The response of foraging eastern chipmunks (*Tamias striatus*) to alarm calls of the black-capped chickadee (*Poecile atricapillus*)

By
Kathryne A. de León
April 2010



Allegheny College
Department of Biology

The response of foraging eastern chipmunks (*Tamias striatus*) to alarm calls of the black-capped chickadee (*Poecile atricapillus*)

By
Kathryne de León
April, 2010

A Senior Comprehensive Project in Partial Fulfillment of the Requirements for a Bachelor of Science Degree from Allegheny College

I hereby recognize and pledge to fulfill my responsibilities as defined in the Honor Code and to maintain the integrity of both myself and the College community as a whole.

_____
Pledge

Approval by the Senior Thesis Committee:

_____
Dr. Ron Mumme

_____
Dr. Chris Lundberg

Abstract

The black-capped chickadee (*Poecile atricapillus*) emits alarm calls that express information about the type of predator and the degree of threat the predator holds. While chickadees produce alarm calls to warn members of their own species of dangerous predators, other animals can eavesdrop on these calls and obtain information regarding common predators. My study tests whether foraging eastern chipmunks (*Tamias striatus*) are able to distinguish and respond appropriately to chickadee alarm calls. Due to the shared habitat and types of predators between the eastern chipmunk and black-capped chickadee, I hypothesized that chipmunks will become more aware of predator risk after hearing chickadee alarm calls and will respond by assuming an alert posture, looking up from foraging, scanning the area, and fleeing the foraging site. Chipmunks responded to alarm calls with vigilant behavior and by decreasing the amount of seeds consumed, demonstrating that chipmunks recognize the alarm calls of chickadees and respond with anti-predator behavior. These findings are consistent with previous studies demonstrating interspecific eavesdropping with several species.

Introduction

To increase their survival and fitness, animals can use different forms of communication, such as eavesdropping, which involves obtaining information from signaling interactions by individuals not directly involved in communication (Peake et al., 2005). Since animal communication often occurs in networks when various species are in close range, individuals may be able to obtain information about neighbors and predators by eavesdropping on other species' signaling interactions. Animals who eavesdrop are able to overhear vital data that can be beneficial for their own survival (McGregor, 1993). Studies show that male nightingales (*Luscinia megarhynchos*) eavesdrop on vocal contests between neighbors and intruders to create

a standard of their own response (Naguib et al., 2004), squirrels eavesdrop to assess site-specific risks of cache robbers (Schmidt and Ostfeld, 2008), and many species eavesdrop on heterospecifics to evaluate predation risk.

While many species of birds use alarm calls, the black-capped chickadee in particular has developed a sophisticated system of alarm signals that transmit information about the size and threat level of potential predators (Miller, 2005). To drive predators away they use mobbing behavior signaled by mobbing calls to prevent predators from entering or remaining on chickadee territory. Additionally, depending on the size of the predator, chickadees increase mobbing intensity or use tactics other than mobbing to try and scare it off (Miller, 2005; Templeton et al., 2005). Templeton et al. (2005) conducted experiments with chickadees revealing that the features and structure of the mobbing calls vary depending on the type of predator and threat it presents. A predator that expresses a higher risk for chickadees elicits a call with a greater number of ‘dee’ notes than a response for a low-risk predator. Moreover, selection appears to have favored variation in alarm signals that encodes information used to provide details about the degree of danger or size a predator presents (Miller, 2005).

Chickadees form two different alarm signals in response to predators. The first is the "seet" alarm, a call of low-amplitude used when flying raptors are detected. In response to a perched or stationary predator, a loud, broadband "chick-a-dee" call composed of many ‘dee’ notes is generated. The two calls elicit different reactions from the flock. While the "seet" call warns the flock of a flying predator, the "chick-a-dee" call is a mobbing alarm call, which recruits other chickadees to harass or “mob” a perched predator (Templeton et al., 2005; Miller 2005).

Although there are only two specific types of chickadee alarm calls, there is a large level of acoustic variation in their calls. In addition, the number of mobbing calls produced in response to each predator is extremely variable. Templeton and Greene (2005) performed an experiment examining the effects of different predators on chickadee calls and found that smaller, higher-risk predators elicited a greater response of alarm calls than larger predators. Results demonstrated that chickadees expressed longer and more intense mobbing behavior when they heard alarm calls in response to the pygmy owl, the smaller predator. Chickadees also approached the hidden speaker, from which the alarm call was being broadcasted, more closely and intensely in response to the small predator call than larger predator calls, illustrating that smaller, more maneuverable predators are more dangerous to the chickadee.

The number of 'dee' notes produced per call is related to predator size. There is a strong inverse relationship between the number of 'dee' notes per call and the wingspan or body length of the predator; the smaller the predator, the more 'dee' notes used in the alarm call. Additionally, the duration of the "dee" note section and the frequency of the 'dee' notes in the alarm call differ depending on the size and threat level of the predator (Templeton et al., 2005). Templeton's study reveals that vocal signals are more likely to give information about the degree of threat a predator presents rather than specifying if the predator is a terrestrial or aerial species. Since maneuverability and body size can influence the results of a predator-prey interaction, calls describing the dangerous features a predator possesses can be more beneficial than identifying the specific type of predator (Templeton and Greene, 2007).

While the effect of chickadee alarm signals on small mammals has not been widely tested, Templeton and Greene (2007) investigated the effect of chickadee calls with red-breasted nuthatches (*Sitta canadensis).* Nuthatches co-occur with chickadees and are commonly found

together in mixed-species flocks. Nuthatches eavesdrop on the calls of chickadees and respond appropriately to defend themselves after hearing chickadee mobbing calls, using mobbing behavior to harass a more dangerous predator. Due to their coexistence, nuthatches responded strongly to the high-threat calls of the chickadees with mobbing behavior and vocalizations of their own. Since nuthatches are not closely related to chickadees, it is interesting that they are able to eavesdrop on chickadees and decode their signals. Furthermore, because nuthatches are able to distinguish between subtle differences in chickadee alarm calls, it shows that animals are able to make sophisticated anti-predator decisions from information contained in a call from a different species (Templeton and Greene, 2007).

Similar to chickadees, eastern chipmunks have three conspecific alarm calls in the presence of predators: chucks, chips, and trills. Chipmunks produce chucks and chips from a stationary position while a predator is in view. Chucks are of a low pitch and give information revealing the sight of an aerial predator while chips are of higher pitch and detail the presence of terrestrial predators (Weary and Kramer, 1995). A chipmunk's voice trills when they are being chased by a predator (Da Silva et al., 2002).

Experiments show that chipmunks respond to all three types of conspecific calls and spend more time alert when calls are played at a higher rate and intensity. There is no significant difference in response to the chips and chucks, although the mean alert time is higher for chucks than for chips. Experiments did not detect differences in responses to the different chipmunk alarm call types (Weary and Kramer, 1995; Baack and Switzer, 2000).

Baack and Switzer (2000) performed experiments evaluating the effect of chip alarm calls on foraging chipmunks. After the call treatments, 10 out of 12 subjects responded with vigilant behavior, defined as looking up, an alert posture, and scanning. Chipmunks also ran a

shorter distance to directly find cover after hearing the alarm call and had a delayed re-emergence time after they escaped into their burrow. After hearing the chip call, they were more alert and had a lighter food load size, but they did not decrease their foraging time. In response to predators, subjects also increased their rates of immobility (freezing posture), keeping all four feet on the ground with their head up (Trouilloud et al., 2004).

Chipmunks have been known to eavesdrop on the alarm calls of the eastern tufted titmouse (*Baeolophus bicolor*) to evaluate predation risk. Three titmouse vocalizations (the contact, seet, and mobbing call) were used as playback stimuli to test the effect of the calls on the giving up densities (GUDs) of the chipmunks which measure changes in perceived predation risk. Variations in GUDs show variation in foraging costs and if chipmunks perceive a higher predation risk, GUDs will increase. Results indicated that chipmunks perceived a higher predation level under the mobbing call and the second highest predation level after hearing the seet call. Chipmunks have much higher GUDs in response to the mobbing and seet call compared to the control titmouse call (Schmidt et al., 2008).

Chickadees and eastern chipmunks share the same environment of deciduous woods throughout North America. Behavioral changes of chipmunks in response to conspecific alarm calls, in addition to evidence of sympatric heterospecifics responding to alarm calls, suggest that eastern chipmunks may interpret and respond to the sophisticated chickadee alarm calls in order to reduce their own predation. By developing the ability to understand chickadee alarm calls, chipmunks would be able to gain a large amount of information regarding predator risk through eavesdropping. To my knowledge, no previous experiments have been done testing the effect of the black-capped chickadee alarm call on foraging and vigilant behavior of eastern chipmunks.

I predicted that chipmunks would recognize the chickadee alarm call as a warning for a possible predator threat and respond appropriately with anti-predator behavior by maintaining an alert posture, scanning the area, and looking up from the foraging site. Additionally, it is hypothesized that chipmunks will have no anti-predator response after a control call, the chickadee song, because a chickadee song does not specify a threat.

Methods

Chickadee Call Manipulation

Three types of chickadee calls were used for playback experiments: a normal chickadee song (no threat to chickadees), a low-D call with three 'dees' (low intensity threat to chickadees), and a high-D call composed of eight 'dees' (high intensity threat to chickadees). Previously recorded chickadee 'fee-bee' songs and calls recorded in response to the playback of screech owl (*Otus asio)* were used as the control and alarm calls (Cornell Laboratory of Ornithology, 1990; Elliot et. al, 1997; Fleming, 2008). Alarm calls were manipulated in the lab to contain the corresponding number of 'dee' notes for each call. For the low-D condition, I used four different low-D alarm calls with variations in pitch, sound, and inflections; I used four different high-D alarm calls with variations in pitch, sound, and inflection for the high-D condition; and I used two 'fee-bee' control song varying in pitch, sound, and inflection to maintain diversity within the calls and avoid habituation during testing.

Experiment Preparation

Experiments were conducted from August 2009 to October 2009 in the wood and brush areas of Allegheny College's Robertson Field in Crawford County, Pennsylvania. In early fall, I explored the woods adjacent to Robertson field in search for locations with chipmunks. Chipmunks surrounding a total of 12 burrow locations (N=12) were tested. I identified a

location close to their burrows and tagged the burrow with a flag so I knew where to place the feeding tray used to observe foraging behavior. A 20 x 20 x 2 cm feeding tray filled with black oil sunflower seeds was placed near each chipmunk burrow before experiments began to familiarize chipmunks with the tray. The trays remained in the same location throughout the entire study. Several days before trials began I observed the trays to be sure seeds were disappearing from the tray. During this time, I fed the chipmunks at the same time every morning in an attempt to train them to use the feeding trays and know to arrive at the feeding trays each day. After filling the trays with seed, I blew a whistle three times to try and condition the chipmunks so they knew when seed would be available.

Playback Experiments

Alarm calls were played on a portable CD player placed about 10 m from the feeding tray hidden in the brush. Each of the playback recordings had the same amplitude and the speaker was at an identical volume for each playback. Testing was initiated only if one chipmunk was present at a burrow location. A total of 33 trials were carried out: 13 control trials, 10 low-D trials, and 10 high-D trials. To avoid habituation, chipmunks were exposed to each condition only once; however, due to the absence of chipmunks at some sites, one burrow location was tested twice for the control and low-D condition. During the trials, chipmunks were exposed to a certain call while foraging. Each chipmunk tested was exposed to one call each day to avoid habituation. Additionally, to reduce the possibility that chipmunks may familiarize themselves to the playbacks and realize no predator threat exists, which could reduce their anti-predator response, only three individuals with three different conditions were tested in the same area each day. By testing three chipmunks each day, there was only one playback of the control, high-D,

or low-D call each day, which reduced the possibility of habituation with the calls. The type of call to which the chipmunk was exposed was randomly assigned.

To begin the trial, I added a previously weighed mass of sunflower seeds (approximately 180 g) to the feeding tray. I hid in the brush about 10 m from the tray and sat waiting for an individual to approach the feeding tray. After the chipmunk began feeding, I played its assigned chickadee call. Each call recording consisted of about 15 seconds of the alarm or control call playback followed by a one-minute pause, and then another playback of the call for 15 seconds.

Data Collection and Vigilant Behavior

During the course of the playbacks the behavior of the chipmunk was recorded. Vigilant behavior, defined as the amount of time spent alert (an upright posture), looking up from foraging while on all fours, and scanning the area for predators was recorded. The amount of time spent foraging, amount of time spent at the feeder, the mass of seeds taken by the chipmunk, amount of time spent scanning, and the number of look ups was recorded and analyzed.

Data were analyzed statistically using a one-way analysis of variance (ANOVA) by comparing the amount (grams) of seeds taken from the feeding tray, the amount of time (seconds) spent on the feeding tray, the amount of time spent foraging, the amount and the number of lookups a chipmunk had.

Results

Chipmunks responded to all black-capped chickadee calls. Chipmunks took a greater amount of seeds and foraged longer during the control call playback, but this result was not significant (Fig. 1, P=0.7987, P=0.2216). Additionally, chipmunks spent less time on the feeder during the low-D and high-D alarm call than the control call, even though results are not

significant (Fig. 2, P=0.5275). During the high-D treatment, chipmunks obtained more seeds per second foraging and on the feeder than the two other treatments, but these results were not significant (Fig. 3, P=0.4195, P=0.3838). Chipmunks had the greatest number of lookups for the high-D call (Fig. 4A, P=0.6503) and spent a greater amount of time scanning the area for the low-D playback (Fig. 4B, P=0.300), but these results are not significant. Trends indicate that as chipmunks spent more time foraging, they obtained more seeds, yet the relationship was not significant (Fig 5B, P=0.0508). There was a significant relationship between the total time spent on the feeder and the amount of seeds taken (P=0.0488). Chipmunks increased the mass of seeds foraged as they spent more time on the feeder (Fig. 5A).

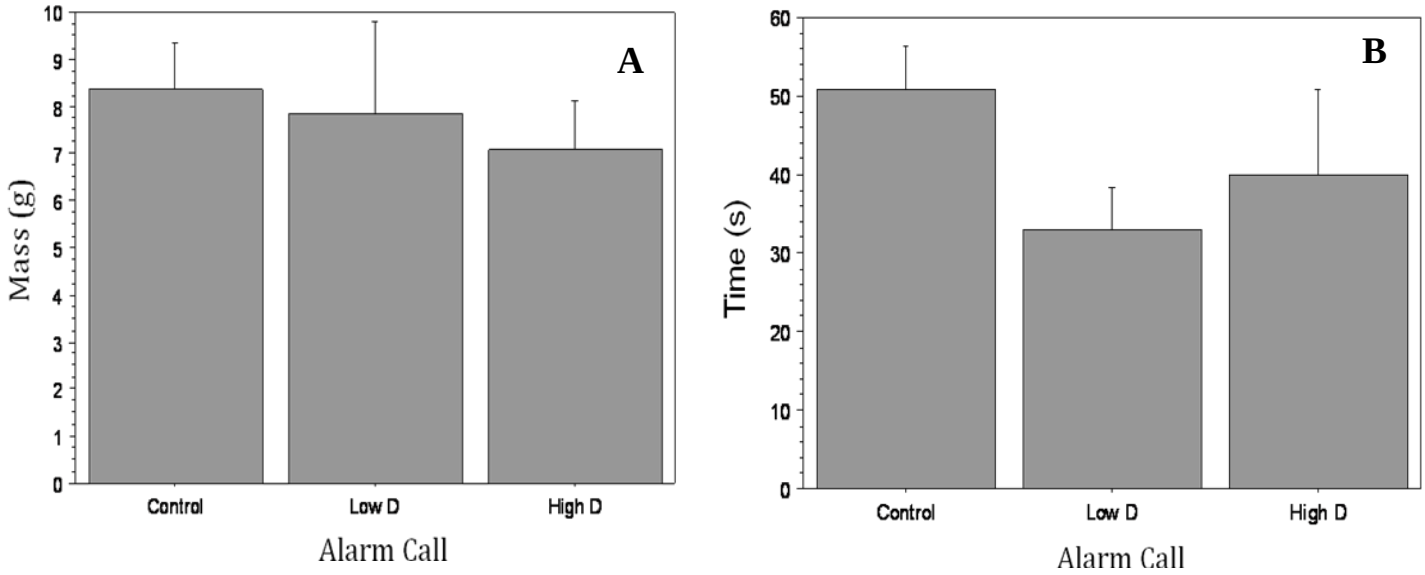


Figure 1: (**A**) Total amount of seeds taken from the feeding tray (P=0.7987). Error bars represent the standard error. (**B**) Total time spent foraging (P=0.2216). Error bars represent the standard error.

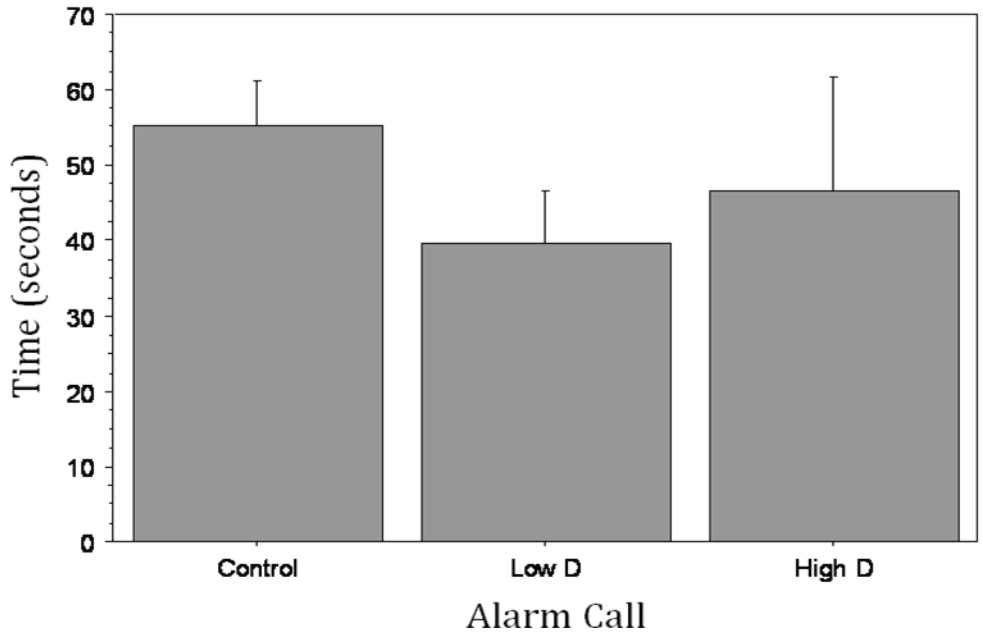


Figure 2: Total Time spent on feeder (P=0.5275). Error bars represent standard error.

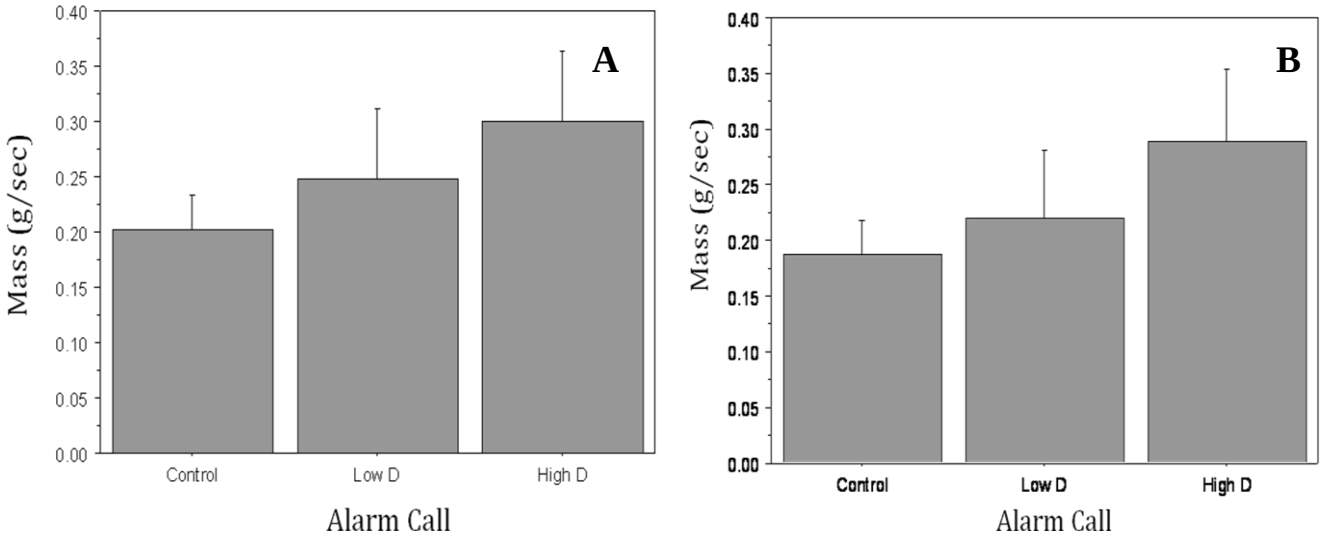


Figure 3: (**A**) Mass of seeds taken per second spent foraging (P=0.4195). Error bars represent standard error. (**B**) Mass of seeds taken per second spent on feeding tray (P=0.3838). Error bars represent standard error.

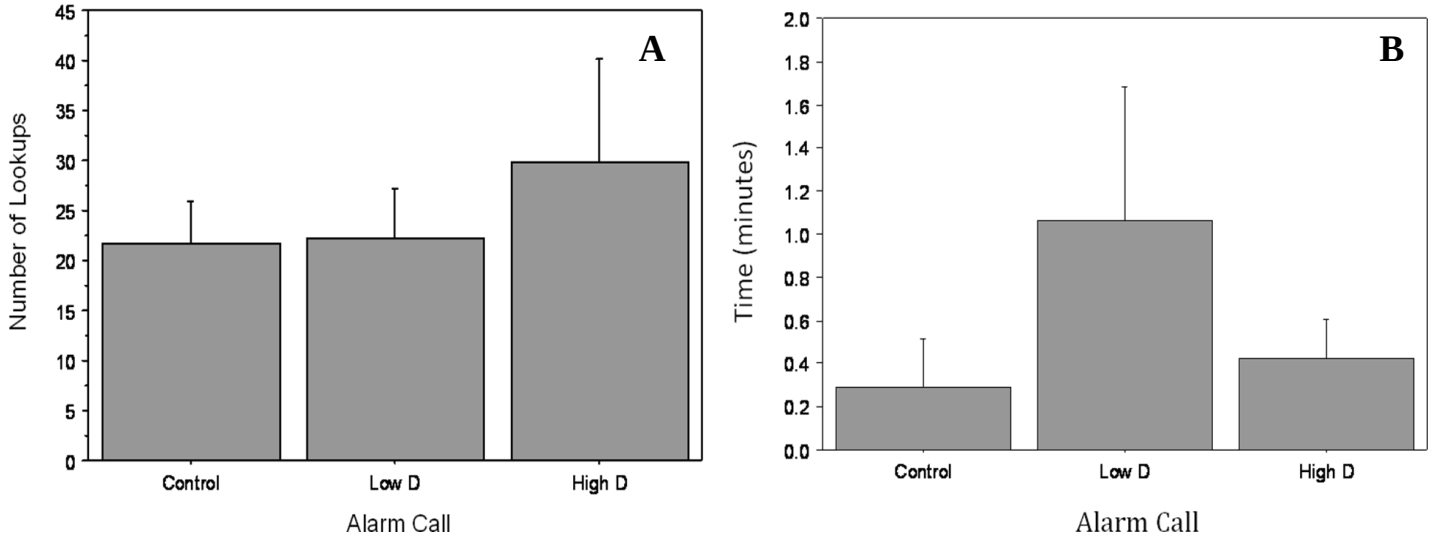


Figure 4: (**A**) Total number of lookups made by the chipmunk (P=0.6503). Error bars represent standard error. (**B**) Amount of time spent scanning by the chipmunk (P=0.300). Error bars represent standard error.

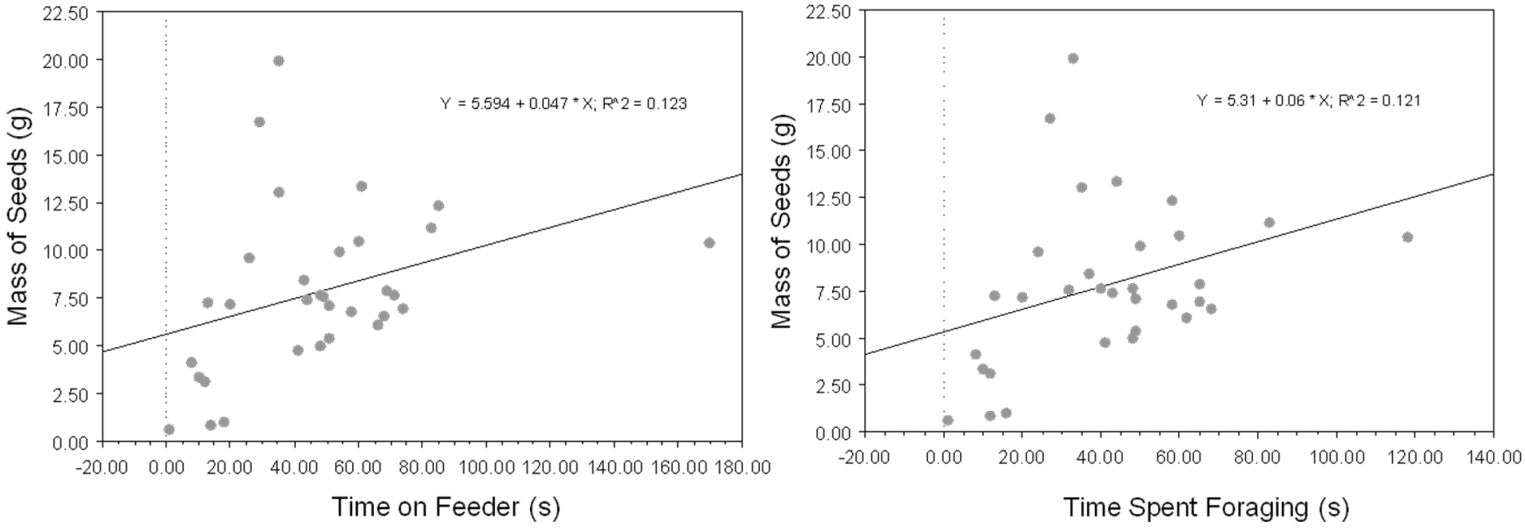


Figure 5: (A) Time on feeder versus the mass of seeds taken (P=0.488). **(B)** Mass of seeds versus amount of time spent foraging (P=0508).

Discussion

It can be advantageous for animals to eavesdrop on the alarm calls of heterospecifics to gain information about threats from shared predators. Individuals that are able to interpret anti-predator information encoded in the alarm calls would then be able to respond accordingly to predator threats (Fallow and Magrath, 2010) and be favored by evolution and natural selection. I hypothesized that chipmunks would respond with vigilant behavior during the low-D and high-D calls. Chipmunks tended to have a greater number of look-ups during the high-D broadcast as expected; however there was little difference in the number of look-ups between the low-D playback and control (Fig. 4A). These data suggest that the low-D alarm call had no effect on vigilant behavior of chipmunks, a result that conflicts with data obtained from scanning rates of chipmunks. During the low-D playback, chipmunks responded more vigilantly and with a higher scan rate while the high-D scan rate was similar to the control (Fig. 4B). An increase in vigilant behavior during the low-D and high-D calls corresponds to previous studies of chipmunks responding to their own alarm calls during a perceived predation risk (Burke da Silva, 2008; Baack and Switzer, 2000; Weary and Kramer, 1995).

Playbacks of chickadee alarm calls had an effect on scanning and look-up behavior of the chipmunks (Fig. 4). Since this behavior was not consistent with the two alarm calls (stronger look up response for high-D call versus stronger scanning response for low-D call) it is possible that scanning and looking up differ depending on a necessary response to a perceived predator. To my knowledge, no research has been done distinguishing the differences in the effect of scanning versus looking up as vigilant behavior or whether a difference exists. If a difference between these behaviors does exist, my results imply that chipmunks can differentiate between the chickadee alarm calls rather than responding to all types of calls in the same manner.

Since there was a different response of vigilant behavior with the low-D and high-D calls (Fig. 4), chipmunks may be able to distinguish between the alarm calls of the chickadee. Chipmunks cannot distinguish between conspecific alarm calls based on the individual emitting the call or its amplitude, but respond more vigilantly based on call rates and volume (Weary and Kramer, 1995). Since chickadee alarm calls are much more distinguished (Templeton et al., 2005) and give more information than a chipmunk call, it is possible that chipmunks sharing a habitat with chickadees will only expend energy learning to distinguish between the different alarm calls of chickadees rather than distinguishing between their own calls.

Similarly, the difference in response of scanning versus look-ups may be due to the predator risk (Fig. 4). Larger predators that cause a low-D alarm call from chickadees may be more dangerous to chipmunks due to their larger size, and a high scanning rate could be the result of a high-risk predator for the chipmunk, or a low-D chickadee alarm call. Smaller predators may be a low-risk predator for chipmunks and therefore cause an increase in look-ups for chipmunks rather than an increase in scanning.

Additionally, chipmunks tended to spend more time foraging and time at the feeder during the high-D calls than the low-D calls (Fig. 1B, 2); however, they took an overall greater mass of seeds during the low-D broadcast (Fig. 1A). My results are consistent with previous experiments analyzing conspecific alarm calls on chipmunk foraging in which chipmunks decreased their load size without reducing the time spent loading seeds (Baack and Switzer, 2000) due to the increased time chipmunks spend vigilant during loading after hearing an alarm call. Additionally, under a perceived predation risk, chipmunks may only forage what they need to increase survival. Chipmunks also foraged at a higher rate (Fig. 3) during the high-D alarm

call, which could be because chipmunks are under a greater threat and forage efficiently to escape once they have enough seed.

Since chipmunks took seeds and foraged at a higher rate for the high-D call than the low-D call, it is possible that chipmunks are able to distinguish between the low-D and high-D threat calls of the chickadee even though they cannot distinguish between their own chipmunk alarm calls (Fig. 3). Due to the high scan and foraging rate in response to the high-D call, results indicate a tendency of chipmunks to increase vigilant behavior for smaller predators (high-D call), suggesting that smaller predators have a higher risk than large predators. However, chipmunks also increased the total number of look-ups and time scanning (Fig. 4), demonstrating an increase in vigilant behavior in response to a low-D call. These results contrast with results in Figures 1, 2, and 3 and suggest that chipmunks may perceive larger predators (low-D call) as high-risk predators. Even though results suggest that response to high- and low-D calls could be due to a difference in predator risk for chipmunks, no studies have been done which detail the level of threat various predators hold for chipmunks.

This study showed that chipmunks eavesdrop and are able to react with anti-predator behavior after hearing a chickadee alarm call. Since experiments were done in the late summer to fall, many chipmunks were observed close to the time when chipmunks were storing seeds for the winter while other chipmunks were observed in late summer before preparation for winter. Conducting experiments in the spring or early summer could result in different data due to a different time of observation. Further changes could be made with data collection, such as the time elapsed while chipmunks return to their burrow after the alarm call and the reemergence time from the burrow after escape. These items were not recorded during my experiment due to time constraints and difficulty of locating and viewing the burrow.

Future studies could test the anti-predator response of males versus females and whether chipmunks respond with their own alarm calls after hearing a chickadee alarm call. Finally, additional studies are needed to determine whether chipmunks are able to distinguish and react differently between low and high D calls, including extensive research on the differences in vigilant behavior of chipmunks and risk levels of chipmunk predators.

Chipmunks responded with vigilant behavior to both chickadee alarm calls. This study suggests that chipmunks may be able to distinguish between different types of chickadee alarm calls and respond with specific behavior, even though this is not the case with their own alarm calls. My experiment provides additional data indicating the benefits and use of interspecific eavesdropping. When chipmunks eavesdrop on chickadee alarm calls and respond with vigilant behavior, they increase their chance of survival without using their own energy to watch for predators. Chipmunks can therefore use this energy in other areas, such as foraging. Further experiments can examine the degree of understanding chipmunks have with the chickadee alarm calls and may reveal a level of cooperation chipmunks and chickadees have to ward away predators.

Acknowledgements

I would first like to thank Dr. Mumme for the many, many hours he spent with me in the summer and fall out in the field looking for chipmunks I could observe. I would also like to thank Dr. Mumme for helping me manipulate chickadee calls, organize my experiment, analyze data, and revise my drafts. To the members of my senior comprehensive project group, thank

you very much for your ideas and suggestions throughout the year. I would also like to thank James Everett Newman for his revisions and suggestions, even when he was a thousand miles away and Kelsey Braun for her revisions and answers to my many questions. Finally, I would like to thank my family and friends for their support. Muchísimas gracias por su ayuda.

Literature Cited

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

Cornell Laboratory of Ornithology. 1990. "A Field Guide to Bird Songs." CD-ROM. Third Edition. Boston: Houghton Mifflin Company.

Da Silva KB, Mahan C, Da Silva J. 2002. The trill of the chase: Eastern chipmunks call to warn kin. *Journal of Mammalogy*. 83: 546-552.

Elliot L, Stokes D, Stokes L. 1997. "Stokes Field Guide to Bird Songs." Nature Sound Studio. CD-ROM. New York: Time Warner Audio Books.

Fallow PM, Magrath RD. 2010. Eavesdropping on other species: mutual interspecific understanding of urgency information in avian alarm calls. *Animal Behaviour*. 79: 411-417.

Fleming, A. 2008. Heterospecific Attraction to Black-capped Chickadee Mobbing Calls: The Role of Call Structure. Senior Comprehensive Project.

McGregor P. 1993. Signaling in territorial systems: A context for individual identification, ranging and eavesdropping. *Philosophical Transactions: Biological Sciences*. 340: 237-244.

Miller G. 2005. Bird alarm calls size up predator. *Science*. 308: 1853-1855.

Naguib M, Amrhein V, Kunc HP. 2004. Effects of territorial intrusions on eavesdropping neighbors: communication networks in nightingales. *Behavioral Ecology*. 15: 1011-1015.

Peake TM, Matessi G, McGregor PK, Dabelsteen, T. 2005. Song type matching, song type switching and eavesdropping in great tits. *Animal Behaviour*. 69: 1063-1068.

Schmidt K, Lee E, Ostfeld RS, Sieving K. 2008. Eastern chipmunks increase their perception of predation risk in response to titmouse alarm calls. *Behavioral Ecology*. 19: 759-763.

Schmidt KA and Ostfeld RS. 2008. Eavesdropping squirrels reduce their future value of food under the perceived presence of cache robbers. *The American Naturalist*. 171: 386-393.

Templeton C, Greene E. 2007. Nuthatches eavesdrop on variations in heterospecific chickadee mobbing alarm calls. *The National Academy of Sciences of the USA*. 104: 5479-5482.

Templeton C, Greene E, Davis K. 2005. Allometry of alarm calls: Black-capped chickadees encode information about predator size. *Science*. 308: 1934-1937.

Trouilloud W, Delisle A, and Kramer, D. 2004. Head raising during foraging and pausing during intermittent locomotion as components of antipredator vigilance in chipmunks. *Animal Behaviour*. 67: 789-797.

Weary D, Kramer D. 1995. Response of eastern chipmunks to conspecific alarm calls. *Animal Behaviour*. 49: 81-93.