Generalization of Prey Fear Response to Predatory Risk in Deer Mice

(*Peromyscus maniculatus*) to Owl Calls

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ABSTRACT:

Predator recognition and foraging are both crucial functions in which an individual must engage for its survival and fitness. Both direct and indirect cues of predatory risk can be utilized to elicit behavioral changes in prey. In this study, we exposed *P. maniculatus* in two different substrates to native and novel owl calls to measure their responses to non-lethal effects in terms of food consumption. Substrate was classified as noisy or quiet. I predicted that the control and the novel owl call treatment would be the most similar, due to inexperience with the novel owl call. Therefore, I predicted that mice in the native owl call trials would consume the least amount of seeds due to an increase in vigilance and other safety related behavior. Mice showed no difference the amount of seeds eaten according to owl calls. Rather, the only difference was in the amount of seeds consumed between the two substrates; mice ate significantly fewer seeds in the noisy substrate. Our results suggest that mice may be more prone to generalize their fear responses instead of specializing to individual predators.

INTRODUCTION:

Predator-prey relationships are an integral part of the dynamics found between species in any ecosystem. Predation ultimately leads to the removal of an individual from the ecological system, which in turn can have great impacts on the prey population dynamics and ecosystem (Lima 1998). There are two approaches to analyzing predator-prey interactions; the first focuses on lethal effects, of predators (Preisser et al. 2007), while the second focuses on the non-lethal effects, of predators (Lima and Dill 1990). In the first approach, the model focuses on the predator, instead of the prey. Rarely does it consider the prey's behavioral response. Much of past discussion concerning predator-prey interactions has been dominated by the lethal effects of predation.

However, more recent literature suggests that the non-lethal effects of predation may be equally, if not more influential on prey behavior (Schmidt 2006, Preisser et al. 2007, Peckarsky et al. 2008). When prey species show altered behavior due to the presence of predators, this is referred to as the nonlethal effect, otherwise known as predation risk effect (Ripple and Beschta 2004); many of these changes in behavior are in response to fear. The prey must balance maximizing energy intake and safety, while minimizing their time and energy expenditure to maximize fitness, as described by optimal foraging theory (Davidson and Morris 2001, Pyke 1984, MacArthur and Pianka 1966).

One assumption concerning predator-prey interactions is that prey have the option of foraging for food or remaining inactive, and thereby safe. Prey must sacrifice feeding rates for safety and select its optimal balance between vigilance in response to its perceptions of a predator (Brown et.al 1999).

Another assumption is that the prey is able to recognize and respond to the threat of predation. In order to do this, they must be able to assess direct and indirect cues of predation risk (Schmidt 2006). In a study by Durant (2000), cheetahs were shown to respond to vocalizations of lions, a direct cue, by moving away and reducing their probability of making a kill and protecting their cubs. Acharya and McNeil (1998) determined that two species of moths temporarily stopped releasing pheromones for mating in response to sounds simulating the echolocation calls of bats. Mating, like foraging for food, is an activity that makes animals more conspicuous and vulnerable to predation. Therefore, prey can become frightened enough by predators to forgo feeding and other such opportunities necessary for their survival (Brown et. al 2001).

Many studies have shown that mice, especially deer mice (*Peromyscus maniculatus*) are a significant portion of owl diets (Swengel and Swenggel 1992). Because of this, there exists a unique predator-prey relationship between these two animals. They are one of the most abundant mammalian species native to North America that have adapted to a wide range of habitats of various elevations, precipitation, and temperature (Dewey and Dawson 2001).

Owls have also been shown to have a preference for different types of mice. In a study by Marti and Hogue (1979), researchers found that screech owls prefer relatively small mice prey over other readily available sizes of prey. Barn owls (*Tyto alba*) have been shown to hunt small, female mice from the population (Dickman et al. 1991). However, the majority of these studies have investigated the predator-prey relationship from the perspective of the owl, the predator: a lethal effect approach to this interaction. As mentioned before, few studies have examined the effect that the owls have on the foraging patterns and behavior of mice, the prey.

Other studies have demonstrated that some prey can assess the risk of predation under various circumstances and can incorporate this information into their behavioral decisions (Berger-Tal et al. 2010). Both *P. maniculatus* and owls are nocturnal species, and therefore they rely heavily upon sound to navigate through the night. *P. maniculatus* can be alerted to the presence of different species of owls by their various calls (direct cues of predation). Furthermore, owls are classified as "sit-and-pursue," relatively sedentary predators (Preisser et al. 2007). Therefore, acoustic cues should be strongly indicative of their presence; thus, also indicative of increased predation risk (Preisser et al. 2007). Research on predator avoidance in the past has mainly focused on animals that use visual or chemical stimuli to detect their predators (Blumstein et al. 2000, Coss 1978); the predator-prey relationship has not been examined for animals that rely upon auditory cues to detect their predators.

Not only can prey detect the presence of predators using auditory cues, predators can also be alerted to the presence of prey by the sounds that they make while moving and foraging through different substrates. Due to these evolutionary selective pressures, Roche et al. (1999) concluded that *P. maniculatus* restrict their movement to routes that reduce the risk of auditory detection by predators. Schmidt (2006) determined that mice reduced their activity space in response to owl vocalizations and illumination provided by the moon. However, without both the presence of owl call and illumination of a full moon, foraging remained unaffected (Schmidt 2006).

In addition to evaluating the changes in foraging patterns of prey, few studies have explored the effects of novel predators on prey populations. Alien predators are considered as one of the leading causes in the decline and extinctions of species around the world (Vitousek et al. 1997). Although it has been also been suggested that there are some stimuli configurations that are inherently aversive and trigger avoidance responses in animals that have no prior experience with the predator (Coss 1978), anti-predatory skills are heavily dependent upon experience (Griffin et al. 2001). In systems in which novel predators are introduced, prey are often naïve – similar in the manner in which juveniles are inexperienced in terms of predators as compared to adults – to the hunting methods of the new predator (Salo et al. 2007). When predation risk is altered due to environmental changes, prey are exposed to previously unfamiliar predators and must learn to recognize and avoid novel dangers (Griffin 2004).

Within the University of Notre Dame Environmental Research Center area, the barred owl (*Strix varia*) is one of the most abundant species. The barn owl (*Tyto alba*) is of similar size to *Strix varia*. However, its habitat range has a northern limit at the southern border of Wisconsin. Thus, with global warming, it is possible for these predators to expand their habitat range into the

UNDERC area and feed upon the *P. maniculatus*. It would therefore be important to examine the responses of the mice to these new predators.

The purpose of this study is to first, see the effects of native owl calls and novel owl calls on mouse foraging patterns. The study will then explore the effects of substrate on mouse foraging patterns in response to owl calls. Finally, we will analyze the differences in vocalizations of the different owls. According to previous studies, the effects owl calls have on *P. maniculatus* may depend heavily on the size of the individual prey. I hypothesized that *P. maniculatus* will respond similarly to both the native and novel owl calls, but to a lesser degree to the novel owl call. Unfamiliar to the sound, but still startled by it, the mouse will eat fewer seeds. I also predicted that *P. maniculatus* will forage at a greater rate in the sand in comparison to the sand and leaves.

MATERIALS & METHODS:

Study site and experimental design

This study was conducted in an *Acer saccharum* dominated forest on the property of the Univerisity of Notre Dame Environmental Research Center (UNDERC) on the Upper Peninsula of Michigan.

Trapping was conducted between June and July of 2010 between the first quarter phase of the moon and the last quarter phase of the moon. One night prior to the experiments, 25 Sherman traps were set at dusk in various 5x5 grids previously established by Dr. Michael Cramer. Traps were checked the following morning between 6:30am and 8:00am. All mice captured were marked using ear tags at the capture site. Following capture, mice were brought to the mouse room in the wet laboratory and housed in 15-gallon aquaria (0.62 x 0.30 x 0.30 m), separated into two equal portions with plexiglass. Mice were provided bedding and cotton for

nesting material. They were also provided with food and water. Lactating and pregnant females were not used for trials.   Six hours prior to the experiment, food was removed from the cages. *Acer saccharum* seeds were dried in the drying oven for at least three hours at 60°C. Immediately after drying, 10g of seeds were measured and separated for each trial. Before each trial, the seeds were scattered randomly throughout 2L of sand. For leaf trials, copy paper was soaked in water, dried, crumpled, and cut into shapes of *Acer saccharum* leaves of various sizes. These synthetic leaves were then dispersed over the sand to mimic leaf cover on the forest floor.

Trials

Each trial was performed in a standard 15-gallon glass aquarium (0.62 x 0.30 x 0.30 m). To simulate nighttime at which time mice are most active, we put a clear lid on the aquarium and lit the area with infrared lights. Each trial was recorded using an infrared sensing camera. Once the mouse was placed into the aquarium, we waited until it began eating a seed to start recording its activity. Upon taping, prerecorded owl calls (approximately 15s long) were played through speakers connected to an iPod and positioned slightly to the left of and level to the aquarium.

Each mouse was randomly given one of six treatments: a combination of one of three calls – a negative control, a native owl call, or a novel owl call – and one of two substrates – a quiet substrate or a loud substrate. For a negative control, speakers were turned on and no call was played. We played the native owl call of the barred owl (*Strix varia*) or the novel owl call of the barn owl (*Tyto alba*). For both calls, maximum amplitude was held constant. For the quiet substrate, we used sand, and for the noisy substrate, we added dried paper leaves to the sand. *S. varia* was chosen for its prevalence in the UNDERC area, and *T. alba* was chosen for the similarity in size to *S. varia*. Each call was repeated twice and the volume of the calls was kept constant. After a 30 minute period, we removed the mouse and sifted the sand for seeds. Broken

and otherwise consumed seeds were removed and dried for at three hours at 60°C. Seeds were

weighed and recorded immediately after being taken out of the drying oven. Between each trial,

sand from the previous trial was replaced with new sand. Each treatment was replicated at least

nine times, and mice were only used for one trial. After testing, all mice were released at the site

of capture. All procedures were reviewed and approved by the University of Notre Dame

Institutional Animal Care and Use Committee.

Owl Calls

Differences in owl calls were examined using Raven Pro 1.4. Considering we were using

a single prerecorded owl call for each of the treatments, there were no variations, and therefore

no way of analyzing the owl calls in a quantitative manner. Rather, we were only able to

qualitatively compare the novel and native owl calls. We investigated the duration of the entire

call and individual notes, maximum and minimum frequency, and rate of repetition of each call.

Statistics

To interpret the data in terms of significance of substrate and owl call on the foraging

patterns of the mice, we conducted a two-way ANOVA; the dependent variable was the amount

of seeds eaten in grams, and the two independent variables were the owl call (none, native, or

novel) and the substrate (quiet or noisy). A correlation was used to see whether amount of seeds

eaten was dependent on the body mass of the mouse. Two hypotheses tests were conducted to

compare owl call treatments to the control. A Lilliefors test was performed to verify normality.

A three-way ANOVA was conducted to examine the data in terms of the independent

variables of age class, owl call, and substrate. Mice with body weight mass less than or equal to

18g were classified as juveniles, while mice heavier than 18g were categorized as adults.

Because of this assumption, the amount of seeds eaten was transformed into a ratio relative to the

mouse body mass (amount of seed eaten/mouse body mass). Since we did not actively collect data according to age, there was no data on juveniles given the control treatment. Thus, the three-way ANOVA examined only two levels of owl calls, novel and native. We also conducted a two-way ANOVA to investigate the significance of owl calls and age class, without substrate, to address the lack in data for the juvenile control treatment Again, hypotheses tests were performed to compare the novel and native owl call treatments to the control. These results will demonstrate whether prey, such as *P. maniculatus*, can recognize unfamiliar forms of dangerous predators by their acoustic cues.

RESULTS:

One outlier was removed from the data before any analysis was done. This mouse did not move from its initial location and shivered the entire time the trial was being run. When age of the mouse was not taken into consideration, *P. maniculatus* showed no difference in the amount of seeds eaten relative to the different owl calls ($F_{2,49} = 1.852$, $P = 0.168$; Figure 1). Mice ate significantly more seeds in the sand substrate compared to the sand and leaf substrate ($F_{1,49} = 4.594$, $P = 0.037$), and there were no significant interactions between owl call and substrate ($F_{2,49} = 0.339$, $P = 0.714$). The Lilliefors test verified that our data was normally distributed ($P = 0.258$). The hypotheses tests determined that there were no significant differences between the control and native owl call ($F_{1,49} = 0.487$, $P = 0.488$). However, mice given the novel owl call treatment ate marginally significantly fewer seeds than those in the control treatment ($F_{1,49} = 3.612$, $P = 0.063$). There was no correlation between mouse body mass and the amount of seeds eaten ($P = 0.325$; Figure 2).

When organized relative to ages of the mice and without substrate, there was no significant difference between the ratio of seeds eaten to mouse body mass according to age class

($F_{1,49} = 0.166$, P = 0.686) and owl calls ($F_{2,49} = 2.015$, P = 0.144). The interaction between age class and owl call was also not significant ($F_{2,49} = 0.140$, P = 0.870). The Lilliefors test verified that our data was still normally distributed (P = 0.595). The hypotheses tests determined that there were no significant differences between the control and native owl call ($F_{1,49} = 0.647$, P = 0.425), but a marginally significant difference between the control and the novel owl call ($F_{1,49} = 3.944$, P = 0.053).

When organized relative to ages of the mice without the control, there were no significant differences between owl call ($F_{1,29} = 2.977$, P = 0.095), age class ($F_{1,29} = 0.213$, P = 0.648), and substrate ($F_{1,29} < 0.001$, P = 0.989). There were no interactions between owl call and age class ($F_{1,29} = 254$, P = 0.618), owl call and substrate ($F_{1,29} = 0.001$, P = 0.982), and age class, owl call, and substrate ($F_{1,29} = 1.169$, P = 0.289). Still, there was an interaction between age and substrate ($F_{1,29} = 5.018$, P = 0.033). The Lilliefors test verified normality.

The *Strix varia* call, "who cooks for you, who cooks for you now," consisted of a repetition of two shorter hoots, followed by a longer hoot (Table 1). The two shorter hoots had an approximate duration of 0.391s. The first of the longer hoots lasted 0.932s and the second hoot lasted 1.712s. The total call was 4.239s, and the frequency of the call ranged between 689.1Hz and 2239.5Hz. The call was repeated twice during the recording. The *Tyto alba* call, much like a human scream, was much higher in frequency; the frequencies ranged between 861.3Hz and 7924.2Hz. The recording consisted of eight repetitions of this call, each lasting between 0.407s and 0.563s: an average of 0.481s.

DISCUSSION:

The results of our study reject our hypothesis that *P. maniculatus* change their foraging patterns according to the direct cues of predators (Figure 1). The amount of seeds that the mice

consumed was only affected by the differences in the noise that the substrate produces during foraging ($P < 0.05$); they ate much fewer seeds in leaf trials regardless of the predator call. This suggests that the mice may be focusing on the aspects of predator avoidance that the individual has control over, instead of the predator itself. There may also be an imbalance in the ways that certain stimuli are associated with fear and predation risk (Griffin et al. 2001). Although mice are prey of a "sit-and-pursue" predator and should therefore rely more heavily upon acoustic cues, it may be necessary for mice to have a visual cue to associate the sound with a predator. Moreover, it has been theorized that prey tend to generalize their acquired predation risk responses to other species of predators (Griffin et al. 2001). This would suggest that the mice are able to infer predation risk associate with novel owls.

The mass of seeds eaten was used in this analysis because there was no clear relationship between the body mass of the mouse and the mass of seeds eaten (Figure 2). One would normally predict that smaller mice would consume less amounts of food because the mouse itself is small. However, this was not the case; the correlation only accounted for approximately 1% of the variation in the data collected. However, when comparing just the control trials to the novel owl call trials, the mice in the novel trials ate significantly fewer seeds (by mass) than those in the control trials (Figure 1). This is particularly unexpected since these calls are from predators that the mice have theoretically never encountered. Previous studies have predicted that because of this lack of encounter, prey are much more vulnerable to introduced predators (Salo et al. 2007); the prey do not know what animal is making the sound.

The lack of significant differences among the native owl call treatment and the control may also allude to the fact that the local mouse population has become habituated to the native predator calls. Assuming that mice would be able to recognize a novel predator as a threat, mice

would need to increase vigilance and allocate more resources to safety, rather than foraging behavior thereby suppressing the amount of food the mouse could consume (Brown et al. 1999). This would happen due to inexperience in how to avoid this new predator in an effective manner.

Owl call comparisons revealed that the two owl calls were extremely different. The novel owl call was much shorter (Figure 5) in comparison to the native owl call (Figure 4). Moreover, the novel owl call had a much greater range in frequency, ranging up to 8kHz, whereas the native owl call only went as high as 2.24kHz. The bottom ranges of the owl calls were relatively similar (approximately 700Hz-800Hz). Also, the novel call was repeated eight times during the treatment, while the native call was only repeated once. Given these stark differences, it would be reasonable that mice would not be able to recognize the novel call as a predator. To account for inexperience, future studies should include treatments that involve the calls of native, non-predatory nocturnal birds. Furthermore, videos of the mouse behavior should be analyzed and compared for similarities and differences in vigilance and foraging behavior.

When our data was organized according to the age of the mouse, interestingly, it highlighted the observation that adults are more aware of their surrounding substrate and predators whereas juveniles are not (Figure 3). Without the juvenile data, the effect of substrate on the ratio of seeds eaten to body weight ratio increased dramatically (all data: $P = 0.037$, adult data: $P = 0.01$; Figure 1 and 3). The significant interaction term between age class and substrate is also indicative of the juvenile's inexperience in recognizing a novel predator call or lack of self awareness and the sound that it is producing. These results may suggest that juveniles place a greater emphasis on foraging for food than adults or that juveniles are inexperienced and have not yet learned to recognize the call or stop foraging and take cover for safety in response to direct cues of predators. It has been shown that certain species generalize their fear response

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techniques to other predators in the same species (Griffin et al. 2001). This would explain the general suppression in food consumption of the adult mice in the noisy substrate regardless of the owl call.

In future experiments, one should collect equal sample sizes of juvenile and adult mice to be able to better compare the two age classes. The effects of age were analyzed after the fact in this study; even so, these results suggest that there is a real difference between these age groups and the method in which they use to forage. One could also test some other aspects of nonlethal, non-consumptive effects of predation such as visual cues and chemical cues in conjunction with auditory cues. Another interesting study would be to see whether the mice in this area become habituated to the novel owl calls over time. If after repeated exposure to the novel call, the mice become habituated to the novel call, there should be no significant differences between the amount of seeds consumed in relation to native and novel calls to the control.

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Table 1. Comparison between the *Strix varia* (Native) call and the *Tyto alba* (Novel) call. The *S. varia* call can be broken further into six sections: two hoots which are shorter in length (0.391s each) followed by a longer hoots (0.932s) followed by another two hoots (0.391s each) and another longer hoot (1.712s).

Owl Call	Maximum Frequency (Hz)	Minimum Frequency (Hz)	Duration of call (s)	Repetition During Recording
Strix varia	2239.5	689.1	4.239	2
Tyto alba	7924.2	861.3	0.481	8

Figure 1. Comparison of amount of *Acer saccharum* seeds consumed (g) by *P. maniculatus* according to owl call. There was no difference between owl calls ($F_{2,49} = 1.852$, P = 0.168). Mice ate significantly more seeds in the sand substrate compared to the sand and leaf substrate ($F_{1,49} = 4.594$, P = 0.037). There were no significant interactions between owl call and substrate ($F_{2,49} = 0.339$, P = 0.714).
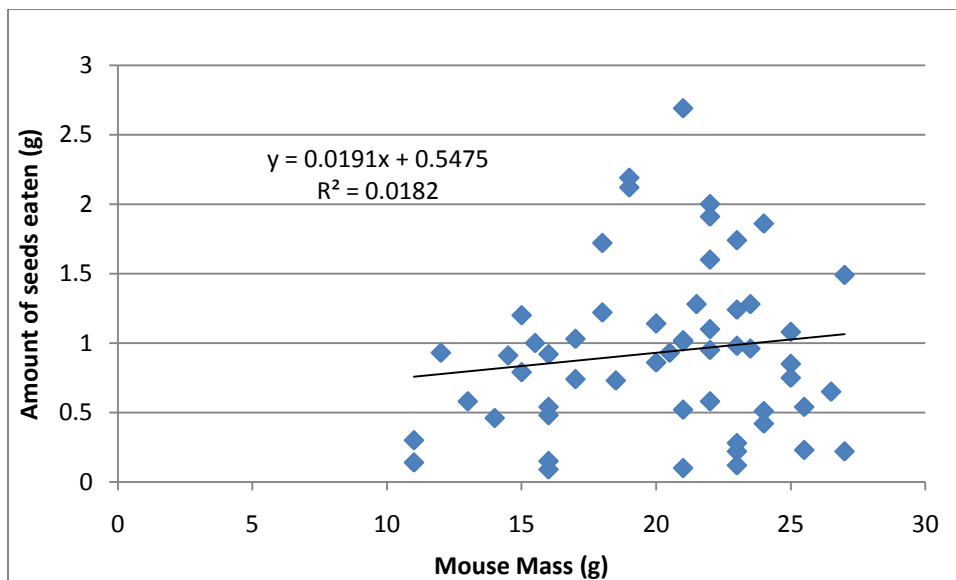

Figure 2. Amount of *Acer saccharum* seeds consumed by *P. maniculatus* (g) in comparison to mouse body mass (g). There was no correlation between mouse body mass and the amount of seeds eaten (P = 0.325).
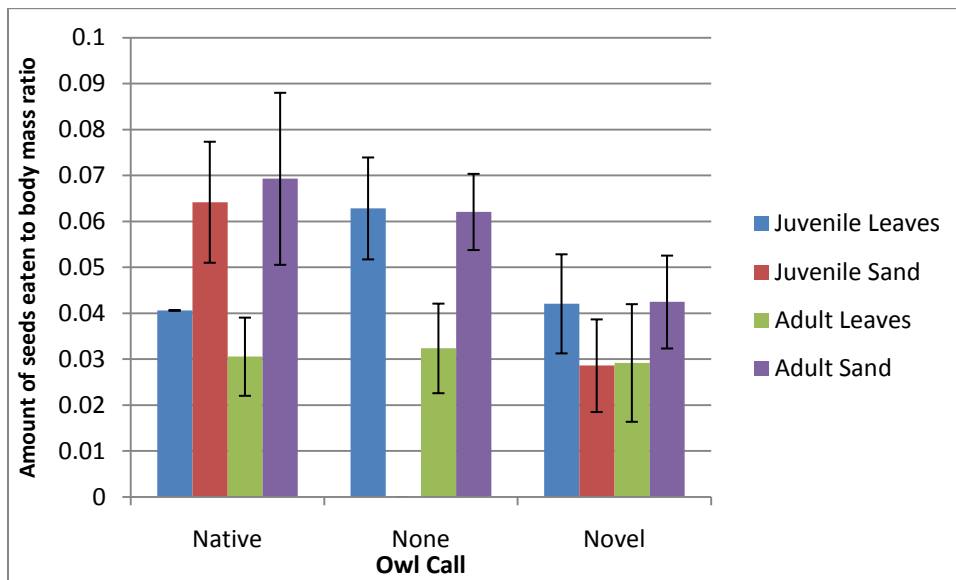
Figure 3. Comparison of amount of *Acer saccharum* seeds consumed to body mass ratio organized according to age class. Relative to age classes of adults (> 18g) and juveniles (≤ 18g),without the control, there were no significant differences between owl call ($F_{1,29} = 2.977$, P = 0.095), age class ($F_{1,29} = 0.213$, P = 0.648), and substrate ($F_{1,29} < 0.001$, P = 0.989). There were no interactions between owl call and age class ($F_{1,29} = 254$, P = 0.618), owl call and substrate ($F_{1,29} = 0.001$, P = 0.982), and age class, owl call, and substrate ($F_{1,29} = 1.169$, P = 0.289). Still, there was an interaction between age and substrate ($F_{1,29} = 5.018$, P = 0.033).
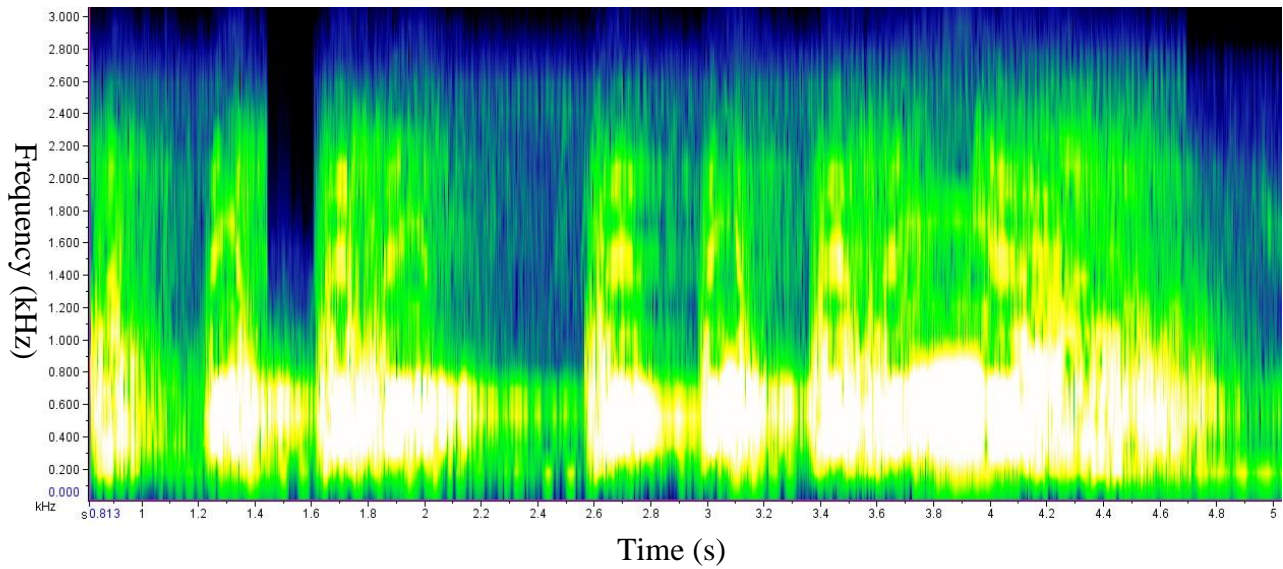
Figure 4. The native owl call of *Strix varia* according to frequency, intensity, and time.
Intensity of the call is represented by the colors, white being most intense and black being the least intense.
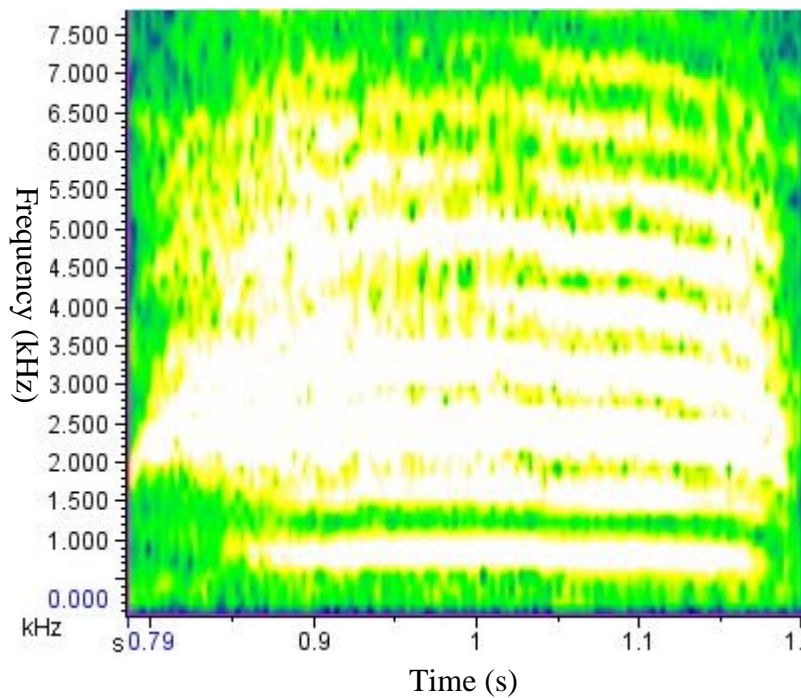

Figure 5. The novel owl call of *Tyto alba* according to frequency, intensity, and time.
Intensity of the call is represented by the colors, white being most intense and black being the least intense.