GEOGRAPHIC VARIATION IN THE MARBLED GODWIT AND DESCRIPTION OF AN ALASKA SUBSPECIES¹

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Abstract. There are three breeding populations of the Marbled Godwit Limosa fedoa (Linnaeus): the prairie-breeding birds of mid-continent North America, and widely separated tundra-breeding populations at James Bay, Canada, and in the vicinity of Ugashik Bay, Alaska, on the north coast of the Alaska Peninsula. The Alaska population, which apparently winters locally on the Pacific coast from Washington to northern California, comprises birds with shorter tarsi, shorter wings, shorter culmens, and more massive bodies than those of the mid-continent population. Believed to have persisted near Ugashik Bay since that area formed part of Pleistocene Beringia, the Alaska birds are described as a new subspecies, L. f. beringiae.

Key words: Alaska; Beringia; Marbled Godwit; Limosa fedoa beringiae.

INTRODUCTION

Three geographically separated populations of the Marbled Godwit Limosa fedoa (Linnaeus) exist in North America (Fig. 1). The largest is a mid-continent population, which breeds from central Alberta, central Saskatchewan, and southern Manitoba south to central Montana, central North Dakota, northeastern South Dakota, and northwestern Minnesota (AOU 1983). The other two are small, isolated, little-known populations. One breeds in southwestern James Bay, Canada, where birds have been found during the breeding season at Akimiski Island (Manning 1952) and at the mouths of rivers draining into James Bay from Fort Albany (specimen ROM 67903) to East Point at the eastern tip of Hannah Bay (Todd 1963), and where a downy young chick weighing 132.7 g and with remiges 8 mm out of sheaths was found at North Point, near Moosonee, on 4 July 1975 (specimen NMC 63284). The other isolated population breeds on the north side of the Alaska Peninsula, from Ugashik Bay (57°35'N, 157°42'W) south and west possibly as far as Port Heiden (56°55'N, 158°41'W). In this paper we report recent information on the Alaska population, compare it morphologically with the other populations, and hypothesize its differentiation in Pleistocene Beringia.

THE ALASKA POPULATION

Marbled Godwits were first recorded in Alaska, at Ugashik Bay, in midsummer 1881 by C. L. McKay, who collected an adult male and a flying juvenal on 16 and 18 July, respectively. Four weeks later, on 14 August 1881, he collected another flying juvenal at Bear Creek, Nushagak, 100 km north of Ugashik Bay (Kessel and Gibson 1978). Although McKay stated in his field notes that the Ugashik Bay juvenal had been "shot out of a flock," his three Marbled Godwit specimens-the only records from Alaska for almost 100 years-were believed to represent, in the absence of additional information from this remote area, accidental occurrences (AOU 1910, 1931, 1957; a godwit [MCZ 317477] taken 5 July 1910 at Nelson Island, Kuskokwim River mouth, and reported as this species [Bent 1927, AOU 1957, Kessel and Gibson 1978] is instead a Bar-tailed Godwit Limosa lapponica).

The first certain contemporary records of this species in Alaska were of spring migrants on 8 May 1967, when a flock of six birds was observed at Katmai Bay, on the Pacific coast of the Alaska Peninsula 165 km east-northeast of Ugashik Bay (Gibson 1970), and on 9 May 1969, when two were observed along the coast north of Cape Fairweather, on the Gulf of Alaska (B. B. Paige, in litt.). Thereafter, as a result of an increase in the number of observers looking for these birds, sight records proliferated during the 1970s, elucidating in just a few years the annual spring

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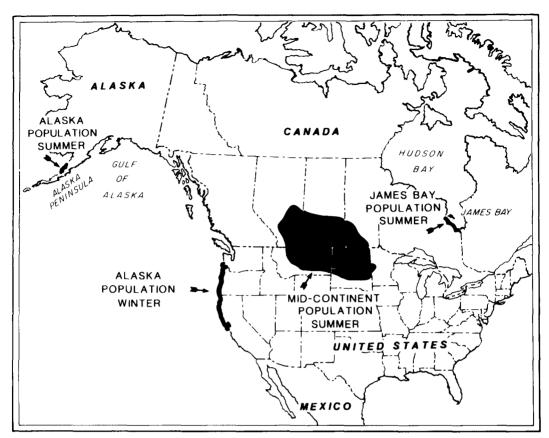


FIGURE 1. Breeding distribution of the Marbled Godwit and winter distribution of the Alaska population.

passage of a small population of Marbled Godwits on the Pacific coast of Alaska (Kessel and Gibson 1978).

The main spring movement takes place during the last few days of April and first 10 days of May, but some migrants continue to move along the coast throughout May. We believe a trans-Gulf of Alaska spring passage is involved for most of the population because (1) the preponderance of spring records, all of the seasonally earliest records, and most records of flocks have come from the northern coast of the Gulf of Alaska-from the Bering River Delta to Chiniak Bay, Kodiak Island-or from the Alaska Peninsula itself, and because (2) the highest counts of passage birds have been recorded at Chiniak Bay (e.g., flock of 20 birds on 5 May 1974; total of 20, including flock of 19, on 1 May 1982; flock of 15 on 2 May 1978; flock of 13 on 1 May 1984; and total of 12, including flock of 10, on 11 May 1986 [all R. A. MacIntosh et al., in litts.]) and at Cinder River lagoon (57°22'N, 158°03'W),

Alaska Peninsula (flocks of 31–220 Marbled Godwits observed daily 27–30 April 1988, maximum count 360 birds on 28 April [R. J. Wilk, pers. comm.]).

Speculating that a breeding population of Marbled Godwits existed at Ugashik Bay, we alerted interested people who might visit Ugashik Bay to look for them there. As a result, the first contemporary Ugashik Bay sightings were made in 1982, when 80–100 birds were identified on U.S. Fish and Wildlife Service aerial waterfowl surveys on 3 June by J. G. King and B. Conant (pers. comm.) and when a high count of 700+ (and an estimated maximum of 1,000+) feeding birds was made on 12 June by M. E. Isleib (in litt.).

We visited Ugashik Bay ourselves in 1983. Marbled Godwits were observed each day 10– 17 June as they flew between a still-undiscovered nesting area—somewhere above the lower reaches of the King Salmon and Dog Salmon rivers and the vast tide flats of the bay, where they fed

	Alaska $(n = 8)$		Mid-continent ^a $(n = 35)$		James Bay ^b $(n = 6)$	
	$\hat{x} \pm SD$	Range	$\bar{x} \pm SD$	Range	$\hat{x} \pm SD$	Range
Diagonal tarsus	62.0 ± 2.1	59.9-64.2	70.5 ± 3.3	63.6°-77.3	66.3 ± 2.8	63.3-70.0
Flattened wing	216.8 ± 3.6	212.5-218.0	229.2 ± 5.9	219.4-240.0	224.1 ± 3.8	219.5-226.5
Exposed culmen	$88.5~\pm~4.2$	83.2-96.1	97.1 ± 5.0	86.1-108.1	93.0 ± 5.2	86.2-100.4

TABLE 1. Measurements (mm) of male specimens of three populations of Marbled Godwits.

^a Specimens from American Museum of Natural History (AMNH), U.S. National Museum of Natural History (USNM), California Academy of Sciences (CAS, ST), Museum of Comparative Zoology (MCZ), and Museum of Vertebrate Zoology (MVZ).
^b Specimens from Carnegie Museum of Natural History (CMNH), National Museum of Canada (NMC), and Royal Ontario Museum (ROM).
^c Minimum is that of the South Dakota bird (USNM 479342); the next shortest in sample is 65.0 mm.

on tiny clams (Macoma balthica). The species was seen at all daylight hours, usually in ones, twos, or threes in flight to or from the tide flats. The maximum seen at once by us was a scattered group of 80 feeding on one area of the tide flats on 12 June.

Of the seven specimens we collected, six were males in breeding condition (left testes 10 to 17 mm by 5 to 8 mm) and one was a female that had recently laid eggs (ova to 5.5 mm in diameter and at least two discharged follicles). They were apparently incubating birds, but the week available to us was not sufficient time to locate specific nesting areas in this vast and logistically difficult region. Thus, although we regard as unequivocal the circumstantial evidence of breeding, the actual nesting substrate, a nest with eggs, and flightless young remain to be discovered. The skewed sex ratio of our specimens is probably due to the activity patterns of incubating birds; the male godwit incubates at night and the female from mid-morning until late afternoon (Nowicki 1973), so most females were probably on their nests during our daytime collecting activities.

Limited evidence, including the spring flocks at Cinder River lagoon and an observation of two birds diving at a caribou in dwarf shrub meadow east of Cinder River about 28 June 1988 (R. J. Wilk, pers. comm.), indicates that the breeding range of this population extends at least 30-40 km southwest of Ugashik Bay; and contiguous, similar habitat suggests the possibility that the breeding range may extend southwestward as far as the vicinity of Port Heiden, 100 km down the coast from Ugashik Bay.

Autumn departure of Marbled Godwits has largely escaped notice. To date, there have been only four fall reports from the Alaska Pacific coast tentatively referable to this species. One Marbled Godwit was reported, as a hypothetical record, at the McNeil River mouth, Kamishak Bay, Cook Inlet, on 27 August 1954 (Cahalane

1959); two were identified at the Kasilof River mouth, Kenai Peninsula, on 19 August 1976 (M. A. Miller, in litt.); one was reported on the East Copper River Delta on 26 August 1979 (P. G. Mickelson et al., in litt.); and five godwits seen flying south-southeast with two Whimbrels Numenius phaeopus over open sea at the entrance to Chatham Strait, Alexander Archipelago, on 22 July 1975 (Gibson and T. G. Tobish, Jr., pers. observ.) were probably this species. These are all early dates and are probably of non- or failed breeders; most Marbled Godwits apparently depart the Alaska Peninsula on a direct overseas flight to the eastern North Pacific coast south of Alaska.

Fall sightings in the Ugashik Bay-Cinder River lagoon area, also an autumn staging area for trans-Pacific-migrant Bar-tailed Godwits, have included Marbled Godwits as late as 15 October 1986 (eight with three Bar-tailed Godwits; R. E. Gill, Jr. et al., in litt.) and 16 October 1985 (one with 20+ Bar-tailed Godwits; R. E. Gill, Jr. et al., in litt.) and a high fall count of 130 Marbled Godwits, accompanying 365 Bar-tailed Godwits, on 30 September 1986 (R. J. Wilk, pers. comm.).

MORPHOLOGIC VARIATION AMONG THE THREE POPULATIONS

Nine adult specimens have been collected from the Alaska breeding grounds—a male on 16 July 1881 by McKay, six males and a female that we collected 11-16 June 1983, and a male collected 15 June 1985 by M. E. Isleib. We compared the linear measurements of the eight Alaska males with those of 35 breeding-season males from the mid-continent population (Table 1) and found that measurements of the Alaska population averaged significantly shorter (t-tests, not assuming equal variances, wings and tarsi $P = \langle 0.001$ and culmen $P = \langle 0.0013 \rangle$. Unfortunately, few weight data are available on specimens from the midcontinent population, but weights of five male

	Alaska $(n = 7 \delta, 1 \mathfrak{P})$		Mid-continent* $(n = 5 \delta, 5 \circ)$		James Bay ^b $(n = 1 \delta)$
	$\bar{x} \pm SD$	Range	$\bar{x} \pm SD$	Range	
Males	333.3 ± 20.0	302-365	303.9 ± 20.4	278.3-321.0	321
Females	402	_	340.9 ± 22.0	311.9-365.5	_

TABLE 2. Breeding-season weights (g) of specimens of Marbled Godwit.

* Specimens from National Museum of Canada.

^b Specimen from Royal Ontario Museum.

and five female National Museum of Canada specimens taken from this population between 30 May and 8 July indicate that Alaska birds may be more massive than mid-continent birds (Table 2). The fat condition of most of the male Alaska specimens was light and ranged from none to moderate. The single Alaska female (UAM 4874) had only light fat and yet was 36 g heavier than the heaviest mid-continent bird.

We performed a stepwise discriminate function analysis (DFA), using the tarsus, wing, and culmen measurements from the eight Alaska males and the 35 mid-continent breeding-season males as "knowns" and measurements from 38 "unknown" males taken south of the breeding grounds, either during migration or on the wintering grounds. In an attempt to exclude stillgrowing young birds, these unknowns were restricted to males in alternate plumage (adults) or males in basic plumage taken after 1 January and before summer. This DFA showed a total separation of the two populations (Fig. 2), with only one known misclassified. We got almost as good a classification when only the single character of "tarsus" was used; only one other bird was misclassified, and the "error" was corrected by adding *either* culmen or wing to the DFA. Similarly, a simple bivariate plot of either tarsus \times culmen or tarsus \times wing separated the two populations, with the exception of the one bird misclassified in the DFA. This "misclassified" specimen (USNM 479342) was taken at Rush Lake, Webster County, South Dakota, on 27 May 1929, and all three measurements fall well within those of the Alaska population (tarsus 63.6 mm, wing 221.0 mm, culmen 90.5 mm), although the wing and culmen also fall within the minimums of the ranges of the mid-continent population.

Linear measurements of six adult males from the James Bay population are intermediate between the Alaska and mid-continent birds, with the means larger than those of the Alaska population and smaller than those of the mid-continent population (Table 1). The minimums of the James Bay population do not reach even the means of the Alaska population, and the maximums are all below those of the mid-continent population. The only breeding-season male

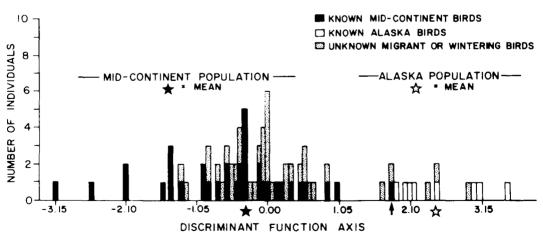


FIGURE 2. Subspecies discrimination based on three measurements of male Marbled Godwits: diagonal tarsus, flattened wing, and exposed culmen. The means of individuals classified as mid-continent birds (-0.41) and those classified as Alaska birds (+2.46) are significantly different (*t*-test, P = <0.001). The "misclassified" specimen from South Dakota, indicated by an arrow, was not included in the calculation of either mean.

weight available from the James Bay population does not refute that population's intermediate size; the specimen was as heavy as the largest mid-continent bird but smaller than the mean of the Alaska birds (Table 2).

NONBREEDING DISTRIBUTION OF THE ALASKA POPULATION

Marbled Godwits winter as far south on the eastern Pacific coast as Colombia, Ecuador, Peru, and northern Chile (AOU 1983). Based on evidence presented below, we believe that the northernmost wintering birds are those of the Alaska population. These birds winter locally in small numbers in bays and estuaries along the coast of Washington and Oregon and, in much larger numbers, northern California-at Willapa Bay, Washington, where a regularly wintering flock of up to 75 birds was discovered in the late 1970s (see Am. Birds 33:307, 1979; 34:300, 1980; 37: 330-331, 1983; 38:350, 1984; 39:202, 1985); at Tillamook and Coos bays, Oregon, where small numbers have been noted at intervals on Christmas Bird Counts (one at Tillamook Bay, 15 December 1979 [Am. Birds 34:638, 1980]; eight at Coos Bay on 19 December 1982 [Am. Birds 37: 737, 1983] and 14 there on 22 December 1985 [Am. Birds 40:970, 1986]); and in northern California at Arcata Bay, where 2,585 birds were counted on 20 December 1986 (Am. Birds 41: 1268, 1987) and 2,914 on 18 December 1987 (Am. Birds 42:1090, 1988), and at the mouth of the Eel River (at 40°38'N, 124°14'W), where 600-4,886 birds have been recorded on the Centerville Beach Christmas Bird Counts, 1972-1988 (see CBC issues, Am. Birds 26:501, 1972, through Am. Birds 42:1093, 1988). And there is one wintering record from as far north as British Columbia (two birds, 28 October 1978 to 20 April 1979, at Cadboro Bay north of Victoria [R. W. Campbell, in litt.]). Farther south, some apparently winter with mid-continent birds in the San Francisco Bay area. We base our supposition on wintering distribution in part on the locations of unknowns classified in the DFA as either Alaska or mid-continent birds, on measurements of determinant specimens that have subsequently come to our attention, and in part on evidence of migration pathways followed to Pacific coast wintering grounds by other, better known bird species.

Alaska birds identified by the DFA include a basic-plumaged male (ST 9856) taken in San Ma-

teo County, California, on 22 March 1938 and three basic-plumaged males from Alameda, California (CAS 11320, 17437, and 17438 taken, respectively, on 30 May 1907 and on 18 and 30 May 1910); the last three birds may have been summering nonbreeders. (Also, a worn adult male was taken in Otero County, New Mexico, on 11 July 1936, apparently a wandering non- or failed breeder.) In addition, three alternate-plumaged males (AMNH 357589-357591) were collected at Shoalwater Bay [=Willapa Bay], Washington, on 17 April 1885, either wintering birds or early migrants.

On the other hand, the 27 Pacific coast specimens identified by the DFA as mid-continent birds were all taken from the San Francisco Bay area (northernmost, MVZ 160436, Bodega Bay, 16 October 1962) and points farther south, including Monterey and Morro bays, Los Angeles and San Diego counties, and Baja California, Mexico. Their more southern wintering distribution is further corroborated by the few band recoveries of Pacific coast-wintering mid-continent Marbled Godwits (Bird Banding Laboratory, U.S. Fish and Wildlife Service): Two godwits banded at the southern end of San Francisco Bay in February 1973 were sighted in Alberta on 6 May 1973 and one banded in Saskatchewan on 2 August 1944 was recovered near Oxnard, southern California, on 15 December 1944. Individuals of each form were collected in San Francisco Bay on 30 May 1907 by E. W. Gifford, on 30 May 1910 by R. H. Beck, and on 22 March 1938 by J. Applegarth and E. W. Martin.

Two of the main migration pathways followed by Pacific Flyway waterfowl and shorebirds from Alaska are (1) a trans-Gulf of Alaska route (e.g., Brant Branta bernicla, Hansen and Nelson 1957, Palmer 1976; "Aleutian" Canada Goose Branta canadensis leucopareia, Woolington et al. 1979; "Cackling" Canada Goose Branta canadensis minima, Nelson and Hansen 1959; Dunlin Calidris alpina, Gill 1979), and (2) a route that follows the Pacific coastline. Either of these routes eventually brings the migrants to the Pacific coast of southern British Columbia, Washington, Oregon, or northern California, west of the Cascade Range. The Alaska Marbled Godwits appear to follow this pattern.

Pacific Flyway waterfowl from breeding grounds in the western prairie provinces of Canada commonly follow a route that crosses western Montana, Idaho, and eastern Oregon and terminates in the Sacramento-San Joaquin River Delta or the San Francisco Bay area (e.g., Northern Pintail Anas acuta, Blue-winged Teal Anas discors, Northern Shoveler Anas clypeata, Gadwall Anas strepera, American Wigeon Anas americana, and Ring-necked Duck Aythya collaris-Bellrose 1980). Tundra Swans Cygnus columbianus from northwestern Alaska (R. J. King, pers. comm.) and from the Mackenzie River Delta (Paullin and Kridler 1988) and Ross' Geese Chen rossii (Dzubin 1965) follow this route into the Pacific Flyway also. The mid-continent Marbled Godwits appear to follow this pathway to their Pacific coast wintering grounds, a routing corroborated in part by observations of migrant godwits at lake areas in the Warner Valley and Malheur National Wildlife Refuge of southeastern Oregon (e.g., see Am. Birds 41:120 and 464, 1987), locations that are major stopover sites for many migrants using this pathway.

DISCUSSION

When or how the mid-continent and Alaska populations became separated is unknown, but the Alaska population could have been breeding in the vicinity of its present range throughout much of the Pleistocene. The last Wisconsin glacial advance, some 10,000–14,000 years ago, did not cover the present breeding grounds on the north coast of the Alaska Peninsula (Detterman 1986). Earlier Pleistocene glaciations barely did (Detterman 1986), but whenever glaciers and ice sheets were extensive, the Bering Land Bridge was exposed and offered other, adjacent areas of suitable breeding habitat—i.e., a steppe-tundra vegetation dominated by sedges, grasses, *Artemisia*, and low willows (Ager 1982, Young 1982).

In southeastern Alaska and British Columbia, the late Pleistocene glaciations may not have been as extensive as previously believed (Fladmark 1978, Mann 1986). Recent analyses indicate a locally variable glaciation along the coastline, with ice reaching the coast mostly in valley glaciers and separated by unglaciated headlands, divides, and outer islands; moreover, sea levels were much lower than today, exposing strips of low-lying terrain between the ice tongues (Fladmark 1978, Mann 1986). These ice-free areas served as biological refugia (Warner et al. 1982), and they were undoubtedly used by migrant birds. Current use by migrant Marbled Godwits (R. W. Campbell, in litt.) of past refugia along the west coast of Vancouver Island and northeastern Graham Island, Queen Charlotte Islands, suggests their use also during the Pleistocene.

The mid-continent population probably bred in grassland habitats in the central United States when the huge Laurentide Ice Sheet covered most of Canada and the northern United States and then shifted northward as appropriate habitat developed in the Canadian prairies with the retreat of ice, beginning some 17,000 years ago. The James Bay birds must be a younger population, since the ice sheet continued to cover that region as recently as 8,000 years ago (Denton and Hughes 1981). The James Bay stock undoubtedly came from the mid-continent population, and it may be evolving morphologically in the same directions as the Alaska birds, i.e., to shorter extremities and perhaps heavier bodies than the mid-continent birds. As yet, however, except at the extremes, the James Bay and the mid-continent birds are not separable from each other.

The morphological indication that the two tundra-breeding populations may be evolving in the same direction suggests some environmental influence. Perhaps longer tarsi and bills are more suitable for the grasslands and prairie wetlands compared to the dwarf shrub meadow tundra and saltwater mud and sand flats of the northern populations, and the more massive bodies more energetically suitable for cooler environments.

Two extralimital distribution records may shed some light on how Marbled Godwits could have reached breeding localities so distant from one another. The birds' propensity to associate with other large sandpipers, especially, in Alaska, with Whimbrels, Bar-tailed Godwits, and Hudsonian Godwits Limosa haemastica, appears to be a contributing factor. We suspect that two Marbled Godwits at Laysan Island on 21 October 1966 (Clapp and Woodward 1968), the only Hawaii record of the species, had accompanied Bar-tailed Godwits across the North Pacific from the Alaska Peninsula. As noted above, late fall associations of Marbled and Bar-tailed godwits have been observed at Alaska Peninsula staging areas, and one Bar-tailed Godwit was recorded on tiny Laysan Island the same day as the two Marbled Godwits (Clapp and Woodward 1968). One of the Laysan Marbled Godwits was collected (USNM 496790); it is a juvenal, but its measurements nonetheless point to its probably being an Alaska bird (male: tarsus 62.2 mm, wing 212.5

mm, culmen 87.0 mm, weight with heavy fat 377 g).

The South Dakota bird that was "misclassified" by the DFA does indeed appear to be from the Alaska population. Perhaps it formed an association with individuals of the mid-continent population while wintering in the San Francisco Bay area. By measurements, the South Dakota bird might not be separable from the smallest James Bay birds, but these latter birds probably are restricted to migration pathways in eastern North America.

DESCRIPTION OF NEW SUBSPECIES

LIMOSA FEDOA BERINGIAE, NEW SUBSPECIES

Holotype. Definitive alternate-plumaged male, U.S. National Museum 600024, formerly University of Alaska Museum 4869; collected near King Salmon River mouth, Ugashik Bay, Alaska (at 57°30'N, 157°37'W), elevation sea level, 11 June 1983, by Daniel D. Gibson and Brina Kessel. Additional data: weight 325 g; no fat; left testis 10 \times 5.5 mm, right testis 7.7 \times 5 mm; flattened wing 216.5 mm, exposed culmen 88.3 mm, diagonal tarsus 64.2 mm; proximal half of bill orange, distal half black; feet and tarsi dark gray; iris dark; one of four birds together flying north towards tidal mudflats from area between King Salmon and Dog Salmon rivers.

Paratypes. Seven definitive alternate-plumaged male topotypes, collected chronologically as follows: (1) U.S. National Museum 86570, 16 July 1881, by C. L. McKay; (2–6) University of Alaska Museum 4868 and 4870–4873, 11–12 June 1983, by Gibson and Kessel; and (7) University of Alaska Museum 5249, 15 June 1985, by M. E. Isleib.

Diagnosis. Adult males of L. f. beringiae are similar in coloration and pattern of plumage to mid-continent Marbled Godwits (nominate fedoa), but have shorter extremities, particularly wing and tarsus lengths (P = <0.001). Linear measurements of eight adult males: diagonal tarsus 62.0 ± 2.1 mm, range = 59.2-64.2 mm; flattened wing 216.8 ± 3.6 mm, range = 212.5-218.0 mm; exposed culmen 88.5 ± 4.2 mm, range = 83.2-96.1 mm. Weight of seven mid-June adult males: 333.3 ± 20.0 g, range = 302-365 g.

Etymology. The designation *beringiae* is derived from "Beringia," a name applied to the geographic area of the Bering Land Bridge by E. Hultén (1937) and more recently applied to the region from the Kolyma River in eastern Siberia

eastward to the Mackenzie River in northwestern North America (Hopkins et al. 1982), a region in which members of the biota reflect to varying degrees the historical influence of Pleistocene patterns of glaciation.

Range. Breeds on the Alaska Peninsula, Alaska, at Ugashik Bay in the vicinity of the King Salmon and Dog Salmon rivers, probably in the Cinder River area, possibly as far south and west as Port Heiden. Migration north and west in spring doubtless includes a transoceanic passage to the Alaska Peninsula, to Kodiak Island, or the mainland coast of the northern Gulf of Alaska for most of the population; fall migration essentially unknown, but apparently involves direct overseas flight from Alaska Peninsula to the eastern North Pacific coast south of Alaska. Apparently winters locally on the Pacific coast from Willapa Bay, Washington, to San Francisco Bay, California.

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