SUNY College of Environmental Science and Forestry
Digital Commons @ ESF

Honors Theses

5-2012

Tail Communication in the Eastern Gray Squirrel, Sciurus carolinensis

Michael A. Pardo

Tail Communication in the Eastern Gray Squirrel, *Sciurus carolinensis*

by

Michael A. Pardo
Candidate for Bachelor of Science
Environmental and Forest Biology
With Honors

May 2012

APPROVED

Thesis Project Advisor: ____________________________
William M. Shields, Ph.D.

Second Reader: __________ ________________________
Guy A. Baldassarre, Ph.D.

Honors Director: _________________________________
William M. Shields, Ph.D.

Date: _________________________________

ABSTRACT

Tree squirrels are known to communicate with their tails, but the only aspects of this communication that have been studied are tail flicking and piloerection. I investigated the communicative significance of tail position in wild eastern gray squirrels by videotaping them at an artificial food source. For each individual, I recorded dominance rank, aggression, avoidance behavior, and three variables describing tail position (tightness of curvature, portion of tail bent, and tail contact with ground). When a subordinate squirrel approached a dominant squirrel I recorded whether the approach was successful, and when a dominant squirrel approached a subordinate squirrel I recorded the distance that the subordinate moved away. All three tail position variables were correlated with the behavior of both the signaler and the receiver. The interaction effect between the tail positions of two interacting squirrels was a better predictor of the more dominant squirrel's degree of aggression than either squirrel's tail position alone. Analysis suggested that different tail variables do not communicate the same information, indicating that tail position may communicate multiple pieces of information simultaneously. I hypothesize that the tightness of the tail's curvature communicates a squirrel's degree of confidence (its status), the portion of the tail that is bent communicates degree of hunger, and whether the tail is touching the ground indicates intent to move.

TABLE OF CONTENTS

LIST OF TABLES

ACKNOWLEDGEMENTS

I extend my sincere gratitude to my academic advisor, Dr. William Shields, for his guidance and mentorship. I am also extremely grateful to my father, Dr. Scott Pardo, for his invaluable assistance with the statistical analyses of this project. Without either of them, this honors thesis would not have been possible. I sincerely thank Gail Pardo, Yudi Pardo, and Jeremy Pardo for providing a camcorder, access to their birdfeeder, and extensive moral support, as well as for engaging me in several discussions leading to the formation of some of my hypotheses. Finally, I thank the SUNY College of Environmental Science and Forestry and its Honors Program for providing additional support.

INTRODUCTION

Eastern gray squirrels *(Sciurus carolinensis)* are known to communicate visually with their tails (Steele & Koprowski, 2001). However, few studies have examined this communication, and those that have have almost exclusively considered tail movements. Tail flagging has been documented as an alarm signal in gray squirrels (Bakken, 1959; Partan et al., 2009; Partan et al., 2010). Gray squirrels also incorporate tail flagging into harassment displays directed at rattlesnakes *(Crotalus horridus)* (Clark, 2005).

Several studies have examined tail communication in other Sciurids, though nearly all have focused on tail movements or piloerection. In fox squirrel *(Sciurus niger)* pre-copulatory displays, male circular tail waves or slow fore-and-aft tail flicks followed by female side-to-side tail flicks inhibit aggression, whereas male rapid jerk tail flicks induce the female to run away (McCloskey & Shaw, 1977). In tassel-eared squirrels *(Sciurus aberti)*, tail piloerection increases with agitation (Farentinos, 1974). California ground squirrels *(Spermophilus beecheyi)* tail flag at snakes (Owings & Coss, 1977; Hennessy et al., 1981) and increase the temperature of their tail when tail flagging at infrared-sensitive rattlesnakes (Rundus et al., 2007). In Uinta ground squirrels *(Spermophilus armatus)*, tail flicks are thought to be intention movements that also communicate species identity (Balph & Stokes, 1963), and tail flicking in thirteen-lined ground squirrels may have a similar function (Wistrand, 1974).

Tree squirrels can hold their tails in a wide range of potential positions. Squirrels can hold their tail flush against their dorsum, ventrum, or sides, fully extend their tail behind their body, or hold their tail at almost any intermediate angle (personal observation). They can bend their tail in any direction (personal observation), and bend their tail simultaneously at both the base and at least one other point along the tail's length (Essner, 2003). This versatility provides the potential for a great deal of information to be encoded in the position of a squirrel's tail. Other species are known to communicate via the position of their tail (see for example: Goddard & Beilharz, 1985 (domestic dogs); McLeod, 1996 (wolves), Pemberton & Renouf, 1993 (Tasmanian devils); Feh, 2005 (Equids)). By only considering tail movements and piloerection, previous studies on squirrel tail communication may have failed to explore all of the potential information conveyed by the tail's position.

Because a squirrel's tail position is defined by multiple aspects that the squirrel can apparently manipulate independently (e.g. angle to body, degree of curvature), the potential exists for squirrels to simultaneously produce multiple signals with their tails. Simultaneous communication of multiple types of information has been documented in other species. For example, meerkats *(Suricata suricatta)* simultaneously encode predator type and urgency in their alarm calls (Manser, 2001). Honeybees *(Apis mellifera)* simultaneously communicate both the distance and direction of a food source in their waggle dance (von Frisch, 1967).

Gray squirrel societies have a well-established dominance hierarchy, in which males dominate females and older individuals dominate younger individuals (Allen & Aspey, 1986). Many species, including jacky dragons *(Amphibolurus muricatus*; Ord et al., 2002), horses *(Equus caballus*; Feh, 2005), and wolves *(Canis lupus*; McLeod, 1996) use tail posture to communicate about dominance relationships. However, to my knowledge, no studies have ever investigated whether gray squirrels communicate with tail postures in dominance-related contexts.

In this observational study I examined three different variables that describe the position of a squirrel's tail. I investigated whether these variables communicate information, and proposed hypotheses about the nature of the information contained in all three variables.

METHODS

Site Description

I conducted all observations at a single birdfeeder in the front yard of a suburban residence in Wesley Hills, NY, USA (41º9'25.524"N, 74º4'45.3612"W). Although it would have been preferable to observe squirrels at multiple locations, eastern gray squirrels have fluid social groups, and cannot readily be observed in groups under many conditions (Thompson, 1978). The fallen sunflower seeds beneath the birdfeeder attracted multiple squirrels to the same location, and allowed me to observe interactions between individuals, which is crucial for an investigation of communication. While the an artificial food source might change the frequency of agonistic interactions, it is less likely to change the signals used in agonistic interactions. The birdfeeder was positioned on a pole between a house and a single-lane street, 8.8 meters from the house and 11 meters from the street. There was at least one tree or shrub within a 5-8 m radius of the birdfeeder in each direction, in which the squirrels took cover when confronted with a threatening stimulus. The squirrels generally remained within a 2-3 m radius of the pole, eating the sunflower seeds that had spilled on the ground. Most of the fallen sunflower seeds were concentrated in the area within a 1.5 m radius of the birdfeeder pole. I observed the squirrels through the second-floor window of the house, which served as a blind. At the start of the study, the house had existed in its current location for 35 years, and the birdfeeder had existed in its current location for 12 years. As the maximum-recorded lifespan of a wild gray squirrel is 12.5 years (Barkalow & Soots, 1975), any squirrels born in the immediate area were almost certainly habituated to the house and the birdfeeder. Any recent immigrants likely dispersed from a similar suburban area, and would also have been habituated to houses, if not necessarily to birdfeeders.

Observation

I conducted observations at arbitrary intervals throughout the day, whenever I saw two or more squirrels at the birdfeeder. Each observation session lasted until the squirrels left or until observer fatigue set in, whichever came first. I used a Panasonic SDR-H80 camcorder with an up to 70x optical zoom to videotape the squirrels. I then uploaded the video clips to an iMac computer and used QuickTime Player to view them, pausing and rewinding as necessary to avoid missing any behavior.

Dominance

Within each video clip, I recorded the relative dominance ranks of each squirrel in the clip. If squirrel A chased, attacked, or lunged towards squirrel B, I assumed that squirrel A was dominant to squirrel B. Similarly, if squirrel B shied away from or was chased by squirrel A, I assumed that squirrel B was subordinate to squirrel A. I never observed a case where one squirrel behaved both “dominantly” and “subordinately” towards a given conspecific within the same video clip. I was unable to keep track of individuals’ identities between video clips. As such, I do not know how many individual squirrels I sampled during my study.

Data Collection

My data collection protocol differed slightly between the first half and second half of the study. All variables recorded in this study are defined in Table 1.

Table 1. Definitions of the variables recorded during this study and their states

Variable	Definition	States	Comments
Dominance Rank	Relative social status compared to other squirrel in video clip	Dominant=chased or attacked other squirrel at least once during video clip Subordinate=avoided or was chased by other squirrel at least once during video clip	
Tightness	How tightly tail was bent (angle b/t distal and proximal halves of tail)	0=rigidly straight 1=relaxed but barely bent 2=very loosely bent (≥90º b/t halves of tail) 3=loosely bent (<90º b/t halves of tail) 4=tightly bent (0º b/t halves of tail)	
Portion Bent	How much of tail was bent (position of kink along length of tail)	0=tail not bent 1=tip of tail bent (kink in distal half) 2=whole tail bent (kink midway or in proximal half)	Part I: only recorded states 1 & 2
Touching Ground	Whether or not tail was touching the ground	0=not touching 1=touching	
Agonistic Behavior	Aggression and avoidance behavior	Aggression=lunging at, jumping at, running at, chasing, biting, or staring at conspecific (if staring squirrel is dominant) Avoidance=shying or running away from conspecific	Only recorded in Part I, when squirrel exhibited either aggression or avoidance
Approaching	Whom the squirrel approached	Appr. Dom=approached more dominant conspecific (or dom & sub simultaneously) Appr. Sub=approached more subordinate conspecific	Only recorded in Part I, when squirrel approached a conspecific
Aggression	Degree of dominant squirrel's aggression	0=no aggression 1=sat up or lifted head 2=turned towards subordinate 3=looked at subordinate 4=lunged or jumped at subordinate 5=ran at subordinate, stopped chase when subordinate fled 6=ran at subordinate, continued chase after subordinate fled	Only recorded in Part II, during final second of an approach
Distance Displaced	Distance subordinate moved away from approaching dominant	0=no visible reaction 1=shied away without moving 2=moved away w/o leaving seed patch or equivalent distance (0.5-1.5 m) 3=left seed patch or equivalent distance (>1.5 m), but stayed in sight of observer 4=moved out of sight (>5m)	Only recorded in Part II, during final second of approach where dominant squirrel approached subordinate
Approach Success	Whether or not subordinate "succeeded" in approaching dominant	Success=remained within 1 m of dominant squirrel for at least 1 second, or dominant moved away Failure=did not meet above criteria	Only recorded in Part II, during final sec of approach where subordinate approached dominant

Part I: August 2008 through December 2008

During this period, I recorded data in any circumstance, as long as at least two squirrels were present. I identified three variables that described the curvature of a squirrel's tail: *Tightness*, *Portion Bent*, and *Touching Ground*. *Tightness* described how tightly the squirrel's tail was bent, or the angle between the distal and proximal halves of the tail. *Portion Bent* described how much of the tail was bent; that is, whether the kink in the tail was located in the distal or proximal half. During Part I of the study, *Portion Bent* was only defined when the tail was at least somewhat bent. *Touching Ground* was a binary variable that indicated whether or not the squirrel's tail was touching the ground. At each second of each video clip, I recorded the values of *Tightness*, *Portion Bent*, and *Touching Ground* for each squirrel. I also recorded whether a squirrel was exhibiting aggression, avoidance behavior, or neither, and whether a squirrel was approaching a more dominant squirrel, approaching a more subordinate squirrel, or not approaching any conspecific. If a squirrel approached two conspecifics simultaneously, one of whom was dominant and one of whom was subordinate, I scored the approach as "approaching dominant". I excluded all instances of "neither aggression nor avoidance" and all instances of "not approaching any conspecific" from my analyses. The data collected in Part I of my study were extracted from a total of four video clips collected on four separate days (8 Aug 2008, 15 Aug 2008, 10 Nov 2008, 14 Dec 2008), and totaled 182 seconds.

Part II: December 2009, January 2010, May 2010, June 2010

During this period, I only recorded data when one squirrel was approaching another. I redefined the variable *Portion Bent* to include a third state, which indicated that the squirrel's tail was not bent at all. I did not change the definition of *Tightness* or

Touching Ground. I recorded the values of all three variables for both the approaching and approached squirrels at each second of each approach. I defined an “approach” as beginning when one squirrel began to approach another. The end of the approaching event was defined differently depending on whether the approaching squirrel was subordinate or dominant. If the approaching squirrel was subordinate, the approaching event ended when one of the following conditions was met:

1) The approaching squirrel was chased away by dominant squirrel
2) The approaching squirrel stopped approaching for at least one second
3) The dominant squirrel moved away from the approaching subordinate squirrel
4) The approaching squirrel turned around without stopping for more than 1 second and moved away from the dominant squirrel

If the approaching squirrel was dominant, the approaching event ended when one of the following conditions was met:

1) The subordinate squirrel moved away from the approaching dominant squirrel or inclined its body away from the dominant squirrel (avoidance behavior)
2) The approaching squirrel stopped for at least 1 second

At the final second of each approach, I recorded the degree of aggression on the part of the dominant squirrel. When the approaching squirrel was subordinate, I recorded whether or not the approach was “successful”. I defined a “successful” approach as occurring when the approaching subordinate squirrel remained within one meter of the dominant squirrel for at least one second, or when the dominant squirrel moved away from the approaching subordinate. When the approaching squirrel was dominant, I recorded the approximate distance that the subordinate squirrel moved away from the approaching dominant squirrel on an ordinal scale. The data collected in Part II of my study came from a total of twelve video clips collected on eight different days (18 Dec 2009, 22 Dec 2009, 23 Dec 2009, 25 Dec 2009, 1 Jan 2010, 4 Jan 2010, 27 May 2010, and 3 Jun 2010). It included 35 instances where a dominant squirrel approached a more subordinate squirrel, and 53 instances where a subordinate squirrel approached a more dominant squirrel. The "dominant approaching subordinate" data came from ten different video clips, and totaled 119 seconds. The "subordinate approaching dominant" data also came from ten different video clips, and totaled 159 seconds.

I designated the final second of a given approach as time "T", the penultimate second "T-1", and so on. For all three tail position variables, I calculated an estimate of the transition probabilities between T-2 and T-1, and T-1 and T. As many approaches were no longer than two seconds, I did not calculate any transition probabilities for times earlier than T-2. Because the T-2→T-1 transition probabilities were very similar to the T-1→T transition probabilities, the process was most likely Markovian. I thus assumed that events at a particular time could best be predicted simply by considering the events at the immediately preceding second. Consequently, in my analyses, I only included the variable values that were recorded at the final second of an approach (time T).

Statistical Analysis

I conducted all statistical analyses with the software program JMP® Version 8.0.2 of SAS Institute Inc.

RESULTS: TIGHTNESS OF TAIL CURVATURE & PORTION OF TAIL BENT

Part I of the Study

Given that agonistic behavior (aggression or avoidance) occurred, squirrels exhibited aggression 78.3% (18/23) of the time, and avoidance behavior 21.7% (7/23) of the time when their tail was loosely bent. When their tail was tightly bent, they exhibited aggression 11.1% (1/9) of the time, and avoidance 88.9% (8/9) of the time (Pearson Chi-square test: X^2_1=12.092, P=0.0005).

Squirrels always exhibited avoidance (never aggression) when only the tip of their tail was bent. When their whole tail was bent, they were aggressive 61.1% (11/18) of the time, and exhibited avoidance behavior 38.9% (7/18) of the time (Pearson Chi-square test: X^2_1=4.889, P=0.0270).

Given that a squirrel's tail was bent, dominant squirrels bent their whole tail (as opposed to only the tip) 94.1% (16/17) of the time, and subordinate squirrels bent their whole tail 29.4% (5/17) of the time (Pearson Chi-square test: X^2_1=15.070, P<0.0001). However, there was no significant relationship between dominance rank and how tightly the tail was bent.

When approaching a more dominant conspecific, squirrels bent their whole tail 33.3% (6/18) of the time. When approaching a more subordinate conspecific, squirrels bent their whole tail 93.8% (15/16) of the time (Pearson Chi-square test: X^2_1=13.092, P=0.0003).

Part II of the Study

There was a significant positive correlation between how tightly the dominant squirrel's tail was bent and the portion of the dominant squirrel's tail that was bent

(Linear Regression: $F_{1,79}$=80.334, P<0.0001, R^2=0.504). There was also a significant positive correlation between how tightly the subordinate squirrel's tail was bent and the portion of the subordinate squirrel's tail that was bent (Linear Regression: $F_{1,73}$=62.845, P<0.0001, R^2=0.463).

I conducted a multiple linear regression with the degree of aggression by the dominant squirrel as the response variable (Multiple Linear Regression: $F_{10,61}$=2.632, P=0.0099, R^2=0.301). The regressors consisted of the dominant squirrel's *Tightness* and *Portion Bent*, the subordinate squirrel's *Tightness* and *Portion Bent*, and the interaction effects for each possible pair of these four variables. The only regressors with significant or marginally significant parameter estimates were the following three interaction effects: Dominant's *Tightness**Subordinate's *Tightness* (P=0.0290), Dominant's *Tightness**Subordinate's *Portion Bent* (P=0.0191), and Dominant's *Portion Bent**Subordinate's *Tightness* (P=0.0527). I conducted another multiple linear regression with the same response variable as before and these three interaction effects as the only regressors (Multiple Linear Regression: $F_{3,68}$=6.420, P=0.0007, R^2=0.221). All three interaction effects had statistically significant parameter estimates (*Dom. Tightness***Sub. Tightness*=0.420, P=0.0274; *Dom. Tightness***Sub. Port. Bent*= –0.666, P=0.0025; and *Dom. Port. Bent***Sub. Tightness*=0.433, P=0.0292).

When both the dominant and the subordinate squirrels' tails were tightly bent, the dominant squirrel tended to react with greater aggression. When the dominant squirrel's tail was tightly bent and the subordinate's tail was loosely bent, the dominant squirrel tended to react with less aggression. When the dominant's tail was loosely bent and the subordinate's was tightly bent, the dominant squirrel tended to react with less aggression, and when both squirrel's tail were loosely bent, the dominant squirrel tended to react with greater aggression (Table 2).

Table 2. The effect of the interaction between the dominant squirrel's *Tightness* and the subordinate squirrel's *Tightness* on the dominant squirrel's aggression

Dominant's Tightness	Subordinate's Tightness	Dominant's Aggression
Tail tightly bent	Tail tightly bent	Higher
Tail tightly bent	Tail loosely bent	Lower
Tail loosely bent	Tail tightly bent	Lower
Tail loosely bent	Tail loosely bent	Higher

When the dominant squirrel's tail was tightly bent and the subordinate bent a large portion of its tail, the dominant squirrel tended to react with less aggression. When the dominant squirrel's tail was tightly bent and the subordinate bent a small portion of its tail, the dominant squirrel tended to react with greater aggression. When the dominant's tail was loosely bent and the subordinate bent a large portion of its tail, the dominant tended to react with greater aggression. When the dominant's tail was loosely bent and the subordinate bent a small portion of its tail, the dominant squirrel tended to react with less aggression (Table 3).

Table 3. The effect of the interaction between the dominant squirrel's *Tightness* and the subordinate squirrel's *Portion Bent* on the dominant squirrel's aggression

Dominant's Tightness	Subordinate's Portion Bent	Dominant's Aggression
Tail tightly bent	Large portion bent	Lower
Tail tightly bent	Small portion bent	Higher
Tail loosely bent	Large portion bent	Higher
Tail loosely bent	Small portion bent	Lower

When the dominant squirrel bent a large portion of its tail and the subordinate squirrel's tail was loosely bent, the dominant squirrel tended to react with less aggression. When the dominant squirrel bent a large portion of its tail and the subordinate's tail was tightly bent, the dominant squirrel tended to react with greater aggression. When the dominant squirrel bent a small portion of its tail and the subordinate's tail was loosely bent, the dominant squirrel tended to react with greater aggression. When the dominant bent a small portion of its tail and the subordinate's tail was tightly bent, the dominant squirrel tended to react with less aggression (Table 4).

Table 4. The effect of the interaction between the dominant squirrel's *Portion Bent* and the subordinate squirrel's *Tightness* on the dominant squirrel's aggression

Dominant's Portion Bent	Subordinate's Tightness	Dominant's Aggression
Large portion bent	Tail tightly bent	Higher
Large portion bent	Tail loosely bent	Lower
Small portion bent	Tail tightly bent	Lower
Small portion bent	Tail loosely bent	Higher

Squirrels bent a large portion of their tail 47.7% (63/132) of the time in winter, and only 31.8% (14/44) of the time in summer (2-Proportion Z Test: Z=1.926, N_1=132, N_2=44, P=0.0541). By contrast, there was no relationship between season and how tightly a squirrel's tail was bent (Pearson Chi-square Test: $X^2{}_1$=0.048, P=0.8263).

DISCUSSION: TIGHTNESS OF TAIL CURVATURE & PORTION OF TAIL BENT

Although it is impossible to know for certain from purely observational data, it seems likely that squirrels communicate information with both the tightness of their tail's curvature and the portion of their tail that is bent. Communication has been defined as "the provision of information that can be utilized by a receiver to make a decision" (Bradbury & Vehrencamp, 1998). Both the *Tightness* and *Portion Bent* of a subordinate squirrel significantly contributed to predicting the severity of subsequent aggression on the part of a more dominant conspecific. This supports the hypothesis that subordinate squirrels' tail postures communicate information, which dominant squirrels use to make a decision about how aggressively to react to the subordinate squirrel. One way to experimentally determine whether this is the case would be to present a high-ranking squirrel with a robotic squirrel with a movable tail, and test the effects of various tail positions on the level of aggression exhibited by the test subject. Robotic squirrels with movable tails have been successfully used with eastern gray squirrels in order to test receivers' responses to various signals (Partan et al., 2009; 2010).

In my multiple regression model, only three of the interactions between the dominant and subordinate squirrels' *Tightness* and *Portion Bent* were significant predictors of the dominant squirrel's aggression; the main effects were not significant. In addition, all three significant interaction effects were antagonistic in nature; the relationship between the dominant squirrel's tail position and the dominant squirrel's aggression was positive given one position of the subordinate squirrel's tail, and negative given the opposite position. Because of this, it is not possible to accurately predict the level of aggression that a dominant squirrel will exhibit by only considering the tail position of the subordinate squirrel or the tail position of the dominant squirrel. The importance of the interaction between the tail positions of the two squirrels implies that squirrels make their decisions about how aggressively to behave towards a conspecific based on the interplay of their own internal state with the signals they receive from the other squirrel. The relative complexity of this decision making process most likely allows for more optimal behavior in a wider range of circumstances than if squirrels made their decision without regard to how their own internal state relates to that of the conspecific with whom they are interacting.

If *Tightness* and *Portion Bent* are communicative, it is unlikely that they communicate the same type of information, even though they were significantly correlated. For example, when the dominant squirrel's tail was tightly bent and the subordinate bent a large portion of its tail, the dominant squirrel tended to react with lower aggression. If *Tightness* and *Portion Bent* communicated the same information, I would have expected the dominant squirrel to react similarly in the reverse situation, where the dominant squirrel bent a large portion of its tail and the subordinate's tail was tightly bent. However, this was not the case. When the dominant squirrel bent a large portion of its tail and the subordinate's tail was tightly bent, the dominant squirrel tended to react with higher aggression.

I speculate that how tightly a squirrel's tail is bent communicates the squirrel's level of confidence, with a more loosely bent tail indicating greater confidence. Here I define confidence as the individual's internal assessment of its status relative to interacting conspecifics. This state of confidence could be based on its assessment of its own health, vigor, and fighting ability as well as on prior interactions with conspecifics. I speculate that the portion of a squirrel's tail that is bent communicates the squirrel's degree of hunger, with a larger portion bent indicating greater hunger. These hypotheses are consistent with all of my results, including the interactions between the tail positions of the dominant and subordinate squirrel. Nonetheless, they remain speculative, and more research is necessary to verify whether they are correct. However, the nature of the interactions between the tail positions of the dominant and subordinate squirrel rules out the competing hypotheses that *Tightness* communicates level of aggressive intent and *Portion Bent* communicates level of fear.

In addition, the fact that squirrels were more likely to bend a large portion of their tail during the winter supports the hypothesis that bending a larger portion of the tail signals a higher degree of hunger. As food is generally scarcer in the winter months (Gurnell, 1996), it is reasonable to expect that the squirrels I observed were hungrier in December than in May and June.

RESULTS: TAIL CONTACT WITH THE GROUND

Part I of the Study

Given that agonistic behavior (aggression or avoidance) occurred, squirrels exhibited aggression 36.6% (15/41) of the time and avoidance behavior 63.4% (26/41) of the time when their tail was not touching the ground. When their tail was touching the ground, they exhibited aggression 100% (10/10) of the time (Pearson Chi-square Test: X^2_1=12.937, P=0.0003).

During approaches in which the approaching squirrel's tail was not touching the ground, the approaching squirrel was subordinate to the squirrel being approached 74% (37/50) of the time. By contrast, during approaches in which the approaching squirrel's tail was touching the ground, the approaching squirrel was subordinate to the squirrel being approached only 36.8% (7/19) of the time (Pearson Chi-square Test: X^2_1=9.869, P=0.0072).

Part II of the Study

I conducted an ANOVA with the degree of aggression by the dominant squirrel as the response variable (ANOVA: $F_{3,83}$=5.924, P=0.0010, R^2=0.176). The factors I included were whether the dominant squirrel's tail touched the ground, whether the subordinate squirrel's tail touched the ground, and the interaction of these two variables.

The dominant squirrel tended to behave less aggressively when its own tail was touching the ground (Parameter Estimate 1= –1.640, P=0.0001), and also tended to behave less aggressively when the subordinate squirrel's tail was touching the ground (Parameter Estimate 2= –1.058, P=0.0897). The interaction effect of these two variables was not significant (Parameter Estimate 3=1.131, P=0.1557).

Using only the data collected when a dominant squirrel approached a subordinate squirrel, I conducted another ANOVA with the same factors, but with the distance that the subordinate squirrel moved away from the approaching dominant squirrel as the response variable (ANOVA: $F_{3,30}$=7.048, P=0.0010, R^2=0.413). The subordinate squirrel tended to move less far from the approaching dominant squirrel when the dominant squirrel's tail was touching the ground (Parameter Estimate 1= –1.463, P=0.0005). The subordinate also tended to move less far away from the dominant squirrel when the subordinate's tail was touching the ground (Parameter Estimate 2= –1.533). The interaction effect of these two variables was marginally significant (Parameter Estimate 3=1.082, P=0.0985).

The dominant squirrel's *Touching Ground* had a greater effect on the distance that the subordinate squirrel moved away when the subordinate squirrel's tail was not touching the ground. Likewise, the subordinate squirrel's *Touching Ground* had a greater effect on the distance that the subordinate moved away when the dominant squirrel's tail was not touching the ground.

Finally, when a subordinate squirrel approached a dominant squirrel, the subordinate squirrel's approach was "successful" 35.7% (10/28) of the time that the subordinate's tail touched the ground, and was "successful" only 12% (3/25) of the time that the subordinate's tail did not touch the ground (Pearson Chi-square Test: X^2_1=4.012, P=0.0452). There was no relationship between the success of the subordinate squirrel's approach and whether the dominant squirrel's tail was touching the ground (Pearson Chi-square Test: X_1=0.164, N=53, P=0.6855).

DISCUSSION: TAIL CONTACT WITH THE GROUND

It is very likely that information is encoded in whether or not a squirrel's tail touches the ground. Based on the observed patterns, it is likely that the information encoded in tail contact with the ground informs the decisions of receiving squirrels.

I speculate that when a squirrel's tail is held off of the ground, it indicates that the squirrel is more likely to move. Conversely, when the tail is held in contact with the ground, it indicates that the squirrel is less likely to move. This hypothesis explains the fact that given some form of agonistic behavior (aggression or avoidance), squirrels were more likely to exhibit aggression when their tail was touching the ground, and were more likely to exhibit avoidance behavior when their tail was not touching the ground. Although both behaviors often involve some movement, an aggressive squirrel (tail touching ground) is probably less willing to move entirely away from the food patch than a squirrel that runs or shies away from a conspecific (tail not touching ground).

Squirrels were more likely to hold their tails off of the ground when approaching a more dominant squirrel because they are more likely to have to quickly flee when approaching a dominant squirrel. Squirrels were more likely to hold their tails in contact with the ground when approaching a more subordinate squirrel because they are less likely to flee from a subordinate.

Dominant squirrels tended to be more aggressive when their tail was not touching the ground because high aggression, such as chasing a conspecific, entails more movement than low aggression (e.g. lunging at a conspecific) or no aggression at all. Dominant squirrels may have been less aggressive toward subordinates whose tails were touching the ground because a subordinate squirrel that is unlikely to move from its present location is also unlikely to attempt to take the dominant squirrel's food or otherwise threaten it. Conversely, subordinates who are less willing to move may be less fearful and therefore less easy "targets" than subordinates who are very willing to move.

Subordinate squirrels tended to move less far away from a dominant squirrel whose tail was touching the ground, because a dominant squirrel that is unlikely to move much closer is also less likely to attack the subordinate squirrel. Likewise, the fact that subordinate squirrels moved less far when their own tail was touching the ground is in concordance with my hypothesis that holding one's tail in contact with the ground signals a decreased likelihood of movement.

The dominant squirrel's *Touching Ground* had a greater effect on the distance that the subordinate squirrel moved away when the subordinate squirrel's tail was not touching the ground. This makes sense because a subordinate squirrel that is likely to move (tail not touching ground) is probably more sensitive to the state of the dominant squirrel than a subordinate squirrel with very little intention of moving (tail touching ground).

The subordinate squirrel's *Touching Ground* had a greater effect on the distance that the subordinate squirrel moved away when the dominant squirrel's tail was not touching the ground. This makes sense because when the dominant squirrel has a high likelihood of moving (tail not touching ground), it may also be more likely to chase the subordinate squirrel, so it is advantageous for the subordinate to be more sensitive to the dominant squirrel's state.

My hypothesis also explains why subordinate squirrels whose tails were touching the ground were more likely to "succeed" in approaching a dominant squirrel. I defined a "successful" approach in part as one where the approaching squirrel does not turn around and flee, which is less likely to occur if the approaching squirrel is not very willing to move (tail touching ground).

If contact between a squirrel's tail and the ground does provide information about the probability that the squirrel will move, it may or may not be a "true" signal that evolved for the purpose of communication. Since allowing the tail to lie on the ground is presumably a more relaxed position than holding it off of the ground, squirrels who are not about to move may hold their tail in contact with the ground for no other reason than that they are more relaxed. Since the tail is often lifted off the ground and extended behind the body for balance during locomotion (Hayssen, 2008), squirrels who are about to move may lift their tails off the ground for no other reason than balance. It is possible that communicating the probability of movement has no adaptive value for the signaling squirrel, but that receiving squirrels are able to extract that information by seeing whether or not a conspecific's tail is touching the ground. Conversely, it is also possible that squirrels have evolved to communicate the probability that they will move. A potential adaptive function of this could be to forewarn other squirrels that the signaler is or is not about to flee or move closer, thus potentially decreasing the likelihood that the receiver will attack the signaler. In this case, what was originally a non-communicative body posture associated with locomotion (i.e. lifting the tail off the ground) may have become ritualized into a display.

DISCUSSION: GENERAL

Because the tail of a tree squirrel has such versatility of movement, it is possible that more than three signals could be conveyed by the tail simultaneously. In addition to the tightness of tail curvature, portion of the tail bent, and whether the tail is touching the ground, information might be encoded in the horizontal or vertical angle of the tail, the degree of piloerection, the direction toward which the tail tip is curved, or any other aspect of tail position. Future research is needed to determine whether any of these aspects are used in communication. However, squirrels use their tails for purposes other than communication, such as balance (Hayssen, 2008) and thermoregulation (Muchlinski & Shump, 1979). Because of this, it might be advantageous for receivers to have evolved a mechanism of determining whether conspecifics are communicating, and for signalers to have evolved a mechanism of indicating when they are communicating. Additional studies should be conducted to determine whether such mechanisms exist.

The fact that I obtained significant results despite small sample sizes strongly suggests the existence of real relationships. Nonetheless, future research should use a more systematic approach to sampling, with a larger sample size. If possible, individual identity should be noted across video clips, in order to avoid collecting all data from a few squirrels. Gray squirrel tail communication should also be investigated in the absence of a provisioned food source, in order to obtain more naturalistic behavior.

REFERENCES

Allen, D. S., & Aspey, W. P. 1986. Determinants of social dominance in eastern gray squirrels *(Sciurus carolinensis)*: A quantitative assessment. *Animal Behaviour*, **34**, 81-89.

Bakken, A. 1959. Behavior of gray squirrels. *Proceedings of the Southeastern Association of Game & Fish Commissioners*, **13**, 393-406.

Balph, D. F. & Stokes, A. W. 1963. On the ethology of a population of Uinta ground squirrels. *American Midland Naturalist*, **69**, 106-126.

Barkalow, F. S., Jr. & Soots, R. F., Jr. 1975. Life span and reproductive longevity of the gray squirrel, *Sciurus c. carolinensis* Gmelin. *Journal of Mammalogy*, **56**, 522-524.

Bradbury, J. W. & Vehrencamp, S. L. 1998. *Principles of Animal Communication*. Sunderland, MA: Sinauer Associates.

Clark, R. W. 2005. Pursuit-deterrent communication between prey animals and timber rattlesnakes *(Crotalus horridus)*: the response of snakes to harassment displays. *Behavioral Ecology and Sociobiology*, **59**, 258-261.

Essner, R. L., Jr. 2003. Locomotion, morphology, and habitat use in arboreal squirrels (Rodentia: Sciuridae). Ph.D. thesis, The Ohio State University.

Farentinos, R. C. 1974. Social communication of the tassel-eared squirrel *(Sciurus aberti)*: A descriptive analysis. *Zeitschrift für Tierpsychologie*, **34**, 441-458.

Feh, C. 2005. Relationships and communication in socially natural horse herds. In: *The Domestic Horse: The Origins, Development, and Management of Its Behaviour* (Ed. by D. S. Mills & S. M. McDonnell), pp. 83-93. Cambridge, UK: Cambridge University Press.

Goddard, M. E. & Beilharz, R. G. 1985. Individual variation in agonistic behaviour in dogs. *Animal Behaviour*, **33**, 1338-1342.

Gurnell, J. 1996. The effects of food availability and winter weather on the dynamics of a grey squirrel population in southern England. *Journal of Applied Ecology*, **33**, 325-338.

Hayssen, V. 2008. Patterns of body and tail length and body mass in Sciuridae. *Journal of Mammalogy.* **89,** 852-873.

Hennessy, D. F., Owings, D. H., Rowe, M. P., Coss, R. G., & Leger, D. W. 1981. The information afforded by a variable signal: Constraints on snake-elicited tail flagging by California ground squirrels. *Behaviour*, **78**, 188-226.

Manser, M. B. 2001. The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency. *Proceedings of the Royal Society of London B*, **268**, 2315-2324.

McLeod, P. J. 1996. Developmental changes in associations among timber wolves *(Canis lupus)* postures. *Behavioural Processes*, **38**, 105-118.

Muchlinski, A. E. & Shump, K. A., Jr. 1979. The Sciurid tail: a possible thermoregulatory mechanism. *Journal of Mammalogy*, **60**, 652-654.

Ord, T. J., Peters, R. A., Evans, C. S., Taylor, A. J. 2002. Digital video playback and visual communication in lizards. *Animal Behaviour*, **63**, 879-890.

Owings, D. H. & Coss, R. G. 1977. Snake mobbing by California ground squirrels: Adaptive variation and ontogeny. *Behaviour*, **62**, 50-69.

Partan, S. R., Larco, C. P., & Owens, M. J. 2009. Wild tree squirrels respond with multisensory enhancement to conspecific robot alarm behavior. *Animal Behaviour*, **77**, 1127-1135.

Partan, S. R., Fulmer, A. G., Gounard, M. A. M., & Redmond, J. E. 2010. Multimodal alarm behavior in urban and rural gray squirrels studied by means of observation and a mechanical robot. *Current Zoology*, **56**, 313-326.

Rundus, A. S., Owings, D. H., Joshi, S. S., Chinn, E., & Giannini, N. 2007. Ground squirrels use an infrared signal to deter rattlesnake predation. *Proceedings of the National Academy of Sciences*, **104**, 14372-14376.

Steele, M. A. & Koprowski, J. L. 2001. *North American Tree Squirrels*. Washington, DC: Smithsonian Institution Press.

Thompson, D. C. 1978. The social system of the grey squirrel. *Behaviour*, **64**, 305-328.

von Frisch, K. 1967. *The Dance Language and Orientation of Bees*. Cambridge, MA: Harvard University Press.

Wistrand, H. 1974. Individual, social, and seasonal behavior of the thirteen-lined ground squirrel *(Spermophilus tridecemlineatus)*. *Journal of Mammalogy*, **55**, 329-347.