugh (1972), in discussing polygamy in the Kirtland's Warbler (*Dendroica kirtlandii*), noted a single case of successive polyandry. Fraga (1972) reported one case of polyandry in the Bay-winged Cowbird (*Molothrus badius*), usually a monogamous species.

Unbalanced sex ratios in the field have led authors to hypothesize that females of some species nested with more than one male, but no detailed studies of these species are available. Such is the case with the Painted Snipe, *Rostratula benghalensis* (Baker, 1935; Cairns, 1940; Lowe, 1963; Pitman, 1912; Serventy and Whittell, 1962; Whistler, 1949).

In the plovers (*Charadriidae*), Nethersole-Thompson (1951, 1972, and in Bannerman, 1961) reports examples of polyandry in the Dotterel (*Eudromias morinellus*). Polyandry has subsequently been proved in the Dotterel in Austria and Finland.

Several authors have suggested that at least two of the three species of phalaropes (*Phalaropodidae*) may sometimes be polyandrous but, as pointed out by Hölin (1965), the evidence was indirect and not very convincing. Raner (1972), however, found polyandry in an individually color-banded population of the Northern Phalarope (*Lobipes lobatus*) in Sweden.

In this paper I discuss serial polyandry in a member of the Scolopacidae, the Spotted Sandpiper (*Actitis macularia*), based on the behavior of a small, individually color-banded population of this species that I watched on Great Gull Island, New York (72° 07' W Long., 41° 12' N Lat.), during the summers of 1970 and 1971.

Observations reported in the literature (Burger, 1968a; Knowles, 1942; Mousley, 1939; Nelson, 1930; van Rossem, 1925) provide a basis for the hypothesis that the male Spotted Sandpiper does much of the diurnal incubation

and brooding. Occasionally, authors reported two birds near nests with eggs or newly hatched young, but the role of the female after the eggs are laid is not described. I, therefore, made a particular effort to follow the females during the breeding season.

The breeding population in both years comprised 17 birds. In 1970, I found six females and 11 males breeding; in 1971, five females and 12 males nested. Most females paired successively with two or more males. Females left the males to incubate as soon as a clutch was complete, with the exception of the final clutch, in which females shared the incubation with the male, but left the care of the young to him.

Study Area and Methods

Study Area

Great Gull Island lies seven miles east-northeast of Orient Point, New York at the eastern end of Long Island Sound. It is half a mile long and a tenth of a mile wide at its widest point, has an area of 17 acres, and is the site of a large tern colony. Spotted Sandpipers nest in the grassy upland areas of the island.

In 1966, we set up a permanent grid on the island (Cooper *et al.*, 1970), dividing it into quadrats, 25 meters square. Nests mentioned in this paper are located by reference to the grid marker in the northeast corner of the quadrat in which the nest was found (Figures 1 and 2).

Determining Sex

Female Spotted Sandpipers are slightly larger than males and, in most cases, have more spotting. The first year females, however, are lightly spotted and indistinguishable from males (Theodora Nelson, pers. commun.). Wing measurements of the sexes overlap (Ridgway, 1919). Due to the problem of distinguishing males and females in the field, I determined the sex of the birds, except where noted, by observing copulation in individually marked birds.

Color Banding

With the help of Donald Cooper and Frederick Schaeffer, I began color banding Spotted Sandpipers in 1967 and 1968. In late May and early June, we mist-netted Spotted Sandpipers in the meadow sections of the island and trapped them on nests. We gave each bird an individual color combination composed of three colored plastic bands and a U. S. Fish and Wildlife Service band. Most of these birds were males.

In 1969, with the help of Grace Donaldson, I tried to trap and individually color mark every Spotted Sandpiper on the island during the last two weeks in May. I felt that by trapping all individuals before they began to nest we could mark enough females so that, in 1970, we could observe any of those that returned. We used treadle traps and funnel traps, baited with maggots from rotting seaweed and set at the tideline on patches of seaweed where small groups of Spotted Sandpipers fed and postured. We also set treadle traps along the paths of the upland sections of the island where the species foraged at high tide. The method worked. Four of the six females, banded in 1969, were back in 1970.

Spotted Sandpipers nesting on the island in 1970 had been color banded a number of years previously: one male, five years before; two males, four;

1970 FEEDING AND DISPLAYING RANGES OF FEMALE
SPOTTED SANDPIPERS ON GREAT GULL ISLAND

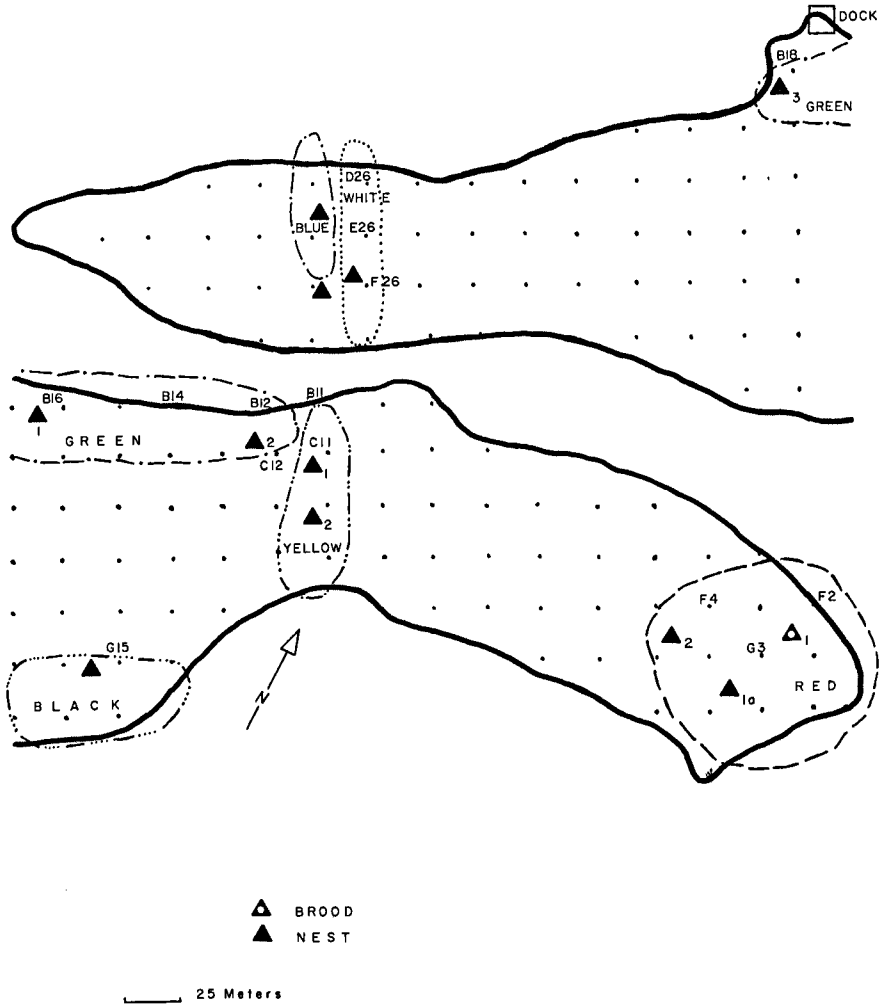


Figure 1. The feeding and displaying ranges of the six female Spotted Sandpipers that nested on Great Gull Island in 1970. A grid divides the island into quadrats 25 meters square. Grid lines running north-south are numbered 1-30 from east to west. Grid lines running east-west are marked B-G from north to south. Females are identified by a color and their ranges marked with dotted, dashed, or dotted and dashed lines. The nests, broods, or nests and broods of each female are numbered consecutively within her range. Female Red's third nest is numbered 1a because she renested with her first mate after he lost his first brood.

1971 FEEDING AND DISPLAYING RANGES OF FEMALE
SPOTTED SANDPIPERS ON GREAT GULL ISLAND

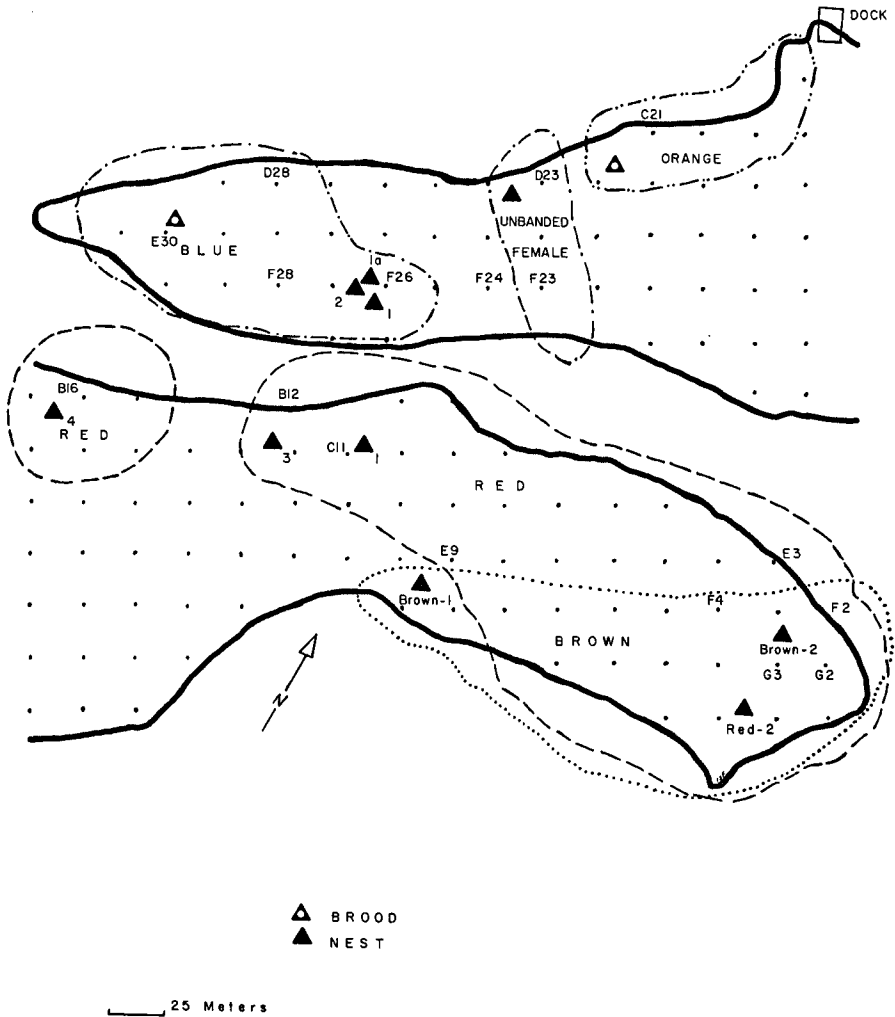


Figure 2. The feeding and displaying ranges of five female Spotted Sandpipers that nested on Great Gull Island in 1971. A grid divides the island into quadrats 25 meters square. Grid lines running north-south are numbered 1-30 from east to west. Grid lines running east-west are marked B-G from north to south. Females are identified by a color or are marked unbanded, and their ranges are marked with a dotted, dashed, or dotted and dashed line. Nests, broods, or nests and broods of each female are numbered consecutively within the range of the female. In the case of female Blue's third nest, it is numbered 1a because she re-nested with her first male after he lost his first brood. Late in the season we found a brood near grid marker E-30 with no female associated with it. Although it was within Blue's feeding and displaying range, I cannot assign it to her.

three males, three; three males and four females, two; two males and two females, less than one. In 1971, the length of time individuals had been banded stood as follows: one male, six years; two males, five; three males, four; two males, one female, three; one male, one female, two; three females less than one. One male in 1971 is omitted because his partial combination prevented me from determining when he had been banded, and one male was unbanded.

Daily Observations

In 1970 and 1971, I was able to follow most of the color-banded Spotted Sandpipers from the time they arrived in early May until 10 June. Reading color combinations with a Bausch and Lomb Zoom Balscope, 15 to 60 \times , I censused the birds daily between 08:00 and 10:00 hours and between 16:00 and 18:00 hours and made additional observations throughout the day. My periods of observation were determined in part by work in the tern colony, the main project during both summers. Regular observations of the Spotted Sandpipers terminated toward the end of May when most of the terns began nesting.

In 1967, Grace Donaldson and I circled the island in a rowboat on the following days: 22, 30 July; 5, 6, 8–11, 19, 20, 26, 27 August; and 2, 3, 9 September. Each day we read bands with Bushnell 9 \times 35 binoculars and recorded the color combinations of the Spotted Sandpipers remaining on the island.

Results

Arrivals

In both 1970 and 1971, I first checked for Spotted Sandpipers on Great Gull Island on 1 May. Females and males arrived at about the same time. In 1970, for example, I saw three banded males and three banded females on 4 May. In 1971, the first banded male arrived on 2 May, three banded males and a female appeared on 8 May, and the last banded birds arrived on 5 June.

Incubation

I computed the beginning of incubation at 20 days before the hatching date. The literature contains a number of different incubation periods for this species. W. M. Tyler (*in* Bent, 1929) gave 15 days. Burger (1968a) reported 14–18 days; but on recalculating, Burger (1968b) gave a range of 19–21 days. Knowles (1942), Miller and Miller (1948), Mousley (1939), Nelson (1930), and Preston (1951) gave incubation periods for Spotted Sandpipers ranging from 20–24 days.

One clutch that was incomplete when I found it hatched 21 days after the laying of the fourth egg. In 1970, the clutch of one female hatched 26 days after I flushed her first mate from four warm eggs. Only 25–30 meters east of this nest, the same female displayed with her second male. I saw the second male chase the first one on two occasions when the first approached the calling female after he began incubating. The proximity of the female and her second mate to the first nest may have delayed the first male's settling down to steady incubation, resulting in a longer incubation period.

Nest Histories of Females in 1970 (Table 1)

In 1970, I followed one female, referred to as "Green" because of the color of her band. She nested with three different males successively and the detailed notes on her behavior show the rapidity with which pairs form and dissolve

TABLE 1
Nest Histories of Spotted Sandpipers on Great Gull Island, 1970

Female	Male	Hatching	Evidence for pair-bond			
			Copulation	Feeding*	Trapped on nest	Flushed from nest
Green	G-m1**	13-14 June	12 May			
	G-m2	19-20 June			Female 28 May Male 19 June	
	G-m3	2 July				Male and female
Red	R-m1	14 June		X		
	R-m2	30 June		X		
	R-m1a	15 July		X		
Yellow	Y-m1	11 June	15 May			
	Y-m2	19 June			Female 15 June	Male
White	W-m1	13 June				Male and female
Blue	B-m1	19 June		X		
Unknown		9 June				
Unknown		2 July				

*Birds fed together at least 8 days.

**Males designated by mate's color and his position in series of mates. G-m1 indicates the first mate, in 1970, of the female with green color bands.

once the female has completed her clutch. Briefer comments on five other females follow.

I observed Green and her first mate, Green-m1, copulating on 12 May 1970, and flushed Green-m1 from four warm eggs on 18 May.

On 19 May, Green ran along the path behind the dock — D-18 — calling. She then flew east to the beach, a short distance from her first nest, and landed on the shore — B-14. In the afternoon, she flew and called near another male, a bird which I had seen daily since 11 May standing on the rocky shoreline — B-11, B-12 — and the one that was to be her second mate, G-m2. On 20 May, Green and Green-m2 postured and called along the shoreline east of the dock, and on 21 May, Green-m2 tried unsuccessfully to mount Green.

From 22 through 24 May, between 14:00 and 18:00 hours, I watched the beach area where I had seen the two displaying. On 24 May at 17:00 hours, Green approached a patch of beach pea (*Lathyrus maritimus*). At 17:05 she went into the beach pea and reappeared at 17:23. At 17:28, I asked Grace Donaldson to check the spot where Green emerged; she found one warm egg in a shallow depression. The nest was not checked on 25 May, but at 05:30 on 26 May there were two cool eggs in the nest. On 27 May, between 05:30 and 08:00, I found a third egg in the nest. On 28 May at 05:23, there were still only three eggs, but they were warm for the first time; at 09:30, when I trapped

the female on the nest, there were still only three. On 29 May, I found a fourth egg. The clutch was complete.

The day that the fourth egg appeared in Green's second nest, I saw Green running and calling along the path behind the dock. On 2 June, Green and an unbanded bird appeared to be foraging in an area used by Green's first mate for feeding when he came off the nest. On 2 June, between 07:30 and 08:15, I watched Green's first mate, Green-m1, dart toward the unbanded bird accompanying Green. The unbanded bird leapt into the air and landed near Green. With that, Green chased Green-m1 away.

On 8 June, I flushed Green from a nest containing two eggs, and on 11 June, I found four eggs in the nest. Green shared the incubation of her third and last clutch with an unbanded male, G-m3, which I later trapped. For the first three to four days after the clutch was completed, I flushed Green from the nest at different times during the day. From the fifth day until 1 July, the day before the young hatched, I flushed her from the nest only at 05:00 hours. At other times of the day G-m3 flew from the nest. This suggests that, at this nest, the male incubated during the day and the female at night.

Of the other five females that nested on the island in 1970, one female, "Black," was unsuccessful. I found her eggs cold and pecked open. The female "White" nested with only one male; I flushed both birds from the nest throughout the incubation period, and saw both birds with the brood for the first two days after hatching; after that only the male attended the brood. Two other females, "Yellow" and "Red," each nested with two males successively. Red's first mate, R-m1, lost his brood and Red nested with him again. This was the third clutch she produced and the second clutch that her first mate incubated. I trapped the sixth and last female, "Blue," on a nest the day before the eggs hatched. I think that this was her second clutch, but I am not sure because I did not observe her earlier in the season when she might have associated with another male.

Nest Histories of Females in 1971 (Table 2)

In 1971, only Red and Blue returned to the island. Both completed their first clutches of eggs within eight to 10 days of their arrival. Red paired successively with four males on the eastern half of the island — eight, seven, and seven days apart. Three of these males nested on the island with other females in 1970. The nest sites for each male in both years were remarkably close together, suggesting that males may influence the choice of site. Red's first mate, R-m1, nested in the east meadow — C-10, 11 — and the site of his 1971 nest was only three meters from the 1970 site. Red's third mate, R-m3, incubated a clutch of eggs in 1971 only one meter from his 1970 nest site. Red's fourth and final mate, R-m4, incubated a clutch on the side of a hill, two meters from the spot where he nested in 1970. Red's second mate, also her second mate in 1970, incubated in 1971 at a spot five meters southwest of Red's third nest in 1970.

Nesting and Feeding Ranges of Red and Blue Contrasted

The feeding and nesting ranges of Red and Blue illustrate the differences in behavior that can exist within a species.

Red nested throughout the eastern half of the island (Figure 2). Her nests were widely spaced, the two closest being some 25 meters apart. During the week that she was with any one male, she spent time feeding both in the area

Spotted Sandpipers, *Actitis macularia*. Painting by Christopher Pineo.



where he waited and later incubated, and also at the extreme eastern end of the island.

Blue remained throughout the breeding season at the extreme western end of the island. Her nests were remarkably close together, all three within seven meters of one another. She fed almost exclusively at the western point, occasionally moving east a short distance along the north and south shores, D-28 and F-26. Males fed and displayed with her at the western point. The only time I saw Blue away from the western tip of the island was when she moved 175 meters east and displayed near a male that waited on the shore.

The interactions of Red and Blue with Red's fourth mate, Red-m4, shows the difference in the behavior of the two females. The female that R-m4 paired with in 1970 did not return in 1971. I first saw him in 1971, feeding and displaying near Red and her first mate on the pavement west of the dock, D-19. I then saw Red and R-m1 175 meters east of the dock, C-11, while R-m4 remained near the dock, B-16, calling. Occasionally, he flew to the south shore

TABLE 2
Nest Histories of Spotted Sandpipers on Great Gull Island, 1971

Female	Male	First sighted	First banded ¹	Hatching	Evidence for pair-bond		
					Copulation	Feeding ²	Flushed from nest
Red		8 May	X				
	R-m1 ³	7 May	X	11 June	13, 15 May		
	R-m2		X	19 June	20 May		
	R-m3	15 May	X	26 June	2, 3 June		
	R-m4	8 May	X	3 July			Male and female
Blue		10 May	X				
	B-m1	2 May	X	12 June		X	
	B-m2	15 May	X	1, 2 July	4, 7 June		
	B-m1a			12-13 July		X	
Brown			26 May				
	Br-m1	17 May	X	25 June		X	
	Br-m2	5 June	X	15 July		X	
Orange			19 May				
	O-m1 ⁴	21 May		5 July ⁵		X	
Unbanded ⁶	M(F-23)	14 May	X	6 July			
Unknown	M(E-30)	5 June	X	23 July ⁵			

¹ X indicates bird banded prior to 1971.

² Birds fed together at least eight days.

³ Males designated by mate's color and his position in series of mates. R-m1 indicates the first mate, in 1971, of the female with the red color band.

⁴ Unbanded male identifiable by pattern of spotting.

⁵ Newly hatched brood; no nest found.

⁶ Female unbanded; mate identified by grid location of his area.

on the eastern end of the island, calling, but he always returned to the dock area.

On 17 May, he accompanied an unbanded bird near the dock. On 22 May, I trapped an unbanded bird — judged to be a female on the basis of spotting, wing measurement, and behavior — on the dock and color banded her “Blue-white.” R-m4 fed with Blue-white during 22 and 23 May, after which I never saw her again.

From 24 May through 4 June, I observed R-m4 daily at the western end of the island, feeding near Blue. Blue had completed her first clutch of eggs on 22 May, and her future second mate, B-m2, had been feeding on the point near her until 21 May when he too disappeared. R-m4 remained near Blue except for a few occasions when he flew to the area east of the dock. On 28 May, R-m4 mounted Blue but did not attempt copulation.

On 4 June, B-m2 was back on the point at the western end of the island. R-m4 chased him and Blue chased R-m4, whereupon R-m4 left the area. B-m2 copulated with Blue later that morning, and by 10 June he was incubating a clutch of four eggs.

On the morning of 5 June, I saw R-m4 flying and calling over the meadow at the western end of the island. A second bird was present, but I could not see whether it was banded. In the afternoon of 5 June, R-m4 stood on the cistern just east of the dock and below him Red stood on a log (B-16).

During the following week Red and R-m4 fed together and postured. By 12 June, they had begun to share the incubation of Red's fourth and final clutch of eggs for 1971.

Observations of the other Spotted Sandpipers that nested on the island in 1971 are much less complete than those for Red and Blue; their nest histories appear in Table 2. The banded birds, associated with the last three nests to hatch on the island, were seen for one month before they began nesting, contrasting sharply with the rapidity with which Red and Blue completed their first clutches. Orange, for example, paired with an unbanded male and completed her clutch 26 days after I trapped her. I saw the banded males at F-23 and E-30 almost daily for 32 and 27 days, respectively, before they began incubating.

Aggressive Behavior by Females

Early in the season I watched groups of Spotted Sandpipers chasing one another and posturing. Often the most aggressive birds appeared larger and more spotted, and I guessed they were females. In 1971, I saw several chases by banded birds early in the season in what appeared to me to be two different situations.

In the first instance I saw Red on 8 May, Blue between 15–20 May, and Brown on 5 June posturing with, and sometimes chasing, two banded males. In all but one instance these females later nested with these males. The exception was a one-legged male, one of two that Brown chased on 5 June and with which she fed later in the season. I do not believe they nested. All chases took place at the time the banded birds were first seen on the island, and in areas where the males had nested before. These chases may serve to establish a kind of bond between a female and the several males with which she will eventually pair.

In a second situation of aggressive chasing by a female, I saw a chase that suggested that the female patrolled the entire area where her first three nests were located (Figure 2). On 20 May at 18:30 hours, I watched Red, now paired

with her second mate, fly across the meadow from the south side of the island, E-9, to the north side, B-10, and land on the path near her first nest. She chased an unbanded bird, which I judged on the basis of size, spotting, and behavior to be a female, along the path. The unbanded female had been posturing near the male which was to become Red's third mate. The future R-m3, as well as R-m1, joined her in the chase. At that moment, a person walked through the meadow, but, before the birds scattered, I had the impression that Red was chasing the unbanded female out of the area. The observation suggests that females, by patrolling and defending large areas, keep potential mates isolated.

Posthatching

In late July and August of 1967, we checked Spotted Sandpipers to determine how long the adults and young remain on the island. No adults from nests that hatched in June were present. One male, from a nest that hatched on 4 July, defended the nest site through 30 July. A female from a nest that hatched 16 July had molted and had lost the spotting on her breast by 8 August. She remained through 20 August.

Of the 34 young Spotted Sandpipers, banded on the island in 1967, we recorded 10 later in the season when they were no longer associated with an adult: two up to four weeks after hatching; two up to five weeks after hatching; three up to six weeks after hatching; and three up to eight weeks after hatching. We saw many of these birds between 22 July and 20 August on more than one day, some on as many as eight days. In all but one instance, the birds foraged along the shore near their hatching sites, seeming to remain within limited sections of the shoreline, and some defended these areas against others of their species.

Discussion

My observations of females Orange, Red, and Blue, as well as their mates, suggest that birds returning to the island nest more quickly than birds coming to the island for the first time. Red and Blue, females that had nested on the island before, completed their first clutches within eight days of their arrival; Orange took 27 days after I banded her to complete her clutch.

The nest histories of Red and Blue suggest that the association of the male with a particular site and the female with a larger area that includes a number of sites may be more critical for rapid pairing than the bond between any particular male and female. The three males that nested for the first time with Red in 1971 nested at almost the same sites in 1970, but with different females. At times, however, the attachment to a site may inhibit pairing away from that site. Thus, the attachment of female Blue and male R-m4 to different areas may have prevented them from pairing with one another. And the attachment of R-m4, as well as the male at F-23, to sites that did not fall within the range of a territorial female, appeared to isolate them, which might function to delay pairing.

A lessening of importance of the pair-bond and the increasing importance of attachment of individuals to particular sites or areas could serve as an adaptation facilitating the development of serial polyandry as is seen in the Spotted Sandpiper, as well as polygyny in other species.

The variability in pairing behavior of female Spotted Sandpipers suggests that this species still may be evolving its polyandrous form of nesting behavior.

Females nest with different numbers of males. White, in 1970, nested with only one male and shared the incubation of the clutch with him. Most of the other females, however, did not incubate until their second, third, or fourth clutch. It is evident that since a number of males incubated and took care of the young without the female's help, her assistance in parental care is not necessary for successful reproduction. That she sometimes does so suggests that a tendency to incubate still exists.

In the Scolopacidae, there is a widespread tendency for reversal of sexual roles, and, in quite a few species, males take over much of the incubation and care of the young. In most of the latter instances, the females tend to be larger and occasionally differ in color with the most extreme examples in the related phalaropes and the painted snipes.

In discussing sexual dimorphism, Amadon (1959) began with Darwin's theory that competition for mates results in one sex, usually the male, being larger than the other. Amadon also noted that in some groups, such as the shorebirds, the females may be larger and more brightly colored because they compete for mates.

Selander (1966) discussed sexual dimorphism in certain species as an adaptation to different niches. Pitelka (1950), when reporting on sexual dimorphism in the Long-billed Dowitcher (*Limnodromus scolopaceus*), in which the female is larger and longer billed than the male, suggested that the female's longer bill gives her an advantage by enabling her to feed in deeper water. On Great Gull Island I can see no difference in feeding areas between the male and female Spotted Sandpiper, and I assume that both sexes eat the same organisms where they do feed, as would be expected, since their bills are about the same length (Ridgway, 1919). The tendency toward sexual dimorphism in this species, from my observations thus far of birds on the breeding ground, suggests competition for mates rather than an adaptation of the sexes to different niches as the selective force influencing sexual dimorphism.

Mayr (1939) suggested that the primary and secondary sex ratios of certain species may be unequal, creating an imbalance in the tertiary sex ratio. Orians (1961) suggested that primary and secondary sex ratios of Red-winged Blackbirds (*Agelaius phoeniceus*) are equal, but that ecological factors have caused the delayed maturation of males, thus creating an imbalance in the tertiary sex ratio.

The primary and secondary sex ratios for the Spotted Sandpiper are not known. The multiple clutches of the females, however, may result in an imbalance of sexes in favor of the males. On the basis of the limited numbers of birds in two years, proportionately more males than females returned to nest in 1971. If, in the course of future observations, this difference is shown to be more than fortuitous, it might suggest that multiple clutches is a factor producing an imbalance in the tertiary sex ratio.

Within the Scolopacidae there is a tremendous variation in sexual behavior. The promiscuous Ruff (*Philomachus pugnax*) and polyandrous Spotted Sandpiper exemplify two extreme forms of behavior. Interestingly, both of these forms are characterized by sexual dimorphism, an imbalance in the tertiary sex ratios, and a strong attachment by the males to particular areas. In the Ruff a number of males remain, when courting, in very restricted areas and the females come to the males in these areas to mate. In the Spotted Sandpiper the males become attached to particular nest sites. The females

may defend areas that include a number of sites or move freely from one site to another following the completion of a clutch.

With the decrease in importance of the pair-bond and an increase in attachment to particular areas, polyandry, polygyny, or promiscuity develops. Determining the factors that influence this development is perhaps not possible, but a closer look at behavior in some of the monogamous members of this group might prove useful. In Temminck's Stint (*Calidris temminckii*), Hilden (1965) reported that the female regularly lays two clutches of eggs; the male incubates the first; the female the second. Parmelee (1970) suggested a similar pattern for the Sanderling (*Crocethia alba*). The production of multiple clutches, as well as the reversal of sexual roles, may represent behavioral and physiological adaptations essential for the evolution of polyandry. The behavior of other forms, not yet described, may prove to represent intermediate behavioral stages from which polygynous forms of behavior have evolved. The Scolopacidae, more than any other family, offers an excellent opportunity to learn about the development of polygynous, polyandrous, and promiscuous forms of sexual behavior.

Summary

During May and June of 1970 and 1971, I observed an individually marked population of Spotted Sandpipers (*Actitis macularia*), comprising 17 birds on Great Gull Island, New York. Females often nested with a number of males successively.

In 1970, six females initiated 12 nests. The females nested with males as follows: two were monogamous; two females each formed pair-bonds with two males successively; one female nested with three males successively. In addition, one nest was destroyed and the female did not nest again; one female nested with two males, but her first male lost his brood and she nested with him a second time — her third clutch and his second; and finally, one nest hatched at which no female had been seen.

In 1971, five females initiated 12 nests; each female nested with the following numbers of males: two females remained monogamous; two females each had two mates; one female mated successively with four males. In addition, one nest hatched, and I had seen no female near it. Again, one male lost his first brood and his female nested with him again — her third clutch, his second.

Females shared the incubation of the final clutch with the male; but on previous nests, the males incubated and reared the young.

Of 34 young Spotted Sandpipers banded on Great Gull Island in 1967, 10 were seen later in the season, three up to eight weeks after hatching.

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