

An ear for fear: the effect of substrate type and background noise on the foraging behavior of *Peromyscus maniculatus gracilis* (Woodland Deer Mice)

BIOS 35502-01: Practicum in Field Biology

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2018

Abstract

The ecology of fear concerns the ways in which organisms alter their behavior in response to perceived predation risk. *Peromyscus* species change their foraging behavior in response to a variety of environmental factors including moonlight intensity, habitat coverage, and substrate type. In general, *Peromyscus* species tend to avoid noisy substrates, presumably to reduce detection by auditory predators. Background noise, however, has the potential to mask prey-generated sounds, making prey species less vulnerable to predation. This study examines whether the presence of background noise affects the behavior of *Peromyscus maniculatus gracilis*, and whether this effect is dependent on substrate type. We predicted that background noise would increase foraging activity on a noisy substrate, but have no effect on a quiet substrate. To test this hypothesis, wild mice were captured and allowed to forage on either leafy or sandy substrates in the presence or absence of a frog chorus. Seed consumption, time spent active, and distance moved were quantified. The results indicated that mice increased their time spent active when on a sandy substrate in the presence of the frog chorus, but did not alter their consumption. These findings demonstrate that elements of the soundscape, both natural and anthropogenic, have the potential to influence the behavior of nocturnal foragers.

Keywords *Peromyscus*, ecology of fear, foraging, granivory, soundscape ecology, noise pollution

Introduction

Trophic cascades are common across terrestrial, freshwater, and marine ecosystems, and have been documented in seemingly unlikely areas including tropical forests and the open ocean (Pace et al. 1999). Traditionally, trophic cascades were thought to function through density-

mediated indirect interactions (DMII), in which predators indirectly increase the abundance of plants via consumption of herbivores (Rosenzweig 1973). However, it is now recognized that many trophic cascades function primarily through trait-mediated indirect interactions (TMII), whereby the presence of a predator indirectly influences the plant community by causing herbivores to divert time away from foraging and towards antipredator behavior (Schmitz et al. 1997, 2004; Preisser et al. 2005; Peckarsky 2008). The study of how these nonlethal predator-prey interactions impact population- and community-level dynamics is known as the ecology of fear (Brown et al. 1999).

The foraging of *Peromyscus* (deer mice) presents a good model system to study how fear of predation may alter trophic interactions. Forest-dwelling *Peromyscus* forage nocturnally for insects, other invertebrates, fruits, nuts, and seeds (Drickamer 1970, 1976; Whitaker 1996). As granivores, deer mice and other rodents can significantly influence plant community structure through selective seed consumption (Garcia et al. 2005). For example, one species of *Peromyscus* exhibits a strong preference for *Acer rubrum* (Red Maple) seeds over *A. saccharum* (Sugar Maple) seeds, which may have implications for the relative recruitment of each tree species (Cramer 2014). In turn, *Peromyscus* populations are subject to predation by a wide range of aerial and terrestrial predators, including owls, snakes, weasels, foxes, and wolves (Kurta 2017). Deer mice therefore inhabit a key position in forest food webs.

Peromyscus species alter their foraging behavior in response to perceived predation risk. Studies have shown that *Peromyscus* evaluate risk based on a variety of indirect cues, such as moonlight intensity and habitat coverage, and that they respond by reducing their activity in or avoiding locations that are more brightly lit and exposed (Clarke 1982; Fanson 2010; Travers et al 1988; Wolfe and Summerlin 1989). These behaviors serve a clear adaptive function, as the

hunting efficiency of owls has been shown to increase under brighter conditions (Clarke 1982). However, these antipredator behaviors come at the cost of time spent foraging.

This study will focus on *P. maniculatus gracilis* (Woodland Deer Mice), a subspecies that is primarily resident in forested areas. In contrast to mice that inhabit exposed areas, namely fields, this species' concealed environment may mean that noise serves as a more relevant indicator of predation risk than light. In particular, patch substrate may affect foraging behavior, as certain nocturnal predators, like owls and bats, rely on the noise created by substrate rustling to locate their prey in dark, cluttered environments (Payne 1971; Arlettaz et al. 2001). Studies indicate that *P. maniculatus* systemically selects quieter substrates, showing preferences for coniferous leaf litter over hardwood leaf litter, wet leaf litter over dry leaf litter, and soft logs over hard logs (Barnum et al. 1992; Fitzgerald and Woff 1988; Roche et al. 1999). This suggests that the noise created by certain substrate types influences a deer mouse's perception of predation risk and resultant foraging behavior.

Background noise that masks the sounds created by noisy substrates may reduce or eliminate these substrate preferences. The noises in an ecosystem, collectively known as the "soundscape," can come from natural sources, like birds and rivers, and well as anthropogenic sources, like roads (Pijanowski et al. 2011). With regards to road noise, a study on bats that rely on passive listening to locate their prey found that more intense highway noise decreased foraging success rates and increased search time (Siemers and Schaub 2011). Presumably because of this, bats tend to avoid both anthropogenic and natural noise (Schaub et al. 2008). Other auditory predators may also experience lowered foraging success in the context of masking background noise. If this is the case, background noise would be expected to shift a

prey species' assessment of the trade-off between predator evasion and foraging, leading them to exhibit less caution in noisy environments.

This study examines whether the foraging behavior of *P. m. gracilis* on different substrate types is affected by the introduction of background noise, specifically a frog chorus. We predicted that, on a quiet substrate, background noise would not impact the movement and seed consumption of *P. m. gracilis*. However, on a noisy substrate, we predicted that mice would show increased activity and consumption in the presence of background noise.

Methods

Study Site

Sampling and experimentation was conducted at the University of Notre Dame Environmental Research Center-East (UNDERC-East), a 7500-acre site situated at the border between Wisconsin and the Upper Peninsula of Michigan. The area hosts *P. m. gracilis* in addition to many other small mammals, and is covered by a mixture of coniferous and hardwood forest.

Trapping and Housing

Deer mice were live-trapped in *A. saccharum*-dominant stands using Sherman traps (7.62 x 8.89 x 22.86 cm; H. B. Sherman Traps, Inc., Tallahassee FL) baited with millet and black oil sunflower seeds. *P. m. gracilis* were distinguished from *P. leucopus* based on tail morphology, facial morphology, and ear length (Stephens et al. 2014; Ridenhour and Cramer 2015). Pregnant and lactating females (identified as those with descended mammae; in addition, pregnant mice were often over 30 g) were excluded from experimentation. Prior to testing, mice were housed in

individual cages (19 x 29 x 12.5 cm) containing paper bedding and polyfill nesting material, and were provided with unrestricted food (Teklad Irradiated Global 19% Protein Extruded Rodent Diet) and water. All animal use followed guidelines provided by the American Society of Mammalogists (Sikes et al. 2016) and the Animal Behavior Society (Ethical and Animal Care Committee of the Animal Behavior Society 2012), and adhered to a research protocol approved by the University of Notre Dame Institutional Animal Care and Use Committee (protocol 17-03-3770).

Experimental Procedure

Mice were randomly assigned to one of four treatments: noisy substrate with background noise, noisy substrate without background noise, quiet substrate with background noise, and quiet substrate without background noise. Trials were carried out in a fifteen-gallon glass aquarium (12" x 12" x 24"). For the noisy substrate treatment, the aquarium floor was covered with artificial *A. saccharum* leaves (36, assorted sizes). For the quiet substrate treatment, the aquarium was filled with sand (approx. 700 mL). The background noise consisted of a pre-recorded chorus of *Hyla versicolor* (Grey Tree Frog), a common species at UNDERC-East. The chorus was played from two speakers (Altec Lansing VS2320) placed at opposite ends of the aquarium, and the volume was set so that the chorus varied between 40 and 70 dB, mimicking natural conditions.

Trials were conducted between 10PM and 1AM. Mice were starved for approximately five hours prior to testing. For each trial, black oil sunflower seeds (2.5 g) were strewn haphazardly on top of the substrate. One mouse was then transferred to the aquarium and allowed to forage in the dark for 30 minutes, during which time its movements were recorded

using two video cameras (Night Owl Color Security Cameras). After this allotted time, the mouse was removed and the remaining seeds were weighed. The amount consumed was determined by subtracting the weight of the uneaten seeds from the initial weight of the seeds. This number was standardized by the mass of the mouse.

Video recordings were analyzed using JWatcher (Version 1.0; Blumstein and Daniels 2007). Videos were coded for mouse behavior (active or stationary) and location (quadrant 1, 2, 3, or 4). For each mouse, the proportion of time spent active and the total number of quadrants visited (a proxy for distance moved) was calculated.

Statistical Analyses

Data were analyzed using a two-way analysis of variance (ANOVA). The two independent categorical variables were substrate type and the presence or absence of background noise. The responses of three different independent variables were tested: standardized mass of seeds consumed, proportion of time spent active, and number of quadrants visited. The Shapiro-Wilk test was used to ensure Normality, and Bartlett's test was used to check the assumption of homoscedasticity. In the case of a significant interaction term, Tukey post-hoc analyses were run. All tests were conducted using R (Version 3.4.1; R Core Team 2017), and significance was determined at an alpha value of 0.10.

Results

A total of 31 mice were tested; seven were tested with the noisy substrate and frog chorus, and eight were tested in each of the other three treatments. The results of Bartlett's test verified that the variances were equal across treatments for each of the three response variables

(consumption: $K^2 = 6.86$, $df = 3$, $p = 0.077$; proportion of time spent active: $K^2 = 4.86$, $df = 3$, $p = 0.182$; quadrants visited: $K^2 = 2.59$, $df = 3$, $p = 0.458$). The assumption of Normality was also met for measures of consumption (Shapiro-Wilk; leaves + silence: $W = 0.95$, $p = 0.662$; sand + silence: $W = 0.91$, $p = 0.362$; leaves + chorus: $W = 0.94$, $p = 0.597$; sand + chorus: $W = 0.96$, $p = 0.789$) and proportion of time spent active (leaves + silence: $W = 0.92$, $p = 0.405$; sand + silence: $W = 0.95$, $p = 0.719$; leaves + chorus: $W = 0.83$, $p = 0.085$; sand + chorus: $W = 0.84$, $p = 0.076$). The number of quadrants visited was non-Normal for one of the treatments (leaves + silence: $W = 0.93$, $p = 0.544$; sand + silence: $W = 0.85$, $p = 0.101$; leaves + chorus: $W = 0.67$, $p = 0.002$; sand + chorus: $W = 0.89$, $p = 0.248$), but due to the robust nature of ANOVA, parametric analysis was still used.

Standardized consumption was compared across treatments (Figure 1). Neither substrate type nor background noise had a significant effect on consumption (2-way ANOVA, substrate type: $F = 0.17$, $df = 1, 27$, $p = 0.686$; background noise: $F = 2.11$, $df = 1, 27$, $p = 0.158$). Furthermore, the effect of background noise did not depend on substrate type ($F = 1.82$, $df = 1, 27$, $p = 0.189$).

The effect of background noise on the proportion of time spent active did depend on substrate type (2-way ANOVA, $F = 6.49$, $df = 1, 27$, $p = 0.017$; Figure 2). On the leafy substrate, background noise did not influence activity levels (Tukey post-hoc, $HSD = -0.12$, $p = 0.628$), but on the sandy substrate activity was 67% higher in the presence of the frog chorus ($HSD = 0.23$, $p = 0.098$). In addition, in the presence of a frog chorus activity was 145% higher on sand than on leaves ($HSD = 0.34$, $p = 0.010$), but no significant difference between substrate types was observed in the absence of the chorus ($HSD = -0.01$, $p = 0.999$).

The results for the number of quadrants entered closely tracked those for proportion of time spent active (Figure 3). As before, the effect of background noise depended on substrate type (2-way ANOVA, $F = 5.16$, $df = 1, 27$, $p = 0.031$). Due to high variation in the data, no pairwise differences were significant (on leaves, effect of background noise: $HSD = -75.64$, $p = 0.450$; on sand, effect of background noise: $HSD = 83.38$, $p = 0.336$; without chorus, effect of substrate type: $HSD = -41.88$, $p = 0.825$; with chorus, effect of substrate type: $HSD = 117.14$, $p = 0.117$).

Discussion

This experiment indicates that background noise may influence the foraging behavior of mice, but that this effect depends on substrate. On the sandy substrate, mice exhibited elevated activity levels in the presence of a frog chorus, whereas on the leafy substrate this effect was not observed. This is contrary to our hypothesis that background noise would affect foraging on leaves but not sand. One explanation for these results may be that the frog chorus did not fully mask the noise created by rustling leaves, but did mask noise created in the sandy substrate. Research on the rustling sounds produced by beetles has shown that sand rustles at about 40 decibels, while dry leaves rustle at about 65 decibels (Goerlitz et al. 2008). The volume of the frog chorus oscillated between 40 and 70 decibels, meaning that leaf rustling may have still been audible during the troughs in the chorus, whereas sand rustling was completely masked. Siemer and Schaub (2011) compared the effect of continuous versus transient (i.e., rising and falling with the passage of cars) highway noise on bat foraging, and found that search time was lower in the context of transient noise. This suggests that predators may still be able to locate prey when background noise levels are variable. A subsequent study could be conducted using a continuous

natural noise, such as a rushing river, to see whether mice exhibit decreased caution on the leafy substrate as well as the sandy substrate.

It's important to note that a sizeable portion of the time spent active was devoted to escape attempts, i.e. jumping up the walls, rather than looking for seeds. Because of this, activity in a lab setting may not be a good indicator of foraging rates, a possibility that is also supported by the fact that standardized consumption did not track time spent active. However, elevated activity does still suggest that the mice experienced a lower perception of predation risk on sand in the presence of a frog chorus. In order to reduce escape behavior, future experiments could use a larger testing aquarium and include an acclimation period in the aquarium prior to addition of the seeds. Laboratory trials could also be supplemented with field-based observations of foraging behavior in locations with different substrate types and varying levels of ambient noise.

The number of quadrants visited mirrored activity levels, but pairwise differences were not significant. Visitation rates were used as a proxy for distance moved, but a more effective way to quantify this variable would be to measure movement directly. Studies have already demonstrated the feasibility of this using software programs such as ImageJ to automatically quantify distance traveled and average speed (Tungtur et al. 2017). Use of this technology would enable us to determine whether, in addition to moving less of the time, mice also moved slower when on leaves or in the silent treatments.

As stated previously, standardized consumption did not follow the same trend as activity. Instead, consumption showed no significant differences between substrate types or noise treatments. This could indicate that seed handling and consumption are relatively quiet tasks and are therefore not reduced in the context of elevated predation risk. Additionally, mice often retreated to the corners of the aquarium to eat their seeds; according to Wurbel (2001), the

structure of corners mimic locations that mice would select for burrow construction in the wild, and as such they may confer a sense of safety and protection. If replicable in the field, the biological significance of these findings would be that background noise, specifically a frog chorus, doesn't impact seed consumption, and therefore has little bearing on seed recruitment.

On the other hand, the finding that background noise doesn't impact consumption could be explained by the fact that there was an abundance of seeds in the aquarium, and that mice could therefore consume their fill without needing to move very much. This may be an accurate reflection of seed density during certain times of the year: one study found that *A. rubrum* seed rain density ranges from 15-425 seeds per square meter in the spring (Lambers and Clark 2005). However, the same study found a much lower abundance in the fall, with seed bank density ranging from 0-63 seeds per square meter. In this case, reduced deer mouse activity could correspond to fewer seeds consumed and higher recruitment the following summer. Furthermore, in this study the seeds were scattered on top of the substrate, but in the natural environment they could be buried under leaves or soil. This would increase the difficulty of finding them, and may further reduce seed predation rates.

In addition to studying the effect of continuous natural noises, future research should also examine how anthropogenic noise, or anthrophony, impacts the foraging behavior of *Peromyscus*. Given the predicted increase in anthrophony in the coming decades (Pijanowski et al. 2011), understanding the effect of urban noise pollution on foraging ecology and predator-prey interactions will become increasingly important. Some studies suggest that organisms take advantage of anthrophony; for example, certain bird species nest preferentially near natural gas extraction sites, where the density of nest predators is lower (Francis et al. 2009). However, other findings indicate that organisms may perceive human-generated noise as an indication of

predation risk, and consequently exhibit more antipredator behavior (Barber et al. 2010). The response of prey to anthrophony therefore appears to be species- and context-dependent.

Overall, this study suggests that background noise does impact the foraging behavior of *P. m. gracilis*, but that this effect is dependent on substrate type, and may not necessarily translate into differential seed recruitment. Mice spent more time active when on a sandy substrate in the presence on a frog chorus, but were less active when the substrate was leafy or the chorus was absent. These findings show that, in addition to environmental factors like lighting and habitat coverage, nocturnal foragers may use the soundscape to evaluate predation risk, and alter their behavior accordingly. Ultimately, more research is needed to fully understand how both natural and anthropogenic noise influence foraging behavior, and what implications this might have for plant communities and predator-prey interactions.

Acknowledgements

I'm grateful for the funding and support supplied for this research by the Bernard J. Hank Family Endowment. Dr. Michael Cramer provided invaluable assistance with trapping, experimental design and set-up, and data analysis, and was always willing to answer questions and offer advice. I would also like to thank expert mouse wranglers Nathalia Rodriguez and Kiana Lee, and fearless flagger Xiomary Serrano Rodriguez. Shannon Jones, Sam Sutton, Ellie Wallace, and Gary Belovsky all dedicated considerable time and effort to make this program a success. Thanks to the rest of the UNDERC class for being a supportive and enthusiastic community, and for helping to catch mice in the dorm. Finally, this research would not have been possible without the participation of the 31 *Peromyscus maniculatus* that graciously ran into our traps, sometimes more than once.

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Figures

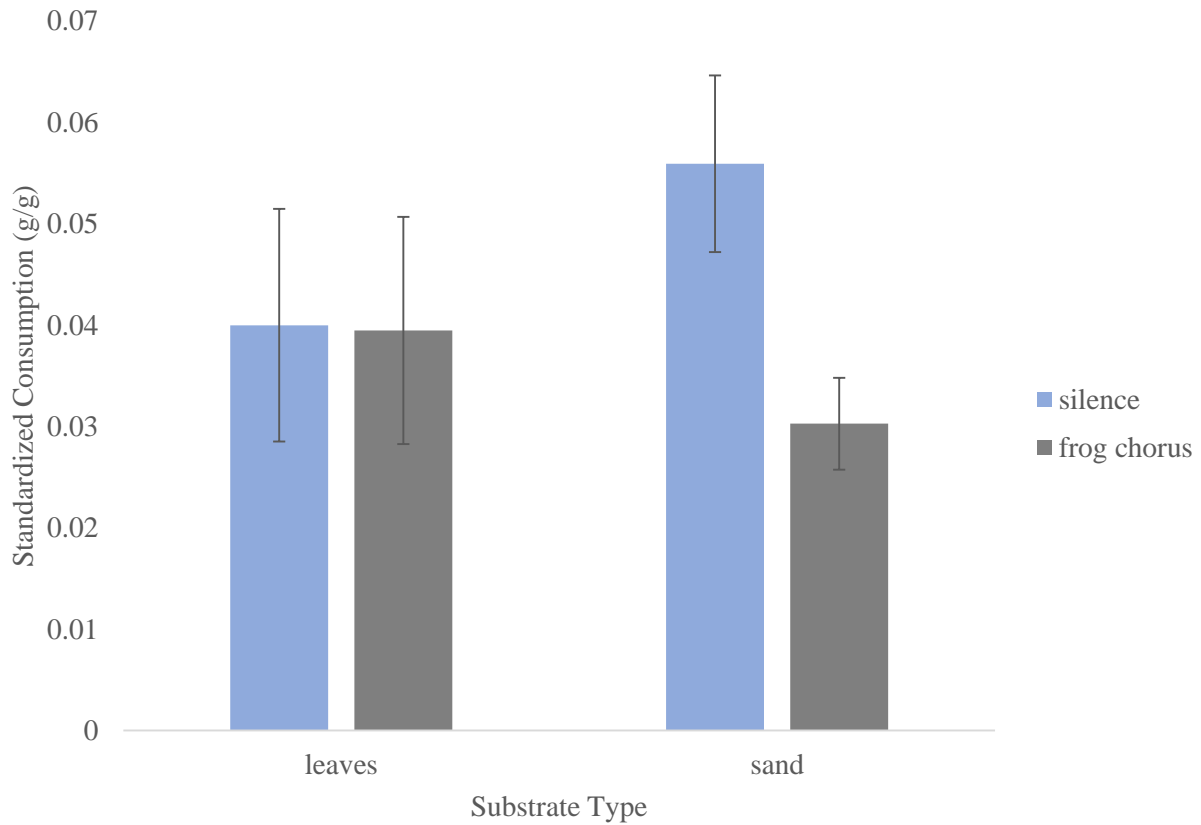


Figure 1. Effect of substrate type and background noise on mass of seeds consumed (\pm SE).

There was no significant effect of substrate type ($p = 0.686$) or background noise ($p = 0.158$) on consumption, nor did the effect of background noise depend on substrate ($p = 0.189$).

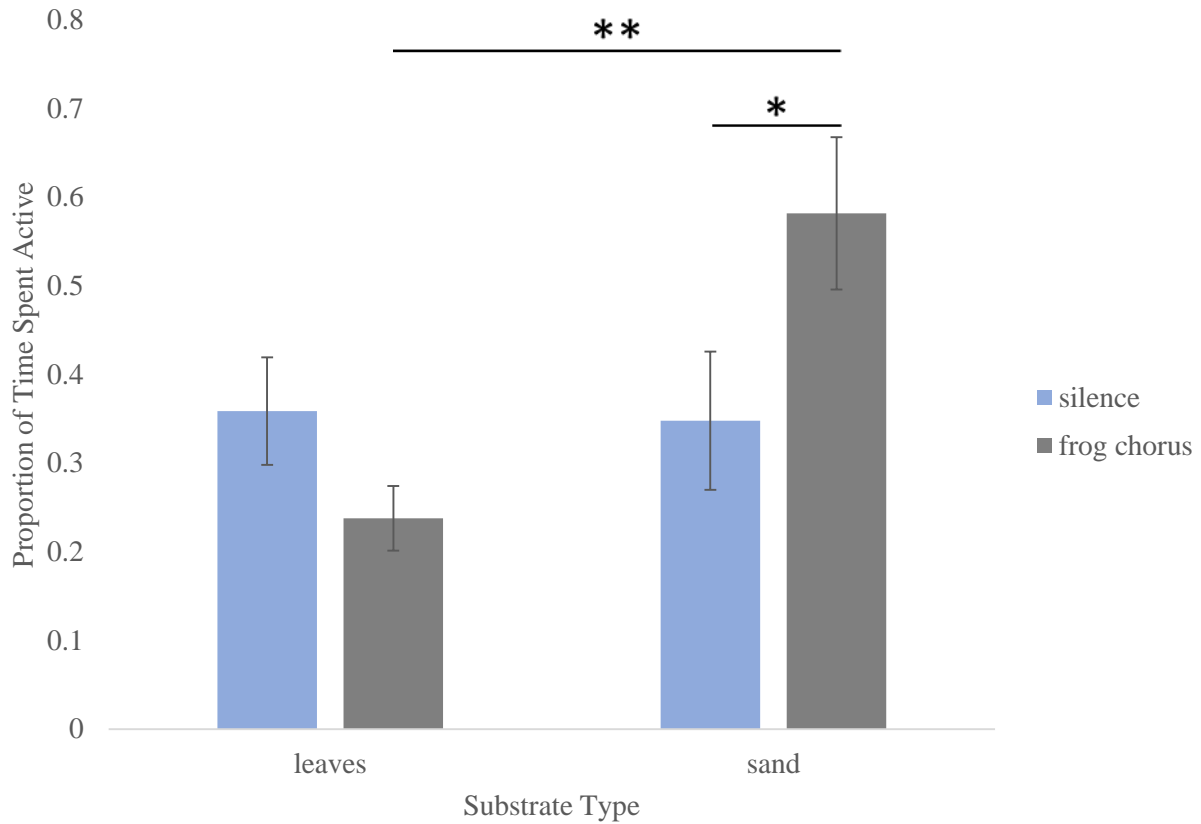


Figure 2. Effect of substrate type and background noise on proportion of time spent active (\pm SE). The effect of background noise depended on substrate type ($p = 0.017$), with the frog chorus increasing activity on the sandy substrate ($p = 0.098$) but not on the leafy substrate ($p = 0.628$). Furthermore, activity was higher on the sandy substrate versus the leafy substrate in the presence of the frog chorus ($p = 0.010$), but not in the silent treatments ($p = 0.999$).

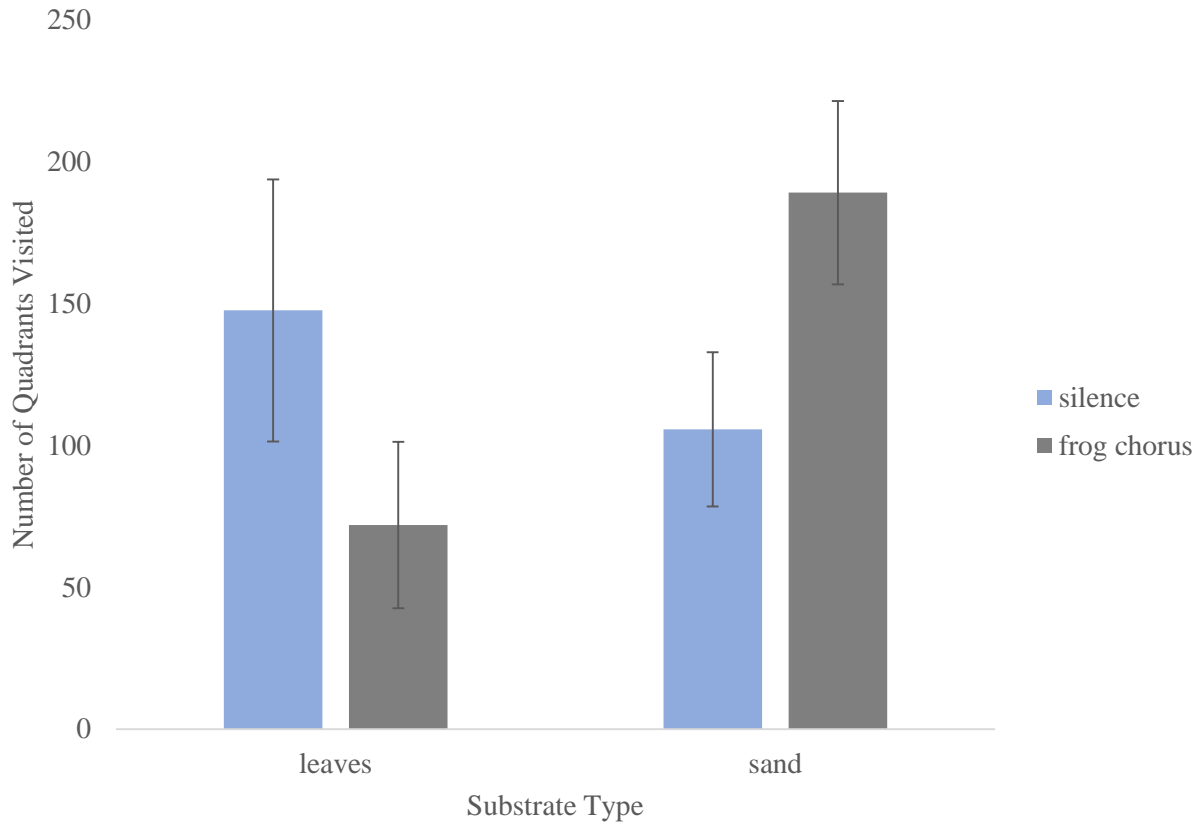


Figure 3. Effect of substrate type and background noise on number of quadrants visited by mice (\pm SE). The effect of background noise depended on substrate type ($p = 0.031$); however, pairwise differences were insignificant.