

Chapter 10 Sexual Size Dimorphism in Rodents

Albrecht I. Schulte-Hostedde

Body size is the result of both natural and sexual selection, and may influence the demography and life history of vertebrates (Sauer and Slade 1988; Roff 1992). In particular, intraspecific variation in body size may have consequences for individual reproductive success and survival. For example, large body size is expected to enhance reproductive success of males through increased success at acquiring mates (Alexander et al. 1979; Clutton-Brock et al. 1988). For females, large size is associated with increased offspring survival through higher-quality maternal care (Ralls 1976). Selection for small body size can occur due to costs such as the time and energy required to support a large body, and the risks of predation, parasitism, or starvation associated with the rapid growth or lengthy development time required to reach large size (Blanckenhorn 2000). These costs can act to counterbalance the benefits of large size.

Sexual size dimorphism (hereafter referred to as simply sexual dimorphism) is defined as any difference in body size between males and females of the same species. Sex differences in the relationship between body size and fitness ultimately lead to different body size optima being favored by natural and sexual selection (Price 1984; Greenwood and Adams 1987; Hedrick and Temeles 1989; Andersson 1994; Blanckenhorn 2000). The sum of selection pressures acting on males and females therefore dictates the direction and magnitude of sexual dimorphism. These selection pressures include niche differentiation between the sexes, fecundity selection, intrasexual selection (male-male competition), and intersexual selection (female mate choice: Andersson 1994).

Underlying these selection pressures are genetic correlations between the sexes that may retard male and female body size from evolving apart (Lande 1980). These correlations can be powerful enough to prevent sexual dimorphism from evolving, despite differential selection for male and female body size (Merilä et al. 1998). Additionally, ecological constraints associated with locomotion and other habits may also limit the degree to which sex-specific selective forces such as sexual selection lead to sex differences in body size. Thus explanations for the evolution and maintenance of sexual dimorphism must not only consider why one sex is larger, but also why the other sex is smaller.

Rodents comprise the largest order of mammals, with over 2,000 species (Nowak 1991), and as such display a diversity of sizes, shapes, and, of particular interest, differences between the sexes. Thus rodents are an excellent phylogenetic group with which to study the selection pressures on body size that result in sexual dimorphism. The objectives of this chapter are to (1) outline several issues related to our understanding of how both body size and sex differences in body size evolve, especially of rodents (see table 10.1), (2) describe interspecific patterns of variation in sexual dimorphism of rodents, (3) examine geographic patterns of intraspecific variation in sexual dimorphism in *Tamias* spp. with respect to climatic variables, and finally (4) develop hypotheses and approaches to the study of the evolution and maintenance of sexual dimorphism, specifically using rodents.

Sexual dimorphism in mammals has been extensively studied, especially in the context of the male-biased sexual

Table 10.1 Sex-specific selective pressures that contribute to the evolution of monomorphism and sexual size dimorphism in rodents

Direction of advantage	Selective pressure	Example	Reference
Large female size	Higher fecundity	Deer mice	Myers and Masters 1983
	Better parental care	—	—
	Dominance in contests over resources	Southern flying squirrel	Madden 1974
Small female size	Early maturation and faster generation times	—	—
	Lower energetic demands for maintenance, and more efficient shunting of energy to reproduction	Yellow-pine chipmunk (?)	Schulte-Hostedde et al. 2002
Large male size	Male-male combat over females	Arctic ground squirrel	Lacey and Wiczorek 2001
Small male size	Success at scramble competition (competition in which manoeuvrability is important)	13-lined ground squirrel	Schwagmeyer 1988b
	Early maturation with more rapid reproduction	—	—

dimorphism prevalent in pinnipeds and ungulates (e.g., Alexander et al. 1979; Weckerly 1998; Loison et al. 1999), but relatively little attention has been paid to the evolution and maintenance of sexual dimorphism in rodents (but see Bondrup-Nielsen and Ims 1990; Yoccoz and Mesnager 1998). This lack of attention may be the result of the relatively subtle size differences between males and females that occur in most rodents—however, there is evidence of both male- and female-biased sexual dimorphism, a pattern that is uncommon among other mammalian orders (Ralls 1977).

Mammals are generally polygynous (Clutton-Brock 1989b), yet the mating systems of rodents are highly variable, ranging from monogamy (prairie voles [*Microtus ochrogaster*; Getz et al. 1993], California mice [*Microtus californicus*; Ribble 1991]), to polygynandry (deer mice [*Peromyscus maniculatus*; Ribble and Millar 1996], yellow-pine chipmunks [*Tamias amoenus*; Schulte-Hostedde 2004]). Sexual dimorphism is predicted to be male-biased in those species that have intense male-male competition for mates, especially if combat takes place on the ground, rather than in arboreal or aerial environments (Alexander et al. 1979; Andersson 1994). This prediction has borne true in North American voles; males had significantly longer bodies than females in polygynous species (*Microtus californicus*, *M. oeconomus*, *M. xanthognathus*; Heske and Ostfeld 1990). Nonetheless, this pattern is not universal. For example, the bushy-tailed woodrat (*Neotoma cinerea*) is highly dimorphic (males weigh approximately 30% more than females; Schulte-Hostedde et al. 2001), yet variation in male and female reproductive success is equal, and there is no genetic evidence that woodrats are polygynous (Topping and Millar 1998; 1999). Thus despite strong evidence that intense male-male competition is associated with male-biased dimorphism, this explanation cannot be universal.

Explanations for why females are larger than males tend to be more complex than explaining male-biased sexual dimorphism in rodents. Most examples of female-biased sex-

ual dimorphism are explained by the fecundity advantage afforded to large females (Andersson 1994). Indeed, in many oviparous taxa such as insects, fish, and reptiles, females are often larger than males (Andersson 1994). However there is little, if any, evidence that fecundity is correlated with body size in rodents (but see Myers and Master 1983; Dobson and Michener 1992). Ralls (1976) hypothesized that larger females were better mothers with respect to parental care, and thus selection should favor larger females. There have been few studies of female-biased sexual dimorphism in mammals, but work on rodents has suggested that the best approach to understanding the evolution of female-biased sexual dimorphism is to consider the selective pressures on both sexes (Bondrup-Nielsen and Ims 1990; Schulte-Hostedde et al. 2002). With the advent of molecular techniques for the assignment of paternity, it is possible to quantify the fitness components of both sexes, such as lifetime reproductive success, allowing sex-specific patterns to be ascertained. It is becoming clear from studies on other taxa that this approach can be fruitful when testing hypotheses related to the evolution and maintenance of sexual dimorphism (Preziosi and Fairbairn 2000; Przybylo et al. 2000).

An important consideration when testing hypotheses related to body size and sexual dimorphism is the definition of body size. Body size can be defined as the magnitude of an individual's physical structure, and two measures of body size are often used—body mass and skeletal size (e.g., Boonstra et al. 1993; Ostfeld and Heske 1993). The interpretation of intraspecific variation in body mass as an index of body size can be compromised, particularly when size dimorphism is small, because body mass can vary for two reasons. First, variation in skeletal structure may lead to large structural size and a concomitant increase in mass. Second, variation in fat reserves or muscle mass may lead to sex differences in body mass. Under the latter scenario, any observed sexual dimorphism would be due to differences in

body composition rather than size. Indeed, male rodents tend to have more muscle mass than females, and thus, at the same structural size, males are heavier than females (Schulte-Hostedde et al. 2001). Additionally, female rodents gain mass during reproduction; therefore the use of mass as an index of sexual dimorphism is inappropriate during the reproductive season. The measurement of structural size components such as body length or skull dimensions is an appropriate alternative; however, it is critical that these components are measured in a repeatable fashion (Bailey and Byrnes 1990; Loughheed et al. 1991). The use of a multivariate index of body size from a factor analysis is preferred over univariate measures because the use of multiple size components in a composite index of size is more likely to accurately reflect overall structural size than a single component (Green 2001). The most appropriate index of overall body size is therefore a multivariate estimate, but when this is not possible a univariate measure of structural size, such as body length, is preferred. The use of an index of structural size avoids the problems associated with body mass.

Hand in hand with issues related to the definition of body size is how to best describe sexual dimorphism. The calculation of a dimorphism ratio is complicated by the misgivings associated with the use of ratios (Atchley et al. 1976), yet ratios have high intuitive value. Both the direction and degree of dimorphism are contained within a ratio index of size dimorphism, without the need to refer to an equation (Lovich and Gibbons 1992). Ratios for multivariate indices of body size are difficult to calculate, because such “factor scores” from factor analyses are not on a ratio scale. However, using the eigenvectors from the factor analysis to calculate the factor score of an animal of zero size, and adding the absolute value of this score to the factor scores of each individual can provide an alternative (Slattery and Alisauskas 1995). Recently, it has been suggested that the arguments against the use of ratios do not preclude their use when studying sexual dimorphism (Smith 1999), and so ratios may provide the most intuitive descriptor of the magnitude of any sex differences in body size. Nonetheless, alternative methods of analysing sexual dimorphism among species or groups have been proposed, including using residuals from a regression between the body size of one sex and the body size of the other (Ranta et al. 1994) as an index of the size of one sex relative to the size of the other sex.

Patterns of Sexual Size Dimorphism in Rodents

Evidence from some genera of rodents indicates that there is substantial variation in sexual dimorphism (Bondrup-

Nielsen and Ims 1990; Heske and Ostfeld 1990; Levenson 1990; Yoccoz and Mesnager 1998). There has not been a comprehensive examination of sex differences in body size across a broad taxonomic range of rodent species.

I compiled data from published sources on structural size (body length) and/or body mass of males and females for a number of rodent species. I collected data on body mass despite misgivings regarding this metric of body size because it was often the only index of size provided. I did not compile data on body size components such as skull and pelvic characters (e.g., Lammers et al. 2001). Where geographic differences in sexual size dimorphism existed, I arbitrarily present the data from only one population. Patterns of monomorphism and sexual dimorphism are reported for 172 species of rodents (tables 10.2 and 10.3).

Male-biased sexual dimorphism

There are several broad patterns that emerge from the compiled data on sexual dimorphism among rodents. Dimorphism ratios associated with body mass tend to be higher than ratios based on body size, likely because males carry more muscle than females of the same size (Schulte-Hostedde et al. 2001). The predominant pattern among species in which dimorphism occurs is that of male-biased sexual dimorphism. In the overwhelming number of species males are larger than females, and this difference is most pronounced among the ground squirrels. The large degree of male-biased size dimorphism is likely the result of sexual selection, because the mating system of many ground squirrels involves polygyny and male-male competition (e.g., Davis and Murie 1985; Lacey and Wiczorek 2001; Hoogland 2003b). Similar patterns of male-biased dimorphism are found among desert rodents (the Heteromyidae) and fossorial rodents (e.g., the Geomyidae and the Bathyergidae). Competition occurs among male kangaroo rats (Randall 1991a; Randall et al. 2002), which may favor large male body size and the evolution of male-biased sexual dimorphism. Interestingly, males often compete through “foot-drumming” (Randall 1997), and it is not clear how patterns of foot-drumming are related to individual male size. Fossorial rodents, including solitary mole-rats and pocket gophers, have high levels of male-biased sexual dimorphism. Males may be significantly larger than females in many fossorial rodents because of the highly aggressive and xenophobic nature of intraspecific interactions (Bennett et al. 2000). The evolution of large male size and male-biased sexual dimorphism may be related to the high degree of male-male combat that occurs. The mating system of fossorial rodents has been characterized as polygynous, in which males mate with multiple females; however, it is unclear whether competition among males occurs through

Table 10.2 Common and scientific names, male and female mean body size, standard deviation (when available) and dimorphism ratio (female: male) for 49 species of the Sciuridae

Common name	Species	n (f)	n (m)	Size trait	Male	SD	Female	SD	f : m	Reference
Southern flying squirrel	<i>Glaucomys volans</i>	90	71	body length (mm)	125.8	5.2	129	6.4	1.03	Robins et al. 2000
Yellow-pine chipmunk	<i>Tamias amoenus</i>	57	37	body length (mm)	122.5	3.4	127.4	3.8	1.04	Schulte-Hostedde et al. 2002
Alpine chipmunk	<i>T. alpinus</i>	28	13	body length (mm)	103.9	4.3	107.3	3.5	1.03	Levenson 1990
Gray-footed chipmunk	<i>T. canipes</i>	21	28	body length (mm)	128.2	5.6	131.1	6.6	1.02	Levenson 1990
Gray-collared chipmunk	<i>T. cinereicollis</i>	17	10	body length (mm)	128.2	5.3	133.2	4.7	1.04	Levenson 1990
Cliff chipmunk	<i>T. dorsalis</i>	70	51	body length (mm)	123.6	8	127.5	10.1	1.03	Levenson 1990
Least chipmunk	<i>T. minimus</i>	204	163	body length (mm)	109.5	7.1	114.6	8.7	1.05	Levenson 1990
Long-eared chipmunk	<i>T. quadrimaculatus</i>	10	10	body length (mm)	131.8	5.6	138.7	6.5	1.05	Levenson 1990
Colorado chipmunk	<i>T. quadrivittatus</i>	21	18	body length (mm)	123.8	9	131.3	7.8	1.06	Levenson 1990
Red-tailed chipmunk	<i>T. ruficaudus</i>	28	24	body length (mm)	122.2	4.3	126.7	5.8	1.04	Levenson 1990
Lodgepole chipmunk	<i>T. speciosus</i>	16	25	body length (mm)	120.2	5.5	127.8	6.5	1.06	Levenson 1990
Townsend's chipmunk	<i>T. townsendii</i>	143	110	body length (mm)	141.9	8.8	146.5	7.6	1.03	Levenson 1990
Uinta chipmunk	<i>T. umbrinus</i>	63	78	body length (mm)	121.8	6.8	125.7	6.2	1.03	Levenson 1990
Buller's chipmunk	<i>T. bulleri</i>	8	11	body length (mm)	132.6	7.6	137.1	5.2	1.03	Levenson 1990
Durango chipmunk	<i>T. durangae</i>	17	18	body length (mm)	135.0	7.8	134.6	8.2	1.00	Levenson 1990
Merriam's chipmunk	<i>T. merriami</i>	40	24	body length (mm)	132.6	5.0	135.6	9.0	1.02	Levenson 1990
California chipmunk	<i>T. obscurus</i>	17	8	body length (mm)	125.2	5.1	128.8	4.8	1.03	Levenson 1990
Palmer's chipmunk	<i>T. palmeri</i>	13	16	body length (mm)	127.0	5.3	126.1	4.2	0.99	Levenson 1990
Panamint chipmunk	<i>T. panamintinus</i>	28	23	body length (mm)	117.9	4.6	118.6	5.4	1.01	Levenson 1990
Siberian chipmunks	<i>T. sibiricus</i>	29	33	body length (mm)	150.2	7.1	149.9	8.9	1.00	Levenson 1990
Sonoma chipmunk	<i>T. sonomae</i>	14	12	body length (mm)	136.0	5.3	140.0	7.0	1.03	Levenson 1990
Eastern chipmunk	<i>T. striatus</i>	45	46	body length (mm)	146.7	7.9	147.6	10.2	1.01	Levenson 1990
North American red squirrel	<i>Tamiasciurus hudsonicus</i>	1075	1231	body mass (g)	265	18.7	251.1	19.5	0.95	S. Boutin, personal communication
Western grey squirrel	<i>Sciurus griseus</i>	—	—	body mass (g)	750		960		1.28	Heaney 1984
Abert's squirrel	<i>S. aberti</i>	—	—	body mass (g)	589		602		1.02	Heaney 1984
Eastern grey squirrel	<i>S. carolinensis</i>	—	—	body mass (g)	593		593		1	Heaney 1984
Red-tailed squirrel	<i>S. granatensis</i>	—	—	body mass (g)	464		440		0.95	Heaney 1984
Fox squirrel	<i>S. niger</i>	—	—	body mass (g)	690		680		0.99	Heaney 1984
Vancouver marmot	<i>Marmota vancouverensis</i>	12	6	total length (mm)	695	32.8	661	39.5	0.95	Nagorsen 1987
Yellow-bellied marmot	<i>M. flaviventris</i>	61	38	body mass (g)	3900	43.8	2800	48.4	0.72	Armitage et al. 1976
Olympic marmot	<i>M. olympus</i>	—	—	body mass (g)	1900		1400		0.74	Armitage 1981
Woodchuck	<i>M. monax</i>	—	—	body mass (g)	3100		3080		0.99	Armitage 1981
Townsend's ground squirrel	<i>Spermophilus townsendii</i>	11	7	body mass (g)	259.8	16.4	173.4	22.6	0.67	Rickart 1982
Richardson's ground squirrel	<i>S. richardsonii</i>	22	13	body mass (g)	363	42.2	218	36.1	0.60	Michener 1984
Thirteen-lined ground squirrel	<i>S. tridecemlineatus</i>	—	—	body mass (g)	135	—	113	—	0.84	Armitage 1981
Round-tailed ground squirrel	<i>S. tereticaudus</i>	—	—	body mass (g)	145	—	100	—	0.69	Armitage 1981
Wyoming ground squirrel	<i>S. elegans</i>	—	—	body mass (g)	266	—	203	—	0.76	Armitage 1981
Uinta ground squirrel	<i>S. armatus</i>	—	—	body mass (g)	333	—	266	—	0.80	Armitage 1981
Franklin's ground squirrel	<i>S. franklinii</i>	—	—	body mass (g)	360	—	280	—	0.78	Armitage 1981
Columbian ground squirrel	<i>S. columbianus</i>	—	—	body mass (g)	492	—	270	—	0.55	Armitage 1981
California ground squirrel	<i>S. beecheyi</i>	—	—	body mass (g)	650	—	500	—	0.77	Armitage 1981
Arctic ground squirrel	<i>S. parryii</i>	—	—	body mass (g)	700	—	635	—	0.91	Armitage 1981
Golden-mantled ground squirrel	<i>S. lateralis</i>	—	—	body mass (g)	155	—	130	—	0.84	Armitage 1981
Belding's ground squirrel	<i>S. beldingi</i>	—	—	body mass (g)	220	—	218	—	0.99	Armitage 1981

Table 10.2 (continued)

Common name	Species	n (f)	n (m)	Size trait	Male	SD	Female	SD	f:m	Reference
Columbian ground squirrel	<i>S. columbianus</i>	19	7	body mass (g)	459	40	393	52	0.86	Dobson 1992
White-tailed prairie dog	<i>Cynomys leucurus</i>	17	28	body mass (g)	790.5	140	579.2	115	0.73	J.L. Hoogland, personal communication
Black-tailed prairie dog	<i>C. ludovicianus</i>	933	481	body mass (g)	727.0	94.1	692.4	94.5	0.95	J.L. Hoogland, personal communication
Gunnison's prairie dog	<i>C. gunnisoni</i>	971	903	body mass (g)	598.7	139	456.1	101	0.76	J.L. Hoogland, personal communication
Utah prairie dog	<i>C. parvidens</i>	363	286	body mass (g)	757.1	156	594.7	102	0.78	J.L. Hoogland, personal communication

NOTES: When available, sample sizes are included (f = female, m = male).

combat, sperm competition (multiple mating by females; Lacey 2000), or both. Thus the logistic difficulties of studying animals that live almost exclusively underground need to be overcome to facilitate the study of mating systems and patterns of sexual dimorphism in mole-rats and pocket gophers.

Female-biased sexual dimorphism

There are two groups in which female-biased sexual dimorphism is prevalent: the chipmunks (*Tamias* spp.) and jumping mice (*Napaeozapus insignis* and *Zapus hudsonius*). Why this pattern exists is unclear, but there is evidence that in the yellow-pine chipmunk, female-biased dimorphism may be the result of the lack of an effect of body size on male reproductive success coupled with selection for large female size with respect to both reproductive success and survival (Schulte-Hostedde et al. 2002). The mating system of most chipmunks is similar to that which is found among tree squirrels (Koprowski, chap. 7, this volume). Females become estrus in early spring and advertise their receptive state by particular vocalizations. On the day of her estrus, males aggregate around the female's burrow and chase her when she emerges (Callahan 1981). In yellow-pine chipmunks, this mating chase results in multiple paternity of the offspring, with no advantage for large males (Schulte-Hostedde et al. 2002; Schulte-Hostedde 2004). However, males with large testes, who are presumably superior at sperm competition, tend to sire more offspring than males with small testes (Schulte-Hostedde and Millar 2004).

In jumping mice, both the mating system and the relationship between body size and fitness components are unknown. Male jumping mice emerge from hibernation earlier than females (Ovaska and Herman 1988), which is

consistent with ground squirrel emergence schedules, when males emerge early to compete for access to emerging females (Michener 1983b). Any inferences about the evolution of female-biased sexual dimorphism in jumping mice are hampered by a lack of information about their basic breeding patterns.

Mixed patterns of sexual dimorphism

Perhaps the most intriguing group of rodents with respect to sexual dimorphism are the voles (*Clethrionomys* and *Microtus*), because sexual dimorphism varies from female-biased to male-biased dimorphism, even among populations of the same species (Yoccoz and Mesnager 1998). This variation has stimulated much of the research on sexual dimorphism in rodents (Bondrup-Nielsen and Ims 1990; Ostfeld and Heske 1993; Yoccoz and Mesnager 1998). Alternating patterns of sexual size dimorphism may exist among voles for a number of reasons, including sex-specific variation in survival rates (Yoccoz and Mesnager 1998). Female bank voles (*Clethrionomys glareolus*) are typically larger than males, yet some alpine populations show male-biased sexual dimorphism (Yoccoz and Mesnager 1998). One hypothesis for this switch in dimorphism is that the evolution of male-biased sexual dimorphism in alpine populations of bank voles is the result of a higher survival rate. This higher survival rate could be due to an absence of predators (weasels) that selects for an increase in somatic mass and a decrease in reproductive effort (Yoccoz and Mesnager 1998). Intense sexual selection occurs when the larger males within these alpine populations compete for mates, ultimately leading to the evolution of male-biased sexual dimorphism. Other explanations are related to variation in male reproductive tactics and how these tactics might be

Table 10.3 Common and scientific names, male and female mean body size, standard deviation (when available) and dimorphism ratio (female:male) for 123 species of rodents from the Erethizontidae, Muridae, Zapodidae, Heteromyidae, Ctenomyidae, Octodontidae, Bathyergidae, Geomyidae, and Chinchillidae

Common name	Species	n (f)	n (m)	Size trait	Male	SD	Female	SD	f:m	Reference
Erethizontidae										
North American porcupine	<i>Erethizon dorsatum</i>	11	12	body mass (kg)	10.2	1.25	8.54	0.93	0.84	Sweitzer and Berger 1997; Sweitzer, personal communication
				vent length (cm)	78	3.46	70.9	2.98	0.91	Sweitzer and Berger 1997; Sweitzer, personal communication
Muridae										
Beach vole	<i>Microtus breweri</i>	25	23	body length (mm)	129.1	6.6	123.3	5.9	0.96	Heske and Ostfeld 1990
Field vole	<i>M. agrestis</i>	—	—	body mass (g)	30.8	—	25.9	—	0.84	Bondrup-Nielsen and Ims 1990
California vole	<i>M. californicus aesterinus</i>	15	16	body length (mm)	142.2	4.9	135.9	5.1	0.96	Heske and Ostfeld 1990
Long-tailed vole	<i>M. longicaudus</i>	6	4	body length (mm)	175	—	172	—	0.98	Smolen and Keller 1987
Singing vole	<i>M. miurus murei</i>	44	38	body length (mm)	123.3	4.9	115.9	5.7	0.94	Heske and Ostfeld 1990
Water vole	<i>M. richardsoni</i>	142	86	body mass (g)	113.7	15.8	98.9	15.7	0.87	Ludwig 1984
				body length (mm)	159	7.1	150.9	8.6	0.95	Ludwig 1984
Root vole	<i>M. oeconomus gilmorei</i>	42	37	body length (mm)	118.9	8.6	113.6	7.1	0.96	Heske and Ostfeld 1990
	<i>M. oeconomus macfarlani</i>	21	18	body mass (g)	29	5.5	24.4	5.4	0.84	Boonstra et al. 1993
Yellow-cheeked vole	<i>M. xanthognathus</i>	14	34	body length (mm)	159.1	10.9	153.1	8.4	0.96	Heske and Ostfeld 1990
Meadow vole	<i>M. pennsylvanicus</i>	43	40	body mass (g)	28.7	5.7	25.8	5.9	0.90	Boonstra et al. 1993
Woodland vole	<i>M. pinetorum</i>	13	5	body length (mm)	117.8	—	122.9	—	1.04	Smolen 1981
Townsend's vole	<i>M. townsendii</i>	58	70	body mass (g)	53.9	7.9	40.9	6.8	0.76	Boonstra et al. 1993
Northern red-backed vole	<i>Clethrionomys rutilus dawsoni</i>	10	11	body length (mm)	100.3	3.6	107.6	8.1	1.07	Heske and Ostfeld 1990
	<i>C. rutilus glacialis</i>	31	21	body length (mm)	110.9	3.9	114.5	4.3	1.03	Heske and Ostfeld 1990
	<i>C. rutilus dawsoni</i>	220	169	body mass (g)	24.4	3.2	23.4	5	0.96	Boonstra et al. 1993
Red-backed vole	<i>C. gapperi</i>	20	66	body length	97.7	0.8	98.0	1.6		Schulte-Hostedde et al. 2001
Bank vole	<i>C. glareolus</i>	176	70	body mass (g)	25.2	2.2	28	2.5	1.11	Bondrup-Nielsen and Ims 1990
Grey-sided vole	<i>C. rufocanus</i>	—	—	body mass (g)	36.4	—	42.6	—	1.17	Bondrup-Nielsen and Ims 1990
Sagebrush vole	<i>Lagurus curtatus</i>	10	10	body length	128	—	127	—	0.99	Carroll and Genoways 1980
Pouched mouse	<i>Saccostomus mearnsi</i>	—	—	body mass (g)	79.5	3.2	62.3	2	0.78	Keesing 1998a
Deer mouse	<i>Peromyscus maniculatus</i>	21	83	body length (mm)	86.5	0.7	88.2	1.6	1.02	Schulte-Hostedde et al. 2001
Volcano mouse	<i>P. alstoni</i>	—	—	body length (mm)	204.4	—	211.1	—	1.03	Williams et al. 1985
Canyon mouse	<i>P. crinitus</i>	81	79	body length (mm)	174.6	—	176.1	—	1.01	Johnson and Armstrong 1987
Yellow-nosed mouse	<i>Abrothrix xanthorhinus</i>	166	194	body length (mm)	80.7	5.2	82.0	7.6	1.02	Lozado et al. 1996
Longtail rice rat	<i>Oryzomys longicaudatus</i>	58	54	body mass (g)	37.7	8.5	27.8	6.3	0.74	Pearson 1983
				body length (mm)	101	7.0	93.2	9.2	0.92	Pearson 1983

Table 10.3 (continued)

Common name	Species	n (f)	n (m)	Size trait	Male	SD	Female	SD	f:m	Reference
South American rock rat	<i>Aconaemys fuscus</i>	4	3	body mass (g)	133	—	134	—	1.01	Pearson 1983
				body length (mm)	177	—	179	—	1.01	Pearson 1983
Long-haired grass mouse	<i>Akodon longipilis</i>	87	121	body mass (g)	38.2	5.9	36.9	6.2	0.97	Pearson 1983
				body length (mm)	104.9	7.0	105.4	7.6	1.00	Pearson 1983
Olive grass mouse	<i>Akodon olivaceus</i>	23	41	body mass (g)	28.2	3.8	25.8	4.8	0.91	Pearson 1983
				body length (mm)	95.6	5.4	93.2	6.1	0.97	Pearson 1983
Bolivian big-eared mouse	<i>Auliscomys micropus</i>	25	20	body mass (g)	72.8	12.3	72.6	12.2	1.00	Pearson 1983
				body length (mm)	133.1	9.3	131.5	5.4	0.99	Pearson 1983
Greater long-clawed mouse	<i>Chelemys macronyx</i>	11	14	body mass (g)	74.6	11.4	72.0	13.6	0.97	Pearson 1983
				body length (mm)	130.0	7.2	130.8	11.7	1.01	Pearson 1983
Long-clawed mole mouse	<i>Geoxus valdivianus</i>	8	15	body mass (g)	31.7	3.2	31.3	4.5	0.99	Pearson 1983
				body length (mm)	101.7	3.2	101.7	6.5	1.00	Pearson 1983
Chilean rat	<i>Irenomys tarsalis</i>	13	11	body mass (g)	44.4	12.9	41.9	9.0	0.94	Pearson 1983
Long-tailed mouse	<i>Pseudomys higginsi</i>	26	29	body length (mm)	131.1	—	131.7	—	0.99	Driessen and Rose 1999
House mouse	<i>Mus musculus</i>	20	20	body length (mm)	79.0	—	77.6	—	0.98	Southern 1977
Harvest mouse	<i>Micromys minutus</i>	47	72	body length (mm)	57.0	—	57.1	—	1.00	Southern 1977
Wood mouse	<i>Apodemus sylvaticus</i>	20	20	body length (mm)	87.6	—	87.7	—	1.00	Southern 1977
Yellow-necked mouse	<i>Apodemus flavicollis</i>	10	22	body length (mm)	105	—	101.6	—	0.97	Southern 1977
Musk-rat	<i>Ondatra zibethicus</i>	14	11	body length (mm)	312.7	20.6	312.5	10.1	1.00	Virgl and Messier 1992
Round-tailed muskrat	<i>Neofiber alleni</i>	108	52	body mass (g)	279	35.4	262	38.3	0.94	Birkenholz 1963
Spiny mouse	<i>Acomys cahirinus</i>	19	14	body mass (g)	43.1	4.4	36.3	4.9	0.84	Khokhlova et al. 2000
Spinifex hopping mouse	<i>Notomys alexis</i>	—	—	body mass (g)	27.9	—	33.3	—	1.19	Breed 1983
Sundevall's jird	<i>Meriones crassus</i>	30	37	body mass (g)	74.7	15.9	67.4	14	0.90	Khokhlova et al. 2000
Desert woodrat	<i>Neotoma lepida</i>	24	16	body length (mm)	174.4	7.8	159.5	6.8	0.91	Hoffmeister 1986
Eastern woodrat	<i>N. floridana</i>	27	41	total length (mm)	384.2	19.4	369.8	17.1	0.96	Birney 1973
Southern plains woodrat	<i>N. micropus</i>	23	31	total length (mm)	370	22.7	355.8	16.6	0.96	Birney 1973
Sonoran woodrat	<i>N. phenax</i>	10	10	body mass (g)	239	—	216	—	0.90	Jones and Genoways 1978
Mexican woodrat	<i>N. mexicana</i>	6	8	body length (mm)	333	—	327	—	0.98	Cornely and Baker 1986
White-throated woodrat	<i>N. albigula</i>	6	9	body mass (g)	215.6	—	162.5	—	0.75	Macedo and Mares 1988
Bushy-tailed woodrat	<i>N. cinerea</i>	40	22	body mass (g)	388	80.3	297.6	37.1	0.77	Schulte-Hostedde et al. 2001
				body length (mm)	234.6	91.3	221.6	31.1	0.94	Schulte-Hostedde et al. 2001
Capromyidae										
Nutria	<i>Myocastor coypus</i>	82	99	body mass (g)	670	79	636	116	0.95	Southern 1977
Zapodidae										
Meadow jumping mouse	<i>Zapus hudsonius</i>	64	42	body length (mm)	81.4	3.5	84.2	4.5	1.03	Whitaker 1963
Woodland jumping mouse	<i>Napeozapus insignis</i>	33	40	body length (mm)	88.8	—	92.1	—	1.04	Wrigley 1972
Heteromyidae										
Pacific kangaroo rat	<i>Dipodomys agilis</i>	1741	1425	body length (mm)	116.1	—	114	—	1.02	Best 1993
Desert kangaroo rat	<i>D. deserti</i>	254	204	body length (mm)	141.2	—	135.3	—	0.96	Best 1993
San Quintin kangaroo rat	<i>D. gravipes</i>	56	54	body length (mm)	130.6	—	127.1	—	0.97	Best 1993

(continued)

Table 10.3 (continued)

Common name	Species	n (f)	n (m)	Size trait	Male	SD	Female	SD	f:m	Reference
Heermann's kangaroo rat	<i>D. heermanni</i>	474	366	body length (mm)	121.6	—	119.4	—	0.98	Best 1993
Giant kangaroo rat	<i>D. ingens</i>	55	47	body length (mm)	147.6	—	144.5	—	0.98	Best 1993
San Jose island kangaroo rat	<i>D. insularis</i>	9	16	body length (mm)	108.2	—	97.3	—	0.90	Best 1993
Merriam's kangaroo rat	<i>D. merriami</i>	433	397	body length (mm)	100.6	—	99.2	—	0.99	Best 1993
Narrow-faced kangaroo rat	<i>D. venustus</i>	65	73	body length (mm)	128.7	—	122.9	—	0.95	Best 1988
California kangaroo rat	<i>D. californicus</i>	191	150	body length (mm)	119.5	—	120.5	—	1.01	Best 1988
Gulf coast kangaroo rat	<i>D. compactus</i>	48	29	body length (mm)	112.5	—	110.6	—	0.98	Best 1988
Texas kangaroo rat	<i>D. elator</i>	120	86	body length (mm)	124.3	—	124.0	—	1.00	Best 1988
Big-eared kangaroo rat	<i>D. elephantinus</i>	38	32	body length (mm)	129.0	—	128.9	—	1.00	Best 1988
Chisel-toothed kangaroo rat	<i>D. microps</i>	156	174	body length (mm)	113.5	—	111.8	—	0.98	Best 1988
Nelson's kangaroo rat	<i>D. nelsoni</i>	112	87	body length (mm)	128.3	—	127.1	—	0.99	Best 1988
Tipton kangaroo rat	<i>D. nitratoides</i>	276	200	body length (mm)	97.1	—	98.1	—	0.99	Best 1988
Ord's kangaroo rat	<i>D. ordii</i>	691	662	body length (mm)	114.2	—	114.0	—	1.00	Best 1988
Panamint kangaroo rat	<i>D. panamintinus</i>	467	385	body length (mm)	120.2	—	121.1	—	1.01	Best 1988
Phillip's kangaroo rat	<i>D. phillipsii</i>	93	77	body length (mm)	105.0	—	104.2	—	0.99	Best 1988
Banner-tailed kangaroo rat	<i>D. spectabilis</i>	296	232	body length (mm)	142.3	—	142.0	—	1.00	Best 1988
Stephen's kangaroo rat	<i>D. stephensi</i>	81	70	body length (mm)	115.7	—	115.8	—	1.00	Best 1988
Tehachapi pocket mouse	<i>Perognathus alticola</i>	20	20	body length (mm)	77.6	—	72.5	—	0.93	Best 1993
Great Basin pocket mouse	<i>P. parvus</i>	20	20	body length (mm)	83.6	—	78.3	—	0.94	Best 1993
Arizona pocket mouse	<i>P. amplus</i>	20	20	body length (mm)	70.8	—	70.1	—	0.99	Best 1993
Olive-backed pocket mouse	<i>P. fasciatus</i>	20	20	body length (mm)	71.2	—	72.1	—	1.01	Best 1993
Plains pocket mouse	<i>P. flavescens</i>	20	20	body length (mm)	72.1	—	70.4	—	0.98	Best 1993
Silky pocket mouse	<i>P. flavus</i>	20	20	body length (mm)	59.0	—	60.4	—	1.02	Best 1993
San Joaquin pocket mouse	<i>P. inornatus</i>	20	20	body length (mm)	72.6	—	72.1	—	0.99	Best 1993
Little pocket mouse	<i>P. longimembris</i>	20	20	body length (mm)	58.5	—	56.9	—	0.97	Best 1993
Narrow-skulled pocket mouse	<i>Chaetodipus artus</i>	20	20	body length (mm)	92.1	—	85.9	—	0.93	Best 1993
Little desert pocket mouse	<i>C. arenarius</i>	20	20	body length (mm)	69.5	—	67.3	—	0.97	Best 1993
Bailey's pocket mouse	<i>C. baileyi</i>	20	20	body length (mm)	94.5	—	92.5	—	0.98	Best 1993
California pocket mouse	<i>C. californicus</i>	20	20	body length (mm)	88.5	—	85.3	—	0.96	Best 1993
San Diego pocket mouse	<i>C. fallax</i>	20	20	body length (mm)	84.6	—	82.0	—	0.97	Best 1993
Long-tailed pocket mouse	<i>C. formosus</i>	20	20	body length (mm)	82.7	—	79.0	—	0.96	Best 1993
Goldman's pocket mouse	<i>C. goldmani</i>	20	20	body length (mm)	81.4	—	83.7	—	1.03	Best 1993
Hispid pocket mouse	<i>C. hispidus</i>	20	20	body length (mm)	101.5	—	106.9	—	1.05	Best 1993
Rock pocket mouse	<i>C. intermedius</i>	20	20	body length (mm)	74.0	—	74.1	—	1.00	Best 1993
Line pocket mouse	<i>C. lineatus</i>	20	20	body length (mm)	74.4	—	73.0	—	0.98	Best 1993

Table 10.3 (continued)

Common name	Species	n (f)	n (m)	Size trait	Male	SD	Female	SD	f:m	Reference
Nelson's pocket mouse	<i>C. nelsoni</i>	20	20	body length (mm)	80.7	—	78.4	—	0.97	Best 1993
Desert pocket mouse	<i>C. penicillatus</i>	20	20	body length (mm)	76.6	—	75.8	—	0.99	Best 1993
Sinaloa pocket mouse	<i>C. pernix</i>	20	20	body length (mm)	75.2	—	68.9	—	0.92	Best 1993
Spiny pocket mouse	<i>C. spinatus</i>	20	20	body length (mm)	85.0	—	82.6	—	0.97	Best 1993
Dark kangaroo mouse	<i>Microdipodops megacephalus</i>	20	20	body length (mm)	65.0	—	66.8	—	1.03	Best 1993
Pale kangaroo mouse	<i>M. pallidus</i>	20	20	body length (mm)	85.0	—	82.6	—	0.97	Best 1993
Southern spiny pocket mouse	<i>Heteromys australis</i>	20	20	body length (mm)	127.5	—	120.3	—	0.94	Best 1993
Mountain spiny pocket mouse	<i>H. oresterus</i>	9	10	body length (mm)	159.4	—	141.1	—	0.89	Best 1993
Forest spiny pocket mouse	<i>H. anomalus</i>	20	20	body length (mm)	133.8	—	128.9	—	0.96	Best 1993
Desmarest's spiny pocket mouse	<i>H. desmarestianus</i>	20	20	body length (mm)	133.1	—	129.7	—	0.97	Best 1993
Gaumer's spiny pocket mouse	<i>H. gaumeri</i>	20	20	body length (mm)	125.3	—	123.4	—	0.98	Best 1993
Goldman's spiny pocket mouse	<i>H. goldmani</i>	20	20	body length (mm)	148.5	—	143.6	—	0.97	Best 1993
Nelson's spiny pocket mouse	<i>H. nelsoni</i>	20	20	body length (mm)	161.5	—	150.6	—	0.93	Best 1993
Mexican spiny pocket mouse	<i>Liomys irroratus</i>	20	20	body length (mm)	125.4	—	118.6	—	0.95	Best 1993
Salvin's spiny pocket mouse	<i>L. salvini</i>	20	20	body length (mm)	114.2	—	107.5	—	0.94	Best 1993
Painted spiny pocket mouse	<i>L. pictus</i>	35	27	total length (mm)	241	12.2	229.7	9.7	0.95	Genoways 1973
Panamanian spiny pocket mouse	<i>L. adspersus</i>	18	6	total length (mm)	265.9	11.2	249.7	7.3	0.94	Genoways 1973
	<i>L. spectabilis</i>	20	20	body length (mm)	109.4	—	101.5	—	0.93	Best 1993
Ctenomyidae										
Tuco-tuco	<i>Ctenomys talarum</i>	110	95	body mass (g)	136.2	18.8	102.3	12.6	0.76	Zenuto et al. 1999
				body length (mm)	145.99	10.7	139.2	9.35	0.95	Zenuto et al. 1999
Octodontidae										
Cururo	<i>Spalacopus cyanus</i>	7	8	body mass (g)	99.3	4.4	80.2	6.4	0.81	Contreras 1986
Bathyergidae										
Giant mole-rat	<i>Cryptomys mechowii</i>	15	18	body mass (g)	345.3	95.4	252	34	0.73	Scharf et al. 2001
Silvery mole-rat	<i>Heliophobius argente-eocinereus</i>	70	74	body mass (g)	190.1	58.1	162.1	47.2	0.85	Sumbera et al. 2003
				body length (mm)	155.3	17.8	148.8	15	0.96	Sumbera et al. 2003
Geomyidae										
Northern pocket gopher	<i>Thomomys talpoides</i>	13	13	body length (mm)	147.5	8.6	139.2	9.8	0.94	Hoffmeister 1986
Southern pocket gopher	<i>T. umbrinus</i>	11	20	body length (mm)	135.9	8.5	128.9	7.6	0.95	Hoffmeister 1986
Desert pocket gopher	<i>Geomys arenarius</i>	10	7	body length (mm)	253	—	233	—	0.92	Williams and Baker 1974
Texas pocket gopher	<i>G. personatus</i>	13	11	body length (mm)	275.0	—	252.9	—	0.92	Williams 1982
Chinchillidae										
Plains viscacha	<i>Lagostomus maximus</i>	65	66	body mass (g)	630	—	400	—	0.63	Jackson et al. 1996
				total length (mm)	753	—	641	—	0.85	Jackson et al. 1996

NOTES: When available, sample sizes are included (f = female, m = male).

size-dependent. For example, variation in patterns of dimorphism in voles may simply be because variation in mating systems occurs with larger males occurring in species and/or populations with intense male-male competition (Heske and Ostfeld 1990). Variation in spacing behaviour can also lead to variation in male mating tactics and size, and therefore can influence the evolution of sexual dimorphism (Bondrup-Nielsen and Ims 1990). To date, no study has incorporated genetic techniques to measure variation in male reproductive success and examine questions related to sexual dimorphism in voles.

Despite these general patterns of sexual dimorphism it is also clear that many species are monomorphic. Few studies have examined sex-specific patterns of selection on body size in rodents, and therefore it is not possible to determine whether the lack of dimorphism is due to a lack of differential selection on male and female body size or because of ecological or allometric constraints that limit the evolution of sexual dimorphism.

Geographic Variation in Sexual Size Dimorphism of the Chipmunks (*Tamias* spp.): Effects of Climate

Geographic variation in sexual size dimorphism has been documented in many taxa, including snakes (Pearson et al. 2002), lizards (Wikelski and Trillmich 1997), and birds (Badyaev et al. 2000), but there are few studies examining this phenomenon in mammals, specifically rodents. Geographic variation in sexual dimorphism has been related to prey size in carnivores (Dayan and Simberloff 1994), but this is unlikely to apply to rodents. Climatic variation can directly affect body size (Smith et al. 1998; Ashton et al. 2000) and the direction and magnitude of sexual dimorphism in mammals (Dobson and Wigginton 1996; Sullivan and Best 1997; Post et al. 1999). Harsh or extreme climates may place selective pressures on body size by affecting individual energy expenditure through factors such as increased thermoregulatory costs due to cold temperatures or increased foraging costs due to lower food availability. Temporal variation in climate has been suggested to affect sexual size dimorphism in tundra voles (*Microtus oeconomus*), a species in which males are heavier than females due to sexual selection, but seem to adjust body mass downward during the winter to counteract the increase in winter mortality associated with large size (Aars and Ims 2002). This process leads to temporal variation in sexual dimorphism.

The chipmunks (*Tamias* spp.) show a strong pattern of female-biased sexual dimorphism—all species with statistically significant differences in body length between the sexes are exclusively female-biased (Levenson 1990). In yellow-pine chipmunks, male body size does not influence re-

productive success (Schulte-Hostedde et al. 2002), perhaps because scramble competition among males for mating opportunities favors small male size (Alexander et al. 1979). The variation in sexual dimorphism in this genus has been partly attributed to the severity of the environment, with females tending to be larger in the most severe environments (“severe” environments were those that were at high altitude and/or more northern latitude; Levenson 1990). Because large female yellow-pine chipmunks tended to have lower reproductive success than small females when rainfall was excessive, yet had greater reproductive success than small females when rainfall was average, Schulte-Hostedde et al. (2002) hypothesized that large female chipmunks were at an energetic disadvantage when environmental conditions were harsh because of their inability to meet the metabolic demands of both maintenance and lactation. The fitness advantage that large females experience under average conditions is hypothesized to occur because they are “better mothers” (Ralls 1976); either providing higher-quality parental care by protecting the offspring or higher-quality milk than small females (Schulte-Hostedde et al. 2002). Similar sex-specific responses to climate that lead to variation in sexual dimorphism have been seen in the blue tit (*Parus caeruleus*), a small size-dimorphic bird (Blondel et al. 2002). Thus if large females are at an energetic disadvantage when climatic conditions are severe, then female-biased sexual dimorphism should be less pronounced in populations that experience climate extremes, in which selection should favor smaller females.

Using a qualitative assessment based on both latitude and altitude, Levenson (1990) argued that female-biased sexual dimorphism was more pronounced in populations with extreme climatic conditions, in contradiction to the suggestions of Schulte-Hostedde et al. (2002). Levenson (1990) published data on sex differences in body size from 40 populations from 11 species of chipmunks of the genus *Tamias*, almost all from the western United States. Here, I determine whether climate influences the evolution of female-biased sexual dimorphism in chipmunks, and if so, which factors are most important. I obtained the location of capture for the specimens from each of the 40 populations (H. Levenson, pers. comm.), and determined the latitude and longitude of these locations. Monthly climate normals (long-term averages; 1961–1990) were obtained from 3,044 weather stations throughout the continental United States (National Oceanic and Atmospheric Association [NOAA] 1994). For each location of capture, the closest weather station was selected.

To quantify the sex differences in body length among the 40 populations, I used the residuals from the regression of female body length on male body length for each population as an index of female size relative to male size (Ranta

Table 10.4 Description, mean and standard deviation (SD) of the 11 climatic variables used in the analysis of geographic patterns of sexual size dimorphism among 40 chipmunk populations

Variable	Description	Mean	SD
Latitude	degrees and decimal number of minutes	41.7	4.11
January min. temp.	average minimum temperature in January (°C)	-9.4	5.52
Year min. temp.	average monthly within-year minimum temperature (°C)	1	4.23
July max. temp.	average maximum temperature in July (°C)	30	4.05
Year max. temp.	average monthly within-year maximum temperature (°C)	16.3	4.74
Year mean temp.	average monthly within-year mean temperature (°C)	8.7	4.37
Max. temp. range	average annual temperature range (max. July-min. Jan.) (°C)	39.4	4.57
Year total precip.	average total yearly precipitation (mm)	483.4	273.3
Max. precip.	average maximum monthly precipitation (mm)	67.2	35.32
Min. precip.	average minimum monthly precipitation (mm)	19.1	17.65
Max. precip. range	average annual precipitation range (max. month-min. month) (mm)	48.1	32.55

et al. 1994). Because these populations are from species that belong to the same genus, phylogenetic correction was not applied to the estimates of sexual size dimorphism. To determine the climatic factors that predict female size relative to male size, I conducted a forward step-wise regression using residual female size as the dependent variable, and 11 climatic and geographic variables as independent variables (table 10.4).

As expected, male and female body lengths were highly correlated (fig. 10.1; $r^2 = 0.744$, $P < 0.001$), and in the majority of populations (32/40), females were larger than males. Based on the step-wise multiple regression ($r^2 = 0.236$, $df = 4,35$, $P = 0.047$), four climatic variables appeared to be important in explaining geographic variation in sexual dimorphism. Average annual range in precipitation was positively related to relative female size ($\beta = 0.50$, partial $r = 0.39$, $P = 0.02$; fig. 10.2a), whereas average yearly total precipitation ($\beta = -0.38$, partial $r = 0.32$, $P = 0.06$; fig. 10.2b), average January minimum temperature ($\beta = -0.33$, partial $r = 0.28$, $P = 0.09$), and latitude ($\beta = -0.28$, partial $r = 0.26$, $P = 0.13$) were negatively related to relative female size. Thus female-biased sexual dimorphism was most pronounced in highly seasonal populations, and least pronounced in populations with high precipitation, cold winters, and at northern latitudes.

These patterns support the hypothesis that in extreme climates, small females have an advantage over large females with respect to reproductive success, leading to a reduction in female size and female-biased sexual dimorphism. How do these results compare with the qualitative assessment offered by Levenson (1990) on the same 40 populations? Levenson (1990) argued that populations that experienced more extreme climate had more pronounced female-biased sexual size dimorphism. This conclusion was based on a series of pair-wise comparisons that indicated that populations that were farther north or at higher elevation had

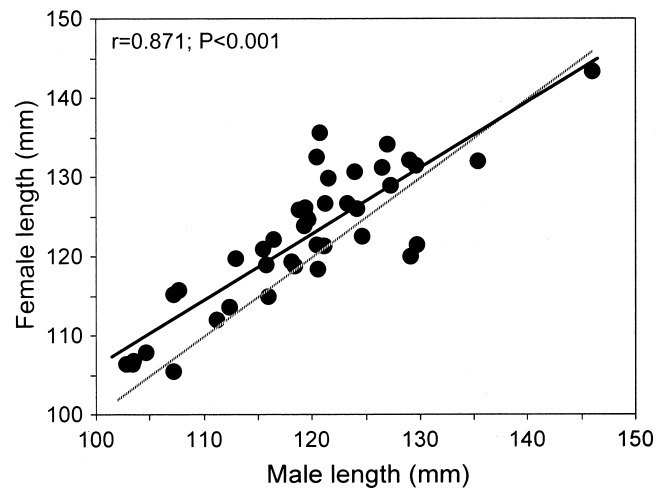


Figure 10.1 Regression between female length and male length for 40 chipmunk populations (*Tamias* spp.; male length = $11.07 + 0.885 \times$ [female length]). The gray line represents a slope of 1, in which male and female size would be equal.

higher dimorphism ratios than populations that were farther south or closer to sea level. My results indicate the opposite trend. Populations that experienced high annual rainfall and low January temperatures (i.e., more extreme climatic conditions) had less female-biased sexual size dimorphism than populations that experienced low rainfall and high January minimum temperatures. What mechanism might be at work that would lead to these patterns? If the mating system is assumed to remain the same across populations, and thus male size is likely to be optimized by sexual selection, then the most likely explanation may be an interaction between the severity of climate and the size dependence of female reproductive energetics.

These contrasting results offer a unique opportunity to present two alternative hypotheses for the evolution of female-biased sexual dimorphism in rodents. Levenson (1990)

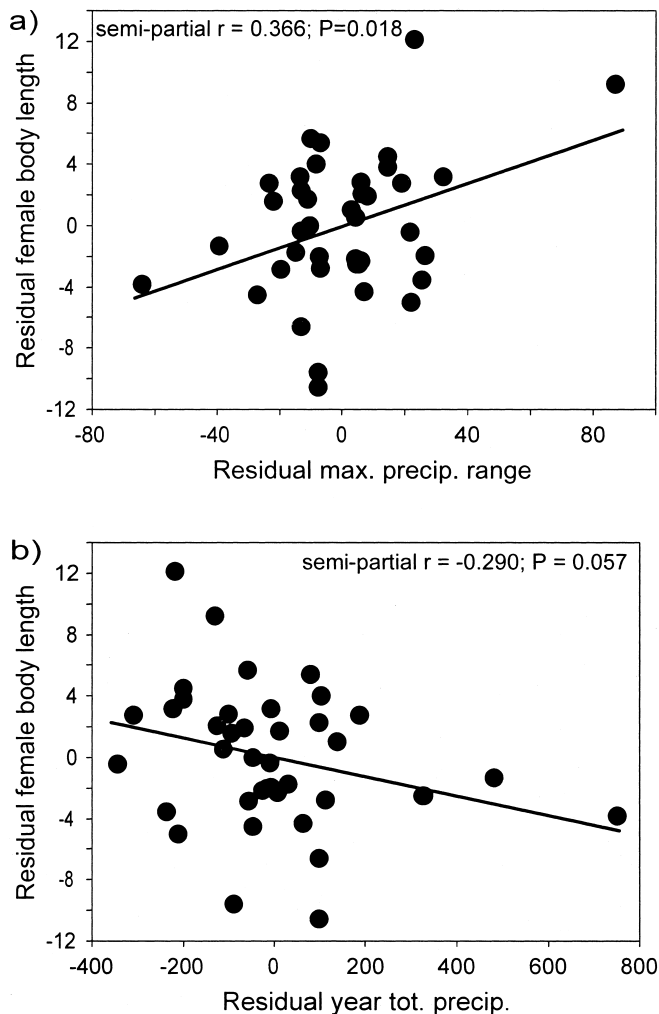


Figure 10.2 Semipartial correlation between residual female body length (female size relative to male size), and (a) residual average monthly within-year maximum temperature and (b) residual total yearly precipitation. Female-biased sexual size dimorphism increases in magnitude with increasing range in within-year maximum temperature, and declines with increased total yearly precipitation.

argued that hibernation imposed strong selection pressure on female body size, because a minimum body size might be required to survive hibernation and subsequently reproduce. Large females with higher energy reserves might be more likely to meet the costs of hibernation, reproduction, and lactation, especially when food availability is low. Thus Levenson (1990) predicted that large females should be favored in severe or seasonal environments. An alternative hypothesis predicts that large females are at a disadvantage when environmental conditions are extreme because of the energetic costs of reproduction and lactation, coupled with the high costs of somatic maintenance associated with large body size. During average conditions large females, emancipated from the prohibitively high maintenance costs associated with extreme climatic conditions, are capable of pro-

viding higher-quality parental care (either through higher quantity/quality of milk or better defence of the offspring) than small females (Schulte-Hostedde et al. 2002). This hypothesis predicts that females should be smaller and female-biased dimorphism less pronounced in extreme environments. The patterns I have found in the chipmunks support the latter hypothesis, but further tests on other groups of rodents should be carried out. An appropriate group may be the voles, because they are variable with respect to sexual size dimorphism. Determining the cause of the observed patterns will also require the determination of size-specific energy expenditure patterns during lactation in female rodents, perhaps with the use of doubly labelled water (Speakman 1997).

Sexual Size Dimorphism in Rodents: Developing Hypotheses and Future Directions

The study of the evolution and maintenance of sexual dimorphism is guided by the fundamental principle that selection acts on both sexes simultaneously, and any hypotheses and tests related to sexual dimorphism must take this principle into account. Thus attributing examples of male-biased sexual dimorphism in rodents to a polygynous mating system in which male size is related to mating success, while perhaps accurate, does not appreciate the complexity of the diverse factors that influence selection on body size. Because of the emphasis on male-biased sexual dimorphism, the role of selection on female size is rarely considered, yet any explanation for sexual dimorphism must consider both sexes. The mating dynamics of both sexes and female reproductive energetics can influence the evolution of sexual size dimorphism. In the following I outline these two factors and suggest future directions for the study of sexual dimorphism in rodents.

Although male-biased sexual dimorphism may evolve from a polygynous mating system, in which males compete through combat for access to females (Heske and Ostfeld 1990), other mating systems may also influence selection on body size and the concomitant evolution of sexual dimorphism. In mating systems described as scramble competition polygyny males actively seek females, and competition among males is not related to combat but rather to mobility and agility (Alexander et al. 1979). The 13-lined ground squirrel (*Spermophilus tridecemlineatus*) exhibits a mating system in which males actively seek females during the breeding season, and males that possess traits associated with mobility have high mating success (Schwagmeyer 1988a). Under these circumstances, there is little selection for large male body size, and the magnitude of sexual dimorphism is predicted to be reduced.

Scramble competition is also often characterized by multiple mating by females, which leads to sperm competition. Female promiscuity and the resulting multiple paternity of litters can reduce variation in male reproductive success relative to mating systems in which males compete through combat. If all males have some probability of siring offspring with a female that mates with multiple males, this will invariably decrease variation in reproductive success relative to situations in which large males can dominate small males and exclude them from any copulations with receptive females. Selection on male body size can therefore be reduced or eliminated by multiple mating by females (Wolff and Macdonald 2004). Evidence for this exists in both interspecific and intraspecific contexts. In polyandrous species of voles, males and females are the same size, and because of multiple mating and sperm competition, males had larger testes than males from polygynous species (Heske and Ostfeld 1990). Intraspecific patterns in the yellow-pine chipmunk indicate that female-biased sexual dimorphism is facilitated by low variation in male reproductive success, which is in part due to (1) scramble competition polygyny, manifested by a “mating chase” by multiple males during the female’s estrus and (2) multiple mating by females, which results in high levels of multiple paternity within litters (Schulte-Hostedde 2004). If selection for large male size is relaxed, whether due to sperm competition or advantages associated with speed and agility, other factors become important in predicting the direction of sexual size dimorphism, including selection for large female body size.

Female reproductive energetics can have a profound influence on the fitness consequences of body size and the evolution of sexual dimorphism, particularly in rodents. Rodents are generally income breeders and depend on increasing ingestion rates to maintain the substantial energetic demands of lactation (Millar 1987). They are therefore susceptible to fluctuations in food resources, and these resources are often influenced by climatological variables. Variation in climate and food resources can fundamentally affect selection on female size. Litter size and offspring survival can be dramatically affected by environmental conditions (King et al. 1991; Wauters and Dhondt 1995; Neuhäus et al. 1999; Kalcounis-Rüppell et al. 2002), and these effects can be size specific, particularly if maintenance costs are high for larger females (Schulte-Hostedde et al. 2002). Geographic patterns of sexual dimorphism may in part be explained by the size-dependence of energetic costs of maintenance and reproduction.

Determining how sexual dimorphism is maintained in rodents will benefit from the study of sex-specific patterns of selection on body size in species that are monomorphic, as well as species that have both male-biased and female-biased sexual dimorphism. The application of modern tech-

niques to answer questions related to (1) the role of male and female mating dynamics in determining the intensity of selection on body size, and (2) size-dependence of female reproductive energetics, will aid in finding general patterns and mechanisms. The use of DNA profiling to determine genetic estimates of reproductive success, levels of multiple paternity (e.g., Ribble 1991; Topping and Millar 1998) and thus the determination of the mating system, particularly in species with female-biased sexual dimorphism, should test the generality of conclusions that have been based on species with male-biased sexual dimorphism (Andersson 1994). The effects of female body size on female reproductive energetics and sexual dimorphism are rarely considered, but the use of techniques such of doubly labelled water (Speakman 1997) will help to understand how females of different size respond energetically to climatic variation, especially during the energetically expensive period of lactation. By considering both sexes and examining examples of sexual monomorphism and male-biased and female-biased sexual dimorphism, our understanding of how sexual selection operates on male and female body size in rodents will be greatly enhanced.

Summary

Sexual size dimorphism is the result of sex-specific patterns of selection on body size. These selective pressures include niche differentiation between the sexes, fecundity selection, and, especially in mammals, sexual selection. Underlying these selection pressures are genetic correlations between the sexes that tend to prevent these selective pressures from creating sex differences in body size. Rodents are highly diverse, both with respect to taxonomy and morphology, yet despite this diversity there has been little study of sexual dimorphism in rodents. A variety of selection pressures is expected to influence rodent body size. These pressures vary from allometry, sexual selection and mating systems, to climatic and other environmental influences. Unfortunately, there are few studies of these pressures in rodents, despite remarkable diversity with respect to the direction of sexual dimorphism. A review of sexual dimorphism among rodents indicates that patterns of diversity include monomorphism, male-biased sexual dimorphism, and female-biased dimorphism. Of particular interest are the ground squirrels (Sciuridae) and the kangaroo rats (Heteromyidae; both almost exclusively male-biased), the chipmunks (*Tamias* spp.) and jumping mice (Zapodidae; both almost exclusively female-biased) and the voles (*Clethrionomys* and *Microtus*; populations within species can vary from male-biased to female-biased sexual dimorphism). The selective pressures resulting in these patterns are likely as varied as

the rodent taxa themselves. One understudied perspective is the effects of climatic variation on sexual size dimorphism. Evidence indicates that climate can have profound effects on the evolution of body size and sexual dimorphism. Chipmunks generally exhibit female-biased sexual dimorphism, and it has been hypothesized that climate may play a role in the evolution of this pattern of body size. Using climate normals and published data on body size of male and female chipmunks from 40 populations (11 species), I used multiple regression analysis to determine which climatic

variables influence the magnitude of sexual dimorphism. The degree of female-biased sexual dimorphism declined with increasing annual rainfall and low winter temperatures, indicating that extreme climatic conditions may influence female size and reproductive energetics. Although much research on mammals has focused on male-biased sexual dimorphism and the role of sexual selection on male size, a more integrated approach examining selection on body size in both sexes will lead to a more complete understanding of the evolution of sexual dimorphism in rodents.