

The effect of predation risk upon giving-up densities (GUDs) of shrew foraging on
invertebrate populations

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Abstract:

Optimal foraging theory states that predators will eventually reach a giving-up density (GUD) in their hunting ground, or a point at which they've depressed the abundance of prey to a point that it is no longer metabolically favorable for them to feed in that particular area. Shrews are insatiable predators on invertebrates and have been demonstrated to have preferential foraging that is at least partially dependent on abundance of prey. In this study I attempted to find if shrews forage in accordance with optimal foraging theory by testing whether or not they seek out areas of high prey density over low density. Using earthworms as bait, we set up multiple bait stations on the UNDERC property in the natural habitat of shrews, some with high density and some with low to test whether they preferred the high prey density. We also treated some of the stations with urine from gray fox (*Urocyon cinereoargenteus*) to test if perceived risk of predation raised their GUD. We found that canid urine had no noticeable effect, yet there was a slight trend towards foraging in higher density areas.

Introduction:

Optimal foraging theory states that in any given area, or 'patch', where food is present, an animal will stay and feed in that area, thereby depressing the amount of available food. Once food is depressed to a certain point, the giving-up density (GUD), foraging in that area will no longer be metabolically favorable and the individual has to move to a new feeding ground. As density of prey is a critical aspect of where predators hunt and how intensely they do so, understanding the dynamics of optimal foraging theory and how predators reach and recognize a GUD would be essential for monitoring predation activity and influence. This project studied GUDs in mammalian foraging on

the UNDERC property, using shrew predation upon earthworms as a model. Studying mammalian predation pattern in the wild is often difficult, even using artificial systems. For most predator species, traits such as low numbers, widespread movement, and timidity make them less than ideal for short-term study. Tracking their prey at the same time can also be difficult. However, unlike most mammalian predators, shrews on the UNDERC property are ideal in that they are small and ubiquitous (Kilcline 2003) and their invertebrate prey is also small and easily handled. Shrews as a group are ravenous predators of invertebrates. Due to their high metabolism a shrew must eat every few hours or expire from starvation (Dr. Cramer, personal communication). As a result of this they greatly reduce large invertebrate populations, as revealed by past enclosure studies (Churchfield et al. 1991). Previously, it was theorized that shrews feed indiscriminately on any prey they are able to catch. While shrews are opportunistic to an extent, this assumption has been moderated by findings that shrews preferentially seek out certain prey species based on numerous factors, such as prey size. (Rychlik and Jancewicz 2002).

There are also indications that abundance and densities will influence shrew selection of prey. It was noted that *Blarina brevicauda* did not occur in otherwise favorable habitats when densities of larger invertebrate prey were low (Getz 1961). Likewise, a study of *Sorex cinereus* revealed that shrews prefer environments of greater moisture, presumably due to the higher number of invertebrates in irrigated land (McCay and Storm 1997). This study also observed that while shrews preferred Lepidoptera larvae to other prey such as gastropods and earthworms this was moderated by relative abundance of prey. In autumn, when Lepidoptera larvae were common, shrews fed preferentially on them. In spring when they were scarce, the diet of shrews contained a

much higher percentage of less favored prey items (McCay and Storm 1997). Another study not only confirmed this dietary shift, but that shrew richness, recruitment and litter size increased with Lepidoptera larvae increases (Bellocq et al. 1994). Furthermore, in an experiment where traps were baited with pine sawfly cocoons, shrews memorized the location of traps favorable to them, all of similar size (Hanski and Parviainen 1985). This data suggests that shrews are aware of relative densities of their prey and alter their foraging patterns accordingly. This sensitivity to prey abundance suggests further that shrews would provide an informative model for studying optimal foraging theory.

Another determining factor upon the foraging patterns of an animal is the risk of predation. A study on GUDs of common voles (*Microtus arvalis*) found that voles have significantly lower GUDs—hence, they are willing to feed longer—in plots of unmowed grass as opposed to mowed grass, in all likelihood due to greater concealment from predators (Jacob and Brown 2000). By the same token, these voles would feed longer in patches at different times of the day with respect to their perceived safety. In the mowed portions they had lower GUDs during the day and in unmowed portions they exhibited lower GUDs at night. The authors hypothesized that this was primarily due to owls and weasels, respectively (Jacob and Brown 2000).

Shrews, like voles, are themselves prey to numerous carnivores, including snakes, owls, other birds of prey, canids, felines and mustelids (George et al. 1986). A study of shrews conducted over 25 years looked at their relative populations in three habitats: bluegrass, tallgrass and alfalfa and found that survival rates of shrews were higher in bluegrass and tallgrass, where they were afforded the greatest cover from predation (Getz, 2004). Similarly, a crash in shrew populations in Finland can most likely be

attributed to predation by mustelids (Henttonen 1985). It is thus reasonable to assume that a perceived greater risk of predation would alter shrew movements, including foraging behavior.

While numerous studies have correlated shrew dietary preferences with prey density and characterized the effect shrews have on invertebrate populations, no direct experiment has been carried out to test whether density of prey cause shrews to favor certain hunting grounds over others, nor have any studies observed whether shrews will avoid food sources out of fear of predators. This project aimed to study these dynamics on the UNDERC property, on the border of Wisconsin and the Upper Peninsula of Michigan. The property is primarily wetland and shrews have been trapped in large numbers there in the past (Kilcline 2003, Nuske 2004, Meyer 2006). The experiment was carried out by setting up bait stations at numerous sites around property, which presented shrews with two densities of prey, high and low. The frequency and ravenous feeding behavior of shrews were expected to have insured their interest in the bait stations once they discovered them. Predator risk at selected sites was simulated by lacing bait stations with fox urine. There were two specific hypotheses to be tested: that shrews would preferentially feed at bait stations with higher density, in accordance with optimal foraging theory, and that they would neglect stations which were scented with predator urine. This would serve as a model for predation patterns and selectivity which could be applied to other mammalian predators.

Materials and Methods:

Shrew GUDs were studied using artificial bait stations, consisting of 86x38x14 cm Rubbermaid® totes. An 8 cm wide wooden board was screwed in halfway down the

length of each tote, bisecting the floor space (see Fig 1). One half was filled with Brown Bear® worm bedding. Earthworms (primarily *Lumbricus rubellus* and *Lumbricus terrestris*) were used due to their place in the natural diet of shrews (Rychlik and Jancewicz 2002) and the ease of acquisition; worms were collected on property or purchased from a local retailer. On the empty side of tote, access to the shrew was provided by a PVC pipe extending 10 cm from a drilled hole and suspended a short distance (~12 mm) above the floor of the tote, to allow the shrew in while preventing worms from escaping by the same route, should they cross the wooden board into the empty half of the tote. Additionally, the seams around the hole were caulked and epoxied and the outside of the pipe and inside rim of the tote were greased with a Teflon®-based lubricant, to further prevent the worms from escaping. The diameter of the inside of the pipe was 22 mm, which allowed ample space to admit the masked shrew, *Sorex cinereus* (the most prevalent shrew on property) (Nuske 2004). Larger species of shrews, such as *Blarina brevicauda* and *Sorex arcticus*, would be hindered, but so would non-shrew species such as *Peromyscus maniculatus* and other small mammals that might be tempted to prey on the worms, providing insurance that only masked shrews would be responsible for predation within the bait stations. The tote was staked into the ground and the top was bolted on to prevent tampering by other curious fauna.

There were six sites at different points on the UNDERC property, each with two bait stations. These sites were Brown Creek, Kickapoo Lake, Plum Creek, Ed's Bog, Northgate Bog, and Tenderfoot Creek. These sites had been selected due to high capture success in these areas in past studies (Nuske 2004, Meyer 2006). The bait stations were placed between 10 and 100 meters from open water, as this was found to be the optimum

habitat for shrews, as determined by trapping experiments in the past (Meyer 2006). The bait stations were placed 25 meters apart to cover sufficient area and the exact GPS coordinates for each can be found in Table 1.

Bait stations were set at the site and the amount of worms within was maintained at 60 per tote for 17 days, a high number intended to elicit the interest of the shrews. During this period, they were checked 3 times. Once it seemed that there were worms disappearing, one station at each site was reduced to 10 worms per tote, while the other was kept at 60 to establish a high and low density. It was observed at most sites that one of the bait stations was already preferred to the other, and this was the one that was reduced, to test if the shrews would alter their foraging patterns. Stations were then checked every 3 to 4 days, and the number of worms missing was counted and recorded. Also at this time, 15x19 mm track plates were placed in the empty half of the tote, with Con-Tact® paper stretched over the wooden board, to capture shrew tracks and confirm predation. At the end of the experiment, the track plates were exchanged for Victor® snap traps baited with peanut butter in half of the totes, while the other half were removed. The total running time of the experiment was 41 days.

Urine from gray fox (*Urocyon cinereoargenteus*) was used to simulate predation risk, as they are natural predators of shrews (George et al.1986) and occur on the UNDERC property. The urine was purchased from R-P Outdoors and applied to cotton balls staked at the entrance of the stations at three randomly selected sites, after 30 days. This allowed a comparison between control stations and ones in which the shrews would perceive a risk of predation. Whenever a station suffered damage, they were repaired or replaced immediately.

The data was graphed using Microsoft Excel and analyzed via MYSTAT 12. The difference in percentage of worms taken from traps with high and low densities both before and after the densities were manipulated was assessed by paired t-tests, to account for the relationship between the high and low densities at each site. The effect of predator scent on predation at both low and high densities was examined with an ANOVA.

Results:

It was observed that even before the densities of prey were manipulated there appeared to be a greater number of worms taken preferentially from one station over the other at each site. Figure 2 illustrates this trend, by plotting the percentage of worms taken from each trap at the dates checked. At all sites, up until Day 17, when the densities were manipulated, one station was more heavily predated than another. A paired t-test revealed this to be nonsignificant with p-values ranging from 0.083 to 0.339. Following Day 17, the stations with high density exceeded that with low density, and in the case of Brown Creek and Tenderfoot creek this trend persisted until the end of the experiment (see Fig 2). At Ed's Bog, the high-density station remains more heavily or equally predated at all times following Day 17 but in the remaining sites, the low-density stations at points surpass the high density stations (see Fig 3). Overall, the traps with higher density were on average predated more heavily, except at Kickapoo Lake and Plum Creek, though there is a wide deviation (see Fig 3). The differences between predation between high- and low-density stations followed a pattern of normal distribution as illustrated by a histogram and probability curve (Fig 4) and these were not significant, according to a paired t-test (Mean difference=0.073, df=34, p=0.097).

Fox urine was applied to stations in the final days of the experiment to test the effect of perceived risk of predation upon shrew foraging at the high and low density sites. Figure 5 displays that while predator scent caused a slight decrease in foraging of low-density stations, high-density stations with fox urine were more heavily predated, though there was a wide deviation. A Shapiro-Wilk test was performed and found that this data was not normally distributed (Shapiro-Wilk=0.883, $p=0.010$), but a Bartlett test demonstrated that the variance within the groups did not differ significantly ($\chi^2=0.488$, 0.922). As an ANOVA is robust with respect to normality in the case of equal variance, one was carried out to compare predation proportions at high- and low- densities and between treated and untreated stations. It determined that there was no significant variation between densities and treatments ($F=0.434$, $df=3$, $p=0.731$).

The track plates within the stations were recovered with a variety of smudges, brushmarks, and negative lines or spots. Some of them were determined to have been left by slugs or earthworms which were recovered in the empty side of the tote, while most were unidentifiable. Others, most of which were found around the periphery of the plates, were possibly left by shrews, when compared to impressions upon undisturbed soot by taxidermied shrews. From station 6 at Plum Creek a partial track was recovered, which exhibited a round pad and three toe marks without claws, approximately 6 mm in total length, possibly left by *Sorex cinereus* or *Blarina brevicauda*. There were no tracks found on the Con-tact® paper. The snap traps caught no shrews or other animals, though peanut butter was missing from two stations, at Ed's Bog and Northgate Bog.

Discussion:

Many past studies have uncovered relationships between shrew presence and foraging and density of prey species, such as those done by McCay and Storm (1997) and Bellocq et al. (1994) correlating shrew abundance with Lepidoptera larvae. These findings can perhaps be explained by the optimal foraging theory, which states that if a plot of habitat has below a certain threshold of available prey, the predator will have to expend more energy capturing prey than it would receive from a meal and would be forced by metabolic constraints to move to a new patch (Charnov 1974). This has many important implications for habitat use and behavior, both for shrews and their prey. It affects which shrew species can live where, as larger shrew species require larger species of invertebrates (Rychlik and Jancewicz 2002, Getz 1961). Conversely, shrews can significantly reduce invertebrate communities where they do occur (Churchfield et al. 1990). Furthermore, which species shrews seek out will also change as a function of density, as when shrews respond to decreases in their preferred prey of Lepidoptera larvae by increasing their predation upon earthworms (McCay and Storm, 1997). Thus, the reciprocal influences of density-dependent shrew foraging and invertebrate abundance on each other are a substantial factor in determining the size and composition of communities in a wetland ecosystem. This grows more interesting when considering that it can be applied to many predator-prey relationships, including those of larger mammals. This project sought to test this interaction in shrews with a direct study on whether density influenced shrew selection of hunting grounds. On the UNDERC property, I set up numerous bait stations at different sites which had been shown by previous researchers Kilcline, Nuske, Meyer, and Francl to have high numbers of shrews. These stations provided shrews with a choice of either a high or low density of prey

(earthworms) with the hypothesis that the shrew would feed preferentially at the high-density stations, due to the greater metabolic reward they represented. These stations were set up with the intention of retaining the worms and allowing access by shrews while prohibiting other small mammals.

Besides energy efficiency, another important factor on foraging is the risk that it exposes the forager to a predator. As other small mammals displayed higher GUDs in response to a perceived risk of predation (Jacob and Brown 2000), I hypothesized that bait stations treated with gray fox (*Urocyon cinereoargenteus*) urine would be less predated upon by shrews.

There was a trend of more worms missing from high-density traps than low-density in four of the six sites, which approached significance ($p=0.097$). Furthermore, there was a nonsignificant but persistent trend before the densities were manipulated of one station being preferentially foraged in over the other at each site, for reasons that were not apparent to the experimenter. These preferred stations were the ones in which the density was lowered, resulting in an immediate increase in the foraging at the other station. This shift held true for three of the six sites until the end of the experiment (see Fig 1). This indicates a possible density-dependent agent responsible for removal of the worms.

The track plates showed a variety of marks, some of them unidentifiable, some left by the worms and other invertebrates that got into the stations, and some which may have been the work of shrews. A number of deceased *B. brevicauda* from previous experiments were stored in a freezer in the lab and from these tracks were taken. It was difficult to obtain a clear, complete track and more commonly claw or toe marks were

produced. Similar markings are found along the periphery of the track plates, though no tracks were distinguishable in the center of the plate. One partial track which may have been left by *Sorex cinereus* or *Blarina brevicauda* was found, which contained three toes and a pad and was too small to belong to *Peromyscus* or similar non-shrew small mammals. This suggests that shrews, upon entering the bait stations, either restricted their movements to the edges of the plates, or were able to jump from the pipe to the wooden board. Such avoidance to traversing a track plate is not atypical behavior of mammals, according to the word of an experienced trapper (Dr. Choate, personal communication). The soot plates also suggest that no *Peromyscus* or other similar small mammals were invading the stations, as they are heavier and were more likely to leave definite tracks on the plate. None of the snap traps caught anything, though the peanut butter bait was missing from two of them. This could have been due to slugs or other invertebrates, which were prevalent in the traps, but was probably not indicative of shrews as it would have been very difficult for them to avoid setting off the snap traps. However, it is possible that the snap traps simply missed the shrews, since they were only added at the end of the experiment and inclement weather at the time may have discouraged shrew movements.

The stringent design of the stations, coupled with the track plates and the possible relation to density indicates that the disappearance of the earthworms were likely the result of shrew predation. Alternative explanations include worms escaping, though this would necessitate them defeating the aforementioned precautions (see Materials and Methods) and no worms were found crawling up the sides of the station or within the pipe at inspection. Arthropod predators could conceivably have been a cause for worm

disappearance, but considering the amount of worms removed, it is likely that some of these arthropod predators would have been found in the stations at the time of inspection which was not the case. Some carrion beetles (*Silpha americanus*) were discovered in one of the stations, but at a time and location of low worm disappearance, and not for a prolonged duration. Spiders were common in the stations, but none of them were large enough to present a threat to the worms.

The application of fox urine did not have a significant effect on the disappearance of worms. In fact, high-density stations treated with urine had more missing worms than others, though this may have been due to chance. This may indicate that shrews were not in fact responsible for the disappearances. It is also possible that the urine did not frighten the shrews because they are used to encountering it in the environment and do not take it as an indication of danger as they might the scent of the predator itself. Foxes are also not the most potent predators of shrews and urine from another species would be better, such as a mustelid, as there are indications that they can have a drastic effect on shrew populations (Henttonen 1985). Fox urine may also have quickly washed out and should perhaps have been reapplied more often than it was to maintain a strong enough signal. Finally, it is possible that shrews do not alter their foraging behavior much in response to predation, relying on their small size or allegedly objectionable odor (George et al. 1986) to ward off most predators.

These findings are inconclusive though trends toward preference of shrews for higher prey densities were found. In the future, further steps should be taken to ensure that shrews are visiting the stations, perhaps by seeding the area with prey which would make the entire area favorable to shrews, though this was not an option in this

experiment, as earthworms are considered invasive species at UNDERC. Earthworms were the only prey that was viable to use at this scale and on property, but if larvae or mealworms could be used in future experiments as bait instead that might attract more shrews, as laboratory experiments indicate that their preferences run this way (Rychlik and Jancewicz 2002). The small size of the access hole may also have discouraged even the shrews as it discouraged other mammals. Confirmation of shrew predation might be attained by more persistent use of track plates or by placing Sherman traps in the bait stations, and checking them frequently enough to prevent shrews from expiring in them, at least until their presence is readily established. It would also be prudent to confirm that worms are not escaping by setting these stations up in a laboratory setting, surrounded by adhesives to catch any escaping worms. The sensitivity to predator scent and its effects may also be best determined in a laboratory setting to see if shrews even perceive an added risk due to this stimulus.

Assuming shrews were foraging in the stations from the data provided by the track plates and considerations taken in the structure of the bait station, the results do indicate a density-dependent aspect of their hunting behavior. Once the reliability of the design, the first as far as we know used for this purpose, was verified, it would also be advised to carry out this experiment again with more replicates for a longer period of time to allow greater statistical analysis. It is possible that these results would be conclusive with more data, as constraints on time and materials were severe. For an even more complete analysis, intermediate densities, in addition to high and low, might be set up, to test how sensitive shrews are to abundance of prey.

In conclusion, the results point towards shrews adhering to some form of the optimal foraging theory and indicate that future experiments in this area may yield clear information for understanding predator behavior and trophic effects in mammalian communities. I propose that given time to explore alternative hunting grounds, shrews will preferentially seek out areas of high-prey density, and that these preferences will be subject to change with numerous other factors, such as predation risk, that influence a shrews perception of the suitability of a habitat.

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Tables and Figures:

Table 1: Location and status of bait stations

Two bait stations were placed 25 m apart at each of the six sites. One was filled with a low density of worms (L=10 worms) and the other with a high density (H=60 worms). Half of the sites were later treated with urine of gray fox (*Urocyon cinereoargenteus*) while the other half were left as control

Station Number	Site Location	GPS	Density	Fox urine
1	Brown Creek	0308213, 5119912	L	Yes
2		0308197, 5119230	H	
3	Kickapoo Lake	0307308, 5121754	H	No
4		0307310, 5121777	L	
5	Plum Creek	0307036, 5121835	L	No
6		0307024, 5121862	H	
7	Ed's Bog	0307834, 5122756	H	Yes
8		0307795, 5122752	L	
9	Northgate Bog	0307961, 5125083	H	Yes
10		0307919, 5125064	L	
11	Tenderfoot Creek	0304909, 5122602	L	No
12		0304908, 5122628	H	

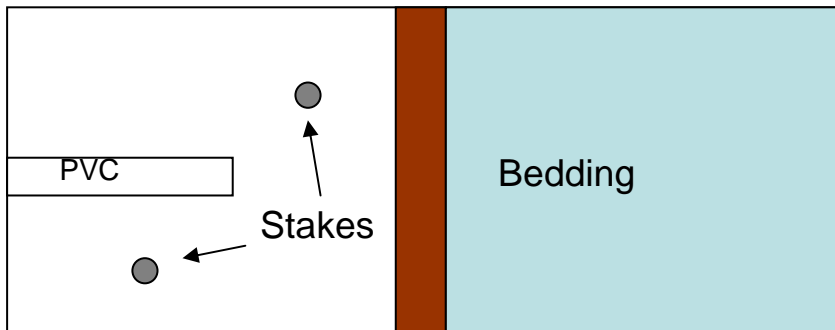


Figure 1: Diagram of bait station.-Consists of a 86x38x14 cm Rubbermaid® tote bisected by an 8 cm wide wooden board. Worms were placed in bedding on one side and a PVC pipe allowed access at the other. Stations were staked into the ground with stakes tight to plastic. Track plates and snap traps were placed in the open half between PVC pipe and wooden board and Con-Tact® paper was stretched over wooden board.

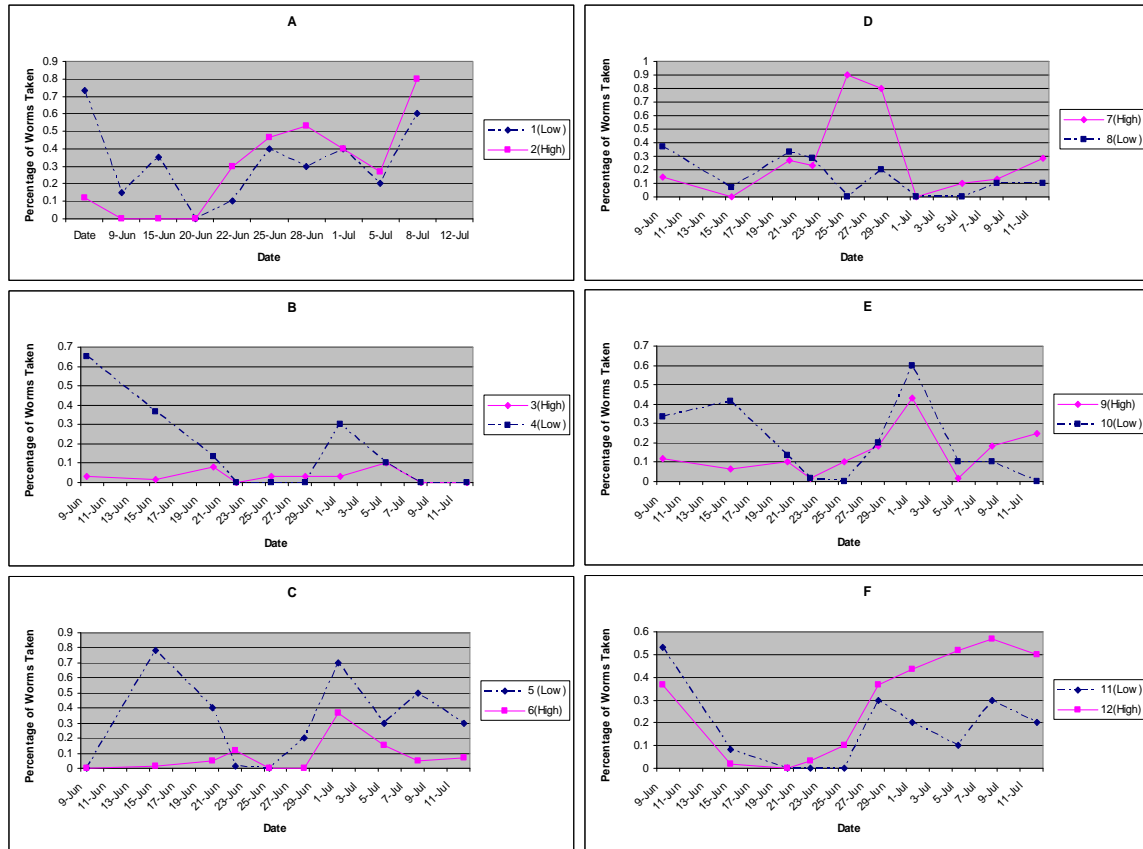


Figure 2: Percentage of worms taken in comparison between high- and low-densities- Graphs of each site (A=Brown Creek, B=Kickapoo Lake, C=Plum Creek, D=Ed's Bog, E=Northgate Bog, F=Tenderfoot Creek), comparing the relative percentage of worms taken from high-density stations (solid/pink) and low-density stations (dashed/blue) at each day. The x-axis contains the date sampled and the y-axis the percentage of worms taken. Day 17 represents the date when the densities were manipulated, after which the high-density stations were all more heavily predated than low-density, those this trend only persisted in Brown Creek, Ed's Bog, and Tenderfoot Creek. Differences in predation both before the densities were manipulated ($0.083 < p < 0.339$) and after ($p = 0.097$) were nonsignificant according to a paired t-test.

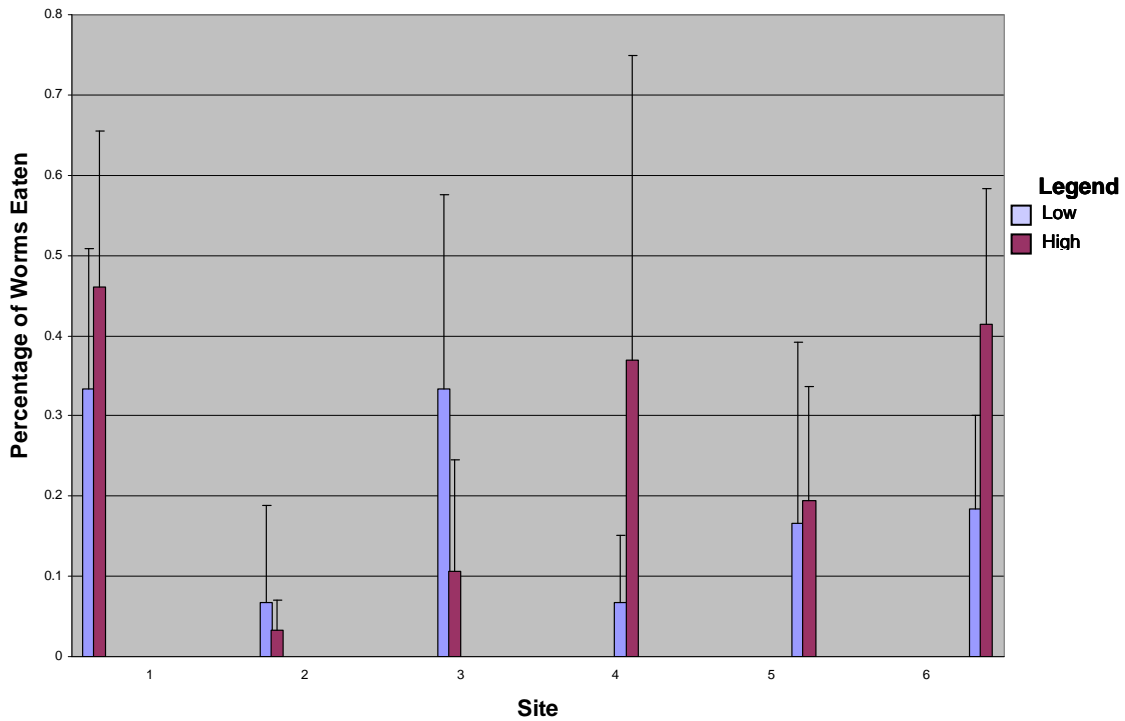


Figure 3: Differences in worms eaten between high- and low- densities at the different sites. The x-axis contains the site (1=Brown Creek, 2=Kickapoo Lake, 3=Plum Creek, 4=Ed's Bog, 5=Northgate Bog, 6=Tenderfoot Creek) and the y-axis contains the percentage of worms taken from each. Except for Kickapoo and Plum, the high-density traps were more heavily predated, though this was not significant according to a paired t-test ($p=0.097$). Standard deviation of the series ranged from 0.037 to 0.379.

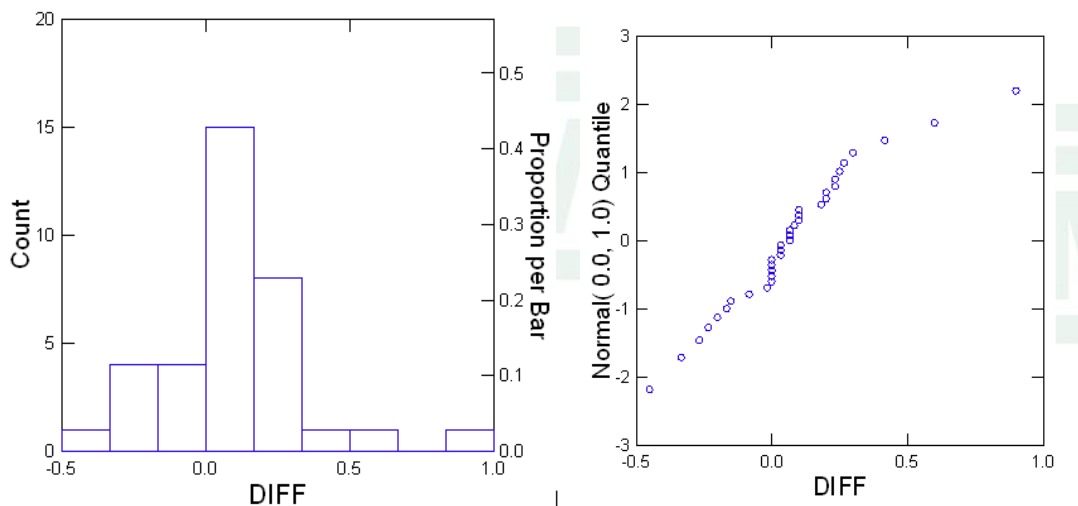


Figure 4: Normal distribution of difference between predation at high- and low- density traps as displayed by a histogram (left) and a probability curve (right). Figure was generated by MYSTAT 12.

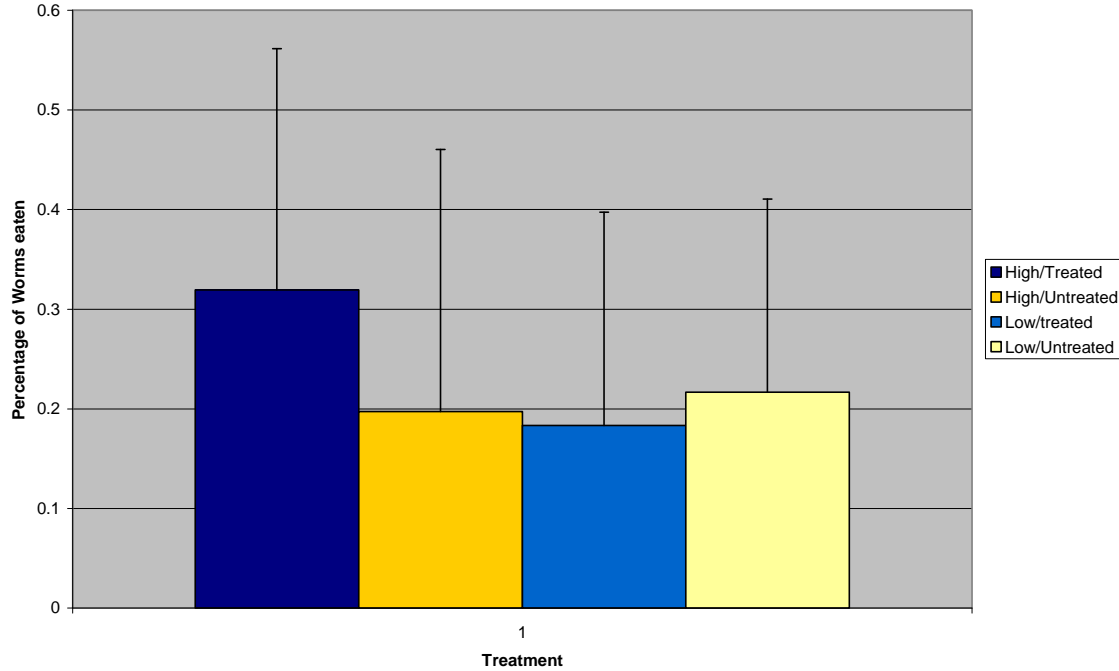


Figure 5: Effect of predator scent application on predation in high- and low-density stations. Application of urine from gray fox (*Urocyon cinereoargenteus*) corresponded with a decrease in predation at low-density stations but an increase at high-density stations. An ANOVA calculated that there was no significant difference between groups ($F=0.434$, $p=0.731$). Standard deviation ranges from 0.194 to 0.263.

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