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Wild tree squirrels respond with multisensory enhancement to conspecific robot alarm behaviour

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Natural social communication in animals involves the use of multiple sensory channels but has traditionally been easier to study one channel at a time. As a consequence we know more about the simplified situation of unitary signal channels than we do about the natural situation in which these sources are integrated. Studies of single channels of communication underestimate, and can even misrepresent, the salience and meaning of messages that are normally communicated via multiple channels. However, new mechanical or robotic animal models allow us to test the meaning of multiple components of a signal, via multiple sensory channels. Being three-dimensional, they also allow these questions to be tested in natural field settings where ambient light may constrain other methods such as video playback. Robotic models have been successfully tested with wild amphibians, reptiles and birds. Here we show that a wild mammal, the eastern grey squirrel, *Sciurus carolinensis*, responds to a robotic model displaying alarm behaviour. Wild squirrels showed enhanced responses to multisensory, audio/visual signals of alarm compared to unisensory (either audio or visual) signals. This is significant for studies of the evolution of communication in that it underscores the importance of taking the complete signal into account, and it provides a method for studying multisensory communication in wild mammals. It is also important for studies of sensory integration, since the squirrels showed an enhanced behavioural response to multisensory signals, providing an overt parallel to brain mechanisms of other mammals that show neural enhancement to multisensory stimuli.

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Animals communicate using multiple sensory channels simultaneously, a phenomenon known as multisensory or ‘multimodal’ communication (Partan & Marler 1999; Rowe 1999). Although multimodal communication has been documented in many animals (reviewed in Partan 2004a), unresolved questions remain. It is unclear, for example, why some species use redundant signals, in which components in multiple channels carry the same message, while other species use nonredundant signal components that can contradict or modify one another (Candolin 2003; Hebets & Papaj 2005; Partan & Marler 2005). An effective way to resolve these questions is to examine responses both to the multimodal signal as a whole and to each of the component parts separately (Partan 2004a). Experimental playback methods are ideal for parsing the contribution of each channel to the overall message.

Multimodal signalling is now commonly studied in laboratory settings where visual, auditory, vibrational, olfactory, and even infrared heat components of the signal can be manipulated and their effects on subjects measured (Uetz & Roberts 2002; Rundus et al. 2007). Experimental field studies of multimodal communication are less common because, among many other constraints, ambient light inhibits use of the video playback method because the screen is hard to see (but see Clark et al. 1997; Burford et al. 2000). One way around this problem is to conduct three-dimensional ‘playbacks’ using mechanical animals (typically dubbed ‘robots’ despite being nonautonomous; Partan 2004b), an approach that overcomes several constraints of video: the need for low ambient light levels, lack of depth and possible issues of screen flicker (D’Eath 1998). This method, called ‘ethorobotics’ (Partan 2004b), has successfully elicited biologically meaningful responses in field studies of bees (Michelsen et al. 1992), frogs (Narins et al. 2003) and birds (Patricelli et al. 2002), as well as laboratory studies of lizards (Martins et al. 2005) and snakes (Rundus et al. 2007). It has yet to be tried with mammalian subjects. Experimental field studies of natural multimodal communication among mammals, however, are important for understanding the evolution of communication. We therefore tested the function of multimodal

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communication among wild mammals using a robotic model as a stimulus.

We chose to study alarm behaviour in tree squirrels (Sciuridae, Sciurini). Auditory signals of alarm have been well studied using audio playback methods (e.g. in sciurids: Lishak 1977; Shriner 1998; Sloan et al. 2005; Blumstein 2007), but multimodal aspects of alarm have been less well studied in any animal. In a survey of 32 studies that explicitly examined separate components of multimodal signals across all animals, only three examined alarm or warning signals (Partan & Marler 2005). These three were studies of warning coloration in aposematic prey animals, and all three found that combinations of visual and chemical cues from the prey can increase unpalatability to a predator (Terrick et al. 1995; Rowe & Guilford 1996; Hatle et al. 2001). Because squirrels have visual as well as audio signals of alarm (described below), they are a good subject for a study of multimodal alarm signals in a nonaposematic species.

The eastern grey squirrel, *Sciurus carolinensis*, is a tree squirrel native to the eastern U.S.A. (Koprowski 1994) that has been well studied for its ecology and management (e.g. Steele et al. 1998; Huxley 2003; Maslovat 2003; Gurnell et al. 2004; Koprowski 2005) but less often for its social behaviour. Early work on general grey squirrel behaviour was reviewed by Steele & Koprowski (2001). More recent work includes studies of reproductive behaviour and nesting (Koprowski 1993, 1996) and of foraging and caching behaviour (Jacobs & Liman 1991; Makowska & Kramer 2007; Steele et al. 2008).

Communication in sciurids has most often been studied in the ground-dwelling members of the family (primarily ground squirrels and marmots), which are highly social and live in tight kin-based groups. The strong kin-based structure of their social system leads to nepotistic behaviours such as alarm calling despite an increased risk of predation (Dunford 1977; Sherman 1977). Tree squirrels, in contrast, are generally less social than ground squirrels. However, Koprowski (1996) found that grey squirrels are somewhat social in that they live in female kin-based groups, nest communally and engage in affiliative as well as agonistic behaviour, suggesting that we might expect nepotistic communication behaviour among female grey squirrels. Urban tree squirrels in particular are found more often in large groups than are rural squirrels (Flyger 1970; Manski et al. 1981; Steele & Koprowski 2001), providing ample opportunity for social interactions and potential selection on communication.

Squirrels use a variety of communication signals in several sensory channels. Multimodal visual and vocal alarm behaviour in squirrels usually involves tail flagging and barking, which have been thoroughly studied in ground squirrels (Balph & Balph 1966; Sherman 1977; Owings & Virginia 1978; Hennessy et al. 1981; Owings & Hennessy 1984). Recently, ground squirrels have been found to extend their auditory and visual signalling outside of the human range into the ultrasonic (*Spermophilus richardsonii*, Wilson & Hare 2004) and infrared ranges (*Spermophilus beecheyi*, Rundus et al. 2007). This leaves open the question of whether these ranges are also used in tree squirrels.

Tree squirrel alarm vocalizations have been documented (grey squirrels, *S. carolinensis*: Horwich 1972; Lishak 1984; red squirrels, *Tamiasciurus* spp.: Smith 1978; Greene & Meagher 1998; African tree squirrels, *Paraxerus* spp.: Viljoen 1983; Malaysian tree squirrels, *Callosciurus* spp.: Tamura & Yong 1993), and tail flagging as a signal of alarm has also been observed (grey squirrels, *S. carolinensis*: Bakken 1959; Steele & Koprowski 2001), but these behaviours have not been studied in tree squirrels to the same extent that they have been studied in ground squirrels.

Although barks and tail movements occur in both tree and ground squirrels, selection pressures imposed by the two very

different habitats that tree and ground squirrels inhabit may have caused these behaviours to evolve for use in different contexts. The ground is a more open habitat for the transmission of visual signals, whereas the arboreal habitat can obscure vision and favour a reliance on auditory communication. In addition, although the effect of predators on squirrel populations is not well known (Wauters 2000; Steele & Koprowski 2001), the predator assemblages and escape routes differ between the two squirrel habitats. Tree and ground squirrels share a number of aerial and terrestrial predators such as raptors, owls, canids, and a variety of small mammals (Koprowski 1994; Steele & Koprowski 2001; Schaufert et al. 2002; Makowska & Kramer 2007), but ground squirrels experience higher predation from badgers (Michener 2004) and snakes, which may lead to communal defence behaviours. For example one consequence of the intense pressure from snake predation on California ground squirrels, *Spermophilus beecheyi*, is that these squirrels have evolved an elaborate multimodal anti-snake mobbing behaviour involving extensive use of tail flagging (Hennessy et al. 1981; Hersek & Owings 1993). Because mobbing behaviour and social cooperation are less common in tree squirrels, there may be less selection for antipredator communication in these squirrels.

The current study was designed to test two questions: first, will a wild mammal, the grey squirrel, respond to mechanical models of conspecifics producing communication signals? Second, how do the visual and vocal components of grey squirrel alarm behaviour interact? Are both signal components required to communicate alarm or will one suffice?

To resolve these questions we created a three-dimensional model of an eastern grey squirrel (*S. carolinensis*) with a mechanical tail and hidden speakers. The experimental design tested the function of the auditory and visual components separately and combined. We also tested both stationary and moving visual features because movement is a key feature of many visual signals, found to be important in other robotic animal studies (Narins et al. 2003). We hypothesized that first, wild squirrels would respond to conspecific robots. We tested the prediction that follows from this hypothesis that the squirrels would respond with alarm more during test periods when they could see or hear the robot than during control periods when they could not. Our second hypothesis was that the auditory and visual signal components of alarm would be redundant (both eliciting similar responses). The combination of components may elicit a qualitatively and quantitatively similar response to isolated components ('equivalence'), or an increased response ('enhancement') (Partan & Marler 2005). The alternative is that the components are not redundant, with one contradicting, modifying or adding to the message of the other (Partan & Marler 2005).

METHODS

Subjects and Sites

Seventy-two wild urban grey squirrels (*S. carolinensis*) on the campus of the University of South Florida St Petersburg and in public parks in St Petersburg, Florida, U.S.A. were tested over the course of one year. All sites are listed in Table 1. Squirrels were not marked but, as in Steele et al. (2008), we avoided resampling the same individuals by keeping track of subjects after their trials were done and by moving to the opposite end of the park before finding a new subject. The smallest parks were one city block, or approximately 150 m lengthwise, which is longer than the greatest linear dimension of grey squirrel home range sizes reported by Doebel & McGinnes (1974; 136.7 m) and Armitage & Harris (1982; 87.4 m). We then moved to an entirely new park on each new data collection day (or for some of the larger sites, we returned to a new end of

Table 1

Locations for data collection in St Petersburg, FL, U.S.A.

Bartlett Park
Campbell Park
Coffeepot Park
Cook Park
Crescent Lake
Demon's Landing
Flora Wylie Park
Fort DeSoto Park at Campground
Fort DeSoto Park near Fort
Ingleside Park
Jorgenson Lake Park
Lake Maggiore Park
Lake Vista Park
Mirror Lake Park
Northshore Park, central
Northshore Park, north end
Northshore Park, south end
Park on the Pier
Pioneer Park
Poynter Park
Roser Park
Sawgrass Lake Park
Straub Park, central
Straub Park, north end
Straub Park, south end
USFSP, north of library
USFSP, by Campus Activities Center
USFSP, by Florida Center for Teachers
USFSP, by HVAC building
USFSP, by waterfront
Vinoy Park, east end
Vinoy Park, west end
Yacht Club near downtown

USFSP: University of South Florida, St Petersburg Campus.

the park or campus on a new day, indicated in Table 1 as 'north end', 'south end', etc.). Given the high density of squirrels in St Petersburg, the fact that we did not visit the same place twice, and the minimal number of times we revisited adjacent areas, we are reasonably confident that we rarely resampled the same individual. If we did, enough time would have passed that the squirrel would be unlikely to remember the previous incident (revisiting a new spot in the same park happened 15 times, with an average of 80 days between visits; range 2–365 days).

Robot Design and Programming

The squirrel robot was made from a life-sized hollow model of an eastern grey squirrel, cast in a heavy plastic and covered with rabbit fur (125 cm long, 105 cm wide, 130 cm high at the head with the tail extending to 180 cm high when upright; Fig. 1). The model sat on a base concealing a circuit board, motor, speakers and amplifier. We constructed a mechanical tail around a 15 cm heavy spring that descended into the base of the model and attached to a small hidden servo motor. The motor moved the tail forward and backward, actuated by a remote switch via a 12 m cable. Eastern grey squirrels move their tails primarily forward and back (Bakken 1959), unlike California ground squirrels, which often incorporate circular movement (Hennessy et al. 1981).

The squirrel robot was controlled using a microcontroller (called 'Stamp' made by Parallax) programmed with 'Basic Stamp' software. The tail was programmed to flick back and forth seven times (duration 3 s), then pause (duration 3 s), repeated for the duration of the test (1 min). This timing was chosen based on our observations of natural tail flagging in local grey squirrels. For audio trials, a compact disc was prerecorded with two tracks: first, two short bursts of white noise were used as a trial-start signal to ensure that

the subject was attending to the stimulus. This sound was chosen as an alerting stimulus because tree squirrels glance briefly towards white noise but do not run away (Tamura 1995). This sound was played at the start of each trial. The second audio track contained eastern grey squirrel alarm vocalizations that were broadcast continuously for the duration of all tests that included audio (1 min).

Playback Protocol

Subjects were presented with 3 min trials during which the squirrel robot was camouflaged from view for the first minute (pre-test control period), presented in one of five conditions for the second minute (the test), and camouflaged again for the final minute (post-test). Trials had to be kept brief because of the rapid baseline movement of the squirrels across the substrate as they foraged.

The five test conditions were as follows: audio only (grey squirrel alarm calls, during which the model remained camouflaged; A); visual only, still (uncovered model, with no tail motion; Vs); visual only, moving (uncovered model, tail waving; Vm); audio/visual still (uncovered motionless model with calls; AVs); and audio/visual moving (uncovered moving model with calls; AVm). Each condition acted as a control for the others, following the design of Narins et al.'s (2003) robotic frog presentations.



Figure 1. Squirrel robot. Photograph copyright Jason Marsh.

Conditions were presented in random order per subject. Each subject was tested for only one set of five trials.

The primary contrast we anticipated was between the pre-test and the test period. We expected that alarm behaviour may continue to be elevated in the post-test period because once squirrels begin to give alarm calls they often continue for many minutes (Loughry & McDonough 1988; Tamura 1995).

Behavioural Data Collection

Squirrel responses were recorded in the field using the one/zero recording method with time intervals of 20 s (presence or absence of behaviour was noted for each time interval; Martin & Bateson 2007). The field team consisted of three people: one to operate the robot and keep track of the squirrel should it move off; one to take the observational data; and one to record backup video.

Data were collected on the subject's alarm behaviour (tail flagging, barking and staring fixedly at the robot) and non-alarm behaviour (general attentiveness, defined by looking up and around in several directions, and approaching the model, defined by moving in the direction of the model, regardless of whether the squirrel was on a tree or the ground). Data were included in the analysis only if the squirrel remained visible for the duration of the entire 3 min trial (which occurred on 134 of 152 trials). If the squirrel ran away during the pre-test period, we did not continue the trial and did not conduct a test. If the squirrel ran away during the test (11 times) or post-test periods (7 times), we did not include the data in the analysis. Although the numbers were too low for a statistical analysis of squirrels lost by condition tested, most of the squirrels ran away during audio (8 of 18) or audio-visual movement trials (5 of 18).

Over the course of the study we used a number of field observers; only those data collected by three observers that attained interobserver reliability were retained for analysis (134 trials were retained: 68 trials from one observer, 61 trials from a second observer, and five trials from a third observer). For the interobserver reliability test, we ran six regular trials with three squirrels (two trials per squirrel) that were observed by all of our field observers simultaneously. Each trial had the usual three phases, pre-test, test and post-test; each phase had the usual three data points at 0 s, 20 s and 40 s. This totalled nine data points per trial for each behaviour. We collected data on the five behaviours listed above, for a total of 45 data points per trial. The three observers whose data were retained attained an average of over 90% reliability (reliability was measured as: number of agreements / (number of agreements + number of disagreements)).

Statistical Analysis

We examined the data at a gross level first, by lumping alarm behaviours (tail flag, bark and stare at the robot) and comparing them against the non-alarm behaviours (general attention, approach). We conducted an ANOVA using period (pre, test, post) and condition (A, Vs, Vm, AVs, AVm) as independent variables, and the categories of alarm and non-alarm behaviour as dependent variables. Because the response metric can affect interpretation of the data, in particular influencing the classification of a signal into redundant and nonredundant categories (Partan & Marler 2005), we also examined the behavioural responses individually. For this second ANOVA we used the same independent variables, but included all five individual behaviours (tail flag, bark, stare, attention, approach) as separate dependent variables. Significance level for all tests was 0.05.

RESULTS

The wild squirrels responded to the mechanical model with the normal suite of alarm responses that are given in response to real squirrels. Supporting our first hypothesis, that the squirrels would respond to the robot, they responded with alarm more often when they could see or hear the robot than when they could not. Alarm behaviour increased significantly during the test period ($F_{2,387} = 11.07$, $P < 0.0001$; Fig. 2a), but non-alarm behaviour did not ($F_{2,387} = 0.26$, $P = 0.77$; Fig. 2b). That the non-alarm behaviours did not vary, but the alarm behaviours did, indicates that the squirrels reacted in a biologically meaningful way to the stimulus.

Our second hypothesis, that the audio and visual components would be redundant, was also supported, with moderate responses shown to unisensory signals and larger responses to multimodal signals. This supports the idea of redundancy with multisensory enhancement. Alarm behaviour was significantly higher during the AVm (Audio, Visual movement) condition than during any other ($F_{4,387} = 4.14$, $P = 0.003$; Fig. 2a), whereas the unisensory conditions were not significantly different from one another. Non-alarm behaviour did not vary across condition ($F_{4,387} = 0.84$, $P = 0.50$; Fig. 2b).

The analysis of individual behaviour by period showed that two of the three alarm behaviours varied significantly across the three test periods: tail flagging ($F_{2,353} = 4.32$, $P = 0.014$; Fig. 3a) and staring at the robot ($F_{2,353} = 15.84$, $P < 0.0001$; Fig. 3b). Tukey HSD post hoc analyses showed that squirrels tail-flagged at significantly higher rates during the test and post-test periods than during the control (pre-test) period. Rates for staring behaviour were also higher during the test period than either the pre- or the post-test periods. In contrast, there were no significant differences across period for either of the two non-alarm behaviours (approach: $F_{2,353} = 0.179$, $P = 0.836$; attention: $F_{2,353} = 0.141$, $P = 0.868$).

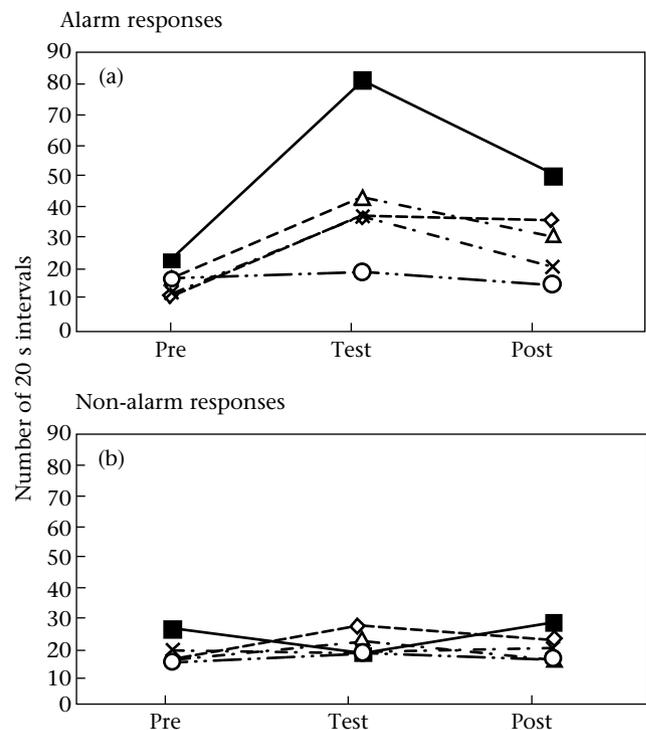


Figure 2. (a) Alarm and (b) non-alarm responses of wild grey squirrels to the squirrel robot. The robot was presented in multisensory conditions (solid square: audio/visual, moving, AVm; open triangle: audio/visual, still, AVs) and in unisensory conditions (open diamond: audio only, A; ×: visual, moving, Vm; open circle: visual, still, Vs).

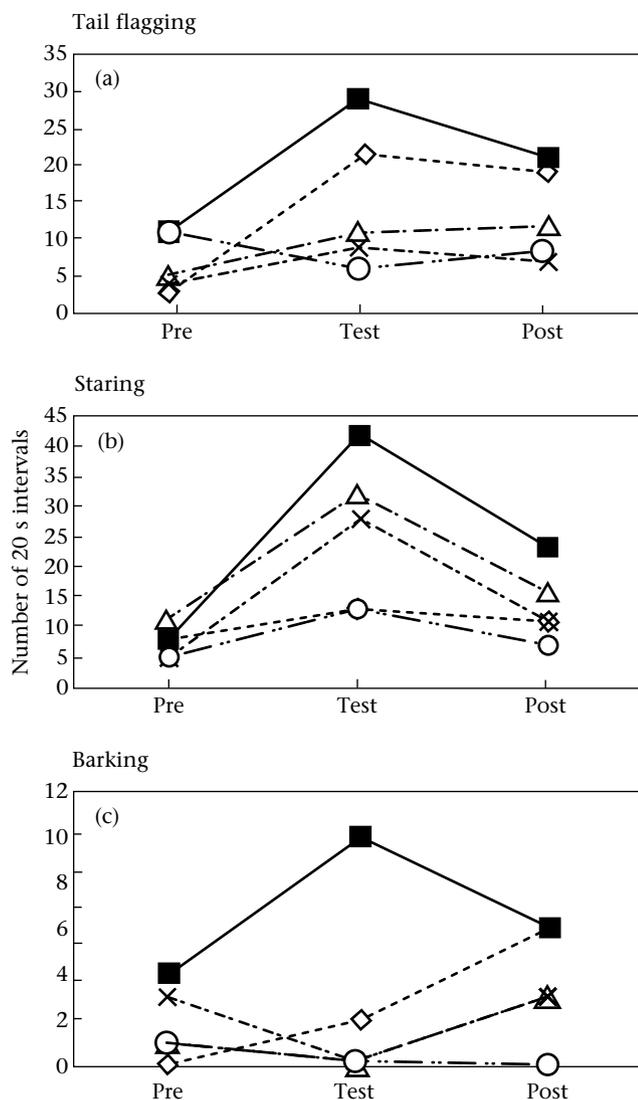


Figure 3. Specific alarm responses by wild grey squirrels to the squirrel robot: (a) tail flagging, (b) staring at the robot and (c) barking. Key as in Fig. 2.

The analysis of individual behaviour by condition showed that two alarm behaviours varied significantly across the five test conditions: staring at the robot ($F_{4,353} = 5.09$, $P = 0.0005$; Fig. 3b) and barking ($F_{4,353} = 2.59$, $P = 0.0365$; Fig. 3c). Tukey HSD post hoc analyses showed that both multimodal conditions (AVm and AVs) elicited more staring behaviour than either of two unimodal conditions (A or Vs), and that AVm elicited the most barking behaviour (and Vs the least). There was also a nonsignificant tendency ($F_{4,353} = 2.25$, $P = 0.0638$; Fig. 3a) for tail flagging to be higher during AVm than during the other conditions. Although the non-alarm behaviours as a group were not significantly different across condition, when analysed separately, approach behaviour was significant ($F_{4,353} = 2.44$, $P = 0.047$) whereas attention remained nonsignificant ($F_{4,353} = 1.37$, $P = 0.244$). Tukey HSD post hoc analyses showed that the squirrels approached more after AVm tests, and less after AVs tests, than during any other condition or period. This may have been because the squirrels tended to run high into the trees during AVm tests, but often returned to a lower spot in the tree during the post-test period, which was coded as 'approach' because it brought the squirrel closer to the robotic model.

DISCUSSION

Our results show that wild grey squirrels responded to presentations of alarm from a mechanical squirrel, distinguishing the test from the control periods. When the mechanical squirrel's signals included only unisensory information (either audio or visual), there was a moderate amount of alarm response from the wild squirrels. However, multimodal, audio/visual-movement displays were highly evocative of alarm behaviour. These two sensory channels appear to work together to enhance the effect of the signal. According to the terminology presented by Partan & Marler (1999, 2005), these signals would therefore be categorized as 'redundant', since they all elicit some type of alarm behaviour, with a subclassification of 'enhancement', because the combination of channels increases the response. In this discussion we first address the topic of multimodality, then we discuss alarm signals, and we conclude with a discussion of the robotic animal method and future studies.

Multimodality

Signal classification

Ours is one of the first studies to examine alarm behaviour from the perspective of multiple sensory modalities, outside of the work on aposematic prey (Terrick et al. 1995; Rowe & Guilford 1996; Hatle et al. 2001). Multimodal communication has been extensively studied, however, in the context of mate choice (see Candolin 2003; Hebets & Papaj 2005). Mate choice involves signalling about quality, and multicomponent courtship signals can convey information about numerous aspects of quality simultaneously. These types of signals are therefore often composed of composite nonredundant signals that carry multiple messages (Johnstone 1996), although they can also be composed of redundant signals. Multiple messages allow a receiver to transmit more information per unit time. Multimodal alarm signals, being of immediate importance to survival, may be likely to be composed of redundant components, as backup signals that all convey the single meaning of alarm. Redundant backup signals ensure that the signal is transmitted even in noise. There may be cases, however, in which multicomponent alarm signals transmit new messages, such as the multiple audio components of chickadee alarm calls (Templeton et al. 2005).

The categorization frameworks that have been developed for hypotheses about multicomponent signals used in mate choice (Candolin 2003; see also Hebets & Papaj 2005; reviewed in: Otovic & Partan 2009) may also be applicable to other communication contexts such as antipredator behaviour, and they each list redundant signals as one category. Although they use a similar definition of redundancy as Partan & Marler (1999, 2005), the latter authors further subdivide redundancy into equivalence and enhancement, useful here because the squirrels showed enhanced responses to the multimodal display.

Multimodal enhancement has also been found in birds experimentally presented with audio and video images in the laboratory (alarm behaviour in chickens: Evans & Marler 1991; avoidance behaviour in chickadees: Baker et al. 1996; courtship behaviour in pigeons: Partan et al. 2005). In field work with animal robots, auditory combined with moving visual signals were also the most effective condition tested for eliciting aggressive responses in frogs (Narins et al. 2003).

Our finding that grey squirrels spent much more time (and presumably energy; Ryan 1988) attending (see Fig. 3b) and responding (see Fig. 3a) to multimodal signals than to unimodal signals is important for understanding time budgets and responses to predation risk. Hebets (2005) found that female wolf spiders that

are attending to multimodal signals of male courtship are more likely to be captured by (human) predators than are females attending to fewer signal channels from the male, presenting empirical evidence for an important cost of multimodal communication suggested by Candolin (2003) and Partan & Marler (2005). In addition, from the predator's point of view, Roberts et al. (2007) found that predatory jumping spiders attack more quickly if the prey, simulated by playback of signals from wolf spiders, uses multiple sensory channels to communicate than if the prey uses just one channel.

Issue of behavioural assay

Partan & Marler (2005) discussed the issue of interpreting data differently when a different number of responses are measured. This issue can be seen clearly here. When we lumped the responses into the gross-level categories of 'alarm' and 'non-alarm' behaviours (see Fig. 2), audio and visual components were redundant, as discussed above. However, when we examined behavioural responses individually, we found more complexity in the data. For example, although two of the three alarm behaviours measured showed the same pattern whether analysed separately (Fig. 3) or combined (Fig. 2a), the third behaviour, bark, did not. Wild squirrels barked in response to multimodal audio/visual-movement presentations, but suppressed barking during the other presentations (Fig. 3c). Therefore, if we had examined barking alone, we might have concluded that the response to the multimodal signal differed over time compared to other types of signals. Perhaps at a gross level, it is fair to conclude that the audio and visual components are redundant because they both elicited alarm behaviour, as opposed to, say, courtship behaviour. Although the degree of alarm differed, as exemplified by the addition of barking in response to the multimodal stimulus, this can be seen as a quantitative rather than qualitative difference (see below for more on barking).

Hebets & Papaj (2005) discussed a similar issue with regard to mate choice signals. They pointed out that multiple cues may signal different aspects of quality, so that in one sense they provide redundant information on quality, but in another sense they provide multiple messages (or nonredundant information) about particular measures of quality.

Effects of unimodal channels

Although the multimodal audio-visual movement condition elicited the highest levels of alarm response across each behaviour tested, the effects of the other conditions were more variable. The other multimodal condition, audio-visual still, elicited staring but not tail flagging or barking, whereas audio-alone was more evocative of tail flagging and barking. Viljoen (1983) suggested that in African tree squirrels, visual signals are used during lower levels of excitation and auditory signals are given with increasing excitement. Our data support this idea to the extent that tail flagging was a more common response to the robot than was barking. Furthermore, tail flagging rates were higher in response to the audio-only signals than to the visual-only signals from the robot (Fig. 3a). California ground squirrels also show less response to conspecific tail movement alone than to vocal alarms (Owings & Hennessy 1984). Our data therefore support the idea that, as with ground-dwelling sciurids (Macedonia & Evans 1993), variation in grey squirrel alarm signals may reflect response urgency (see below).

Compared to tail flagging, staring and barking were suppressed in the audio-only condition. This makes sense in the case of staring, because the robot was covered during audio-only trials so there was nothing to draw visual attention. In the case of barking, this may have been suppressed because the squirrels could not listen and bark at the same time; immediately following the test interval,

barking behaviour increased after the audio-only tests (Fig. 3c). In Malaysian tree squirrels, alarm barks also cause other squirrels to stay silent until the barking ceases (Tamura & Yong 1993).

The one condition that was routinely ignored by the squirrels was the visual-only still condition. This was biologically appropriate, because the still model evoked the image of a foraging squirrel, producing no communication signals, and no cause for alarm. Since the still model did not display signalling behaviour, it can be considered a control condition, useful for ensuring that the squirrels were not responding to the robot itself, in the absence of any interpretable signal.

Alarm Signals

Signal addressee and contagion of alarm

Squirrel tail flags and barks may be given as alarm signals to warn conspecifics of danger for a variety of reasons, such as kin selection or possible reciprocation (Sherman 1977; Smith 1986; Loughry & McDonough 1988). In many species of rodents and birds, individuals repeat alarm calls given by conspecifics. Our observation that grey squirrels often responded to the robotic presentations of alarm signals by repeating the alarm suggests that they are at least active recipients of these conspecific alarm signals, regardless of whether they (or their predators) are the intended recipient(s) of these signals. Caro (1986) discussed many possible reasons for prey to signal to predators, such as informing the predator that it has been detected, as Bildstein (1983) found for the tail flagging of white-tailed deer, or deterring the predator from attacking, as Rundus et al. (2007) suggested for tail flagging in California ground squirrels. Shelley & Blumstein (2005) surveyed 209 rodent species and found support for the idea that alarm calls evolved to communicate to predators (although grey squirrels were not included in the survey). We cannot address this possibility with our data because we did not study the predators. Thorington & Ferrell (2006) acknowledged that it is difficult to tell whether tree squirrel alarm behaviour is directed towards conspecifics or predators, but given that tree squirrels are not as social as ground squirrels and that they usually give alarm calls from the safety of the treetops after a predator has been detected, these authors suggested that predator deterrence may be the primary function. However, Koprowski (1996) found that grey squirrels do have kin-based social groups, so there is a potential for nepotistic use of alarm calls. An alternative hypothesis presented by Taylor (1966) is that grey squirrel calling is used in social behaviour rather than in alarm or antipredator behaviour, because she found that the prevalence of calling varied throughout the year, whereas one might expect alarm behaviour to occur year-round. All three hypotheses, that tail flagging and barking function as signals of alarm to conspecifics, as signals to the predator, or as other types of social behaviour, may actually be mutually compatible explanations, as Craig (1982) suggested for tail flicking in swamphens.

Referentiality

An extensive literature on the question of referentiality in alarm calls of primates and ground-dwelling sciurid rodents was analysed by Macedonia & Evans (1993). These authors suggested that the necessity for some primates to use different escape tactics in the face of different predators drove the evolution of referential signalling to indicate which escape route to use. In contrast, ground-dwelling sciurid rodents have one escape: the burrow. They need information on predator location but would not necessarily benefit from further information regarding predator identity. Response urgency is therefore more likely to be encoded into their calls, rather than referential information. The data (summarized in Macedonia & Evans 1993) indicate that although ground-dwelling

sciurids may have specific calls used for different predator classes, they also use these calls across classes depending on the degree of response urgency. Blumstein (2007) discussed this issue in marmots, and added the suggestion that the degree of sociality affects the evolution of referentiality in alarm calling as well. Tree squirrels present an interesting angle on this debate: they are taxonomically related to the ground rodents, but live primarily in trees like the arboreal primates. Tamura & Yong (1993) and Tamura (1995) found that Malaysian and Formosan tree squirrels give predator-class-specific calls. These two species of squirrels also show different escape strategies to the different calls: they run into the trees in response to terrestrial predator calls, freeze in response to aerial predator calls, and approach snake calls (these squirrels mob snakes). Greene & Meagher (1998) studied red squirrels, *Tamiasciurus hudsonicus*, which are sympatric with grey squirrels in North America, and they found that red squirrels also have predator-class-specific alarm calls and use multiple escape routes. Our review of the work on grey squirrel alarm calls has not yet indicated the existence of predator-specific calls in this species. Furthermore, Makowska & Kramer (2007) found that foraging urban grey squirrels are less vigilant when overhead views are obstructed than they are with lateral obstructions, suggesting that overhead cover found in trees may reduce threat from aerial predators. Although our study did not address these topics specifically, and we played only one type of alarm call from our robotic model, we observed only one primary type of response (running up into the trees). More work should be done on this question in grey squirrels.

Robotic Animal Method

Mammal responses to robots

This is the first demonstration to our knowledge of a wild mammal responding to a conspecific robotic model in the field. There have been two laboratory studies, however, of other mammals responding to conspecific robots: Sony's autonomous toy dog, 'AIBO', elicited either aggressive or playful responses from live dogs, depending on the context (Kubinyi et al. 2004). 'AIBO' was not designed to realistically simulate a live dog, nor to accurately mimic movements of a live dog, however. The other laboratory study was a study of learning in rats, in which the rats followed a robotic rat model to sources of food (Takanishi et al. 1998), similar to a recent study of cockroaches following a robot to sources of shelter (Halloy et al. 2007). In both the rat and cockroach studies, the focus was on creating an autonomous robot that would seek out the appropriate resource and elicit a following response from the live subjects. In the rat study it was possible that the rats simply learned that the robot could be used as a discriminative stimulus for food arrival. We are aware of two other studies that have used robots modelled after mammals, but in both cases the subjects tested were nonmammals: Rundus et al. (2007) elicited caution in snakes by presenting realistic-looking robotic ground squirrels that were programmed to modulate the degree of warming of their tails; and Vaughan et al. (2000) managed to herd ducks within a round enclosure with what they called a 'robotic sheepdog', although their robot was a round canister that did not resemble an animal form. In contrast, our mechanical squirrel was designed to mimic a live animal's shape, form and movement and to interact with live, wild conspecifics, as with the studies of wild bower birds (Patricelli et al. 2002) and frogs (Narins et al. 2003).

Further work

There are several further studies that could be done to add to our understanding of the squirrels' reaction to the robots, which would be useful for any robotic animal study. First, it would be good to compare the response of the animals to the robot with their

natural responses to conspecifics. This is hard in many cases because the behaviours being tested, such as tail flagging and barking, may be infrequent in the wild. Quantitative data on this question have not yet been taken with grey squirrels. An ideal approach would be to set up observation blinds and record the responses of squirrels to alarm calls and displays made by conspecifics.

Second, it would be informative to test various renditions of the mechanical models to determine which features of the model are important in eliciting a response. In this present study, we tested the presence and absence of the entire model as well as the tail movement and vocalizations of the model, but there are other aspects of the model to consider, such as the material from which it is made. Is it important that the model be fur-covered? In the AIBO studies, live dogs reacted more strongly to AIBO robots that were covered in puppy-scented artificial fur than to robots without fur (Kubinyi et al. 2004). In our study, we used rabbit fur to cover the model. Future studies could examine whether a taxidermied squirrel would be more or less effective than our fabricated model. Taxidermied birds have been used successfully in studies using robotic bird models (Patricelli et al. 2002; Göth & Evans 2004). The squirrels in our study did not approach the model closely enough to get much olfactory information, although we did not keep track of wind direction. We could also systematically degrade the lifelike appearance of the model to determine the minimum stimulus required to get a meaningful reaction from the squirrels. Tinbergen (1948) pioneered this method with dummy animal models and it is worth revisiting in the current context of robotic models, to better understand the perceptual basis of communication behaviour.

In summary, our results indicate that the message of alarm can be carried in either the audio component or the moving visual component, suggesting that the two components are redundant. Together, audio and visual movement components were highly evocative of alarm responses, creating an enhanced multimodal signal. For animal taxa whose multimodal audio/visual communication has been most commonly studied (insects, amphibians and birds), it is common for the combination of signal channels to interact such that the composite signal is modulated or enhanced above the level of the unisensory components (Seitz 1940; Partan 2004a; Hebets & Papaj 2005; Partan & Marler 2005). If this is also true for mammals, as our results suggest for grey squirrel alarm signals, and as studies of neural multisensory integration in cats and rhesus monkeys have found at the cellular level (Meredith & Stein 1983; Stein et al. 1993), it has implications for the evolution of mammalian communication, including current debates on the role of gesture in the evolution of human speech (Corballis 2003; Pollick & de Waal 2007).

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