MATING SYSTEMS AND SEXUAL DIMORPHISM IN MASS IN MICROTINES

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Sexual dimorphism in body size is expected to vary as a function of mating system. Heske and Ostfeld (1990, J. Mammal. 71:510-519) found no difference in body-length dimorphism between the majority of promiscuous and monogamous microtines. In five species we used body mass and in three species, length of body to test the robustness of these findings. We found no significant dimorphism in length of body in any species, but significant dimorphism in body mass in all species, independent of mating system. We propose that 1) mass rather than length is the measure needed to assess dimorphism in microtines, and 2) the bias in favor of large males should rank as follows with respect to mating system: facultative monogamy = polygyny > promiscuity > obligate monogamy.

Key words: *Microtus,* sexual dimorphism, mating systems, body mass

Sexual dimorphism is expected to occur when one sex competes for access to the other (Darwin, 1871). In mammals, where the dominant mating system is polygyny (Kleiman, 1977) and where males do the competing, they may obtain an advantage by being large (Reiss, 1989). Emlen and Oring (1977) predicted that the greater the potential for multiple-mate monopolization, the more intense intrasexual selection should be and hence the greater the tendency for polygyny. Thus, knowledge of the mating system should allow one to predict the degree of sexual dimorphism: in polygynous mating systems, where one male has exclusive access to multiple females, selection should cause dimorphism to be greatest; in a promiscuous mating system, where no one male may gain exclusive access to a female, dimorphism should be less; and finally, in a monogamous mating system, where each male has exclusive access to only one female, dimorphism should be minimal. Therefore, the expectation is that sexual dimorphism (male/female body size) would rank as follows with respect to mating system: polygynous > promiscuous > monogamous. In contrast, in a comparative study on microtine species of the genera *Microtus* and *Clethrionomys,* Heske and Ostfeld (1990) found the following ranking with respect to sexual dimorphism: polygynous > promiscuous = monogamous. None of their monogamous species and only one of 12 promiscuous species showed male-biased sexual dimorphism. Two of the promiscuous species showed female-biased sexual dimorphism. These results are counter-intuitive and we believe they are incorrect because length of body rather than mass was used as a measure of sexual dimorphism.

METHODS

We used two lines of evidence to examine sexual dimorphism in microtines. To avoid drawing conclusions from comparisons in which different aged cohorts were included, both our tests involved examining only animals that had overwintered. First, a population of *Microtus pennsylvanicus* was intensively live-trapped at the onset of breeding and the mass of males and females determined. The major disadvantage of using mass from live-trapped animals to assess dimorphism is that the early stages of pregnancy cannot be detected and hence may make males and females more similar than they really are. However, if dimorphism were to be found in spite of this bias, it would only serve to strengthen the conclusion that the sexes were different with respect to mass. From March to May 1983, a dense population of *M. p. pennsylvanicus* was live-trapped weekly for 2 days/week at a site near Toronto, Ontario, and females were removed near the end of pregnancy to allow parturition to occur in the laboratory. Thus, we knew the pregnancy status of most females and hence were able to minimize the effect of pregnancy on body mass. Breeding had not occurred the previous winter and since almost no animals survived to breed in 2 different years (Cockburn, 1988), the voles present in March must have been born in the previous summer and autumn and thus were similar in age. When trapping started in March only 10% of the males were in breeding condition and none of the females were pregnant. By 30 March, 96% of the males were in breeding condition and 6% of the females were pregnant. No other females had a litter before 14 April.

Second, we collected samples of four species of voles and performed autopsies, thus allowing us to subtract the contribution of pregnancy to body mass in females. In the southern Yukon, we obtained snap-trap samples of *M. oeconomus, M. pennsylvanicus,* and *C. rutilus* from 1974–1977 (see Krebs and Wingate, 1985 for details). Only overwintered animals collected in spring (April–June) were included in the analysis and spring samples were pooled. In southern British Columbia, we obtained a large sample of overwintered *M. townsendii* from 6 March to 29 April 1974 using live-traps (see Boonstra, 1976 for details). In both studies, embryo plus uterine mass were taken in pregnant females and this was subtracted from total mass to obtain body mass comparable to that of males. In the former study, length of body (excluding length of tail) and body mass were recorded; in the latter study only body mass was recorded.

RESULTS AND DISCUSSION

Our two methods to assess sexual dimorphism were consistent and showed the same result. First, the meadow vole, *M. pennsylvanicus,* is known to have a mating system with female territoriality and male promiscuity (Boonstra and Rodd, 1983; Madison, 1980; Ostfeld et al., 1988; Webster and Brooks, 1981), yet Heske and Ostfeld's (1990) results indicate that this species is monomorphic with respect to length. Fig. 1 shows the distribution of body masses of field-captured voles on 30 March 1983, excluding obviously pregnant females. Males ($\bar{X}$ = 47.9 g, *SD* 6.09, n = 105) were significantly heavier than females ($\bar{X}$ = 39.9 g, *SD* 4.91, n = 86) (t = 9.86, *d.f.* = 189, $P <$ 0.0001). The male:female ratio is thus 1.20:1 compared with that of between 0.99:1 and 1.04:1 for the three subspecies obtained by Heske and Ostfeld (1990). Our study thus indicated a pronounced sexual dimorphism in this promiscuous species. Second, significant sexual dimorphism in mass, but not length, occurred in all species examined through autopsy (Table 1). Thus, males were significantly heavier than females in all species independent of mating system. These results are similar to those found by Dewsbury et al. (1980) in a laboratory study of equal-aged animals in three species of *Microtus.*

Therefore, we believe that Heske and Ostfeld (1990) used the wrong index to assess sexual dimorphism in microtines. All studies that we know of in microtines indicate mass is the crucial measure and the consistent result is that heavier males are dominant or have greater breeding success than lighter males (Kawata, 1988; Sheridan and Tamarin, 1988; Turner and Iverson, 1973). Unfortunately, none of these studies measured length of body, so a similar assessment is not possible. Other species of mammals show the same advantage of being heavier (e.g., *Mus musculus*—Franks and Lenington, 1986; *Cervus elaphus*—Clutton-Brock et al., 1982; *Sciurus vulgaris*—Wauters and Dhondt, 1989). It is likely that the differences in the relationship between length and body mass in males and females do not occur until puberty, but thereafter androgenic and estrogenic hormones act to dif-

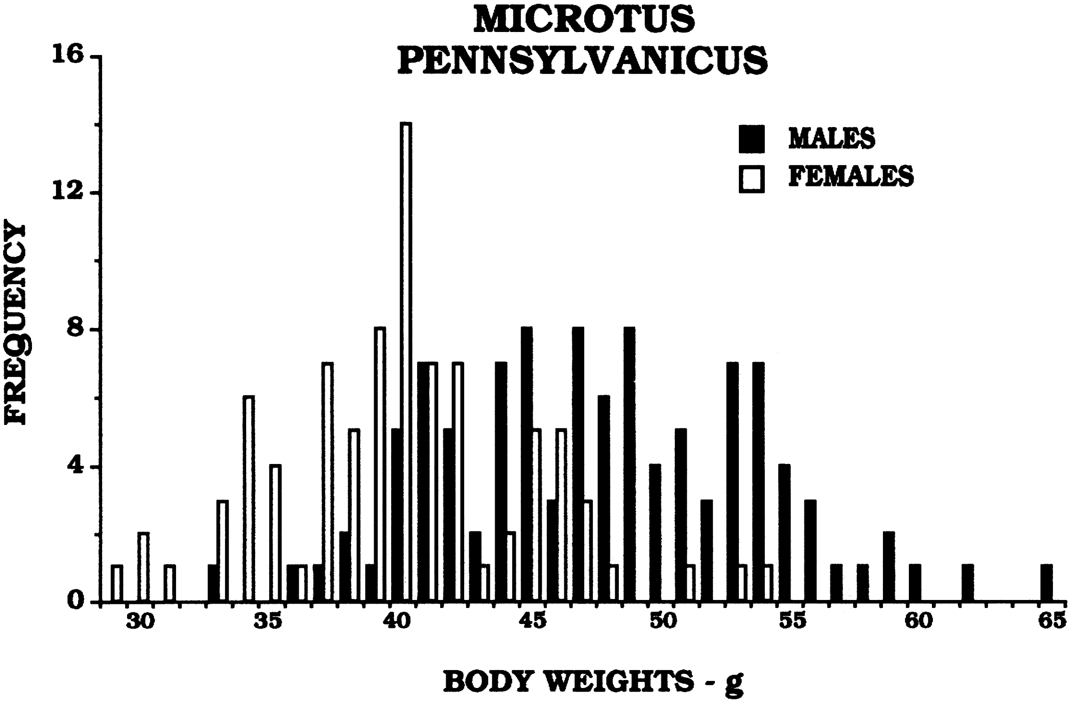

FIG. 1.—Distribution of body mass of a population of *M. pennsylvanicus* from southern Ontario on 30 March 1985.

ferentiate between the sexes (Glucksmann, 1974; Widdowson, 1976; Wilson and Foster, 1985). Androgens working in conjunction with growth hormone are known to have an additional anabolic effect on protein synthesis, causing increased protein deposition to all parts of the body, especially to skeletal muscle and cartilage. Our results indicate that in adult breeding microtines, length of body is similar in both sexes, but males are more robust.

The most pronounced sexual dimorphism in mass occurred in *M. townsendii*, a species that primarily is monogamous (Lambin and Krebs, 1991). The least-pronounced sexual dimorphism in mass occurred in *C. rutilus*, a promiscuous species, which Heske and Ostfeld (1990) found to exhibit female-biased sexual dimorphism. Thus, our ranking of sexual dimorphism in mass relative to mating system was as follows: monogamous > polygynous > promiscuous. These results are contrary to those found by Heske and Ostfeld (1990), but also contrary to our prediction that polygynous species should have the largest males. Why? The generality of our conclusions could be strengthened by including more species with various mating systems. However, we propose that for microtines, a larger sample of species will show the following trend in sexual dimorphism with respect to mating system: facultative monogamy = polygyny > promiscuity > obligate monogamy. A monogamous and a polygynous mating system are closely related if the males can switch between either tactic and thus selection should operate to give larger males a competitive advantage if polygyny is a possibility. Monogamy is known to occur in three *Microtus* species, but in at least two of them it is facultative. Lambin and Krebs (1991) found that although monogamy was the predominant mating system in *M. townsendii* in spring, polygyny increased in summer. In *M. ochrogaster* monogamy is the main type

TABLE 1.—*The relationship between mating system and sexual dimorphism in length of body and mass* ($\bar{X}$ ± SD) *in three species of* Microtus *and one species of* Clethrionomys.

Species	Length of body (mm)				Male: Female ratio	Body weight (g)		Male: Female ratio	Mating system	References
	n	Females	*n*	Males		Female	Male			
M. p. alcorni	40	106.9 ± 7.7	43	109.9 ± 6.6	1.03	25.8 ± 5.9	28.7 ± 5.7*	1.11	promiscuous	Madison, 1980; Boonstra and Rodd, 1983; Ostfeld et al., 1988; Webster and Brooks, 1981
M. oeconomus macfarlani	18	111.3 ± 9.2	24	111.7 ± 5.9	1.00	24.4 ± 5.4	29.0 ± 5.5**	1.19	polygynous	Lambin et al., 1992; Tast, 1966
M. t. townsendii	70	—	58	—		40.9 ± 6.8	53.9 ± 7.9***	1.32	monogamous	Lambin and Krebs, 1991
C. rutilus dawsoni	169	102.6 ± 7.1	220	101.6 ± 4.5	0.99	23.4 ± 5.0	24.4 ± 3.2*	1.04	promiscuous	Burns, 1981

* $P < 0.05$, ** < 0.01, *** < 0.001.

of social system (Getz and Hofmann, 1986; Getz et al., 1987; Thomas and Birney, 1979), but polygyny is common (Getz and Hofmann, 1986). Conversely, preliminary evidence indicates that *M. pinetorum* is monogamous (or perhaps even polyandrous), but not polygynous (FitzGerald and Madison, 1983). Thus, we would expect sexual dimorphism to occur in the first two species, but to be minimal in the last one. Indeed, Dewsbury et al. (1980) found significant sexual dimorphism in *M. ochrogaster* at 90 days of age (male:female ratio of 1.17:1).

In this discussion we assume that the major reason for a sex bias in mass is because of intraspecific competition among males for access to females. As Ralls (1976) points out, there may be other reasons why sexual dimorphism could evolve, especially when it favors females, ranging from differential niche utilization by the sexes to intense competition among females for access to resources. However, we suggest that, although the latter explanations may account for sexual dimorphism in other organisms, such as raptors, the bias we see favoring male microtines is most parsimoniously explained by competition among males for access to females.

In conclusion, sexual dimorphism in body mass, but not length of body, follows a predictable pattern based on an understanding of the mating system. However, to understand the selective forces acting to promote sexual dimorphism it is crucial to know the full range of mating tactics occurring among males and females within a species.

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