Eastern Gray Squirrels (Sciurus carolinensis) Communicate with the Positions of their Tails in an Agonistic Context

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Notes and Discussion

Eastern Gray Squirrels (Sciurus carolinensis) Communicate with the Positions of their Tails in an Agonistic Context

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. We investigated the communicative significance of tail position in wild eastern gray squirrels (*Sciurus carolinensis*) by videotaping tails on squirrels at an artificial food source. We determined the relative dominance ranks of each individual in each video clip. Each time one squirrel approached another, we recorded the degree of aggression exhibited by the more dominant individual, as well as two variables describing tail position (tightness of curvature and portion of tail bent) for each squirrel. Both tail position variables and their interaction effects significantly predicted the dominant squirrel's degree of aggression in a multiple regression analysis, suggesting tail position communicates information related to aggression in eastern gray squirrels.

INTRODUCTION

Eastern gray squirrels (*Sciurus carolinensis*) are known to communicate visually with their tails (Steele and Koprowski, 2001). However, few studies have examined this communication and those that have almost exclusively considered tail movements. Tail flagging has been documented as an alarm signal in gray squirrels (Bakken, 1959; McRae, 2012; Partan *et al.*, 2009; Partan *et al.*, 2010). Gray squirrels also mob rattlesnakes (*Crotalus horridus*) with tail flagging displays (Clark, 2005).

Several studies investigated tail communication in other Sciurids, though nearly all focused on tail movements or piloerection. In fox squirrel (*Sciurus niger*) pre-copulatory displays, males use different tail flicks to signal aggressive vs. nonaggressive intent, and females respond with other tail flicks to signal receptivity (McCloskey and Shaw, 1977). In tassel-eared squirrels (*Sciurus aberti*), tail piloerection increases with agitation (Farentinos, 1974). California ground squirrels (*Spermophilus beecheyi*) wave their tails at snakes (Owings and Coss, 1977; Hennessy *et al.*, 1981) and increase the temperature of their tail when tail waving at infrared-sensitive rattlesnakes (Rundus *et al.*, 2007). In Uinta ground squirrels (*Spermophilus armatus*) and thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*), tail flicks may be intention movements that also communicate species identity (Balph and Stokes, 1963; Wistrand, 1974).

Tree squirrels can hold their tails in a wide range of positions (Essner, 2003). This versatility provides the potential for squirrels to encode a great deal of information in the position of their tail. By only considering tail movements and piloerection, previous studies may not have explored all of the information conveyed by the tail.

Gray squirrel societies have a well-established dominance hierarchy, in which males dominate females and older individuals dominate younger individuals (Allen and Aspey, 1986). Many species use tail position to communicate about dominance relationships [Ord *et al.*, 2002 (*Amphibolurus muricatus*); Feh, 2005 (*Equus caballus*); McLeod, 1996 (*Canis lupus*); Goddard and Beilharz, 1985 (*Canis lupus familiaris*)]. However, to our knowledge, no studies have investigated whether gray squirrels communicate with tail positions in dominance-related contexts.

In this observational study we examined two different variables that describe the position of a squirrel's tail. We investigated whether these variables communicate information in an agonistic context.

METHODS

SITE DESCRIPTION

We conducted all observations at a single birdfeeder in the front yard of a suburban residence in Wesley Hills, NY, U.S.A. (41°9′25.524″N, 74°4′45.3612″W). Eastern gray squirrels have fluid social groups and cannot readily be observed in groups under many conditions (Thompson, 1978), but the fallen sunflower seeds beneath the birdfeeder attracted multiple squirrels to the same location. The

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birdfeeder was positioned on a pole between a house and a single-lane street, 8.8 m from the house and 11 m from the street. At least one tree or shrub was within a 5–8 m radius of the birdfeeder in each direction, in which the squirrels took cover when threatened. 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 in the area within a 1.5 m radius of the pole, with some seeds further away. We observed the squirrels through the second-floor window of the house, which served as a blind. Although the window was elevated above the squirrels' level, the viewing angle was shallow enough to afford a mostly lateral view of the squirrels, thus approximating a ''squirrel's eye view.''

OBSERVATION

We conducted observations at arbitrary intervals throughout the day, whenever we 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. We used a Panasonic SDR-H80 camcorder with an up to 70× optical zoom to videotape the squirrels and viewed the video clips with QuickTime Player on an iMac computer.

DOMINANCE

Within each video clip, we recorded the relative dominance ranks of each squirrel in the clip. If squirrel A chased, attacked, or lunged towards squirrel B, we assumed squirrel A was dominant to squirrel B. If squirrel B shied away from or was chased by squirrel A, we assumed squirrel B was subordinate to squirrel A. We never observed a case where one squirrel behaved both ''dominantly'' and ''subordinately'' towards a given conspecific within the same video clip. After watching the entire video clip to determine the relative dominance ranks of the squirrels in that clip, we replayed the clip to collect more detailed data on dyadic interactions between the squirrels (*see* below). As we were unable to mark the squirrels or keep track of individual identities between video clips, we do not know how many individuals we sampled during our study.

DATA COLLECTION

We collected twelve video clips totaling 2 h, 7 min, and 37 s over 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). Each clip contained footage of at least two squirrels feeding simultaneously beneath the birdfeeder. In this study, we only recorded data at those instances in the video clips where one squirrel approached another. We observed 35 instances where a dominant squirrel approached a more subordinate squirrel, and 53 instances where a subordinate squirrel approached a more dominant squirrel. We defined an ''approach'' as beginning when one squirrel began to move towards another. We defined the end of the approach differently depending on whether the approaching squirrel was subordinate or dominant. If the approaching squirrel was subordinate, the approach ended when one of the following conditions was met: (1) the approaching squirrel was chased away by the dominant squirrel, (2)the approaching squirrel stopped approaching for at least 1 s, (3) the dominant squirrel moved away from the approaching subordinate squirrel, or (4) the approaching squirrel turned around without stopping for more than 1 s and moved away from the dominant squirrel.

If the approaching squirrel was dominant, the approach 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) or (2) the approaching squirrel stopped for at least 1 s.

As we had no *a priori* information about which aspects of tail position or movement might be relevant to communication, we arbitrarily defined twelve variables that described tail position and movement. We restrict the scope of this note to two variables that described the curvature of a squirrel's tail: *Tightness* and *Portion Bent*. *Tightness* described how tightly the squirrel's tail was bent, or the angle between the distal and proximal halves of the tail (Fig. 1). *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, or whether the tail was not bent at all (Fig. 2). We recorded the values of *Tightness* and *Portion Bent* for both the approaching and approached squirrels at each second of each approach. At the final second of each approach, we recorded the degree of aggression on the part of the dominant squirrel on an ordinal

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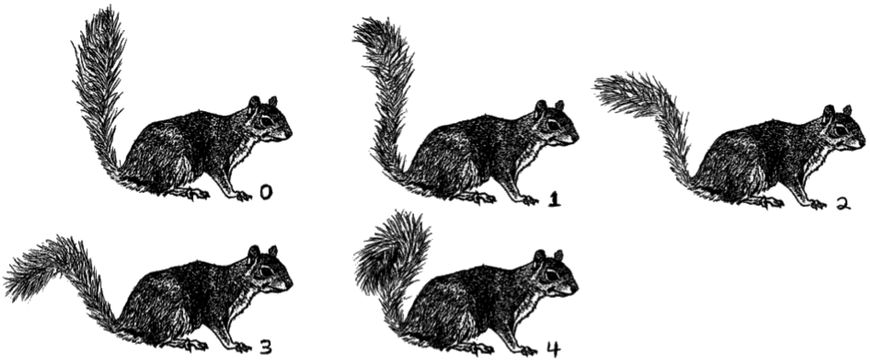

FIG. 1.—Illustrations of the five different states of the variable *Tightness*

scale. This variable (*Aggression*) was both more fine-grained and more temporally specific than our categorization of squirrels as ''dominant'' or ''subordinate,'' in which we simply recorded whether an individual exhibited aggressive or submissive behavior towards a given conspecific at any point during the video clip (*see* subsection DOMINANCE). The states of *Tightness*, *Portion Bent*, and *Aggression* are defined in Table 1.

TIME SEQUENCE OF BEHAVIORS

After comparing the transition probabilities of behaviors at each second of an approach, we concluded that events at a particular time were best predicted by the events at the immediately preceding second. Consequently, in our analyses, we only included the variable values that were recorded at the final second of an approach.

STATISTICAL ANALYSIS

We conducted all statistical analyses in JMP® Version 8.0.2 of SAS Institute Inc. (Cary, NC, U.S.A.). We used multiple linear regression to determine whether the dominant squirrel's degree of aggression

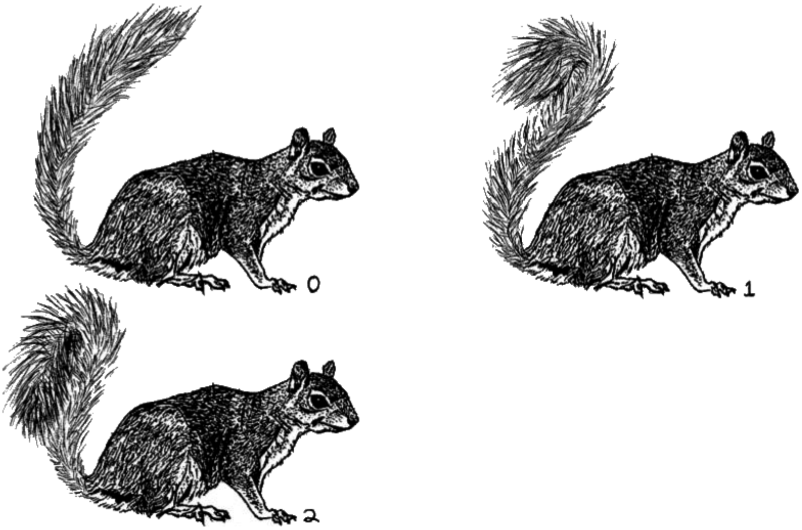

FIG. 2.—Illustrations of the three different states of the variable *Portion Bent*

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

Variable name	Definition	States
Tightness	How tightly tail was bent (angle between distal and proximal halves of tail)	0 = rigidly straight 1 = relaxed but barely bent 2 = very loosely bent (90° $<$ angle b/t halves of tail $<$ 180°) 3 = loosely bent ($<$90° b/t halves of tail) 4 = tightly bent (0° 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)
Aggression	Degree of dominant squirrel's aggression towards subordinate squirrel at end of approach	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

could be predicted by some combination of either squirrel's *Tightness* and *Portion Bent* and any two-way interaction effect of these variables. We employed three different model-building methodologies: forward stepwise regression, backward stepwise regression, and nondynamically reducing the full model by excluding all nonsignificant terms ($\alpha = 0.05$). If an interaction between two variables was significant, then each of the variables was included in the reduced model, even if their P-values in the full model were greater than 0.05. We compared each model on the basis of adjusted R^2 and Mallow's C_p. An optimal Mallow's C_p value equals the number of parameters in the model. However, a model with a slightly sub-optimal C_p may be considered superior if it has a higher adjusted R^2 value (Draper and Smith, 1998).

RESULTS

Of all the models fit, the only one with all significant co- efficients was the nondynamically reduced model without an intercept (n = 31, Adj-R^2 = 0.3080, C_p = 5.65, 6 parameters). When an intercept term was included the C_p value was improved, but the adjusted R^2 was lower (n = 31, Adj-R^2 = 0.2985, C_p = 6.99, 7 parameters). Therefore, we elected to use the reduced model without an intercept. This model included the *Tightness* and *Portion Bent* of both the dominant and subordinate squirrels, as well as the interaction effects *D-Tightness***S-Portion Bent* and *D-Portion Bent***S-Tightness* (where ''D'' denotes the dominant squirrel's tail and ''S'' denotes the subordinate squirrel's tail). Table 2 displays the parameter estimates and associated P-values for the final model.

FIRST INTERACTION EFFECT

When the dominant squirrel's tail was tightly bent and the subordinate bent a large portion of its tail, the dominant squirrel's average aggression was lowest. Conversely, when the dominant squirrel's tail was tightly bent and the subordinate bent a small portion of its tail, the dominant squirrel's aggression was highest (Fig. 3).

SECOND INTERACTION EFFECT

When the dominant squirrel bent a small portion of its tail and the subordinate squirrel's tail was loosely bent, the dominant squirrel's average aggression was lowest. When the dominant squirrel bent a large

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TABLE 2.—Parameter estimates and their associated standard errors, t-ratios, and P-values for the final model (nondynamically reduced model without an intercept term)

Term	Estimate	Std error	t Ratio	Prob > |t|
D-Tightness	3.18	0.8547	3.7265	0.0010
D-Portion Bent	−4.22	1.5011	−2.8092	0.0095
S-Tightness	−1.84	0.7819	−2.3547	0.0267
S-Portion Bent	4.23	1.3232	3.1964	0.0037
D-Tightness*S-Portion Bent	−1.92	0.5068	−3.7870	0.0037
D-Portion Bent*S-Tightness	1.26	0.4990	2.5304	0.0181

portion of its tail and the subordinate's tail was tightly bent, the dominant squirrel's aggression was highest. Overall, the dominant squirrel was more aggressive when the subordinate's tail was tightly bent (Fig. 4).

DISCUSSION

Our data suggest that squirrels communicate information with both the tightness of their tail's curvature and the portion of their tail that is bent. Communication is defined as the provision of information that can be utilized by a receiver to make a decision (Bradbury and Vehrencamp, 1998, p. 2). Both the *Tightness* and *Portion Bent* of a subordinate squirrel's tail significantly contributed to predicting the degree of subsequent aggression by 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.

The importance of the interaction effects between the tail positions of the two squirrels implies that dominant squirrels make their decisions about how aggressively to behave towards a conspecific based

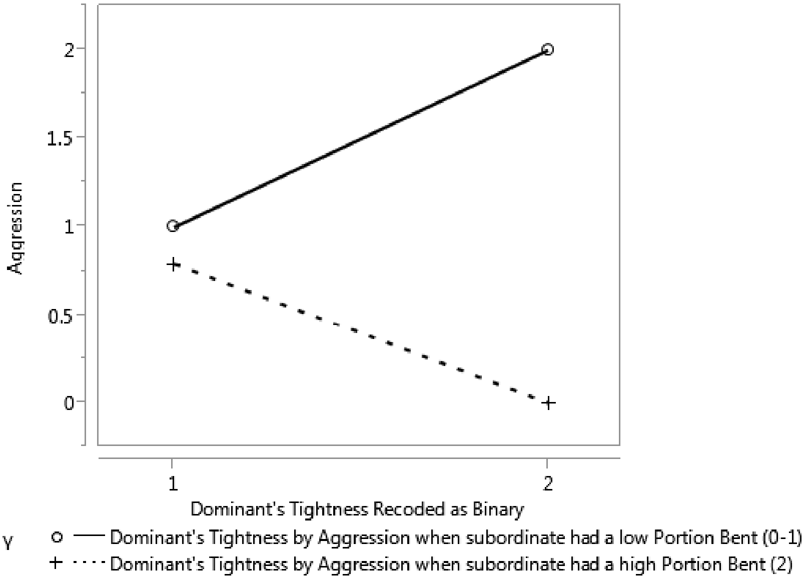

FIG. 3.—Effect of the interaction between the dominant squirrel's *Tightness* and the subordinate squirrel's *Portion Bent* on the dominant squirrel's *Aggression.* Both tail position variables were recoded as binary variables in order to produce this graph. *Tightness* values of 0–2 were rescored as ''1'' (low *Tightness*), and values of 3–4 were rescored as a ''2'' (high *Tightness*). *Portion Bent* values of 0–1 were rescored as ''1'' (low *Portion Bent*), and values of 2 were left untouched (high *Portion Bent*)

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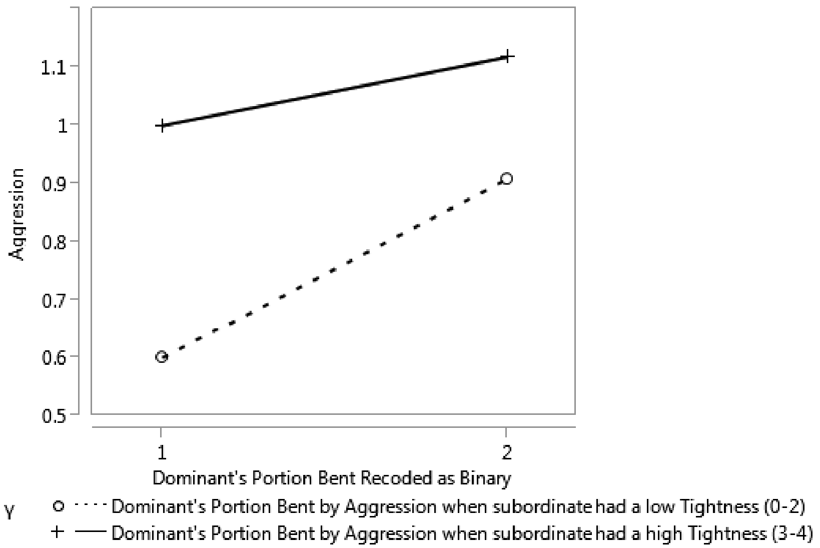

FIG. 4.—Effect of the interaction between the dominant squirrel's *Portion Bent* and the subordinate squirrel's *Tightness* on the dominant squirrel's *Aggression.* Both tail position variables were recoded as binary variables in order to produce this graph. *Portion Bent* values of 0–1 were rescored as "1" (low *Portion Bent*), and values of 2 were left untouched (high *Portion Bent*). *Tightness* values of 0–2 were rescored as "1" (low *Tightness*), and values of 3–4 were rescored as a "2" (high *Tightness*)

on the interplay of their own internal state with the signals they receive from the subordinate squirrel. The relative complexity of this decision making process most likely allows for adaptive behavior in a wider range of circumstances than if squirrels made their decision without regard to how their own state relates to that of the conspecific with whom they are interacting.

Although the sample size in this study was small, significance of the effects indicates potential repeatability. Thus, future study of tail position in gray squirrel communication is warranted.

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