

SEXUAL DIMORPHISM AND MATING SYSTEMS IN VOLES

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Here we respond to the criticism that use of body length is an incorrect and misleading measure of sexual dimorphism in body size (Boonstra et al., 1993, *J. Mammal.*, 74:224-229). Despite the contention by Boonstra et al. that body mass is a more sensitive metric for detecting dimorphism, some vole populations show statistically significant dimorphism for length, but not mass. Published studies based on length and mass corroborate many of our conclusions based on length only (Heske and Ostfeld, 1990, *J. Mammal.*, 71:510-519) and are in opposition to the results of Boonstra et al. based on mass. We question the reasoning behind Boonstra et al.'s expectation of sexual dimorphism in promiscuous and facultatively monogamous species, and urge that clearer predictions be formulated.

Key words: *Microtus*, sexual dimorphism, mating systems, size

Because male mammals often compete more actively among themselves for access to mates than do females, sexual selection is assumed to be a stronger force among males (Darwin, 1871). The outcome of sexual selection will be the evolution of traits that confer an advantage in acquiring mates and siring their offspring. The particular traits that evolve will depend on the mating system. Heske and Ostfeld (1990) provided evidence that in North American voles (Rodentia: Arvicolidae), sexual selection has resulted in sexual dimorphism for size in polygynous species, and in large testes (relative to body size), but a lack of sexual dimorphism, in promiscuous species. Our expectation of a lack of sexual selection on either body size or testis size in monogamous systems was met for only one of the two monogamous species of voles we analyzed.

Boonstra et al. (1993) have criticized our use of body length to assess sexual dimorphism for size, arguing that body mass is preferable. They contend that our results are "counter-intuitive and . . . incorrect." Their discussion centers on three issues, which we

will address in turn: mass versus length as a measure of body size; discrepancies among data sets using mass and length; the relationship between dimorphism and mating systems.

Mass versus length.—A primary reason for using body length as a measure of size was that it allowed us to measure relative size of testis (testis length/body length), from data recorded on museum tags (Heske and Ostfeld, 1990). Although body mass typically is recorded on tags, testis mass is not. We recognized that mass scales to length by an exponential function between two and three, and that consequently the range in variation in length would be less, thus increasing the chance of a Type II statistical error.

Boonstra et al. (1993) claim that Heske and Ostfeld "used the wrong index to assess sexual dimorphism," implying that their index based on body mass is right. Their justification for this assertion is that "heavier males are dominant and/or have greater breeding success than lighter males." However, they are quick to point out that these

heavier males also may be longer, but that length was not recorded in the studies they cite. Mass and length are highly correlated in California voles (Lidicker and Ostfeld, 1991), and we suspect in other voles as well.

The critical issue is, which measure of size is most directly responsive to sexual selection? We are not aware of studies that provide an unequivocal answer, but suspect that body length will be found to be more responsive. Body mass is notoriously variable as a result of recent or current endocrine and nutritional state, body composition (e.g., percent fat—Lidicker and Ostfeld, 1991), and the presence of food in the digestive tract, which in arvicolids is relatively large (Batzli, 1985). These sources of variation probably are not heritable, weakening the power of selection acting directly on body mass. Thus, we view the smaller probability of including nonheritable variation to be an advantage in our analysis based on length.

Discrepancies among data sets.—Boonstra et al. (1993) found that some vole species Heske and Ostfeld (1990) considered monomorphic based on body length were sexually dimorphic for body mass. Their interpretation was that our failure to detect dimorphism in these species represented a flaw in our analysis (namely, using body length). An alternative explanation is that interpopulational variation in body size occurs in voles, and that the discrepancies in our data sets reflect real differences.

For example, Boonstra et al. (1993) found statistically significant sexual dimorphism in mass, but not length, for *Microtus oeconomus*; Heske and Ostfeld (1990) found significant dimorphism for length in this species. Boonstra et al. (1993) found significant dimorphism in mass, but not length, for *M. pennsylvanicus*; Bondrup-Nielson and Ims (1990) found no significant dimorphism in mass for this species, based on a sample of 7,860 voles. Boonstra et al. (1993) found statistically significant dimorphism in mass for *Clethrionomys rutilus* (males > females); Heske and Ostfeld (1990) found *C. rutilus* to be the only species with females

significantly longer than males; Bondrup-Nielson and Ims (1990) found that females were significantly *heavier* at the 0.001 level. Moskvita and Suchkova (1976) also found significant sexual dimorphism in body length, with females longer, in five populations of *C. rutilus*.

In the data set of Bondrup-Nielson and Ims (1990), of eight populations of voles having both mass and length measurements, six showed statistically significant dimorphism in both metrics, and two showed significant dimorphism in length only. Thus, in some instances, length may be a more sensitive metric than mass.

We conclude that length and mass measure somewhat different aspects of size; that discrepancies between data sets may result from real differences in populations sampled rather than inherent inadequacies in methods; and that although the range of phenotypic variation in mass may be greater than that in length, mass is not necessarily more likely to detect dimorphism when it occurs.

Relationship between sexual dimorphism and mating system.—Boonstra et al. (1993) predict that sexual dimorphism (males > females) will be greatest in polygynous species, intermediate in promiscuous species, and least in monogamous ones. In contrast, their results show a ranking of mating systems with monogamous > polygynous > promiscuous. As a result, they modify their prediction as follows: facultatively monogamous = polygynous > promiscuous > obligately monogamous. The reasons for both the original and the modified predictions are not clear. In particular, we do not understand the rationale for the equal status of facultative monogamy and polygyny, nor for the intermediate status of promiscuous species.

We believe some confusion results from the assignment of species to the category, facultative monogamy. Boonstra et al. (1993) place both *M. townsendii* and *M. ochrogaster* in this category; however, the social systems of these species seem fun-

damentally different. *M. townsendii* begins the breeding season with individual territoriality in both females and males. Because individual territories of males and females overlap, mating may be predominantly monogamous during this time. During most of the breeding season, however, females show a high degree of intrasexual overlap, and mating appears to be polygynous (Lambin and Krebs, 1991). In fact, this mating system seems to be most similar to that of *M. californicus* (Heske, 1987; Ostfeld, 1986; M. Salvioni and W. Z. Lidicker, Jr., pers. comm.), a species typically considered polygynous. In *M. ochrogaster*, mating is monogamous throughout the breeding season of most years. At high population density, or under certain weather conditions, monogamy appears to erode into a promiscuous system (Getz et al., 1987). We believe it is important to specify both the type of nonmonogamous system employed by facultatively monogamous species, and the frequency with which that nonmonogamous system operates, before reliable predictions can be made regarding sexual selection on body size.

The expectation of intermediate levels of dimorphism for promiscuous species (Boonstra et al., 1993) appears to be based on some hidden assumptions about the form of sexual selection under this system. These assumptions need to be made explicit. Do males of promiscuous species compete directly just as polygynous males do, but to a lesser degree? Or is intrasexual competition of a different form entirely? Our data (Heske and Ostfeld, 1990) indicated that a fundamental form of competition among promiscuous males was sperm competition within reproductive tracts of females, and therefore selection acted on testis size but not necessarily on body size. Whether or not direct behavioral competition among males, as well as female choice, would select for large body size in these species is not known (Heske and Ostfeld, 1990:513). One obvious result of this discourse is the need

for clear models of sexual selection on body size in promiscuous and facultatively monogamous species.

In conclusion, we suggest that variation in sexual dimorphism, both within and among species, may be caused by concordant variation in mating systems. Variation in both dimorphism and mating system probably is continuous rather than discrete. Thus, rather than asking whether or not each species or population is sexually dimorphic, we should ask to what degree it is dimorphic. To ask whether variation in mating system is driving variation in dimorphism will require more thorough descriptive studies of social behavior, a more sensitive scheme for categorizing systems according to the predicted strength of sexual selection, and clearer predictions regarding the traits in males and females most likely to respond to sexual and natural selection.

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