

## NOTE / NOTE

# Influence of female-biased sexual size dimorphism on dominance of female Townsend's chipmunks

A.J. Edelman and J.L. Koprowski

**Abstract:** Female-biased sexual size dimorphism (SSD), a condition common in North American chipmunks, occurs when females are larger than males in a species. We examined the influence of body size on dominance of captive female Townsend's chipmunks (*Tamias townsendii* Bachman, 1839), a species that exhibits female-biased SSD, in all-female and mixed-sex dyadic encounters. In all-female dyads, large female chipmunks were more frequently dominant over small female opponents. In mixed-sex dyads, large females were always dominant over small males. Female-biased SSD in Townsend's chipmunks appears to indirectly allow large females to more frequently dominate small female and male conspecifics. Greater dominance could increase reproductive success of large female chipmunks by increasing access to resources.

**Résumé :** Le dimorphisme sexuel de la taille (SSD) qui favorise les femelles, une condition commune chez les tamias d'Amérique du Nord, se produit lorsque les femelles d'une espèce sont plus grandes que les mâles. Nous étudions l'influence de la taille corporelle sur la dominance chez des tamias de Townsend (*Tamias townsendii* Bachman, 1839) femelles en captivité, une espèce qui possède un SSD favorisant les femelles, lors de rencontres entre des dyades de femelles ou d'individus de sexe différent. Dans les dyades formées seulement de femelles, les femelles de grande taille dominant plus souvent leurs adversaires plus petits. Dans les dyades formées d'individus des deux sexes, les grandes femelles dominant toujours les petits mâles. Le SSD favorisant les femelles chez les tamias de Townsend semble permettre indirectement aux femelles plus grandes de dominer plus fréquemment les petites femelles et les mâles de leur espèce. La dominance accrue peut sans doute accroître le succès reproductif des grandes femelles de tamias en facilitant leur accès aux ressources.

[Traduit par la Rédaction]

## Introduction

Male-biased sexual size dimorphism (SSD), where males of a species are larger than the females (Trivers 1972; Alexander et al. 1979), is a widely reported phenomenon. In some taxa, female-biased SSD is more prevalent (Shine 1988). While female-biased SSD is commonly found in invertebrates (Trivers 1972) and birds (Andersson and Norberg 1981), some mammal species also exhibit this trait (Ralls 1976). Unlike male-biased SSD, female-biased SSD in mammals is hypothesized to be the product of natural selection rather than sexual selection (Ralls 1976). Probable

natural selection pressures leading to female-biased SSD include reduction of interspecific competition for resources (Ralls 1976), social dominance over males (Madden 1974; Ralls 1976; Bowers and Smith 1979), strong competition for resources among females (Madden 1974; Ralls 1976), increased reproductive ability after hibernation (Bronson 1980; Levenson 1990; Svendsen and White 1997), and production of larger offspring (Ralls 1976). Sexual selection could favor smaller male body size if agility is important in finding mates (Ralls 1976; Levenson 1990).

In North American chipmunks (order Rodentia, family Scuriidae, genus *Tamias* Illiger, 1811), female-biased SSD is exhibited in 12 species (Levenson 1990; Schulte-Hostedde and Millar 2000). Female chipmunks in these species are 2% to 6% larger than males (Levenson 1990). Large body size may be beneficial to females because female survival and reproductive success are positively correlated with body size in yellow-pine chipmunks (*Tamias amoenus* J.A. Allen, 1890), a species with female-biased SSD (Schulte-Hostedde et al. 2002). Increased survival and reproductive success of large females could be due to dominance over small conspecifics that allows greater access to resources (e.g., food and burrows). In the southern flying squirrel (*Glaucomys volans*

Received 12 August 2006. Accepted 31 October 2006. Published on the NRC Research Press Web site at <http://cjz.nrc.ca> on 23 January 2007.

A.J. Edelman<sup>1,2</sup> and J.L. Koprowski<sup>3</sup> Department of Biology, Willamette University, Salem, OR 97301, USA.

<sup>1</sup>Corresponding author (e-mail: [andrew@unm.edu](mailto:andrew@unm.edu)).

<sup>2</sup>Present address: Department of Biology, University of New Mexico, Albuquerque, NM 87131, USA.

<sup>3</sup>Present address: Wildlife Conservation and Management, School of Natural Resources, University of Arizona, Tucson, AZ 85721, USA.

L., 1758), female-biased SSD allows large females to better defend nest sites, food, and water sources (Madden 1974). In field studies of eastern chipmunks (*T. striatus* L., 1758), a species without female-biased SSD, individuals successfully defended core areas (i.e., high-use areas centered on burrows) from most intruders regardless of sex or size (Dunford 1970; Elliott 1978). The area of space-dependent dominance can vary greatly between individuals, probably because of space-independent factors such as size and age (Elliott 1978). The space-dependent dominance effect is minimized by placing the chipmunks in captivity (Elliott 1978). Dominance in agonistic encounters between captive eastern chipmunks is positively associated with body size (Wolfe 1966; Ickes 1974).

Although dominance between males has been examined in chipmunks that exhibit female-biased SSD (Schulte-Hostedde and Millar 2002a), the effect of female-biased SSD on female chipmunk dominance is not known. We examined the influence of body size on dominance of female Townsend's chipmunks (*T. townsendii* Bachman, 1839), a species that exhibits female-biased SSD (Levenson 1990), by observing agonistic encounters in two types of dyads: (1) dyads consisting of females differing in body size and (2) mixed-sex dyads where females were larger than males. To independently examine the effect of body size on dominance, we minimized the space-dependent dominance effect by staging dyadic encounters in captivity. We hypothesized that within dyads, (i) large females would be dominant over small females and (ii) large females would be dominant over small males.

## Materials and methods

### Study species

Townsend's chipmunks inhabit coniferous forests of western North America from British Columbia to northern California (Ingles 1965). Townsend's chipmunks are diurnal sciurids that feed on seeds, berries, insects, and fungi. Individuals inhabit a single burrow up to 10 m in length (Thomas 1974). Chipmunks generally have overlapping home ranges of 0.5 ha but actively defend only the core area within 9–12 m of the burrow (Dunford 1970; Elliott 1978), and they larder hoard food in one dense aggregation within the burrow (Clarke and Kramer 1994). During winter, Townsend's chipmunks at high elevations experience periods of torpor and rely on their food larder rather than fat deposits for survival (Kenagy and Barnes 1988). At lower elevations, where snow is uncommon, Townsend's chipmunks can be found above ground the entire year (Maser 1998). Female-biased SSD in Townsend's chipmunks is well documented, with females 2.5% to 10% larger, on average, than males depending on the population and time of year (Gashwiler 1976; Levenson 1990; Rosenberg and Anthony 1993; Hayes et al. 1995).

### Behavioral testing

To capture individuals for dyadic trials and document the extent of female-biased SSD, Townsend's chipmunks were livetrapped from September to November 1998 in second-growth Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) forest in Macleay, Marion County, Oregon, USA. We used 41 cm × 14 cm × 14 cm box traps (model 201, Tomahawk

Live Trap Co., Tomahawk, Wisconsin, USA) baited with a mixture of peanut butter and oats. Sunflower seeds were placed around the traps between trapping periods. Captured animals were placed in a mesh bag and sex, body length, tail length, and mass ( $\pm 0.5$  g) of each animal were recorded. Individuals were marked with a uniquely numbered ear tag (model 1005-1, National Band and Tag Co., Newport, Kentucky, USA). Handling of animals was in accordance with the guidelines of the Canadian Council on Animal Care.

Chipmunks livetrapped during October–November 1998 were transported 30 min to Willamette University, Salem, Oregon, for dyadic trials. Animals were placed in plastic cages (39.3 cm × 28.5 cm × 19.4 cm) and provided with water, housing, and ad libitum rat chow supplemented with seeds, carrots, and apples. The light regime of the caged chipmunks simulated natural light conditions. Following a period of trials usually lasting 4 days, the animals were released at the location of capture.

Dyadic trials started on the day after the animals were captured and were conducted from 0800 to 1700. Trials were conducted outside of the breeding season. Each animal participated in a maximum of five trials and had at least 1 h of rest between trials. Dyadic trials were conducted in an arena with wooden sides, a wire mesh top, and dimensions of 1.5 m × 0.75 m × 0.3 m. Tree branches, pine cones, and several food items were placed within the arena. The arena was housed in a room with one-way glass to diminish interference from the observer. Trials were recorded using a video camcorder to allow post-trial analysis of encounters.

Two types of dyadic trials were conducted: (1) pairs of females differing in body size (i.e., all-female dyads) and (2) male–female pairs in which the female was larger than the male (i.e., mixed-sex dyads). Large opponents weighed  $\geq 1$  g more than small opponents. Chipmunks were weighed on the day of participation in dyadic trials. Dyads for each trial were selected based on individual sex, body mass, and previous trial history. Fourteen females were used in all-female dyads and 11 females and 6 males were used in mixed-sex dyads. Nine females were used in both types of dyads. The lower number of males used in mixed-sex dyads was due to the trapping success being skewed towards females. Individuals were never paired with the same partner more than once during trials. The mean total number of dyadic trials that each male participated in (mean  $\pm$  SE =  $2.8 \pm 0.5$  trials) was similar to the number that each female participated in (mean  $\pm$  SE =  $2.9 \pm 0.4$  trials) (two-tailed *t* test,  $t_{[20]} = 0.16$ ,  $n = 22$ ,  $P = 0.876$ ).

One animal from each dyad was randomly selected and placed in the arena first. To allow acclimatization, a trial did not begin until an agonistic encounter occurred or 10 min had passed. During a 15 min trial, the observer recorded when an agonistic encounter occurred and which individual was dominant in the encounter. Agonistic encounters consisted of one or more of the following behaviors (developed from Dunford 1970; Aniskowicz and Vaillancourt 1979): (i) attack (dashing or leaping at a conspecific), (ii) fight (both animals locked together, kicking and biting each other while tumbling), and (iii) chase (running after a conspecific). An agonistic encounter ended when one individual fled from the other individual. During an agonistic encounter, the animal whose opponent fled from the encounter was considered

**Table 1.** Body measurements (mean  $\pm$  SE) and mean percent dimorphism of female ( $n = 27$ ) and male ( $n = 20$ ) adult Townsend's chipmunks (*Tamias townsendii*).

Sex	Mass (g)	Body length (mm)	Tail length (mm)	Total length (mm)
Female	84.5 $\pm$ 1.0	119 $\pm$ 1	120 $\pm$ 2	239 $\pm$ 2
Male	78.6 $\pm$ 1.3	115 $\pm$ 2	113 $\pm$ 2	228 $\pm$ 3
% dimorphism <sup>a</sup>	7.5	3.5	6.2	4.8

<sup>a</sup>Calculated using the equation [(mean female body measurement/mean male body measurement) - 1.000]  $\times$  100.

dominant. Individuals in dyads were identified by observers based on unique natural markings, placement of ear tags, and visual differences in body size. Video footage was used to confirm the outcome of encounters. Overall dominance in a trial was assigned to the individual who was dominant in at least one more agonistic encounter than its conspecific. Trials without agonistic encounters were excluded from analyses (8 of 31 trials).

### Data analysis

One-tailed  $t$  tests were used to analyze body measurements between the sexes. Total length of each chipmunk was calculated from the sum of body and tail length. Mean percent dimorphism of body measurements was calculated using the equation [(mean female body measurement / mean male body measurement) - 1.000]  $\times$  100 (Levenson 1990). Pearson's  $\chi^2$  test was used to examine dominance in all-female dyadic trials. One-tailed paired  $t$  tests were used to analyze body size and number of encounters between opponents in both types of dyadic trials.

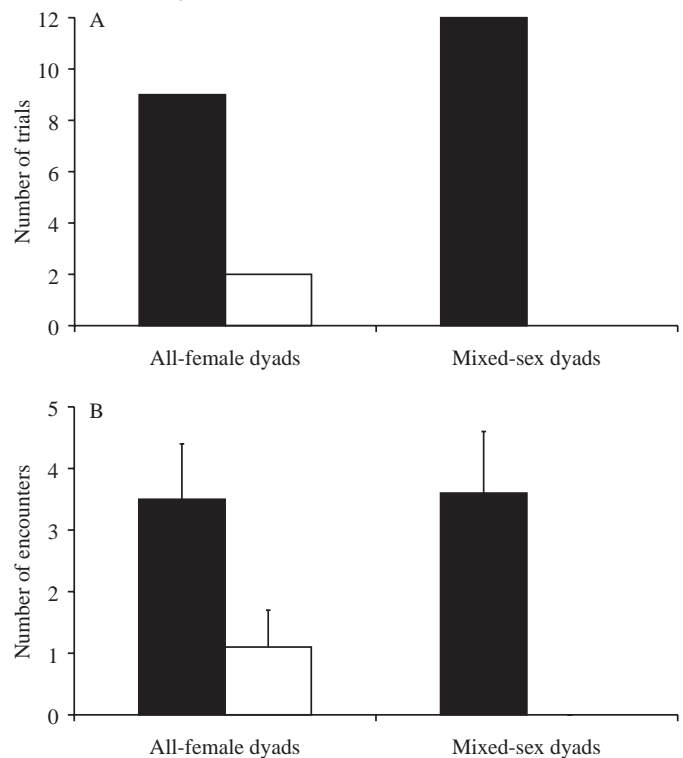
### Results

Livetrapped females ( $n = 27$ ) were heavier ( $t_{[45]} = 3.57$ ,  $P < 0.001$ ) and had greater tail length ( $t_{[45]} = 2.25$ ,  $P = 0.015$ ) and total length ( $t_{[45]} = 2.99$ ,  $P = 0.002$ ) than males ( $n = 20$ ) (Table 1). Body length also tended to be greater in females than in males (Table 1,  $t_{[45]} = 1.54$ ,  $P = 0.065$ ). Mean percent dimorphism was greatest between females and males for body mass and least for body length (Table 1).

For both mixed-sex and all-female trials, novice individuals (i.e., chipmunks that had never previously participated in a trial with at least one agonistic encounter) were dominant in all trials in which they were larger than opponents (13 of 13 trials) and subordinate in most trials in which they were smaller than opponents (8 of 9 trials). Within all-female dyads, the difference in body mass between opponents averaged  $7.8 \pm 1.3$  g ( $t_{[10]} = 5.88$ ,  $P < 0.001$ ). Large females were most frequently the dominant individual in all-female dyadic trials (Fig. 1A,  $\chi^2_{[1]} = 4.46$ ,  $P = 0.035$ ). Within dyadic trials, large females were dominant in more agonistic encounters than small female opponents (Fig. 1B,  $t_{[10]} = 1.84$ ,  $P = 0.048$ ).

Within mixed-sex dyadic trials, females averaged  $6.5 \pm 1.1$  g heavier (mean percent dimorphism = 8.4%) than male opponents ( $t_{[11]} = 5.86$ ,  $P < 0.001$ ), which is similar to the female-biased SSD exhibited naturally in this population (Table 1). Large females were always dominant over small males in mixed-sex dyadic trials (Fig. 1A). Within a dyadic trial, large females were always dominant over

**Fig. 1.** Number of dyadic trials (A) and mean ( $\pm$ SE) number of agonistic encounters per dyadic trial (B) in which large (shaded bars) and small (unshaded bars) Townsend's chipmunks (*Tamias townsendii*) were dominant over opponents. Two types of dyadic trials were conducted: (i) all-female dyads consisting of females differing in body size ( $n = 11$ ) and (ii) mixed-sex dyads in which females were larger than males ( $n = 12$ ).



small males in agonistic encounters (Fig. 1B,  $t_{[11]} = 3.65$ ,  $P = 0.002$ ).

### Discussion

Body size appears important in predicting female dominance in agonistic encounters of Townsend's chipmunk dyads in captivity. In both all-female and mixed-sex dyads, large females were dominant more frequently than small females and males. Dominance in agonistic encounters was also positively related to body size in captive eastern chipmunks, which do not exhibit female-biased SSD (Wolfe 1966; Ickes 1974). In the three dyadic trials we observed in which males were larger than females, males were always dominant (A.J. Edelman and J.L. Koprowski, unpublished data). Thus, gender likely does not directly affect dominance in chipmunks with female-biased SSD; however, because females are, on average, larger than

males, female-biased SSD appears to indirectly cause more frequent female dominance over males. Alternatively, our results could be due to a winner or loser effect (Rutte et al. 2006) because individuals were used in more than one dyadic trial. However, such an effect appears unlikely because all novice large individuals were dominant in trials and almost all novice small individuals were subordinate in trials.

Dominance in chipmunks in the wild is closely linked to distance from the home burrow. Individual chipmunks are usually dominant over opponents regardless of size if they are close to their burrow (Dunford 1970; Elliott 1978). The area of dominance surrounding burrows, however, varies widely among individuals and is likely due to individual differences such as age and size (Elliott 1978). We minimized the effect of space-dependent dominance in chipmunks by observing dyadic encounters in a captive setting, which allowed us to examine how body size affects dominance. Female yellow-pine chipmunks, a species with female-biased SSD, exhibit a positive correlation between body size and survival and female reproductive success in some years. Large females may have lower reproductive success than small females in poor environmental conditions owing to greater energetic demands (Schulte-Hostedde et al. 2002). In the wild, female-biased SSD could contribute to greater reproductive success in large females by allowing them to more frequently dominate small neighbors in encounters and expand the size of core areas. By increasing the area of dominance, a large female would have access to a larger foraging area, possibly increasing the amount of available food resources. In mammals, females usually have greater parental investment than males (Trivers 1972); therefore, an increase in resources would potentially raise a female chipmunk's reproductive success.

Our results support large body size as a good indicator of female dominance in all-female and mixed-sex dyads during the non-breeding season. However, in all-male dyads of breeding yellow-pine chipmunks, small males were more frequently dominant over large males in agonistic encounters (Schulte-Hostedde and Millar 2002a). Small males may improve mating success by being aggressive towards other males, whereas large males may be able to gain matings through increased ability to find or chase receptive females (Schulte-Hostedde and Millar 2002a, 2002b). These alternative mating tactics likely yield similar numbers of sired offspring because male reproductive success of yellow-pine chipmunks is independent of body size (Schulte-Hostedde et al. 2004). Breeding condition could also affect dominance of females and should be examined in future studies.

In conclusion, we observed that body size was positively associated with female dominance in all-female and mixed-sex dyads of captive Townsend's chipmunks, a species that exhibits female-biased SSD. The ecological implications of female dominance may be that large female chipmunks can obtain more resources than small females and males. Future studies of chipmunks with female-biased SSD should examine how body size and sex affect core-area size and dominance of chipmunks in the wild and whether these factors are predictive of female reproductive success.

## Acknowledgments

We thank Willamette University for partial support of this research. This project was completed in partial fulfillment of the requirements for a B.Sc. degree in biology at Willamette University. We thank Nicki Shaw, the Tolar family, Ian Silvernail, Nan Perigo, and Jenna Edelman for their assistance with this research.

## References

- Alexander, R.D., Hoogland, J.L., Howard, R.D., Noonan, K.M., and Sherman, P.W. 1979. Sexual dimorphisms and breeding systems in pinnipeds, ungulates, primates, and humans. *In* Evolutionary biology and human social behavior: an anthropological perspective. Edited by N.A. Chagnon and W. Irons. Duxbury Press, North Scituate, Mass. pp. 402–435.
- Andersson, M., and Norberg, R.A. 1981. Evolution of reversed sexual size dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. *Biol. J. Linn. Soc.* **15**: 105–130.
- Aniskowicz, B.T., and Vaillancourt, J. 1979. Agonistic interactions among wild eastern chipmunks (*Tamias striatus*). *Can. J. Zool.* **57**: 683–690.
- Bowers, M.A., and Smith, H.D. 1979. Differential habitat utilization by sexes of the deermouse, *Peromyscus maniculatus*. *Ecology*, **60**: 869–875. doi:10.2307/1936854.
- Bronson, M.T. 1980. Altitudinal variation in emergence time of golden-mantled ground squirrels (*Spermophilus lateralis*). *J. Mammal.* **61**: 124–126. doi:10.2307/1379967.
- Clarke, M.F., and Kramer, D.L. 1994. Scatter-hoarding by a larder-hoarding rodent: intraspecific variation in the hoarding behaviour of the eastern chipmunk, *Tamias striatus*. *Anim. Behav.* **48**: 299–308. doi:10.1006/anbe.1994.1243.
- Dunford, C. 1970. Behavioral aspects of spatial organization in the chipmunk, *Tamias striatus*. *Behaviour*, **36**: 215–231.
- Elliott, L. 1978. Social behavior and foraging ecology of the eastern chipmunk (*Tamias striatus*) in the Adirondack Mountains. *Smithson. Contrib. Zool.* **265**: 1–107.
- Gashwiler, J.S. 1976. Biology of Townsend's chipmunks in western Oregon. *Murrelet*, **57**: 26–31.
- Hayes, J.P., Horvath, E.G., and Hounihan, P. 1995. Townsend's chipmunk populations in Douglas-fir plantations and mature forests in the Oregon Coast Range. *Can. J. Zool.* **73**: 67–73.
- Ickes, R.A. 1974. Agonistic behavior and the use of space in the eastern chipmunk, *Tamias striatus*. Ph.D. thesis, University of Pittsburgh, Pa.
- Ingles, L.G. 1965. Mammals of the Pacific states: California, Oregon, Washington. Stanford University Press, Stanford, Calif.
- Kenagy, G.J., and Barnes, B.M. 1988. Seasonal reproductive patterns in four coexisting rodent species from the Cascade Mountains, Washington. *J. Mammal.* **69**: 274–292. doi:10.2307/1381378.
- Levenson, H. 1990. Sexual size dimorphism in chipmunks. *J. Mammal.* **71**: 161–170. doi:10.2307/1382163.
- Madden, J.R. 1974. Female territoriality in a Suffolk county, Long Island, population of *Glaucomys volans*. *J. Mammal.* **55**: 647–652. doi:10.2307/1379554.
- Maser, C. 1998. Mammals of the Pacific Northwest: from the coast to the High Cascades. Oregon State University Press, Corvallis, Ore.
- Ralls, K. 1976. Mammals in which females are larger than males. *Q. Rev. Biol.* **51**: 245–276. PMID:785524.
- Rosenberg, D.K., and Anthony, R.G. 1993. Differences in Townsend's chipmunk populations between second- and old-growth forests in western Oregon. *J. Wildl. Manag.* **57**: 365–373.

- Rutte, C., Taborsky, M., and Brinkhof, M.W.G. 2006. What sets the odds of winning and losing? *Trends Ecol. Evol.* **21**: 16–21. doi:10.1016/j.tree.2005.10.014. PMID:16701465.
- Schulte-Hostedde, A.I., and Millar, J.S. 2000. Measuring sexual size dimorphism in the yellow-pine chipmunk (*Tamias amoenus*). *Can. J. Zool.* **78**: 728–733. doi:10.1139/cjz-78-5-728.
- Schulte-Hostedde, A.I., and Millar, J.S. 2002a. ‘Little chipmunk’ syndrome? Male body size and dominance in captive yellow-pine chipmunks (*Tamias amoenus*). *Ethology*, **108**: 127–137. doi:10.1046/j.1439-0310.2002.00765.x.
- Schulte-Hostedde, A.I., and Millar, J.S. 2002b. Effects of body size and mass on running speed of male yellow-pine chipmunks (*Tamias amoenus*). *Can. J. Zool.* **80**: 1584–1587. doi:10.1139/z02-164.
- Schulte-Hostedde, A.I., Millar, J.S., and Gibbs, H.L. 2002. Female-biased sexual size dimorphism in the yellow-pine chipmunk (*Tamias amoenus*): sex-specific patterns of annual reproductive success and survival. *Evolution*, **56**: 2519–2529. doi:10.1554/0014-3820(2002)056[2519:FBSSDI]2.0.CO;2. PMID:12583591.
- Schulte-Hostedde, A.I., Millar, J.S., and Gibbs, H.L. 2004. Sexual selection and mating patterns in a mammal with female-biased sexual size dimorphism. *Behav. Ecol.* **15**: 351–356. doi:10.1093/beheco/arh021.
- Shine, R. 1988. The evolution of large body size in females: a critique of Darwin’s “fecundity advantage” model. *Am. Nat.* **131**: 124–131. doi:10.1086/284778.
- Svendsen, G.E., and White, M.M. 1997. Body mass and first-time reproduction in female chipmunks (*Tamias striatus*). *Can. J. Zool.* **75**: 1891–1895.
- Thomas, K.R. 1974. Burrow systems of the eastern chipmunk (*Tamias striatus pipilans* Lowery) in Louisiana. *J. Mammal.* **55**: 454–459. doi:10.2307/1379017.
- Trivers, R.L. 1972. Parental investment and sexual selection. In *Sexual selection and the descent of man: 1871–1971*. Edited by B. Campbell. Aldine Publishing Company, Chicago. pp. 136–179.
- Wolfe, J.L. 1966. Agonistic behavior and dominance relationships of the eastern chipmunk, *Tamias striatus*. *Am. Midl. Nat.* **76**: 190–200. doi:10.2307/2423242.