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## MOLT CYCLE OF THE RED-BACKED SANDPIPER (*CALIDRIS ALPINA*) IN WESTERN NORTH AMERICA

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THE placement of molts in relation to other events of the annual cycle differs among shorebirds breeding in the arctic. For example, in some, such as the Red-backed Sandpiper, the complete molt occurs in summer, even though reproductive and molt activities then necessarily overlap in time and energy demands. In other species, including many of the Red-back's congeners, this molt does not take place until after southward migration. Such species-specific differences in molt scheduling represent adaptive responses, at least in part, to the stringent environmental conditions of high latitudes (Holmes, 1966*a*).

The main objective of this paper is to describe the molts and their scheduling in one arctic shorebird, the Red-backed Sandpiper or Dunlin (*Calidris alpina*), on Alaskan breeding grounds and on migrating and wintering areas along the west coast of North America from Alaska to California. This information will provide the basis for later comparisons and evaluations of the ecological and evolutionary significance of molt schedule specializations in *Calidris* sandpipers and perhaps in other shorebirds as well. For *C. alpina*, the information given here on molt cycle is integrated with other aspects of its annual-cycle ecology when appropriate, but a broader discussion is given in another paper (Holmes, 1966*a*).

### ACKNOWLEDGMENTS

I am indebted to Frank A. Pitelka for his continuing assistance and encouragement and for his constructive criticism of this manuscript. The field work in Alaska was done under the auspices of a grant from the Arctic Institute of North America to Dr. Pitelka. For use of the facilities at the Museum of Vertebrate Zoology, I am indebted to N. K. Johnson, and to the late Alden H. Miller.

In addition to the material of *C. alpina* at the Museum of Vertebrate Zoology, other specimens of this species from western North America examined in this study were located in the collections of the following institutions: University of Alaska, Arctic Health Research Center (Anchorage), British Columbian Provincial Museum (Victoria), University of British Columbia, Royal Ontario Museum of Zoology

	Primaries		Seco- nd's		Rec- tr's	
	1,5	10	1,10	1,6		
O	0	0	0	0		
M	.38	0.7	.38	.19		
A	.75	1.3	.75	.38		
B	1.12	1.9	1.12	.56		
1/4 C	1.5	2.5	1.5	.75		
1/3 C	2.0	3.8	2.0	1.25		
1/2 C	3.0	5	3.0	1.5		
2/3 C	4.0	6.8	4.0	2.0		
3/4 C	4.5	7.5	4.5	2.25		
4/5 C	5.0	8	5.0	2.5		
D	5.4	9	5.4	2.7		
E	6	10	6	3		
A	x2 =12	x1 =10	x2 =12	x2 =6	Total = 40 Points	

	O	A	B	C	D	E
O	0	4	8	12	16	20
A		8	12	16	20	24
B			16	20	24	28
C				24	28	32
D					32	36
E						40
	For 4 areas					total = 160

Figure 1. A. Scoring system for selected flight feathers (see text). B. Scoring system for each of four selected areas of body feathers. The least advanced stage represented is read down, the most advanced is read across. See text for further detail.

Key: O, old feathers; M, missing; A, pin feather; B, "brush" stage; C, partly grown feather; D, feather completely grown or nearly so, but still sheathed basally; E, feather completely grown, no basal sheath.

(Toronto), National Museum of Canada (Ottawa), Washington State University, Humboldt State College (California), California Academy of Sciences, University of California at Los Angeles, Los Angeles County Museum, Denver Museum of Natural History, University of Kansas Museum of Natural History, Chicago Natural History Museum, University of Michigan Museum of Zoology, Carnegie Museum, Museum of Comparative Zoology, American Museum of Natural History, and the United States National Museum. To the curators of these collections, I extend my appreciation.

MATERIALS AND METHODS

Information on pterylosis, molt, and molt schedule of *C. alpina* (race *pacifica*, A.O.U., 1957) was obtained from individuals collected during ecological and behavioral studies of this species at Barrow, Alaska (71° N lat., 157° W long.) in the summers of 1959 through 1964 and on the Berkeley-Emerlyville shore of San Francisco Bay, Alameda County, California (37° N, 122° W) during the corresponding winters. In addition, all specimens of *C. alpina* from the west coast of North America in those museums designated above were examined for molt and feather characteristics.

For pterylographic studies, molting and non-molting Red-backs were collected and preserved in 70 per cent alcohol; later, their feathers were clipped and their pterylae mapped. Some flat skins were prepared for internal views of feather tracts.

To document the timing of molt, I used a modification and extension of the system developed by Pitelka (1958). Representative remiges and rectrices and particular

areas in the body feather tracts were chosen for recording of molt, because they included the sites first to begin molt, the last to finish, and graded stages between the extremes. Those flight feathers chosen were primaries 1, 5, and 10, secondaries 1 and 10, and rectrices 1 and 6. Each was classed according to the scheme shown in Figure 1, A (after Pitelka, 1958). For recording body molt, a one cm square area centrally located in each of the following sites was selected: (1) coronal region, capital tract; (2) interscapular region, dorsal tract; (3) cervical and (4) sternal regions of the ventral tract. In each area, the range of molt stages present was recorded; the same designations as for flight feathers were used (see legend of Figure 1, A), except that it was impossible to detect missing ("M") body feathers and to record the fractional lengths of growing body feathers. For additional quantification of body feather molt, the molt stage of the most abundantly represented feathers within the area examined was noted. For example, if some feathers were of the old generation, but molt was just beginning, the reading would be O-A (the underline denoting "O" as the predominant stage); likewise, O-C-E would indicate that all feather stages from old through fully grown were present but that the intermediate stages were the most common.

Once recorded, the molt stages were assigned numerical values (Figure 1), using a scoring system developed to reflect the relative dry weights (biomass) of the different feathers and feather groups. The result was a quantitative measure of the stage of molt at a given time in each individual and, with a large sample size, in the population. In establishing weighting factors, feathers were removed from 19 fresh specimens which had completed their molt; the plucked feathers were oven-dried at 85°C for three days (at which time there was no further loss of weight) and then weighed by groups (primaries, secondaries, rectrices, and body feathers); the flight feathers were also weighed individually. Results indicated that the flight feathers represented 20 per cent, and the body feathers 80 per cent of the feather mass. Using an arbitrary 200 points for a total score, 40 were allotted to flight feathers, 160 to body feathers.

Of the flight feathers (Figure 1, A), the primaries comprise 55 per cent by weight (and receive 22 of the 40 points), the secondaries 30 per cent (12 points), and the rectrices 15 per cent (6 points). In the last two groups, points were divided evenly between the two feathers for which records were taken, since all secondaries and all rectrices were approximately of the same size and weight. With primaries, however, the size of feathers varies from the small inner ones to the larger outer ones. Since the inner six are similar in size and weight, primaries 1 and 5 were given 6 points each, but primary 10, representing the molt of larger feathers was given 10 points.

To each of the four body areas recorded, 40 points were given; these were further subdivided arithmetically so that advancing growth stages received proportionately increasing values (see Figure 1, B). Furthermore, the most abundant feather stage was weighted in order to represent the molt stage more accurately. This was done by using the value halfway between the predominant stage and the most advanced stage when the latter was not the most common one; thus, O-A = 2 points, whereas O-A = 4; and O-C-D = 14, while C-D-E = 30. Although the readings are somewhat subjective and the scoring system relatively crude, this method of representing feather molt proved to be satisfactory (see later sections).

#### PTERYLOGRAPHY

Requisite to a study of molts and plumages is a description of feather distribution in the particular species being considered. Surprisingly little

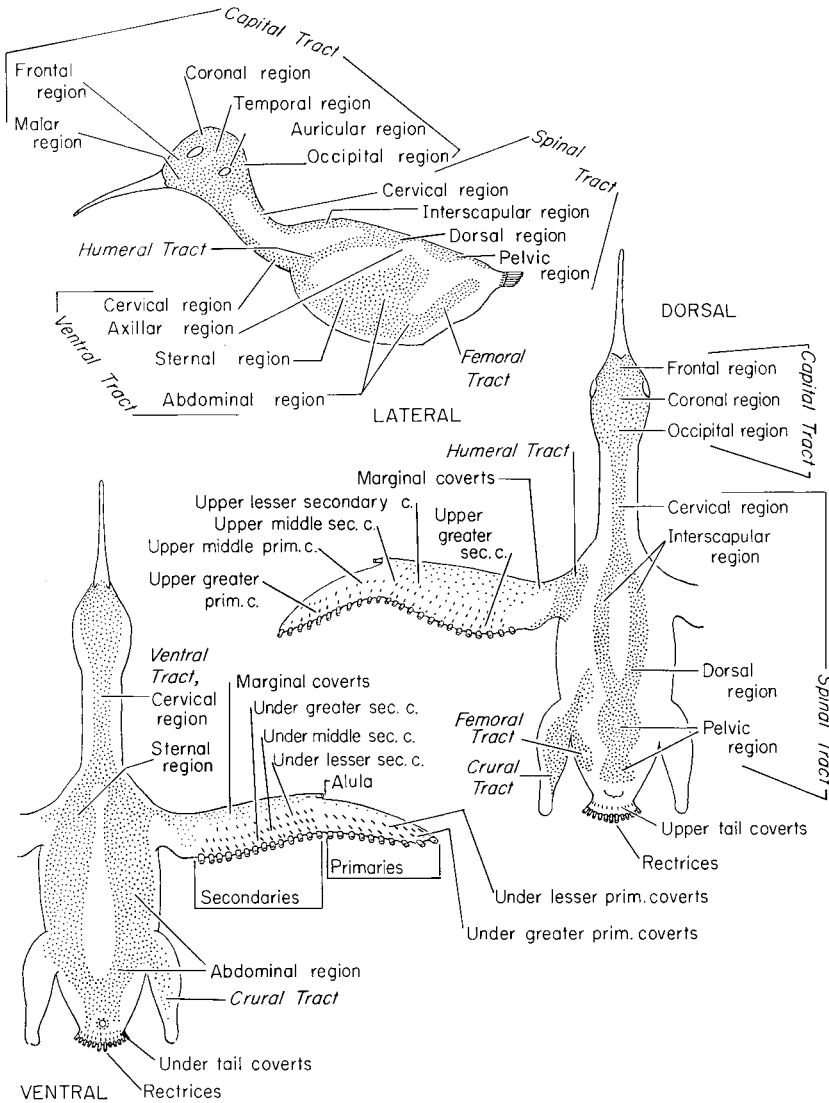


Figure 2. Pterylography of *Calidris alpina* shown in lateral, dorsal, and ventral views.

information is available on the pterylosis of Limicolae, let alone of any *Calidris* sandpiper. The pterylographic sketches of Nitzsch (1867) for *Charadrius* and *Scolopax*, of Lowe (1927) for *Scolopax* and (1931) for *Limnodromus*, and of Pettingill (1936) for *Philohela* were of use, but in general they did not provide sufficient detail for comparative purposes.

The drawings (Figure 2) of *C. alpina* feather tracts provide a basic description of sandpiper pterylographic pattern; feather tracts of several other *Calidris* species (*melanotos*, *bairdii*, and *pusilla*) were also examined, but no obvious differences from *C. alpina* were evident.

The arrangement of sandpiper pterygiae resembles, at least in over-all configuration, that found in passerine birds. Therefore the nomenclature employed is based on that used for passerine pterylography, particularly by Miller (1928) and Pitelka (1945).

*Capital tract.*—Feathers on the head form an essentially continuous and unseparated covering with but one small apterium immediately behind the eye (Figure 2). Feathers are slightly more dense in the coronal, frontal, and malar regions than in other areas.

*Spinal tract.*—Of this tract, four divisions, varying in extent and distribution, can be recognized (Figure 2). Covering the dorsal surface of the neck is the cervical region, which is separated from ventral pterygiae by large lateral apteria. The cervical region joins with the interscapular region, which splits into two rami that continue posteriorly as the dorsal region. This divided dorsal region with its central apterium is characteristic of charadriiforms (Nitzsch, 1867; Lowe, 1927; Pettingill, 1936) and differs markedly from the single, but often irregularly shaped, dorsal region found in passerines (Miller, 1928; Pitelka, 1945). In *C. alpina* the two halves of the dorsal region meet posteriorly and form a relatively wide, two-lobed patch, the pelvic region.

*Humeral, femoral, and crural tracts.*—Each of these constitutes a single region, covering the area(s) shown in Figure 2; they differ very little from those reported for other Limicolae and from apparently homologous tracts in passerines.

*Caudal tract.*—Red-backs have 6 pairs of rectrices, which is the usual number found in shorebirds (Witherby *et al.*, 1940), although Pettingill (1936) reports 7 pairs in *Philohela*, and Baker (1929) reports 7 to 13 pairs in *Capella*. In *Calidris alpina* the central pair of tail feathers is slightly longer and differs in color and pattern from the others. Each tail feather has an upper and lower covert.

*Ventral tract.*—Feathers on the under surface of the head are distributed continuously from the base of the bill to the base of the neck, where the tract divides into two sternal components. The anterior portion (inter-ramal and sub-malar regions of passerines; Pitelka, 1945) merges laterally with the capital tract. The axillary region in Red-backs is not easily distinguishable. The abdominal area is relatively wide and densely feathered.

*Alar tract.*—In his description of the pterylosis of *Philohela*, Pettingill (1936) reported only 10 primaries and discounted earlier reports of a rudimentary 11th primary in shorebirds. In *C. alpina*, however, there are 11 primaries, each with its greater and lesser coverts; the outermost primary is reduced in length to about 6 mm. Aside from this, the proximal five primaries are shortest, ranging from 55 to 70 mm in length. The more distal ones are increasingly large, the tenth being approximately 105 mm long.

Red-backs have 14 secondaries, of which the proximal 4 are thinner and more flexible than the others and in addition differ in color. The secondaries are all of the same general size. They are diastataxic with a slight gap between secondaries 4 and 5, above which there is an "extra" secondary covert. The greatest, middle, and lesser secondary coverts are present on both the upper and lower sides of the wing and are arranged in regular rows above their respective secondaries (Figure 2). There are roughly five rows of marginal coverts.

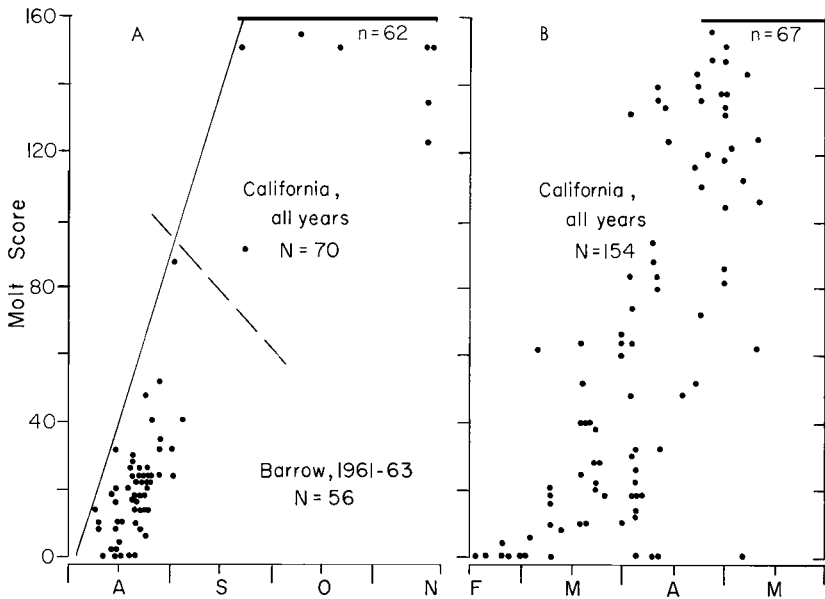


Figure 3. A. Timing of first prebasic molt of *Calidris alpina*, recorded from specimens taken at Barrow, Alaska, and in California. B. Timing of prealternate molt of *Calidris alpina*, recorded from specimens taken in California.

See text for explanation of molt score. Solid lines at top span the period when individuals (number given by *n*) with molt completed were taken. Overall sample size, including *n*, is given by *N*.

#### PLUMAGE SUCCESSION

Some fragmentary information on the timing and sequence of molt in *C. alpina* is available (Dwight, 1900*b*; Jackson, 1917; Witherby *et al.*, 1940; Kozlova, 1962; Stresemann, 1963), but no systematic studies with large sample sizes from relatively few localities have previously been made. In this investigation, 1,449 specimens of *C. alpina* from the west coast of North America were examined for the occurrence of molt. For interpretative purposes, emphasis is placed on the molt of Red-backs in their Alaskan breeding quarters and their wintering areas in California, as sample sizes from these areas are largest.

Since the placement of molts in the annual cycle varies markedly among the *Calidris* species, I have found the molt terminology of Dwight (1900*a*) to be inconvenient when applied to sandpipers, especially when interspecific comparisons are to be made. The molt classification scheme of Humphrey and Parkes (1959), even though the implications of some terms (such as "basic") seem unfortunate, does fit more satisfactorily, and consequently

will be used here. For detailed descriptions of plumages of *C. alpina*, the reader is referred to Witherby *et al.* (1940) and to Gabrielson and Lincoln (1959).

*Postnatal and first prebasic (postjuvenile) molts.*—Young Red-backs, upon hatching, are covered with down feathers, which begin within a week to be replaced through a postnatal molt. The incoming juvenal feathers first appear on the humeral tract and in the interscapular region, then ventrally in sternal and cervical regions. From these loci, molt spreads laterally and posteriorly until the chick is covered with large contour feathers of the juvenal plumage. Flight feathers begin to break sheaths when the chick is about 15 days old and are fully grown two to three weeks later. The young sandpipers are able to fly about three weeks after they hatch, this being one week or so prior to completion of growth of the flight feathers (Holmes, 1966*a*).

The juvenal plumage has a fleeting existence, almost as short as that of the downy plumage. In fact, it is difficult to observe any pause in feather replacement between postnatal and first prebasic molts. All young Red-backs taken in July at Barrow (N = 125) had downy plumage or were undergoing the postnatal molt. The first prebasic molt usually begins before the juvenal plumage is complete. Thus, as the later portions of the juvenal plumage are still in growth stages, feathers which had been completed just days or weeks earlier are being replaced by feathers of the first basic plumage.

The first prebasic molt involves the replacement of most of the juvenal feathers (Dwight, 1900*b*: 381). However, all flight feathers, most wing coverts, and certain portions of the juvenal body plumage (the pelvic region and frequently a few feathers in the humeral tract and interscapular region) are retained. Replacement begins in the capital tract and in the dorsal and interscapular regions of the spinal tract, and is followed shortly by molt along the mid-ventral line. Molt then spreads rapidly to all remaining feather tracts that are to molt, so that once started, it occurs in practically all those areas at once. Except for those feathers not replaced, the sequence of this molt is the same as that of later body molts.

The first prebasic molt, as recorded in the Red-back population at Barrow in summer, begins during the first week of August (Figure 3, A), at a time when the family groups are beginning to disperse. By 15–20 August, every immature Red-back is in molt. At the time of their departure from the Barrow region, mainly during the last 10 days of August and the first few days of September, young Red-backs have completed approximately one quarter to one third of their first prebasic molt (Figure 3, A).

Upon arrival on the wintering grounds in California in late September and October, most immature Red-backs have completed molt and are in their

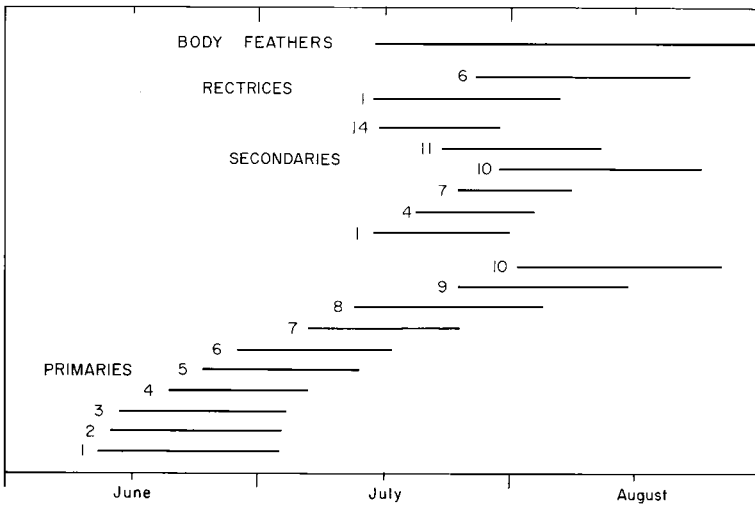


Figure 4. Inclusive period in which molt of particular flight feathers was in progress, in the population as a whole, during the prebasic molt of adult *Calidris alpina* at Barrow, Alaska.

first basic plumage (Figure 3, A). Among the few exceptions were two birds that had arrived in California earlier than normal (before 20 September) and four individuals collected in mid-November, 1963. Although the delay in the latter cases cannot be explained without knowing the histories of the individuals involved, it was noted that when collected, each had partially molted into the basic plumage but showed no active molt, suggesting that molt may be suspended during migration (see Discussion).

*Prealternate (prenuptial) molt.*—In spring, the change from basic to alternate plumage is practically identical in sequence and timing in both first-year and adult Red-backs. All flight feathers and their coverts are retained, except that in a small number of adults (less than 10 per cent), the central pair of rectrices and the innermost secondaries are replaced. Most body feathers are molted, excepting those in the pelvic region, and occasional ones in the dorsal and humeral regions and in the posterior part of the abdominal region. The pattern of feather replacement follows that described below for the prebasic molt of body feathers.

Of the 126 specimens collected between 15 November and 20 February at west coast localities (British Columbia to California), none was in molt. In California, the earliest individual in prealternate molt was detected in late February (Figure 3, B). Farther north, in coastal areas of Washington, British Columbia, and southeastern Alaska, 21 Red-backs taken be-



tween 2–25 March had not yet begun to molt. Specimens collected in early April in the northwest, however, show molt in early stages.

In California and probably farther north, molt continues as the Red-backs drift slowly northward in migration. Of the birds still present in California in mid to late April, most have completed molt (Figure 3, B). Among 36 specimens collected in April from the northwest, a great variety of molt stages was observed, while from the same region in May, only 2 of 78 were not in their completed alternate plumage.

*Second and succeeding prebasic (postnuptial) molts.*—In summer and early fall, adult Red-backs renew all flight and body feathers. This molt starts with the flight feathers. Onset of molt is signalled by the loss of the proximal primary, followed closely by primaries 2 and 3 (Figure 4). Molt in the remaining primaries progresses distally, one feather dropping every few days until number 10 has been lost. Normally several of the innermost primaries are simultaneously missing or in very early growth stages. Although the gap so produced is very conspicuous in the field, it is not large enough to impair flight, especially since the adjacent secondaries are not lost until these proximal primaries have been replaced. In fact, during this part of the molt, the birds are actively advertising and defending territories (Holmes, 1966a: 30–32). The more distal primaries are lost individually.

Within the period when the primaries are being replaced, all other remiges, plus the rectrices and associated coverts, are renewed (Figure 4). Molt in secondaries begins with loss of the outermost (number 1) and proceeds proximally until number 10 is replaced; within this time span, the inner four secondaries are also molted. Wing and marginal coverts are renewed concurrently with the secondaries and are usually fully grown before the last primary is completed. Molt in the rectrices begins with the central pair and progresses laterally ending with the replacement of the outermost tail feathers (Figure 4).

Replacement of body feathers begins after flight feather molt is well underway, but once started, the molt occurs almost simultaneously in all feather tracts. Contrary to observations of Dwight (1900b: 372), new feathers usually appear first in the frontal and coronal regions of the capital tract and not in the humeral and interscapular regions. From the coronal region, molt spreads posteriorly along the spinal tract, and then feathers in the humeral, crural, and femoral tracts begin to molt. Soon after molt begins in the capital areas, it does so ventrally near the base of the bill and along the midline of the cervical region and then spreads in all directions. The last areas in which molt can be detected are those on the sides of the head, mostly in the auricular patch, and in sternal and

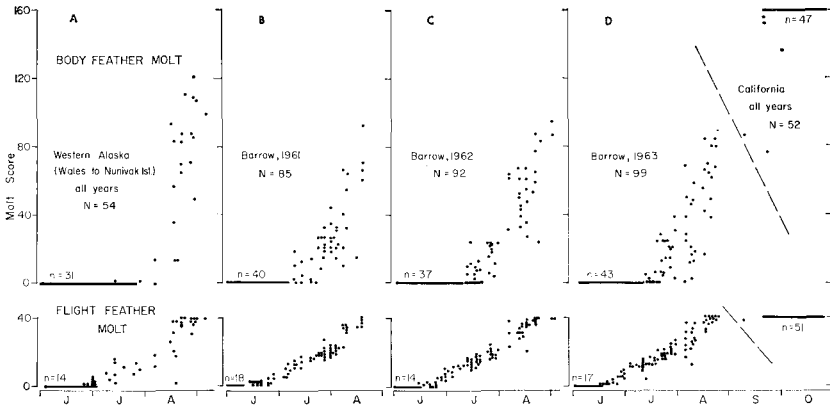


Figure 5. Timing of prebasic molt in adult *Calidris alpina* in summer (A) in western Alaska (Wales to Nunivak Island in various years), (B–D) at Barrow, Alaska, in 1961–1963, and (D) in California in various years. Overall sample size for each area is given by N; the portion of each sample consisting of individuals showing no molt or molt completed is given by n, with the inclusive period when such specimens were taken shown by the heavy line.

abdominal regions. One of the last visible features of the alternate plumage to be lost is the ventral black patch.

The timing of the second and presumably all following prebasic molts in the populations studied is given in Figure 5, B–D. Kozlova (1962: 121) states that the prebasic molt of *C. a. sakhalina* (*pacifica* of A.O.U., 1957) begins in July, but it is evident that in northern Alaska, it starts even earlier. At Barrow, the first individual in molt was collected on 14 June, at which time it showed several primaries in young growth stages. Within the period 14–20 June in each year of study at Barrow, almost every adult Red-back started wing molt; the only individual after 22 June not yet in molt was one collected on 24 June 1961 (Figure 5, B). Thus, onset of molt is highly synchronous and occurs early in the season, and in fact concurrently with egg laying (Holmes, 1966a).

In the Red-back population at Barrow, molt of flight feathers continues through July and nears completion by mid-August (Figure 5, B–D). Although some adult Red-backs leave the Barrow tundra during the first half of August when their flight feathers are not yet fully replaced, most remain long enough so that growth of remiges is usually complete before they move south. Those that have not finished molt when they depart from the breeding areas apparently do so during a period of migratory drift, an early phase of fall migration (see Discussion).

At the time of their arrival in California, almost all Red-backs have a

completed set of flight feathers (Figure 5, D). The only exception encountered was a female taken at Santa Barbara, California, on 9 September 1911 (Carnegie Museum no. 38726), whose outer primaries were still in terminal growth stages. This may have been a non-breeding individual not newly or recently arrived in southward migration. Completion of flight-feather replacement before arrival in California is further indicated by 67 fall-collected Red-backs from Washington and British Columbia, all of which show completed molt of remiges.

At Barrow, replacement of body feathers in the prebasic molt begins in most Red-backs between 5 and 10 July, and by 20 July molt is usually occurring in all individuals and in all feather tracts. The spread of scores for the body molt within each season is greater than that recorded for flight feather molt in the corresponding years (Figure 5, B-D). Although this increased variation may be an artifact resulting from the greater subjectivity in recording and scoring body molt, it is likely that molt of body feathers may be more influenced by variations of climate than is flight feather molt. For instance, in mid-summer, 1963, adverse weather conditions caused a reduction in availability of insect food supplies (Holmes, 1966b: 37). At this time, some Red-backs shifted feeding sites and judging from the variability in molt scores (Figure 5, D) may have stopped or at least slowed the molting process. In this season, however, the flight feather molt was not as strongly affected (Figure 5, D). Probably the molt schedule of flight feathers is relatively fixed so that replacement is completed before southward migration, and thus any variation in conditions affecting timing and extent of molt will influence the body molt first.

At the time of departure from Barrow, adult Red-backs have completed approximately one half of their body feather molt (Figure 5, B-D). Upon arrival in the California wintering quarters, most birds are in completed basic plumages, the only exceptions being a few early arrivals (again possibly non-breeders). Likewise, all fall-collected Red-backs from the northwest referred to above were through molting. Thus, the last half of the adult prebasic molt is completed in late summer and early fall, during the interval of migratory drift (Holmes, 1966a: 40), just as is true for the first prebasic molt.

In addition to northern Alaska, *C. alpina* also nests on tundra in the western part of the state, mostly along the Bering Sea coast, as far south as the Kuskokwim River delta and Nunivak Island and possibly to the Alaska Peninsula (Gabrielson and Lincoln, 1959: 387). At present, there is no detailed information on the ecology of these west coast populations, but 54 *alpina* specimens collected between Cape Prince of Wales (66° N) and Nunivak Island (60° N) in various years were available for examination of molt. The results are plotted in Figure 5, A.

Red-backs breeding in western Alaska begin molt later than those at Barrow. The first individual with flight feathers in molt was not recorded until 25 June, and even at the end of that month, several Red-backs had not yet begun to molt and others were only in very early stages. Likewise, a Red-back collected on 12 July was just starting its body molt, while many individuals taken during the last days of July had not yet started molt of body feathers (Figure 5, A).

If lines are roughly fitted to the molt scores in Figure 5, A–D (omitting the late August individuals because of the uncertainty of their breeding localities), it appears, most noticeably in the flight feathers, that the slope for the Bering Sea coast sample is lower than for those farther north, which suggests that the prebasic molt of adults in the former area may occur at slightly slower rates. Thus, not only does molt begin later at more southerly breeding latitudes, but it appears to be more protracted in time.

#### AGE DETERMINATION

For more concise information on those plumage features useful in aging Red-backed Sandpipers, the following points are summarized from the preceding sections. These features are in general agreement with those given by Witherby *et al.* (1940) for *C. a. schinzii*.

Plumage of immatures in fall and winter is like that of adults, except for juvenal feathers in the pelvic region of the spinal tract and a few that occasionally remain in the humeral tract (scapulars) and in the mid-dorsal area. The juvenal wing coverts and innermost secondaries are retained, but confusion with adults can result because some new coverts (mainly the greater coverts) and the new inner secondaries of the basic plumage of adults may have the same buffy coloration as the corresponding juvenal feathers.

Immatures in late spring and individuals in their first summer are very difficult to separate from older birds. In general, the buffy edges of the retained juvenal wing coverts are most useful. The central tail feathers are replaced in spring in some but not all adults, but apparently never in one-year-olds. The latter statement is based on the examination of two banded Red-backs of known first-year age and of other collected specimens. All flight feathers of the banded one-year-old individuals were very frayed and worn, significantly more so than in older Red-backs.

A combination of all criteria mentioned above provides the best basis for determination of age.

#### DISCUSSION

The major ecological significance of molt in avian populations lies in its timing with relation to other annual cycle events, since the schedules among

these activities reflect the evolutionary results of energy and time budgeting at the population level. Two aspects of scheduling, the integration of molt with breeding and of molt with migration, will be considered here.

*Molt and breeding.*—The prebasic molt in arctic-breeding bird species is scheduled in one of two ways. In some, as in *C. alpina* described here and in the Glaucous Gull (*Larus hyperboreus*) studied by Johnston (1961), the molt occurs during the summer season while the birds are in or near breeding quarters. In other sandpipers, such as *C. melanotos*, *C. bairdii*, and *C. pusilla*, molt does not take place in the arctic (Pitelka, 1959: 256–257; Holmes, MS), but instead occurs after departure from the tundra. In *C. minuta*, a species similar to *melanotos* and *bairdii* in that it also winters in the southern hemisphere, molt occurs during the winter months (Middlemiss, 1961: 120). More details on the relationship between timing of molt and location of winter quarters are considered by Stresemann (1963) and Holmes (1966a: 39–40).

The former situation is more germane to our discussion. The fact that molting and breeding take place simultaneously is in contrast to the exclusiveness of these two events as usually observed in other bird species, particularly those at temperate and lower latitudes (Pitelka, 1958; Miller, 1961; Johnson, 1963), and raises questions concerning energy relations in these arctic populations.

In Figure 6, the occurrence of molt is summarized for the *alpina* population at Barrow, using the results of the scoring procedures as an index to the relative amounts of energy being expended on molt. From this over-all view of annual events, it becomes apparent that most of the metabolic energy for the prebasic molt is needed in late summer. At this time, (1) the main breeding effort is already completed, (2) most of the young are full grown, (3) the adults and young occupy different habitats and consequently exploit different food supplies, and (4) the adults of other congeners, which are potential competitors for food, have already left the tundra on southward migration (for details, see Holmes, 1966a). Thus, with the body feathers representing a proportionately large percentage of the feather mass, the bulk of energy cost for molt comes later in the summer after the main outlay of energy for breeding. This same conclusion probably holds for the timing of molt in the arctic gull species (Johnston, 1961), since there, too, wing molt begins in early summer, body molt later.

The overlap of breeding and molt in *C. alpina* is a result of the compression of almost the entire prebasic molt into the short span of the high latitude summer. Moreover molts of body and flight feathers are overlapped and telescoped in time, and the duration of the molt is not more than about three months. So that flight feathers may be completely replaced and full-sized before southward migration, the molt of remiges

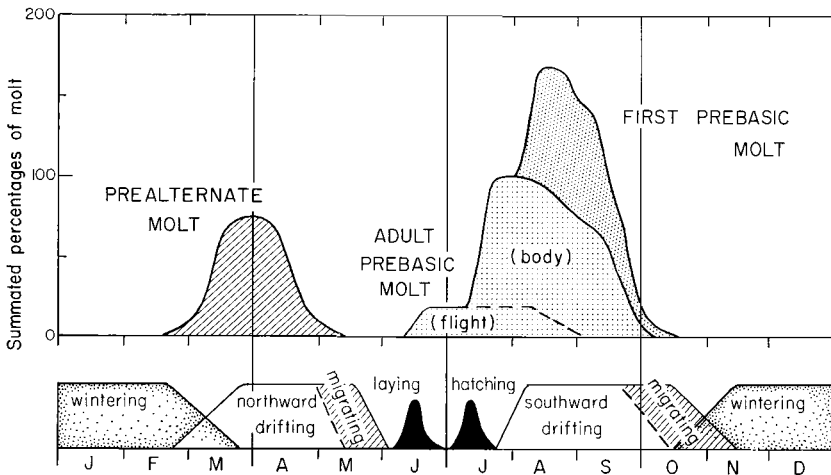


Figure 6. Summary of molt schedule in the Alaskan-breeding, California-wintering populations of *Calidris alpina*, showing proportion of feathers in molt in relation to other events of the annual cycle. The breeding cycle given is that of the population at Barrow, Alaska ( $71^{\circ}20' N$  lat.).

starts soon after Red-backs arrive on the tundra in early summer, but the main energy drain for molt occurs later.

The significance of this compaction of molt is evident when the molt schedule of *C. alpina* is compared with those of other *Calidris* species. In *C. minuta* (Middlemiss, 1961), body feathers are replaced in the prebasic molt between October and early December, after which molt of the remiges and rectrices begins. The latter feathers are not fully grown until late winter, just prior to the prealternate molt and spring migration. In *C. minuta* and similar species, this spacing of the different components of the prebasic molt is correlated with a longer season, in the south-temperate latitude wintering quarters, available for the complete molt.

Further evidence for the selective pressures of the arctic environment on time and energy schedules is derived from analyses of molts of *C. alpina* in breeding areas along the Bering Sea coast (Figure 5, A). In this more southerly region, the summer season begins earlier and lasts longer than at Barrow (Conover, 1926). Here, Red-backs not only start to breed earlier, but the prebasic molt starts later. This greater separation of breeding and molt a few degrees latitude south of Barrow attests to the stringency of selective factors acting to compress these events into the shorter season to the north.

Since, in the other *Calidris* sandpipers at Barrow which leave the tundra in mid-summer, molt is postponed until after arrival in wintering quarters,

it might be asked why the Red-backs have not evolved a similar schedule. Although this question is presently unanswerable on several grounds, I have suggested in another paper (Holmes, 1966a: 40) that *C. alpina*, by remaining longer in the arctic in summer, is able to capitalize on a then-abundant food supply at a time when there are few if any potential competitors present. This later stay is permitted by the relatively short migration which Red-backs make in fall. The relationship between molt and breeding in other *Calidris* species, such as *mauri*, *ptilocnemis*, and *maritima*, that also winter in north temperate regions is not yet sufficiently documented to permit comparisons.

*Molt and migration.*—In most passerine birds, individuals in migration rarely undergo a significant amount of molt (Johnson, 1963: 879), but in *C. alpina*, the migration and molt periods in both spring and fall do overlap (Figure 6). It is necessary, however, to elaborate upon and to qualify the term "migration" for this species. Although little is known about the early phases of their southward movement in fall, Red-backs apparently travel only a few hundred miles in a period of two to three months and probably spend considerable time in favorable sites along the way (Holmes, 1966a: 25–27). It is in this period that the prebasic molt is completed. By the time the birds are ready to fly long distances, e.g., from Alaska to California, they have a full set of new flight and body feathers. Likewise, on spring migration Red-backs move very slowly, gradually drifting northward so that no mass movement is detectable at this season (Storer, 1949; Holmes, 1966a). Thus, even though molt does take place during migratory periods, the migrations are relatively slow and leisurely, and at least in part for this reason, energy costs of both processes can be met concurrently.

Some additional evidence suggests that molt and rapid migration are normally exclusive events. Several Red-backs collected during the late and more rapid phases of both fall and spring migrations were in partially completed plumages but showed no active molt. This implies that if molt is not finished at a time when a rapid or long distance move, or both, is imperative (e.g., when the early advance of cold weather in October forces birds to move south), it is suspended, except that new feathers already started will continue to grow until completed. Thus, the cessation of molt when rapid migration begins suggests that at this time energy reserves are switched from molt processes to migratory flight processes.

It is known that other geographical races of *C. alpina*, particularly those in western Eurasia (Witherby *et al.*, 1940), differ both in timing of molt and in timing of fall migration from the Pacific coast populations. Further study of comparative molt cycles and of the ecology of shorebird groups is needed to provide more information on the range of differences, both

inter- and intra-specific, and on the environmental correlates of such differences. Such evidence will provide further clues to selective forces acting on the evolution of molt schedules.

#### SUMMARY

The pterylography, molts, molt schedule, and criteria for age determination of *Calidris alpina* along the west coast of North America are described. The relationships of molt with breeding and with migration are discussed for this species, which nests at arctic latitudes and winters in north-temperate regions.

In breeding populations of *C. alpina* in northern Alaska (71° N), the prebasic molt of adults is condensed into the short span of the arctic summer and overlaps with almost the whole of the breeding season. Molt begins early in the summer, and new flight feathers are completely grown before departure for winter quarters. At lower-latitude breeding localities in western Alaska (60–66° N), molt apparently starts later and breeding begins earlier than at the higher latitudes, with the result that less overlap occurs. Even in the northern populations, however, the major portion of energy expenditure on molt comes in late summer when breeding is over and young Red-backs are fully grown.

Molt takes place during slow phases of both fall and spring migrations, energy reserves evidently being sufficient to support both activities. In periods of rapid migration, molt is suspended.

The specializations in the molt schedule of *C. alpina* relate to the fact that this species, with its winter quarters in north-temperate regions, remains in the arctic through the end of summer, during which time it exploits tundra food sources in the absence of possible competitors.

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