CONSIDER THE CHIPMUNK; RECONSIDER THE ROAD: ROAD NOISE EFFECTS ON EAVESDROPPING SYSTEMS IN EASTERN CHIPMUNKS

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Abstract. The ability of a forager to gain information about its surrounding environment may influence its decision of where and how long to forage (Brown 1988, Valone and Giraldeau 1993). Typically eastern chipmunks, *Tamias striatus*, eavesdrop on the alarm calls of birds in the Paridae family such as eastern tufted titmice *Baeolophus bicolor* and black capped chickadees *Poecile atricapilus* to gather information about the cost of predation in the surrounding area. Since chipmunks vary their time spent foraging in relation to perceived foraging costs, the giving-up density (GUD) or the amount of food left over when the chipmunk decides to stop foraging is an indication of the animal's patch use behavior and perception of predation risk. The purpose of this research is to measure giving-up densities (GUDs) of chipmunks in the presence of different alarm calls with and without background road noise to quantify the consequential changes in perceived predation risk. If road noise masks sounds in the environment, including alarm calls, chipmunks may have elevated predation risk. Chipmunks that perceive a greater risk from road noise increase vigilance and cease risky behavior faster as a result, leaving more food behind and yielding a greater giving-up density. Our results indicate that road noise can interfere with the chipmunk's eavesdropping systems and consequently affect their cost-benefit analysis of foraging.

INTRODUCTION

Eavesdropping Systems

When making decisions about how to navigate the world, many of us eavesdrop or take cues from the people around us. Eavesdropping is the use of information in signals by individuals other than the primary target (Schmidt et al. 2008, Peake 2005). This behavior is not species specific; small mammals shift their day-to-day activities based on the vocalizations of their avian neighbors. Con- or heterospecific alarm calls that vocally communicate a predator's presence create public information regarding predation risk in the environment (Schmidt et al. 2008, Valone and Giraldeau 1993). For instance, eastern chipmunks alter their feeding behavior based on the alarm calls of tufted titmice. Titmice are small grey songbirds that are vigilant and vociferous. When they identify a threat, they announce it by engaging in a sophisticated system of alarm calls that conveys information about both the size of a predator and its degree of threat (Templeton et al. 2005). Two different alarm calls are supposed to help organize titmouse defense: a soft, high-pitched "seet" call warns of flying predators while a louder "mobbing" call recruits others to harass or mob a perched predator (Templeton et al. 2005, Hetrick and Sieving 2011). This elaborate system of vocalizations mediates social interactions within flocks; but more than that, since chipmunks share many of the same predators as titmice, their decision of where and how long to forage is strongly influenced as a result of this information transfer. The purpose of this research is to test whether and to what degree chronic road noise alters this transfer of information through eavesdropping.

Road Noise Effects

Roads are ubiquitous across vast stretches of the world. In fact, 83% of the United States is within 1 km of a road (Riitters and Wickham 2003). Although some authors have suggested the positive effects of

roads on wildlife, the overall effects across taxa are overwhelmingly negative (McClure et al. 2013). Many studies document declines in populations of wildlife near roads; In order to identify noise as one of the primary mechanisms underlying these effects, McClure et al. (2013) experimentally apply traffic noise to a roadless area at a landscape scale. Here, we will note how the foraging patterns of chipmunks change as a result.

Patch-Use Intensity and the Giving-Up Density

Optimal foraging theory assumes that an individual should exploit a patch until the benefits from foraging equal the costs. Foraging costs should include the predation cost of foraging, the missed opportunity costs of not engaging in alternative activities, and the metabolic costs of foraging (Brown 1988, Stephens and Krebs 1986). When you consider the marginal rates of substitution of different inputs into fitness, all inputs can be expressed as a single currency of energy in Joules (Brown 1992). As long as harvest rates are a function of patch type and resource density, the giving up density, or the amount of food remaining in a patch at the cessation of foraging, is a highly correlated surrogate for the quitting harvest rate (QHR) and an accurate measure of the animal's costs and patch use intensity (Whelan 2005, Brown 1988). If predation cost increases in response to a stimulus, the forager spends less time foraging and the GUD increases. In order to quantify road noise effects, we measure GUDs of chipmunks in the presence of different alarm calls with and without background road noise.

METHODS AND MATERIALS

Study Site and Species

The study area was located on the Cary Institute of Ecosystem Studies (IES), Dutchess County, NY. The site contains oak-dominated forest home to several diurnal rodents such as chipmunks, gray and red squirrels, and woodchucks and a diverse avian community including the veery *(Catharus fuscescens)* and two species of parids: eastern tufted titmouse *(Baeolophus bicolor)* and black capped chickadee *(Poecile atricapilus)*. We chose to study the titmice, eastern chipmunks, and veeries because titmice demonstrate alarm calls that contain information about the type of predator and immediacy the threat (Hetrick and Sieving 2011, Templeton 2005, Schmidt et al. 2008); chipmunks are diurnal rodents that are small enough to potentially share common predators with titmice (Schmidt et al. 2008); and the veery's song is distinct, commonly heard in our research location, and nonthreatening to chipmunks.

Experimental Food Patches and Design

There are four sites total in the Greens region of IES near a setup of three speakers playing recorded road noise placed about 25m apart (Figure 1). Each site takes up a space about 50m by 50m at least 200m away from each other and contains five subsites arranged equal distances away from the speaker broadcasting alarm calls and varying distances away from the line of speakers sounding road noise (Figure 1). Each subsite should in turn have two artificial resource patches, provided by plastic trays (30 x 20 x 6cm) filled with millet seeds mixed into about 3 pints of sifted sand. One tray should have 10g of seeds mixed into the sand and the other only 5g seeds to provide a lower food density. This dual patch design can detect density-dependent or independent harvest by chipmunks and tell us if the chipmunks are foraging with no, little, or perfect information.

After a baiting period of a couple weeks to allow chipmunks to associate the trays with a food source, confirmed by identifying chipmunk spoor, we collected foraging data from the seed trays for 10 days with one treatment played per site per day. Trays were open roughly between 0700 and 1430 h. The playback equipment was positioned at a height of 1.5 m in a nearby tree approximately 20m away from each

subsite of trays at each site. At the end of each experimental day, we noted any footprints in the sifted soil to identify the forager, took down the playback equipment, and sieved trays to recover uneaten food, which was then taken back to the lab, cleaned of debris, and weighed to measure giving-up density.

Recordings

There were four treatments or acoustic stimuli rotated at each of the four sites over nine days in July-August, 2014. The treatments included a veery control (represents a non-threatening song), a titmouse seet call, a titmouse mobbing call, and a grey squirrel chipping call. We recorded three exemplars of each of the four vocalizations together with tracks of various lengths of silence and uploaded the playlists onto an iPod shuffle. The pattern of vocalizations with respect to random intervals of silence was then determined by random shuffling of tracks. Vocal tracks played only 30% of the time on average. Although this frequency of vocalizing is higher than what naturally occurs, rapid rates are observed to occur over a period of 15 minutes or more (Schmidt et al. 2008). Furthermore, since individual chipmunk foraging bouts in the food patches take within 5 and 20 minutes, a relatively high call rate is necessary to insure that chipmunks are exposed to the vocalizations while they are actively foraging (Schmidt et al. 2008).

Statistical Analysis

We used a Latin-square design to randomize presentations over time while giving chipmunks only one treatment per day for 9 days (Table 1). Analysis of Variance (ANOVA) used rank-transformed means to test for differences in GUDs among several sources of variance. Our model includes day (to check for chipmunk habituation to calls or road noise), site, treatment, initial seed density (to test for density-dependent foraging), presence of road noise, and distance to road noise. If the resulting F-ratio is high in each of these analyses, there is a more statistically significant variance in GUDs.

RESULTS & DISCUSSION

Our model for ANOVA found several sources of variance, including a road effect, to be statistically significant (Table 2). In particular, we found that different call treatments significantly affect chipmunks' perceived risk of predation. This finding corroborates that of a previous study (Schmidt et al. 2008). Chipmunks perceive their highest level of predation risk under the mobbing and seet calls, and lower levels under chipmunk and veery vocalizations (Figure 2). Statistically, GUDs during mobbing and seet calls were not significantly different from each other (P=1.000; Bonferroni HSD), and likewise between chipmunk and veery vocalizations (P>0.05; Bonferroni HSD).

Brown (2004) suggests a model of fitness where the energetic cost of predation is the predation risk multiplied by survivor's fitness divided by the marginal fitness value of energy: $\mu F/(\delta F/\delta e)$. Houston et al. (1993) also derive the same model for the cost of predation. You can think of the marginal fitness value of energy ($\delta F/\delta e$) as the "benefit of harvesting" or "what you have to fain from foraging." It makes sense that this value is in the denominator because if that value is super high (i.e. the forager is starving), the cost of predation is relatively low and the forager is likely to continue to forage despite predation risk (μ) as a result. "Survivor's fitness" (F) is like what you have to lose when you get killed. For example, pregnant or young squirrels have relatively more to lose. This term considers current and future reproductive success, likelihood of surviving, etc. We should consider how the model of predation cost $\mu F/(\delta F/\delta e)$ would change with the addition of road noise.

For instance, our main finding is that there is a significant road effect on eavesdropping systems in eastern chipmunks (Figure 3). Road noise may generally enable predators to get closer to their prey before they are recognized, increasing predation risk (μ), cost of predation, and GUD. Road noise could also have an impact from the perspective of the forager: noisy environments may mask alarm calls and render chipmunks less able to eavesdrop and collect useful information regarding predators, thus increasing predation risk (μ) and yielding the observed increase in GUD.

Since our sources of variation (road, treatment, and distance) could impact each other, we include interaction effects in our model. The one we found to be significant is the road × treatment effect, meaning that not all treatments respond the same way to roads. When road noise is present, mobbing and chipmunk calls yield increased GUDs whereas seet and veery vocalizations decrease GUDs (Figure 4).

The chipmunk treatment might signal to nearby foragers that there are more of them around. As a result, foragers sense a greater value for "survivor's fitness" (F) and that they have more to lose in the event of predation. So, in the presence of road noise or potential danger, GUDs collected under chipmunk calls increase (Column 1, Figure 4).

The decrease in GUDs observed under seet treatments might be because the traffic noise masks the warning call. The chipmunk consequently cannot tell where the predator is coming from, so they forage more (Column 3, Figure 4).

This observation is reversed in mobbing because while seet calls have an average frequency of around 8000 Hz, mobbing calls have a much wider range of frequencies. Since anthropogenic noise usually occurs at low frequencies (<200 Hz), chipmunks may be able to hear these mobbing frequencies even in the presence of a road. Since there is not as much masking of mobbing occurring, the chipmunks have more information regarding predation risk, so it is less risky for them to forage more (Column 2, Figure 4).

In the last 10 years, eavesdropping behavior has blossomed into a rapidly growing field of behavioral ecology. Auditory cues are given and received all the time. This finding that road noise has the ability to disrupt eavesdropping systems and GUDs collected under mobbing calls in particular are enhanced in the presence of road noise may be an indication that chronic road noise could also disrupt other activities like mating, avoiding predators, finding nests. When you consider that 83% of the US is within 1km of a road, this is a conservation issue that no one is considering enough. In a day like ours with species in decline and roads being built every day, it is more important than ever to understand these interactions when making decisions about conservation needs.

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APPENDIX

TABLE 1. Treatment times and locations. Green background indicates the presence of road noise, while red indicates its absence.

| Day	Site 1	Site 2	Site 3	Site 4
1	veery	chipmunk	mobbing	seet
2	chipmunk	seet	veery	mobbing
3	mobbing	veery	seet	chipmunk
4	seet	mobbing	chipmunk	veery
5	veery	seet	mobbing	chipmunk
6	chipmunk	seet	veery	mobbing
7	mobbing	veery	seet	chipmunk
8	mobbing	seet	chipmunk	veery
9	veery	chipmunk	seet	mobbing

TABLE 2. Analysis of Variance results.

| Source	df	MS	F ratio	P
DAY	6	0.289	8.449	0.000
SITE	3	1.718	50.150	0.000
INITIAL	1	6.490	189.432	0.000
TREATMENT	3	0.208	6.064	0.001
DISTANCE	1	0.296	8.636	0.004
ROAD*TREATMENT	3	0.157	4.579	0.004
ROAD	1	0.153	4.468	0.036
TREATMENT*DISTANCE	3	0.070	2.029	0.112
ROAD*DISTANCE	1	0.043	1.257	0.264
Error	152	0.034		
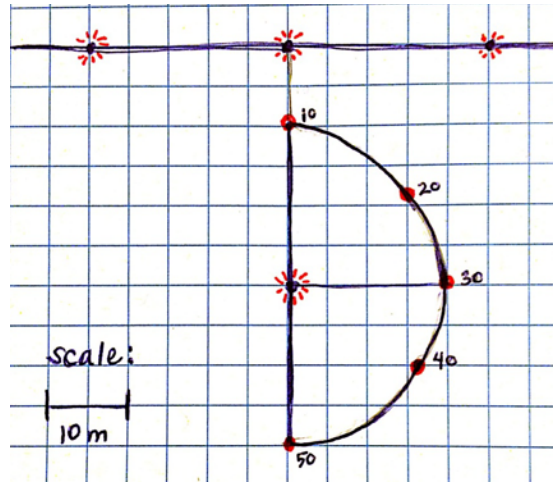
FIGURE 1. Schematic diagram of each site with 3 speakers playing road noise in a line, treatment speaker in middle, and 5 subsites numbered with distance (m) from road.
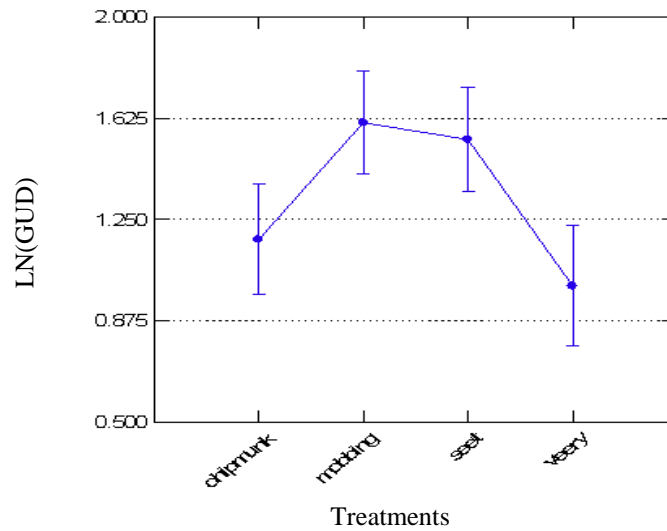
FIGURE 2. Mean treatment ranks (±standard error) based on least square means.
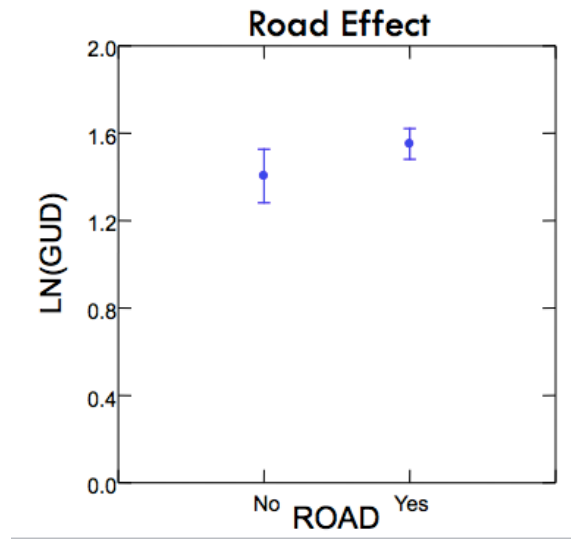
FIGURE 3. Log-transformed GUDs based on least square means when road noise is and is not present.
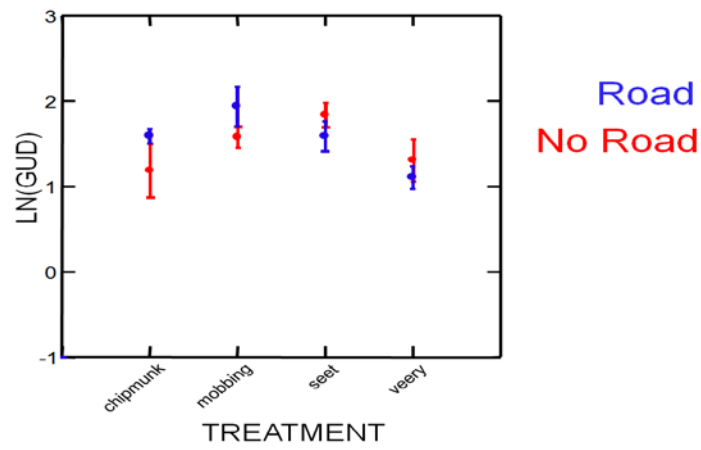
FIGURE 4. Log-transformed GUDs of road × treatment effects based on least square means.