


# Prey responses to predation risk under chronic road noise

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## Keywords

anthropogenic disturbance; foraging; vigilance;  
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predation risk effects; road noise.

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## Abstract

Anthropogenic noise has dramatically increased over the past decades with potentially significant impacts on wildlife and their community interactions. Using giving-up densities (GUDs) paired with camera traps, we examined the concurrent influence of chronic road noise and predation risk on free-living small mammals. Specifically, we looked for differences in foraging and vigilance behavior during various noise treatments. We found that small mammals significantly reduced food intake when exposed to predation risk; however, concurrent exposure to road noise eliminated this effect; small mammals increased food intake when exposed to road noise and risk compared to risk alone. Furthermore, road noise reduced the number of visits and time spent at foraging trays while it increased vigilance behavior of small mammals in risky situations, meaning they were able to increase their foraging efficiency. Mice also ate less when moon illumination was greater; however, this had no effect on our overall results. This is one of the first studies to concurrently examine the effects of road noise and predation risk on free-living prey. It shows the complex responses of prey exposed to chronic noise conditions as they attempt to gain reliable information about predation risk and respond appropriately. We highlight the potential consequences road noise may have on the survival of prey as it interferes with their appropriate risk responses.

## Introduction

Predators can alter prey populations not only through direct killing and consumption but also through non-consumptive, predation risk effects (Creel et al., 2014; Hoverman & Reylea, 2012; Peacor et al., 2020). Such effects include changes to behavior, morphology, physiology, and life history (Sheriff et al., 2020b). While such predation risk effects may reduce reproduction and ultimate survival (e.g., MacLoed et al., 2018; Sheriff et al., 2009; Zanette et al., 2011), the risk-induced trait responses increase immediate survival in the face of increased predation (Sih, 2005). To respond appropriately, prey's ability to gather and respond to reliable cues about the level of predation risk they face is critical (Sih, 1992; Sih et al., 2011). In many animal's environments, however, the soundscape they are exposed to is being degraded by anthropogenic inputs (Barber et al., 2010; Butler et al., 2016). The impact of noise on free-living animals has been shown to alter their physiology and behavior (Brouček, 2014; Nichols et al., 2015; Tennesen et al., 2018), have effects on space use and nest selection sites, reduce fecundity, and increase offspring abandonment (Halfwerk et al., 2011; Plummer et al., 2021; Strasser & Heath, 2013). A major, yet relatively unexplored noise input comes from roads, which may affect prey's ability to perceive predation risk cues and alter their risk responses (Berlow et al., 2021; Francis & Barber, 2013; Luo et al., 2015; Shannon

et al., 2016a). This article will focus specifically on behavioral risk responses.

Chronic road noise, a widespread source of anthropogenic noise pollution, has shown dramatic increases over the last few decades with the expansion of resources and transportation (Shannon et al., 2016b) and is poised to become increasingly pervasive. Indeed, while the US' population increased by about one third, traffic nearly tripled between 1970 and 2007 (Barber et al., 2010). Anthropogenic noise pollution, including road noise, can affect prey's ability to perceive predation risk cues, altering their responses which can be critical to survival (Francis & Barber, 2013; Shannon et al., 2016a). Road noise is hypothesized to alter prey responses to predation risk in three distinct ways. One is through increasing responses because prey have more difficulty in detecting predators or conspecific alarm calls with background noise, leading to more caution; termed the masking hypothesis (Barber et al., 2010; Meillère et al., 2015). For example, Quinn et al. (2006) found chaffinches to increase vigilance behavior toward predation risk when background noise was also present. Alternatively, prey may reduce responses because noise causes prey to have more difficulty in detecting predators but distracts them from risk cues. In this scenario, prey become less cautious and perceive an area as less risky; termed the distracted prey or reduced detectability hypothesis (Chan & Blumstein, 2011; Chan et al., 2010). For example, Simpson et al. (2015) found that while

exposed to ship noise, European eels were both less likely and slower to startle, and got caught much quicker by simulated predators. The third way is by increasing responses because prey perceive road noise itself as a threat; termed the risk disturbance hypothesis or increased threat hypothesis (Gill et al., 1996; Owens et al., 2012; Tyack et al., 2011). For example, Shannon et al. (2014) found that prairie dogs reduced foraging and increased vigilance when exposed to traffic noise. Curé et al. (2016) found that sperm whales interrupted foraging and avoided sonar disturbance similarly to if they perceived a killer whale, a major predator. This can be teased apart from the first hypothesis due to prey responding to just road noise alone, rather than predation risk plus road noise. This helps us understand the anti-predator response to predation risk and road noise; whether it is driven by prey perceiving road noise as a threat or whether road noise impedes prey detection of predation risk cues.

While there is evidence supporting each of the above hypotheses, there is yet to be a study that examines how chronic exposure to road noise alters the longer term responses of prey to predation risk. Furthermore, most studies tend to focus on avian and marine animals, while examples on terrestrial mammals are sparse (Shannon et al., 2016b).

Here, we tested the effects of road noise on responses of small mammals exposed to predation risk. Small mammals are known to respond to predation risk by changing their activity patterns and foraging behavior (Kotler et al., 1993; Schmitz et al., 1997) as they attempt to minimize their risk of predation while maximizing foraging opportunities (Loggins et al., 2019). Studies have also shown that animals will increase their vigilance when exposed to increased predation risk (Creel et al., 2014; Shannon et al., 2016a).

We exposed free-living small mammals to four playback (auditory calls) treatments: non-predators (as a control), owls and hawks (predation risk), predation risk plus road noise, and road noise alone, and measured small mammals' food intake, foraging behavior, and vigilance. We tested three alternative hypotheses:

- (1) Road noise, during risk, would cause prey to perceive the area as riskier. As such, we would expect small mammals to reduce food intake and time spent foraging, and increase vigilance while foraging when exposed to predation risk plus road noise as compared to risk alone.
- (2) Road noise, during risk, would cause prey to perceive the area as less risky. As such, we would expect small mammals to increase food intake and time spent foraging, and reduce vigilance while foraging when exposed to predation risk plus road noise as compared to risk alone.
- (3) Road noise itself would be perceived as a threat. As such, we would expect small mammals to behave similarly to risk only exposed prey, reducing food intake and time spent foraging, and increasing vigilance while foraging when exposed to road noise only as compared to control prey.

## Materials and methods

We exposed chipmunks (*Tamias striatus*) and mice (*Peromyscus leucopus*) to four independent treatments: control, predation

risk, road noise + predation, and road noise alone using auditory playbacks of animals that reside in the area and of recordings of road noise (Suraci et al., 2016; Zanette et al., 2011). We broadcasted each treatment through a speaker at levels equaling approximately 62 dB ("A" filter playing through a KB6000 speaker) at the experimental site (described below). Each treatment lasted 72 h with 48 h of silence between treatments and was temporally replicated three times. The total duration of the experiment occurred from July 1, 2020 to September 13, 2020.

## Study area

The study occurred at one site in a 2 km × 0.6 km deciduous woodland in Southern Massachusetts, with surrounding rural neighborhoods and farmland. No major roadways are within the vicinity. Small mammals common in the area include chipmunks (*Tamias striatus*) and white-footed mice (*Peromyscus leucopus*) (hereafter "small mammals"). It is possible that deer mice (*Peromyscus maniculatus*) are also present; however, the study site is outside of their known geographic range. Through camera trapping and handling, it is almost impossible to tell the two species apart (Feldhamer et al., 1983; Tessier et al., 2004). Common diurnal predators include red-tailed hawks (*Buteo jamaicensis*) and barred owls (*Strix varia*), and nocturnal predators include barred owls, horned owls (*Bubo virginianus*), and eastern screech owls (*Megascops asio*) at lower prevalence. Diurnal non-predators include mourning dove (*Zenaidura macroura*) and northern flicker (*Colaptes auratus*), while veery (*Catharus fuscescens*), eastern whip-poor-will (*Caprimulgus vociferous*), wood frog (*Lithobates sylvaticus*), gray treefrog (*Hyla versicolor*), and spring peeper (*Pseudacris crucifer*) are nocturnal.

## Risk and road noise manipulation

Our control treatment playbacks consisted of calls from above-mentioned resident non-predator species. We used a playback control as opposed to no-noise control to control for "noise and speakers" themselves, time constraints limited our ability to use both no-noise and playback controls. Our risk treatment playbacks consisted of calls from abovementioned relevant predators. We downloaded avian playbacks from the Cornell Ornithology laboratory, cleaned, and cut them using the program Audacity (v. 2.4.2). These two treatments broadcasted calls at random times and random lengths for 10% of the time during the day and 40% of the time during the night (see Zanette et al., 2011 for details).

We downloaded road noise playbacks from YouTube (Relaxing White Noise Sounds – Topic 2018; Swineberg, 2015; TexasHighDef, 2016) rather than live recording given the reduced traffic from COVID-19 restrictions during the study. We manipulated playbacks using Audacity to reflect patterns of highway traffic over a 24-h period, using traffic patterns laid out in Järv et al. (2012), that is, increased prevalence during rush hour and reduced during late night and mid-day. In the predation risk plus road noise treatment, we manipulated risk exactly as outlined above and road noise was played from a

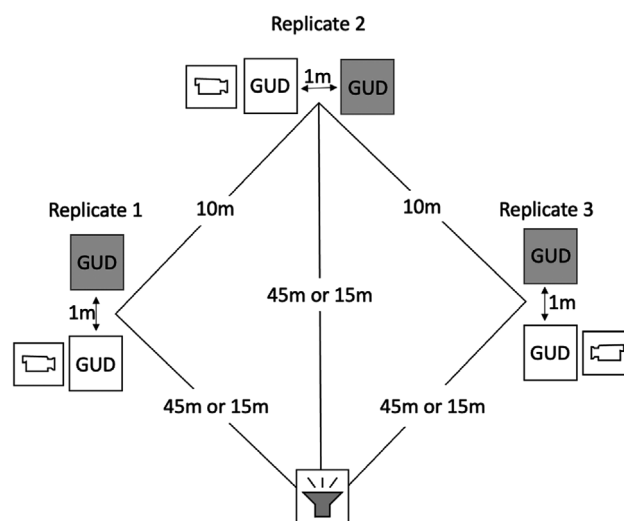
different speaker 100% of the time reflecting 24-h traffic patterns. In the road noise alone treatment, only road noise played 100% of the time reflecting 24-h traffic patterns. We selected noise level (for all treatments) from preliminary measurements we took during rush hour 50 m into the forest, which showed that levels were approximately 62 dBA. This is similar to our previous studies where we played predator playbacks at approximately 68 dBA.

### Foraging and vigilance estimates

To measure foraging behavior and vigilance, we used a combination of the giving-up density (GUD) technique (Brown, 1988) and motion detecting cameras. GUDs, based on the marginal value theorem and the cost of diminishing returns (Charnov, 1976), are widely accepted to quantify foraging behavior (Kotler et al., 1993; Mella et al., 2018; Zhang et al., 2020) and is a measure of the amount of food left in a foraging tray after an animal has ceased foraging. GUD values have been shown to be impacted by many environmental and ecological factors, including the risk of predation an animal is exposed to (Brown, 1988; Schmidt et al., 2008). Here, we used plastic foraging trays (32 cm × 11 cm × 17.5 cm) with holes cut into the sides to allow unrestricted access, filled with 500 mL of sand and 2.5 g of millet seed. Pairs of foraging trays were placed 1 m apart and 10 m apart from other pairs, which gave six trays total in three pairs during each treatment replicate. Each tray was approximately 45 m from the playback speaker used for the control and predator audio and 15 m from the road noise speaker (noise levels at trays regardless of speaker placement or treatments were approximately 62 dB). See Fig. 1.

Three of the six foraging trays (one per pair) had motion detection cameras (Apeman H70 Trail Cameras) to estimate the number of visits, length of visits, number of vigilance events, and duration of vigilance events of small mammals. We determined vigilance based on head positioning; if the animal raised its head higher than its backside, it was determined to be vigilant (Suraci et al., 2016). We set the cameras to record video for 45 s, with a delay of 5 s between continuous motion. We only used cameras during experimental replicates 2 and 3 due to logistical constraints. We analyzed camera data using the program JWatcher (v. 1.0) to score visits and vigilance. The use of camera traps in observational studies has been shown to give invaluable data on animal communities; however, it has not been well used in experimental research (Smith et al., 2020), particularly in combination with audio playbacks (Buxton et al., 2018). Some limitations of camera trap data include camera detection and triggering, species identification, and behavioral responses to cameras themselves (Meek et al., 2015). The problem of a subject entering the camera's view and the camera not detecting it could lead to sampling error (Burton et al., 2015; Williams et al., 2002). Additionally, the camera itself could potentially alter the subject's behavior. These effects are likely the same in all treatments and should not affect our interpretation of the results (Meek et al., 2015).

The study was conducted by repeating the same set-up in one area and alternating the order of treatments to control for



**Figure 1** Experimental setup of the GUD and speaker system replicated for two consecutive nights across four treatments that were replicated three times. Three pairs of GUD trays were 15 meters from the road noise speaker and 45 meters from the speaker with all other playbacks. Cameras were set up at three of the trays. GUD, giving-up density.

potential variation due to timing of each experiment. While we were limited by space, future studies may examine treatments concurrently in time over a larger area. During an experimental period, we initiated playbacks at 07:00 h on day 1, placed foraging trays into the field 24 h later at 07:00 h on day 2 (cameras turned on), and trays were first collected and replaced 24 h later at 07:00 h on day 3, and finally collected at 07:00 h on day 4 (camera data collected). We turned off the speakers for 48 h and repeated the experiment for a different treatment. No experiments were conducted during rain. We sifted seeds from the sand and dried at 60°C for 2 h (to control for moisture absorption while in the field) prior to weighing. We recorded 389 videos and observed 738 behaviors.

### Study design and statistics

Experiments proceeded in a randomly selected order of: Predation (P), Control (C), Predation + Road (P + R), Road (R), P + R, P, R, C, P, R, P + R, and C. We collected six GUDs for two consecutive nights in each experiment, thus yielding 144 GUDs (with three discarded due to rain) after three total replicates of each of the four treatments.

To compare food intake among treatments, we analyzed the variation in GUD, that is, weight of seeds eaten by small mammals. We constructed a linear regression model including treatment (C, P, P + R, and R) as the main predictor. We also included replicate ( $n = 3$ ) and night ( $n = 2$ ) as additive predictors, accounting for potential variation among replicates and sampling nights. Additionally, we included moon illumination and date to control for effects of moonlight and environmental confounders across time. Moon illumination was determined by the date of the experiment and retrieved from the R

package *lunar* (function *lunar.illumination*; v.0.1-04), used as a continuous variable. Date was included as a fixed continuous predictor to account for autocorrelation. We could not use mixed effects models for this analyses as all our blocking variables had 3 or less levels, which is far below the suggested minimum of 5 for random effects. In this case, it is suggested to include blocking variables as fixed effects. We tested the model using an ANOVA, and performed a post hoc analyses using the Tukey method *p*-value correction (*emmeans* v. 1.5.2-1). The response variable was log-transformed to approximate a normal distribution of the model residuals. Even so, model residuals were not normally distributed (Shapiro–Wilk normality test;  $P < 0.001$ ) due to outliers. Running the model without outliers ( $N = 10$ ; GUDs that were not eaten, i.e., had a weight of 2.5 g) resulted in normally distributed model residuals (Shapiro–Wilk normality test;  $P = 0.22$ ) and did not change the interpretation of our results. Model residuals were visually checked for heteroscedasticity; no patterns were observed.

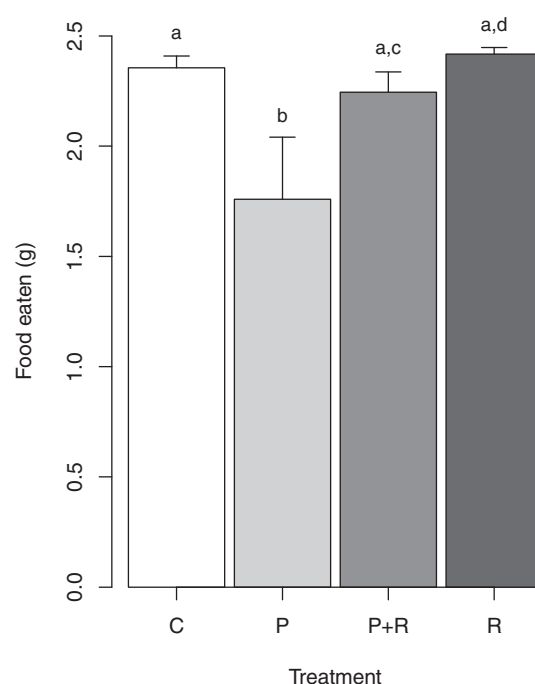
To assess visitation and vigilance behavior recorded from cameras among treatments, we first tested for differences between number of visits and number of vigils between the treatments. The data did not allow us to apply negative binomial regression models, as their number of visits and vigils was too irregular. We instead performed Chi-square tests using the Holm *P*-value correction method for multiple testing (Holm, 1979). Second, to test for differences in average time spent on visits and vigilance between treatments and species (chipmunks and white-footed mice), we constructed negative binomial general linear regression model (*MASS* v. 7.3-53) (Fig. 2c and d). The model included a three-way interaction between playback treatment, behavior, and species as predictor. We also included replicate, night, moon illumination, and date to control for potential variation due to our blocking design and environmental variation across time. Post hoc tests with the Holm-Bonferroni method were performed to compare between groups, where applicable (*emmeans* v. 1.5.2-1). All statistical analyses were performed with R (v. 4.0.3) in Rstudio (v. 1.3.1093).

## Results

### Food intake

We found that treatment had a significant effect on GUDs ( $F_{3,132} = 22.43$ ,  $P < 0.001$ ; Fig. 2). In the risk treatment, small mammals ate 24% less compared to the control treatment ( $t = -4.703$ ,  $df = 132$ ,  $P < 0.001$ ). However, in the risk plus road noise treatment, *T. striatus* and *P. leucopus* ate similar amounts compared to the control treatment ( $t = -1.727$ ,  $df = 132$ ,  $P = 0.314$ ). When exposed to the road treatment, small mammals ate similar amounts compared to the control treatment ( $t = 1.766$ ,  $df = 132$ ,  $P = 0.294$ ) but 26% more compared to the risk treatment ( $t = 6.552$ ,  $df = 132$ ,  $P < 0.001$ ).

Small mammals ate significantly less in the risk treatment compared to the risk + road treatment ( $t = 3.288$ ,  $df = 132$ ,  $P = 0.007$ ), and ate significantly less in risk + road treatment compared to the road treatment ( $t = 3.528$ ,  $df = 132$ ,  $P = 0.003$ ).



**Figure 2** The amount of food (i.e., seeds) eaten at foraging trays by chipmunks (*Tamias striatus*) and mice (*Peromyscus leucopus*) during exposure to four audio playback treatments: control (C), predation (P), predation risk + road noise (P + R), and road noise (R). Arrows indicate 95% confidence interval. Letters denote significant differences between groups ( $P < 0.05$ ).

Small mammals ate significantly less on the second sampling night ( $F_{1,132} = 16.18$ ,  $P < 0.001$ ); however, this effect was the same among treatments ( $F_{3,132} = 0.312$ ,  $P = 0.817$ ). There was no effect of replicate or date on food eaten. With increasing moon illumination mice ate less ( $F_{1,132} = 10.665$ ,  $P < 0.001$ ) but we found no interaction between moonlight and treatment ( $F_{3,132} = 1.441$ ,  $P = 0.234$ ). Both date ( $F_{1,132} = 0.216$ ,  $P = 0.643$ ) and replicate ( $F_{2,132} = 2.163$ ,  $P = 0.119$ ) were not significant. The model fit the data well and had an adjusted  $R^2$  value of 0.39.

### Foraging behavior

Time spent on visits was significantly different between chipmunks and mice, such that chipmunks spent on average 36 s on a visit compared to 21 s in mice, a 43% difference ( $F_{1,721} = 29.099$ ,  $P < 0.001$ ). All comparisons are shown in Tables 1 and 2.

### Chipmunks

We found that overall visitation behavior was significantly different among treatments ( $\chi^2 = 6.70$ ,  $df = 3$ ,  $P = 0.082$ ; Table 1; Fig. 3a). There was no difference in number of visits of chipmunks between risk and control treatment. However, chipmunks visited the trays 46% less in risk plus road treatment compared to the risk treatment. Visitation behavior was

**Table 1** Post hoc test results from chi-squared tests; Holm-Bonferroni correction was applied to obtain *P*-values adjusted for multiple testing (Adj. *P*)

Number of visits						Number of vigils		
Chipmunks			Mouse			Chipmunk		
Contrast	<i>P</i> -value	Adj. <i>P</i>	Contrast	<i>P</i> -value	Adj. <i>P</i>	Contrast	<i>P</i> -value	Adj. <i>P</i>
C – P	1.000	1.000	C – P	0.071	0.283	<b>C – P</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>
C – P + R	0.030	0.147	C – P + R	0.435	0.870	<b>C – P + R</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>
C – R	0.814	1.000	C – R	0.071	0.283	C – R	0.869	0.869
P – P + R	0.030	0.147	<b>P – P + R</b>	<b>0.010</b>	<b>0.063</b>	P – P + R	0.218	0.437
P – R	0.814	1.000	P – R	1.000	1.000	<b>P – R</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>
<b>P + R – R</b>	<b>0.016</b>	<b>0.097</b>	<b>P + R – R</b>	<b>&lt;0.001</b>	<b>0.063</b>	<b>P + R – R</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>

Bold values indicate significant difference between groups (*P*-value < 0.05). Audio playback treatments: control (C), predation (P), predation risk + road noise (P + R), and road noise (R).

**Table 2** Post hoc test results from regression analysis of the audio playback treatments

		Contrast	Ratio	SE	<i>t</i> -ratio	<i>P</i> -value
Time spent on visits	Chipmunk	C – P	0.81	0.22	–0.80	0.856
		C – P + R	0.52	0.16	–2.12	0.149
		C – R	1.13	0.29	0.46	0.969
		P – P + R	0.64	0.17	–1.62	0.367
		P – R	1.40	0.34	1.40	0.503
		<b>P + R – R</b>	<b>2.17</b>	<b>0.60</b>	<b>2.78</b>	<b>0.028</b>
	Mouse	C – P	1.15	0.32	0.50	0.959
		C – P + R	0.52	0.17	–2.05	0.171
		C – R	0.64	0.19	–1.50	0.438
		<b>P – P + R</b>	<b>0.45</b>	<b>0.12</b>	<b>–2.93</b>	<b>0.018</b>
		P – R	0.56	0.13	–2.45	0.068
		P + R – R	1.24	0.36	0.73	0.884
Time spent on vigils	Chipmunk	<b>C – P</b>	<b>0.50</b>	<b>0.10</b>	<b>–3.48</b>	<b>0.003</b>
		C – P + R	0.58	0.13	–2.49	0.062
		C – R	0.73	0.14	–1.58	0.389
		P – P + R	1.16	0.14	1.23	0.610
		P – R	1.46	0.24	2.34	0.091
		P + R – R	1.26	0.22	1.33	0.543

Bold values indicate significant difference between groups (*P*-value < 0.05). Audio playback treatments: control (C), predation (P), predation risk + road noise (P + R), and road noise (R).

similar between the road and control treatment, and between the road and risk treatment.

We also found that the average time spent per visit was significantly different among treatments (Table 2; Fig. 3c). Chipmunks spent a similar amount of time per visit between the risk and control treatments. However, they spent 54% more time per visit in the risk plus road noise treatment compared to the risk treatment. Chipmunks spent on average a total of 1384 s foraging in the control treatment, 1199 s foraging in the risk treatment, 972 s in risk plus road treatment, and 1004 s in the road treatment.

## Mice

We found overall visitation behavior to be significantly different among treatments ( $\chi^2 = 9.90$ , *df* = 3, *P* = 0.019; Table 1; Fig. 3a). Though not significant, mice visited the trays 38% more in the risk treatment compared to the control. However, mice visited the trays 49% less in the risk plus road treatment compared to the risk treatment. Mice tended to visit the trays

38% more in the road treatment compared to the control but this is also not significant. Mice visitation behavior did not differ between the road treatment and risk treatment.

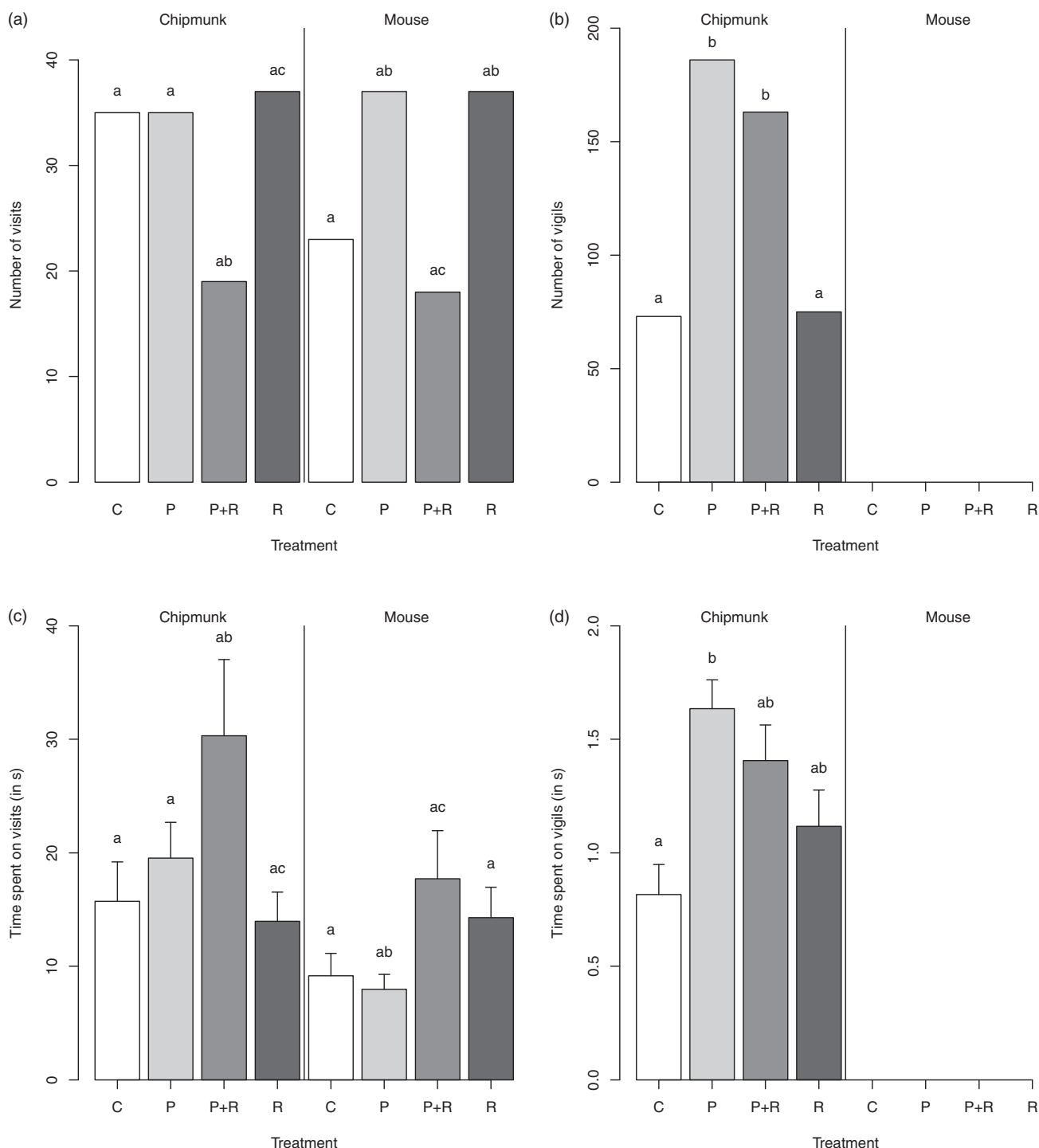
We also found that the time spent per visit was significantly different among treatments (Table 2; Fig. 3c). Mice spent similar amounts of time on visits in the risk treatment compared to the control, and similar amounts of time on visits in the risk treatment compared to the road noise treatment. Mice spent 55% less time per visit in the risk treatment compared to the risk plus road noise treatment. Mice spent on average a total of 448 s foraging in the control treatment, 594 s foraging in the risk treatment, 389 s in risk plus road treatment, and 973 s in the road treatment.

## Vigilance behavior

### Chipmunks

Number of vigils was significantly different among treatments ( $\chi^2 = 83.44$ , *df* = 3, *P* < 0.001; Table 1; Fig. 3b and d).





**Figure 3** Visit and vigilance behavior of eastern chipmunks (*Tamias striata*) and white-footed mice (*Peromyscus leucopus*) at foraging trays during experimental exposure to audio playbacks of control (C), predation risk (P), predation risk + road noise (P + R), and road noise (R). (a) The number of visits to foraging trays from *T. striata* and *P. leucopus*. (b) The number of vigilance events in *T. striata*; no data in *P. leucopus*. (c) The average amount of time spent during visits by *T. striata* and *P. leucopus*. (d) The average time spent being vigilant in *T. striata*; no data in *P. leucopus*. Arrows denote 95% confidence interval. Letters denote significant differences between groups ( $P < 0.05$ ).

Chipmunks displayed 155% more vigils in the risk treatment compared to the control. Chipmunks displayed a 12% decrease in vigils in the risk plus road treatment compared to the risk treatment. Number of chipmunk vigils was not different between the road and control treatment. However, chipmunks displayed a 60% decrease in vigils in the road treatment compared to the risk treatment.

The amount of time spent per vigil was significantly different among treatments (Table 2; Fig. 3d). Chipmunks spent 50% more time per vigil in the risk treatment compared to the control treatment. Chipmunks spent a similar amount of time on vigils in the control treatment compared to the risk plus road noise treatment and the road treatment.

## Mice

We found that mice did not display any recordable vigilance behavior during any of the treatments (Fig. 3b and d).

## Discussion

In this study, we examined how concurrent exposure to road noise and predation risk manipulations altered small mammal foraging and vigilance. Overall, we found that when compared to predation risk alone, *T. striatus* and *P. leucopus* increased their food intake when exposed to road noise, whether in risky (when predation risk playbacks concurrently occurred) or safe (road noise alone) situations. Road noise also had a significant effect on small mammal foraging behavior and vigilance, generally reducing time spent foraging and vigilant in risky situations and reducing time spent foraging but having no effect on vigilance in safe situations. Increasing moonlight also reduced foraging in mice, but had no effect on our overall findings. Generally, our results support our second hypothesis that road noise caused animals to perceive the area as less risky; however, it did cause animals to reduce time spent foraging (but not food intake).

## Food intake

We found small mammals ate significantly less when exposed to predation risk, as compared to the control. However, road noise exposure eliminated this effect: when small mammals were exposed to road noise plus predation risk they ate a similar amount as when exposed to control conditions and road noise alone.

This is different than many other studies examining noise effects, that often find noise reduces animal foraging. For example, Voellmy et al. (2014) found that both sticklebacks and minnows reduced the number of daphnia consumed during noise playbacks. Luo et al. (2015) found that traffic noise reduced Daubenton's bat foraging success and food intake. However, such studies most often examine short-term effects of acute noise exposure (i.e., examining the immediate response of animals to a noise stimuli) and as such may overestimate the effects of noise (Lima & Bedenkoff, 1999; Wolff & Davis-Born, 1997). In such studies, animal responses may represent their response to an acute disturbance of a novel

experience. On the contrary, Francis et al. (2012) found increased foraging and Willems et al. (2021) found no change in mouse trapping success with increased noise. Our study exposed animals for 72 h and measured foraging behavior 24 h after the start of the experiment. As such, our findings may represent a more realistic response of animals to the chronic exposure of noise. Habitat structure, including distance to refuge has been shown to play a part in prey's antipredator behavior, even more so than the type of risk presented (Verdolin, 2006). Woods offer refuge with a steady perceived risk, and thus the decision to forage rather than flee may be tolerated longer (Frid & Dill, 2002). The increase in food intake that we found supports our second hypothesis, that road noise reduces prey's risk perception or masking hypothesis (Chan & Blumstein, 2011; Chan et al., 2010). An alternative explanation may be that road noise reduces actual owl predation (Mason et al., 2016), and small mammals recognize the reduction in risk and increase their foraging. Large birds like owls are sensitive to noise as it may mask acoustic cues of prey (Francis et al., 2012). If these predators do avoid noisy areas, road noise may provide shelter for small mammals. While the driving mechanisms still need to be explored, our findings support the hypothesis that road noise reduces prey's risk response.

We also found mice reduced food intake on nights with greater moonlight illumination. Although we could not differentiate the relative effect on the foraging trays between mice and chipmunks, as chipmunks are diurnal, moonlight should not affect their foraging behavior. Other studies have also found increasing moonlight reduces small mammal foraging and activity (Guiden & Orrock, 2019; Loggins et al., 2019; Prugh & Golden, 2014). Moonlight likely increases the potential for small mammals to be spotted by a predator, and thus, they respond by engaging in anti-predator responses even before encountering a predator (Sheriff et al., 2020a).

## Foraging behavior

Overall, our foraging behavior results did not align with our food intake results. We found that road noise generally reduced total time spent foraging in risky situations but had species specific responses in safe situations: reducing total time spent foraging in chipmunks but greatly increasing total time spent foraging in mice. We would have expected an increase in time spent foraging when animals were exposed to road noise given our food intake results. Thus, it is likely that road noise altered the foraging performance of animals, particularly in risky situations; reducing the time spent foraging but increasing food intake. While other studies have examined foraging behavior under noise exposure, few have concurrently examined behavior and outcome (i.e., food intake). Luo et al. (2015) found that Daubenton's bats foraged less in noisy environments. Purser and Radford (2011) found that three-spined sticklebacks exposed to noise had decreased foraging efficiency, although there was no significant change in food intake compared to controls. In laboratory rats exposed to predation risk, Chaby et al. (2015) found that animals also altered their foraging performance, reducing visitation number to foraging patches but increasing food intake. By measuring multiple aspects of

foraging, our findings on road noise effects becomes much more complex. It is possible that small mammals fear road noise, and as such reduce their use of foraging patches, but increase their overall food intake while foraging. However, our results from road noise alone treatments as compared to control treatments do not support the explanation that small mammals fear road noise as the risk disturbance hypothesis suggests. Alternatively, as we originally proposed, road noise may reduce small mammal perception of risk and therefore increase their foraging efficiency (i.e., food intake per foraging bout) because they reduced their assessment of risk (vigilance) during road plus risk treatments (as compared to risk alone).

## Vigilance behavior

We found that road noise significantly increased vigilance behavior in chipmunks but not in mice – we actually did not observe any vigilance behavior in mice, potentially due to mice not being vigilant or because our set-up failed to record such behavior. Other studies found similar increases in vigilance. For example, Quinn et al. (2006) found chaffinches increased vigilance when exposed to background noise. Shannon et al. (2014) also saw an increase in prairie dog vigilance in response to road noise. In the absence of risk, we found chipmunks exposed to road noise alone had similar vigilance (time per vigil) as compared to control treatments. We also found vigilance was greater in the road noise plus risk treatment as compared to the control; however, it was reduced in this treatment compared to the risk treatment alone (both number of vigils and time spent per vigil). Thus, while road noise did not alter vigilance in the absence of risk (road noise compared to controls), it reduced vigilance in the presence of risk (road noise plus risk compared to risk). We suggest that road noise may reduce prey's perception of risk (thus, reducing vigilance during risky times – leading to increased foraging efficiency), but prey do not perceive road noise as risky itself.

We found that mice did not engage in vigilance behavior at all. This discrepancy between the species may be due to their life history differences. Chipmunks are a diurnal species and rely on visual detection of predators (Wall & Peterson, 1996). Whereas, white-footed deer mice are primarily a nocturnal species and as such, likely rely more heavily on auditory detection of their predators as eyesight is poor (Ohlemiller et al., 2016). These differences may also be related to the different response in foraging behavior. For example, heightened mouse hearing may have allowed them to distinguish safety better than chipmunks during road noise playbacks, leading them to alternate responses. Unfortunately, our approach did not allow us to measure auditory vigilance in mice, though they likely rely on it much more. In future studies, this limitation needs to be addressed to better our understanding of how road noise may alter mouse vigilance.

## Conclusion

Overall, our findings suggest that road noise reduces small mammal perception of predation risk (our second hypothesis);

resulting in increased food intake and influencing their foraging performance and vigilance. Such noise-induced effects could have severe consequences to the population dynamics of small mammal prey and their predators if such changes in behavior alter their survival. While other studies have found that road noise reduces the ability of predators to kill prey (Siemers & Shaub, 2011), our study shows that road noise may reduce the ability of prey to appropriately detect and respond to their predators (e.g., the overall reduction in vigilance).

This is the first study to examine how chronic road noise alters small mammals' responses to predation risk over multiple days. Predation risk and disturbance are most often studied separately and disturbance manipulation is often provided as only an acute exposure. Future studies are needed that concurrently manipulate chronic noise exposure and predation risk to examine prey response and predator–prey interactions. In particular, studies examining prey dispersal and survival are of critical importance, as are community based studies that examine hunting success (given the potential impact on both predators and prey), and prey and predator population dynamics. Through this work, we highlight an issue of global importance as humans expand and develop land around the world, and our findings add an understanding of prey's ability to respond to risk under chronic conditions of increased noise.

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