Effects of red fox urine on foraging behavior in forest and residential populations of nocturnal rodents

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Abstract – Rodents perceive odors exuded by mammalian predators, and may alter foraging behaviors based on such information. The literature is mixed, however, and the extent to which wild rodents actually rely on olfaction to assess predation risk is not known. Aversion to predator scents may be innate or learned, and few studies have considered the potential importance of previous experience in determining rodent reactions to scent cues. We measured the effects of red fox (*Vulpes vulpes*) urine on the foraging activity of nocturnal rodents at track plates baited with sunflower seeds. To test the influence of previous experience, we set track plates both in areas close to human habitation (where rodents are presumably "predator naïve"), and in forest habitats where active predation by mammalian carnivores is likely. In both areas, a urine treatment and a scentless control were alternated in nightly trials. We discovered a significant difference between forest and residential populations of rodents in their response to red fox urine, though urine treatments did not differ from control treatments within either area. The difference in response to urine treatments was opposite of expected, with residential rodents significantly less active at urine-treated track plates than forest rodents.

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INTRODUCTION

Rodents are capable of detecting mammalian predators by scent. A review of the literature by Apfelbach et al. (2005) indicates that at least twenty-nine species representing seven rodent families respond to odors derived from the fur, feces, urine, or anal glands of predators (Table 1). Behavioral responses to predator scent include: initiation of defensive strategies such as immobility or retreat (Jedrzejewski et al., 1993), inhibition of foraging (Koivisto and Pusenius, 2003), reduction of normal scent-marking behaviors (Roberts et al., 2001), and avoidance of affected areas (Dickman, 1992; Jedrzejewski et al., 1993; Herman and Valone, 2000).

Rodent aversion to coyote (*Canis latrans*) urine is most intense when the urine contains a high proportion of sulfur compounds, which indicate the amount of meat in a coyote's diet (Nolte et al., 1994). This suggests that prey broadly identify *meat-eaters* – rather than specific predators – via olfaction. However, reactions unique to particular rodent-predator systems have also been demonstrated. In an experiment by Jedrzejewski et al. (1993), wild-caught bank voles (*Clethrionomys glareulus*) used scent cues to recognize and avoid cages in which one of several predators (including *Mustela erminea, M. nivalis, M. putorius*, and *Vulpes vulpes*) had recently been present. When the weasel scents were perceived, voles abandoned plastic and rubber tubes (simulating burrows) in favor of above-ground refuge on twigs (simulating shrubs). Fox scent caused voles to abruptly cease activity and become immobile on the ground.

The role of scent cues in determining wild rodent behavior is not well understood. In general, effects of predator scent appear to be strongest and most consistent in laboratory experiments (Herman and Valone, 2000), while free-living rodents may respond weakly or not at all (Thorson et al., 1998; Orrock et al., 2004; Fanson, 2010). Experimental results vary from rodent to rodent and predator to predator, and may depend on the origin of the odors tested (e.g. fur, feces, urine, or anal scent glands), the amount of odor used, and the context in which odors are presented (Dickman, 1992; Apfelbach et al., 2005).

Previous exposure of the focal rodents to actual predation may be important: Dickman (1992) found that house mice (*Mus domesticus*) are indifferent to red fox (*Vulpes vulpes*) and cat (*Felis catus*) feces unless these are presented in conjunction with the predators themselves, after which mice avoid the scents.

We tested predator-scent avoidance in wild populations of nocturnal rodents in northern Michigan. Foraging activity was measured at track plates baited with sunflower seeds. A cotton ball soaked in red fox urine was suspended on a flag near the track plate in scent treatments, and a flag without cotton or urine was used as a scentless control. Track plates were located both in forested areas where predation on rodents by mammalian carnivores is likely, and in a human residential area were carnivores (both wild and domesticated) are not found. Statistical analyses were performed to compare the inhibitive effects of fox urine on foraging activity in these two areas. Based on the conclusions of Dickman (1992), we hypothesized that "predator naïve" rodents living near human habitation would exhibit a weak response to fox urine compared with "predator savvy" populations in the forest.

MATERIALS AND METHODS

Study Location

The experiment was conducted at The University of Michigan Biological Station (UMBS), a seasonal research and teaching facility on the south shore of Douglas Lake in Cheboygan County, Michigan. Station property includes 4047 hectares of forested land and a residential campus with cabins and labs. Summer populations of around 200 people are normal at UMBS, and small mammals living within camp are habituated to humans. White-footed mice (*Peromyscus leucopus*) move about openly in occupied cabins. Other local rodents include: diurnal tree and ground squirrels (*Sciurus carolinensis*, *Tamiasciurus hudsonicus*, *Tamias striatus*, *Spermophilus tridecemlineatus*), nocturnal flying squirrels (*Glaucomys volans*), and voles (*Microtus pennsylvanicus*). Soricopmorphs occurring at UMBS include shrews (*Sorex*

cinereus, *Blarina brivicauda*) and moles (*Scalopus aquaticus*, *Condylura cristata*). Raccoons (*Procyon lotor*) are common, and visited our track plates on several occasions. Tree communities in and around camp are typical of northern Michigan successional forest and forest-edge, with aspens, birches, and maples predominating and pines occurring intermittently.

Track plates were located either within the residential campus (Camp), or approximately 1.5km to the west on Grapevine Point (Forest). Three sites in each area were utilized. In both Camp and Forest areas, track sites were separated from each other by a distance of at least 100m. Distances from Douglas Lake varied by site but did not exceed 300m.

Sites in Camp were located near cabins, labs, and regularly trafficked foot paths. They varied somewhat in the amount of vegetative cover available to foraging rodents, but were always more exposed than Forest sites. Forest sites were located in a stand of mature aspens with a sparse understory of young maple. Leaf litter was uniform across the forest floor, and proximity to fallen logs and other cover was similar at all Forest sites.

Rodent communities in Camp and Forest were comparable. The white-footed mouse *Peromyscus leucopus* is the most abundant nocturnal rodent everywhere in the region (Myers et al., 2009), and accounted for most of the tracks collected at both Camp and Forest plates. The meadow vole *Microtus pennsylvanicus* was likely rare in Camp (sites offered marginally-acceptable habitat for meadow voles) and totally absent in the Forest. No vole tracks were positively identified at any track plate, and it is unlikely that differences in the density of *Microtus* affected our results.

Track Plates

Track plates were aluminum sheets (0.57m X 0.76m) with white contact paper (0.46m X 0.27m) centered on the aluminum and attached adhesive-side up (Fig. 1). A solution of blue carpenter's chalk in 97% isopropyl alcohol was used as tracking medium. With a foam paintbrush, we applied the medium in a thin, even layer to the 0.15m wide region of exposed aluminum on all sides of the contact paper.

Black-oil sunflower seeds were weighed to 150g and placed at the center of the track plate in a shallow, open plastic container. Rodents crossing the aluminum picked-up chalk, which was then deposited on the contact paper registering a reasonably high-fidelity footprint.

The predator scent used was red fox (*Vulpes vulpes*) urine obtained from Jay's Sporting Goods in Gaylord, Michigan (Jay's Sporting Goods in-house brand). We stored the urine in a refrigerator prior to use. In scent treatments, a urine-soaked cotton ball was suspended 0.3m above ground on a flag located at one corner of the track plate. In control treatments, a flag without cotton or urine was used.

Trials started between 9 and 10pm and ended between 6:30 and 7:30am. This interval was selected to minimize the presence of *Tamias striatus* – a diurnal food-hoarder – and maximize the presence of *Peromyscus leucopus* and other nocturnal rodents. At the start of each trial, a clean sheet of contact paper was attached to the plate and a fresh layer of tracking medium was applied. Trials began when the plate was baited and (in scent treatments) the urine was introduced. At the end of each trial we collected the contact paper and any uneaten seeds. Nine nights of trials were conducted at each of the six sites, though some data were rendered unusable by rain. In all, twenty-three track-nights were collected.

Tracks were roughly identified as Raccoon, Large Squirrel (*S. carolinensis*), Small Squirrel (*T.striatus*, *S. tridecemlineatus*, *T. hudsonicus*, *G. volans*) or Mouse (*Peromyscus leocopu*s). No shrew or vole tracks were positively identified at any track plate, but it is possible that these animals were present. Any shrew or vole tracks that went unrecognized are included in the Mouse category.

Data Analysis

We counted total tracks for each category and calculated tracks/minute based on the start and stop times of the trial. We also weighed the uneaten seeds and calculated the mass of seeds consumed per minute of trial. Statistical tests (One-Way ANOVA and Tukey's post-hoc) were performed using SPSS (SPSS Inc.) to determine differences in tracks/minute and seeds/minute consumed between controls

and treatments and between Camp and Forest sites. A Pearson correlation was used to determine whether results were correlated with date. This was important because a significant correlation with date would indicate that rodents became habituated to scent treatments over the course of the experiment.

RESULTS

Tracks Per Minute

We compared mean tracks/minute values between four separate treatments: Forest Control, Forest Red Fox, Camp Control, and Camp Red Fox. To isolate any species-unique effects, we ran a separate One-Way ANOVA for each category of tracks.

Mouse: In the Mouse category, tracks/minute means differed significantly (One-Way ANOVA; $F=4.428$; $p=0.016$). Tukey's post-hoc analysis revealed that the Forest Red Fox mean was significantly greater than the Camp Red Fox mean ($p=0.009$). All other Tukey's comparisons within Mouse were non-significant. Means for the Mouse category are illustrated in Figure 2.

Small Squirrel: Tracks/minute means did not differ significantly (One-way ANOVA; $F=0.314$; $p=0.815$). All Tukey's post-hoc comparisons were non-significant. Means for the Small Squirrel category are illustrated in Figure 3.

Large Squirrel: Tracks/minute means did not differ significantly in the Large Squirrel category (One-Way ANOVA; $F=1.145$; $p=0.357$). All Tukey's post-hoc comparisons were non-significant. Means for the Large Squirrel category are illustrated in Figure 4.

Raccoon: Tracks/minute means did not differ significantly in the Raccoon category (One-Way ANOVA; F=2.701; p=.075). Tukey's post-hoc analysis revealed that the tracks/minute mean for Forest Control was greater than that for Camp Control, but this difference was only marginally significant (p=0.058). All other Tukey's comparisons within Raccoon were non-significant. Means for the Raccoon category are illustrated in Figure 5.

Mass of Seeds Consumed Per Minute

We also compared mean seeds/minute values between the four treatments. Tukey's post-hoc tests showed that means for Forest Control and Camp Red Fox were significantly higher than the mean for Camp Control (p=0.022 and p=0.048, respectively). All other Tukey's post-hoc comparisons were non-significant. Seeds/minute means are illustrated for all treatments in Figure 6.

Correlation Analysis

A correlation analysis of the entire data set plus date revealed no significant correlation of tracks/minute or seeds/minute with date (Pearson correlation; r=0.390; N=23; p≥0.313). Seeds/minute was positively correlated with Raccoon tracks/minute (r=0.482; N=23; p=0.02).

DISCUSSION

Mice in camp were significantly less active at urine-treated track plates than were mice in the forest. This implies that mice *did* notice the scent of fox urine, and that Camp mice and Forest mice differed in either the nature or the intensity of their response to it. In neither area, however, was there a significant change in mouse activity between urine treatment and scentless control. This implies that mice in general *were not* sufficiently motivated to forgo feeding.

The observed difference in mouse activity between Camp and Forest scent treatments is inconsistent with a major prediction of our hypothesis. We expected that Camp mice, which are protected from fox

predation by their proximity to humans, would be more willing to feed near a urine-soaked cotton ball than Forest mice. The opposite was true. One explanation for this result is that Forest mice, having had previous experience with foxes, can tell the difference between fresh scent and refrigerated urine. Predator naïve camp mice may have reacted instinctively to the urine and avoided it, even though it was not fresh.

Another possible explanation is suggested by the fact that Camp track plates were relatively more exposed than Forest track plates. Previous studies show that rodents prefer to forage in areas where plant cover is heavy and visibility is low (Thorson et al., 1998; Herman and Valone, 2000; Orrock et al., 2004; Fanson, 2010). In control treatments, activity was no lower in Camp than at Forest sites. This suggests that Camp rodents were not especially inhibited by the less-secure microhabitat. When predator scent was perceived, however, Camp mice may have been unwilling to move in the open.

We also observed a difference in seed consumption between all Forest treatments and the Camp control. This result is explained by differences in the intensity of raccoon activity in the Forest and in Camp. Across all sites, there was a positive correlation between raccoon tracks/minute and seeds/minute consumed. This relationship makes sense, given the greater size and metabolic requirement of raccoons compared to the small rodents feeding at our track plates. Forest Control and Forest Red Fox were the treatments with the highest mean raccoon activity. Camp Control was the one treatment were raccoons were never present. This discrepancy easily accounts for the significantly lower seeds/minute values recorded in Camp.

Our results suggest that small rodents do pay attention to the presence or absence of predator odors, but that the effect of scent cues on rodent behavior is not clean cut. In particular, the importance of microhabitat and the affects of past experience deserve to be better understood.

ACKNOWLEDGEMENTS

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Table 1

Rodent taxa in which a response to predator scent has been demonstrated experimentally. *After Apfelbach et al., 2005.*

Family	**Subfamily**	**Genus**	**Species**
Aplodontiidae		Aplodontia	*A. rufa*
Castoridae		Castor	*C. canadensis*
			C. fiber
Caviidae		Cavia	*C. porcellus*
Cricetidae	Arvicolinae	Arvicola	*A. terrestris*
		Clethrionomys	*C. glareolus*
			C. rufocanus
		Microtus	*M. agrestis*
			M. arvalis
			M. montanus
			M. oeconomus
			M. pennsylvanicus
	Cricetinae	Cricetulus	*C. triton*
		Mesocricetus	*M. auratus*
		Phodopus	*P. campbelli*
	Neotominae	Peromyscus	*P. maniculatus*
Geomyidae		Thomomys	*T. talipoides*
Heteromyidae		Dipodomys	*D. merriami*
Muridae	Deomyinae	Acomys	*A. cahrinus*
	Murinae	Apodemus	*A. sylvaticus*
		Melomys	*M. cervinipes*
		Mus	*M. domesticus*
			M. musculus
		Pseudomys	*P. albocinereus*
		Rattus	*R. exulans*
			R. fuscipes
			R. norvegicus
			R. rattus
		Uromys	*U. caudimaculatus*

LIST OF FIGURES

Figure 1. Diagram of a baited track plate with red fox scent. An aluminum sheet was painted with tracking medium (carpenter's chalk and isopropyl alcohol), and tracks were collected on white contact paper centered on the aluminum and attached adhesive-side up. Red Fox urine was soaked into a cotton ball and placed on a flagpole at the corner of the plate. In control treatments, cotton ball and scent were not used.

Figure 2. Mean Mouse tracks per minute for each treatment group. Error bars represent $\pm$ 1 SE. Difference between treatments is significant (One-Way ANOVA; p=0.016). Forest Red Fox was significantly greater than Camp Red Fox (Tukey's post-hoc; p=0.009). All other comparisons were non-significant (p>0.251).

Figure 3. Mean Small Squirrel tracks per minute for each treatment group. Error bars represent $\pm$ 1 SE. Treatments did not significantly differ in Small Squirrel tracks per minute (One-Way ANOVA; p=0.815).

Figure 4. Mean Large Squirrel tracks per minute for each treatment group. Error bars represent $\pm$ 1 SE. No large squirrel tracks were counted in Forest Red Fox or Forest Control treatments, even though *Sciurus carolinensis* was commonly observed near Forest track sites. Treatments did not significantly differ in Large Squirrel tracks per minute (One-Way ANOVA; p=0.357).

Figure 5. Mean Raccoon tracks per minute for each treatment group. Error bars represent $\pm$ 1 SE. No raccoon tracks were counted for Camp Control treatments. Treatments did not significantly differ in Raccoon tracks per minute (One-Way ANOVA; p=0.075).

Figure 6. Mean mass of seeds (in grams) consumed per minute for each treatment group. Error bars represent $\pm$ 1 SE. Treatments differed significantly in mass of seeds consumed per minute (One-Way ANOVA; p=0.012). Forest Control was significantly greater than Camp Control (Tukey's post-hoc; p=0.022) and Forest Red Fox was significantly greater than Camp Control (p=0.048). All other comparisons were non-significant (p>0.109).

Figure 1.

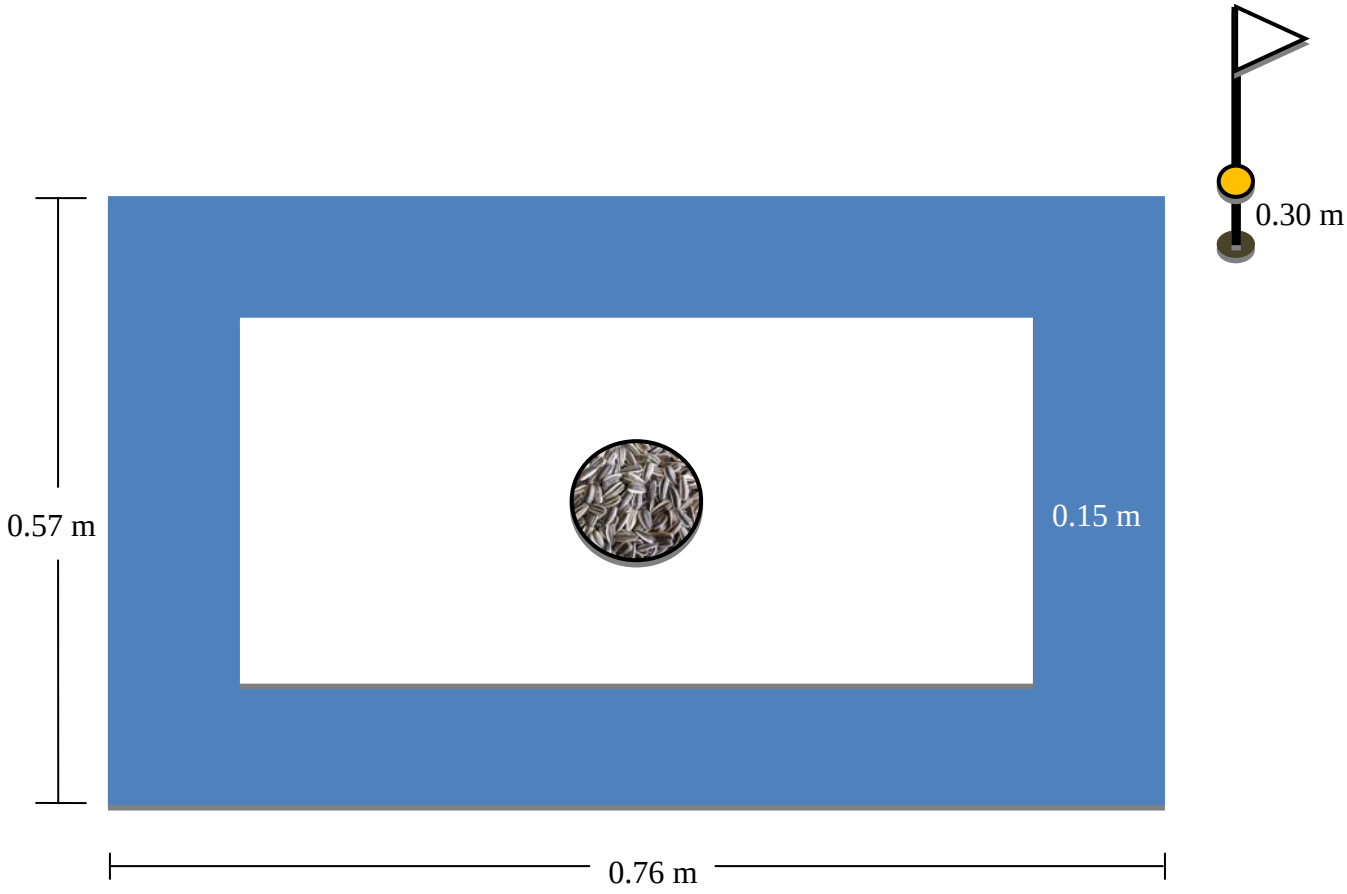


Figure 2.

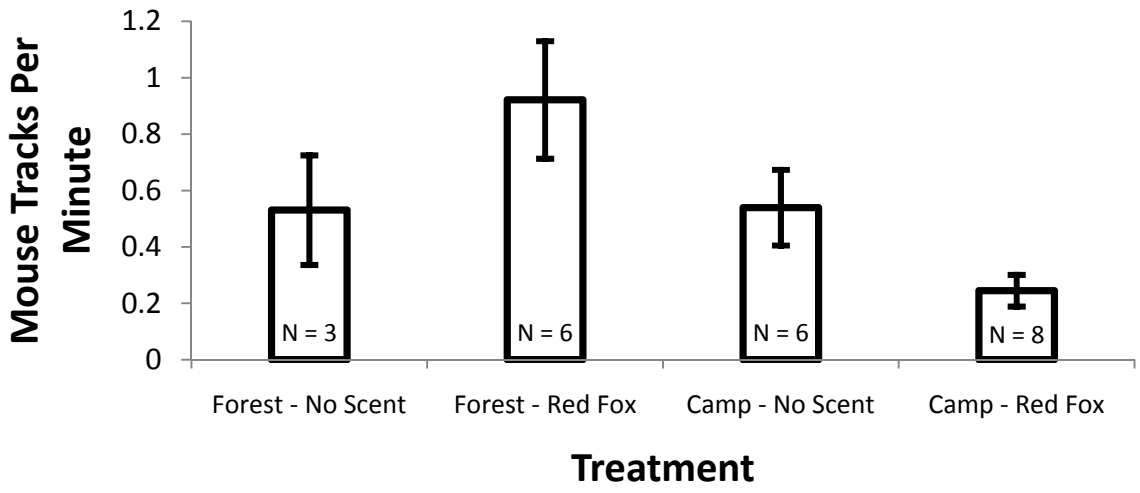

Mouse Tracks Per Minute
1.2
1
0.8
0.6
0.4
0.2
0
N = 3
N = 6
N = 6
N = 8
Forest - No Scent
Forest - Red Fox
Camp - No Scent
Camp - Red Fox
Treatment

Figure 3.

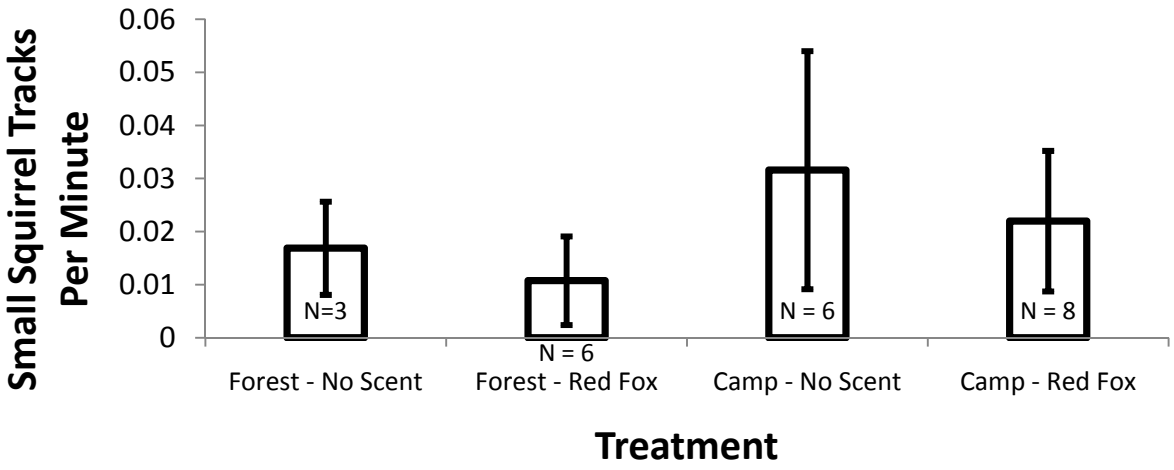

Small Squirrel Tracks Per Minute
0.06
0.05
0.04
0.03
0.02
0.01
0
N=3
N = 6
N = 6
N = 8
Forest - No Scent
Forest - Red Fox
Camp - No Scent
Camp - Red Fox
Treatment

Figure 4.

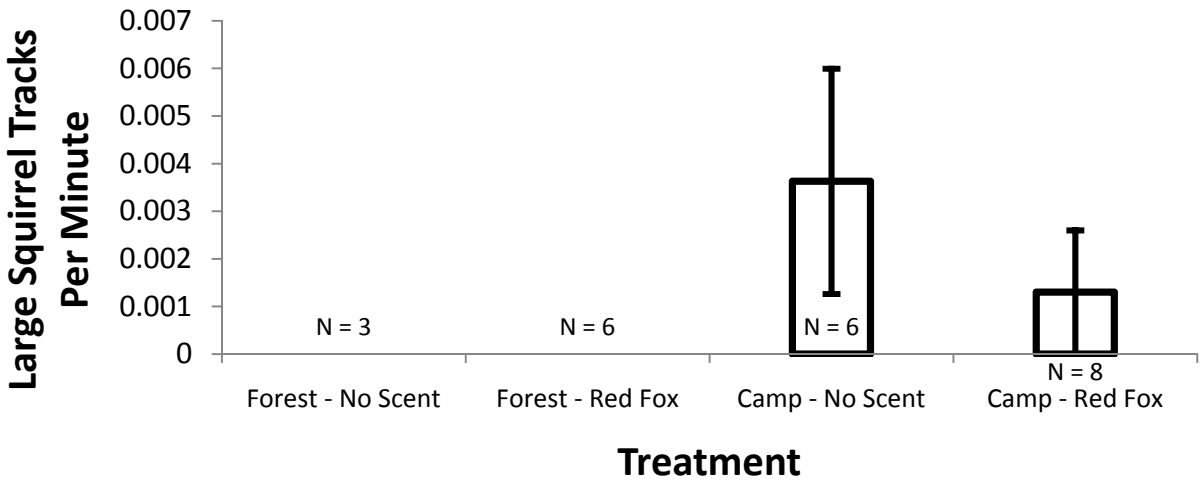

Large Squirrel Tracks Per Minute
0.007
0.006
0.005
0.004
0.003
0.002
0.001
0
N = 3
N = 6
N = 6
N = 8
Forest - No Scent
Forest - Red Fox
Camp - No Scent
Camp - Red Fox
Treatment

Figure 5.

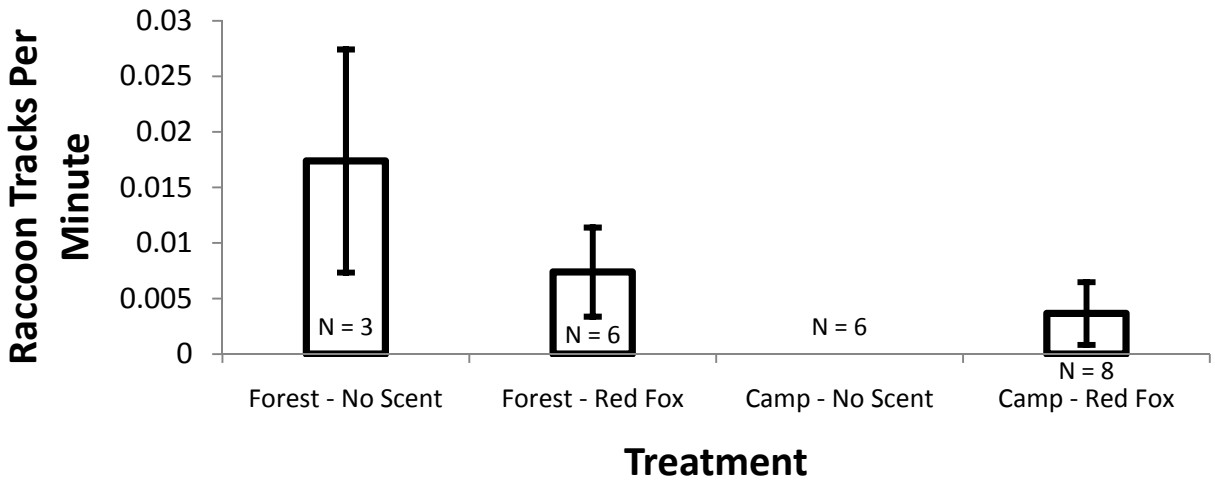
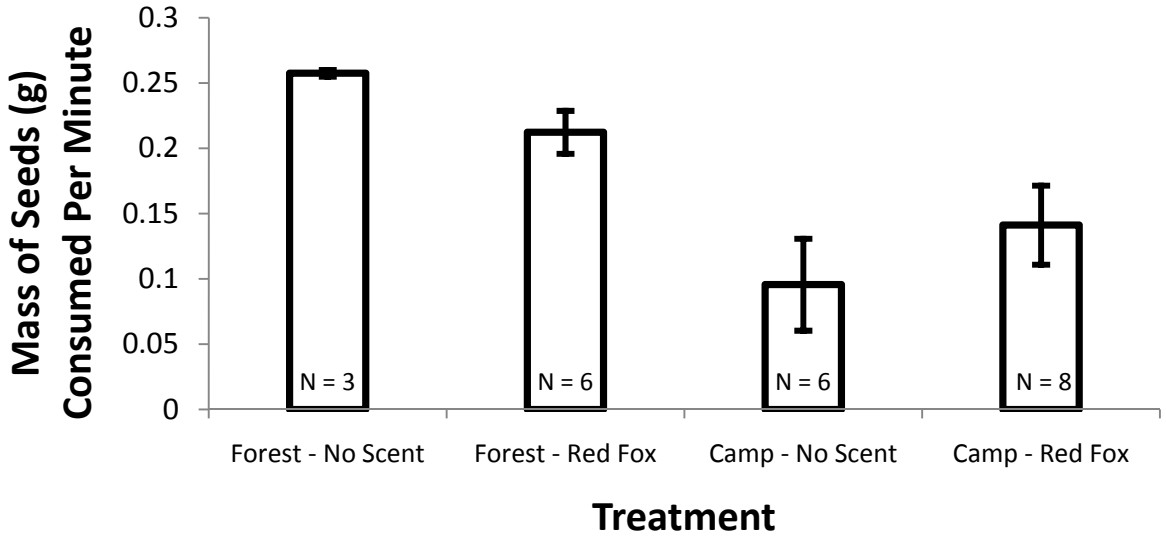

Raccoon Tracks Per Minute
0.03
0.025
0.02
0.015
0.01
0.005
0
N = 3
N = 6
N = 6
N = 8
Forest - No Scent
Forest - Red Fox
Camp - No Scent
Camp - Red Fox
Treatment

Figure 6.


Mass of Seeds (g) Consumed Per Minute
0.3
0.25
0.2
0.15
0.1
0.05
0
N = 3
N = 6
N = 6
N = 8
Forest - No Scent
Forest - Red Fox
Camp - No Scent
Camp - Red Fox
Treatment