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GEOGRAPHIC VARIATION IN TESTIS SIZE IN SAVANNAH SPARROWS (*PASSERCULUS SANDWICHENSIS*)

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Abstract.—Body size and testis size are positively correlated among 1165 Savannah Sparrows (*Passerculus sandwichensis*) from 48 localities. Body size accounts for 5–7% of the variation among individuals in testis size, and for about 30% of the variation in average testis size among populations. Testis size and latitude are negatively correlated, and latitude per se better predicts testis size than does a variety of direct measures of the climatic environments at the collecting sites. The testis sizes of males from polygynous populations average larger than those of males from monogamous populations. However, the differences between "polygynous" and "monogamous" males are slight, and males from Halifax and Sable Island, Nova Scotia, where the species is known to be polygynous, have *smaller* testes than predicted. There is no correlation between testis size and the amount or extent of yellow in the superciliary stripe—a measure of plumage brightness. The average testis volume of Savannah Sparrows resident in saltmarshes along the west coast of Mexico and southern California is greater than that from other populations. *Received 22 Jan. 1986, accepted 14 July 1986.*

In birds, there is a pronounced increase in the size of the testes during the breeding season. Histologically, this increase in size occurs primarily as a consequence of the enlargement of the seminiferous tubules, in which sperm are produced (Lofts and Murton 1973). In Great Tits (*Parus major*), resident in Sweden, the testes remain large throughout the mating season even though the size of the Leydig cells (where testosterone is produced) decreases after the period of time during which male territoriality is maximal (Silverin 1978, Röhss and Silverin 1983). Similarly, Wingfield (1984) found that testes of male Song Sparrows (*Melospiza melodia*) are maximally enlarged when females are laying, and hence when they are copulating. The testes of Song Sparrows from New York, where birds are double-brooded, remain maximally large until after the second brood has been laid, even though endocrine activity decreases substantially before the young in the first brood have hatched. Therefore, it is reasonable to assume that the testis size is an approximate reflection of the quantity of sperm produced, and hence of sperm demand, although this has not been shown directly for any bird species.

In primates, males in genera with multimale breeding systems have relatively larger testes than do males in genera with single-male breeding

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systems. In multimale species, several males may copulate with an estrous female, and it appears that sperm competition selects for large testis size (Harcourt et al. 1981). In birds, Cartar (1985) found that among 18 species of sandpipers (Subfamily Calidridinae), males of species with nonmonogamous mating systems generally had larger testes (relative to body mass) than did males of species with monogamous mating systems. In shorebirds the opportunity for males of nonmonogamous species to mate with several females in a season is probably a more important factor than sperm competition in the evolution of testis size (Cartar 1985).

Here, I relate interpopulational variation in testis size within Savannah Sparrows (*Passerculus sandwichensis*) to body size and presumed age, as well as to various aspects of natural history, including differences in breeding biology.

Savannah Sparrows are widespread and abundant North American songbirds. Throughout most of their range, they breed in mesic sedge or grass meadows, hayfields, or pastures. In the southwestern United States and western Mexico, however, they breed in coastal saltmarshes. In contrast to other Savannah Sparrows, which are migratory, these saltmarsh sparrows are resident, although there is some postbreeding wandering (van Rossem 1947). There have been several studies of the natural history of nonsaltmarsh Savannah Sparrows, but little is known about the biology of the saltmarsh birds. Therefore, I shall analyze interpopulational variation in testis size in the nonsaltmarsh and the saltmarsh birds separately.

The mating system of Savannah Sparrows varies from population to population. Stobo and McLaren (1975) and Welsh (1975) found that males are frequently polygynous on Sable Island and near Halifax, Nova Scotia, whereas Weatherhead (1979) and Bédard and Meunier (1983) found them to be monogamous near Churchill, Manitoba, and Isle Verte, Quebec.

I assume that sperm demands are highest in the populations where males are commonly polygynous, where males are selected to be capable of fertilizing two clutches of eggs in relatively less time than in "monogamous" populations, and, on occasion, to do so virtually simultaneously. I predict that this would select for relatively larger testes (greater volume of seminiferous tubules) in such places.

METHODS

I collected samples of Savannah Sparrows from sites throughout North America, including Sable Island and Halifax, Nova Scotia, and Churchill, Manitoba. When possible, I measured the length and width of the largest (almost always the left) testis on each specimen. I made the majority of the measurements, but for some samples others took the measurements. Each specimen was weighed and the skin and skeleton saved and measured (these are in the Royal Ontario Museum, Toronto, Canada); thus I have information about both body and testis size and plumage coloration for each individual.

I used testis volume as a measure of testis size and estimated volumes using the formula for the volume of a prolate spheroid, where volume = 0.52(length)(width)^2. Because these volumes are log-normally distributed, I used a log transformation of volume to facilitate statistical analyses. Cartar (1985) used testis length as a measure of testis size.

As mentioned above, of the many factors that may affect testis size within a species, seasonal variation in gonadal activity is surely the most important. Here I present data only on "breeding" males, that is, males that, when collected, were apparently on territories during a time of the year when the majority of males were establishing territories, defending territories, or feeding young. In total, I have information on 1433 "breeding" male Savannah Sparrows, but for these analyses not all of these were used. I have omitted samples taken either very early or very late in the breeding season, and discarded small samples, leaving 1020 nonsaltmarsh and 145 saltmarsh birds from 48 different localities. From two localities, Kleinburg, Ontario, and Woodruff, Utah, there are two different samples taken on different dates and in different years (Table 1).

Among the 48 samples from different localities, several, in addition to those from Sable Island and Halifax, are from maritime Canada (Table 1). Because the ecological conditions at these sites are similar to those at Sable Island and Halifax, I assume that males in these populations are similarly selected to be polygynous. While this seems a reasonable assumption, it might not be a correct one. Dixon (1978) did not find polygyny in Savannah Sparrows breeding on Kent Island, New Brunswick, although this was not apparently an aspect of breeding biology that she was especially studying.

For a sample of populations probably selected to be monogamous, I used, in addition to Churchill, Manitoba, 7 other samples from high latitudes, where the breeding season is short; Weatherhead (1979) found that it was the short nesting season that selected for monogamy at Churchill. Additionally, Lein (1968, pers. comm.) and Potter (1972, 1974, pers. comm.), who studied Savannah Sparrows near Saskatoon, Saskatchewan, and Ann Arbor, Michigan, respectively, found that, on their study sites, the sparrows were almost always monogamous. On the basis of these studies, I included 3 samples from the Canadian prairies and one from Wallaceburg, Ontario (close to Ann Arbor) in the monogamous sample (Table 1). Because monogamy is apparently widespread in the species, it is probable that many if not all of the samples in the "unknown mating system" category are composed of generally monogamous males; the selection of these 11 samples for the "monogamous" group is conservative.

In the following analyses, I used the information on each individual when relating testis size to characteristics of individuals (e.g., body size, "age"). Because all of the variables are normal deviates and the variances are homogeneous, I used parametric correlation analyses to assess the significance of relationships between variables, and t-tests or ANOVA to assess significance of differences between or among groups. I used regression and correlation analyses to assess the relationship between testis size and the log of weight among individuals. Because there is a significant relationship between testis size and weight (see below), in some analyses I used the residual values of testis volume, regressed against log weight, to "correct" for variation in body size.

In Northern ("Baltimore") Orioles (*Icterus galbula*), males breeding in their first year have smaller testes than do older breeding males (Flood 1980). As in orioles, Bédard and LaPointe (1984) found that the proportion of yearling Savannah Sparrow males that obtained mates was significantly less than the proportion of older males that obtained mates. Therefore, the average sperm demand on yearling males would be less than that for older ones, perhaps leading to (or because of) smaller testis size. I have no direct way to assess the age of the Savannah Sparrows used in this study (they were all at least one year old). However, the brightness of the plumage increases with age in many species. There is little apparent

TABLE 1

SAVANNAH SPARROW TESTIS VOLUMES AND FEMUR LENGTHS

Location	*N*	Femur length[a]	Volume[b]	Latitude[c]
"Polygynous" samples				
Sable Island, Nova Scotia	24	19.0	5.61	44.00
Halifax, Nova Scotia	12	17.7	5.50	44.67
River John, Nova Scotia	31	17.6	5.78	45.84
Parson's Pond, Newfoundland	13	17.7	5.45	50.00
Bedeque, Prince Edward Island	25	17.3	5.56	46.33
St. Andrews, New Brunswick	21	17.4	5.69	45.16
Magdalen Islands, Quebec	28	17.6	5.44	47.50
"Monogamous" samples				
Churchill, Manitoba	28	17.2	5.30	58.84
Gillam, Manitoba	17	17.2	5.28	56.33
Ft. Chimo, Quebec	20	17.5	5.39	58.16
Winisk, Ontario	40	17.3	5.42	55.33
Yellowknife, Northwest Territories	15	16.9	5.15	62.50
Norman Wells, N.W.T.	21	17.0	5.18	65.33
Coppermine, N.W.T.	30	17.1	5.49	67.84
Inuvik, N.W.T.	14	16.8	5.07	68.33
Wallaceburg, Ontario	37	17.3	5.45	42.67
Milk River, Alberta	29	16.9	5.35	49.16
Grande Prairie, Alberta	26	16.9	5.50	55.16
Samples with unknown mating system				
Matane, Quebec	29	17.2	5.59	48.84
Kleinburg, Ontario (16 May)	17	17.1	5.72	43.84
Kleinburg, Ontario (20 May)	25	17.1	5.63	43.84
Sowerby, Ontario	23	17.4	5.51	46.33
Cochrane, Ontario	22	17.4	5.18	47.84
Moosonee, Ontario	44	17.0	5.43	51.33
Attawapiskat, Ontario	35	17.1	5.41	53.00
Portage La Prairie, Manitoba	35	17.1	5.30	50.16
The Pas, Manitoba	20	17.1	5.37	53.84
Owen's Lake, California	18	17.2	5.37	36.50
Brandonville, West Virginia	24	17.2	5.66	39.58
Woodruff, Utah (18 May)	21	17.1	5.36	41.50
Woodruff, Utah (10 June)	24	17.3	5.54	41.50
Elberta, Utah	18	17.0	5.41	40.00
Halleck, Nevada	18	17.1	5.38	40.87
Sheridan, Wyoming	31	17.1	5.51	44.78
Creston, Washington	33	17.0	5.44	47.67
Eureka, California	24	17.4	5.50	40.67
Wasilla, Alaska	26	16.9	5.44	61.16
Fairbanks, Alaska	21	16.7	5.20	65.00
Umnak Island, Alaska	26	18.5	5.68	55.33

TABLE 1
CONTINUED

Location	*N*	Femur length[a]	Volume[b]	Latitude[c]
Port Heiden, Alaska	16	17.6	5.67	56.83
Cold Bay, Alaska	15	18.2	5.74	55.00
Middleton Island, Alaska	25	17.8	5.51	59.50
Saltmarsh samples				
Puerto Peñasco, Sonora	9	17.9	5.50	31.33
Kino, Sonora	21	18.1	5.89	28.84
El Molino, Sinaloa	17	18.3	5.86	24.50
Magdalena Bay, Baja Cal. S.	14	18.2	5.34	24.33
Guerrero Negro, Baja Cal. N.	33	17.7	5.85	28.00
Bahia San Quintin, Baja Cal. N.	20	17.2	5.68	30.33
San Diego, California	19	17.0	5.56	33.33
Morro Bay, California	17	17.1	5.56	35.33

[a] Average (mm).
[b] Log of testis volume (mm^3).
[c] Converted to decimals (i.e., 47°40′ = 47.67).

variation in plumage coloration in Savannah Sparrows, but there is a variable amount of yellow in the superciliary (of both sexes) that might be of some significance in display and that might increase with age. I scored each specimen on a scale of 1 (no yellow) to 5 (extensive and bright yellow). As a possible test of the relationship between age and testis size, I correlated this superciliary score with the log of the testis volume.

To assess patterns of interpopulational variation, I used stepwise multiple regression (SPSSX Subroutine REGRESSION), regressing the log of the average testis size from each site, against seemingly relevant characteristics of the site or the sample, namely: (1) day of collection, (2) latitude, (3) longitude, (4) elevation, (5) average June temperature at a weather station near the site, (6) average femur length of the males at the site (skeletal measurements), (7) log of average mass of the males, and (8) an estimate of the reproductive condition of the females at the time the birds were collected. At each locality I collected females as well as males, and also examined their gonads. The estimate of female reproductive condition was the percentage of these females that were either pre-laying or laying. The percentages were transformed by arcsin to reduce skewness.

I selected these independent variables to reflect geographic variation in both climate and the birds' size. The timing of reproduction varies from locality to locality. For example, judging from the reproductive condition of the females collected, the birds at Owen's Lake, California, on 14 May and those at Moosonee, Ontario, on 12 June were at comparable stages in their nesting cycle. The variables latitude, longitude, elevation, day of collection, percentage of females laying, and June temperatures relate to this interpopulational variation in climate and seasonality. The average femur length and mass reflect body size, and these variables were included to account for geographic variation in body size.

RESULTS AND DISCUSSION

The correlation between date of collection and log testis volume among the 1020 nonsaltmarsh males is $r = -0.08$ ($P < 0.01$), and that between volume and date for the 145 saltmarsh males is $r = 0.10$ ($P > 0.05$). Thus, less than 1% of the variation in testis size among the birds used in these analyses is explained by differences in the dates of collection.

The correlation between the log body weight and the log testis volume in the total sample is $r = 0.26$ (N = 1157, $P < 0.01$). Within the nonsaltmarsh birds, this correlation is $r = 0.23$ (N = 1011; $P < 0.01$), and within the saltmarsh birds, it is $r = 0.27$ (N = 146; $P < 0.01$). Thus, 5–7% of the variation among individuals in testis volume is explained by variation in body size; this relationship does not appear to differ between saltmarsh and nonsaltmarsh birds.

The correlation between the testis volume and the extent and intensity of the superciliary stripe is $r = -0.02$ (N = 1011; $P > 0.05$).

The average testis volume of the 154 males collected from "polygynous populations" is significantly larger than that of 277 males from "monogamous populations" (5.59 vs 5.36; $t = 5.99$, df = 429, $P < 0.001$). Also, the testis volume of the saltmarsh sparrows is larger than that of the nonsaltmarsh birds (5.66 vs 5.46, $t = 2.66$, df = 1163, $P = 0.01$). Both the polygynous and the saltmarsh birds, however, are larger on average than nonsaltmarsh birds (see femur lengths in Table 1). I regressed log testis volume on log weight to correct for the relationship between testis size and body size, and used the residuals as a measure of testis size that is independent of body size. There is a significant difference between the average residual variation of the 154 polygynous males and the 277 monogamous males (0.015 vs −0.107; $t = 3.07$, $P = 0.002$), and a significant difference between the 146 saltmarsh vs the 1011 nonsaltmarsh birds (0.165 vs −0.023; $t = 6.09$, $P < 0.001$). Thus, the differences in testis size between monogamous and polygynous birds, on the one hand, and nonsaltmarsh and saltmarsh birds, on the other, are significant even when the among-individual variation in size is accounted for.

In the stepwise multiple regression, only two variables, "femur length" and "latitude," were entered (in that order) using a significance criterion of $P < 0.05$. Thus, with the covariation with femur length and latitude accounted for, none of the other measures—log weight, longitude, elevation, June temperature, date of collection, and reproductive condition of females—are significantly correlated with testis volume. Femur length is a measure of "body size" (the correlation with the log of weight in these samples is 0.93). Size and latitude taken together explain 41.6% of the variation in testis volume among the 42 samples of nonsaltmarsh Savannah Sparrows.

There is a significant correlation between average femur length and average testis volume ($r = 0.55$, $P < 0.01$) (Fig. 1). Testis volume decreases with latitude ($r = -0.35$, $P < 0.05$). The equation describing the

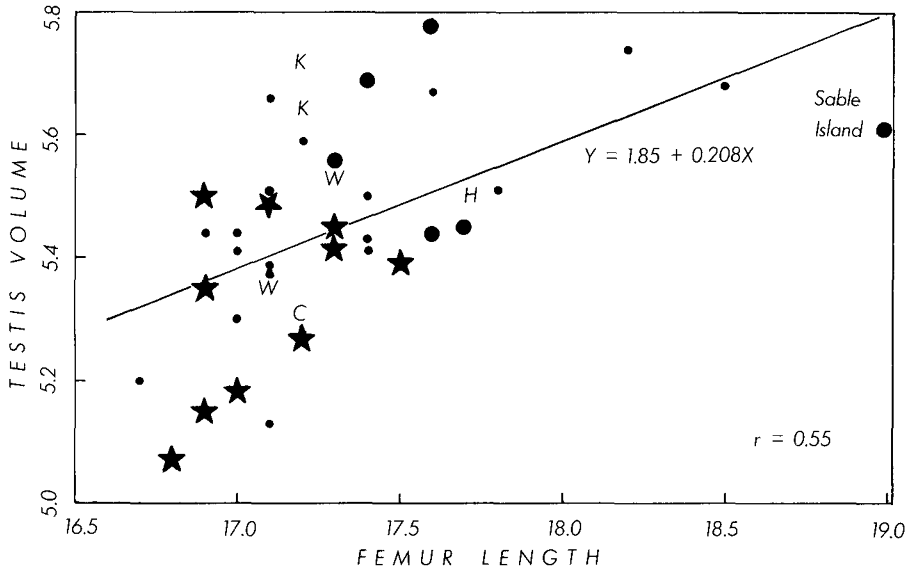

FIG. 1. Relationship between the natural log of testis volume and the average femur length (in mm) among 42 samples of nonsaltmarsh Savannah Sparrows from 40 different localities. Stars indicate the positions of samples of birds that are presumed to be monogamous, and large dots positions of samples presumed to be polygynous. The two "K"s and "W"s indicate the positions of the two samples from Kleinburg, Ontario, and Woodruff, Utah, respectively. "H" and "C" indicate the positions of the samples from Halifax and Churchill; Halifax is a "polygynous" sample and Churchill a "monogamous" one.

relationship of log testis volume as a function of both femur length (FL) and latitude (L) is, $Y = 2.52 + 0.019FL - 0.007L$. Throughout the season monogamous nonsaltmarsh birds consistently have smaller testes than predicted by the combination of body size and latitude, whereas the testis size of the polygynous birds is smaller than predicted early in the year, but appears to increase through the season. Sable Island and Halifax, where polygyny has actually been found to occur regularly, contain birds with testes that average less than predicted by body size and latitude, contra hypothesis. The repeated samples from Kleinburg (K) and Woodruff (W) give an estimation of variation among samples from the same site. Thus, the results of multiple regression using sample means confirm, where comparable, those of the univariate analyses of individuals.

It is not clear why average testis size would decrease with latitude. At high latitudes (e.g., Churchill), Savannah Sparrows are single-brooded, whereas at lower latitudes two or more broods are commonly raised. Among monogamous sparrows it would seem that the sperm demand

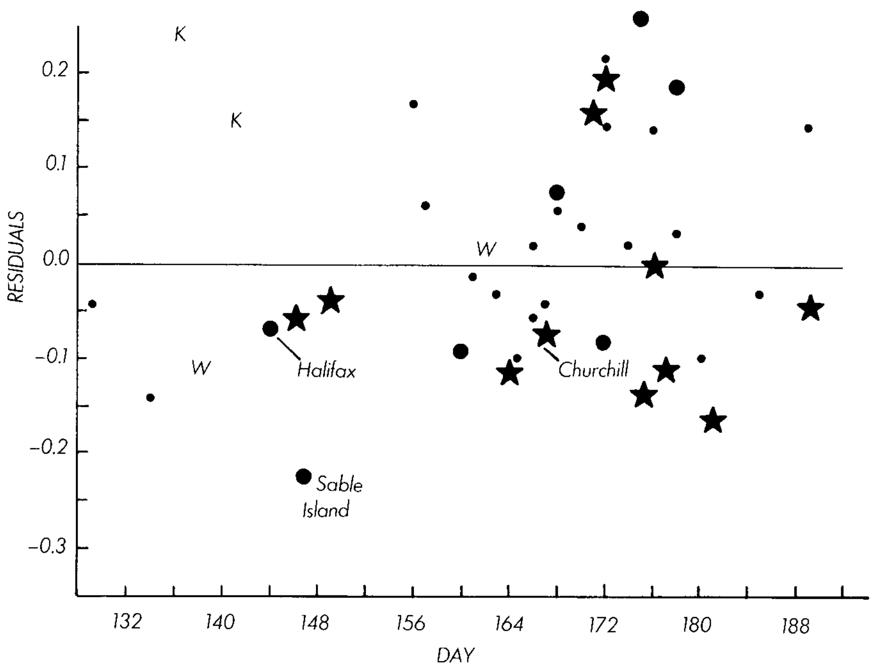

FIG. 2. Relationship between the residuals of samples from multiple regression of testis volume against latitude and femur length, plotted against the day of collection. Overall, the correlation between the residuals and day of collection is not significant. The stars indicate the positions of the 11 samples presumed to be monogamous, and the large dots the positions of the 7 samples presumed to be polygynous. The "W"s and the "K"s indicate the positions of the two samples from Woodruff, Utah, and Kleinburg, Ontario. Day 132 is 12 May, and 188 is 7 July.

during laying would be similar in single- and multi-brooded populations (although the testes would doubtless remain enlarged for a longer period of time in the latter), but perhaps this is not the case.

The relationship between relative testis size and mating system is not clear. As predicted, the testis volume of polygynous males averages greater than that of monogamous males even with the covariation between testis volume and body size accounted for, but the average testis volumes of males from Sable Island and Halifax, Nova Scotia, the only two localities from which polygyny has been found to occur frequently, are smaller than predicted by size alone (Fig. 1) or by the combination of body size and latitude (Fig. 2). Also, 8 of the presumed 11 monogamous samples are from high latitudes, whereas all of the presumed polygynous males are from lower latitude sites. Therefore, the slight differences in the testis sizes of the polygynous and monogamous males may be an extension of the latitudinal trend.

Saltmarsh Savannah Sparrows have larger testes than their migratory conspecifics (Table 1), and, although there is a great deal of interpopulational variation in size and other features of these birds, relatively large testes are apparently a general characteristic of them (the exceptions, Puerto Peñasco and Magdalena Bay, are based on small samples). Because of their southerly occurrence it seems likely that in all cases they are multibrooded; their mating systems are not known, although they are apparently usually monogamous at Pt. Mugu, California (J. B. Williams, pers. comm.). More knowledge of the breeding biology of these saltmarsh birds is needed.

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