Role of sex, body size, and sexual state in determining aggression in *Tamias striatus* (eastern chipmunk)

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Abstract. We studied dominance structure in a human-acclimated population of *Tamias striatus* on University of Michigan Biological Station (UMBS) property in the northern Lower Peninsula of Michigan. We predicted that larger, sexually mature individuals who were closer to their burrows would be dominant over smaller, immature animals that were farther from their burrows, and that males would be more aggressive than females. We captured and marked chipmunks and observed them over several weeks. We found that sex and sexual state did not have an effect on aggression but that chipmunks further from their burrows won more fights than chipmunks closer to their burrows. We attribute these unexpected results to the presence of juveniles on the peripheries of the community with a high drive for food who were less willing to back down from confrontations.

Tamias striatus (eastern chipmunk) is a small-bodied sciurid with a wide geographic range that includes most of the American Northeast and the Laurentian Great Lakes region, and extends west almost to the Rocky Mountains and south to the Gulf of Mexico (Kurta 2005). With its distinctive striped pelage, loud chirping alarm calls, and the ease with which it adapts to the presence of humans, it is often a conspicuous member of ecosystems in parks, around camps, and even in urban environments. The University of Michigan Biological Station (UMBS) in the northern Lower Peninsula of Michigan is blessed with an extremely dense and human-acclimated population of *T. striatus*, making it an ideal site to study the dominance hierarchy and social interactions of these energetic and boisterous animals.

Chipmunks devote much of their time to aggressive interactions with other chipmunks. We sought to find what determines success in intraspecific conflict. We established feeding stations at five sites around the UMBS campus, and observed over the course of several weeks the interactions of *T. striatus* as individuals competed for food. We looked for both feeder success (measured by time spent on the feeder) and how often individuals won conflicts with other chipmunks. Competition over resources to cache is fierce. Chipmunks that do not have large enough caches when they enter their winter torpor hibernate until later in the spring than

chipmunks that cached excess amounts of food (French, 2000). Since chipmunks breed in the springtime (Kurta 2005), emerging from torpor earlier could confer a reproductive advantage over chipmunks that hibernate longer. We wished to determine what makes a chipmunk more successful in competition over resources to cache, and therefore perhaps have a better chance at reproductive success. We examined the importance of sex, sexual condition, distance from home burrow, and body weight to determine if any of these factors contributed to the success of an individual animal in intraspecific interactions.

We predicted that males would be more aggressive than females. Female chipmunks often form close associations with their mothers and live near them, while male chipmunks tend to disperse further away (Loew 1999). Some females probably interact as mother-daughter pairs and are expected to show less aggression towards each other. We predicted that chipmunks closer to their burrows would win more fights than chipmunks farther away from their burrows. In captivity, chipmunks establish an area of dominance close to their nest boxes, and have been observed fighting fiercely to defend them (Brenner et al. 1978). Because larger animals tend to be older, more experienced and more mature reproductively, we predicted that they would dominate smaller animals (Bowers and Carr 1992, Brenner et al. 1978).

Methods and Materials

Observations

Observations were conducted late June and early July of 2010. The study site was the UMBS campus, located near Pellston, in the northern Lower Peninsula of Michigan. The campus is approximately seven acres in area and feeding stations were distributed throughout campus.

Sites were chosen to represent a variety of ground and tree cover as well as variation in the level of human activity (see Fig. 1 and Table 1).

Prior to beginning the study, we trapped chipmunks at all five sites using Havahart® live traps baited with sunflower seeds. We placed 14 large traps and 1 small trap at each station and checked the traps once each hour. Trapping occurred over the course of 3 days. When an animal that had already been trapped and labeled was re-captured in a trap, we immediately released it unless its mark was illegible. We weighed the animals, sexed them, determined reproductive condition, and then marked them with unique numbers using Nyanzol-D fur dye applied with Q-tips. The animals were then released at the site where they had been captured.

The class was divided into five teams of three people each. For each observation session, two team members recorded chipmunk observations while the third located home burrows. Observation sessions lasted one hour, with one session during the chipmunks' morning active time and one during the afternoon active time. Approximately half an hour prior to observations beginning, the sites were pre-baited with a small handful of sunflower seeds scattered on the ground to bring in the animals. At the beginnings of observation sessions, approximately one cup of sunflower seeds was placed in a cardboard dish on a 12" x 12" wooden platform and replenished throughout the session as necessary. Observers used stopwatches to determine how much time animals spent on the feeder and also recorded when a conflict occurred, which animals were involved, and which individual won the conflict. In the case of unmarked animals, teams recorded observations, then attempted to capture and mark them after the observation session had been completed. Individuals for which we had observations but had been unable to capture by the end of the study were arbitrarily given numbers and were not used in analysis of body weight, sexual condition or distance to home burrow. Burrows were located by following

chipmunks as they left feeding stations and were marked with labeled flags. Distance from feeding station to home burrow was measured using a 150 m measuring tape and walking the most direct line from the station to the burrow possible. Each site had a feeding station placed in open cover and one in closed cover; however these two conditions were analyzed separately only to determine distance from home burrow.

Data Analysis

We conducted three types of data analyses. First, we examined the importance of sex in how much time an animal spent on the feeder, its mass, the number of fights it had, the percentage of fights it won and the average time it spent on the feeder. We organized these data in a table and conducted t-tests using Microsoft Excel® and SPSS®.

Second, we looked at individual animals and their overall success as a function of their mass, number of fights, time on feeder and distance to home burrow. We organized these variables into a Microsoft Excel® spreadsheet and used t-tests and correlations to determine the relationships among them.

Finally, we analyzed encounters on a pairwise basis. We examined interactions between two individuals and related the winner's success to the difference in their body size, distance from home burrows, and differences in sex and sexual condition.

Results

Differences between males and females

Females are significantly smaller than males ($p = 0.042$) (Table 2). Average weight for females is 97.55 g while average weight for males is 103.21 g. Males spent more time on feeders on average (male average = 51.7 seconds, female average = 42.9 seconds); however, the difference was not significant ($p = 0.437$). There was no significant difference between how

many fights males and females had (p = 0.855) or the fraction of fights that were won by males vs. females (p =0.382).

Differences between winners and losers

We defined a "winner" as a chipmunk that won more than 50% of its fights and a "loser" as a chipmunk that lost more than 50% of its fights (Table 3). Winners were marginally significantly larger than losers (winner average = 107.67 g, loser average = 98.20 g, p = 0.058). Winners fought marginally significantly more fights than losers (winner average = 33.7 fights, loser average = 18.4 fights, p = 0.069). Winners were on average farther from their burrows both at open feeding stations (winner average = 24.6 m, loser average = 19.0 m) and closed feeding stations (winner average = 24.6 m, loser average = 24.8 m), however the difference was not significant in either case (p = 0.248 and p = 0.564, respectively). We found no significant difference in the time that winners and losers spent at the feeders (p = 0.831).

We also used a Pearson product-moment correlation analysis to examine the relationship between mass and tendency to fight, tendency to win, and tendency to spend more time on the feeder. We found that larger chipmunks won a high fraction of fights (r=0.625, n=19, p=0.004) but did not fight more often (r=0.315, n=19, p=0.189) or feed for longer periods of time (r=0.134, n=19, p=0.584). Chipmunks that were more aggressive (had more fights) had a marginally significant tendency to spend less time on the feeder (r=0.373, n=26, p=0.061), but chipmunks that won a higher proportion of fights did not differ from chipmunks that lost more fights in the time they spent on the feeder (r=0.182, n=26, p=0.373).

Differences between reproductive states

We found no significant differences between scrotal and non-scrotal males in terms of number of fights (p=0.886), proportion of fights won (p=0.660), or time spent at the feeder

(p=0.423) (Table 4). Similarly, we found no significant differences between females with enlarged nipples and females with tiny nipples in terms of number of fights (p=0.771), proportion of fights win (p=0.185) or time spent at the feeder (p=0.772) (Table 5).

Pairwise comparisons

On average, looking at members of each pair, the winner is significantly heavier then the loser (p = 0.020) (Table 6). Difference in mass is positively correlated with the fraction of fights won between members of a pair (r=0.390, n=45, p=0.008) and average time spent on the feeder (r=0.415, n=44, p=0.005), but not with the number of fights (r=0.140, n=45, p=0.360).

Contrary to individual analyses, in the pairwise analysis, more fights did not relate to less time spent on the feeder (r=0.034, n=82, p=0.759). Chipmunks that won a higher proportion of their fights spent more time feeding (r=0.335, n=82, p=0.002).

For distance to home burrow from open feeding stations, winners were farther from their home burrow than losers significantly more often than expected (16 observed, 12.4 expected), and losers were closer to their burrow than winners significantly more often than expected (11 observed, 7.4 expected) (chi-square=5.465, df=1, p=0.026) (Table 7). The trend is the same for the closed feeding station (chi-square=4.91, df=1, p=0.05) (Table 8).

Discussion

We found that neither males nor females were more aggressive. We had predicted that females would be less aggressive due to the presence of mother-daughter bonded pairs. Perhaps the high population densities of *T. striatus* around UMBS property increase competition to the point where these post-weaning mother-daughter bonds are weak. Certainly, the population

dynamics of the extremely human-acclimated animals around camp should be expected to differ from those of the wild chipmunks studied by Loew in 1999.

Contrary to our prediction, we found that chipmunks farther from their burrows won more encounters than expected and chipmunks closer to their burrows lost more encounters than expected. One reason this may have occurred is the age structure within the population. *Tamias striatus* has litters in the spring. After approximately two months, the young disperse from their mother's burrow and create or find burrows of their own (Kurta 2005). Younger individuals are pushed to the peripheries of the community into less favorable burrows (Clarke and Kramer 1994). Juvenile chipmunks have been observed scatter hoarding in the wild. This behavior may be because they cannot adequately defend one large cache of food from intruders, so instead they bury many smaller caches in shallow holes. Theft from these small hoards is a common event, however the animal also faces less risk of fighting an opponent against whom it cannot defend itself (Clarke and Kramer 1994). Due to high rates of theft from shallow hoards, younger chipmunks need to store more seeds overall to establish an adequate cache. This higher requirement might make younger chipmunks more desperate for resources, and therefore less likely to back down from a confrontation. Our study took place during early summer, not long after juvenile chipmunks left their mothers' burrows. This may explain why chipmunks that lived farther away from the feeding stations fared better than predicted.

We found that larger-bodied animals won a greater proportion of their encounters, which is not surprising, given the often surprisingly physical nature of fights. However, we did not find that sexual condition played a role in establishing dominance. This is surprising, particularly in females with enlarged nipples, given that individuals who have bred are older and more experienced. This unexpected result could also be explained by the desperation of

marginalized juvenile chipmunks. Many confrontations observed did not involve a physical fight, and instead consisted of a vocalization or a hard stare in which one individual backed down without having to be physically attacked. Body size did not necessarily factor into these non-physical confrontations, so perhaps immature juveniles were simply more determined to gain access to cache resources. Mature chipmunks presumably have access to better burrows and are more able to defend them, making it easier to establish a large central cache. If they had been hoarding food since spring, perhaps their caches were already quite large, making them more willing to back down and avoid physical confrontations in which they could potentially be injured.

We cannot conclude what confers an advantage in the competition over resources to cache due to the unforeseen effects of age structure on the study. Marginalized juveniles on the outskirts of the community showed greater success than was expected, perhaps due to greater competitive pressure felt. Perhaps if the study were conducted later in the season once juveniles became more integrated into the community, or before juvenile chipmunks dispersed from their home burrows, it would give a more complete picture as to what gives a chipmunk the ability to cache excess food, and therefore be able to wake up earlier in the spring.

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Appendix

Table 1: Summarizes habitat conditions at all five feeding station sites.

Site #	Tree Cover	Ground Cover	Level of human activity	Comments
1	Pines	Bare dirt, concrete, pine needles	Heavy	Near student cabins, nearly constant foot traffic, maintenance staff was feeding here
2	Deciduous	Bare dirt, short leafy vines	Moderate	Near classroom and dining hall, periodic bouts of foot traffic
3	Open in center, pines	Tall grasses	Light	In field near dorm lounge, almost no foot traffic through field, many burrows, across street from lake
4	Deciduous and pines	Short grass and moss, reeds near shoreline	Moderate	Open area near sidewalk, occasional foot traffic, moderate foot traffic on nearby road, near lake
5	Pines	Short leafy vines, short grass, concrete	Light	Quiet back yard, very light foot traffic on nearby road, bird feeders animals were accustomed to feeding at, near lake

Table 2: Shows difference between males and females in mass, number of encounters, fraction of fights won, and average time spent on feeder.

	sex	N	Mean	Std. Deviation	df	t	p
Mass (g)	male	28	103.21	8.513	59	2.08	0.042
	female	33	97.55	12.065			
# fights	male	8	24.4	18.677	17	-0.186	0.855
	female	11	26.3	24.017			
fraction fights won	male	8	.56	0.318	17	0.897	0.382
	female	11	.42	0.354			
Avg. time on feeder	male	8	51.7	29.967	17	0.797	0.437
	female	11	42.9	18.646			

Table 3: Shows differences between individuals who won more than 50% of their fights (winners) and those who lost more than half of their fights (losers), in average time on feeder, and distance from open and closed feeders to the home burrow.

	winner	N	Mean	Std. Deviation	df	t	p
Mass (g)	yes	9	107.67	11.630	17	2.03	0.058
	no	10	98.20	8.600			
# fights	yes	13	33.7	24.642	24	1.91	0.069
	no	13	18.4	15.207			
Avg. time on feeder	yes	13	45.5	27.975	24	-2.15	0.831
	no	13	47.6	20.490			
Burrow to Open (m)	yes	10	24.6	9.506	15	1.20	0.248
	no	7	19.0	9.246			
Burrow to Closed (m)	yes	10	28.7	16.068	15	0.59	0.564
	no	7	24.8	7.480			

Table 4: Shows comparison of number of encounters, fraction of fights won, and average time on feeder for scrotal and non-scrotal males**.**

	repro. cond.	N	Mean	Std. Deviation	df	t	p
# fights	scrotal	5	25.2	17.021	6	0.150	0.886
	non-scrotal	3	23.0	25.239			
fraction fights won	scrotal	5	0.52	0.390	6	-0.462	0.660
	non-scrotal	3	0.63	0.193			
Avg. time on feeder	scrotal	5	58.9	34.911	6	0.859	0.423
	non-scrotal	3	39.7	18.998			

Table 5: Shows comparison of number of encounters, fraction of fights won, and average time on feeder for females with tiny nipples (NTNL) vs. those with enlarged nipples (NENL).

	Repro. cond.	N	Mean	Std. Deviation	df	t	p
# fights	NTNL	8	24.9	18.271	9	-0.301	0.771
	NENL	3	30.0	41.073			
fraction fights won	NTNL	8	.33	0.230	9	-1.436	0.185
	NENL	3	.66	0.570			
Avg. time on feeder	NTNL	8	41.7	21.356	9	-0.299	0.772
	NENL	3	45.7	11.177			

Table 6: Shows comparison of masses of members of pair of interacting chipmunks.

	winner?	N	Mean	Std. Deviation	df	T	p
difference in mass	no	18	-6.28	13.033	43	-2.41	p=0.020
	yes	27	2.78	11.866			

Table 7: Shows pairwise comparison of winners and losers vs. distance from the open feeder to their home burrow.

			winners		
			no	yes	Total
1st animal closest to burrow (open)?	yes	Count	11	6	17
		Expected Count	7.4	9.6	17.0
	no	Count	6	16	22
		Expected Count	9.6	12.4	22.0
Total		Count	17	22	39
		Expected Count	17.0	22.0	39.0

Table 8: Shows pairwise comparison of winners and losers vs. distance from the closed feeder to their home burrow.

			winners		
			no	yes	Total
1st animal closest (closed)	no	Count	20	12	32
		Expected Count	16.0	16.0	32.0
	yes	Count	7	15	22
		Expected Count	11.0	11.0	22.0
Total		Count	27	27	54
		Expected Count	27.0	27.0	54.0

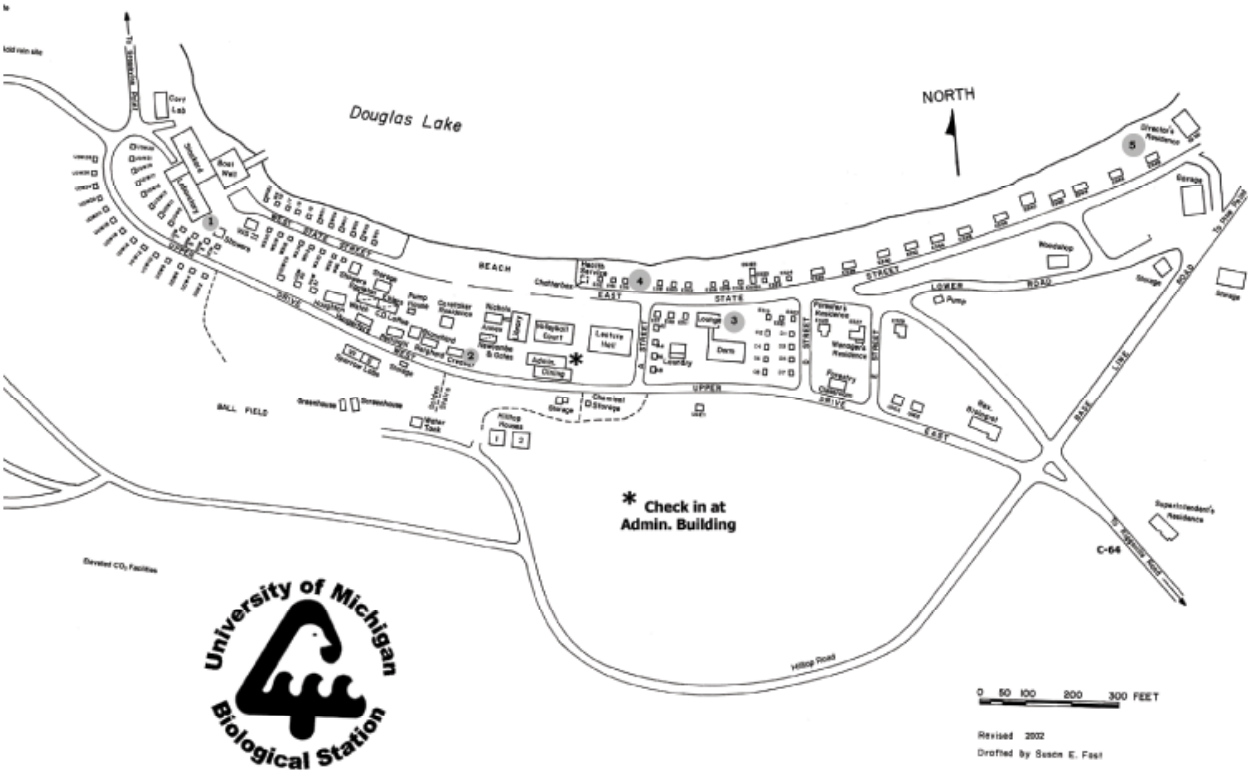

Figure 1: Shows a map of UMBS property. Grey circles mark sites of feeding stations. Site 1 is located west of the shower house and east of Lakeside Lab, Site 2 is located just east of Creaser, Site 3 is located north of the dorm, Site 4 is located east of the Chatterbox and Site 5 is located west of the Director's residence.