

FEMALE-BIASED SEXUAL SIZE DIMORPHISM IN THE YELLOW-PINE CHIPMUNK (*TAMIAS AMOENUS*): SEX-SPECIFIC PATTERNS OF ANNUAL REPRODUCTIVE SUCCESS AND SURVIVAL

ALBRECHT I. SCHULTE-HOSTEDDE,^{1,2} JOHN S. MILLAR,¹ AND H. LISLE GIBBS^{3,4}

¹Ecology and Evolution Group, Department of Zoology, University of Western Ontario, London, Ontario K7L 3N6 Canada

³Department of Biology, McMaster University, Hamilton, Ontario L8S 4K1 Canada

Abstract.—Sexual size dimorphism is ultimately the result of independent, sex-specific selection on body size. In mammals, male-biased sexual size dimorphism is the predominant pattern, and it is usually attributed to the polygynous mating system prevalent in most mammals. This sole explanation is unsatisfying because selection acts on both sexes simultaneously, therefore any explanation of sexual size dimorphism should explain why one sex is relatively large and the other is small. Using mark-recapture techniques and DNA microsatellite loci to assign parentage, we examined sex-specific patterns of annual reproductive success and survival in the yellow-pine chipmunk (*Tamias amoenus*), a small mammal with female-biased sexual size dimorphism, to test the hypothesis that the dimorphism was related to sex differences in the relationship between body size and fitness. Chipmunks were monitored and body size components measured over three years in the Kananaskis Valley, Alberta, Canada. Male reproductive success was independent of body size perhaps due to trade-offs in body size associated with behavioral components of male mating success: dominance and running speed. Male survival was consistent with stabilizing selection for overall body size and body size components. The relationship between reproductive success and female body size fluctuated. In two of three years the relationship was positive, whereas in one year the relationship was negative. This may have been the result of differences in environmental conditions among years. Large females require more energy to maintain their soma than small females and may be unable to maintain lactation in the face of challenging environmental conditions. Female survival was positively related to body size, with little evidence for stabilizing selection. Sex differences in the relationship between body size and fitness (reproductive success and survival) were the result of different processes, but were ultimately consistent with female-biased sexual size dimorphism evident in this species.

Key words.—Body size, microsatellites, reproductive success, sexual size dimorphism, survival, yellow-pine chipmunks.

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Sexual size dimorphism is ultimately the result of independent, sex-specific selection acting on body size (Price 1984a; Greenwood and Adams 1987; Hedrick and Temeles 1989; Andersson 1994; Blanckenhorn 2000). Sex differences in the sum of all selective pressures acting on body size may lead to different optima for males and females. These selective pressures may include niche differentiation between the sexes (Slatkin 1984; Shine 1989) or fecundity selection (Andersson 1994). Intrasexual selection (male-male competition), intersexual selection (female mate choice), and sex differences in survival may also underlie patterns of sexual size dimorphism (Andersson 1994). Contemporary patterns of selection can provide insights into the selective pressures influencing the evolution and maintenance of sexual size dimorphism (e.g., Price 1984a; Weatherhead and Clark 1994; Weatherhead et al. 1995; Badyaev and Martin 2000; Ferguson and Fairbairn 2000).

Because of the polygynous nature of mammalian mating systems (Clutton-Brock 1989), male-male competition for access to females is usually thought to have driven the evolution of male body size and thus the male-biased sexual size dimorphism that predominates in most mammals (Andersson 1994; Weckerly 1998). However, some mammals have female-biased sexual size dimorphism (Ralls 1976), so this

singular explanation for sexual size dimorphism in mammals cannot be universal. Indeed, because of high genetic correlations between the sexes (Lande 1980), selection for increased size in one sex should result in increased size of the other, therefore any explanation of sexual size dimorphism must not only explain why one sex is larger but why the other sex is smaller. Selection on body size acts on both sexes simultaneously (Greenwood and Adams 1987; Hedrick and Temeles 1989; Karubian and Swaddle 2001), so a first step in evaluating any hypotheses is establishing sex-specific patterns of reproductive success and survival in relation to body size. In addition, by examining exceptions to the general pattern of male-biased sexual size dimorphism we can gain insights into the general mechanisms underlying the evolution and maintenance of sexual dimorphism in mammals.

The yellow-pine chipmunk (*Tamias amoenus*) is a small, ground-dwelling sciurid (35–65 g) and, like many other North American chipmunks, exhibits female-biased sexual size dimorphism (Levenson 1990; Schulte-Hostedde and Millar 2000), despite having a mating system in which either male-biased sexual size dimorphism or no dimorphism would be expected to evolve. Most tree squirrels and chipmunks have a promiscuous mating system involving intense male-male competition for access to estrous females (Koprowski 1998). Female yellow-pine chipmunks are in estrus for only one day each year in late April or early May. Three to five days prior to estrus, females advertise the onset of estrus through vocalizations, perhaps to incite competition among males (Callahan 1981). Typically, two to six males aggregate near the

² Present address: Department of Biology, Queen's University, Kingston, Ontario K7L 3N6, Canada; E-mail: albrecht@biology.queensu.ca.

⁴ Present address: Department of Evolution, Ecology and Organismal Biology, Ohio State University, Columbus, Ohio 43210-1253.

female's den and pursue her on the day of estrus. The female copulates with one or more males during this mating chase (Callahan 1981). Many chipmunks and tree squirrels, including eastern chipmunks (*T. striatus*; Elliott 1978; Yahner 1978), eastern gray squirrels (*Sciurus carolinensis*; Koprowski 1993), and Eurasian red squirrels (*S. vulgaris*; Wauters et al. 1990) exhibit a mating chase during breeding. All three of these species are monomorphic, that is, males are the same size as females (Wauters and Dhondt 1989; Levenson 1990; J. Koprowski, pers. comm.). Red squirrels (*Tamiasciurus hudsonicus*) also have a similar mating system and males are larger than females (Boutin and Larsen 1993).

Most research on sexual size dimorphism in mammals has focused on species with male-biased sexual size dimorphism (e.g., Dobson and Wigginton 1996; Loison et al. 1999; McElligott et al. 2001), and few studies have examined sex differences in survival and reproductive success in relation to body size in species with female-biased sexual size dimorphism (but see Bondrup-Nielsen and Ims 1990; Yoccoz and Mesnager 1998). In addition, obtaining data on male reproductive success is problematic in mammals because observations of copulations are rare in most species, and females of many species engage in multiple mating (Gomendio et al. 1998). Nonetheless, it is critical to determine variation in male reproductive success to understand its role in the evolution and maintenance of sexual size dimorphism. The use of molecular techniques is therefore required to assign parentage and thus quantify male reproductive success. Here we use mark-recapture and molecular techniques to test the hypothesis that female-biased sexual size dimorphism in the yellow-pine chipmunk (Schulte-Hostedde and Millar 2000) is related to sex differences in annual reproductive success (the number of young emerged from the maternal den) and annual adult survival in relation to body size.

MATERIALS AND METHODS

Field Studies

Chipmunks were sampled on three trapping grids in the Kananaskis Valley, Alberta, in the Front Ranges of the Rocky Mountains (51°N, 115°W) in 1998–2000. These grids were located on Mount Kidd (3.8 ha), at Grizzly Creek (4.8 ha), and at the Kananaskis Village junction (2.4 ha; hereafter "Village"). In 1999 and 2000 we did not sample the grid at Grizzly Creek due to a low density of chipmunks. We expanded the grid at the Kananaskis Village junction for 1999 and 2000 from 2.4 ha to approximately 3.4 ha. All grids were located on rocky creek beds and consisted of an array of traps that were distributed evenly (20 m apart) along the rocky creek bed. For all grids, except for Village in 1998 (which had 60 traps), there was one trap placed at 100–120 locations on each grid. These grids followed the form of the creek bed and were generally rectangular in shape. The Longworth traps were baited with sunflower seeds, oats, and cotton bedding. Each grid was trapped two mornings each week from early May to late August.

In 1998 we individually marked chipmunks using ear tags Monel #1005, National Band and Tag Co., Newport, KY) with unique numbers, but encountered some tag loss. Therefore in 1999 and 2000 we used passive integrated transponder

(PIT) tags (Anitech Enterprises, Inc., Markham, Ontario, Canada) to mark individuals.

Upon capture, chipmunks were individually marked (1998, ear tags; 1999 and 2000, PIT tags), weighed with a pesola scale (± 1 g), and the sex and reproductive condition of each animal recorded. 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. Body size components of individual adults were measured approximately every two weeks; they were not measured at each capture. Four measurements were made: total body length (including tail; ± 1 mm), tail length (± 1 mm), skull length (± 0.1 mm), and skull width (± 0.1 mm; see Schulte-Hostedde and Millar 2000). We collected tissue samples from one ear from each individual for subsequent DNA analysis. Putative parents were first captured in May or early June each year, whereas juveniles emerged in July or early August. All chipmunks were monitored by trapping until late August.

In 1998 we used fluorescent tracking powder (Radiant Color, Richmond, CA) to track lactating females to their nests (Sharpe and Millar 1990), but we were unable to successfully locate nests using this technique because of the long distances between the sites at which we captured the chipmunks and their nest sites (up to 400 m apart). Therefore, in 1999 and 2000 we radio-collared lactating female chipmunks (Model MD-2C, Holohil Systems Ltd., Carp, Ontario, Canada) and used radio-telemetry to track them to their nests. These radio-collars weighed 1.35 g (2.2–2.7% of body mass) and were assumed not to affect the chipmunks (Bertheaux et al. 1996). Once a nest was found, we set out four or five Longworth traps around the nest two or three times per week from late June to late August to capture emerging juveniles.

Genetic Analysis of Reproductive Success

DNA was extracted from tissue samples taken from juveniles and all putative parents using Qiagen (Mississauga, Ontario, Canada) tissue kits (Schulte-Hostedde et al. 2000). Individuals were then genotyped for 11 microsatellite loci using the techniques described in Schulte-Hostedde et al. (2000). Briefly, primers for each locus (one end-labeled with ^{32}P) were used to amplify sample DNA using the polymerase chain reaction (PCR) at optimized annealing temperatures (see Schulte-Hostedde et al. 2000). PCR products were resolved on 6% denaturing polyacrylamide gels at 70 W. Gels were dried and exposed to X-ray film overnight. Product sizes were determined with a clone of known size for each locus. Only one locus deviated from Hardy-Weinberg equilibrium (EuAmMS 114, heterozygote excess).

We assigned parentage using the likelihood-based approach and simulation procedures of CERVUS 1.0 (Marshall et al. 1998). Simulations were performed and delta criteria determined for each grid-year combination. We ran the simulations for 10,000 cycles and the parameters entered into each simulation included the number of candidate parents on the grid, the proportion of candidate parents sampled (0.95), the proportion of loci typed (1.0), and the rate of typing error (0.02). We used 80% confidence as our relaxed criteria for parentage assignment and 95% confidence as our strict cri-

teria for parentage assignment (Marshall et al. 1998). Our general approach was to initially assign maternity to each individual (because there were fewer breeding females than males and our sampling technique allowed us to be reasonably certain who the mother was before genetic assignment of parentage) and then assign paternity using the identity of the assigned mother as the known parent.

To identify potential effects of age on annual reproductive success, we examined the data from individuals who remained on the grids for more than one year. For these individuals (males $n = 13$, females $n = 9$), reproductive success was partitioned into the first year, t , in which they were present on the grid and subsequent years ($t + 1$, and $t + 2$ if the individual was present for all three years of the study). We then conducted analysis of variance (ANOVA) to determine whether there was any significant difference in annual reproductive success among these three categories (t , $t + 1$, and $t + 2$). Only one male was captured in all three seasons and we removed this male from our analysis because there would only be one datapoint in the $t + 2$ category.

To determine the relationship between body size and annual reproductive success, we first quantified overall structural size for each sex, using principal components analysis (PCA) of mean log-transformed values of body size components: body length (measured as total body length minus tail length), skull length, and skull width (Pimentel 1979; Dobson 1992). We then calculated univariate selection gradients using least squares regression following the general procedures outlined by Lande and Arnold (1983) (for examples of calculations see Fairbairn and Preziosi 1996; Przybylo et al. 2000). For each year, we regressed relative reproductive success (individual reproductive success divided by the mean reproductive success of that year) on standardized scores from the first principal component (PC1) of body size components. PC scores for each year were standardized to a mean of zero and a standard deviation of one (Fairbairn and Preziosi 1996). The slopes (β) of these regression models were used as univariate directional selection gradients (Fairbairn and Preziosi 1996; Przybylo et al. 2000). To determine if there was any evidence of stabilizing or disruptive selection on body size, we calculated univariate nonlinear selection gradients (γ) from quadratic regressions between relative reproductive success and PC1 scores (Fairbairn and Preziosi 1996; Przybylo et al. 2000). The coefficient of the quadratic term (β_2) was used to calculate γ ($2\beta_2 = \gamma$ Fairbairn and Preziosi 1996). It is not standard to correct for multiple comparisons in estimations of selection gradients (Fairbairn and Preziosi 1996). However, we estimated two selection gradients for each year (β and γ); thus, the correct α for each analysis of selection gradients is $0.05/2 = 0.025$.

Both male and female yellow-pine chipmunks may forego reproduction as yearlings (Sheppard 1969). In 1998 five females did not breed (i.e., there was no evidence of pregnancy) and we assumed that these females were yearlings. To determine whether body size played a role in the propensity for a female to breed, we compared mean body size (PC1) and body length between females who bred in 1998 and those who did not breed, but we did not include these nonbreeding females in the analysis of reproductive success.

Survival

We used two approaches to examine the effects of body size on annual survival. First, we modeled survival using the mark-recapture models (Cormack-Jolly-Seber [CJS] model; Lebreton et al. 1992) of the program MARK (White and Burnham 1999). Individual capture histories were constructed and separate models developed (using the logit link function) for males and females. Only individuals considered resident (i.e., those captured three times over one month) were included in the analysis, and we assumed that residents who disappeared were dead rather than having emigrated. The time between captures was set at one year to examine annual survival. Thus, our capture histories had three capture occasions (1998, 1999, and 2000) and two survival intervals. Our first step was to determine which of the four submodels of the general CJS model (both survival and recapture time dependent; survival constant, recapture time dependent; survival time dependent, recapture constant; and both survival and recapture constant) was the most parsimonious. We then used goodness of fit bootstrap procedures (500 simulations) from MARK to determine whether the most parsimonious model fit the data adequately. Finally, to determine the relationship between survival and body size, we used the most parsimonious model to develop survival functions, each using one of three measures of body size as covariates. We compared models using PC1; body length; and body length, skull length, and skull width as individual covariates. Parsimony was based on the Akaike's information criterion coefficient (AICc) and the AICc weight (Burnham et al. 1995a,b) as determined by MARK. The model with the lowest AICc was considered the most parsimonious, and when models differed by >2 with respect to AICc coefficients, we concluded that there was strong support for real differences between the models (Burnham et al. 1995a,b).

Second, as with the data on reproductive success, we calculated univariate directional (β) and nonlinear (γ) selection gradients between standardized body size (PC1) and relative survival (calculated by dividing individual survival value [1, survivor; 0, nonsurvivor] by the average survival in that year) for each interval between years (e.g., 1998–1999 and 1999–2000; Fairbairn and Preziosi 1996; Przybylo et al. 2000). Because of the estimation of two selection gradients from each year (β and γ), the correct α is 0.025 (see *Reproductive Success* below).

RESULTS

Body Size

The mean and standard deviation of body size components were consistent with values reported previously (Schulte-Hostedde and Millar 2000). Females had 4% longer bodies and skulls that were 1.5% longer and 2.1% wider than males (Table 1). PCA was conducted on males and females separately. PC1 explained 53.6% and 57.0% of the variation in body size components of males and females, respectively (Table 1). PC1 was used as an index of overall body size for both males and females because of the consistent direction and high loadings of each body size component.

TABLE 1. Mean and standard deviation (SD) of body size components (all in mm) for male and female yellow-pine chipmunks and dimorphism ratio (female/male). Also included are the loadings of the morphological traits on the first principal component (PC1) from a principal component analysis; % variance refers to the proportion of variation in the morphological data explained by PC1.

	Male (<i>n</i> = 57)			Female (<i>n</i> = 37)			Dimorphism ratio
	Mean	SD	PC1	Mean	SD	PC1	
Body length	122.48	3.40	0.745	127.39	3.76	0.909	1.040
Skull length	36.29	0.59	0.756	36.82	0.45	0.794	1.015
Skull width	18.14	0.71	0.693	18.53	0.64	0.503	1.021
% variance	—	—	53.6	—	—	57.0	

Reproductive Success

We assigned maternity to 81 of 92 (88.0%) and paternity to 78 of 92 (84.8%) young of the year (YY) captured in 1998, 1999, and 2000 (Table 2). Our confidence in these procedures was bolstered by the general concordance between maternity assignment based on CERVUS and maternity assignment based on the location of the nest at which YY were captured. Genetic assignment of maternity matched the identity of the breeding female who occupied the maternal den that YY were captured at in 78.6% (22 of 28) of captures at maternal dens. In the remaining 21.4% (six of 28) of cases, the den of mother assigned by CERVUS was within 10–20 m of the maternal den at which YY were captured.

We found no significant effects of age on annual reproductive success. Annual reproductive success did not vary with age for males ($F_{1,24} = 0.555$, $P = 0.463$) or females ($F_{2,19} = 1.023$, $P = 0.378$).

There was a significant difference in annual reproductive success of females among 1998 ($n = 19$, $\bar{x} = 1.316 \pm 1.250$ [SD]), 1999 ($n = 13$, $\bar{x} = 2.615 \pm 1.121$), and 2000 ($n = 12$, $\bar{x} = 1.750$; ± 1.215 ; $F_{2,41} = 4.52$, $P = 0.017$). A least significant difference (LSD) test indicated significantly lower mean reproductive success of females in 1998 than 1999 ($P = 0.005$). There was no significant difference in annual reproductive success of males among 1998 ($n = 28$, $\bar{x} = 0.893 \pm 0.875$), 1999 ($n = 20$, $\bar{x} = 1.500 \pm 1.357$), and 2000 ($n = 15$, $\bar{x} = 1.533 \pm 1.555$; $F_{2,60} = 2.02$, $P = 0.14$).

Annual reproductive success of females was significantly related to body size in 1998 and 1999, albeit in opposite directions. In 1998 the directional selection gradient between PC1 and relative reproductive success was negative ($\beta = -0.480 \pm 0.213$ [SE], $P = 0.037$), whereas in 1999 the

directional selection gradient was positive ($\beta = 0.521 \pm 0.257$, $P = 0.067$; Fig. 1). In 2000 the directional selection gradient was nonsignificant ($P = 0.71$); however, when we excluded an outlier (a small yearling that produced four young: Cook' $D = 1.55$), the directional selection gradient was positive ($\beta = 0.626 \pm 0.260$, $P = 0.039$; Fig. 1). In all three years the nonlinear selection gradients (γ) were not significantly different from zero ($P > 0.3$).

Females who did not breed in 1998 had shorter bodies (breeders, 128.80 ± 3.05 mm [SD] nonbreeders, 124.75 ± 3.021 mm) than breeding females ($t_{1,22} = 2.647$, $P = 0.015$) and tended to be smaller in overall size (breeders, mean PC1 = 0.276 ± 0.977 ; nonbreeders, mean PC1 = -0.423 ± 0.703 ; $t_{1,22} = 1.491$, $P = 0.15$).

Annual reproductive success of males was independent of overall body size. There was no relationship between annual reproductive success and body size (PC1) in all three years (Fig. 2). In all cases the directional selection gradients were not different from zero ($P > 0.3$). Nonlinear selection gradients (γ) in 1998 and 1999 were not different from zero ($P > 0.19$). However, in 2000 there was evidence of a trend toward stabilizing selection ($\gamma = -1.360 \pm 0.220$ [SE], $P = 0.079$). This trend appeared to be driven by a single outlier ($P = 0.14$ when outlier is removed).

Males who were captured on the periphery of the grids may have mated with unsampled females, thus leading to a bias in our estimates of male reproductive success. We conducted two tests to determine if such a bias existed in our data. First, for each year we assigned each male as a peripheral or interior male using the locations of captures. We then conducted ANOVA to compare mean reproductive success of peripheral and interior males. We found no significant differences ($P > 0.14$) in mean reproductive success between categories of males in all years. In addition, for each year we regressed the number of times a male was captured on reproductive success. Males who are captured less often may be peripheral relative to those captured more often. In 1998 and 1999 we found no relationship between number of captures and reproductive success ($P > 0.35$). In 2000, however, we found a significant relationship between these two variables ($r^2 = 0.27$, $P = 0.047$). This relationship, however, was driven by a single male who was captured 29 times in 2000 (often more than once a trapping session) and sired six young. When this male was removed, the significant relationship disappeared ($P = 0.615$). Thus, there was little evidence that our estimates of male reproductive success were biased by peripheral males mating with unsampled females.

TABLE 2. Summary of parentage assignment using CERVUS 1.0 (Marshall et al. 1998). Assignments for maternity and paternity were categorized as being < 80% confident (parentage not assigned), 80–95% confident (relaxed) and > 95% confident (strict). Numbers represent the number of young of the year (YY) assigned to a mother or father for each level of confidence. Proportion of parents assigned to YY for each level of confidence in each year in parentheses.

	No. of YY	Parent	Confidence level		
			< 80%	80–95%	> 95%
1998	30	maternity	4 (13.3%)	10 (33.3%)	16 (53.3%)
		paternity	5 (16.7%)	14 (46.7%)	11 (36.7%)
1999	33	maternity	0	16 (48.5%)	17 (51.5%)
		paternity	3 (9.1%)	8 (24.2%)	22 (66.7%)
2000	29	maternity	7 (24.1%)	11 (37.9%)	11 (37.9%)
		paternity	6 (20.7%)	3 (10.3%)	20 (69.0%)

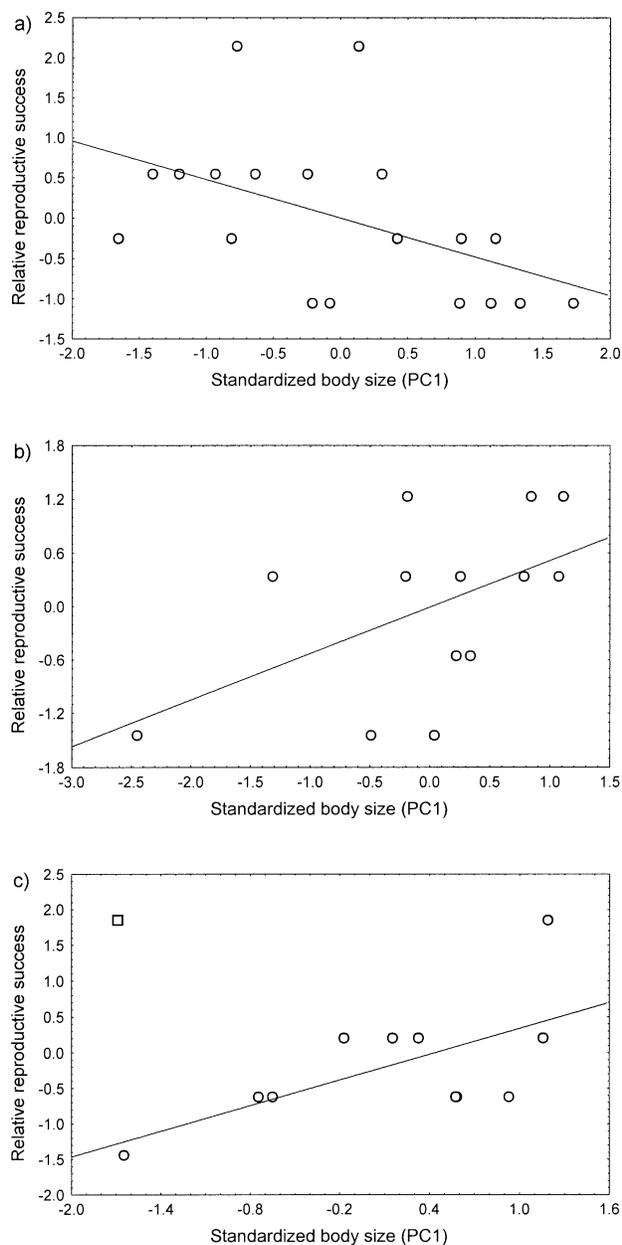


Fig. 1. Regressions of relative female reproductive success on body size (PC1) from (a) 1998, (b) 1999, and (c) 2000. The regression for 1998 showed a negative relationship ($\beta = -0.480 \pm 0.213$ SE; $r^2 = 0.230$, $P = 0.037$) and for 1999 a positive relationship ($\beta = 0.521 \pm 0.257$ SE; $r^2 = 0.272$, $P = 0.067$). The regression from 2000 was nonsignificant ($P > 0.7$) but when an outlier was removed (marked as a box), the regression was significant ($\beta = 0.626 \pm 0.278$ SE; $r^2 = 0.392$, $P = 0.039$). Nonlinear selection gradients (γ) were all nonsignificant ($P > 0.2$).

Survival

A total of 22 females and 40 males were considered residents and included in the survival analysis. Figure 3 presents the mean body size of males and females who were recaptured (survived) and not recaptured (assumed dead) between 1998 and 1999 and between 1999 and 2000. When analyzing the data using MARK, the most parsimonious model for both

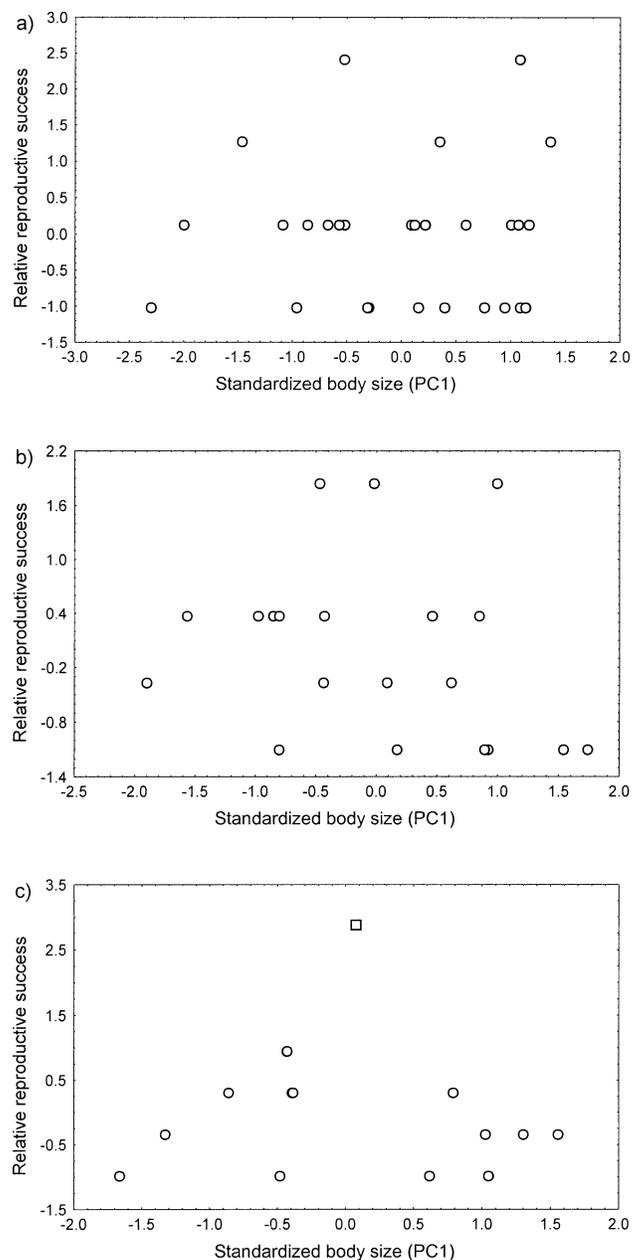


Fig. 2. Regressions of relative male reproductive success on body size (PC1) for (a) 1998, (b) 1999, and (c) 2000. β was nonsignificant for all years ($P > 0.3$). Nonlinear selection gradients (γ) were nonsignificant for 1998 and 1999; however, there was evidence of stabilizing selection in 2000 ($\gamma = -0.967 \pm 0.252$ SE, $P = 0.079$; $P = 0.14$ when outlier [marked as a box] was removed).

males and females was the fully constant model (survival and recapture probabilities independent of time; Table 3). MARK was unable to estimate the recapture parameter probabilities of any of the models; recapture probabilities were consistently estimated as 1.0 with no standard error. This likely occurred because our data did not contain individuals who had a capture history of 1-0-1 (captured in 1998, not captured in 1999, and captured again in 2000). Survival of males was estimated at $\phi = 0.375 \pm 0.07$ (SE) and female survival was estimated at $\phi = 0.594 \pm 0.09$. The goodness-of-fit bootstrap

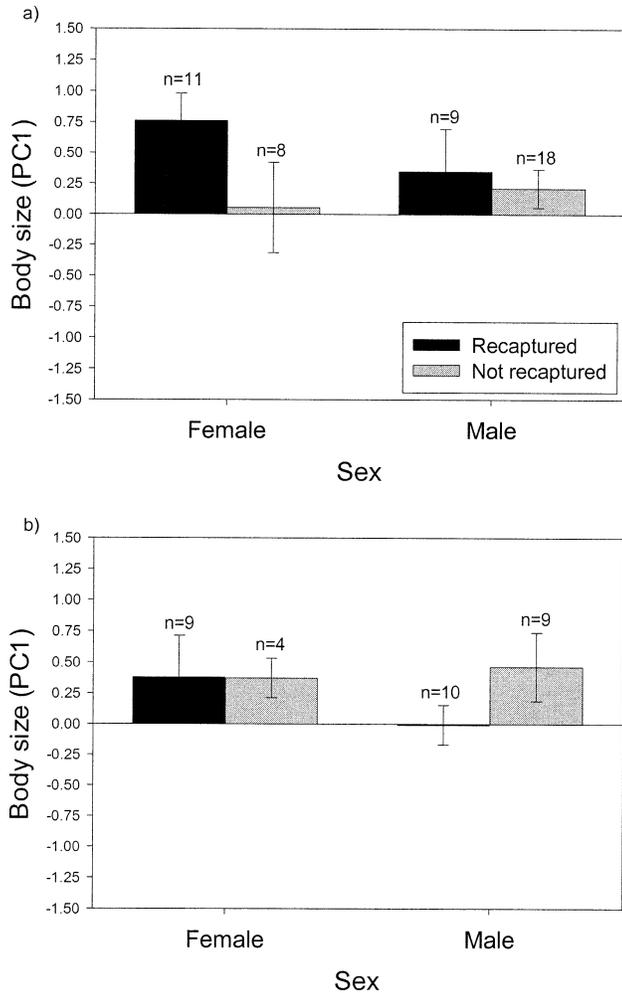


Fig. 3. Body size (PC1; mean \pm SE) of male and female yellow-pine chipmunks that had been recaptured (survived) and not been recaptured (assumed dead) between (a) 1998 and 1999 and (b) 1999 and 2000. Sample sizes are indicated.

procedures of MARK indicated that the time-independent model adequately explained the data for both males ($P > 0.07$) and females ($P > 0.50$).

We used the fully constant model (ϕ, p) to construct three models, each using one of three estimates of body size (PC1; body length; and body length, skull length, and skull width). In all but one model the recapture parameter could not be estimated, again likely due to the lack of individuals with a capture history of 1-0-1. For females, the models including body length and PC1 as covariates had very similar AIC coefficients ($\Delta AICc = 0.25$; Table 4). We therefore elected to use the model with PC1 as the covariate as our most parsimonious model because PC1 better represents overall body size than body length. For males, the model that included all three body size components was the most parsimonious. $\Delta AICc$ was < 2.0 between the model that included all three body size components and the model that used PC1 as a covariate, suggesting that both adequately described the data.

We additionally explored the possibility that survival was normally distributed, rather than a linear function of body

TABLE 3. Akaike's information criteria coefficient (AICc), difference in AICc (defined as the difference between the AICc for a model and the AICc for the current minimum AICc model), AICc weight, model likelihood, the number of estimated parameters, and the deviance of the model, all as calculated by MARK (White and Burnham 1999) from four submodels of the Cormack-Jolly-Seber mark-recapture models (ϕ, p , constant survival and recapture probabilities; ϕ, p_t , constant survival and time-dependent recapture probabilities; ϕ_t, p , time-dependent survival and constant recapture probability; ϕ_t, p_t , time-dependent survival and recapture probabilities) for male and female yellow-pine chipmunks. Because MARK could not estimate the recapture parameter (p), models in which p is time dependent are not presented.

Model	AICc	$\Delta AICc$	AICc weight	Model likelihood	No. parameters	Deviance
Female						
ϕ, p	45.36	0.00	0.367	1.000	1	0.737
ϕ_t, p	47.39	2.03	0.133	0.362	2	0.487
Male						
ϕ, p	65.60	0.00	0.364	1.000	1	6.366
ϕ_t, p	67.58	1.98	0.136	0.372	2	6.165

size. To do so, we constructed a quadratic model using both PC1 and $(PC1)^2$ as covariates for males and females. For females, this normal model was not an improvement on the linear models using PC1 and body length as covariates ($\Delta AICc > 2.00$). However for males, the normal model had twice as much support as the linear model that combined all three body size components (Table 4).

The function of the most parsimonious model for survival of females was

$$\text{logit}(\phi) = 0.3199629 + 0.5393456(PC1_s) \quad (1)$$

and the function of the most parsimonious model for male survival was

$$\text{logit}(\phi) = -0.6902285 + 0.1913686(PC1_s) - 0.9056849(PC1_s)^2, \quad (2)$$

TABLE 4. Akaike's information criteria coefficient (AICc), difference in AICc (defined as the difference between the AICc for a model and the AICc for the current minimum AICc model), AICc weight, model likelihood, the number of estimated parameters, and the deviance of the model, all as calculated by MARK (White and Burnham 1999) from constant survival and recapture models (ϕ, p Cormack-Jolly-Seber mark-recapture models) using the following variables as covariates: body length (BL); PC1; body length, skull length, and skull width (ALL); and PC1 and $PC1^2$ ($PC1^2$ for males only) for male and female chipmunks.

Model	AICc	$\Delta AICc$	AICc weight	Model likelihood	No. parameters	Deviance
Female						
BL	45.62	0.00	0.512	1.000	2	41.202
PC1	45.87	0.25	0.451	0.882	2	41.454
ALL	50.86	5.25	0.037	0.073	5	38.556
Male						
$PC1^2$	63.80	0.00	0.562	1.000	3	57.250
ALL	65.22	1.42	0.276	0.491	4	56.290
BL	67.59	3.80	0.084	0.150	2	63.327
PC1	67.73	3.94	0.078	0.140	2	63.469

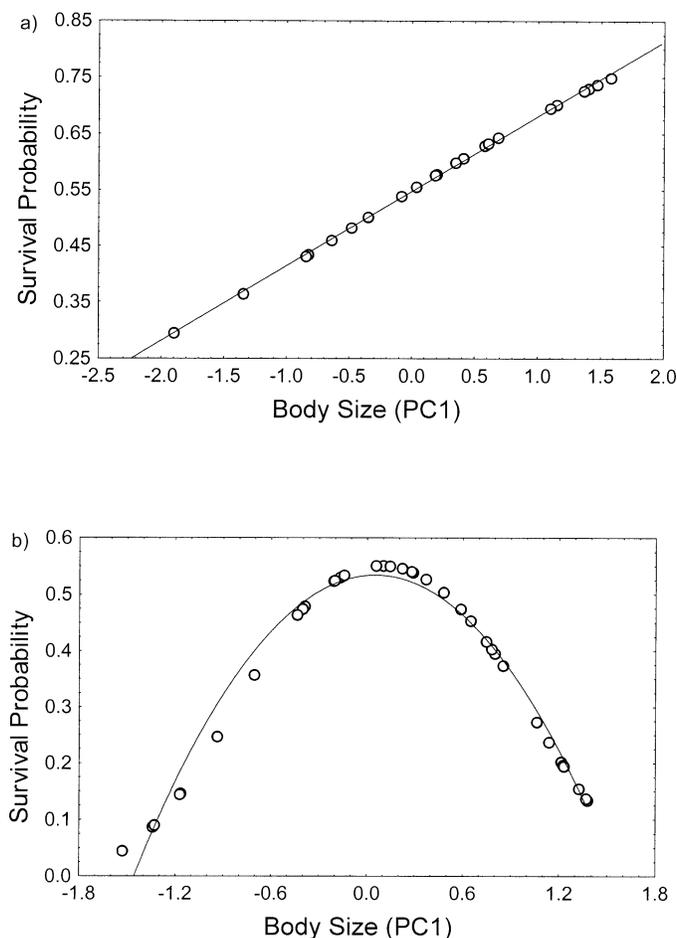


Fig. 4. Most parsimonious survival functions using body size (PC1) as a covariate for (a) female and (b) male yellow-pine chipmunks. Plotted values are based on values back-transformed from survival functions (function 1: $\text{logit}[\phi] = 0.3199629 + 0.5393456[\text{PC1}_S]$; function 2: $\text{logit}[\phi] = -0.6902285 + 0.1913686[\text{PC1}_S] - 0.9056849[\text{PC1}_S]^2$).

where $\text{logit}(\phi)$ is the logit function of survival (ϕ) and PC1_S is the standardized PC scores from PC1 (Fig. 4).

Our analysis of selection gradients for relative survival indicated a trend toward directional selection on female body size in 1998–1999 ($\beta = 0.392 \pm 0.223$, $P = 0.097$) but not in 1999–2000 ($P = 0.99$). There was no evidence of stabilizing or disruptive selection for female body size in relation to relative survival ($P > 0.1$). Directional selection gradients for survival were not different from zero for male body size ($P > 0.1$ for both 1998–1999 and 1999–2000), although there was some evidence of stabilizing selection ($P < 0.1$; Fig. 5).

Pooling Data

Data for each year were pooled among grids (Kidd, Village, and in 1998, Grizzly). Individuals did not travel between grids because distances between grids ranged between 8 km and 15 km (Schulte-Hostedde et al. 2001), well beyond dispersal distances of chipmunks. However, there is evidence of gene flow among the grids (Schulte-Hostedde et al. 2001), suggesting that there is some continuity among them. None-

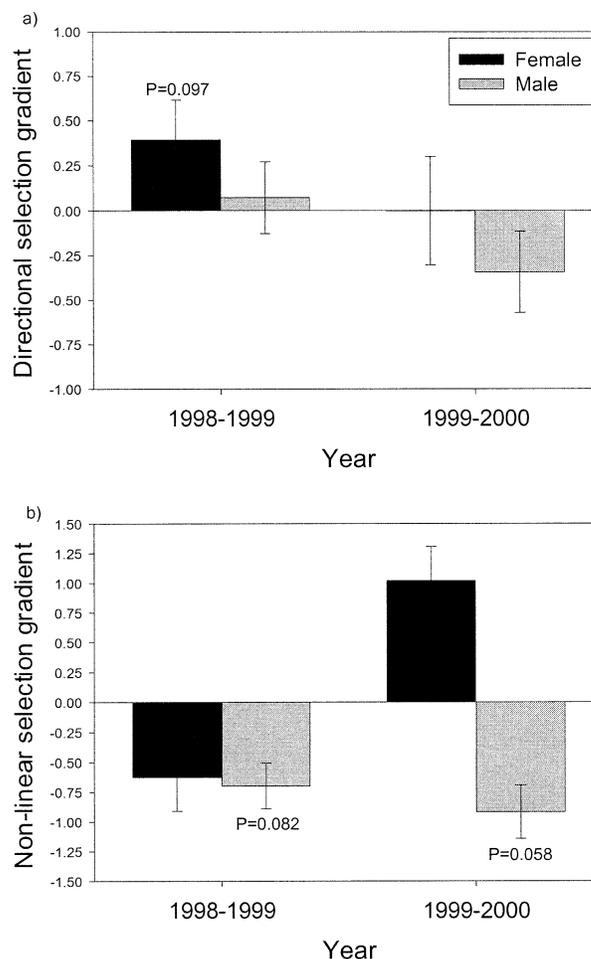


Fig. 5. Univariate (a) directional (β) and (b) nonlinear (γ) selection gradients (\pm SE) for relative survival and body size (PC1). All selection gradients are nonsignificant ($P > 0.1$) except for male nonlinear selection gradients ($\gamma > 0.7$, $P < 0.1$).

theless, we tested for differences among grids in the relationship between body size and relative fitness (relative reproductive success and survival). For each sex and year, we constructed regression models between relative fitness (reproductive success and survival) and body size. We then added the grid identity (Kidd, Village, and Grizzly) as a dummy variable and an interaction (between grid identity and body size). If the grid identity or interaction term were significant factors in the analysis, then it could be concluded that selection was acting differentially among the grids. We found no evidence of this, as in all cases both the interaction and grid terms were nonsignificant ($P > 0.05$), suggesting no significant differences in selection gradients among grids. Thus, pooling data among grids should not have biased our results.

DISCUSSION

Sexual selection does not appear to be acting to maintain sexual size dimorphism in the yellow-pine chipmunk, in sharp contrast to mammalian species that exhibit male-biased sexual size dimorphism. In many large ungulates and pin-

nipeds, large males have higher mating success than small males, thus selecting for large male size (Maynard Smith and Brown 1986; Clutton-Brock et al. 1988; Le Beouf and Reiter 1988; Weckerly 1998; Loison et al. 1999; McElligott et al. 2001). The decoupling of the correlation between body size and reproductive success in male yellow-pine chipmunks, combined with stabilizing survival selection for male body size, may contribute to the evolution of female-biased sexual size dimorphism by providing an opportunity for female body size to evolve to a size greater than that of males. There are fitness advantages afforded to large females; female survival was positively related to body size and, in two of three years, reproductive success of females was positively related to body size. Thus, selection for large female size in the absence of selection for large male size ultimately results in female-biased sexual size dimorphism. Sex differences in reproductive success and survival in relation to body size are a consistent characteristic found in species with sexual size dimorphism, although the pattern varies. For instance in Darwin's ground finch (*Geospiza fortis*) and the house finch (*Carpodacus mexicanus*), two species with male-biased sexual size dimorphism, large males have a mating advantage over small males and small females have a fecundity advantage over large females (Price 1984b; Badyaev and Martin 2000). In contrast, in the waterstrider *Aquarius remigis*, a species with female-biased sexual size dimorphism, lifetime fitness as measured by reproductive success and survival favors an intermediate body size in both males and females (stabilizing selection), with the optimal body size being larger in females than males (Preziosi and Fairbairn 2000).

Because of the emphasis on the role of sexual selection on male-biased sexual size dimorphism in mammals (Andersson 1994), there is often little consideration given to the role of survival in the evolution of sexual size dimorphism (but see Yoccoz and Mesnager 1998). Survival may play an important role in the female-biased sexual size dimorphism of the yellow-pine chipmunk because of stabilizing selection on male body size and positive directional selection on female body size. Sex differences in survival also occur in other taxa with sexual size dimorphism. In marine iguanas (*Amblyrhynchus cristatus*) male body size, but not female body size, was negatively related to survival (Wikelski and Trillmich 1997). This pattern was attributed to starvation, where large male marine iguanas were unable to meet their energetic requirements. A similar pattern has been observed in house finches—large males were less likely to survive than small males and large females were more likely to survive than small females (Badyaev and Martin 2000). Both of these species exhibit male-biased sexual size dimorphism. Survival may be highest at a body size intermediate between male and female body size and this may cause sex differences in survival. However, this scenario cannot apply to our study, where females are larger than males, because survival selection for females is positive and survival selection for males is stabilizing. This suggests that the body size at which adult survival is optimal is different for male and female chipmunks. Why this is the case is unclear, but there is some evidence that, in mammals, large females have higher survival than small females (Wauters and Dhondt 1989; Gaillard et al. 2000). Large males may have low survival if the energetic costs of territoriality or

female defense are high. In chipmunks, male survival is highest at an intermediate size, with small and large chipmunks suffering from low probabilities of survival. This may be due to the costs of aggression associated with small males (Schulte-Hostedde and Millar 2002) and the costs of maintaining a large body (Blanckenhorn 2000).

The absence of a correlation between male reproductive success and body size may be the result of a trade-off between two behavioral components of male mating success: dominance and running speed. To copulate during the mating chase, a male must be fast enough to catch a female and dominant, so that rival males do not displace him (Wauters et al. 1990; Koprowski 1993). Large chipmunks tend to be faster than small chipmunks (Schulte-Hostedde and Millar 2002b), and small chipmunks are behaviorally dominant (aggressive) over large males (Schulte-Hostedde and Millar 2002a). It has been suggested that aggressive behavior in small male chipmunks may represent an alternative mating tactic (Schulte-Hostedde and Millar 2002a) relative to large males. If large males gain matings through tactics other than dominance (such as the ability to successfully find and/or chase receptive females), then small males may adopt aggression as an alternative tactic and thus accept the high costs of aggression (Huntingford and Turner 1987) to compensate for their lack of success in finding and chasing receptive females. In other words, they may be "making the best of a bad job"; small male chipmunks may only be able to attain copulations by being aggressive. This may allow small males to achieve near or the same level of reproductive success as large males, thus contributing to the evolution of female-biased sexual size dimorphism. This type of trade-off may explain the lack of a relationship between male body size and reproductive success found in some other mammalian species (e.g., Topping and Millar 1999), and the preponderance of small (< 1 kg) mammals that exhibit female-biased sexual size dimorphism (Ralls 1976).

The fluctuating relationship between annual female reproductive success and body size may be the result of the differential effects of environmental conditions on female reproduction. Levenson (1990) observed that female-biased sexual size dimorphism in chipmunks tended to be most pronounced in severe environments, suggesting that climate may play a role in the evolution of size dimorphism. Adverse weather conditions and reduced food availability are known to affect female reproductive success in mammals (King et al. 1991; Wauters and Dhondt 1995; Neuhaus et al. 1999), possibly through reduced offspring survival (Clutton-Brock et al. 1988; Packer et al. 1988). Small female mammals depend on increased ingestion rather than stored energy to support gestation and lactation (Millar 1987). Therefore large females, who must support a large soma as well as maintain lactation to support their young, may suffer nestling mortality under reduced food availability. Alternatively, when environmental conditions are favorable, large females may have higher reproductive success than small females because of a fecundity advantage or higher quality maternal care (Ralls 1976). Parturition in chipmunks takes place in late May to early June and average June temperatures in the Kananaskis Valley were not substantially different among years (1998, 11.0°C; 1999, 9.9°C; 2000, 10.9°C), but precipitation was

dramatically different among years. In 1998, when female reproductive success was negatively related to body size, the amount of rainfall was 265.0 mm (2.6 mm of snow also fell), whereas in 1999 and 2000, when female reproductive success was positively related to reproductive success, rainfall was only 63.2 mm and 53.2 mm, respectively, with no snow. These vastly different environmental conditions may contribute to the differences in the relationship between female reproductive success and body size in 1998 and 1999. Since 1981, only two other years have approached precipitation levels of 1998 in the Kananaskis Valley, 178 mm in 1995 and 188.4 mm in 1992. In all other years, precipitation was less than 150 mm, with most years under 100 mm. If female reproductive success is negatively related to body size in years of abnormally high rainfall, then female-biased sexual size dimorphism might be maintained because high precipitation is reasonably rare in the Kananaskis Valley.

There appears to be clear evidence of fitness benefits to large female size. However, what limits female size? One possibility is that genetic correlations between the sexes may limit the evolution of female body size. For example, Merilä et al. (1998) attributed the absence of sexual size dimorphism in collared flycatchers (*Ficedula albicollis*), despite differential selection on male and female size, to high genetic correlations between the sexes. Alternatively, body size may affect age at first reproduction (Roff 1992). Up to one-third of female yellow-pine chipmunks do not breed as yearlings, but delay maturation until they are two years old (Shepherd 1969). In our study, five of 24 female chipmunks did not breed in 1998, and these nonbreeders tended to be smaller than breeding females. This sample is small, and a proper comparison between body size and the propensity to breed as yearlings should be among yearlings alone. Among species of mammals, age at first reproduction is dependent on body size with larger species having a later age at first reproduction than small species. There are also fitness advantages to breeding early. In deer mice, females breeding first as young-of-the-year, rather than as yearlings, suffered no costs with respect to survival or future reproductive success (Teferi and Millar 1993). Even if small female chipmunks have lower annual reproductive success than large females, they may compensate by breeding as yearlings, leading to a longer breeding life span than large females. This scenario may act to limit the evolution of female body size (Shine 1988).

Sex differences in reproductive success and survival are consistent with female-biased sexual size dimorphism in the yellow-pine chipmunk yet there are several interesting and unresolved questions that arise from this research. Perhaps the most striking question, as outlined above, is what limits female body size? The role of age structure and body size in female reproductive success, particularly with respect to reproduction by yearling females, is also an interesting question because selection on body size can vary depending on the life stage of the organism (Schluter et al. 1991). Trade-offs between growth and survival may be influenced by body size (Schluter and Smith 1986). The effects of body size on specific determinants of reproductive success such as breeding longevity, fecundity, mating success, and offspring survival (Clutton-Brock 1988) are also critical to understand the

mechanism behind the maintenance of female-biased sexual size dimorphism.

Finally, the scale of this study is localized and it would be interesting to examine geographic variation in sexual size dimorphism. Yoccoz and Mesnager (1998) suggested that female-biased sexual size dimorphism in bank voles (*Clethrionomys glareolus*) occurs in populations in which survival is low, leading to a decrease in somatic investment (small size) and a concomitant decline in male-male competition. This is interesting because Levenson (1990) suggested that female-biased sexual size dimorphism is most pronounced in populations of chipmunks that are in "severe" environments, where survival may be low.

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