BILL LENGTHS, WINTERING AREAS, AND TAXONOMY OF NORTH AMERICAN DUNLINS, *CALIDRIS ALPINA*

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THE Dunlin or Red-backed Sandpiper (*Calidris alpina*) is a common shorebird that breeds on circumpolar tundra and winters along north temperate seacoasts. The breeding ecology and behavior of this species have recently been studied in Finland by Soikkeli (1967), in northern Germany by Heldt (1966), in northern and western Alaska by Holmes (1966a, 1966b, 1966c; 1970; 1971) and MacLean (1969), and in north-central Canada by Jehl (pers. comm.). These studies have revealed a number of ecological and behavioral differences between breeding populations, such as variations in the timing of the breeding cycle, of molt, and of migration. Breeding populations in Finland and northern Alaska were compared by Soikkeli (1967). The differences between these geographically distant and morphologically distinct populations are not too surprising. Recently Holmes (1970, 1971) has reported significant differences in breeding density and scheduling of breeding season events in Dunlin populations of northern and western Alaska, breeding grounds separated by 10° of latitude and approximately 550 miles. These findings led us to question the taxonomic relationship of the two Alaskan populations and their relationships to other breeding populations of *C. alpina*.

The Alaskan Dunlins Holmes studied are presently considered to belong to a single North American subspecies, *Calidris alpina pacifica* (A.O.U., 1957; Gabrielson and Lincoln, 1959). Todd (1953) divided the North American Dunlins into three subspecies: "*arcticola*," "Range—Northern Alaska in summer; migration and winter ranges not yet ascertained;" "*pacifica*," breeding in western Alaska and wintering along the Pacific coast of North America; and "*hudsonia*," breeding in arctic Canada and migrating across eastern North America to winter on the Gulf Coast. Thus, according to Todd's scheme, the two populations studied by Holmes are subspecifically distinct. Todd claimed that both "*pacifica*" and "*arcticola*" are distinguishable from the Siberian form, *C. a. sakhalina*. His analysis was based on bill length and coloration of the breeding plumage.

During the course of our studies of *C. alpina* we, too, noticed differences in bill lengths of birds nesting in different parts of Alaska and from different wintering grounds. As bill length, unlike plumage, remains constant from breeding to wintering grounds, this characteristic can be used to determine the specific wintering range of each population,

TABLE 1

Bill Lengths of Adult Dunlins from Breeding and Wintering areas of North America and East Asia[1]

Breeding Areas Northern Alaska, Siberia	Western Alaska	Northern Canada
* "arcticola" Todd 1953	* "pacifica" Todd (1953)	* "hudsonia" Todd (1953)
♂ : 33.7 (33 –35) 10	♂ : 37.4 (35 –43) 10	♂ : 36 (35 –38.5) 10
♀ : 37.0 (34 –39.5) 8	♀ : 41.4 (38 –43.5) 10	♂ : 39 (37 –41) 10
* *"sakhalina"* Kozlova (1962)		
♂ : 34.1 (29.0–38.8) 16		
♀ : 37.1 (33.0–39.8) 18		
	Kolomak River, Yukon- Kuskokwim R. Delta, Alaska	Southampton Island, NWT and Churchill, Manitoba
Barrow, Alaska		
♂ : 33.7 (30.5–36.5) 25	♂ : 36.4 (32.0–40.0) 55	♂ : 36.2 (33.0–39.0) 23
♀ : 37.0 (34.5–38.5) 25	♀ : 40.1 (37.0–42.0) 29	♀ : 39.4 (37.0–43.0) 17
Northeast Siberia		
♂ : 32.9 (30.0–37.0) 41		
♀ : 37.3 (33.0–41.0) 20		
Wintering Areas **East Asia**	**Western North America**	**Eastern North America**
♂ : 33.2 (30.0–36.5) 46	♂ : 37.2 (34.0–41.0) 112	♂ : 36.6 (30.0–41.0) 90
♀ : 36.8 (32.5–40.5) 33	♀ : 40.5 (34.5–45.0) 111	♀ : 39.2 (34.0–43.5) 105

[1] Values given are mean and sample range, in mm, and sample size. Values preceded by an asterisk (*) are taken from the literature, as cited.

TABLE 2

AVERAGE BODY WEIGHT OF DUNLINS COLLECTED ON THE BREEDING GROUNDS IN JUNE, JULY, AND AUGUST

	Northern Alaska[1]	Western Alaska[2]	Northern Canada[3]
Males	55.4 (N = 267)	53.4 (N = 140)	53.5 (N = 24)
Females[4]	59.7 (N = 177)	59.4 (N = 67)	54.5 (N = 13)

[1] MacLean, 1969.
[2] Holmes, field data.
[3] C. G. Yarbrough, pers. comm.
[4] Values for egg-laying females excluded.

and thus may help to clarify the relationships between breeding populations.

METHODS

All measurements reported in this paper were obtained from *C. alpina* specimens in museum collections. The exposed culmen was measured middorsally to the nearest 0.5 mm. Wing chord and tarsus lengths were taken on many specimens, but these characters show little variation (for examples see Todd, 1953, and Kozlova, 1962) and are not considered here.

RESULTS

Morphological differences between breeding populations.—The Dunlins of northern Alaska are clearly separable from those of western Alaska and northern Canada on the basis of bill length (Table 1). The birds of northern Alaska have shorter bills than the Dunlins of the other two areas. This difference is not related to a difference in absolute size of the birds (Table 2), as the *alpina* of northern Alaska are slightly heavier than those collected in the other breeding grounds.

The bill lengths of northern Alaskan Dunlins are indistinguishable from the values published for the Siberian subspecies, *C. a. sakhalina*, by Kozlova (1962) and from those of the sample of Siberian birds available to us in museum collections (Table 1). Thus in this trait the Dunlins that breed in northern Alaska are more similar to their conspecifics in Asia than they are to Dunlins of other North American breeding areas.

Migration routes and wintering areas.—A survey of the bill lengths of Dunlins wintering in North America (Table 1) reveals that neither the west coast nor the east coast populations includes the birds that breed in northern Alaska. The mean values of bill lengths for each sex for both wintering areas are well above the means for northern Alaskan birds. In fact, the range of bill lengths in the sample from the Pacific coast of North America excludes most of the northern Alaskan males.

The values recorded for birds collected along the Pacific coast match most closely those of the birds that breed in western Alaska.

All males in the large sample from the east coast of North America, except one with a bill length of 30 mm, had bills of 33 mm or more, again excluding a large proportion of the males of northern Alaska. The eastern wintering population appears to match the birds breeding in northern Canada, and the two regions are connected by large series of birds collected in migration in north central United States.

The bill lengths of northern Alaskan Dunlins agree well with the measurements of birds that winter in Asia along the coasts of the Yellow Sea and Sea of Japan (Table 1). The latter regions constitute much of the reported wintering grounds of *C. a. sakhalina.*

Thus, it appears that the Dunlins of northern Alaska migrate in fall westward and southward, across the Bering Straits and along the Pacific coast of Asia, where they may mix with Dunlins from Siberia. The *C. alpina* populations of western Alaska and northern Canada, on the other hand, migrate southward and eastward after breeding to form the wintering populations of the two coasts of North America.

Taxonomic implications.—This evidence that the North American Dunlins are separable into three distinct populations supports the conclusion of Todd (1953), and we agree with Todd that these populations should be accorded subspecific status. The name *C. a. pacifica* should be restricted to the long-billed, brightly-colored birds that breed in western Alaska and winter along the Pacific coast of North America. Likewise, in our opinion, Todd's name *C. a. hudsonia* is rightfully applied to the Dunlins that nest in north central Canada and winter along the Atlantic and Gulf coasts of North America. These two forms have similar bill length, *pacifica* averaging somewhat longer, but are separated geographically by the population of shorter-billed birds that breed in northern Alaska.

We see no reason for separating the Dunlins of northern Alaska ("*arcticola*" of Todd, 1953) from the Siberian birds of *C. a. sakhalina.* We found that the plumage differences described by Todd (*arcticola*: "upper parts darker colored; throat and breast more decidedly streaked; and black abdominal area averaging more extensive.") too variable to be useful consistently for separating birds breeding on the two sides of the Bering Straits. In view of the evidence for convergence on a common wintering ground, we believe that the Dunlins of northern Alaska should be included in *C. a. sakhalina* until conclusive evidence to the contrary is presented.

The separation between *pacifica* and *sakhalina* occurs in northwestern Alaska; birds collected on the Seward Peninsula near Nome are clearly

pacifica, while a series of *alpina* collected at Cape Thompson about 200 miles farther north belong to *sakhalina*. The subspecies *sakhalina* and *hudsonia* do not come into contact, as no Dunlins nest in northwestern Canada.

Discussion

Dunlins that breed in North America and northeastern Asia are similar in body size and coloration, but they differ significantly in bill size. The selective pressures influencing bill length include the size and kind of prey species available for exploitation and the presence or absence of ecologically similar species that might compete for the same food items. Geographic variation in either of these parameters might lead to divergence in bill length between different populations.

Four species of *Calidris* sandpipers, including *alpina*, breed sympatrically near Point Barrow in northern Alaska. Holmes and Pitelka (1968) show that these species overlap considerably in food items taken, although some separation occurs. MacLean (1969) investigated feeding microhabitats of the four species and reached a similar conclusion: the species overlap broadly in microhabitats used, but differ significantly in their frequencies of utilization of each habitat type. It is significant that the greatest separation (least overlap) occurs when food is least plentiful. Thus ample evidence indicates that, at least in this area, competition with congeners for food, only partly alleviated by differences in selection of feeding sites or prey items, may be a potent force influencing the evolution of bill length. MacLean (1969) shows that when the four *Calidris* species found near Barrow are arranged in sequence according to bill length, the degrees of difference of larger over smaller species throughout the sequence are constant (and relatively large, according to the analysis of Schoener, 1965). This, again, indicates that interspecific relationships are important factors in the evolution of bill length.

Yet interspecific relationships alone cannot explain the divergence in bill length seen in the several populations of *C. alpina*. The Point Barrow Dunlins, although the smallest-billed of the North American populations of *alpina*, are the longest-billed of the four *Calidris* species that nest near Barrow. Thus their short bills cannot be explained as the result of competition on the breeding grounds with some longer-billed form. Presumably they could evolve longer bills and thereby reduce the potential for competition with their shorter-billed congeners. Any tendency to do so, however, must be opposed by selective pressures, probably resulting from the kinds and quantities of food available, which favor shorter-billed over longer-billed Dunlins.

In western Alaska *C. alpina pacifica* is sympatric with but one other calidridine sandpiper, *C. mauri*, and the two species occupy different habitats (Holmes, 1970). These are the Dunlins with the longest bills and the greatest amount of sexual dimorphism in bill length. Holmes (1970) discusses differences in food availability and diet of Dunlins in northern (*C. a. sakhalina*) and western (*C. a. pacifica*) Alaska. In western Alaska the birds feed heavily on a food source—larval Chironomidae—that is both plentiful and dependable. In northern Alaska, in contrast, the food supply is generally less abundant and subject to large variations in abundance, some of which are predictable (seasonal variations) and some of which are unpredictable (weather-induced) (MacLean and Pitelka, 1971). As a result, the Dunlins of northern Alaska are more opportunistic in feeding behavior and more diverse in diet. Perhaps the longer bill of *pacifica* is a more efficient tool for extracting chironomid larvae from pond-margin sediments, but is a less efficient tool for the more diverse feeding conditions that Dunlins must cope with on northern Alaskan tundra. The available data from Siberia (Chernov, 1967) indicate that the insect fauna and diet of *C. a. sakhalina* there are more similar to the conditions found in northern than in western Alaska.

Thus far we have emphasized selective pressures operating on the breeding grounds, but these birds spend two thirds of the year on coastal mudflats in north temperate areas of the world, where different populations may mix with the same or different congeners. Differentiation could result from pressures exerted at this point in the season. Although the ecology of mudflat birds is poorly known, the available evidence indicates a strong separation in food habits among sympatric wintering shorebirds (Ehlert, 1964; Recher, 1966; Bengston and Svensson, 1968; Wolff, 1969; G. Chaniot, pers. comm.). The fact that ecological separating mechanisms have evolved supports the notion of the evolutionary importance of feeding relationships on the wintering grounds.

The northern Alaskan Dunlin population must be added to the short list of species that winter in Asia but regularly migrate across the Bering Straits to breed in Alaska. Irving (1960) noted this phenomenon in the Bar-tailed Godwit (*Limosa lapponica*), Bluethroat (*Luscinia svecica*), Wheatear (*Oenanthe oenanthe*), Kennicott's Willow Warbler (*Phylloscopus borealis*), and Yellow Wagtail (*Motacilla flava*). All of these are primarily Palearctic species that probably spread to northern Alaska while it was connected to Asia via the Beringial land mass and separated from other parts of North America by the glacial barrier. *C. a. sakhalina* also probably reached Alaska at this time, and quite possibly other Holarctic species developed similar distribution patterns

with the geographic separations imposed by glaciation. Pitelka and his colleagues (F. A. Pitelka, pers. comm.) banded large numbers of Snow Buntings (*Plectrophenax nivalis*) near Barrow in three summers, 1951–53. The only returns came from two birds recovered in winter and spring in the upper Lena River Valley, Siberia. It seems unlikely that this is simply a coincidence; the Snow Buntings that breed near Barrow probably migrate westward to Siberia after breeding. This hypothesis could be verified by the discovery of a morphological feature, such as bill length in *C. alpina,* that would permit the identification of birds on their wintering areas.

The discovery that northern Alaska Dunlins migrate to the Asian coast might be expected to raise some difficulties with the conclusions reached by Holmes (1966a, 1966c) in his study of this species in northern Alaska and coastal California. However studies of *C. a. pacifica* in western Alaska (Holmes, 1970, 1971) and of *C. a. sakhalina* in Japan (Kobayishi, 1959) indicate that these two subspecies are identical in timing of migration and occupy very similar wintering habitats. Thus, the conclusions relating activities on the breeding and wintering areas are still valid, and, in fact, have been verified by subsequent studies of *C. a. pacifica.* [See page 927, this issue, ed.]

ACKNOWLEDGMENTS

Holmes' research in western Alaska was supported by NSF Grant GB-6175; MacLean's research in northern Alaska was supported by grants from the Arctic Institute of North America to Frank A. Pitelka and by a Frank M. Chapman Award from the American Museum of Natural History. We are grateful to C. Lensink, U. S. Fish and Wildlife Service, Bethel, Alaska and Max C. Brewer, Director, Naval Arctic Research Laboratory, Barrow, Alaska for logistic support in western and northern Alaska, respectively.

We extend our thanks to the following Museums and their curators for lending specimens: American Museum of Natural History (Dean Amadon); British Museum of Natural History; California Academy of Sciences (Robert T. Orr); The Carnegie Museum (Kenneth C. Parkes); Museum of Comparative Zoology, Harvard University (Raymond A. Paynter, Jr.); Museum of Vertebrate Zoology, University of California (Ned K. Johnson); Museum of Zoology, University of Michigan (Robert W. Storer); and the Washington State Museum, University of Washington (Frank Richardson).

SUMMARY

The Dunlins that breed on arctic tundra of North America are separable into three distinct groups on the basis of bill length, with those of northern Alaska having shorter bills than those of western Alaska or north central Canada. The Dunlins of northern Alaska do not winter in North America but cross the Bering Straits to winter along the Pacific coast of Asia. The Dunlins of northeast Siberia, which also

winter along the east Asian coast, have bills indistinguishable from those of northern Alaskan birds. These two populations should be included together in *C. alpina sakhalina*. The name *C. a. pacifica* should be restricted to the birds that breed in western Alaska and winter along the Pacific coast of North America. The name *C. a. hudsonia*, first used by Todd (1953), is applied to Dunlins that breed in north central Canada and winter along the east coast of North America.

The selective pressures influencing the evolution of bill length include the size and kind of prey species available for exploitation and the presence or absence of ecologically similar species that might compete for the same food items. Geographic variation in these parameters is discussed.

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