

‘Little Chipmunk’ Syndrome? Male Body Size and Dominance in Captive Yellow-Pine Chipmunks (*Tamias amoenus*)

A. I. Schulte-Hostedde & J. S. Millar

*Ecology and Evolution Group, Department of Zoology, University of Western
Ontario, London, Ontario, Canada*

Abstract

In mammals, large males are often assumed to have higher mating success because they have greater success at contest competition. This relationship is often used to explain the prevalence of male-biased sexual size dimorphism in mammals. However, in many small vertebrates, large individuals are not always dominant. Using staged dyadic encounters, we examined the relationship between male body size and social dominance in captive male yellow-pine chipmunks (*Tamias amoenus*), a species with female-biased sexual size dimorphism. The yellow-pine chipmunk has a mating system in which males participate in mating chases and dominant males may have an advantage in acquiring matings with oestrous females. Captive male chipmunks were aggressive in only 28% of 144 paired encounters; however, several lines of evidence indicated that smaller chipmunks were dominant over large chipmunks: (1) small males were dominant in more dyads than large males; (2) within dyads, dominant males were smaller than subordinate males; and (3) small males performed more aggressive behaviour than large males. These results are not consistent with the prediction that large males are typically dominant. If large chipmunks are able to gain matings with females because of qualities other than dominance (such as the ability to successfully find and/or chase receptive females), then the costs of aggression to large chipmunks may outweigh any potential benefits. Small males, but not large males, may improve their mating success by being aggressive.

Corresponding author: Albrecht I. Schulte-Hostedde, Department of Biology, Queen’s University, Kingston, Ontario, Canada K7L 3N6. E-mail: albrecht@biology.queensu.ca

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 (Andersson 1994). The role of combat in the acquisition of matings has been well studied (Clutton-Brock 1988; Andersson 1994). However, mating success may be determined by contests that are not combative or in which combat plays a smaller role. Work on many species of mammals has suggested that larger males are behaviourally dominant to smaller males (e.g. Clutton-Brock 1988; Le Boeuf & Reiter 1988). If large dominant males tend to have high mating success, then the ultimate result may be the evolution of large male body size (Maynard-Smith & Brown 1986) and male-biased sexual size dimorphism.

The yellow-pine chipmunk (*Tamias amoenus*), like many other North American chipmunks, exhibits female-biased sexual size dimorphism (Levenson 1990; Schulte-Hostedde & Millar 2000). This is despite a competitive 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 that involves intense male–male competition for access to oestrous females (Koprowski 1998). Female yellow-pine chipmunks are in oestrus for only 1 d in late Apr. or early May. Three to 5 d prior to oestrus, females advertise the onset of oestrus through vocalizations, perhaps to incite competition among males (Callahan 1981). Several (two to six) males aggregate near the female's den and pursue her on the day of oestrus, and 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 grey squirrels, *Sciurus carolinensis* (Koprowski 1993), and Eurasian red squirrels, *S. vulgaris* (Wauters et al. 1990) exhibit a mating chase during breeding.

In this type of mating system, a male must be dominant to successfully fend off other males for access to females. Females are often described as mating with dominant males, but they also mate with males that use alternative tactics such as 'satellite' behaviour (Callahan 1981; Koprowski 1993). If dominant males are also large, then male-biased sexual size dimorphism may evolve. For example, red squirrels (*Tamiasciurus hudsonicus*) have a mating system typical of tree squirrels and chipmunks and males are larger than females (Boutin & Larsen 1993).

Some studies of small vertebrates have found either no relationship between body size and dominance (e.g. Robinson 1986; Garland et al. 1990; Tarvin & Woolfenden 1997) or evidence that small animals are dominant (e.g. Beacham 1987; Beaugrand et al. 1991; Belthoff & Gauthreaux 1991; Solberg & Ringsby 1997). If large males are not dominant over small males, and thus do not have greater reproductive success than small males, then female-biased sexual size dimorphism may evolve. Here, we used staged dyadic encounters between captive male yellow-pine chipmunks to determine whether large males are dominant over small males. If dominance is negatively related to body size, then this may provide

some explanation for the evolution of female-biased sexual size dimorphism in this species.

Methods

Dyadic encounters were conducted over 12 d during the mating season (early to mid May) 1999. Eighteen adult male chipmunks (16 with enlarged testes, indicative of breeding condition) were captured over 1 wk from seven sites in the Kananaskis Valley, Alberta, Canada and kept at the Kananaskis Field Station, University of Calgary. They were housed individually in plastic or metal cages (40 × 30 × 15 cm; L × W × H). Food (sunflower seeds and rat chow) and water were provided *ad libitum*, and apple was occasionally provided. The average mass (\pm SD) of chipmunks upon capture was 51.33 ± 5.21 g; range 42–65 g and they gained an average of 2.67 g over the course of the study. Only three of the 18 chipmunks lost weight (range 1–4 g). Animals were maintained on a 14-h light : 10-h dark illumination regime. Chipmunks were introduced into dyadic pairs within 48 h of capture.

Dyadic encounters were conducted between 08 : 00 h and 17 : 00 h MST in a neutral Plexiglas arena (80 × 60 × 40 cm) that could be divided into two compartments with a sliding partition. After each chipmunk in a dyad had the end of the tail dipped in fluorescent powder (Radiant Colour, Richmond, California) for individual identification, it was placed in one half of the arena for a 5-min acclimation period before the partition was removed, allowing the two males to interact freely. Observations were made from behind a blind for 10 min by one of us (AISH). Following the trial, both individuals were weighed (± 1 g) by an assistant. The observer was therefore 'blind' to the mass of the chipmunks prior to all trials. The arena was cleaned with dilute acetic acid to remove odours following each trial.

Each chipmunk was paired with all 17 other chipmunks for a total of 144 behavioural dyads. The order in which the dyads were formed was randomly determined, although the order was changed if individuals were assigned to dyads which occurred three or more times in a row. Each individual male was paired up to five times per day to complete the number of trials required over the course of the study.

We assigned dominant status for each dyad based on aggressive dominance. When aggressive encounters occurred (see Table 1 for descriptions of aggressive behavioural acts), it was always unidirectional and unambiguous (i.e. only one individual in each dyad initiated aggressive contact). We quantified aggressive behaviour by counting the number of times an aggressive behaviour (Table 1) was performed. The aggressive individual was considered dominant ($n = 40$). We also observed encounters in which some individuals climbed on top of the other without eliciting a response from its opponent ($n = 34$). In some dyads, either both individuals showed only amicable behaviour ('nuzzling' or nose-genital contact; $n = 43$) or no interaction took place (e.g. both chipmunks self-groomed

Table 1: Mean (\pm SD) frequency of five observed aggressive behavioural acts, percentage of aggressive encounters in which each behaviour occurred, and rank correlation ($n = 18$; Kendall's tau) between both body size (PCI) and body length and the frequency of the five aggressive behavioural acts counted during staged dyadic encounters between male yellow-pine chipmunks. Two frequently observed, non-aggressive behavioural acts are also described

Behaviour	Description	Mean \pm SD	% Occurrence	PCI	Body length
Aggressive					
Chase	One animal runs/leaps towards the other.	5.23 \pm 7.89	67.5	$\tau = -0.261$	$\tau = -0.471^{**}$
Lunge	One animal moves the whole body or the head and forequarters towards the other.	1.35 \pm 2.05	50.0	$\tau = -0.410^*$	$\tau = -0.385^*$
Fight	Both animals lock together ventrally and roll over	0.48 \pm 1.11	25.0	$\tau = -0.350^*$	$\tau = -0.493^{**}$
Mount	One animal climbs on top of another from behind.	0.05 \pm 0.22	5.0	$\tau = -0.086$	$\tau = -0.206$
Threat posture	One animal is in a crouched position with tail moving slowly and head oriented towards the other.	0.03 \pm 0.16	2.5	$\tau = 0.176$	$\tau = 0.283$
Non-aggressive					
Nuzzle	One animal approaches the other with nose extended and establishes contact with nose, neck, cheek and/or forehead.	—	—	—	—
Nose-genital	One individual establishes nasal contact with genital–anal region of the other.	—	—	—	—

* $p < 0.05$, ** $p < 0.01$.

for the 10-min observation period; $n = 27$). In these cases ($n = 104$), dominance status was not assigned.

Following completion of all behavioural dyads, chipmunks were euthanized (with an overdose of anaesthetic (isoflurane)) and measured to quantify overall body size. Total body length was measured using a graduated board (1 mm increments) 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 extended on the board with its nose against the perpendicular surface and its body pressed against the board. Total body length was measured to the nearest 1 mm from the tip of the nose to the last vertebra of the tail. Tail length was measured to the nearest mm from the base of the tail to the last vertebra using a ruler. Skull length was measured from the tip of the nose to the back of the skull, and skull width was measured to the nearest 0.1 mm across the widest point of the skull (the zygomatic arch) using dial calipers. We conducted a principal components analysis using log-transformed body length (total body length minus tail length), skull length and skull width, and the first principal component (PC1) was used as an index of overall body size (Dobson 1992). We also determined body condition using the residuals from a regression of body size (PC1) on mean body mass (calculated from body mass determined after each dyadic encounter; Schulte-Hostedde et al. 2001).

We confined most of our analyses to the 40 dyads in which dominance was exhibited. However, to determine whether pairs of males of similar body size were more likely to interact aggressively than males of widely different size, we conducted an independent t-test between the difference in body size (PC1) of males (i.e. body size of larger male minus the body size of smaller male) in dyads which resulted in aggressive interactions and those eliciting no aggressive interactions. We did the same with differences in log-transformed body length. We also conducted an independent t-test on the mean relative difference in body length (i.e. body length of larger male divided by body length of smaller male) between dyads, which resulted in aggressive interactions and dyads in which aggressive interactions did not occur.

We determined the number of dyads in which an individual established aggressive dominance (data were not normally distributed; Kolmogorov–Smirnov test, $d = 0.311$, $p < 0.05$), and conducted rank correlations (Kendall's tau) between the number of trials in which an individual was dominant and body size (PC1), log-transformed body length, mass and condition. We also conducted paired t-tests of body size (PC1) and log-transformed body length between dominant and subordinate individuals from each trial. Finally, we analysed the total number of aggressive acts performed per dyadic encounter relative to body size (PC1), log-transformed body length, mass and condition using rank correlation (Kendall's tau). We used rank correlation instead of least-squares regression because the data were not normally distributed (Kolmogorov–Smirnov test, $d > 0.313$; $p < 0.05$ for all aggressive behavioural acts, except for 'lunge' ($d = 0.243$, $p > 0.1$)).

Results

Of the yellow-pine chipmunks used in the behavioural dyads, over 75% of the variation in body measurements was described by the first principal component (PC1) and all measurements loaded positively on PC1 (Table 2). We were therefore able to use PC1 as an index of overall body size. We also used residuals from the body mass–body size (PC1) regression as an index of condition ($r^2 = 0.48$, $p = 0.001$). Rank correlations were not significant between the number of dyads in which an individual was aggressively dominant and mass (Kendall's tau = -0.103 ; $p = 0.549$) and condition (Kendall's tau = 0.089 ; $p = 0.608$). However, dominance was significantly negatively related to both body size (PC1) and body length (Fig. 1).

Although all 18 male chipmunks were involved in dyads in which aggressive behaviour was observed, only 11 of 18 males exhibited aggression. When aggressive behaviour occurred, chasing was the most common behaviour observed, followed by lunging. Very few threat postures and mounts were observed (Table 1). There was no significant relationship between either body mass or body condition, and the frequency of any aggressive behaviours ($p > 0.1$ for all behavioural acts). There was a significant negative relationship between body size (PC1) and frequency of two aggressive behaviours, lunging and fighting (Table 1). Lunging, fighting, and chasing showed a significant negative relationship with log-transformed body length (Table 1).

When dominance was exhibited, there was a marginally non-significant difference in body size (PC1) between the dominant (PC1 = -0.355) and subordinate males (PC1 = 0.066); smaller individuals were more likely to be dominant (paired t-test, $df = 39$, $t = -1.935$, $p = 0.060$). To investigate the result of this paired t-test further, we conducted a power analysis using the one sample model (normal distribution) of POWER CALCULATOR (available at <http://ebook.stat.ucla.edu/calculators/powercalc>). The power of this test was 0.466 ($\beta = 0.534$) and the sample size required to detect a significant difference (with $\beta = 0.20$, $SD = 1.375$, and $\delta = 0.421$) was 86. We removed one chipmunk which was an outlier (he was aggressively dominant in 15 out of 18 trials) and this improved the significance level of the paired t-test ($df = 24$, $t = -2.348$, $p = 0.027$). This 'outlier' chipmunk was in the bottom quartile in body length

Table 2: Mean, standard deviation and range of morphological measurements, and principal components analysis for male yellow-pine chipmunks used in behavioural trials (PC1) ($n = 18$). % variance refers to the percentage variance in the data explained by first principal component (PC1)

	Mean (mm)	SD	Range (mm)	PC1
Body length	128.39	5.679	117–135	0.809
Skull length	36.47	0.558	35.2–37.1	0.909
Skull width	18.67	0.379	17.8–19.1	0.880
% variance	–	–	–	75.2

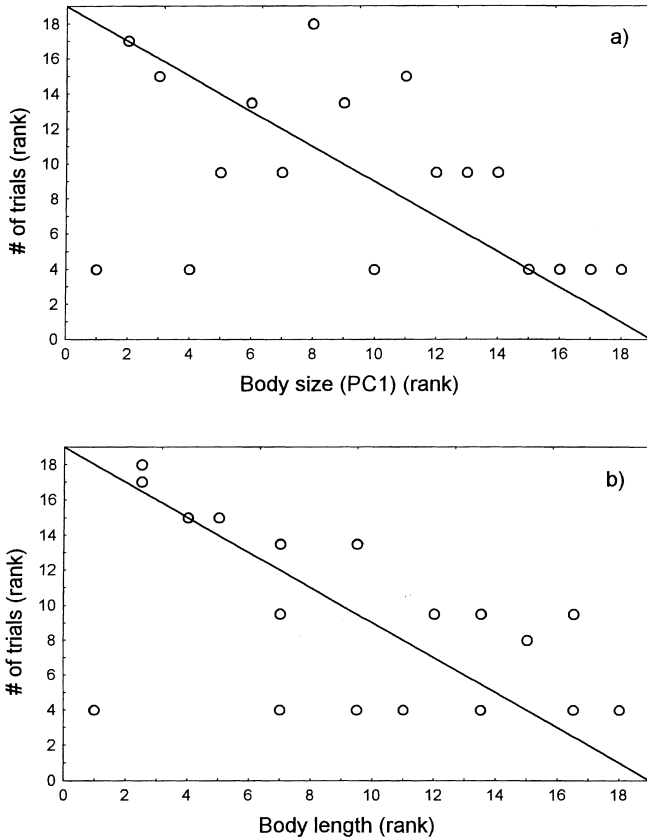


Fig. 1: Plot of the ranks between the number of trials an individual male yellow-pine chipmunk was dominant and body size (PC1) (a) (Kendall's tau = -0.354 ; $p = 0.04$), and body length (b) (Kendall's tau = -0.456 ; $p = 0.008$). A rank of 1 was given to the smallest male (a rank of 18 was given to the largest individual, and the individual that was aggressive in the most dyadic encounters). The line in (a) and (b) represents the null hypothesis of a negative rank correlation between the independent variable (body size (PC1) or body length) and the number of trials in which an individual was dominant. The rank assigned to tied observations is the mean of the ranks that would have been assigned had they not been tied

but not for any of the other body size components (skull length, skull width) or overall body size (PC1). Mean (\pm SD) log-transformed body length was significantly different between dominant (124.3 ± 0.01 mm) and subordinate (128.9 ± 0.02 mm) male chipmunks ($df = 39$, $t = -4.064$, $p < 0.001$).

The mean difference (\pm SD) in body length between males in dyads that resulted in aggressive encounters was 7.00 ± 5.03 mm and in dyads in which aggression did not occur, the mean difference in male body length was 6.14 ± 4.91 mm. There were no significant differences in the mean difference in log-transformed body length ($df = 142$, $t = -0.944$, $p = 0.346$), mean difference

in male body size (PC1; $df = 142$, $t = -0.529$, $p = 0.597$) and mean relative difference in body length ($df = 142$, $t = -1.018$, $p = 0.310$) between dyads which resulted in aggressive interactions and dyads in which aggressive interactions did not occur.

Discussion

In the current study, we assumed that aggressive behaviour was the expression of dominance, so that those individuals exhibiting aggressive behaviour were assumed dominant over those that were not aggressive. We also assumed that male chipmunks which were recipients of aggressive behaviour were subordinate. This may not always be the case but, in the context of a mating chase, male chipmunks which chase or drive away rival males are more likely to have access to an oestrous female than males which flee from other aggressive males. 'Chase' was the aggressive behaviour that occurred most often and in most of the dyads in which aggression took place, males which were chased always fled from their opponent. Therefore, it seems likely that aggressive males would be able to displace other males during a mating chase. A positive relationship between aggression and dominance has been found in other studies of sciurid mating strategies (e.g. Farentinos 1972; Murie & Harris 1978), especially when placed in the context of a dominance hierarchy (Koprowski 1993). A positive relationship between aggression and dominance has also been established in other vertebrate taxa (e.g. Robinson 1986; Beaugrand et al. 1991; Bryant & Newton 1994).

The negative relationship between body size (PC1 and body length) and dominance found here for the yellow-pine chipmunk is not consistent with that found in many larger mammals (e.g. Clutton-Brock 1988; Le Boeuf & Reiter 1988). However, our results are consistent with Sheppard (1965) who also found a negative relationship between body mass and dominance rank among a small sample of yellow-pine chipmunks. Many studies of small animals, such as passerine birds, lizards and fish, have found either no relationship between body size and dominance (e.g. Robinson 1986; Garland et al. 1990; Tarvin & Woolfenden 1997) or evidence that smaller individuals are dominant over larger individuals (i.e. the so-called 'little man' syndrome) (Beacham 1987; Beaugrand et al. 1991; Belthoff & Gauthreaux 1991; Solberg & Ringsby 1997).

The positive relationship between body size and aggressive dominance found in many large vertebrates may not be universal among relatively small (<1 kg) vertebrate species. If small males are more likely to be aggressively dominant than large males in small-bodied vertebrate species, then this may partly explain the relatively higher incidence of female-biased sexual size dimorphism among these groups of animals. Chipmunks (*Tamias* spp.) are among the smallest squirrels, and female-biased sexual size dimorphism is pervasive among species within the genus (Levenson 1990). Ralls (1976) summarized data from several sources and documented the mammalian species in which females were reported to be larger

than males. The vast majority of examples of female-biased sexual size dimorphism were from small mammals, including marsupials, insectivores, bats and rodents. Other taxa of small vertebrates also show this trend, including many fishes, amphibians, snakes and small birds such as waders, hummingbirds and some raptors (Andersson 1994). Factors such as the fecundity advantage of large female size may be responsible for these trends. Nonetheless, it is worth speculating whether small males are also dominant over large males, as seems to be the case in some taxa.

Despite the negative relationship between body size (PC1 and body length) and dominance, aggressive behaviour in captive male yellow-pine chipmunks was rarely displayed. A dominant chipmunk could only be assigned in 40 of our 144 staged dyads (27.8%). Field observations confirm this. Wounding was rarely observed in males during the breeding season (Schulte-Hostedde, pers. obs.).

Male chipmunks may assess their opponent on the basis of body size and choose not to challenge a much larger opponent. Dyads composed of chipmunks of similar size may be more likely to produce aggressive interactions than dyads in which male chipmunks are widely different in body size. However, we found that the mean difference in male body size (PC1) and body length was not significantly different between dyads in which aggression took place and dyads in which aggression was not evident. Alternatively, male yellow-pine chipmunks may use other traits, such as odours or body posture, to assess the competitive ability of opponents.

Although many studies have examined dominance in tree squirrels, few have examined it in relation to body size. Wauters et al. (1990) found that heavier male red squirrels (which are not necessarily larger in skeletal size; Wauters & Dhondt 1989) were ranked highest in a dominance hierarchy. Conversely, Allen & Aspey (1986) found that body mass did not influence social status in grey squirrels. Factors such as age and residence status may better explain dominance in tree squirrels and chipmunks (Farentinos 1972; Wauters et al. 1990; Koprowski 1993), especially if old animals are larger than young animals. The chipmunks used in our study were all adults and there is little evidence that chipmunks continue to grow once they have reached their first winter of life (Schulte-Hostedde & Millar 2000). In the context of a mating chase, residence status is probably irrelevant because yellow-pine chipmunks are only territorial near their burrow and mating chases occur in the vicinity of oestrous females (Broadbrooks 1970). Although our chipmunks could not be accurately aged, we did control for residence status by using a neutral arena.

When aggression takes place, why don't large chipmunks respond to aggressive small chipmunks? The costs of aggression can be high (Huntingford & Turner 1987) and include increased risk of injury and increased energetic requirements to maintain activity levels (e.g. Rowher & Ewald 1981; Appleby 1983; Tiebout 1993; Olsson 1994; Nicieza & Metcalfe 1999). These costs are presumably offset by increased mating success. The assumption that dominant individuals have higher mating success than subordinates has been questioned (Dewsbury 1982; Qvarnström & Forsgren 1998). Nonetheless, in many tree squirrels, dominant males tend to achieve more copulations than subordinate individuals (Koprowski 1998).

However, if large chipmunks are able to gain matings because of success at tactics other than dominance over other males (such as the ability to successfully find and/or chase receptive females), then the costs of aggression to large chipmunks may outweigh any potential benefits. Small males may adopt aggression as an alternative tactic relative to large males and thus accept the high costs of aggression 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 or may not result in a positive relationship between male body size and reproductive success, but the use of an aggressive tactic may allow small males to achieve almost or the same level of reproductive success as large males, thus contributing to the evolution of female-biased sexual size dimorphism.

Acknowledgements

Special thanks to G. Eccles for assistance in conducting the dyadic encounters and the Small Mammal Discussion Group for suggestions. Helpful suggestions on the manuscript were provided by J.-G. Godin, J. Koprowski and an anonymous reviewer. We also acknowledge the University of Calgary Kananaskis Field Station for logistical support. This study was supported by an NSERC operating grant to JSM and an NSERC postgraduate scholarship to AISH. The protocols used in this study were approved by University of Western Ontario Animal Care Committee (protocol #99083-04).

Literature Cited

- Allen, D. S. & Aspey, W. P. 1986: Determinants of social dominance in eastern gray squirrels (*Sciurus carolinensis*): a quantitative assessment. *Anim. Behav.* **34**, 81—89.
- Andersson, M. 1994: *Sexual Selection*. Princeton Univ. Press, Princeton.
- Appleby, M. C. 1983: Competition in a red deer stag social group: rank, age, and relatedness of opponents. *Anim. Behav.* **31**, 913—918.
- Beacham, J. L. 1987: The relative importance of body size and aggressive experience as determinants of dominance in pumpkinseed sunfish, *Lepomis gibbosus*. *Anim. Behav.* **36**, 621—623.
- Beaugrand, J., Goulet, C. & Payette, D. 1991: Outcome of dyadic conflict in male green swordtail fish, *Xiphophorus helleri*: effects of body size and prior dominance. *Anim. Behav.* **41**, 417—424.
- Belthoff, J. R. & Gauthreaux, S. A. Jr 1991: Aggression and dominance in house finches. *Condor* **93**, 1010—1013.
- Boutin, S. & Larsen, K. W. 1993: Does food availability affect growth and survival of males and females differently in a promiscuous small mammal, *Tamiasciurus hudsonicus*? *J. Anim. Ecol.* **62**, 364—370.
- Broadbrooks, H. E. 1970: Home ranges and territorial behavior of the yellow-pine chipmunk, *Eutamias amoenus*. *J. Mammal.* **51**, 310—326.
- Bryant, D. M. & Newton, A. V. 1994: Metabolic costs of dominance in dipper, *Cinclus cinclus*. *Anim. Behav.* **48**, 447—455.
- Callahan, J. R. 1981: Vocal solicitation and parental investment in female *Eutamias*. *Am. Nat.* **118**, 872—875.
- Clutton-Brock, T. H. 1988: Reproductive success. In: *Reproductive Success* (Clutton-Brock, T. H., ed.). Univ. of Chicago Press, Chicago, pp. 472—485.
- Dewsbury, D. A. 1982: Dominance rank, copulatory behavior, and differential reproduction. *Q. Rev. Biol.* **57**, 135—159.
- Dobson, F. S. 1992: Body mass, structural size, and life-history patterns of the Columbian ground squirrel. *Am. Nat.* **140**, 109—125.
- Elliott, L. 1978: Social behaviour and foraging ecology of the eastern chipmunk (*Tamias striatus*) in the Adirondack mountains. *Smithsonian. Contr. Zool.* **265**, 1—107.

- Farentinos, R. C. 1972: Social dominance and mating activity in the tassel-eared squirrel (*Sciurus aberti ferreus*). *Anim. Behav.* **20**, 316–326.
- Garland, T. Jr, Hankins, E. & Huey, R. B. 1990: Locomotor capacity and social dominance in male lizards. *Funct. Ecol.* **4**, 243–250.
- Huntingford, F. A. & Turner, A. K. 1987: *Animal Conflict*. Chapman & Hall, London.
- Koprowski, J. L. 1993: Alternative reproductive tactics in male eastern gray squirrels: 'making the best of a bad job'. *Behav. Ecol.* **4**, 165–171.
- Koprowski, J. L. 1998: Conflict between the sexes: A review of social and mating systems of the tree squirrels. In: *Ecology and Evolutionary Biology of Tree Squirrels* (Steele, M. A., Merritt, J. F. & Zegers, D. A., eds). Virginia Museum of Natural History, Spec. Publishers **6**, pp. 33–41.
- Le Boeuf, B. J. & Reiter, J. 1988: Lifetime reproductive success in northern elephant seals. In: *Reproductive Success* (Clutton-Brock, T. H., ed.). Univ. of Chicago Press, Chicago, pp. 344–362.
- Levenson, H. 1990: Sexual size dimorphism in chipmunks. *J. Mammal.* **71**, 161–170.
- Maynard-Smith, J. & Brown, R. L. 1986: Competition and body size. *Theor. Popul. Biol.* **30**, 166–179.
- Murie, J. O. & Harris, M. A. 1978: Territoriality and dominance in male Columbian ground squirrels (*Spermophilus columbianus*). *Can. J. Zool.* **56**, 2402–2412.
- Nicieza, A. G. & Metcalfe, N. B. 1999: Cost of rapid growth: the risk of aggression is higher for fast-growing salmon. *Funct. Ecol.* **13**, 793–800.
- Olsson, M. 1994: Why are sand lizard males (*Lacerta agilis*) not equally green? *Behav. Ecol. Sociobiol.* **35**, 169–173.
- Qvarnström, A. & Forsgren, E. 1998: Should females prefer dominant males? *Trends Ecol. Evol.* **13**, 498–501.
- Ralls, K. 1976: Mammals in which females are larger than males. *Q. Rev. Biol.* **51**, 245–276.
- Robinson, S. K. 1986: Benefits, costs and determinants of dominance in a polygynous oriole. *Anim. Behav.* **34**, 241–255.
- Rowher, S. & Ewald, P. W. 1981: The cost of dominance and advantage of subordination in a badge signaling system. *Evolution* **35**, 441–454.
- Schulte-Hostedde, A. I. & Millar, J. S. 2000: Measuring sexual size dimorphism in the yellow-pine chipmunk (*Tamias amoenus*). *Can. J. Zool.* **78**, 728–733.
- Schulte-Hostedde, A. I., Millar, J. S. & Hickling, G. J. 2001: Evaluating body condition in small mammals. *Can. J. Zool.* **79**, 1021–1029.
- Sheppard, D. H. 1965: Ecology of the chipmunks, *Eutamias amoenus luteiventris* (Allen) and *E. minimus oreocetes*, with particular reference to competition. PhD Thesis, Univ. of Saskatchewan, Saskatoon.
- Solberg, E. J. & Ringsby, T. H. 1997: Does male badge size signal status in small island populations of house sparrows, *Passer domesticus*? *Ethology* **103**, 177–186.
- Tarvin, K. A. & Woolfenden, G. E. 1997: Patterns of dominance and aggressive behaviour in blue jays at a feeder. *Condor* **99**, 434–444.
- Tiebout, H. M. III 1993: Mechanisms of competition in tropical hummingbirds: metabolic costs for losers and winners. *Anim. Behav.* **74**, 405–418.
- Wauters, L. A. & Dhondt, A. A. 1989: Variation in length and body weight of the red squirrel (*Sciurus vulgaris*) in two different habitats. *J. Zool. Lond.* **217**, 93–106.
- Wauters, L. A., Dhondt, A. A. & De Vos, R. 1990: Factors affecting male mating success in red squirrels (*Sciurus vulgaris*). *Ethol. Ecol. Evol.* **2**, 195–204.
- Yahner, R. H. 1978: The adaptive nature of the social system and behaviour in the eastern chipmunk, *Tamias striatus*. *Behav. Ecol. Sociobiol.* **3**, 397–427.

Received: January 22, 2001

Initial acceptance: August 15, 2001

Final acceptance: August 27, 2001 (J.-G. Godin)