

Multimodal alarm behavior in urban and rural gray squirrels studied by means of observation and a mechanical robot

Sarah R. PARTAN*, Andrew G. FULMER, Maya A. M. GOUNARD, Jake E. REDMOND

Hampshire College School of Cognitive Science, Amherst, MA 01002 Massachusetts, USA

Abstract Urbanization of animal habitats has the potential to affect the natural communication systems of any species able to survive in the changed environment. Urban animals such as squirrels use multiple signal channels to communicate, but it is unknown how urbanization has affected these behaviors. Multimodal communication, involving more than one sensory modality, can be studied by use of biomimetic mechanical animal models that are designed to simulate the multimodal signals and be presented to animal subjects in the field. In this way the responses to the various signal components can be compared and contrasted to determine whether the multimodal signal is made up of redundant or nonredundant components. In this study, we presented wild gray squirrels in relatively urban and relatively rural habitats in Western Massachusetts with a biomimetic squirrel model that produced tail flags and alarm barks in a variety of combinations. We found that the squirrels responded to each unimodal component on its own, the bark and tail flag, but they responded most to the complete multimodal signal, containing both the acoustic and the moving visual components, providing evidence that in this context the signal components are redundant and that their combination elicits multimodal enhancement. We expanded on the results of Partan et al. (2009) by providing data on signaling behavior in the presence and absence of conspecifics, suggesting that alarm signaling is more likely if conspecifics are present. We found that the squirrels were more active in the urban habitats and that they responded more to tail flagging in the urban habitats as compared to the rural ones, suggesting the interesting possibility of a multimodal shift from reliance on audio to visual signals in noisier more crowded urban habitats [*Current Zoology* 56 (3): 313–326, 2010].

Key words Alarm behavior, Communication, Gray squirrel, *Sciurus carolinensis*, Multisensory signaling, Redundancy, Urbanization, Ethorobotics

Increasing urbanization calls for increased scientific focus on the ecology of urban systems and the unique selective pressures they present. Urban centers may be characterized by high human density, a landscape dominated by artificial structures, and elevated noise levels (Warren et al., 2006). Species must be able to compensate for these unique stresses to thrive in the urban environment - and most urban areas experience a corresponding decrease in biodiversity. Wildlife found in these areas often display behavioral adaptations to living in close proximity to humans. The contrast in behaviors between rural and urban populations of a species can highlight the direction of these small evolved or learned changes (Ditchkoff et al., 2006). Communication behavior in particular has the potential to be affected by urbanization (Rabin and Greene, 2002; Patricelli and Blickley, 2006).

To understand how animals communicate, it is useful to conduct playback experiments in which one simulates the signal of interest and presents it to the animal to see

how the animal will respond. This has been done with great success for decades with bird song. Visual signals are harder to simulate, but interesting work is being done with video playbacks (reviewed by Rosenthal, 1999; Uetz and Roberts, 2002). Video playbacks are of limited utility in natural field settings, however, due to the high ambient light, limited electricity sources, and difficulty replicating realistic depth and spectral cues (d'Eath, 1998; Zeil, 2000). A solution to these issues is to create three-dimensional mechanical or "robotic" animals to simulate visual displays in the field. Robotic models have been used successfully to study courtship, foraging and social behavior in birds (Patricelli et al., 2002; Göth and Evans, 2004; Fernandez-Juricic et al., 2006; Patricelli and Krakauer, 2010), territoriality in frogs and lizards (Narins et al., 2003, 2005; Martins et al., 2005), and antipredatory behavior of squirrels (Rundus et al., 2007; Partan et al., 2009).

Biomimetic mechanical models (informally called "robots") can be designed to produce sound or other

Received Nov. 16, 2009; accepted Feb. 17, 2010.

* Corresponding author. E-mail: partan@hampshire.edu

© 2010 *Current Zoology*

vibration along with moving visual components, making them useful for studying multimodal communication. Multimodal communication (Partan and Marler, 1999; Rowe, 1999; Hebets and Papaj, 2005), involving more than one sensory system, can be difficult to study because multiple signals are emitted and perceived simultaneously, and our equipment is usually designed for one process at a time. However it is important to gather information on all components of an animal's signaling behavior in order to understand the behavior, because the gestalt of the whole signal can have effects that go beyond the individual components (Partan, 2004a; Partan and Marler, 2005). Ethorobotics, the use of robotic or mechanical models in ethology (Partan, 2004b), handily resolves this issue.

We examined communication behavior of the Eastern gray squirrel *Sciurus carolinensis* in urban and semi-rural areas. Communication behavior of gray squirrels has not been often studied, although alarm barks have been described (Lishak, 1984), and tail flagging as a component of alarm and aggressive behavior has been reported (Bakken, 1959; Steele and Koprowski, 2001; Clark, 2005). Gray squirrels are well studied on other topics, however, including reproductive behavior (Koprowski, 1993, 1996) and foraging (Makowska and Kramer, 2007; Steele et al., 2008). In terms of urban/rural comparisons, urban and rural gray squirrels have been studied in the context of resource acquisition (Bowers and Breland, 1996) and antipredator behavior (Cooper et al., 2008). Aggression and flight distance have also been studied in urban populations of gray squirrels (Gustafson and Van Druff, 1990; Parker and Nilon, 2008).

Our current study expands upon our earlier work in which we examined responses of wild squirrels living in urban parks in St. Petersburg, Florida, to alarm barks and tail flags of a robotic squirrel (Partan et al., 2009). In the earlier study we found that the vocal and visual signals of alarm were redundant in that they each elicited alarm responses on their own and the combination of signals elicited more alarm than either did alone. In the current study we extended this work in a number of ways. First, we conducted the study in Western Massachusetts, overall a more rural area than St. Petersburg Florida, but we included a variety of field sites that varied along the urban-rural continuum. In this way we could compare the responses of squirrels in relatively urban and more rural settings, a useful exercise for understanding adaptations to urban environments. Second, we collected data on the presence of conspecifics, so

that we could explore the question of the addressee of alarm signals (see Partan et al., 2009). Third, we updated our robotic model with a number of technical improvements, including a new computer-controlled interface that automated the control of the robot and allowed us to record behavioral responses into a customized data collection program live in the field. Finally we collected some additional observational data on naturalistic behavior of squirrels in the rural setting to augment our experimental study.

Strong population differences in communication behavior are relatively rare in mammals. Although songbirds learn their songs and therefore show clear dialect differences in different regional populations (Marler and Tamura, 1964), most mammals appear not to have a strong learned component in their signaling behavior and do not exhibit large regional differences (except for humans and some marine mammals and other species; see review in Janik and Slater, 1997). We did not expect to find regional differences in our squirrel communication behavior. We therefore predicted that, as with the Florida squirrels (Partan et al., 2009), the Massachusetts squirrels studied here would show redundant responses to both visual and vocal components of their alarm behavior.

Between our relatively urban and relatively rural sites, we predicted that squirrels living in the more urban environments would show lower levels of alarm responses, given that they are more habituated to human presence, as McCleery (2009) found in a study of fox squirrels. However, there is also precedent for the finding that Sciurids may be more reactive around humans, rather than less: Magle et al. (2005) found that rather than habituating, prairie dogs became sensitized to repeated human intrusions and increased their reactivity over time. Ultimately however, the prairie dogs in rural areas were still more sensitive to the intrusions than were the urban colonies.

We did not have a prediction as to levels of vigilance in urban versus rural areas because the literature is equivocal on this issue. McCleery (2009) suggests that because of habituation, fox squirrels have lower levels of vigilance in urban areas, whereas other studies have found that some animals, such as crows (Ward and Low, 1997), show higher vigilance in more urban areas (reviewed by Frid and Dill, 2002). Rabin et al. (2006) found that California ground squirrels increased levels of vigilance and caution in areas of high anthropogenic mechanical noise. Vigilance levels are related to the degree of predator pressure, but the literature varies on

the question of predation differences between urban and rural environments, which of course also depends on the species. On the one hand, urban prey may be subject to intensive predation due to the high density of prey available in a relatively small area for predators that can capitalize on this situation, such as Cooper's hawks preying on city doves (Estes and Mannan, 2003). On the other hand, many predators large enough to predate on squirrels would be likely to avoid areas of high human occupancy; a study of mortality in fox squirrels found that predation took a much greater toll on rural than urban populations (McCleery et al., 2007). We therefore collected data on vigilance behavior without an *a priori* prediction as to direction of difference.

Finally, we collected some additional descriptive data on natural squirrel behavior in a rural environment, including activity levels and behavior in the presence or absence of conspecifics. Our goals with the observational work were to document the natural incidence of alarm behavior to compare to the levels of alarm elicited in our experimental work, and to gather some clues on the question of whether squirrel alarm signals are directed toward conspecifics or predators (see discussion in Partan et al., 2009).

1 Materials and Methods

1.1 Observational pilot study

We conducted a short observational pilot study of natural alarm behavior of wild Eastern gray squirrels on Hampshire College campus. The data were collected with the help of 20 undergraduate students enrolled in an Animal Behavior Field Methods class. Students collected data in pairs, one observing with binoculars and calling out behaviors, and the other recording the data by hand onto check-sheets. We collected data three times a day for an hour each session, for 21 days in a row from March 25 to April 15, 2009. Sessions were held at 8am, noon, and 5pm. Focal animal observations were conducted from an observation blind located just

outside a building (Adele Simmons Hall) on the perimeter of Hampshire College campus woods. The squirrels visible from the blind were either in the woods or in a grassy area near a bird feeder at the edge of the building. Data on six behaviors were recorded using one-zero frequencies (Martin and Bateson, 2007), recording the presence or absence of behavior for every 30-second time block over the one-hour session. We used the one-zero method because it is good for capturing rare behaviors of short duration, such as tail flagging and barking, and it is also good for improving reliability among multiple observers. Data were taken primarily on the focal individual, but the presence of other squirrels and other animals in the area was also noted for each time period. The six behaviors recorded were: bipedal vigilance, quadrupedal vigilance, tail flicking, tail flagging, vocalizing, and locomotion (see Table 1 for definitions). Squirrels were unmarked, so it is likely that individual squirrels contributed unevenly to the data set over the course of the observational pilot study.

All students underwent training to recognize the behaviors, and an interobserver reliability test was conducted by having every student watch ten minutes of video footage (from three different focal squirrels) and record data for all behaviors using the same data sheets used for the field work. The students' data were then compared to that taken by the primary author, and only field data from those students who attained above 70% reliability for each behavior were included in the final data set. Average reliability for the 20 students whose data were included was 84%. With so many relatively inexperienced observers the consistency of these observations is likely to be lower than desired, but sufficient for the purposes of pilot work supplementing and giving context to the main experimental study. Any inconsistencies would increase noise in the data but not bias, since in this portion of the study we were collecting observational data without a hypothesis that could drive expectations in any particular direction.

Table 1 Observational study: definitions of behaviors

Behavior name	Definition
Quadrupedal vigilance	Head is at or above the plane of the shoulders, body motionless although the head or eyes may be scanning, all four feet are on the ground or rarely one forepaw is lifted.
Bipedal vigilance	Head is above the plane of the shoulders, body motionless although the head or eyes may be scanning, squirrel is sitting or standing on hind legs only.
Tail flick	Tail moved quickly with medium vigor, short duration, usually only a portion of tail moves while the rest of the tail remains parallel to body.
Tail flag	Tail waved with high vigor, longer duration, above the axis of the back, usually up over the head, involves most of the tail in movement.
Vocalize	Any vocal emission.
Locomotion	Movement across the terrain, including walking, running and climbing.

1.2 Experimental playbacks of the mechanical squirrel model

A mechanical squirrel model (Fig. 1) displaying auditory or visual signals of alarm, or both, was presented to wild squirrels whose responses were documented. Methods for this experiment closely followed those described by Partan et al. (2009).



Fig. 1 Photograph of the mechanical squirrel model

The camouflage cover is retracted and folded up at the base behind the model (motor for cover is visible on the right). Speaker was hidden under camouflage cloth in front of the model. Copyright Steven E Frischling for Hampshire College.

1.2.1 Subjects and field sites

Sixty-eight wild gray squirrels *Sciurus carolinensis* were tested over the course of one year. Squirrels were unmarked but we were unlikely to have sampled the same individual twice because, as with the studies by Steele et al. (2008) and Partan et al. (2009), we moved to a new location for each new focal individual's test. We tested in four general locations in Amherst, Massachusetts: on the campus of Hampshire College (51 trials), on the campus of the University of Massachusetts Amherst (75 trials), and a small number of trials in downtown (12 trials) and in residential areas (12 trials) of the town of Amherst. Because some sites were more highly urbanized and others more rural, we classified sites into relatively urban and relatively rural groups by estimating the percent impervious surface for each general location. To do so we loaded images of the surveyed areas in Google Earth™ and took a screen capture of each research area. Using a digital metric, we delineated the borders of all impervious surfaces in these areas (paved areas and buildings), as well as the total available area, to calculate percent impervious surface. Two of us took independent estimates, which were significantly correlated (correlation for unordered pairs, $F_{3,4}=10.96$, $P=0.02$) and were then averaged. Two sites had over 50% impervious surface, which we lumped together and classified as relatively “urban”: the Uni-

versity of Massachusetts campus (an average of 64.5% impervious surface) and the downtown Amherst areas (an average of 58% impervious surface); the other two sites had less than 20% impervious surface, which we lumped together and classified as relatively “rural”: Hampshire College campus (an average of 16.5% impervious surface) and residential Amherst (an average of 17.5% impervious surface). Although not quantified, pedestrian traffic in our relatively urban sites was substantially greater than that at the relatively rural sites.

1.2.2 Robot design and programming

The mechanical squirrel (see Fig. 1) was designed to be able to flag its tail (moving it rapidly and repeatedly high over its body) and emit alarm barks from embedded speakers. The body, tail, and speakers of the model were the same as those used in Partan et al. (2009) and described therein, however several hardware upgrades were made and the programming platform was entirely redone. One upgrade was to install an automated cover. The cover was made from cloth with a camouflage pattern stretched over thin plastic battens and attached with a servo motor to the robot. The cover motor was programmed in conjunction with the robot to open for appropriate trials (those that included the visual components of the robot) for the duration of the test phase and remain closed at all other times. Another upgrade was to install an audio chip (“VMusic2” sound board made by Viniculum) so that the alarm sounds could be played on command from the microcontroller (in the previous model they were played by hand using a CD player). We used two different gray squirrel alarm call sequences that were broadcast at random. One sequence was from Cornell University's Library of Natural Sounds (recording #LNS127048), from an originally longer recording that we trimmed down to one minute in length, and containing a number of calls from the same individual. The other sound was the sound that was used in our Florida study (Partan et al., 2009), an alarm call from a gray squirrel recording that we looped to repeat for a length of one minute.

A new programming platform was designed to automate the robot. The program was written using “Processing” (an open source programming language, processing.org) and was implemented on an Arduino microcontroller (arduino.cc). The program allowed us to automatically control the robot in the field and to record behavioral data into data files that were linked to the input variables. The user interface allowed the experimenter to designate trial type and collect data into the same file. The program introduced naturally realistic

variability into the behavior of the robot in two ways beyond the original design: for audio trials there were two sound files of alarm calls that were played in random order; for the visual tail flag trials there was variability programmed into the speed and duration of the motor rotation that controlled the tail flagging. The program called up a sequence of 5 sets of tail flag motions that were made of short and long motions repeated in different orders. These sources of additional variability in display behavior were added in an attempt to mitigate the potential pseudoreplication issue of using only one mechanical squirrel model and one sound (as was done in the earlier study, Partan et al., 2009). Using only one robot is a type of pseudoreplication (McGregor, 2000), but including the variability in tail movements and the multiple audio exemplars helps to ameliorate this issue (cf. Patricelli and Krakauer, 2010).

1.2.3 Trial protocol and data collection

At the start of each trial, the experimenter entered independent variables (date, time, location, names of observers, squirrel number, trial number, number of squirrels present) and trial type (see below), determined in advance by a random number generator. He or she then started the trial, which was timed automatically by the computer. A second observer, naive to the trial type, stood by with binoculars calling out behaviors of the focal animal. The first experimenter entered these behaviors into the computer by clicking boxes on a customized screen. Each entry was automatically time stamped, and the phase (pre—test—post) was indicated. After a one-minute pre-test during which the model was stationary, quiet and covered, a one-minute test phase commenced presenting one of six conditions. There were five experimental conditions and a baseline condition during which nothing happened (the robot remained stationary, quiet and covered). The experimental test conditions were: Audio only (A), in which the robot was covered but alarm calls were broadcast; Visual still (Vs), in which the robot was uncovered but stationary and quiet; Visual moving (Vm), in which the robot was uncovered and the tail was flagged; Audio Visual still (AVs), in which the robot was uncovered and alarm calls played; and Audio Visual moving (AVm) in which the robot was uncovered, alarm calls played and the tail flagged. The conditions were presented in random order per subject. The five test conditions were the same ones used by Partan et al. (2009), but the baseline was new in the current study. After the one-minute test, the cover was automatically drawn over the robot and a one-minute post-test was conducted during which the

model was once again covered, quiet and stationary and any behavioral responses of subjects continued to be scored. Each subject was tested for a maximum of six trials (one of each type), or fewer if they ran away before finishing (as was common: most squirrels, 47%, departed after the first trial, thereby completing only one of the six conditions; 22% completed two conditions, 18% three, 6% four, 4% five, and only 3% completed all six conditions). We handled this variability by randomizing the order of conditions presented, so that the first trial could be any of the six conditions in random order. We then compared the results of the data from first trials only to the results from all the data to ensure that there were no differences in patterns of response.

Because we had a new automated system for continuous recording of behavioral data, we could increase the number of behaviors coded above what was collected either in our pilot observational study (see Table 1), or in our earlier Florida study (Partan et al., 2009). We recorded twelve behaviors, listed in Table 2, along with some location variables (in tree, on ground, out of view). In our analysis, we lumped behaviors into three types: alarm, vigilance, and calm behavior (see Table 2 for details). Our software did not allow us to measure durations of behaviors, but rather start times only. This means that every time a squirrel ceased foraging to lift its head to be vigilant, and then lowered its head to return to foraging, we coded “forage-vigilant-forage”, which tended to equate the number of foraging and vigilance bouts. The vigilance behaviors tended to be of very short duration, however, with foraging bouts much longer. Durations are not reflected in our frequency data.

Interobserver reliability was measured for the two teams of researchers that collected the field data. To conduct the test, we ran five trials exactly as usual except that two teams collected data independently on two separate computers. We then compared the data from the two teams and found an average of 86.6 % agreement across the five trials.

1.3 Data analysis

Data analysis was conducted using SPSS/PASW Statistics 18. For F tests we used Wilks' Lambda statistic to assess significance, and alpha levels were set at 0.05 for all analyses. For the observational study we used a chi-square test to examine squirrel presence by time of day, and conducted a MANOVA to examine the effects of conspecific presence (included as an independent variable) and all six behaviors as dependent variables

(see Table 1).

For the experimental study we began with a complete four-way MANOVA with all four independent variables: experimental condition, phase of trial, conspecific presence, and habitat type; and the composite variables of alarm, vigilance and calm (see Table 2) as dependent variables. We also included follow-up contrasts to compare each test condition to the baseline (control) condition, and contrasts to compare the test and post-test phases to the pretest (control) phase. It is worth clarifying that the “alarm behavior” category is not the inverse of the “calm behavior” category, because it is possible for each category of behavior to increase or decrease independently.

We were interested in which particular behaviors were given in the presence of conspecifics, so we broke apart the composite dependent variables that were significant in our first analysis and conducted T-tests on individual behaviors by conspecific presence or absence (independent samples T-tests, two-tailed). To pursue an interaction observed in our first analysis and find out whether test conditions were responded to differently in urban and rural habitats we ran a MANOVA on habitat with the data file split by condition.

Finally, to compare the incidence of alarm behaviors from the observational study, in which behaviors were sampled using one-zero or Hansen frequencies (Martin and Bateson, 2007), to the incidence of behaviors in the experimental study, in which real frequencies were taken using continuous data collection, we utilized Altmann and Wagner’s (1970) formula for estimating rates

from Hansen frequencies.

2 Results

2.1 Observational study: natural squirrel behavior

Almost fifty hours of observations were conducted for the pilot observational study. Squirrels were present in the study area on and off during the observations, for a total of 12.4 hours that squirrels were visible to us (summed over 1488 30-s time intervals of data collected on behavior throughout the study). Squirrels were significantly more likely to be present during the morning sessions (100% of 8am sessions had squirrels for at least a part of the session) than midday (62% of noon sessions) or evening sessions (58% of 5 pm sessions; $\chi^2_1 = 11.95$, $P=0.0005$).

One goal of the observational study was to document the natural incidence of alarm behavior. We witnessed few of the classic alarm behaviors of tail flagging or vocalizing (Table 3). Tail flicking, which may be an alarm behavior as well, was more common (Table 3), but students may have recorded flicking as used during locomotion in addition to alarm flicking. In fact 80% of intervals with flicks also contained locomotion (187 out of 234 intervals). Vigilance was also common (Table 3).

Another goal of the observational study was to document whether or not alarm behavior occurred in the presence of conspecifics, to help us answer the question of whether alarm signals are directed toward conspecifics or toward predators. Toward that end we had students note the presence of conspecifics: during 293 (20%) of intervals conspecifics were noted. Conspecific

Table 2 Experimental study: definitions of behaviors

Group Name	Behavior Name	Definition
Vigilance	Quadrupedal vigilance	See Table 1.
	Bipedal vigilance	See Table 1.
Alarm	Tail flick	See Table 1. In addition, this was only coded when squirrel was not locomoting
	Tail flag	See Table 1.
	Vocalize	Alarm barks, including the “kuk” and “quaa” described by Lishak (1984).
	Mount tree	Move from the ground onto the trunk of a tree.
	Ascend tree	Locomote up a tree.
Calm	Groom	Moving the mouth or forepaws over own body, or scratching with hind feet.
	Forage	Manipulation of food or substrate including eating, digging, nosing at the ground or locomoting with head down.
Other	Go to tree	Locomote toward a tree.
	Descend tree	Locomote down a tree.
	Leave	Depart the study area.

All behaviors were recorded once per bout; if the behavior ceased for >1 s then a new bout was recorded upon recommencement of the behavior.

Table 3 Observational study: frequency counts of the number of 30-s time intervals in which each behavior occurred

Behavior	Frequency of intervals	Proportion of intervals
Quadrupedal vigilance	399	26.81%
Bipedal vigilance	325	21.84%
Tail flick	234	15.66%
Tail flag	24	1.61%
Vocalize	11	0.74%
Locomotion	831	55.85%

presence had a significant effect overall, across all six dependent behaviors ($F_{6, 218}=2.568$, $P=0.02$). Between-groups tests showed that focal squirrels were more likely to vocalize during intervals with conspecifics present ($F_{1, 223}=5.045$, $P=0.026$), and less likely to show quadrupedal vigilance behavior in the presence of conspecifics ($F_{1, 223}=6.379$, $P=0.012$).

2.2 Experimental study: presentations of mechanical squirrel model

2.2.1 Condition and phase of trial

A total of 150 trials were conducted, with 25 of each condition type, on 68 squirrels. A four-way MANOVA showed that there were main effects of all four independent variables, experimental condition, phase of trial, conspecific presence, and habitat type, along with several interactions (F values are listed in Table 4). In order to ensure that results were not affected by the uneven distribution of squirrels across trials, we also ran a four-way MANOVA using only the first trial for each squirrel ($n=68$ trials), which also found that the four main effects were significant (Condition: $F_{15, 376}=3.786$, $P<0.001$; Phase: $F_{6, 272}=6.267$, $P<0.001$; Habitat: $F_{3, 136}=5.944$, $P<0.01$; Conspecific presence: $F_{3, 136}=8.453$, $P<0.001$), with the more detailed results following the same patterns. Therefore for the rest of the results reported, we analyzed all 150 trials.

As with our earlier Florida study (Partan et al., 2009), squirrels responded in a biologically meaningful way to the presentations of the mechanical squirrel model: the highest levels of alarm (Fig. 2a) and vigilance (Fig. 2b) occurred during the test phase when the robot was presented. In the current study we also collected data on foraging and grooming, which were lumped for analysis as non-alarm or “calm” behaviors; these dropped during the post-test phase (Fig. 2c). Raw frequencies of the specific behaviors that made up the composite grouped variables are given in Table 5, for the one-minute test phase only.

Contrast tests for condition were significant for alarm behavior ($F_{5, 432}=6.015$, $P<0.001$), with four of the five test conditions significantly different from the baseline condition: Audio (A, $P=0.018$), Visual movement (Vm, $P=0.006$), Audio Visual still (AVs, $P=0.006$), and Audio Visual movement (AVm, $P<0.001$). Visual still (Vs) was not different from baseline ($P=0.288$). Contrasts for condition were not significant for vigilance or calm behavior overall. Bonferroni pairwise posthoc comparisons showed that AVm elicited the most alarm behavior (AVm was significantly higher than baseline, $P<0.001$, and significantly higher than Vs, $P<0.001$, whereas other conditions were significantly higher than only the baseline condition, at $P<0.05$).

Table 4 Experimental study: F values for four-way MANOVA of experimental condition, phase, habitate and conspecific presence

Source	Overall	Alarm	Vigilance	Calm
Condition	$F_{15, 1038}=2.708^{***}$	$F_{5, 378}=6.112^{***}$	$F_{5, 378}=0.799$	$F_{5, 378}=0.360$
Phase of Trial	$F_{6, 752}=14.871^{***}$	$F_{2, 378}=11.098^{***}$	$F_{2, 378}=19.835^{***}$	$F_{2, 378}=4.213^*$
Habitat	$F_{3, 376}=18.436^{***}$	$F_{1, 378}=7.530^{**}$	$F_{1, 378}=47.798^{***}$	$F_{1, 378}=29.363^{***}$
Conspecific	$F_{3, 376}=4.077^{**}$	$F_{1, 378}=8.546^{**}$	$F_{1, 378}=4.208^*$	$F_{1, 378}=0.858$
Condition x Phase	$F_{30, 1104}=1.803^{**}$	$F_{10, 378}=3.270^{***}$	$F_{10, 378}=0.966$	$F_{10, 378}=0.425$
Condition x Habitat	$F_{15, 1038}=1.976^{**}$	$F_{5, 378}=3.347^{**}$	$F_{5, 378}=2.202$	$F_{5, 378}=1.196$
Phase x Habitat	$F_{6, 752}=3.954^{**}$	$F_{2, 378}=3.588^*$	$F_{2, 378}=4.461^*$	$F_{2, 378}=0.106$
Condition x Habitat x Conspecific	$F_{15, 1038}=2.440^{**}$	$F_{5, 378}=2.366^*$	$F_{5, 378}=3.073^*$	$F_{5, 378}=2.998^*$

* $P<0.05$, ** $P<0.01$, *** $P<0.001$. The six conditions included Audio, Visual still, Visual moving, AudioVisual still, AudioVisual moving, and Baseline. Phases of Trial included Pretest, Test, and Post-test, Conspecific reflected Presence or Absence of conspecifics. Habitat Type included Urban or Rural. All four main effects are listed; beyond that only the four interactions that were significant are listed. All between-groups effects are listed for these eight sources.

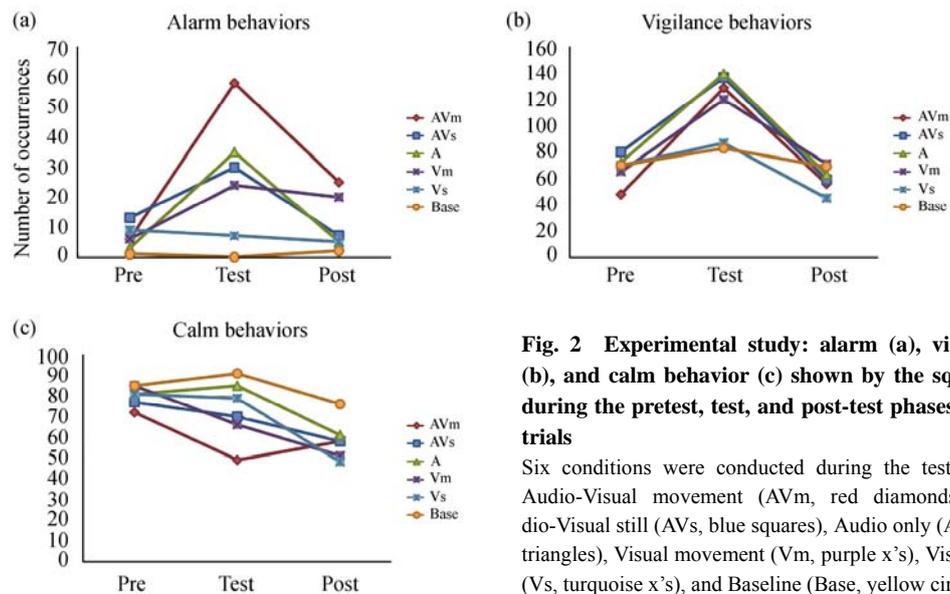


Fig. 2 Experimental study: alarm (a), vigilance (b), and calm behavior (c) shown by the squirrels during the pretest, test, and post-test phases of the trials

Six conditions were conducted during the test phase: Audio-Visual movement (AVm, red diamonds), Audio-Visual still (AVs, blue squares), Audio only (A, green triangles), Visual movement (Vm, purple x's), Visual still (Vs, turquoise x's), and Baseline (Base, yellow circles).

Table 5 Experimental study: frequency counts of each specific behavior that occurred during the Test Phase only (the middle minute, during which the test stimulus was presented)

Condition	Alarm Behavior				Vigilance Behavior		Calm Behavior		
	Tail Flag	Tail Flick	Vocalize	Mount Tree	Ascend Tree	Quad Vig	Biped Vig	Forage	Groom
AVm	19	20	3	4	12	83	46	47	2
AVs	0	23	2	3	2	102	35	69	1
A	3	13	0	4	15	103	37	80	5
Vm	2	17	1	1	3	85	35	62	4
Vs	0	5	0	0	2	68	19	76	3
Base	0	0	0	0	0	74	9	87	4

Contrast tests for phase were significant for all three dependent variables, alarm ($F_{2, 432}=12.966$, $P<0.001$), vigilance ($F_{2, 432}=22.027$, $P<0.001$), and calm ($F_{2, 432}=4.344$, $P=0.014$). Specifically, alarm behaviors ($P<0.001$) and vigilance ($P<0.001$) rose during the test phase in comparison to the pretest phase, and calm behaviors ($P=0.004$) decreased during the post-test phase in comparison to the pretest phase.

We graphed tail movements separately in order to examine differences between tail flick and tail flag (two of the “alarm” behaviors; Fig. 3). We found that while tail flicks increased during many conditions, tail flag increased only during AVm, the Audio Visual Movement condition.

2.2.2 Conspecific presence and habitat

Although we attempted to find and test lone squirrels, almost half of our trials (68, or 45%) were in fact conducted when the focal squirrel was not alone. This allowed us to test conspecific presence and absence as a factor in our model. Alarm and vigilance behaviors, but not calm behaviors, differed with presence or absence of conspecifics (see the four-way MANOVA results in Table 4); both alarm and vigilance increased in the presence of conspecifics (Fig. 4). We looked into these groups in

more detail to determine which of the behaviors making up the composite variables were responsible for the findings. We found that Tail Flagging was significantly higher when there were conspecifics present ($t=-2.817$, $P=0.005$). Vocalization did not differ significantly by presence of conspecifics ($t=-1.388$, $P=0.166$). Quadrupedal vigilance was significantly higher in the presence of conspecifics ($t=-2.892$, $P=0.004$), while bipedal vigilance was not significantly different ($t=-0.466$, $P=0.642$).

Squirrels were more plentiful in the urban habitats than the rural ones: there were an average of 2.0 squirrels present per trial in the relatively urban habitats (range 1–8) and an average of 1.4 squirrels present per trial in the rural areas (range 1–3). All three dependent variables, alarm, vigilance, and calm behavior, were higher in urban than rural habitats (Fig. 5). To follow up on the significant interaction between condition and habitat (see Table 4) and to find out whether communication signals were responded to differently in urban and rural areas we ran a MANOVA on habitat with the data file split by condition. We found that alarm responses were higher in the urban habitat for two conditions (Fig. 6): Vm and AVm (Vm: $F_{1, 73}=6.431$, $P=0.013$; AVm: $F_{1, 73}=5.65$, $P=0.020$).

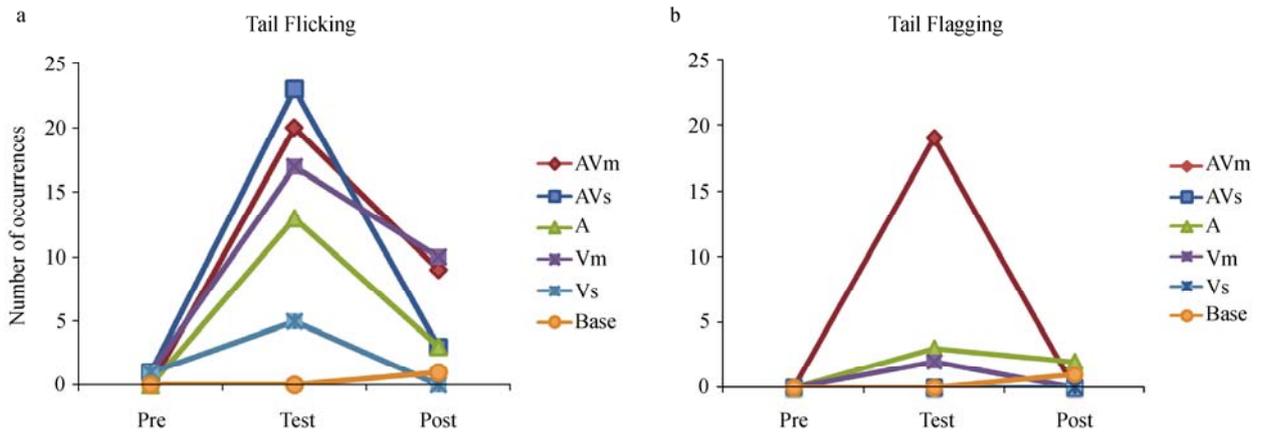


Fig. 3 Experimental study: tail movements in response to the squirrel robot

Two of the behaviors making up the Alarm Behavior Group in Fig. 2. Tail flicking (a) was more common, whereas tail flagging (b) was reserved primarily for the most evocative test condition, AVm. Key as in Fig. 2.

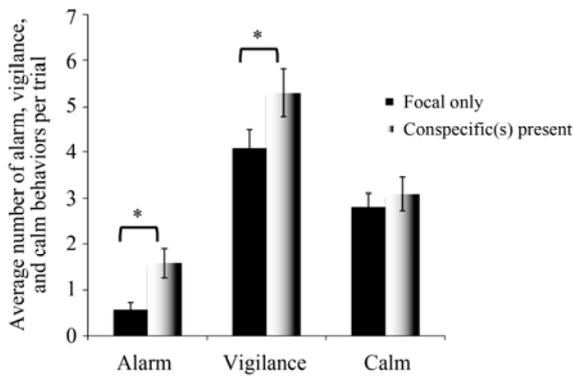


Fig. 4 Experimental study: behavioral responses with conspecifics present or absent, during the test presentations (test minute only)

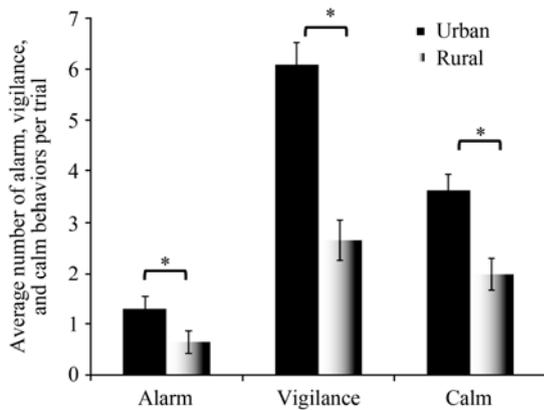


Fig. 5 Experimental study: behavioral responses in urban versus rural habitats, during the test presentations (test minute only)

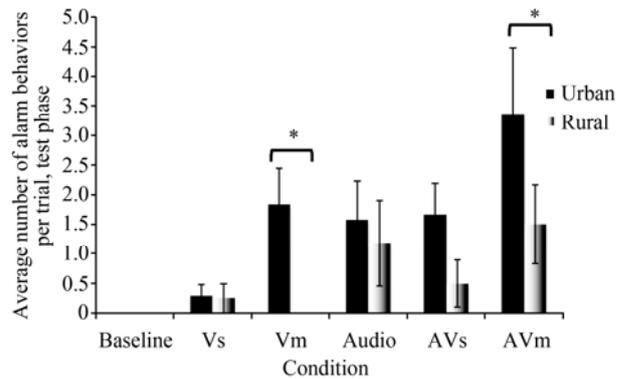


Fig. 6 Experimental study: alarm behaviors by condition, in urban and rural habitats, during the test presentations (test minute only)

2.3 Comparison of observational and experimental studies

Our data on natural squirrel behavior was intended to serve as a contrast for the experimental data in that it would provide us with a baseline estimate of the frequency of alarm behavior in a relatively undisturbed population. The squirrels in both studies emitted few tail flags or barks, however (see Tables 3 and 5, keeping in mind that Table 5 represents only a third of the experimental data because it includes the test phase only). Using Altmann and Wagner’s (1970) formula for estimating rates from Hansen frequencies, we calculated that during the observational study, for a length of time equivalent to the total duration of time that squirrels were observed in our experimental study, the squirrels gave an estimated 14.66 tail flags and 6.69 vocalizations. This was about

50% of that shown in the experimental study, in which there were 27 tail flags and 15 vocalizations overall.

3 Discussion

3.1 Multimodal enhancement

The Eastern gray squirrels tested in this Massachusetts study responded most strongly to a simulated mechanical conspecific producing alarm behavior when the presentations included both an audio component (bark) and moving visual component (tail flag; see Fig. 2a). Squirrels also responded to each signal component when it was presented on its own, but the multimodal signal was the most evocative of alarm responses in the subjects. This type of response is termed “multimodal enhancement” and it was also seen in an earlier study with gray squirrels in Florida (Partan et al., 2009). Both studies suggest that the auditory and visual components of these alarm signals are redundant in this context, in that they each evoke alarm responses in the observing squirrels, and together they evoke a higher level of alarm behavior than either does on its own. In fact, the system studied here exhibits properties of a linear system satisfying the principle of superposition, in that the responses to the audio and visual unimodal signals sum to the response to the multimodal one. Specifically, figure 2a shows that there were 24 alarm responses to tail flagging (Vm), and there were an average of 32.5 alarm responses to barking (averaging A and AVs, since these conditions both displayed barking without any other signal), and there were 58 alarm responses to the multimodal signal (AVm), which is about equal to the addition of the other two. This property has also been termed summation (Partan, 2004a), after Seitz’s Law of Heterogeneous Summation (Lorenz, 1981). Vigilance and calm behaviors did not exhibit this property.

Redundant signals are common in the animal kingdom and they have the benefit of ensuring that messages are transmitted even in noise (Wilson, 1975; Krebs and Dawkins, 1984; Johnstone, 1996; Rowe, 1999; Partan and Marler, 2005), although nonredundant signals are also important in many species and contexts, particularly mate choice (Candolin, 2003; Partan and Marler, 2005). Redundant multimodal signals that elicit enhanced responses, above the level of the unimodal components, are the most common type of redundant signaling (Partan, 2004a); further discussion of these topics can be found in Partan et al. (2009).

3.2 Conspecific presence and signal addressee

Alarm signals can be addressed toward conspecifics

(Sherman, 1977; Smith, 1986) or toward the predator (as predator deterrence, Caro, 1986; Shelley and Blumstein, 2005). To get an idea of the intended addressee of the gray squirrel alarm signals, we examined whether the squirrels were more likely to produce alarm behavior in the presence of conspecifics than when they were alone. In our experimental study we found that squirrels were more likely to tail flag in response to the robot when conspecifics were present than otherwise, suggesting that tail flagging may be directed toward conspecifics. We did not have predator presence data to ask whether this signal might also be directed toward predators. California ground squirrels use tail flags as a predator deterrent signal, directed specifically at snakes (Hennessy et al., 1981; Rundus et al., 2007), and there is recent documentation of gray squirrels tail flagging at snakes as well (Clark, 2005). It is possible that an anti-predator or alarm signal such as tail flagging has multiple addressees and functions (see Craig, 1982).

Our results regarding vocalizations were equivocal: our experimental study found that the incidence of vocalizing did not differ by conspecific presence, but our observational pilot data indicated that more vocalizations occurred when conspecifics were present. It is worth noting that in both studies the incidence of vocalizing was low (we noted fifteen vocalizations in the experimental study, and eleven 30-s time intervals in which vocalizations were heard in the observational one); a larger sample size of vocalizations would be useful before making generalizations. In addition, the vocalizations reported in our observational study came primarily from one particular session in which two squirrels were involved in a chase, so these were likely to be sounds involved in agonistic or reproductive behavior rather than alarm calls. In contrast to our experimental study, we did not require observers to distinguish among vocalization categories for the observational data collection.

3.3 Tail flicking and flagging

In both our observational and experimental studies we coded two tail movements, tail flicking and tail flagging, because we wanted to distinguish the classic, high intensity alarm behavior of tail flag from the lower intensity flicking. We found that tail flagging was in fact much less common than flicking and it was reserved primarily for situations of high alarm, e.g. during the AVm condition of the experiment (Fig. 3). We did not code the lowest level of tail movement, which could be called a “twitch”, that occurs commonly upon locomotion, because we assumed that twitches were not used for communication, but rather are associated with spinal flexion in locomotion (Hennessy et al., 1981).

Tail flagging has received far more attention in the literature than has flicking (e.g. in ground squirrels: Hennessey et al., 1981; Hersek and Owings, 1993; Rundus et al., 2007). While specific attention to tail flicking as a discrete behavior has been scant, several researchers have proposed that tail flagging represents one extreme end of a gradient of tail movements (Hennessey et al., 1981; Hersek and Owings, 1993; Tamura and Yong, 1993). In ungulates, Stankowich (2008) explicitly distinguishes between tail flicking and flagging and places the behaviors on a continuum from association with locomotion to agitation, although these behaviors are morphologically and functionally different in ungulates than in squirrels. Our data supports the suggestion that different levels of tail motion are positively associated with increasing levels of alarm.

In our experimental study, the moving visual component of tail flagging, rather than the static view of the tail, was found to be very important. Two visual conditions were tested: in one, the robot flagged its tail (Vm), and in the other, the robot was simply presented as a still model (Vs). The moving visual signal evoked significant responses in the observing squirrel, whereas the still model was treated no differently than the control condition (baseline trials in which the robot remained covered with camouflage cloth). This result suggests that the squirrels were responding specifically to the simulated tail flag signal, rather than just to the presence of a model squirrel. It also emphasizes the importance of motion in the signaling system of squirrels. Motion is important in most visual signaling systems. One advantage of using mechanical models is that motion can be disentangled from other cues, such as was shown in the frog studies in which frogs only responded when a mechanical frog model included vocal sac movement along with sound (Narins et al., 2003, 2005). A similar result was found in a study of foraging birds in which movement of robotic birds was important for responses from the live birds (Fernandez-Juricic et al., 2006).

3.4 Urban/rural comparisons

Our experimental study was carried out at different field locations, which varied along a number of dimensions including level of urbanization. The more urban areas tended to have more pedestrian traffic and the squirrels were more habituated to human presence than in the rural areas. We initially expected, therefore, that they would be less responsive to a simulated conspecific showing alarm behavior, based on the rationale from a study of fox squirrels in which it was found that squirrels in more urban areas showed reduced alarm re-

sponses to predator stimuli, likely due to a generalization of their habituation to humans (McCleery, 2009). However we found the opposite: the squirrels in the urban areas were more reactive, and showed more of every type of behavior overall (alarm, vigilance, and calm) than did the rural squirrels, similar to findings by Magle et al. (2005) and Rabin et al. (2006) for other Sciurids.

There are a number of key differences between McCleery's (2009) study and ours, including that we were studying different species and his was a study of responses to predators whereas ours was a study of responses to conspecific alarm behavior. Our terminology may also have differed in regard to the level of urbanization of our sites; his urban and rural sites were clearly distinguished at opposite ends of the urban-rural continuum, whereas our sites were probably less different from one another, being somewhat closer to each other on the urban-rural continuum, and perhaps more similar to McCleery's suburban category. Furthermore, the sites chosen by McCleery clearly differed with regard to predation risk, whereas our sites are likely more similar to one another in terms of predation, although the higher incidence of human pedestrian and vehicular traffic in our urban sites probably keeps predators further at bay than at our rural sites. Red-tailed hawks, red foxes and domestic dogs are fairly frequent visitors to both campuses in our study and feral cats, gray foxes, coyotes, bobcats, fisher, and other raptors occasional visitors, although there are likely more bobcats near the University of Massachusetts area and more coyotes and fishers in the Hampshire College area (Noah Charney and Brian Schultz, pers. comm., and SRP pers. obs.). Although these are all important differences between McCleery's (2009) study and ours, they do not easily explain why we found an opposite pattern of response by habitat type.

There are a number of possible explanations for the finding that our urban squirrels were more active and reactive than our rural squirrels. The high level of activity that we found in the urban squirrels supports earlier studies reporting high gray squirrel activity levels in crowded urban parks in Washington, D.C. (Manski et al., 1981). Higher levels of urban noise may have contributed to increases in vigilance in urban areas, as was found in ground squirrels by Rabin et al. (2006). Another possible explanation is that the rural squirrels may have been more likely to freeze than the urban squirrels, a behavior that we failed to code. Therefore the freezing behavior could have decreased the measured levels of all active behaviors that were recorded in the study. Or

the availability of tree refuge may have been closer and more abundant in the rural areas, leading the rural squirrels to be less reactive because they were closer to safety. Woodchucks who are close to refuge (<2m) run more slowly to safety than if they are further away, suggesting that distance to refuge can affect activity levels (Bonenfant and Kramer, 1996). Although we did not take data on this, we did notice that the urban squirrels were often found further from tree cover than were the rural squirrels. Another possible explanation has to do with self selection: it is possible that, since some squirrels in the rural areas tended to run off before we could even begin a trial, the only squirrels left in those areas to test may have been relatively unresponsive individuals. In the urban areas, where fleeing was not as common, we would have sampled a wider range of individuals who varied in their tendency toward responsiveness. Stankowich and Coss (2006) suggested that black-tailed deer vary individually in responsiveness and tendency toward flight. Webb and Blumstein (2005) suggested that there may be individual differences in tolerance of human disturbances in seagulls, which could lead to group differences if seagulls self-select their habitat.

We found that there were consistently more squirrels present at our urban sites than the rural sites, as is typical for other squirrel populations (Flyger, 1970; Manski et al., 1981; Steele and Koprowski, 2001). Differences in behavior between the two locations, therefore, might be attributable to the higher likelihood that conspecifics were present in higher numbers at the urban areas. In fact, Parker and Nilon (2008) found that squirrels in areas with higher population density were less wary, measured by shorter flight distances to human approach, than squirrels in areas with lower population density.

3.5 Population differences in acoustic behavior

Although population differences in signaling behavior of tree squirrels are not commonly reported, we found that these Massachusetts gray squirrels differed from the Florida gray squirrels studied by Partan et al. (2009) in at least one noticeable regard: the squirrels in the Massachusetts study vocalized far less frequently than the squirrels in the Florida study. The raw numbers are difficult to compare in the two studies because the Massachusetts study counted actual frequencies of barks using continuous recording, whereas the Florida study used one-zero recording (Hansen frequencies) to count number of 20s intervals in which barking occurred. Using Altmann and Wagner's (1970) formula for estimating rates from Hansen frequencies, we calculated that for an equivalent number of hours of data, the Florida

squirrels vocalized an estimated 44 times, in comparison to the 15 vocalizations heard in the Massachusetts experimental study. There are a number of possible explanations for this finding. Although data on conspecific presence was not recorded during the Florida study, it is likely that there were more conspecifics present at the Florida sites (SRP pers. obs.), and our current data suggests that the presence of conspecifics influences likelihood of alarm signaling behavior. We did find that the number of conspecifics was higher in the more urban of the Massachusetts sites, and the Florida study area was even more urbanized than any of the Massachusetts areas (using the same method described above we calculated the approximate percent of impervious surface for the earlier study area in St. Petersburg, Florida, to be 67%, which was higher than any of our Massachusetts sites).

Another possible explanation for the finding that the Florida squirrels vocalized more than the Massachusetts squirrels is that squirrels might vocalize more frequently in more urban environments, perhaps due to a need to overcome high noise levels. Animals do modify their vocal behavior under noisy urban conditions. California ground squirrels shift the emphasis of their calls from lower to higher harmonics to avoid traffic noise (Rabin et al., 2003); great tits increase the pitch of their songs in noisy urban environments (Slabbekoorn and Peet, 2003); orca increase the duration of calls once boat traffic exceeds a threshold level of noise (Foote et al., 2004); and humans and other animals increase the amplitude of vocalizations in noisy environments (known as the Lombard effect; Warren et al., 2006). In support of this idea, all 15 of the calls heard in our Massachusetts experimental study (6 during the test phase and 9 during the post-test phase) occurred on the University of Massachusetts campus, our most urban site, and none occurred at our rural sites. If urban squirrels do vocalize more frequently than rural squirrels, this may be the first documentation of changes in vocal *rate* due to urbanization, although in the visual modality, lizards increase their rate of visual display in more visually "noisy" habitats (Ord et al., 2007).

3.6 Multimodal shift in urban habitat?

We looked into the responses of the squirrels in the two habitats by experimental condition and found that the urban squirrels responded more strongly to visual tail flagging signals from the robotic stimulus than did the rural squirrels. The two conditions that were reacted to significantly more in urban sites were Vm, tail flagging on its own, and AVm, tail flagging with barking (see Fig. 6). There was no difference by habitat in the

response to audio signals on their own. This suggests the possibility that urban squirrels, perhaps due to elevated levels of auditory noise in the urban environment (Warren et al., 2006), might shift from a reliance on audio perception toward more reliance on visual perception (or a shared reliance on audio and visual signaling) for gathering information about environmental threats. Rabin et al. (2006) suggested that high levels of anthropogenic mechanical noise may cause acoustic masking of ground squirrel alarm calls, requiring behavioral changes to cope, such as reliance on visual scanning tactics rather than listening. Multimodal shifts due to noise may be commonplace; they are predicted by the so-called “cocktail party phenomenon” in which people in acoustically noisy situations rely more on visual cues from mouth articulation than they would otherwise (Cherry, 1953; Sumbly and Pollack, 1954; see discussions in Partan, 2004a, and Partan and Marler, 2005). Brumm and Slabbekoorn (2005) reviewed work on birds and frogs suggesting that visual signals may augment vocal ones in noisy environments. They concluded that more work is needed on these topics, but reasoned that especially in noisy environments where acoustic signals are masked, close-range visual signals should be favored by evolution. We are planning further work to investigate the possibility of multimodal shifts in urban noise in squirrels.

Acknowledgements We are grateful to Christian Larco and Max Owens for initial work on the squirrel robotic model; to Adam Sax for programming the upgraded model; Sean Nunley and Dan Taub for field work; Dana Morrison for help with class study and all of the students enrolled in the Spring 2009 Animal Behavior Field Methods class at Hampshire College; Jane Couperus, Phil Kelleher, and Richard Lowry for statistical help; Ted Stankowich, Paige Warren, and Mark Feinstein for discussion of results; Beth Jakob, Renae Brodie, Denise Pope, Peter Narins and an anonymous reviewer for comments on the manuscript; Martin Stevens for the invitation to submit to this special issue; and Hampshire College School of Cognitive Sciences and Dean of Faculty Office for support.

References

- Altmann SA, Wagner SS, 1970. Estimating rates of behavior from Hansen frequencies. *Primates* 11: 181–183.
- Bakken A, 1959. Behavior of gray squirrels. *Proceedings of the Southeastern Association of Game & Fish Commissioners* 13: 393–406.
- Blumstein DT, 2003. Flight-initiation distance in birds is dependent on intruder starting distance. *Journal of Wildlife Management* 67: 852–857.
- Bonenfant M, Kramer DL, 1996. The influence of distance to burrow on flight initiation distance in the woodchuck *Marmota monax*. *Behavioral Ecology* 7: 299–303.
- Bowers MA, Breland B, 1996. Foraging of gray squirrels on an urban-rural gradient: Use of the GUD to assess anthropogenic impact. *Ecological Applications* 6: 1135–1142.
- Brumm H, Slabbekoorn H, 2005. Acoustic communication in noise. *Advances in the Study of Behavior* 35: 151–209.
- Candolin U, 2003. The use of multiple cues in mate choice. *Biological Reviews* 78: 575–595.
- Caro TM, 1986. The functions of stotting: A review of the hypotheses. *Animal Behaviour* 34: 649–662.
- Cherry EC, 1953. Some experiments on the recognition of speech, with one and two ears. *Journal of the Acoustical Society of America* 25: 975–979.
- Clark RW, 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.
- Cooper CA, Neff AJ, Poon DP, Smith GR, 2008. Behavioral responses of Eastern gray squirrels in suburban habitats differing in human activity levels. *Northeastern Naturalist* 15: 619–625.
- Craig J L, 1982. On the evidence for a ‘pursuit deterrent’ function of alarm signals of swamp hens. *American Naturalist* 119: 753–755.
- D’Eath RB, 1998. Can video images imitate real stimuli in animal behaviour experiments? *Biological Reviews* 73: 267–292.
- Ditchkoff SS, Saalfeld ST, Gibson CJ, 2006. Animal behavior in urban ecosystems: Modifications due to human-induced stress. *Urban Ecosystems* 9: 5–12.
- Estes WA, Mannan RW, 2003. Feeding behavior of Cooper’s hawks at urban and rural nests in southeastern Arizona. *The Condor* 105: 107–116.
- Fernandez-Juricic E, Gilak N, McDonald JC, Pithia P, Valcarcel A, 2006. A dynamic method to study the transmission of social foraging information in flocks using robots. *Animal Behaviour* 71: 901–911.
- Flyger VF, 1970. Urban gray squirrels: Problems, management, and comparisons with forest populations. *Transactions of the Northeast Fish and Wildlife Conference* 27: 107–113.
- Foote AD, Osborne RW, Hoelzel AR, 2004. Whale-call response to masking boat noise. *Nature* 428: 910.
- Frid A, Dill LM, 2002. Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology* 6: 11–26.
- Göth A, Evans CS, 2004. Social responses without early experience: Australian brush-turkey chicks use specific visual cues to aggregate with conspecifics. *Journal of Experimental Biology* 207: 2199–2208.
- Gustafson EJ, VanDruff LW, 1990. Behavior of black and gray morphs of *Sciurus carolinensis* in an urban environment. *American Midland Naturalist* 123: 186–192.
- Hebets EA, Papaj DR, 2005. Complex signal function: Developing a framework of testable hypotheses. *Behavioral Ecology and Sociobiology* 57: 197–214.
- Hennessy DF, Owings DH, Rowe MP, Coss RG, Leger DW, 1981. The information afforded by a variable signal: Constraints on snake-elicited tail flagging by California ground squirrels. *Behaviour* 78: 188–226.
- Hersek MJ, Owings DH, 1993. Tail flagging by adult California ground squirrels: A tonic signal that serves different functions for males and females. *Animal Behavior* 46: 129–238.
- Janik VM, Slater PJB, 1997. Vocal learning in mammals. *Advances in the Study of Behavior* 26: 59–99.
- Johnstone RA, 1996. Multiple displays in animal communications: ‘Backup signals’ and ‘multiple messages’. *Philosophical Transactions of the Royal Society of London, Series B* 351: 329–338.
- Koprowski JL, 1993. Alternative reproductive tactics in male eastern gray squirrels: “Making the best of a bad job”. *Behavioral Ecology*

- 4: 165–171.
- Koprowski JL, 1996. Natal philopatry, communal nesting, and kinship in fox squirrels and Eastern gray squirrels. *Journal of Mammalogy* 77: 1006–1016.
- Krebs JR, Dawkins R, 1984. Animals signals: Mind-reading and manipulation. In: Krebs JR, Davies N ed. *Behavioural Ecology*. 2nd edn. Blackwell, Oxford: 380–402.
- Lishak RS, 1984. Alarm vocalizations of adult gray squirrels. *Journal of Mammalogy* 65: 681–684.
- Lorenz K, 1981. *The Foundations of Ethology*. New York: Springer-Verlag.
- Magle S, Zhu J, Crooks KR, 2005. Behavioral responses to repeated human intrusion by black-tailed prairie dogs *Cynomys ludovicianus*. *Journal of Mammalogy* 86: 524–530.
- Makowska IJ, Kramer DL, 2007. Vigilance during food handling in grey squirrels *Sciurus carolinensis*. *Animal Behavior* 74: 153–158.
- Manski DA, Vandruff LW, Flyger V, 1981. Activities of gray squirrels and people in a downtown Washington, D.C. park: Management implications. *Transactions of the North American Wildlife & Natural Resources Conference* 46: 439–454.
- Marler P, Tamura M, 1964. Culturally transmitted patterns of vocal behavior in sparrows. *Science* 146: 1483–1486.
- Martin P, Bateson P, 2007. *Measuring Behaviour*. 3rd edn. Cambridge: Cambridge University Press.
- Martins EP, Ord TJ, Davenport SW, 2005. Combining motions into complex displays: Playbacks with a robotic lizard. *Behavioral Ecology and Sociobiology* 58: 351–360.
- McCleery RA, Lopez RR, Silvy NJ, Gallant DL, 2007. Fox squirrel survival in urban and rural environments. *The Journal of Wildlife Management* 72: 133–137.
- McCleery RA, 2009. Changes in fox squirrel anti-predator behaviors across the urban-rural gradient. *Landscape Ecology* 24: 483–493.
- McGregor PK, 2000. Playback experiments: Design and analysis. *Acta Ethologica* 3: 3–8.
- Narins PM, Hödl W, Grabul DS, 2003. Bimodal signal requisite for agonistic behavior in a dart-poison frog *Epipedobates femoralis*. *Proceedings of the National Academy of Sciences U.S.A.* 100: 577–580.
- Narins PM, Grabul DS, Soma KK, Gaucher P, Hödl W, 2005. Cross-modal integration in a dart-poison frog. *Proceedings of the National Academy of Sciences* 102: 2425–2429.
- Ord TJ, Peters RA, Clucas B, Stamps JA, 2007. Lizards speed up visual displays in noisy motion habitats. *Proceedings of the Royal Society B* 274: 1057–1062.
- Parker TS, Nilon CH, 2008. Gray squirrel density, habitat suitability, and behavior in urban parks. *Urban Ecosystems* 11: 243–255.
- Partan SR, 2004a. Multisensory animal communication. In: Calvert G, Spence C, Stein BE ed. *The Handbook of Multisensory Processes*. Cambridge: MIT Press, 225–240.
- Partan SR, 2004b. Animal robots. In: Bekoff M, ed. *Encyclopedia of Animal Behavior*. Westport: Greenwood, 952–955.
- Partan SR, Marler P, 1999. Communication goes multimodal. *Science* 283: 1272–1273.
- Partan SR, Marler P, 2005. Issues in the classification of multisensory communication signals. *The American Naturalist* 166: 231–245.
- Partan SR, Larco CP, Owens MJ, 2009. Wild tree squirrels respond with multisensory enhancement to conspecific robot alarm behavior. *Animal Behaviour* 77: 1127–1135.
- Patricelli GL, Uy JAC, Walsh G, Borgia G, 2002. Male displays adjusted to female's response. *Nature* 415: 279–280.
- Patricelli GL, Blickley JL, 2006. Avian communication in urban noise: Causes and consequences of vocal adjustment. *The Auk* 123: 639–649.
- Patricelli GL, Krakauer AH, 2010. Tactical allocation of display effort reduces trade-offs among multiple sexual signals in greater sage-grouse: An experiment with a robotic female. *Behavioral Ecology* 21: 97–106.
- Rabin LA, Greene CM, 2002. Changes to acoustic communication systems in human-altered environments. *Journal of Comparative Psychology* 116: 137–141.
- Rabin LA, Coss RG, Owings DH, 2006. The effects of wind turbines on antipredator behavior in California ground squirrels *Spermophilus beecheyi*. *Biological Conservation* 132: 410–420.
- Rabin LA, McCowan B, Hooper SL, Owings DH, 2003. Anthropogenic noise and its effect on animal communication: An interface between comparative psychology and conservation biology. *International Journal of Comparative Psychology* 16: 172–192.
- Rosenthal GG, 1999. Using video playback to study sexual communication. *Environmental Biology of Fishes* 56: 307–316.
- Rowe C, 1999. Receiver psychology and the evolution of multicomponent signals. *Animal Behaviour* 58: 921–931.
- Rundus A, Owings D, Joshi S, Chinn E, Glanini N, 2007. Ground squirrels use an infrared signal to deter rattlesnake predation. *Proceedings of the National Academy of Sciences* 104: 14372–14376.
- Shelley EL, Blumstein DT, 2005. The evolution of vocal alarm communication in rodents. *Behavioral Ecology* 16: 169–177.
- Sherman PW, 1977. Nepotism and the evolution of alarm calls. *Science* 197: 1246–1253.
- Slabbekoorn H, Peet M, 2003. Birds sing at a higher pitch in urban noise. *Nature* 424: 267.
- Smith R J F, 1986. Evolution of alarm signals: Role of benefits of retaining group members or territorial neighbors. *The American Naturalist* 128: 604–610.
- Stankowich T, 2008. Tail-flicking, tail-flagging, and tail position in ungulates with special reference to black-tailed deer. *Ethology* 114: 875–885.
- Stankowich T, Coss RG, 2006. Effects of predator behavior and proximity on risk assessment by Columbian black-tailed deer. *Behavioral Ecology* 17: 246–254.
- Steele MA, Koprowski JL, 2001. *North American Tree Squirrels*. 1st edn. Washington: Smithsonian Institution Press.
- Steele MA, Halkin SL, Smallwood PD, McKenna TJ, Mitsopoulos K et al., 2008. Cache protection strategies of a scatter-hoarding rodent: Do tree squirrels engage in behavioural deception? *Animal Behaviour* 75: 705–714.
- Sumby WH, Pollack I, 1954. Visual contribution to speech intelligibility in noise. *Journal of Acoustical Society of America* 26: 212–215.
- Tamura N, Yong H-S, 1993. Vocalizations in response to predators in three species of Malaysian *Callosciurus* (Sciuridae). *Journal of Mammalogy* 75: 703–714.
- Uetz GW, Roberts JA, 2002. Multisensory cues and multimodal communication in spiders: Insights from video/audio playback studies. *Brain Behaviour and Evolution* 59: 222–230.
- Ward C, Low BS, 1997. Predictors of vigilance for American crows foraging in an urban environment. *The Wilson Bulletin* 109: 481–489.
- Warren PS, Madhusudan K, Ermann M, Brazel A, 2006. Urban bioacoustics: It's not just noise. *Animal Behaviour* 71: 491–502.
- Webb NV, Blumstein DT, 2005. Variation in human disturbance differentially affects predation risk assessment in western gulls. *The Condor* 107: 178–181.
- Wilson EO, 1975. *Sociobiology*. Belknap: Cambridge, MA.
- Zeil J, 2000. Depth cues, behavioral context, and natural illumination: Some potential limitations of video playback technique. *Acta Ethologica* 3: 39–48.