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Relationship Between Testis Size and Mating Systems in American Sparrows (Emberizinae)

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Considerable interspecific variation in the relative testis size of birds has long been apparent to ornithologists. Testis size, as would be expected, is positively correlated with body size in birds (Cartar 1985, Møller 1988a, 1991), as it is in primates (Harcourt et al. 1981). Many species characteristically have testes that are larger than would be predicted by body size alone. Some recent studies have correlated interspecific variation in relative testis size to the mating systems of species (Birkhead and Møller 1992). Harcourt et al. (1981) found that testes were relatively small in primate species in which estrous females generally copulate with only one male (single-male mating systems), whereas testes were substantially larger in species in which females copulate with several males (multimale mating systems), presumably because of sperm competition. In both birds and mammals there is a positive correlation between testes mass and both the volume of the ejaculate and the number of sperm per ejaculate, suggesting that individuals with relatively large testes indeed, do, potentially deliver more sperm than individuals with relatively small ones (Møller 1988a, b). Among several closely-related sandpipers (*Calidris* spp.), the testes of nonmonogamous species average larger than those of monogamous ones (Cartar 1985). Although some of the nonmonogamous *Calidris* practice lek polygyny (terminology following Alcock 1989:467), others show resource-defense polygyny, in which presumably only one male copulates with his mates. In these latter birds, sperm competition would not seem to be a significant factor in selecting for relatively large testis size. Cartar (1985) suggested that sperm depletion might select for relatively large testes, as a polygynous male perhaps would copulate with several females daily. Thus, sperm depletion and sperm competition are two different hypotheses that have been put forth to explain some of the interspecific variation in relative testis size. There is no evidence to suggest that testis size is related to clutch size, that is, to the number of sperm needed to assure fertilization (Birkhead et al. 1987).

I recently collected samples of breeding males of 19 species of North American sparrows (Emberizinae), including samples from several populations of Nelson's Sharp-tailed Sparrows (see Table 1 for scientific names), Saltmarsh Sharp-tailed Sparrows, and Savannah Sparrows, as well as two samples of LeConte's Sparrow. This offers the opportunity to examine intra- and interspecific variation in relative testis size, and to assess the significance of sperm competition in the evolution of testis size. This work augments Møller's (1991) review of 16 orders, focusing on a small group of closely-related species with diverse mating biologies.

Of the species discussed here, Nelson's Sharp-tailed Sparrow, Saltmarsh Sharp-tailed Sparrow, and Smith's Longspur have a multimale mating system: males are apparently not territorial, and laying females solicit copulations from many different males (Post and Greenlaw 1982, Briskie 1992, 1993a, b). These are among the few species of birds that practice scramble-competition polygyny, and in this way resemble chimpanzees (*Pan troglodytes*), a species in which males have very large testes relative to mass (Harcourt et al. 1981). Another of the emberizids collected, the Lark Bunting, practices resource-defense polygyny (Pleszczynska 1978). Of the other species collected, the Seaside Sparrow is apparently monogamous (Post and Greenlaw 1982, 1994), and the Savannah Sparrow from the region from which I have data is generally so (Wheelwright and Rising 1993). White-crowned Sparrows from the western coast of North America are occasionally polygynous (Petrinovich and Patterson 1978), but the data I have are from birds from northern Manitoba, where they have not been studied. There is one record of a polygynous Lark Sparrow (Knowles 1938), and Lapland Longspurs are rarely polygynous (Lyon and Montgomerie 1987). McCown's Longspurs apparently are monogamous (With 1994). The mating systems of the other species have not been closely studied, but all are territorial and seemingly generally monogamous (Murray 1969, Verner and Willson 1969, Ford 1983). However, the monogamy/nonmonogamy dichotomy is not a reliable indicator of intensity of sperm competition because it is increasingly evident that extrapair copulations are a significant factor in the mating systems of many apparently monogamous birds. For example, on the basis of genetic evidence Westneat (1987) found that at least 14.4% of 257 Indigo Buntings (*Passerina cyanea*) had genotypes that were incompatible with those of one of their apparent parents, and Wetton et al. (1987) similarly found evidence of frequent extrapair copulation in House Sparrows (*Passer domesticus*).

In many instances males can increase their probability of paternity either by mate guarding or by frequent copulation, but this is not always the case (Morton et al. 1990). The latter option is perhaps the only one available in species whose behavior or habitat use makes close guarding impractical. Birds of prey and colonial species, for example, generally do not guard, as effective guarding probably is not possible (Birkhead et al. 1987). Close guarding would be impractical for species (e.g. Indigo Bunting) that nest in dense habitats, such as deciduous thickets or tall grass,

TABLE 1. Average testis volume and mass of several populations and species of emberizine sparrows.

Species/population	n	Volume (0.52 *LW*)	Mass (g)	Mating system[a]	Habitat[b]
Bachman's Sparrow (*Aimophila aestivalis*)	1	5.54	18.2	1	1
Botteri's Sparrow (*A. botterii*)	6	5.28	19.9	1	2
Cassin's Sparrow (*A. cassinii*)	12	4.99	18.2	1	2
Rufous-crowned Sparrow (*A. ruficeps*)	3	5.33	19.7	1	1
Vesper Sparrow (*Pooecetes gramineus*)	8	5.78	25.8	1	2
Lark Sparrow (*Chondestes grammacus*)	12	5.69	30.3	1	1
Lark Bunting (*Calamospiza melanocorys*)	8	6.28	40.4	2	2
Savannah Sparrow (*Passerculus sandwichensis*)					
Southern Ontario (1987)	15	5.47	19.1		
Southern Ontario (1990)	19	5.86	18.9		
James Bay Lowlands	11	5.67	19.3		
Prairies	1	5.32	19.3		
Total	46	5.67	19.1	1	2
Baird's Sparrow (*Ammodramus bairdii*)	18	5.30	19.3	1	2
Grasshopper Sparrow (*A. savannarum*)	11	5.45	17.6	1	2
LeConte's Sparrow (*A. leconteii*)					
Prairies	11	5.47	13.2		
James Bay Lowlands	9	5.89	13.7		
Total	20	5.69	13.5	1	4
Nelson's Sharp-tailed Sparrow (*A. nelsoni*)					
Sackville, New Brunswick	18	6.03	17.6		
St. Lawrence River, Quebec	19	6.32	17.1		
Upham, North Dakota	10	5.69	14.7		
Last Mountain Lake, Saskatchewan	10	5.84	15.0		
Attawapiskat, Ontario	16	6.08	16.8		
Moosonee, Ontario	17	6.97	16.8		
Total	90	6.20	16.6	3	4
Saltmarsh Sharp-tailed Sparrow (*A. caudacutus*)					
Prime Hook Refuge, Delaware	19	6.31	19.9		
Brigantine Refuge, New Jersey	11	6.43	20.3		
Long Island, New York	14	6.16	20.1		
Plum Island, Massachusetts	13	6.47	21.1		
Popham Beach, Maine	18	6.62	18.5		
Total	75	6.20	19.9	3	4
Seaside Sparrow (*A. maritimus*)	13	5.49	23.9	1	4
White-crowned Sparrow (*Zonotrichia leucophrys*)	14	5.60	27.9	1	1
McCown's Longspur (*Calcarius mccownii*)	6	5.21	25.3	1	2
Lapland Longspur (*C. lapponicus*)	13	5.45	27.7	1	3
Smith's Longspur (*C. pictus*)	12	6.58	29.7	3	3
Chestnut-collared Longspur (*C. ornatus*)	6	5.16	19.7	1	2

[a] (1) Apparently monogamous or unknown; (2) polygynous; and (3) promiscuous.
[b] (1) Edge; (2) grassland; (3) tundra; and (4) marsh.

but may be easy for species breeding in shortgrass prairie.

Methods.—I used a plastic ruler to measure the length and width of the largest (usually the left) testis of 366 freshly collected specimens in 32 samples of 19 species of sparrows. Prior to dissection, 362 of these birds were weighed (nearest 0.1 g using Pesola spring scale). The species, numbers of birds measured, and natural logs of average testis volumes and masses are listed in Table 1. Here I use testis volume (V) as a measure of testis size, and estimate it using the formula for the prolate spheroid: $V = 0.52\ L^2$. Because these volumes are log-normally distributed, I use a log transformation of volume in statistical analyses (Rising 1987). Cartar (1985) used testis length as a measure of testis size; Møller (1991) used mass, commonly calculated on the basis of length and width measurements written on specimen labels.

In birds there is considerable seasonal variation in testis size. Within the breeding season, however, testes in sparrows remain large throughout the time during which copulation occurs (Wingfield 1984, Rising 1987). All of the males collected for this study were singing and apparently on their breeding grounds. With the exception of the females collected in southern Ontario in 1987, all of the females collected at the same time were either laying or incubating. The 1987 collection from southern Ontario apparently was taken prior to laying (most collected on 14 May, the remainder on 21 May). Females collected on those days were not yet laying and, thus, males there probably were not in maximal reproductive condition. The females in a sample collected from the same fields in late May were laying. Therefore, these two samples afford an opportunity to evaluate a possible seasonal effect.

I used ANOVA (SAS/GLM; SAS Institute 1986) to quantify interpopulational variation in testis size in the three species for which more than one sample was available, and Pearson's correlation (SAS/CORR) to quantify the relationship between logs of testis volume and logs of mass. I regressed average testis volume with average mass for 20 samples, splitting the sharp-tailed sparrows into three groups, one from the prairies and James Bay (average of North Dakota, Saskatchewan, Attawapiskat and Moosonee), one from the Maritimes (Quebec and New Brunswick), and one from the Atlantic coast (Delaware, New Jersey, New York, and Massachusetts). These populations are geographically, phenotypically, behaviorally, and biochemically distinct (Rising and Avise 1993).

Although the phylogenetic relationships of these sparrows are not known, phylogenetic constraints (Harvey and Pagel 1991) for the most part probably are not important here, as some of the largest and the smallest testes are found in males in *Calcarius* and *Ammodramus* (probably monophyletic, or at least paraphyletic taxa). Also, sharp-tailed sparrows and Seaside Sparrows—whose testes differ substantially in size—are certainly closely related and may be sister taxa (Robins and Schnell 1971, Zink and Avise 1990). Sequence data from mtDNA (Dawson et al. in prep.) confirms the close relationships among Seaside, LeConte's, Nelson's Sharp-tailed, and Saltmarsh Sharp-tailed sparrows, as well as the close relationship between the Chestnut-collared and McCown's longspurs. These two longspurs, however, are quite distinct from the other North American sparrows. To evaluate possible differences within *Ammodramus* and within *Calcarius*, I used ANOVA to compare relative testis size based on the residuals from the regression testis size versus mass. I selected only prairie (North Dakota and Saskatchewan) and James Bay (Attawapiskat) sharp-tailed and LeConte's sparrows, and coastal (Delaware and New Jersey) sharp-tailed and Seaside sparrows, as these samples were collected at the same time and generally from the same marshes. I similarly analyzed the four *Calcarius* separately. These four species are nowhere jointly sympatric, but the former two were collected from the same sites in the northern Prairies, whereas the latter were collected from northern Canada.

Results.—The correlation between log body mass and log testis volume of the 362 sparrows pooled across 19 species is not significant ($r = -0.01$, $P > 0.05$). However, if only the 165 Nelson's and Saltmarsh sharp-tailed sparrows or the 197 sparrows of other species are considered separately, there is a significant positive correlation between mass and testis volume ($r = 0.63$ and 0.20, respectively; $P < 0.001$ and <0.01). ANOVA also shows highly significant (df = 10 and 154, $P < 0.001$) differences in relative testis size (ln[mass] − ln[testis volume]) among the 11 samples of sharp-tailed sparrows. An *a posteriori* (Student-Newman-Keuls) test delimits four statistically homogeneous subsets; there is considerable overlap among three of these, but the population from Popham Beach, Maine, has significantly larger relative testis size than the others (Table 1). The differences in relative testis volume of the two samples of LeConte's Sparrow also are significant ($F = 16.1$, df 1 and 18, $P < 0.001$), as are those among the three samples of Savannah Sparrow $F = 10.5$, df 2 and 43, $P < 0.001$). There are two overlapping statistically homogeneous groups among Savannah Sparrows, but the two samples from southern Ontario are significantly different from each other.

The correlation between average testis volume and average body mass among 20 samples (19 species and two sets of samples of Nelson's Sharp-tailed Sparrows) is not significant ($r = 0.26$, $P > 0.05$; Fig. 1). Of the 20, 6 fall above the regression line (Fig. 1)—the three sets of sharp-tailed sparrows, along with Smith's Longspur, Lark Bunting, and LeConte's Sparrow (i.e. these six have relatively larger testes than average for sparrows of their sizes).

The ANOVA of the residuals from the regression of ln[testis volume] versus ln[mass] of the prairie and James Bay LeConte's sparrows and sharp-tailed sparrows showed that those of the sharp-tailed sparrows were significantly larger ($F = 9.24$, df = 1 and 43, $P < 0.004$). Similarly, the coastal sharp-tailed sparrows had significantly larger testes than Seaside Sparrows ($F = 78.6$, df = 1 and 40, $P < 0.001$), the difference being greater than that between the prairie Nelson's Sharp-tailed and LeConte's sparrows. There was also a significant difference among the four longspur species ($F = 13.24$, df = 3 and 24, $P < 0.001$); an *a posteriori* test identified two statistically homogenous subsets, one containing only Smith's Longspur, and the other the remaining three longspur species. Cassin's Sparrows, and Chestnut-collared, McCown's, and Lapland longspurs have relatively small testes.

Discussion.—Testis size among all 362 male sparrows of 19 species is not correlated with body size. There is, however, a strong positive correlation between body size and testis size for the 165 sharp-tailed sparrows, similar to that found by Rising (1987) for the Savannah Sparrow, as well as a positive correlation among the 197 individuals of the other 17 sparrow species studied here.

The significant difference in relative testis size between the two different samples of Savannah Sparrows taken in southern Ontario should be viewed with caution, as the male Savannah Sparrows in the 1987 sample were taken earlier in the season than the

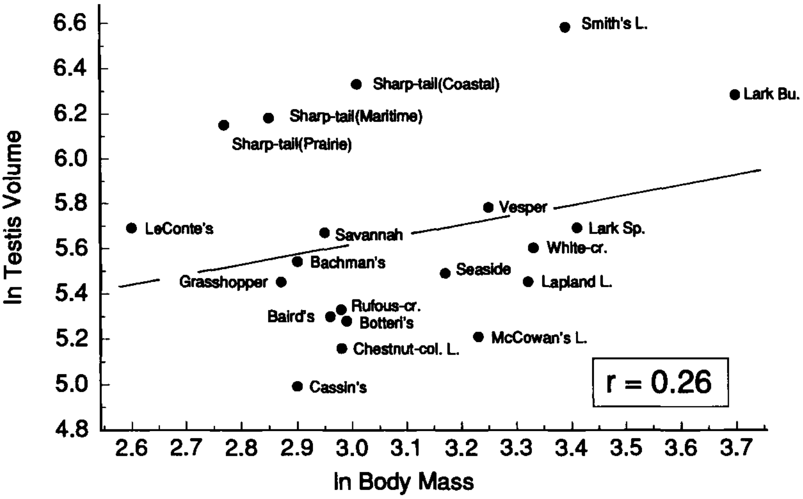

Fig. 1.—Relationship between log mean testis volume and log mean body mass among 20 samples of 19 species of emberizine sparrows, buntings, and longspurs. Slope of regression line is not significantly different from 0. However, relationship within the sharp-tailed sparrows (taken alone) and within the other species (i.e. sharp-tailed sparrows excluded) is significant.

1990 sample. Therefore, they may not have been in full reproductive condition, and their testes not fully enlarged.

As predicted from the sperm-competition hypothesis, the sharp-tailed sparrows and Smith's Longspur, species with multimale mating systems, have relatively larger testes than the other sparrows. However, the testes of the LeConte's Sparrow, which is territorial and thought to be monogamous, are nearly comparable (although significantly smaller) in size to those of similar-sized sharp-tailed sparrows. Atlantic coastal sharp-tailed sparrows have significantly larger testes than do the sympatric and closely-related, but monogamous, Seaside Sparrows. Lark Buntings, which are frequently polygynous, also have relatively large testes. These live in xeric grassland, where mate guarding would likely to be effective, and males accompany their mates when feeding; however, it would not be possible for a polygynous Lark Bunting to accompany both mates because they nest simultaneously (Pleszczynska 1978). The species with the smallest testes—Cassin's Sparrow, and Chestnut-collared, McGowan's, and Lapland longspurs—all breed in xeric grasslands or open tundra. Male Lapland Longspurs always stay close to their fertilizable mates (Lyon and Montgomerie 1987), and this probably is true for the other three species as well (Mickey 1943, pers. obs.). With the occasional exception of the Lapland Longspur, these four species probably are monogamous (although virtually nothing is known about the breeding biology of Cassin's Sparrow). Where they are sympatric, Lark Buntings often nest in the same fields as Cassin's Sparrows, Chestnut-collared Longspurs, and McCown's Longspurs; likewise, Smith's and Lapland longspurs often nest in the same fields where their ranges overlap. Breeding biology, not habitat preference, best predicts which species have evolved relatively large testes.

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