Measuring sexual size dimorphism in the yellow-pine chipmunk (*Tamias amoenus*)

Albrecht I. Schulte-Hostedde and John S. Millar

Abstract: Body size was examined in the yellow-pine chipmunk (*Tamias amoenus*), which is reported to have female-biased sexual size dimorphism. Our objective was to determine if yellow-pine chipmunks from the Kananaskis Valley were dimorphic. Three methods were used. We compared body mass, 5 univariate components of body size, and multivariate centroids between males and females, and quantified measurement error. Females were significantly heavier (10–20%) and had a longer body (4%) and a longer (0.9%) and wider (2.2%) skull than male chipmunks, as well as being larger in overall size of skeletal tissue (structural body size). Multivariate methods such as discriminant functional analysis can robustly determine whether the sexes are significantly different in overall structural body size. However, univariate measures of body size provide an intuitively clear index of the magnitude of the difference in size of a particular character between the sexes.

Résumé : Chez le Tamia amène (*Tamias amoenus*), le dimorphisme sexuel quant à la taille avantage les femelles; nous avons étudié la variable taille au moyen de trois méthodes chez cet animal dans le but de déterminer si les Tamias amènes de la vallée de Kananaskis sont dimorphiques. Nous avons comparé la masse totale, 5 composantes unidimensionnelles de la taille du corps et des centroïdes multidimensionnels chez des mâles et des femelles et nous avons quantifié les erreurs de mesure. Les femelles sont significativement (10–20 %) plus lourdes, ont le corps plus long (4 %) et le crâne plus long (0,9 %) et plus large (2,2 %) que les mâles, et ont également une taille structurelle globale plus grande. Les méthodes multudimensionnelles, comme l'analyse des fonctions discriminantes, peuvent déterminer de façon robuste si les mâles e les femelles ont une taille structurelle globale significativement différente. Cependant, les mesures unidimensionnelles de la taille fournissent un indice intuitivement clair de l'amplitude des différences de taille de caractères particuliers entre mâles et femelles.

[Traduit par la Rédaction]

Introduction

The evolution and maintenance of sexual size dimorphism (SSD) has been the topic of much discussion and debate (e.g., Hedrick and Temeles 1989; Kozlowski 1989; Abouheif and Fairbairn 1997; Fairbairn 1997). Hypotheses to explain SSD have focused on ecological-niche divergence, sexual selection, and fecundity selection. SSD due to ecological-niche divergence occurs when each sex has adapted to different ecological niches (Slatkin 1984; Shine 1989). Male-biased SSD may evolve through sexual selection on male body size. Larger males can be more successful at acquiring mating opportunities, usually through combat, which can lead to the evolution of larger male body size (Andersson 1994). Finally, female-biased SSD may evolve through fecundity selection: larger females produce more young than smaller females, leading to higher lifetime reproductive success and the evolution of larger female body size (Andersson 1994). In mammals, male-biased SSD is usually attributed to a polygynous mating system, in which larger males achieve greater reproductive success because of success in contest competition (Andersson 1994). Most mammalian species exhibit male-biased SSD, particularly those with polygynous mating systems (Eisenberg 1981), but some species of mammals exhibit female-biased SSD (Ralls 1976, 1977).

Explaining the evolution and maintenance of SSD first requires measuring and quantifying dimorphism to prove that SSD actually exists. Various methods of measuring and quantifying SSD have been used (e.g., Lovich and Gibbons 1992; Ranta et al. 1994), but studies of SSD and intraspecific variation in body size of mammals have focused on differences in mass (e.g., Sauer and Slade 1987, 1989; Boonstra et al. 1993; Yoccoz and Mesnager 1998). Interpreting intraspecific variation in body mass can be problematic, particularly when size dimorphism is small, because body mass varies for two reasons. Body mass may reflect the size of skeletal tissue (structural body size), so large individuals are also heavy (Dobson 1992). Alternatively, body mass may reflect body condition: heavy individuals may have larger stores of metabolizable tissue, such as fat, than light individuals (Dobson 1992).

A clearer method of documenting SSD is through the measuring structural body size. For instance, length of the hind foot has been used to determine structural body size in red squirrels (*Sciurus vulgaris*) (Wauters and Dhondt 1989), and body length has been used to assess SSD in voles (*Microtus* spp. and *Clethrionomys* spp.) and chipmunks (*Tamias* spp.) (Heske and Ostfeld 1990; Levenson 1990). However, univariate analysis of body-size components assumes that characters are uncorrelated and does not describe contrasting patterns

Received September 30, 1999. Accepted December 9, 1999.

A.I. Schulte-Hostedde[1] and J.S. Millar. Ecology and Evolution Group, Department of Zoology, University of Western Ontario, London, ON N6G 5B7, Canada.

[1]Author to whom all correspondence should be addressed (e-mail: aischult@julian.uwo.ca).

of variation, necessitating the use of multivariate methods to adequately describe variation in body size (Pimentel 1979; Willig et al. 1986).

Whenever structural body size is measured, it is important to quantify measurement error, or repeatability (Bailey and Byrnes 1990; Lougheed et al. 1991). Quantifying SSD can be compromised when measurement error is high because type II statistical errors (accepting a false null hypothesis) can occur (Lougheed et al. 1991). Identifying measurements that have a large error may aid in the interpretation of statistical analyses. Few studies of morphometric variation have included a calculation of measurement error, although many contain an acknowledgement that it may have affected the results (e.g., Heske and Ostfeld 1990; Levenson 1990).

In this study, body size is examined in the yellow-pine chipmunk (*Tamias amoenus*), which has been reported to have female-biased SSD. Female chipmunks are, on average, 2.4% longer (Levenson 1990) and 16% heavier (Kenagy and Barnes 1988) than males. This dimorphism is subtle compared with that in large mammals such as pinnipeds and ungulates (in which mean ratios of average mass of males to females reach 2.98 (Weckerly 1998), with some males of larger species weighing up to 8 times the females (Fairbairn 1997)). There also appears to be geographic variation in dimorphism of yellow-pine chipmunks: dimorphism ratios (female/male) in body length range from 1.059 to 0.936 among populations (Levenson 1990). This means that in some populations SSD is male-biased, while in others it is female-biased.

Our objective was to determine if the chipmunks in our study area are dimorphic and, if so, in which direction. To do this we used three methods to quantify SSD. First, we compared body masses between males and females, second, we conducted univariate analyses of 5 measured components of body size, and third, we conducted a multivariate analysis to determine if males and females are significantly different in structural body size. We also evaluated measurement error for each of the body-size-component measurements.

Methods

Chipmunks were sampled on three trapping grids in the Kananaskis Valley, Alberta, in the Front Ranges of the Rocky Mountains (51°N, 115°W). These grids were located at the base of Mount Kidd (3.8 ha), at Grizzly Creek (4.8 ha), and at the Kananaskis Village junction (2.4 ha). All grids were located on rocky creek beds and consisted of single Longworth traps placed approximately 20 m apart and baited with sunflower seeds, oats, and cotton bedding. Each grid was trapped two mornings each week from early May to late August 1998.

Upon capture, individual chipmunks were ear-tagged (Monel No. 1005), weighed with a pesola scale (±1 g), and sexed, and reproductive condition was assessed as scrotal (enlarged testes and black scrotum) or nonscrotal for males and as imperforate, perforate, pregnant (swollen abdomen), or lactating (enlarged nipples) for females. Individuals were then lightly anaesthetized with methoxyflurene (Metofane-Jannssen Pharmaceutica) to facilitate accurate measurement of body-size components. Individuals were measured approximately every 2 weeks, not at each capture. Six measurements were taken: total body length (including tail), tail length, skull length (SKL), skull width (SKW), forefoot length (FFL), and hind-foot length (HFL). Most chipmunks were alert when released (i.e., the effects of the anaesthetic had worn off), but when this was not the case, the trap was locked open and the chipmunk was placed inside to recover.

Total body length was measured using a graduated (1 mm) board approximately 3 cm wide and 30 cm long. A second piece of wood was attached perpendicular to the end of the first. The chipmunk was placed on the board with its nose against the perpendicular surface and its body pressed against the board. Total body length was measured from the tip of the nose to the last vertebrae of the tail (±1 mm). Tail length was measured from the base of the tail to the last vertebrae, using a ruler (±1 mm). SKL was measured from the tip of the nose to the back of the skull, and SKW was measured across the widest point of the skull (the zygomatic arch), using dial calipers (±0.1 mm). FFL and HFL were measured by pressing the foot on a ruler and measuring from the tip of the longest toe (without the nail) to the carpus (wrist) or tarsus (ankle) (±1 mm). All measurements were performed by the senior author.

We used data from chipmunks that had been measured at least three times, the mean being used in all statistical analyses except those related to measurement error. Twenty-two female and 28 male chipmunks fit this criterion. Statistical analyses were performed using 5 body-size components: BL (total body length minus tail length), SKL, SKW, FFL, and HFL. Tail length could not be used as a body-size component because some chipmunks had injured, and thus shortened, their tails. Dimorphism ratios were calculated by dividing the mean female component by the mean male component. Independent *t* tests were performed to compare the 5 body-size components between male and female chipmunks.

Because mass increases during pregnancy, it was inappropriate to compare male and female body masses when females were pregnant. Therefore, we calculated mean mass of reproductive females using data from prebreeding (not yet pregnant) and postbreeding (postlactating) females. The mean Julian date was calculated for the onset of obvious pregnancy (124 = May 24) and the end of obvious lactation (197 = August 5). To make a valid comparison between male and female body masses we calculated the male body mass corresponding to the females' pre- and post-breeding periods. In some cases, individuals were not captured before or after breeding, and calculating mean body mass was not possible. Independent *t* tests were used to determine if mean masses of males and females were significantly different. To satisfy the assumption of equal variances, the *t* test between the sexes for the postbreeding period was performed on log-transformed data. Untransformed prebreeding data were homoscedastic. The dimorphism ratio ((mean female mass)/(mean male mass)) was also calculated for both the pre- and post-breeding periods.

Discriminant function analysis (DFA) was performed to determine how well the 5 log-transformed body-size components distinguished between males and females. The DFA first used a multivariate analysis of variance (MANOVA) to establish a significant difference among groups (Pimentel 1979) and then classified each individual to the sex it most resembled, calculated the Mahalanobis' distances between the group centroids, and calculated a canonical vector that maximized the variation in the body-size components in discriminant space (analogous to a principal components analysis) (Pimentel 1979).

Chipmunks were measured at least three times from May to August 1998, so measurement error was assessed for 6 body-size-component measurements using analysis of variance (ANOVA). Because BL was calculated by subtracting tail length from total body length, we calculated the measurement error for tail length and total body length, as well as for the other body-size components (SKW, SKL, FFL, HFL). We estimated variance of body-size components both among and within chipmunks (s^2_{among} and s^2_{within}) (as described in Lessels and Boag 1987) and calculated percent measurement error (%ME) using the following formula (Bailey and Byrnes 1990):

Table 1. Body masses (mean and standard error (SE)), sample sizes (*N*), and dimorphism ratios (female/male) for yellow-pine chipmunks (*Tamias amoenus*) during the pre- and post-breeding periods.

	Females			Males					
	N	Mean (g)	SE (g)	*N*	Mean (g)	SE (g)	Dimorphism ratio	*t*	*P*
Prebreeding period	14	56.50	1.74	15	49.91	0.87	1.207	3.46	0.0018
Postbreeding period	10	59.68	1.03	13	53.86	0.93	1.108	3.50	0.0016

Note: The results of independent *t* tests are also presented; df = 27 for the prebreeding period and df = 21 for the postbreeding period. Significance is accepted for $P < 0.05$.

Table 2. Descriptive statistics and dimorphism ratios (female/male) for 5 body-size components of yellow-pine chipmunks in the Kananaskis Valley, Alberta.

	Females (N = 22)			Males (N = 28)					
	Mean (mm)	SD (mm)	CV	Mean (mm)	SD (mm)	CV	Dimorphism ratio	*t*	*P*
BL	127.91	3.804	0.113	122.89	3.552	0.103	1.041	4.805	<0.0001
SKL	36.95	0.479	0.006	36.49	0.582	0.009	1.013	2.976	0.00456
SKW	18.36	0.711	0.039	17.95	0.629	0.022	1.023	2.174	0.0347
FFL	14.05	0.375	0.010	14.14	0.448	0.014	0.993	–0.818	0.417
HFL	30.00	0.535	0.009	29.93	0.539	0.010	1.002	0.4667	0.643

Note: The results of independent *t* tests comparing 5 body-size components between male and female chipmunks are also provided. For all *t* tests, df = 48, and significance is accepted for $P < 0.05$. For a description of body-size components see the text. SD, standard deviation; CV, coefficient of variation.

$$[1] \qquad \%ME = (s^2_{within})/(s^2_{among} + s^2_{within}) \times 100$$

Because s^2_{within} was estimated over the summer, it may reflect growth as well as measurement error. However, chipmunks only breed once each year (in May) in Kananaskis and young of the year reach adult size before they enter hibernation (Broadbrooks 1970; Sutton 1992). Because we only used adult chipmunks in our analysis, we assumed that all individuals had reached asymptotic growth. Therefore, s^2_{within} should reflect only measurement error. To test our assumption we used repeated body-size-component measurements from male and female chipmunks that had measurements spanning May through August and regressed these repeated measurements against Julian date. Therefore, we conducted 6 regressions on both male and female chipmunks, using total body length and tail length as well as the other body size components (SKW, SKL, FFL, HFL). In total, 12 regressions were performed to determine the average adult growth rate for males and females.

All statistical analyses were performed on Statistica 5.0 (Statsoft, Inc.).

Results

Female chipmunks were heavier ($P < 0.01$) than males in both the pre- and post-breeding periods (Table 1), although dimorphism ratios were larger for prebreeding than for postbreeding chipmunks (Table 1). Females were 20% heavier in the prebreeding period and 11% heavier in the postbreeding period than males.

Dimorphism ratios for all 5 body-size components ranged from 0.993 (FFL) to 1.041 (BL) (Table 1). Females had longer bodies, longer skulls, and wider skulls than males (Table 2).

The initial MANOVA indicated a significant difference between the sexes (Wilk's $\lambda = 0.6223$, $F_{[5,44]} = 5.341$, $P < 0.0006$). The squared Mahalanobis' distance between male and female centroids was 2.463 ($P = 0.000645$). The DFA correctly classified the sex of 78% of individuals (72.7% of males and 82.1% of females).

Table 3. Factor structure of canonical vector for 5 body-size components of yellow-pine chipmunks.

	Canonical structure
BL	0.884
SKL	0.549
SKW	0.399
FFL	–0.150
HFL	0.087

Note: For a description of body-size components see the text.

Four of the 5 body-size components were positively correlated with the canonical vector (Table 3), suggesting that males and females differ in structural body size. Only FFL was weakly negatively correlated with the canonical vector. The distribution of canonical scores is presented in Fig. 1. Correlations among body-size components showed that BL was correlated with SKL, SKW, and HFL (Table 4).

Measurement error was lowest for tail length and total body length, and highest for SKW, FFL, and HFL (Table 5). There were some noticeable differences in measurement error between males and females for both foot measurements. Measurement error for foot measurements was higher for males. Generally, measurement error was highest for male body-size-component measurements.

We found little evidence that male and female chipmunks grew over the summer. Five male and five female chipmunks

Fig. 1. Frequency distribution of canonical discriminant scores for male and female yellow-pine chipmunks (*Tamias amoenus*). The mean canonical scores are –0.677 for males and 0.861 for females.

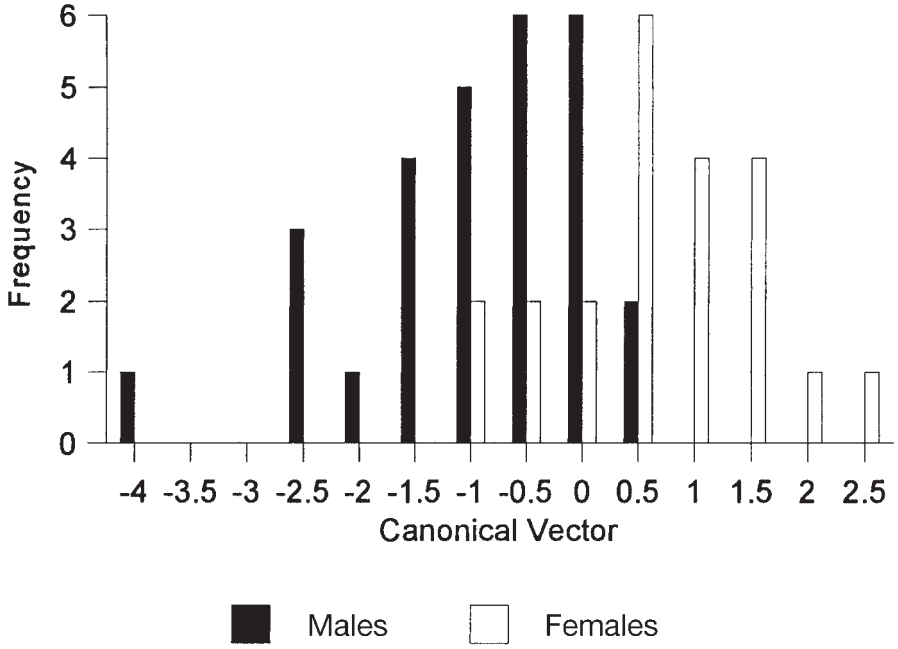

Table 4. Correlation matrices of 5 body-size-component measurements taken from yellow-pine chipmunks.

	BL	SKL	SKW	FFL	HFL
Males					
BL	1	0.53*	0.45*	–0.15	0.45*
SKL		1	0.44*	0.22	0.06
SKW			1	–0.34	0.16
FFL				1	0.04
HFL					1
Females					
BL	1	0.50*	0.53*	0.26	0.61*
SKL		1	0.23	0.26	0.36
SKW			1	–0.02	0.31
FFL				1	0.23
HFL					1

Note: Matrices for male and female body-size components are presented. For a description of body-size components see the text.
*Significant at $P < 0.05$.

Table 5. Measurement error (%) for 6 measurements taken from male and female yellow-pine chipmunks.

	Females	Males	Pooled
Total body length	8.30	12.77	9.97
Tail length	4.14	10.62	6.37
SKL	50.17	34.82	35.60
SKW	82.25	89.06	83.59
FFL	79.46	97.30	92.75
HFL	68.14	84.14	77.94

Note: Measurement errors for each sex and both sexes (pooled) are presented. For a description of body-size components see the text.

had measurements spanning May to August 1998. Nine of 12 regressions were nonsignificant ($P > 0.05$); male BL was marginally significant, and Julian date explained less than 10% of the variance in body-size measurements ($r^2 = 0.091$, $P = 0.049$). SKW was the only body-size-component measurement that increased over the summer (males: $r^2 = 0.576$, $P < 0.001$; females: $r^2 = 0.348$, $P = 0.007$).

Discussion

The dimorphism ratios for yellow-pine chipmunks in the Kananaskis Valley are comparable to those of other populations. Levenson (1990) found a dimorphism ratio of 1.024 in length among populations of yellow-pine chipmunks, measured from museum specimens. Kenagy and Barnes (1988) found that females weigh 16% more than males (excluding pregnant females) in Washington State. Female chipmunks from Kananaskis were longer, had larger skulls, and were heavier than male chipmunks. Our DFA confirmed that female chipmunks were, in fact, structurally larger than male chipmunks.

There are several fundamental problems with the use of body mass as an index of SSD. There is temporal variation in mass in both the short term (gut contents can change over the course of a day) and the long term (mammals that hibernate store fat prior to the winter and females gain mass when pregnant). Kenagy and Barnes (1988) excluded reproductive females when they determined that female yellow-pine chipmunks were 16% heavier than males, but there is evidence that heavy female chipmunks are more likely to breed than light females (Svendsen and White 1997). Excluding reproductive females may result in a conservative estimate of sexual dimorphism in mass. When dealing with hibernating species, males and females may not be in similar condition before breeding because males often emerge from hibernation before females (Sheppard 1969; Michener 1983). This compromises the arbitrary selection of a set time period prior to

reproduction in which body mass can be used for calculating a dimorphism ratio.

Using univariate measures of body size to determine SSD can be advantageous. It is simple to quantify dimorphism by determining the ratio of the mean of a morphological trait, such as body length, between the sexes. This approach provides an intuitively clear index of the magnitude of the difference in size of a particular character between males and females (Lovich and Gibbons 1992). However, concluding that one sex is larger than the other can be an arbitrary decision based on the number of characters that are found to be significantly different using univariate statistics (Willig et al. 1986). This approach also assumes that the characters being measured are uncorrelated, an assumption that is often violated (Willig et al. 1986).

Determining whether males and females are significantly different in overall structural body size can best be evaluated by testing the null hypothesis that the multivariate centroids are equal (Pimentel 1979). The DFA clearly showed that females were larger than males in overall structural body size. However, it is difficult to determine the extent to which females are larger than males with this approach because the canonical axis is not a ratio scale, so a meaningful ratio between mean male and female body sizes cannot be computed.

Assessing measurement error when quantifying body size can be very important. Type II statistical errors (accepting a null hypothesis when it is in fact false) can occur when variables with high measurement error are used (Lougheed et al. 1991). The error assessed for our body-size-component measurements was >20%, for SKW, FFL, and HFL. SKW measurements may have had high error because of bending of the zygomatic arch during measurement. Foot measurements were taken ±1 mm, so the precision necessary to quantify the variation among individuals was lacking. Despite bias toward a type II error, however, it is important to note that the *t* tests still indicated that female chipmunks had significantly longer and wider skulls than males. It is also important to note that a high measurement error does not necessarily indicate little among-individual variation. It reflects the probability that measurements taken from one individual are different from measurements taken from other individuals in the population (Yezerinac et al. 1992). The high measurement error found in some of the measurements emphasizes the importance of taking several measurements from an individual and using the mean value to minimize the impact of measurement error.

The evolution and maintenance of SSD in mammals is usually considered to be the result of the polygynous mating system of most mammals in which larger males are more successful at procuring mates, leading to the evolution of male-biased SSD (Eisenberg 1981; Andersson 1994). In many chipmunk populations, including those in the Kananaskis Valley, females are larger than males (Levenson 1990). Why this is so is not known. Niche differentiation between the sexes may explain female-biased SSD in many bird species (Mueller 1990; Andersson 1994). For chipmunks, in which the dimorphism is more subtle than in birds, this is unlikely. Ralls (1976) concluded that the most likely explanation for female-biased SSD in mammals is that larger females may be better mothers. Larger mothers may be able to produce more or larger offspring, provide more or better quality milk, and (or) provide better maternal care than smaller mothers can (Ralls 1976). There is some evidence that larger female rodents can produce larger litters than smaller females (Myers and Master 1983; Dobson and Michener 1995). Female-biased SSD may also be the result of selection for smaller males. Smaller males can spend more time mate-searching and less time feeding because of lower absolute energy requirements (Blanckenhorn et al. 1995). Smaller males may also be faster and more agile (e.g., Trombulak 1989). Female chipmunks advertise the onset of estrus and many males will aggregate near a burrow to chase the female on the day of her estrus in an attempt to copulate (Callahan 1981). Speed and agility, as well as strength and dominance, may be advantageous in this kind of competition. Because SSD is the result of sex-specific selection pressures acting on body size, one or more of these hypotheses may be correct. Female-biased SSD may therefore be the result of selection for smaller males and (or) larger females. As well, there may be selection for both large male size through male–male competition and large female size because of the "big mother" hypothesis. Selection for female size may be stronger than selection for larger males, which may result in females being larger than males (Greenwood and Adams 1987).

Acknowledgements

We thank Monica Guzkowski and Andrew McAdam for help in the field, the Kananaskis Field Station for logistic support and accommodation, and C.D. Ankney, R.C. Bailey, D.J. Fairbairn, and M.C. Kalcounis for constructive criticism of the manuscript. This study was supported by an operating grant from the Natural Sciences and Engineering Research Council of Canada to J.S.M. and an Ontario Graduate Scholarship to A.I.S.-H.

References

Abouheif, E., and Fairbairn, D.J. 1997. A comparative analysis of allometry for sexual size dimorphism: assessing Rensch's rule. Am. Nat. **149**: 540–562.

Andersson, M. 1994. Sexual selection. Princeton University Press, Princeton, N.J.

Bailey, R.C., and Byrnes, J. 1990. A new, old method for assessing measurement error in both univariate and multivariate morphometric studies. Syst. Zool. **39**: 124–130.

Blanckenhorn, W.U., Preziosi, R.F., and Fairbairn, D.J. 1995. Time and energy constraints and the evolution of sexual size dimorphism—to eat or mate? Evol. Ecol. **9**: 369–381.

Boonstra, R., Gilbert, B.S., and Krebs, C.J. 1993. Mating systems and sexual dimorphism in mass in microtines. J. Mammal. **74**: 224–229.

Broadbrooks, H.E. 1970. Populations of the yellow-pine chipmunk *Eutamias amoenus*. Am. Midl. Nat. **83**: 472–488.

Callahan, J.R. 1981. Vocal solicitation and parental investment in female *Eutamias*. Am. Nat. **118**: 872–875.

Dobson, F.S. 1992. Body mass, structural size, and life-history patterns of the Columbian ground squirrel. Am. Nat. **139**: 109–125.

Dobson, F.S., and Michener, G.R. 1995. Maternal traits and reproduction in Richardson's ground squirrels. Ecology, **76**: 851–862.

Eisenberg, J.F. 1981. The mammalian radiations. University of Chicago Press, Chicago.

Fairbairn, D.J. 1997. Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. Annu. Rev. Ecol. Syst. **28**: 659–687.

Greenwood, P.J., and Adams, J. 1987. Sexual selection, size dimorphism, and a fallacy. Oikos, **48**: 106–108.

Hedrick, A.V., and Temeles, E.J. 1989. The evolution of sexual dimorphism in animals: hypotheses and tests. Trends Ecol. Evol. **4**: 136–138.

Heske, E.J., and Ostfeld, R.S. 1990. Sexual dimorphism in size, relative size of testes, and mating systems in North American voles. J. Mammal. **71**: 510–519.

Kenagy, G.J., and Barnes, B.M. 1988. Seasonal reproductive patterns in four co-existing rodent species from the Cascade Mountains, Washington. J. Mammal. **69**: 274–292.

Kozlowski, J. 1989. Sexual size dimorphism: a life-history perspective. Oikos, **54**: 253–255.

Lessels, C.M., and Boag, P.T. 1987. Unrepeatable repeatabilities: a common mistake. Auk, **104**: 116–121.

Levenson, H. 1990. Sexual size dimorphism in chipmunks. J. Mammal. **71**: 161–170.

Lougheed, S.C., Arnold, T.W., and Bailey, R.C. 1991. Measurement error of external and skeletal variables in birds and its effects on principal components. Auk, **108**: 432–436.

Lovich, J.E., and Gibbons, J.W. 1992. A review of techniques for quantifying sexual size dimorphism. Growth Dev. Aging, **56**: 269–281.

Michener, G.R. 1983. Spring emergence schedules and vernal behavior of Richardson's ground squirrels: why do males emerge from hibernation before females? Behav. Ecol. Sociobiol. **14**: 29–38.

Myers, P., and Master, L.L. 1983. Reproduction by *Peromyscus maniculatus*: size and compromise. J. Mammal. **64**: 1–18.

Pimentel, R.A. 1979. Morphometrics: the multivariate analysis of biological data. Kendell/Hunt Publishing Co., Dubuque, Iowa.

Ralls, K. 1976. Mammals in which females are larger than males. Q. Rev. Biol. **51**: 245–276.

Ralls, K. 1977. Sexual dimorphism in mammals: avian models and unanswered questions. Am. Nat. **111**: 917–938.

Ranta, E., Laurila, A., and Elmberg, J. 1994. Reinventing the wheel: analysis of sexual dimorphism in body size. Oikos, **70**: 313–312.

Sauer, J.R., and Slade, N.A. 1987. Size-based demography of vertebrates. Annu. Rev. Ecol. Syst. **18**: 71–90.

Sauer, J.R., and Slade, N.A. 1989. Body size as a demographic categorical variable: ramifications for life-history analysis of mammals. *In* Evolution of life histories of mammals: theory and pattern. *Edited by* M.S. Boyce. Yale University Press. New Haven, Conn. pp. 107–121.

Sheppard, D.H. 1969. A comparison of reproduction in two chipmunk species (*Eutamias*). Can. J. Zool. **47**: 603–608.

Shine, R.S. 1989. Ecological causes for the evolution of sexual size dimorphism: a review of the evidence. Q. Rev. Biol. **64**: 419–441.

Slatkin, M. 1984. Ecological causes of sexual dimorphism. Evolution, **38**: 622–630.

Sutton, D. 1992. *Tamias amoenus*. Mamm. Species, **390**: 1–8.

Svendsen, G.E., and White, M.M. 1997. Body mass and first-time reproduction in female chipmunks (*Tamias striatus*). Can. J. Zool. **75**: 1891–1895.

Trombulak, S.C. 1989. Running speed and body mass in Belding's ground squirrels. J. Mammal. **70**: 194–197.

Wauters, L.A., and Dhondt, A.A. 1989. Variation in length and body weight of the red squirrel (*Sciurus vulgaris*) in two different habitats. J. Zool. (Lond.), **217**: 93–106.

Weckerly, F.W. 1998. Sexual-size dimorphism: influence of mass and mating systems in the most dimorphic mammals. J. Mammal. **79**: 33–52.

Willig, M.R., Owen, R.D., and Colbert, R.L. 1986. Assessment of morphometric variation in natural populations: the inadequacy of the univariate approach. Syst. Zool. **35**: 195–203.

Yezerinac, S.M., Lougheed, S.C., and Handford, P. 1992. Measurement error and morphometric studies: statistical power and observer experience. Syst. Biol. **41**: 471–482.

Yoccoz, N.G., and Mesnager, S. 1998. Are alpine bank voles larger and more sexually dimorphic because adults survive better? Oikos, **82**: 85–98.