Change in resource consumption and selectivity of food types by nocturnal rodents as a result of direct and indirect cues of predation risk

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Abstract

The purpose of this study was to examine the effect of seed quality and predation risk on the foraging behavior of nocturnal rodents and determine whether diet selection is influenced by both direct and indirect cues of predation risk. Two types of sunflower seeds, black oil and striped, were used to study the influence of seed quality. Predator urine and lack of vertical cover were used as direct and indirect cues of predation risk, respectively. Foraging choices of nocturnal rodents were evaluated based on giving-up densities (GUDs), the amount of food remaining in feeding trays. Rodents fed more in the covered trays than in the open trays and consumed more black oil than striped sunflower seeds. They did not respond to the coyote urine, but they consumed fewer seeds and became more selective when mink urine was added around the stations. Because this response was only observed in open trays, it may be due to the combined effect of the direct predation risk cue, the mink odor, and the indirect cue, the lack of microhabitat cover. There was a lag in the response of the prey to the removal of the mink urine from the stations, because of site assessment and association or residual odor. Last, there was evidence that rodents carried seeds from the open trays to covered trays.

Introduction

Natural selection favors the optimal behavioral alternative, whose benefits outweigh its costs by the greatest amount. This theory applies to various aspects of animal behavior, including foraging. Two foraging strategies have been

proposed for fitness maximization (Schoener 1971). The first one is the energy maximization strategy, which states that foragers maximize their net energy gain for a given time spent feeding (Schoener 1971). These are animals whose potential reproductive success is positively correlated with their net energy gain (Hixon 1982). The second one is the time minimization strategy, according to which animals feed until they meet a given energy requirement (Schoener 1971). Any additional food intake after this minimum energy is gained does not increase potential reproductive success (Hixon 1982). Foragers employ this strategy when it is more beneficial to spend time avoiding predators and engaging in other behaviors than it is to continue feeding.

Prey animals may sacrifice energy gain for safety by foraging in areas with the highest perceived safety, even though these patches may be less energetically rewarding (Altendorf et al. 2001, Brown 1988, Goodenough et al. 2001, Lima and Dill 1990). Variation in patch quality and predation risk influences the balance between safety and energy gain, thereby affecting foraging decisions (Brown 1988, Pyke 1984). Determining how prey perceive predation risk remains a challenge for behavioral ecologists (Frid et al. 2007, Lima and Steury 2005, Schmidt et al. 2008, Thorson 1998). Without physically encountering or directly observing a predator, prey may use cues to determine the immediate level of predation risk (Thorson 1998). A predation risk cue is considered direct when prey encounter a cue that indicates a predator is present (Galef and Whiskin 2006). This includes predator vocalizations (Schmidt 2006) and olfactory cues, such as urine and feces (Orrock et al. 2004, Powell and Banks 2004). An indirect

cue is an environmental factor that increases the probability that the prey will be killed in the case of an attack (Galef and Whiskin 2006). Habitat cover, precipitation, and moon illumination are examples of indirect cues of predation risk (Leaver and Daly 2003, Orrock et al. 2004, Powell and Banks 2004).

Giving-up densities (GUDs) are commonly used as measures of the foraging activity of rodents (Bouskila 1995, Herman and Valone 2000, Kotler et al. 1991, Morris and Davidson 2000, Orrock et al. 2004, Powell and Banks 2004, Shaner et al. 2007, Thorson et al. 1998). GUD is the amount of food remaining in feeding trays. At that food density, there is a balance between energetic gain, metabolic costs of the foraging activity, risk of predation, and missed fitness opportunities (Powell and Banks 2004).

When predation risk changes, prey might respond by altering not only the amount of resources consumed, but also their selection of food types, if more than one food type is present in a patch (Shaner et al. 2007). There are two competing hypotheses that explain foraging behavior at different degrees of predation risk. The "higher requisite profit" model predicts that as the threat of predation increases, prey animals become more selective about the nutritional quality of the food they consume. This is because less profitable items no longer cover the increased cost of predation risk, so they are dropped from the diet (Leaver and Daly 2003). By comparison, the "reduced finickiness" model suggests that increased risk leads to decreased selectivity, because more extensive assessment and search behavior are associated with selectivity; this prolongs the exposure of foragers to predation risk (Leaver and Daly 2003).

The purpose of this study was to examine the effect of seed quality and predation risk on the foraging behavior of nocturnal rodents and determine whether diet selection is influenced by both direct and indirect cues of predation risk. Two types of sunflower seeds, black oil and striped, were used to study the influence of seed quality. The former provide a higher fat and protein gain per unit handling time. Lack of vertical cover in the microhabitat was used as an indirect cue of predation risk (Leaver and Daly 2003, Orrock et al. 2004). Predator urine placed around feeding trays was used as a direct cue of predation risk. I used urine from a canid species, *Canis latrans*, and a mustelid species, *Mustela vison*, to test whether different types of predators have a different effect on rodent foraging behavior.

The first hypothesis tested was that foragers will consume less food in the presence of predator odors, because the marginal value of food will decline as predation risk increases. My second hypothesis was that prey would become less selective of food types in the presence of predator odor, as proposed by the "reduced finickiness" model. This behavior is related to the time minimization strategy proposed by Schoener (1971); decreasing the time that foragers spend feeding reduces exposure to predators. My third hypothesis was that the presence of vertical cover would reduce the effect of predator odor on foraging behavior; therefore GUDs would increase more in the absence of vertical cover. Increased foraging has been observed in the presence of vertical cover, because it offers protection from aerial predators (Szewczyk, unpublished).

Even though other studies have examined the individual effect of seed quality, habitat, and predator odor on rodent foraging behavior (Arcis and Desor 2003, Leaver and Daly 2003, Orrock et al. 2004, Powell and Banks 2004), their combined influence has not been previously studied. This research provides important information about foragers' response to simultaneous changes in patch quality, habitat structure, and predation risk.

Methods

Foraging choices of nocturnal rodents were evaluated based on GUDs of the two seed types (Brown 1988). A repeated-measures, before-after-control-treatment (BACI) design (Scheiner and Gurevitch 2001) was used to evaluate the effect of seed quality, microhabitat cover, and olfactory predator cues (Fig. 1) on rodent foraging in artificial patches (i.e., trays filled with sand and seeds). A BACI experiment was conducted for each of the two predator odor treatments. I conducted all experiments at one site, rather than at several sites, because large habitat differences could affect foraging behavior. Even though there was some habitat heterogeneity within my field site, I am assuming that it will not affect my results, since it has previously been shown that habitat-wide vegetation structures, such as ground and canopy cover do not influence rodent foraging behavior (Seilie, unpublished). I did not apply all of the treatments at the same time in the same site, because predator odor could have diffused to stations where it was not intended to be present. The distance required between trays of different treatments to prevent this diffusion of predator odor is not clearly known (Conover 2007).

Study Area and Experimental Design. The study was conducted in a mixed deciduous forest on the University of Notre Dame Environmental Research Center (UNDERC) property in the Upper Peninsula of Michigan. Nocturnal foragers present in this area include white-footed mice (*Peromyscus leucopus*), deer mice (*Peromyscus maniculatus*), meadow voles (*Microtus pennsylvannicus*), southern red-backed voles (*Myodes gapperi*), and southern flying squirrels (*Glaucomys volans*). The two *Peromyscus* species are the most abundant rodents in the field site (Cramer, unpublished).

The field site contained 30 open trays and 30 trays with vertical cover provided by a shade cloth screen suspended 20 cm above the feeding tray (Figs. 2 and 3). This offered protection from aerial predators, such as owls. Previous studies have used vegetative cover, such as small trees or shrubs, as a shelter for the trays (Leaver and Daly 2003, Orrock et al. 2004). For my study, however, I used artificial cover because it can be standardized across stations, avoiding variability caused by different sizes and species of vegetation that provide different types of vertical and horizontal cover.

Pairs of open and covered trays were placed 50 m apart throughout an area with uniform habitat features, including vegetation type and density (Fig. 3). These plastic cafeteria trays were filled with 1.5 L of sand and 7.50 ± 0.02 g of each of the two seed types distributed evenly in the trays. The seeds were heated in a microwave oven for 2 minutes before use to prevent germination (Bouskila 1995, Leaver and Daly 2003). I added seeds to the feeding trays within 30 minutes of sunset and I collected and weighed uneaten seeds the following

morning right after sunrise. The first three nights of the study, seeds and sand were placed in trays at the site to allow the animals to acclimate to the trays. After this pre-baiting period, the odor-free experiment was repeated for two more nights prior to the application of the predator-odor risk treatment. Three days were planned for each trial, but fewer were run due to rain. After the trials with odor, GUDs were measured for additional days with no odor present (Fig. 1)

For the predator-odor risk treatments, scent dispensers were placed on two sides of each tray. The dispensers consisted of a plastic film canister with a cotton swab to which 1 mL of predator urine was added. I used coyote urine in the first predator-odor risk experiment and mink urine in the second experiment (Fig. 1). Between the two odor treatments, GUDs were measured with no odor present. These periods of no predator odor were essential because multiple visits of rodents may facilitate site assessment and association due to learning. This method also mitigated potential problems caused by residual odor between treatments. During these odor-free intervals, GUDs were expected to return to pre-treatment levels. Because of complete consumption of seeds in several stations during the coyote odor treatment, 250 mL of a 50:50 mixture of black oil and striped sunflower seeds were scattered around each station as augmentation during the mink odor experiment (including pre-, during, and post- odor treatments). This was done to reduce the marginal value of the seeds in the trays and thereby increase the GUDs to a measurable level.

During the collection of seeds from feeding trays every morning, I observed that there were more empty shells in the covered trays compared to the open ones.

I speculated that the rodents were carrying the seeds from the open trays and consuming them at the covered trays, or other places that were perceived to be safer. To test whether this was occurring, I painted all the seeds that were placed in the open trays, using colorless blacklight paint (Starlight and Magic, Inc, Invisible Blacklight Paint, Lexington, KY). Based on a measured sample of painted seeds, a negligible weight (0.240 ± 0.093 g) was added to the seeds without affecting the shell thickness or texture. Therefore, the thin paint coating should not have influenced handling time by the rodents. This experiment was done on the last odor-free night of the study period, after the mink odor experiment. After the uneaten seeds and shells were collected, they were examined with a UV transilluminator. Ten open and ten covered trays were also randomly selected and the empty shells collected from those trays were weighed according to seed type.

Data Analysis. Data collected during the coyote and mink odor treatments were analyzed separately because seed augmentation was necessary for the mink experiment. Only GUD data from the coyote odor treatment needed to be ln-transformed to meet the assumptions of normality and homogeneity of variances. The two seed types were analyzed separately across time, using Repeated Measures ANOVA (RM ANOVA) to evaluate the effect of cover and predator urine. The dependent variable was the GUD for each seed type in each foraging tray (n=60 trays). The effect of odor treatment was evaluated as a significant effect across days in the presence or absence of odor, therefore trial day was used

as the repeated measure. The effect of cover type was evaluated as the independent variable. To test for changes in selectivity, I calculated the difference between the GUDs of striped and black oil seeds and used this as a selectivity index. I then used this index as the dependent variable in RM ANOVAs for each of the two treatment periods. Significant effects were further examined with post-hoc tests using a Bonferroni correction. A paired t-test was performed to compare GUDs of black oil and GUDs of striped sunflower seeds at all stations across the entire study period. A two-sample t-test was used to compare the total amount of empty shells found in a random sample of 10 open versus 10 covered trays on the last odor-free night of the mink odor treatment. SYSTAT 12.0 (SYSTAT 2009) was used for all statistical analyses; p-values ≤ 0.05 were considered statistically significant.

Results

In the coyote odor experiment, rodents consumed more black oil and striped sunflower seeds in covered trays (i.e., GUDs were lower) than open trays (RM ANOVA, cover: black oil, $F_{1,58}$=20.27, P<0.001, striped, $F_{1,58}$=5.91, P=0.018; Table 1A). GUDs of black oil and striped sunflower seeds declined across treatment days (day: $F_{4,232}$=20.11, P<0.001). There was no interaction between the effect of day and cover (day × cover: black oil, $F_{4,232}$=1.53, P=0.194; striped, $F_{4,232}$=1.29, P=0.276). The Greenhouse-Geisser epsilon values were 0.929 and 0.925 for black oil and striped, respectively, suggesting that sphericity was not seriously violated.

Coyote odor was applied on days 2, 3, and 4; days 1 and 5 were odor-free (Fig. 4A). The amount of black oil sunflower seeds consumed on day 5 was significantly higher than that consumed on days 1, 2, and 3 (Bonferroni-corrected probabilities, day 1: P=0.023, day 2: P<0.001, day 3: P<0.001). The amount of striped sunflower seeds consumed on day 1 was significantly lower than that consumed on days 2, 3, 4, and 5 (P<0.001). Total GUDs in the covered trays were lower than in the open trays throughout the coyote odor treatment (P<0.001; Fig. 5A). Rodents consumed more black oil than striped sunflower seeds (paired t-test, t=7.087, df=299, P<0.001).

In the mink odor experiment, rodents consumed more black oil and striped sunflower seeds in covered trays than open trays (RM ANOVA, cover: black oil, $F_{1,50}$=23.97, P<0.001, striped, $F_{1,50}$=29.7, P<0.001; Table 1B). GUDs of black oil and striped sunflower seeds changed across treatment days (day: black oil, $F_{4,200}$=8.27, P<0.001, striped, $F_{4,200}$=10.8, P<0.001). There was no interaction between the effect of day and cover (day × cover: black oil, $F_{4,200}$=2.19, P=0.072; striped, $F_{4,200}$=1.65, P=0.164). The Greenhouse-Geisser epsilon values were 0.893 and 0.895 for black oil and striped, respectively, which means that sphericity was not seriously violated.

Mink odor was applied on days 2 and 3; days 1, 4, and 5 were odor-free (Fig. 4B). The rodents consumed more black oil sunflower seeds on day 5 than days 1, 2, and 4 (Bonferroni-corrected probabilities, day 1: P=0.013, day 2: P<0.001, day 4: P<0.001). They also consumed more striped sunflower seeds on days 1, 2, 3, and 4, than day 5 (P<0.01). Total GUDs in covered trays were significantly lower

than in the open trays throughout the mink odor treatment (P<0.001; Fig. 5B). Rodents consumed more black oil than striped sunflower seeds (paired t-test, t=-9.496, df=296, *P*<0.001).

In the coyote odor experiment, there was no difference in selectivity for seed types between the open and covered trays (RM ANOVA, cover: $F_{1,58}$=0.337, *P*=0.564; Table 2; Fig. 6A). Rodents did not change their selectivity of seed types across treatment days (day: $F_{4,232}$=0.000, *P*=1.000). There was no statistically significant interaction between day and cover (day × cover: $F_{4,232}$=0.357, *P*=0.839). The Greenhouse-Geisser epsilon value was 0.835, suggesting that sphericity was not seriously violated.

In the mink odor experiment rodents were more selective in the open trays cover (RM ANOVA, cover: $F_{1,58}$=5.84, *P*=0.019; Table 2; Fig. 6B). Rodents changed their selectivity of seed types across treatment days (day: $F_{4,232}$=5.25, *P*<0.001). They were more selective on day 3 compared to day 5 (Bonferroni-corrected probabilities, *P*<0.01). The difference in selectivity between days 1 and 3 and days 3 and 4 approached statistical significance (*P*<0.06). There was no statistically significant interaction between day and cover ($F_{4,232}$=1.63, *P*=0.167; Table 2). The Greenhouse-Geisser epsilon value was 0.815, so sphericity was not seriously violated.

More empty shells were found in the covered (μ ± SE = 0.167 ± 0.022) than in the open (0.028 ± 0.011) trays (t=-5.529, df=18, *P*<0.001; Fig. 7). More empty black oil (0.123 ± 0.019) shells were collected than empty striped (0.037 ± 0.007) shells (paired t-test, t=-3.053, df=9, *P*=0.0137). Painted shells were found in the

covered feeding trays at five stations, indicating that seeds had been carried from the open tray and were eaten under the protective cover.

Discussion

Microhabitat cover was an important factor in influencing GUDs during both odor-free and predator-odor risk treatments. The artificial vertical cover provided protection from aerial predators, such as owls, so the covered tray was perceived as a safer foraging patch by the rodents, leading to lower GUDs as I had predicted. They also consumed more black oil than striped sunflower seeds, regardless of microhabitat cover and olfactory cues.

The two predator odors did not have the same effect on GUDs. There was no response to the coyote urine; GUDs consistently decreased throughout the coyote odor treatment. An explanation for this decrease is acclimation of rodents to the seeds in the trays. During the mink odor treatment, rodents did not change the amount of seeds they consumed or their selectivity in the covered trays. This indicates that covered trays were still considered relatively safe foraging patches, because nocturnal rodents perceive aerial predators as a greater threat than terrestrial predators (Szewczyk, unpublished).

However, rodents did change their foraging behavior in the open trays. They not only responded to the mink urine by decreasing the amount of seeds they consumed but they also became more selective, consuming a greater proportion of black oil sunflower seeds in the open trays. Striped sunflower seeds, the less profitable items, were not completely excluded from the rodents' diet as predicted

by the "higher requisite profit" model (Leaver and Daly 2003). Selectivity decreased again after the odor was removed. These results were contrary to my hypothesis that rodents would be less selective when predation risk increased due to time minimization. Since the change in selectivity was only observed in open trays during the mink odor experiment, this response may be a result of the combined effect of a direct predation risk cue, the mink odor, and an indirect cue, the lack of microhabitat cover.

The decrease in foraging activity was evident until the first odor-free night. This is a significant finding because it suggests a lag in the response of the prey to the removal of the predator urine from the stations. This may be a result of site assessment and association due to learning by the rodents. Another explanation is residual odor from the predator urine at the stations. On the second odor-free night, GUDs decreased significantly, becoming lower than the GUDs observed before the addition of the mink odor. Rodents may have consumed more seeds because they perceived the habitat as safer, responding in a similar manner as in the coyote odor experiment, in which a steady decline in GUDs was observed over time. This could also arise as more rodents visit the trays.

The reason for the response to an olfactory cue from a mustelid, but lack of response to that from a canid, may be the abundance of these predators on the UNDERC property. Smaller-bodied carnivores, such as mink, tend to be more abundant than large-bodied carnivores, such as coyotes (Choate, personal communication). If coyotes are a rare threat, the coyote urine may not cause a response, which was what I observed. The increase in GUDs during the mink

odor experiment suggests that mink are perceived as a greater threat by the rodents.

Based on the unidirectional movement of painted seeds and the higher mass of empty shells in the covered trays, rodents appeared to carry seeds from the open trays to the protective cover of the covered trays. I also found that more striped than black oil sunflower seeds get moved from the feeding trays. Black oil sunflower seeds provide a greater energy gain per unit handling time, covering the increased costs of predation risk. These results are consistent with those of Lima and Valone (1986), who found that grey squirrels (*Sciurus carolinensis*) carried larger and less energetically profitable items to protective cover for consumption. Lima and Valone (1986) collected data by observing several individuals forage; the use of blacklight paint or other marking techniques may be a more efficient method for obtaining qualitative and quantitative information about the movement of food items in a patch. Since these items are not always eaten at the patches where they are encountered (Lima and Valone 1986), GUDs may be unreliable as quantitative measures of foraging behavior (Price and Correll 2001), so they should not be used to directly estimate energetic or metabolic losses. My results, however, are robust for determining the effect of predation risk cues on rodent foraging, as indexed by GUDs.

In conclusion, seed type selectivity increased in the trays with the greatest perceived predation risk: open trays with mink odor. Even though other studies have shown that selectivity is affected by certain indirect cues of predation risk (Leaver and Daly 2003), there have been no previous studies, to my knowledge,

examining the effect of direct cues on selectivity of similar food types. My results also highlight the importance of taking lag effect into consideration when designing foraging experiments. For example, Orrock et al. (2004) found that direct predation risk cues do not affect foraging decisions of rodents, but these results could be an artifact of their experimental design. Different predator scents were added around the trays on consecutive nights with no odor-free trials between them. The lack of a decrease in GUDs when predator odors were removed may be attributed to a lagged response of the prey; residual odor or patch association due to learning may have led to continued wariness across all odor days in their study.

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Table 1 Results of Repeated Measures ANOVA for the coyote (A) and the mink (B) odor treatments. Ln-transformed GUD data were used for the analysis of the former.

Source	Black oil sunflower seeds				Striped sunflower seeds			
	df	MS	*F*	*P*	*df*	MS	*F*	*P*
A) Coyote odor								
Between subjects								
Cover	1	310.7	20.27	<0.0001	1	259	5.91	0.018
Residual	58	15.3			58	43.85		
Within subjects								
Day	4	119.8	20.11	<0.0001	4	255.6	21.5	<0.0001
Day × Cover	4	9.11	1.53	0.194	4	15.29	1.29	0.276
Residual	232	5.96			232	11.88		
B) Mink odor								
Between subjects								
Cover	1	142.8	23.97	<0.0001	1	345.2	29.7	<0.0001
Residual	50	5.96			50	11.62		
Within subjects								
Day	4	15.87	8.27	<0.0001	4	30.96	10.8	<0.0001
Day × Cover	4	4.20	2.19	0.072	4	4.70	1.65	0.164
Residual	200	1.92			200	2.86		

Table 2 Results of Repeated Measures ANOVA for selectivity of seed types during the coyote and mink odor treatments. Selectivity was defined as the difference between GUDs of the two seed types (d = striped – black oil, g).

Source	Coyote odor treatment				Mink odor treatment			
	df	MS	*F*	*P*	*df*	MS	*F*	*P*
Between subjects								
Cover	1	7.95	0.337	0.564	1	44.40	5.84	0.019
Residual	58	23.61			58	7.61		
Within subjects								
Day	4	0.000	0.000	1.000	4	10.41	5.25	<0.001
Day × Cover	4	2.403	0.357	0.839	4	3.23	1.63	0.167
Residual	232	6.74			232	1.98		

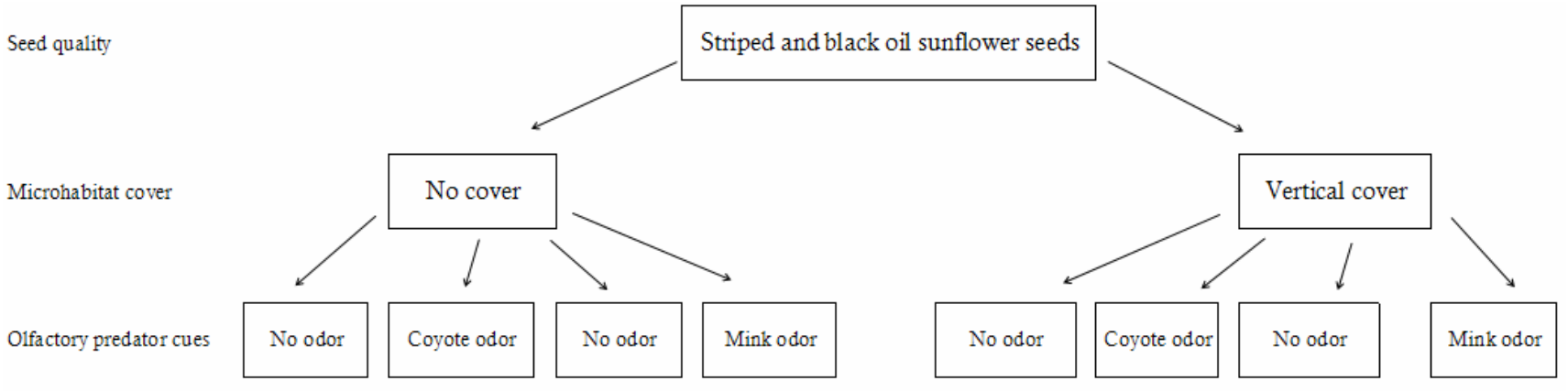

Fig. 1 Experimental design used to examine the effect of seed quality, microhabitat cover, and olfactory predator cues on nocturnal rodent foraging behavior. Each treatment consisted of two foraging trays: one with vertical cover and an open tray as the control for vertical cover. In the absence of odors, these served as the controls for the odor treatments in a repeated measures BACI design. Equal amounts of striped and black oil sunflower seeds were placed in each tray.

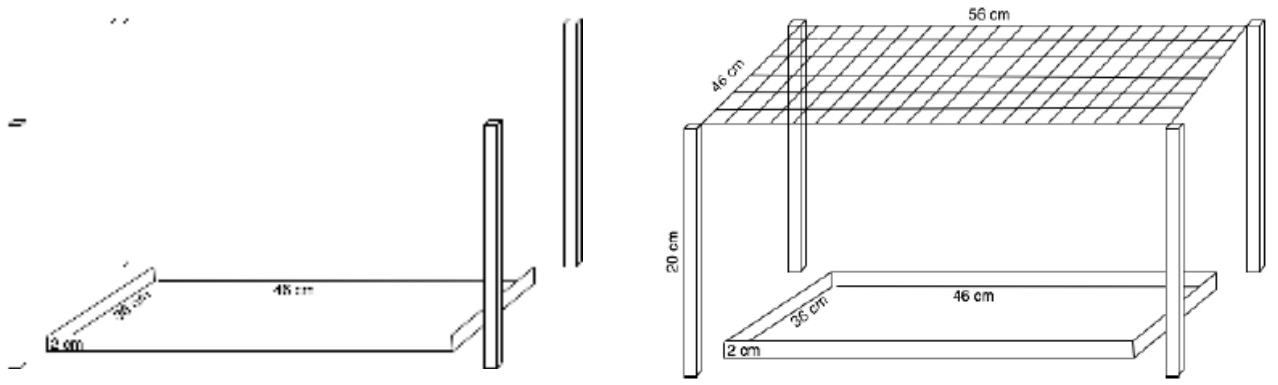

Fig. 2 Design of control trays (left) and trays with vertical cover (right), provided by shade cloth (from Szewczyk, unpublished).

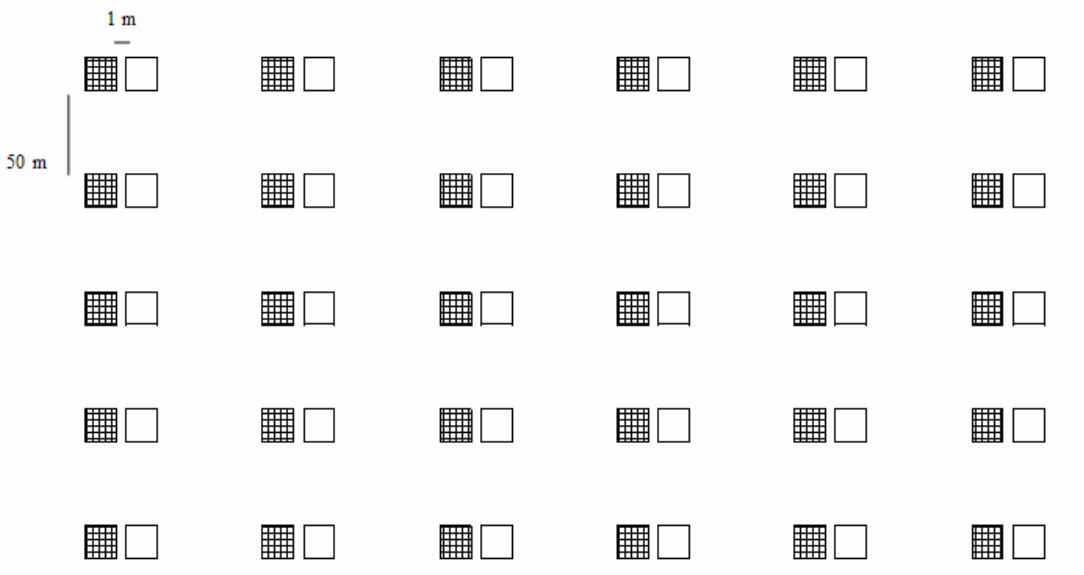

Fig. 3 The field site contained 30 stations in a 5 x 6 grid with a distance of 50 m between stations. Each station consisted of one covered (crosshatch) and one open (white) feeding tray placed 1 m apart.

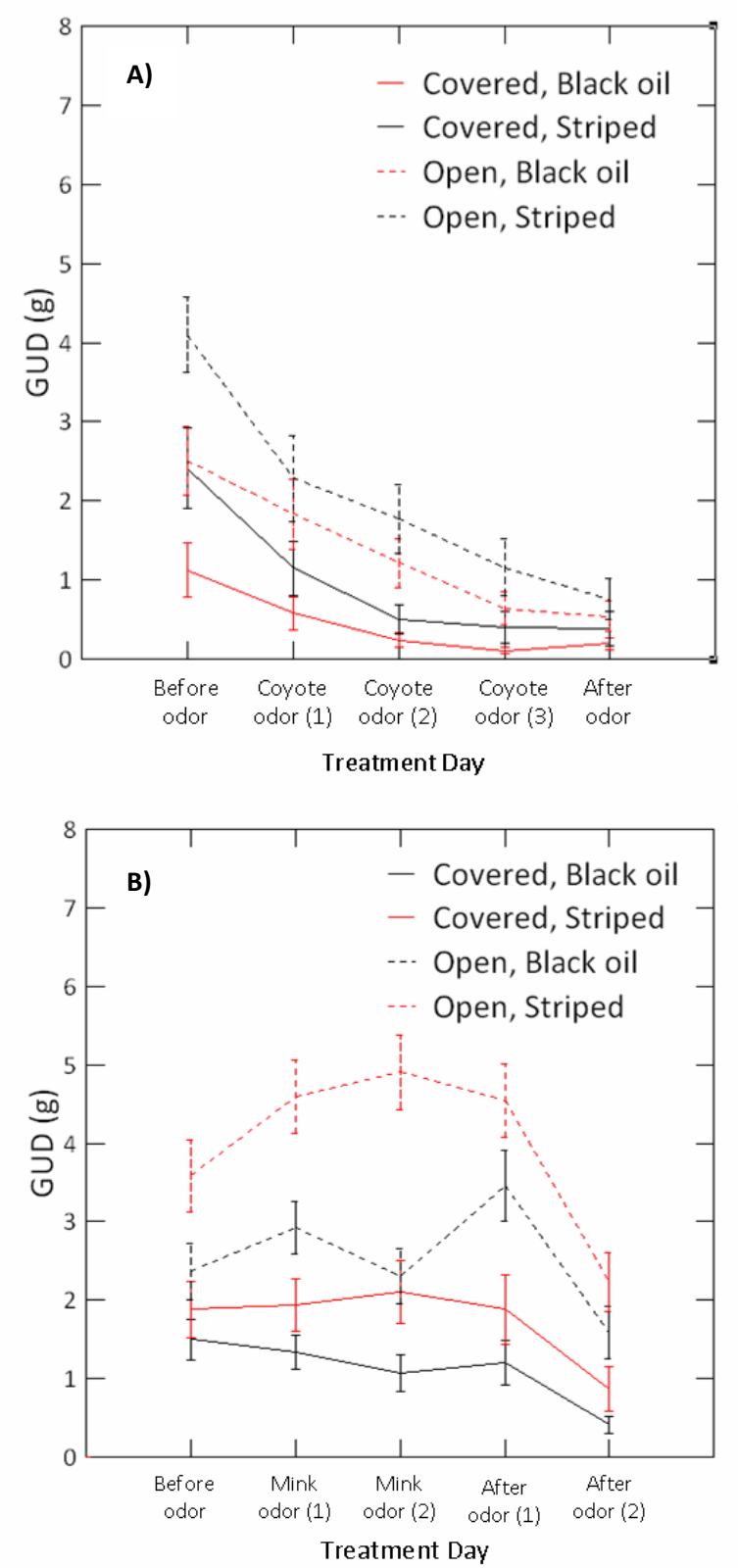

Fig. 4 Mean giving-up densities (± SE) of black oil and striped sunflower seeds in open (*n*=30) and covered (*n*=30) trays throughout the coyote odor treatment (A) and the mink odor treatment (B).

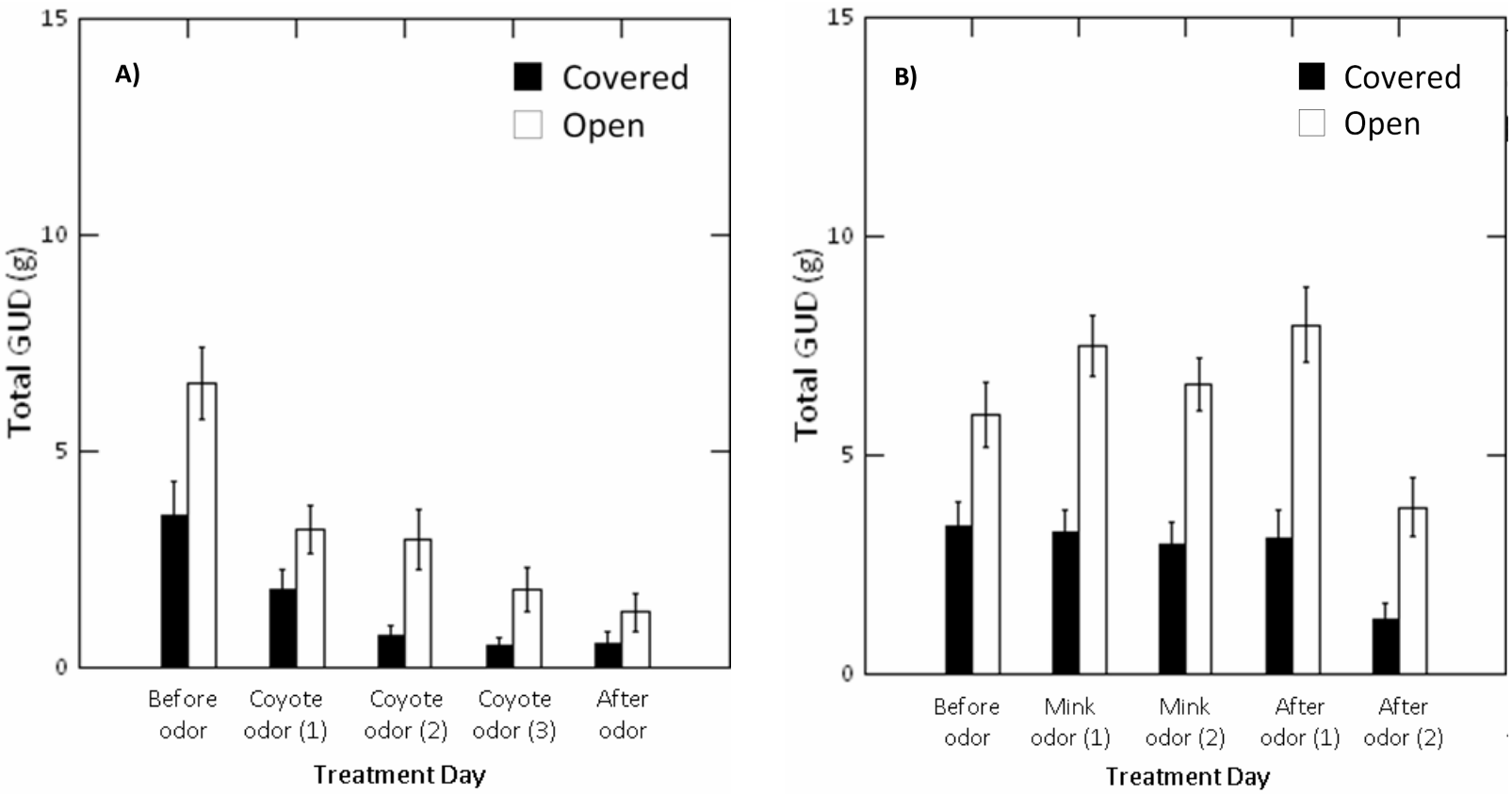

Fig. 5 Mean total giving-up densities (± SE) in open (*n*=30) and covered (*n*=30) trays throughout the coyote (A) and the mink (B) odor treatment.

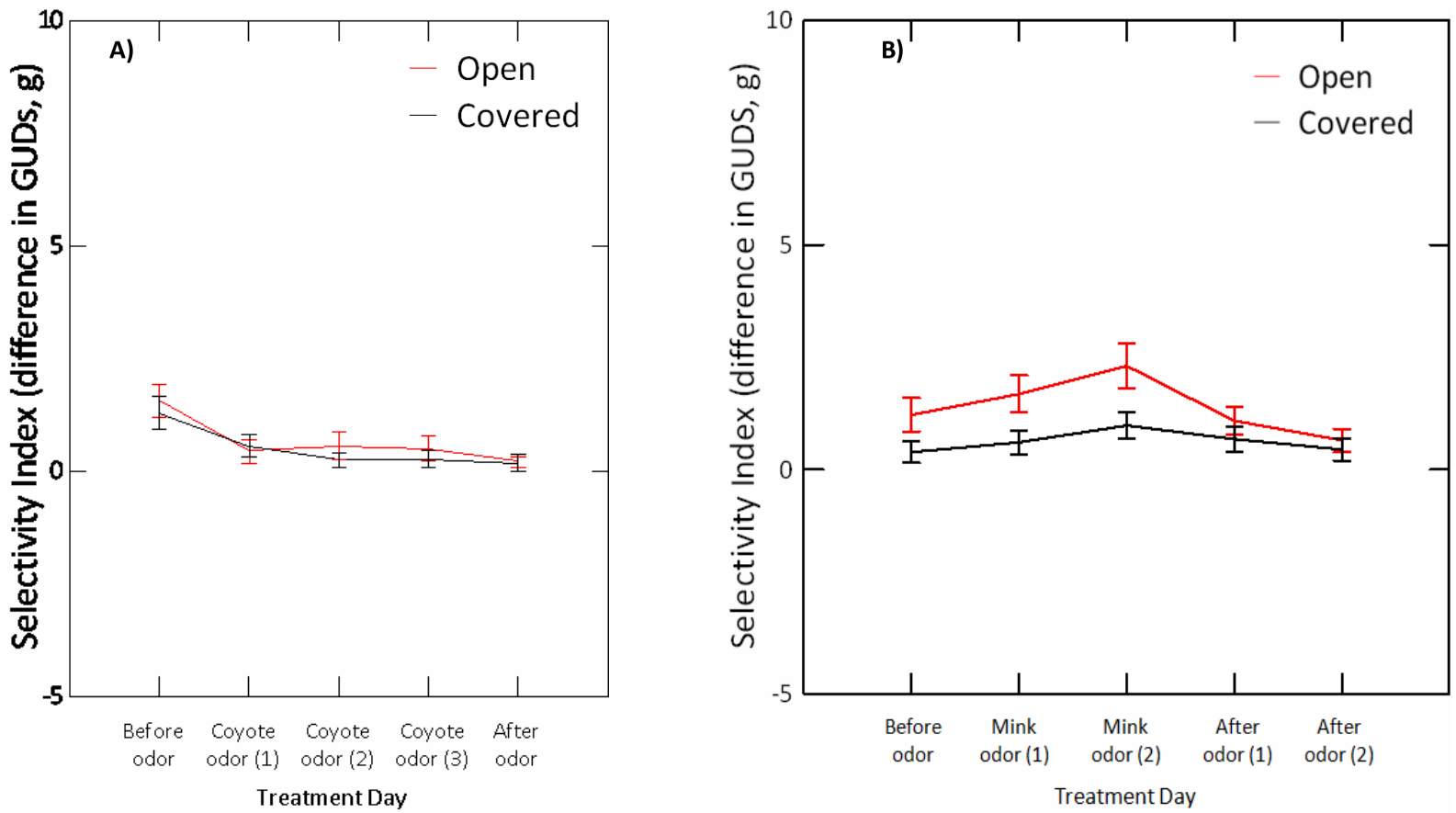

Fig. 6 Mean seed type selectivity (± SE) in open (*n*=30) and covered (*n*=30) trays throughout the coyote (A) odor treatment and the mink (B) odor treatment.

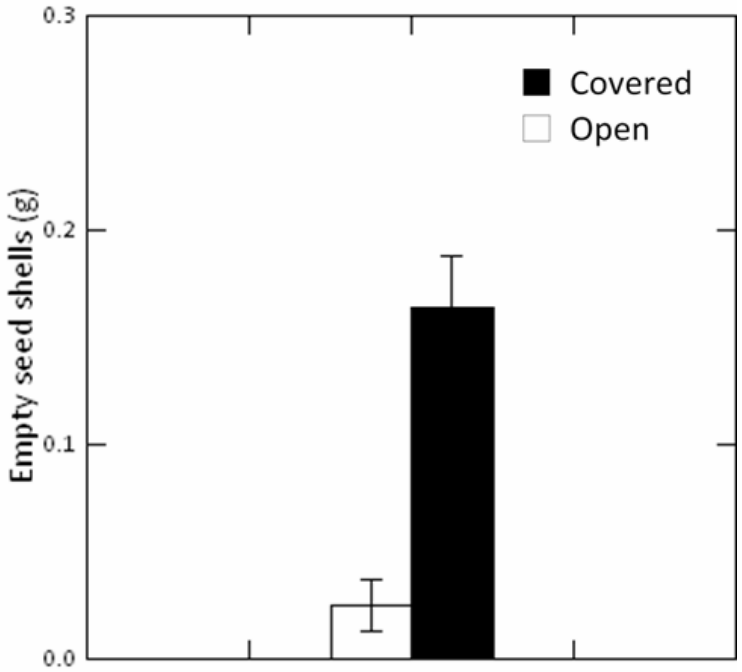

Fig. 7 Mean weight of empty shells (± SE) from both seed types found in randomly selected open (*n*=10) and covered (*n*=10) trays, during a post-odor trial.