Prey Selection by Owls on the National Bison Range

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ABSTRACT
The object of this study was to determine whether Great Horned Owls (*Bubo virginianus*) on the National Bison Range in Moiese, MT selectively feed on certain prey species. By surveying the small mammal community of known owl prey near Mission Creek, chiefly *Microtus pennsylvanicus* and *Peromyscus maniculatus*, I compared the abundance of prey in the environment to that found in egested owl pellets throughout July of 2006. In total, seventy five prey individuals were identified in thirty five pellets. A statistically significant difference was discovered between the diet of the owls and the local relative abundance of potential prey. The owls appeared to select *Microtus pennsylvanicus*, suggesting that this small mammal species makes better prey for *Bubo virginianus*. Possible reasons are because they are more active when the owls are hunting, have less effective anti-predator behaviors compared to *Peromyscus maniculatus*, or are more efficient sources of energy given capture and handling times for their size.

Key Words: Prey selection, Optimal Foraging Theory, Great Horned Owls, *Bubo virginianus*, Owl Pellets, *Microtus pennsylvanicus*, *Peromyscus maniculatus*, National Bison Range

INTRODUCTION

Optimal foraging theory attempts to explain the mix of food items that will maximize net energy intake and guide an animal to certain behavior in foraging for meals (MacArthur and Pianka 1966). A highly efficient food provides a significant amount of nutrients or energy for little effort or cost to the animal. Foraging cost to an herbivore takes into account the energy that is needed to process a meal, such as digging, cracking open hard seeds or nuts, chewing, and digesting, to name a few. Time spent searching for food is also considered a cost. For animals higher on the food chain, getting a meal includes additional challenges. Beyond finding appropriate food, pursuing, capturing, and killing live prey are often the major activities of predatory animals. Not only does this require much time, but also energy. Hunting for worthy prey can also entail risk of injury to the predator itself, certainly a formidable potential cost. Optimal foraging theory therefore says that the fruits of such labor should be well worth the input. This guiding force becomes especially pertinent when a predator has the option of allocating its time and energy towards many different foraging strategies.

An animal is considered a generalist feeder when it has the ability to take a wide variety of foods, as opposed to specializing on only one or two. A generalist predator may be able to effectively consume a number of different prey species depending on what is available. The Great Horned Owl (*Bubo virginianus*), is known to be a remarkably opportunistic hunter. Craighead and Craighead (1956) asserted that the Great Horned Owl eats the widest range of prey out of all North American raptors. It is accepted by some scientists that Great Horned Owl food habits reflect the relative abundance of prey in the environment (Baumgartner and Baumgartner 1944). If this were true in all cases, then one should be able to describe the diet of a Great Horned Owl by characterizing the potential prey existing in its environment, usually accomplished through small mammal trapping (Ward et al. 1998).

Different prey species provide different amounts of nourishment, even if slight. It is also probable that it takes different amounts of time and energy to capture and manipulate these same prey animals. If these discrepancies add up to a significant difference in net energy, optimal foraging theory would push the predator to focus on one prey over another. Even a versatile predator, such as the Great Horned Owl, may favor one of its prey species if there is imbalance between hunting plus handling cost and energy gained (Molles). If searching and sighting prey takes a long time, the best strategy would be to eat anything encountered. On the other hand, if prey was fairly abundant and the main costs to owls involved capture, handling, and digestion, it would be most efficient to target the species with highest energy yields.

Great Horned Owls are "perch and pounce" hunters (Carolina Raptor Center). Unlike other raptors that may scan a large area on the wing, Great Horned Owls perch on a suitable lookout, such as a branch or fencepost, and dive a short distance to the ground with wings folded, talons forward. These powerful predators will crash through thick brush to reach prey, killing them instantly upon capture. Small enough prey are swallowed whole and deposited directly into the gizzard. There, digestive fluids and small stones dissolve usable parts, leaving behind fur, feathers, bones, teeth, and claws. These parts cannot pass safely through the digestive tract, and are instead compacted into a smooth, rounded pellet which is later regurgitated. The pellet may be stored in a special organ, the proventriculus, for up to twenty hours, meanwhile preventing the owl from eating again, though three to six hours is more average (Carolina Biological-The Secret Lives of Owls: Owl Pellets). A pellet may contain several individual prey species, especially if the prey were small and were eaten soon after one another. The regurgitated pellets can be collected and dissected for the indigestible parts of their prey, such as fur, bones, and possibly feathers, scales, and chitin. This method enables extraction of qualitative and quantitative data on owl diet (Marti 1987). Pellet analysis, in conjunction with a small mammal census, can be used to detect whether or not owls are eating prey in the same ratios that they exist in the environment.

Vertebrate predation studies are difficult to accomplish in the field, particularly in birds (Götmark and Post 1996). Despite the familiarity of the Great Horned Owl, there is scarce data on its dietary habits (Marti and Kochert 1996). Since this owl boasts an enormous home range throughout North America, its feeding behavior must vary with the local ecosystem accordingly. Hence, knowledge of local prey species is imperative in understanding the feeding habits of Great Horned Owls. The meadow vole *Microtus pennsylvanicus* is the main prey of several other owl species on the Bison Range, including the Short Eared Owl (*Asio flammeus*) and Long Eared Owl (*Asio otus*). This herbivorous rodent is active both day and night. The smaller deer mouse *Peromyscus maniculatus* is chiefly nocturnal. Great Horned owls begin hunting at dusk, often long before complete darkness (Marti 1974).

As rodent populations are subject to significant, sometimes severe fluctuations, predator populations that rely exclusively on them must either migrate in and out of the area or fluctuate in turn. Great Horned Owl populations are not affected by *Microtus pennsylvanicus* numbers, at least not to the extent other owl species are, but it might be demonstrated that they respond to the presence or absence of this prey species, which is especially noted for extreme population oscillations. Great Horned Owls may still selectively feed and take prey in ratios that do not reflect relative abundances of prey in the environment. Despite the common perception that Great Horned Owls will eat anything they can, it may be better for them to selectively avoid some prey and selectively choose others. At the same time, owl hunting techniques and time of activity coupled with variant prey behaviors could have a significant effect on whether the owls are choosing all prey equally.

HYPOTHESES AND PREDICTIONS

General Hypothesis: Owls will selectively feed on small mammal prey.

Prediction: Prey abundance in owl pellets will not reflect the relative abundance of prey available in the habitat.

Statistical Null Hypothesis: There will be no statistical difference in the relative abundance of small mammals in the diets of owls and in the local community.

Statistical Alternate Hypothesis: There will be a statistically significant difference in the makeup of the local prey population and that which will be found in the owl pellets.

MATERIALS AND METHODS

Location: The site for the study was located where Mission Creek intersects the north side of the National Bison Range in Moiese, Montana (see Map 1). The surrounding riparian zone and meadow (up to 70 meters on either side of the creek) was evaluated in terms of small mammal community and was also the area used to obtain owl pellets.

Method of Survey: The riparian zone surrounding Mission Creek was scouted for owl pellets bi-weekly for three weeks. Ground beneath trees, the primary feature of the riparian zone where owls could roost and regurgitate pellets, was carefully examined. Other vertical features that were likely owl hunting perches and roosting spots were also checked (Zimmerman et al. 1996). Knowledge of owl sightings from local biologists was also considered to help find owl dwellings.

A colleague completed a simultaneous small mammal survey in the Mission Creek riparian zone, recording species trapped and body masses.

Pellet Collection: Located pellets were assigned numbers (1-35), placed in their own sealed plastic bag, and labeled with the date collected and location. A handheld GPS unit assigned each pellet its own UTM coordinates at the point it was regurgitated. Pellet collection took place in or near the trapping locations, as well as a public picnic area adjacent to Mission Creek.

Pellet Dissection: Pellets were dissected by hand with forceps and a dissecting needle. *Microtus pennsylvanicus* and *Peromyscus maniculatus* were distinguished by skull and mandible features, particularly the molars. Larger prey was keyed out to the extent possible, however as there was no attempt to survey these animals in the environment, identifying them would have been superfluous. Three groups were tallied for statistical purposes: *Peromyscus maniculatus*, *Microtus pennsylvanicus*, and "other."

Data Analysis: The Chesson Electivity Index (Chesson 1978) was employed to detect any difference between species eaten by the owls and species available in the environment. The Chesson Electivity Index uses the parameter α_i, which calculates the probability of the prey encounter for the capture probability. $\alpha_i = (r_i/p_i)/ \Sigma\, (r_i/p_i)$ where (r_i) is the proportion of prey "i" in the diet, (p_i) is the proportion of prey "i" in the environment, and $\Sigma\alpha_i=1$. If the total number of prey species is (m), then when $\alpha_i= 1/(m)$, there is no evidence of selection. When $\alpha_i > 1/(m)$, selective predation may be occurring. Alternatively, if $\alpha_i < 1/(m)$, prey avoidance may be occurring.

A Chi-square test was run to compare the expected diet of owls based on prey abundance in the environment and the actual diets discovered from pellets ($p<0.05$). JMPIN 5.1 statistical program was used.

Owl Species Census: Recorded calls of the owls known to exist on the National Bison Range were played in order of smallest to largest owl at or near the locations of pellet collection to find out if species besides *Bubo virgnianus* inhabited the particular location under study. An amplifyer and speaker played the calls for two minutes with a quiet period of five minutes in between the calls. If no calls were returned or no owl was sighted flying into the area, the next call began. The order of calls happened as follows: Burrowing Owl (*Athene cunicularia*), Northern Saw-Whet Owl (*Aegolius acudicus*), Northern Pygmy Owl (*Glaucidium gnoma*), Western Screech Owl (*Otus kennicottii*), Long-Eared Owl (*Asio otus*), Short-Eared Owl (*Asio flammeus*), Barn Owl (*Tyto alba*), Barred Owl (*Strix varia*), Great Horned Owl (*Bubo virginianus*). The number of owls heard or seen was recorded at each location.

RESULTS

Three hundred fifty-six animals were trapped in the trap survey (see Figure 1). Two hundred thirty-one *P. maniculatus* individuals were trapped (average mass= 19.9 +/- 5.8 grams). One hundred sixteen *M. pennsylvanicus* (average mass= 34.5 +/- 10.5 grams) were also trapped. Eight other individual mammals were found and pooled as "other", including *Sorex cinereus*, *Sorex monticulus*, and *Zapus princes*.

Thirty five owl pellets were collected, yielding a total of seventy-two prey individuals (see Figure 2). Three individuals in the pellets were not identified to species as they were of animals larger than we trapped. They were probably lagomorphs, though for the purposes of this study, they were grouped as "other" with one *Pica pica* and one *Thomomys talpoides*. Two *Peromyscus maniculatus* were found, while the remaining sixty five individuals were all *Microtus pennsylvanicus*

The Chesson Electivity Index produced an $\alpha_{Microtus}$ of 0.985 and $\alpha_{Peromyscus}$ of 0.015. Species that appeared in the owls' diets that were not included in the small mammal census (*Thomomys talpoides, Pica pica,* other large prey) were not examined or calculated in the Chesson Index.

There was a significant difference between owl diet composition and prey composition in the environment ($\chi 2$: $p<0.001$, df= 2, see Table 1). Therefore, the null hypothesis that samples of prey in the environment and in the owl pellets are not different can be rejected. The alternative hypothesis, that the abundances of prey are in the environment and in the owls' diets are significantly different, can now be considered.

The Great Horned Owl (*Bubo virginianus*) was the only owl drawn into sight with call recordings. Three Great Horned Owls appeared near the bridge across Mission Creek at 9:30 pm on July 19th (see Map 1). On July 20th at 10:30 pm, six Great Horned Owls were drawn into the picnic area where many pellets had already been discovered. No other owl species were detected.

DISCUSSION

Early characterization of the Great Horned Owl claimed that they were hardly choosy with their food and would eat anything that was available (Baumgartner and Baumgartner 1944, Errington et al. 1940). More recent studies have found that these owls do not always demonstrate the most varied diets and will focus their hunting efforts in a smaller area if prey is abundant enough (Marti and Kochert 1996). The results from this particular study on the National Bison Range, at least, indicated that Great Horned Owls may be selectively feeding to a serious degree. The Chesson Elecvtivity Index results were strongly suggestive of non-random prey selection. Conversely, prey behavior might be the biggest factor in terms of explaining why owls were not eating small mammals in ratios anywhere close to the relative abundances in the environment.

To assert that owls were intentionally selecting some prey over others assumes at least two things. First, we must accept that our small mammal survey correctly estimated the relative abundances of the two mammals under scrutiny. If our traps were biased and wildly overestimated the numbers of *P. maniculatus* while diminishing the count of *M. pennsylvanicus*, it would weaken the claim that the owls were selecting meadow voles. The roughly 2:1 ratio of mice to voles in the mammal survey, however, compared to the approximately 30:1 ratio of voles to mice in the owl pellets is so tremendous that a trapping bias is unlikely, especially given that trapping took place in different microenvironments and censused over 300 individuals. Additionally, stating that owls are actively choosing *Microtus pennsylvanicus* over *Peromyscus maniculatus* assumes that these two rodents are equally likely to be encountered. It would be inaccurate to cite predator foraging behavior as a cause for this diet peculiarity if deer mice were in some way unavailable to the owls. Prey behavior and activity, though, might be a worthwhile area to explore.

Of the two small mammals under scrutiny, *Peromyscus maniculatus*, for several reasons, is probably a less ideal prey for a Great Horned Owl. These mice are completely nocturnal. Great Horned Owls begin hunting in the evening while meadow voles are active and mice are still inactive. This does not rule out the deermice, however, as Great Horned Owls continue to hunt into the night. Behavioral differences between mice and voles could also be important.

Peromyscus maniculatus has been shown by Clarke (1983) to be able to adapt their nightly activities depending on the intensity of moonlight. Owl hunting effectiveness increases with a waxing moon, but behavioral experiments have shown that deer mice respond in kind by limiting risky behavior, such as foraging in open areas under brighter moonlight. The majority of owl pellets collected for this study were taken on July 13, 2006, just two days after a full moon. If the pellets were egested after July 3, they were done so in the presence of a half moon waxing towards full (Phases of the Moon). Should meadow voles lack the behavioral adaptations that deer mice possess, they may be more vulnerable in strong moonlight. Moreover, it has been suggested that voles may have difficulty in wisely selecting habitat under high predation risk (Jacob and Brown 2000). Again, the owls might be eating voles because they are inferior predator-avoiders. On the other hand, Great Horned Owls cannot be considered superior hunters in low levels of light. Marti (1974) demonstrated through manipulative experiments that under lower levels of light, Great Horned Owls were poor at locating mice except by random encounter. Therefore, Great Horned Owls are probably best suited to hunting when there is significant sunlight left (when voles are active, but not mice) or when there is strong moonlight (when mice behave cautiously).

All other factors being equal, Great Horned Owls should almost certainly select a prey species of a larger size over a smaller species. Marti (1974) claimed that small prey would be too inefficient for a Great Horned Owl to eat, unless it was very easy to capture. Dietary habit studies on Great Horned Owls have estimated average prey weight at 44.5 grams (Marti and Kochert 1996) when the prey is predominantly comprised of rodents. Although body mass of prey was not estimated from salvaged skulls an mandibles in the pellets, the average weights of mammals trapped in the survey were 19.9 +/- 5.8 grams for the *P. maniculatus* (n=231) and 34.9 +/- 10.5 grams for the *M. pennsylvanicus* (n=116). Deer Mice may be too small to be worth capturing if there are larger voles present. Moreover, studies on barn owls, Deer Mice, and meadow voles (Lyman et al. 2001) revealed disparate prey vulnerability based on the ages of the rodents. Juvenile mice were preyed upon at a higher rate because they were dispersing into unfamiliar territory. Interestingly, adult voles were taken more often than the juveniles, which theoretically should have had the highest risk of capture as they were searching for suitable habitat. This occurrence supports similar findings by Derting and Cranford (1989).

This study has inferred much from owl pellets assumed to be produced by Great Horned Owls. Certainly there are other species of owls on the National Bison Range that could have produced them. However, several reasons support the conclusion that the pellets came from Great Horned Owls. Recorded calls only drew responses from this single species across several different spots near Mission Creek. Additionally, the riparian zone is particularly suitable habitat for Great Horned Owls to roost and hunt, while the Short-Eared Owl, a major predator of *M. pennsylvanicus*, prefers to hunt in open fields. However, preferred feeding habitats of these two owls overlap at the edge of the wooded riparian zone which was included in the survey and pellet search. The meadow outside the riparian zone is hypothetically good hunting ground for Short-Eared Owls. Still, Great Horned Owls are considered the dominant bird of prey in most ecosystems for good reason. It has been documented that Great Horned Owls have killed and eaten Short-Eared Owls near the interface of their hunting habitats (Bluhm and Ward

1979). The high abundance of Great Horned Owls in the Mission Creek area lends further assurance that other owls probably do not hunt and roost in the immediate area.

Finally, one must be cautious when using pellet data. Although it is widely accepted as the most reliable way to deduce owl diets, there is a risk of underestimating certain species' contributions to an owl diet. Animals with fragile bones (birds, especially) may be chemically digested by the owl before it egests a pellet. Additionally, larger animals, such as rabbits, may make several meals for an owl and appear spread out over many pellets, though only tallied once. Though pellet study is the best way known to study owl diets, it may not tell the entire story, which might be elucidated through observations of owls as they hunt.

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APPENDIX

Level	Estim Prob	Hypoth Prob	
Mp	0.90278	0.327	
Pm	0.02778	0.65	
other	0.06944	0.023	
Test	**ChiSquare**	**DF**	**Prob>Chisq**
Likelihood Ratio	130.4565	2	<.0001
Pearson	122.6333	2	<.0001

Table 1: Chi-square output comparing the observed composition of owl diets with the expected diets based on the survey of small mammals in the environment. (Mp= Microtus pennsylvanicus, Pm= Peromyscus maniculatus)

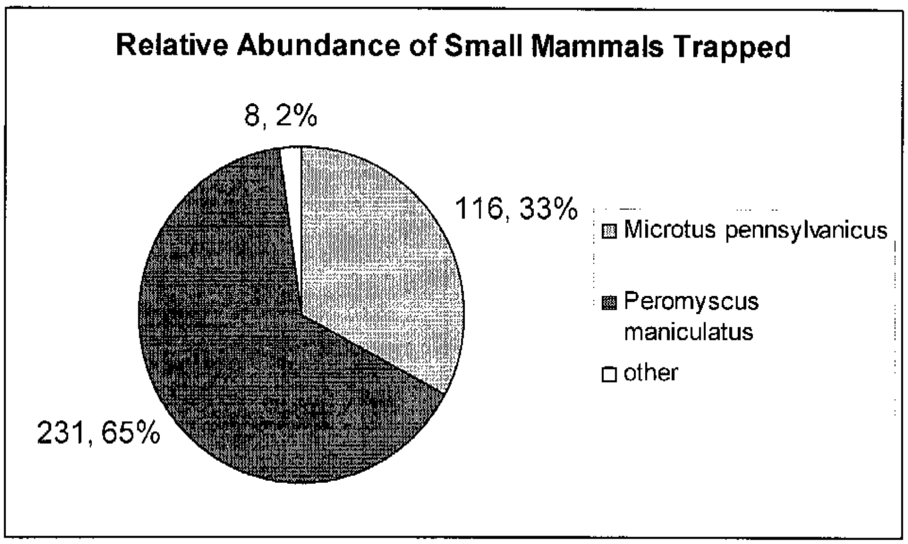


Figure 1: Compares the numbers of different species found in the trapping survey (total number trapped, percent of total). "Other" includes *Sorex cinereus*, *Sorex monticulus*, and *Zapus princes*.

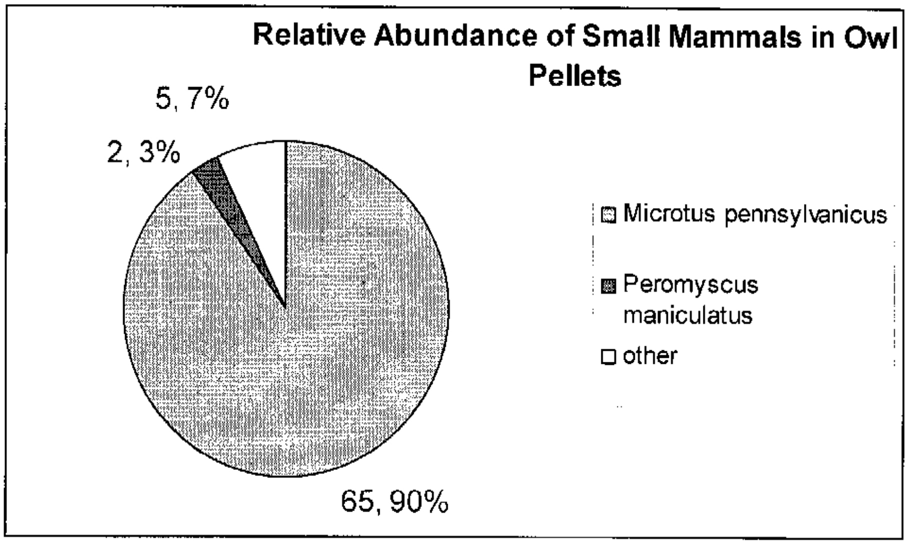
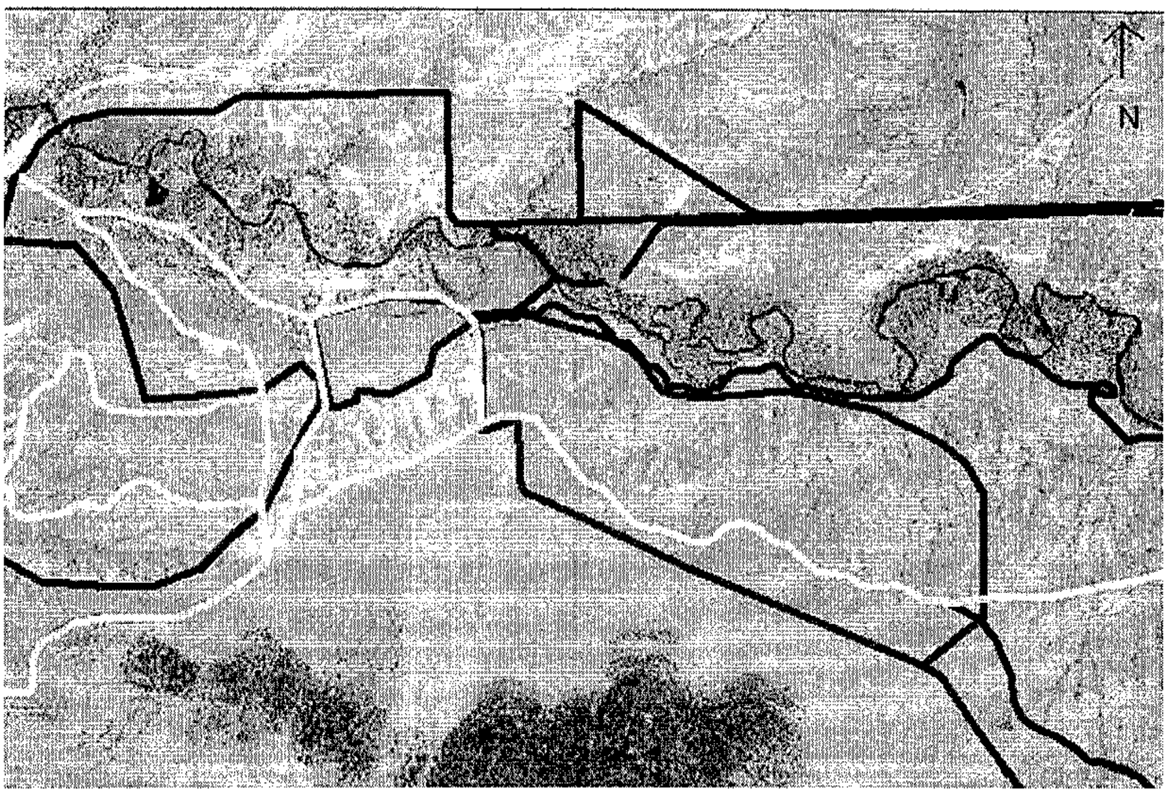


Figure 2: Shows the numbers of each species of prey found in dissected owl pellets (total number found, percent of total). "Other" includes *Thomomys talpoides*, *Pica pica*, and unknown larger prey.



Map 1: Aerial view of Mission Creek on the National Bison Range. Yellow and blue lines represent roads. Brown lines indicate fences. Black line shows the outer boundary of the bison range. Locations of owl pellet sites are highlighted with orange points. Green points denote spots where owls were successfully called in. Scale 1:24,000.