

Sexual dimorphism in body composition of small mammals

A.I. Schulte-Hostedde, J.S. Millar, and G.J. Hickling

Abstract: Differences in reproductive roles between the sexes may lead to sexual dimorphism in body composition. Body size and composition of three species of small mammals (bushy-tailed wood rats (*Neotoma cinerea* Ord), deer mice (*Peromyscus maniculatus* Wagner), and red-backed voles (*Clethrionomys gapperi* Vigors)) were analyzed to test the predictions that (i) males will have more muscle mass than females and (ii) females will have more fat than males. Results supported the first prediction but not the second. For all three species, males had more lean dry mass relative to body size than females, but females did not have relatively more fat than males. Muscle mass of males may aid in mate-searching and mate-guarding activities, but fat content may not differ between the sexes because female small mammals depend on increased ingestion rates, rather than fat stores, to support reproduction.

Résumé : La différence des rôles reproducteurs chez les mâles et les femelles peut donner lieu au dimorphisme sexuel de la composition du corps. La taille du corps et sa composition ont été analysées chez trois espèces de petits mammifères, le Néotoma à queue touffue (*Neotoma cinerea* Ord), la Souris à pattes blanches (*Peromyscus maniculatus* Wagner) et le Campagnol-à-dos-roux de Gapper (*Clethrionomys gapperi* Vigors), dans le but de vérifier les prédictions suivantes : (i) la masse musculaire est plus importante chez les mâles que chez les femelles et (ii) la masse des graisses est plus importante chez les femelles que chez les mâles. Nos résultats confirment la première prédiction, mais pas la seconde. Chez les trois espèces, la masse sèche sans les graisses est plus importante relativement à la masse totale chez les mâles que chez les femelles, mais les femelles n'ont pas une masse relative de graisses plus grande que celle des mâles. La masse musculaire développée chez les mâles peut faciliter les activités de recherche et de surveillance de leurs partenaires, mais l'absence de différence entre la masse de graisse des mâles et celle des femelles peut s'expliquer par le fait que les femelles ont recours à des taux d'ingestion accrus plutôt qu'à l'utilisation de leurs réserves de graisse lors de la reproduction.

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Introduction

Males and females often have different reproductive roles because males can maximize reproductive success by seeking, defending, and mating with many females, whereas females typically invest a larger amount of energy in reproduction (Trivers 1972). Although female animals may mate with multiple males, female reproductive success is limited by the amount of energy required to successfully produce, and in some cases, raise these offspring (Andersson 1994).

Males and females differ fundamentally in many ways, including reproductive organs, behaviour, and morphology. One difference, sexual dimorphism in size and appearance, occurs throughout the animal kingdom (Hedrick and Temeles 1989), and often reflects the roles that males and females have in relation to reproduction (Andersson 1994). In many taxa, females are larger than males because of fecundity se-

lection; large females can produce more gametes than small females (Andersson 1994; but see Shine 1988). Mammals are predominantly polygynous and competition among males for females has led to adaptations that enhance success at combat, such as large male body size (Eisenberg 1981).

Although sex differences in body size are the most conspicuous form of dimorphism, other forms of dimorphism that are not immediately obvious may occur. Differences in reproductive roles may lead to dimorphism in organ systems and body composition. Males produce large numbers of energetically inexpensive gametes and are often under selection to locate and mate with multiple females. Selection should favour the development of a robust musculature, which would aid in mate-searching and be advantageous during male-male combat. Alternatively, females produce energy-rich gametes, and in mammals invest a tremendous amount of energy raising offspring. In this case, selection should favour the acquisition and storage of energy for use during reproduction. Females should carry more fat than males to facilitate the successful production of offspring. These predictions have been upheld among several species of snakes. Males have more muscle mass and larger kidneys (which produce constituents that are combined with semen) than females, perhaps because of the differences in reproductive roles (Bonnet et al. 1998). These traits may be favoured because they confer an advantage in terms of mate-searching and male-male combat (muscle mass) and sperm competition (kidneys).

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A.I. Schulte-Hostedde¹ and J.S. Millar. Ecology and Evolution Group, Department of Zoology, University of Western Ontario, London, ON N6G 5B7, Canada.

G.J. Hickling. Ecology and Entomology Group, Soil, Plant and Ecological Sciences Division, P.O. Box 84, Lincoln University, Canterbury, New Zealand.

¹Corresponding author (e-mail: aischult@julian.uwo.ca).

Table 1. Body length, total mass, lean dry mass, fat content, and water content of male and female deer mice (*Peromyscus maniculatus*), red-backed voles (*Clethrionomys gapperi*), and bushy-tailed wood rats (*Neotoma cinerea*).

	Deer mice		Red-backed voles		Wood rats	
	Male	Female	Male	Female	Male	Female
Body length (mm)	86.45 ± 5.97	88.19 ± 7.21	97.73 ± 6.65	97.95 ± 6.98	234.63 ± 14.43	221.59 ± 6.63
Total mass (g)	21.78 ± 0.23	20.09 ± 0.48	26.31 ± 0.43	24.38 ± 0.71	387.98 ± 12.71	297.63 ± 7.91
Lean dry mass (g)	4.54 ± 0.62	4.19 ± 0.91	6.03 ± 0.85	5.55 ± 0.69	75.67 ± 19.06	61.02 ± 8.23
Fat content (g)	1.06 ± 0.45	1.03 ± 0.63	0.51 ± 0.14	0.59 ± 0.26	12.71 ± 7.73	12.13 ± 7.41
Water content (g)	16.17 ± 1.61	14.87 ± 1.77	19.76 ± 2.69	18.24 ± 2.54	267.55 ± 59.80	224.49 ± 29.75

Note: Values are given as the mean ± SD.

Small mammals are suitable for testing predictions related to sex differences in body composition. Although sexual size dimorphism exists in some species, there is substantial overlap in body size between the sexes. Morphologically, males and females do not differ in relative size of particular body parts. This means that any differences found between the sexes cannot be easily attributed to allometry or differences in morphological shape.

Selection should act on the sexes in relation to their reproductive roles and should be reflected in sex differences in body composition. Here, we use data from three species of small mammals to test adaptive predictions about their body composition. Because of activities such as mate-searching and male–male combat, males should have more muscle mass than females. Also, females should be under selection to store energy to facilitate future reproduction, and thus should have more fat than males.

Methods

We used data from three species of small mammals (bushy-tailed wood rats (*Neotoma cinereus* Ord), deer mice (*Peromyscus maniculatus* Wagner), and red-backed voles (*Clethrionomys gapperi* Vigors)) all collected in the Kananaskis Valley, Alberta, in the Front Ranges of the Rocky Mountains (51°N, 115°W). All animals used in the analyses were either adult males or adult females that were not pregnant or lactating, and were collected as part of other studies of these species. We removed pregnant and lactating females from our analysis to remove any bias that might occur if embryos and (or) mammary tissue were included in the body-composition analysis. Composition analysis was not done on mothers and embryos separately. Most females, however, were not nonbreeders because most of the females were captured prior to becoming pregnant in the spring or had finished lactating from their last litter in the fall.

Wood rats (40 males, 22 females) were collected in the summer and winter of 1984–1985 using Conibear kill-traps (Hickling 1987; Hickling et al. 1991). Body mass (±0.1 g), total body length (including tail) (±1 mm), and tail length (±1 mm) were measured and each body was frozen. Deer mice (83 males, 21 females) and red-backed voles (66 males and 20 females) were collected from early May to late August 1987 using snap traps baited with a small string soaked in aromatic oils that was tied to the treadle (Millar et al. 1990). Body mass (±0.1 g), total body length (including tail) (±1 mm), and tail length (±1 mm) were measured and each body was frozen (Millar 1987; Millar et al. 1990).

Fat extractions were performed following Kerr et al. (1982) and Dobush et al. (1985). For deer mice and red-backed voles, whole bodies excluding stomach contents were dried, ground in a Wiley Mill or a Moulinex coffee grinder, and fat content was determined using petroleum ether in a Soxhlet fat extractor. Wood rat carcasses

(excluding stomach contents, skull, and pelt) were ground in a meat grinder and dried. The dried carcass was then ground in a Moulinex coffee grinder. Fat extraction was performed on two 4-g subsamples. Fat content of the pelt was determined by soaking the intact pelt in ether for 24 h. Total fat content was calculated as the mean of the two replicate estimates of carcass fat plus pelt fat (Hickling et al. 1991). Fat extractions for all species were performed in the Department of Zoology, University of Western Ontario, within the year that the carcasses were collected. For all species, we calculated water content as the difference between fresh mass (without stomach contents) and the mass of the carcass after drying. Lean dry mass was determined as the mass of the carcass following the removal of fat.

For all three species, analysis of covariance (ANCOVA) was performed between sex and log-transformed total mass and log-transformed mass of each of three body components (fat, lean dry mass, and water content). To correct for variation in dependent variables due to variation in body size, body length (calculated by subtracting tail length from total body length) was used as a covariate.

Results

Table 1 presents mean body length (mm), whole mass (g), lean dry mass (g), fat (g), and water content (g) for males and females of each species. There was no sexual dimorphism in body length for deer mice and red-backed voles (deer mice: $t_{[102]} = -1.14$, $P = 0.35$; red-backed voles: $t_{[84]} = -0.129$, $P = 0.90$). Male wood rats were significantly longer than female wood rats ($t_{[60]} = 4.00$, $P = 0.002$), although there was considerable overlap in body length (males: BL = 205–267 mm; females: BL = 209–232 mm).

Analysis of covariance showed that the sex-specific pattern of body composition was similar among the three species. When corrected for body size, females and males of all three species did not differ significantly in total fat (Table 2). Males consistently had more total mass, lean dry mass (composed mostly of protein (muscle)) and water content than did females (Fig. 1, Table 2). In all cases in which the ANCOVA showed a significant difference between males and females, slopes for male and female data were not significantly different ($P > 0.05$).

Discussion

Selection should reflect differences in reproductive roles between the sexes, particularly in relation to body composition. Males should be under selection to have large muscle mass to aid in male–male combat and mate-searching. Females should be under selection to acquire and store energy to facilitate the production of offspring.

Table 2. Results of analysis of covariance on sex differences (M, male; F, female) in total mass (TOTAL), relative mass of fat (FAT), lean dry mass (LDM), and water content (WATER) for deer mice, red-backed voles, and bushy-tailed wood rats.

	Regression equations	<i>F</i>	df	<i>P</i>	Larger sex
Deer mice					
Total mass					
M	BL = 0.0018 log(TOTAL) + 1.178	15.75	1,101	0.001	M
F	BL = 0.0027 log(TOTAL) + 1.059				
Fat					
M	BL = 0.0114 log(FAT) - 0.110	0.623	1,101	0.430	—
F	BL = -0.0159 log(FAT) + 1.35				
Lean dry mass					
M	BL = 0.0021 log(LDM) + 0.468	7.240	1,101	0.008	M
F	BL = 0.0070 log(LDM) - 0.009				
Water content					
M	BL = 0.0017 log(WATER) + 1.060	14.98	1,101	<0.001	M
F	BL = 0.0027 log(WATER) + 0.931				
Red-backed voles					
Total mass					
M	BL = 0.0064 log(TOTAL) + 0.795	10.85	1,83	0.001	M
F	BL = 0.0062 log(TOTAL) + 0.777				
Fat					
M	BL = 0.002 log(FAT) - 0.329	0.490	1,83	0.484	—
F	BL = -0.0015 log(FAT) - 0.423				
Lean dry mass					
M	BL = 0.0066 log(LDM) + 0.155	9.947	1,83	0.002	M
F	BL = 0.0056 log(LDM) + 0.195				
Water content					
M	BL = 0.0066 log(WATER) + 0.650	11.06	1,83	0.001	M
F	BL = 0.0065 log(WATER) + 0.617				
Wood rats					
Total mass					
M	BL = 0.0052 log(TOTAL) + 1.471	9.92	1,59	0.003	M
F	BL = 0.0047 log(TOTAL) + 1.316				
Fat					
M	BL = 0.0088 log(FAT) - 1.024	1.892	1,59	0.174	—
F	BL = 0.0078 log(FAT) - 0.699				
Lean dry mass					
M	BL = 0.0050 log(LDM) + 0.748	17.11	1,59	<0.001	M
F	BL = 0.0047 log(LDM) + 0.746				
Water content					
M	BL = 0.0046 log(WATER) + 1.378	9.517	1,59	0.003	M
F	BL = 0.0055 log(WATER) + 1.137				

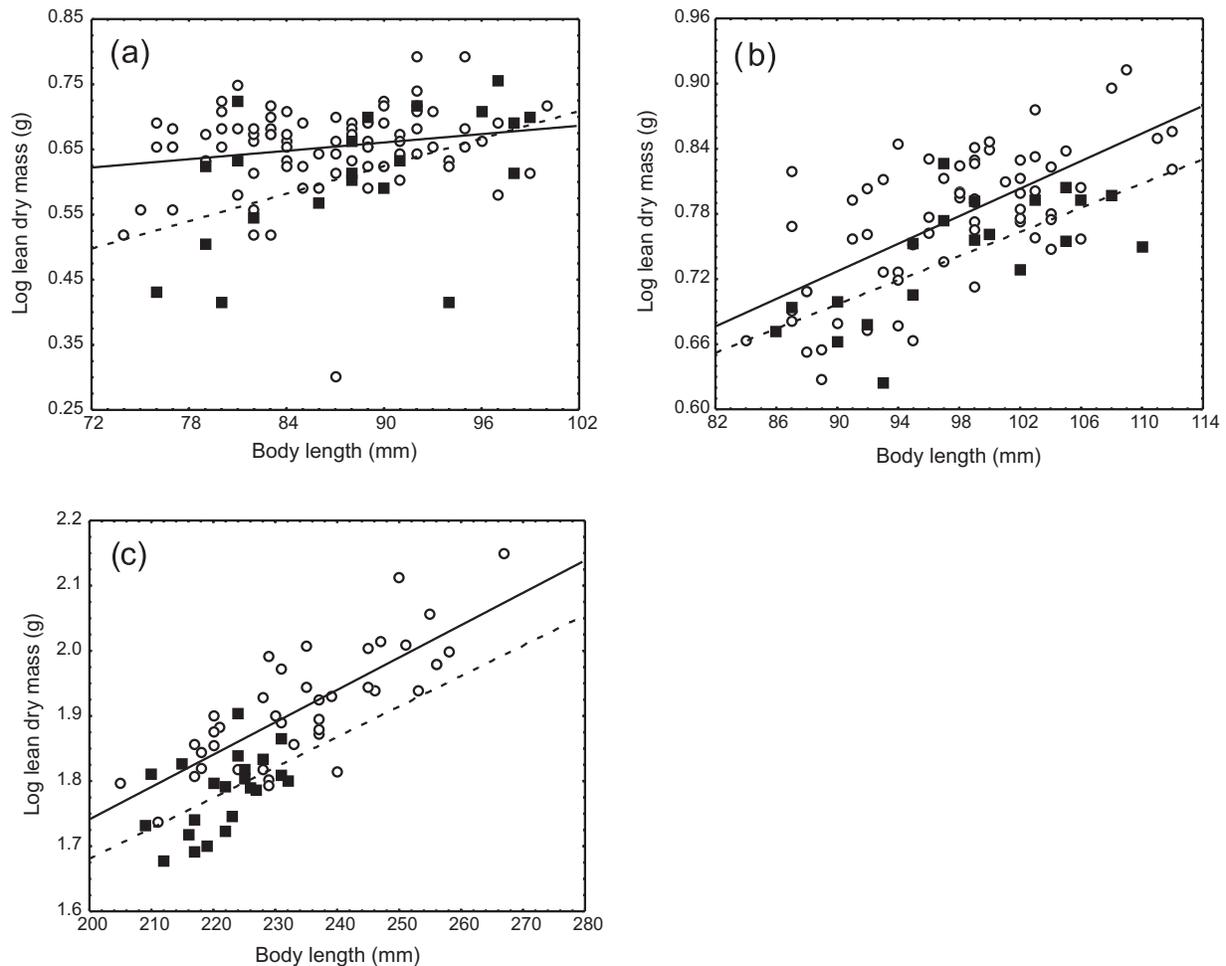
Note: Body length (BL) was used as a covariate. Masses of body components were log-transformed prior to analysis.

In all three species, males weighed more in overall mass than females when corrected for body size. There was no difference in corrected total fat content between males and females. Males had more lean dry mass and water content than did females in all three species. The majority of lean dry mass is protein derived from muscle, therefore dimorphism in lean dry mass likely reflects differences in muscle mass between the sexes. For instance, in water snakes (*Nerodia sipedon*) protein made up 78% of lean dry mass on average (Weatherhead and Brown 1996). In muskrats (*Ondatra zibethicus*), approximately 83% of lean dry mass was composed of protein (Virgl and Messier 1992). In both cases, the balance of lean dry mass was composed of ash. Variation in lean dry mass may also reflect some variation in skeletal

structure (ash). Males may require a robust skeleton to support heavy muscle mass. Water content is more closely associated with protein than fat (which is hydrophobic), so animals with more protein should have more water as was found in our study. The result that males have more muscle than females is consistent with that found for three snake species (Bonnet et al. 1998) and also with the broad prediction made by Bonnet et al. (1998) that sexual dimorphism in muscle mass may be one of the most fundamental morphological differences between males and females.

The fact that there was no sexual dimorphism in fat content may not be surprising. Although some fat is used in reproduction in wood rats (Hickling et al. 1991), most non-hibernating small mammals are "income breeders" (Jonsson

Fig. 1. Sexual dimorphism in lean dry mass relative to body length for male (○, solid line) and female (■, broken line) deer mice (*Peromyscus maniculatus*) (a), red-backed voles (*Clethrionomys gapperi*) (b), and bushy-tailed wood rats (*Neotoma cinerea*) (c). Males for all three species have more lean dry mass than females when corrected for body size.



1997) and depend on increased ingestion rather than fat for reproduction (Millar 1987), so the initial prediction that females should have more fat to support reproduction may not apply. In addition, our analysis was confined to males and nonbreeding females. Millar and Schieck (1986) did not statistically test for differences in fat reserves between male and female deer mice, but fat reserves relative to lean dry mass were similar between breeding males and nonbreeding females. Breeding male mice had more fat than lactating female mice, but less fat than pregnant mice and mice that were simultaneously pregnant and lactating (Millar and Schieck 1986). Breeding male red-backed voles had similar levels of fat as nonbreeding females, but females lactating late in the breeding season had more fat than breeding males, nonbreeding females, and pregnant females (Innes 1984). Lactating female wood rats consistently had less fat than females that were nonbreeding or pregnant (Hickling et al. 1991). If nonbreeding female wood rats and breeding males have similar levels of fat relative to body size (Table 2), then when pregnant, female wood rats should have more fat than males.

Fat deposition is a seasonal phenomenon that depends on the predictability and level of food resources (Millar and Schieck 1986), and could have affected the patterns we ex-

amined in our analysis. Deer mice and red-backed voles were collected May–August, minimizing any effects that season may have had. Wood rats, however, were collected in the summer and winter, so seasonality of fat deposition may have affected these results. Sex differences in fat content were consistent among all three species, suggesting that seasonal differences in fat content did not affect the patterns that we observed.

More muscle mass may be advantageous for males in all three species. Both deer mice and red-backed voles are promiscuous (Ribble and Millar 1996; Heske and Ostfeld 1990) and mate-searching activities by males may be enhanced by an increase in muscle mass. Male wood rats, although not monogamous, may guard an estrous female from other males (Topping and Millar 1998). Wounds on large males indicate that aggressive encounters among males may occur (Hickling 1987). Under these circumstances, it would be advantageous for males to have heavy musculature. Additionally, females of all three species may carry less metabolically expensive tissue (protein) than males in order to devote more energy to reproduction. For instance, when energetically stressed during periods of low food-resource levels in winter, northern red-backed voles (*Clethrionomys rutilus*) and muskrats have lower protein reserves than when food resources are high (Virgl

and Messier 1992; Zeurcher et al. 1999). Protein reserves may act as energy sources, as well as serving to minimize metabolic requirements.

Few studies have examined how variation in muscle mass affects male reproductive success in wild populations. To prove that increased muscle mass is adaptive in terms of the acquisition of mating opportunities, it must be shown that muscle mass of males is a heritable trait and related to lifetime reproductive success. Testing this hypothesis must be done to put our results in the proper context.

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