

## Density, Habitat, and the Mating System of the Western Sandpiper (*Calidris mauri*)

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*Summary.* The hypothesis that intense predation, variable food availability, and increased social interactions in high density populations have been important factors promoting the evolution of polygynous and promiscuous mating systems in certain Calidridine sandpipers (Holmes and Pitelka, 1966) is examined in breeding populations of the Western Sandpiper (*Calidris mauri*) in subarctic Alaska.

Western Sandpipers breed in a habitat consisting of a complex mosaic of wet low-lying marshes and relatively well-drained, heath-covered tundra. They defend small territories and nest on the latter, while some feeding also occurs there. Most foods however are obtained off territory in the wet marshes and along the shores of lakes, rivers and sloughs.

Densities in the nesting areas ranged from 132–196 pairs/40 ha at the base of a low range of hills to 200–300/40 ha on hummocks surrounded completely by marsh. These densities, the highest reported for a Calidridine sandpiper, are relatively constant from year to year.

The mating system of the Western Sandpiper is monogamous, both sexes incubate and care for young. Correlated with a strong single pair-bond and stable populations is a strong tendency to return to the same site. Of sandpipers marked, an average of 57.6% of males and 48.8% of females returned in succeeding years, frequently to the same territory or its immediate vicinity. Of the pairs returning to the study area in subsequent years, 61.5% reunited.

The restriction of nesting activities to heath tundra is considered to be a result of the protection it provides for nests. With the separation of nesting and feeding areas and with relatively abundant food sources that are not significantly affected by weather, a large nesting area is not required, allowing high densities of Western Sandpipers to occupy the patches of heath-covered tundra. In this ecological context, the high intensity of social interactions has not resulted in the evolution of a nonmonogamous mating system. Indeed, the increased protection afforded offspring by the presence of both parents is probably the most important selective force promoting the evolution of the monogamous mating pattern in Western Sandpipers.

### Introduction

Within the last decade there has been renewed interest in the factors influencing the social groupings of animals, especially birds (Orians, 1961, 1969; Crook, 1964, 1965, 1970; Verner, 1964; Verner and Willson,

1966; Lack, 1968; and others). The main thrust of recent investigations has been to demonstrate that social structure and its components (e.g. territoriality, pair-bonds and mating systems, patterns of parental care, flocking, and sociality) are adaptive characteristics of a species' biology and can best be interpreted through analyses of the behavior and ecology of individual populations in their natural environments.

The ecological factors influencing the evolution of mating systems, however, are not well understood. In a review of avian breeding patterns Lack (1968) indicates that approximately 90% of all bird species are monogamous, with the remainder being polygynous, polyandrous, or promiscuous. Verner and Willson (1966) show that polygyny is more frequent among bird species occupying two dimensional habitats, such as grasslands or marshes, in which food resources are concentrated into a narrow plane and in which potential areal differences in food availability among bird territories exist. As a result more than one female might choose to pair with a male on the better territory, even though this might form a polygynous association. More recently Orians (1969) has extended this idea and proposed a generalized model relating the evolution of polygyny to increased reproductive success of females choosing males on the best quality habitat even though these males may already possess one or more mates. Habitat quality in these author's considerations refers to adequate nesting sites, food abundance, and other features affecting reproduction and survival.

From studies of the breeding and social systems of sandpipers (Calidridinae) nesting on high arctic tundra, Holmes and Pitelka (1966) and Pitelka, Holmes, and Maclean (MS) proposed an hypothesis relating the type of mating system to the ways in which the species exploit the arctic environment. The basic features of the model follow.

The environmental factors most influential on sandpiper breeding systems are the geographic and seasonal variations in the timing of snow melt and especially the abundance of food resources. Both vary markedly and unpredictably with changes in the rigorous and severe arctic weather (Holmes, 1966a, b). Such variations in habitat quality have generated two major adaptive responses among the sandpipers, one promoting a monogamous mating system, the other polygynous or promiscuous ones.

Those species with monogamous pair-bonds, such as *Calidris alpina*, are widely spaced on relatively large territories in which feeding and nesting take place. In these, sufficient food is available for each pair and their offspring in the event of a food shortage. The nests are widely dispersed, reducing the probability of predation. The monogamous pair-bond is adaptive because of the increased care given to the nest and young by both parents.

The evolution of non-monogamous mating systems in certain other species, such as *C. melanotos*, *C. fuscicollis*, and *Tryngites subruficollis* in North America, is related to the high density of their populations which occur in localized areas of high quality habitats. With dense groupings of such ground-nesting birds with relatively exposed nests, predators might be attracted, resulting in increased nest destruction and loss of young. There is thus a selective advantage for only one adult to be present at the nest, thereby reducing the nest's conspicuousness to predators. Furthermore, with food abundance on high arctic tundra being lowest and most variable in mid summer before the period of sandpiper hatching (Holmes, 1966a, b), it is adaptive for one adult to depart from the tundra by early July, and to move south to localities where the food supply is greater and more dependable.

If these factors operate in this way and the male is emancipated from nest duties, his primary remaining function would be to fertilize the eggs. He could then spend more time in display, which might result in increased competition for females. This would lead to the evolution of increased sexual dimorphism which would further facilitate mate attraction and faster mating. In addition, the heightened social interactions among individuals in these dense populations would provide greater opportunity for males to encounter and court more than one female, thus enhancing the possibility of polygynous or promiscuous matings.

In contrast to the breeding systems of the species described above on which the model was based, the Western Sandpiper (*C. mauri*) had been reported to occur in dense populations in western Alaska (Brandt, 1947) but from indirect evidence appeared to be monogamous. The present study therefore was designed to examine the relationship between density and the mating system in this species. The results, presented here, provide a test of the proposed model and further insight into the factors influencing the evolution of sandpiper mating systems.

### Breeding Distribution and Study Area

The breeding range of the Western Sandpiper is principally along the west coast of Alaska, with a small breeding population located in easternmost Siberia (Kozlova, 1962). Within Alaska, the species breeds in tundra habitats, from the mouth of the Kuskokwim River (59° N Lat.) north to the vicinity of Point Barrow and Camden Bay (71° N) (Gabrielson and Lincoln, 1959). The central and major parts of the breeding range, however, are the Yukon-Kuskokwim Delta, an area about 323 kilometers square, and the tundra near the coast north of the

Delta, extending to Nome and Cape Prince of Wales on the Seward Peninsula.

This study was conducted in the summers of 1966 through 1969 in the west-central portion of the Delta, along the Kolomak River (61° 31' N; 164° 50' W), approximately 30 km northeast of Hooper Bay and about 16 km inland from the Bering Sea. The main study area was located at the base of the south slope of the Askinuk Mountains, a low isolated range of hills (highest elevation, 745 m) along the Kolomak River. A 10 ha census plot was established on a level bench of heath tundra where it meets and interdigitates with low-lying marsh tundra. Another study plot, 5 ha in area, was located on the mountain slope of nearby Kikuktok Mountain at an elevation of 150 m and about 2 km away from the wet marsh. Information on the occurrence and habitat utilization of Western Sandpipers was also obtained from visits to Hooper Bay and Old Chevak, and from Dr. C. J. Lensink who was conducting extensive waterfowl nesting surveys from the air and on the ground over large portions of the Delta.

In three seasons (1966 through 1968) the sandpipers were censused by standardized procedures (see Holmes, 1966a) several times per week from mid May through late June; during the censuses territorial boundary conflicts and observations of individually marked birds were recorded on a gridded map. All or most nests on the plot were found, and in the summers of 1967 to 1969 most adult sandpipers on the main study area were captured and marked for individual identification. This was essential for sorting out territorial and mating relationships and for providing data on site tenacity and mate faithfulness.

### Habitat

The Delta consists of essentially flat terrain, with a few isolated hills and low ranges of mountains. It is dotted with numerous lakes and ponds and is transected by many rivers and sloughs (Fig. 1). The latter connect to the larger Delta river channels, and all fluctuate with the tide, even many miles inland from the sea. With particularly high, storm-driven tides which occur at most once or twice a year, usually in the late fall, much of the low-lying tundra is covered with water.

In the spring and early summer when the sandpipers are breeding, water covers perhaps 50% or more of the Delta surface. The remaining areas can be divided into two major habitat categories on the basis of vegetation and drainage. The low-lying wet tundra is poorly drained, contains numerous ponds and lakes, and is vegetated mainly by grasses (*Elymus*, *Poa*) and sedges (mostly *Carex aquatilis* and *Eriophorum* spp).

Within these marshes there are raised and slightly better drained sites ranging in diameter from 1 m to several hectares (Fig. 2). Long



Fig. 1. An aerial view of the Yukon-Kuskokwim Delta, about 20 km east of Hooper Bay, Alaska

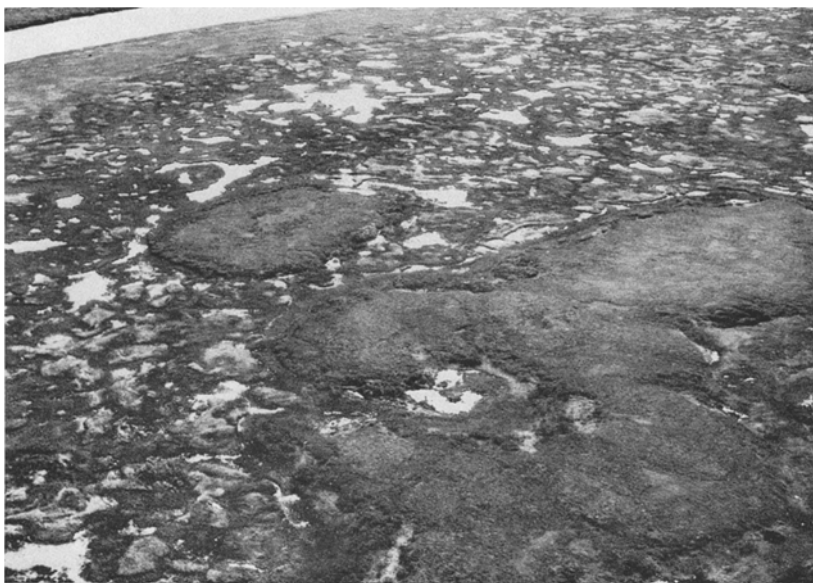


Fig. 2. "Islands" of dwarf shrub-heath tundra surrounded by marsh, Yukon-Kuskokwim Delta, Alaska

ridges extending several km or more also occur. These hummocks, ridges and the better drained slopes of the hills are vegetated with mosses, lichens, and plants normally characterized as representing dwarf shrub-heath tundra (Britton, 1957). The main low-growing woody plants consist of one or more species of *Betula*, *Salix*, *Empetrum*, *Arctostaphylos*, *Vaccinium*, and *Rubus*. In addition various herbs, grasses and sedges also occur commonly. This heath tundra is the nesting habitat for Western Sandpipers, while both the marsh and heath sites are used as feeding areas. The only other common and widespread Calidridine sandpiper on the Delta is the dunlin (*Calidris alpina*) which occurs exclusively in the low-lying marshy habitats (Holmes, 1970). Other wader species nesting in the heath tundra are the Black-bellied Plover (*Squatarola squatarola*), Northern Phalarope (*Lobipes lobatus*), and the Bar-tailed Godwit (*Limosa lapponica*).

### Dispersion and Density

The dispersion pattern of breeding Western Sandpipers is directly related to the occurrence of the dwarf shrub-heath tundra. Extensive bird population surveys on the 720 000 ha Clarence Rhode National Wildlife Range and surrounding areas on the Delta by U.S. Fish and Wildlife Service personnel indicate that Western Sandpipers are common wherever slightly elevated, better-drained, heath-covered tundra occurs, with a trend toward denser populations in the western part of the Delta (Lensink, pers. comm.). Since this nesting habitat is distributed irregularly, i. e. on small to large islands surrounded by wet marsh, along elevated ridges, and on the hill slopes, the overall distribution of Western Sandpipers on the Delta is clumped, population units occurring on most such patches of heath tundra.

At the Kolomak study area, Western Sandpipers nest from the upper slopes of the hills down to the edge of the flat marsh and within the marsh on patches of heath tundra larger than 0.2 ha in area. Westerns occupy these sites from the time of their arrival in mid to late May until after the young hatch about a month later. Nests are placed on the heath tundra, usually under a dwarf birch (*Betula nana*) where they are well camouflaged and difficult to find.

Within the heath tundra habitat, the nesting populations of Western Sandpipers are regularly dispersed (Fig. 3), as a result of a strongly developed territorial system. Upon arrival on the tundra male Westerns establish centers of activity which they defend against conspecific males and advertise by species-specific displays (Brown, 1962; Holmes, MS). These territories are small, ranging in size between 0.2–0.3 ha (Table 1; Fig. 3). Display activity and chasing by males are greatest early in the

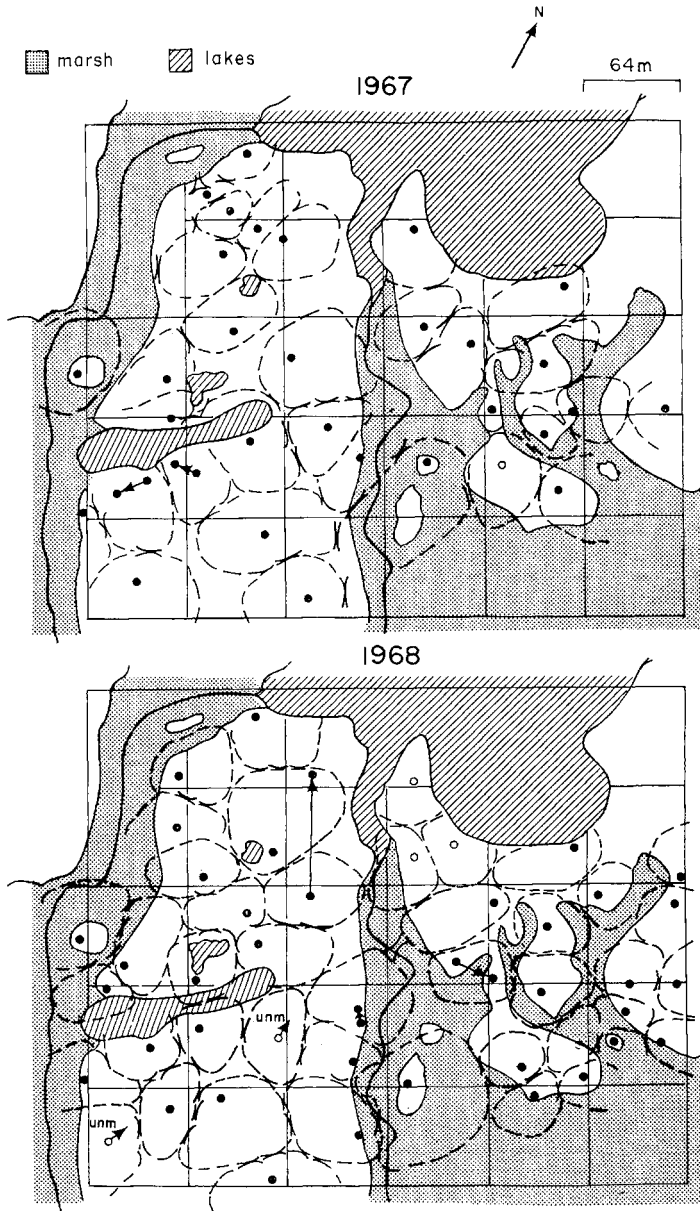


Fig. 3. Spacing of male Western Sandpipers in two summers on the main study area, Kolomak River, Alaska. Paired lines represent observed territory boundary contact points between adjacent males; broken lines approximate territorial boundaries. Solid dots represent location of nests found; open circles indicate nests not actually found but known to be present in that general vicinity. Arrows between two nests indicate sites of second nesting following failure of the first. Each square of the grid equals 0.4 ha (1 ac). "Unm ♂" refers to the territory of an unmarked and unmated ♂

Table 1. *Densities and territory sizes of Western Sandpipers on the main study area, Kolomak River, Alaska*

	No. pairs/ 7.2 ha <sup>a</sup>	No. pairs/ 40 ha	Aver. territory size (ha)/pair
1966	24	134.4	0.3
1967	31	173.6	0.23
1968	35 <sup>b</sup>	196.0 <sup>b</sup>	0.21
1969	24 +	134.4 +	0.3

<sup>a</sup> 10 ha study area, contained 2.8 ha of marsh tundra and lakes, which were not occupied by Western Sandpipers.

<sup>b</sup> 2 additional unmated males that were present on the plot are not included in these figures.

nesting season and decline once eggs are laid, although aggressive encounters continue until late in the incubation period. The decline in defense during the nesting season is due in part to the males being absent from their territories when they go off to other areas to feed (Holmes, 1972).

The adult Westerns obtain some food in the vicinity of their nests but more commonly, especially as the time of hatching approaches, in communal feeding areas along the shores of lakes, rivers, and sloughs in the low-lying marshes. Birds nesting on the hill slopes also fly to the marshes to feed. From the mountain-side census plot, Westerns were seen flying about 2 km down to the wet tundra; they would usually return to their territories within an hour and continue defense, courtship or incubation activities.

After the young fledge, Western Sandpipers leave the nesting habitat and move into the marshes. At this time they usually frequent the margins of lakes and rivers where they prey on insect larvae and other invertebrates. They then gradually shift to the Bering Sea coast, from which they move south on migration in late July and early August (Holmes, 1972).

The densities of Western Sandpipers in the nesting habitat are relatively high. On the main study area during the four years, the numbers ranged from 24 to 35 pairs/10 ha (Table 1; see Fig. 3). Since about 2.8 ha of this plot were marsh tundra, the effective ecological densities were 24 to 35 pairs/7.2 ha or 134 to 196 pairs/40 ha. The lower figures in 1966 and 1969 may reflect less complete census activities in those two seasons. On the census plot located on the mountain slope, the density of Westerns averaged about 11 pairs/5 ha for three seasons or 88 pairs/40 ha, about half that recorded on the heath tundra adjacent



to the marshes. Subjective estimates of Western Sandpiper densities on other sections of the hills indicated that density declined with altitude or more likely with distance from the marsh since this latter habitat is an important feeding area.

Few quantitative records are available of breeding densities of Western Sandpipers on patches of upland tundra located within the marshes. However, on several such patches near the Kolomak study site, the densities were similar to or greater than those on the main study area. Two islands of 0.2 ha supported one pair of Westerns apiece, while patches smaller than this had no breeding pairs. Another of 0.5 ha had 4 resident pairs which nested successfully. Extrapolated, these data indicate densities of 200 pairs/40 ha and 320/40 ha, respectively.

These densities of Western Sandpipers are the highest for any Calidridine species that have thus far been studied, with the possible exception of *C. temminckii* in northern Sweden. In the latter case Southern and Lewis (1938) found 4 males occupying a 0.2 ha island; they gave no information on how representative this figure was. Other estimates for Calidridines are considerably lower. For dunlin, the average densities range from 5 to 6 pairs/40 ha at Barrow Alaska (Holmes, 1966a) to 25–30 pairs/40 ha in marsh tundra at the Kolomak (Holmes, 1970). For *C. melanotos* and *C. fuscicollis*, the two opportunistic species which occur densely in some years in northern Alaska and which have non-monomagous mating systems, the maximum recorded densities at Barrow are 30 males/40 ha (Holmes, 1966a) and 20 males/40 ha (Holmes, unpub. data), respectively. In northern Canada Drury (1961) found the latter species at a density of 6 males/sq. mi. (0.9 males/40 ha) on Bylot Island and Parmelee *et al.* (1968) found it at 22 males/sq. mi. (3.4 males/40 ha) on Victoria Island. None of these approach the densities of Western Sandpipers recorded in this study on the Yukon-Kuskokwin Delta.

#### Population Stability and Site Tenacity

In addition to having relatively high, localized, densities, the opportunistic Calidridine species in northern Alaska appear to be very mobile, settling in one place one year, somewhere else the next. For instance at Barrow, *C. melanotos* and *C. fuscicollis* varied in density from near 0 to 20 or 30/ha (Holmes, 1966a, and unpubl. data).

In contrast, Western Sandpipers although dense appear to be comparatively stable. The census data for four years at the Kolomak (Table 1; also Fig. 3 for 1967 and 1968) indicate an annual variation of about 50%, although even this may be an artifact of sampling due to incomplete census work in 1966 and 1969. In any case, there is no indication of a 10 to 20 fold change as reported above for other species.

Table 2. *Mark and recovery records for adult Western Sandpipers on the main study area, Kolomak River, Alaska*

	1966		1967		1968		1969	
	♂	♀	♂	♀	♂	♀	♂	♀
No. Captured	0	1	19	20	33	32	22	22
No. Marked 1 year previously	—	—	0	1	12 (1) <sup>a</sup>	10 (1)	9 (1)	5 (3)
No. Marked 2 years previously	—	—	—	—	—	1	5	4
Return rate (%)					68.4	60.0	45.5	37.5

<sup>a</sup> Number of sandpipers recaptured on nests near but not on the main study area.

Further evidence supporting the stability of breeding Western Sandpipers is provided by data on their tendency to return to their former breeding sites and/or places of hatching. These data were obtained by an intensive marking and recapture program on the main study plot. In 1967 and 1968, 66% and 99%, respectively, of the adult breeding Western Sandpiper population on the study area was captured and marked. In 1969, the study area was visited for only a nine day period just prior to and during the time of hatching; as many nests as possible were found, and the adults captured and checked for the presence of bands. In 1968 and 1969 many but not all nests within 100 m of the study plot were also located and the adults caught and the presence of bands ascertained. In all four years of study many young Westerns hatching on or near the plot were banded before they left the nest.

*Return of Adult Sandpipers.* Of the 19 male Western Sandpipers caught and marked on the main study area in 1967, 13 (68.4%) were recaptured on or near the plot the next year; in 1969, 15 (45.5%) of the 33 captured in the preceding year returned (Table 2). The average return rate for males in the two recovery seasons was 57.6%. The estimates for female Western Sandpipers returning in 1968 and 1969, respectively, were 60.0% and 37.5% (Table 2), averaging 48.8%. Those not recaptured either died during the preceding year or settled outside the survey radius. The lower figure for the second year in both sexes may be a result of incomplete captures, although the density in that year for unknown reasons was less than in the preceding two seasons (see Table 1).

Those individuals that did return to the study area showed a strong tendency to return to specific sites. The data on nesting locations of males that returned two or more times are given in Fig. 4. With two

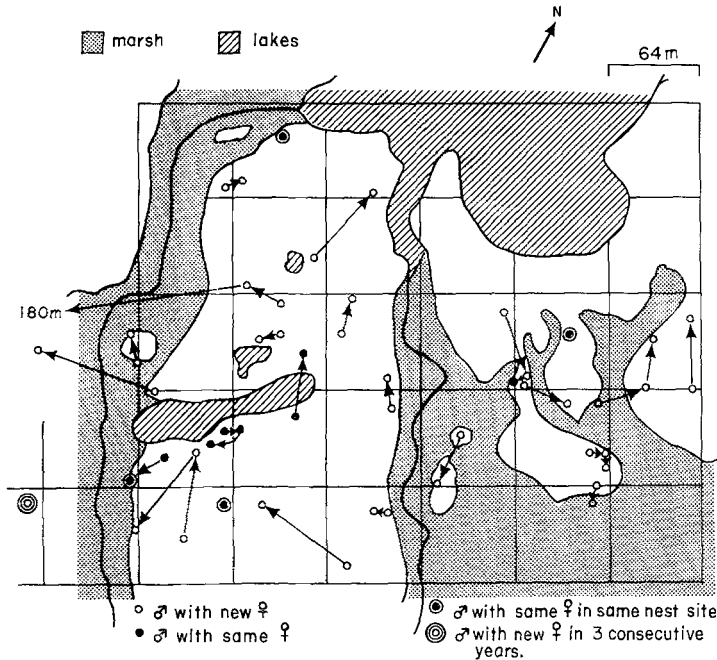


Fig. 4. Nest sites and mate faithfulness of male Western Sandpipers that bred two or more times on the main study area, Kolomak River, Alaska, 1967-1969

or perhaps three exceptions, every male that returned occupied the same part of the plot as in the previous season. Four males used the same nest cup in two consecutive years, one used the same cup in three. The average distance between nests of returning males was 37.7 m (range 0 to 221 m,  $n = 38$ ). Thus for those males returning, there is a strong attachment to the same territory they occupied in the preceding year. This is remarkable considering the fact that territory sizes average slightly less than 0.3 ha and that these are located on relatively featureless tundra terrain.

The nesting sites of female Western Sandpipers which returned for two or more years are shown in Fig. 5. Four of these used the same nest cup in two successive years, one of which had a new mate, the other three being paired with the same male who had also returned. The average distance between nest sites of returning females was 68.8 m (range = 0 to 241 m,  $n = 25$ ). The slightly poorer return and site attachment of females may be due to the fact that they arrive slightly later than males, so that where they settle is determined by the presence of unmated males rather than a territory *per se*. The situations where

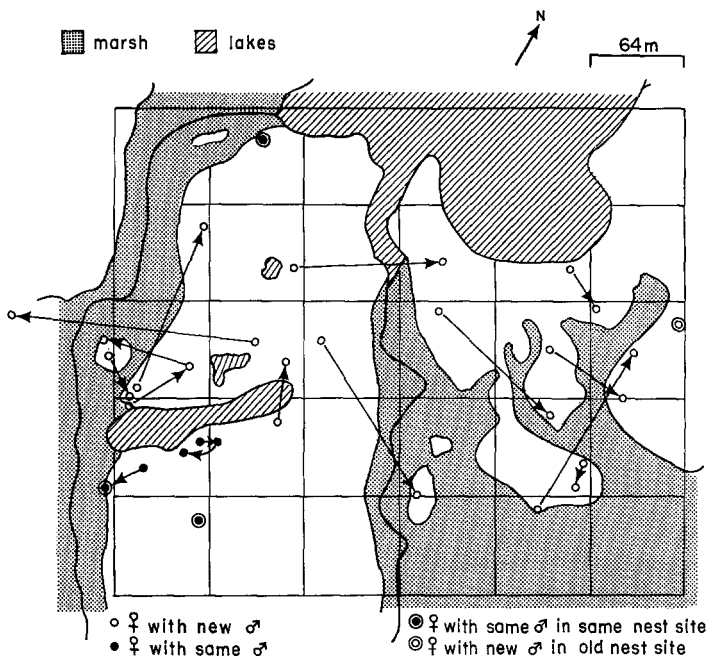


Fig. 5. Nest sites and mate faithfulness of female Western Sandpipers that bred two or more times on the main study area, Kolomak River, Alaska, 1967-1969

pairs reunited probably involve females returning to specific areas to which the same males had also returned, rather than a year-long association of the pair.

The only comparative data for other Calidridine sandpipers are those for dunlin (*C. a. schinzii*) in southern Finland (Soikkeli, 1967, 1970) and in northern Germany (Heldt, 1966). In these studies which were conducted over a number of seasons, the average return rates (calculated from data in Soikkeli, 1967) were approximately 73% for Finnish Dunlin and 62% for those in northern Germany. In reviewing comparable data for other Charadrii, Soikkeli (1970) indicated an average annual survival rate of adult birds of roughly 60 to 75%. Thus the return rates for *C. mauri* of 57.6% for males and 48.8% for females are relatively low, reflecting either a higher mortality rate or incomplete recapture at the breeding area. The latter may be the case, since the breeding areas of the Western Sandpiper at the Kolomak were large and extensive relative to the size of the study plot, with the result that a returning bird shifting its breeding site by 50 to 100 m could easily be missed. In Soikkeli's study area, dunlin are confined to rela-

tively small isolated coastal meadows in which almost every individual could be captured or observed.

Nevertheless many adult Western Sandpipers, in contrast with the "opportunistic" sandpiper species, do return to very specific areas in succeeding years.

*Return of Young Sandpipers.* In 1967, 33 juvenile Western Sandpipers were banded as they left their nests on or near the study plot. Of these two were recaptured as nesting birds in 1968 and one other was located for the first time nesting on the plot in 1969. Of 152 juveniles marked in 1968, four were nesting there in 1969. This means about 3.0% of the young sandpipers returned to breed in the immediate vicinity of their place of hatching.

For those returning the average distance from hatching site to their nesting place in subsequent years was 156.3 m (range = 42.7 to 262.2 m,  $n = 7$ ). The only figures for comparison for Calidridine sandpipers are an 11% return of young dunlin in southern Finland (Soikkeli, 1970) and a 2.8% return for the same species in northern Germany (Heldt, 1966). In Finland, the young birds settled at distances of 70 m to nearly 5 km from their hatching site, although more than half were within a 2 km range. No doubt a wider search at the Kolomak would have yielded a higher number of returning young.

Considering that mortality of young waders may be quite high (Boyd, 1962) and that young tend to disperse over a relatively wide area (Soikkeli, 1970), the 3.0% return of *C. mauri* young represents a significant tendency of these birds to return to areas near their site of hatching.

### The Mating System

*The Pair-Bond.* A strong pair-bond is maintained between male and female Western Sandpipers during the nesting season. Observations of marked pairs showed that mate fidelity was maintained and that no polygynous or polyandrous associations existed. In 1968 all birds on the plot with the exception of 3 unmated males, were marked and were associated with a nest. Each female laid one clutch, which if lost to predators early in the summer, was replaced (Holmes, 1972) usually in a nest site close to the original (see Fig. 3). Both members of each pair incubated, females usually from late afternoon through mid morning, males during the remainder of the day. As the incubation period proceeded, males performed a greater share of incubation duties. After hatching, both adults usually accompanied the brood, although the male was more attentive. This same pattern of pair responsibilities is found in *C. alpina* (Holmes, 1966a; Soikkeli, 1967) and *C. bairdii* (Holmes, unpublished data).

Table 3. *Return rates and mate faithfulness of Western Sandpipers on the main study area, Kolomak River, Alaska*

	1968		1969	
	♂	♀	♂	♀
No. marked in previous year	19	20	33	32
No. returned	13	12	15	12
No. pairs returned	7		6	
No. pairs returned and reunited	4		4	
No. returning ♂♂ paired to different but returned ♀♀	3	—	0	—
No. returning ♀♀ paired to different but returned ♂♂	—	5	—	1
No. returning ♂♂ paired to unmarked ♀♀	6	—	11	—
No. returning ♀♀ paired to unmarked ♂♂	—	3	—	7

Since there was only one active clutch per female, the situation reported by Hilden (1965) for *C. temminckii* and Parmelee (1970) for *C. alba* in which the female lays two clutches, one of which is taken by the male to incubate and one by the female, was not found in these dense populations of *C. mauri*.

*Mate Faithfulness.* The monogamous pair-bond described above refers to the relationship between male and female Western Sandpipers during a single summer. Data from the capture and marking of nesting sandpipers on the main study plot during three summers allows for an assessment of the degree of mate fidelity from one year to the next in this population (Table 3).

In the two years for which there are return data, 13 pairs of *mauri* were recaptured on or near the plot. Eight (61.5%) of these reunited, the others splitting and obtaining new mates. Two of these 8 records are pairs that remained faithful for three consecutive seasons. The only comparative data are those again of Soikkeli (1967) for Finnish Dunlin. In this species he found that in three seasons approximately 80% of the returning pairs rejoined while in a fourth year only 44% did so. Thus, while the degree of mate faithfulness in *C. mauri* appears to be slightly less than that for *C. a. schinzii*, they probably are comparable.

The information on pair-bonds of returning Western Sandpipers which obtained new mates is given in Table 3. Nine individuals (3 males, 6 females) formed pair-bonds with other returning Westerns who had not been their mates in the preceding year. A larger percentage of returning birds (about 45% of males and 55% of females) paired with unmarked and presumably new individuals. Four of the latter were

juveniles from the preceding year, having hatched on or near the plot. None of these four however returned to nest in the same vicinity of their hatching site, nor was any one mated to its own parents.

This relatively high degree of mate faithfulness probably reflects the strong site tenacity of this species, birds returning to the same areas in successive years (see p. 200). The adaptive significance of mate faithfulness and site tenacity probably lies in the fact that individuals are more familiar with their territories, expediting pair formation and nesting. This is probably adaptive for the Western Sandpiper since food abundance on and near the nesting areas decreases rapidly through the breeding period (Holmes, 1972); thus early breeding may produce more surviving offspring.

### Discussion and Conclusions

The most significant feature of the Western Sandpiper's social system is that with dense localized populations, monogamy is the type of mating system that has evolved. In light of this finding, the model proposed by Holmes and Pitelka (1966) and Pitelka, Holmes, and Maclean (MS) to account for the evolution of sandpiper mating systems on high arctic tundra can be refined, especially with regard to its applicability to species in other ecological settings.

In the Western Sandpiper, despite heavy predation, there has been no selection against both adults attending the nest. Indeed, both adult Westerns participate actively in incubation, although the presence on the territory of the non-incubating sex is decreased because the birds often go elsewhere to feed. The protection afforded to nests by the low shrubby heath vegetation probably reduces predation and may be the reason that nesting is restricted to the better drained heath tundra. With greater nest camouflage, both adults can incubate and can be present to escort and protect the young once they leave the nest site. The impact of predation on these dense populations of Westerns is therefore reduced by the availability of a habitat type which provides protection for sandpiper nests.

The food supply of the Western Sandpiper during the early summer breeding period is not subject to the vagaries of weather (Holmes, 1970) as it is for the species on the tundra of northern Alaska (Holmes, 1966b). This fact in combination with the occurrence of a longer summer season in subarctic Alaska allows Western Sandpipers to complete their nesting activities before food shortages occur. There is thus no selective advantage for part of the Western Sandpiper population (e.g. the males) to depart from the tundra before their breeding effort is completed, as occurs in *C. melanotos* in northern Alaska (Pitelka, 1959).

The higher population densities of Western Sandpipers on heath tundra where it adjoins the lowland marshes are probably a function of access to areas where food is readily available and abundant. Since Westerns do obtain much of their food away from their territories, a large nesting area is not required. Therefore, territories can be small and many pairs are able to occupy the patches of heath tundra, resulting in the observed dense populations.

Even with the great intensity of social interactions that take place in these extremely dense groupings of Western Sandpipers, however, a monogamous mating system persists. It is evident therefore that frequent social interactions, in themselves, do not necessarily promote the development of non-monogamous pair-bonds.

Since food procurement by the Western Sandpiper is not confined to the territory and since nesting sites are probably unlimited as long as the territory is on heath tundra, differences in habitat quality between territories appear to be minimal and would not likely be a factor in females' choice of mates, as proposed by Verner (1964) and Orians (1969).

For the Western Sandpiper, the selective advantage of monogamy can best be attributed to the increased protection afforded the young by the presence of both adults. On the Delta, the post-hatching period is particularly crucial, since predators are then abundant and actively hunting. At this time, young Westerns accompanied by their parents move from the heath tundra to lowland feeding areas where they are conspicuous and in greater need of protection. Thus, a monogamous pair-relationship in this species probably results in greater reproductive success. This supports the earlier contentions of Holmes and Pitelka and is in full agreement with the generalizations of Lack (1968) and Orians (1969) that monogamy will be favored where the cooperation of two parents results in more young being raised than would be possible by a single unaided adult.

These same findings do not negate the hypothesis concerning the evolution of polygynous or promiscuous mating systems in other sandpiper species. Indeed, in the ecological context of northern Alaska and other high arctic sites, the features of habitat quality such as predation rates, habitat structure, food abundance, and climatic conditions differ markedly from those described in this paper for subarctic Alaska. More detailed studies on the breeding and social systems of these non-monogamous species are needed before the factors influencing their evolution can be better understood.

In conclusion, the findings presented here for the Western Sandpiper provide another dimension to the range of variability in social organization of Calidridine sandpipers. The clumped dispersion pattern in the



Western is a direct result of the distribution pattern of heath tundra which provides protected nesting sites. Within this nesting habitat, the populations are relatively stable, and individuals return to the same areas year after year. The high densities on the patches of heath tundra are made possible by the separation of feeding and nesting areas, which is permitted by the complex mosaic arrangement of the slightly elevated nesting habitat and lowland areas where food is abundant. Monogamy has evolved as a result of the increased protection afforded to the precocial offspring by the presence of two parents.

The results of this study on the Western Sandpiper demonstrate clearly the importance of examining avian social systems in relation to the ecological setting in which they function.

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