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## BREEDING ECOLOGY AND ANNUAL CYCLE ADAPTATIONS OF THE RED-BACKED SANDPIPER (*CALIDRIS ALPINA*) IN NORTHERN ALASKA

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During summer months sandpipers of the inclusive genus *Calidris* are conspicuous and important components of tundra communities. All 18 species in the genus are arctic or subarctic breeders, either in circumpolar distribution or in restricted sectors of the Arctic on one or both continents. After the breeding period they migrate southward to overwintering areas characteristic for each species. In annual cycles of sandpipers species-specific modifications are found that reflect different ways of adapting to high-latitude environments and to other features of their annual routines. This study examines the ecology and behavior of a common arctic-nesting species, the Red-backed Sandpiper or Dunlin (*Calidris alpina*), during its annual cycle, and emphasizes the breeding season near Barrow, Alaska. Some comparisons will be made with several congeners also breeding there, particularly the Pectoral Sandpiper (*C. melanotos*).

Information on breeding shore birds is derived chiefly from observations made by naturalists during faunistic surveys, for instance those of Murdoch (1885), Nelson (1887), Stone (1900), and Sutton (1932). For sandpipers breeding in Eurasia, observations have been compiled by Pleske (1928), Grote (1937), Johansen (1960), and Kozlova (1962), and for those in North America by Bent (1927). Some data, often only fragmentary, on behavior and ecology of particular species of *Calidris* in their breeding areas are available from the studies of Moore (1912), Haviland (1915, 1916), Dixon (1917, 1918), Southern and Lewis (1938), Keith (1938), Portenko (1957, 1959), and Drury (1961). Breeding of the Dunlin has received relatively little attention; the only specific reports available are those on populations in Great Britain by Brown (1938) and in northern Germany by König (1956). The principal deficiency of many of these studies is a lack of information on the populations throughout a series of years or even through one season. Thus it is impossible to analyze and compare fluctuations in timing of arrival, pair formation, density, nesting time, and flocking, which are common in arctic bird populations. The only investigation on an arctic shore bird sufficiently intensive to allow comparisons with the Dunlin is Pitelka's (1959) study of *C. melanotos* in northern Alaska.

### METHODS

Summer field studies of breeding sandpiper populations were conducted within 10 miles of the Arctic Research Laboratory near Barrow, Alaska (latitude 71° 20' N), from 1959 to 1963. Each year field work began before or during the arrival period of the birds in late May or early June and terminated in late August or early September after most sandpipers had departed.

The primary method of study was direct observation, and details on behavior, habitat, nesting, and local movements were recorded in a field notebook. Information obtained in censuses of established plots and in repeated visits to specific areas of the tundra provided systematic coverage of events through each season. Red-backs collected from those parts of the study area where

quantitative observations were not being made were examined for reproductive status, fatness, weight, and molt. Some were prepared as specimens, but only the wings of others were saved for later studies of molt.

In the Red-back, sexes are similar in coloration and plumage, but they do differ in size. Females are slightly larger than males, as evidenced by mensural characters (Witherby *et al.*, 1940) and body weights (see fig. 4). In spite of overlap in these characteristics the sexes can be distinguished in the field by length of bill and general body size in an estimated 60 per cent of observations or, when direct comparison of a pair is possible, in 90 per cent. In field observations sexes were usually distinguished by these criteria. In many instances identification of sex was further substantiated by collection of the individuals under observation.

Censusing provided data on breeding densities and also on timing of breeding-season events and other features of behavior. The census methods employed, including an evaluation of their advantages and difficulties, are described in detail by Pitelka (1959). Maps of territories were obtained by compiling records of territorial boundary conflicts and observations on locations of settled males on a master map. If the data were extensive enough they circumscribed the defended area and gave information on the activity centers of territorial birds. In addition the frequent and systematic coverage of a given area allowed for standard observations on seasonal changes in numbers and behavior, location and survival of nests, movements of broods after they left the nest site, and local movements of breeding and nonbreeding birds.

Censusing at Barrow was conducted primarily on a 100-acre plot ( $4 \times 25$  acres), located on upland polygonized tundra, one-quarter mile west of Ikroavik Lake and six miles south of the Arctic Research Laboratory. This plot was censused at three- to five-day intervals from early June through late July, and at less frequent intervals during August in the summers of 1960 to 1963. Another area used less regularly for census work was a 40-acre plot of ridge and upland tundra along the north sector of a beach ridge, one mile south of the laboratory and west of Pitelka's (1959) plot number one. Observations were made also on sandpiper populations on all parts of the tundra covered during daily travels.

Data on timing of breeding were obtained from (1) nests with incomplete clutches; (2) collected females in the process of laying; and (3) nests found during the incubation period, both on census plots and elsewhere on the tundra, for which, by using an incubation period of 21 to 22 days, laying could be determined from hatching dates. Observations of nests also gave an estimate of the number of nests remaining until hatching and therefore provided a rough measure of nesting success.

Information on growth of young could not be obtained by following individual chicks. But young Red-backs were collected, usually one per brood, whenever they were encountered in the field, and additional young were obtained from small mammal traplines that were in operation through parts of each summer. Plotting the weights of these chicks, which represent a sample of the growing population at any given period, provided an index to the time and rate of growth of young on a population basis. Those young sandpipers not collected were banded.

Seasonal changes in the availability and abundance of the insect food supply were followed by standardized sampling of insect populations through the summers, 1961 to 1963. A detailed report on seasonal changes in insect populations and on food habits of breeding Red-backed Sandpiper adults and their young is given elsewhere (Holmes, 1966).

For information on nonbreeding activities wintering populations of Red-backs were studied in coastal central California, chiefly on the east shore of San Francisco Bay near Emeryville and Berkeley, Alameda County. Field work was conducted also at the following localities: Humboldt Bay, Humboldt County, in the winters of 1957 to 1959; Morro Bay, San Luis Obispo County, and also San Quintin Bay, Baja California, in April 1961; and at frequent intervals at Bay Farm Island and Albany, Alameda County, and Bodega Bay, Sonoma County, in the winters of 1960 to 1964. Migrating populations were studied near Anchorage, Alaska, in May 1962.

In the nonbreeding period observations were made on arrival and departure dates, seasonal changes in population numbers, winter behavior, and interspecific relations among the shore-bird species coexisting on mudflat habitats. Specimens were collected at intervals throughout the period of migration and wintering in California for data on weights, food habits, fat condition, and molt.

Specimens collected in California and northern Alaska, combined with series borrowed from the major museums in North America, were examined for evidence on the timing and extent of molt. The results are to be described in another paper (Holmes, MS) but are reviewed briefly here in discussion of the annual schedule.

#### DISTRIBUTION

*Calidris alpina* is circumpolar in breeding distribution with recognized subspecies in Europe and Iceland, Scandinavia and western Siberia, central Siberia, North America, and Greenland (Peters, 1934). Although known to breed as far south as the British Isles and northern continental Europe (Witherby *et al.*, 1940) and into the taiga region of Siberia (Johansen, 1960), the species breeds mainly in the arctic tundra biome of high latitudes. In migration and in the winter it is found at North Temperate latitudes (AOU, 1957; Nørrevang, 1955; Kozlova, 1962), chiefly at coastal localities. Since the various subspecies of *C. alpina* differ in important features of their ecology (see discussion), all references to *C. alpina* in this paper, unless otherwise noted, are to the North American race (given as *pacifica* by AOU, 1957).

In North America the breeding range of *C. alpina* extends from the south shore of Bristol Bay on the Alaska Peninsula northward in tundra habitats along the west coast of the Alaskan mainland, on Nunivak and St. Lawrence islands, to the Arctic coast and thence east to the vicinity of Point Barrow and sparsely as far as the Mackenzie Delta, Northwest Territories, Canada (Gabrielson and Lincoln, 1959). Farther east the species is apparently absent for several hundred miles and then occurs on several islands of the Canadian arctic archipelago, on the northern Canadian mainland, and locally along the west and south shores of Hudson Bay (AOU, 1957; Snyder, 1957).

In western North America migrating Red-backs follow a coastal route along western Alaska, British Columbia, and the Pacific states; but farther east they pass through the midwestern United States and the Great Lakes region before moving to the Atlantic seaboard or to the Gulf coast (Cooke, 1910; AOU, 1957). In winter this species is found along the Pacific coast from British Columbia (rarely southeastern Alaska) to Baja California and the coast of Sonora, and on the gulf coast of the southern United States and the Atlantic coast from Massachusetts to Florida (AOU, 1957).

#### HABITAT IN NORTHERN ALASKA

In northern Alaska *C. alpina* breeds mainly on wet coastal plain tundra but is occasionally found in low foothill areas. General features of environment and vegetation near Barrow and inland on the arctic slope in general are described by Britton (1957) and Wiggins and Thomas (1962).

The habitats of the arctic coastal plain are a mixture of wet marshy lowlands, including ponds and lakes of varying sizes, and small raised mounds or ridges of relatively well-drained ground. These elevated areas vary in extent from old beach ridges several hundred yards wide, rising several feet above the lowlands, to large expanses of patterned ground with interspersed ponds and wet marshy troughs. Although these drained or upland areas form only slight relief above the relatively flat lowland tundra, they do provide some diversification of habitat. The resulting pattern is a mosaic of wet and drained habitat types that are available locally to all Red-backs, even within the confines of most territories. The habitats at Barrow that provide important feeding sites for shore birds, particularly Red-backs, are described by Holmes (1966).

Habitat selection by breeding Red-backs during the summer season varies with moisture conditions of the tundra and with food availability. Seasonal weather changes affect habitat conditions. Melt-off of the snow cover usually begins at Barrow during the last days of May and in most years is complete by mid- to late June. During this time flood waters collect in depressions and lowlands, and temperature fluctuations subject nesting birds to a period of uncertainty. The tempera-

ture sometimes drops below freezing, thus halting and prolonging the melt, or may rise suddenly, accelerating melt and causing severe flood conditions. Once melt is completed, the days generally become warmer, and in some seasons the partly drained sites on the tundra begin to dry. This warm weather continues, with year-to-year variation, through mid-July, and then, because of the shallowness of the melted layer over permafrost, the first rains quickly saturate the tundra. The weather normally continues rainy, and temperatures drop during August. By the end of the month the first regularly occurring freezes and snowfalls begin. Variations in this weather pattern occur from season to season and within each summer, and although the significance of these changes will be considered later, it should be noted that rain, snow, and freezing temperatures may occur at any time during the arctic summer.

Upon arrival, Red-backs generally occupy and begin to defend territories in the relatively well-drained or upland tundra and rarely in the expanses of lowland marsh. The uplands provide (1) the first snow-free areas, (2) suitable sites for nest locations, and (3) the most available and apparently preferred food of Red-backs in early summer—crane-fly larvae of the family Tipulidae, order Diptera (Holmes, 1966). The lowlands on the other hand are often flooded with melt waters at least during the first half of June and sometimes later. After hatching has occurred, the adults and their young move for two or three weeks into the wet marshes, which by then are relatively drained and in most years provide good cover for young. After the young birds can fly, they generally move toward the seacoast, where they feed along the shores of coastal lagoons and adjacent ponds. At the same time the adults begin to flock together on the uplands, in the same areas where breeding had previously taken place.

There are no detailed studies of the habitat of this species in other parts of its breeding range. However, Conover (1926) mentions that Red-back populations at Hooper Bay, Alaska, were found in wet marshy tundra and not on the slopes of the foothills that occur near there. At Wales, Alaska, Red-backs breed in the wet grass-sedge communities where there is little or no topographic relief and not in the adjacent hill country (Bailey, 1948; Holmes, MS). On the Taimyr Peninsula in northern Siberia, Tolmatschew (in Grote, 1937) states that *C. alpina* was found most often in the extensive wet lowland tundra; this was also true for the species in other parts of the tundra zone of western Siberia (Johansen, 1960). The fact that Red-backs are not commonly found in the foothill or mountain tundra of northern Alaska suggests that their breeding distribution is restricted to relatively wet grass and sedge tundra, as found on the coastal plain of northern and western Alaska.

#### ARRIVAL AND DISPERSAL ON BREEDING GROUNDS

At Barrow the timing of arrival of Red-backed Sandpipers and most other shore birds differs in each season. This variation is correlated with year-to-year differences in climatic events that either prolong or accelerate snowmelt, thereby influencing the availability of snow-free tundra.

The most complete sequence of early-season events for Red-backs was witnessed in 1962 when melt-off, once started, proceeded rapidly, making large areas of suitable habitat available to birds early in June. In this season the first Red-backs arrived in late May, coincident with the appearance of snow-free tundra. These were single birds, mostly males, which were still unsettled, moving from one open patch to another. By 1 June some individuals were settled, as evidenced by localized activities, display,

and territorial behavior. The main influx of birds began in early June with the arrival of flocks, consisting of three to 10 birds, which fed together on the rapidly expanding but still unclaimed areas of snow-free tundra. Initially these flocks were composed entirely of males. However, by the middle of the first week of June, flocks contained both males and females, and finally small groups seen between 6 and 8 June contained only females. In the second week of June a few pairs arrived, and as they moved across the tundra, they were chased successively from the territories of already-established birds.

In 1960 and 1961 melt-off started at roughly the same time as in 1962 but was delayed by cold weather in early June. As in 1962 the advance guard of individual Red-backs arrived in late May. But the main influx of birds was delayed for several days, and then they arrived mostly in pairs, not flocks. Thus when conditions are unfavorable in the breeding area, Red-backs apparently linger farther south where pairing may take place.

In 1963 snowmelt began very early so that by the end of May large expanses of tundra were already exposed. At this time, however, only a few individual Red-backs had arrived, corresponding closely to the number present at that period in other years, even though large areas of tundra were then available to birds. This suggests that migration in Red-back populations may be closely synchronized with the usual or average time of availability of inhabitable tundra, that is, for arrival at Barrow in early June, and that the birds are not always moving north just behind the advancing line of melting snow. The possibility remains, however, that conditions along the migratory route may have slowed them in this particular season. After the initial period in 1963 the major influx and sequence of arrival events followed closely those described for 1962.

Individuals arriving earliest settle on patches of open ground, and males perform territorial flights over tundra mainly covered by snow. Snow-free areas are not always continuous, so that displaying opponents are generally not in close proximity at this period. Yet the settled birds rigorously chase migrant or wandering individuals or flocks, patrol their boundaries regularly, and exhibit other signs of area attachment. As more and more tundra becomes exposed during the first two weeks of June, more males begin settling, females arrive, and frequency of courtship and aggressive actions increases.

Flocks in early June disperse by a gradual increase in aggressive behavior of their component members and by contact with already-settled individuals. In the first days of June no interactions among flock members were noted. But by the end of the first week, intragroup chasing began. Several individuals from the same flock either simultaneously or alternately would perform abbreviated flight displays. In these situations the individuals would fly into the air, circle 10 to 20 feet above the feeding group, at the same time giving the trilled song, and then land near the flock on the ground and resume their feeding activity. In two recorded instances, a bird that had just performed one of these displays returned to his flock and actively began to chase the other members. When he finally succeeded in supplanting the entire group, he gave a more intense aerial territorial display and remained in the area although the flock moved on. Whether or not these individuals were already settled before the arrival of the flock is not known, but the observations do suggest the initial phase of territorial behavior.

TABLE 1  
 NUMBERS OF ADULT RED-BACKED SANDPIPERS REMOVED FROM ELSON BLUFF  
 EXPERIMENTAL PLOT IN TWO SUMMERS

	1961		1962	
	Males	Females	Males	Females
1-5 June	2	1	4	2
6-10	6	5	4	0
11-15	2	0	2	2
16-20	0	0	1	0
21-25	0	0	0	0
26-30	0	0	0	0
Totals	10	6	11	4

Territorial claims develop gradually. In some instances a locally settled male will tolerate the presence of a flock in his territory and at the same time will defend against neighboring (and displaying) individuals. In fact, several cases were recorded in early June in which a local defending male would associate with a flock while feeding but would rise to display or defend the area when a neighboring, apparently settled bird began to advertise nearby or intrude upon his area. This ambivalent behavior occurred only for a week or so. By the second week of June territorial boundaries became more rigid, and settled males were intolerant of other males, occurring singly or in flocks.

Once some individuals had settled and most flocks had dispersed, it was difficult to detect newly arriving birds. To document better the duration of the arrival period and at the same time to determine the presence or absence of wandering or unsettled birds in the breeding population, locally settled (*i.e.*, displaying) Red-backs were systematically collected on a given area approximately five acres wide and 20 acres long, on upland tundra adjacent to Elson Lagoon, three miles southeast of the Arctic Research Laboratory. This area was typical breeding habitat, and in the summer of 1960 had supported four or five pairs of breeding Red-backs. The results of this removal experiment in the two seasons are given in table 1. Red-backs, either new arrivals or individuals from dispersing flocks, continued to settle in the area through 15 June, but after that time, with one exception on 17 June 1962, no additional Red-backs established territories on the experimental plot. From mid-June until wandering flocks appeared in late summer, no resident birds of this species were present on the plot although other pairs were breeding on adjoining tundra. Likewise, in other localities near Barrow where specimens were collected intensively during the first half of June, Red-backs would continue to arrive and to begin territorial and breeding activities until 15 to 20 June. But after that time no Red-backs were present.

This general pattern of arrival, local dispersal, and spacing is common for most sandpipers and other shore birds at Barrow, with the exceptions of the Red Phalarope (*Phalaropus fulicarius*) and the Pectoral Sandpiper, both of which arrive in numbers on the average slightly later than do the Red-backs and other shore birds (Pitelka, 1959; Pitelka and Holmes, MS). Furthermore, in the Pectoral, not only does the bulk of the population appear slightly later but arrival of individuals, perhaps first-year birds, continues through the month of June, thus contrasting sharply with the situation in *alpina*.

It is apparent that in northern breeding populations of Red-backed Sandpipers,

such as those at Barrow and probably in other high-latitude nesting shore-bird species, the time and place of pair formation are dependent on the environmental conditions of each particular year, and that pairing does not normally occur until the birds are on or close to their breeding quarters. The facts that (1) in years of late melt Red-backs arrive already paired, (2) in other seasons the latest birds to arrive are paired, and (3) all Red-backs are apparently present and settled by mid-June indicate that for this population there is a critical period by which arrival and pairing must be completed to maximize time available for breeding in the short summer.

#### BREEDING BEHAVIOR

*Territorial displays and aggressive behavior.* From the time of their arrival until early mid-July male Red-backs advertise their territorial claims by flight displays accompanied by song. The male rises from the ground in a relatively steep, rapid flight to a height of 10 to 150 feet (average about 50 feet) where he hovers on out-stretched and down-curved wings, stiffly beating or quivering through a shallow arc. At regular intervals of five to 10 seconds the wings are held rigidly in a down-curved position, the bird glides for one to two seconds, and then the vibrating hover is resumed. In the course of this flight display, which may last from a few seconds to several minutes (longest record was 3.5 minutes), the male moves slowly in a wide circle over the major part of his territory and thus performs a type of boundary patrol. Often in June one male is stimulated to display when an adjacent bird begins his hovering flight and song, and countersinging follows, with both birds displaying simultaneously.

Throughout flight display the male gives a series of short trill notes, repeated at a rate of approximately one per second. This series is occasionally interrupted by another trill (coincident with the occurrence of brief glides in the flight path), longer in duration (3 to 6 seconds), more musical, and descending in pitch and volume. This long trill is also delivered as the bird terminates his aerial display and descends to the ground on canted wings. As he lands, his wings remain in a vertical, up-stretched position for one to two seconds before they are lowered into normal resting posture. This pronounced landing display is observed only in the period of territorial defense, from early June to early July.

Territorial advertisement and defense also occur in other ways. Long aerial chases of one male by another are common in the period of local settling and spacing in early June but become less frequent when territorial boundaries are more firmly established and when wandering or unsettled birds are not present. When one neighboring bird begins to intrude upon another, the defender will take flight, set his wings at an angle of about 45° to 60° above the horizontal, and give the long trill. If this does not deter the oncoming bird, the local individual will begin to chase. In addition to aerial maneuvers, aggressive actions between males in early June also take place on the ground; these involve much chasing, ritualized posturing, and occasional physical combat.

In addition to the wing-up landing display described above, Red-backs also perform in a variety of contexts a wing-raising display given while standing on the ground, in which one or both wings are raised to the vertical, held there for one or two seconds, then lowered slowly into normal position. This action may be repeated several times in rapid succession, resulting in a type of wing-flashing. Frequently, the long trill accompanies this behavior. The wing-raising display, given by both males and females but more commonly by the former, is primarily performed during the prenesting and

incubation periods, becoming less frequent by mid- to late July. Provocations for the display are varied: it is given in response to other Red-backs in courtship and aggressive contexts, to birds of other species (even to individuals of unrelated groups, such as passerines, jaegers, and owls), to mechanical vehicles, and to man. This type of display is widespread among waders (Limicolae), where it probably has evolved from an intention movement to take flight, and in some species it has become ritualized and often integrated into other displays (Lind, 1961). Wing-raising in the Red-backed Sandpiper appears in many instances to indicate disturbance and/or awareness of a changing situation, but in this species it is also part of courtship and pairing behavior (see below). This display is not seen as frequently in *alpina* as it is in *C. bairdii* (Holmes, MS) or *C. maritima* (Keith, 1938).

*Courtship and pair-formation.* Pairing takes place either on the tundra within the territory of the male or during migration before arrival on the breeding grounds. The process of pair-formation consists of an increasing association between the sexes, and the bond is formed or at least reinforced through frequent aerial courtship flights involving both sexes, through ground displays including ritualized nest-scraping that progresses to nest-construction behavior, and through precopulatory actions.

The aerial activity of the pair consists of long, erratic flights or chases low over the tundra, in which the male pursues the female; this has been substantiated by identification of the sexes of birds under observation (p. 4) and by collection of chasing birds. Upon landing, both birds usually start to feed, and often the male will begin to perform a nest-scraping display. In doing this he settles into a depression on the tundra and begins to scrape the bottom of the cuplike hollow with his feet, throwing bits of grass and lichen onto the tundra surface behind him. He then settles down, presses and rotates his breast against the bottom of the cup, and vigorously wags his tail and folded wingtips, which are extending vertically into the air. The exposed white undertail coverts are conspicuous and may aid in attracting the female. The male then stands up and starts to pick up bits of grass or sedge blades from the vicinity of the cup and tosses them sideways with a flick of the head so that they fall next to him into the depression. This display is given by an individual male for a period of at least three to four days, often several times a day, and usually in several different depressions within his territory. The female gradually begins to take part, first by standing nearby, then by stepping into the cup after the male has stepped out but then moving off immediately, and finally by settling into the depression in a routine incubation posture, not generally performing the same exaggerated rotation motions of the male. She may, however, do some sidling in the cup and also pick some grass blades from the rim of the depression and toss them into the cup in the same way as the male had previously done. The female takes part in this display in several different cups, one of which is probably chosen for the nest site; she then apparently completes the lining of the cup. This nest-cup or nest-scraping display is found in many Limicolae and has been described in detail for *Limosa limosa* by Lind (1961) and for *C. ferruginea* by Holmes and Pitelka (1964).

The precopulatory behavior of *alpina* is not as complex as that of *ferruginea* (Holmes and Pitelka, 1964) or of *melanotos* (Pitelka, 1959). The male Red-back follows behind the female, raises the tail slightly (angle of 45° above the horizontal), raises one or both wings to an angle of about 60° (underwing surfaces face to the side, not toward the female who is in front of the male), and gives a trill note that is similar to the long trill of the aerial display song but is longer, uneven in pitch, and not so loud. After this, the male lifts himself into the air, hovers above the female,



lands on her back, and flutters there while copulation ensues. Afterward, both birds preen briefly, and then usually feed, or the male performs a flight display.

*Nesting behavior and the pair relationship.* From the time of pair-formation in early June until after hatching the pair remains together within the territory and then later in the season with the brood. Once eggs are laid, both the male and female incubate. From nonquantified observations females appear to do a greater share of the incubation early in the nesting period, and the share of the male increases as hatching approaches. This statement is based on several pieces of evidence. Early in the nesting cycle males are actively defending and advertising their territories, and females are found more often on nests. However, judging by observations in mid-June of males being flushed from nests and from well-developed brood patches of collected male specimens, males do incubate early in the nesting cycle but probably for only short periods. By late June and early July males are more likely to be found brooding than females, although the females are usually present and are occasionally flushed from nests. Perhaps as a result of being associated more closely with the nest later in the nesting period, males give more intense distraction displays than do females, especially in early July as the time of hatching approaches. If both adults are present at hatching, the male is the more solicitous and excited by the approach of an observer, while the female stands nervously nearby, giving a disturbance call but not performing a distraction display. Both sexes usually accompany the brood as it leaves the nest site a few hours or perhaps a day after hatching. When both adults are with young chicks, the male is the more active in decoy behavior, as at the nest. If only one adult is with the brood, it is usually the male, although in several cases when the female was found alone with the young, she performed full distraction behavior.

In *alpina* the female is usually the first adult to leave the family group, and the first flocks of adult Red-backs to form on the tundra in mid- to late July are composed almost entirely of females. However, this does not mean that the pair-bond is always broken during the fledging period, since in late July and as late as mid-August flocks of three to four flying young and two accompanying adults (male and female)—apparently a family group—have been observed feeding together on the tundra. Suschkin (in Johansen, 1960) stated that on the steppes of Siberia, south of the breeding grounds, adult male *alpina* were the first to arrive on southward migration in midsummer, indicating that females remain longer with the young. This is not borne out by the present study of *alpina* in Alaska.

Increased participation of males in nesting duties and care of the young as the nesting cycle advances is found in other *Calidris* species at Barrow, namely *bairdii* and *pusilla* (Holmes, MS). It is completely lacking in *melanotos*, in which the male takes no part in nesting activities and normally departs before the young hatch (Pitelka, 1959). Witherby *et al.* (1940) state that in *C. temminckii*, males do most of the incubating, and that in *C. minuta*, birds collected from nests were predominantly males. A contradictory report on *minuta* is given in Grote (1937), who quotes Russian sources indicating that females do most of the incubating, although no information is given on how the sexes were distinguished.

#### TERRITORIALITY AND BREEDING DENSITY

Spacing of breeding Red-backed Sandpipers is accomplished by a well-developed territorial system, including area defense against conspecific males, patrol of established territorial boundaries, announcement of occupancy by ritualized aerial displays

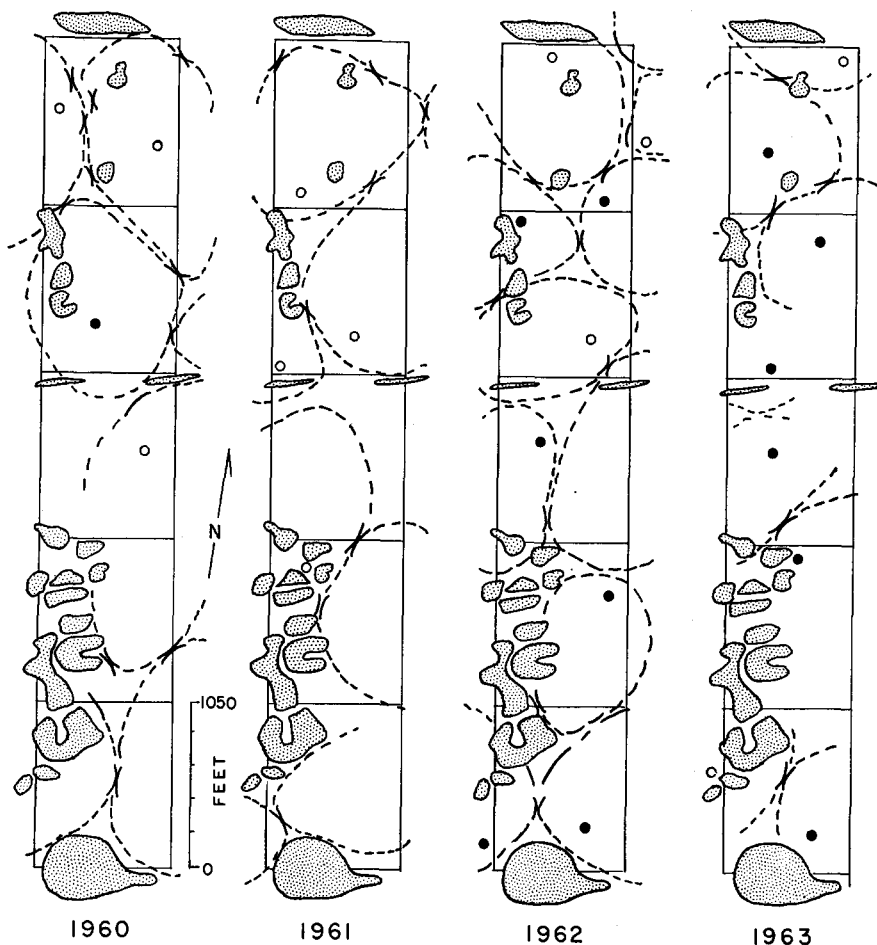


Figure 1. Spacing of male Red-backed Sandpipers in four summers on the Ikroavik census plot, six miles south of Barrow, Alaska. Paired lines represent observed territory boundary contact points between adjacent males; broken lines approximate territorial boundaries. Solid dots represent location of nests found; open circles indicate nests that were not actually found but were known to be present in the general vicinity. Stippled areas are large ponds.

with song, and restriction to a localized area. Since this territorial behavior regulates, at least in a proximate sense, the density of the breeding population (see below), it is important to know how this spacing is maintained, what intra- and interseasonal fluctuations in territory size and characteristics exist, how long the spacing mechanisms are in effect in the short summer, and what relationship the territorial behavior has to other events of the nesting cycle and to changes occurring in the environment. Data will also be given here on territoriality in populations of *C. melanotos*, the other common sandpiper species at Barrow, which provides a striking contrast with *alpina*.

Dispersal of Red-backs onto the tundra upon their arrival has already been described. It is clear that the Red-back, like other *Calidris* sandpipers in the Arctic (Pitelka, 1959), exhibits classical territorial behavior as defined by Howard (1920) and Nice (1941). But as is true of many precocial bird species, the territory contains

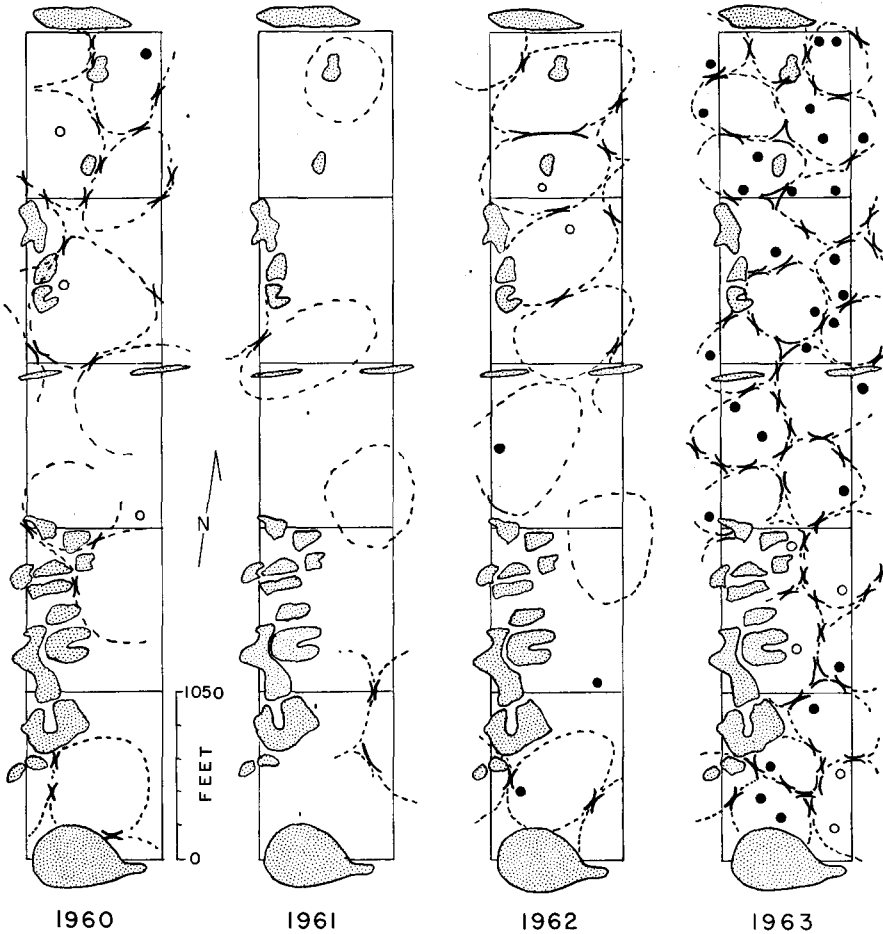


Figure 2. Spacing of male Pectoral Sandpipers in four summers on the Ikroavik census plot, six miles south of Barrow, Alaska. Symbols are the same as given in figure 1.

the nest site and feeding areas for the adults only during the incubation period (Hinde, 1956). Thereafter the adults with young often move away from the breeding territories.

Sizes of territories defended by male Red-backs range between 12 and 17 acres, as shown by data from populations in four seasons on the Ikroavik census plot (fig. 1). Variability was only slight within a season and only moderate from year to year. In 1960 territories were 14 to 17 acres in area, whereas in 1961, although fewer Red-backs were present, territory size or at least the area of ground frequented by the pair did not change appreciably. In the latter year it appeared that fewer individuals arrived at Barrow, so that with an initially low population density, many territorial males had no opponents against which to display, and correspondingly there was an early decline in territorial behavior. It is significant that when neighboring individuals were absent, the settled birds stayed within occupied areas of approximately 15 to 17 acres. They continued to patrol these weakly, apparently not increasing their activity or foraging radius, thus indicating that adequate space had already been obtained.

Furthermore, in two seasons (1961, 1962) when some individuals left in late June because of nest failure, remaining birds stayed within their original territories and showed no tendency to move into the adjacent areas vacated by departed pairs.

In 1962 territory size varied from 12 to 14 acres, slightly smaller than in other seasons, indicating that with a denser population some compression of the defended area can occur. Although display activity of Red-backs in 1963 was low, resulting in fewer observed aerial territorial boundary encounters (fig. 1), the nesting density as indicated by spacing of located nests was as high as in 1962 (fig. 1); each pair was occupying approximately 12 acres of upland tundra. However, the change in territory size exhibited by *alpina* was insignificant when compared with that of *melanotos* in the same four years on the Ikroavik census plot (fig. 2), where territory size varied from only two to more than 20 acres per male. In *melanotos*, in which the pair-bond is weak and brief, more than one nest can occur within the territory of a male, and the species is polygamous.

In all bird populations at Barrow, territorial boundaries on the tundra, as shown for the two sandpiper species on a fixed plot in successive seasons (figs. 1 and 2), varied greatly from year to year. This can be attributed to the relative uniformity of topographical and vegetational features. Since territory size was less in years of high density, the location and size of territories were undoubtedly influenced by the number of neighboring birds present during the main period of territorial establishment, and boundaries became fixed through territorial encounters with adjacent males. Since there is no direct evidence concerning the degree to which the same individuals return to particular areas on the tundra, no information is available on the role experience plays in causing a bird to occupy a particular territory. In two instances on census plots a nest was found in the same site in two successive years, and the territories occupied in both years had approximately the same boundaries, indicating that perhaps the same adults had returned to familiar territory.

It is noteworthy that at least some young Red-backs apparently return to the vicinity of their hatching site to breed in their first breeding season. Of 34 young Red-backs banded in five years of field work, two were collected at Barrow in the summer following their hatch. When taken (27 June 1961; 7 July 1962), each was defending a territory within one-quarter mile of its hatching site; both were males in breeding condition with well-developed incubation patches. Thus, if the ability of young to home is quite well developed, it might be expected that adults may also return to former breeding areas in successive years.

Changes in territorial activity and occupancy of male Red-backs in each season were measured by recording the number of males actively defending territories on the Ikroavik census plot; the results are given in figure 3 as number of males defending per 100 acres during each summer from early June to late July. Territorial display activity of male Red-backs was maximal between 15 and 25 June. In each year (except 1963) the major decline in early July corresponds with the hatching of eggs, at which time males ceased defending and advertising territories. The slightly earlier decline in 1961 and 1962 was due to increased nest failures (from predation by jaegers, *Stercorarius parasiticus*, and/or *S. longicaudis*), resulting in early departure by some of the adults, their spaces not being filled by others. In 1961 a very heavy loss of eggs due to nest predation combined with a low initial number of breeding birds resulted in a low frequency of encounters between individuals and therefore a low intensity of display (fig. 3). In 1963 display activity was at a minimum, although as demonstrated previously, nesting density was at least as great as that of other

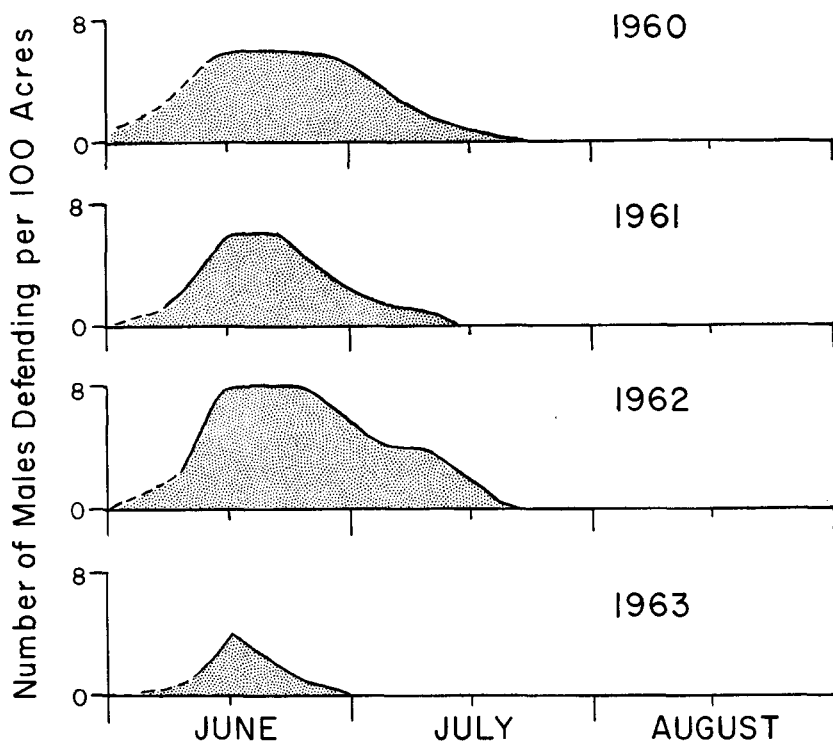


Figure 3. Duration of territorial-defense behavior and occupancy of territories by Red-backed Sandpipers on the Ikroavik census plot in four summers at Barrow.

seasons. A major difference between the summers being compared was that in 1963 when aerial activity of Red-backs was low, the density of Pectoral Sandpipers was exceedingly high (fig. 2). Because male Pectorals are extremely active and vocal in display and because they were so abundant, it is suggested that in 1963 their dominant activity may have inhibited the aerial display of *alpina*. However, very few encounters or interactions between these two species were noted. When occurring they were the result of one bird getting in the way of the other, and produced nothing more than an alarm note or, in two cases, a brief chase of the Red-back by the Pectoral. It should be noted that the two species are sympatric over a wide part of their breeding range. At Barrow some nests of Red-back and Pectoral were only 30 feet apart. No detectable interference between incubating birds was seen, and both species had approximately the same nesting success (Holmes, MS). Yet the fact remains that the aerial activity of *alpina* was significantly lower in 1963 than at any other time in the five seasons studied, and no other explanation for this presents itself.

Red-backs hold territories mostly on the upland tundra, including those areas of well-developed polygonized ground. As implied in the foregoing discussion, the Red-back pair is confined to its territory from the time of arrival until midsummer, and all activities including courting (if it has not occurred before arrival), nesting, and feeding occur within the defended area. Occasionally, individuals whose territories bordered on large lowland marshes where there were no settled pairs of Red-backs moved off the defended area to feed. But these situations were rare.

After the eggs hatch, territorial behavior rapidly subsides, and the two adults and their chicks begin to wander freely, often from the now-dry uplands into the wetter marshes that usually were not included within the previously held territories. If family groups moved onto an actively defended territory, that is, one in which the eggs had not yet hatched, the occupant whose aggressive tendencies were already waning at this time remained unconcerned, and no conflict resulted. Occasionally, family units met and intermingled as they fed. But no interactions were noted, the groups separating and moving off independently.

From the results of the removal experiments and other observations on arrival behavior (see above), it is seen that limits are imposed on the number of breeding birds early in the breeding period. Extension of territorial behavior beyond late June would seem energetically wasteful, and in any event the ceiling on breeding numbers is by then adequately established. A more important feature of the decline in territorial behavior at or near the time of hatching is that from then on adults and their precocial chicks are able to move freely over the tundra beyond boundaries of the parents' former territories. Territoriality in this precocial species therefore functions as a spacing mechanism only in the period when birds can possibly settle and undertake nesting with a likelihood of success. Once this critical period is past, territorial activity wanes, and, as in *alpina*, the male becomes more involved with the nest and chicks or, as in *melanotos*, he begins his southward migration (Pitelka, 1959).

The striking feature of the territorial system in *alpina* populations is that territory size does not vary greatly from year to year. Instead, the breeding density in the four years of this study remained relatively stable, averaging approximately seven pairs per 100 acres. In addition, once a pair was established on a territory, it remained there at least until the eggs hatched, and, with the exception of the few individuals leaving after their nests were destroyed, there was little flocking or significant movement of birds on the tundra during the nesting period. In contrast the spacing of *C. melanotos* showed a high degree of yearly fluctuation, as evidenced by differences in territory size (fig. 2) and by a significant amount of flocking of unsettled, newly arriving, and/or nonbreeding birds during late June and early July (Pitelka, 1959; Pitelka and Holmes, MS). These characteristics, together with the fact that in *melanotos* the pair relationship is a brief, almost transitory affair, produce a population structure that is more variable in both time and space.

A question that arises concerning these different spacing phenomena but that is not answerable within the scope of this study, is: To what degree are sandpiper densities observed at Barrow representative of those occurring throughout the Alaskan breeding range? My impression from brief visits in the nesting season to several localities in Alaska (Meade River Coal Mine, 60 miles southwest of Barrow, in 1960; Wainwright, 100 miles southwest of Barrow, in 1960; Wales, Alaska, in 1961) and from a 12-year record of bird populations at Barrow (Pitelka, personal communication) is that *alpina* densities are in general similar to those recorded at Barrow in this study. On the other hand, the density of *melanotos* characteristically varies by year and locality. The only other species in northern Alaska that fluctuates in numbers as much as *melanotos* is the Red Phalarope, a shore bird that has other characteristics of population dynamics and social organization in common with *melanotos*.

Thus the highly compressible population together with other special features of population structure and social system of *C. melanotos* may allow it opportunistically to take advantage of local situations in which environmental factors are particularly favorable. On the other hand, the population density of *alpina*, unvarying from year

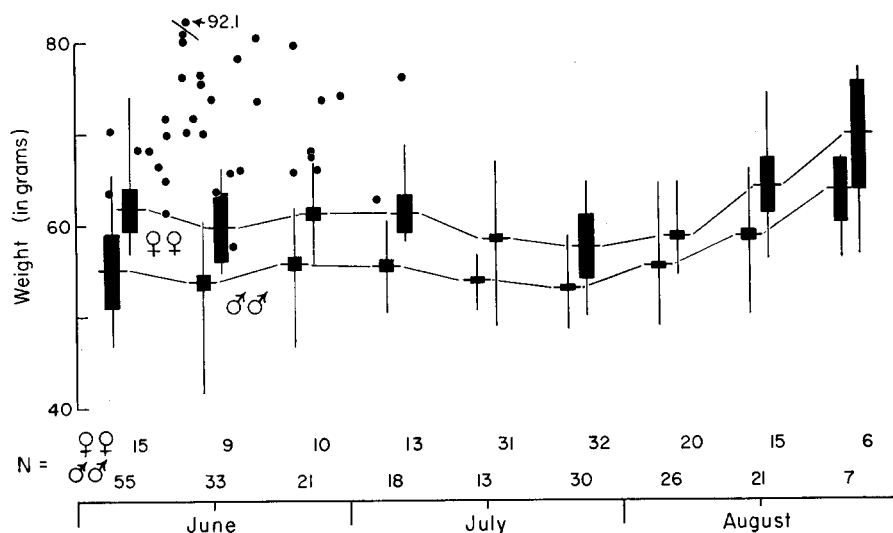


Figure 4. Body weights of adult *C. alpina* at Barrow, Alaska, in the summers 1959 to 1963. Mean weights for each 10-day time interval are connected by the horizontal line; the vertical lines represent range, and the bars a distance twice the standard error on each side of the mean. Weights of egg-laying females are shown individually by dots.

to year, and the large territory occupied by each pair may be corollaries of the fact that adults of *alpina*, unlike those of *melanotos*, remain on the tundra through the summer, utilizing the food resources there for the completion of molt and for pre-migratory conditioning. In *alpina* the number of birds present in late summer is limited early in the season, and the large, rather fixed territory size may have evolved as part of a long-term adjustment of population density to average environmental conditions exploited for both breeding and molt. In *alpina* the spacing system may represent a more conservative way of adapting to the variable conditions at high latitudes.

#### ADULT BODY WEIGHTS IN SUMMER

Body weights of adult Red-backed Sandpipers collected in summers at Barrow are given in figure 4. Since differences in weight between summers were insignificant, weights from specimens taken in all five summers, 1959 to 1963, were pooled and then divided into 10-day intervals before statistical summary. For egg-laying females weights are given separately as individual points on the graph.

In both sexes weights fluctuate only slightly during June and July, females being consistently heavier than males. Red-backs arriving in early June have little if any body fat, their weights being close to the minimum recorded. As females begin to lay eggs, their body weight increases markedly; the heaviest recorded weighed 92.1 gm. A general decline in weight in midsummer is evident in both sexes (fig. 4). Most individuals examined from this period were lean. This low point in the weight cycle in mid- and late July may be a result of increased energy drain brought on by nesting activities and by physiological processes involved in molt, which begins to increase in intensity at this time (see discussion). In late summer Red-backs begin to increase in weight as a result of deposition of fat. This occurs during the period of postbreeding drift, before migratory departure.

## REPRODUCTIVE CONDITION AND NESTING ACTIVITIES

Depending on times of arrival, weather conditions in the breeding area, and stage of pair formation, Red-backed Sandpipers begin nesting activities within less than a week after arrival. After they are paired, courting behavior grades into a series of ritualized nest-scraping displays that lead to the location of a nest site. The nest is situated on relatively well-drained upland tundra within the territory and is placed in a natural cuplike depression in the ground, usually surrounded by low-growing but dense vegetation. After the nest is formed, the female begins to lay one egg per day until a set of four has been completed. Incubation usually starts when the clutch is complete but occasionally with the laying of the third egg.

Upon arrival at Barrow in the last days of May and early June male Red-backs have fully developed gonads, as indicated by size of left testis (fig. 5). Late-wintering and/or early-migrant males collected between early April and mid-May along the California coast had recrudescing gonads 2 to 5 mm in length (winter size  $\leq 1$  mm); two specimens collected near Anchorage on 22 and 24 May 1962 had gonads nearly the size (9 and 10 mm, respectively) of those birds taken at Barrow in early June.

Variation in testis size in early summer was most marked in 1961 (fig. 5). In this particular season in contrast to other years, the snowmelt was delayed, and fewer birds arrived in late May and early June. Those that did appear had smaller testes than did individuals at comparable times in other summers. Adverse weather conditions associated with that season at Barrow and probably also farther south along the Bering Sea coast (migratory route) not only delayed arrival but also retarded gonadal development (see later comments on nesting dates in 1961).

Regression of male gonads begins in late June and is complete in less than a month, before the birds begin to leave the tundra. Decrease in gonad size corresponds closely with the decline in territorial and aggressive activity in most seasons (see fig. 3).

In contrast to males, gonadal recrudescence in female Red-backs occurs chiefly in the first two weeks of June after arrival on breeding grounds, although some growth may take place before arrival. Females collected in April and early May along the coast of central California showed slight signs of ovarian enlargement, some follicles being 1 or 2 mm in diameter (winter size,  $\leq 1$  mm), and one bird taken 24 May 1962 near Anchorage, Alaska, a site several hundred miles from the nearest breeding area, had follicles to 3 mm. Females taken in the first days of June at Barrow have follicles no larger than 3 to 4 mm in diameter, apparently slightly more developed than in migrating birds farther south.

Early in the second week of June at Barrow as the main laying period approaches, follicular size increases rapidly, reaching 20 to 22 mm at the time of ovulation. Most females collected in mid-June were in the process of laying, and occasional females in late June or early July were also found with recently collapsed follicles or eggs about to be laid. After eggs are laid, the remaining follicles rapidly regress in size, and most female Red-backs (with the exception of the late layers) have small follicles (1 mm in diameter or less) by 25 June.

*Egg-laying.* Timing of egg-laying in the Red-back population as measured by the dates at which a clutch is complete in each of four summers, 1960 to 1963, and for all four seasons combined, is given in figure 6. The period during which clutches were completed was 6 June to 6 July with the peak of laying occurring in the interval 12 to 18 June. Early and late clutch dates account for only a relatively small percentage of the total, and the significant effort in egg-laying occurs in mid-June.

The lack of distinct peaks in egg-laying in 1960 and 1961 and other variations in



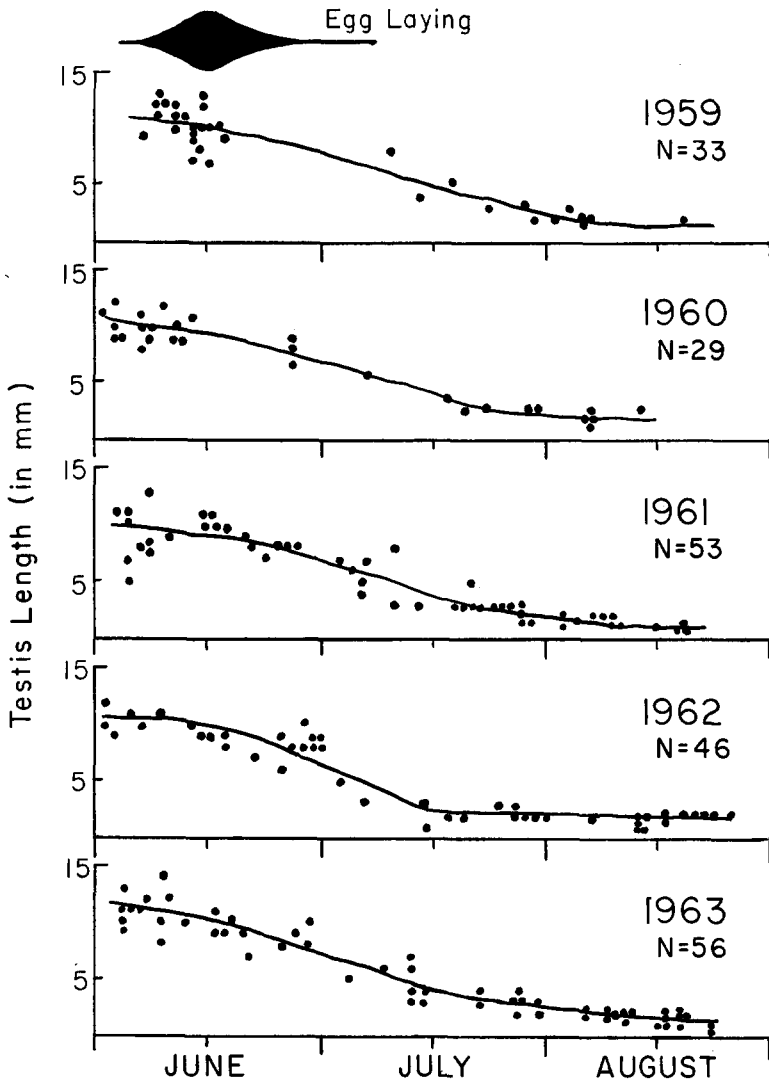


Figure 5. Reproductive condition of male Red-backed Sandpipers collected in the breeding area at Barrow, as indicated by length of left testis.

the data can be attributed, at least in part, to small sample sizes in those years, especially because the ability of the observer to find nests increased during the course of the study. Nevertheless, some yearly differences are apparent. In 1961 there is a suggestion that the mean time of laying was either later than in other years or at least that there was a greater spread in the time of laying. The latter explanation seems more plausible and is given further support by variation in reproductive conditions of males in 1961 (fig. 5) and by data on growth of young, which in that season show a wider scatter of ages (by weight) in the growth period (fig. 7). This variability in 1961 can be accounted for by an early, then delayed melt that allowed some individuals to begin nesting early but delayed the arrival and nesting of others.

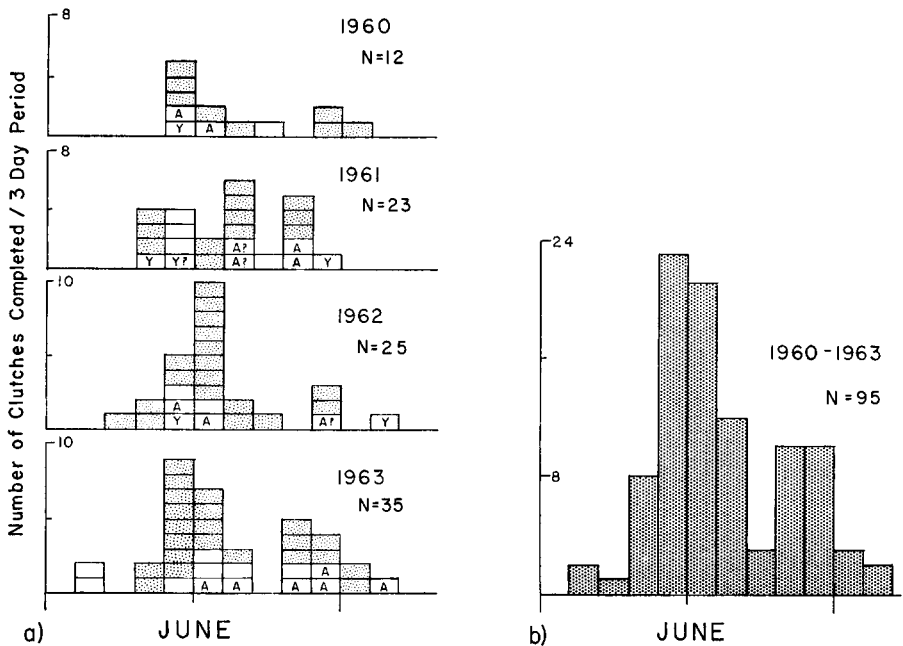


Figure 6. Dates of egg-laying in the Red-backed Sandpiper population near Barrow in each of four summers, 1960 to 1963 (in a) and in all four summed (in b). Each block represents a clutch completed in each three-day interval (1-3 June, 4-6 . . .). In a, the blank open boxes represent clutches incomplete when found and then followed until completion; open boxes with letters represent egg dates obtained from females collected during the laying period, the letter indicating age (Y = one-year-old females in their first breeding season; A = females older than one year); stippled boxes represent clutch dates obtained by extrapolation from hatching dates (see text).

In all seasons a few clutches were completed before 12 June (fig. 6), the earliest records being two on 6 June 1963 and one 9 June 1962. Since one egg is usually laid each day, this places the time of first oviposition on 2 and 5 June respectively; both of these dates are very early, although the melt in both seasons began promptly in late May and proceeded rapidly. These early nests were in areas that had been the first to become free of snow, and the adults that had formed them had most likely been among the first to arrive, for only such individuals would have had time to establish themselves, court, and mate before laying the first egg on 2 June. The extreme earliness of these records is emphasized by the fact that in all five summers at Barrow, I did not find evidence of earlier breeding in any other shore bird. Since none of the females collected in early June was in laying condition and only a few nests have been found in this interval, it can be concluded that nesting before approximately 10 June is relatively infrequent, occurring only in those years when local conditions permit.

In each year several clutches were completed during the last days of June and the first week of July (fig. 6). The latest was on 6 July 1963, when a female was collected that had just laid three eggs and had a fourth in the oviduct.

Because of the shortness of the summer and a three-week incubation period in

this species, it is impossible for Red-backs at Barrow to lay two consecutive and successful clutches. A second clutch, however, may be laid if the first is lost or destroyed.

Before considering renesting, two alternative explanations for late nestings must be mentioned. First, it is possible that these may be late-arriving or surplus birds that begin to breed later in the season than do most members of the population. However, the results of the removal experiment (p. 8) demonstrate that the arrival period of Red-backs is past by mid-June. Second, the late nesters may be nonbreeding yearlings. Although Kozlova (1962) states that *alpina* does not breed in its first year, contrary evidence was obtained for the Alaskan populations, based on recoveries of two banded breeding male Red-backs of known first-year age (see p. 14), and on age determination of collected breeding Red-backs. For the latter, criteria based on plumage characters were developed using individuals of known age in conjunction with a large series of Red-back specimens (Holmes, MS). This technique was applied to female Red-backs collected in the egg-laying period; results are given in figure 6. Of several females completing clutches after 26 June, five were adults and two were birds in their first breeding season. Since first-year birds were breeding as commonly as adults early in the season, the data indicate that year-old females do nest early as well as late in the laying period.

Finally, the adult female depositing eggs on 6 July, as well as others laying in late June, had well-formed, vascularized, and opaque brood patches, a condition that normally occurs only after a bird has incubated actively for at least several days. Because nest losses occur owing to predation (mostly by jaegers) and occasionally to floods during the late stages of melt, it becomes clear that late-nesting individuals represent birds whose earlier nests have failed. The height of the second peak in laying dates (fig. 6b), although cumulative for the four different seasons, suggests that a significant number of birds do renest. Although the large dip separating the second clutches from the primary peak may result from inadequate data for that interim period, it seems more likely that, since egg production represents a heavy energy drain, the gap results from the period required for a female to attain the physiological capacity to lay a second set of eggs. If nest loss is concentrated in one period as it might be in event of a weather catastrophe, this would also account for the relative synchrony among the late nesters in some years.

Laying of a second clutch by other shore birds at Barrow has not been recorded, although the laying span in other sandpiper populations, for example, in *C. melanotos* (Pitelka, 1959), is similar to that shown here for *alpina*. It may be that laying of a second clutch when the first has been destroyed is more common among arctic sandpipers than formerly supposed. No reports of renesting in any other high-latitude shore birds have been found in the literature, although several exist for shore birds, particularly plovers, breeding at temperate and lower latitudes (Witherby *et al.*, 1940; Boyd, 1962).

The breeding effort in the Red-back population as measured by egg-laying is therefore concentrated in mid-June with earlier nesting possible when environmental conditions permit; attempts at renesting are made following nest loss within a certain restricted period. Since nesting does not begin immediately upon arrival but is delayed until mid-June on the average, and in addition, since breeding activities of other sandpipers on the tundra are synchronous with those described here for *alpina*, a timing mechanism for breeding in arctic bird populations other than the mere availability or accessibility of habitat or favorable weather conditions may be in operation. This will be considered later.

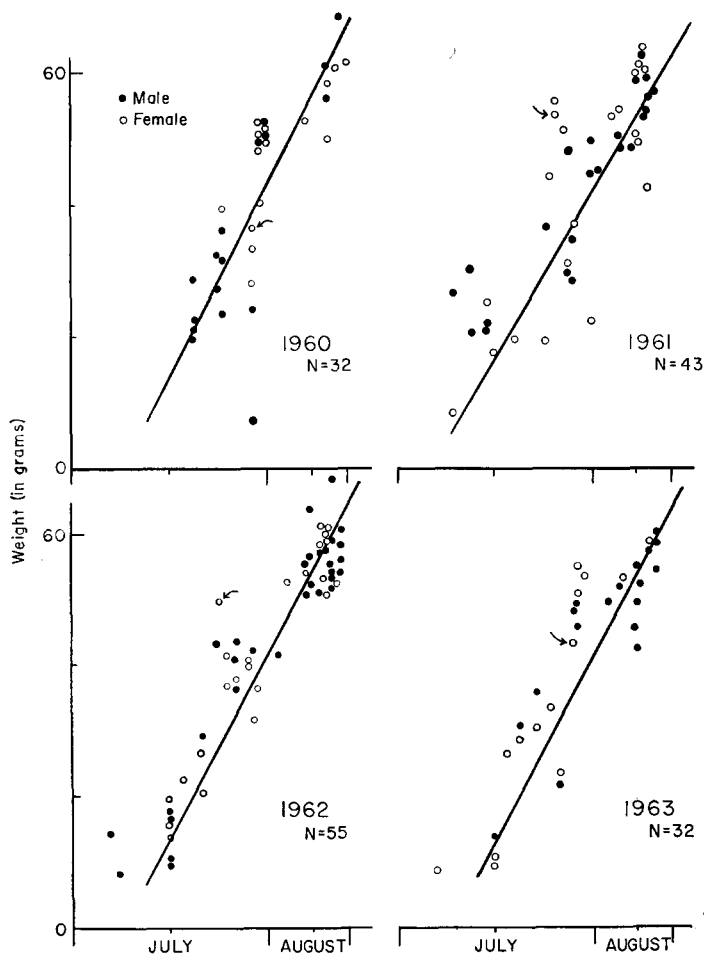


Figure 7. Regressions of weights of young Red-backed Sandpipers collected at Barrow in four summers, 1960 to 1963, against time (log). Arrows indicate first flying immatures.

*Hatching and growth of young.* Eggs begin to hatch after 21 or 22 days of incubation. Hatching of all four eggs in one nest is usually completed in 12 to 24 hours, but occasionally may take as long as 48 hours, depending on the time at which incubation had started. Time of hatching in nests in which this was not recorded directly was obtained by adding 22 days to the dates for clutch completion. The hatching period recorded at Barrow in this five-year study extended from 28 June through 26 July, the extreme dates, but the peak of hatching fell between 4 and 10 July.

Within hours after the last egg hatches, the precocial chicks leave the nest site, usually accompanied by both adults. Attempts were made to follow the movements of broods after they left the vicinity of the nest by banding the young as soon after hatching as possible; however, in most cases these marked individuals were never encountered again, even on the succeeding days when arduous searches were made for them. The only marked brood found subsequently was one banded in its nest

1 July 1962 and found 10 days later a half mile away. This brood and others, as judged from field observations on location of broods in mid-July, were in wet lowland *Carex* and *Dupontia* marshes at this time of the summer, or in the vicinity of small ponds or wet polygon troughs; they rarely remained in upland tundra where nesting had occurred.

Because of difficulties in relocating broods and in maintaining shore birds in captivity, it was not feasible to measure directly the growth rates of individual birds. Instead, an estimate of growth in the population as a whole was obtained by plotting weights of collected young Red-backs against time from their first appearance until their departure in late summer. These are given in figure 7 for young in each of the four seasons, 1960 to 1963.

At hatching, young Red-backs weigh approximately 7 gm; within three to four weeks they reach adult size of 50 to 60 gm. No differences in growth rates or absolute weights between the sexes were noted until they approached adult weight, when the females tended to be slightly heavier (see table 2).

The first flying young observed or collected in each season is indicated in figure 7. The time between hatching and first flight, calculated in minimum time from the earliest hatching date possible, ranged between 21 and 26 days. Thus, chicks are able to fly in slightly more than three weeks following hatching, at which time they are about three-quarters adult size.

The regression lines for growth in each of the four years (fig. 7) are nearly identical; but when distribution of weights is compared between seasons, it appears that in 1961, a year in which the melt-off was late, there was a greater scatter in weights than in any other year. The occasional points far below the line late in July in most seasons represent offspring from renestings.

The similarity in growth rates in different seasons in which melt-off of snow, times of arrival, amount and temporal distribution of rainfall, number and frequency of freezes and snowfalls differed suggests that in these arctic sandpiper populations, surviving young follow a relatively constant rate of growth regardless of the phenologic and weather characteristics of the particular season, and that there is a rather fixed time of breeding in each summer. Also, with such rapid growth, young Red-backs are nearly adult size and able to fly weeks before the usual onset of winter conditions (late August). Therefore, the last month of the arctic summer is used for final growth, especially for late-hatching chicks if they survive at all, in preparation for migration, and for part of the postjuvinal molt that begins during this period (see below).

*Breeding success and mortality factors.* Estimates of reproductive success in the Red-back population were obtained from observational data on potential mortality factors (e.g., presence of predators), on amount of flocking, and on relative differences in survival of nests and young in different seasons.

On the breeding grounds at Barrow the only significant predators on shore birds are wandering, nonbreeding Long-tailed and Parasitic jaegers. In 1961 and 1962 the Parasitics were present in small numbers throughout the summers, but Long-tails appeared in flocks as large as 50 or more in mid-June and remained on the tundra until late July. During this time both species fed on birds' eggs and young, insects (mostly crane-fly imagoes), and occasionally on lemmings (*Lemmus trimucronatus*). In 1960, in the presence of dense populations of nesting Pomarine Jaegers and Snowy Owls (*Nyctea scandiaca*), which rarely feed on shore birds (Maher, MS; Pitelka *et al.*, 1955), the flocks of Long-tails and Parasitics were not present; consequently, nest loss in that season appeared to be low, and survival of chicks, judging by the

number found on the tundra in midsummer, was high (see below). In 1963 scattered pairs of Pomarines bred at Barrow, and other species of Jaegers did not arrive early in the season; however, flocks of Long-tails and scattered Parasitics did appear in mid-July after most of the shore-bird nests had hatched, resulting in predation on young birds.

Effects of weather on nesting success are varied. One nest was flooded by melt water in mid-June 1962, but in 1963 another with young about to hatch was lost when the adults were prevented from returning to the nest by a three-inch layer of snow. The occurrence of snow and rain during July 1963 demonstrated how vagaries of weather can change conditions in midsummer. In addition to causing the above-described mortality, adverse weather reduces the availability of important food species (Holmes, 1966). The effect of weather-caused food shortage on survival of young Red-backs was not measurable directly, but it was my impression in 1963 that in comparison with the four previous seasons fewer young Red-backs were present on the tundra, although no starving young were found. The fact that the population growth rates of young Red-backs in 1963 were closely comparable with those found in other years indicates that in spite of yearly differences in survival and food supply, the remaining young continue to grow at virtually identical rates in each season.

Nest loss also resulted through the activity of lemmings on the tundra in 1960, a year of their maximum abundance. In June of this season these rodents were very active on the tundra surface, and several records of nest-site disruption were obtained. In one case a lemming had undermined the nest of a Red-back; eventually the eggs rolled out of the nest into the burrow, whereupon the adult birds deserted.

The amount of flocking of adult Red-backs in July, a time when they should have been incubating or attending their young, is another indirect indicator of nesting success. In 1960 flocking of adult Red-backs before the end of the fledging period (late July-early August) was not conspicuous. In 1961 and 1962 groups of both males and females (4 to 8 individuals) were frequently observed on the tundra between 1 and 20 July. Specimens collected from these flocks had well-developed incubation patches, indicating recent brooding activity. Because the flocks contained males as well as females, there is little likelihood that the females left the broods early, leaving males with young, as they do to some extent later in July in all years when flocks are composed chiefly of females. In 1963 flocks were not noted until after 15 July when small groups (3 to 6 individuals) were observed, correlating with increased loss of young, due to a later arrival of important predators and to the inclement weather in July.

Although data on breeding success are difficult to obtain, and most information that I have is indirect, rough approximations can be attempted from the few figures available. Nest loss in each season, given as the number of nests lost before hatching per number of nests found in the particular season, is as follows: 1960, 1/4; 1961, 2/4; 1962, 4/17; 1963, 1/17. The sample sizes in the first two years are too low to be useful. But the difference between 1962 and 1963, although not statistically significant, correlates with the presence of a large number of predators early in the summer of 1962. On the basis of all figures available, it appears that nest loss during the egg stage is relatively low, less than 50 and probably about 20 to 25 per cent. This agrees with the generalization made by Boyd (1962) that in the Charadrii, 66 to 96 per cent of eggs hatch. Survival of newly hatched and growing young is even more difficult to quan-

tify. But data were recorded on the number of young per brood (nonflying) encountered on the tundra during July; the average numbers of young and the number of broods found are as follows: 1960, 3.7 (6); 1961, 2.6 (5); 1962, 2.3 (6); 1963, 2.0 (6). Although the samples are small, they show that in 1960 in the absence of shore-bird predators, more young survived through July, whereas in 1961 and 1962, more were lost, probably to Jaegers. In 1963, the low survival of young represents the combined impact of predation and adverse weather conditions. Thus, a posthatching mortality as high as 50 per cent, at least in some seasons, is possible. Estimates by Boyd (1962) for shore birds in general indicate that success from hatching to fledging averages from 40 to 80 per cent.

Thus in the Red-back and apparently in other Charadrii (Boyd, 1962), nest success and survival of young to fledging are relatively high as compared with those of passerine birds (see Farner, 1955). Martin-Lof (1961), using Swedish banding records, estimated first-year mortality for juvenile Dunlin at 62 per cent, but Boyd (1962) gives the value at approximately 75 per cent. Using plumage characteristics as age criteria (Holmes, MS), the fractions of one-year-old Red-backs in the breeding population at Barrow (sample collected between 1 June and 10 July in the four years 1960 to 1963) are 30 per cent for males ( $N = 65$ ) and 28.6 per cent for females ( $N = 45$ ). Thus an average first-year mortality rate of 70 per cent is indicated.

#### POSTBREEDING DRIFT OF FLOCKS

After the end of the arrival period flocks of Red-backs are not seen in some seasons until the first week in July, when small groups of adults are found wandering in marshy tundra habitats. These groups contain both males and females that have presumably lost their nests or broods. Flocks in mid- and late July are composed of the first adults, usually females, to leave their mates and broods. After 20 July, as young Red-backs are beginning to fly, family bonds begin to weaken. The immatures gain their independence, and there is a gradual separation of young from adults. These two age groups remain relatively segregated in habitat for the remainder of their stay at Barrow, the young moving to coastal areas or along the larger lakes and rivers, the adults remaining on the inland tundra. From the last days of July through the end of August, adult Red-backs move together in loosely organized flocks, consisting of from two to 30 birds. Flock size generally decreased during late summer, except for one large group of 47, which included four immatures, noted in the latter half of August 1961. Departure of adults begins in late July and continues through August; nearly all have left the tundra at Barrow by 1 September. In 1963 adult Red-backs were difficult to locate on the tundra in late July and early August, suggesting that they had left, at least temporarily, or changed habitats, for example, had moved to and along the coast, perhaps because of the local food shortage mentioned above.

It is possible that some adult Red-backs at Barrow in August are not from the local breeding population but are migrants from farther east or from inland localities. This might be particularly true in a season like 1963 when birds were scarce in late July but then became relatively common again in August. However, the fact that no late-summer increase in numbers is known to occur at Barrow and that the number of Red-backs normally declines gradually suggests that the birds there represent mainly if not wholly the local breeding population and that they leave gradually and move south and westward on migration. Movement at Barrow is across the

tundra and not along the coastline, but Bailey (1948) observed flocks of adults and young "on the flats" near Wainwright in the last week of August.

Once free of their parents young Red-backs at Barrow move coastward and are found most commonly during August feeding near the gravel-bordered lagoons, along the shores of larger lakes and ponds near the coast, and along rivers and their deltas. Most of the young remain in flocks of their own at least through August and early September. They are only occasionally seen on upland tundra, sometimes with a flock of adults. Departure of immatures from Barrow begins during the last half of August and occurs precipitately before 1 September. Immature Red-backs have been seen at Barrow as late as 18 September (Mullen, personal communication), but most are gone at least two weeks before that time.

#### NONBREEDING SEASON

To obtain information on activities of *C. alpina* in the nonbreeding season, studies were made of its populations in central California, mainly on San Francisco Bay. The emphasis here will be on temporal changes in numbers and body weights, with brief comments on winter habitat, food, and interspecific relations.

Although numerous reports and notes have been published on migratory and winter activities of shore birds in North America, very few provide systematic data on changes in abundance of species through one or more seasons. The only useful information of this type on *C. alpina* is in the studies of Storer (1951) in California and Urner and Storer (1949) on the Atlantic seaboard. There is a dearth of satisfactory information on winter ecology of shore birds, although the recent investigation by Ehlert (1964) is a major contribution to this subject.

At present, shore-bird populations near San Francisco Bay in winter have a discontinuous distribution along the shoreline because of filling and development of these areas by industry. For this study shore-bird populations were examined at one of the remaining pockets of mudflats and adjoining shore and levee systems that serve as feeding and loafing sites for many wintering species. The study area, the Emeryville crescent, is a curving two-mile-long shoreline on the east side of San Francisco Bay near the Oakland-San Francisco Bay bridge. The nearest similar mudflat habitat to the south is in the Alameda-Bay Farm Island area 11 miles away; six miles to the north are mudflats at Point Isabelle and Brooks Island, the only locality where wading birds are found in any significant numbers south of the end of the Bay (about 10 miles farther north).

Large numbers of shore birds occur on the mudflats along the central California coast; the frequent species and their seasonal abundance in central California are described by Storer (1951). It should be noted that the usual congeners that breed sympatrically with *alpina* at Barrow are not usually found in California. *C. melanotos* and *C. bairdii* migrate primarily through the interior United States and Canada east of the Rocky Mountains to their Southern Hemisphere wintering areas; only occasional stragglers reach the California coast in fall, and these usually are immature birds (Holmes, MS). *C. pusilla* moves east and south from Alaska and arctic Canada and winters from the southern Atlantic coast of the United States south along the Gulf of México to northern South America (AOU, 1957).

*Seasonal changes in numbers and body weights in California.* Censuses of wintering and migrating Red-backed Sandpipers taken at frequent intervals in the Emeryville area from September to May 1960 to 1964 provide an estimate of relative changes in numbers present in this locality in four consecutive winters. Results are given in



TABLE 2  
WEIGHTS OF *C. alpina* COLLECTED ON SAN FRANCISCO BAY,  
CALIFORNIA IN THE WINTERS, 1960 TO 1964

	Mean	SE	♂ N	Range	Mean	SE	♀ N	Range
15 Sept.–10 Oct.	53.6 ± 1.0		11	48.7–58.7	63.5 ± 4.0		5	50.3–73.6
11–20 Oct.	52.5 ± 1.2		10	47.7–61.1	59.3 ± 1.3		21	47.5–70.0
3–17 Nov.	53.1 ± 0.2		25	44.7–59.1	57.7 ± 0.3		13	51.7–64.0
20 Dec.–24 Jan.	56.5 ± 0.3		7	53.7–60.3	58.1 ± 0.3		16	51.7–63.7
1–15 April	53.8 ± 0.3		10	50.9–58.3	57.4 ± 0.3		11	53.6–63.4
16–30 April	65.2 ± 1.7		6	60.0–72.2	70.8 ± 3.0		11	53.7–85.1
1–10 May	48.7 ± 2.6		2	46.1–51.2	58.0 ± 4.8		2	53.2–62.8

figure 8 together with one year's (1948–1949) data on this species at Bay Farm Island from Storer (1951). To provide an index to the general physiological state and amount of fat deposition at different parts of the season, the weights of specimens collected in the four years near the study area are summarized in table 2.

Although other sandpipers such as *C. mauri* arrive in central California in significant numbers in mid-July and continue to do so through the fall (Storer, 1951), Red-backs do not arrive until the last days of September (fig. 8). The earliest occurrence in the present study was 22 September, while Storer (see fig. 8) first saw this species at Bay Farm Island in the last days of September. Records earlier than this in California are uncommon, although several exist, for example, a specimen collected 9 September 1911 at Santa Barbara (No. 38726, Carnegie Museum) and observations of Red-backs in August and early September (Grinnell, Bryant, and Storer, 1918). In some cases such late-summer birds may represent nonbreeders that have spent the summer at these latitudes. In general, most Red-backed Sandpipers arrive in California after 1 October, at which time they are decreasing in weight (table 2); this is unlike *C. mauri*, which arrive earlier and show heavy fat (Holmes, MS).

From this and other investigations (Storer, 1951; Urner and Storer, 1949) it is apparent that *C. alpina* is one of the last shore-bird species to arrive at temperate latitudes in North America in fall. Since there are no banding recoveries of this species from the Pacific area (Duvall, U.S. Banding Office records) and since observational data from northern latitudes in fall are essentially lacking, evidence for events of the interval between the end of breeding and arrival in wintering areas is mostly indirect. From a summary of available information on movements of Red-backs along the west coast of North America from Alaska to California (Holmes, MS), it appears that both adult and immature Red-backs probably drift slowly southward in arctic and subarctic regions and remain in western Alaska during late August and most of September. During this time they inhabit either the tundra adjacent to the coast as they do at Barrow in late summer or the mudflats of the Bering Sea, perhaps mainly in extensive bays such as Bristol Bay where large expanses of mud are exposed at low tide. Then in late September and October they fly directly and rapidly to their winter quarters in western North America. One result of this leisurely migration is that both adult and immature Red-backs concentrate in southwestern Alaska and then migrate and arrive together in California in October in about equal numbers (Holmes, MS). This migration pattern differs from that of most shore-bird species arriving at temperate latitudes (e.g., *C. mauri*, Holmes, MS; *Limnodromus griseus*, Jehl, 1963) whereby adults arrive first, followed later by immatures.

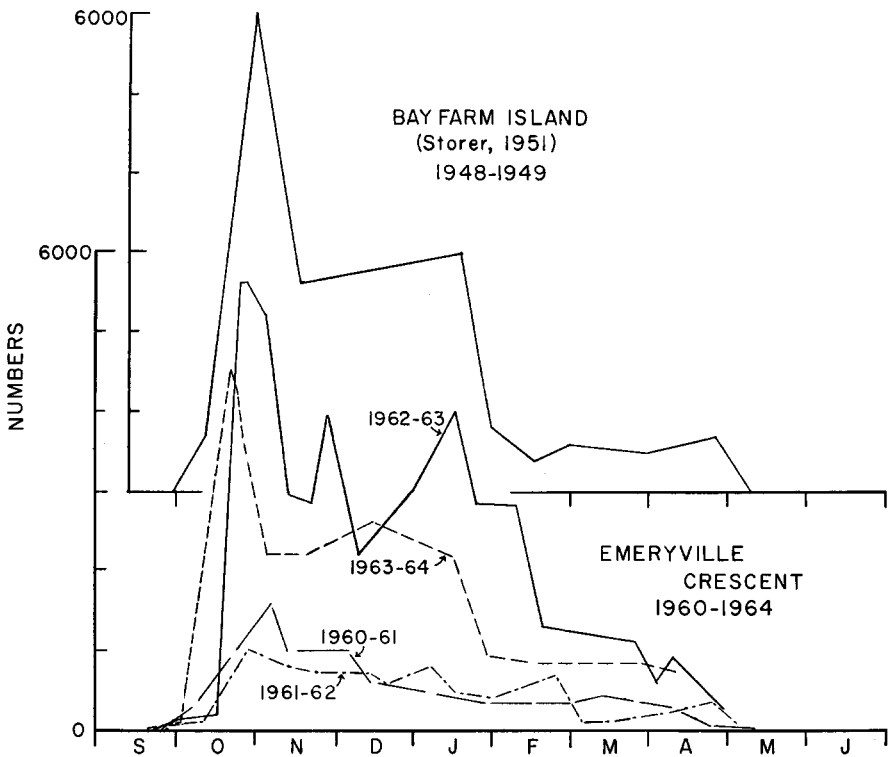


Figure 8. Seasonal changes in Red-backed Sandpiper populations on San Francisco Bay at Bay Farm Island in 1948 to 1949 (from Storer, 1951) and at the Emeryville crescent in 1960 to 1964.

In California numbers of Red-backs increase markedly through October and reach a peak in late October and early November (fig. 8); in this period they outnumber any other shore bird in the area. In November their abundance declines slightly as some individuals continue to move southward; the population then stabilizes at a winter level for the months November to January. Differences in maximum numbers of Red-backs in the fall population in the four years studied at Emeryville (fig. 8) probably result from changes in condition of the mudflat, which permitted a general increase in total number of birds in this area in successive years. The rapidly disappearing habitats in other parts of the Bay may also contribute to greater concentrations of shore birds in remaining habitats.

In late winter and spring Red-backs decrease in numbers in coastal central California (fig. 8), and there are no records for increases either to the south or north at this season (Holmes, MS). This decline, as recorded here and by Storer (1951), may represent (1) a dispersal of Red-backs to other parts of the Bay or to other regions of California, or (2) an early, slow-moving spring migration. From a review of published observational evidence (Holmes, MS), the latter explanation seems more likely, and it appears that the entire wintering population shifts gradually northward so that no observable build-up in numbers occurs. Movement in spring is primarily coastal, but Red-backs do increase in occurrence in marshy areas of California's central valley

in March and April, indicating some shift inland at this time. Numbers along the east side of San Francisco Bay and on the outer California coast at Bodega Bay, Tomales Bay, Bolinas Bay, and Monterey Bay remain low with no significant increase in spring, but those present are depositing fat, as indicated by increases in weight (table 2). The final decrease in numbers of Red-backs in California occurs in the first two weeks of May (fig. 8). The few Red-backs recorded in California in June and July (Grinnell and Miller, 1944) are almost certainly nonbreeding individuals. Four specimens collected in May in the course of this study were light in weight (table 2). These probably represent birds that might have remained to spend the summer as nonbreeders.

Migration routes farther north in spring have not been well documented. No noticeable increase has been observed in the Pacific Northwest, either coastally or inland, but judging by the paucity of inland records, the Pacific populations probably move northward, primarily along the coast to British Columbia, and then migrate across the Gulf of Alaska to western Alaska and then into breeding areas (Holmes, MS). There are some records of individual or small groups of Red-backs as early as March in southeastern Alaska (Gabrielson and Lincoln, 1959) and in May in southern Alaska near Anchorage (Holmes, MS) and near the base of the Aleutians (Murie, 1959). Observations of Conover (1926) at Hooper Bay, Yukon Delta, indicate that Red-backs arrive on or near 10 May; as stated above, the earliest arrive at Barrow in northern Alaska during the last days of May.

This same pattern of migratory and wintering events is found in other populations of *C. alpina* in North America and in the western Pacific. Urner and Storer (1949), reporting the results of 10 years of observation of Red-backs along the New Jersey coast, observed arrival in late September, high numbers from October to December, then a decline in January through March similar to that in California; but on the Atlantic coast a slight increase in May was detected, representing a weak mass movement northward. On the west side of the Pacific, a similar routine is observed, with a more constant population level maintained through the winter (Kobayashi, 1959; Kuroda, 1919).

In populations of *C. alpina* in western Europe another timing pattern is found. In the British Isles the main period of fall migration is mid-July to mid-September; numbers decrease through October, with only a few remaining to overwinter (Nisbet, 1957). At Öland in southeastern Sweden and in Denmark fall migration of *C. alpina* (races *alpina* and *schinzii*, apparently mixed) is at a peak in the first week of August, the birds being mainly adults, and immatures appear later (Nørrevang, 1955). At Jaeren, on the southern tip of Norway, the peak of Dunlin migration is reached about 1 October; Nørrevang (1955) states that this consists chiefly of immature birds that use a different route than that of the adults, which move farther south along the north coast of the main mass of continental Europe. Migration patterns of this species in Europe are more complex than in North America since the species nests at lower latitudes in these regions. Thus the relative contribution of different populations (e.g., from western Siberia, Scandinavia, or northern continental Europe) to the migratory routes is varied and undoubtedly makes analysis of migration difficult. In any event, it does seem that in Europe there is a well-defined separation of adults and immatures during migration, a situation not observed in *alpina* in California, and that the migration schedule followed by the European races differs significantly from that of Pacific and western Atlantic populations.

*Habitat, food, and interspecific relations in winter.* In all parts of its winter

range *C. alpina* occurs mainly in coastal or estuarine habitats. It is found occasionally on open sandy beaches but more commonly on intertidal mudflats (Witherby *et al.*, 1940; Grinnell and Miller, 1944; C. M. Fennell, personal communication; Holmes, MS). In spring Red-backs occur at inland localities around the edges of fresh-water lakes, ponds, and marshes.

On mudflats of coastal bays and lagoons this species primarily feeds, frequently by deep-probing methods, at the edge of the advancing or receding tide, although at low tide it may feed along drainage channels or in small puddles of water remaining on the mud. Other small sandpipers in California have different spacing patterns while feeding. Western Sandpipers do not generally follow the tideline but scatter over the exposed mud, the individuals being two to three feet apart. They remain evenly distributed, although spreading out as more surface becomes available until the upcoming tide crowds them together and finally forces them to leave the flat. Least Sandpipers do not generally feed on the open mud but chiefly at the edges of mudflats close to marsh vegetation (mostly *Salicornia* and *Spartina*). They also feed more frequently along mud channels or ditches traversing the vegetated part of the marsh, and only occasionally do they move onto open mud with the Western Sandpipers or out near the tideline with the Red-backs. High-tide roosts of all three sandpipers at Emeryville were usually the same areas, with all species congregating on sandspits or dikes. As feeding areas begin to appear with a changing tide, they again separate as described above.

Analysis of stomach contents taken from specimens collected at Emeryville in the course of the present study indicates that polychaete worms are important prey of *alpina* in this area (Chaniot, personal communication). *C. alpina* in other areas have also been found to feed on polychaetes (McAtee, 1911; Ehlert, 1964). Based on analyses that are still incomplete, it appears that other small sandpipers occurring with *alpina* in California winter habitats take different prey as a result of the local habitat segregation discussed above, although considerable overlap does occur (Chaniot, personal communication). At Helgoland, Ehlert (1964) demonstrated that *alpina* concentrates on annelids, *C. canutus* takes mostly mollusks, and *C. alba* feeds predominately on insects.

#### TIMING OF MOLT

The annual timing of molt in *Calidris* sandpipers varies from species to species. In some, such as the New World populations of *alpina*, the postnuptial (prebasic) molt occurs during their stay in the Arctic, where in others, as *melanotos* and *bairdii*, it takes place after fall migration. In all species the incomplete prenuptial (prealternate) molt occurs just before or during the early phases of spring migration. Only a synopsis of the timing of molt of *alpina* will be given here, since a detailed analysis of sandpiper pterylography and molt processes, together with method of scoring and graphing molt, will appear elsewhere. Figure 9 shows the periods when molt occurs in Red-back populations at Barrow and in California. All individuals in molt fall within the trapezoids.

Briefly, the postnuptial molt of adult Red-backs begins almost synchronously in the population in mid-June; replacement of primaries occurs first, followed shortly thereafter by secondaries and rectrices, and molt of flight feathers is generally complete before southward migration. Body feather molt begins between 10 and 25 July and occurs almost simultaneously in all feather tracts. It is at least half-completed by the time of departure from the Arctic in late summer (fig. 9). The postjuvenile

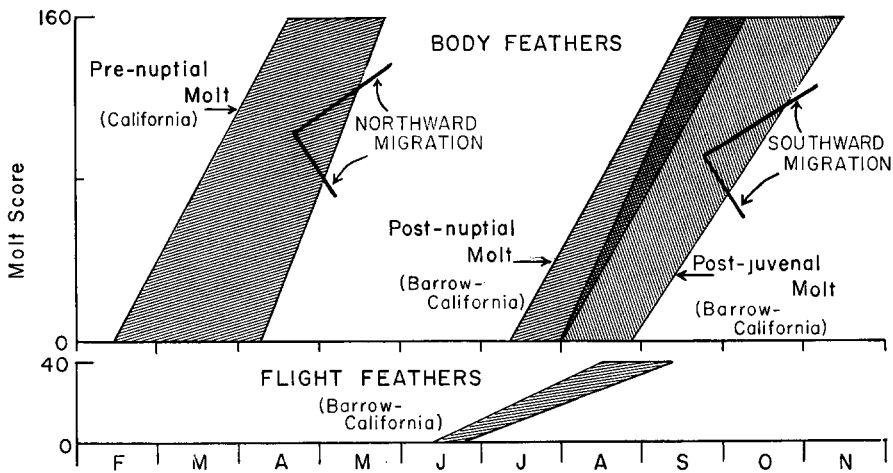


Figure 9. Summary of annual molt schedule of the Red-backed Sandpiper at Barrow, Alaska, and in California.

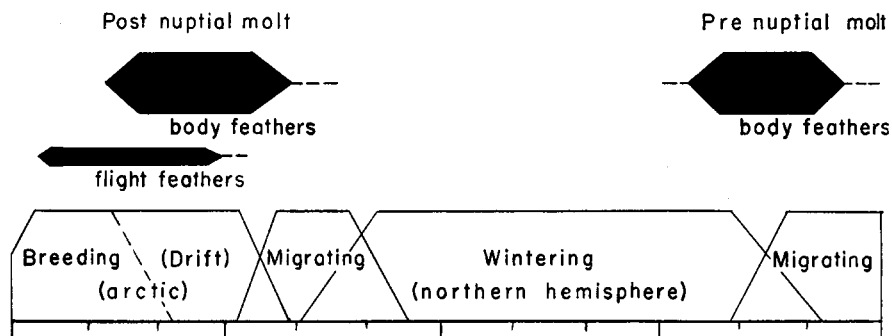
(first prebasic) molt of immature Red-backs is an incomplete molt and follows the same general time sequence as that of body feathers of adults mentioned above, except for a slightly later start (late July–early August). Prenuptial molt begins in mid-February and March and proceeds rapidly to completion by mid-April or early May (fig. 9).

In populations of *alpina* along the Bering Sea coast in Alaska the postnuptial molt begins slightly later than at Barrow, and overlaps less with the breeding season. Therefore, with the longer summer period at more southerly latitudes, there is greater separation in time of these two energy-demanding events. Likewise there is evidence that if molt is not completed at the time when migration begins, it is suspended or delayed until after the southward movement is completed (Holmes, MS).

A schematic comparison of molt cycles of several *Calidris* species including summaries of other major annual cycle events is presented in figure 10. The information on molt of species other than *alpina* is derived from a knowledge of their breeding ecology (Holmes, MS; Pitelka, 1959; Witherby *et al.*, 1940) and from an excellent study by Middlemiss (1961) on molt in *minuta* wintering in South Africa. The justification for using the latter data in this general way is based on additional information in the literature (Dwight, 1900; Wetmore, 1927; Witherby *et al.*, 1940) and from correspondence (D. L. Serventy, personal communication), which suggest that most if not all *Calidris* species wintering exclusively in the Southern Hemisphere, whether in South America, Africa, or Australia, have a molt pattern similar to that shown in the lower part of figure 10, which is based primarily on information for *minuta*. This is verified also by the fact that none of the species occurring at Barrow, other than *alpina*, molts to any extent while in the Arctic, and only rare individuals, usually the last ones to depart, show inception of molt.

Not only is molt postponed until later in the annual cycle in those species that are transequatorial migrants, but it occurs in a different sequence (fig. 10). Molt of body feathers begins first and is completed by mid-November; molt of rectrices and remiges then begins and is completed in February, followed by a partial (body-feather) molt in spring, mostly before migration. This means that flight-feather molt occurs during

## NORTH TEMPERATE WINTERING SPECIES

*C. alpina*

## SOUTH TEMPERATE WINTERING SPECIES

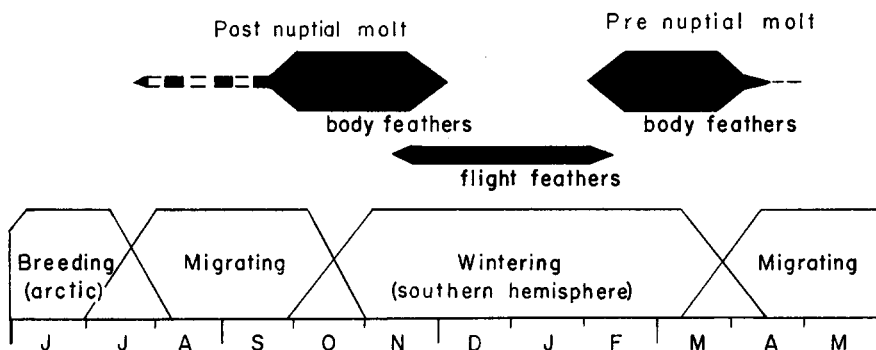
*C. melanotos, C. bairdii, C. minuta*

Figure 10. Molt schedules of several arctic *Calidris* sandpipers in relation to other major events of their annual cycles.

the part of the year when the birds are relatively sedentary in their winter quarters and not in or near a migratory period. Another feature of winter molt in these species is that it is protracted in time, occurring in a five-month period, whereas that of *alpina* is completed in less than four months, when it is not only compressed in time but overlapped with the breeding effort. In the latter species molt of flight feathers is also complete before migration.

The correlation between Southern Hemisphere wintering and winter molt seems to hold well for all species wintering there. However, other species and, indeed, even the European races of *alpina* that winter in North Temperate regions do not appear to follow the specific pattern shown here for Alaskan Red-backs. In *C. a. schinzii* in the British Isles where breeding starts in May, the postnuptial molt occurs between July and November (Witherby *et al.*, 1940), suggesting a very different time schedule from that reported here for Alaskan populations. Kozlova (1962) indicates that molt in Siberian populations begins during the breeding season and thus follows a pattern similar to that reported here; but complete information on molt schedules and sequences in these and other Eurasian populations of *alpina* is not available. Another

*Calidris* species that breeds as far north as *alpina* and winters exclusively in northern zones is *maritima*. Witherby *et al.* (1940) state that its fall plumage is acquired between August and November, indicating a later molt than in Alaskan Red-backs. Two other species from North America that are in North Temperate zones in winter are *C. mauri* and *C. minutilla*, both of which are sub- or low-arctic nesters; their post-nuptial molt occurs after they have finished breeding, either before they migrate southward or during migration. Individuals of both species arrive in their winter areas by August (Storer, 1951), and some collected in California in early September were molting body feathers and some flight feathers (Holmes, MS). More information on molt schedules of these and other *Calidris* species, especially *C. alba* and *C. pusillus*, which winter in both hemispheres, is needed.

#### DISCUSSION

From the foregoing examination of events in the annual cycle of *Calidris alpina* in western North America, it is evident that (1) breeding takes place at the same time each season in spite of yearly and seasonal variations in weather, (2) molt overlaps with the breeding effort, (3) adult Red-backs remain longer on the tundra in fall than do adults of other sandpiper species, and (4) their migration is late in fall and prolonged in spring.

We may first consider the factors regulating the breeding seasons of avian populations at high latitudes. In all shore-bird populations at Barrow, breeding occurs mainly in mid-June. But the time of pairing varies with the early season weather, occurring before the birds' arrival on the tundra when snowmelt is delayed and after arrival when melt proceeds rapidly with favorable weather. In the latter situation several days to a week are spent in courtship activities on the breeding areas. As a result of simultaneous nesting in all insectivorous shore-bird populations at Barrow (Holmes, MS), there is a synchronous hatch followed by a period of rapid growth of young that are flying and independent of the adults by late July or early August, a month before the onset of winter weather. With this apparent lability in the time of pairing in early summer, it appears that timing of breeding in these populations does not depend merely on the availability of snow-free tundra. If the shortness of the season were in itself critical, pair-formation would occur early every year so that nesting could begin immediately after arrival instead of being delayed until mid-June. Likewise, a safety margin of a month's duration in late summer seems extreme if breeding is actually curtailed by the abbreviated season.

A plausible explanation suggested by the regular onset and synchrony of nesting activities is that breeding is timed to correlate with some factor other than the beginning of summer, such as a seasonal peak in food supply. The ultimate importance of food in regulating breeding seasons has been discussed by Lack (1954) and has been examined for many bird populations, mostly passerines at temperate and lower latitudes (Lack, 1954; Dunnet, 1955; Snow, 1962a, 1962b; Murton *et al.*, 1963; Kahl, 1964). The general premise of Lack's hypothesis, which has received general support from the above studies, is that breeding schedules have evolved directly in relation to food supply so that young are produced in the season most favorable for their growth and survival.

To test the applicability of Lack's hypothesis for a nonpasserine, precocial species breeding in a high arctic environment, availability and abundance of the food source (mostly insects) in relation to food intake of breeding Red-backed Sandpipers, both adults and young, were assessed near Barrow in three summers, 1961 to 1963. De-

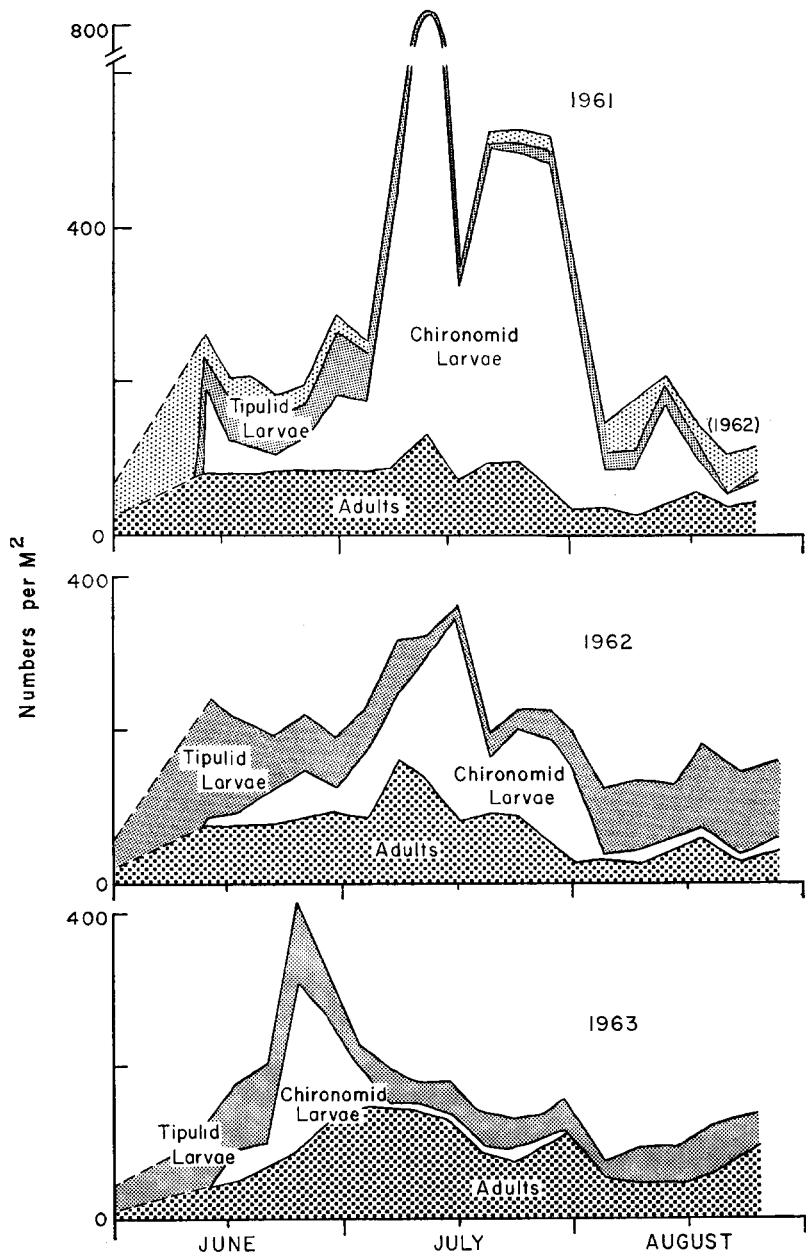


Figure 11. Changes in availability of insect prey in numbers per square meter in three summers at Barrow. For clearer comparisons, gaps in the data for tipulid larvae in 1961 have been filled by data from the 1962 sampling (see fig. 12 and Holmes, 1966).



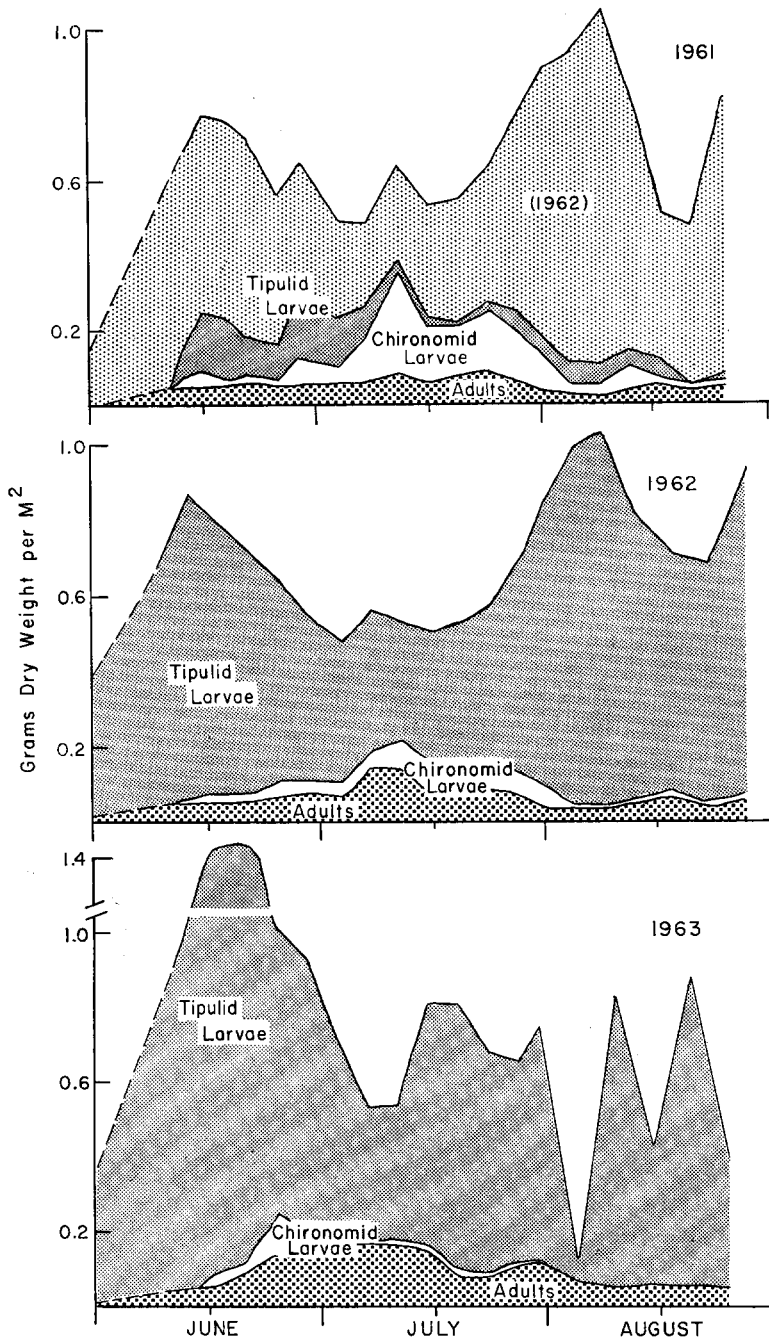


Figure 12. Changes in availability of insect prey in biomass (grams dry weight per square meter) in three summers at Barrow. Data for tipulid larvae in 1961 have been partly substituted from those of 1962 (see Holmes, 1966).

tails of insect sampling and Red-back feeding behavior and food habits are included in another report (Holmes, 1966), but are summarized here for discussion purposes in figures 11 and 12.

The results showed that the insect fauna at Barrow and other arctic regions is low in taxonomic diversity compared with that of temperate latitudes, and only a limited variety of food items is available to birds. The most important prey species at Barrow are Diptera of the families Tipulidae (3 species) and Chironomidae (numerous species not easily separable taxonomically); other insect orders and dipteran families are represented but to a lesser degree. Availability of acceptable prey for sandpipers changes in the course of a summer season, varying with the life-cycle phenomena of the insects and with effects of weather. The latter also cause large fluctuations in insect availability in different years. Results of the insect-sampling program accurately reflected changes in prey availability; in addition, food taken by Red-backs was closely correlated with these changes in each season. Adult Red-backs concentrate primarily on subsurface prey, mostly tipulid and chironomid larvae, but take adult insects in early July; young Red-backs feed first on small adult insects and later in the summer on chironomid larvae.

When time of hatching of Red-back chicks is plotted against seasonal rise and fall in their food supply (adult Diptera, fig. 13), it is evident that hatching does occur at the time of the summer when the food utilized by young is most available. Within a few hours after hatching, sandpiper chicks are active and feeding independently. Food-gathering by a small chick is limited to those prey items, such as adult insects, which it can obtain from the tundra surface. At this time its bill is not yet strong enough to probe. Because adult insects, particularly chironomids, are found most commonly in lowland marshes, the chicks (and accompanying adults) usually move to this habitat-type soon after hatching.

Midsummer is when the greatest number of changes are taking place in the insect populations, and more importantly, in the weather. Larvae that have overwintered and grown during June are then pupating, imagoes are emerging and laying eggs that in turn are hatching, and new larvae are beginning to grow. With such changes occurring in the prey populations, variable weather can have direct effects on the rates of emergence and survival of metamorphosing insects and on their availability (Holmes, 1966). Adverse weather conditions are known to persist for days or weeks during the arctic summer (see Bird and Bird, 1940; Marshall, 1952), and in such instances, adult insects would be totally eliminated, causing a severe food shortage and lowered survival of young. Thus, even if young sandpipers hatch when their food is usually most readily available, they are being reared in the most unpredictable part of the summer, a time when there is less total food in terms of available biomass for the population as a whole and for adult sandpipers in particular (fig. 12), and when changing environmental conditions can significantly alter the availability of food resources with threat of food shortage. At first this seems to contradict Lack's postulate, since for adaptive timing in which young are growing during the most favorable season, it is usually stated or implied that the favorable interval is the time of maximal food abundance and optimum conditions for feeding. Nevertheless, in the Arctic, the mid-July interval remains the only part of the season in which young sandpipers can find adequate food, and breeding is timed to the availability of food for the precocial young, even though this part of the season is not necessarily the most favorable for the adults (see below).

Precociality may be a particular advantage in arctic environments, especially with

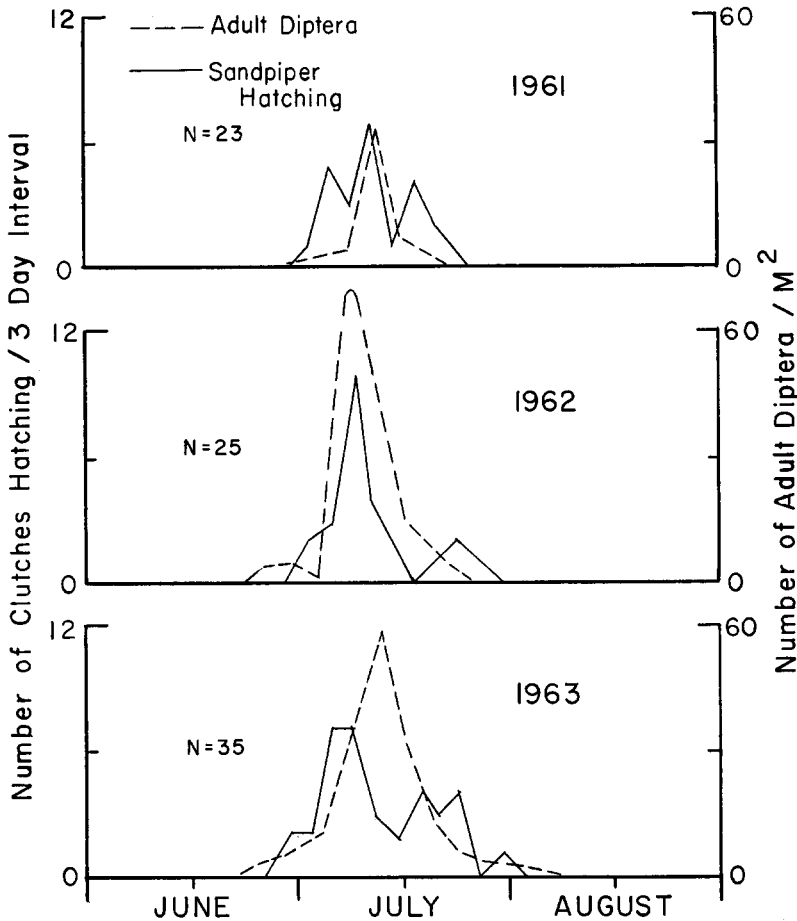


Figure 13. Hatching times of Red-backed Sandpiper nests in relation to availability of adult Diptera on tundra surface.

the temporal and spatial variability in food supply found there, in that the young are able to move, even long distances, to locally favorable feeding sites. This precociality, coupled with the short span of territorial defense, allows feeding birds of all ages access to all parts of the tundra. It is suggested that this may be one reason why shore birds are so successful in high-latitude communities as compared with passerines, which are poorly represented.

On a weight basis, less food is available in midsummer (fig. 12), and the supply varies with the accessibility of chironomids. It has been shown that adult Red-backs prefer tipulid larvae to chironomid larvae and that they apparently prefer the latter to adult insects. This preference is correlated with size of prey (*i.e.*, the larger the individual organism, the more highly preferred) and therefore probably with energy value in relation to unit foraging effort (Holmes, 1966). Thus, in early and mid-July when only adult insects are available and later in some years when the chironomids become inaccessible, feeding conditions for adult Red-backs are suboptimal. Not

only can weather-induced food shortages occur in midsummer, but adult Red-backs are feeding on less-preferred and perhaps poorer-quality foods, although this is the time when food for young sandpipers is maximal.

Since food availability is characteristically variable, especially in midsummer, specializations in breeding ecologies of these sandpipers that perhaps alleviate the effects of such a food shortage may be expected. As discussed earlier, territoriality declines by late June or early July; this allows the adults and their precocial young to wander freely during the midsummer season, particularly into lowland marshes that are not usually included within breeding territories, but where adult insects and, later in some seasons, larval chironomids are most available.

In response to a food shortage in mid- or late summer, adult Red-backs apparently begin to migrate southward to more favorable feeding areas or to leave the tundra, shifting to other habitats, such as the coastal lagoons and ponds. The latter occurred in late July–early August 1963 when food availability was exceedingly low because of the inaccessibility of chironomid larvae, declining numbers of adult insects, and a not-yet-available source of tipulid larvae on the tundra (see fig. 11). At this time adult Red-backs could be found only at coastal feeding sites where they were preying on chironomid larvae (Holmes, 1966). Later in the season they, or other individuals in migration, again appeared in the upland tundra feeding on tipulid larvae. In addition to the habitat shift, adult Red-backs collected near the coast in that season showed more variation in extent and timing of body-feather molt than is recorded in the local population in any other season. This could have been a result of metabolic adjustment, because of food deficiency or change in diet to coastal chironomids; or perhaps the sample includes a mixture of individuals from various breeding localities. In most seasons, however, adult Red-backs apparently survive the critical period of midsummer on the tundra, and begin to gain weight during August while molting intensively.

In other shore-bird populations in northern Alaska, different responses to midsummer food conditions have evolved. In *C. melanotos* and *P. fulvicarius* populations one sex (male in *melanotos*; female in *fulvicarius*) leaves the tundra before the midsummer period, and the remaining adult stays until the young are essentially grown and then departs (Pitelka, 1959). In *C. bairdii* and *C. pusillus* both adults incubate and both stay with their young until the young are flying. But then they leave immediately, apparently on southward migration. Occasionally, in these species, as in *alpina*, one sex (usually the female) leaves the brood before the other, and thus it is not uncommon in late July to find only the male adult with the young. But in *bairdii* and *pusillus*, unlike *alpina*, the males leave when the young are becoming independent, and adults of the former two species are rarely found on the tundra at Barrow after late July. Furthermore, adults of all species mentioned above except *alpina* do not molt or increase in weight before their departure. Therefore, by late summer, all other adult sandpipers that early in the season take food similar to that of *alpina* (Holmes, 1964) have departed; the young that may still be present are feeding primarily on chironomid larvae (Holmes, MS), as are the immature Red-backs at this time of the season (Holmes, 1966). Adult *alpina* thus exploit the late-summer tipulid populations at a time when few, if any, other species are taking this food item.

A summary of annual fluctuation in weights of Red-backed Sandpipers (fig. 14) demonstrates the importance of the food resources of the tundra during late summer in furnishing energy reserves for fall migration. The fact that their body weights are approaching the minimum level at the time of arrival in central California indicates

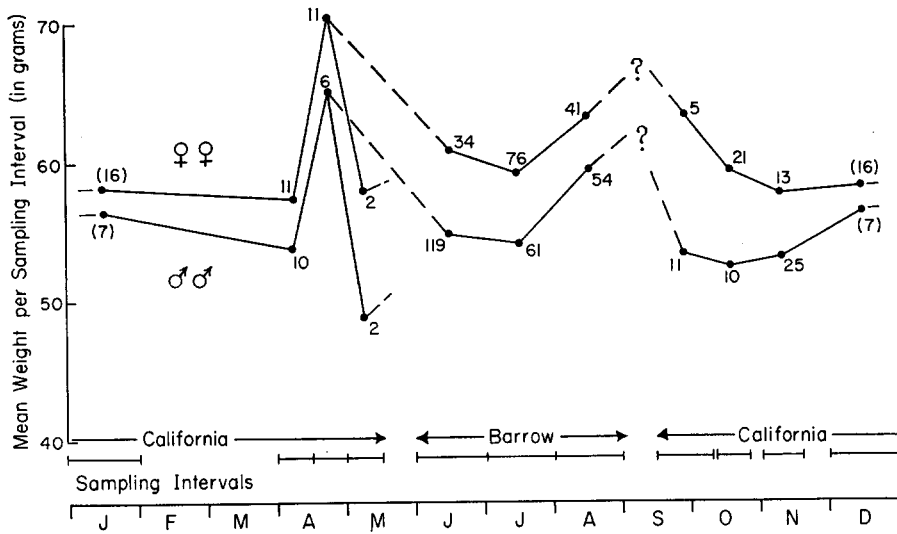


Figure 14. Annual body-weight cycle of *Calidris alpina*, as recorded at Barrow, Alaska, and coastal central California. Dots represent mean weights for 10-day intervals in June-July-August (see fig. 4) and for 15- to 25-day intervals during the remainder of the year (see table 2).

that the fat reserves are depleted during the southward movement in late September and October and are not renewed until the following spring (fig. 14). In other sandpiper populations at Barrow, for example, in *C. melanotos*, the weights of both sexes are maximum in June, and then decline in July as the individuals depart; these birds delay fat deposition until they have arrived in other habitats farther south (see Pitelka, 1959; Hamilton, 1959).

It has been observed in many bird populations, particularly those at temperate or tropical latitudes where most studies of avian ecology have been made, that the complete molt usually follows the breeding period and rarely overlaps it (Kendeigh, 1949; Miller, 1961). Both processes require considerable energy, and thus in the evolution of an annual schedule, selection would act to separate them in time so that limited energy resources are apportioned and used most efficiently. Lack (1954) states that breeding is correlated with maximal food availability, and although he acknowledges molt as a significant part of the annual schedule, he does not fully consider it as a competing process. Pitelka (1958) has shown for a resident corvid species at a cold temperate latitude (54° N), where the favorable summer season is relatively short, that breeding and molt encroach upon each other and overlap slightly, so that both molt in adults and growth of young occur when food is most abundant. This finding represents a compromise in the utilization of the food resource for breeding and molt activities in a markedly seasonal environment.

The striking differences noted among *Calidris* sandpiper species, such as the timing of postnuptial molt in relation to other annual cycle events, reveal different solutions to the problem of adaptation to a severe environment. With the exception of *alpina*, the complete molt of all sandpipers at Barrow occurs after the birds have reached their winter quarters. In *alpina* molt is included in the schedule of events on the tundra. But when molt is scored, using dry weight of feathers as an index to the

amount of metabolic energy needed to replace plumage (Holmes, MS), it becomes evident that the majority of molt activity and therefore of energy expended on molt comes during August and early September. This is after the main breeding effort, yet within the period when the birds are being supported by tundra food sources. It is also in this late-summer period that adult Red-backs normally return to upland tundra and begin to drift southward, feeding again on tipulid larvae.

From the comparisons of molt schedules and major annual cycle events (see fig. 9), it can be suggested that for those species that go a long distance to winter, selection favors an early departure from the Arctic. Tundra resources are not used for molt, nor for premigratory conditioning, and the early departure has probably evolved because of the great uncertainty in food availability in midsummer (see Pitelka, 1959). In *alpina*, however, which migrates only short distances to temperate latitudes, a longer stay on the tundra is possible, and in the absence of other adult sandpipers in late summer, it exploits the major food source (tipulid larvae), completes its molt, and accumulates premigratory fat. With compression of molt into the relatively short time span of the arctic summer, body and flight feathers are being replaced at the same time, but molt in the latter is projected forward so that it begins in mid-June. The result is, however, that the flight feathers are renewed before the onset of southward migration.

When breeding and molting schedules of shore birds are compared with those of coexisting passerines, an interesting fact emerges that sheds further light on the relative abundance of these two groups. At Barrow there are only two passerines, both fringillids—the Lapland Longspur, *Calcarius lapponicus*, and the Snow Bunting, *Plectrophenax nivalis*. In these species, as in many temperate-zone passerines, molt follows the breeding effort and is complete before the birds begin to migrate (Pitelka, personal communication). In the two passerines molting and breeding do not overlap in time; molt apparently must be complete before departure, and breeding occurs earlier in the season. This, in conjunction with a short incubation period, results in hatching of young before the time of optimal food availability on the tundra. In July molting adults and growing young both depend on the same food supply. Among shore birds, on the other hand, with a longer incubation period and precocial young, breeding is more closely timed with the food supply so that their young are produced at the most favorable part of the season; in addition, young and adult sandpipers in later summer are generally in different habitats and are exploiting different prey populations (see below). This fundamental difference suggests a second reason why shore birds are more successful in arctic regions than are passerines.

A summary of the breeding period for *alpina* is given in figure 15. The lower part of this illustration shows biomass, as measured by average wet weight of Red-backs per unit area in the Arctic during a summer. The line for young birds is drawn to allow for 50 per cent survival at or shortly after the time of hatching and through the main period of growth, a relatively conservative estimate (see p. 25).

The compression of breeding and most molting activities of the Red-back population into the arctic summer, together with their longer stay in the Arctic, contrasts with the scheduling of events in populations of other arctic shorebirds and reveals major differences in their adaptive characteristics. For *melanotos* Pitelka (1959) suggested that the early departure by the adults represented an adaptation for alleviating food shortages during midsummer, a hypothesis that is generally supported by the results of the present study. In *alpina* populations, although there is no differential departure of the adults and no early departure, there is a populational adaptation com-

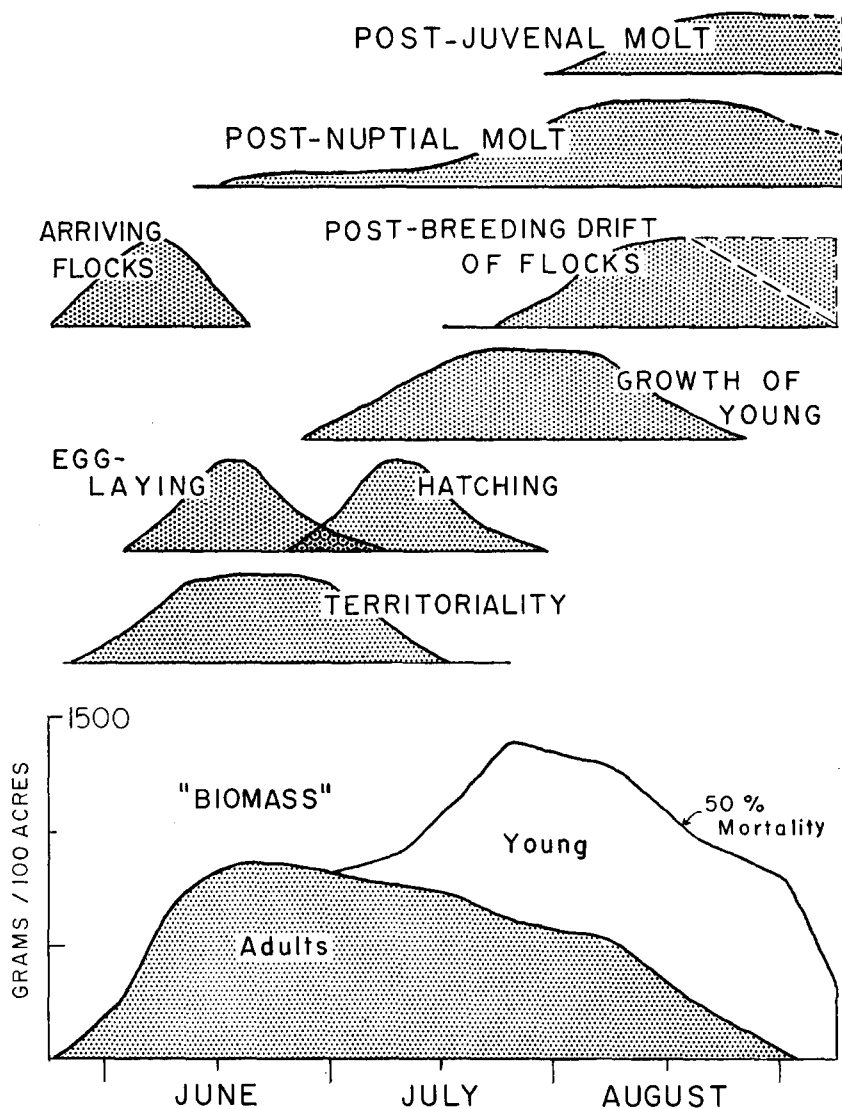


Figure 15. Summary of breeding schedule and associated events occurring on the tundra at Barrow in populations of the Red-backed Sandpiper. The lower part, labeled "biomass," represents wet weight of birds on a population basis through the summer.

parable to that found in *melanotos*. Since in August most young Red-backs move to the coast or to lake margins, they are not being supported by the tundra proper; for this reason, the line for young in figure 15 falls sharply in early August. With the adult and young Red-backs occupying different habitats and taking different foods, especially in late summer when both are molting, an effective ecological separation in this period is achieved.

The long-term result of this system is similar to that of *melanotos* in that the

adults and young are separated in late summer. The major difference is that adult Red-backs remain in the Arctic longer in summer and feed on the late-season tipulid populations whereas adult *melanotos* move south and feed in fresh-water marshes along the migratory route. However, the opportunistic settling and compression of populations into favorable areas for breeding that is characteristic of *melanotos* is not found in *alpina*.

The long summer residence on the tundra, large and stable territory size, occurrence of molt, and generally intense utilization of tundra resources suggest that *C. alpina* is more firmly committed in its adaptive characteristics to the Arctic than is a species, such as *C. melanotos*, which, in its more opportunistic and labile breeding system, stays on the tundra only long enough to produce young. The relatively short migration and northerly wintering areas of *alpina* have probably been necessary concomitants to the evolution of its breeding system.

#### SUMMARY

Ecological and behavioral specializations in the annual cycles of sandpipers of the inclusive genus *Calidris* nesting in the Arctic reveal adaptive adjustments to the environment, particularly to the shortness of the summer. In the comparative study of this general problem, the breeding ecology of one species, the Red-backed Sandpiper (*Calidris alpina*), was investigated in five consecutive summers, 1959 to 1963, in northern Alaska; for the nonbreeding phases of the annual cycle, wintering populations in California were observed from 1960 to 1964.

At Barrow, Alaska, latitude 71° 20' N, the arctic summer lasts from early June until late August. Red-backs arrive throughout a two-week period singly, in small flocks, or in formed pairs, depending on local weather conditions. Self-contained territories of 12 to 17 acres are established on upland tundra. Egg-laying is relatively synchronous, most clutches being completed between 12 and 18 June; later clutches mainly represent attempts at renesting following early-season nest loss. Both sexes incubate, the male's role increasing as hatching approaches. Hatching occurs primarily in early to mid-July, after which the precocial young, accompanied by their parents, move into lowland marshes. Growth of young proceeds rapidly; the immatures fly within three weeks of hatching. Survival of young to fledging is relatively high but varies in different seasons, with weather and predation being the major mortality factors. In late July and August young Red-backs move to coastal or lake-margin habitats, and adults flock to uplands; both depart by late August or early September.

In fall Red-backs apparently stay in the Arctic or sub-Arctic until mid- to late September, drifting slowly across the tundra or along the coast. Their arrival in California winter quarters occurs in late September and early October, reaching a peak on San Francisco Bay in late October and November. Numbers then remain relatively constant until late January, after which the population declines. Spring migration probably consists of a gradual northward shift of the wintering population, although this is not well understood.

Postnuptial molt of *C. alpina* is compressed into the short summer at high latitudes, beginning in mid-June concurrently with egg-laying and terminating by mid-September before the species reaches its coastal North Temperate wintering quarters; most other *Calidris* sandpipers breeding at Barrow molt after the fall migration.

Lack's (1954) postulate concerning the ultimate importance of food in the evolution of breeding schedules is supported by this study. Although food supply in terms of total available biomass is higher in June and August than in midsummer, the num-



ber and variety of surface insects required as food by precocial young are maximal in mid-July when young sandpipers are growing most rapidly. The distinction between food for young and that for adults is thus stressed. Furthermore, it is suggested that the precociality of arctic shore birds that allows young to move to favorable feeding habitats may be one factor permitting this group of birds to be so successful in high arctic regions.

With the food maxima for adult sandpipers that utilize chiefly subsurface prey coming early and late in the season, several populational adaptations of the sympatric *Calidris* species have evolved, particularly in relation to midseason food shortages and perhaps to other features of the environment, such as highly variable weather. In all sandpipers territorial behavior sets an early ceiling on breeding density, and then declines. In its absence in midsummer, adults and young move into lowlands that contain the most available food. In *C. melanotos* there is a highly compressible territorial system that permits settling in locally favorable areas; this is coupled with a brief pair-bond and with early departure of adults. However, for *alpina*, mean breeding density is constant and relatively low, and adults remain longer on the tundra. In late summer, in the absence of other potentially competitive species, they exploit abundant upland insect larvae, and during this time molt increases in intensity. Also, habitat separation of young and adults in late summer relieves intraspecific competition. The adaptiveness of these different breeding systems and their ecological and behavioral correlates are discussed.

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