Effects of body size and mass on running speed of male yellow-pine chipmunks (*Tamias amoenus*)

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Abstract: Male-biased sexual size dimorphism in mammals is usually attributed to the success of large males in intrasexual combat for mates. However, mating success may be determined by contests that are not combative. In the mating chase of the yellow-pine chipmunk (*Tamias amoenus*), a mammalian species with female-biased sexual size dimorphism, fast males may have an advantage in acquiring matings with estrous females. However, the effects of intraspecific variation in body size on running speed are not obvious; heavy individuals may run more slowly than light individuals because excess mass can be a hindrance to locomotion, but individuals that are structurally large may run faster than small individuals because of longer stride length. We examined the effects of both body mass and structural size on running speed in male yellow-pine chipmunks using manipulated runs in which male chipmunks were chased over a known distance. Structurally large male chipmunks had faster running speeds than small males, potentially giving large males an advantage when chasing estrous females. However, small male chipmunks are known to be aggressively dominant over large males. This leads to a potential trade-off in male body size between two behavioural components of mating success (running speed and dominance) that may constrain the evolution of male body size, ultimately leading to female-biased sexual size dimorphism.

Résumé : Chez les mammifères, le dimorphisme sexuel quant à la taille est généralement attribué au succès plus grand des plus gros mâles au cours des combats pour se gagner des partenaires. Cependant, le succès d'un accouplement peut résulter de confrontations dans lesquels il n'y a pas de combat. Chez le tamia amène (*Tamias amoenus*), une espèce à fort dimorphisme sexuel chez laquelle les femelles ont une taille plus grande, les mâles les plus rapides ont plus de chance de s'accoupler à une femelle en chaleur. Cependant, les effets de la variation intraspécifique de la taille sur la vitesse de la course ne sont pas évidents; des mâles lourds courent souvent moins vite que des mâles plus légers parce que l'excès de masse peut nuire à leur locomotion, mais les individus qui sont plus costauds peuvent courir plus vite que les petits individus parce qu'ils font de plus longues enjambées. Nous avons étudié les effets de la masse et de la carrure sur la vitesse de course chez des tamias amènes sur des pistes contrôlées sur lesquelles des tamias mâles étaient pourchassés sur une distance prédéterminée. Les mâles costauds courent plus vite que les mâles plus petits, ce qui devrait théoriquement leur conférer un avantage dans la poursuite de femelles en chaleur. Cependant, il arrive que des mâles plus petits fassent preuve de dominance agressive à l'égard des mâles de grande taille. Ce compromis dans la taille des mâles entre deux composantes comportementales du succès de l'accouplement (la vitesse de course et la dominance) peut imposer des contraintes à l'évolution de la taille des mâles, résultant en bout de ligne à un dimorphisme sexuel de la taille qui favorise les femelles.

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Introduction

In mammals, male-biased sexual size dimorphism is usually attributed to a polygynous mating system in which large males achieve greater mating success than small males because of success at contest competition through combat (Andersson 1994). However, mating success may be determined by contests that are not combative or in which combat plays a small role. For instance, running speed rather than

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combat ability may be particularly important in mating systems in which males chase potential mates (e.g., Elliott 1978; Callahan 1981).

The yellow-pine chipmunk (*Tamias amoenus*), like many other North American chipmunks, exhibits female-biased sexual size dimorphism (Levenson 1990; Schulte-Hostedde and Millar 2000). Chipmunks, like many tree squirrels (Yahner 1978; Koprowski 1993, 1998; Wauters et al. 1990) have a promiscuous mating system in which males compete intensely for access to an estrous female during a "mating chase"; several (2–6) males aggregate near the female's den and pursue her on the day of estrous (Elliott 1978; Callahan 1981). Pursuit of the female involves a series of short chases rather than a prolonged chase (Elliott 1978; Callahan 1981). Under these conditions, male-biased sexual size dimorphism or no dimorphism would be expected to evolve.

Success in the mating chase requires that a male be fast enough to outrun his competitors and dominant enough to successfully fend off other males for access to females. Understanding the relationship between body size and behav-

ioral components of mating success (dominance and running speed) can provide insights into the evolution and maintenance of sexual size dimorphism. Small male yellow-pine chipmunks are known to aggressively dominate large males (Schulte-Hostedde and Millar 2002); however, little is known about the effect of body size on their running speed.

Among mammals, large species tend to be faster than small species (Garland 1983). However, the effects of intraspecific variation in body size on running speed are not obvious; heavy individuals may be expected to run more slowly than light individuals because their large mass may impede locomotory function, but individuals that are structurally large may be expected to run faster than small individuals because they may have long limbs and long strides. Few studies have examined the effects of body mass and structural size on running speed in rodents, but Trombulak (1989) found heavy Belding's ground squirrels (*Spermophilus beldingi*) to be slower than light squirrels, and Djawden and Garland (1988) found that the lightest least chipmunk (*Tamias minimus*) was faster than heavier chipmunks. Here, we examine the effects of body mass and structural size on running speed using manipulated runs in which male chipmunks are chased over a known distance.

Methods

We conducted running speed trials in July and August 2000. Nineteen adult male chipmunks were captured from seven sites in the Kananaskis Valley, Alberta, and kept at the Kananaskis Field Station, University of Calgary, for a maximum of 24 h before the running trial. Chipmunks were housed in plastic or metal cages measuring $40 \times 30 \times 15$ cm. Food (sunflower seeds and rat chow) and water were provided ad lib, and apple was occasionally provided. Animals were maintained on a 14 h light –10 h dark photoperiod.

A running trial was conducted only once for each individual. Before a running speed trial took place, all chipmunks were weighed (± 1 g) and measured to quantify structural size. Total body length was measured using a graduated board (± 1 mm) 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). Skull length was measured from the tip of the nose to the back of the skull, and skull width was measured across the widest point of the skull (the zygomatic arch) using dial calipers (± 0.1 mm).

Trials took place on the grounds of the Kananaskis Field Station on a flat, mowed field between 2:00 and 4:00 pm. For each trial, a chipmunk was placed in a bag of flourescent tracking powder (Radiant Color, Richmond, Calif.) and released 15–18 m from the edge of the field. We motivated the chipmunk to run towards the edge by having an assistant shout and wave their arms. This approach has been used successfully on other rodents (e.g., Trombulak 1989; Blumstein 1992; Djawden 1993; Smith 1995). One observer (AISH) timed the runs from the point at which the chipmunk began running until it reached the edge of the field. We assumed

that these manipulated runs generated maximum running speeds. The same assistant and methodology was used for each of the 19 running trials. We measured the distance traveled using a tape measure along the powder trail left behind on the grass. We removed five chipmunks from the analysis because either they paused during the chase or their trajectory was not linear.

We quantified overall structural size by conducting a principal components analysis on log-transformed values of body length (total body length minus tail length), skull length, and skull width. We selected these morphological traits to describe overall body size because they are reasonably repeatable (Schulte-Hostedde and Millar 2000) and we have used these measurements in other studies related to female-biased sexual size dimorphism in yellow-pine chipmunks (Schulte-Hostedde and Millar 2002; Schulte-Hostedde et al. 2002).

We calculated running speed (metres/second) and regressed running speed on body size and mass.

Results

Variation in body-size components (Table 1) was generally the same as variation reported in larger samples of chipmunks (Schulte-Hostedde and Millar 2000), suggesting that the chipmunks we sampled were representative of natural variation.

Only 36% of the variation in the body size measurements of the chipmunks was explained by the first principal component (PC1) and the three body size components did not load in a consistent direction (Table 2), suggesting that PC1 described variation in shape rather than size. The second principal component (PC2), however, explained 33% of the variation of the body-size measurements (marginally less than PC1) and the body-size components all loaded in a consistent direction (Table 2). Although PC2 is almost entirely body length, it does explain some minor variation in skull dimensions. Therefore, we used both PC2 scores (which provide some information on variation in skull dimensions) and body length as indices of body size. The regression of body mass on body size (PC2) was not significant (df = 1,13; $r^2 = 0.023$; $P = 0.59$), nor was the regression of body mass on body length (df = 1,13, $r^2 = 0.01$, $P = 0.60$), meaning that heavy chipmunks were not necessarily large chipmunks. Because PC2 was not normally distributed (Shapiro–Wilk W test, $W = 0.871$, $P < 0.05$) and body length was approaching non-normality ($W = 0.908$, $P < 0.15$), we used nonparametric procedures (Spearman's rank correlation) for data analysis.

Male chipmunks ran a distance of 13.8 ± 2.50 m (mean ± SD) in a time of 3.28 ± 1.01 s. Distance traveled was independent of body size (PC2, $r = 0.345$, $P = 0.226$; body length, $r = 0.297$, $P = 0.302$) and body mass ($r = 0.137$, $P = 0.639$), indicating that measures of running speed in relation to body size and mass were unlikely to be biased with respect to distance traveled. Running speeds (3.33–5.66 m/s) approached previously published estimates of maximal running speeds found in the smaller least chipmunk (3.2 m/s; Smith 1995) and the larger golden-mantled ground squirrel (*Spermophilus lateralis*; 6.0 m/s; Kenagy and Hoyt 1989); therefore, we are confident that our manipulated runs reflect

Table 1. Mean, standard deviation (SD), and range of body mass and measured morphological variables for male yellow-pine chipmunks (*Tamias amoenus*) used in running speed trials ($n = 14$).

	Mean ± SD	Range
Body mass (g)	51.21 ± 3.21	45–57
Body length (mm)	121.86 ± 3.44	114–129
Skull length (mm)	36.36 ± 0.50	35.2–37.3
Skull width (mm)	18.57 ± 0.41	17.9–19.3

Table 2. Factor loadings from principal components analysis for male yellow-pine chipmunks used in running speed trials (PC1 and PC2) ($n = 14$).

	PC1	PC2
Body length	−0.040	0.996
Skull length	−0.740	0.034
Skull width	0.737	0.088
% variance[a]	0.364	0.334

[a]The percent variance in the data explained by PC1 or PC2.

Fig. 1. Plot of the ranks between running speed and (*a*) body size (PC2) and (*b*) body length of male yellow-pine chipmunks (*Tamias amoenus*). The line in (*a*) and (*b*) represents the hypothesis of a positive rank correlation between the independent variable (body size (PC2) or body length) and running speed. The rank assigned to tied observations is the mean of the ranks that would have been assigned had they not been tied.
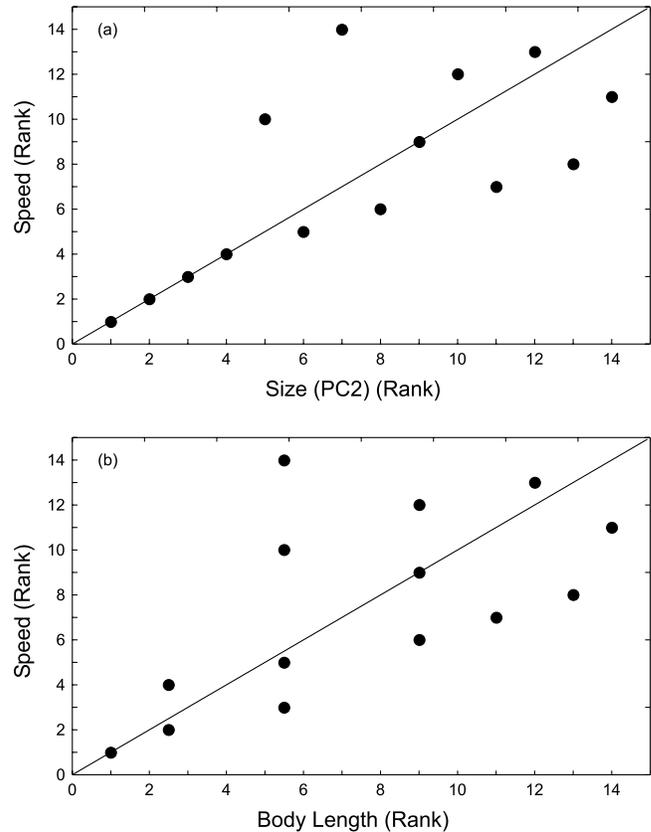

maximum running speeds. There was a significant, positive relationship between body size (PC2) and running speed ($r_S = 0.705$, $P = 0.005$) and between body length and running speed ($r_S = 0.619$, $P = 0.018$; Fig. 1). There was no relationship between body mass and running speed ($r_S = 0.221$, $P = 0.447$).

Discussion

Structural size, but not body mass, explained a significant amount of variation in running speed. Large male chipmunks ran faster than small males, but running speed was independent of mass. Given this result, structurally large males may reach receptive females during the mating chase sooner than small males. Variation in running speed in relation to structural size among male chipmunks is not the result of differences in age because adult chipmunks show little evidence of growing during the summer (Schulte-Hostedde and Millar 2000) and young-of-the-year, which are born in June, are usually indistinguishable by mass from adults by September (Broadbrooks 1970).

The lack of a relationship between body mass and running speed is consistent with some other work on small vertebrates. Garland (1983) suggested that running speed among the Rodentia was independent of body mass, and Djawden and Garland (1988) found no correlation between body mass and running speed within 18 species of rodents. Similar results have been found in lizards (Garland et al. 1990). These results contrast with those of Trombulak (1989), who found a negative relationship between body mass and running speed in Belding's ground squirrels. Hibernators, such as ground squirrels, may be at a particular disadvantage when a large proportion of body mass is fat (Trombulak 1989). Under these circumstances, body mass is more likely to limit running speed. Yellow-pine chipmunks are lean (total body fat is only 2.8% of total mass (Schulte-Hostedde et al. 2001)), and they deposit little fat before hibernation (Kenagy

and Barnes 1988). In this context, fat is unlikely to hinder locomotion.

The positive relationship between structural size and running speed may be related to stride length, i.e., individuals with long limbs are able to travel more quickly than individuals with short limbs. Rodents with long strides tend to run more quickly than those with short strides (Strang and Steudel 1990). Hind-foot length is correlated with body length in yellow-pine chipmunks (Schulte-Hostedde and Millar 2000), suggesting that large chipmunks have longer limbs than small chipmunks.

It is worth noting that PC1 explained only 36% of the variation in structural size and that structural size components loaded in conflicting directions. Analyses of other samples of yellow-pine chipmunks have shown PC1 to explain >50% of the variation in body-size components (Schulte-Hostedde et al. 2001). This suggests that the sample of chipmunks used here may have varied more in shape than in overall body size. The differences in shape among the chipmunks used in the running speed trials may explain the lack of correlation between body size and body mass.

Large male chipmunks have an advantage over small chipmunks in running speed and this is particularly interesting in the context of female-biased sexual size dimorphism. Small male chipmunks (as measured by both body length and a

multivariate index of body size) are known to be aggressively dominant over large males (Schulte-Hostedde and Millar 2002). Small males may use aggression to gain matings because of poor success at chasing females. This suggests an interesting trade-off in male body size between two behavioural components of mating success, dominance and running speed. This trade-off may provide the potential for the evolution and maintenance of female-biased sexual size dimorphism in this species by limiting the evolution of male body size. The motivation provided in this study of male behaviour (running speed) was not chasing an estrous female; therefore, it would be interesting to examine running speed in this species by either timing chases that occur in the field or using odour cues from estrous females to motivate male chipmunks.

Acknowledgements

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