

Sexual selection and mating patterns in a mammal with female-biased sexual size dimorphism

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In mammals, species with highly male-biased sexual size dimorphism tend to have high variance in male reproductive success. However, little information is available on patterns of sexual selection, variation in male and female reproductive success, and body size and mating success in species with female-biased size dimorphism. We used parentage data from microsatellite DNA loci to examine these issues in the yellow-pine chipmunk (*Tamias amoenus*), a small ground squirrel with female-biased sexual size dimorphism. Chipmunks were monitored over 3 years in the Kananaskis Valley, Alberta, Canada. We found evidence of high levels of multiple paternity within litters. Variation in male and female reproductive success was equal, and the opportunity for sexual selection was only marginally higher in males than females. Male and female reproductive success both depended on mating success. We found no evidence that the number of genetic mates a male had depended on body size. Our results are consistent with a promiscuous mating system in which males and female mate with multiple partners. Low variation in male reproductive success may be a general feature of mammalian species in which females are larger than males. *Key words*: body size, chipmunks, mammals, mating patterns, microsatellites, multiple paternity, reproductive success, *Tamias amoenus*. [*Behav Ecol* 15:351–356 (2004)]

Mammalian mating systems vary greatly (Clutton-Brock, 1989), from monogamy (males are socially bonded to a single female; Ribble, 1991) to polygyny (males mate with multiple females; Clutton-Brock et al., 1983) to promiscuity (both males and females mate with multiple partners; Boonstra et al., 1993). Despite this variation, most mammals are polygynous (Clutton-Brock, 1989). The male-male competition that results from polygyny is thought to have driven the evolution of male-biased sexual size dimorphism, a pattern that predominates among mammals (Andersson, 1994; Weckerly, 1998). A necessary condition for the evolution of male-biased sexual size dimorphism by male-male competition is high variation in male reproductive success (Andersson, 1994). Bighorn sheep (*Ovis canadensis*; Coltman et al., 2002) and other large ungulates (Coltman et al., 1999b; Pemberton et al., 1992) are highly dimorphic, with males being substantially larger than females, and variation in male reproductive success is also high in these species. In contrast, male harbor seals (*Phoca vitulina*) are only slightly larger than females, and variation in male reproductive success is low (Coltman et al., 1998). Nonetheless, these patterns are not universal. 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 (Topping and Millar, 1998). Thus, general patterns relating variation in male and female reproductive success to sexual size dimorphism in mammals remain unclear.

Determining mating patterns and variance in reproductive success in mammals is complicated by the general lack of paternal care, making it difficult to quantify male mating success unless copulations are directly observed (Koprowski, 1993; Schwagmeyer et al., 1998). An additional complication occurs when females mate with multiple males, leading to multiple paternity of the young. Under these circumstances, the unambiguous assignment of parentage requires the use of DNA profiling (Hughes, 1998; Westneat, 2000). Genetic techniques have been used in some mammals (Coltman et al., 1998, 2002; Topping and Millar, 1998), but their application lags behind studies of other vertebrate taxa such as birds (Bonnet et al., 2001; Petrie and Kempenaers, 1998). Despite this bias, small mammals are attractive subjects with respect to the study of mating patterns for several reasons. First, they produce relatively large litters, increasing the possibility of multiple paternity. Second, gestation periods are short and population densities are often high. Finally, many other aspects of the behavior and ecology of small mammals have been studied, providing important background for the development of hypotheses relative to mating patterns.

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). Males and females differ in overall structural size, and females weigh 10–20% more than males (Schulte-Hostedde and Millar, 2000). Female chipmunks are in estrus for 1 day a year in late April or early May. Females advertise their estrous state through vocalizations 3–5 days before its onset. Several males (2–6) aggregate near the 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 also exhibit a mating chase during breeding (Elliott, 1978; Koprowski, 1993; Wauters et al., 1990; Yahner, 1978).

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Here, we used microsatellite DNA loci to assign parentage of offspring to quantify variation in both male and female reproductive success and examined several questions related to sexual selection, mating patterns, and body size in the yellow-pine chipmunk. First, we determined the degree of multiple paternity evident in litters from which we captured at least two offspring. Second, we compared variance in genetic estimates of male and female reproductive success and calculated the opportunity for sexual selection (I , standardized variance in reproductive success; Ferguson and Fairbairn, 2001) and sexual selection gradients (the degree to which reproductive success depends on the number of genetic mates; Arnold and Duvall, 1994) for both sexes. Finally, there is some evidence that males may use different size-dependent tactics to acquire mates (Schulte-Hostedde and Millar, 2002a,b; Schulte-Hostedde et al., 2002). Although male reproductive success is independent of body size, reproductive success can be gained by siring a few offspring with many females or siring many offspring with a few females. We therefore determined whether the number of genetic mates depended on male body size.

METHODS

Field methods

We sampled chipmunks on three trapping grids in the Kananaskis Valley, Alberta, Canada 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). 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 which were distributed evenly (20 m apart) along the rocky creek bed. For all grids, except for Kananaskis Village in 1998 (which had 60 traps), there was 1 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 Monel #1005 ear tags with unique numbers but encountered some tag loss. Therefore, in 1999 and 2000 we used PIT (passive integrated transponder) tags (Anitech Enterprises Inc., Markham, Ontario, Canada) to mark individuals.

Upon capture, we individually marked chipmunks (1998, ear tags; 1999 and 2000, PIT tags), weighed them with a Pesola scale (± 1 g), and recorded the sex and reproductive condition of each animal. 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 2 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, for details). 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, California) 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; Hoholil 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 (Berteaux et al., 1996). Once a nest was found, we set out four or five Longworth traps around the nest two to three times per week from late June to late August to capture emerging juveniles.

Genetic analysis of reproductive success

We extracted DNA from tissue samples taken from juveniles and all putative parents using QIAGEN 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 ^{33}P) were used to amplify sample DNA using the polymerase chain reaction (PCR) at optimized annealing temperatures (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; Schulte-Hostedde et al., 2000).

We based genetic estimates of reproductive success on DNA extracted from tissue samples taken from the young that were captured upon emergence from the maternal nest. 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” criteria 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 because 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.

RESULTS

We estimated trapability of each individual adult chipmunk that was captured at least three times within a year by calculating the number of times an individual was caught divided by the number of trap nights when the animal is known to be alive, excluding first and last capture. Using this approach, we determined that individual chipmunks were, on average, captured in 60–70% of all trapping sessions (1998: $66\% \pm 21\%$ [SD]; 1999: $66\% \pm 24\%$; 2000: $61\% \pm 27\%$).

Multiple paternity and sexual selection

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 with at least 80% confidence (see Schulte-Hostedde et al., 2002, for details). 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 young were captured. Genetic assignment of maternity matched the identity of the breeding female that occupied the maternal den at which the young were captured in 78.6% (22 of 28) of captures at maternal dens. In the remaining 21.4% (6 of 28) of cases, the den of the mother assigned by CERVUS was within 10–20 m of the maternal den at which the young were captured.

Over the 3-year study period, we captured young from 37 litters. Of these 37 litters, 24 consisted of two or more offspring, allowing us to examine the incidence of multiple paternity in these litters. Twenty-two of 24 litters (91.7%) with 2 or more young were multiply sired (i.e., young were assigned to the same mother but to different fathers).

Variance in male and female reproductive success was not significantly different in 1998, 1999, 2000, nor when the data were pooled (Figure 1; variance ratio test, $p > .05$ for all comparisons). We conducted a power analysis of the pooled variance ratio test using G-Power (Faal and Erdfelder, 1992). Indeed, with a sample size of 107, our ability to detect medium to large effects ($f^2 = 0.15$ and 0.35 ; Cohen, 1988) had low power ($1 - \beta = 0.30$ and 0.74). We therefore conducted an additional test to determine whether the distribution of reproductive success varied between males and females using contingency table analysis. Again, we found no significant differences between males and females ($\chi^2 = 8.05$, $df = 6$, $p > .1$). Statistical power to detect medium to large effect sizes ($w = 0.3$ and 0.5 ; Cohen, 1988) was improved compared with the variance ratio test ($1 - \beta = 0.62$ and 0.98). Thus, if there were relatively large differences in variation of reproductive success between male and female chipmunks, we should have been able to detect them.

The opportunity for sexual selection (I ; standardized variance in reproductive success defined as the variance in reproductive success divided by the square of mean reproductive success; Ferguson and Fairbairn, 2001) varied between 0.480 and 1.186 for females and between 0.858 and 1.551 for males among the 3 years of the study (Table 1). When data were pooled, I was higher for males (1.243) than for females (0.928; Table 1).

Reproductive success depended on the number of genetic mates for both males and females (Figure 2), but the slopes of these relationships were significantly different. There was a significant interaction between sex and the number of genetic mates (ANCOVA: $F_{1,76} = 5.41$, $p = .02$), suggesting that this slope was significantly shallower for females than males (see Figure 2).

Males that 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 have previously conducted two tests to determine if such a bias occurred in our data (Schulte-Hostedde et al., 2002). First, we found no evidence that males captured on the periphery of the trapping grids had lower reproductive success than males captured at the center of the grids (Schulte-Hostedde et al., 2002). Second, males that were captured more often did not have higher reproductive success than males captured less often (Schulte-Hostedde et al., 2002). Thus, there was little evidence that our estimates of male reproductive success were biased.

Body size and the number of genetic mates

The first principal component (PC1) from a principal components analysis on body size measurements (body length, skull length, and skull width) was used as an index of body size (see Schulte-Hostedde et al., 2002, for details). The analysis was conducted separately for each sex. PC1

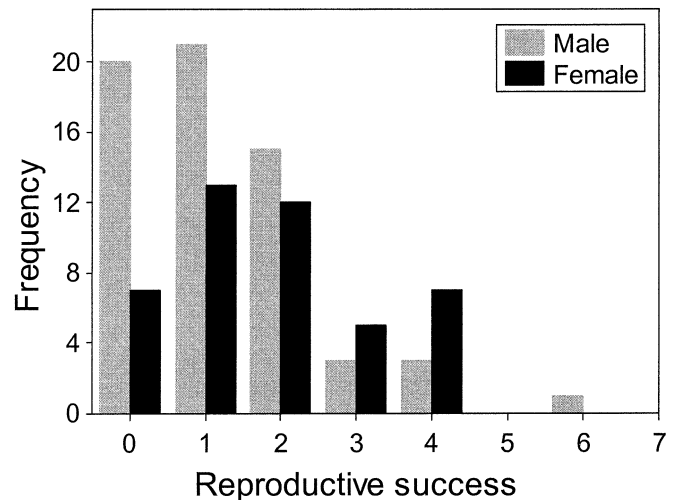


Figure 1
Frequency distribution of annual male and female reproductive success for yellow-pine chipmunks. Data are pooled from 1998–2000. There was no significant difference in the distribution of reproductive success between the sexes ($\chi^2 = 8.05$, $p > .1$).

explained 53.6 and 57.0% of the variation in body size components of males and females, respectively. Body size components consistently loaded heavily on PC1. The loadings of body size components ranged from 0.503 to 0.909 for females and from 0.693 to 0.756 for males.

We found no evidence of a linear (1998: $p = .96$; 1999: $p = .17$; 2000: $p = .89$) or a quadratic relationship between male body size and the number of genetic mates (1998: $p = .99$; 1999: $p = .08$; 2000: $p = .21$); see Figure 3.

DISCUSSION

Sexual selection does not seem to be acting differently on male and female chipmunks. The relationship between mating success and reproductive success was not significantly different between males and females, nor was variance in reproductive success. Finally, there was evidence of multiple paternity, as young that were assigned to the same mother were often assigned to different fathers. The genetic evidence is therefore consistent with a mating system in which both male and female chipmunks mate with multiple partners.

The proportion of litters that we determined to have been sired by more than one male was very high (91.7%), similar to that in other mammalian species. Some studies of rodents in seminatural conditions have found comparable levels of multiple paternity (Bartmann and Gerlach, 2001; Keil et al., 1999). Other field studies of sciurids have also found high levels of multiple paternity, such as 89% of litters in California ground squirrels (*Spermophilus beecheyi*) and 78% in Belding's ground squirrel (*S. beldingi*; Birkhead and Appleton, 1998). Nonetheless, our estimate of levels of multiple paternity in yellow-pine chipmunks should be interpreted cautiously because we did not bring pregnant females into the lab and collect DNA samples from the entire litter directly at parturition.

The low opportunity for sexual selection in male yellow-pine chipmunks is consistent with the female-biased sexual size dimorphism evident in this species (Schulte-Hostedde and Millar, 2000). High variance in male reproductive success and a size advantage in male–male competition for mates is thought to have driven the evolution of male-biased sexual size dimorphism that is common in mammals (Andersson,

Table 1
Reproductive success in female and male yellow-pine chipmunks

	<i>n</i>	Mean	<i>s</i> ²	<i>I</i>
Female				
1998	19	1.32	1.56	1.186
1999	13	2.62	1.26	0.480
2000	12	1.75	1.48	0.844
Pooled	44	1.82	1.69	0.928
Male				
1998	28	0.89	0.77	0.858
1999	20	1.50	1.84	1.228
2000	15	1.55	2.41	1.551
Pooled	63	1.24	1.54	1.243

The mean and three measures of variation in reproductive success (variance, *s*², and standardized variance (*I*)) are presented.

1994). For instance, bighorn sheep show highly male-biased dimorphism; 4-year-old males are up to 50% heavier than females (Festa-Bianchet et al., 1996) and have massive curled horns that are used in combat, and, depending on the year, the opportunity for selection (*I*) for males ranged between 2.45 and 8.32 (Coltman et al., 2002). Northern elephant seals are also highly dimorphic, and estimates of *I* ranged from 7.08 to 27.00 (Le Beouf and Reiter, 1988), similar to measures of *I* from other large, highly dimorphic ungulates (e.g., Coltman et al., 1999b; Pemberton et al., 1992). Recently, we concluded that the female-biased sexual size dimorphism evident in yellow-pine chipmunks may result from the decoupling of the correlation between male body size and reproductive success (Schulte-Hostedde et al., 2002). As shown here, variation in male reproductive success is also quite low and not significantly different from variation in female reproductive success. Thus, it appears that male reproductive success is independent of body size because there appears to be little variation in reproductive success to explain. Another example of this pattern is the harbor seal, which has low levels of male-biased sexual size dimorphism (males are only 7% longer than females); large males do not have higher reproductive success than small males (Coltman et al., 1999a), and measures of *I* for male harbour seals are also low (0.88–1.29; Coltman et al., 1998). The absence of high variation in male reproductive success (low *I*) may limit the evolution of male size in mammals.

The dependence of male reproductive success on the number of genetic mates is not surprising. In species in which males provide no parental care, males can maximize reproductive success by seeking, defending, and mating with many females (Trivers, 1972). This relationship is expected in both promiscuous and polygynous species (Arnold and Duvall, 1994) and has been found in both northern water snakes (Prosser et al., 2002) and brown-headed cowbirds (*Molothrus ater*; Woolfenden et al., 2002), which have a promiscuous and polygynous mating system, respectively. A more interesting question is why does female reproductive success increase with the number of genetic mates? In Gunnison's prairie dogs (*Cynomys gunnisoni*), female litter size likewise increased with the number of mates a female had (Hoogland, 1998). A common explanation may be that multiple paternity of the young enhances the genetic diversity of the offspring, leading to higher survival of the young (Jennions and Petrie, 2000; Reynolds, 1996). In our study, juveniles were sampled after they had emerged from the maternal den, a period of approximately 35 days from birth (Sutton, 1992). We found that mean female reproduc-

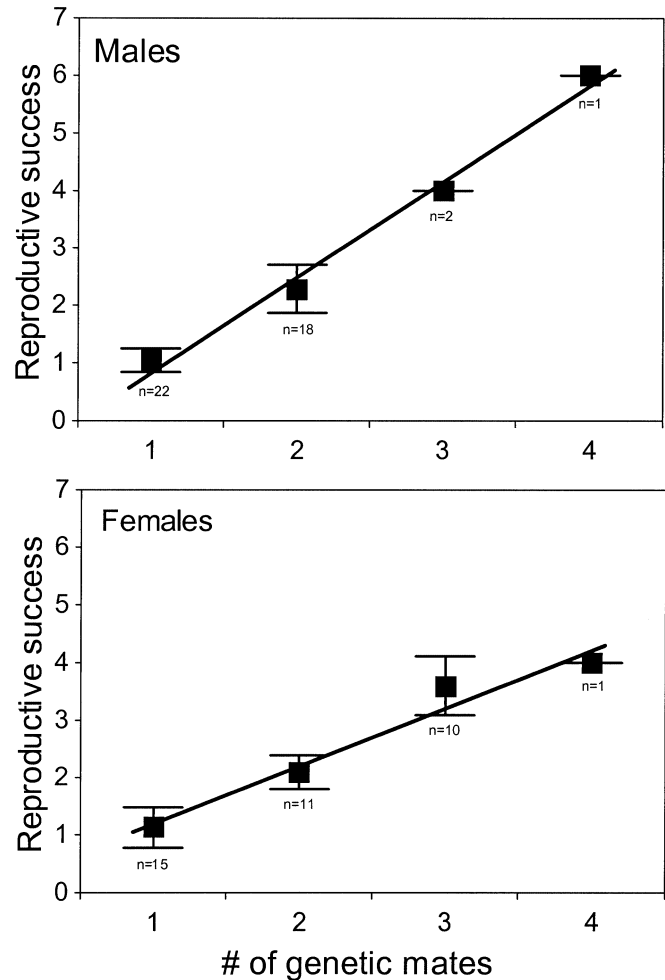


Figure 2

Annual reproductive success (based on the number of offspring emerged from the maternal den) (mean \pm SD) as a function of annual mating success (the number of partners an individual was genetically identified having mated with) for male and female yellow-pine chipmunks. In both males and females, reproductive success is highly correlated with the number of genetic mates (male: $r^2 = .85$, $df = 1,41$, $p < .001$; female: $r^2 = .87$, $df = 1,35$, $p < .001$).

tive success was substantially lower than reported litter sizes for yellow-pine chipmunks (1.32–2.6). Sheppard (1969) reported mean embryo counts of 4.80, and Kenagy and Barnes (1988) reported mean litter size at birth as 5.02. This suggests that female yellow-pine chipmunks suffer from moderate to complete loss of the litter in the nest, a situation not uncommon in sciurids (e.g., Neuhaus, 2000). It is interesting to speculate whether those females that mated with multiple males may have had litters with higher survival during the period before emergence. This pattern has been found in northern water snakes: multiply sired litters showed higher overwinter survival than singly sired litters, perhaps due to genetic benefits associated with increased genetic diversity (Kissner, 2002).

An alternative explanation of the dependence of female reproductive success on mating success and the small sizes of emerged litters is that incomplete sampling of the young may bias the likelihood of detecting multiple paternity within litters. Thus, we may have been less likely to find evidence of multiple mates of females if we had incompletely sampled their litters. Unfortunately, we cannot directly test this

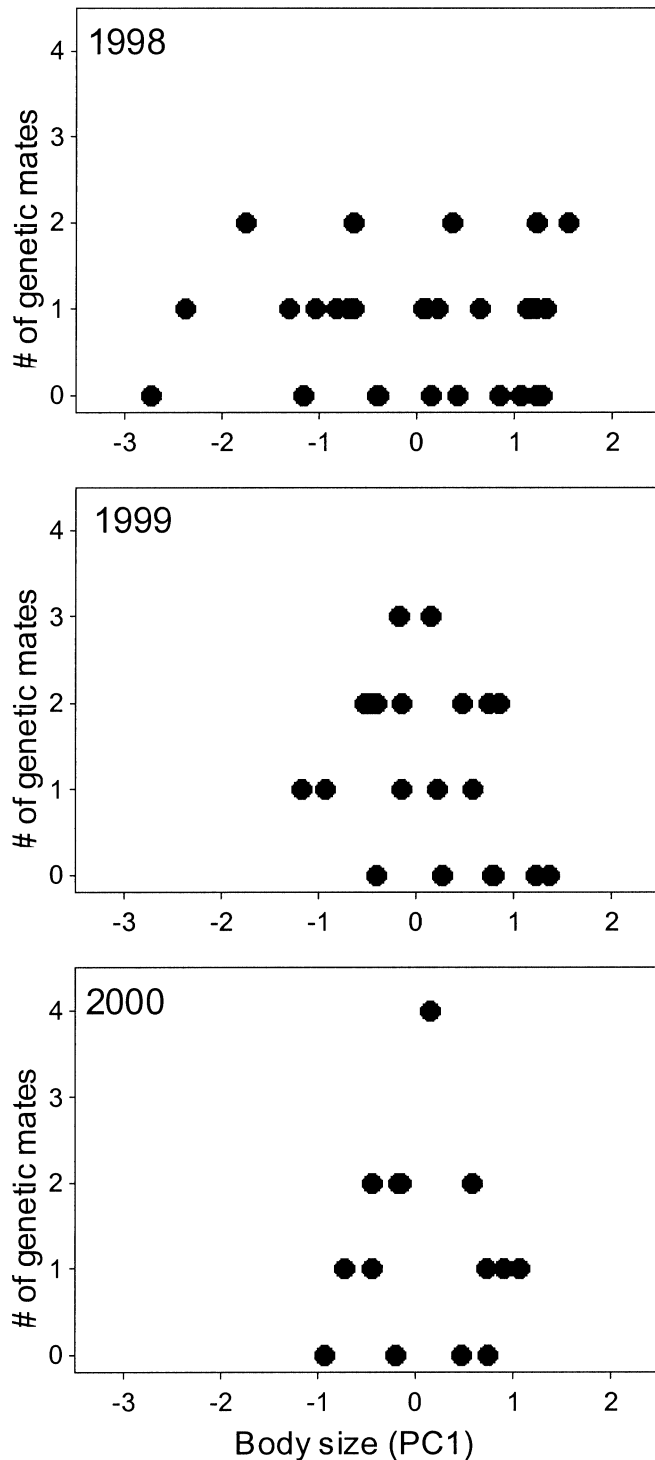


Figure 3
Regressions of annual number of genetic mates for males and body size for 1998, 1999, and 2000. There was no relationship between body size and mating success in all 3 years.

possibility, but it is unlikely that our trapping protocol would have missed capturing so many (three or four young per litter) juvenile chipmunks. Trapability estimates for adult chipmunks were high (>60%), and on average we captured individual adult males 11–12 times per season. We also regularly captured breeding females at their nest sites (as determined by radio

telemetry; A.I. Schulte-Hostedde, unpublished data), suggesting that chipmunks are easily captured.

It has been hypothesized that large male chipmunks might be better able to chase and/or find females, and small males may use aggression as an alternative tactic to obtain matings (Schulte-Hostedde and Millar, 2002a,b; Schulte-Hostedde et al., 2002). Males engaging in alternative mating tactics may have similar reproductive success yet have a different number of genetic mates. For example, large males may have acquired reproductive success by having few offspring with many females, and small males may have many offspring with a few females. We found no evidence of a relationship between the number of genetic mates and body size, and this is consistent with previous work which found that male reproductive success was independent of body size (Schulte-Hostedde et al., 2002). Our results indicate that if size-dependent alternative tactics are present in this species, they do not differ with respect to the number of genetic mates. This is in contrast to what has been observed in gray squirrels, where small young males have lower mating success than large old males due to the adoption of a “satellite” tactic during mating chases (Koprowski, 1993).

There are two research directions stimulated by these results. First, the genetic benefits of multiple paternity have not received much attention in mammals, and our results hint that females that mate multiply have high offspring survival. Observational and experimental approaches should be used to test the prediction that litters with multiple sires have higher survival than litters with single sires. Second, testing the generality of the conclusion that low standardized variation in male reproductive success (I) is characteristic among mammalian species that are monomorphic or exhibit female-biased sexual size dimorphism should provide insight into the evolution of sexual size dimorphism in mammals.

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