Ecological Factors Influencing the Breeding Season Schedule of Western Sandpipers (Calidris mauri) in Subarctic Alaska

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ABSTRACT: Studies of the breeding system ecology of the Western Sandpiper (*Calidris mauri*) were conducted in the summers of 1966-1969 on the Yukon-Kuskokwim Delta in western Alaska. Western Sandpipers arrive as soon as the snow begins to melt, establish territories on heath tundra, pair and nest once. Second nestings are restricted to replacement clutches. As soon as breeding is completed, the adults shift to coastal habitats, begin molt, and by early to mid-July move S on migration. Young *mauri* follow about 2 to 3 weeks later. After their arrival on Pacific coast feeding areas, the adults continue their prebasic molt, completing it by late October.

The single nesting and early departure of Western Sandpipers from the breeding areas are related to a decreasing food supply in an otherwise favorable environment. The only other congener sympatric with *mauri* on the Delta, *C. alpina,* follows an identical breeding schedule, but remains longer in the N, occupying riverbank and intertidal habitats, and completes its molt before migrating S in late September. This extended residence of *alpina* in Alaska is possible because it is able to exploit marine invertebrates there during late summer, whereas *mauri* apparently is not. Therefore, the changes in food abundance near the nesting areas and the lack of suitable food supply in midsummer are the primary factors influencing the scheduling of breeding season events in Western Sandpiper populations.

INTRODUCTION

Avian breeding systems and the timing of molt and migration vary markedly from one species to another. Recent studies by Orians (1961), Crook (1964), Lack (1968) and others have begun to demonstrate that these systems represent adaptive responses to environmental conditions and that the functioning of these systems and, therefore, their evolutionary significance can only be understood through studies of individual species populations in relation to the environments in which they live.

Among tundra-nesting sandpipers of the inclusive genus *Calidris*, marked and various specializations occur in breeding systems, which have been hypothesized to result from the influence of the rigorous arctic climate and its impact on the availability and abundance of the sandpiper's food supply (Holmes, 1966a; Holmes and Pitelka, 1966, 1968). To test the validity and generality of this hypothesis, I have been conducting studies on *Calidris* sandpipers breeding in a subarctic environment, characterized by less severe weather, a longer summer season and a food supply differing in several respects. The effects of differences in latitude on population structure of one species, *C. alpina*, have already been reported (Holmes, 1970, 1971a).

The Western Sandpiper (*Calidris mauri*) was chosen for detailed study because it is principally a subarctic nester, and it is the only abundant congener sympatric with *C. alpina* in western Alaska. The influence of high population density and habitat utilized on the type of mating system of this species is discussed elsewhere (Holmes, 1971b). The present paper considers another aspect of the breeding system ecology of the Western Sandpiper, that of the summer schedule of events in relation to length of season, weather and food supply.

STUDY SITES AND METHODS

Western Sandpipers were studied on the Yukon-Kuskokwim Delta in western Alaska in four summers, 1966-1969. The main study area was located along the Kolomak River (61°30′N, 164°50′W), 30 km NE of Hooper Bay and about 16 km inland from the Bering Sea (Fig. 1).

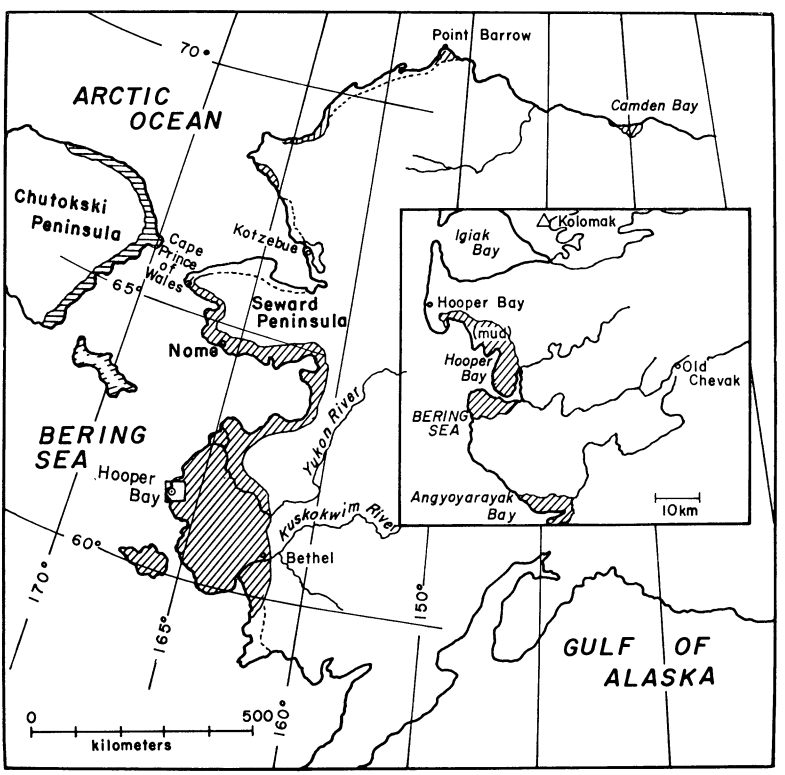

Fig. 1.—Breeding range of the Western Sandpiper, *Calidris mauri* (hatched zone). The inset provides detail on the area of study on the Yukon-Kuskokwim Delta near Hooper Bay. Hatched zone on inset represents extensive mudflats at low tide

In the summers of 1966-1968 field work at the Kolomak began in mid-May and ended in mid-July. In the latter 2 years the studies were continued through late August at Old Chevak, a U.S. Fish and Wildlife Service camp about 40 km SE of Hooper Bay. From this locality, frequent trips were made along many of the Delta river channels and along the coast of the Bering Sea, S of Hooper Bay (*see* Fig. 1). In 1969, studies were conducted at the Kolomak study area from 10 to 17 June.

The method of study was direct observation with details on numbers, habitat, behavior, nesting and movements recorded in field notebooks. On the main study area which consisted of a 10-ha gridded plot, Western Sandpipers were observed, censused, captured and marked with aluminum and colored bands for individual recognition. Specimens were collected in areas away from the main study sites; these were examined for reproductive status, fat, weight, molt and stomach contents. Additional information on molt was obtained by examining specimens in several museum collections.

Information on the diet of Western Sandpipers came from analyses of stomach contents of collected specimens. Data on food availability was obtained by sampling pond edge sites, mainly in lowland marshes (for details and results, *see* Holmes, 1970).

Observations on migrating and wintering Western Sandpipers were made in many locations along the California coast from 1957 to 1965. The most intensively studied populations were those on Humboldt Bay, Humboldt Co. (1957-1959) and along the east side of San Francisco Bay near Emeryville, Contra Costa Co. (1959-1964).

DISTRIBUTION AND HABITAT

The breeding range of the Western Sandpiper (Fig. 1) extends from near the mouth of the Kuskokwim River (59°N) in southwestern Alaska to the vicinity of Point Barrow and Camden Bay (72°N) in arctic Alaska (Gabrielson and Lincoln, 1959) and overlaps into easternmost Siberia (Kozlova, 1962). The main concentration of breeding Western Sandpipers, however, is in the Yukon-Kuskokwim Delta of Alaska, an area approximately 323 km sq, and the tundra near the coast N of the Delta, extending to Nome and Cape Prince of Wales on the Seward Peninsula (Fig. 1).

The habitat utilized by this species in the breeding areas has been described elsewhere (Holmes, 1971b). Briefly, it consists of a mosaic of slightly elevated and better-drained dwarf shrub-heath tundra and low-lying wet marsh tundra. The former is the nesting habitat of the Western Sandpiper and is vegetated with mats of mosses, lichens, grasses, prostrate shrubby plants (mostly species of *Betula, Arctostaphylos, Salix, Vaccinium, Empetrum,* etc.) and scattered forbs. The marshes contain many ponds, lakes, streams, and sloughs which interconnect in a complex pattern with each other and with the Delta river channels. The latter drain into the sea and have tidal fluctuations of 2-4 m, even many kilometers inland. The marsh tundra is

vegetated principally by grasses (*Elymus, Poa*) and sedges (mostly *Carex*). These marsh sites comprise major feeding areas for nesting Western Sandpipers.

The climate on the Delta is less severe than that in northern Alaska (Holmes, 1970, 1971a). The snow-free season lasts roughly from late May through late September. Summer temperatures range between 7 and 15 C. Rains are frequent in summer, but snow and freezing temperatures are rare after 1 June and before 1 September. The period of favorable weather lasts about 2 months longer than in northern Alaska.

Western Sandpipers migrate in autumn, mainly along the Pacific coast of North America, from southeastern Alaska to Baja California and farther S, rarely in the central interior from North Dakota and southern Ontario southwards and in small numbers along the Atlantic coast (A.O.U. Checklist, 1957). In winter, the species is found along the Pacific coast from northern California to Ecuador and Peru and on the southern Atlantic coast, along the Gulf of Mexico, S to Central America and northern South America (A.O.U. Checklist, 1957).

The relative distribution and abundance of Western Sandpipers within the winter range are not clear. Large numbers are present along the California coast (Storer, 1951; Recher, 1966; Holmes, pers. observ.) and the southern Atlantic and Gulf coasts (Sprunt, 1954; Lowery, 1955). Farther S, Wetmore (1965) reports that in Panama they are locally abundant, flocks of thousands occurring in favorable areas along the Pacific coast, but less common on the Caribbean side. DeSchaunasee (1964) indicates that Westerns are common on the Caribbean coast of Colombia.

The habitat of migrating and wintering Western Sandpipers is usually coastal estuaries where they feed on marine invertebrates. They also occur occasionally on sandy beaches. When they do migrate inland, they frequent fresh-water marshes, lake shores, settling ponds of sewage disposal plants, etc.

SUMMER SCHEDULE

Arrival and dispersal onto nesting habitat.—Western Sandpipers begin to arrive on their breeding areas with the first appearance of snow-free tundra. This period of melt varies yearly depending on weather conditions. In the 3 years of this study arrival occurred between 12 and 20 May.

They first appear in small flocks consisting of about two to 10 individuals, some of which still possess large quantities of fat, as indicated by weights of collected specimens (Table 1). As these groups arrive, they move slowly from one patch of tundra to another, all the individuals feeding actively along the edges of small tundra pools or along the shores of lakes. Aggressive interactions among flock members increase within a few days, and the individuals gradually disperse onto the newly exposed tundra. Some courting activity was noted

among flock members, suggesting that the flocks contained both males and females.

Within 10 days after the first Westerns appear, the breeding population is usually settled onto nesting habitat. Males establish territories which they defend actively against conspecific males and to which they attract females. These territories at the Kolomak averaged about 0.3 ha in area and were located exclusively on the dwarf shrub-heath tundra, although occasionally the edges overlapped onto adjacent marsh habitat (Holmes, 1971b). Since this heath tundra is distributed irregularly in patches over the Delta and surrounding areas, the overall dispersion pattern of nesting Western Sandpipers is consequently clumped.

Egg-laying and incubation.—Within days of establishing a territory, most male Western Sandpipers attract, court and pair with a female. The pair-bond is monogamous, as determined through intensive observations of color-marked sandpipers on the main study area (Holmes, 1971b).

Once paired, it is only a matter of days before the nest site is chosen and the female lays the first egg. Laying occurs at no particular time of day; some females laid early in the morning, others late in the afternoon or evening. Eggs are laid by a given female at 23- to 28-hr intervals, averaging 24-25 hr. This was determined by detailed observations of the laying schedules at seven nests. Approximately the same interval has been reported for *C. alpina* in northern Alaska (Holmes, 1966a), but it differs from the 36-hr period for *C. alpina* in Finland and northern Germany given by Soikkeli (1967) and Heldt (1966), respectively. The significance of geographic and species differences in laying intervals is not known, but may represent the effects of different environmental conditions, including food availability for the egg-laying females (Soikkeli, 1967).

The timing of egg-laying in the Western Sandpiper population was determined from: (1) observations of clutches as they were laid; (2) hatching dates of clutches found after completion, from which the dates of laying could be extrapolated, knowing the incubation period, and (3) examination of gonads of female specimens collected during the early summer.

Laying dates at the Kolomak varied in different years, depending

TABLE 1.—Summer weights of adult Western Sandpipers (laying females excluded) collected on the Yukon-Kuskokwim Delta, Alaska, 1966-1968

	Males			Females		
	N	Mean	± S.E.	N	Mean	± S.E.
18-30 May	12	26.5	± 0.17	7	31.0	± 1.09
31 May-10 June	13	26.8	± 0.21	4	30.2	± 1.05
11-20 June	13	26.3	± 2.00	9	30.2	± 0.16
21-30 June	20	26.6	± 1.26	11	27.7	± 0.25
1-9 July	15	26.9	± 0.31	20	30.6	± 0.28
10-19 July	14	25.4	± 0.21	7	32.8	± 1.69
20-28 July	5	25.5	± 1.25	3	26.2	± 0.22

on timing of melt. In 1966, laying commenced on 27-28 May, with the first complete clutch of four eggs recorded on 1 June; the peak occurred between 4-6 June. Because of earlier melt in the 1967 and 1969 seasons, the first eggs in those years were produced on or about 19-20 May, most clutches being completed between 25 and 28 May (Fig. 2).

The late clutches in each season represent the attempts of birds to renest after the loss of the first clutch. The evidence for this is derived from observations of several individually marked pairs on the main study plot which, when their nests were destroyed, then renested within the same territory. Several females were also collected in mid-June which were in the process of laying eggs but which had thickened, well-developed brood patches, suggesting that they had previously incubated. It thus appears that renesting is relatively com-

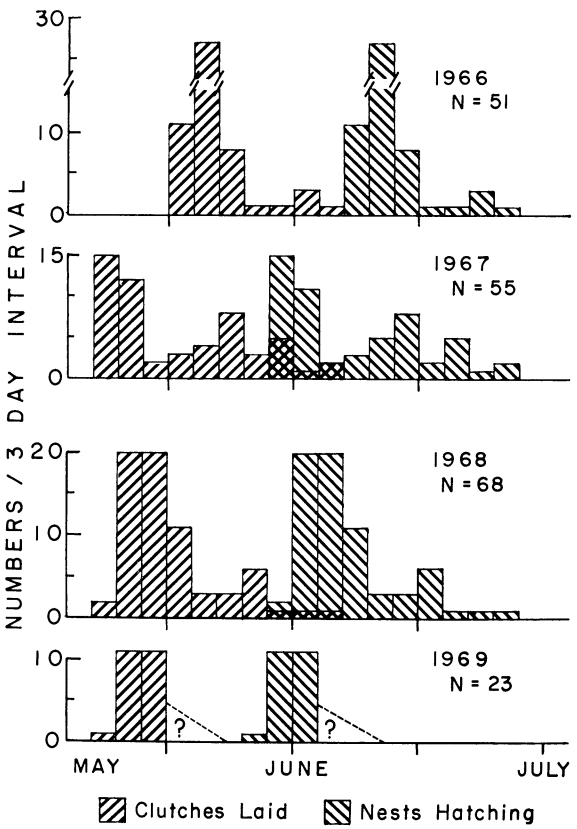

Fig. 2.—Dates of laying and hatching in the *C. mauri* population at the Kolomak study site in four summers. The data for 1969 are based on hatching dates recorded during an 8-day period in mid-June, and are thus incomplete

mon. However, no pairs were found to lay a second clutch after successfully hatching their first.

Once the clutch is complete, both sexes participate in its incubation. The length of incubation varied from 20.5 to 22.0 days, averaging 21.0 (N = 27 nests). This is roughly the same length of incubation period recorded for most other Calidridine species (Holmes, 1966a; Soikkeli, 1967; Parmelee *et al.*, 1968).

Hatching and growth of young.—The hatching period is relatively synchronous, with an early peak representing the results of the main breeding effort, followed by the hatching of young from renestings (Fig. 2).

Within a clutch, the young usually hatch over a period of about 24 hr. The first to hatch usually stay in the nest until the last chick has hatched and dried. If this occurs during the night or early morning, the brood leaves the nest site within a few hours. If hatching is not completed until late afternoon or evening, the young will usually stay in the nest overnight and move off the following morning.

When the young leave the nest cup, they are accompanied by one or both parents. The male is almost invariably found with the brood; the female may or may not be there. The attending parent(s) stays with the young and broods them frequently during the 1st few days after hatching, especially on cold nights and during periods of rainy weather. The adult also provides protection by giving alarm signals and distraction displays upon approach of a predator (Brown, 1962). The family group is maintained until the young are able to fly, after which the adults and young flock separately prior to departure.

Although the Western Sandpiper is strongly territorial during the nesting season, area defense wanes late in incubation. After hatching, the family groups wander freely both on upland heath tundra and in nearby marshes. The young forage for themselves during this period, while the adults feed nearby.

Once the young leave the nest and move off with their parents, they are exceedingly difficult to locate and very few were actually found and captured, even though the distressed parents were very conspicuous. Data on growth rates were therefore hard to obtain. The weight of young Westerns at hatching ranged between 4.4 and 5.4 g, averaging 5.0 g (N = 8). The first flying young Western was recorded 18 days after the first hatching occurred in the population, and one collected 19 days after the first clutch had hatched was adult size, weighing 20.3 g. It thus appears that the young grow rapidly, and are probably capable of flight within 2½-3 weeks following hatch. This is roughly comparable to the figures for the growth of young *alpina* in northern Alaska (Holmes, 1966a) and in Finland (Soikkeli, 1967).

Mortality factors and breeding success.—The major mortality of breeding Western Sandpipers is caused by predators taking eggs, young and, perhaps rarely, adult sandpipers.

At the Kolomak and more widely on the Delta, there are several

important predators, namely red foxes (*Vulpes fulva*) and breeding populations of two species of jaegers, the long-tailed jaeger (*Stercorarius longicaudis*) and the parasitic jaeger (*S. parasiticus*). All are predators on small birds and have been seen hunting and in some cases successfully taking birds' eggs at the Kolomak. In contrast to the situation in northern Alaska where there are very few predators on birds (Holmes, 1966a), these on the Delta are common and regularly present throughout the early summer when sandpipers are nesting. Thus predation pressure on sandpiper eggs and young is probably greater on the Delta than it is in northern Alaska.

The impact of weather likewise differs in the two areas being compared. At Barrow, when snows and freezing temperatures occur during the nesting period, some clutches are abandoned and if young are present their mortality may be increased. At the Kolomak, the weather is significantly more moderate, and in the 4 years of this study it did not appear to have any direct effect on sandpiper nesting success.

The numbers of Western Sandpiper clutches found at the Kolomak, their size and fate through the time of hatching are given in Table 2. The normal clutch size is four; the occurrence of three- and of two-egg clutches was restricted to those late in the season, many of which may have been renesting efforts. Of the clutches found, 83.7% hatched, while most if not all of the others were lost to predators. A total of 20 successful clutches in the 3-year period contained one egg which did not hatch. When examined later, these had no visible embryos and were apparently sterile.

On the basis of these figures, it appears that the nest loss prior to hatching is approximately 15 to 25%, slightly lower than that recorded for *C. alpina* in northern Alaska (Holmes, 1966a), but within the range of 4 to 44% for the Charadrii reviewed by Boyd (1962). The protection afforded nest sites of Western Sandpipers by the low shrubby heath tundra may be important in maintaining a relatively high hatching success in the face of heavy predation pressure (Holmes, 1971b).

Since the young were extremely difficult to locate after they had left their nest sites, no information was obtained on their survival and/or mortality. Boyd (1962) estimates for Charadrii in general that

TABLE 2.—Clutch size and hatching success of Western Sandpipers on the Kolomak study area

	N	Clutch size 4	3	2	No. of clutches hatching	% Hatching	No. and (%) of clutches with 1 unhatched egg
1966	69	65	4		50	72.5	5 (7.3)
1967	62	58	2	2	53	85.5	4 (6.5)
1968	84	79	5	0	77	91.7	11 (13.1)
	215				180	83.7	

posthatching mortality (to fledging) ranges from about 40 to 80%. From entirely subjective estimates for this Western Sandpiper population, I would place the figure in the lower part of this range.

Postbreeding movements and migration.—About the time of hatching, small flocks of adult sandpipers begin to appear on the heath tundra and along the shores of nearby rivers, sloughs and lakes. These range in size from two to 20 birds, and consist mainly of adults which, as judged by the presence of well-developed brood patches on all individuals collected from such flocks, have recently lost their eggs or broods.

These flocks were first noted at the Kolomak on 24 June in 1966 and 15 June in 1967 and 1968. They were present through the first half of July, the numbers increasing to about 25 to 30 per flock due to the addition of other adults finishing breeding.

By mid-July, the numbers of adult Westerns began to decrease at the Kolomak, Old Chevak and other inland areas, but increased along the river channels toward the coast and along the shores of the Bering Sea near Hooper Bay. The greatest concentration at this time was found on shallow brackish pools and marshes just inland from the coast. By the end of July all adult Western Sandpipers had left the Old Chevak-Hooper Bay section of the Delta, apparently having moved S on migration. The last adult Western identified was a male collected S of Hooper Bay on 28 July (1967).

From examination of body weights of adult Western Sandpipers on the Delta (Table 1) it is apparent that weights remain relatively constant through the entire summer stay in Alaska and, most importantly, that no significant increase in weight occurred prior to autumn departure, as is found in other Alaskan Calidridines (Holmes, 1966a, and unpubl. data).

After fledging, young Westerns occasionally associate with the flocks of adults, but more typically remain separate. During July they occurred individually or in flocks, some of which consisted of 200 or more birds, along the river channels and near the coast of the Bering Sea. By the 1st week of August, however, their numbers decreased sharply, and afterwards only singles and small groups of two to 10 birds were recorded. A few young Westerns were still present along the coast near Hooper Bay when our observations ended in late August.

This departure schedule from the Delta is confirmed by the arrival times of Western Sandpipers on California estuaries. Both Storer (1951) and Gerstenberg (pers. comm.) report that Western Sandpipers first arrive in late June or early July on San Francisco Bay and Humboldt Bay, respectively, after which two peaks in movement are noted. One occurs in early to mid-July, which, according to the data from the Alaskan breeding grounds, must consist mostly of adult Westerns; the second is in mid- to late August, caused by the influx of juveniles. Judging from the short time between departure from

Alaska and arrival in California, this first phase of migration must be rapid and direct.

Many of the Western Sandpipers moving through California in late summer continue to move S. This is shown by the fact that in California the numbers of Westerns are greater in mid- to late summer than during the winter months (Storer, 1951; Recher, 1966). Adult Westerns probably move farther S than the young, since a migratory wave of adults does move through California in July, and since more immatures relative to adults are found in California in late autumn and winter. The evidence for the latter is derived from the age distribution of specimens in museum collections.

Migratory routes and movement patterns of Western Sandpipers to Atlantic and Gulf coasts and especially to wintering areas farther S have not been documented. However, judging again from observations of Western Sandpipers in California, migration becomes slow there relative to the rapid move S from Alaska. This may also be true for movements from there on S. At this time, the Westerns are usually found in coastal habitats and are undergoing extensive molt, which for the adults includes that of flight feathers.

MOLT OF ADULT SANDPIPERS

Since molt is an energy-demanding process, its timing in relation to breeding and migration must be considered in any discussion of breeding season schedules. The prebasic molt of adult sandpipers is the most critical, and will be the only one considered here for the Western Sandpiper.

Information on the timing of the prebasic molt of adult Westerns in Alaska was gathered from specimens collected between mid-May and mid-July at the Kolomak and between mid-July and late August at Old Chevak and along the Bering Sea coast a few miles S of the village of Hooper Bay. Molt data were also obtained from specimens of adult Westerns (in museum collections) taken in summer and autumn along the Pacific coast from British Columbia to Baja California.

Since the pattern of molt in most Calidridine sandpipers is nearly identical (Holmes, unpubl. data), I have used the same methods for recording molt stages and for assigning scores for Western Sandpiper molt, as those developed and used in the study of *C. alpina* (Holmes, 1966c). This involves recording the occurrence and stage of molt in several selected flight feathers and in feathers on several regions of the body; these include the areas first and last to molt and graded stages in between. A bird that has not begun to molt scores 0; one just completing molt, 200 (40 and 160 for completed flight and body feathers, respectively).

The prebasic molt of adult Western Sandpipers begins in late June (Fig. 3) with the replacement of feathers on the capital tract and within a few days on nearly all parts of the body. Most individuals collected at the Kolomak from small flocks during late June and the

first half of July were beginning molt, while adults associated with nests or young were not. The nonmolting individuals in the sample from mid- to late July probably represent such late nesters. No molt of

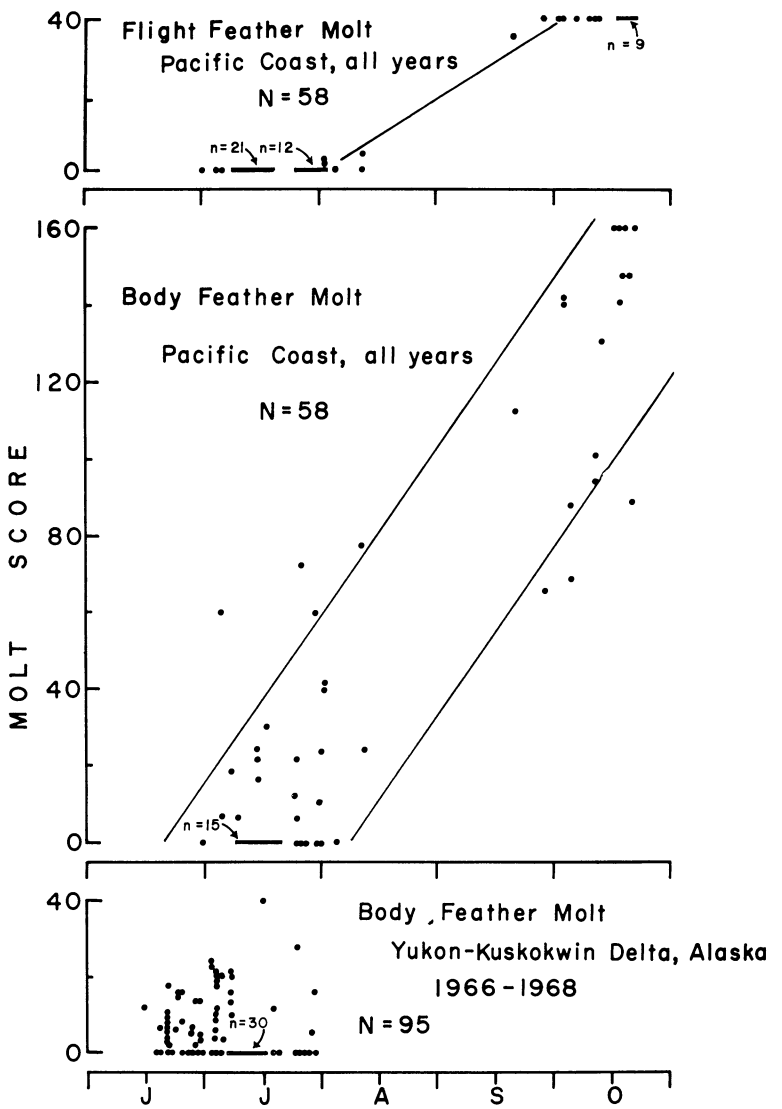

Fig. 3.—Molt schedule of *C. mauri,* determined from specimens collected on the Yukon-Kuskokwim Delta, 1966-1968 (lower) and from museum specimens which had been collected in various years along the Pacific coast from British Columbia to Baja California (middle and upper)

remiges or rectrices was recorded from any adult Western Sandpiper collected on the Delta.

From the museum specimen data, it is apparent that some individuals arrive on the Pacific coast without having started molt (Fig. 3), while others are relatively far along. Those with molt scores of 60 to 80 for body feathers in July may be individuals which migrated early due to nest loss or birds which did not go N to the breeding grounds and oversummered at temperate latitudes.

The synchrony of molt inception in the sample from the Delta and from the Pacific coast supports the conclusion that the movement of adults from Alaska to their wintering areas is a rapid event. Some Westerns collected in July along the Pacific coast had completed part of their body feather molt, but had no new molt started, suggesting that molt may be arrested during migration.

The first individuals with complete sets of new body feathers were recorded in mid-October (Fig. 3), giving a period of 3½-4 months needed for the replacement of body feathers. This contrasts with a 2½-month period for body feather molt of *C. alpina* in Alaska (Holmes, 1966c, 1971a).

The first individuals' molting flight feathers were collected in early August in California, while birds with newly completed flight feather molt were not recorded until early October (Fig. 3). The replacement time for flight feathers is therefore about 2-2½ months. This is comparable to the rate of flight feather replacement in the *C. alpina* population in northern Alaska but shorter than the 3-month period taken by *C. alpina* on the Yukon Delta (Holmes, 1971a).

Unlike either *C. alpina* population, however, the Western Sandpiper starts its flight feather molt after body molt is well under way, and this occurs after their arrival in coastal habitats along the Pacific coast, not near the summering grounds.

FOODS OF ADULT AND YOUNG SANDPIPERS

The diets of adult and young Western Sandpipers were determined from analyses of the contents of stomachs of 208 individuals collected on the Delta during three summers. The results are grouped into 10-day periods, except for late May when a 14-day interval is used. The data are presented using the enumeration method of Hartley (1948), in which the abundance of each prey species in all stomachs from one time period is expressed as a per cent of the total numbers of food items present in those stomachs. The advantages and disadvantages of this technique are discussed elsewhere (Holmes, 1966b). Since almost no taxonomic studies of the invertebrate fauna of western Alaska have been made, the prey species are identified here to order or family. The breakdown is comparable to that used for analyzing the invertebrate prey of sandpipers in northern Alaska.

Foods of adult Western Sandpipers.—During their stay on the tundra, adult Westerns feed predominately on larval and pupal insects, most of which belong to the families Chironomidae and Muscidae,

order Diptera (Table 3). In addition, they take adult flies of the above-mentioned families, larval and adult craneflies (Diptera, Tipulidae), adult and larval beetles (Coleoptera, mostly Staphilinidae), spiders, a few small crustacea and occasionally other items. All stomachs contained one to many small stones, and many had one or more kinds of seeds, the most common of which was of an aquatic plant, *Hippurus tetraphylla*, found in shallow ponds. These seeds are frequently used in case-building by caddis fly larvae (order Trichoptera) and may have entered the stomachs when these larvae were ingested, rather than having been selected directly.

The intraseasonal change in diet of adult Western Sandpipers on the Yukon Delta is not as great as that of *Calidris* species in northern Alaska (Holmes and Pitelka, 1968). Early in the season at the Kolomak when many of the ponds and marshlands are still snow- or ice-covered, Westerns take more adult beetles and spiders than they do later; at this time they are settling onto and defending territories on heath tundra and evidently feeding there. When snow melts from the lowlands and the spring floods subside, Westerns leave their territories to feed in these now accessible areas, and take mostly muscid and chironomid larvae and later pupae. These two food items then make up the bulk of the diet for the rest of their stay on the Delta (Table 3).

During June, chironomid larvae are utilized heavily. These occur along the margins of ponds, particularly those in lowland marshes, and are most abundant early in the summer, declining sharply through June and early July (Holmes, 1970). As this occurs, the adult Westerns shift back to the muscid larvae and pupae which they obtain primarily from the shores of rivers and sloughs.

The adult Westerns in the sample from mid- and late July were collected in the region between Old Chevak and the Bering Sea coast. They were taken wherever they could be found, which was mostly in lowland marshes and at shallow pools just above the riverbanks or just inland from the coast. These were feeding primarily on larval and pupal Diptera, and even the few that were taken from coastal mudflats did not have such marine invertebrates as amphipods or ostracods on which this species feeds during the winter (Recher, 1966).

Foods of young Western Sandpipers.—All young Westerns in the sample were fully grown and able to fly, except for the birds collected in late June which varied in weight from 5 to 9.4 g.

Being precocial, young Western Sandpipers leave the nest site and begin foraging for themselves within 12 to 24 hr after hatching. At this time, they take mostly surface-active insects, such as adult flies and beetles, along with some muscid larvae (Table 4). The timing of hatching coincides closely with the first major emergence of adult insects (Holmes, 1970), thus supporting Lack's (1954) hypothesis which links the timing of breeding to the availability of food for young.

TABLE 3.—Proportion (%) of prey items in stomachs of adult *Calidris mauri* in three summers, 1966-1968, at the Kolomak River, Yukon-Kuskokwim Delta

	18-31 May	1-10 June	11-20 June	21-30 June	1-10 July	11-20 July	21-31 July
Larval Diptera							
Tipulidae	4.8	5.9	0.7	0.9	0.7	1.0	0.0
Muscidae	33.9	25.8	7.3	35.1	62.4	45.0	35.5
Chironomidae	9.7	62.7	74.7	49.1	17.1	5.0	0.0
Pupal Diptera (Muscidae & Chironomidae)	0.0	0.2	1.1	5.6	16.2	20.0	55.3
Adult Diptera	4.8	1.0	8.4	4.1	0.2	6.0	6.6
Larval Coleoptera	0.0	0.8	1.8	0.9	0.0	10.0	0.0
Adult Coleoptera	24.2	2.8	5.4	3.6	2.8	12.0	1.3
Arachnida	21.0	0.4	0.2	0.0	0.1	1.0	1.3
Others	1.6	0.4	0.4	0.7	0.5	0.0	0.0
"Seeds"	+	+	+	+	+	+	+
Total (%)	100.0	100.0	100.0	100.0	100.0	100.0	100.0
Total no. of items	62	502	454	558	1306	100	76
No. of stomachs examined	9	17	22	33	37	19	10

Once fledged, the young concentrate on muscid larvae, pupae and adults and at this time have a diet very similar to that of the adults. This general pattern of prey utilization continues during their stay on the Delta. By late July and early August, young Westerns inhabit coastal areas, but continue feeding on the ponds and marshes just inland from the shore. Like the adults, the young do not feed on marine invertebrates from the coastal mudflats of the Bering Sea.

DISCUSSION AND CONCLUSIONS

From the foregoing examination of breeding season and molt schedules of the Western Sandpiper in Alaska, it is evident that: (1) breeding takes place as early as possible, the actual dates varying with the timing of snow melt; (2) only one clutch is laid which may be replaced if lost early in incubation; (3) there is no attempt to produce a second nesting after successfully completing the first, in spite of favorable climatic conditions; (4) adults leave the nesting habitat soon after their young fledge and then depart southward on migration by early to mid-July, the young following 2 to 3 weeks later, and (5) adults may begin molt of body feathers while in Alaska but the bulk of feather replacement occurs after arrival on temperate or more southerly feeding grounds.

These events for the Western Sandpiper are summarized in Figure 4, and contrasted with those of the only other *Calidris* sandpiper occurring commonly on the Delta, *C. alpina*. The ensuing discussion focuses on the similarities and differences in breeding and molt schedules of these two species inhabiting the same subarctic environment and on the underlying ecological factors.

The nesting schedule.—Both *mauri* and *alpina* arrive on the Delta

TABLE 4.—Proportion (%) of prey items in stomachs of immature *Calidris mauri* in three summers, 1966-1968 at the Kolomak River

	21-30 June	1-10 July	11-20 July	21-31 July	1-10 Aug	11-20 Aug
Larval Diptera						
Tipulidae	0.0	0.0	31.8	13.3	0.0	0.0
Muscidae	27.8	29.4	45.5	41.4	26.3	0.0
Chironomidae	0.0	0.0	0.0	14.0	0.0	0.0
Pupal Diptera (Muscidae & Chironomidae)	0.0	0.0	0.0	6.7	19.7	0.0
Adult Diptera	33.3	35.3	6.1	11.3	48.8	50.0
Larval Coleoptera	0.0	0.0	1.5	0.0	0.0	0.0
Adult Coleoptera	33.3	11.8	12.1	11.3	2.6	50.0
Arachnida	0.0	5.9	0.0	0.0	0.0	0.0
Others	5.6	17.6	3.0	2.0	2.6	0.0
"Seeds"						
Total (%)	100.0	100.0	100.0	100.0	100.0	100.0
Total no. of items	18	17	66	150	76	12
No. of stomachs examined	9	7	11	21	11	2

as soon as the snow begins to melt, and, within 1 to 2 weeks, have established territories, paired and laid eggs. In both populations most nests hatch in mid-June, coinciding with the first major emergence period of adult insects on which the precocial young sandpipers feed. At Barrow, sandpiper hatching is closely synchronized with the occurrence of adult insects on the tundra surface, which is a period of only 2 to 3 weeks. On the Delta, adult insects are present for a much longer time, at least through early August, and the sandpiper hatching season is considerably longer. As noted below, however, breeding does terminate before this time of decreasing abundance of the adult insects. It is significant that the sandpipers, except for the young in the 1st few days after hatching, take very few adult insects and instead apparently prefer the larval forms.

Renesting in both sandpiper populations on the Delta is more frequent than in higher latitude Calidridines, including *C. alpina* at Barrow. This means that a second nest, started 1 to 2 weeks after the first, has a relatively high probability of successfully producing young. The lack of a second complete nesting in both populations on the Delta, however, suggests that some environmental condition in mid- to late July is not conducive to the successful production of young and that food resources are instead channelled into processes other than breeding, such as molt or possibly premigratory fat deposition.

The ecological factors most likely to affect breeding success are length of season, weather, predators and food supply. At this sub-

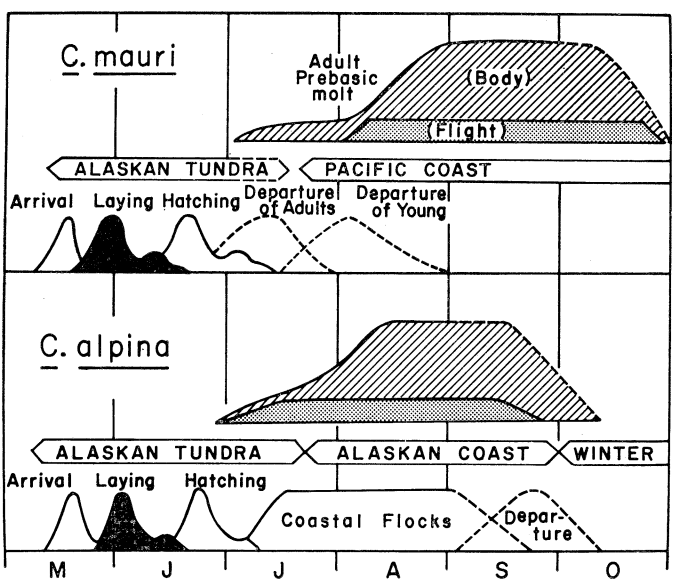

Fig. 4.—Comparison of breeding season schedules of *C. mauri* and *C. alpina* populations on the Yukon-Kuskokwim Delta (approximately 61°N lat)

arctic locality, the snow-free season lasts until late September, almost 3 months after the cessation of sandpiper breeding, and thus does not appear to be limiting. The weather is colder in late May and early June when nesting is at its peak than in July or August. Rains occur throughout the snow-free season but these do not seem to have any direct effect on nesting activities of sandpipers, although as a result pond levels may rise, making insect larvae less available. There is no evidence for any change in predation pressure during the summer, although the food demands of resident predators are doubtless higher in late June and early July when they have young to feed.

The main factor affecting length of breeding season is probably food supply. While breeding, both species feed intensively on insect larvae in the shallow, muddy-edged pools in the marshes. These larvae are extremely abundant in late May and early June, but decrease precipitously by mid-July, due to life cycle changes and in some years to the filling of ponds with rain water (Holmes, 1970). With the decline in availability of insect larvae near the breeding areas, adult sandpipers and their fledged young move quickly, soon after breeding is completed, to feeding sites along the rivers and sloughs and finally to the coast of the Bering Sea. The foods taken by *mauri* in July before their departure are almost exclusively insects; no change to marine invertebrates occurs while on or near the Delta. In contrast, once adult and young *alpina* reach the coast, they begin taking small molluscs and annelids while continuing to feed on some insects (Holmes, unpubl. data). At this point, the *mauri* population departs on migration; *alpina* stays longer and completes its molt.

The molt schedule and migration.—An earlier analysis of *Calidris* sandpipers breeding sympatrically in northern Alaska demonstrated two major patterns of breeding and molt schedules (Holmes, 1966a, c and ms.). In one, exemplified by *alpina,* all individuals stay longer in the N and molt is compressed into the short summer season so that it is completed before southward migration. In the other, shown by *C. melanotos, C. bairdii* and *C. pusilla,* the individuals leave the tundra in midsummer, move S to southern hemisphere wintering grounds, and molt during the winter months. From the studies in northern Alaska, I hypothesized that the early departure of the latter species was adaptive because it allows them to avoid mid- and late summer food shortages which frequently occur on the tundra and to complete more easily their long transequatorial migration. Also, the later stay of *alpina,* made possible by the close proximity of its N temperate winter quarters, permitted it to utilize late summer food resources in the arctic in the absence of potentially competing species.

From the results presented in this paper, it is now apparent that *C. mauri* represents a third and intermediate case. It nests early and then leaves the breeding areas by midsummer due to the environmental conditions discussed above. Although the adult's prebasic molt may commence while they are on or near the breeding areas, most molt is accomplished after arrival in N temperate or more southerly feeding

grounds. For this species, then, the relatively short migratory route has not resulted in a longer stay in Alaska.

Indeed, rather than lingering along the coast of the Bering Sea, Western Sandpipers move rapidly S in midsummer. The reason for this departure is likely a direct response to the lack of suitable prey, although it could conceivably be a result of interspecific competition with *C. alpina*. There is essentially no information on interactions, if any, between *mauri* and *alpina* along Alaskan coasts, but since the length of *alpina's* bill is nearly twice that of *mauri's*, they are undoubtedly capable of taking different kinds of prey. They do, in fact, during their period of coexistence on California winter grounds (Recher, 1966).

Although there is no information on the occurrence, distribution or abundance of marine invertebrates along the Bering Sea coast, very few amphipods, ostracods or other items that normally make up the Western's diet in coastal habitats farther S (Recher, 1966) were found in the stomachs of any sandpipers collected near Hooper Bay. This suggests that these kinds of invertebrates may not be common in this region. Therefore, Western Sandpipers, with their short bills not adapted for deep probing, may not have an exploitable food source along the Bering Sea in mid- to late summer. As a result, they move at this time to more favorable feeding areas in estuaries farther S along the Pacific coast. In contrast, *C. alpina* with its longer bill can exploit the food resources along the western Alaskan coast. At this time its stomachs contained annelids, small molluscs, isopods and other small marine invertebrates (Holmes, unpubl. data).

The result is again that *C. alpina* is left as the only abundant sandpiper along the outer river channels and the shores of the Bering Sea during the period when its molt is most intensive. Likewise, the Western Sandpiper is the only common small sandpiper along the Pacific coast in late July through early September. Each one thus exploits a food source and molts in the absence of other small, potentially competing species.

Therefore, it is evident that the timing of breeding season events, molt and migration of the Western Sandpiper is less affected by length of summer season and climate, than is true of *Calidris* species nesting at higher latitudes. The timing in these subarctic populations of Westerns, however, is significantly influenced by the changes in abundance of insect prey near the nesting areas and by the lack of alternative prey along the coast of the Bering Sea.

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