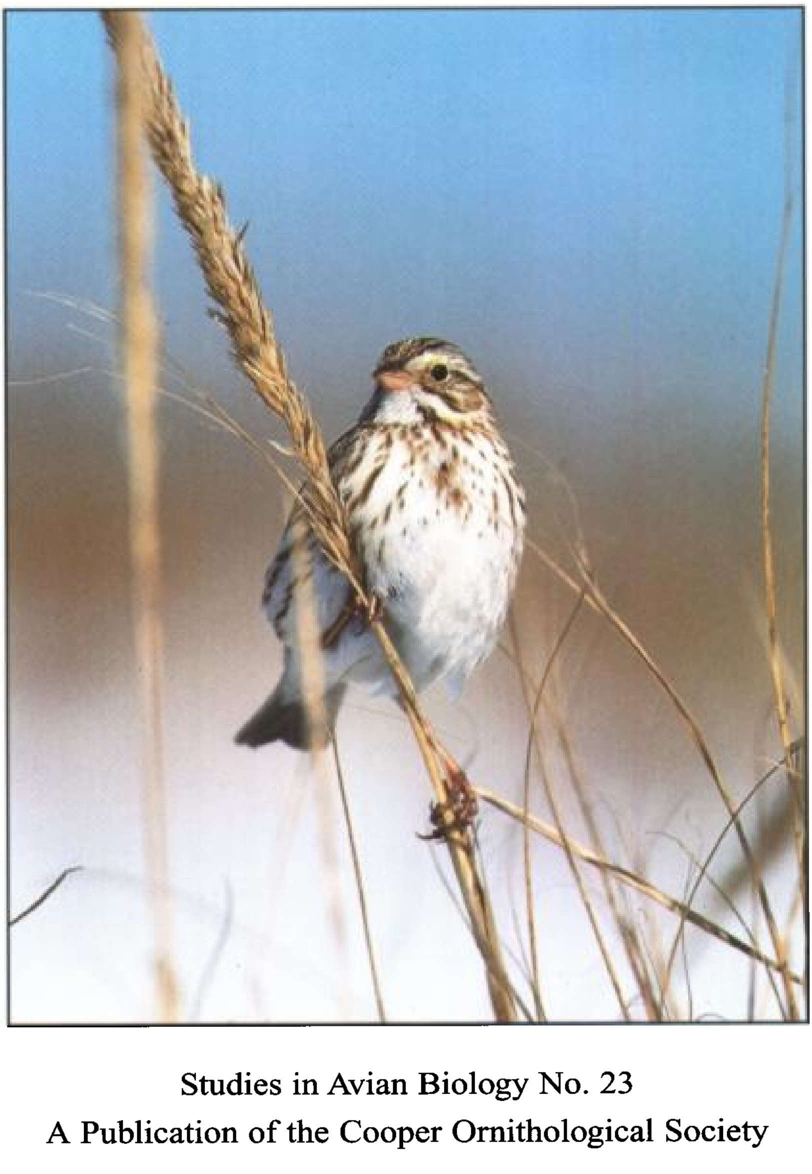
GEOGRAPHIC VARIATION IN SIZE AND SHAPE OF SAVANNAH SPARROWS (*PASSERCULUS SANDWICHENSIS*)

JAMES D. RISING



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Cover photograph of "Ipswich" Savannah Sparrow (*Passerculus sandwichensis princeps*) on beach grass (*Ammophila breviligulata*), Point Lookout, Long Island, NY, by Michael D. Stubblefield (January 2000)

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ABSTRACT

I analyzed variation in 24 measurements on the skeletons of 2281 breeding Savannah Sparrows (*Passerculus sandwichensis*) from 65 different localities to describe patterns of geographic variation in size and shape. The samples come from virtually throughout the species' breeding range, from northern Canada and Alaska, south to the northeastern United States, central Great Plains, and in the highlands of the west, south to central Mexico.

For the most part, the interpopulational variation in size is clinal, with considerable overlap among geographically contiguous populations. The most striking finding of this study is that Savannah Sparrows are large on islands, as would be predicted by some theory.

The largest Savannah Sparrows are from Sable Island, Nova Scotia, and the Aleutian Islands, Alaska. Although both are islands, these two areas are ecologically different in many ways. On Sable Island, the Savannah Sparrow is the only breeding passerine, whereas on the Aleutians, Lapland Longspurs (*Calcarius lapponicus*) as well as Savannah Sparrows are abundant, and seemingly found in the same habitat; Song Sparrows (*Melospiza melodia*) and Gray-crowned Rosy-Finches (*Leucosticte tephrocotis*) also breed there, but generally in different habitats. Thus, one site is sparrow poor, and the other relatively sparrow rich. Savannah Sparrows are also relatively large on the Magdalen Islands, Quebec, and on Middleton Island, Alaska. On the Magdalen Islands, Nelson's Sharp-tailed Sparrows (*Ammodramus nelsoni*) and Swamp Sparrows (*M. georgiana*) overlap with Savannah Sparrows in habitat use, and Song Sparrows are common as well. On Middleton Island, Fox Sparrows (*Passerella iliaca*) and Lapland Longspurs are both common, as are Savannah Sparrows. Thus, while Savannah Sparrows tend to be small where species diversity is highest (see below), this alone does not appear to be an adequate explanation for their large body size on islands. One characteristic of all of these islands is that they have long, cool, and moist summers; this may result in a predictable and fairly rich food supply. On Sable Island, Savannah Sparrows are often socially polygynous, which, at least in many species, leads to enhanced competition for high quality territories and enhanced body size, at least in males, but sexual size dimorphism is not enhanced there.

There is also significant geographical variation in bill shape, with western Savannah Sparrows having relatively more slender bills. Variation in bill shape, however, is clinal and slight, and there is a great deal of overlap among populations.

I calculated correlations between various multivariate measures of size and shape (derived from Discriminate Function and Principal Component analyses) and a variety of measures of climatic variation, latitude, longitude, elevation, and species diversity. Savannah Sparrows tend to be large where it is moist, and small where it is hot and dry. They are also smallest in the west and at high elevations, and large where they coexist with few other sparrow-like birds. These trends remain even when the samples from islands, which are outliers, are removed from the analyses. The significant negative relationship between body size and species diversity supports hypotheses that relate body size to interspecific competition. Overall, there is no significant relationship between body size and latitude, and although they tend to be small where maximum summer temperatures are highest, the species does not follow the trend described by Bergmann's Rule. This is true when all samples are considered as well as when the eastern and western samples are analyzed separately

Savannah Sparrows from the coastal saltmarshes of Sinaloa and Sonora also have large body sizes. They are the only sparrow-like birds that breed in these saltmarshes, and they are abundant in them. They also have notably large bills, probably reflecting their diet, which includes fiddler-crabs (*Uca*).

Interpopulational variation in wing length is related to migratory status: birds from sedentary populations, where only short-distance movement occurs, have relatively short wings; those that presumably migrate the greatest distances have relatively long wings. The birds with the relatively longest wings are from the northern Great Plains and high elevations.

The location of the two inland Mexican populations in multivariate space is interesting, in that Lerma, México, is close to the samples from northeastern North America, whereas Charco Redondo, Jalisco, is close to birds from the Northwest Territories. Although Lerma and Charco Redondo are only about 500 km apart, Lerma is higher in elevation and more mesic than Charco Redondo.

There is also clinal variation in both body size and bill size among the non-migratory populations in saltmarshes along the Pacific Coast; the smallest birds are from Morro Bay, San Luis Obispo County, California, and the largest from Bahía Magdalena, Baja California Sur. The birds from coastal California have relatively gracile bills whereas those from Bahía Magdalena have stout bills.

Seventeen subspecies of Savannah Sparrows are generally accepted. Many of these have been named on the basis of coloration, which is not examined here, as well as body size and bill shape. *P. s. princeps*, from Sable Island, is large (and pale in coloration); my results show that they are significantly larger in size than birds from the adjacent mainland, but not different in shape, thus supporting this subspecific separation. *P. s. sandwichensis* from the Aleutian Islands and the tip of the Alaskan Peninsula are also significantly larger than (but similar in coloration to) those from the mainland, but there is clinal variation down the Alaskan Peninsula; it is my opinion, therefore, that these should not be recognized as subspecifically distinct because there is no benefit to more or less arbitrarily delimiting taxa that overlap on a phenetic continuum. Viewed in this way my analyses support the recognition of only one subspecies of Savannah Sparrow from North America, *P. s. sandwichensis,* other than *P. s. princeps* and the birds resident in west coastal saltmarshes. The nine subspecies of saltmarsh Savannah Sparrows all seem to be clearly separable, and my analyses support the retention of these as valid and distinct taxa.

Key Words: Bergmann's Rule, geographic variation, islands, morphology, *Passerculus sandwichensis,* Savannah Sparrow, subspecies.

INTRODUCTION

Evolutionary biologists use studies of geographic variation as a means of testing hypotheses about adaptation, because the evolution of variation among populations of a species across its range, where is it exposed to a variety of different environments, reflects changes that could take place in a single population, exposed to changing environments, through time (Gould and Johnston 1972). Patterns of geographic variation within a species allow us to test hypotheses about adaptations to different environmental conditions, and thus by inference to environmental changes (biotic and abiotic) over time. Why, for example, do features such as body size, wing length, or bill size and shape differ across a species' range? If these differences reflect adaptations to the different environments to which the species is exposed, what are the selection agencies that have resulted in them? This perhaps cannot ever be answered by field studies, but correlations with environmental factors may point to possible experiments that could clarify these questions.

The Savannah Sparrow (*Passerculus sandwichensis*) is one of the commonest and most wide-spread of American songbirds. It breeds from Alaska, west to the Aleutian Islands (Amukta Island), eastward across northern Canada, south of the Arctic Archipelago and central Nunavat ("Northwest Territories"), south (in mountains) to eastern Tennessee and northern Georgia, southern Ohio, central Indiana, central Iowa (formerly or irregularly south to western Missouri and northwestern Arkansas), central Nebraska, and locally in the western mountains south in the Mexican highlands to Guatemala, and along the Gulf coast of Sonora and Sinaloa, and the Pacific Coast to southern Baja California (south to Bahía Magdalena; Rising 1996) (Fig. 1). Savannah Sparrows have been the subject of a number of systematic reviews, most importantly by Peters and Griscom (1938), van Rossem (1947), and Hubbard (1974), and a large number of subspecies have been described, indicating that there is considerable geographic variation in the species. The 5th Edition of the AOU Check-list (1957) recognized the "Ipswich" Sparrow (*P. princeps*), which breeds on Sable Island, Nova Scotia, as a separate species, and listed 16 subspecies of other Savannah Sparrows from Baja California, Canada, and the United States; a 17th subspecies has been described from Guatemala, but where breeding has not been confirmed. Most current lists (Sibley and Monroe 1990, AOU 1998) merge the Ipswich Sparrow with the other Savannah Sparrows. Most populations of Savannah Sparrows are migratory (Rising 1988, Wheelwright and Rising 1993). There are, however, resident populations in coastal saltmarshes in California and Baja California (five or six subspecies in the *P. s. beldingi* group), and coastal Sonora and Sinaloa (two subspecies in the *P. s. rostratus* group). Preliminary analyses of mitochondrial DNA indicate that the *P. s. rostratus* birds may best be recognized as a distinct species, and little if any

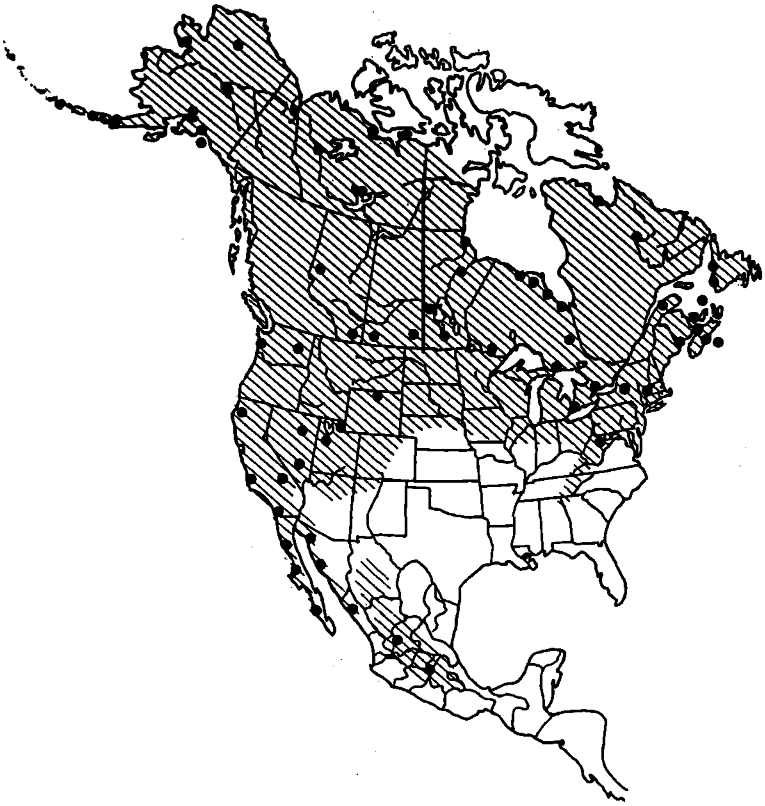

FIGURE 1. Range of the Savannah Sparrow (*Passerculus sandwichensis*). Dots represent sites from which I have examined specimens (Table 1).

interbreeding occurs between *P. s. beldingi* and "typical" Savannah Sparrows (Zink et al. 1991). Preliminary mtDNA sequence data suggest that Savannah Sparrows belong in the *Ammodramus* clade, close to Baird's Sparrow (*A. bairdii*; R. J. G. Dawson and J. D. Rising, pers. obs.).

The objective of this study is to describe and quantify geographic variation in size of Savannah Sparrows from throughout their breeding range, and to relate trends in phenotypic variation to environmental variation (Zink and Remsen 1986). The species breeds in a wide range of climatic conditions, from places with hot, fairly dry summers to places with cool, mesic summers; in some parts of their range, the Savannah Sparrow is the only sparrow that breeds, but in others it is but one of a complex guild of breeding sparrow species, often occurring with similar species (*Ammodramus*) that have similar habitat requirements.

One pattern of geographic variation that seems to appear in more songbird species than one would expect to find by chance alone is the trend summarized by Bergmann's Rule, namely that within species of homeothermic vertebrates, individuals from relatively cold areas average larger in body size than other individuals from relatively warmer areas. A second trend, Allen's Rule, states that within such species, individuals from relatively cold areas have smaller appendages relative to their body size than individuals from relatively hot areas (Mayr

TABLE 1. SAMPLE LOCALITIES AND NUMBERS OF SAVANNAH SPARROWS MEASURED

Locality	N (♂)	N (♀)	Alleged Subspecies	Latitude	Longitude	Elevation (m)	Annual precipitation[a]	June precipitation[a]	Average minimum summer temperature[b]	Average maximum summer temperature[b]	Minimum summer temperature[b]	Maximum summer temperature[b]	Cook's Index
Nova Scotia: Sable Island	24	16	*princeps*	44.00	60.00	16	50.01	3.12	46.7	68.0	35	86	01
Nova Scotia: Halifax Co., Lawrencetown Beach, Seaforth	12	10	*savanna*	44.67	63.67	16	51.92	3.30	49.5	73.3	35	93	17
Nova Scotia: Pictou Co., River John	31	22	*savanna*	45.84	63.00	16	43.33	2.47	44.9	74.8	27	90	16
Newfoundland: Pasadina, Steady Brook, Doyles	12	10	*labradorius*	49.00	57.67	61	—[c]	—	—	—	—	—	—
Newfoundland: Parson's Pond, Bellburns	13	8	*labradorius*	50.00	57.67	16	—[c]	—	—	—	—	—	—
Prince Edward Island: Prince Co., Bedeque	27	8	*savanna*	46.33	63.67	3	—[c]	—	—	—	—	—	—
New Brunswick: Charlotte Co., St. Andrews	24	18	*savanna*	45.15	67.00	16	48.50	3.37	48.6	72.9	36	96	18
Quebec: Matane Co., Matane	29	22	*savanna*	48.84	67.5	305	37.73	3.28	46.7	69.3	30	91	16
Quebec: Terr. Nouveau Quebec, Schefferville	5	4	*labradorius*	54.84	66.84	52	—[c]	—	—	—	—	—	—
Quebec: Magdalen Islands	29	15	*savanna*	47.50	61.75	3	55.16	4.28	43.1	63.8	30	82	16
Quebec: Terr. Nouveau Quebec, Kuujjuaq (Fort Chimo)	23	24	*labradorius*	58.16	68.33	34	19.05	1.83	35.3	62.5	17	90	10
Massachusetts & eastern New York	11	5	*savanna*	42.50	73.50	460	—[c]	—	—	—	—	—	—
New York: Syracuse & Jordon	8	2	*savanna*	43.16	76.50	150	—[c]	—	—	—	—	—	—
West Virginia: Preston Co., Brandonville	25	11	*savanna*	39.58	79.58	610	—[c]	—	—	—	—	—	—
Ontario: Peel Co., Wildfield & Kleinburg	42	11	*savanna*	43.84	79.67	120	—[c]	—	—	—	—	—	—
Ontario: Durham R.M., Pickering	15	4	*savanna*	43.84	79.67	120	—[c]	—	—	—	—	—	—

TABLE 1. CONTINUED.

Locality	N (♂)	N (♀)	Alleged Subspecies	Latitude	Longitude	Elevation (m)	Annual precipitation[a]	June precipitation[a]	Average minimum summer temperature[b]	Average maximum summer temperature[b]	Minimum summer tem perature[b]	Maximum summer temperature[b]	Cook's Index
Ontario: Lampton Co., Wallaceburg	41	15	*savanna*	42.67	82.33	183	30.77	3.00	56.5	81.5	34	104	24
Ontario: Algoma Dist., Sowerby	25	9	*oblitus*	46.33	83.24	183	—[c]	—	—	—	—	—	—
Ontario: Cochrane Dist., Cochrane	35	8	*oblitus* > *labradorius*	47.84	83.33	245	—[c]	—	—	—	—	—	—
Ontario: Kenora Dist., Sutton Ridges	8	1	*labradorius*	54.50	84.92	100	—[c]	—	—	—	—	—	—
Ontario: Cochrane Dist., Moosonee	50	30	*labradorius*	51.33	80.67	9	30.92	3.46	41.5	71.2	21	96	16
Ontario: Kenora Dist., Attawapiskat	39	26	*labradorius*	53.00	82.33	6	30.92	3.46	41.5	71.2	212	96	16
Ontario: Kenora Dist., Winisk	47	21	*labradorius*	55.33	85.16	8	15.61	1.58	34.7	62.5	15	91	15
Ontario: Thunder Bay Dist., Kaministikwia	16	12	*oblitus*	48.45	89.67	45	—[c]	—	—	—	—	—	—
Manitoba: Delta	39	21	*nevadensis* > *oblitus*	50.16	98.33	260	22.05	3.23	50.0	79.5	25	106	24
Manitoba: The Pas	22	6	*oblitus* > *nevadensis*	53.84	101.33	275	—[c]	—	—	—	—	—	—
Manitoba: Gillam	19	6	*oblitus*	56.33	94.67	150	—[c]	—	—	—	—	—	—
Manitoba: Churchill	30	18	*oblitus*	58.84	94.16	30	15.61	1.58	34.7	62.5	15	91	14
Northwest Terr.: Yellowknife	5	5	*anthinus* > *nevadensis*	62.50	114.33	180	—[c]	—	—	—	—	—	—
Nunavut: Kugluktuk (Coppermine)	29	16	*anthinus*	67.84	115.16	30	8.51	0.66	31.8	56.2	5	90	08
Northwest Terr.: Norman Wells	22	22	*anthinus*	65.33	126.84	72	13.17	1.44	46.0	71.3	21	91	15
Northwest Terr.: Inuvik	14	14	*anthinus*	68.33	133.67	30	10.25	0.51	38.6	66.5	21	89	12
Saskatchewan: Maple Creek, Consul, Estuary	24	4	*nevadensis*	50.00	109.50	1100	—[c]	—	—	—	—	—	—
Saskatchewan: Courval, Dundurn, Gurn	14	4	*nevadensis*	50.00	106.00	880	—[c]	—	—	—	—	—	—
Saskatchewan: Fleming	7	0	*nevadensis*	50.00	101.90	500	—[c]	—	—	—	—	—	—
Alberta: Milk River	29	7	*nevadensis*	49.16	111.67	1050	—[c]	—	—	—	—	—	—

TABLE 1. CONTINUED.

Locality	N (♂)	N (♀)	Alleged Subspecies	Latitude	Longitude	Elevation (m)	Annual precipitation[a]	June precipitation[a]	Average minimum summer temperature[b]	Average maximum summer temperature[b]	Minimum summer temperature[b]	Maximum summer temperature[b]	Cook's Index
Alberta: Grande Prairie	32	24	*nevadensis*	55.16	118.84	670	17.40	2.54	45.3	72.5	27	94	21
Alaska: Anuktuvuk Pass	4	0	*anthinus*	68.16	151.67	670	—[c]	—	—	—	—	—	—
Alaska: Koyuk	15	21	*anthinus*	65.00	161.16	152	14.05	0.90	41.6	60.5	25	87	12
Alaska: Fairbanks	21	8	*anthinus*	65.00	147.67	305	—[c]	—	—	—	—	—	—
Alaska: Wasilla	27	23	*anthinus*	61.16	150.00	15	15.06	1.13	47.0	65.1	33	85	14
Alaska: Aleutian Is., (Umnak Island)	30	24	*sandwichensis*	55.33	168.00	61	35.58	2.16	40.1	62.1	33	78	12
Alaska: Cold Bay	15	8	*sandwichensis*	55.00	163.00	15	—[c]	—	—	—	—	—	—
Alaska: Port Heiden	16	14	*sandwichensis* > *anthinus*	56.83	159.00	15	—[c]	—	—	—	—	—	—
Alaska: Middleton Island	29	16	*anthinus*	59.50	146.33	17	61.25	4.18	43.3	62.9	30	86	12
Alaska: Gakona, Kenny Lake, Valdez	8	9	*anthinus*	62.30	145.20	20	—[c]	—	—	—	—	—	—
Wyoming: Sheridan Co., Sheridan	33	17	*nevadensis*	44.78	107.17	1372	15.64	2.35	47.6	86.0	27	106	28
Utah: Rich Co., Woodruff	48	16	*nevadensis*	41.50	111.16	1921	9.05	0.71	43.3	90.4	23	107	27
Utah: Utah Co., Elberta	19	3	*nevadensis*	40.00	111.92	1402	—[c]	—	—	—	—	—	—
Nevada: Elko Co., Halleck	30	10	*nevadensis*	40.87	115.33	1646	—[c]	—	—	—	—	—	—
Nevada: Lincoln Co., Alamo	6	4	*nevadensis*	37.84	115.16	1070	—[c]	—	—	—	—	—	—
Washington: Lincoln Co., Creston	34	17	*nevadensis*	47.67	118.50	700	16.23	1.29	45.0	96.0	34	108	25
Washington: Grays Harbor Co., Hoquiam	19	22	*brooksi*	47.0	124.00	15	107.47	3.18	46.5	68.6	33	99	21
California: Inyo Co., Owens Lake, 17 mi S Lone Pine	20	22	*nevadensis*	36.50	118.00	1085	5.74	0.12	70.7	97.5	29	109	21
California: Humboldt Co., Eureka	26	14	*alaudinus*	40.67	124.22	3	39.44	0.71	50.2	61.3	41	85	21
California: San Luis Obispo Co., Morro Bay	17	11	*alaudinus* > *beldingi*	35.33	120.84	3	—[c]	—	—	—	—	—	—
California: San Diego Co., Solidad Creek and Rio Santa Margarita	20	15	*beldingi*	33.33	117.84	3	—[c]	—	—	—	—	—	—

TABLE 1. CONTINUED.

Locality	N (♂)	N (♀)	Alleged Subspecies	Latitude	Longitude	Elevation (m)	Annual precipitation[a]	June precipitation[a]	Average minimum summer temperature[b]	Average maximum summer temperature[b]	Minimum summer temperature[b]	Maximum summer temperature[b]	Cook's Index
Baja California N.: Bahia San Quintin	21	15	*beldingi*	30.33	116.00	3	—[c]	—	—	—	—	—	—
Baja California S.: Guerrero Negro	34	19	*anulus*	28.00	114.16	3	—[c]	—	—	—	—	—	—
Baja California S.: Bahia Magdalena, San Carlos and Estero Salinas	15	15	*magdalenae*	24.33	111.16	3	—[c]	—	—	—	—	—	—
Sonora: Puerto Peñasco	9	4	*rostratus*	31.33	113.33	3	—[c]	—	—	—	—	—	—
Sonora: Bahia Kino	21	15	*atratus*	28.84	112.00	3	—[c]	—	—	—	—	—	—
Sinaloa: El Molina	16	8	*atratus*	24.50	107.40	3	—[c]	—	—	—	—	—	—
Jalisco: Charco Redondo, 20 mi W Ojeulos de Jalisco (Cienega de Mata)	16	7	*rufofuscus*	21.67	101.84	2100	—[c]	—	—	—	—	—	—
México: ½ km N. Lerma (Lerma Marshes)	21	6	*rufofuscus*	19.33	99.50	2560	—[c]	—	—	—	—	—	—
Total (65 samples)	1459	822											

[a] Inches.
[b] F°.
[c] Sample not used in environmental regression analyses.

1963, Zink and Remsen 1986). The considerable debate about these "ecogeographic rules" (McNab 1971, Zink and Remsen 1986) has focused on two separate and unrelated issues: (1) do these trends occur in birds (and mammals) more often then we would expect to find by chance, and (2) if so, why? It is surprisingly difficult to answer the first question, both because it is, in practice, difficult to measure body size (Rising and Somers 1989) and because there have been few in-depth studies of geographic size variation, especially across the entire range of a species. However, at least so far as North American birds are concerned, it does appear that the majority of species that show geographic variation in size follow Bergmann's Rule, and this is especially so for non-migratory species, although many species show the trend only weakly (James 1970, Zink and Remsen 1986). The traditional answer to the second question has been that an individual that has a relatively large body and relatively small appendages has a thermoregulatory advantage in cold climates, and conversely one with a relatively slight body and large appendages has a similar advantage in warm ones (Mayr 1963). However, it has been argued that body size is far more significantly influenced by food size and abundance (McNab 1971), and by interspecific competition (Schoener 1969, McNab 1971), the latter being taken as perhaps the principal reason why populations on islands tend to be larger on average than their mainland counterparts (Case 1978).

Because the Savannah Sparrow breeds in a wide range of climates, occurs both in species-rich and species-poor sparrow guilds, and is found on the American mainland as well as on several islands, it is an ideal species to use to test these hypotheses about the evolution of geographic variation in size and shape in birds.

MATERIALS AND METHODS

I measured a total of 2281 Savannah Sparrows (1459 males, 822 females) that were collected from 65 different sites from virtually throughout the species' range (Fig. 1; Table 1). These birds were all collected during the breeding season, had little fat, and had enlarged and apparently active gonads; in all probability, most if not all were breeding birds that were collected at their breeding site.

Each was prepared as a skin and skeletal specimen, and is in the collection of the Royal Ontario Museum. I made 24 skeletal measurements on each specimen, to the nearest 0.1mm. These were skull length (to the tip of the premaxilla; all measures were maxima), skull width, premaxilla length and depth, narial, premaxilla, and interorbital widths, mandible length, gonys length, mandible depth, coracoid and scapula length, femur length and width, tibiotarsus, tarsometatarsus, humerus, ulna, carpometacarpus, and hallux lengths, sternum length and depth, keel length (from apex to posterior margin), and synsacrum width. I made all measurements, and they are the same that I have used in other studies (Rising 1987, 1988). These measurements are illustrated in Robins and Schnell (1971). I also took five measurements on the skins, and noted the weight of each specimen. Some of these data are published elsewhere (Wheelwright and Rising 1993, Rising 1996). When it was not possible to measure all 24 skeletal variables, I estimated missing or broken elements using multiple regression (BMDP Statistical Software, Method = Twostep; Dixon 1983); if a specimen was missing more than three measurements, the specimen was omitted from multivariate analyses that involved any of the missing values.

The Savannah Sparrow is sexually dimorphic in size (Rising 1987) so I have assessed patterns of geographic variation for the two sexes separately. ANOVA was used to test for geographic variation for each variable; for these analyses, only reasonably large samples ($N > 9$) were used. I identified statistically homogeneous subsets of samples using an *a posteriori* Student-Newman-Kuels (snk) multiple range test (SAS PROC ANOVA; SAS Institute 1985).

To reduce the dimensionality and complexity of the data, I used a Principal Components Analysis, operating on the matrix of correlations among the 24 characters (Rohlf et al. 1982); this is a standard procedure in morphometric analyses, and makes little difference in practice whether a correlation or covariance matrix is used (Rising and Somers 1989). ANOVA was used to test for geographic variation in each of the first three Principal Components (PCs), again using only the larger samples. I did not use additional PCs as their eigenvalues were small and were of similar magnitude.

To assess the significance of differences among populations in multivariate space, I used Discriminant Functions Analysis (DFA; SPSSX Program Discriminant; SPSS 1986). To do DFA among the larger samples (excluding those from saltmarsh localities, see below), I reduced the number of variables to 12, using skull length and width, premaxilla length and width, and mandibular, gonys, coracoid, femur, tibiotarsus, ulna, hallux, and keel lengths. I selected these variables because they had relatively low within-group variances, and included measures of the different parts of the birds' bodies (e.g. head size, bill size, wing size, and leg size). Birds missing any of these variables were omitted from analyses, and only samples with $N > 12$ were used: for males, this included 1152 individuals from 47 different localities; for females, 501 individuals from 27 localities.

With the exception of the sample from Morro Bay, California (which is intermediate in size between the resident "Belding's" sparrows of the saltmarshes of southern California and Baja California and non-saltmarsh sparrows), the Savannah Sparrows from the saltmarshes of southern California (San Diego), Baja California, Sinaloa, and Sonora were not included in these analyses as they are very different in size and shape (see RESULTS). Because several of the saltmarsh samples are relatively small, to assess the significance among differences among these, I used a step-wise DFA, limiting the number of steps to eight. The Morro Bay sample was included in both sets of analyses to facilitate comparisons. For males, the eight variables selected in the step-wise analysis were: premaxilla depth and width, mandible length and depth, tibiotarsus and ulna length, sternum depth, and synsacrum width. For females: premaxilla length and depth, mandible depth, tarsometatarsus, ulna, sternum, and keel lengths, and synsacrum width.

To relate patterns of variation to the climatic environment and geography, I calculated Spearman's non-parametric correlations and regressed multivariate measures of size and shape from the Principal Component (PC) and Discriminant Function (DF) analyses (see RESULTS), namely PC 1, PC 2, DF 1, and DF 2 scores, with measures of the (1) average annual precipitation, (2) average June precipitation, (3) average minimum summer (June–August) temperature, (4) extreme low summer temperature, (5) extreme high summer temperature, (6) latitude, (7) longitude, and (8) elevation. The climatic data for each site were based on the nearest weather station of similar elevation, and were obtained from Canadian and United States government sources (Environment Canada 1973, National Oceanic and Atmospheric Administration 1983), and are given in Table 1. I also related these to four measures of "sparrow" diversity: (1) the number of potentially competing species (e.g., other sparrows [Emberizinae], Bobolinks [*Dolychonyx oryzivorus*], meadowlarks [*Sturnella* spp.]) that I found in the fields with Savannah Sparrows ("All Species"), (2) the number of species of sparrows in these fields ("Sparrows"), (3) a measure of the abundance of potentially competing species that I found in the fields ("Abundance"; using my field notes, the abundance of each species was scored as: 3, abundant; 2, common; or 1, present, but not common, and the sum of all of the species present was used in these analyses), and (4) the number of species of Fringillidae reported breeding in the general vicinity of the collecting site ("Cook's Index"; Cook 1969). The Fringillidae of Cook (1969) included the Cardinalini, Emberizini, and Carduelini of Sibley and Monroe (1990), or the Emberizidae, Cardinalidae, and Fringillidae of the AOU Check-list (1998); that is, an apparently paraphyletic assemblage of phenetically similar, conical-billed birds. If competition were to affect the evolution of body size and shape, phenetically similar species (whether closely related or not) represent potential competitors. In these analyses I omitted the samples from Lerma and Charco Redondo, Mexico, as I did not have comparable information on the environment or species diversity for those sites.

Because the environmental variables selected are to varying degrees correlated with each

I did principal components analyses on these, and then correlated the Environmental PC scores with the Phenotypic PC scores.

Lastly, to determined the association between the Environmental PC scores and the Phenotypic PC scores I used the average morphological data for males from the 42 samples for which I had good climatic data and the climatic data set (not including latitude, longitude, elevation, or the measures of species diversity). I used a redundancy analysis (SAS PROC CANCOR; SAS Institute 1985), which links the morphological data with the climatic data with a canonical correlation analysis. This can be done both ways (morphological data vs. climatic data, or climatic data vs. morphological data) with parallel principal components analyses between the two data sets where the correlation between them is maximized. Lastly, for a multivariate measure of the concordance between these two matrices, I used Procrustes Analysis (PROTEST; Jackson 1995; D. A. Jackson, pers. comm.); many more commonly used procedures for such comparisons are unsuitable because of non-linearity among locality and environmental data. I looked at the residuals from a Procrustian analysis of the two largest axes combined from both the morphological and climatic data principal components to identify from which localities the morphology was least well explained by the climatic variation.

RESULTS

The patterns of variation in the saltmarsh Savannah Sparrows from the coast of southern California and Baja California, and Sonora and Sinaloa are substantially different, and are discussed separately. I included the sample resident in the saltmarshes near Morro Bay, California, in both groups because they are phenetically intermediate (Fig. 2; see discussion below).

NON-SALTMARSH SAVANNAH SPARROWS

Univariate analyses of size

The ANOVA's (which are not presented here) showed significant geographic variation with regard to all 24 skeletal variables for both sexes. Appendices 1 and 2 list means, ranges, and standard deviations for the larger samples of males and females, respectively. The patterns of variation for the two sexes are similar, and a number of overlapping statistically homogeneous (snk) subsets were identified. I will only describe general trends.

Birds from Sable Island, Nova Scotia, and Umnak Island in the Aleutians are the largest (Figs. 1 and 4; Appendices 1 and 2). There is clinal variation along the Alaska Peninsula, with large birds, nearly as large on average as those on Umnak Island, at the tip (Cold Bay), intermediate birds at Port Heiden, about half-way eastward down the Peninsula, and small birds at Wasilla, Alaska (near Anchorage). Birds from Middleton Island, Alaska, in the north Pacific, are also large, nearly comparable in size to birds from Cold Bay. Savannah Sparrows from the coast of maritime Canada, including those from the Magdalen Islands, Quebec, in the Gulf of St. Lawrence, are larger than those from farther inland. "Ipswich" sparrows (*P. s. princeps*) from Sable Island, Nova Scotia, are especially large and are comparable in size (although slightly larger) with birds from the Aleutian Islands. At the other end of the spectrum, the smallest birds are from the interior of California (Owens Lake), Washington (Creston, Hoquiam), and from Nevada (Elko, Alamo), Utah (Elberta), Alberta (Milk River, Grande Prairie), Wyoming (Sheridan), the interior of Alaska (Koyuk, Wasilla, Fairbanks), and the Mackenzie River Valley, Northwest Territories (Norman Wells, Inuvik). It needs to be emphasized, however, that, with the exception of birds from Sable Island, Umnak

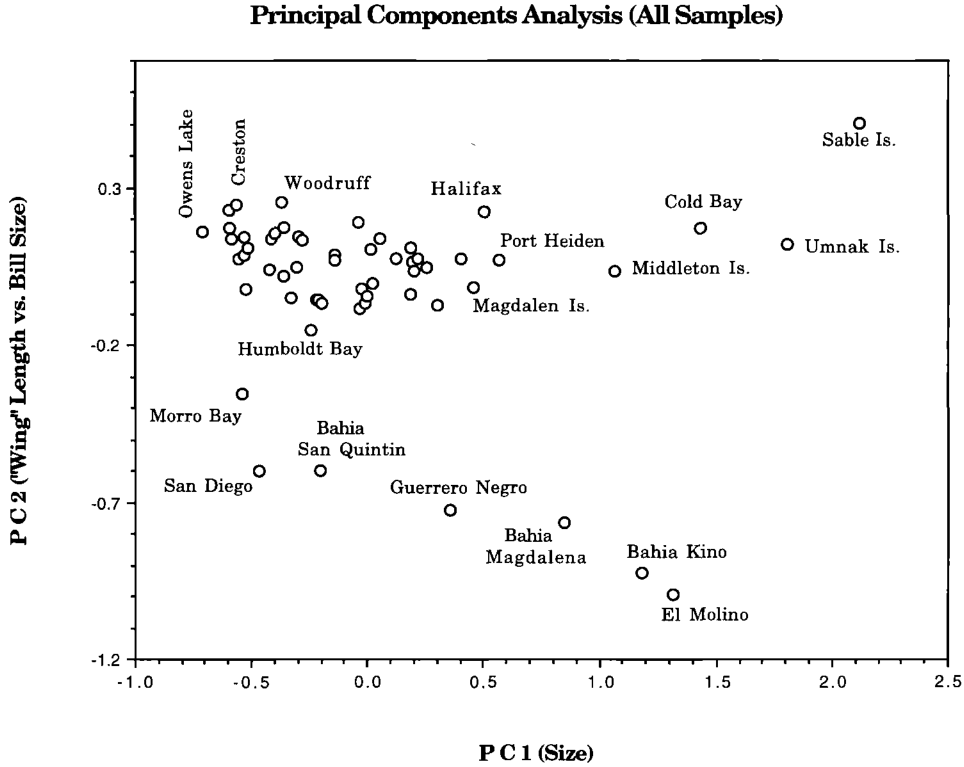

FIGURE 2. Sample averages of male Savannah Sparrows in the space defined by principal components 1 and 2 from a principal component analysis based on the correlations among 24 variables. PC 1 explains 52.4% of the total variance, and represents increasing overall size. PC 2 accounts for 12.9% of the total variance; increasing scores are associated with increasing wing size and decreasing bill size.

Island, and the Alaska Peninsula, the differences in size are small, and there is an enormous amount of overlap in all dimensions (see Appendices). For example, the tibiotarsus length (a good univariate measure of size; i.e., it is highly correlated with PC 1 [Table 2]) of males from Halifax, Nova Scotia (where they are relatively large), range from 29.4–30.6 mm (average = 30.0 mm), those from Woodruff, Utah, (where they are relatively small) range from 25.3–29.5 mm (average = 28.0 mm), and those from Churchill, Manitoba, (where they are intermediate in size) range from 27.2–29.6 mm (average = 28.5 mm); males from Sable Island range from 30.3–32.7 mm (average = 31.7 mm); those from Umnak Island, Aleutian Islands, range from 29.2–32.2 mm (average = 30.8 mm), and those from Wasilla, near Anchorage, Alaska, range from 26.9–29.3 mm (average = 28.2 mm; Appendix 1).

Bill size also varies geographically, with birds from both coastal and the interior of California, the Great Basin, the Great Plains, and north into the Northwest Territories having generally more gracile bills than birds from the northeast or central Mexico (Lerma). Again, however, the amount of interpopulational variation is slight. The ratio of premaxilla depth to premaxilla width ranges only between 0.55 and 0.61, with almost all 0.58–0.60 (see Appendices). Thus, although there is interpopulational variation in bill proportions, the variation is slight.

TABLE 2. CORRELATIONS BETWEEN VARIABLES AND PRINCIPAL COMPONENT SCORES FROM A PCA OF THE CORRELATION MATRIX OF THE RAW MEASUREMENTS OF 1459 MALE AND 822 FEMALE SUMMER-TAKEN SAVANNAH SPARROWS (*Passerculus sandwichensis*)[a]

	Males		Females	
Variable	PC 1	PC 2	PC 1	PC 2
Skull length	0.85	−0.37	0.83	−0.40
Skull width	0.81	—	0.79	—
Premaxilla length	0.66	−0.55	0.60	−0.66
Premaxilla depth	0.72	−0.37	0.66	−0.43
Narial width	0.64	—	0.67	—
Premaxilla width	0.74	−0.37	0.73	−0.40
Interorbital width	0.47	—	0.49	—
Mandible length	0.82	−0.40	0.79	−0.47
Gonys length	0.68	−0.49	0.61	−0.62
Mandible depth	0.72	−0.50	0.71	−0.54
Coracoid length	0.78	0.40	0.77	0.42
Scapula length	0.67	0.47	0.70	0.48
Femur length	0.85	—	0.88	—
Femur width	0.48	—	0.58	—
Tibiotarsus length	0.88	—	0.90	—
Tarsometatarsus length	0.86	—	0.85	—
Humerus length	0.78	0.36	0.79	0.38
Ulna length	0.75	0.47	0.77	0.47
Carpometacarpus length	0.74	0.41	0.78	0.42
Hallux length	0.68	—	0.71	—
Sternum length	0.69	0.47	0.73	0.44
Sternum depth	0.59	0.35	0.58	0.36
Keel length	0.57	0.55	0.59	0.54
Synsacrum width	0.77	—	0.78	—
Eigenvalue	12.6	3.1	12.7	3.6
% variance explained	52.4%	12.9%	52.9%	15.1%

[a] Correlations <0.30 are not included.

Principal components analysis

The correlations between all 24 skeletal measurements of male and female Savannah Sparrows and the first principal component (PC 1) are all relatively large and positive (Table 2), and therefore PC 1 can be taken to be a multivariate measure of overall size (Rising and Somers 1989). Thus, individuals with large PC 1 values are relatively large. The correlations between the measures of bill size (including skull length, which includes the entire premaxilla length) and PC 2 are negative and all greater than 0.36, whereas the correlations between the eight measures of wing and sternum length and PC 2 are all positive and 0.35 or larger. Thus, PC 2 is a measure of shape: individuals with large PC 2 values have relatively large pectoral bones (wings) and small bills, whereas individuals with small PC 2 values have relatively large bills and small wings (Table 2). The first two principal components, taken together, explain 65.3 % (males) and 68.0% (females) of the total variance in the correlation matrices (Table 2); all of the other principal components individually explain less than 7% of the total variance, and are not discussed here.

In two-dimensional, PC 1 vs. PC 2 space, the saltmarsh birds (Morro Bay, San Diego, Bahía San Quintin, Guerrero Negro, Bahía Magdalena, Bahía Kino, and El Molino) are separated on the PC 2 axis from the others because they have relatively large bills and short wings (Fig. 2). The birds from El Molino and

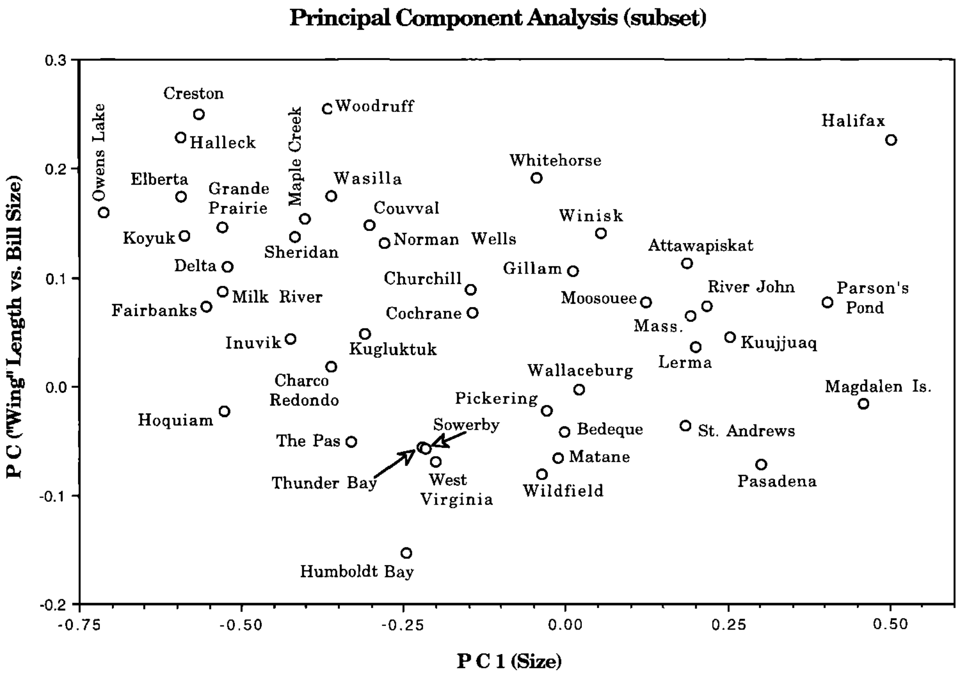

FIGURE 3. Male Savannah Sparrows in PC 1 vs. PC 2 space with the samples from Sable, Umnak, and Middleton islands, and Cold Bay and Port Heiden, Alaska, and the saltmarsh localities removed (see Fig. 2).

Bahía Kino are, in the broad sense, the "large-billed" Savannah Sparrows (the "*rostratus*" group; van Rossem 1947, Rising 1996); they are relatively large as well as large-billed.

The individuals on the islands (Sable Island, Umnak Island, and Middleton Island) as well as Cold Bay (at the tip of the Alaskan Peninsula) are larger than the other non-saltmarsh birds. There is a clear size cline from the Aleutian Islands eastward along the Alaskan Peninsula, with the largest individuals coming from the Aleutians (Umnak Island), then Cold Bay, then Port Heiden (about mid-Peninsula; Fig. 2).

To get a clearer picture of the variation among the remaining populations, I removed the seven saltmarsh samples, plus the samples from Sable, Umnak, and Middleton islands, Cold Bay, and Port Heiden (Fig. 3). For this, no new analyses were done. Rather the "outlier" populations were removed from the figure to give a clearer view of the arrangements of the remaining populations in the principal component ordination. This figure shows a basically east to west cline in body size, with the largest birds being from Halifax (on mainland Nova Scotia, about 300 km west of Sable Island), the Magdalen Islands in the Gulf of St. Lawrence, and Parson's Pond on the west coast of Newfoundland. Although the sparrows on the Aleutians, Middleton Island (in the north Pacific, southeast of Anchorage, Alaska), and the Alaskan Peninsula are large, those from the coastal mainland or inland Alaska are small (Wasilla, near Anchorage; Koyuk, on Norton Bay; Fairbanks).

On the PC 2 axis, Humboldt Bay (coastal northern California) is separate from

TABLE 3. STANDARDIZED CANONICAL DISCRIMINANT FUNCTION COEFFICIENTS FROM A DFA OF 12 MEASUREMENTS OF 1152 MALE SAVANNAH SPARROWS (*Passerculus sandwichensis*) FROM 47 LOCALITIES AND 501 FEMALES SAVANNAH SPARROWS FROM 27 LOCALITIES

	Males		Females	
Variable	DF 1	DF 2	DF 1	DF 2
Skull length	0.15	−0.17	0.13	−0.22
Skull width	0.33	−0.05	0.24	−0.16
Premaxilla length	0.00	0.23	0.10	0.40
Premaxilla width	0.26	0.18	0.31	0.13
Mandible length	0.23	−0.13	0.24	−0.07
Gonys length	0.17	0.26	0.13	−0.26
Coracoid length	0.01	0.34	−0.07	0.11
Femur length	0.12	0.05	0.18	0.09
Tibiotarsus length	0.34	−0.38	0.48	−0.33
Ulna length	−0.36	0.84	−0.34	1.00
Hallux length	0.27	−0.75	0.22	−0.44
Keel length	−0.02	0.12	−0.11	0.38
Eigenvalue	3.53	0.77	4.43	0.70
% variance explained	59.7%	13.0%	66.7%	10.5%
Canonical Correlation	0.88	0.66	0.90	0.64

the others (Fig. 3), intermediate on this axis between the saltmarsh birds and the others (Fig. 2). There is clinal variation, south to north, along the Pacific Coast, from San Diego, Morro Bay, and Humboldt Bay. Hoquiam, on the Washington coast, is widely separated from Humboldt Bay on the PC 2 axis (Fig. 3). The same applies to the two inland Mexican populations (Charco Redondo, Jalisco, and Lerma, México), but they differ only on the PC 1 (size) axis (Fig. 3).

Discriminant functions analysis

Non-saltmarsh males.—The discriminant functions (DF) analysis of the 1152 male Savannah Sparrows from the 47 large (N > 12) non-saltmarsh samples identified 10 significant functions. The first explains 59.7% of the total variance; the second an additional 13.0%; the third and forth 6.8% and 6.0%, respectively; and the remaining ones less than 4% (Table 3). I will discuss variation only in the first two DF dimensions. The ellipses in Figs. 4–10 are 95% confidence ellipses (i.e., 95% of the individuals in the sample are found within the ellipse). Figure 4 shows the positions of all 47 samples; the standardized discriminant function coefficients of the 12 variables used in these analyses are shown in Table 3. The DF 1 coefficients for premaxilla length, coracoid length, and keel length are very small and, with the exception of ulna length and keel length (both measures of the size of the pectoral girdle), all of these are positive. Thus samples to the right in Fig. 4 are made up of relatively large individuals with relatively short wings. The largest DF 2 coefficients are ulna length (0.84) and hallux length (−0.75); thus samples toward the top of the figures contain individuals with relatively long wing and short toes.

The large birds from Sable Island, Cold Bay, and Middleton Island are significantly different from the other samples on the DF 1 axis. There is a great deal of overlap among the other 43 samples. I replotted these 43, with the above four samples removed, to obtain a clearer picture of the relationships among them (Fig. 5). Again, this did not involve a new analysis; the samples were removed

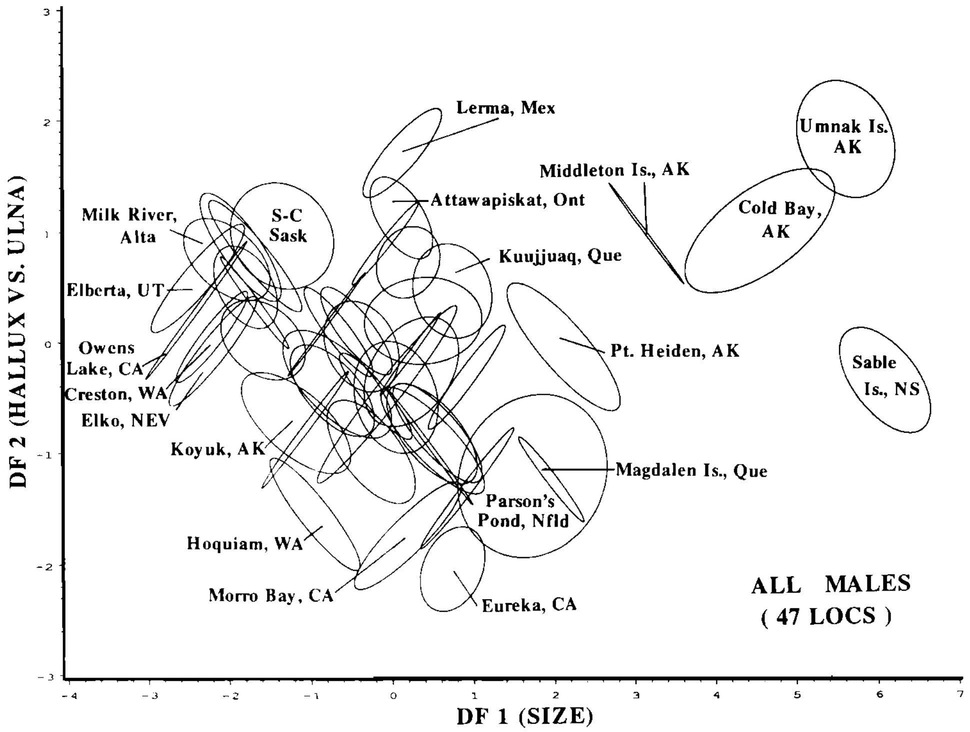

FIGURE 4. Samples of male Savannah Sparrows in the space defined by Discriminant Function (DF) 1 and DF 2; 95% confidence ellipses are shown. DF 1 explains 59.7% of the total variance and can be interpreted as summarizing size variation, with larger birds to the right; DF2 explains an additional 13.0% of the variance and contrasts hallux length with ulna length, with birds toward the top having relatively long ulnas (wings) and short halluxes.

only to better illustrate the relationships among the remaining 43 samples. Samples from Port Heiden, Alaska, the eastern maritime provinces, northern Quebec (Kuujjuaq = Ft. Chimo), northern Ontario (Attawapiskat, Moosonee), coastal California (Morro Bay, Eureka), West Virginia, and central Mexico (Lerma) are to the right in this figure, whereas the relatively small birds from the prairies and intermontane west are to the left. Birds from the north and prairies have relatively long wing and short toes, whereas those from coastal Washington and California, and Newfoundland, the Magdalen Islands, and West Virginia have relatively short wings and long toes. These trends are more clearly illustrated in plots of just the 22 eastern samples (Fig. 6) and 19 western samples (Fig. 7).

Non-saltmarsh females.—The DF results for 501 females from 27 samples are similar, with the birds from Sable and Umnak islands significantly different and substantially larger than those from the other sites. The relationships among samples, with Sable and Umnak islands removed, are shown in Fig. 8; Middleton Island is significantly larger than the other samples, and Magdalen Islands are somewhat (and significantly) larger than mainland maritime and Labrador samples (Halifax and Pictou, Nova Scotia, St. Andrews, New Brunswick, and Matane and Kuujjuaq, Quebec; Fig. 9). Among the western females, the smallest birds come

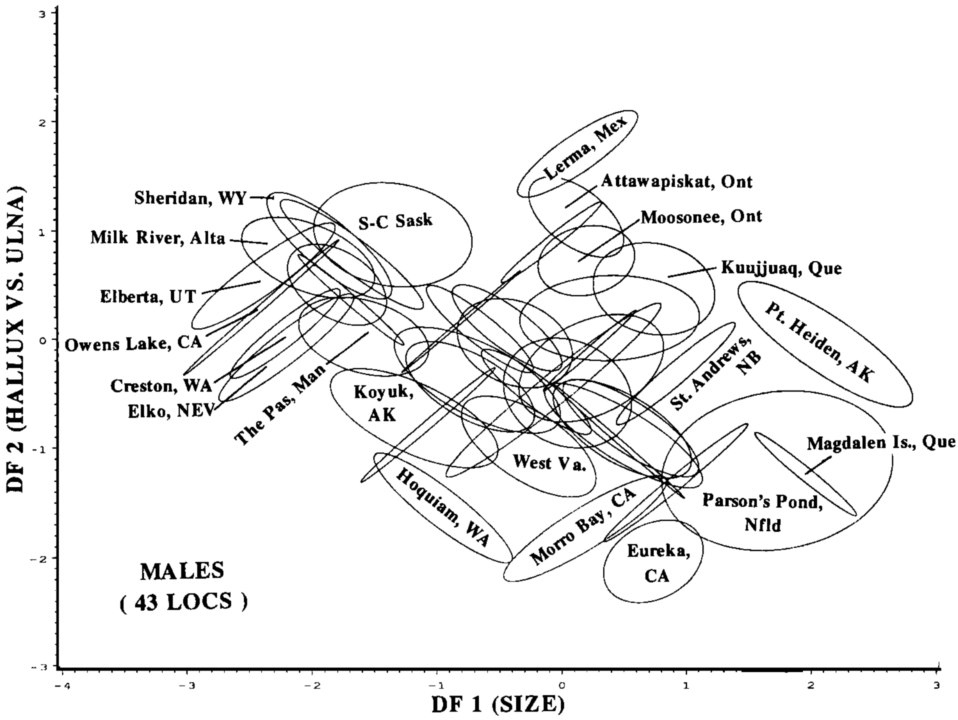

FIGURE 5. Samples of male Savannah Sparrows in the DF 1 vs. DF 2 space, with samples of larger birds removed to improve the resolution of the remaining ones (see Fig. 4).

from the arid west and Great Plains (Sheridan, Wyoming, Creston, Washington, Grande Prairie, Alberta, and Owen's Lake, California; Fig. 10).

Correlations between environmental variables and size

Spearman's correlations between principal component (PC) and discriminant function (DF) scores and a variety of environmental measures from the 45 largest ($N > 10$) male and 27 female samples from non-saltmarsh localities are given in Table 4 (only localities for which reliable environmental data were available were used in these analyses [Table 1]). Because the Savannah Sparrows from Sable Island, Nova Scotia, and Umnak Island, Middleton Island, Cold Bay, and Port Heiden, Alaska, are substantially larger than others, they are outliers in these correlation analyses. Thus, I also calculated the Spearman's correlations between male size and environmental variables, with these localities omitted, reducing the number samples of males to 40, and the number of samples of females to 25 (Table 5). Samples of females from Cold Bay, Port Heiden, and Middleton Island are small, and they are not included in either set of correlation analyses.

For both sexes, there is a significant correlation between PC 1 score (size) and both average annual precipitation and average June precipitation; that is, Savannah Sparrows tend to be large where the precipitation is high. This is true not only for all samples (Table 4), but also when the samples of especially large sparrows are omitted (Table 5). There is also a significant negative correlation between PC 1 scores and the average minimum summer temperature, average maximum sum-

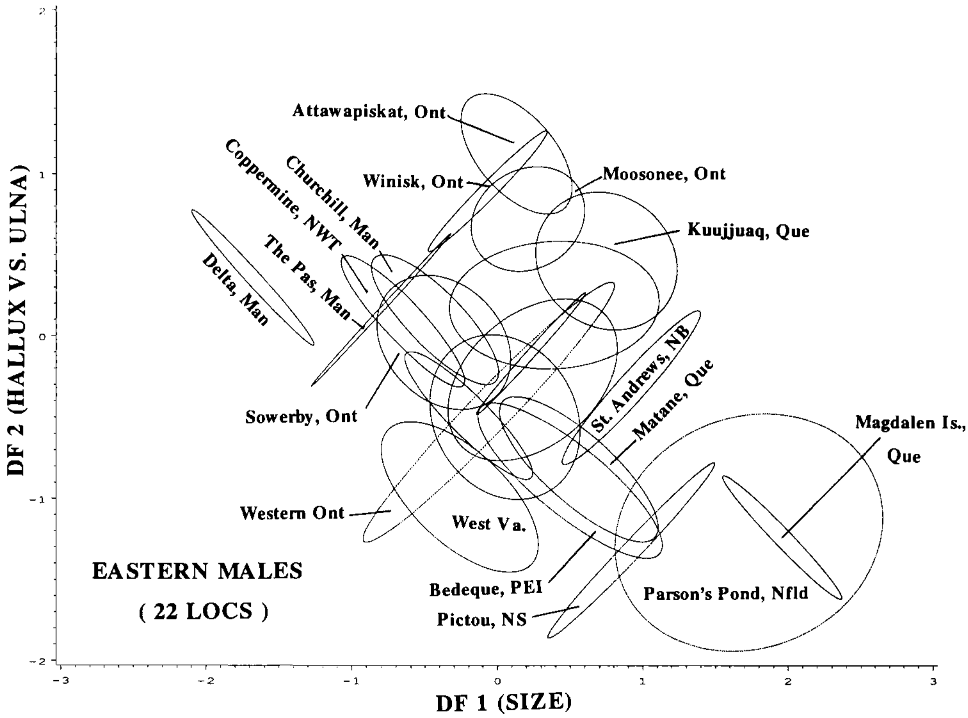

FIGURE 6. Samples of eastern male Savannah Sparrows in the DF 1 vs. DF 2 space (see Fig. 4).

mer temperature, and maximum summer temperature for males; for females, correlation values are similar, but only the last is significant (Table 4), and for both sexes these correlations similar when all of the sparrow samples are considered as well as when the largest ones are omitted (Table 5). Also, there is a significantly negative correlation between both longitude and elevation and PC (Tables 4 and 5). Thus, Savannah Sparrows are smallest in the west and at high elevations. Lastly, there is a significantly negative correlation between body size and Cook's Index, illustrating that Savannah Sparrows tend to be relatively large where they co-occur with few potential competing species.

The second principal component (PC 2) scores are negatively correlated with measures of bill size, and positively correlated with measures of pectoral girdle size (Table 2); thus, individuals with large PC 2 scores have relatively small bills and long wings. PC 2 scores are significantly negatively correlated with both average annual precipitation and average June precipitation in both sexes (Table 4). With the samples of the largest sparrows removed from the analyses, the size of the correlation between PC 2 and average annual precipitation is larger, and the same is true for females (Table 5). As well, there is a positive correlation between PC 2 score and both longitude and elevation; the correlation between elevation and PC 2 score in males is significant, and in both sexes with the largest sparrows omitted (Tables 4 and 5). Thus Savannah Sparrows from the west and high elevations have relatively small bills and long wings.

Some of these relationships in bivariate space are illustrated in Figs. 11–20. The correlation coefficients used in these figures are Pearson's correlations (cf. Tables

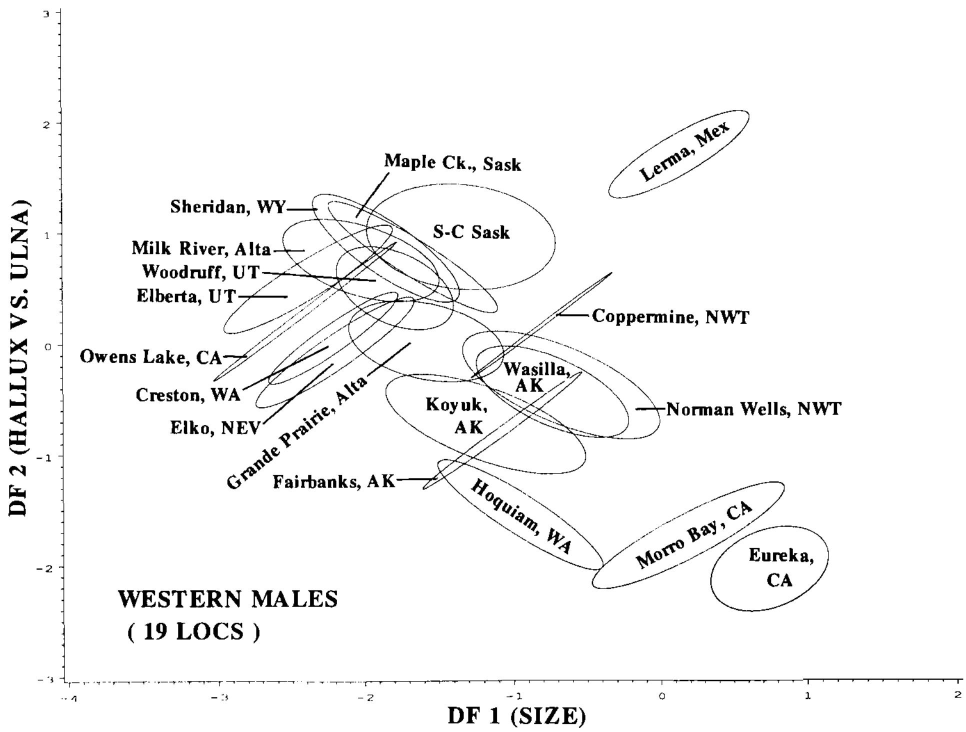

FIGURE 7. Samples of western male Savannah Sparrows in the DF 1 vs. DF 2 space (see Fig. 4).

4 and 5). There is a negative correlation between DF 1 scores (body size) of males and the maximum temperature (Fig. 11); with the three populations with the largest body size, Sable and Umnak islands and Cold Bay, removed this correlation drops from −0.69 to −0.60 (Fig. 12), but it is still statistically significant; thus, they are smallest where ambient temperatures may be high. There is a positive correlation between DF 1 scores of males and the average annual precipitation (Fig. 13). With Sable and Umnak islands and Cold Bay removed, the correlation increases from 0.56 to 0.64 (Fig. 14); both correlations are statistically significant. Females are largest (PC 1 scores) where the maximum recorded temperature is relatively low (Fig. 15); with the largest birds, those from Umnak and Sable islands, removed (Fig. 16) the correlation decreases from −0.58 to −0.46, showing that the inclusion of those samples substantially affects the apparent relationship. Females are also relatively large where the annual precipitation is high (Fig. 17), and in the east (Fig. 18). They have relatively small bills and large wing bones (PC 2) where the precipitation is low (Fig. 19). Lastly, males are relatively large (DF 1 scores) where species diversity (Cook's Index) is low (Fig. 20).

The principal components analysis of the environmental variables produced two principal components with nearly equal and large eigenvalues, which combined explained 74% (males) to 77% (females) of the variation among localities (Table 6). Environmental principal component 1 (EPC 1) is positively correlated with all of the temperature variables and rather weakly correlated with the precipitation variables; thus, localities with high values for EPC 1 tended to be warm, and

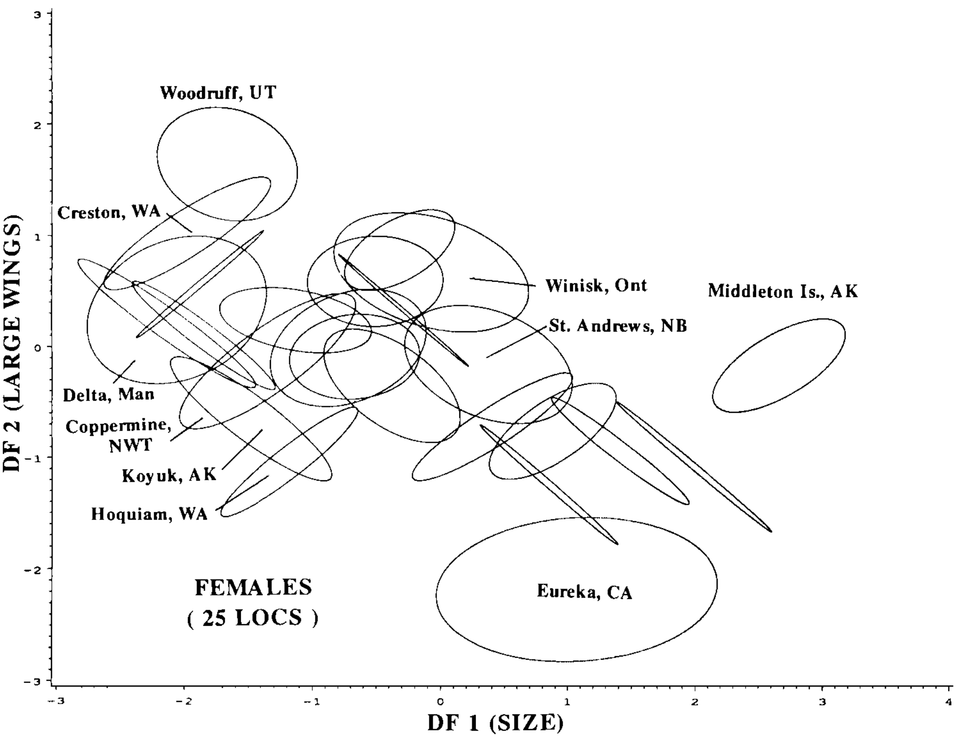

FIGURE 8. Samples of female Savannah Sparrows in the DF 1 vs. DF 2 space. Individuals to the right of the plot are relatively large; those toward the top have relatively large wings.

perhaps moister than average. EPC 2 is positively correlated with the precipitation variables and the extreme low summer temperature; thus, localities with high values for EPC 2 are moist and tend not to have extremely high summer temperatures (Table 7). Phenotypic principal component 1 (PPC 1) scores (large values for large birds) are negatively correlated the EPC 1 (that is, large birds are found where it is cool; Table 7) and positively correlated with EPC 2 (that is, large birds are found where it is moist and extreme summer high temperatures are low; Table 4). These correlations were calculated only for 45 male and 27 female samples. The correlations between PPC 2 and EPC 1 are not significant, and those between PPC 2 and EPC 2 are negative (birds in relative mesic areas have large bills and relatively small wings; Table 4).

Thus, Savannah Sparrows are smallest in the west and at high elevations. Latitudinal trends are slight and not significant, and this is so even when only the 27 eastern samples are examined ($r = 0.01$, ns; Sable Island not included), or the 23 western are examined ($r = 0.06$, ns; Umnak Island, Cold Bay, Port Heiden, and Middleton Island not included). Lastly, there is a significantly negative correlation between body size and Cook's Index, indicating that Savannah Sparrows tend to be relatively larger where they co-occur with few potential competing species (Table 4). This remains true when the samples of the largest birds (which includes three of the four island samples) are removed (Table 5).

PC 2 scores (which reflect bill size and pectoral girdle size) are significantly negatively correlated with both average annual precipitation and average June

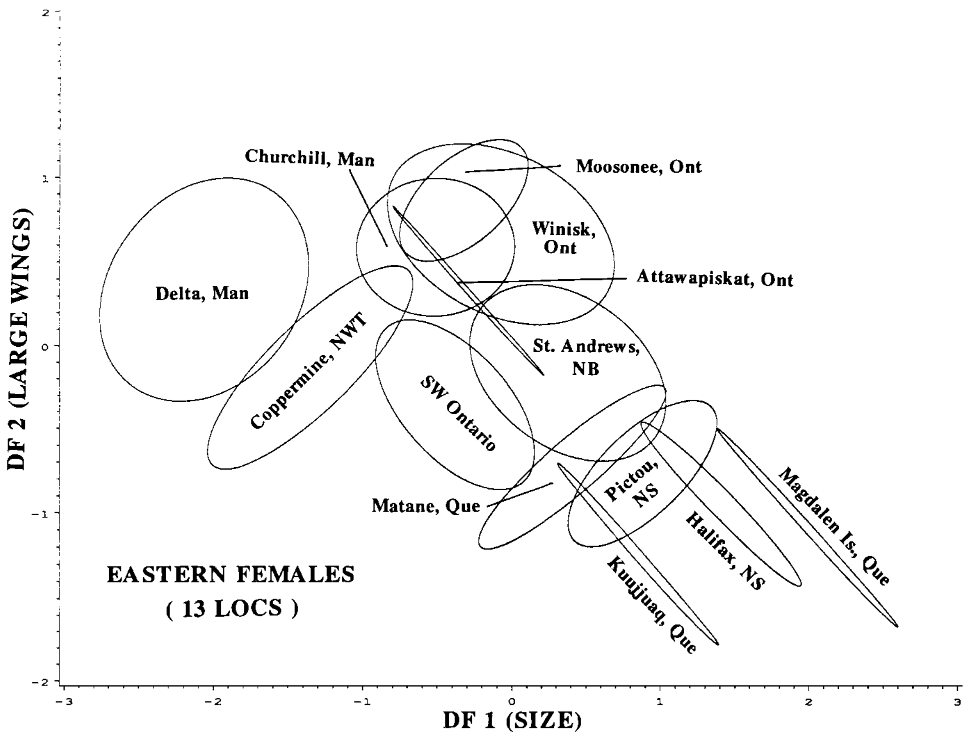

FIGURE 9. Samples of female Savannah Sparrows from eastern North America in the DF 1 vs. DF 2 space (see Fig. 8).

precipitation in both sexes (Table 4). Thus, Savannah Sparrows have relatively large bills and small wings where both annual and June precipitation are low. With the samples of the largest sparrows removed from the analyses (Table 5), the sizes of these correlations are larger. As well, there is a positive correlation between PC 2 score and both longitude and elevation; the correlation between elevation and PC 2 score is significant in males, and in both sexes with the largest sparrows omitted. Thus, Savannah Sparrows from the west and high elevations have relatively small bills and large wings.

Canonical correlations and redundancy analysis

The correlations between the morphological variables (averages for each of 42 different populations) and the first canonical variable based on the morphological canonical variable (MCV1) are all relatively high and negative, that is, large birds have small MCV1 values (Table 8). This axis, then, can be taken as a measure of size, and explains 27.9% of the morphological variance. The measures of bill size and hallux (toe) length are positively correlated with MCV2; that is, birds with relatively large bills and long toes have large MCV2 values. This second axis explains 10.2% of the variance. Lastly, measures of wing and leg length are negatively correlated with MCV3, and explains an additional 9.6% of the morphological variability.

The first climatic canonical variable (CCV1) from the analysis of the climatic variables range from relatively cool and moist localities to relatively hot and dry ones (Table 9); approximately 35.4% of the climatic variation among localities is

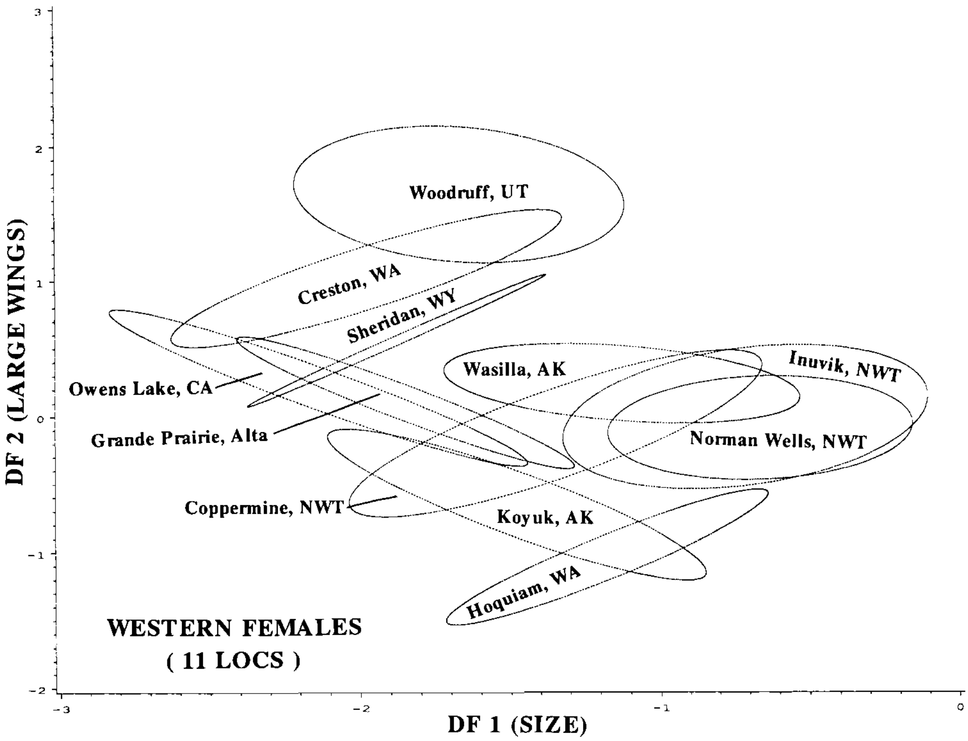

FIGURE 10. Samples of female Savannah Sparrows from western North America in the DF 1 vs. DF 2 space (see Fig. 8).

explained along this axis. CCV2 explains an additional 28.9% of the climatic variation, and contrasts localities with relatively warm and wet (as measured by rainfall) climates with those that are relatively cool. CCV3 explains 7.3% of the climatic variability, but is not particularly highly correlated with any of the climatic variables (Table 9).

For the most part, the residuals from the Procrustean analysis of the morphological and climatic principal components (two axes of each combined) are small (Table 10). The only large values are those for the localities where the birds are especially large (Sable Island, Umnak Island, and Cold Bay), two coastal localities, one of which is found in the far north (Kugluktuk and Hoquiam), and Owens Lake in east-central California (where the summers are hot and dry, but the birds are found in relatively mesic vegetation along the shores of the lake). These are, thus, either places where the birds are unusually large or where the data taken from weather stations are probably a poor indication of the environmental conditions in the microhabitat of the birds. There is strong agreement between the climatic and morphological data sets (probability of rejection is 0.0001).

Saltmarsh Savannah Sparrows

Males

There are four significant discriminant functions among the eight samples of saltmarsh Savannah Sparrow; of these, the first explains nearly 85% of the vari-

TABLE 4. SPEARMAN'S CORRELATIONS BETWEEN PRINCIPAL COMPONENTS (PC) AND DISCRIMINANT FUNCTIONS (DF) SCORES AND ENVIRONMENTAL MEASURES FOR SAVANNAH SPARROWS FROM 45 (MALES) AND 27 (FEMALES) LOCALITIES

Variable	PC 1		PC 2		DF 1		DF 2	
	Male	Female	Male	Female	Male	Female	Male	Female
Average annual precipitation	0.62 (0.0001)[a]	0.57 (0.002)	−0.66 (0.0001)	−0.59 (0.001)	0.71 (0.0001)	0.68 (0.0001)	0.39 (0.009)	−0.41 (0.03)
Average June precipitation	0.43 (0.004)	0.50 (0.008)	−0.51 (0.0005)	−0.39 (0.05)	0.44 (0.003)	0.47 (0.01)	0.21 (0.18)	−0.17 (0.41)
Average minimum summer[b] temperature	−0.36 (0.02)	−0.26 (0.19)	−0.13 (0.39)	−0.11 (0.59)	−0.33 (0.03)	−0.16 (0.43)	0.33 (0.03)	−0.21 (0.29)
Average maximum summer temperature	−0.51 (0.0005)	−0.31 (0.12)	0.27 (0.08)	0.28 (0.17)	−0.56 (0.0001)	−0.45 (0.02)	−0.01 (0.95)	0.21 (0.29)
Minimum summer temperature	0.00 (0.98)	0.19 (0.34)	−0.25 (0.11)	−0.28 (0.16)	0.08 (0.58)	0.30 (0.12)	0.25 (0.10)	−0.25 (0.22)
Maximum summer temperature	−0.63 (0.0001)	−0.53 (0.005)	−0.40 (0.008)	0.32 (0.10)	−0.67 (0.0001)	−0.67 (0.001)	−0.11 (0.47)	0.29 (0.14)
Environmental PC 1	−0.62 (0.0001)	−0.41 (0.03)	−0.26 (0.09)	0.10 (0.60)	—	—	—	—
Environmental PC 2	0.38 (0.01)	0.49 (0.01)	−0.64 (0.001)	−0.56 (0.002)	—	—	—	—
Latitude	0.14 (0.37)	−0.02 (0.89)	0.09 (0.58)	0.11 (0.60)	0.15 (0.34)	−0.04 (0.82)	−0.34 (0.02)	0.06 (0.76)
Longitude	−0.40 (0.007)	−0.43 (0.03)	0.22 (0.16)	0.11 (0.59)	−0.36 (0.02)	−0.37 (0.06)	−0.30 (0.05)	0.13 (0.53)
Elevation	−0.63 (0.0001)	−0.56 (0.002)	+0.38 (0.01)	0.29 (0.14)	−0.68 (0.0001)	−0.61 (0.0007)	−0.26 (0.08)	0.33 (0.10)
Competitor abundance	−0.18 (0.26)	−0.23 (0.25)	+0.17 (0.26)	0.22 (0.28)	−0.17 (0.27)	−0.25 (0.20)	−0.22 (0.14)	−0.14 (0.49)
Number of competing species	0.07 (0.65)	−0.13 (0.51)	+0.09 (0.55)	0.13 (0.51)	−0.08 (0.61)	−0.16 (0.43)	−0.28 (0.07)	0.19 (0.33)
Number of sparrow species	0.13 (0.42)	0.01 (0.95)	+0.07 (0.69)	0.14 (0.47)	0.13 (0.41)	−0.03 (0.87)	−0.21 (0.17)	0.19 (0.35)
Cook's Index	−0.59 (0.001)	−0.44 (0.02)	+0.20 (0.19)	0.04 (0.85)	−0.58 (0.0001)	−0.50 (0.009)	0.03 (0.84)	0.03 (0.88)

[a] Exact probabilities are in parentheses.
[b] June, July, and August.

TABLE 5. SPEARMAN'S CORRELATIONS BETWEEN PRINCIPAL COMPONENTS (PC) AND DISCRIMINANT FUNCTIONS (DF) SCORES AND ENVIRONMENTAL MEASURES FOR SAVANNAH SPARROWS FROM 40 (MALES) AND 25 (FEMALES) LOCALITIES

Variable	PC 1		PC 2		DF 1		DF 2	
	Male	Female	Male	Female	Male	Female	Male	Female
Average annual precipitation	0.59	0.53	−0.73	−0.69	0.69	0.66	0.55	−0.55
	(0.0001)[a]	(0.007)	(0.0001)	(0.0001)	(0.0001)	(0.0003)	(0.0003)	(0.004)
Average June precipitation	0.50	0.55	−0.57	−0.44	0.51	0.51	0.26	−0.19
	(0.001)	(0.004)	(0.0002)	(0.03)	(0.0009)	(0.009)	(0.11)	(0.35)
Average minimum summer[b] temperature	−0.29	−0.29	+0.22	−0.19	−0.22	−0.16	0.23	−0.22
	(0.08)	(0.17)	(0.19)	(0.37)	(0.17)	(0.44)	(0.17)	(0.29)
Average maximum summer temperature	−0.41	−0.26	+0.30	0.30	−0.47	−0.43	−0.20	0.33
	(0.01)	(0.21)	(0.07)	(0.14)	(0.002)	(0.03)	(0.22)	(0.10)
Minimum summer temperature	−0.24	0.05	−0.25	−0.38	−0.11	0.19	0.37	−0.43
	(0.14)	(0.80)	(0.13)	(0.06)	(0.51)	(0.37)	(0.02)	(0.03)
Maximum summer temperature	−0.51	−0.43	+0.46	0.41	−0.56	−0.61	−0.33	0.54
	(0.001)	(0.03)	(0.004)	(0.04)	(0.0002)	(0.001)	(0.04)	(0.005)
Latitude	0.07	0.00	+0.18	−0.22	0.06	−0.02	−0.26	0.14
	(0.66)	(0.99)	(0.28)	(0.30)	(0.71)	(0.94)	(0.10)	(0.50)
Longitude	−0.81	−0.53	+0.48	0.30	−0.74	−0.46	−0.14	0.17
	(0.0001)	(0.007)	(0.002)	(0.15)	(0.0001)	(0.02)	(0.14)	(0.42)
Elevation	−0.64	−0.62	+0.45	0.37	−0.70	−0.68	−0.35	0.38
	(0.0001)	(0.001)	(0.005)	(0.07)	(0.0001)	(0.0002)	(0.03)	(0.06)
Competitor abundance	0.07	−0.08	−0.19	−0.34	−0.06	−0.11	0.38	0.36
	(0.66)	(0.70)	(0.25)	(0.09)	(0.73)	(0.60)	(0.02)	(0.60)
Number of competing species	0.14	−0.02	−0.11	0.26	0.10	−0.05	−0.37	0.37
	(0.41)	(0.93)	(0.49)	(0.21)	(0.53)	(0.83)	(0.02)	(0.07)
Number of sparrow species	0.29	0.11	0.10	0.28	0.26	0.05	−0.26	0.34
	(0.08)	(0.60)	(0.56)	(0.17)	(0.11)	(0.82)	(0.11)	(0.10)
Cook's index	−0.47	−0.33	−0.28	0.13	−0.45	−0.39	−0.12	0.22
	(0.003)	(0.11)	(0.09)	(0.53)	(0.004)	(0.051)	(0.47)	(0.29)

[a] Exact probabilities given in parentheses.
[b] June, July, and August.

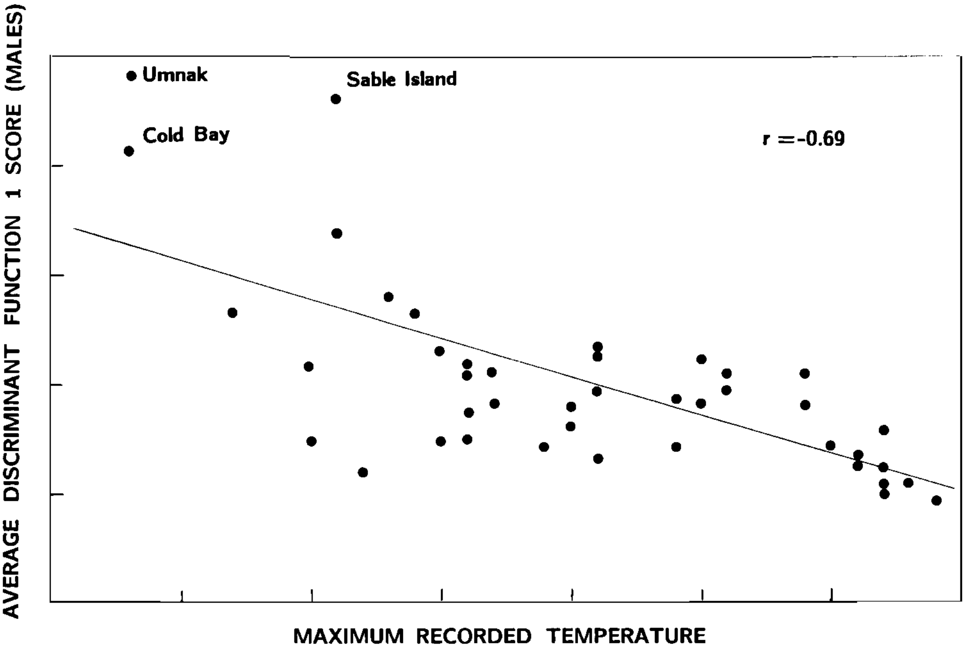

FIGURE 11. Relationship between average DF 1 score of males (Fig. 4) vs. the maximum recorded temperature. The product-moment correlation coefficient between the variables is −0.69, and it is statistically significant ($P < 0.001$).

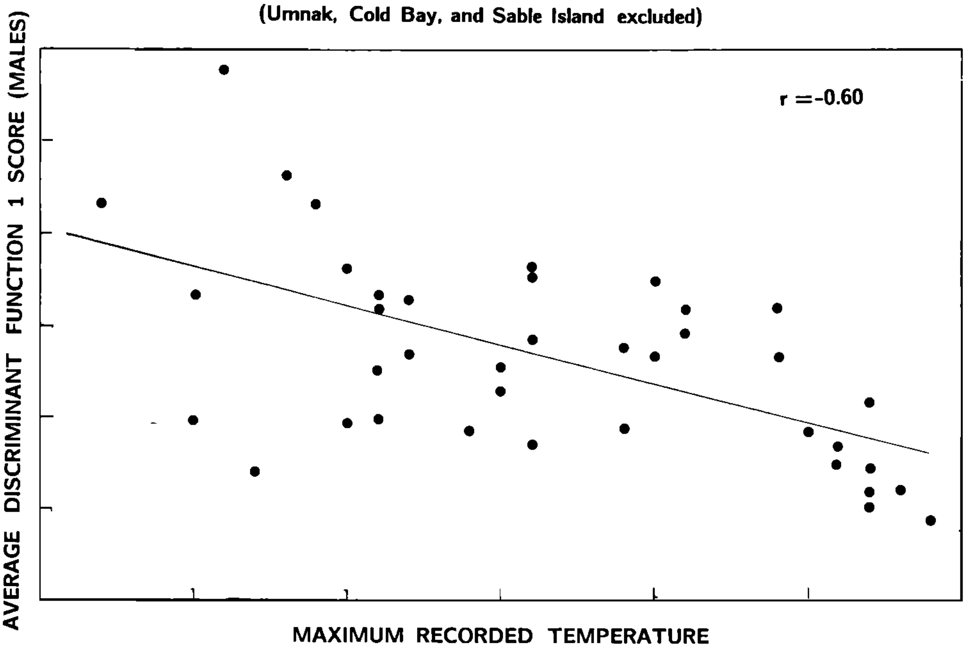

FIGURE 12. Relationship between the average DF 1 score of males (Fig. 4) vs. the maximum recorded temperature with the three samples of the largest individuals (Umnak Island, Cold Bay, and Sable Island) removed. The product-moment correlation of −0.60 is statistically significant ($P < 0.001$).

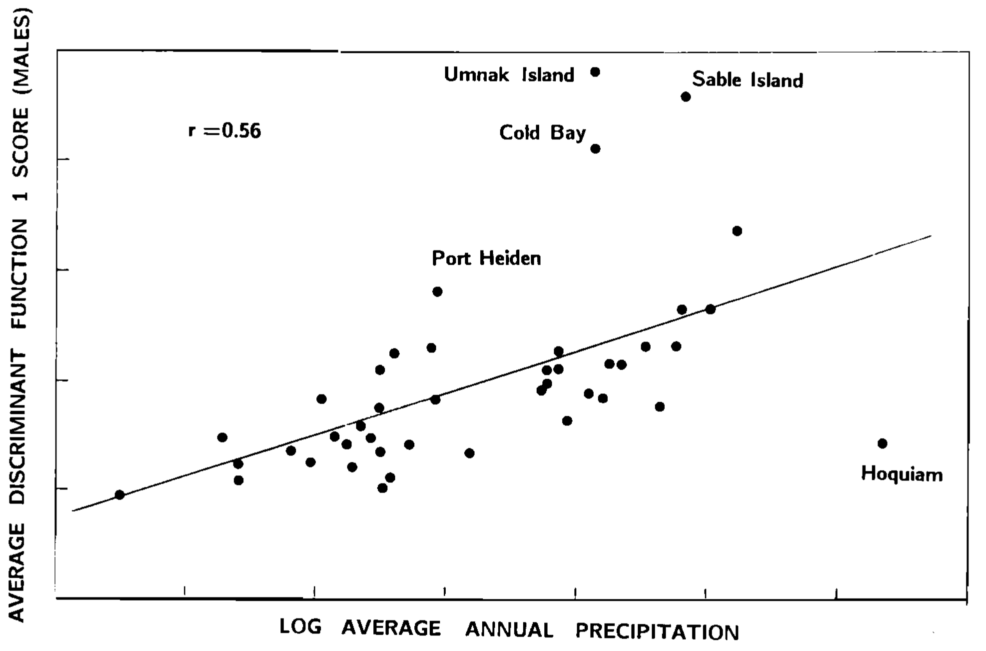

FIGURE 13. Relationship between the average DF 1 score of males (Fig. 4) vs. the log of the average annual precipitation. The product-moment correlation of 0.56 is statistically significant (P = 0.004).

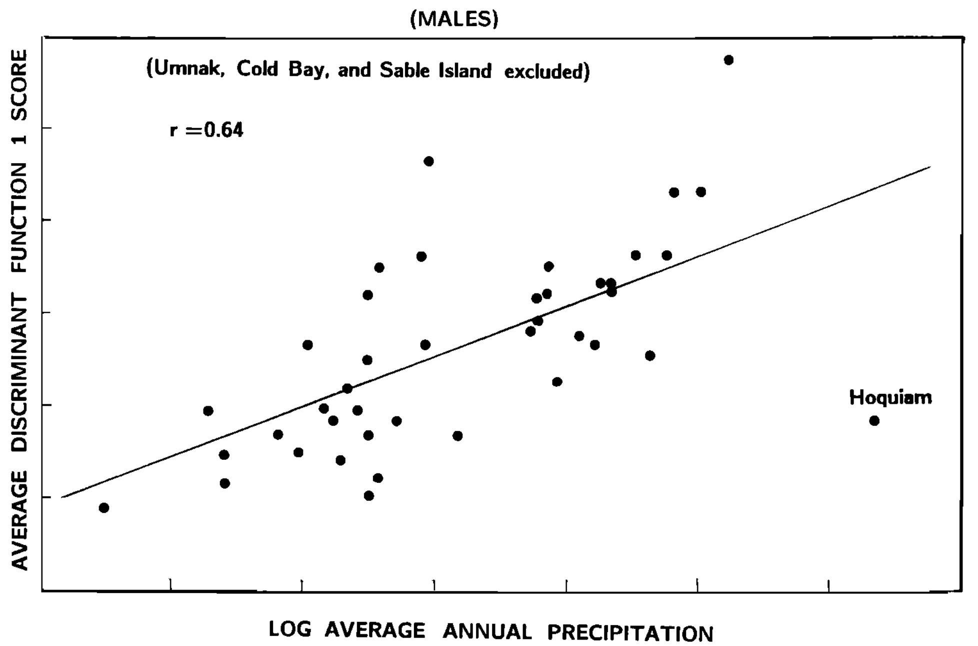

FIGURE 14. Relationship between the average DF 1 scores of males (Fig. 4) vs. the log of the average annual precipitation with the three samples of the largest individuals (Umnak Island, Cold Bay, and Sable Island) removed. The product-moment correlation of 0.64 is statistically significant P = 0.003).

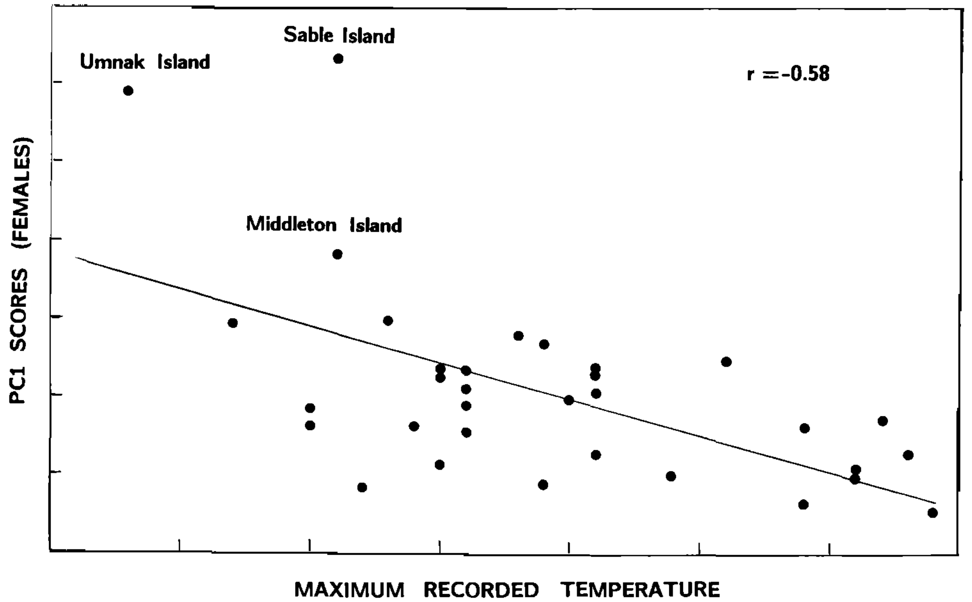

FIGURE 15. Relationship between the average PC 1 scores of female Savannah Sparrows from 33 localities vs. the maximum recorded temperature. PC 1 scores are a measure of overall body size (see text). The product-moment correlation of −0.58 is statistically significant (P = 0.002).

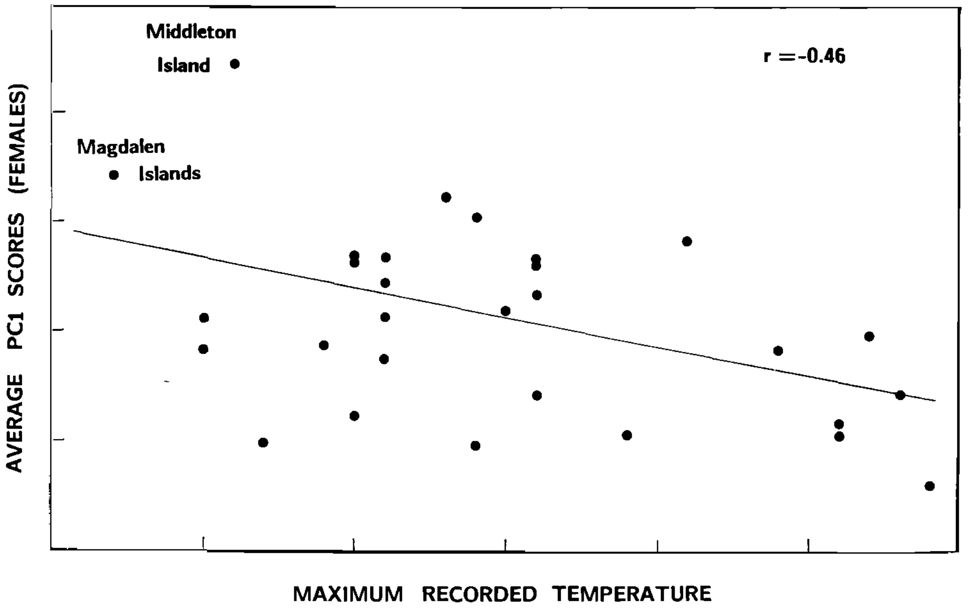

FIGURE 16. Relationship between the average PC 1 scores of female Savannah Sparrows from 29 localities (Sable and Umnak islands omitted) vs. the maximum recorded temperature. The product-moment correlation of −0.46 is statistically significant (P = 0.008).

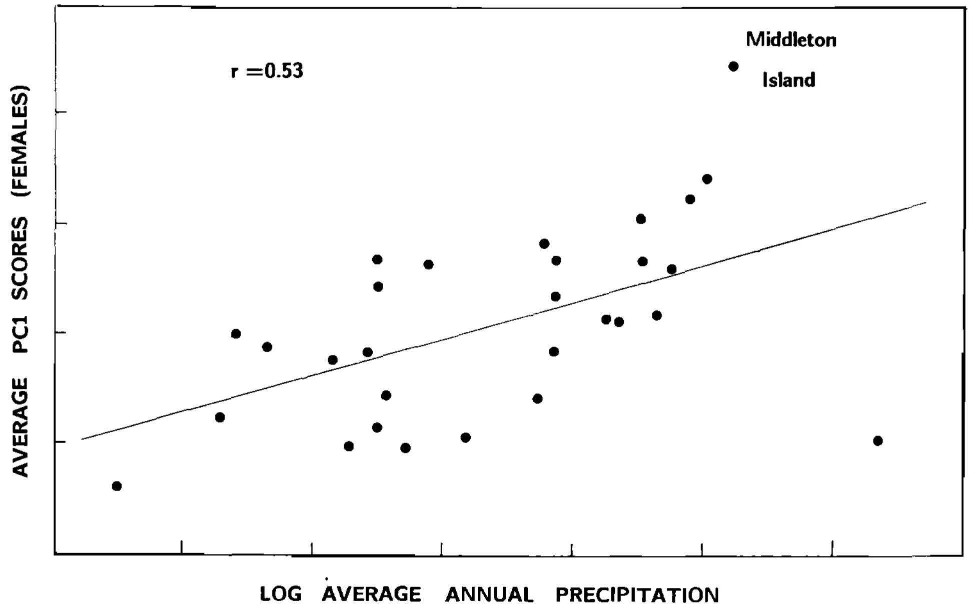

FIGURE 17. Relationship between the average PC 1 scores of female Savannah Sparrows from 29 localities vs. the log of the average annual precipitation. The product-moment correlation of 0.53 is statistically significant (P = 0.008).

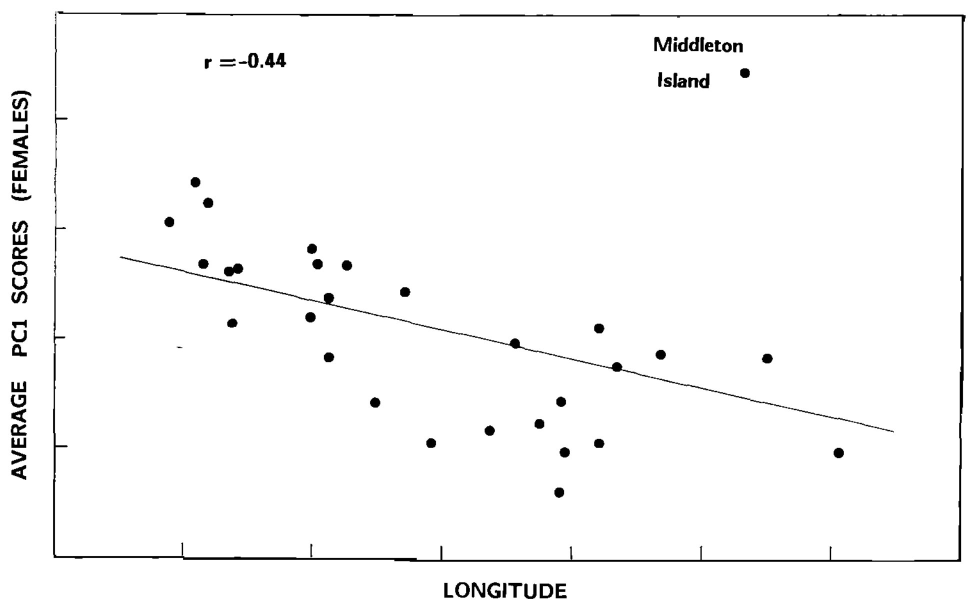

FIGURE 18. Relationship between the average PC 1 scores of female Savannah Sparrows from 29 localities vs. longitude. The product-moment correlation of −0.44 is statistically significant (P = 0.03).

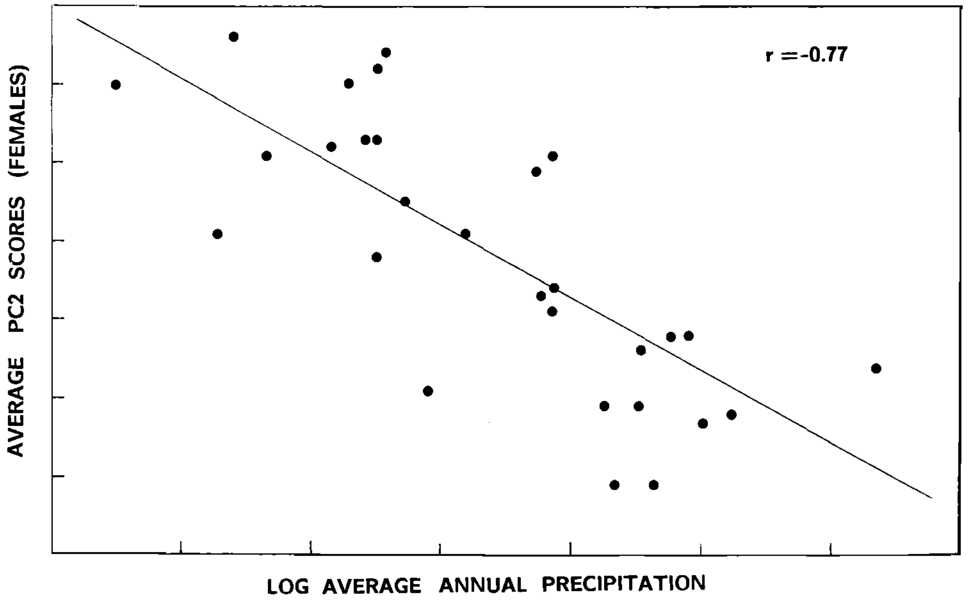

FIGURE 19. Relationship between the average PC 2 scores of female Savannah Sparrows from 29 localities vs. the log of the average annual precipitation. PC 2 scores contrast bill size with wing size (see text). The product-moment correlation of −0.77 is statistically significant (P = 0.001).

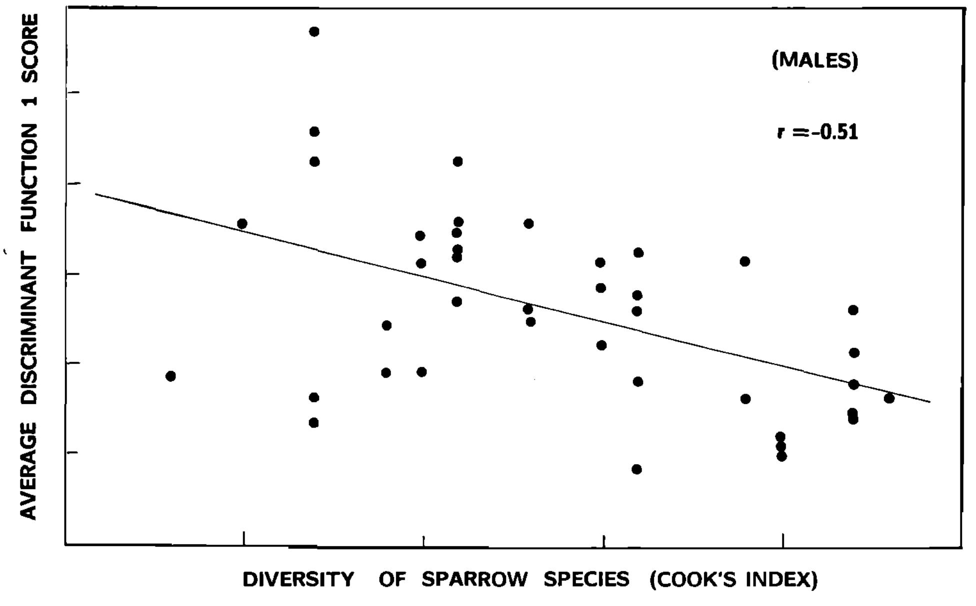

FIGURE 20. Relationship between the average DF 1 scores of male Savannah Sparrows vs. Cook's Index of sparrow species diversity (see text). The product-moment correlation of −0.51 is statistically significant (P < 0.001).

TABLE 6. STANDARDIZED CANONICAL DISCRIMINANT FUNCTION COEFFICIENTS FROM A DFA OF 8 MEASUREMENTS OF 153 MALE SAVANNAH SPARROWS FROM 8 SALTMARSH LOCALITIES AND 98 FEMALE SAVANNAH SPARROWS FROM 7 LOCALITIES

	Males		Females	
Variable	DF 1	DF 2	DF 1	DF 2
Premaxilla depth	0.48	−0.34	0.42	0.43
Premaxilla width	0.22	−0.13	0.61	0.49
Mandible length	0.34	0.43	—	—
Mandible depth	0.54	−0.01	0.66	−0.51
Tibiotarsus length	0.27	0.58	—	—
Tarsometatarsus length	—	—	0.26	0.87
Ulna length	−0.11	−1.12	−0.12	−0.73
Sternum length	—	—	−0.40	0.84
Sternum depth	−0.17	0.38	—	—
Synsacrum width	−0.15	0.77	−0.10	−0.63
Eigenvalue	9.75	1.08	12.85	0.83
% variance explained	84.9%	9.5%	87.20%	5.66%
Canonical Correlation	0.95	0.72	0.96	0.67

ance among the groups, and the second an additional 9.5% (Table 11). I will discuss only these two. The first DF separates the males principally on the basis of bill size; birds with large DF 1 scores have relatively large bills. This function separates the large-billed sparrows of coastal Sonora and Sinaloa from the small-billed birds of coastal California and Baja California. The southern-most Baja sample, that from Bahía Magdalena, is intermediate on this axis between the large-billed birds and the sample from Guerrero Negro, midway north on the Baja coast (Fig. 21; because of the small sample size, the ellipse for the birds from Puerto Peñasco is not included in the illustration). Males with large DF 2 scores have short wings, wide synsacra, long legs, and long mandibles. Samples from Baja California, especially Guerrero Negro, have relatively large DF 2 scores; the birds from Puerto Peñasco, Sonora, and Morro Bay, California, are similar on the DF 2 axis; the birds from Morro Bay and San Diego are virtually identical on this axis (Fig. 21).

Retrospectively, overall in the DFA 72.2% of the males are correctly identified as to sample. In general, misidentified individuals are grouped with the nearest population; interestingly two of the nine males from Puerto Peñasco were identified as belonging to the Magdalena Bay population, and one of the 15 males

TABLE 7. RELATIONSHIP BETWEEN MORPHOLOGICAL PRINCIPAL COMPONENTS AND ENVIRONMENTAL PRINCIPAL COMPONENTS

	Environmental			
	PC 1		PC 2	
Male				
Morphology PC 1	−0.52	$P < 0.001$	0.32	$P = 0.04$
Morphology PC 2	−0.30	$P > 0.05$	0.48	$P = 0.001$
% Variation Explained	42%		32%	
Female				
Morphology PC 1	−0.34	$P > 0.05$	0.45	$P = 0.02$
Morphology PC 2	0.45	$P = 0.02$	−0.48	$P = 0.01$
% Variation Explained	42%		35%	

TABLE 8. Squared Multiple Correlations Between the Morphological Variables and the First Three Canonical Climatic Variables

Morphological Variable	MCV1	MCV2	MCV3
Skull length	0.44	0.51	0.58
Skull width	0.47	0.48	0.63
Premaxilla length	0.25	0.32	0.38
Premaxilla depth	0.20	0.47	0.50
Narial width	0.15	0.55	0.61
Premaxilla width	0.23	0.44	0.49
Interorbital width	0.04	0.45	0.46
Mandible length	0.43	0.51	0.57
Gonys length	0.32	0.42	0.45
Mandible depth	0.19	0.49	0.50
Coracoid length	0.20	0.29	0.38
Scapula length	0.20	0.26	0.42
Femur length	0.18	0.28	0.38
Femur width	0.13	0.21	0.21
Tibiotarsus length	0.32	0.42	0.51
Tarsometatarsus length	0.30	0.43	0.50
Humerus length	0.08	0.14	0.20
Ulna length	0.09	0.15	0.27
Carpometacarpus length	0.22	0.24	0.37
Hallux length	0.27	0.50	0.57
Sternum length	0.19	0.28	0.35
Sternum depth	0.12	0.24	0.26
Keel length	0.12	0.21	0.32
Synsacrum width	0.35	0.42	0.49
Mass	0.26	0.34	0.39
% Morphological variation explained	27.9%	10.2%	9.6%

from Bahía Magdalena was identified with the Puerto Peñasco sample and another with the Bahía Kino sample. Otherwise, none of the coastal birds from California or Baja California were identified with the coastal Sonora and Sinaloa birds, and vice versa.

Females

There are four significant discriminant functions in the DFA of seven samples of females (the sample from Puerto Peñasco was too small for inclusion in this analysis). DF 1 explains 87.2% of the total variation among samples, and DF 2 only an additional 5.7% (Table 11); variation on only these dimensions is discussed. The first DF is sensitive to variability in bill size, especially bill depth; it

TABLE 9. Correlations Between Climate Variables and Their Canonical Variables (CCV)

Climatic Variable	CCV1	CCV2	CCV3
Average annual precipitation	−0.48	0.67	0.29
Average June precipitation	0.02	0.89	0.28
Average minimum summer temperature	0.49	0.37	−0.17
Average maximum summer temperature	0.88	0.05	−0.14
Minimum summer temperature	−0.16	0.46	−0.32
Maximum summer temperature	0.84	−0.15	0.33
% morphological data explained by climate axes	26.5%	8.8%	7.1%
% climatic data explained by climate axes	35.4%	28.9%	7.3%

TABLE 10. Residuals for Dimensions 1 and 2 of Procrustean Analysis of Morphological and Climatic Principal Components (2 Axes of Each) Combined

Site	Residual	Site	Residual
Sable Island, NS	0.43	Grande Praire, AB	0.12
Parsons Pond, NF	0.01	Courval, SK	0.05
Bedeque, PEI	0.05	Kaministikwia, ON	0.07
River John, NS	0.03	Owens Lake, CA	0.22
St. Andrews, NB	0.08	Brandonville, WV	0.11
Matane, PQ	0.07	Woodruff, UT	0.12
Kuujjuaq, PQ	0.16	Creston, WA	0.12
Wildfield, ON	0.09	Hoquiam, WA	0.31
Wallaceburg, ON	0.15	Morro Bay, CA	0.06
Sowerby, ON	0.09	Humboldt Bay, CA	0.12
Cochrane, ON	0.05	Koyuk, AK	0.09
Moosonee, ON	0.03	Wasilla, AK	0.11
Attawapiskat, ON	0.02	Fairbanks, AK	0.07
Winisk, ON	0.17	Umnak Is, AK	0.29
Delta, MB	0.07	Port Heiden, AK	0.10
The Pas, MB	0.05	Cold Bay, AK	0.20
Gillam, MB	0.09	Middleton Is., AK	0.10
Churchill, MB	0.19	Magdalen Is., PQ	0.10
Coppermine, NU	0.30	Halleck, NV	0.05
Norman Wells, NT	0.07	Elberta, UT	0.13
Inuvik, NT	0.16	Sheridan, WY	0.06
Maple Creek, SK	0.04	Residual sum of squares:	0.93
Milk River, AB	0.07	Probability of Rejection:	0.0001

is negatively correlated with sternum length and positively correlated with keel length. To the degree that the same variables were used in the male and female analyses, the DF coefficients on the DF 1 axis are similar between the sexes. As with the males, DF 1 separates the bird from coastal Sonora and Sinaloa from those from coastal California, with the birds from Bahía Magdalena closer to the birds from Sinaloa and Sonora than to those from coastal California. DF 2 is positively correlated with tarsometatarsus, sternum, and premaxilla lengths, premaxilla depth, and negatively correlated with ulna length, synsacrum width, man-

TABLE 11. Standardized Canonical Discriminant Function Coefficients from a DFA of 8 Measurements of 153 Male Savannah Sparrows from 8 Saltmarsh Localities and 98 Female Savannah Sparrows from 7 Localities

	Males		Females	
Variable	DF 1	DF 2	DF 1	DF 2
Premaxilla depth	0.48	−0.34	0.42	0.43
Premaxilla width	0.22	−0.13	0.61	0.49
Mandible length	0.34	0.43	—	—
Mandible depth	0.54	−0.01	0.66	−0.51
Tibiotarsus length	0.27	0.58	—	—
Tarsometatarsus length	—	—	0.26	0.87
Ulna length	−0.11	−1.12	−0.12	−0.73
Sternum length	—	—	−0.40	0.84
Sternum depth	−0.17	0.38	—	—
Synsacrum width	−0.15	0.77	−0.10	−0.63
Eigenvalue	9.75	1.08	12.85	0.83
% variance explained	84.9%	9.5%	87.20%	5.66%
Canonical Correlation	0.95	0.72	0.96	0.67

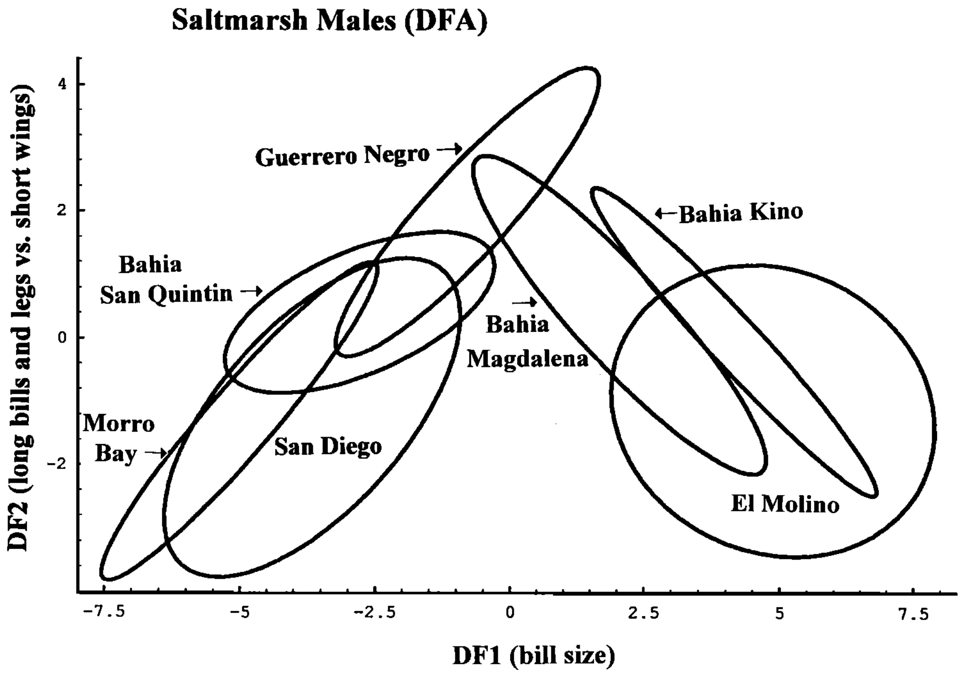

FIGURE 21. Samples of male Savannah Sparrows from coastal saltmarsh sites (95% confidence ellipses) in the space defined by DF 1 and DF 2. DF 1 explains 84.9% of the total variance and contrasts bill size and leg length with measures of wing size. DF 2 explains an additional 9.5% of the variance, and contrasts ulna length and premaxilla depth with leg length, sternum depth, and synsacrum width.

dible depth, and keel length (Table 11). Females from Bahía Magdalena have the largest DF 2 scores, whereas those from Bahía San Quintin have the smallest. Overall, 86% of the females are correctly identified in this analysis. As with the males, misidentified individuals are generally grouped with those of a geographically adjacent sample. One female from Bahía Magdalena is clustered with the Bahía Kino sample; otherwise, none of the birds from California, Baja California are identified as belonging to a sample from Sonora or Sinaloa. One bird from El Molino is clustered with the females from Bahía Magdalena.

DISCUSSION

For the most part, the interpopulational variation in size of Savannah Sparrows is clinal. The most striking finding of this study is that Savannah Sparrows are large on islands. Case (1978) argued that, unless tightly constrained by other factors, we should expect large body size to evolve on islands because (1) islands usually contain fewer competitors as well as predators, so food availability for colonists would initially be expected to be high, and (2) intraspecific interactions for food would be relatively more important for island species than mainland ones, favoring individuals with relatively large body size. Additionally, larger individuals would be able to take advantage of a larger range of foods, and are thermally more efficient. Schoener (1969) found an inverse relationship between body size of *Anolis* and the number of species of *Anolis* (and other potentially competing lizards) on West Indian islands.

The largest Savannah Sparrows are from Sable Island, Nova Scotia, and the Aleutian Islands, Alaska. Although both are islands, these two areas are ecologically different in many ways. On Sable Island, the Savannah Sparrow is the only passerine bird that nests, whereas on the Aleutians, Lapland Longspurs (*Calcarius lapponicus*) as well as Savannah Sparrows are abundant, and seemingly found in the same habitat; Song Sparrows (*Melospiza melodia*) and Gray-crowned Rosy-finches (*Leucosticte tephrocotis*) also breed there, but generally in different habitat. The Song Sparrows and rosy-finches on the Aleutians also have notably large body size (J. D. Rising, pers. obs.). Thus, one site is sparrow poor and the other relatively sparrow rich. Savannah Sparrows are also relatively large on the Magdalen Islands, Quebec, and on Middleton Island, Alaska. On the Magdalen Islands, Nelson's Sharp-tailed Sparrows (*Ammodramus nelsoni*) and Swamp Sparrows (*M. georgiana*) overlap Savannah Sparrows in habitat, and Song Sparrows are common as well. On Middleton Island, Fox Sparrows (*Passerella iliaca*) and Lapland Longspurs are both common, as are Savannah Sparrows. (Although I have not analyzed them here, the Savannah Sparrows from the Islas San Benito, Baja California, Mexico, are also large in size, and they are the only sparrow-like species that breeds on those islands.) Thus, while Savannah Sparrows do tend to be small where species diversity is highest (see discussion below), this alone does not appear to be an adequate explanation for their large body size on islands. One common feature of all of the islands on which Savannah Sparrows live is that they have long, cool, moist summers; this may result in a predictable and fairly rich food supply. On Sable Island, the length of the breeding season seems to permit them to be multi-brooded (commonly three or four broods in a season) and also polygynous (Stobo and McLaren 1975), perhaps leading to enhanced competition for high quality territories. This is apparently generally true for islands in the Maritimes (Wheelwright and Rising 1993). Either competition with conspecifics for food or territories seemingly selects for large body size on these islands.

Murphy (1938) noted that 78% of insular races of North American songbirds have larger bills than their mainland counterparts, and cites Savannah Sparrow (both from the Aleutian Islands and Sable Island) as among those species illustrating this trend. My results confirm this for Savannah Sparrows, but it would appear that the bills are large because the birds are large; the bills are not noticeably larger relative to body size.

Savannah Sparrows are also somewhat larger from the mainland at Halifax, Nova Scotia, than in other maritime sites. This may reflect gene flow from Sable Island as "Ipswich" sparrows are sometimes reported in the Halifax area mated to mainland birds, although I know of no proof that any of these "mixed" pairs have successfully fledged young (Stobo and McLaren 1975; I. A. McLaren, pers. comm.). Other maritime Savannah Sparrows are also relatively large, but not so large as the Halifax ones.

The correlation analyses show that Savannah Sparrows tend to be large where it is moist, and small where it is hot and dry. They are also smallest in the west and at high elevations, and large where they coexist with few other sparrow-like birds. These trends are true even with the samples of the largest birds removed from the analyses. The significant negative relationship between body size and species diversity supports hypotheses that relate body size with interspecific competition. Overall, there is no significant relationship between body size and latitude, and although they tend to be small where maximum summer temperatures are highest, the species does not seem to follow the trend described by Bergmann's Rule. Although the Bergmann trend is shown by many species that are migratory (James 1970), it is less prevalent among these than among sedentary species (Zink and Remsen 1986).

There is clinal variation in size eastward from the Aleutian Islands down the Alaska Peninsula, with the birds at the tip of the Peninsula (Cold Bay) being nearly as large as those from the Aleutians, and those from Port Heiden, midway down the Peninsula, being intermediate in size between the larger birds and those from the Alaskan mainland. This suggests that there is selection for large birds on the Aleutians and probably also on the Alaskan Peninsula, and selection for smaller birds on the mainland, and gene flow among these populations.

Savannah Sparrows from the coastal saltmarshes of Sinaloa and Sonora also have large body sizes. They are the only sparrow-like birds that breed in these saltmarshes. They also have notably large bills. Fiddler-crabs (*Uca*) are abundant in these marshes, and stomach analyses reveal that the Savannah Sparrows there commonly eat *Uca,* at least during the breeding season (February–March; J. D. Rising, pers. obs.). The large bill would seem to facilitate handling these relatively large prey items. *Uca* are also abundant in the marshes around Bahía Magdalena where the sparrows are also large-billed.

Interpopulational variation in wing length is related to migratory status: sedentary populations or populations where only short-distance movement occurs have relatively short wings; those that presumably migrate the greatest distances have relatively long wings. The birds with the relatively longest wings are from the northern Great Plains and high elevations. Rising (1988) supplied indirect, phenetic, evidence that in fall migration, birds tend to move more or less south, so that birds that breed in the Maritimes and northeast probably generally winter in the southeastern United States, whereas those that breed in the Great Plains probably generally winter from central Texas and California south into Mexico. A sparrow migrating from Coppermine in the northern Northwest Territories (near the northern-most part of their range in the western arctic) to northern Mexico would fly at least 4000 km, whereas one flying from Kuujjuaq in northern Quebec (near the northern-most part of their range in the eastern arctic) to northern Florida would fly about 3000 km. Banding data (although limited) do indicate that migratory movement is principally in a north to south direction (Brewer et al. 2000)

The arrangement of the two inland Mexican populations is somewhat surprising. Lerma, México, clusters with the samples from northeastern North America, and populations from Charco Redondo, Jalisco, with birds from the Northwest Territories. These two sites, however, are quite different ecologically; Lerma is higher in elevation and considerably more mesic than Charco Redondo. The separation between these two samples is on the PC 1 axis (Fig. 3); that is, the birds differ in size, but not shape. The sample collected at Charco Redondo was collected 7–8 May, and may have contained some migratory birds, although that is unlikely as many of the males were singing and had recrudescing testes, and all had little fat. The sample from Lerma was collected on 11 May, and the condition of the birds was similar to that of the birds from Charco Redondo.

My results confirm that there is an east to west trend in bill size, with western birds tending to have more slender bills than eastern ones. There is, however, a tremendous amount of overlap among populations, and the total range of variation is slight.

There is also clinal variation in both body size and bill size among the populations in saltmarshes along the Pacific Coast, from Morro Bay, San Luis Obispo County, California, south to Bahía Magdalena, Baja California Sur, with the birds from Morro Bay and San Diego being the smallest, with relatively gracile bills, and those from Bahía Magdalena being the largest, with stout bills. The latter birds are intermediate in size and shape between the birds from Guerrero Negro and those from along the coast of the Gulf of California in Sonora and Sinaloa.

CONCLUSIONS

Savannah Sparrows show clinal variation in size, with birds from the northeast being slightly larger than those from the west. Additionally, they are strikingly larger on islands than from mainland sites. This is not obviously related to species diversity as the diversity of sparrows is high on some islands, and low on others. I speculate that the rather long breeding season and predictability of the weather select for individuals to be multibrooded, and this, in turn, may select for large body size. Savannah Sparrows tend to be larger in cool, moist areas, and small where it is hot and dry. They also tend to be smallest where they co-occur with several other sparrow species. They do not follow Bergmann's Rule. In general, measures of the climatic environment (summer temperature, precipitation) explain well patterns of morphological size variation.

Bill proportions vary subtly, with birds from the northeast having bills that average slightly more conical than those from the west.

Savannah Sparrows from isolated saltmarshes in California, Baja California, and coastal Sonora and Sinaloa show a great deal of interpopulational variation, with a clinal increase in body size from north to south along the Pacific Coast, and to a lesser extent along the east coast of the Gulf of California. Relative to other Savannah Sparrows, they have short wings and large bills, with the birds from the Gulf coast having the largest bills. As with body size, there is clinal variation with regard to these features, with an increase in bill size relative to body size from north to south along the Pacific Coast.

TAXONOMIC COMMENTS

Sixteen subspecies of Savannah Sparrows were recognized in the 5th edition of the AOU Check-list of North American Birds (AOU 1957). In addition, they treated the Ipswich Sparrow as a separate species, *Passerculus princeps.* More recently, *P. princeps* has been treated as a subspecies (AOU 1998), *P. s. princeps,* bringing the number of subspecies recognized to 17. These subspecies were described on the basis of a variety of attributes relating to size, shape, and coloration.

Philosophically, I do not see much value in delimiting subspecies on the basis of clinal variation, unless there are well-defined steps in the clines. Chopping clinal variation into subspecies results in more or less arbitrarily delimiting overlapping groups on a phenetic continuum. I see no virtue in naming subspecies when the only way they can be reliably separated is on the basis of locality. Trying to identify to subspecies migratory and wintering individuals of such subspecies is problematic and leads to circularity.

EASTERN SAVANNAH SPARROWS

Four subspecies of eastern Savannah Sparrows are generally recognized: *P. s. princeps,* which breeds on Sable Island, Nova Scotia, and winters along the Atlantic coast; *P. s. labradorius,* which breeds in Labrador, Newfoundland, and northern Quebec; *P. s. oblitus,* which breeds in northern Ontario west to eastern Keewatin; and *P. s. savanna,* which breeds south of *P. s. labradorius* and *P. s. oblitus.* Aldrich (1940) split *P. s. savanna* into *P. s. savanna* and *P. s. mediogriseus,* restricting the range of the former to Nova Scotia; *P. s. mediogriseus* was not recognized in the AOU Check-list (AOU 1957).

P. s. princeps are significantly larger than any other eastern Savannah Sparrows (Fig. 4); these birds are also noticeably more pallid in color than other Savannah Sparrows (J. D. Rising, pers. obs.).

P. s. labradorius was described by Howe (in Todd 1963) because of its supposed larger size on the basis of only three specimens from Labrador. The distinctiveness of *P. s. labradorius* was debated for some years until Austin (1932), on the basis of 18 adult specimens from Labrador, concluded that *P. s. labradorius* was both larger and darker than *P. s. savanna,* although his assessment of size appears to have been qualitative. Peters and Griscom (1938:452) examined over 150 specimens of this subspecies and upheld its validity as "A dark Savannah Sparrow with relatively stout bill, its depth more than half the length of the culmen." However, they examined only 30 birds from Newfoundland and Labrador, the rest being migrating or wintering birds. Todd (1963) noted that birds from the interior of Labrador are also, on average, dark as are those from the James Bay and Hudson Bay lowlands, and he extended the range of *P. s. labradorius* westward to Churchill, the type locality of *P. s. oblitus,* a subspecies named by Peters and Griscom in 1938 as a "... gray Savannah Sparrow with relatively stout bill, its depth more than half the length of the culmen ... [S]imilar ... to *P. s. labradorius* ..., but the browns much paler and reduced in area" (Peters and Griscom 1938:455). Todd (1963:673–674), on comparing series from Churchill and the Labrador Peninsula, commented that "the general more grayish tone of the upperparts [of the birds from Churchill], as against the more brownish appearance in the latter series [from Labrador] is apparent, but it is quite possible to select specimens from one series which resemble some in the other." *P. s. savanna* is said to be a "brown Savannah Sparrow with relatively stout bill; its depth equal to or exceeding half the length of the culmen. Similar to *P. s. oblitus* ... but browner throughout" (Peters and Griscom 1938:450).

My analyses show that there is clinal variation in size, with a decrease from east to west; birds from Churchill, southern Ontario, and West Virginia are significantly smaller than those from the northeast, but there is a great deal of overlap of individuals from different samples (Figs. 6 and 9). My measures of bill size are based on skeletal features (Appendices 1 and 2), and thus are not comparable to those used by Peters and Griscom (1938). The ratio of premaxilla length to premaxilla depth for birds from the northeast range from 1.7 to 1.8. The bill proportions of the sample from Kuujjuaq, in Labrador, is 1.8; that from Churchill

1.7. Although no one (including myself) has published a quantitative analysis of color variation (J. D. Rising, in prep.), my studied opinion supports that of Todd (1963), namely that there is subtle clinal variation in color, but that intrapopulational variation is great, obfuscating even the clines. Thus, there seems to be little to support any of these eastern subspecies except for *P. s. princeps,* which is distinctive

WESTERN SAVANNAH SPARROWS

Other than the Savannah Sparrows that breed in coastal saltmarshes, six subspecies of western Savannah Sparrows are generally recognized. *P. s. sandwichensis* breeds in the Aleutian Islands and the western Alaskan Peninsula. *P. s. anthinus* breeds from the base of the Alaskan Peninsula east across Canada to Nunavut, and south to central Saskatchewan and Alberta. These are replaced to the south by *P. s. nevadensis* of the northern and central Great Plains and the Great Basin, south to central New Mexico and Arizona (Hubbard 1974). *P. s. brooksi* breeds on Vancouver Island, along the southwestern coast of British Columbia, south through western Washington to northwestern California. *P. s. brunnescens* (= *P. s. rufofuscus*; Hubbard 1974) breeds on the Central Plateau of Mexico. *P. s. wetmorei* is known only from the type series of five birds, which were collected in Guatemala in 1897; I have not seen these birds, and no one has reported Savannah Sparrows from Guatemala since 1897.

P. s. sandwichensis is nearly as large in size as *P. s. princeps* from which it differs on both the PC2 and DF2 axes (Figs. 2 and 4), as well in coloration, which is like that of other "typical" Savannah Sparrows. There is clinal variation on the Peninsula with the largest birds at the western tip (Cold Bay), and birds from Port Heiden intermediate in size between *P. s. sandwichensis* and *P. s. anthinus.* Birds from Middleton Island, Alaska, are also large, and probably best placed in *P. s. sandwichensis. P. s. sandwichensis* are said to be slender-billed, with the ". . . depth at base about one-half the length of the culmen" (Peters and Griscom 1938). The ratio of premaxilla length to premaxilla depth of birds from Umnak Island is 1.7; that of birds from Cold Bay 1.7; that of birds from Port Heiden 1.8; that of birds from Middleton Island 1.7; and that of birds from Wasilla (*P. s. anthinus* from near Anchorage) 1.8. Thus, there is little justification for separating these two subspecies on bill shape, but the size difference is considerable.

Peters and Griscom (1938:461) characterize *P. s. brooksi* as being "Smallest of the races . . . ; bill intermediate between the stout-billed and slender billed forms; depth of bill averaging just about one-half of length of culmen." My sample from Hoquiam, in western Washington (which on geographical grounds would be *P. s. brooksi*), certainly is not one of notably small-sized Savannah Sparrows, the birds from the Great Plains and Great Basin being the smallest (Figs. 7 and 10). The premaxilla length to depth ratio of this sample is 1.6; that of the sample from Eureka, northwestern California is 1.7, again not indicating a different bill shape. Peters and Griscom (1938:461) write, "In spring general coloration nearest *nevadensis,* averaging very slightly browner . . . ," that is, the supposed differences in coloration are slight. Also, spring birds may well be migrants of unknown breeding provenance.

P. s. nevadensis is a pale gray Savannah Sparrow, paler than *P. s. anthinus,* and with less streaking below. The yellow supercilium is frequently pale. They are said to be relatively slender billed (Peters and Griscom 1938), but in this group, as with others, variation in bill shape is slight. Hubbard (1974) places the birds from the southwestern United States in *P. s. nevadensis.*

According to Hubbard (1974) *P. s. brunnescens* do not differ mensurally from *P. s. nevadensis* and in my analyses the sample from Charco Redondo, Jalisco, is close to birds from the Canadian north (*P. s. anthinus*) and the sample from Lerma, México, with birds from the northeast (*P. s. savanna*). Savannah Sparrows from the interior of Mexico are said to be reddish brown in upperpart color and streaking, compared to the grayer and duller birds from the southwest United States (Hubbard 1974); to my eye, the difference is slight.

SALTMARSH SAVANNAH SPARROWS

The nine subspecies of saltmarsh Savannah Sparrows all seem to be clearly separable; here I have examined material for seven of these.

P. s. alaudinus breeds from Humboldt Bay south to Morro Bay, in California. *P. s. beldingi* breeds from Santa Barbara south to northwestern Baja California; my samples from San Diego and Bahía San Quintin, on geographic grounds, belong to this subspecies. Phenetically, the birds from Morro Bay are intermediate between the birds from Humboldt Bay (Eureka) and San Diego, which are, in turn, intermediate between Morro Bay and Bahía San Quintin. The birds that I collected at Humboldt Bay, although from along the coast, were not in a saltmarsh, whereas all birds I collected and examined from along the coast south of there were. I am inclined to place the birds from Morro Bay in the same subspecies as the birds from San Diego and Bahía San Quintin as they all overlap in the discriminant functions analysis (Fig. 21). In the San Francisco Bay area there are populations that do breed in saltmarsh habitats (Mailliard 1916, 1917; Squires 1916; J. D. Rising, pers. obs.), but there also are birds in non-saltmarsh habitats. Apparently, the birds in these two habitats are very similar in appearance, although the upland individuals may be lighter in coloration; I have not examined material from the San Francisco area.

P. s. annulus breed in the marshes around Bahía Viscaíno, where my Guerrero Negro sample was collected; these are phenetically intermediate between the birds from Bahía San Quintin and those from Bahía Magdalena, where *P. s. magdalenae* breed. Bahía Magdalena is the southern-most place on the coast of Baja California where Savannah Sparrows breed. I have not rigorously examined material from Laguna San Ignacio, where *P. s. guttatus* are resident, but I have seen them in the field and they appear to be very like *P. s. annulus,* as Van Rossem (1947) asserts. The birds from the Islas San Benito where *P. s. sanctorum* are resident are quite distinctive.

From north to south along the coast there is clinal variation in bill size (Appendices 1 and 2): premaxilla length of males increases from 5.7 mm at Humboldt Bay, which is like the bill size of typical Savannah Sparrows, to 7.1 mm at Bahía Magdalena. The length of the bill relative to its depth (premaxilla) also increases from north to south, with the premaxilla length/premaxilla depth ratio being 1.7 at Humboldt Bay, typical for the species, and 1.9 at Bahía San Quintin and Guerrero Negro. It is 1.8 at Bahía Magdalena.

The samples from Bahía Kino, Sonora, and El Molino, Sinaloa, represent *P. s. atratus.* These are darker in coloration than *P. s. rostratus* from the coast of northwestern Sonora; I measured a sample from Puerto Peñasco, Sonora, which is not included in the figures as I have only nine male and four female specimens. On the basis of my specimens, these have somewhat smaller bills than *P. s. atratus*. I feel that we should defer changing the taxonomy of the saltmarsh Savannah Sparrows until additional information is available.

In conclusion, I see no justification in retaining either *P. s. oblitus* or *P. s. brooksi*. Careful field work along the coast of northern California is needed to clarify the status of the saltmarsh birds there. Many of the other subspecies are poorly differentiated, and all of the geographic variation among the non-saltmarsh localities is clinal. A careful analysis of plumage variation in needed. I suspect that it will appear reasonable to recognize only three subspecies of non-saltmarsh Savannah Sparrows, *P. s. sandwichensis* (large size), *P. s. savanna* (typical Savannah Sparrows), and *P. s. princeps* (large and pallid). However, because *P. s. sandwichensis* merges clinally into *P. s. savanna* (as defined above), I would prefer to recognize only two subspecies of non-saltmarsh Savannah Sparrows, *P. s. sandwichensis* and *P. s. princeps*. As mentioned in the introduction, a preliminary study (Zink et al. 1991) suggests that the large-billed Savannah Sparrows (*P. S. rostratus*) may be specifically distinct; the same may be true for "Belding's" sparrows. Biochemical studies (J. D. Rising and R. M. Zink, in prep.) of the typical Savannah Sparrows may help us better understand the relationships among the populations.

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APPENDIX 1. MEASUREMENTS (IN MM) AND SAMPLE STATISTICS FOR MALE SAVANNAH SPARROWS (*Ammodramus sandwichensis*)

	Skull length				Skull width				Premaxilla length				Premaxilla depth			
Locality	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.
Sable Is., N.S.	29.7	23	28.4–31.0	0.61	15.2	24	14.3–15.7	0.31	6.4	23	5.6–7.0	0.34	3.8	24	3.5–4.0	0.13
Halifax, N.S.	27.7	10	27.1–28.8	0.53	14.5	10	14.1–14.9	0.27	5.9	12	5.3–6.4	0.38	3.5	12	3.4–3.6	0.09
River John, N.S.	27.6	29	26.2–28.4	0.57	14.4	31	13.8–15.0	0.36	5.8	31	5.2–6.5	0.36	3.5	29	3.2–3.6	0.12
Pasadena, NFLD	27.9	11	27.3–28.7	0.49	14.5	12	14.2–14.8	0.20	5.9	12	5.2–6.5	0.37	3.5	12	3.3–3.6	0.11
Parson's Pond, NFLD	27.7	13	26.8–28.2	0.41	14.5	13	14.0–15.1	0.33	5.8	13	5.5–6.2	0.23	3.5	13	3.4–3.8	0.13
Bedeque, P.E.I.	25.6	26	26.7–28.8	0.60	14.3	27	13.6–15.1	0.31	5.8	26	5.4–6.5	0.30	3.5	26	3.2–3.7	0.13
St. Andrews, N.B.	27.7	21	26.5–28.7	0.64	14.4	24	13.7–14.8	0.26	6.0	21	5.2–6.7	0.49	3.5	21	3.2–3.9	0.16
Matane, QUE	27.6	28	26.8–28.5	0.47	14.4	28	14.0–14.8	0.26	5.8	29	5.2–6.5	0.31	3.5	29	3.2–3.9	0.13
Magdalen Is., QUE	27.9	27	27.0–29.0	0.41	14.5	29	14.0–14.8	0.20	6.1	27	5.2–6.6	0.30	3.6	29	3.4–3.9	0.10
Kuujjuaq, QUE	27.8	20	26.9–28.6	0.42	14.3	23	14.0–14.7	0.22	6.0	21	5.5–6.6	0.27	3.4	23	3.2–3.7	0.13
MA and eastern NY	27.6	10	26.9–28.2	0.38	14.3	11	14.0–14.7	0.20	5.7	10	5.3–5.9	0.21	3.4	10	3.3–3.6	0.11
Brandonville, WV	27.2	22	26.3–27.8	0.40	14.2	24	13.5–14.7	0.26	5.9	23	5.4–6.5	0.28	3.4	24	3.2–3.6	0.11
Wildfield, ON	27.6	41	27.0–28.5	0.41	14.3	41	13.9–14.7	0.20	5.8	41	5.2–6.8	0.33	3.5	43	3.1–3.7	0.13
Pickering, ON	27.3	14	26.6–28.1	0.46	14.3	15	14.1–14.9	0.20	5.8	14	5.3–6.2	0.28	3.4	15	3.1–3.6	0.17
Wallaceburg, ON	27.5	40	26.5–28.8	0.52	14.3	40	13.7–14.8	0.28	5.9	40	5.3–6.4	0.30	3.4	40	3.2–3.7	0.14
Sowerby, ON	27.4	24	26.5–28.0	0.43	14.2	24	13.7–14.7	0.24	5.8	24	5.4–6.2	0.23	3.4	25	3.3–3.7	0.12
Cochrane, ON	27.2	31	26.2–28.1	0.47	14.3	34	13.9–14.6	0.19	5.7	32	5.3–6.2	0.29	3.4	35	3.0–3.7	0.16
Moosonee, ON	27.4	43	26.2–28.3	0.49	14.4	48	13.6–15.0	0.28	5.9	46	5.3–6.4	0.29	3.4	49	3.2–3.7	0.11
Attawapiskat, ON	27.6	36	26.8–28.6	0.50	14.4	39	14.0–14.8	0.23	5.9	37	5.2–6.5	0.34	3.4	38	3.2–3.7	0.12
Winisk, ON	27.5	38	26.2–28.5	0.59	14.4	46	13.9–15.0	0.25	5.9	40	5.3–6.6	0.33	3.4	45	3.1–3.7	0.14
Thunder Bay, ON	27.5	16	26.2–28.6	0.67	14.3	16	13.7–14.9	0.31	5.7	16	4.7–6.3	0.41	3.3	16	3.1–3.6	0.15
Delta, MAN	26.8	38	25.4–28.3	0.53	13.9	39	13.2–14.5	0.28	5.6	38	4.9–6.1	0.29	3.4	39	3.0–3.7	0.17
The Pas, MAN	27.2	22	26.2–28.1	0.56	14.3	22	13.6–14.6	0.23	5.8	22	5.1–6.3	0.30	3.4	22	3.2–3.5	0.10
Gillam, MAN	27.7	18	26.6–28.5	0.56	14.5	19	13.8–15.5	0.35	5.8	18	5.3–6.3	0.24	3.4	19	3.2–3.7	0.12
Churchill, MAN	27.5	29	26.7–28.6	0.46	14.2	30	13.7–15.0	0.31	5.8	29	4.9–6.4	0.35	3.3	29	3.1–3.6	0.13
Coppermine, N.W.T.	27.5	26	26.3–28.8	0.65	14.2	28	13.8–14.7	0.25	5.9	26	5.2–6.6	0.31	3.4	26	3.1–3.7	0.14
Norman Wells, N.W.T.	27.5	20	26.9–28.2	0.38	14.2	22	13.7–14.5	0.23	5.6	20	5.2–6.1	0.25	3.4	22	3.2–3.6	0.13
Inuvik, N.W.T.	27.6	10	26.6–28.2	0.58	14.2	11	13.8–14.6	0.23	5.9	11	5.3–6.3	0.26	3.2	13	3.0–3.5	0.15
Whitehorse, Yukon T.	27.5	10	26.7–28.0	0.47	14.3	10	13.7–14.7	0.30	5.8	11	5.3–6.2	0.38	3.3	11	3.2–3.5	0.11
Maple Creek, SASK	26.7	20	25.7–27.7	0.54	13.9	23	13.4–14.6	0.28	5.6	20	4.9–6.2	0.31	3.4	24	3.0–3.8	0.16
Courval, SASK	27.0	13	26.4–27.5	0.36	14.0	14	13.6–14.5	0.26	5.7	13	5.2–6.0	0.28	3.4	14	3.1–3.5	0.11
Milk River, ALTA	26.7	29	25.5–28.2	0.55	13.9	29	13.6–14.4	0.24	5.7	28	4.9–6.2	0.29	3.4	29	3.1–3.7	0.15
Grande Prairie, ALTA	26.7	30	25.6–28.4	0.58	14.1	32	13.7–14.7	0.22	5.5	31	4.8–6.1	0.30	3.4	31	3.1–3.7	0.14
Koyuk, AK	27.2	15	26.2–27.8	0.52	14.1	15	13.8–14.3	0.17	5.5	15	5.1–6.0	0.26	3.1	15	2.9–3.5	0.17
Fairbanks, AK	27.2	20	26.6–28.2	0.40	14.1	20	13.8–14.5	0.19	5.6	20	5.1–6.1	0.27	3.3	21	3.0–3.5	0.14

APPENDIX 1. CONTINUED.

Locality	Skull length				Skull width				Premaxilla length				Premaxilla depth			
	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.
Wasilla, AK	27.4	27	26.8–28.1	0.39	14.3	27	13.8–14.6	0.20	5.7	27	5.3–6.2	0.23	3.2	27	3.0–3.4	0.11
Umnak Is., AK	29.7	29	28.7–30.9	0.53	15.4	30	14.5–16.4	0.43	6.7	29	6.0–7.2	0.32	3.9	29	3.7–4.1	0.12
Cold Bay, AK	29.4	12	28.5–30.2	0.52	15.1	15	14.7–15.7	0.27	6.6	12	6.1–7.1	0.31	3.9	15	3.7–4.2	0.14
Port Heiden, AK	28.4	12	26.8–29.1	0.63	14.6	16	14.2–15.0	0.24	6.3	12	5.6–6.7	0.32	3.6	16	3.4–3.9	0.17
Middleton Is., AK	28.9	29	27.8–29.9	0.63	14.9	29	14.5–15.8	0.27	6.5	29	5.9–7.0	0.26	3.8	29	3.5–4.1	0.14
Sheridan, WY	27.0	32	25.9–28.0	0.51	13.9	33	13.2–14.5	0.31	5.8	33	5.1–6.3	0.31	3.3	32	3.1–3.5	0.12
Woodruff, UT	26.9	46	25.6–27.9	0.49	14.0	48	13.5–14.5	0.24	5.6	46	5.0–6.3	0.34	3.3	48	2.9–3.5	0.12
Elberta, UT	26.7	18	25.7–27.5	0.51	13.9	19	13.4–14.1	0.20	5.6	19	5.0–6.1	0.30	3.3	17	3.1–3.5	0.13
Halleck, NV	26.7	26	25.2–27.8	0.55	13.9	29	13.2–14.2	0.26	5.7	29	5.9–6.4	0.31	3.2	29	2.9–3.5	0.15
Alamo, NV	26.3	6	25.8–26.7	0.33	13.7	6	13.2–14.1	0.34	5.4	6	5.0–5.7	0.25	3.2	6	3.0–3.4	0.14
Creston, WA	26.8	31	25.6–27.9	0.51	14.0	33	12.8–14.5	0.32	5.5	33	4.9–6.2	0.26	3.2	34	3.0–3.5	0.14
Hoquiam, WA	27.0	18	26.0–27.8	0.52	14.2	19	13.8–14.7	0.25	5.4	18	4.8–6.1	0.37	3.3	18	3.0–3.6	0.17
Owen's Lake, CA	26.4	16	24.8–27.4	0.63	14.0	20	12.8–14.2	0.36	5.5	19	5.2–5.9	0.22	3.2	20	2.8–3.4	0.15
Eureka, CA	27.5	25	26.5–28.3	0.50	14.4	25	13.9–14.8	0.22	5.7	25	4.9–6.4	0.36	3.4	26	3.2–3.8	0.15
Morro Bay, CA	27.4	17	26.3–28.2	0.65	14.1	17	13.8–14.6	0.22	5.8	17	5.0–6.7	0.44	3.3	17	3.1–3.5	0.10
San Diego, CA	27.7	19	26.3–28.7	0.58	14.2	19	13.8–14.5	0.21	6.1	19	5.6–6.8	0.33	3.5	20	3.2–3.8	0.17
Bahia San Quintin, B.C.N.	28.3	17	27.5–28.8	0.43	14.4	21	13.9–14.9	0.24	6.5	17	6.1–7.0	0.28	3.5	19	3.2–3.7	0.13
Guerrero Negro, B.C.S.	28.9	31	27.7–30.3	0.64	14.6	32	14.0–15.3	0.29	6.9	32	6.2–7.6	0.39	3.6	34	3.3–3.9	0.13
Bahia Magdalena, B.C.S.	29.4	15	28.2–30.3	0.66	14.7	15	14.4–15.3	0.26	7.1	15	6.4–7.5	0.37	3.9	15	3.5–4.2	0.21
Puerto Peñasco, Sonora	29.4	9	28.7–38.0	0.43	14.7	9	14.5–15.	0.19	7.2	9	6.7–8.0	0.40	4.0	9	3.8–4.2	0.11
Bahia Kino, Sonora	30.0	21	29.1–30.8	0.50	14.9	21	14.4–15.4	0.25	7.6	21	6.6–8.4	0.39	4.0	21	3.8–4.3	0.15
El Molino, Sinaloa	30.1	16	29.0–31.0	0.54	14.9	16	14.5–15.2	0.24	7.6	16	7.0–8.2	0.41	4.1	16	3.7–4.4	0.19
Charco Redondo, Jalisco	26.8	15	26.0–27.7	0.53	14.1	16	13.6–14.7	0.28	5.6	15	5.3–6.2	0.26	3.4	16	3.1–3.6	0.18
Lerma, México	27.4	20	26.7–28.6	0.51	14.4	21	14.0–14.8	0.20	5.8	20	5.4–6.5	0.30	3.5	21	3.3–3.8	0.15

APPENDIX 1. CONTINUED

Locality	Narial width				Premaxilla width				Inter-orbital width				Mandibular length			
	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.
Sable Is., N.S.	7.2	24	6.5–7.8	0.27	5.8	24	5.5–6.0	0.13	2.8	24	2.3–3.2	0.19	20.5	24	19.8–21.6	0.49
Halifax, N.S.	6.9	12	6.5–7.3	0.24	5.3	12	4.9–5.6	0.19	2.5	11	2.0–3.0	0.23	18.8	10	18.2–19.7	0.45
River John, N.S.	6.9	30	6.3–7.3	0.29	5.2	28	4.9–5.7	0.22	2.8	31	2.3–3.6	0.28	18.4	29	17.2–19.3	0.5
Pasadena, NFLD	6.9	11	6.6–7.4	0.26	5.4	12	5.0–5.6	0.22	2.7	11	2.5–3.1	0.19	18.9	10	18.3–19.5	0.45
Parson's Pond, NFLD	6.7	13	6.2–7.3	0.34	5.4	13	5.1–5.7	0.21	2.7	13	2.3–3.1	0.22	18.7	12	18.0–19.6	0.44
Bedeque, P.E.I.	6.8	26	6.4–7.5	0.24	5.2	26	4.9–5.5	0.20	2.7	27	2.2–3.1	0.22	18.5	25	17.2–19.5	0.58
St. Andrews, N.B.	6.8	24	6.5–7.3	0.23	5.3	21	5.0–5.6	0.18	2.7	24	2.3–3.0	0.21	18.8	19	17.6–19.7	0.50
Matane, QUE	6.8	29	6.3–7.3	0.22	5.3	29	4.9–5.7	0.17	2.5	29	2.1–2.9	0.18	18.6	27	17.4–19.2	0.24
Magdalen Is., QUE	6.8	29	6.3–7.5	0.31	5.3	29	5.0–5.6	0.18	2.7	29	2.4–3.2	0.19	19.0	28	18.2–19.6	0.39
Kuujjuaq, QUE	6.7	21	6.1–7.3	0.25	5.2	23	5.0–5.5	0.16	2.6	23	2.1–3.2	0.24	18.9	21	17.6–19.5	0.45
MA and eastern NY	6.7	11	6.1–7.1	0.30	5.2	10	4.7–5.7	0.30	2.8	11	2.5–3.0	0.16	18.7	10	18.0–19.5	0.46
Brandonville, WV	6.8	25	6.2–7.6	0.30	5.2	24	4.7–5.7	0.22	2.6	24	2.1–3.0	0.19	18.2	24	17.2–18.7	0.42
Wildfield, ON	6.8	42	6.2–7.3	0.28	5.2	42	4.8–5.7	0.21	2.7	43	2.4–3.2	0.21	18.4	40	17.3–19.1	0.40
Pickering, ON	6.8	15	6.3–7.3	0.32	5.2	15	4.9–5.5	0.19	2.7	15	2.4–3.0	0.23	18.5	13	17.8–19.3	0.44
Wallaceburg, ON	6.9	40	6.1–7.2	0.25	5.2	40	5.0–5.6	0.18	2.7	38	2.3–3.1	0.16	18.4	37	17.7–19.0	0.36
Sowerby, ON	6.7	25	6.2–7.1	0.22	5.2	25	4.8–5.6	0.17	2.6	25	2.3–2.9	0.18	18.4	24	17.6–19.1	0.40
Cochrane, ON	6.7	32	6.2–7.1	0.23	5.1	33	4.7–5.5	0.21	2.6	32	2.3–3.0	0.17	18.3	33	17.1–19.0	0.48
Moosonee, ON	6.8	49	6.2–7.3	0.25	5.2	49	4.6–5.6	0.22	2.7	50	2.3–3.1	0.22	18.4	43	17.3–19.5	0.47
Attawapiskat, ON	6.7	38	6.2–7.4	0.25	5.2	38	4.9–5.6	0.16	2.7	38	2.4–3.2	0.22	18.5	37	17.8–19.3	0.41
Winisk, ON	6.6	47	5.9–7.5	0.29	5.1	43	4.8–5.6	0.19	2.6	46	2.2–3.0	0.19	18.5	40	17.5–19.4	0.54
Thunder Bay, ON	6.7	16	6.3–7.1	0.24	5.2	16	4.9–5.6	0.20	2.6	16	2.2–3.0	0.24	18.5	15	17.3–19.4	0.63
Delta, MAN	6.6	39	6.0–7.2	0.26	5.1	39	4.8–5.5	0.16	2.5	39	2.2–3.0	0.19	18.0	38	17.0–18.8	0.45
The Pas, MAN	6.7	22	6.2–7.3	0.27	5.2	22	4.9–5.5	0.14	2.6	22	2.3–2.9	0.19	18.2	22	17.6–19.3	0.42
Gillam, MAN	6.6	19	6.3–7.2	0.25	5.3	19	5.0–5.6	0.18	2.5	19	2.2–2.8	0.16	18.5	18	17.4–19.5	0.59
Churchill, MAN	6.5	29	6.0–7.1	0.29	5.1	29	4.7–5.6	0.23	2.6	30	2.2–2.9	0.21	18.4	28	17.6–19.2	0.43
Coppermine, N.W.T.	6.3	28	5.6–7.1	0.33	4.9	27	4.5–5.3	0.18	2.4	28	1.9–2.8	0.24	18.5	23	17.7–19.9	0.56
Norman Wells, N.W.T.	6.6	22	6.1–7.1	0.25	5.0	21	4.8–5.3	0.14	2.5	22	2.1–2.7	0.16	18.4	21	17.6–19.1	0.42
Inuvik, N.W.T.	6.5	12	5.9–7.1	0.35	5.1	13	4.8–5.3	0.16	2.4	14	2.1–2.8	0.21	18.4	14	17.6–19.3	0.51
Whitehorse, Yukon T.	6.5	10	6.1–6.9	0.24	5.0	11	4.6–5.4	0.25	2.6	10	2.1–2.8	0.23	18.6	11	17.7–19.7	0.61
Maple Creek, SASK	6.6	23	6.0–7.2	0.31	5.1	24	4.8–5.5	0.19	2.5	24	2.3–3.0	0.21	17.9	24	16.9–18.7	0.45
Courval, SASK	6.5	14	6.0–7.1	0.33	5.2	13	4.9–5.7	0.22	2.5	14	2.2–2.8	0.18	18.0	13	17.3–18.4	0.38
Milk River, ALTA	6.5	29	5.9–7.0	0.29	5.0	29	4.7–5.5	0.19	2.5	29	2.2–2.9	0.67	17.9	26	17.3–18.7	0.36
Grande Prairie, ALTA	6.5	31	6.0–7.0	0.24	5.1	32	4.7–5.4	0.19	2.5	31	2.1–3.1	0.24	17.9	28	17.3–19.1	0.39
Koyuk, AK	6.4	13	6.1–6.9	0.22	4.9	15	4.6–5.1	0.15	2.4	15	2.2–2.6	0.14	18.3	15	17.6–18.9	0.34
Fairbanks, AK	6.5	21	6.0–7.0	0.27	5.1	21	4.8–6.1	0.27	2.4	21	2.0–2.7	0.18	18.1	21	16.9–19.0	0.47

APPENDIX 1. CONTINUED

Locality	Narial width				Premaxilla width				Inter-orbital width				Mandibular length			
	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.
Wasilla, AK	6.5	27	6.0–6.9	0.24	5.0	27	4.7–5.4	0.15	2.5	26	2.2–2.9	0.18	18.4	25	17.9–19.3	0.34
Umnak Is., AK	7.3	29	6.6–8.0	0.36	6.0	29	5.6–6.6	0.23	2.8	30	2.3–3.3	0.25	20.4	29	19.6–20.5	0.49
Cold Bay, AK	7.0	15	6.6–7.5	0.29	5.7	15	5.3–6.3	0.28	2.	15	2.3–3.0	0.22	20.0	14	19.1–21.3	0.66
Port Heiden, AK	6.8	16	6.3–7.3	0.29	5.3	15	5.0–5.6	0.15	2.6	16	2.1–3.0	0.22	19.3	14	18.3–19.9	0.42
Middleton Is., AK	6.9	29	6.6–7.4	0.23	5.5	29	5.2–5.7	0.14	2.8	29	2.4–3.1	0.19	19.9	28	18.9–20.8	0.48
Sheridan, WY	6.6	32	5.8–7.2	0.37	5.1	31	4.7–5.8	0.23	2.6	33	2.1–2.8	0.19	18.0	31	17.1–18.9	0.47
Woodruff, UT	6.6	48	6.1–7.1	0.22	4.9	48	4.5–5.3	0.19	2.6	48	2.1–3.1	0.25	18.0	47	17.0–19.1	0.46
Elberta, UT	6.5	18	5.7–7.0	0.30	4.9	19	4.4–5.3	0.24	2.6	19	2.3–2.8	0.17	17.7	17	16.3–18.2	0.56
Halleck, NV	6.4	30	5.8–6.8	0.28	4.9	28	4.3–5.4	0.27	2.5	30	2.0–2.9	0.22	17.7	28	16.7–18.7	0.54
Alamo, NV	6.3	6	6.0–6.5	0.19	4.9	6	4.5–5.3	0.30	2.4	6	2.3–2.5	0.08	17.5	4	16.8–18.0	0.55
Creston, WA	6.4	33	5.9–6.9	0.27	5.0	34	4.5–5.6	0.23	2.5	33	2.1–4.6	0.43	17.8	30	15.4–18.7	0.66
Hoquiam, WA	6.6	18	6.3–7.2	0.23	5.0	19	4.7–5.4	0.20	2.6	19	2.3–2.9	0.18	17.9	17	17.3–18.7	0.40
Owen's Lake, CA	6.4	19	5.9–7.0	0.29	4.9	19	4.7–5.3	0.17	2.5	20	2.0–3.0	0.28	17.7	18	17.2–18.6	0.39
Eureka, CA	6.7	25	6.1–7.4	0.28	5.2	26	4.8–5.6	0.17	2.5	26	2.1–2.9	0.23	18.5	26	17.5–19.4	0.41
Morro Bay, CA	6.3	17	6.0–6.6	0.19	5.2	16	4.9–5.5	0.15	2.6	17	2.3–2.9	0.16	18.6	17	17.4–19.2	0.52
San Diego, CA	6.5	20	5.7–6.9	0.27	5.2	20	4.9–5.6	0.19	2.6	20	2.2–2.9	0.19	18.9	19	18.1–19.9	0.55
Bahia San Quintin, B.C.N.	6.4	20	6.1–6.8	0.18	5.3	18	5.0–5.6	0.15	2.6	21	2.2–3.0	0.20	19.5	12	18.7–20.1	0.46
Guerrero Negro, B.C.S.	6.7	33	5.9–7.1	0.33	5.6	34	5.2–6.1	0.23	2.7	34	2.3–3.1	0.22	19.9	30	19.1–21.2	0.43
Bahia Magdalena, B.C.S.	7.2	15	6.7–7.7	0.31	5.8	15	5.3–6.2	0.24	2.8	15	2.4–3.3	0.23	20.3	11	19.1–21.1	0.55
Puerto Peñasco, Sonora	7.1	8	6.7–7.3	0.20	6.0	8	5.6–6.4	0.26	2.8	9	2.6–3.2	0.19	20.5	8	20.1–20.9	0.31
Bahia Kino, Sonora	7.1	21	6.0–7.6	0.34	6.0	19	5.7–6.3	0.15	3.0	21	2.5–3.5	0.24	20.9	19	20.0–21.6	0.41
El Molino, Sinaloa	7.3	16	6.8–7.8	0.27	5.9	16	5.6–6.5	0.26	3.1	16	2.7–3.4	0.21	21.0	15	20.0–21.5	0.42
Charco Redondo, Jalisco	6.7	16	6.2–7.2	0.25	5.1	16	4.7–5.4	0.21	2.7	15	2.5–2.9	0.12	17.9	14	17.0–18.7	0.43
Lerma, México	6.8	21	6.1–7.2	0.26	5.5	21	5.1–5.7	0.15	2.8	21	2.3–3.3	0.27	18.5	20	17.7–19.5	0.51

APPENDIX 1. CONTINUED

Locality	Gonys				Mandible depth				Coracoid length				Scapula length			
	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.
Sable Is., N.S.	5.5	24	4.7–6.3	0.34	2.1	22	1.9–2.3	0.09	18.9	24	17.9–19.7	0.48	21.8	20	20.4–23.4	0.66
Halifax, N.S.	5.1	10	4.5–5.6	0.33	1.9	11	1.8–2.0	0.08	18.0	12	17.3–18.5	0.37	20.4	12	19.3–21.0	0.52
River John, N.S.	4.9	30	4.2–5.3	0.29	2.0	28	1.8–2.1	0.07	17.5	31	16.2–18.6	0.55	20.1	31	18.9–21.9	0.77
Pasadena, NFLD	5.1	9	4.7–5.7	0.31	1.9	9	1.8–2.1	0.09	17.5	10	16.9–18.1	0.40	20.1	10	19.6–20.6	0.33
Parson's Pond, NFLD	5.1	13	4.6–5.6	0.29	1.9	13	1.8–2.1	0.10	17.7	13	16.9–18.4	0.49	20.3	13	19.0–21.1	0.61
Bedeque, P.E.I.	4.9	25	4.5–5.5	0.24	1.9	22	1.8–2.0	0.07	17.3	26	16.5–18.2	0.46	19.6	24	18.6–20.6	0.46
St. Andrews, N.B.	5.1	19	4.7–5.7	0.28	2.0	17	1.8–2.1	0.09	17.5	24	16.8–18.6	0.42	19.8	22	18.4–21.2	0.72
Matane, QUE	5.0	28	4.4–5.4	0.25	1.9	29	1.8–2.0	0.07	17.3	29	16.4–18.5	0.50	19.9	27	18.7–20.6	0.50
Magdalen Is., QUE	5.2	28	4.8–6.1	0.26	1.9	27	1.8–2.0	0.06	17.7	29	17.1–18.5	0.38	20.2	27	19.5–21.4	0.54
Kuujjuaq, QUE	5.2	21	4.6–5.7	0.27	1.9	22	1.8–2.0	0.08	17.6	22	17.1–18.5	0.47	20.0	21	19.1–21.1	0.52
MA and eastern NY	5.0	10	4.7–5.4	0.21	1.9	9	1.8–2.1	0.09	17.5	11	16.9–18.0	0.31	20.2	11	19.6–20.6	0.28
Brandonville, WV	4.7	24	4.2–5.1	0.23	1.9	24	1.7–2.1	0.10	17.2	25	16.4–17.9	0.46	19.7	25	18.7–20.7	0.55
Wildfield, ON	4.8	40	4.2–5.4	0.29	1.9	39	1.8–2.1	0.07	17.3	43	16.2–18.3	0.50	19.9	40	18.1–21.0	0.65
Pickering, ON	5.0	13	4.7–5.2	0.14	1.9	13	1.8–2.0	0.08	17.4	15	16.5–18.2	0.44	19.7	15	18.9–20.5	0.50
Wallaceburg, ON	4.9	36	4.4–5.4	0.26	1.9	38	1.8–2.2	0.09	17.4	39	16.7–18.3	0.40	19.9	40	18.5–20.8	0.48
Sowerby, ON	4.9	24	4.2–5.4	0.33	1.9	25	1.8–2.0	0.07	17.3	25	16.3–18.1	0.48	19.8	25	18.9–21.1	0.53
Cochrane, ON	4.9	33	4.4–5.4	0.23	1.9	31	1.6–2.0	0.09	17.3	34	16.6–18.1	0.37	19.9	33	19.0–21.1	0.47
Moosonee, ON	5.0	47	4.2–5.9	0.32	1.9	47	1.7–2.2	0.10	17.6	48	16.2–18.5	0.49	20.3	48	18.5–21.7	0.61
Attawapiskat, ON	5.1	37	4.5–5.7	0.31	1.9	38	1.7–2.0	0.08	17.7	38	17.0–18.5	0.39	20.2	38	19.1–20.0	0.50
Winisk, ON	5.0	42	4.2–5.5	0.29	1.9	42	1.7–2.0	0.07	17.6	46	16.9–18.7	0.41	20.2	44	19.1–21.2	0.54
Thunder Bay, ON	4.8	15	4.1–5.6	0.44	1.9	15	1.8–2.0	0.06	17.3	16	16.6–18.0	0.41	19.8	15	18.8–20.8	0.51
Delta, MAN	4.6	38	4.1–4.9	0.22	1.8	39	1.6–1.9	0.07	17.2	34	16.3–18.2	0.37	19.6	38	17.9–20.6	0.51
The Pas, MAN	4.8	22	4.4–5.3	0.25	1.8	21	1.7–1.9	0.07	17.1	22	16.6–17.8	0.36	19.4	21	17.9–20.9	0.68
Gillam, MAN	4.9	18	4.3–5.3	0.24	1.8	19	1.7–1.9	0.06	17.6	18	17.0–18.1	0.33	20.0	18	19.4–21.1	0.46
Churchill, MAN	4.8	29	4.2–5.4	0.29	1.8	27	1.7–2.0	0.06	17.4	29	16.5–18.3	0.38	19.9	28	18.7–21.1	0.58
Coppermine, N.W.T.	4.8	24	4.1–5.5	0.34	1.8	27	1.6–1.9	0.07	17.3	29	16.2–18.0	0.44	19.7	29	18.5–20.9	0.67
Norman Wells, N.W.T.	4.8	20	4.4–5.3	0.25	1.7	21	1.6–1.9	0.08	17.3	22	16.1–18.3	0.52	19.9	22	19.1–21.4	0.51
Inuvik, N.W.T.	4.7	13	4.0–5.5	0.45	1.8	11	1.6–1.9	0.09	17.1	13	16.1–17.9	0.49	19.9	14	19.0–20.7	0.52
Whitehorse, Yukon T.	5.0	11	4.5–5.7	0.37	1.8	11	1.7–1.9	0.06	17.4	9	16.7–18.1	0.50	19.9	10	18.8–20.8	0.70
Maple Creek, SASK	4.7	24	4.1–5.3	0.32	1.8	23	1.7–1.9	0.06	17.4	23	16.6–18.0	0.42	19.8	20	18.6–21.0	0.60
Courval, SASK	4.8	13	4.4–5.2	0.23	1.8	11	1.7–1.9	0.07	17.3	14	16.1–18.1	0.49	19.8	13	19.0–20.7	0.50
Milk River, ALTA	4.7	27	4.1–5.1	0.25	1.8	25	1.6–1.9	0.07	17.2	29	15.6–18.2	0.46	19.7	28	17.7–20.8	0.64
Grande Prairie, ALTA	4.6	30	4.0–5.2	0.31	1.7	31	1.6–1.9	0.08	17.2	31	16.5–18.1	0.43	19.8	31	18.7–20.9	0.54
Koyuk, AK	4.8	15	4.4–5.2	0.21	1.6	14	1.5–1.7	0.07	17.0	15	16.8–17.6	0.22	19.7	15	18.7–20.8	0.58
Fairbanks, AK	4.6	21	4.0–5.4	0.34	1.7	21	1.6–1.9	0.07	17.0	21	16.4–17.6	0.36	19.6	20	18.5–20.7	0.50

APPENDIX 1. CONTINUED

Locality	Gonys				Mandible depth				Coracoid length				Scapula length			
	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.
Wasilla, AK	4.7	25	4.2–5.0	0.24	1.7	25	1.6–1.8	0.05	17.4	27	16.5–18.2	0.41	20.0	26	19.0–21.0	0.59
Umnak Is., AK	5.8	25	5.2–6.4	0.33	2.1	29	1.9–2.3	0.11	18.8	30	18.0–19.8	0.40	21.6	29	20.1–22.7	0.59
Cold Bay, AK	5.5	14	4.4–6.1	0.45	2.0	15	1.9–2.2	0.10	18.6	15	17.9–19.7	0.49	21.5	15	20.6–22.7	0.65
Port Heiden, AK	5.3	14	4.5–5.8	0.30	1.9	12	1.8–2.0	0.07	17.8	16	17.2–18.5	0.37	20.6	16	19.9–21.7	0.57
Middleton Is., AK	5.5	27	5.0–6.0	0.32	2.0	27	1.8–2.1	0.09	18.2	29	17.8–18.8	0.28	21.0	29	20.3–22.1	0.46
Sheridan, WY	4.6	31	4.0–5.0	0.24	1.8	31	1.6–1.9	0.07	17.3	33	16.3–18.1	0.41	19.8	32	18.8–20.6	0.47
Woodruff, UT	4.6	47	4.1–5.1	0.26	1.8	44	1.6–2.0	0.10	17.3	48	16.2–18.0	0.42	19.8	48	18.6–21.1	0.56
Elberta, UT	4.5	17	4.1–4.8	0.20	1.7	17	1.6–1.8	0.07	17.2	18	16.1–17.8	0.39	19.6	18	18.2–20.2	0.52
Halleck, NV	4.4	28	3.9–5.0	0.27	1.7	28	1.5–1.8	0.09	17.2	30	16.2–18.3	0.45	19.8	28	18.0–21.1	0.65
Alamo, NV	4.4	4	4.0–4.9	0.39	1.7	4	1.6–1.8	0.10	16.8	6	16.3–17.5	0.41	19.0	6	18.7–20.8	1.11
Creston, WA	4.5	31	3.9–4.9	0.24	1.7	33	1.5–1.9	0.08	17.2	33	16.4–18.5	0.44	19.8	33	18.3–21.2	0.60
Hoquiam, WA	4.6	16	4.2–5.0	0.21	1.9	18	1.8–2.0	0.07	17.0	19	16.4–17.6	0.32	19.3	19	18.4–20.0	0.43
Owen's Lake, CA	4.7	19	4.3–5.0	0.24	1.7	19	1.6–1.8	0.07	17.1	20	16.1–17.8	0.48	19.5	20	18.3–20.7	0.66
Eureka, CA	4.7	25	4.2–5.2	0.31	1.9	25	1.7–2.0	0.09	17.2	26	16.7–18.1	0.33	19.7	26	18.5–20.7	0.59
Morro Bay, CA	4.9	17	4.3–5.5	0.37	1.8	16	1.6–2.0	0.11	16.9	17	16.5–17.5	0.31	19.3	17	18.5–20.0	0.47
San Diego, CA	5.1	19	4.5–5.7	0.30	1.9	20	1.7–2.0	0.09	16.9	20	15.8–17.5	0.37	18.9	18	18.0–19.6	0.40
Bahia San Quintin, B.C.N.	5.4	13	5.0–6.0	0.29	2.0	15	1.8–2.1	0.09	17.0	20	16.6–17.5	0.24	19.2	21	17.4–20.2	0.72
Guerrero Negro, B.C.S.	5.7	30	5.0–6.9	0.37	2.1	32	1.9–2.3	0.09	17.1	34	16.1–18.2	0.48	19.4	33	18.2–20.7	0.58
Bahia Magdalena, B.C.S.	5.8	11	5.4–6.4	0.29	2.2	13	2.1–2.4	0.09	17.5	15	16.7–18.6	0.47	19.7	15	18.9–21.1	0.61
Puerto Peñasco, Sonora	5.8	9	5.5–6.7	0.41	2.3	9	2.2–2.6	0.14	17.4	9	16.9–18.1	0.47	19.3	9	18.5–20.0	0.51
Bahia Kino, Sonora	6.1	19	5.6–6.8	0.30	2.5	18	2.1–2.6	0.13	17.6	21	16.9–18.4	0.44	19.7	21	19.0–20.4	0.44
El Molino, Sinaloa	6.1	16	5.6–6.7	0.30	2.4	16	2.3–2.6	0.10	17.5	16	16.9–18.1	0.30	19.7	15	18.4–20.6	0.74
Charco Redondo, Jalisco	4.7	14	4.4–5.0	0.21	1.8	12	1.7–1.9	0.06	17.2	16	16.4–18.5	0.48	19.4	16	17.2–21.0	0.92
Lerma, México	4.9	20	4.3–5.5	0.31	1.9	19	1.7–1.9	0.06	17.7	19	16.7–18.3	0.50	19.9	21	18.8–21.0	0.56

APPENDIX 1. CONTINUED

Locality	Femur length				Femur width				Tibiotarsus length				Tarsometatarsus length			
	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.
Sable Is., N.S.	19.1	23	18.2–20.1	0.48	1.4	24	1.3–1.5	0.06	31.7	23	30.3–32.7	0.70	22.8	24	21.9–24.0	0.60
Halifax, N.S.	17.7	12	17.3–18.5	0.34	1.3	12	1.2–1.4	0.05	30.0	11	29.4–30.6	0.41	21.7	11	21.4–22.2	0.28
River John, N.S.	17.6	28	16.4–18.6	0.45	1.3	31	1.2–1.5	0.07	29.1	28	27.2–30.8	0.94	20.9	29	19.3–22.0	0.71
Pasadena, NFLD	17.4	10	16.9–18.1	0.37	1.3	12	1.2–1.3	0.04	29.5	11	28.0–31.0	0.81	21.5	11	20.4–22.5	0.63
Parson's Pond, NFLD	17.7	12	16.9–18.8	0.55	1.3	13	1.1–1.3	0.07	29.5	12	28.0–13.1	0.84	21.6	13	21.6–22.4	0.49
Bedeque, P.E.I.	17.6	28	16.4–18.6	0.45	1.3	31	1.2–1.5	0.07	29.1	28	27.2–30.8	0.94	20.9	29	19.3–22.0	0.71
St. Andrews, N.B.	17.4	23	16.6–18.3	0.39	1.3	23	1.1–1.4	0.06	29.0	20	28.0–30.5	0.64	20.9	22	19.9–21.6	0.38
Matane, QUE	17.2	29	16.6–18.2	0.40	1.2	29	1.1–1.3	0.07	28.6	29	27.0–30.5	0.93	20.6	24	19.5–22.0	0.69
Magdalen Is., QUE	17.6	29	17.0–18.1	0.31	1.3	29	1.2–1.4	0.05	29.6	29	28.4–30.6	0.61	21.4	28	20.2–22.5	0.47
Kuujjuaq, QUE	17.5	22	16.7–18.3	0.37	1.3	23	1.2–1.5	0.07	29.1	22	28.1–30.7	0.67	21.0	20	20.1–22.0	0.54
MA and eastern NY	17.7	10	17.3–18.2	0.28	1.2	11	1.2–1.3	0.03	29.4	7	29.1–29.9	0.30	21.1	10	20.4–21.7	0.39
Brandonville, WV	17.1	25	16.4–17.8	0.41	1.2	25	1.1–1.3	0.07	28.6	23	26.5–29.7	0.70	20.5	24	18.7–21.5	0.65
Wildfield, ON	17.2	42	16.4–17.8	0.40	1.3	42	1.1–1.4	0.07	28.7	40	27.3–30.1	0.74	20.7	40	19.5–21.8	0.56
Pickering, ON	17.3	15	16.4–18.0	0.43	1.2	15	1.2–1.3	0.05	29.0	13	28.3–29.7	0.50	20.9	13	20.2–21.7	0.43
Wallaceburg, ON	17.3	38	16.1–18.3	0.40	1.3	41	1.1–1.4	0.07	28.8	38	24.7–30.2	0.69	20.6	38	19.6–22.1	0.59
Sowerby, ON	17.1	25	16.0–18.0	0.44	1.3	25	1.2–1.4	0.06	28.3	22	26.7–29.4	0.76	20.4	23	19.0–21.4	0.60
Cochrane, ON	17.1	35	16.2–17.8	0.36	1.3	35	1.1–1.4	0.06	28.4	28	26.5–29.9	0.82	20.5	31	19.1–21.7	0.58
Moosonee, ON	17.3	49	16.3–18.4	0.40	1.3	50	1.1–1.4	0.06	28.8	43	27.2–30.2	0.69	20.7	47	18.1–21.8	0.63
Attawapiskat, ON	17.4	38	16.4–18.3	0.38	1.3	39	1.2–1.4	0.07	28.6	35	27.1–30.5	0.66	20.8	37	19.5–21.9	0.56
Winisk, ON	17.3	45	16.4–18.8	0.46	1.3	47	1.1–1.4	0.06	28.6	43	27.2–29.8	0.71	20.5	37	19.2–21.7	0.68
Thunder Bay, ON	17.1	15	16.6–17.6	0.24	1.2	16	1.1–1.3	0.04	28.3	13	27.5–29.6	0.50	20.3	15	19.8–21.2	0.38
Delta, MAN	17.0	39	15.9–17.7	0.40	1.2	39	1.1–1.3	0.07	27.7	37	24.7–29.0	0.80	20.0	39	17.9–21.5	0.67
The Pas, MAN	17.1	22	16.3–18.0	0.37	1.3	22	1.1–1.4	0.08	27.9	20	26.8–29.3	0.72	20.0	21	19.0–21.2	0.59
Gillam, MAN	17.2	19	16.5–17.9	0.35	1.2	19	1.1–1.3	0.05	28.6	19	27.8–29.6	0.45	20.6	19	20.1–21.0	0.28
Churchill, MAN	17.2	28	16.7–17.8	0.28	1.3	30	1.2–1.4	0.06	28.5	26	27.2–29.6	0.54	20.5	27	19.5–21.5	0.51
Coppermine, N.W.T.	17.1	29	16.3–17.8	0.31	1.2	29	1.1–1.4	0.07	28.5	27	27.3–29.6	0.58	20.5	27	19.5–21.4	0.49
Norman Wells, N.W.T.	17.0	21	16.4–17.8	0.43	1.2	22	1.1–1.3	0.06	28.5	21	27.5–30.1	0.74	20.4	21	19.6–21.7	0.60
Inuvik, N.W.T.	16.8	14	16.1–17.5	0.43	1.2	14	1.1–1.3	0.06	28.0	13	26.6–29.4	0.92	19.8	14	18.6–21.3	0.85
Whitehorse, Yukon T.	17.2	11	16.7–17.6	0.29	1.3	11	1.2–1.4	0.09	28.5	9	27.9–29.5	0.63	20.8	11	19.9–21.7	0.52
Maple Creek, SASK	17.1	22	16.4–17.8	0.34	1.3	24	1.2–1.4	0.06	27.9	22	26.2–29.7	0.77	20.1	24	18.9–21.3	0.57
Courval, SASK	17.1	14	16.4–17.7	0.44	1.3	14	1.2–1.3	0.05	28.1	12	26.0–29.1	0.87	20.2	12	18.5–21.2	0.76
Milk River, ALTA	16.9	28	16.4–17.8	0.35	1.2	29	1.1–1.4	0.08	27.5	23	26.0–29.1	0.62	20.0	27	18.3–21.1	0.65
Grande Prairie, ALTA	16.9	31	16.1–17.9	0.45	1.2	32	1.1–1.3	0.05	27.6	26	26.5–29.0	0.75	19.9	28	18.7–21.3	0.62
Koyuk, AK	16.8	15	16.1–17.3	0.36	1.2	15	1.1–1.2	0.04	28.1	15	27.3–28.8	0.45	20.3	15	19.5–20.9	0.43
Fairbanks, AK	16.7	21	15.9–17.3	0.37	1.2	21	1.1–1.3	0.06	28.0	21	26.6–29.1	0.71	20.1	18	19.1–21.6	0.62

APPENDIX 1. CONTINUED

Locality	Femur length				Femur width				Tibiotarsus length				Tarsometatarsus length			
	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.
Wasilla, AK	16.9	27	16.1–17.8	0.41	1.2	27	1.1–1.3	0.06	28.2	24	26.9–29.3	0.63	20.3	24	19.2–21.1	0.46
Umnak Is., AK	18.5	29	17.4–19.0	0.36	1.4	30	1.3–1.5	0.06	30.8	29	29.2–32.2	0.75	22.3	30	21.2–23.2	0.48
Cold Bay, AK	18.2	15	17.6–18.9	0.41	1.3	15	1.2–1.5	0.09	30.7	13	29.5–31.6	0.63	22.1	14	21.4–23.0	0.50
Port Heiden, AK	17.6	16	17.1–18.5	0.42	1.3	16	1.2–1.4	0.08	29.6	16	28.8–31.0	0.63	21.4	16	20.6–22.8	0.65
Middleton Is., AK	17.8	29	17.1–18.5	0.36	1.4	29	1.3–1.5	0.06	29.8	28	28.6–31.5	0.61	21.7	28	20.9–23.5	0.69
Sheridan, WY	17.1	32	16.1–18.0	0.43	1.2	33	1.1–1.3	0.06	27.8	32	26.3–29.2	0.70	20.0	32	19.0–21.3	0.55
Woodruff, UT	17.2	46	15.5–17.8	0.45	1.3	48	1.2–1.4	0.06	28.0	47	25.3–29.5	0.77	20.2	47	18.4–21.6	0.69
Elberta, UT	17.0	18	15.8–17.5	0.46	1.2	18	1.2–1.3	0.05	27.8	16	26.4–29.0	0.71	20.1	18	18.4–21.0	0.65
Halleck, NV	17.1	29	15.9–18.2	0.50	1.2	29	1.1–1.4	0.06	28.0	27	25.4–29.1	0.80	20.2	30	18.0–21.3	0.62
Alamo, NV	16.7	6	15.6–17.6	0.70	1.2	6	1.2–1.3	0.04	27.2	6	25.2–28.4	1.22	19.5	6	18.1–21.4	0.84
Creston, WA	17.0	34	16.4–17.8	0.34	1.2	34	1.1–1.4	0.07	27.8	33	26.4–28.7	0.59	19.9	33	19.0–20.8	0.48
Hoquiam, WA	16.8	19	16.2–17.4	0.33	1.3	19	1.2–1.4	0.70	27.9	19	27.2–28.5	0.39	20.3	17	19.5–21.2	0.49
Owen's Lake, CA	17.1	20	16.2–17.8	0.52	1.2	20	1.1–1.4	0.08	27.9	19	26.7–30.3	0.90	20.3	17	19.0–22.0	0.68
Eureka, CA	17.4	26	16.2–18.1	0.44	1.2	26	1.1–1.3	0.62	28.5	26	27.8–29.7	0.47	20.5	26	19.7–21.4	0.43
Morro Bay, CA	17.1	17	16.6–17.6	0.26	1.2	17	1.1–1.3	0.06	28.3	15	27.5–29.0	0.44	20.3	15	19.7–21.0	0.46
San Diego, CA	17.0	19	16.3–17.6	0.41	1.2	20	1.1–1.3	0.05	28.4	19	26.9–29.6	0.78	20.3	18	19.1–21.0	0.53
Bahia San Quintin, B.C.N.	17.2	19	16.8–18.3	0.35	1.2	21	1.1–1.2	0.05	28.5	19	27.5–29.5	0.56	20.6	21	19.8–21.5	0.50
Guerrero Negro, B.C.S.	17.7	34	16.6–18.6	0.44	1.2	34	1.1–1.4	0.07	29.7	33	27.4–31.9	0.85	21.3	33	19.8–22.5	0.59
Bahia Magdalena, B.C.S.	18.2	15	17.5–19.4	0.47	1.2	15	1.1–1.3	0.07	30.4	15	29.1–32.0	0.81	21.9	15	20.8–23.2	0.80
Puerto Peñasco, Sonora	17.9	9	17.3–18.6	0.41	1.3	9	1.2–1.3	0.05	30.2	8	29.5–30.9	0.54	21.9	9	21.3–22.6	0.39
Bahia Kino, Sonora	18.1	21	17.4–18.8	0.37	1.3	21	1.2–1.3	0.05	30.3	19	28.8–32.2	0.88	21.9	19	20.7–22.9	0.65
El Molino, Sinaloa	18.3	16	17.6–19.3	0.41	1.3	16	1.1–1.4	0.07	30.7	16	29.7–31.8	0.63	22.1	16	21.2–22.9	0.47
Charco Redondo, Jalisco	17.3	16	16.4–18.0	0.47	1.2	16	1.1–1.3	0.05	28.3	14	27.4–29.4	0.60	20.9	15	20.0–21.8	0.61
Lerma, México	17.7	21	17.1–18.3	0.41	1.3	21	1.2–1.4	0.06	28.9	20	27.5–30.0	0.67	21.2	21	19.6–22.4	0.67

APPENDIX 1. CONTINUED

Locality	Humerus length				Ulna length				Carpometacarpus length				Hallux length			
	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.
Sable Is., N.S.	20.3	24	19.2–21.2	0.50	23.5	23	22.3–24.3	0.58	13.1	22	12.0–13.8	0.40	9.5	23	8.9–10.2	0.37
Halifax, N.S.	19.0	11	18.5–19.4	0.30	22.1	12	21.6–22.4	0.27	12.1	12	11.7–12.5	0.24	8.5	11	8.0–8.8	0.24
River John, N.S.	18.7	30	17.3–19.7	0.60	21.7	30	20.2–22.6	0.66	11.9	27	11.3–12.4	0.33	8.5	27	7.6–9.2	0.35
Pasadena, NFLD	18.5	12	18.0–19.1	0.27	21.6	12	21.0–22.1	0.28	12.0	11	11.8–12.3	0.17	8.7	10	8.1–9.2	0.40
Parson's Pond, NFLD	18.9	13	18.1–19.3	0.37	22.0	13	20.7–22.6	0.58	12.1	13	11.5–12.7	0.37	8.7	12	8.1–9.4	0.34
Bedeque, P.E.I.	18.6	23	17.9–19.4	0.36	21.6	26	20.9–22.4	0.45	11.8	23	11.0–12.5	0.33	8.3	23	7.4–9.2	0.43
St. Andrews, N.B.	18.7	24	18.1–19.8	0.41	21.7	22	21.1–22.3	0.36	11.9	22	11.4–12.4	0.26	8.3	24	7.8–8.6	0.21
Matane, QUE	18.5	29	17.8–19.5	0.40	21.5	28	20.7–23.1	0.49	11.8	22	11.1–12.6	0.32	8.3	28	7.7–9.0	0.32
Magdalen Is., QUE	18.8	28	18.2–19.7	0.37	21.8	29	21.1–22.6	0.39	12.1	26	11.5–12.6	0.26	8.6	29	8.1–9.1	0.26
Kuujjuaq, QUE	18.8	21	17.9–19.6	0.46	21.9	23	21.2–22.8	0.50	12.1	21	11.0–12.6	0.41	8.2	21	7.6–8.7	0.34
MA and eastern NY	18.8	11	18.2–19.1	0.29	21.9	8	21.4–22.3	0.31	12.0	11	11.4–12.7	0.33	8.4	10	8.1–8.7	0.19
Brandonville, WV	18.3	25	17.5–18.9	0.38	21.4	25	20.5–22.1	0.42	11.7	23	11.1–12.1	0.28	8.2	23	7.4–9.0	0.32
Wildfield, ON	18.5	41	17.6–19.6	0.42	21.5	43	20.5–22.8	0.53	11.8	38	11.4–12.5	0.29	8.2	41	7.7–9.0	0.31
Pickering, ON	18.5	15	18.0–19.1	0.30	21.6	15	20.9–22.6	0.44	11.8	14	11.3–12.5	0.30	8.2	13	7.9–8.7	0.28
Wallaceburg, ON	18.5	38	17.6–19.2	0.37	21.7	39	20.8–23.0	0.44	11.8	39	11.0–12.7	0.32	8.2	38	7.3–8.9	0.30
Sowerby, ON	18.3	25	17.0–19.3	0.52	21.4	25	19.9–22.8	0.58	11.8	24	11.0–12.4	0.32	8.0	22	7.2–8.5	0.33
Cochrane, ON	18.5	35	17.6–19.3	0.43	21.6	32	20.6–22.6	0.48	11.8	34	10.7–12.5	0.38	8.2	32	7.4–8.8	0.30
Moosonee, ON	18.7	50	17.6–19.9	0.40	21.8	49	20.2–23.2	0.46	12.0	49	11.0–12.8	0.30	8.0	48	7.4–8.8	0.28
Attawapiskat, ON	18.8	38	18.2–20.0	0.43	21.9	36	21.1–22.8	0.49	12.1	37	11.6–12.7	0.34	8.0	36	7.5–8.8	0.26
Winisk, ON	18.8	42	17.9–19.5	0.40	21.9	45	20.7–22.9	0.47	12.1	44	11.3–12.7	0.29	8.0	41	7.3–8.5	0.23
Thunder Bay, ON	18.4	15	18.1–19.3	0.31	21.5	16	21.0–22.8	0.51	11.8	15	11.3–12.4	0.30	8.0	14	7.7–8.6	0.29
Delta, MAN	18.4	36	17.1–19.1	0.40	21.4	36	19.4–22.4	0.58	11.8	35	11.2–12.4	0.30	7.8	37	7.0–8.3	0.30
The Pas, MAN	18.4	22	17.7–19.0	0.34	21.4	21	20.7–22.1	0.45	11.8	22	10.0–12.3	0.33	8.0	21	7.3–8.5	0.25
Gillam, MAN	18.7	19	18.0–19.5	0.41	21.8	19	21.0–22.6	0.39	12.0	17	11.6–12.6	0.24	8.1	18	7.8–8.4	0.20
Churchill, MAN	18.5	29	18.0–19.2	0.28	21.6	29	20.8–22.6	0.44	12.0	30	11.5–12.8	0.30	8.0	29	7.3–8.5	0.32
Coppermine, N.W.T.	18.6	28	17.8–19.3	0.39	21.6	28	20.6–22.6	0.45	11.9	28	11.1–12.5	0.30	7.8	27	7.1–8.3	0.27
Norman Wells, N.W.T.	18.5	22	17.9–19.2	0.41	21.7	22	21.0–22.8	0.45	12.0	20	11.7–12.4	0.22	8.1	21	7.4–8.	0.29
Inuvik, N.W.T.	18.3	14	17.4–19.2	0.47	21.4	14	20.5–22.3	0.58	12.0	13	11.3–12.5	0.37	7.8	13	7.3–8.4	0.34
Whitehorse, Yukon T.	18.5	11	17.9–19.1	0.39	21.9	10	21.4–22.3	0.30	12.1	10	11.9–12.4	0.19	8.2	10	7.5–8.7	0.34
Maple Creek, SASK	18.6	23	17.7–19.3	0.34	21.6	24	20.7–22.3	0.42	11.9	22	11.4–12.3	0.29	7.9	22	7.4–8.4	0.28
Courval, SASK	18.6	13	17.9–19.4	0.42	21.6	14	20.8–22.0	0.44	11.9	13	11.4–12.3	0.26	7.8	11	7.5–8.2	0.21
Milk River, ALTA	18.4	29	17.6–19.2	0.34	21.4	24	20.6–22.4	0.50	11.7	27	11.1–12.3	0.31	7.8	24	7.1–8.7	0.31
Grande Prairie, ALTA	18.4	32	17.8–19.2	0.38	21.3	30	20.1–22.3	0.51	11.8	30	11.2–12.2	0.28	7.9	29	7.3–8.5	0.29
Koyuk, AK	18.2	15	17.4–18.8	0.38	21.2	15	20.2–21.8	0.43	11.9	15	11.6–12.2	0.23	7.8	14	7.4–8.4	0.25
Fairbanks, AK	18.1	21	17.4–19.6	0.53	21.2	21	20.4–22.4	0.48	11.8	21	11.4–12.4	0.28	7.9	19	7.6–8.5	0.27

APPENDIX 1. CONTINUED

Locality	Humerus length Mean	N	Range	S.D.	Ulna length Mean	N	Range	S.D.	Carpometacarpus length Mean	N	Range	S.D.	Hallux length Mean	N	Range	S.D.
Wasilla, AK	18.2	27	17.4–19.0	0.38	21.5	27	20.6–22.7	0.46	11.9	26	11.5–12.3	0.22	8.0	27	7.4–8.5	0.29
Umnak Is., AK	19.5	30	18.6–20.0	0.34	23.0	29	21.8–23.9	0.48	13.0	29	12.5–13.5	0.26	8.7	30	7.9–9.2	0.30
Cold Bay, AK	19.3	15	18.6–20.3	0.48	22.8	15	21.9–23.5	0.51	12.9	14	12.4–13.4	0.33	8.7	14	8.1–9.2	0.30
Port Heiden, AK	18.6	16	18.0–19.4	0.41	21.9	15	21.1–22.6	0.47	12.4	15	11.8–13.1	0.36	8.3	14	7.7–9.1	0.35
Middleton Is., AK	19.0	29	18.4–19.7	0.35	22.5	29	2.8–23.2	0.40	12.6	29	12.1–13.1	0.29	8.4	28	8.0–9.0	0.28
Sheridan, WY	18.4	32	17.7–19.2	0.44	21.5	33	20.6–22.5	0.43	11.9	32	11.0–12.6	0.37	7.8	30	7.3–8.2	0.24
Woodruff, UT	18.6	48	17.5–19.5	0.43	21.7	47	20.2–23.0	0.55	18.9	43	11.1–12.6	0.37	7.9	45	7.3–8.7	0.32
Elberta, UT	18.4	17	17.8–19.2	0.37	21.5	18	20.5–22.5	0.50	11.8	18	11.1–12.5	0.39	7.7	18	7.2–8.1	0.21
Halleck, NV	18.5	29	17.8–19.2	0.35	21.6	29	20.5–22.6	0.53	11.8	29	11.1–12.4	0.31	7.9	27	7.4–8.5	0.25
Alamo, NV	18.1	6	17.1–18.6	0.56	21.4	6	20.3–22.0	0.65	11.5	6	10.7–12.0	0.47	7.7	6	7.0–8.2	0.45
Creston, WA	18.4	32	17.5–19.4	0.36	21.5	34	20.3–22.4	0.41	11.8	32	11.3–12.4	0.24	7.8	33	7.2–8.5	0.30
Hoquiam, WA	18.1	19	17.7–18.6	0.28	21.0	16	20.5–21.5	0.35	11.6	18	11.1–12.1	0.26	8.1	18	7.4–8.6	0.34
Owen's Lake, CA	18.5	20	17.6–19.4	0.52	21.5	20	20.6–23.3	0.67	11.7	17	11.2–12.6	0.33	7.9	19	7.5–8.5	0.28
Eureka, CA	18.4	25	17.8–19.4	0.36	21.1	25	20.4–22.1	0.39	11.6	25	11.0–12.3	0.30	8.4	23	7.6–9.1	0.33
Morro Bay, CA	18.1	17	17.4–18.7	0.36	20.7	17	20.1–21.3	0.31	11.5	16	11.2–11.9	0.21	7.9	16	7.6–8.3	0.20
San Diego, CA	18.0	20	16.7–18.7	0.49	20.5	20	19.2–21.4	0.50	11.3	19	10.7–11.9	0.31	7.9	18	7.4–8.4	0.25
Bahia San Quintin, B.C.N.	18.2	21	17.4–19.1	0.38	20.7	19	20.2–21.2	0.32	11.5	19	10.9–12.0	0.25	7.9	20	7.5–8.6	0.34
Guerrero Negro, B.C.S.	18.4	34	17.3–19.3	0.44	21.0	34	19.6–22.6	0.53	11.7	32	11.0–12.4	0.32	8.0	33	7.6–8.5	0.22
Bahia Magdalena, B.C.S.	18.8	15	17.9–20.1	0.51	21.6	15	20.7–22.6	0.53	11.9	14	11.2–12.5	0.33	8.2	15	7.7–9.1	0.41
Puerto Peñasco, Sonora	18.8	9	18.3–19.2	0.31	21.9	8	21.3–22.3	0.40	12.0	9	11.6–12.4	0.30	8.0	9	7.8–8.5	0.25
Bahia Kino, Sonora	19.0	21	18.2–19.7	0.42	21.8	21	21.1–22.6	0.44	12.0	19	11.3–12.5	0.30	8.1	20	7.5–8.5	0.28
El Molino, Sinaloa	19.2	15	18.7–19.6	0.27	22.1	15	21.4–22.9	0.44	12.1	15	11.6–12.6	0.25	8.1	15	7.7–8.4	0.18
Charco Redondo, Jalisco	18.6	16	17.9–19.5	0.46	21.8	15	21.0–22.6	0.47	11.6	15	11.2–12.1	0.29	8.0	15	7.4–8.6	0.37
Lerma, México	19.1	20	18.3–19.8	0.40	22.4	20	21.2–23.2	0.49	11.9	20	10.5–12.5	0.42	8.0	18	7.5–8.4	0.25

APPENDIX 1. CONTINUED

Locality	Sternum length				Sternum depth				Keel length				Synsacrum width			
	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.
Sable Is., N.S.	23.0	23	22.0–24.2	0.57	10.8	24	10.4–11.6	0.32	22.4	23	21.1–23.9	0.73	11.8	23	10.4–13.2	0.60
Halifax, N.S.	21.2	11	20.4–22.0	0.50	10.0	11	9.1–10.6	0.42	20.5	10	19.0–21.3	0.67	10.7	11	10.3–11.2	0.30
River John, N.S.	21.0	30	19.7–22.5	0.73	9.6	29	8.7–10.7	0.51	20.2	29	18.9–21.6	0.78	10.7	29	9.5–11.4	0.42
Pasadena, NFLD	20.8	12	20.1–21.4	0.36	9.3	12	8.9–9.8	0.26	19.8	12	18.4–20.8	0.77	10.8	10	10.1–11.1	0.31
Parson's Pond, NFLD	20.9	13	19.7–22.2	0.66	9.3	13	8.5–10.0	0.43	20.1	13	18.9–21.2	0.76	10.7	13	9.7–11.3	0.46
Bedeque, P.E.I.	20.6	27	19.1–21.6	0.61	9.4	26	8.6–10.4	0.47	19.8	26	18.2–21.2	0.64	10.7	26	10.1–11.3	0.31
St. Andrews, N.B.	20.8	24	19.7–22.1	0.60	9.5	23	8.6–10.2	0.38	19.9	23	17.4–21.12	0.94	10.7	24	10.3–11.1	0.26
Matane, QUE	20.6	28	19.2–22.1	0.60	9.4	29	8.5–10.6	0.50	20.0	28	18.2–21.7	0.70	10.6	28	10.1–11.3	0.32
Magdalen Is., QUE	20.9	28	19.2–21.8	0.63	9.5	28	9.0–10.0	0.31	19.9	29	18.5–21.0	0.65	10.8	29	10.4–11.3	0.25
Kuujjuaq, QUE	20.9	21	20.1–21.7	0.44	9.6	2	9.1–10.4	0.32	20.1	21	19.2–20.9	0.56	10.8	23	10.1–11.5	0.37
MA and eastern NY	20.7	10	19.9–21.6	0.54	9.7	10	9.4–10.1	0.20	19.9	10	19.2–20.9	0.51	10.6	10	10.3–11.0	0.20
Brandonville, WV	20.5	25	18.7–23.1	0.83	9.3	25	8.6–10.7	0.48	19.7	25	18.3–21.0	0.81	10.6	23	10.0–11.0	0.29
Wildfield, ON	20.7	41	19.5–22.5	0.67	9.4	40	8.8–10.6	0.42	20.0	42	18.5–21.7	0.74	10.5	42	9.7–11.1	0.28
Pickering, ON	20.6	15	19.7–21.3	0.49	9.6	15	8.8–10.0	0.33	19.8	15	18.7–20.5	0.52	10.5	14	9.9–11.2	0.37
Wallaceburg, ON	20.7	40	19.6–21.7	0.59	9.4	39	8.7–10.1	0.36	20.0	40	18.5–21.3	0.73	10.7	38	10.0–11.1	0.26
Sowerby, ON	20.4	25	19.2–21.6	0.49	9.2	25	8.6–9.6	0.29	19.8	25	18.9–20.5	0.47	10.4	25	9.9–11.0	0.33
Cochrane, ON	20.6	32	19.5–21.4	0.50	9.5	32	8.5–10.3	0.34	20.0	32	18.7–21.8	0.71	10.4	33	9.9–11.0	0.28
Moosonee, ON	20.9	49	19.3–22.3	0.62	9.6	47	8.8–10.3	0.39	20.1	46	18.3–22.4	0.80	10.7	48	10.0–11.5	0.34
Attawapiskat, ON	20.9	38	19.7–22.3	0.60	9.6	37	8.8–10.5	0.42	20.2	38	18.2–21.6	0.70	10.7	37	10.2–11.4	0.32
Winisk, ON	20.8	42	19.6–22.6	0.61	9.7	37	9.0–10.4	0.39	20.1	36	18.6–22.2	0.89	10.6	39	9.9–11.1	0.29
Thunder Bay, ON	20.1	16	19.3–21.2	0.56	9.3	15	8.7–9.8	0.31	19.5	15	18.2–20.7	0.60	10.4	16	10.1–11.0	0.22
Delta, MAN	20.4	36	19.6–21.3	0.43	9.3	38	8.4–10.2	0.38	19.7	36	18.3–21.3	0.75	10.4	37	9.8–10.9	0.27
The Pas, MAN	20.2	21	19.5–21.3	0.53	9.2	21	8.5–10.0	0.37	19.6	22	18.5–20.5	0.53	10.4	22	9.9–10.9	0.31
Gillam, MAN	20.7	17	19.9–22.1	0.62	9.5	17	8.9–10.4	0.37	20.0	19	18.6–21.6	0.70	10.6	19	10.1–11.4	0.30
Churchill, MAN	20.7	29	19.7–23.2	0.70	9.2	29	8.7–9.6	0.24	19.8	30	18.6–21.3	0.67	10.7	29	9.8–11.3	0.28
Coppermine, N.W.T.	20.4	28	19.1–21.6	0.58	9.1	27	8.5–10.0	0.34	19.4	27	17.7–20.7	0.87	10.6	27	9.9–10.3	0.34
Norman Wells, N.W.T.	20.3	19	19.5–21.3	0.47	9.3	20	8.4–10.0	0.42	19.8	20	18.5–21.4	0.70	10.5	22	9.7–10.8	0.26
Inuvik, N.W.T.	20.5	12	19.7–21.5	0.48	9.2	9	8.8–9.7	0.33	19.9	11	18.3–21.1	0.85	10.5	14	9.9–11.4	0.41
Whitehorse, Yukon T.	20.8	11	19.8–21.4	0.53	9.3	11	8.4–9.8	0.38	20.4	11	19.1–21.2	0.59	10.6	8	10.1–11.2	0.38
Maple Creek, SASK	20.4	23	19.0–21.5	0.58	9.3	23	8.8–9.9	0.33	19.8	23	18.6–21.0	0.72	10.3	22	9.8–10.9	0.24
Courval, SASK	20.7	14	19.6–22.1	0.65	9.4	14	8.8–10.0	0.45	20.1	14	18.8–21.0	0.70	10.5	14	9.9–11.2	0.34
Milk River, ALTA	20.4	29	18.7–21.3	0.63	9.2	29	8.1–9.8	0.43	19.7	29	18.3–21.6	0.76	10.4	28	9.9–10.8	0.26
Grande Prairie, ALTA	20.3	30	18.7–21.3	0.57	9.3	30	8.8–9.9	0.30	19.8	30	18.2–21.2	0.78	10.3	27	9.9–10.7	0.24
Koyuk, AK	20.4	15	19.6–21.4	0.52	9.2	15	8.9–9.8	0.30	19.8	15	19.2–21.1	0.53	10.6	14	10.2–11.1	0.29
Fairbanks, AK	20.4	20	19.2–21.3	0.56	9.2	20	8.4–9.8	0.45	19.8	21	18.1–20.9	0.67	10.4	21	9.8–10.8	0.25

APPENDIX 1. CONTINUED

	Sternum length				Sternum depth				Keel length				Synsacrum width			
Locality	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.
Wasilla, AK	20.6	25	19.2–21.6	0.62	9.4	26	8.9–10.3	0.36	20.2	25	18.4–21.4	0.78	10.5	26	9.9–11.4	0.35
Umnak Is., AK	22.2	30	21.0–23.1	0.60	10.1	29	9.1–10.7	0.42	21.5	28	20.2–22.8	0.64	11.7	29	11.1–12.3	0.30
Cold Bay, AK	22.3	13	21.5–23.1	0.46	9.7	14	9.1–10.3	0.43	21.1	14	20.2–22.7	0.66	11.4	13	10.7–12.5	0.45
Port Heiden, AK	21.2	16	19.7–22.6	0.80	9.7	15	8.8–10.7	0.58	20.6	15	18.9–22.6	1.12	11.0	16	10.3–11.4	0.33
Middleton Is., AK	21.6	29	20.0–23.0	0.63	9.5	27	8.5–10.6	0.42	20.7	26	19.1–22.6	0.73	11.2	29	10.2–11.7	0.31
Sheridan, WY	20.6	29	19.5–21.6	0.54	9.3	29	8.6–10.3	0.42	19.9	32	18.9–21.7	0.71	10.3	32	9.8–11.0	0.28
Woodruff, UT	20.6	45	19.1–21.8	0.64	9.3	43	8.1–10.1	0.39	20.0	46	17.9–21.6	0.83	10.4	45	9.8–11.0	0.29
Elberta, UT	20.2	17	19.3–21.4	0.51	9.2	17	8.7–9.8	0.33	19.7	19	18.9–21.2	0.64	10.3	18	9.7–10.9	0.29
Halleck, NV	20.1	30	18.2–21.4	0.75	9.2	29	8.0–9.8	0.43	19.5	29	17.0–21.4	0.98	10.3	30	9.8–10.9	0.30
Alamo, NV	20.0	5	19.0–20.4	0.57	8.7	5	8.2–9.0	0.36	19.2	6	18.8–19.6	0.35	9.7	4	9.1–10.2	0.45
Creston, WA	20.5	31	18.7–21.4	0.53	9.3	33	8.4–10.1	0.43	20.0	31	17.4–21.3	0.92	10.3	34	9.9–11.0	0.26
Hoquiam, WA	20.1	19	19.2–21.4	0.58	9.4	18	8.0–10.0	0.48	19.6	18	18.4–20.7	0.62	10.3	19	10.0–10.7	0.22
Owen's Lake, CA	19.9	18	19.2–20.9	0.44	9.0	19	8.5–9.9	0.39	19.3	18	18.2–20.7	0.73	10.1	20	9.8–10.6	0.22
Eureka, CA	20.0	26	18.8–21.5	0.71	9.1	26	8.4–9.1	0.36	19.4	26	18.1–21.0	0.70	10.5	25	10.0–11.0	0.23
Morro Bay, CA	19.9	17	19.5–20.5	0.27	8.9	16	8.2–9.4	0.42	18.7	16	16.8–20.7	0.86	10.5	16	10.0–11.0	0.28
San Diego, CA	19.8	20	18.7–20.3	0.45	8.8	19	8.5–9.4	0.26	18.7	19	17.4–20.2	0.71	10.5	19	9.7–11.0	0.37
Bahia San Quintin, B.C.N.	19.8	20	18.9–20.4	0.40	9.3	20	8.5–9.9	0.37	18.6	19	18.0–19.6	0.47	10.7	20	10.0–11.2	0.25
Guerrero Negro, B.C.S.	20.2	34	18.9–21.4	0.57	9.3	32	8.7–10.2	0.39	19.3	32	18.0–21.2	0.71	11.1	33	10.6–11.7	0.27
Bahia Magdalena, B.C.S.	20.2	15	18.5–22.1	0.78	9.3	15	8.7–10.2	0.37	19.2	15	17.8–21.7	0.96	11.2	14	10.8–11.8	0.32
Puerto Peñasco, Sonora	20.3	9	19.9–20.9	0.40	9.3	9	8.9–10.0	0.35	19.5	9	18.9–20.3	0.47	10.9	8	10.4–11.1	0.25
Bahia Kino, Sonora	20.6	21	19.6–22.1	0.56	9.5	20	8.7–10.5	0.45	19.8	20	19.2–20.7	0.50	11.2	21	10.5–11.8	0.30
El Molino, Sinaloa	20.6	16	19.5–21.3	0.47	9.3	16	8.4–9.9	0.40	19.5	15	18.6–20.1	0.52	11.1	15	10.5–11.8	0.37
Charco Redondo, Jalisco	20.1	14	19.4–21.7	0.64	9.3	15	8.7–10.0	0.42	19.4	15	18.1–21.1	0.84	10.2	15	9.6–10.8	0.34
Lerma, México	20.5	21	19.1–21.6	0.53	9.3	21	8.5–9.8	0.29	19.7	20	17.8–21.1	0.81	10.5	20	9.9–11.5	0.38

APPENDIX 2. MEASUREMENTS (IN MM) AND SAMPLE STATISTICS FOR FEMALE SAVANNAH SPARROWS (*Ammodramus sandwichensis*)

	Skull length				Skull width				Premaxilla length				Premaxilla depth			
Locality	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.
Sable Is., N.S.	29.0	14	28.1–29.8	0.51	14.7	16	14.1–15.1	0.28	6.3	13	5.8–6.7	0.34	3.6	16	3.3–4.0	0.20
Halifax, N.S.	27.4	14	26.6–27.8	0.43	14.2	15	13.7–14.6	0.24	5.8	14	5.2–6.1	0.27	3.5	15	3.2–3.6	0.13
River John, N.S.	27.1	23	25.7–27.9	0.55	14.1	24	13.6–14.5	0.23	5.7	22	4.8–6.6	0.42	3.4	24	3.0–3.6	0.14
Pasadena, NFLD	27.4	9	26.5–28.3	0.58	14.2	9	13.7–14.6	0.31	5.8	10	5.3–6.3	0.32	3.5	10	3.2–3.7	0.16
St. Andrews, N.B.	27.1	17	26.0–28.0	0.48	14.1	18	13.5–14.6	0.27	5.8	16	5.2–6.3	0.32	3.4	17	3.2–3.7	0.16
Matane, QUE	26.9	21	25.6–28.2	0.69	14.1	22	13.6–14.7	0.24	5.7	22	4.6–6.3	0.40	3.5	22	3.2–3.9	0.17
Magdalen Is., QUE	27.4	15	27.0–28.4	0.40	14.2	15	13.7–14.6	0.23	6.0	15	5.5–6.6	0.31	3.5	15	3.3–3.8	0.13
Kuujjuaq, QUE	27.3	22	26.5–27.8	0.39	14.1	24	13.3–14.6	0.32	5.8	22	5.2–6.3	0.31	3.4	24	3.2–3.7	0.14
Brandonville, WV	26.9	8	23.6–27.2	0.30	14.1	11	13.7–14.5	0.25	5.7	8	5.4–5.9	0.16	3.4	11	3.2–3.7	0.14
Wildfield, ON	27.0	11	25.7–27.7	0.59	14.0	11	13.6–14.6	0.33	5.7	11	5.3–6.2	0.30	3.4	11	3.3–3.5	0.08
Wallaceburg, ON	26.7	15	25.8–27.5	0.41	13.8	15	13.5–14.2	0.21	5.6	15	5.0–6.3	0.36	3.3	15	3.0–3.5	0.13
Sowerby, ON	26.6	9	26.0–27.3	0.45	14.0	9	13.7–14.6	0.26	5.5	9	5.0–5.8	0.27	3.3	9	3.2–3.5	0.10
Moosonee, ON	27.0	26	26.1–27.8	0.40	14.1	30	13.6–14.5	0.23	5.7	27	5.2–6.4	0.26	3.3	31	3.1–3.6	0.13
Attawapiskat, ON	27.0	25	25.8–27.8	0.52	14.0	26	13.6–14.6	0.26	5.8	24	5.2–6.2	0.29	3.4	25	3.1–3.7	0.17
Winisk, ON	27.1	16	25.8–27.6	0.44	14.0	20	13.5–14.5	0.23	5.8	19	5.1–6.3	0.32	3.3	19	3.1–3.5	0.11
Thunder Bay, ON	26.5	10	26.0–27.1	0.36	13.7	12	13.4–14.2	0.28	5.4	10	4.7–5.7	0.34	3.3	12	3.0–3.5	0.17
Delta, MAN	26.4	17	25.4–27.6	0.65	13.7	21	13.1–14.5	0.34	5.4	18	4.9–5.9	0.28	3.3	21	3.1–3.6	0.15
Churchill, MAN	27.1	17	25.6–28.0	0.53	14.0	18	13.6–14.6	0.25	5.7	17	5.2–6.3	0.29	3.3	18	3.1–3.6	0.13
Coppermine, N.W.T.	26.9	15	25.6–27.6	0.58	13.8	16	13.1–14.2	0.36	5.7	14	5.2–5.9	0.25	3.2	15	3.0–3.5	0.15
Norman Wells, N.W.T.	26.9	21	25.5–28.0	0.55	13.9	21	13.2–14.3	0.31	5.5	21	4.6–6.1	0.41	3.3	21	3.1–3.5	0.12
Inuvik, N.W.T.	27.2	13	26.1–27.9	0.48	13.8	14	13.2–14.4	0.28	5.7	13	5.0–6.2	0.34	3.2	14	3.0–3.5	0.16
Grande Prairie, ALTA	26.1	22	25.4–26.9	0.37	13.7	24	13.3–13.6	0.30	5.4	22	4.8–6.2	0.30	3.2	23	3.1–3.5	0.12
Koyuk, AK	26.6	21	25.4–27.4	0.60	13.9	21	13.4–14.7	0.29	5.3	21	4.8–5.8	0.27	3.2	21	2.9–3.5	0.15
Wasilla, AK	26.9	21	26.4–27.7	0.29	14.0	22	13.5–14.3	0.19	5.6	22	5.1–6.2	0.23	3.3	23	3.0–3.5	0.15
Umnak Is., AK	29.2	23	28.3–30.5	0.61	15.0	23	14.5–15.4	0.28	6.6	23	6.0–7.1	0.24	3.8	24	3.6–4.0	0.13
Cold Bay, AK	28.0	7	27.6–28.7	0.37	14.4	6	14.2–14.7	0.18	6.4	8	6.2–6.8	0.23	3.8	8	3.6–4.0	0.14
Port Heiden, AK	27.6	12	27.0–28.3	0.39	14.4	13	14.0–14.8	0.23	6.0	12	5.8–6.5	0.21	3.5	13	3.3–3.7	0.13
Middleton Is., AK	28.3	20	27.5–28.9	0.36	14.6	17	14.2–15.2	0.26	6.3	20	5.8–6.7	0.31	3.7	20	3.5–4.0	0.16
Sheridan, WY	26.4	14	25.7–27.2	0.44	13.8	17	13.3–14.3	0.27	5.7	14	5.3–6.1	0.27	3.3	17	3.1–3.5	0.12
Woodruff, UT	26.5	16	25.9–27.2	0.41	13.8	16	13.5–14.0	0.14	5.7	16	5.1–6.0	0.25	3.3	16	3.0–3.7	0.18
Halleck, NV	26.4	9	25.7–27.0	0.52	13.6	9	13.4–14.0	0.19	5.6	9	5.2–6.1	0.31	3.1	9	3.0–3.4	0.13
Creston, WA	26.3	16	25.3–27.4	0.51	13.8	19	13.5–14.5	0.24	5.4	15	5.0–5.9	0.29	3.2	19	3.0–3.5	0.13
Hoquiam, WA	26.6	22	25.7–27.5	0.43	13.9	24	13.4–14.6	0.31	5.5	24	5.0–5.9	0.25	3.2	25	3.0–3.5	0.12
Owen's Lake, CA	26.0	22	24.9–26.8	0.50	13.5	23	12.9–14.1	0.31	5.4	22	5.0–5.9	0.27	3.1	23	2.8–3.6	0.18
Eureka, CA	27.3	14	26.5–29.4	0.80	14.1	14	13.5–14.6	0.30	5.7	14	5.1–6.1	0.33	3.3	14	3.1–3.6	0.15

APPENDIX 2. CONTINUED

Locality	Skull length				Skull width				Premaxilla length				Premaxilla depth			
	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.
Morro Bay, CA	26.7	11	26.0–27.2	0.34	13.9	11	13.6–14.2	0.17	5.6	11	5.0–5.9	0.26	3.2	11	2.8–3.4	0.18
San Diego, CA	27.1	15	26.4–27.9	0.46	13.9	15	13.2–14.4	0.29	6.0	15	5.3–6.4	0.28	3.4	15	3.2–3.6	0.11
Bahia San Quintin, B.C.N.	27.6	10	26.7–28.5	0.57	13.8	15	13.1–14.3	0.29	6.4	13	5.9–7.0	0.31	3.4	14	3.2–3.7	0.14
Guerrero Negro, B.C.S.	27.9	21	26.5–29.3	0.60	14.3	23	13.6–14.9	0.27	6.6	21	5.8–7.3	0.36	3.5	23	3.2–3.9	0.15
Bahia Magdalena, B.C.S.	28.8	14	27.3–30.1	0.60	14.4	13	13.9–15.0	0.31	7.1	14	6.5–7.6	0.32	3.7	15	3.6–3.9	0.10
Puerto Peñasco, Sonora	28.5	4	28.1–28.9	0.46	14.3	4	13.9–14.5	0.26	6.8	4	6.5–7.0	0.22	3.9	4	3.8–4.0	0.10
Bahia Kino, Sonora	29.0	13	28.2–29.7	0.48	14.5	14	13.8–15.3	0.32	7.3	14	6.9–7.9	0.33	3.9	14	3.7–4.2	0.16
El Molino, Sinaloa	29.1	8	28.6–29.9	0.45	14.4	8	14.2–14.8	0.22	7.5	8	7.0–7.7	0.21	4.0	8	3.9–4.2	0.10
Charco Redondo, Jalisco	26.2	7	25.0–27.0	0.70	13.7	7	13.5–14.0	0.19	5.4	7	5.0–5.7	0.29	3.3	7	3.2–3.5	0.11
Lerma, México	27.4	5	26.9–28.0	0.43	14.0	6	13.7–14.3	0.22	6.3	6	6.0–6.5	0.22	3.5	5	3.0–3.6	0.11

APPENDIX 2. CONTINUED

Locality	Narial width				Premaxilla width				Inter-orbital width				Mandibular length			
	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.
Sable Is., N.S.	6.9	16	6.3–7.4	0.30	5.9	16	5.3–6.8	0.45	2.7	16	2.3–2.9	0.19	20.0	13	19.5–20.4	0.35
Halifax, N.S.	6.5	15	6.0–6.8	0.24	5.2	15	4.8–5.5	0.17	2.6	15	2.3–2.9	0.15	18.4	14	17.7–19.0	0.48
River John, N.S.	6.5	24	6.1–7.3	0.28	5.1	24	4.1–5.6	0.28	2.6	24	2.0–3.0	0.23	18.2	21	17.2–19.3	0.53
Pasadena, NFLD	6.6	10	6.1–7.1	0.28	5.3	10	5.0–5.5	0.21	2.5	10	2.2–2.8	0.21	18.6	8	17.0–19.5	0.81
St. Andrews, N.B.	6.5	17	6.0–7.0	0.25	5.2	17	4.9–5.6	0.19	2.5	18	2.2–3.0	0.18	18.3	14	17.3–18.7	0.35
Matane, QUE	6.4	22	5.9–7.0	0.27	5.1	22	4.7–5.6	0.22	2.5	20	2.1–2.9	0.21	18.1	18	16.9–19.1	0.52
Magdalen Is., QUE	6.5	15	6.1–7.1	0.28	5.1	15	4.9–5.3	0.14	2.7	14	2.4–3.1	0.20	18.7	14	18.1–19.5	0.43
Kuujjuaq, QUE	6.4	23	5.9–6.8	0.28	5.1	24	4.8–5.5	0.18	2.5	24	2.1–2.9	0.20	18.5	21	17.2–19.3	0.46
Brandonville, WV	6.7	11	6.6–6.9	0.12	5.2	11	5.0–5.5	0.14	2.5	11	2.1–2.7	0.17	18.1	9	17.3–18.5	0.34
Wildfield, ON	6.5	11	5.9–7.0	0.30	5.2	11	5.0–5.6	0.21	2.6	11	2.2–3.0	0.20	18.2	11	17.5–18.6	0.38
Wallaceburg, ON	6.4	14	5.9–6.9	0.28	5.1	14	4.7–5.3	0.16	2.5	15	2.2–2.9	0.20	17.8	15	17.2–18.5	0.37
Sowerby, ON	6.5	9	6.1–7.0	0.24	5.1	9	4.9–5.3	0.13	2.6	9	2.3–2.8	0.18	17.9	8	17.5–18.5	0.34
Moosonee, ON	6.4	31	5.9–7.0	0.26	5.1	31	4.6–5.5	0.19	2.5	31	2.1–3.0	0.19	18.0	26	17.1–18.8	0.36
Attawapiskat, ON	6.4	26	5.9–6.9	0.26	5.0	26	4.6–5.3	0.19	2.6	26	2.2–3.0	0.23	18.1	24	17.1–19.2	0.46
Winisk, ON	6.3	19	5.8–6.7	0.25	5.1	19	4.9–5.4	0.13	2.1	21	2.2–2.9	0.21	18.2	18	16.8–19.0	0.48
Thunder Bay, ON	6.2	12	5.9–6.7	0.28	5.0	11	4.7–5.3	0.17	2.5	12	2.0–2.9	0.24	17.8	10	17.4–18.5	0.35
Delta, MAN	6.3	20	5.8–6.7	0.27	5.0	21	4.7–5.4	0.19	2.4	21	1.9–2.9	0.21	17.6	21	16.6–19.2	0.61
Churchill, MAN	6.3	18	5.7–6.8	0.32	5.0	18	4.7–5.4	0.18	2.3	17	2.0–2.7	0.17	18.0	16	17.1–18.9	0.39
Coppermine, N.W.T.	6.0	14	5.8–6.5	0.25	4.8	15	4.4–5.2	0.21	2.3	15	1.9–2.8	0.26	17.9	12	17.4–18.7	0.44
Norman Wells, N.W.T.	6.3	22	5.7–6.6	0.22	5.0	22	4.7–5.4	0.18	2.4	21	2.0–2.7	0.17	18.0	20	17.2–18.9	0.50
Inuvik, N.W.T.	6.1	14	5.8–6.8	0.30	4.9	14	4.7–5.2	0.14	2.4	14	2.1–2.6	0.17	18.2	14	17.3–18.7	0.41
Grande Prairie, ALTA	6.2	24	5.8–6.7	0.23	5.0	23	4.5–5.5	0.19	2.3	23	1.9–2.6	0.20	17.6	21	16.6–18.4	0.48
Koyuk, AK	6.2	20	5.6–6.9	0.32	4.8	21	4.6–5.2	0.16	2.2	21	1.9–2.5	0.17	17.9	20	16.9–18.6	0.54
Wasilla, AK	6.3	22	5.9–7.0	0.27	4.8	21	4.6–5.1	0.15	2.5	23	2.1–2.8	0.22	18.0	22	17.4–18.5	0.28
Umnak Is., AK	7.0	24	6.4–7.4	0.29	5.8	24	5.3–6.3	0.26	2.7	23	2.4–3.3	0.22	20.1	22	19.2–20.9	0.51
Cold Bay, AK	6.8	8	6.5–7.1	0.18	5.5	8	5.4–5.6	0.08	2.7	8	2.4–3.1	0.21	19.1	6	18.8–19.4	0.24
Port Heiden, AK	6.4	13	6.1–6.9	0.24	5.2	11	5.0–5.3	0.11	2.6	13	2.2–3.0	0.24	18.8	12	18.3–19.4	0.34
Middleton Is., AK	6.6	20	6.3–6.9	0.17	5.3	20	4.9–5.7	0.19	2.6	20	2.3–2.8	0.15	19.1	18	18.4–19.9	0.40
Sheridan, WY	6.3	17	5.8–6.7	0.25	4.9	16	4.3–5.2	0.22	2.5	17	2.3–2.7	0.16	17.6	16	17.2–18.1	0.30
Woodruff, UT	6.4	16	6.0–6.7	0.20	4.9	16	4.6–5.3	0.18	2.6	16	2.3–2.8	0.16	17.7	15	17.0–18.1	0.28
Halleck, NV	6.3	9	6.0–6.6	0.20	4.8	9	4.6–5.0	0.12	2.4	9	2.2–2.6	0.15	17.4	9	16.6–17.9	0.51
Creston, WA	6.3	19	5.6–6.7	0.29	4.9	18	4.6–5.8	0.27	2.4	19	2.1–2.7	0.21	17.7	19	17.0–19.3	0.58
Hoquiam, WA	6.3	22	5.8–6.7	0.24	5.0	24	4.8–5.3	0.15	2.4	25	2.0–2.8	0.20	17.7	23	17.0–18.4	0.42
Owen's Lake, CA	6.1	23	5.3–6.8	0.38	4.8	23	4.5–5.2	0.19	2.4	23	2.0–2.7	0.20	17.4	23	16.9–18.2	0.40
Eureka, CA	6.6	11	6.4–6.9	0.14	5.1	14	4.8–5.5	0.20	2.3	13	1.8–2.7	0.20	18.4	14	16.7–19.9	0.91

APPENDIX 2. CONTINUED

Locality	Narial width				Premaxilla width				Inter-orbital width				Mandibular length			
	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.
Morro Bay, CA	6.1	10	5.8–6.4	0.20	5.1	11	4.8–5.5	0.22	2.5	11	1.9–2.8	0.24	18.0	10	17.6–18.5	0.28
San Diego, CA	6.2	15	5.6–6.5	0.26	5.2	15	4.7–5.7	0.24	2.4	14	2.0–2.7	0.19	18.4	12	17.6–19.1	0.44
Bahia San Quintin, B.C.N.	6.1	15	5.5–6.7	0.35	5.1	13	4.9–5.3	0.10	2.4	15	2.1–2.6	0.15	18.9	14	17.8–20.0	0.58
Guerrero Negro, B.C.S.	6.4	23	5.9–6.8	0.20	5.4	22	4.9–5.7	0.20	2.6	22	2.2–2.9	0.19	19.2	18	18.1–19.0	0.50
Bahia Magdalena, B.C.S.	6.7	15	6.3–7.0	0.22	5.6	15	5.2–6.0	0.23	2.7	14	2.4–3.0	0.17	20.0	10	18.9–20.7	0.62
Puerto Peñasco, Sonora	6.7	4	6.4–6.9	0.21	5.9	4	5.7–6.0	0.13	2.4	4	2.2–2.6	0.18	19.6	4	19.3–19.7	0.19
Bahia Kino, Sonora	6.7	14	6.3–7.4	0.27	5.8	14	5.5–6.1	0.17	2.0	13	2.3–3.2	0.36	20.1	11	19.3–20.8	0.40
El Molino, Sinaloa	6.9	8	6.4–7.2	0.33	5.9	8	5.6–6.1	0.19	2.9	8	2.6–3.1	0.15	20.3	5	19.7–20.6	0.36
Charco Redondo, Jalisco	6.2	7	5.8–6.7	0.29	4.9	7	4.7–5.0	0.12	2.4	7	2.1–2.7	0.21	17.5	6	16.9–19.7	0.39
Lerma, México	6.5	6	6.2–6.8	0.24	5.4	5	5.2–5.5	0.13	2.6	6	2.3–3.0	0.24	18.4	5	18.0–18.7	0.30

APPENDIX 2. CONTINUED

Locality	Gonys				Mandible depth				Coracoid length				Scapula length			
	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.
Sable Is., N.S.	5.3	12	5.0–5.7	0.22	2.1	11	1.9–2.2	0.08	18.1	16	17.2–19.2	0.53	20.8	16	18.8–21.9	0.83
Halifax, N.S.	4.9	13	4.4–5.4	0.37	1.9	14	1.8–2.0	0.07	16.9	14	16.3–17.5	0.33	19.3	14	17.9–20.0	0.57
River John, N.S.	4.8	21	4.2–5.9	0.35	1.9	21	1.7–2.2	0.12	16.7	24	16.2–17.0	0.37	19.1	23	17.8–20.1	0.59
Pasadena, NFLD	4.9	8	4.3–5.3	0.34	1.9	8	1.8–2.0	0.06	16.8	8	16.1–17.9	0.63	18.9	9	17.8–19.7	0.68
St. Andrews, N.B.	4.8	15	4.3–5.2	0.29	1.9	16	1.8–2.1	0.08	16.7	18	16.1–17.5	0.38	19.1	16	17.9–20.6	0.70
Matane, QUE	4.8	20	4.2–5.4	0.29	1.8	19	1.7–2.0	0.08	16.5	22	15.7–17.4	0.44	19.0	20	18.0–20.0	0.52
Magdalen Is., QUE	5.0	14	4.4–5.7	0.31	1.9	14	1.7–2.0	0.10	16.9	15	16.4–17.7	0.32	19.4	15	18.3–20.4	0.48
Kuujjuaq, QUE	5.1	20	4.4–5.6	0.32	1.9	24	1.7–2.0	0.07	16.7	24	15.8–17.5	0.44	19.0	23	17.6–20.1	0.58
Brandonville, WV	4.7	9	4.4–5.1	0.26	1.8	9	1.7–2.0	0.09	16.5	11	16.0–16.8	0.24	19.0	10	18.4–20.4	0.63
Wildfield, ON	4.8	11	4.4–5.3	0.27	1.9	11	1.7–2.0	0.09	16.8	11	16.1–17.3	0.42	19.4	11	18.6–20.6	0.63
Wallaceburg, ON	4.7	14	4.2–5.1	0.21	1.8	15	1.7–1.9	0.06	16.5	15	16.0–17.0	0.31	19.0	15	18.2–19.7	0.45
Sowerby, ON	4.7	9	4.4–5.3	0.32	1.8	9	1.7–2.0	0.09	16.6	9	16.1–17.3	0.38	19.3	9	18.5–20.7	0.68
Moosonee, ON	4.7	25	4.3–5.5	0.32	1.8	27	1.7–2.0	0.08	16.9	30	16.3–17.7	0.34	19.5	29	18.2–20.4	0.55
Attawapiskat, ON	4.8	23	4.2–5.4	0.30	1.8	24	1.7–1.9	0.07	16.7	25	16.0–17.5	0.43	19.2	24	18.1–20.5	0.63
Winisk, ON	4.8	18	4.1–5.2	0.31	1.9	19	1.7–2.1	0.10	16.9	21	16.1–17.8	0.38	19.3	21	17.9–20.0	0.53
Thunder Bay, ON	4.5	11	4.2–4.9	0.24	1.8	11	1.7–1.9	0.07	16.6	12	15.9–17.1	0.39	19.0	12	18.2–19.7	0.43
Delta, MAN	4.5	21	4.2–5.1	0.24	1.8	21	1.6–1.9	0.07	16.5	21	15.5–17.8	0.52	19.0	19	18.0–19.8	0.52
Churchill, MAN	4.6	16	4.3–5.1	0.20	1.8	15	1.6–1.8	0.06	16.9	18	16.3–17.7	0.36	19.4	17	18.4–20.5	0.54
Coppermine, N.W.T.	4.7	13	4.5–5.2	0.18	1.7	14	1.6–1.8	0.06	16.4	16	15.3–17.1	0.48	18.6	15	17.7–19.7	0.58
Norman Wells, N.W.T.	4.6	19	4.1–5.1	0.27	1.7	20	1.6–1.9	0.06	16.6	21	16.0–17.3	0.36	19.1	21	18.4–19.9	0.51
Inuvik, N.W.T.	4.8	13	4.3–5.3	0.24	1.7	14	1.6–1.8	0.07	16.6	14	15.5–17.2	0.40	19.2	13	18.1–20.1	0.52
Grande Prairie, ALTA	4.6	21	4.0–5.2	0.34	1.7	21	1.6–1.8	0.06	16.5	24	15.5–16.9	0.37	18.9	23	17.8–19.6	0.40
Koyuk, AK	4.6	20	4.1–5.1	0.28	1.6	19	1.5–1.7	0.05	16.4	21	15.8–17.3	0.45	18.9	21	18.0–20.2	0.67
Wasilla, AK	4.6	20	4.3–4.8	0.14	1.7	22	1.6–1.9	0.10	16.7	23	15.9–17.6	0.41	19.2	22	17.8–20.1	0.61
Umnak Is., AK	5.5	22	4.9–6.1	0.36	2.1	23	1.9–2.2	0.08	17.8	23	17.2–18.8	0.44	20.8	23	18.9–21.9	0.71
Cold Bay, AK	5.3	6	5.0–5.4	0.17	2.0	6	1.9–2.1	0.06	17.5	8	17.2–18.0	0.27	20.2	8	19.6–20.7	0.39
Port Heiden, AK	5.1	12	4.6–5.5	0.25	1.8	13	1.6–2.0	0.09	16.8	12	16.4–17.2	0.28	19.4	13	18.7–20.1	0.44
Middleton Is., AK	5.3	18	4.2–5.7	0.38	1.9	20	1.8–2.0	0.06	17.2	20	16.5–18.1	0.40	19.9	20	18.7–20.7	0.52
Sheridan, WY	4.6	16	4.1–4.9	0.24	1.7	16	1.6–1.9	0.09	16.4	17	15.7–17.0	0.33	18.9	17	18.2–19.6	0.40
Woodruff, UT	4.4	15	4.1–5.0	0.24	1.7	15	1.6–1.9	0.07	16.8	16	15.6–17.6	0.54	19.1	16	18.3–19.7	0.33
Halleck, NV	4.3	9	4.3–4.7	0.31	1.7	8	1.6–1.8	0.09	16.4	8	15.8–17.1	0.43	19.0	8	17.9–20.0	0.67
Creston, WA	4.5	19	4.1–5.1	0.28	1.7	19	1.6–1.9	0.07	16.7	19	15.8–17.8	0.53	19.2	19	17.7–20.5	0.67
Hoquiam, WA	4.7	21	4.4–5.0	0.17	1.8	23	1.6–1.9	0.07	16.3	24	15.3–16.9	0.38	18.6	25	17.6–19.4	0.48
Owen's Lake, CA	4.5	23	4.0–5.1	0.29	1.7	23	1.5–1.8	0.07	16.4	22	15.6–17.4	0.47	18.5	23	17.2–20.1	0.75
Eureka, CA	4.9	14	4.3–5.6	0.40	1.8	13	1.7–2.1	0.11	16.4	14	15.6–17.3	0.56	19.0	14	18.0–20.6	0.74

APPENDIX 2. CONTINUED

Locality	Gonys				Mandible depth				Coracoid length				Scapula length			
	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.
Morro Bay, CA	4.7	10	4.2–5.1	0.26	1.8	10	1.7–1.8	0.05	15.9	11	15.4–16.4	0.36	18.3	11	17.5–19.0	0.44
San Diego, CA	5.0	12	4.2–5.4	0.29	1.8	14	1.7–1.9	0.08	16.1	15	15.3–16.8	0.41	17.9	14	16.6–18.8	0.68
Bahia San Quintin, B.C.N.	5.2	13	4.8–6.0	0.32	1.9	11	1.8–2.0	0.06	15.8	14	15.4–16.2	0.25	18.2	13	17.1–18.8	0.49
Guerrero Negro, B.C.S.	5.4	19	4.5–5.9	0.28	2.0	20	1.8–2.1	0.08	16.2	22	15.4–16.7	0.28	18.4	21	17.7–19.1	0.40
Bahia Magdalena, B.C.S.	5.9	10	5.4–6.5	0.36	2.1	14	2.0–2.3	0.08	16.7	15	16.2–17.4	0.30	18.6	13	17.7–19.8	0.51
Puerto Peñasco, Sonora	5.5	4	5.0–5.8	0.33	2.3	4	2.2–2.5	0.13	16.3	4	16.1–16.6	0.22	18.2	4	17.5–19.0	0.61
Bahia Kino, Sonora	5.8	11	5.4–6.2	0.28	2.3	13	2.1–2.4	0.09	16.7	12	16.1–17.4	0.37	18.6	14	17.4–19.2	0.47
El Molino, Sinaloa	5.9	6	5.5–6.3	0.33	2.3	8	2.1–2.4	0.10	16.6	8	16.1–17.2	0.39	18.8	8	17.6–19.7	0.63
Charco Redondo, Jalisco	4.7	6	4.4–4.9	0.19	1.7	5	1.6–1.7	0.04	16.3	7	15.9–16.8	0.32	18.6	7	17.7–19.4	0.60
Lerma, México	5.0	5	4.7–5.3	0.24	1.9	5	1.8–1.9	0.05	17.2	6	16.7–17.3	0.23	19.3	6	18.7–19.9	0.46

APPENDIX 2. CONTINUED

Locality	Femur length				Femur width				Tibiotarsus length				Tarsometatarsus length			
	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.
Sable Is., N.S.	18.7	16	18.1–19.5	0.42	1.4	16	1.3–1.5	0.04	31.3	14	29.8–32.5	0.71	22.3	16	21.0–23.1	0.64
Halifax, N.S.	17.2	15	16.6–17.6	0.27	1.2	15	1.2–1.4	0.06	28.7	14	27.5–29.4	0.51	20.7	15	19.9–21.5	0.46
River John, N.S.	17.0	24	16.3–17.7	0.38	1.3	24	1.2–1.3	0.05	28.5	23	26.5–30.2	0.96	20.5	23	18.8–21.8	0.72
Pasadena, NFLD	17.1	10	16.4–18.0	0.55	1.3	10	1.2–1.4	0.06	28.8	8	25.5–30.3	1.05	20.7	10	19.5–21.9	0.90
St. Andrews, N.B.	16.9	17	16.3–17.5	0.27	1.2	17	1.1–1.3	0.06	28.1	15	27.1–29.2	0.62	20.3	15	19.4–21.2	0.53
Matane, QUE	16.8	21	16.0–18.1	0.46	1.2	22	1.1–1.4	0.07	28.0	19	26.5–30.6	0.92	20.0	21	18.8–21.5	0.76
Magdalen Is., QUE	17.3	15	16.9–17.6	0.21	1.3	15	1.3–1.4	0.04	29.0	15	27.8–29.6	0.49	20.9	15	20.2–21.7	0.49
Kuujjuaq, QUE	16.9	24	15.9–17.7	0.43	1.3	24	1.1–1.4	0.07	28.5	21	26.9–29.7	0.59	20.4	24	18.7–21.1	0.56
Brandonville, WV	16.7	11	16.2–17.2	0.30	1.3	11	1.2–1.4	0.04	27.9	11	27.1–28.9	0.62	20.0	10	18.7–20.9	0.70
Wildfield, ON	17.1	11	16.4–17.5	0.34	1.3	11	1.2–1.3	0.04	28.4	1	27.6–29.4	0.60	20.1	11	19.3–20.9	0.61
Wallaceburg, ON	16.7	14	16.3–17.4	0.35	1.2	15	1.1–1.3	0.08	27.9	15	27.2–7	0.52	20.1	15	19.4–20.6	0.37
Sowerby, ON	16.6	9	16.2–16.9	0.25	1.3	9	1.2–1.3	0.05	27.5	9	26.4–28.4	0.58	20.0	8	19.2–20.5	0.49
Moosonee, ON	17.0	31	16.0–17.7	0.40	1.2	31	1.2–1.3	0.05	28.0	31	26.9–29.6	0.61	20.1	28	19.2–21.2	0.56
Attawapiskat, ON	16.9	26	16.1–17.9	0.40	1.2	26	1.1–1.4	0.06	27.9	20	26.8–29.5	0.66	20.1	23	19.1–21.0	0.43
Winisk, ON	17.1	21	16.3–17.5	0.30	1.2	21	1.2–1.3	0.05	28.3	17	27.0–29.5	0.59	20.2	19	19.2–21.1	0.48
Thunder Bay, ON	16.7	12	16.2–17.4	0.42	1.2	12	1.1–1.3	0.06	27.5	12	26.5–28.4	0.59	19.7	12	19.1–20.3	0.39
Delta, MAN	16.5	20	15.8–17.5	0.36	1.2	21	1.1–1.3	0.07	26.9	21	25.7–27.7	0.48	19.4	20	18.4–20.1	0.52
Churchill, MAN	16.9	18	16.2–17.6	0.36	1.3	18	1.2–1.3	0.05	28.0	18	26.7–28.9	0.64	20.3	16	19.6–21.2	0.53
Coppermine, N.W.T.	16.6	16	16.0–17.4	0.40	1.3	16	1.2–1.3	0.05	27.5	16	26.7–29.0	0.77	19.7	16	18.7–20.9	0.66
Norman Wells, N.W.T.	16.7	22	16.2–17.0	0.27	1.2	22	1.1–1.3	0.05	27.9	19	26.3–28.9	0.68	20.1	22	19.0–21.3	0.58
Inuvik, N.W.T.	16.7	14	16.2–17.5	0.35	1.2	14	1.1–1.3	0.07	27.8	13	26.5–28.7	0.66	20.0	13	19.0–21.0	0.52
Grande Prairie, ALTA	16.5	23	15.5–17.3	0.43	1.2	24	1.1–1.3	0.06	26.9	17	26.0–28.2	0.62	19.3	22	18.3–20.3	0.50
Koyuk, AK	16.5	21	15.8–17.2	0.38	1.1	21	1.0–1.3	0.07	27.4	21	25.9–28.2	0.66	19.8	21	18.7–20.8	0.54
Wasilla, AK	16.6	21	16.1–17.4	0.32	1.3	23	1.1–1.4	0.07	27.7	21	26.9–28.5	0.56	20.0	23	19.1–21.2	0.56
Umnak Is., AK	18.3	22	17.6–19.3	0.43	1.4	24	1.3–1.4	0.05	30.5	24	29.3–31.5	0.55	21.9	24	20.9–22.7	0.52
Cold Bay, AK	17.7	8	17.1–18.1	0.39	1.3	8	1.2–1.3	0.05	29.5	8	28.4–30.1	0.61	21.2	8	20.7–21.8	0.38
Port Heiden, AK	17.2	13	16.3–18.0	0.42	1.3	13	1.1–1.4	0.07	28.6	13	26.7–29.6	0.72	20.6	13	19.6–21.3	0.46
Middleton Is., AK	17.3	20	16.7–18.1	0.42	1.3	20	1.2–1.4	0.05	28.9	20	27.5–30.0	0.69	21.0	20	19.6–22.2	0.65
Sheridan, WY	16.6	17	15.4–17.0	0.45	1.2	17	1.1–1.3	0.07	26.9	14	25.5–27.7	0.54	19.4	17	18.1–20.4	0.60
Woodruff, UT	16.9	17	15.8–17.5	0.48	1.2	17	1.2–1.3	0.05	26.8	15	26.9–28.5	0.51	20.2	16	19.0–21.1	0.58
Halleck, NV	16.6	9	16.1–17.3	0.42	1.2	9	1.2–1.3	0.04	27.4	9	26.6–28.3	0.61	19.7	9	18.9–20.4	0.51
Creston, WA	16.7	18	16.1–17.7	0.51	1.2	19	1.1–1.4	0.08	27.5	19	26.3–28.9	0.72	19.5	19	18.5–21.3	0.71
Hoquiam, WA	16.4	24	15.7–17.2	0.44	1.2	25	1.1–1.3	0.04	27.0	22	26.1–28.2	0.62	19.6	21	18.4–20.2	0.48
Owen's Lake, CA	16.7	23	15.9–17.4	0.39	1.2	23	1.1–1.3	0.05	27.4	18	26.5–28.6	0.58	19.7	23	18.7–20.9	0.59
Eureka, CA	17.0	14	16.1–17.8	0.47	1.2	14	1.1–1.3	0.06	28.0	12	26.3–29.9	0.86	20.1	12	19.3–21.3	0.57

APPENDIX 2. CONTINUED

Locality	Femur length				Femur width				Tibiotarsus length				Tarsometatarsus length			
	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.
Morro Bay, CA	16.6	10	15.6–17.2	0.61	1.2	11	1.1–1.3	0.05	27.2	10	25.3–28.1	0.88	19.6	11	18.4–20.7	0.75
San Diego, CA	16.6	15	16.2–17.4	0.43	1.2	15	1.1–1.4	0.08	27.5	14	26.5–28.7	0.58	19.8	15	18.4–20.9	0.58
Bahia San Quintin, B.C.N.	16.5	15	15.9–17.3	0.37	1.1	15	1.1–1.2	0.05	27.5	15	26.2–28.4	0.70	19.7	15	18.7–20.6	0.58
Guerrero Negro, B.C.S.	17.1	23	16.0–17.9	0.45	1.1	23	1.1–1.2	0.05	28.6	22	26.9–29.8	0.70	20.5	21	19.7–21.5	0.47
Bahia Magdalena, B.C.S.	17.7	15	16.9–18.2	0.38	1.2	15	1.1–1.3	0.06	29.3	15	28.6–30.0	0.43	21.1	15	20.4–22.0	0.40
Puerto Peñasco, Sonora	17.2	4	16.9–17.5	0.25	1.2	4	1.2–1.3	0.05	29.0	4	28.4–29.8	0.61	21.3	4	20.5–21.7	0.53
Bahia Kino, Sonora	17.5	14	16.3–18.3	0.46	1.2	14	1.1–1.3	0.05	29.1	12	26.9–30.3	0.91	21.1	13	19.2–22.6	0.83
El Molino, Sinaloa	17.5	8	16.8–17.0	0.40	1.2	8	1.2–1.3	0.05	29.4	8	28.3–30.5	0.85	20.9	7	19.9–22.0	0.71
Charco Redondo, Jalisco	17.0	7	15.9–18.0	0.69	1.2	7	1.1–1.3	0.06	27.8	7	26.2–29.3	0.92	20.4	6	19.6–21.0	0.48
Lerma, México	17.4	6	16.7–18.2	0.50	1.3	6	1.2–1.3	0.05	28.5	6	27.7–29.1	0.56	20.7	6	20.0–21.2	0.39

APPENDIX 2. CONTINUED.

Locality	Humerus length				Ulna length				Carpometacarpus length				Hallux length			
	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.
Sable Is., N.S.	19.7	15	19.0–22.0	0.75	22.2	14	21.5–22.7	0.40	12.5	16	12.0–13.1	0.32	9.2	16	8.5–10.1	0.40
Halifax, N.S.	18.0	15	17.7–18.5	0.25	20.7	15	20.2–21.3	0.31	11.4	15	11.0–11.9	0.28	8.3	14	8.0–8.8	0.25
River John, N.S.	17.9	24	17.2–18.8	0.43	20.4	24	19.3–21.5	0.52	11.3	21	10.7–11.7	0.26	8.1	24	7.7–8.8	0.26
Pasadena, NFLD	17.8	8	17.2–18.8	0.50	20.6	9	19.8–21.3	0.49	11.3	8	11.0–11.7	0.26	8.2	10	7.8–8.7	0.31
St. Andrews, N.B.	17.9	16	17.4–18.6	0.33	20.6	18	19.9–21.4	0.35	11.4	18	10.9–11.7	0.24	8.0	16	7.6–8.5	0.26
Matane, QUE	17.8	21	17.0–9.3	0.46	20.4	20	19.7–21.9	0.49	11.1	20	10.1–12.0	0.38	8.0	21	7.5–8.4	0.25
Magdalen Is., QUE	18.1	14	17.2–18.5	0.31	20.7	15	20.2–21.1	0.27	11.4	15	11.1–11.9	0.23	8.3	15	7.8–8.9	0.34
Kuujjuaq, QUE	17.9	23	17.0–18.6	0.43	20.5	24	19.4–21.3	0.52	11.3	24	10.8–12.0	0.30	7.9	24	7.5–8.4	0.26
Brandonville, WV	17.8	11	17.4–18.4	0.29	20.2	10	19.6–20.7	0.35	11.2	10	10.7–11.5	0.22	7.9	10	7.3–8.3	0.32
Wildfield, ON	18.1	11	17.5–18.8	0.34	20.8	11	20.4–21.7	0.39	11.4	11	11.0–11.8	0.24	8.0	11	7.5–8.5	0.29
Wallaceburg, ON	17.7	14	17.3–18.0	0.23	20.4	15	19.8–20.9	0.32	11.2	15	10.7–11.8	0.27	7.9	14	7.5–8.2	0.23
Sowerby, ON	17.7	9	17.2–18.0	0.27	20.2	9	19.8–20.6	0.25	11.1	9	10.9–11.5	0.19	7.8	9	7.4–8.3	0.29
Moosonee, ON	18.1	31	17.3–19.2	0.42	20.8	31	20.0–22.3	0.49	11.5	28	11.0–12.1	0.24	7.9	28	7.5–8.9	0.30
Attawapiskat, ON	17.9	26	17.0–18.6	0.43	20.6	25	19.7–21.3	0.40	11.3	26	10.6–11.8	0.27	7.8	26	7.3–8.3	0.23
Winisk, ON	18.2	18	17.4–18.8	0.33	20.9	21	20.1–21.5	0.44	11.6	20	11.1–12.0	0.27	7.9	17	7.5–8.3	0.29
Thunder Bay, ON	17.8	12	17.2–18.3	0.33	20.3	12	19.8–21.0	0.41	11.3	12	10.8–11.8	0.30	7.8	11	7.5–8.3	0.27
Delta, MAN	17.7	20	16.7–18.2	0.40	20.1	20	19.1–21.0	0.54	11.1	17	10.6–11.8	0.31	7.6	21	6.8–8.3	0.36
Churchill, MAN	18.0	18	17.5–18.9	0.39	20.7	18	19.6–21.6	0.53	11.5	18	10.9–12.2	0.32	7.8	14	7.4–8.4	0.27
Coppermine, N.W.T.	17.8	15	17.4–18.4	0.29	20.3	15	19.1–21.2	0.57	11.2	16	10.6–11.9	0.35	7.6	15	7.2–8.0	0.25
Norman Wells, N.W.T.	17.8	22	17.1–18.1	0.27	20.5	21	19.6–21.3	0.40	11.3	19	10.8–11.8	0.28	7.8	17	7.4–8.3	0.23
Inuvik, N.W.T.	17.8	14	16.9–18.2	0.26	20.5	14	19.8–20.9	0.34	11.4	14	11.0–11.8	0.23	7.9	14	7.5–8.3	0.26
Grande Prairie, ALTA	17.6	22	17.0–18.5	0.38	20.1	22	19.2–20.8	0.46	11.2	23	10.6–11.7	0.27	7.7	24	7.0–8.5	0.36
Koyuk, AK	17.4	21	16.8–18.1	0.34	20.2	21	19.4–21.1	0.38	11.3	21	10.8–11.7	0.25	7.7	21	7.1–8.1	0.25
Wasilla, AK	17.6	23	16.9–18.4	0.36	20.5	23	19.8–21.2	0.38	11.4	23	10.9–12.1	0.29	7.8	21	7.4–8.3	0.23
Umnak Is., AK	18.8	24	18.2–19.4	0.37	21.8	24	21.2–22.7	0.47	12.4	24	11.8–12.8	0.30	8.5	24	8.1–9.0	0.24
Cold Bay, AK	18.4	8	17.8–19.0	0.42	21.2	8	20.3–21.7	0.45	11.9	7	11.6–12.1	0.17	8.3	8	8.0–8.7	0.24
Port Heiden, AK	17.8	12	17.0–18.4	0.35	20.6	13	19.8–21.3	0.35	11.7	12	11.2–11.8	0.17	8.1	13	7.5–8.5	0.30
Middleton Is., AK	18.1	20	17.4–18.8	0.42	21.0	20	20.0–21.9	0.48	11.8	20	11.3–12.3	0.29	8.2	20	7.9–8.6	0.21
Sheridan, WY	17.7	17	16.9–18.3	0.39	20.2	17	19.1–21.0	0.51	11.2	17	10.6–11.7	0.31	7.6	17	7.2–8.0	0.24
Woodruff, UT	18.0	15	17.2–18.6	0.39	20.8	15	20.0–21.4	0.36	11.5	15	11.0–11.8	0.28	7.9	13	7.5–8.3	0.26
Halleck, NV	17.8	9	17.1–18.4	0.38	20.6	9	19.9–21.4	0.41	11.3	9	10.8–11.8	0.34	7.8	9	7.1–8.4	0.41
Creston, WA	17.8	17	17.3–19.2	0.45	20.6	19	20.0–21.9	0.53	11.3	19	10.7–12.1	0.32	7.6	19	7.2–8.4	0.33
Hoquiam, WA	17.4	21	16.7–18.0	0.43	19.9	24	19.1–20.6	0.43	11.0	22	10.5–11.4	0.26	7.8	24	7.3–8.4	0.32
Owen's Lake, CA	17.7	23	17.0–18.5	0.45	20.3	22	19.3–21.2	0.43	11.1	22	10.7–12.0	0.30	7.7	22	7.2–8.2	0.31
Eureka, CA	17.6	14	17.0–18.4	0.41	20.0	13	19.3–21.1	0.50	11.1	14	10.7–11.8	0.33	8.1	14	7.7–8.9	0.38

APPENDIX 2. CONTINUED.

Locality	Humerus length				Ulna length				Carpometacarpus length				Hallux length			
	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.
Morro Bay, CA	17.3	10	16.9–17.8	0.30	19.6	11	18.9–20.1	0.33	10.8	11	10.3–11.2	0.24	7.6	11	7.2–7.9	0.24
San Diego, CA	17.1	15	16.7–17.5	0.30	19.3	15	18.7–19.8	0.32	10.7	13	10.4–11.1	0.22	7.6	15	7.3–8.0	0.20
Bahia San Quintin, B.C.N.	17.1	14	16.5–17.6	0.32	19.3	14	18.9–20.2	0.40	10.7	15	10.3–11.2	0.24	7.6	14	7.2–8.3	0.33
Guerrero Negro, B.C.S.	17.5	22	16.6–18.2	0.37	19.8	21	18.7–20.4	0.38	11.0	21	10.0–11.8	0.32	7.7	23	7.2–8.2	0.27
Bahia Magdalena, B.C.S.	18.0	14	17.5–18.2	0.19	20.4	15	19.9–20.8	0.25	11.2	14	10.9–11.8	0.21	7.9	15	7.5–8.2	0.20
Puerto Peñasco, Sonora	17.9	4	17.6–18.4	0.34	20.6	4	20.0–20.9	0.39	11.5	4	11.2–11.6	0.19	7.8	4	7.5–8.0	0.22
Bahia Kino, Sonora	18.1	13	17.0–18.6	0.45	20.5	12	19.2–21.2	0.65	11.3	13	10.7–11.8	0.30	7.7	13	7.5–8.2	0.24
El Molino, Sinaloa	18.0	8	17.3–18.6	0.46	20.5	7	19.8–21.3	0.56	11.3	8	10.9–11.6	0.22	7.6	8	7.2–8.1	0.30
Charco Redondo, Jalisco	17.9	6	17.6–18.6	0.37	20.6	6	20.0–21.4	0.57	11.1	7	10.8–11.5	0.24	8.0	6	7.6–8.5	0.33
Lerma, México	18.5	6	18.4–18.8	0.16	21.5	5	21.4–21.6	0.09	11.4	6	11.1–11.6	0.22	8.0	6	7.9–8.2	0.12

APPENDIX 2. CONTINUED.

Locality	Sternum length				Sternum depth				Keel length				Synsacrum width			
	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.
Sable Is., N.S.	21.5	16	20.3–22.0	0.46	10.0	16	9.4–10.9	0.40	20.3	16	18.6–21.6	0.83	11.6	16	10.9–12.4	0.41
Halifax, N.S.	19.8	14	18.6–20.6	0.56	8.8	14	8.3–9.5	0.37	18.3	14	17.0–19.6	0.74	10.4	14	9.8–11.2	0.40
River John, N.S.	19.5	23	18.6–20.6	0.59	9.0	23	8.2–9.5	0.36	18.2	21	17.3–19.4	0.59	10.3	23	9.7–10.8	0.26
Pasadena, NFLD	19.9	6	19.4–21.1	0.66	8.9	7	8.1–9.4	0.42	18.9	5	18.5–19.3	0.34	10.5	8	10.0–10.9	0.28
St. Andrews, N.B.	19.7	16	19.2–20.5	0.41	8.9	17	8.2–9.4	0.37	18.3	16	17.1–19.6	0.78	10.4	17	9.7–11.1	0.35
Matane, QUE	19.4	20	18.2–21.2	0.62	8.9	20	8.3–9.4	0.32	18.1	22	17.0–19.7	0.59	10.2	20	9.7–10.8	0.32
Magdalen Is., QUE	19.4	13	18.2–20.4	0.56	8.6	13	8.1–9.0	0.22	17.9	13	16.7–19.4	0.76	10.5	15	9.9–11.1	0.35
Kuujjuaq, QUE	19.3	22	18.7–20.4	0.51	8.8	23	7.9–9.4	0.37	18.1	23	16.8–19.9	0.81	10.4	23	9.8–10.9	0.28
Brandonville, WV	19.3	10	19.1–19.7	0.18	8.7	11	8.3–9.1	0.24	18.0	10	17.4–18.5	0.37	10.2	9	9.8–10.5	0.24
Wildfield, ON	19.5	9	18.6–20.3	0.56	8.7	10	8.3–9.2	0.27	18.4	10	17.5–19.2	0.63	10.4	11	10.0–10.8	0.23
Wallaceburg, ON	19.2	15	18.2–20.2	0.63	8.9	15	8.3–9.8	0.39	18.1	15	17.1–19.5	0.75	10.3	14	9.7–10.8	0.28
Sowerby, ON	19.0	9	18.4–19.6	0.45	8.6	9	8.2–9.1	0.29	17.9	9	16.9–19.2	0.63	10.0	9	9.5–10.5	0.31
Moosonee, ON	19.6	30	18.9–20.7	0.49	9.0	30	8.0–10.0	0.43	18.6	29	17.4–20.0	0.66	10.4	28	9.9–11.0	0.23
Attawapiskat, ON	19.3	26	18.0–20.5	0.73	9.0	25	8.3–9.6	0.34	18.3	24	18.6–20.3	0.97	10.3	23	9.7–11.0	0.36
Winisk, ON	19.5	19	18.7–20.4	0.48	8.9	21	8.4–9.9	0.34	18.2	18	16.9–19.0	0.66	10.5	17	10.0–11.1	0.31
Thunder Bay, ON	19.3	11	18.0–20.2	0.70	8.5	10	8.0–9.3	0.43	18.2	11	16.9–19.5	0.82	10.1	12	9.7–10.4	0.22
Delta, MAN	19.3	20	17.6–20.5	0.72	8.7	20	8.0–9.4	0.41	18.1	21	16.2–19.9	0.92	10.0	15	9.0–10.3	0.33
Churchill, MAN	19.8	16	19.2–20.5	0.43	8.6	15	8.0–9.1	0.34	18.7	16	17.5–19.8	0.52	10.5	16	9.9–11.3	0.32
Coppermine, N.W.T.	19.0	14	18.2–20.0	0.49	8.4	14	7.8–9.0	0.38	17.9	15	17.0–19.2	0.55	10.2	16	9.6–10.8	0.30
Norman Wells, N.W.T.	19.3	22	18.2–20.2	0.58	8.8	19	8.2–9.6	0.35	18.3	20	17.1–19.4	0.56	10.2	22	9.7–10.9	0.28
Inuvik, N.W.T.	19.3	14	18.5–20.4	0.43	8.6	14	7.8–9.1	0.36	18.5	14	17.5–19.4	0.47	10.3	14	10.0–10.9	0.23
Grande Prairie, ALTA	19.1	22	17.7–19.9	0.55	8.6	22	8.2–9.1	0.28	18.0	22	16.7–19.2	0.69	10.1	19	9.7–10.7	0.29
Koyuk, AK	19.2	21	18.2–20.6	0.73	8.6	21	7.7–9.5	0.46	18.2	21	16.5–20.4	1.05	10.3	21	9.9–10.8	0.23
Wasilla, AK	19.4	23	18.2–20.3	0.56	8.8	23	8.2–9.2	0.28	18.5	23	17.0–19.4	0.72	10.2	22	9.7–10.7	0.26
Umnak Is., AK	21.0	23	19.7–22.6	0.57	9.3	23	7.8–10.2	0.50	19.6	23	18.6–21.7	0.57	11.3	23	10.8–12.2	0.36
Cold Bay, AK	20.6	8	19.5–21.8	0.90	9.1	7	8.4–9.6	0.42	19.2	7	18.0–20.2	0.82	10.8	7	10.5–11.0	0.21
Port Heiden, AK	20.0	12	19.2–20.9	0.47	9.1	12	8.2–10.0	0.47	18.8	12	18.0–20.4	0.74	10.6	13	10.2–11.3	0.31
Middleton Is., AK	20.3	20	19.5–21.3	0.53	8.7	20	8.1–9.3	0.31	18.7	19	17.5–20.2	0.69	10.8	19	9.8–11.5	0.43
Sheridan, WY	19.2	16	18.3–20.0	0.56	8.7	16	8.1–9.1	0.30	18.2	16	16.9–19.5	0.75	10.0	16	9.3–10.6	0.29
Woodruff, UT	19.4	17	17.6–20.1	0.58	8.6	17	7.8–9.0	0.37	18.6	17	16.7–19.6	0.67	10.2	16	9.7–10.6	0.26
Halleck, NV	19.1	7	18.6–19.8	0.50	8.7	7	8.2–9.2	0.36	18.2	9	17.5–18.9	0.54	10.1	9	9.7–10.8	0.31
Creston, WA	19.3	19	18.1–21.1	0.79	8.7	19	8.3–9.4	0.34	18.4	18	16.6–19.6	0.75	10.2	19	9.6–10.7	0.30
Hoquiam, WA	18.9	23	17.9–19.9	0.52	8.8	24	8.1–9.4	0.31	18.1	23	17.0–19.4	0.73	10.1	25	9.1–10.8	0.41
Owen's Lake, CA	18.8	21	17.3–20.2	0.73	8.4	22	7.6–9.3	0.43	17.7	21	16.3–19.8	0.80	9.9	22	9.2–10.3	0.26
Eureka, CA	19.1	13	18.3–20.5	0.69	8.6	14	8.0–9.0	0.30	18.0	13	16.8–19.4	0.76	10.4	13	10.0–10.8	0.20

APPENDIX 2. CONTINUED.

Locality	Sternum length				Sternum depth				Keel length				Synsacrum width			
	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.	Mean	N	Range	S.D.
Morro Bay, CA	18.6	11	17.9–19.5	0.47	8.4	11	7.6–8.6	0.29	17.0	11	15.7–18.2	0.74	10.4	10	10.1–10.6	0.19
San Diego, CA	18.6	15	17.8–19.6	0.49	8.4	15	7.9–8.8	0.32	17.1	15	15.5–18.2	0.69	10.1	14	9.7–10.4	0.23
Bahia San Quintin, B.C.N.	18.3	12	17.4–18.9	0.45	8.3	14	7.6–9.1	0.47	16.9	13	15.7–17.7	0.61	10.3	12	10.0–10.7	0.24
Guerrero Negro, B.C.S.	18.8	21	18.2–19.6	0.38	8.6	20	8.1–9.0	0.24	17.4	21	16.5–18.7	0.58	10.7	20	10.1–11.3	0.30
Bahia Magdalena, B.C.S.	19.0	15	18.5–19.7	0.33	8.8	15	8.4–9.4	0.27	17.6	15	17.1–18.4	0.38	10.7	15	9.9–11.1	0.29
Puerto Peñasco, Sonora	18.5	4	18.2–18.8	0.25	8.2	4	7.9–8.4	0.22	18.9	4	16.4–17.6	0.57	10.4	4	10.3–10.5	0.08
Bahia Kino, Sonora	19.1	13	18.0–20.3	0.69	8.7	13	8.1–9.2	0.28	18.0	13	16.2–19.2	0.85	10.8	12	10.4–11.4	0.33
El Molino, Sinaloa	19.2	8	18.2–20.0	0.59	8.5	8	8.1–8.8	0.26	17.7	8	16.4–18.5	0.80	10.9	8	10.6–11.2	0.23
Charco Redondo, Jalisco	18.8	7	18.1–19.6	0.51	8.5	7	8.2–8.9	0.28	17.7	7	16.7–19.2	0.8	10	6	9.2–10.5	0.44
Lerma, México	19.5	5	18.7–20.4	0.62	8.7	5	8.2–9.3	0.47	18.3	5	17.9–19.2	0.53	10.1	4	9.8–10.3	0.24