LATITUDINAL DIFFERENCES IN THE BREEDING AND MOLT SCHEDULES OF ALASKAN RED-BACKED SANDPIPERS (*CALIDRIS ALPINA*)

RICHARD T. HOLMES

Department of Biological Sciences
Dartmouth College
Hanover, New Hampshire 03755

Breeding cycles of birds at high latitudes are frequently modified, so that some events are compressed in time, delayed, overlapped with one another, or eliminated entirely from the schedule of activities on the tundra. It has been hypothesized that these temporal specializations in breeding systems result from strong selective pressures imposed by the short arctic summer and by the impact of highly variable and severe summer weather (Pitelka 1959; Holmes 1966a).

To test this hypothesis, a study was conducted on the breeding populations of the Red-backed Sandpiper (*Calidris alpina*) on the Yukon-Kuskokwim Delta in western Alaska (61°N), and the results contrasted with those from previous studies of the same species at a higher latitude (71°N) in northern Alaska (Holmes 1966a, b, c). This comparison provides a basis for evaluating the relative importance of various components of the environment on the breeding system ecology and the timing of annual cycle events of this tundra nesting sandpiper.

In this report, the influence of length of summer season and of climate on the timing of breeding and molt in the lower latitude red-back population is described and contrasted with the more northerly population. Latitudinal differences in territory size, density, and food supply and their implications for understanding the red-back's breeding system are considered in another paper (Holmes 1970).

STUDY AREAS AND HABITAT

Nesting populations of Red-backed Sandpipers were studied from mid-May through mid-July 1966–1968 on the Yukon-Kuskokwim Delta near the Kolomak River (61°31'N, 164°50'W), 17 mi. NE of Hooper Bay and 10 mi. inland from the Bering Sea. In 1967 and 1968 studies continued from mid-July through late August at Old Chevak, 20 mi. SE of the Kolomak and about 10 mi. inland from the sea. From there red-backs were observed and collected wherever they could be found, which was primarily along the rivers and sloughs and at the coast on the large intertidal mudflats of Hooper Bay and Angyoyaravak Bay.

The nesting habitat of red-backs in the Delta consists of flat, marshy tundra, covered mostly by grasses (*Elymus, Poa*) and sedges (*Carex* spp.), dotted with numerous lakes and ponds, and transected by many river channels which wind tortuously, anastomose frequently, and fluctuate with the tide, even many miles inland. Red-backs feed primarily on insect larvae and other invertebrates obtained from the edges of ponds, the banks of rivers and sloughs, and, later in the summer, from coastal habitats (Holmes 1970).

BREEDING SCHEDULE

Red-backs arrive on the Yukon-Kushkokwim Delta between 10 and 20 May, coincident with the appearance of patches of snow-free tundra. Males appear first in small flocks of two to eight birds; these groups quickly disperse, each male establishing a territory which he continues to defend and advertise for a period of about four weeks. Females begin to arrive shortly after the males and typically are actively pursued and courted by the males.

In 1966 territories were established and the pair-bonds formed by the last days of May, while in 1967 and 1968, both seasons with earlier snow-melt, these activities were completed by approximately 20 May. The earliest known date for a completed four-egg clutch in 1966 was 1 June, while in both 1967 and 1968 the first completed clutches were recorded on 24 May (fig. 1). Egg-laying and clutch completion within each season were relatively synchronous, the peak occurring at the end of the first week of June in 1966 and between 26 and 28 May in 1967 and 1968 (fig. 1). These events on the Delta occur, on the average, one and one-half to two weeks before they do at Barrow (Holmes 1966a).

Those nests completed in mid- and late June at the Kolomak (fig. 1) represent, probably in most if not all cases, a second attempt at nesting following the failure of the first clutch. Evidence for this is of two kinds: 1) two female red-backs collected on 20 June 1967 and 22 June 1968 in the process of laying had opaque, thickened, and heavily vascularized brood patches, a condition that is attained only after several days or more of incubation; and 2) two known (color-banded) pairs lost their first clutches to predators and subse-

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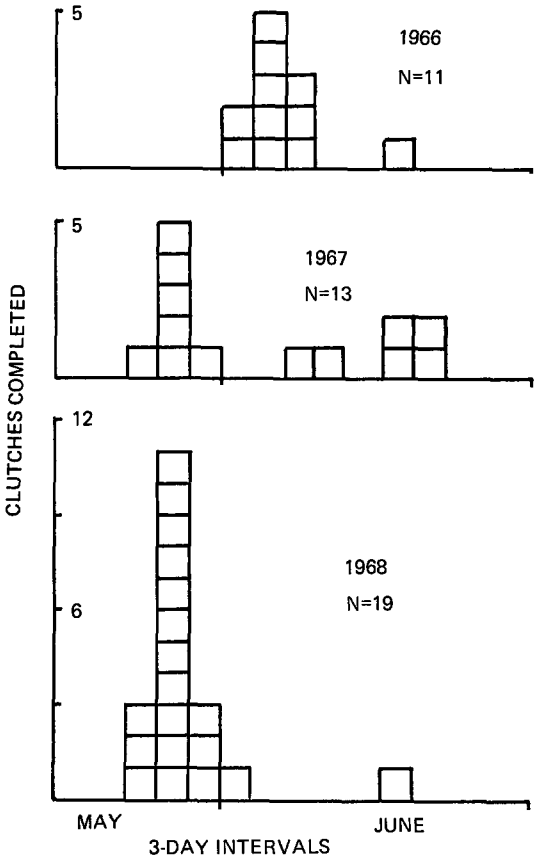

FIGURE 1. Dates of egg-laying in the Red-backed Sandpiper population near the Kolomak River, western Alaska, during three summers (each block represents a clutch completed during a three-day interval).

quently prepared new nest sites within their original territories and laid and incubated a second set of eggs. Similar renesting following early nest failure was found in the red-back population at Barrow (Holmes 1966a).

Both male and female red-backs share incubation duties, and hatching begins approximately 21 days after completion of the clutch. In 1966 the period of hatching at the Kolomak occurred mainly between 24 and 26 June; and, in both 1967 and 1968, between 18 and 20 June. Once hatched, the young sandpipers grew rapidly, reaching adult weight and starting to fly in three to four weeks. This rate of development is similar to that of young red-backs at Barrow. At the Kolomak no attempts to lay a second clutch after successfully completing a first one were recorded, even though mild weather and seemingly favorable environmental conditions prevail in this locality through mid-September (Lensink, pers. comm.).

Following fledging, young red-backs and the adults leave the marshy tundra and begin to gather along the major rivers and sloughs of the Delta. Gradually adults, followed later by the immatures, begin shifting toward the coast of the Bering Sea. In late July flocks of approximately 5000–10,000 red-backs, almost all adults, were observed on the mudflats of Angyoyaravak and Hooper Bays. By the end of the first week of August many flocks, varying in size from a few hundred to as many as 25,000, were recorded along the same section of coast. At this time about a tenth were immatures, mainly in flocks separate from the adults. By 22–23 August, tens of thousands of red-backs, approximately half adults and half immatures, were seen along the several miles of coastline surveyed.

Although I have no direct field observations from western Alaska during the month of September, red-backs apparently remain there through most of that month before moving southward. This conclusion is based on the facts that they are abundant there in late August, that they do not begin to arrive in their temperate migrating or winter quarters in any numbers until late September or early October, and that they have not been recorded in any significant numbers along the coasts of southern and southeastern Alaska, British Columbia, Washington or Oregon during this period (see Holmes 1966a).

MOLT SCHEDULE

While on or near their Alaskan breeding grounds, adult red-backs undergo a complete molt, involving the replacement of essentially all body and flight feathers. This molt, the second or succeeding prebasic molt in the terminology of Humphrey and Parkes (1959), is referred to hereafter as the prebasic molt. Because of its variation in timing with respect to latitude and to breeding schedules (see below), only it is treated here in detail. Although I have little information on the juvenal and first prebasic molts of young Delta red-backs, these appear to be essentially identical with those in the Barrow population (see Holmes 1966c), following the same patterns of timing in relation to hatching and growth periods.

Information on the pattern and timing of the prebasic molt of the Delta red-backs was obtained from specimens collected between mid-May and mid-July at the Kolomak, and between mid-July and late August at Old Chevak and along the Bering Sea coast a few miles south of Hooper Bay. The methods of recording molt stages and of assigning numerical scores were the same as those used in

the study of the Barrow red-back population. Briefly, these involved recording the occurrence and stage of molt in several selected flight feathers and of feathers on four areas of the body, which included those areas first and last to molt and graded stages in between. These data were then converted to scores, based on the total mass of feathers represented by each feather or area recorded. A bird that had not begun to molt scored 0, one just completing molt, 200 (40 and 160 for completed flight and body feathers, respectively).

The sequence of feather replacement in the prebasic molt of adult red-backs on the Delta is identical to that at Barrow, but differs in overall scheduling. The molt begins with the loss of the innermost primary. On the Delta, the first bird molting primaries was recorded on 27 June, but even by 15 July many had not yet started to molt (fig. 2). The last individual not molting primaries was recorded on 23 July. By contrast, at Barrow, where snow melt occurs between late May and mid-June, primary molt starts on about 14 June, coincident with egg laying, and every individual is in molt within a 10-day period. Therefore, even though spring melt occurs two weeks earlier on the Delta, the red-backs there are two weeks later in starting to replace primaries. Furthermore, the period during which molt is initiated on the Delta is far longer than that in the Barrow population (three weeks vs. 10 days).

The molt of flight feathers continues through the summer, with secondaries and rectrices starting to be replaced in late July and early August. By 22–23 August, when our field work on the Delta ended, we had collected only one individual with fully completed wing and tail feathers (fig. 2). Since most red-backs arrive on their winter quarters in complete basic plumage and do not molt during migration, they must finish molt between the end of August and the time of their southward migration in late September to mid-October. This agrees with the projected end of the regression line in figure 2, which indicates that flight feather molt will be completed in this population by late September.

The molt of body feathers in the Alaskan red-backs begins on the crown, then on the cervical region, and quickly spreads to all feather tracts (Holmes 1966c). The onset of body feather molt in the Delta red-backs was highly variable, as was the case for the Barrow birds. The first red-back on the Delta undergoing body molt was collected at the Kolomak on 27 June 1966, the second not until 7 July 1966, while most started body molt in the last ten days of July (fig. 2). By 22 August, few birds in the sample had replaced more than half of their body feathers, as indicated by the molt score. At Barrow the body feather molt began about 10 July, with most individuals in molt by 20 July, and the last not in molt recorded on 5 August (Holmes 1966c). Little difference in the timing of body feather molt therefore exists between the two populations.

Since red-backs arrive in their winter areas in complete basic plumage (Holmes 1966c), their molt of body feathers, like that of flight feathers, must be completed during September while they are still in northern regions.

DISCUSSION

To exploit the tundra during the short arctic summer, birds must strictly budget their time and energy resources. The forms taken by these budgets vary, even among closely related species, suggesting that several different but apparently successful evolutionary strategies of responding to the stringent environment are possible (Pitelka, Holmes, and MacLean, MS). In the Calidridine sandpipers of northern Alaska, this is most apparent in the scheduling of the major energy-requiring events of reproduction, molt, and migration.

In this group, two major patterns are evident. Several species (e.g., *C. melanotos, C. bairdii,* and *C. pusilla*) migrate northwards in spring, breed, depart from the tundra between mid-July and mid-August, migrate south, and then molt during their relatively long stay in south temperate winter quarters. The other pattern is shown by *C. alpina* in which breeding and molt take place on the summering grounds between the two migrations; this is permitted, at least in part, by the nearness of their north temperate wintering areas, allowing a longer stay in the northern regions. As this paper demonstrates, however, the two Alaskan *alpina* populations, separated by 10° of latitude, exhibit some differences in the timing of their breeding season events.

EFFECT OF SHORT SUMMER

In the *C. alpina* population of the Yukon-Kuskokwim Delta the breeding and molting seasons do not overlap. With the long snow-free period, there is sufficient time for molt to be completed between the end of the breeding effort and the fall migration. The lack of any attempts to produce second broods

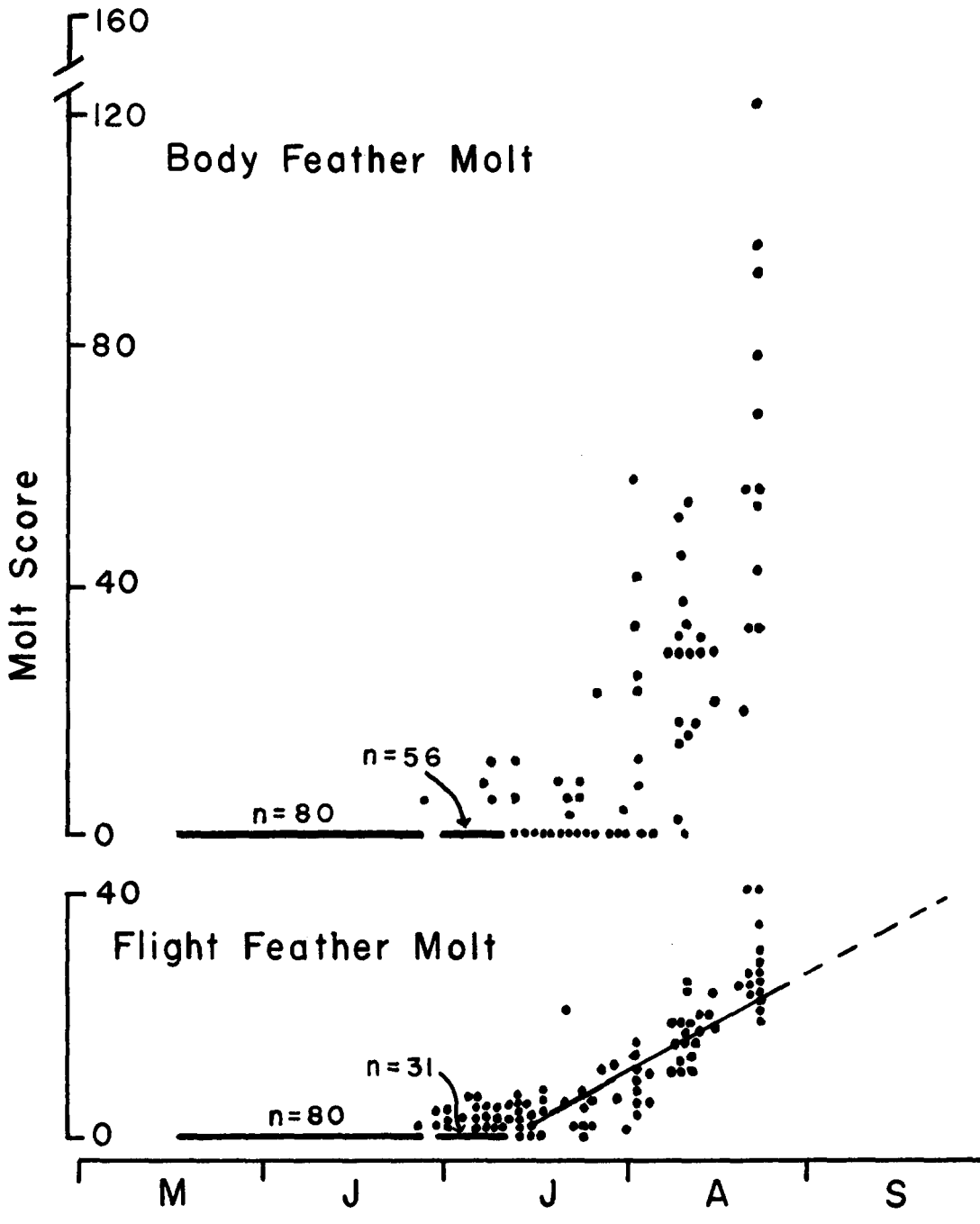

FIGURE 2. Molt schedule, as indicated by molt scores (see Holmes 1966c and text), of 202 adult Red-backed Sandpipers, collected on the Yukon-Kuskokwim Delta, western Alaska, in the summers of 1966–1968. Regression equation for flight feather molt: $Y = 0.47X - 5.44$.

after successfully rearing the first, even though the weather remains relatively mild, is probably due to a precipitiously declining food supply on marsh tundra at this time (Holmes 1970). This results in a movement of the redbacks away from the nesting habitat to better feeding areas at the coast. In addition, molt is intensifying in late June and July and the available food-energy resources may then be channeled into the molt process.

This illustrates, through comparisons with the Barrow population (fig. 3), the effects of the longer snow-free season at the lower latitude. At Barrow, with an abbreviated summer, breeding and molt are compressed into a shorter period and necessarily overlap. In

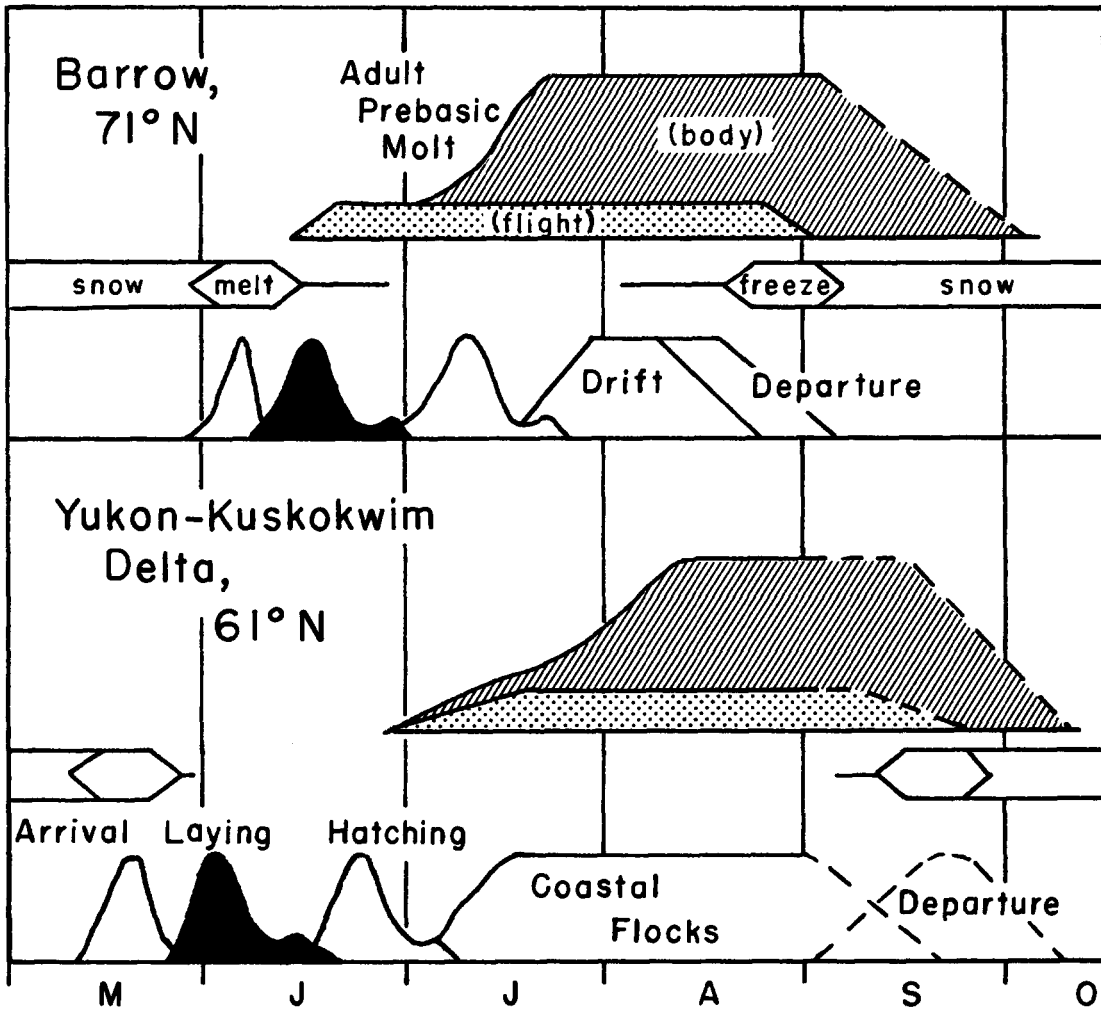

FIGURE 3. Comparison of breeding season schedules of two Alaskan Red-backed Sandpiper populations.

addition, red-backs at Barrow have also responded evolutionarily to the short season by molting at a faster rate. This is demonstrated by a comparison of regression lines of flight feather molt scores for two red-back populations (fig. 4) in which the two regression coefficients ($b = 0.75$ for Barrow and $b = 0.47$ for the Delta) were significantly different ($P > 0.01$). From this analysis, the average length of time required to replace flight feathers is about 70 days for the Barrow red-backs and about 97 days for the Delta birds. Therefore, molt at Barrow starts earlier and progresses faster, both apparently adaptive responses to the shorter summer season.

Although the overlap of breeding and molt at Barrow appears to represent an exception, or compromise (Payne 1965), to the general tenet that breeding and molt are temporally exclusive events (Lack 1954; Pitelka 1958), it has been shown previously (Holmes 1966c; see fig. 3) that the bulk of feather replacement and presumably of energy expended on molt takes place after the main breeding effort. Furthermore, the portion of molt which does overlap breeding, that of some flight feathers, is minimally demanding of energy.

EFFECT OF WEATHER

The impact of weather on scheduling of events in the red-back populations is not as easily evaluated. The times of spring melt and fall freeze-up set the outside limits to the birds' stay on the tundra, but these relate to the length of season discussed above. At Barrow the weather is more severe and unpredictable than on the Delta, and there it has significant and direct effects on the availability and abundance of insects which are the major foods for sandpipers (Holmes 1966b). The results of freezing temperatures and snow storms during the summer months are lowered

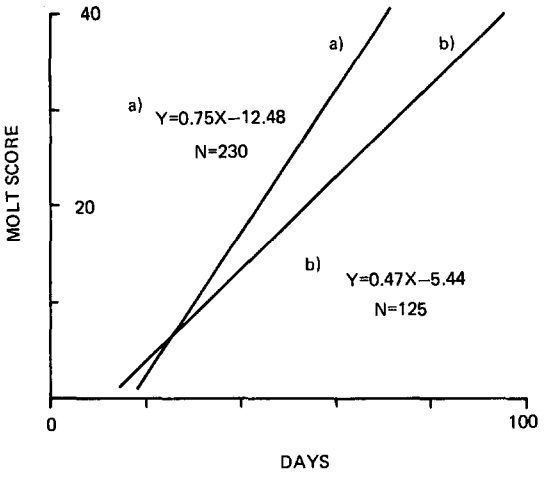

FIGURE 4. Regression of molt scores of flight feathers on time for Alaskan *C. alpina* populations at (a) Barrow and (b) on the Yukon-Kuskokwim Delta. Time axis is given in days from when the first individual was recorded in molt. The data for line (a) are from figure 5b, c, d in Holmes (1966c); those for line (b) are from figure 2 of this paper.

survival of young and the forced movement of adult birds to other feeding areas, e.g., to the coast or river banks. This weather-induced variability in food abundance, which is greatest at Barrow in mid- to late summer, may have been a major force in the evolution of the early departure schedules of *C. melanotos*, *C. bairdii*, and *C. pusilla*. The red-back, however, stays longer on the tundra in summer, moves to locally favorable feeding sites in periods of adverse weather, and utilizes the tundra's food resources in late summer for completion of its molt.

On the Delta the weather is relatively mild, with freezing temperatures and snowfall being rare after late May and before mid-September. The amount of rain varies from one year to the next, but apparently does not affect food availability. Breeding in the Delta red-backs takes place as early in the summer as possible and, in contrast to Barrow, does not appear to be so exactly timed to the emergence of adult insects, although the latter are usually present at the time of red-back hatching. The early breeding pattern may have evolved to leave the maximum amount of time after completion of breeding for molt to be accomplished. Insect abundance on the marsh does decline markedly through the first half of the summer (the only part for which data are available, Holmes 1970), and as soon as breeding is over, the red-backs quickly move to feeding sites along the rivers and the coast. None of these events seems to be correlated, directly or indirectly, with weather.

In conclusion, the telescoping of breeding and molt in the Barrow red-back population represents an adaptive response to the shortness of the summer season, while the Delta red-backs, living in a less stringent environment, have evolved a more typical schedule in which these activities do not overlap. Climatic events have greater effects at higher latitudes by their influence on the timing of reproduction and on breeding success.

SUMMARY

On the Yukon-Kuskokwim Delta in western Alaska, adult *C. alpina* arrive in mid-May, establish territories, pair, nest, and care for young before starting their prebasic molt. After the young fledge, the red-backs shift from inland marsh tundra to coastal habitats, at which time molt intensifies. Feather replacement is complete prior to arrival in late September and October on their north temperate wintering quarters. The result is that breeding and molt are fitted, in sequence, into the summer schedule of events and do not overlap.

In the *C. alpina* populations at Barrow, Alaska, 10° latitude farther north, breeding and molt overlap and molt proceeds at a faster rate. Such modifications are results of adaptive responses to the shorter summers at the higher latitudes and, to a lesser extent, to the more severe and unpredictable weather there. Results support the hypothesis that the timing of breeding season events in arctic shorebird populations is strongly affected by the length and character of the summer season.

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