

Department of Biological Sciences, Eastern Illinois University, Charleston

Alarm Calls Affect Foraging Behavior in Eastern Chipmunks (*Tamias striatus*, Rodentia: Sciuridae)

Jessica K. Baack & Paul V. Switzer

Baack, J. K. & Switzer, P. V. 2000: Alarm calls affect foraging behavior in eastern chipmunks (*Tamias striatus*, Rodentia: Sciuridae). *Ethology* **106**, 1057–1066.

Abstract

We used playback experiments to test whether alarm calls affected the foraging behavior of eastern chipmunks (*Tamias striatus*). We subjected chipmunks, foraging at artificial feeding stations, to three playback treatments (silent, control noise, and alarm call) and examined changes in vigilant and foraging behavior. Chipmunks responded to alarm calls with a greater degree and duration of vigilant behavior, such as look-ups and alert postures. Chipmunks also ran a shorter distance to cover and took longer to re-emerge from the burrow after hearing an alarm call. Alarm calls caused individuals to spend more time exposed at the feeding stations; however, individuals also took significantly fewer seeds after hearing an alarm call. This was not due to a difference in the time spent handling food, but rather to a slower rate of loading. Chipmunks appear to sacrifice energy gain by increasing vigilance after hearing an alarm call. This study suggests that to avoid the costs of unnecessary escape behavior, individuals directly assess their own risk rather than relying only on indirect cues such as alarm calls.

Corresponding author: Jessica K. Baack, Department of Biology, Montgomery College, Rockville Campus, Rockville, MD 20850, USA. E-mail: jbaack@mc.cc.md.us

Introduction

Foraging often carries with it a danger of predation. Predation risk is characterized by the probability of being encountered by and being attacked or killed by a predator (Newman et al. 1988; Lima & Dill 1990), and may affect various components of foraging such as diet selection (Dill & Fraser 1984; Lima & Valone 1986; Phelan & Baker 1992), habitat choice (Anderson 1986; Gilliam & Fraser 1987; Holmes 1991; Hughes & Ward 1993; Brown & Morgan 1995), the distribu-

tion of competitors among resources (Newman & Caraco 1987), and patch exploitation (Holmes 1984; Lima et al. 1985). For central place foragers, who repeatedly carry food items back to a central location, other factors such as time needed to travel to and from the food patch, and the constraints associated with carrying multiple items, may alter classical predictions of foraging behavior. Thus, animals face a trade-off in which they must balance two conflicting, but necessary demands (energy gain and not getting eaten) and may compromise one or both objectives (Sih 1980).

Individuals' perception of risk may be affected by the direct detection of predators (Dill & Fraser 1984; Kieffer 1991) and by the proximity to or the amount of cover (Valone & Lima 1987; Dill & Houtman 1989; Bowers & Ellis 1993). In addition, many species make use of alarm calls to signal potential danger (Dunford 1970; Lishak 1984; Thompson & Liebreich 1987; Blumstein 1995; Blumstein & Arnold 1995; Weary & Kramer 1995; Hoogland 1996; Blumstein & Armitage 1997). In response to alarm calls, animals may assume an alert posture (Weary & Kramer 1995), become more vigilant (Carey & Moore 1986; Shriner 1998), or flee into a refuge (Weary & Kramer 1995; Shriner 1998). These behaviors are consistent with those observed in other studies that have looked at other aspects of predation risk (Dill & Fraser 1984; Valone & Lima 1987; Kieffer 1991), which suggests that alarm calls also increase an individual's perception of risk and may increase the probability of early detection of a predator (Hauser & Wrangham 1990). Interestingly, many studies have looked at how foraging behavior is affected by correlates of predation risk, such as distance to cover, amount of cover, and the presence of a predator (Dill & Fraser 1984; Valone & Lima 1987; Dill & Houtman 1989; Holmes 1991; Bowers & Ellis 1993). On the other hand, studies investigating responses to alarm calls have generally measured vigilance. Rarely have studies tested whether hearing an alarm call affected other aspects of an individual's behavior, such as foraging, as we would predict if alarm calls do indeed increase an individual's perception of risk (but see Bachman 1993). In this study we examine how the foraging behavior of eastern chipmunks (*Tamias striatus*) is affected by conspecific alarm calls.

Eastern chipmunks are small, solitary, diurnal, terrestrial rodents (Kramer & Nowell 1980; Giraldeau & Kramer 1982; Clarke et al. 1993; Giraldeau et al. 1994; Otter 1994; Bowers 1995). They are often found in deciduous woods in habitats with high over-story and ground cover (Bowers 1995; Brown & Morgan 1995). Chipmunks have small (usually less than 0.5 ha), but widely overlapping home ranges (Dunford 1970; Wood 1993; Giraldeau et al. 1994). They are central place foragers, and center their activity around their burrow system of underground runways in which they forage, cache, and defend food from conspecifics (Dunford 1970; Kramer & Weary 1991; Clarke et al. 1993; Wood 1993).

Chipmunks are excellent subjects for studying the effects of alarm calls on foraging behavior. They are abundant, readily habituate to humans, and exhibit virtually insatiable hoarding behavior (Kramer & Nowell 1980; Kramer & Weary 1991). Chipmunks give alarm calls in response to conspecifics, humans, and other large animals (Dunford 1970). An individual hearing these calls often assumes an

upright or crouched alert posture, characterized by a lack of movement, and may flee the area (Dunford 1970; Weary & Kramer 1995). Thus, these behavioral changes, along with the contexts in which alarm calls are often given, suggest that hearing an alarm call does increase a chipmunk's perception of risk. If alarm calls do alter perceived predation risk, we can make the following predictions on how alarm calls will affect foraging behavior. First, chipmunks should respond to alarm calls with more vigilant behavior, as has been previously demonstrated in other studies of alarm call behavior (e.g. Carey & Moore 1986; Weary & Kramer 1995). Secondly, individuals should spend less time in a food patch after hearing an alarm call, in order to minimize the time spent exposed to potential predators (Bowers & Ellis 1993). Thirdly, chipmunks should take fewer seeds per trip (Kieffer 1991; Bowers & Ellis 1993) after hearing an alarm call, due either to lower foraging rates as a result of vigilance or less time spent in the food patch.

Materials and Methods

This study was conducted in and around residential areas of Charleston, IL, USA, with study sites averaging approximately 0.75 ha in size and temperatures ranging from 18°C to 34°C, over a 6-month period. Most contained grass lawns surrounded by woods and brush, creating an edge habitat through which chipmunks readily traveled.

Subjects were caught at the study sites from late May through Jun. 1998 using Sherman live traps baited with sunflower seeds. We marked each individual with varying spot patterns on the shoulder, midsection, and rump using different combinations of blond and black Clairol Nice 'N' Easy hair dye applied with a paintbrush. Metal numbered ear-tags with plastic colored discs were also applied as a second measure of identification. Individuals were released immediately after handling and observations were made to identify frequently used burrow entrances, home ranges, and common pathways of travel. Capture and handling of chipmunks was compliant with governmental and institutional regulations.

Feeding stations were constructed from a 20 × 20 × 2 cm³ piece of wood with a plastic Petri dish nailed to the center. These were set out for each individual approximately 5 m from the central burrow so that chipmunks would find the feeding stations quickly (Bowers & Ellis 1993). To habituate individuals to the feeding stations, we supplied striped sunflower seed for 1 mo prior to experiments. Three different 'playback' treatments were used: a 'chip' alarm call, shown to be elicited in response to terrestrial predators (Burke da Silva et al. 1994); a control sound (white noise); and silence. We recorded alarm calls using a Marantz Model PMD222 portable cassette recorder, a Sennheiser System K6 microphone, and parabolic reflector. Chipmunks do not distinguish among playback calls of different individuals (Weary & Kramer 1995). To control for chance recognition of a specific call, we obtained calls from multiple individuals from areas at least 1 mile from the study sites to create a set of playback stimuli for the playback trials. Using Canary Software (Charif et al. 1995), we eliminated background noise and selected three series of notes with the least amount of background noise; each ser-

ies was spliced with itself to produce a given 20 s playback stimulus. The rate of calls in a playback stimulus mimicked natural bouts of calls (approximately 1.5 notes per s). A similar method was used to create control sounds of white noise (Weary & Kramer 1995; Mateo 1996). All playbacks were broadcast from a Marantz portable cassette recorder through a single Advent Powered Partners AV570 speaker, powered by a Bescor PRO 10 Amp battery pack model PRB-10. The sound level of the playback was calibrated to 90 dB using a Radio Shack sound level meter to mimic the volume of chipmunk vocalizations heard in nature (Weary & Kramer 1995). The speaker was housed in a wooden box with a camouflage cover; the speaker and observer were hidden approximately 3–4 m from the feeding station and approximately 10 m from the burrow entrance.

Trials were conducted Jul. through Nov. between 09:00 h and 17:00 h. During this study period natural chipmunk alarm calls were frequently heard at the study sites at times other than those during which we conducted playback trials. Feeding stations contained 60 sunflower seeds (Kramer & Nowell 1980; Bowers & Ellis 1993). All trials were videotaped with a HI 8 Canon camcorder, model ES3000, mounted on a tripod.

Each subject received all three playback treatments; all three treatments were given to an individual on the same day. At least 0.5 h (mean \pm SE, 42.6 ± 1.5 min) was allowed between control and alarm call playbacks for each individual to increase the likelihood of independence of treatments. Prior to a trial a subject had two undisturbed trips to the feeding station. The order of the treatments for an individual (silent, control, alarm call) as well as the particular playback stimulus was chosen at random for each trial. The order of the treatments which an individual received did not affect the responses. For example, the percentage of individuals responding in a particular manner consistent with the overall result (e.g. increased rather than decreased residence time after hearing an alarm call) was similar regardless of whether the individual was played an alarm call or control sound first (84% vs. 81%, respectively, with foraging behavior analyses pooled, $\chi^2 = 0.05$, $df = 1$, $p = 0.82$).

We recorded a number of observations for each trial. We first recorded whether travel to the dish was direct, with no stops between the burrow and the dish, or delayed, in which the individual periodically stopped and scanned (McAdam & Kramer 1998). Just before the subject began to load seeds, we broadcast the playback stimulus (either control sound or alarm call); for silent trials, no recording was played. For the time that an individual was at a feeding station, we recorded handling time (time spent loading, chewing, or manipulating food items) and the frequency and duration of vigilant behavior. Vigilant behavior included looking up, alert postures, and scanning (Otter 1994; Weary & Kramer 1995). Residence time was defined as the total time spent at the feeding station, or vigilance time plus handling time. As response behavior, we recorded the distance an individual ran to cover (i.e. burrow or vegetation that concealed the individual from the observer) after collecting seeds, whether its travel away from the dish was direct or delayed, and its recovery time (the time from which the subject entered the burrow until the time it re-emerged from the burrow). Load size was deter-

mined by removing the remaining seeds from the feeding station and counting them. This constituted the end of a single trial.

Statistical tests were non-parametric and corrected for ties where appropriate. We used McNemar's test to conduct frequency comparisons of changes in behaviors within individuals for different treatments (Zar 1996). Wilcoxon signed rank tests were used for within-individual comparisons of means. For simplicity, we present only the results of call vs. control sound comparisons. No significant differences existed between silent and control treatments, and Friedman's test incorporating all three treatments yielded results consistent with those presented below. All means are reported as \pm SE.

Results

Ten out of 12 subjects responded with vigilant behavior to call treatments and did not respond to control treatments. Of the other two, one responded to both the control and call sound and one did not respond to either playback treatment (McNemar's test, $P=0.002$). Chipmunks exhibited more vigilant behavior with the alarm treatment than they did with the control treatment as shown by the higher frequency of look-up events and the trend towards more alert postures (Table 1). Thus, they spent a greater proportion of time vigilant throughout an entire trial after hearing an alarm call (Table 1). Interestingly, however, although they responded to alarm calls, total residence time was greater for individuals following an alarm call treatment than following the control (Table 1).

Foraging behavior was also affected by alarm calls. Chipmunks took significantly fewer seeds after hearing an alarm call as opposed to a control sound (control = 36.1 ± 3.7 seeds, call = 30.8 ± 4.1 seeds; Wilcoxon $n=12$; $T=13$; $p < 0.05$). The lowered load size was not due to a decrease in the time spent handling food (control = 42.3 ± 5.9 s, call = 64.2 ± 13.4 s; Wilcoxon $n=12$; $T=24$; $p =$

Table 1: Results of Wilcoxon signed rank tests for responses to control and alarm call treatments by Eastern chipmunks at feeding stations ($n=12$ individuals)

	Mean \pm SE		df	Wilcoxon T	p
	Control	Call			
Total Residence time (s)	60.5 \pm 6.0	108.1 \pm 20.8	11	13	0.050
Rate of loading (seeds/s)	0.97 \pm 0.1	0.66 \pm 0.1	11	11	0.035
Number of look-ups	12.0 \pm 1.5	15.4 \pm 2.1	11	13	0.050
Number of alert postures	0.3 \pm 0.1	0.9 \pm 0.4	5	2	0.100
Proportion vigilance time	0.3 \pm 0.1	0.4 \pm 0.1	11	5	0.005
Recovery time (s)	143.9 \pm 17.1	339.5 \pm 65.1	11	1	0.001
Distance to cover (m)	3.9 \pm 0.4	2.8 \pm 1.0	11	2.5	0.003

0.3125); rather, individuals loaded food items at a slower rate after hearing an alarm call (Table 1).

Alarm calls continued to affect an individual's behavior after it left the feeding station. After collecting seeds, chipmunks ran a shorter distance to cover following the alarm treatments than following the control (Table 1). Individuals also took significantly longer to re-emerge from the burrow and resume normal activity after the call treatments than after control treatments (Table 1). Type of travel to and from the feeding station did not differ significantly between the two treatments. All 12 individuals exhibited a delayed approach to the feeding station regardless of the treatment (McNemar's test, $p > 0.90$). Only four of the 12 individuals changed travel type away from the feeding station; all four delayed their travel (periodically stopped and scanned) back to the burrow after hearing the control sound but traveled directly back to the burrow after hearing an alarm call (McNemar's test, $p = 0.2$).

Discussion

In this study we found that eastern chipmunks generally react to and alter their foraging behavior in response to conspecific alarm calls. When exposed to alarm calls individuals exhibited more vigilant behavior while foraging at the feeding station. Such reactions to alarm calls have been found in a wide variety of sciurids (Leger et al. 1979; Harris et al. 1983; Carey & Moore 1986; Mateo 1996; Blumstein & Armitage 1997). These responses to alarm calls are consistent with responses observed in studies which varied predation risk with respect to openness of habitat, presence and proximity of a model predator, and distance to a refuge (Carey & Moore 1986; Dill & Houtman 1989; Kieffer 1991; Otter 1994) and thus suggest that alarm calls may also affect an individual's perception of risk. In addition to increased vigilance at the feeding station, chipmunks in our study ran a shorter distance and more directly to cover and delayed their re-emergence from the burrow after hearing an alarm call, suggesting that the call had a lasting effect on their behavior.

As predicted, chipmunks decreased their load size (number of seeds taken per trip) after hearing an alarm call. Other studies found similar shifts in load size after manipulating openness of habitat or proximity of a model predator (Brown 1988; Kieffer 1991; Bowers & Ellis 1993; Bowers et al. 1993; Otter 1994; but see Giraldeau & Kramer 1982; Giraldeau et al. 1994). However, individuals were not decreasing the number of seeds by simply reducing the total time spent at the feeding station, nor did they reduce the amount of time they spent loading seeds. Instead, they were being more vigilant and were loading at a slower rate after hearing an alarm call. Furthermore, chipmunks actually spent more time at the feeding station after hearing an alarm call due to an increase in not only the proportion of time spent vigilant, but also in the total amount of time spent vigilant (residence time minus handling time). Our results suggest that hearing an alarm call results in a cost to the efficiency of foraging, and when combined with the slower rate of

coming back out to forage again, implies that individuals are trading off gaining food with the risk of being eaten.

We predicted that animals would have shorter residence times after hearing alarm calls. Otter (1994) found residence time for eastern chipmunks to be greater in open and presumably more risky habitats and attributed this increase to a greater amount of time spent being vigilant. However, in their study of use of canopy cover, Bowers & Ellis (1993) found that individuals minimized the time they spent in areas of presumably higher potential predation risk. Our results, similar to Otter (1994) but counter to our prediction, suggested that individuals were not minimizing their time exposed to potential predation risk: chipmunks spent more time at the feeding stations after hearing an alarm call. Two, non-exclusive possibilities may explain the increase in residence time after hearing an alarm call.

First, the increased residence time may be due to an individual spending time to directly assess its risk of predation or to ensure a safe escape route if detected by a predator. Although characteristics such as distance from the refuge, amount of cover in the habitat, and alarm calls may indirectly relate to the risk of predation (Lima & Dill 1990; Weary & Kramer 1995), an individual may benefit from directly assessing whether it is in imminent danger of being eaten. To always respond to indirect cues, such as alarm calls, may impose unnecessary temporal and energetic costs and lowered energy gain to a foraging individual (Burger et al. 1991). By becoming more alert and assuming a motionless posture, chipmunks can increase their awareness of visual and auditory stimuli (Weary & Kramer 1995) and may ultimately benefit if their longer residence time leads to either a more accurate assessment of their risk or to a better escape route. Our feeding stations were relatively close to a refuge. However, if individuals are foraging in more 'risky' areas (e.g. further away from a refuge or in an area with less cover), we might expect that they would have more immediate responses to alarm calls and thus decrease their reliance on direct assessment of predation.

A second explanation for increased residence time after hearing an alarm call may be that chipmunks were being vigilant for conspecifics, not predators. Indeed, Ydenberg et al. (1986) predicted that the presence of conspecific competitors would increase residence time, and Giraldeau et al. (1994) found that some aspects of chipmunk foraging behavior, such as load size and travel time, were affected by the presence of nearby individuals. However, previous studies have implicated predation risk rather than competition when explaining responses to alarm calls (e.g. Carey & Moore 1986; Thompson & Liebreich 1987; Macedonia & Evans 1993; Blumstein & Arnold 1995; Weary & Kramer 1995; Mateo 1996; Blumstein & Armitage 1997; Blumstein 1998). For some aspects of foraging behavior, distinguishing responses to alarm calls due to the risk of predation and responses due to the threat of competition may be difficult. For example, increased predation risk and the presence of conspecifics are both predicted to increase vigilance and result in smaller load sizes (Ydenberg et al. 1986; Brown 1988; Giraldeau et al. 1994). In our study, however, we found that in addition to altering their foraging behavior, alarm calls caused individuals to run a shorter distance to cover and have longer

recovery times. Such results are more consistent with predation risk than competition explanations and strongly suggest that some of the responses to alarm calls that we observed were related to effects on perceived risk of predation. In any case, looking for singular, functional explanations of responses to alarm calls may be inappropriate, as individuals may gain more than one type of information from hearing an alarm call. Investigating whether multiple interpretations to 'alarm' signals exist and exploring how the social and environmental contexts of the signal affect its interpretation would be an interesting avenue for future research.

Acknowledgements

We thank T. Nelson for assistance with trapping and marking and for his comments on the manuscript. Thanks also to D. Blumstein, E. Bollinger, D. Baack, and I. and J. Switzer for manuscript suggestions and assistance throughout the study, an anonymous reviewer for manuscript suggestions, and D. Kramer and S. Lima for valuable discussions. Special thanks to Connie Huber, Andrew Methven, Kipp McGilliard, Susie Mounce, Britto Nathan and their respective families for the use of their property on which experiments were conducted.

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Received: July 20, 1999

Initial acceptance: December 25, 1999

Final acceptance: May 30, 2000 (J. Brockmann)