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).