A Statistical Analysis and Decoding of the Tail Communication System of Eastern Gray Squirrels (*Sciurus carolinensis*)

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Introduction

A great deal of research has been conducted on squirrel communication, most of which has focused on ground squirrels. Slobodchikoff and his colleagues have decoded a significant portion of the vocal communication of Gunnison's prairie dog (a type of ground squirrel), and Rundus and his colleagues have made several novel discoveries about the communication of California ground squirrels. However, very little is known about the visual communication of tree squirrels, beyond the simple facts that they communicate in part with their tails and that a higher rate and degree of flicking is correlated with a higher degree of agitation (Steele and Koprowski, 2001; Friend, 2004). The object of this two-year, four-season study was to investigate the tail communication system of eastern gray squirrels (*Sciurus carolinensis*), a type of tree squirrel.

Data Collection Methods

Throughout this study, squirrels were observed at a variety of locations, but the site at which the most communication was observed was an artificial food source (a bird feeder). Eastern gray squirrels are naturally semi-solitary and do not interact with each other very frequently under normal circumstances (Koprowski, 1994), but because they congregated at the bird feeder, they were forced to interact with each other, and a great deal of tail communication was observed. Sometimes soybeans were used to attract more squirrels to the bird feeder. The researcher observed the squirrels interacting at the bird feeder through the window of his house, in order to avoid influencing their behavior with his presence.

The first difficulty faced in decoding tail communication was recording all the relevant data at the rate at which squirrels communicate (often several tail signals per second). A complex shorthand code was developed for recording data quickly in the field (Figure 1 shows examples) and data recording charts were prepared. In the first year (Winter 2007) of the investigation, the following variables were recorded: tail position, direction of tail movement, degree of tail movement, and rate of tail movement of the communicating squirrel (these were collectively called "tail state"). Simultaneous activities of the communicating squirrel, external stimuli that may have affected the squirrel's behavior, and the reactions of other squirrels to the tail state and activities of the communicating squirrel were also recorded. In the first year of the investigation all of these data were recorded by hand and *in situ* as the squirrels communicated, using the shorthand code.

In the second year (Jun. 2007- Feb. 2008), a video camera was used, making it possible to record more data as well as details too complicated to record by hand in a split second. The videos were uploaded to the computer and analyzed frame-by-frame, to ensure that no interactions were missed. Because more information could now be collected and similar tail states and activities could be better differentiated, the shorthand code was revised to include more symbols and new categories of data. Figure 1 displays the tail position codes used in the second year of the investigation.

Hypotheses

In the first year of research, several hypotheses about the possible meanings of different tail states were developed, based on months of previous casual observation. The Chi-squared statistic was used to determine if there was a causal relationship between any of the tail state components (tail position, direction of tail movement, degree of tail movement, and rate of tail movement) and each of the underlined variables listed in below. The research hypotheses with significant p-values in the winter of 2007 are numbered and listed as follows.

1) There is a relationship between the tail position and the <u>other activities</u> of a single given squirrel ($p < .0001$).

2) There is a relationship between the tail position of a given squirrel and the <u>external stimuli</u> present ($p < .0001$).

3) There is a relationship between the tail position of a given squirrel and the <u>threatening stimuli</u> present (i.e. moving motorized vehicles and humans) ($p = .0223$).

4) There is a relationship between the tail position of a given squirrel and whether that squirrel is currently exhibiting <u>dominant or submissive behavior</u> ($p = .0263$).

During the analysis of the second data set, the researcher tested hypotheses based on the questions that the first analysis suggested. In addition to this, old hypotheses that previously had p-values greater than .05 were retested in order to determine if a larger sample size would alter the conclusions.

From the beginning of the 2007-2008 investigation the video camera's ability to record fine details had been fully exploited, and the codes for tail positions and activities had been accordingly revised to be much more specific than they had been in the winter of 2007. However, over-specifying details with additional codes created so many unique states in the variables that few relationships were statistically significant. To solve this problem, the researcher aggregated some of the codes into more general categories. For example, the three "activities" "EE", "E", and "E?" (severe, medium, and slight piloerection (hair raised), respectively) were combined into one symbol ("E") that stood for any piloerection, regardless of degree. Most of the aggregated symbols were the same as the more general symbols that had been used in the winter of 2007. Figure 1 shows the aggregated tail position codes. Figure 2 is a histogram of the tail positions from the winter of 2007. Figure 3 is a histogram of the tail positions from 2007-2008. Figure 4 is a histogram of the aggregated tail positions from 2007-2008.

Even after the aggregation of the "tail position" codes, "tail state" was so complex and included so many different variables that it was necessary to analyze its individual components (tail position, degree of tail movement, etc.) separately, as in the winter of 2007. As in the first year's data analysis, in 2008 several relationships were found to be significant. The hypotheses with significant p-values in the second year of the investigation are numbered and listed as follows.

1) There is a relationship between the rate of a given squirrel's tail movement and whether or not any other squirrels are reacting to that squirrel ($p < .0001$).

2) There is a relationship between the tail position of a given squirrel and that squirrel's hierarchical status ($p < .0001$).

3) There is a relationship between whether a given signaling squirrel is behaving dominantly or submissively and whether the reacting squirrel is behaving dominantly or submissively ($p < .0001$).

4) There is a relationship between whether a given signaling squirrel is behaving dominantly or submissively and the tail position of the reacting squirrel ($p = .0028$).

5) There is a relationship between a given squirrel's hierarchical status and whether or not that squirrel exhibits piloerection ($p < .0001$).

Results

All the variables observed in this study are categorical. Their values are discrete, qualitative states, unlike variables such as height and weight, whose values are expressed as decimal numbers. Consequently, contingency tables and the Chi-squared statistic were used to test hypotheses about relationships between any two variables. Contingency tables are two-dimensional arrays of the joint frequency distribution for two variables (see Figure 5). The Chi-squared statistic is a sum over all cells of the squared differences between the observed and expected numbers, divided by the expected number for each cell. The expected number is based on the null hypothesis that the frequency distributions of the two variables are independent of each other. The Chi-squared test indicates whether the frequency distribution of one variable depends on the state of another. The statistical analysis program JMP was used to calculate the value of the Chi-squared statistic, and its corresponding p-value. The p-value is the probability that the values of two variables could have coincided by chance and are not truly related (the null hypothesis). The alternate to the null hypothesis is that the likelihood of observing any state of one variable depends on the state of the other variable. The alternate is sometimes called the research hypothesis. The convention is to reject the null hypothesis if the p-value is *less* than .05. If the null hypothesis is rejected, the alternate hypothesis is accepted as true (though there is always the 5% chance that the variables were not truly related). However, failure to reject the null hypothesis does not mean that the variables are not related. A p-value could be greater than .05 due to an inadequate sample size or sources of error.

Eastern gray squirrels have a well-established social dominance hierarchy (Koprowski, 1994). It seemed to the researcher that dominant squirrels tended to hold their tails lower and more relaxed than submissive squirrels. Was this impression a reality? The data analysis conducted in the winter of 2007 had shown that the tail touching the ground (coded "D") was the most common tail position exhibited by squirrels behaving in a dominant manner, and that the tail held in the "b" position (a tail position of middling height) was the most common tail position for squirrels behaving submissively. These results seemed to support the hypothesis about tail position height and dominance, but more research was required.

Many animals, including some species of squirrels, warn others of impending danger, and even differentiate between different types of danger with different calls (Kiriazis and Slobodchikoff, 2006). Eastern gray squirrels are known to have a few vocal alarm calls (Thorington and Ferrell, 2006), but it was unclear if they signaled warnings with their tails as well. The significance of hypothesis #3 from the winter of 2007 (tail position by threatening stimuli) indicated that they might. Squirrels exhibited different tail positions depending on whether a moving motorized vehicle or a human was in the area. These results are particularly interesting because gray squirrels are mostly solitary. Why should a solitary creature invest energy to warn others of a potential threat when that energy could be spent escaping? Perhaps future studies could be conducted to determine if there is a relationship between tail position and the presence of different predators, or if squirrels are more likely to signal a warning if close relatives or sharers of their nests are nearby.

Hypothesis #1 from 2007-2008 reaffirms the fact that eastern gray squirrels communicate by tail signaling (ref. cit.). This study had already determined that tail position is crucial to communication. What about tail motion? If tail motion is part of the signaling, the inference is that squirrels are more likely to flick their tails when other squirrels are in the area and reacting to him/her. The hypothesis test showed that not only do eastern gray squirrels communicate with their tails, but also that the communication involves tail movement. Squirrels were most likely to exhibit no tail speed (coded "N") because they were most frequently not moving their tails. However, if they moved their tails at all, not only were they most likely to do it in the presence of another squirrel, but they were much more likely to flick their tail *rapidly* when interacting with another squirrel than when not interacting.

Hypotheses #2-5 from 2007-2008 were related to tail communication between dominant and submissive squirrels. In the winter of 2007, the researcher had discovered that there was a significant relationship between dominant/submissive *behavior* (*not* necessarily hierarchical status) and tail position. Based on trends observed among the data, the researcher had postulated that dominant squirrels were more likely to hold their tails lower to the ground than submissive squirrels. If this were the case it would be interesting for several reasons, especially because many other mammals (e.g. wolves, ring-tailed lemurs, and horses) do just the opposite: dominant individuals hold their tails *higher* in the air (Mech, 1999; Preston-Mafham and Preston-Mafham, 1999; http://www.esc.rutgers.edu/publications/general/fs525.htm). In the winter of 2007, the researcher had found that the tail position “b” (Winter 2007 code) was the most common tail position among squirrels behaving submissively, and that tail position “D” (Winter 2007 code) was the most common tail position among squirrels behaving dominantly. However, different methods for collecting, recording, and analyzing data were used in 2007-2008. Would the same results be obtained for similar tests of the relationship between tail position and dominance when using the 2007-2008 data?

In 2007-2008 a new variable, “dominance number”, was created, which indicated the relative hierarchical status of a particular squirrel to all of the other squirrels observed in that same video/session. Each squirrel was assigned a number based on his/her hierarchical status: “1” was the most dominant, “2” was the second most dominant, and so on. A squirrel’s relative dominance status was determined based on an observation of that squirrel’s behavior throughout the video/session. For example, if squirrel A consistently “stared down” and appeared to threaten squirrel B, but squirrel A was often chased by squirrel C, then it was inferred that squirrel C was dominant to squirrel A who was in turn dominant to squirrel B.

Hypothesis #2 expanded upon the hypothesis from the previous year (tail position by dominant/submissive *activity*). The test of hypothesis #2 showed that there was also a statistically significant relationship between tail position and dominance *number*.

Squirrels with lower dominance numbers (e.g. 1 and 2), which signify *greater* hierarchical status, were more likely to exhibit tail positions “s” (a fairly low position) and “B” (a fairly *high* position) than squirrels with the dominance number 4 (for example), who were most likely to exhibit tail position “b” (the same as submissively behaving squirrels in the winter of 2007). This seemed only partly in keeping with the significance of hypothesis #4 from the previous year (tail position by dominant/submissive activity), and seemed to only partially support the hypothesis that dominant squirrels hold their tails lower than submissive squirrels. These results suggested that while there almost certainly is a relationship between tail position and dominance, it is probably more complicated than the researcher’s original “low=dominant, high=submissive” idea.

It seemed probable that if a squirrel were behaving dominantly while interacting with another squirrel, then the squirrel with whom he/she was interacting would behave submissively. Hypothesis #3, (dominant/submissive activity of signaling squirrel by dominant/submissive activity of reacting squirrel), confirmed this.

It was postulated that dominant/submissive behavior on the part of a signaling squirrel would elicit a response in the tail position of a reacting squirrel. Testing hypothesis #4 showed that there is a relationship between dominant/submissive activity on the part of the signaling squirrel and the tail position of the reacting squirrel. This result strongly indicated that dominant or submissive behavior induces other squirrels to *respond* with particular tail positions. The most common response to dominant behavior was the (aggregate) tail position “s” closely followed by “H”, and the most common response to submissive behavior was the (aggregate) tail position “B”.

Piloerection has already been shown to play a part in squirrel communication (Thorington and Ferrell, 2006). Hypothesis #5 showed that squirrels behaving dominantly are much more likely to exhibit piloerection than squirrels behaving submissively.

Conclusion

The conclusions drawn from all the results of the two-year investigation can be summarized as follows. Eastern gray squirrels definitely communicate with their tails. Faster flicking is more characteristic of communication than slower flicking, possibly because fast flicking is indicative of agitation (ref. cit.), and most squirrel communication is probably centered on aggression and other agitation-inducing circumstances (Steele and Koprowski, 2001).

Different tail positions are positively correlated with different external stimuli. Eastern gray squirrels might warn other squirrels about impending danger with tail signals, and they may differentiate between different threats with different tail positions.

A squirrel's tail position is related to that squirrel's dominance. Dominant squirrels *may* tend to hold their tails lower than submissive squirrels. If this high/low hypothesis is true, then a possible explanation is that holding one's tail lower down is a more comfortable or relaxed position, and dominant squirrels are more relaxed and less worried about being chased away from their food or attacked by another squirrel. Tail position may also differ depending on whether a squirrel is merely higher or lower in the social hierarchy than his/her fellow or is actually behaving dominantly or submissively at the moment. Dominant/submissive behavior elicits a tail position response in reacting squirrels, possibly a higher tail position in response to dominant behavior and a lower tail position in response to submissive behavior. It is probable that these responses are conveying some information but their meaning is unknown. Tail positions probably serve to communicate both a squirrel's overall hierarchical status and whether the squirrel is submitting or exhibiting dominance at the moment. Dominant squirrels might use tail positions to warn submissive squirrels to leave, and submissive squirrels may use tail positions to tell dominant squirrels that they submit, in order to avoid being attacked. It is also possible that dominant squirrels communicate to submissive squirrels whether or not they are allowed to approach. To date, it can only be said that squirrels probably communicate their relative dominance/submissiveness with tail position signals. Squirrels with high dominance are the most likely to exhibit piloerection. This indicates that piloerection probably serves to proclaim dominance in eastern gray squirrels, as it does in many other animals (Frijda, 1986).

This study has provided some insight into the meaning of the tail signals of the eastern gray squirrel. However, much more research will need to be done in order to decode the entire system of communication. Squirrel communication also involves other visual signals, vocalizations, and chemical scents (Thorington and Ferrell, 2006). Though the latter two areas are better documented in tree squirrels than visual communication, there is still more research to be done on them. Future studies could focus on the visual communication of other species of tree squirrels, besides *S. carolinensis*. It would be helpful to collect some *S. carolinensis* communication data during the spring as well as during the summer, autumn, and winter. More squirrel communication should be observed at sites other than artificial food sources, and other populations of eastern gray squirrels should be observed in order to verify that the communication analyzed in this study is not specific to one population of squirrels. Eastern gray squirrels probably have regional dialects (as do many animals, including prairie dogs, orcas, and parrots) (Slobodchikoff and Coast, 1980; http://www.tagate.com/whale_resource_center/whales_species/orca_killer_whale.shtml; Wright, 1996). In conclusion, this study has shed some light on the little-understood phenomenon of tree squirrel visual communication, and equally importantly, has opened the door for future investigations on the topic.

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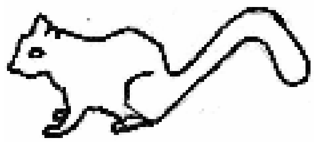
Figure 1: Tail Position Codes

Fig. 1.1 Tail Position **B** (Winter 2007, 2007-2008, and Aggregate)



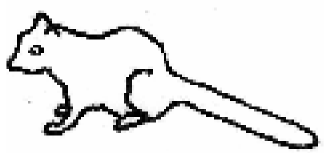
b

L

c

T

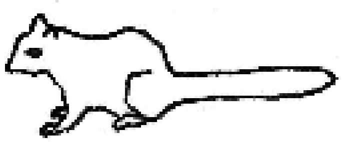
Fig. 1.2 Winter 2007 and Aggregate Tail Position **b**



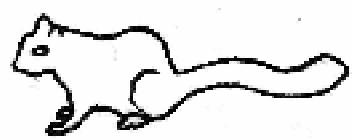
D

d

Fig. 1.3 Winter 2007 and Aggregate Tail Position **D**



S Winter 2007 and 2007-2008

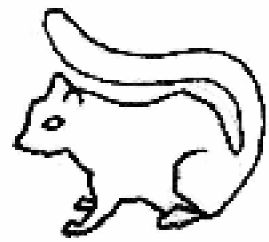


S Winter 2007 and 2007-2008

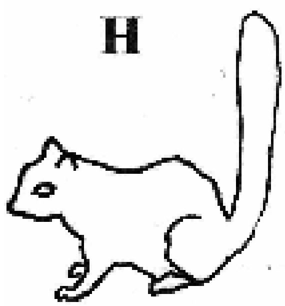
Fig. 1.4 Aggregate Tail Position **S**

Figure 1: Tail Position Codes (Continued)

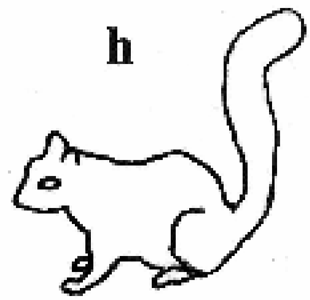
H



h

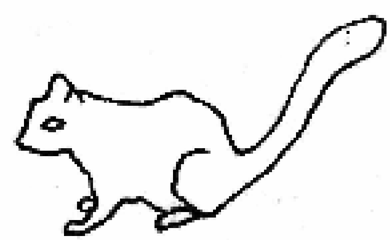


90H



90h

45H

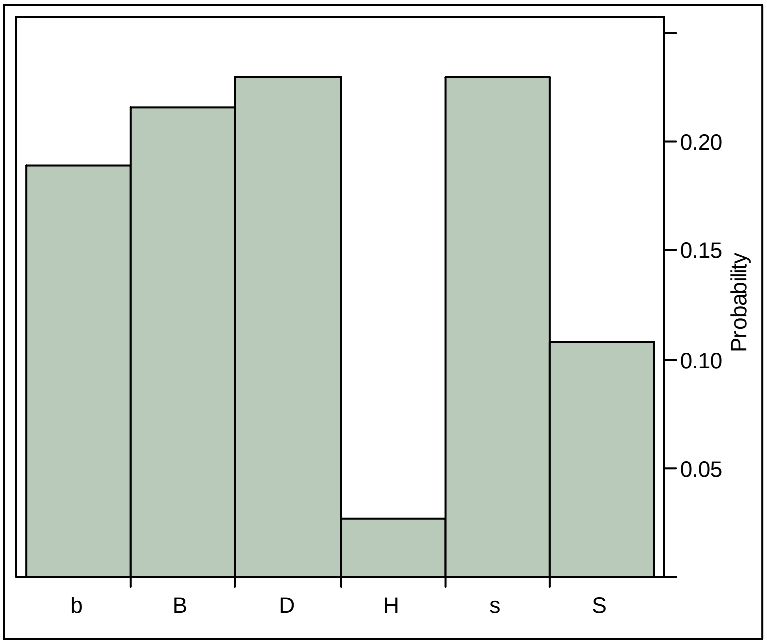


45h

C

Fig. 1.5 Winter 2007 and Aggregate Tail Position **H**

Figure 2
Distributions
Tail Position – Winter 2007

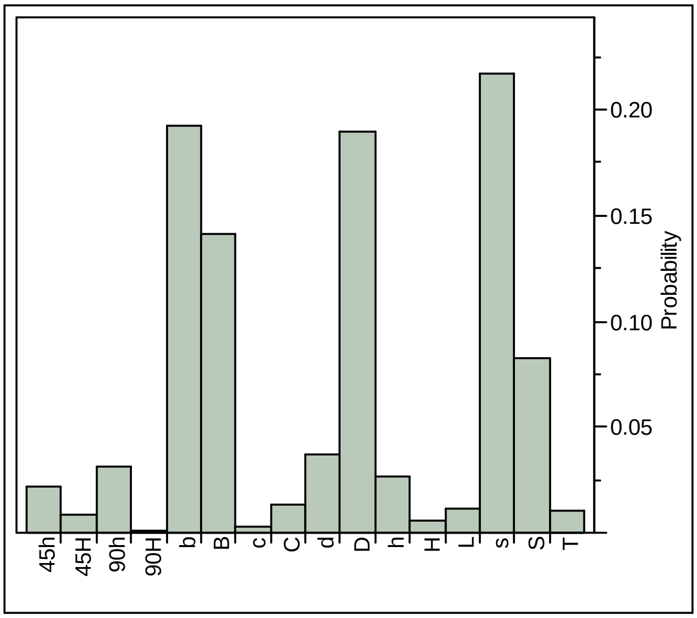


Frequencies

Level	Count	Prob
b	14	0.18919
B	16	0.21622
D	17	0.22973
H	2	0.02703
s	17	0.22973
S	8	0.10811
Total	74	1.00000

N Missing
0
6 Levels

Figure 3
Distributions
Tail Position 1 2007-2008

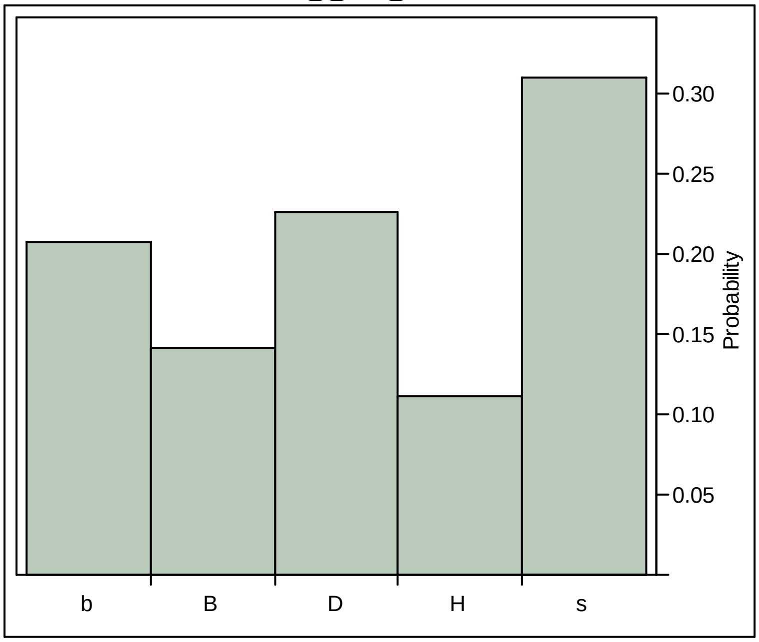


Frequencies

Level	Count	Prob
45h	15	0.02262
45H	6	0.00905
90h	21	0.03167
90H	1	0.00151
b	128	0.19306
B	94	0.14178
c	2	0.00302
C	9	0.01357
d	25	0.03771
D	126	0.19005
h	18	0.02715
H	4	0.00603
L	8	0.01207
s	144	0.21719
S	55	0.08296
T	7	0.01056
Total	663	1.00000

N Missing
29
16 Levels

Figure 4
Distributions
Tail Position 1 Aggregate – 2007-2008



Frequencies

Level	**Count**	**Prob**
b	138	0.20814
B	94	0.14178
D	151	0.22775
H	74	0.11161
s	206	0.31071
Total	663	1.00000

N Missing
29
5 Levels

Figure 5
A Sample Contingency Table
(Chi-Squared) Analysis

Dominant / Submissive Activity of Signaling Squirrel by Tail Position of Reacting Squirrel

Count Total % Col % Row %	Submissive	Dominant	
b	0 0.00 0.00 0.00	5 13.16 15.63 100.00	5 13.16
B	4 10.53 66.67 66.67	2 5.26 6.25 33.33	6 15.79
H	1 2.63 16.67 8.33	11 28.95 34.38 91.67	12 31.58
s	1 2.63 16.67 6.67	14 36.84 43.75 93.33	15 39.47
	6 15.79	32 84.21	38

Tests

N	**DF**	**-LogLike**	**RSquare (U)**
38	3	5.6391012	0.3402

Test	**ChiSquare**	**Prob>ChiSq**
Likelihood Ratio	11.278	0.0103
Pearson	14.059	0.0028