UNDERSTANDING THE TRADEOFF BETWEEN SAFETY AND FOOD QUALITY IN A MAMMALIAN HERBIVORE SPECIALIST, THE PYGMY RABBIT

by

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DEDICATION

For mom and dad.

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ABSTRACT

Conserving a sensitive animal species requires understanding the simultaneous tradeoffs between food and shelter within a landscape. Most management approaches only consider single factors like percent cover at landscape spatial scales. Quantifying the synergy between cover and food quality at a scale relevant to a foraging animal could better reveal the forces that shape habitat use. To better understand habitat use components, I investigated tradeoffs between predation risk and diet quality in a sagebrush endemic, the pygmy rabbit (*Brachylagus idahoensis*). This species is a rare example of a specialist herbivore that relies almost entirely on sagebrush for cover and 50-99% of its diet. I hypothesized that pygmy rabbits would forage in areas with low predation risk and high quality food, but would trade off lower predation risk for higher quality food. I compared food intake of pygmy rabbits during three double-choice trials designed to examine tradeoffs by varying the levels of predation risk (cover) and food quality (toxicity). Rabbits ate under dark cover and preferred non-toxic food. However, interaction results suggested that the value of cover can decrease if food quality is low and that the value of quality food can be reduced if cover is not optimal. Furthermore, foraging decisions by individual rabbits suggested strong variation in tolerance of toxins or predation risk. Preliminary field studies also show that heterogeneity of cover and diet quality in the sagebrush landscape can influence habitat use by pygmy rabbits, creating the potential for tradeoffs between cover and food quality. I measured physical and chemical plant characteristics to map habitat heterogeneity, and measured pygmy rabbit

use of each plant using counts of fecal pellets. These measurements allowed me to estimate how pygmy rabbits are responding to microhabitat heterogeneity in their landscape. Interactions between cover and diet quality can influence risk associated with foraging, thus ultimately shaping habitat use and should be considered in management decisions for pygmy rabbits and other mammalian herbivore specialists.

TABLE OF CONTENTS

DEDICATION iv

ACKNOWLEDGEMENTS v

ABSTRACT vii

LIST OF TABLES xii

LIST OF FIGURES xiii

CHAPTER ONE: INVESTIGATING THE TRADEOFF BETWEEN COVER AND FOOD QUALITY IN CAPTIVE PYGMY RABBITS 1

- Introduction 1
- Methods 5
  - Study Organism 5
  - Rabbit Capture 6
  - Experimental Procedures 6
  - Statistical analyses 10
- Results 11
- Discussion 13
- Literature Cited 20
- Figures 32

CHAPTER TWO: HOW SAGEBRUSH COVER AND CHEMICAL COMPOSITION IMPACT HABITAT USE OF FREE-RANGING PYGMY RABBITS 35

- Introduction 35

Methods 41

  Location 41

  Transects 41

  Cover Quality 42

  Diet Quality 43

  Habitat Use 44

Statistical Analyses 44

Results 45

Discussion 47

Literature Cited 57

Figures 74

Tables 79

CHAPTER THREE: SUGGESTIONS FOR INVESTIGTAING TRADEOFFS BETWEEN COVER AND FOOD USING CAPTIVE AND FREE RANGING HERBIVORES 80

Introduction 80

  Measuring Concealment 80

  Fecal Pellet Surveys 83

  Browsing as an Indicator of Habitat Use 84

  Habitat Use Cause and Effect 85

  Sampling in Varied Geological Features 86

  Testing a Predictive Model 88

Literature Cited 89

Figures 95

APPENDIX A 100

Scent Feeding Trials 100

Introduction 101

Methods 101

Statistical Analysis 102

Results 103

Discussion 103

APPENDIX B 105

Outdoor Feeding Trials 105

Introduction 106

Experimental Design 107

Video Behavioral Observation 109

Results 109

Conclusions 110

Appendix Figures 112

APPENDIX C 115

Appendix Literature Cited 115

LIST OF TABLES

Table 2.1 Number of variables (K), Akaike's Information Criterion corrected for small sample size (AICc), change in AIC from the top model (Δi), rank of model, and model weight (wi) from top models for habitat variables (Concealment, Total monoterpene (Monoterpene), and Distance) affecting habitat use (presence or absence of fecal pellets) by pygmy rabbits. 79

Table 2.2 Conditional logistic regression variable estimates, odds ratio estimates and 95% confidence intervals for each habitat variable (Concealment, Total monoterpene (Monoterpene), and Distance) from the top habitat use model... 79

LIST OF FIGURES

Figure 1.1 Schematic of the experimental arena used to test toxin and predation risk preferences by pygmy rabbits. Rectangles labeled treatment A and B represent the cover treatments containing food treatments offered in bowls (circles). Treatments were switched to the opposite location every 24h, as represented by the arrow between them. The nest box provided insulated refuge open to the rabbit at all times, and the curve behind the box was a length of plastic tubing that simulated a burrow and provided additional refuge. 32

Figure 1.2 Intake (mean + SEM, grams dry wt/day) of food by pygmy rabbits on each choice treatment during three trials. Striped bars represent foods with high toxin risk, dashed borders represent cover with high predation risk, and asterisks denote significance between treatments within a trial. The Toxin Only Trial provided rabbits the choice of toxic food (5% cineole by dry weight) or non-toxic food (no cineole added) under constant cover. The Cover Only Trial provided rabbits with the choice of non-toxic food under high predation risk (transparent cover) or under low predation risk (dark cover). The Tradeoff Trial provided rabbits with a choice of toxic food under low predation risk or non-toxic food under high predation risk. ... 33

Figure 1.3 Proportional intake of each choice treatment on the Tradeoff Trial for individual rabbits when rabbits were offered a choice to feed under a low predation risk (dark cover) that contained toxic food or high predation risk (transparent cover) with non-toxic food. The dashed line represents equal intake of both choice treatments. 34

Figure 2.1 Schematic of line transects on an active pygmy rabbit mound where habitat quality and use was measured. The line transect began at the center of mounds and extended out 30m in a random direction. Distance from mound (m), aerial concealment (%), monoterpene concentration (AUC/ $\frac{1}{10}$ mg DW) and habitat use (presence of fecal pellets) were measured on one randomly selected sagebrush plant within each 5x1m segment. 74

Figure 2.2 Concealment was measured by placing a checkered cube beneath a sagebrush plant, and counting the number of squares >50% covered by vegetation. 75

Figure 2.3 Concealment (%) according to fecal pellet presence at sagebrush plants (n=47) along eight 30m transects. "No" represents plants non used by pygmy rabbits and "Yes" represents plants used by pygmy rabbits. 76

Figure 2.4 Total monoterpene concentration (AUC/ $^1/_{10}$ mg DW) at sagebrush plants (n=47) along eight 30m transects according to fecal pellet presence. "No" represents plants non used by pygmy rabbits and "Yes" represents plants used by pygmy rabbits. 77

Figure 2.5 An example of mapping cover (concealment, %) and diet quality (the monoterpene β-pinene, AUC/g) variables at a mound occupied by pygmy rabbits. 78

Figure 3.1 The relationship between the average measurement of log-transformed concealment and cover from each mound (n=8, $f_{1,6}$=12.8, P=0.01). 95

Figure 3.2 This image was taken by an unmanned aerial vehicle flying over a field site managed by Bureau of Land Management (Shoshone Field Office, Shoshone, ID) near Magic Reservoir, located 20 miles south of Hailey, ID (43°3'N, 114°8'W). The red polygons are tracings of sagebrush plants on and around a mima mound. 96

Figure 3.3 The diagonal clip mark found on a sagebrush plant is evidence of browsing by pygmy rabbits. Note the relatively bright orange or yellow appearance, indicating fresh browsing. Fresh clip marks might also occasionally include a bright green ring of cambium. Old browsing marks are gray and sometimes splintered. 97

Figure 3.4 Suggested design for measuring quality of habitat resources and use by herbivores in habitats with a central area of activity used by herbivores (e.g. mounds). A high activity area should be established based on presence of active burrows, fresh fecal pellets, and recent browsing, along with four equidistant low activity areas. Total area should be equivalent in high and low activity areas. 98

Figure 3.5 Suggested design for measuring quality of habitat resources and use by herbivores in habitats with a decentralized area of activity (e.g. ridgelines, washes, flat plains, etc). Four high activity quadrants should be established using the same 'mound' criteria as in Figure 3.8, along with a single equidistant low activity area with a total area that is equal to the active areas. 99

Figure A.1 The top left, top right and bottom left images show the dark and transparent feeding stations set up on active pygmy rabbit burrows and < 1.5m away from an open burrow hole. The bottom right image displays the three sprigs of sagebrush anchored by plastic holders. The bottom left image also includes a researcher placing a motion-sensitive wildlife trail camera. 112

Figure A.2 A pygmy rabbit emerges from a burrow (bottom center) to investigate feeding stations. The transparent feeding station on the right represents high predation risk, and the feeding station on the left represents low predation risk. 113

Figure A.3 Time (s) spent on specific behaviors by pygmy rabbits captured by video over the course of a 3 day feeding trial in November, 2011. Light gray bars represent behaviors recorded while a rabbit was in or around a transparent feeding station, and black bars represent behaviors recorded while a rabbit was in or around a dark feeding station. 114

CHAPTER ONE: INVESTIGATING THE TRADEOFF BETWEEN COVER AND FOOD QUALITY IN CAPTIVE PYGMY RABBITS

Introduction

The direct and indirect interactions among trophic levels have been instrumental in understanding the ecology of plants, herbivores and predators. Although the strength, direction and importance of top-down and bottom-up effects on herbivores and their impact on community level dynamics are largely debated (Strong 1992; Polis and Strong 1996; Pace et al. 1999; Persson 1999; Polis 1999; Polis et al. 2000; Shurin et al. 2002; Schmitz 2004), it is becoming increasingly clear that predators and plants do not have isolated impacts upon herbivores. Predation and plant diets with toxic components can be simultaneously risky to herbivores (McArthur et al. 1991; Wiggins et al. 2006; McArthur et al. 2012), and the interaction between these variables can influence patterns of habitat use by herbivores.

Predators can shape the ecology of prey organisms through multiple direct and indirect pathways, including inducing behavioral shifts that can decrease the fitness of prey animals. In the presence of a predation threat, prey species might respond by altering foraging patterns and habitat use (Brown and Kotler 2004; Bakker et al. 2005; Jacob 2008). For example, dugongs (*Dugong dugon*) employed safer but less nutritionally rewarding foraging tactics when faced with increased shark presence (Wirsing et al. 2011). Schmidt (2000) showed that fox squirrels (*Sciurus niger*) decreased intake in response to both poor food quality and areas of high predation risk, as cued by open habitat. In addition to altered foraging patterns, prey species can suffer negative physiological effects from perceived predation risk. Increased predation risk reduced immunity and infection resistance in male lab rats (*Rattus norvegicus*, Horak et al. 2006), and lowered reproductive rates in a variety of bird species (Cresswell 2008). Pregnant snowshoe hares (*Lepus americanus*) exposed to simulated increased predation risk bore underweight, undersized litters as a result of elevated stress hormones (Sheriff et al. 2009). Thus, prey species often prefer habitat features that lower predation risk (Lima and Dill 1990; Bowers and Dooley 1993; Hik 1995).

Consumption of plants with chemical defenses also affects herbivores through direct and indirect pathways. For example, plant secondary metabolites can be toxic (Koppel et al. 1981; Sorensen et al. 2005a) or capable of reducing digestibility (Karban and Agrawal 2002). Furthermore, the necessary detoxification process can be energetically expensive for herbivores (Sorensen et al. 2005c). As expected, many herbivores preferred plants with lower plant secondary metabolite concentrations (Karban and Agrawal 2002; Sorensen et al. 2005a; Marsh et al. 2007). Such plant defenses likely have a particularly strong influence on the foraging patterns of specialist herbivores that rely on a narrow dietary range of well-defended plants (Shipley et al. 2009).

Predators and plant defenses do not act in isolation, but can synergistically shape the ecology and behavior of herbivores (Lima and Dill 1990; Kirmani et al. 2010). Browsing by herbivores can induce volatile emissions in plants that recruit predators (Dicke and Sabelis 1988). Some plant species are capable of inducing different chemical defenses based on the type of herbivory (Kahl et al. 2000). The negative metabolic and digestive effects of some toxic plants induce herbivores to behaviorally lengthen or slow their feeding events to mitigate consequences (Marsh et al. 2007). Such behavioral disruptions could, in turn, increase herbivore exposure to predators (Fedriani and Boulay 2006). These varied outcomes show that forage-induced responses in plants have the potential to be detrimental to herbivores in physical (predation) or physiological (toxic) ways.

Given the potential for interactions between predators and plant toxins, herbivores involved in multi-level trophic interactions must make foraging decisions based on simultaneous risks. The risks of predation and toxicity can be mitigated through foraging tradeoffs that determine where, when, and how to feed, as well as what to consume (Lima and Dill 1990). Prey species weigh food benefits against predation risk in accordance with cover provided by patchy, heterogeneous landscapes (Brown and Kotler 2004). Variation in toxin concentration can also influence the costs of consuming chemically defended foods relative to predation risk. For example, the presence of toxins in the diet was shown to have a greater effect on foraging patterns compared to perceived risk of predators by brushtail possums (*Trichosurus vulpecula*, Kirmani et al. 2010) and fox squirrels (*Sciurus niger*, Schmidt 2000). Moreover, herbivore foraging behavior is constrained to a greater extent when toxin and predation risks are combined compared to when either risk is present alone (Kirmani et al. 2010). These studies reveal complex explanations for foraging patterns by vertebrate herbivores: risk of predation can influence the value of food and risk of toxicity can influence the value of refuge from predators.

Most studies evaluating the tradeoffs between predation risk and dietary toxins have focused on generalist vertebrate herbivores. Yet for dietary or habitat specialists, the perceived value of non-toxic food or refuge from predators might be unique. For example, dietary specialists often possess higher tolerance for toxins in their selected diet but lower tolerance for novel toxins (Sorensen et al. 2005b). Dietary specialists might also be less flexible in their pursuit of safe habitats due to a restricted dietary breadth (Dearing and Cork 1999), as opposed to generalists that practice diet mixing behaviors (Wiggins et al. 2003; Villalba et al. 2004). The potentially disparate behavioral tradeoffs associated with toxins and refuge between generalists and specialists are important to better understand the structure of food webs and community dynamics.

I examined the tradeoffs between predation risk and toxins in a dietary specialist mammalian herbivore, the pygmy rabbit (*Brachylagus idahoensis*). I investigated these tradeoffs by addressing the following questions: 1) do pygmy rabbits have behavioral preferences to limit the risk from predators and toxins, and 2) do pygmy rabbits trade off the risk associated with either predators or food to lower the risk of the other? Because the cover quality and toxicity of sagebrush varies spatially and temporally within rabbit habitat (Kelsey et al. 1982; Katzner and Parker 1997; Karban 2007; Larrucea and Brussard 2008a), I predicted that pygmy rabbits can discriminate among that variation. The variation in both cover and food quality and the selective use of these resources by free-ranging pygmy rabbits make this system ideal for studying tradeoffs between cover and food resources in a specialist herbivore. To address tradeoffs, I conducted three experimental feeding trials to measure the foraging preference of captive, wild-caught pygmy rabbits. Rabbits were offered food choices that varied in potential risk of predation and toxin concentration. I hypothesized that pygmy rabbits would prefer to eat under cover that provided the greatest concealment and would choose to consume foods with the fewest toxins. In addition, I hypothesized that pygmy rabbits would trade off refuge from predators for non-toxic food when the alternative was poor refuge paired with toxic food. Investigating the interactions between predation risk and food quality in a specialist mammalian herbivore is crucial to understanding the mechanisms that drive herbivore diet selection and whether the constraints of herbivory differ between specialists and generalist mammalian herbivores. This type of information can provide an understanding of habitat use on two interacting dimensions, allowing for a more comprehensive approach to understanding habitat use by herbivores.

Methods

Study Organism

The pygmy rabbit is an ideal species for studying foraging tradeoffs in a specialist mammalian herbivore because it uses sagebrush (*Artemisia* spp.) for both refuge and food (Green and Flinders 1980). Moreover, pygmy rabbits are highly sensitive to variation in both predation risk and toxins. The majority of pygmy rabbit literature stresses the importance of vegetative cover as a predictor of habitat use (Green and Flinders 1980; Katzner and Parker 1997; Gabler et al. 2000; Heady and Laundré 2005; Larrucea and Brussard 2008a). In accordance, avian predation is identified as a main source of mortality for pygmy rabbits (Crawford et al. 2010). Sagebrush comprises more than 55% of the summer diet and nearly 100% of the winter diet of pygmy rabbits (Green and Flinders 1980; Weiss and Verts 1984; Thines et al. 2004). Recent research has demonstrated that highly browsed sagebrush plants contained lower concentrations of several toxins relative to unbrowsed plants, and captive feeding trials confirmed that pygmy rabbits select browsed over unbrowsed sagebrush (Ulappa 2011). In addition, field observations revealed a range of browsing intensity on adjacent sagebrush plants by pygmy rabbits. This evidence suggests that pygmy rabbits have thresholds to sagebrush toxins that influence diet selection and possibly habitat use.

Rabbit Capture

During summer and fall of 2010, I live-trapped eight adult +300g pygmy rabbits (five females and six males) from three sagebrush-dominated sites in Idaho, USA: Magic Valley (43°3’N, 114°8’W), Raft River (42°8’N, 115°8’W), and Lemhi Valley (45°2’N, 113°8’W). Live-trapping consisted of flushing pygmy rabbits from concealed locations and chasing them into nearby burrows, after which Tomahawk traps (48x15x15cm) were inserted into burrow entrances. The physical health of captured rabbits was assessed by a licensed veterinarian. Rabbits were then placed into quarantine for two weeks at Washington State University’s Small Mammal Research Facility.

During non-testing phases, rabbits were housed indoors within 65x65x40cm individual pens and fed 70g of commercial rabbit pellets (Purina Rabbit Chow Professional Natural AdvantEdge, hereafter ‘control pellets’) and 15g of fresh mixed greens (lettuce, clover, cilantro, and greenhouse grown sagebrush) daily (hereafter ‘basal diet’). All fresh food was grown on site without fertilizers. Water was provided *ad libitum*. Rabbits were used in experiments within one month of capture.

Experimental Procedures

During outdoor trials, individuals were housed in 5.5x3.35m wire enclosures and allowed to feed from two feeding stations (30.5x27x30.5cm plastic boxes) placed equidistant from each other and from a nest box refuge (Figure 1.1). Feeding stations were manipulated to elicit choices involving cover or food quality. During indoor trials, rabbits were housed in individual pens (as described above) so cover remained constant but food quality was manipulated. In all trials, rabbits had the choice to feed from each of two ceramic bowls containing foods of different quality. Each independent trial was designed to gauge the relationship between food quality and cover as factors driving foraging behavior. Before all trials, rabbits were weighed to insure normal body mass. If an individual ate <30g in the course of a feeding trial, the individual was removed from the study and returned to indoor pens and the basal diet, hence the varying sample size between trials.

I used daily intake as a biomarker of the value that individual pygmy rabbits placed on the availability of cover and food. I compared intake under varying cover and food quality treatments using three independent trials in the following chronological order:

1) A Toxin Only Trial in which only food quality was varied to validate that pygmy rabbits preferred food without toxins (Shipley et al. 2006).
2) A Cover Only Trial in which cover quality was varied to determine if pygmy rabbits preferred to consume non-toxic food under dark (low predation risk) or transparent (high predation risk) cover.
3) A Tradeoff Trial in which both cover and food quality were varied to determine which resource rabbits tradeoff for the other.

I provided at least five days (and no more than 30 days) between each trial to allow rabbits to regain any lost weight. Each four day treatment trial was preceded by two control days during which rabbits were allowed to acclimate to the experimental setting without manipulation of the treatment variable. During the control days, rabbits were offered the basal diet of fresh mixed greens and two bowls each containing 35g of commercial rabbit pellets under different cover treatments depending on the trial. The control days for the Toxin Only Trial consisted of no manipulation of cover. The control days for the Cover Only Trial consisted of two opaque feeding stations. The control days for the Tradeoff Trial consisted of one transparent cover feeding station and one dark cover feeding station. Preliminary studies using outdoor exclosures revealed a trend of directional bias between sides of the enclosures; some rabbits consistently ate more out of the dish on one side of the pen compared to the opposite side of the pen even when food and cover quality was equal on each side (paired t test, t_{17} =1.96, P=0.065). To compensate for this directional bias, treatment location was randomly determined at the onset of trials and switched every 24h to the opposite side of the enclosure (Figure 1.1). Water was provided *ad libitum*.

During the trials, the diets offered to rabbits consisted of commercial rabbit pellets, which were either left unaltered (non-toxic, low risk food treatment) or mixed with 1,8 cineole (hereafter cineole, Alfa Aesar, stock #: A12269), a monoterpene naturally found in sagebrush (Kelsey et al. 1982; Welch and McArthur 1981; Shipley et al. 2006). The cineole treatment represented a toxic, high risk food treatment. Monoterpenes are considered toxins, as they can disrupt cellular function (Wink 2008), can irritate mucous membranes (Hedenstierna et al. 1983), cause diuresis and nephritis

(Dearing et al. 2000), and can be energetically costly (Sorensen et al. 2005a). Monoterpenes can deter herbivores from feeding (Sinclair et al. 1988), including pygmy rabbits (Shipley et al. 2006). Cineole was added to commercial rabbit pellets at 5% by dry weight (DW). The toxic food was prepared fresh each morning of the trial by thoroughly mixing 300g dry pellets with 15g of cineole in a glass jar. Although 5% cineole is higher than that found naturally in sagebrush, the total monoterpene content in sagebrush can be as high as 4% (White et al. 1982; Shipley et al. 2006), allowing for a comparable total toxin load. Furthermore, 5% is known to deter feeding by pygmy rabbits but allows rabbits to maintain sufficient body mass (Shipley et al. 2012). During trials that contained toxic food, I collected and replaced all food every 12h to minimize volatilization of cineole.

Experimental Days

For the Toxin Only Trial, rabbits were given a choice of two bowls containing either non-toxic or toxic food under constant cover (that is, indoor, individual pens used during non-testing phases). For the Cover Only Trial, non-toxic food was offered to rabbits under each of the two feeding stations. The “dark” cover treatment consisted of a plastic box (i.e., feeding station) that was blacked-out with contact paper to simulate greater concealment associated with putative lower predation risk found under dense sagebrush plants. The “transparent” cover treatment (i.e., feeding station) consisted of a completely transparent box to simulate higher predation risk found in open habitat. The Tradeoff Trial used the same experimental design as the Cover Only Trial, except toxic food was paired with dark cover and non-toxic food was paired with transparent cover.

The Cover Only Trial was conducted first to validate that cover quality is a parameter that influences habitat use by pygmy rabbits (Katzner and Parker 1997; Gabler et al. 2000; Heady and Laundré 2005; Larrucea and Brussard 2008a). The Cover Only Trial was followed by the Tradeoff Trial to determine if diet quality could influence the value of cover. Although I did not control for the order of trials, the five day period between trials was provided to minimize carryover effects.

Food intake by individual rabbits was determined for each treatment for each day of the trial by calculating the difference between the dry matter of food offered and the dry matter of food rejected. Rejected food was collected during the experimental days every 12h or 24h and dried for 24h at 100°C. A subsample of food was weighed each day and dried for 12h to determine percent dry matter; these values were used to convert fresh food offered and rejected into dry matter offered and rejected. Mean intake (DW/day) was calculated for the four days of each trial. The ratio of mean intake under dark cover relative to transparent cover was calculated for the Cover Only Trial and Tradeoff Trial. This ratio indicated the relative value that rabbits placed on cover when diet quality was constant (Cover Only Trial) and when diet quality varied (Tradeoff Trial).

Statistical analyses

The dependent variables were the mean intake of food (4 day average) on each treatment within a trial and the ratio of food eaten under dark relative to transparent cover in the Cover Only and Tradeoff Trials. Trials have varying sample sizes because some rabbits failed to eat a minimum of 30g/day. Separate paired t-tests were used to compare intake between toxic vs. non-toxic diet on the Toxin Only Trial, between high risk vs.

low risk cover on the Cover Only Trial, and to compare the ratio of intake under dark relative to transparent cover between the Cover versus Tradeoff Trial. Intake data is presented as means with standard error of the mean (mean ±SEM). Outliers were identified with box plots and removed. Data was tested for normality using Shapiro-Wilks prior to analysis, and data sets that were not normally distributed were log-transformed to meet the assumptions of normality. Finally, a power analysis was conducted to investigate population effect size for Tradeoff trial results. All statistical analyses were performed using JMP version 8.0 software of the SAS Institute 2008.

Results

During trials that contained toxic food, I collected and replaced all food every 12h to minimize volatilization of cineole. Analysis of rejected toxic food using gas chromatography methods developed for monoterpenes in sagebrush (Ulappa 2011) confirmed that an average of 1.05% of cineole volatilized during the 12h period. There was no difference in cineole concentration between what was offered and rejected by pygmy rabbits (t_7 = -0.31, P=0.76).

Toxin Only Trial – Pygmy rabbits preferred non-toxic food to toxic food dosed with cineole at 5% of DW. Rabbits consumed nearly four times more non-toxic food (36.1g ± 3.82) relative to toxic food (9.3g ±0.95) when predation risk was constant (t_7=6.0, P=<0.001 Toxin Only Trial, Figure 1.2).

Cover Only Trial – Pygmy rabbits preferred to forage under low predation risk conditions associated with high concealment. Rabbits consumed more than twice as much food under the low predation risk treatment (dark cover, 26.2g±2.53) than under the high predation risk (transparent cover, 10.2g±1.43) when food was non-toxic (t_9= -4.36, P=0.002, Cover Only Trial, Figure 1.2).

Tradeoff Trial – Neither cover nor food quality were dominant in driving pygmy rabbit foraging decisions in trials when they were forced to trade off one resource for the other. During the control days of the Tradeoff Trial when food was held constant (i.e., non-toxic food) and placed under dark or transparent cover, rabbits preferred to feed under low predation risk (14.2g±2.55) relative to high predation risk (5.0±1.34, t_6=-5.54, P=0.002). However, when cover and toxin treatments were combined during treatment days, there was no significant difference in intake between non-toxic food under high predation risk (25.5g±4.4) and toxic food under low predation risk (19.0g±4.11, t_7 = 0.79, P=0.46, Figure 1.2). The ratio of intake under dark relative to transparent cover was significantly higher in the Cover Only Trial (4.0 ± 0.87) than in the Tradeoff Trial (1.3 ± 0.54; t_7=-3.13, P=0.017).

I documented a gradient of individual variation in predation risk behavior during the Tradeoff Trial (Figure 1.3). Out of eight rabbits, three showed preferences for toxic food under low predation risk, while five showed strong preferences for non-toxic food under high predation risk. These results do not support our hypothesis that rabbits would trade off greater cover for high food quality. Instead, no single variable emerged as the driving factor behind pygmy rabbit foraging due to variation among individuals in foraging behavior. A power analysis using the mean difference in individual intake between toxic food and non-toxic food (6.56g, SD = 23.52) during the Tradeoff Trial as the effect size indicated that a sample size of 103 rabbits would be required to detect significance at alpha = 0.05 with a power level of 0.8.

Discussion

Our results demonstrate how value assigned to both predator and toxin risks can shape foraging patterns of a dietary specialist herbivore. Previous studies have demonstrated the influence of one or more factors on the foraging behavior of generalist herbivores (Fedriani and Boulay 2006; Kirmani et al. 2010; Wirsing et al. 2011). However, the present study offers important insight into how the dynamics among plants, specialist herbivores and risk of predation can be shaped by interactive relationships, rather than highlighting linear relationships between single factors. Our study is unique in exploring the tradeoffs that stem from conflicting factors that govern habitat use by a specialist mammalian herbivore, and highlights the individual variation that can accompany such tradeoffs.

While our results concur with previous research that stresses the importance of cover to pygmy rabbits (Katzner and Park 1997; Gabler et al. 2001; Heady and Laundré 2005; Larrucea and Brussard 2008a&b; Camp et al. 2012), our experiments suggested that the presence of toxins in the diet might force individuals to trade off toxin and predation risk. As expected, pygmy rabbits avoided toxic foods during the Toxin Only Trial, but were willing to consume higher amounts of toxins in the Tradeoff Trial. The choice to avoid cineole and other toxins is likely associated with negative consequences of toxin intake (Dearing et al. 2000). Previous research has demonstrated that intake declines when herbivores are fed diets containing cineole above 4% (Boyle and McLean 2004). Despite the negative effects of ingestion of toxins including cineole, our results demonstrated that under certain conditions, pygmy rabbits chose to consume toxic food when the alternative non-toxic food was associated with high predation risk (poor cover).

I propose that this short-term response to minimize immediate predation risk by consuming more toxins under high cover would not be sustainable. Food tradeoffs that have the potential to decrease fitness are not unusual for a prey species. For example, snowshoe hares had poorer body condition scores, despite an abundance of forage, in experimental plots with predators, whereas snowshoe hares in plots without predators had higher body condition scores (Hik, 1995). Furthermore, long term intake of toxins cannot be sustained due to energetic and detoxification costs (Sorensen, 2005a), leading to severe consequences. For example, snowshoe hares fed paper birch (*Betula neoalaskana*) sprigs rich with naturally-occurring triterpenes in no-choice feeding trials would reduce food intake to the point of starvation (Reichardt et al., 1984) when birch sprigs without the toxin were not available. More research is needed to identify a temporal tipping point in the food risks undertaken by pygmy rabbits under threat of predation.

Pygmy rabbits also chose to forage under cover, even in the absence of a true predation risk. No true predator threat was applied during the trials. However, previous studies investigating habitat use by prey species have demonstrated that a predator's presence was not always required to elicit avoidance behaviors (i.e., seeking cover, Dickman 1992a; Kotler et al. 2010). I assumed that strong selection for predator avoidance behaviors should influence selection of cover, even under captive conditions. The importance of cover as a predictor variable for suitable habitat has been well-documented (Green and Flinders 1980; Weiss and Verts 1984;Katzner and Parker 1997; Gabler et al. 2000; Heady and Laundré 2005; Larrucea and Brussard 2008a&b) and can be attributed primarily to a high risk of predation (Crawford et al. 2010). Given the definitive preference for cover in our trials, I consider it a principal mechanism relative to other variables for which value can depreciate over time. For example, the effect of predator scent on herbivore foraging patterns diminishes over time (Kirmani et al. 2010). This time effect might be attributed to the risk allocation hypothesis (Lima and Bednekoff 1999), which states that prey species can become habituated over time to a cue that has lost its reliability as an honest signal. It is possible that pygmy rabbits ate more food under transparent cover than dark cover during the Tradeoff Trial compared to the Cover Only Trial not because of toxins in the food, but because of habituation to conditions. It is also possible that pygmy rabbits learned that there was no true predation risk associated with feeding under the transparent cover and therefore did not tradeoff low predation risk when choosing the low toxin, poor cover treatment. However, the control days during the Tradeoff Trial control period offered the same transparent and dark cover options, but both contained non-toxic foods. During the control days of the Tradeoff Trial there was a foraging preference under dark cover (15.2g±2.1) over transparent cover (4.5g±1.0), which was similar to preference on the Cover Only Trial that occurred approximately 10 days earlier. The preference for dark cover on the control days of the Tradeoff Trial was followed by no significant difference between cover treatments during subsequent experimental days when low predation risk (dark cover) was paired with toxic food and high predation risk (transparent cover) was paired with non-toxic food. These results demonstrate true tradeoffs among risk treatments, rather than habituation or learning. Additional studies are needed to identify which factors are most important in explaining foraging tradeoffs in herbivores.

Results from the Tradeoff Trial suggested that individuals responded heterogeneously to a combination of adverse foraging conditions. Studies that ignore individual variation and focus on population-level trends risk overlooking disparate environmental challenges that can stem from a myriad of behavioral and physiological traits. For example, responses to predation risk can vary widely with an individual's 'personality,' a trait largely defined by consistent patterns of behavior, that lead to direct fitness tradeoffs (Wilson 1998; Gosling 2001; Boon et al. 2008). The age of an individual and its experience with risk also can affect predator-prey dynamics (Lima and Dill 1990; Panzacchi et al. 2008). The sex of an individual can affect predation risk, usually due to a combination of inherent predator choice, sexual dimorphism, and other sex-specific behaviors or traits that increase exposure to predators (Fitzgibbon and Fanshawe 1989; Norrdahl and Korpimaki 1998). Individuals vary in their response to forage quality, a phenomenon mostly studied in carnivores, which can significantly impact trophic levels of an ecosystem (Bolnick et al. 2003). Habitat preference can also differ widely among individuals, but it is mostly thought to be influenced by a combination of other risk-influenced factors like age, sex, and personality (Bolnick et al 2003; Hillen et al. 2011). Given the combination of genetic factors and environmental variation in driving individual preferences, ecologists suggest that the preservation of intraspecific genetic diversity will aid in improving overall population fitness (Smith et al. 2001; Bolnick et al. 2003). These extrinsic, continually interacting variables highlight the potential for tradeoffs to drive habitat use in specialist herbivores. While no significance was found between intake of toxic food during the Tradeoff Trial and sex, age, length of time in captivity, intake during the Toxin Only trial or trapping location, these variables should not be ruled out as possible explanations for the range of individual responses.

More research and a larger sample size are needed to determine potential sources of individual preference. The power analysis results show that the variation observed in this study would require a much larger sample size to achieve the same results within a population. However, the results of the Tradeoff Trial demonstrate the variability of responses and show that no single risk variable drives intake. Furthermore, the usefulness of conducting post-hoc power analyses is debated (Steidl et al. 1997), given the inclusion of arbitrary parameters and an assumption of known rather than estimated input values, among other arguments (Johnson 1999).

I acknowledge that a captive study might not directly reflect conditions in a field setting. Captive herbivores often tolerate larger amounts of toxin given their lack of options (Marsh et al. 2006) and receive a quality of food (i.e., commercial pellets) that differs from those that occur in their natural habitat. My experimental design did not incorporate a true predation risk, but rather sought to modify perceived predation risk indirectly through manipulation of concealment. The clear foraging patterns related to cover between trials, despite the lack of a true predator cue, allow me to conclude authentic tradeoff results. In nature, pygmy rabbits are exposed to avian and terrestrial predators (Crawford et al. 2010). Tall, dense sagebrush provides critical cover from such threats (Green and Flinders 1980; Weiss and Verts 1984; Katzner and Parker 1997; Gabler et al. 2000; Heady and Laundré 2005; Himes and Drohan 2007; Larrucea and Brussard 2008a). The use of darkened and transparent cover treatments was intended to simulate natural foraging scenarios that pygmy rabbits would encounter under sagebrush with varying amounts of cover. Further studies are needed to translate thresholds and tradeoffs of predator and toxin risks from captive studies to the field (Kirmani et al.

2010), especially with respect to individual variation in mammalian herbivore foraging strategies.

As might be expected, the majority of literature that examines tradeoffs that drive habitat use feature generalist herbivores. My study is the first to examine this same dynamic tradeoff between cover and food in a specialist mammalian herbivore. Foraging choices between generalist and specialist mammalian herbivores might exhibit distinct patterns. Generalists typically tolerate a variety of toxins at low thresholds, whereas specialists have higher tolerance thresholds of fewer toxins that correspond to their primary browse species (Sorensen and Dearing 2003; Sorensen et al. 2004). Generalists often practice diet mixing to reduce the potentially harmful consequences of toxin ingestion (Provenza et al. 2003), a practice that might not apply to a specialist herbivore. Shipley et al. (2006) found that pygmy rabbits, when compared to a generalist counterpart, the eastern cottontail rabbit (*Sylvilagus floridanus*), could better tolerate diets high in cineole concentration. However, the Tradeoff Trial demonstrated that a dietary tolerance to toxins does not necessarily trump other habitat factors. In comparison, a study by Kirmani et al. (2010) used cineole and owl pellets to induce foraging tradeoffs in wild brushtail possums (*Trichosurus vulpecula*), a dietary generalist. In that study, cineole was the most reliable feeding deterrent, trumping the predation risk cue provided by the owl pellets.

Although the predation method of each study is different (i.e., cover treatments versus predator scent), the results suggest that values placed on habitat cues are different between specialists and generalists. Given the results of my study, specialists still respond to dietary quality but not as strongly or unanimously as generalists, perhaps because of a greater physiological tolerance to toxins in their diet (Shipley et al., 2006). Generalists are expected to respond more strongly than specialists to variation in dietary quality due to physiological constraints that limit intake of toxins in any one plant. Existing data suggests that although both specialist and generalist herbivores do make tradeoffs between predation and toxin risk, the tipping points of these tradeoffs may be influenced by foraging strategy. Comparing the threshold at which specialists and generalists tradeoff risks deserves further attention.

My findings support the conclusion that cover and diet quality simultaneously interact to drive foraging decisions by pygmy rabbits. Results suggest that the foraging tradeoffs between predation risk and toxin risk do exist in a specialist herbivore and might be driven by individual variation. These results are consistent with recent work showing the importance of diet quality largely driving the foraging decisions of generalist herbivores and the overwhelming focus of the importance of cover in pygmy rabbit literature. Variation is present in both cover and diet quality within and among individual plants. Specifically, refuge from predation varies among sagebrush plants (Katzner and Parker 1997; Katzner et al. 1997; Gabler et al. 2000; Larrucea and Brussard 2008a&b) and can also influence selection of habitats by pygmy rabbits (Sanchez and Rachlow 2008). In addition, toxin concentration in sagebrush varies spatially (Ulappa 2011) and temporally (Welch and McArthur 1979; Welch and McArthur 1981; Behan and Welch 1986), and this variation might influence habitat use by rabbits. My research showed that cover and food hold different values among individual animals, thus indicating that individuals can make markedly diverse foraging choices within a heterogeneous environment. This wide array of variability of habitat features and herbivore tolerance to those features on several different scales could influence management practices. Conservation efforts should begin on a scale relevant to the foraging animal in order to understand the microhabitat features that drive habitat use. Steps to conserve diet quality within a habitat will complement the existing emphasis on cover (Gabler et al. 2000; Gabler et al. 2001; Heady and Laundré 2005). Incorporating diet quality into efforts to predict habitat use will improve our understanding of foraging patterns and identify the habitats for conservation efforts.

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Figures

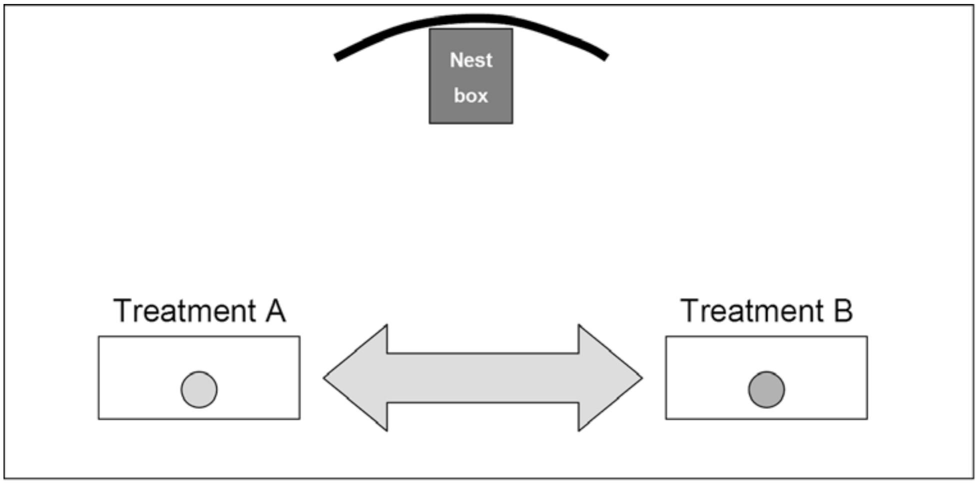

Figure 1.1 Schematic of the experimental arena used to test toxin and predation risk preferences by pygmy rabbits. Rectangles labeled treatment A and B represent the cover treatments containing food treatments offered in bowls (circles). Treatments were switched to the opposite location every 24h, as represented by the arrow between them. The nest box provided insulated refuge open to the rabbit at all times, and the curve behind the box was a length of plastic tubing that simulated a burrow and provided additional refuge.

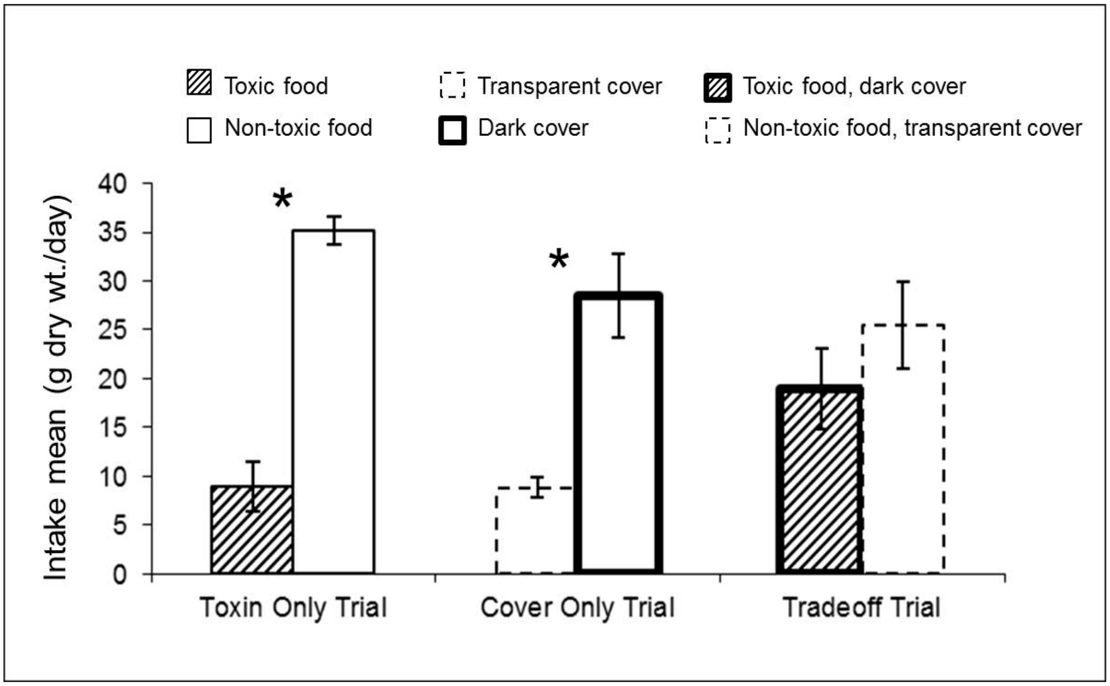

Figure 1.2 Intake (mean + SEM, grams dry wt/day) of food by pygmy rabbits on each choice treatment during three trials. Striped bars represent foods with high toxin risk, dashed borders represent cover with high predation risk, and asterisks denote significance between treatments within a trial. The Toxin Only Trial provided rabbits the choice of toxic food (5% cineole by dry weight) or non-toxic food (no cineole added) under constant cover. The Cover Only Trial provided rabbits with the choice of non-toxic food under high predation risk (transparent cover) or under low predation risk (dark cover). The Tradeoff Trial provided rabbits with a choice of toxic food under low predation risk or non-toxic food under high predation risk.

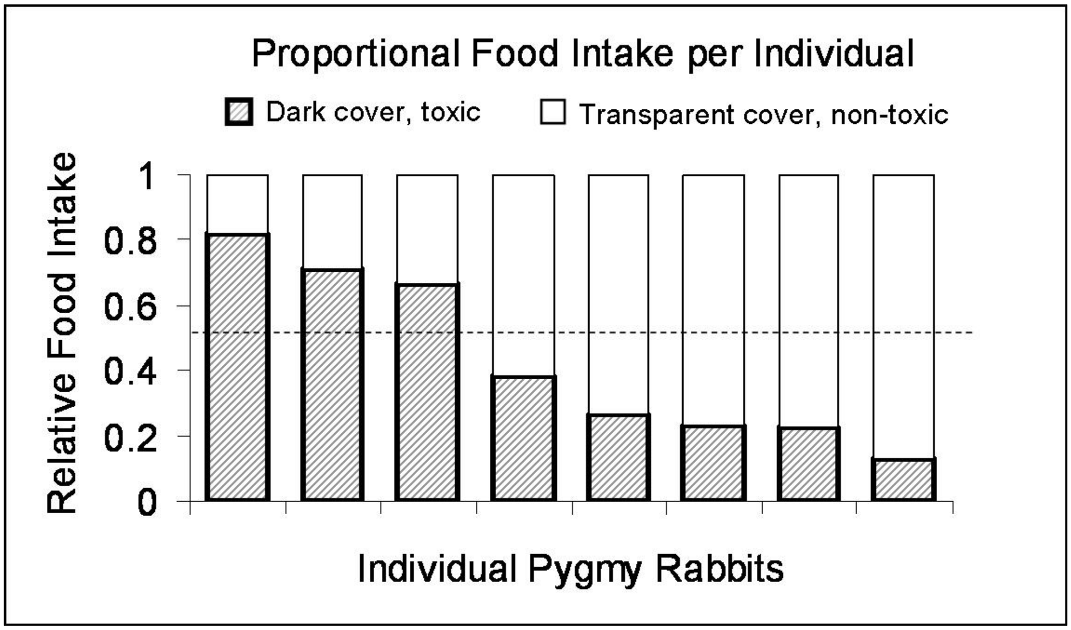

Figure 1.3 Proportional intake of each choice treatment on the Tradeoff Trial for individual rabbits when rabbits were offered a choice to feed under a low predation risk (dark cover) that contained toxic food or high predation risk (transparent cover) with non-toxic food. The dashed line represents equal intake of both choice treatments.

CHAPTER TWO: HOW SAGEBRUSH COVER AND CHEMICAL COMPOSITION IMPACT HABITAT USE OF FREE-RANGING PYGMY RABBITS

Introduction

For the majority of prey species, vegetation is a critical component of habitat quality. Vegetation can mitigate negative consequences associated with predation risk by providing refuge for prey. Prey often seek safer spaces within a landscape according to presence, abundance, or spatial arrangement of predators or predation risk (Formanowicz and Bobka 1989; Creel et al. 2005; Creswell et al. 2010; Wilson et al. 2012). For example, elk (*Cervus elaphus)* abandoned prime grassland habitat for wooded areas that offered subpar grazing but greater protection from predators (Creel et al. 2005). Mice (*Peromyscus spp.*) decreased foraging activity during bright lunar phases as compared to darker phases, indicating a perceived link between greater illumination and increased detection and therefore risk of predation (Dickman 1992; Kotler et al. 2010; Gutman et al. 2011). Wild guinea pigs (*Cavia aperea*) took advantage of agricultural borders by foraging in short grasses immediately adjacent to uncut, taller grasses, which provide effective escape from predator threats (Cassini and Galante 1992). Familiarity with available refuges in a habitat also can also aid a prey animal in avoiding or decreasing chances of predation, as shown by greater escape ‘efficiency’ by chipmunks (*Tamias striatus*) in familiar versus novel habitats (Clarke et al. 1993). The removal or degradation of habitat that provides cover can alter movement and forage patterns and negatively affect body condition (Amo et al. 2007).

For herbivores, vegetation also serves as a food resource that can vary by quantity and quality. Availability of food plants can drive herbivore population dynamics, even entire ecosystems (Polis and Strong 1996; Polis 1999). Plant characteristics, like nutrients and chemical composition, can influence herbivore habitat selection as well. For example, European rabbits (*Oryctolagus cuniculus*) chose to forage on plants with the highest protein (Somers et al. 2008). Moose (*Alces alces*) browsed according to the lowest concentration of chemical defenses (Stotler et al. 2009). Furthermore, variation in vegetation diet quality also can shape distribution of herbivores. For example, habitat occupancy patterns of round-tailed muskrats (*Neofiber alleni*) reflected variation in quality of patches of suitable foods (Schooley and Branch 2007). In addition, the concentration of chemical defenses in plants explained the distribution of koalas (*Phascolarctos cinereus*) within a habitat (Moore and Foley 2005). Selecting plants that have optimal dietary constituents can increase forager fitness. For instance, populations of brushtail possums (*Trichosurus vulpecula*) for which habitat contained trees with greater digestible nitrogen had higher reproductive success compared to neighboring populations associated with trees lower in digestible nitrogen (DeGabriel et al. 2009).

Given the potential fitness consequences associated with vegetative quality from both refuge and dietary perspectives, spatial and temporal variability in quality of vegetation could influence habitat use by herbivores. Vegetation cover and the refuge it provides can vary across spatial and temporal scales. Although refuge quality can vary for a prey species at a landscape level (Anderson et al. 2010), variation in refuge quality at smaller spatial scales is likely to be more relevant to a foraging animal. Specifically, plant characteristics like crown height, width, or cover density can vary at a habitat scale relevant to the foraging animal (Stapp 1997; Butler et al. 2005a; Price 2009). Vegetation cover characteristics can shift with seasons. For example, prey species that rely on deciduous plants for cover must alter anti-predator behavior according to the season (Martin and Lopez 1995). Game animals select habitats with varying levels of cover during high and low risk hunting seasons, indicating that they perceive and respond to spatiotemporally variable habitat characteristics (Tolon et al. 2009). Habitat use also can be explained through variation in diet, like nutrient concentration and defensive chemicals. For example, big sagebrush plants (*Artemisia tridentata*) grown in controlled conditions can vary markedly in monoterpenoid and protein content (Welch and McArthur 1979; Welch and McArthur 1981). These chemical and nutrient profiles of individual plants can also vary seasonally (Wilt and Miller 1992), which could affect herbivore browsing patterns (Bray et al. 1991). Quantity and quality of available winter forage are thought, in part, to be responsible for mountain hare (*Lepus timidus*) population cycles (Pulliainen and Tunkkari 1987).

The functional values of cover and food might not co-vary, and therefore, variation in these resources has the potential to present tradeoffs for herbivores. Predation pressure can cause foraging animals to alter or restrict foraging efforts (Wirsing et al. 2011), thus leading to a potential decline in fitness (Arthur et al. 2004; Creel and Christianson 2008; Tuft et al. 2011; Wirsing et al. 2011). When given a choice, wood mice (*Apodemus sylvaticus*) deliberately foraged on ripe fruits in safe microhabitats (Fedriani and Boulay 2006). However, when these mice were placed in microhabitats without refuge (i.e., heightened predation risk), they foraged indiscriminately on ripe and unripe fruits. Fedriani and Boulay (2006) hypothesized that although the consumption of unripe fruits can yield physiological costs, the risk of potential predation outweighed the time-consuming cost of selectively foraging on ripe fruits in unsafe microhabitats. Additional habitat features, like distance to a food source, can further complicate foraging choices. For instance, distance between complimentary foods can increase travel time and thus exposure to predators (Wiggins et al. 2006a). In another study investigating tradeoff consequences, house mice (*Mus musculus*) in enclosed habitats with predators not only avoided open areas, but also had slower growth rates and delayed reproduction compared to mice in habitats without predators (Arthur et al. 2004).

Herbivorous prey species can sometimes alter both the cover and food quality provided by a single plant given repeated selection. Selective grazing by herbivores can significantly transform cover components over time through the alteration of characteristics like shrub height and visual obstruction (Karban et al. 2006; Price 2009). In extreme cases, like the population explosion of white-tailed deer (*Odocoileus virginianus*) in the eastern United States, heavy browsing pressure can severely reduce cover options not only for the browser in question but other animals as well (Casey and Hein 1983). Selective grazing pressure also can alter habitat characteristics like soil nutrients and plant species richness (Olofsson et al. 2008). Browsing changes the quality of food by altering plant nutrition, growth, regeneration, and plant chemical defenses like plant secondary metabolites (Bryant et al. 1992; Gowda 1997; Agrawal 2000; Stotler et al. 2005; Karban et al. 2006). Predation risk also can shape landscape features by decreasing or re-routing herbivorous browsing pressure, as demonstrated by a correlation between the recent return of wolves (*Canis lupus*) and a decrease in browse intensity of aspen by ungulates in Yellowstone National Park (Beschta and Ripple 2009; Kauffman et al. 2010; Kimble et al. 2011). Some plants can produce volatile emissions in response to damage by herbivores that recruit predators of the offending herbivore (Dicke and Sabelis 1988; Karban 2007). These examples highlight how predators, prey, and plants interact to influence the quality of plants as cover and food for herbivores.

Despite the importance of cover and diet quality in understanding trophic interactions, few studies investigate how variation in both cover and food quality simultaneously influence habitat use by a free-ranging vertebrate herbivore. The complex interactions between cover and food could help to explain why single variables of vegetative quality do not always explain habitat use. The few studies that have investigated how natural variation of cover and food quality influences free-ranging herbivores generally conclude that both factors interact to shape habitat use. A field study with brushtail possums demonstrated that different artificial levels of predator cues and a toxic diet will deter foraging according to the severity of the deterrent (Kirmani et al. 2010). Habitat use by koalas was determined by tree width in addition to lower concentrations of chemical defenses of trees (Moore and Foley 2005). Locations of preferred forage patches for grazing herbivores on the Serengeti can be explained by incorporating both predation risk and dietary quality of plants (Anderson et al. 2010). In addition, although overstory cover primarily explained the establishment of burrows by pygmy rabbits (*Brachylagus idahoensis*), sometimes cover quality was sacrificed for areas with high abundance of food resources (Wilson et al. 2012). Although these examples represent progress towards a synthesis of interacting factors that influence habitat use, overall, foraging ecology literature lacks the integration of contributing, synergistic variables like predation risk and dietary quality (Heino et al. 2008). My study will contribute further understanding of these factors and their impact upon habitat use.

My objective was to investigate the interactive role of cover and diet quality on habitat use by a mammalian herbivore. I used the pygmy rabbit-sagebrush system to answer two questions:

1. Does the cover and dietary quality of a plant vary spatially within a habitat?
2. Does the cover and dietary quality of that plant influence habitat use by a mammalian herbivore?

This is the first study to investigate how spatial variation of two potentially interacting habitat features influences habitat use by free-ranging pygmy rabbits. The pygmy rabbit-sagebrush system provides an ideal model with which to address these questions. First, the quality of cover influences pygmy rabbit foraging behavior. In captivity, pygmy rabbits demonstrated a preference for feeding in well-concealed locations (Chapter 1). Cover has been established as a critical variable in the prediction of suitable habitat for pygmy rabbits (Weiss and Verts 1984; Katzner and Parker 1997; Gabler et al. 2000; Larrucea and Brussard 2008). However, recent work suggests that diet quality also might shape habitat use by pygmy rabbits. Captive research has shown that foraging patterns by pygmy rabbits can be altered by the presence of feeding deterrents, or toxins, naturally found in sagebrush (Shipley et al. 2006). In the field, free-ranging pygmy rabbits selected individual sagebrush within foraging patches with the lowest concentration of chemical defenses and highest nutritional quality (Ulappa 2011). In captivity, both cover *and* diet influenced habitat use by the pygmy rabbit (Chapter 1).

When poor cover was paired with good food and vice versa, tradeoffs made by individuals revealed no single factor determined foraging. Finally, cover (Price 2009) and diet quality (Kelsey et al. 1982; Behan and Welch 1986; Personius et al. 1987; Bray et al. 1991; Welch et al. 1991; Wilt and Miller 1992; Ulappa 2011) can vary naturally in the sagebrush ecosystem. Therefore, the quality of cover and diet have the potential to interact to influence habitat use by free-ranging pygmy rabbits.

Methods

Location

I conducted this study on public land managed by the Bureau of Land Management (Shoshone Field Office, Shoshone, ID) near Magic Reservoir, located 20 miles south of Hailey, ID (43°3’N, 114°8’W). Two sagebrush species dominate the site, Wyoming big sagebrush (*Artemisia tridentate* spp. *wyomingensis*), and low sagebrush (*Atremisia tridentata* var. *arbuscula*). The former species grows mostly on the extensive mima mounds found throughout the site. Mima mounds are generally round (radius of 10m ± 5m) and slightly elevated patches of deeper soil where pygmy rabbits prefer to excavate burrow systems. Native bunch grasses, mustards, and wild onions, as well as invasive cheatgrass (*Bromus tectorum*), are the most common plants found growing in spaces between sagebrush plants.

Transects

I took measurements of cover, diet quality, and habitat use at eight active mima mounds within our study area in late November, 2011. I classified active mounds as those having a pygmy rabbit burrow system with one or more open burrow entrances, at least five fresh fecal pellets, and evidence of recent foraging by pygmy rabbits as indicated by a diagonally clipped sagebrush sprig with an orange to white cambium. I determined the freshness of fecal pellets using color and consistency criteria provided by Sanchez et al. (2009). After a mound was confirmed to be active, I established a 30m transect that began in the center of the mound outward in a randomly chosen direction (Figure. 2.1). Pygmy rabbits spend the majority of time in an area of 60m^2 around burrows in summer (Heady and Laundré 2005), and high use areas can be as small as 13m^2 around burrows in winter (Katzner and Parker 1997). Therefore, the 30m transect I used should include both 'high activity areas' near the burrow and lower activity areas. I divided each 30m transect into six segments of 5x1m, for a total of 48 samples (Figure 2.1). However, one transect contained a segment without a sagebrush plant, so total sample number for analysis was 47. I took measurements of cover, diet quality, and habitat use by pygmy rabbits for a randomly selected sagebrush plant within each segment along each transect. I recorded the distance from the center of the mound to each randomly selected plant.

Cover Quality

I measured aerial concealment using a rabbit analog on the randomly selected plant within each segment. I created the analog using a 20cm cube composed of 25 alternating red and white squares. I placed the cube on the ground at a randomly determined point as close to the sagebrush trunk as possible (without damaging the plant by forcing the concealment cube underneath the plant) and on the opposite side of the shrub for two measurements per plant (Figure 2.2). I counted the number of squares that were > 50% concealed by the vegetation observed from 1m above the plant for each of the two locations and averaged these values. Given that pygmy rabbit mortality often results from avian predators (Crawford et al. 2010), aerial concealment offers a functionally relevant measure of cover.

Diet Quality

I measured the concentration of monoterpenes, a group of plant defenses known to influence browsing by captive (Shipley et al. 2006) and free-ranging (Ulappa 2011) pygmy rabbits, as the functional measure of diet quality. I collected approximately 10± 1g of stems with leaves from each randomly selected sagebrush plant. I placed sagebrush samples in individual plastic bags and stored on ice until they were transferred to -20°C for storage prior to analysis. I analyzed all sagebrush samples for concentration of monoterpenes in leaves using headspace gas chromatography analysis. Prior to analysis, I removed leaves from samples and ground them in liquid nitrogen to $\leq$ 2mm pieces, and placed 0.05g of each homogenized ground sample into a 20ml glass autosampler headspace vial.

I incubated samples in headspace vials at 100°C for 20min in a Hewlett-Packard 7694 headspace sampler (Agilent Technology, Santa Clara, CA). One milliliter of headspace gas was injected into a J&W DB-5 capillary column (30m x 250µm x 0.25µm) installed in an Agilent 6890N GC. Headspace zone temperatures were as follows: oven 100°C, loop 110°C, transfer line 120°C. Incubation time was 20min with a loop size of 1ml. The flame ionized detector (FID) was maintained at 300°C. Splitless injection mode was used and injector temperature was 250°C. The flow rate of helium as the carrier gas was 1ml/min. Chromatographic separation was achieved with a column temperature program initially held at 40°C for two min, increasing 3°C/min until reaching 60°C. The second ramp was 5°C/min until reaching 120°C. The third and final ramp increased at a rate of 20°C/min until it reached 300°C, and was held at 300°C for seven min for a total program length of 36.67min. The order of samples was randomized.

I determined the total area under the curve (AUC) in milligrams of dry weight (DW) for all monoterpenes with retention times on the gas chromatograph less than 30min. Monoterpene values were divided by 10,000 to make the data sets more manageable (AUC/ $\frac{1}{10}$ mg DW). I also determined the concentration (AUC/ $\frac{1}{10}$ mg DW) of two individual monoterpenes, cineole and β-pinene. These specific monoterpenes were chosen because they are known to limit browsing by pygmy rabbits (Shipley et al. 2006; Ulappa 2011).

Habitat Use

I chose the presence of fecal pellets as an indicator of habitat use by pygmy rabbits. Scat surveys can be effective in determining habitat use (Jarman and Caparano 1997; Tuft et al. 2011), density (Sugimura and Yamada 2004) and abundance (Forsyth et al. 2007) of herbivores. In this study, I searched for the presence or absence of rabbit pellets of any age directly under the plant crown circumference. I scored plants with pellets present as ‘yes’ for habitat use, and plants without pellets were scored as ‘no.’

Statistical Analyses

Because samples at a mound were not independent and could be confounded by mound characteristics, I first tested the effect of mound by using mixed effects model with mound as the random effect using R 2.14 (2011). I did not find mound to be a significant random effect, so it was not included in final analyses. To test the spatial variation in quality of vegetation, I ran a separate correlation analysis between distance and each of my habitat variables (% cover, total monoterpenes, and individual monoterpenes). To determine which habitat variables (concealment, distance, and monoterpenes (individual and total)) best explained habitat use (i.e., presence or absence of fecal pellets), I used an information theoretic approach with Akaike Information Criterion adjusted for the small sample size (AICc). Due to the small sample sizes, interactive effects of models and the exploratory nature of this study, I also used individual t-tests (2-tailed) to determine if habitat variables in the top models differed between plants that were used (presence of feces) or not used (absence of feces) by pygmy rabbits. I adjusted the p-value based on the number of comparisons (n=3) to P=0.02 using a Bonferroni correction (Alldredge and Ratti 1992). All data were checked for normality and *log* transformed if needed to meet assumptions of normality. Outliers were identified with box plots and removed (Frigge et al. 1989) for following variables: cineole (n=1 removed), β-pinene (n=3 removed), and total monoterpene (n=2 removed). Means (mean ± SE) are reported for results concerning habitat use (i.e., fecal pellet presence/absence). Statistical analyses were performed using JMP version 8.0 software of the SAS Institute.

Results

Distance from the mound was correlated with some habitat variables but not others. Concealment did not significantly correlate with distance from the mound (r^2 = 0.03, $f_{1,45}$=1.7, P=0.19). However, both β-pinene concentration (r^2=0.10, $f_{1,42}$=4.62, P=0.03) and cineole concentration (r^2 = 0.09, $f_{1,45}$=4.58, P=0.03) decreased with distance from the center of the mound. Total monoterpenes also tended to decrease with distance from mound (r^2=0.06, $f_{1,43}$=3.1, P=0.08). The two monoterpenes were not correlated with each other (P=0.89) or concealment (β-pinene: $f_{1,42}$=1.78, P=0.18, cineole: $f_{1,45}$=0.06, P=0.41).

The top model contained distance, cover, and toxin as the three habitat variables explaining the use of the sagebrush plants by rabbits based on presence or absence of feces. The highest ranking model included distance from the mound (m), concealment (%), and total monoterpenes (AUC/ ⅒ mg DW, Table 2.1). The top two models both contained concealment and total monoterpenes (AUC/ ⅒ mg DW) as the two most influential variables explaining habitat use by pygmy rabbits.

Variables that we estimated indicated that used plants provided greater concealment, had lower concentrations of total monoterpenes, and were closer to the center of the mound. For every one unit increase of concealment, the probability of the presence of fecal pellets increased by 7% (Table 2.2). Total monoterpenes decreased the probability of pellets present by 2%, and distance from the mound decreased pellet probability by 12% with every one unit increase in these variables.

Concealment and concentration of total monoterpenes differed significantly between plants that were used or not used by pygmy rabbits. Concealment was twice as high when fecal pellets were present (n=33, 33.5% ± 3.4) than when pellets were absent (n=14, 16.6%± 5.2, $f_{1,45}$ =7.3, P=<0.01, Figure 2.3). Total monoterpenes were 12% lower when fecal pellets were present (n=32, 397.6 AUC/ ⅒ mg DW $\pm$ 10.7) than when fecal pellets were absent (n=13, 447.4 AUC/ ⅒ mg DW $\pm$ 16.8, $f_{1,43}$=6.2, P=0.02, Figure 2.4). Distance from the mound did not differ between plants with (n=33, 15.1m± 2.2) and without fecal pellets (n=14, 17.3m ± 1.5, t_{47}=-0.82, P=0.79).

Discussion

Overall, I found evidence that the relative quality of cover and food within a habitat varied and that pygmy rabbits responded to this variation. Concealment was not correlated with distance from center of activity (i.e., burrow entrances), whereas chemical defenses decreased with increasing distance from center of activity. Both concealment and diet quality differed between plants used or not used by pygmy rabbits. This relationship was potentially confounded by the distance of plants from the center of activity and perhaps the cause and effect nature between selective foraging and the level of cover and toxins in a plant. When plants with fecal pellets occurred farther away from burrows of pygmy rabbits, these plants had higher concealment and fewer chemical defenses. If pygmy rabbits restrict their foraging to areas near burrows for safety, these areas may contain plants that are more toxic. However, if they forage farther away from less toxic plants, they could experience elevated predation risk. The risk of foraging farther away from a burrow refuge could be mitigated if the plant consumed by the rabbit also has high concealment. This spatial variation in access to refuge and quality food can force individuals to make tradeoffs between resources. My results exhibit the occasionally conflicting choices, occurring on two dimensions, which a specialist herbivore faces in a landscape dominated by a single but variable resource. In the sections that follow, I explain the ecological significance of these results. Chapter 3 offers suggestions to further investigate tradeoffs of habitat features for free-ranging prey species.

Objective 1. Determine if the physical and dietary quality of a plant varies spatially within a habitat.

Physical Characteristics: Cover and Distance

In my study, vegetative cover was not homogenous across the habitat. Plants measured along the line transects provided from 0% to 70% concealment, however, distance from the center of activity did not explain the variation in concealment. This suggested that, if safety provided by the burrow was removed, pygmy rabbits close to or far from the mound would have the same theoretical risk of aerial predation. Beyond shaping habitat use, vegetative cover can have significant impacts on species (Bazazz 1975). For example, the 'habitat heterogeneity hypothesis' (MacArthur and Wilson 1967; Lack 1969) states that the physical structure of vegetation adds another dimension of habitat intricacy and potential for richness (Tews et al. 2004). Refuge provided by vegetation influences habitat use in many animals (Brown 1988; Longland and Price 1991; Cassini and Galante 1992; Dickman 1992; Kindvall 1996; Cowlishaw 1997; Arthur et al. 2004; Creel et al. 2005; Cresswell et al. 2010) even those that are fossorial or semi-fossorial like the pygmy rabbit (Blaum et al. 2007). Moreover, the inability to find adequate refuge can have serious negative consequences for a species (Amo et al. 2007; Arthur et al. 2004; Cresswell 2008; Nelson et al. 2004; Tuft et al. 2011). For example, Iberian rock lizard (*Iberolacerta cyreni*) populations in habitats disturbed by humans had poorer body condition scores (e.g., higher parasite loads, lower body mass) compared to lizards in undisturbed habitats (Amo et al. 2007).

In *Artemisia* dominated landscapes, physical shrub characteristics like cover density, height or visual obstruction are not correlated to measurable environmental variables like precipitation, aspect, or elevation (Davies et al. 2007). However, other factors, such as soil composition and moisture, can influence the extent of concealment provided by a particular plant (Strauss and Schickhoff 2007). In this study, the pygmy rabbit burrow systems were centered on top of and close to mima mounds. Mima mounds have soil that differs in clay, moisture, and pebble content compared to surrounding habitat and thus have different plant communities or productivity (Scheffer 1947; Ross et al. 1968; Hill et al. 2005). The comparatively loamy soil found on mounds is known to attract burrowing and non-burrowing animals (Huntly and Reichman 1994; Ross et al. 1968). Furthermore, the very act of burrowing can change vegetative structure in addition to soil structure via aeration and waste deposition (Huntly and Reichman 1994), which can encourage the growth of woody shrubs (Cox and Gakahu 1985; Hill et al. 2005) that might provide refuge for small animals. Burrowing by animals can enhance the health, diversity, and productivity of plants in proximity to fossorial activity (Hill et al. 2005; Davidson and Lightfoot 2008). This seemingly creates a positive feedback loop of plant success, animal activity, and soil enrichment.

Based on the presence of deeper soils associated with mounds and burrowing by pygmy rabbits, I predicted that concealment would decrease with distance from the mound. However, I did not find greater vegetative concealment of sagebrush plants closer to mounds where burrows are concentrated. This result contrasts with findings from Hill et al. (2005) who reported that taller sagebrush plants with greater leaf biomass were found near or on top of mounds compared to plants in between mounds (Hill et al. 2005). However, previous research on the effects of pygmy rabbit burrow occupancy on vegetation drew conclusions similar to my own regarding similar vegetation structure on and off mounds. Specifically, a functional cover variable like concealment was not correlated with increasing distance from burrow refuge (Price 2009). Concealment that is not restricted to specific patches could represent an advantage for pygmy rabbits when considering movement patterns of this species. After emergence from natal burrows, pygmy rabbits typically disperse 1-3km, depending on sex (Estes-Zumpf and Rachlow 2009). Adults will continue to move between burrows and beyond (Estes-Zumpf et al. 2010). The occurrence of a range of concealment options throughout a landscape offered by sagebrush and other plants might represent an advantage for dispersal. For instance, translocated European rabbits released into habitats of high vegetative cover had less mortality and greater dispersal distances compared to rabbits released in habitats with low vegetative cover (Calvete and Estrada 2004).

Dietary Characteristics: Monoterpene Concentration

The chemical quality of sagebrush plants varied spatially. The individual monoterpenes, cineole and β-pinene, and total monoterpene (AUC/mg DW) concentration varied along line transects and generally decreased with increasing distance from center of activity. As distance increased from 0 to 30m, cineole concentration decreased by 41.4%, β-pinene concentration decreased by 28.6%, and total monoterpene concentration decreased by 13.2% to the end of the transect. The wide variation in monoterpene concentrations that I observed is consistent with variation observed in other studies. Variation in chemical concentration can occur in sagebrush plants grown in identical conditions (Behan and Welch 1986) as well as in a natural setting. The chemistry of sagebrush plants differs between species and subspecies (Wambolt 2004), seasons (Wilt and Miller 1992; Wambolt 2004), soil conditions (Huntly and Reichman 1994), and browsing pressure (Karban 2007).

The spatial variation in chemistry of sagebrush could have significant implications for pygmy rabbits. Because rabbits browse selectively on plants with the lowest monoterpene concentration (Ulappa 2011), rabbits might be forced to browse on plants farther from burrow refuge. If the correlation between monoterpene concentration and distance from the mound continues to strengthen with time, pygmy rabbits might increase distance required to forage and eventually abandon the burrow site. Optimal foraging theory states that herbivores should first exploit the closest resource patches. However, if close plants are poor quality, the net maximum energy intake may be harder to attain given toxin digestion consequences or energetic costs of increasing foraging behaviors to attain higher intake masses of poor quality plants. Herbivores that forage more widely and increase movement to higher quality plants could incur elevated energetic costs (Schoener 1979; Charnov 1976; Stephens and Krebs 1986; Heino et al. 2008). Greater movement could increase predation risk if the plants browsed farther from refuge do not provide adequate cover. For example, when European rabbits (*Oryctolagus cuniculus*) ventured beyond regular foraging patches to obtain higher quality diets, they were exposed to greater predation risk (Bakker et al. 2005).

Although there is ample evidence that chemistry influences browsing by herbivores, plant chemistry can be spatially and temporally variable. This may confound correlations between habitat use and dietary quality. For example, the full variation in chemistry measured might not always be available to rabbits. During the winter, movement by pygmy rabbits can be severely restricted by snow, which might limit foraging choices for rabbits. The spring season sees a steep increase in sagebrush plant growth, resulting in leaves that are lower in chemical defenses compared to leaves of the same plant in peak summer months (Cedarleaf et al. 1983). In addition, spring brings heavy forb growth, which decreases the reliance of pygmy rabbits on sagebrush for food (Green and Flinders 1980). Hot and dry summer seasons prompt sagebrush to drop ephemeral leaves and the availability of other plants in the habitat declines (Miller and Shultz 1987). Finally, during the fall season, any alternative to sagebrush has vanished and difficult winter conditions might follow. Researchers investigating the correlation between habitat use and chemical composition of a highly variable food source in a dynamic environment should attempt to sample at all seasons to gain understanding of habitat use on a temporal scale.

Another complication is that there are a variety of chemicals and nutrients in sagebrush that can influence foraging and therefore habitat use by herbivores. Both concentration of nutrients and monoterpene in sagebrush influenced diet selection by free-ranging pygmy rabbits (Ulappa et al. 2011). Other semi-fossorial animals, like Attwater's pocket gopher (*Geomys attwateri*), also selectively forage based on the concentration of chemicals and nutrients in their diet (Rezsutek and Cameron 2011). Although monoterpenes are the most frequently documented class of chemical that deters sagebrush herbivores, including pygmy rabbits (Personius et al. 1987; Bray et al. 1991; Shipley et al. 2006), it is not the only chemical defense in sagebrush. Sagebrush contains phenolic compounds (Tahvanainen et al. 1985; Wilt and Miller 1992) and sesequiterpene lactones (Personius et al. 1987), both of which deter foraging by mammalian herbivores (Burnett et al. 1977; Tahvanainen et al. 1985). A focus on individual monoterpenes (i.e., cineole and β-pinene) is still valuable in that a specific compound can be isolated as a potential causal variable subject to testing in controlled dietary studies. Measuring total monoterpene concentration is also practical in that the impact of an entire chemical class can be weighed against foraging patterns, rather than relying upon a single chemical that might or might not influence foraging. Total monoterpene assessment also has the advantage of possible *post-hoc* analysis of a chemical not previously known or suspected of influencing foraging patterns. Overall, my results and that of others (Ulappa, 2011) showed that pygmy rabbits likely respond behaviorally to avoid monoterpene concentration in plants. Similar investigations about how pygmy rabbits respond to nutrients, sesquiterpene lactones, and phenolics found in sagebrush might strengthen the link between habitat use and diet quality.

Foraging might influence the chemistry of sagebrush as much as chemistry influences foraging. Optimal foraging models predict that animals will feed close to safety for as long as possible if food quantity and quality allow (Charnov 1976; Schoener 1979). This intense browsing could reduce the quality of forage. For example, intense foraging can increase plant chemical defenses (Martinsen et al. 1998; Kessler et al. 2006). Reduced quality of forage near safety due to intense browsing could shift foraging by herbivores into potentially risky habitat. Yet, in the case of the pygmy rabbit and other ‘burrow-obligate’ animals (Heady and Laundré 2005), the value of safety provided by a burrow might outweigh the costs of ingesting higher concentrations of chemicals in plants closer to burrows.

Objective 2. Determine if the cover and dietary quality of a plant influence habitat use by an herbivore.

Plants that were used by pygmy rabbits along transects had higher concealment and lower chemical defenses, but were not closer to the center of activity for pygmy rabbits. These results suggest that pygmy rabbits will use plants close and far from the mound in equal measures as long as those plants offer relatively high cover and food quality. Rabbits might selectively choose plants with characteristics that offer lower predation risk and are less toxic.

Because the relative quality of concealment and diet did not co-vary, results demonstrate that pygmy rabbits might engage in tradeoffs between safety and food quality. Optimal foraging theory (Macarthur and Pianka 1966; Charnov 1976; Schoener 1979) states that animals will attempt to maximize energy intake but might be forced to limit foraging efficiency given certain energetic costs associated with obtaining food. In this case, pygmy rabbits might trade off between concealment from predation and dietary quality of food from a single resource. The balance between safety and food for a prey species is well documented (Holmes 1984; Formanowicz and Bobka 1989; Lima and Dill 1990; Cassini 1991; Dickman 1992; Bowers and Dooley 1993; Kotler and Blaustein 1995; Lima and Bednekoff 1999; Bakker et al. 2005; Fedriani and Boulay 2006; Kirmani et al. 2010). However, studies examining both perceived predation risk and specific attributes of dietary quality, such as chemical defenses, are rare (Schmidt 2000; Moore and Foley 2005; McArthur et al. 2012). In addition, I am not aware of any tradeoff studies concerning predation risk and food quality in a mammalian specialist. Results from Chapter 1 demonstrated that, in captivity, pygmy rabbits value both cover and food quality but these values can shift when high quality options are not met for both factors. In other words, some rabbits selected high quality food at the expense of potentially higher exposure to predators, whereas other rabbits ate under areas with low predator exposure but at the expense of consuming more toxic food. No single driving variable emerged when rabbits were faced with the tradeoffs. This finding has ecological significance for the conservation of existing populations and the comprehensive habitat evaluation of future generations. Traditional conservation efforts tend to focus on preserving single ecosystem variables that affect foragers (Heino et al. 2008). However, a variety of factors drive habitat use by animals and my results indicate that land managers should approach conservation of herbivores along at least two interacting dimensions: cover and dietary quality of plants.

It is possible that my measure of habitat use (fecal pellet survey) might be influenced by extraneous factors, like season or type of predator present. Sagebrush chemicals are capable of fluctuating throughout seasons (Cedarleaf et al. 1983; Wilt and Miller 1992; Wambolt 2004), which might influence fecal pellet deposition patterns. Predation can also fluctuate seasonally. Both aerial and terrestrial predation rates vary throughout the year with peaks in the springtime (Sanchez and Rachlow 2008) when the aerial predation rate eclipses terrestrial predation rates (Sanchez and Rachlow 2008; Crawford et al. 2010). A constant oscillation of different predation pressures might cause rabbits to value cover differently. Habitat structure relative to terrestrial predation on pygmy rabbits has been measured with a Robel pole in an effort to capture horizontal cover quality (Price 2009). Risk of aerial predation is typically measured via vertical cover using a tool similar to Wien’s pole (Wiens and Rotenberry 1981), according to the perspective of some airborne predator. If a more comprehensive understanding of predation pressure is sought, measuring concealment from all predator perspectives during defined seasons is essential.

Most important to studying tradeoffs is to establish that variation in cover and food choices exists and decisions that weigh predation risk and food quality are actively made by the species of interest. Previous work that emphasizes relationships between an herbivore, its food source, and predation can be difficult and tend to be focused on invertebrate species (Hartvigsen et al. 1995; Turnlings and Benrey 1998; Stamp 2001; Rudgers 2004; Turlings and Wackers 2004) due to the ease of controlling variables like herbivore access to food resources and level of predation risk. Specific characteristics will aid tradeoff studies in vertebrate systems by reducing complexity of interacting factors. Detecting tradeoffs between cover and food is simplified if one plant genus provides the primary food source to the herbivores and this food source varies in dietary quality. A robust predator presence is also necessary to observe if and how prey species adjust foraging patterns relative to predation risk. The variation between predation risk and dietary quality should be measured on a scale relevant to the foraging animal to ensure incorporation of the nuances of relationships between these factors. Furthermore, given certain life history characteristics of the pygmy rabbit and the dynamic environment it occupies, I suggest that simultaneous cover and chemical surveys be conducted at different seasons throughout the year to capture the complex connection between variables across temporal scales.

Few ecologists have explored the connections between the cover and chemical characteristics that vegetation provides (Heino et al. 2008), but understanding how wild animals respond to these interacting variables is critical. Mapping habitat on more than one important dimension that affects habitat use might provide a critical tool for conserving ideal habitat (Figure 2.5). Variable landscapes can be especially vulnerable to rapid changes caused by development activities (Schooley and Branch 2007) and species sensitive to environmental change might need much larger areas to compensate for unfavorable new conditions (Verboom et al. 2010). In a global landscape increasingly threatened by habitat fragmentation and degradation, the importance of capturing the habitat heterogeneity that species select for or against has never been greater (Mortelliti et al. 2010).

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Figures

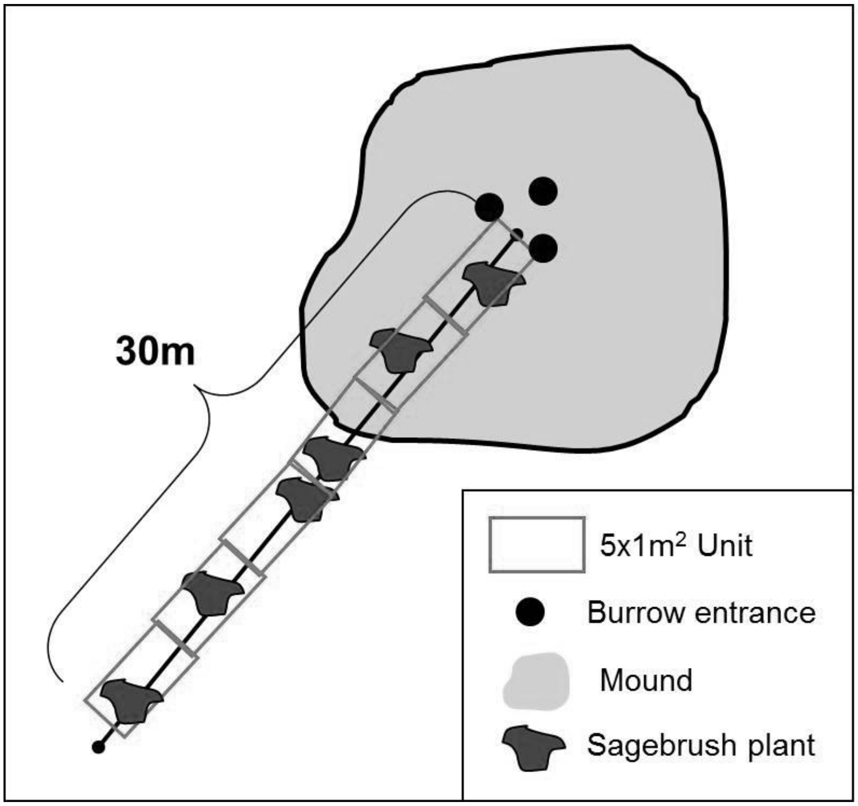

Figure 2.1 Schematic of line transects on an active pygmy rabbit mound where habitat quality and use was measured. The line transect began at the center of mounds and extended out 30m in a random direction. Distance from mound (m), aerial concealment (%), monoterpene concentration (AUC/ $\frac{1}{10}$ mg DW) and habitat use (presence of fecal pellets) were measured on one randomly selected sagebrush plant within each 5x1m segment.

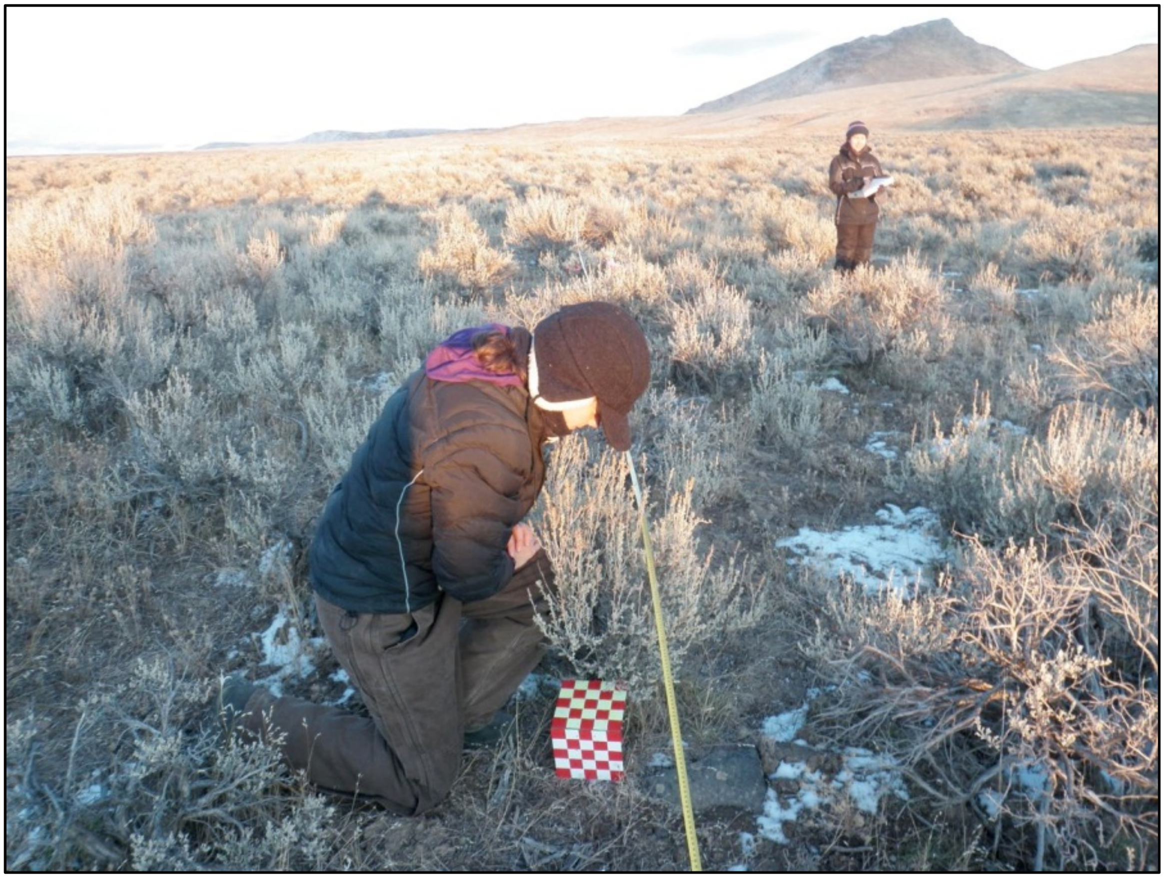

Figure 2.2 Concealment was measured by placing a checkered cube beneath a sagebrush plant, and counting the number of squares >50% covered by vegetation.

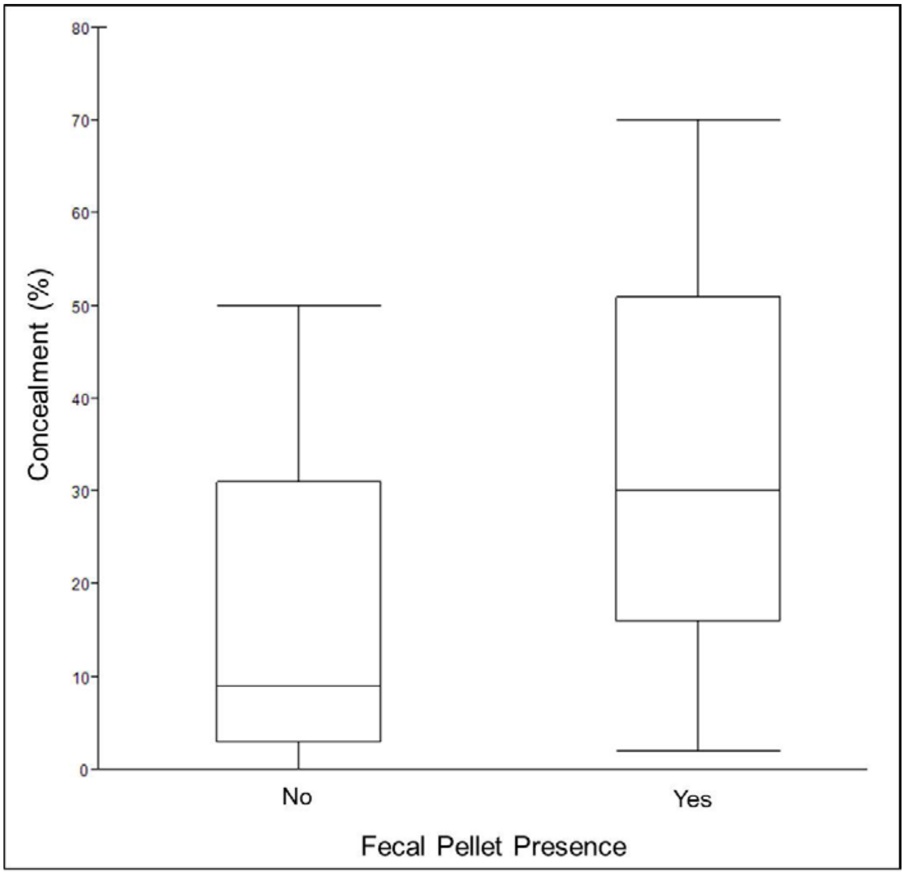

Figure 2.3 Concealment (%) according to fecal pellet presence at sagebrush plants (n=47) along eight 30m transects. "No" represents plants non used by pygmy rabbits and "Yes" represents plants used by pygmy rabbits.

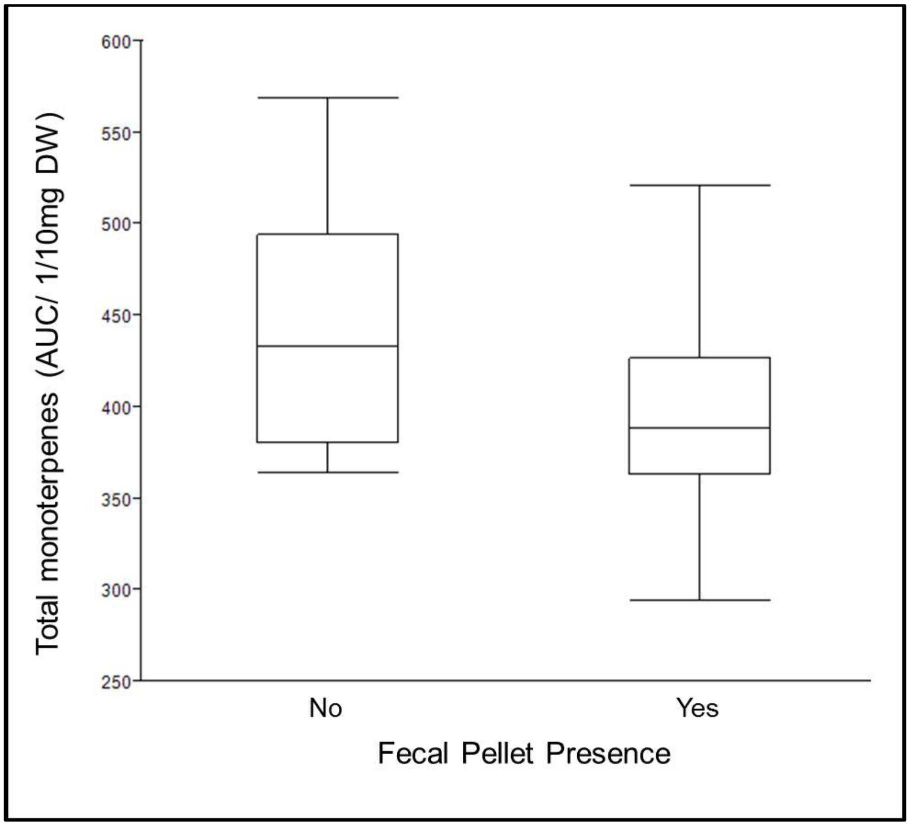

Figure 2.4 Total monoterpene concentration (AUC/ $\frac{1}{10}$ mg DW) at sagebrush plants (n=47) along eight 30m transects according to fecal pellet presence. “No” represents plants non used by pygmy rabbits and “Yes” represents plants used by pygmy rabbits.

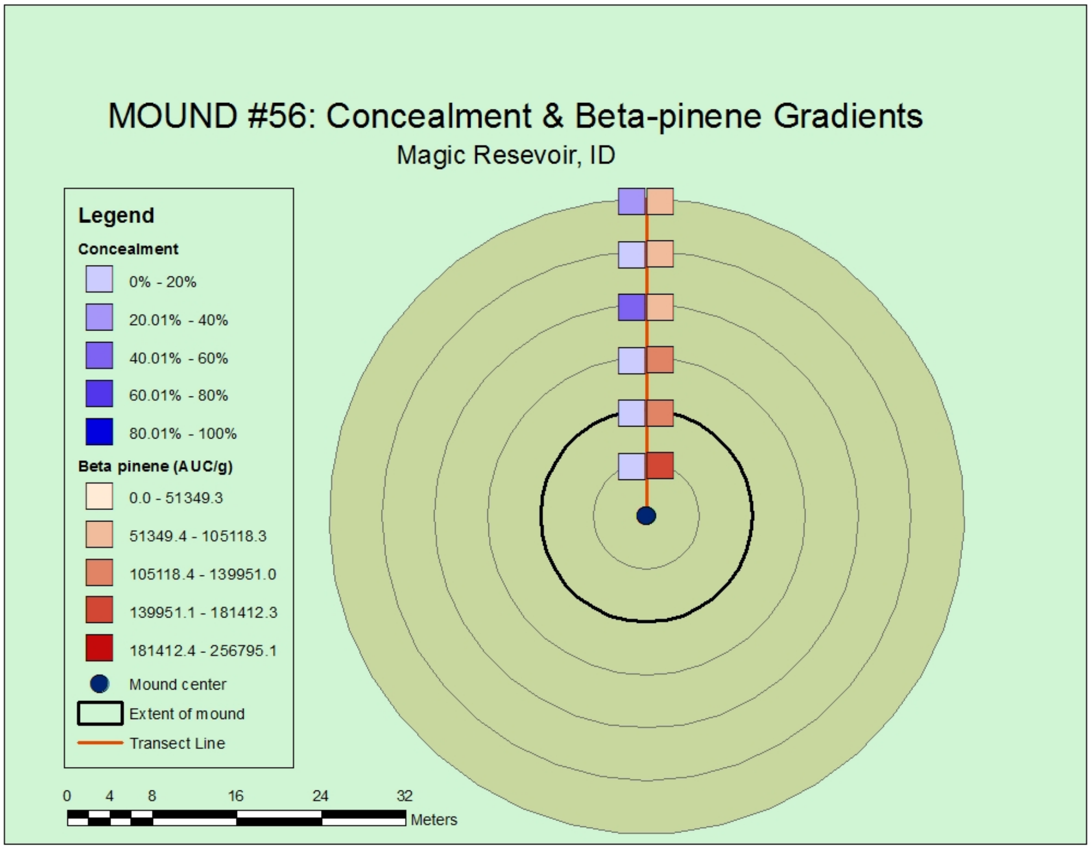

Figure 2.5 An example of mapping cover (concealment, %) and diet quality (the monoterpene β-pinene, AUC/g) variables at a mound occupied by pygmy rabbits.

Tables

Table 2.1 Number of variables (K), Akaike's Information Criterion corrected for small sample size (AICc), change in AIC from the top model (Δi), rank of model, and model weight (wi) from top models for habitat variables (Concealment, Total monoterpene (Monoterpene), and Distance) affecting habitat use (presence or absence of fecal pellets) by pygmy rabbits.

Model Variables	K	AICc Value	Rank	Δi	Wi
Concealment, Monoterpene, Distance	4	47.3	1	0	0.624
Concealment, Monoterpene	3	49.8	2	2.5	0.179
Concealment	2	52	3	4.7	0.059
Concealment, Distance	3	52.3	4	5	0.051
Monoterpene	2	52.6	5	5.3	0.044
Monoterpene, distance	3	53.2	6	5.9	0.033
Null	1	56.2	7	8.9	0.007
Distance	2	57.9	8	10.6	0.003

Table 2.2 Conditional logistic regression variable estimates, odds ratio estimates and 95% confidence intervals for each habitat variable (Concealment, Total monoterpene (Monoterpene), and Distance) from the top habitat use model.

Variables	Estimate	Lower 95% CI	Upper 95% CI	Odds Ratio
Concealment	0.0678	0.0191	0.1342	1.07
Monoterpene	-0.017	-0.0335	-0.004	0.98
Distance	-0.118	-0.2553	-0.013	0.88

CHAPTER THREE: SUGGESTIONS FOR INVESTIGTAING TRADEOFFS BETWEEN COVER AND FOOD USING CAPTIVE AND FREE RANGING HERBIVORES

Introduction

The preceding chapters demonstrated that foraging decisions of pygmy rabbits are affected by tradeoffs between cover and diet quality in Chapter 1, and habitat use in wild populations reflects similar tradeoffs in the face of vegetative heterogeneity in Chapter 2. The following paragraphs provide suggestions for how to overcome some of the limitations associated with measuring habitat tradeoff by herbivores in the field (Chapter 2).

Measuring Concealment

Aerial concealment is not the only choice for assessing or measuring perceived predation risk for prey species. There are a variety of vegetative measurements that can be used to assess the quality of vegetation to provide refuge for prey from predators and therefore assess habitat quality for prey (Daubenmire 1959; Robel et al. 1970; Griffith and Youtie 1988; Limb et al. 2007). The density of foliage is often associated with potential cover for prey species (Canfield 1941) and variations of this method are often used to estimate cover quality in habitat for a variety of herbivores (Eng and Schladwep 1972; Giffith and Youtie 1988; Fischer and Lindenmayer 2002; Wambolt et al. 2006). Estimating visual obstruction using a Robel pole could offer a more functional measure of refuge than percent cover and density specifically from the perspective of a terrestrial predator (Robel et al. 1970). The Robel pole was used to estimate horizontal cover on pygmy rabbit mounds, which tended to decrease with length of burrow occupancy by rabbits (Price 2009). Cover boards (i.e., similar to the concealment cube but on a flat board) have been used on a horizontal plane to estimate terrestrial concealment provided by vegetation for prey (Griffith and Youtie 1998).

Although there are a variety of measures of cover (Robel poles, cover boards, etc.) that are valid, my project focused on aerial concealment for several reasons. Specifically, I used a checkered cube the size of the rabbit's body (Rachlow, personal comm.) from a vertical angle of 90°. This method was inspired by another well-established method known as Wien's pole used for assessing vertical cover over bird nests in shrub-steppe grasslands (Wiens and Rotenberry 1981). The aerial concealment method I chose has several advantages over other approaches that estimate cover. Like concealment measurements using a Robel pole, aerial concealment is a functional measure of how well a prey species can be concealed from an aerial predator. In addition, the analog used is approximately the size and shape of the prey species, rather than a narrow pole. Finally, by viewing the analog from a static viewpoint directly above the object, the problem of determining distance and direction from which to view is eliminated. Because aerial predation is a significant cause of predation-related mortality for pygmy rabbits (Crawford et al. 2010; Price et al. 2010), I considered an aerial concealment measurement to accurately represent functional cover relevant to the foraging animal. I ran correlation analyses between each cover assessment variable (percent cover, concealment, density). Only concealment and percent cover were found to correlate (Figure 3.1), suggesting my measure of concealment relates to the traditional measure of percent cover. Given this correlation, an argument could be made to reject concealment and continue with traditional percent cover. However, I argue that concealment accounts for the role of animal visibility as seen by the predator, whereas percent cover does not. Percent cover measurements do not encompass the subtle structure characteristics of a plant that might enable an animal to exploit refuge options.

To further improve measuring heterogeneity of cover in the sagebrush steppe, I suggest several modifications. I recommend conducting an *a prioi* power analysis (or observing a plateau of sample coefficients of variation) to assess the fewest number of samples that will accurately reflect concealment offered by a plant. I also recommend that other measures of cover be considered as each might have different relative values of refuge for prey from predators. Selection of the particular measurement should be chosen carefully based on habitat characteristics relevant to the research question. For instance, if a researcher is considering a prey species range of vision, a horizontal, terrestrial measure of cover using cover boards (or a similar tool) would be most appropriate. Landscape characteristics must also drive choice of methods. If a sagebrush plain is dominated by short shrubs like dwarf sagebrush (e.g., *Artemisia arbuscula*), a line intercept method to measure plant density might prove more useful than a measure of horizontal cover. Life history characteristics of the species in question could also influence decisions. That is, why the species might need cover (i.e., predation risk, thermal benefits, etc.). Finally, some measures such as percent cover and density are more readily scaled up to larger areas using remote sensing. For example, I collaborated with U.S. Geological Survey to remotely sense percent cover and density of sagebrush at my site using unmanned aerial vehicles. The images demonstrated that remote sensing can be used to measure cover across landscapes (Figure 3.2). We are currently analyzing these images relative to habitat use by pygmy rabbits.

Fecal Pellet Surveys

One possible limitation of this study was the use of fecal pellet presence as evidence for habitat use. Fecal pellet counts are a valuable tool for habitat use surveys of mammalian herbivores, including estimation of populations, range, and density (Rogers et al. 1958; Jarman and Caparano 1997; Krebs et al. 2001; Murray et al. 2002; Sugimura and Yamada 2004; Forsyth et al. 2007). Given extensive use of pellet surveys for evaluation of *Leporid* populations (Angerbjorn 1983; Krebs et al. 1987; Krebs et al. 2001; Sugimura and Yamada 2004; Pierce et al. 2011), my designation of fecal pellet presence as an indicator of microhabitat use was valid. However, the inferences that can be made using fecal pellet surveys can be strengthened further. Two critical components that were not encompassed in my survey techniques were pellet age and density. Using both old and new fecal pellets introduced potential spatial separation between measured habitat quality and use. Previous studies note that deposition and decay rate of fecal pellets are not always consistent over time, and can change with diet quality and weather (Cochran and Stains 1961; Murray et al. 2002). Although concealment is relatively stable across time, chemistry can vary seasonally (Cedarleaf et al. 1983; Wilt and Miller 1992; Wambolt 2004). Therefore, measurements of the dietary quality of plants need to coincide with detection of recent use by rabbits. To use fecal pellets as a measure of recent use associated with the quality of existing habitat features, researchers should exclude evidence of old fecal pellets. Old fecal pellets can generally be distinguished from new by color, as most old pellets will be light tan and dry in texture, whereas new pellets are moist and darker brown, dark green or black (Sanchez et al. 2009). However, I suggest caution with fecal pellet age assignment. If old pellets are moist with snow or rain, they can appear new. In addition, I did not account for density of pellets, a factor that could indicate frequency of use by a single individual, or visits by a number of individuals over time. If the size of the surveyed area permits, I suggest that all fecal pellets are removed during the initial sampling period so that subsequent sampling trips will only contain truly fresh fecal pellets and allow opportunity to quantify use by counting density of new pellets. Surveying of fresh pellets also could provide insight about potential shifts in plant preferences by rabbits across seasons.

Browsing as an Indicator of Habitat Use

In this ecosystem, bite marks from browsing offer an additional indicator of habitat use by pygmy rabbits. While fecal pellets reveal general patterns of habitat use and do not necessarily infer feeding, browsing marks offer true evidence of foraging. Pygmy rabbits clip sagebrush stems at a 45° angle and fresh forage marks will have a yellow or orange woody center, surrounded by a green cambium ring (Figure 3.3). Old browsing evidence can be distinguished from new by the faded gray color of the remaining woody stem. However, no documentation exists of these changes on a temporal scale. In a preliminary study, I did not detect any browsing further than five meters away from the center of the burrow along a transect. Browsing might be present further away from the mound but was not sampled along a transect or was simply not detected. If bite marks are chosen as an indicator of habitat use, plants should be thoroughly inspected for clip marks at the beginning and end of a field season. Existing clip marks should be recorded with precise field notes or tagged with a weather-resistant marking that would not cause physical changes to the plant or influence foraging by herbivores. The presence of both browsing and fecal pellets might be a more significant measure of use than either parameter alone as it represents plants that are both palatable and safe.

Habitat Use Cause and Effect

A limitation of the field study I conducted is the inability to identify cause and effect between variation in habitat features and use by pygmy rabbits. Extensive plant selection by pygmy rabbits might alter the structural and chemical quality of plants, rather than the reverse scenario of these habitat features driving habitat use by pygmy rabbits. Intense browsing by ungulates can alter vegetation structure, therefore changing or reducing cover resources (Van Deelen 1999; Kimble et al. 2011). Concentrated pygmy rabbit browsing can also change vegetation structure and is thought to be responsible for dead sagebrush present on and around burrows that have been occupied for long periods of time (i.e., ≥ 6 years, Price 2009). In addition, burrowing behaviors of semi-fossorial animals can drastically change soil composition, which might have a substantial impact on plant quality (Huntly and Reichman 1994). Furthermore, intense browsing by herbivores can induce a plant to release chemicals on short and long-term scales (Kessler et al. 2006; Karban 2007).

I offer several suggestions to tease out cause and effect of habitat features and use by herbivores in future studies. First, radio-collars fitted on herbivores would provide spatial and temporal data concerning microhabitat use. Combined with high-resolution aerial photography, tracks drawn by GPS-enabled collars would provide even greater detail. Second, recording length of occupancy in addition to vegetation surveys will provide a more thorough assessment of cover and chemical changes over time. Collecting long-term occupancy data might be difficult for some species. However, species that rely on specific habitat features like burrows or exhibit central foraging behaviors might provide acceptable circumstances for studying temporal trends. Third, controlled studies such as those presented in Chapter 1 would minimize many extraneous variables associated with a field setting. If the influence of herbivores upon plants is in question, plants grown in uniform conditions sampled for chemical constituents before, during, and after controlled simulated browsing events could provide precise data on potential chemical changes. Fecal pellet surveys before and after manipulation of vegetative structure in a field setting might also illuminate cover preferences relative to the same temporal shifts in chemical quality.

Sampling in Varied Geological Features

The experimental sampling design in my field study can also be improved and adapted to apply to different environments. The experimental design of this study highlighted the difficulties of measuring the physical characteristics of a patchily distributed habitat. I designated circular, dome-shaped mima mounds as epicenters of rabbit activity and confirmed evidence of rabbit occupation (Rachlow et al. 2005). However, I might not have fully captured the heterogeneity that comprise pygmy rabbit habitat both on and off mima mounds by measuring six plants along a single 30m transect. To improve vegetative sampling efforts in the sagebrush around a central activity area, I suggest the following method. Form an 8m^2 plot on top of the central activity area (Figure 3.4) such that the square encompasses most, if not all of the activity of the mound: i.e., burrow entrances, trails, heavy browsing, and dense fecal piles. Vegetative characteristics measured in this area represent “high activity” areas. For “low activity” areas, identify four $2m^2$ plots placed at cardinal points (or four random directions placed equidistant) equidistant to each other and the activity center. Measuring four low activity areas will be more representative of the habitat surrounding the active center than a single transect. For all four squares, a distance of at least 25m from the center of the active center is recommended to ensure a spatial separation between high and low activity areas. The distance between activity areas will be dependent on localized movement within the rabbit population. Observing or otherwise tracking rabbit movement within and between mounds will enhance efforts to distinguish between high and low activity areas. Vegetative measurements and associated calculations should be chosen according to relevance to square areas rather than linear planes. Also, the number of plants surveyed within high and low activity areas should be the same. This design will increase the intensity of data within and outside of high activity areas.

While pygmy rabbits require healthy sagebrush stands (Green and Flinders 1980; Weiss and Verts 1984), populations are not always centered on or around mima mounds. Populations have been located in other geographic features like slopes and washes (Larrucea and Brussard 2008), which might require vegetation assessment techniques different from those used for mounds. Unlike mima mound populations, rabbits residing in these geographic features can have unpredictably clumped burrow entrances and activity centers. For pygmy rabbit populations in flat or sloped habitats, I recommend identifying several small, high activity areas paired with a single large, low activity area (Figure 3.5). As with the mima mound survey method, a buffer of at least 25m between high and low activity areas should be established, and activity areas should be the same total square area. The paired design increases the power of comparisons because it allows for paired t-tests or conditional logistic regression analysis, which controls for the variation within each experimental unit.

If mound-centered line transects are used, I recommend surveying more plants at the end of the transect, as determined by a proximity standardization, to reduce the possibility of lower detection probabilities by pygmy rabbits. Observing how the animals move through the surrounding habitat, whether via visual observation techniques or GPS-enabled collars, might also decrease the probability of surveying unused or undiscovered habitat.

Testing a Predictive Model

Chapter 2 outlined a descriptive model used to describe how habitat use by pygmy rabbits might be influenced by the quality of cover and diet. The top model contained total monoterpene concentration, concealment, and distance variables. However, models only estimate reality by revealing how a limited set of variables best explained our observations of use by pygmy rabbits in the field. Several design modifications are necessary to test this model. To ensure control over extraneous variables, I recommend testing cover and dietary quality in a captive setting but with values of each parameter presented as close to the natural level as possible. For example, live sagebrush grown in controlled conditions and offered to pygmy rabbits in pots would offer a more accurate food source, compared to commercial rabbit pellets dosed with a single chemical as I did in Chapter 1. This approach would allow a researcher to obtain an *a priori* chemical profile that might shed light on the possibility of how plant toxins influence foraging by herbivores in the field. Cover options can also be improved using more natural components, such as inedible plant materials woven together and arcing over food options. In this circumstance, concealment can be measured using an approach similar to the cover board (Griffith and Youtie 1988; Limb et al. 2007). By beginning with an independent test of parameters and progressing to simultaneously combinations of test parameters, a causative model will emerge. Testing a similar model in the field might be difficult given confounding obstacles like detection probability, distance from burrow, fluctuating predator presence, etc.

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Figures

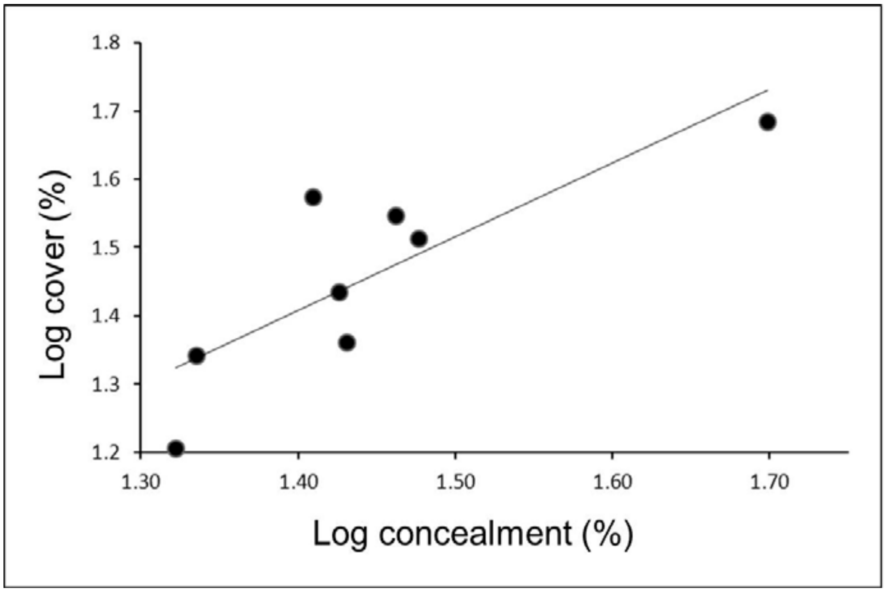

Figure 3.1 The relationship between the average measurement of log-transformed concealment and cover from each mound (n=8, $f_{1,6}$=12.8, P=0.01).

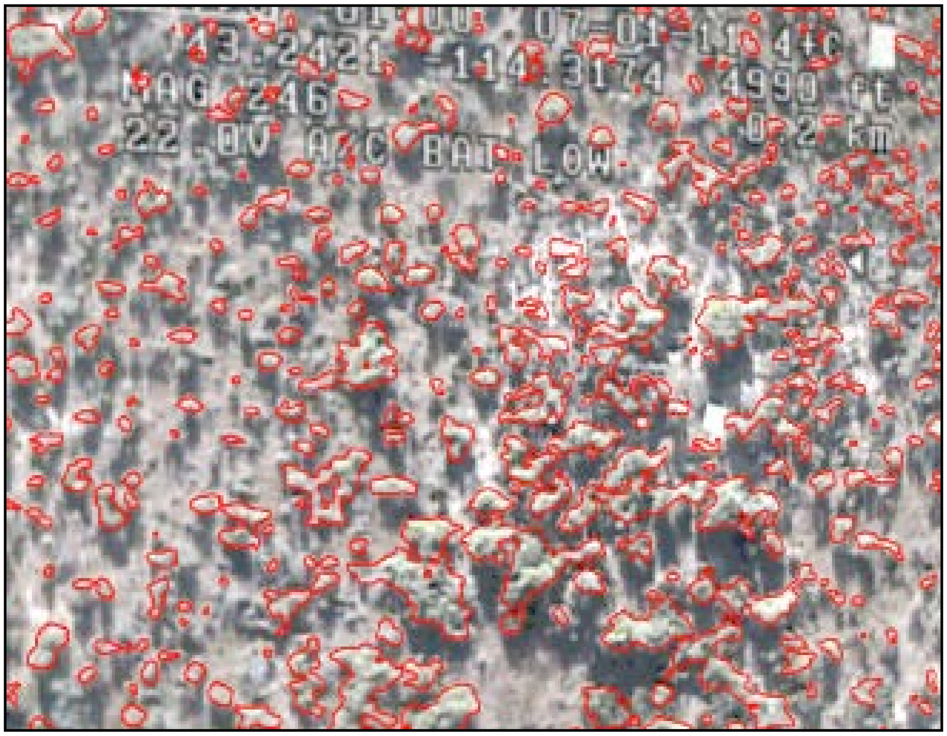

Figure 3.2 This image was taken by an unmanned aerial vehicle flying over a field site managed by Bureau of Land Management (Shoshone Field Office, Shoshone, ID) near Magic Reservoir, located 20 miles south of Hailey, ID (43°3’N, 114°8’W). The red polygons are tracings of sagebrush plants on and around a mima mound.

Figure 3.3 The diagonal clip mark found on a sagebrush plant is evidence of browsing by pygmy rabbits. Note the relatively bright orange or yellow appearance, indicating fresh browsing. Fresh clip marks might also occasionally include a bright green ring of cambium. Old browsing marks are gray and sometimes splintered.

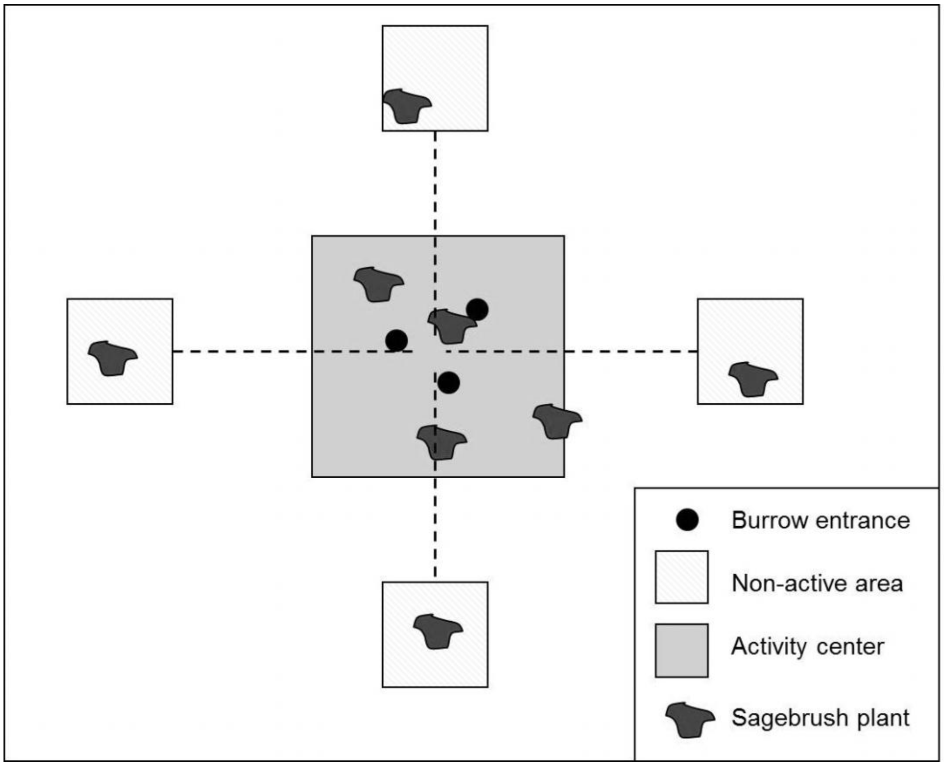

Figure 3.4 Suggested design for measuring quality of habitat resources and use by herbivores in habitats with a central area of activity used by herbivores (e.g. mounds). A high activity area should be established based on presence of active burrows, fresh fecal pellets, and recent browsing, along with four equidistant low activity areas. Total area should be equivalent in high and low activity areas.

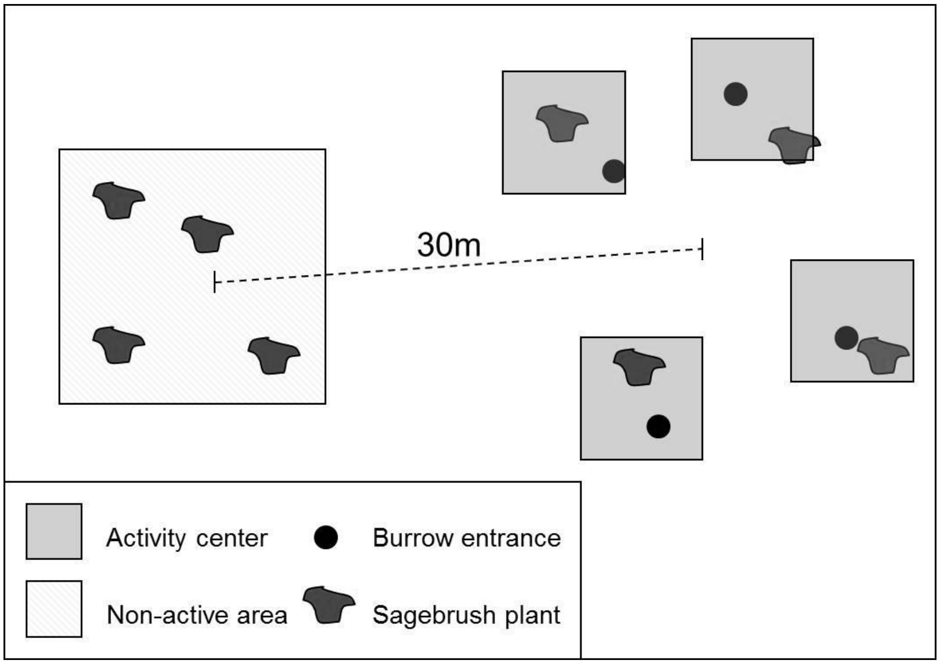

Figure 3.5 Suggested design for measuring quality of habitat resources and use by herbivores in habitats with a decentralized area of activity (e.g. ridgelines, washes, flat plains, etc). Four high activity quadrants should be established using the same 'mound' criteria as in Figure 3.8, along with a single equidistant low activity area with a total area that is equal to the active areas.

APPENDIX A

Scent Feeding Trials

Introduction

The manipulation of predatory olfactory cues as a means to investigate how predation risk influences foraging patterns of herbivores has seen success in previous studies (Koivula and Korpimaki 2001; Bakker et al. 2005; Monclus et al. 2005; Ramp et al. 2005; Kirmani et al. 2010). For example, European rabbits (*Oryctolagus cuniculus*) significantly decreased their food intake in the presence of an odor from a predatory fox compared to exposure to a neutral odor from sheep (Monclus et al. 2005). In addition to altered foraging behavior, rabbits exposed to the fox scent had significantly higher stress hormones compared to rabbits exposed to the sheep odor.

To determine if olfactory cues influence the foraging behavior of pygmy rabbits, I conducted feeding trials where food was associated with predatory or neutral scents. I hypothesized that rabbits would prefer to feed from stations with a neutral scent (mule deer), as opposed to predator scent (coyote). I chose the following combinations of olfactory cues: coyote (*Canis latrans*) or mule deer (*Odocoileus hemionus*) urine, and coyote or mule deer feces. The range of both coyotes (Laundré and Keller 1981) and mule deer (Russell 1931) overlap that of the pygmy rabbit (Weiss and Verts 1984), thus preventing a reaction to novel scent. I chose both delivery methods in an attempt to determine if one was more effective in eliciting a foraging pattern shift.

Methods

I housed wild-caught pygmy rabbits (n=6) in outdoor 5.5mx3.5m enclosures. The enclosure contained a nest box, water *ad libitum*, and two identically opaque feeding stations. During the first two control days of the trial, I fed rabbits 70g of commercial rabbit pellets under each feeding station. Testing occurred during the subsequent four days. If a rabbit did not eat more than 20g, I removed the individual from the trial. I refreshed food every 24h in the afternoon. Within each enclosure, I outfitted each feeding station with either a predator or neutral olfactory cue, and cues were paired by delivery method. I purchased commercially available coyote urine (http://www.predatorpee.com/) and I collected urine from mule deer from captive deer located at the Washington State University Small Mammal Research Facility in Pullman, WA. Cues were either comprised of urine, where I suspended a urine-soaked cotton ball from the roof of the feeding station using nylon hosing, or a fecal sample suspended from the feeding station roof within a tea strainer. The porous nature of the items used for cue suspension ensured adequate scent dispersal while limiting direct contact with pygmy rabbits. After several days of experimentation, I chose urine as the cue delivery method because fecal samples tended to dry out at different rates, which might affect the olfactory strength of the cue. I refreshed scents every 24h and treatment location switched to prevent directional bias as described in Chapter 1 (Figure 1.1).

Statistical Analysis

I assigned dependent variables as mean food intake (4 day average) on each treatment of food eaten under predator or herbivore olfactory cue. I found data to be normally distributed, and a paired sample t-test was conducted between mean intakes of each treatment. I performed all statistical analyses using JMP version 8 software of the SAS Institute.

Results

Foraging patterns of pygmy rabbits were not influenced by olfactory cues. No difference was found between mean intake under a predator treatment (15.45g$\pm$2.54) compared to mean intake under an herbivore treatment (11.62g$\pm$2.23, t_5=1.42, P= 0.21).

Discussion

Despite evidence that rabbit species will respond to olfactory cues (Monclus et al. 2005), my results show that pygmy rabbits did not alter foraging patterns as a response to olfactory cues. Indeed, I made several observations of individuals inside feeding stations (i.e., not feeding, but remaining inside the station nonetheless) baited with predator olfactory cues. In addition, despite treatment switching, some animals still displayed strong directional bias toward a particular side of the enclosure, an issue addressed in Chapter 1.

There are some possible explanations for why pygmy rabbits did not respond to predator scent. The sample size was small (n=6) due to some rabbits not maintaining the minimum daily intake of 20g necessary to sustain health. A larger sample size might have revealed different results. Also, an enclosure without any discernible differences in sides (i.e., sides with the same view rather than one side oriented towards a forest) might have discouraged directional bias and promoted response to cues. To my knowledge, no literature exists that tests a pygmy rabbit's response to odor. Pygmy rabbits might not be as sensitive to terrestrial olfactory cues because 1) the main source of predation-related mortality is avian (Crawford et al. 2010) and 2) fecal deposits by terrestrial predators like coyotes or badgers (*Taxidea taxus)* are common in and around areas of high activity by pygmy rabbits (personal observation). Previous research using olfactory cues to induce predation risk found that a cue might be unreliable if applied with a lack of spatial or temporal association to the probability of predator presence (Powell and Banks 2004). In addition, while many small mammals respond to predator olfactory cues (Sullivan et al. 1985; Sullivan 1986; Lima and Dill 1990; Jedrzejewski et al. 1993; Monclus et al. 2005), some do not. For example, both fox squirrels (*Sciurus niger*) and thirteen-lined ground squirrels (*Spermophilus tridecemlineatus)* showed no change in giving-up density at food patches that contained predatory olfactory cues (Thorson et al. 1998).

Pygmy rabbits showed no response to olfactory cues. This does not mean that an olfactory cue is insignificant to the pygmy rabbit. However, improvements to experimental design, such as a greater number of individuals tested in a highly-controlled setting, are recommended to ensure greater certainty. In comparison, the Cover Only Trial (Chapter 1) served to reinforce the “honest cue” concept (Dall et al. 2005) that cover offers a true cue of risk that is less likely to be misinterpreted, whereas scent might possibly be misconstrued given any number of factors (i.e., age of scent, location of scent, diet of scent provider, etc.). Despite the lack of a true predator threat, pygmy rabbits still selected the dark cover, low predation risk feeding stations. It is imperative to choose honest and unambiguous but variables that can be manipulated when studying tradeoffs and habitat use

APPENDIX B

Outdoor Feeding Trials

Introduction

The results of Chapter 1 demonstrated that in captivity, foraging pygmy rabbits respond to both cover and diet quality. The values placed on cover and food are not independent but instead interact to influence foraging choices of herbivores. That is, high quality food paired with poor cover might outweigh the option of poor quality food paired with good cover or vice versa. The application of Chapter 1 results in a field setting would provide greater relevance in revealing the parameters that drive habitat use in wild populations, thus providing land managers with a more comprehensive approach to conservation. Therefore, I made repeated attempts to conduct feeding trials testing the value of cover and diet quality with wild pygmy rabbits.

For an herbivorous prey species, vegetation often serves a dual purpose: refuge from predation risk and primary food source. Refuge provided by vegetation in a habitat is often a crucial tool for avoiding predation (Cassini and Galante 1992; Clarke et al. 1993; Creel and Christianson 2008; Cresswell et al. 2010). Previous literature has established that vegetative cover, the majority of which is provided by sagebrush (*Artemisia* spp), is a predicting variable for habitat use by pygmy rabbits (Katzner and Parker 1997; Gabler et al. 2001; Heady and Laundré 2005). That cover is important is not a surprise, given the high pressure pygmy rabbits face from aerial predators (Crawford et al. 2010). This same vegetation might also double as a food source. For the pygmy rabbit, sagebrush acts as a dietary cornerstone, composing 55% of the summer diet and 99% of the winter diet (Green and Flinders 1980; Thines et al. 2004).

My objective was to present choices of cover and food quality to wild pygmy rabbits in a design similar to the captive trials of Chapter 1. I hypothesized that rabbits would prefer to feed from dark cover feeding stations (i.e., low predation risk) at the expense of consuming poor quality food. I arrived at this hypothesis given current literature on pygmy rabbits and the determination of cover as a predicting variable of habitat use (Katzner and Parker 1997; Gabler et al. 2001; Heady and Laundré 2005). However, if the quality of food offered far surpassed surrounding options, I predicted that a tradeoff would occur and pygmy rabbits would consume high quality food at the expense of poor or no cover. In addition, I hypothesized that pygmy rabbits would spend more time in covered stations that provide greater refuge from predators than transparent feeding stations.

Experimental Design

Outdoor feeding trials were similar to captive trial methods of Chapter 1. I began by identifying active pygmy rabbit mounds in public land managed by the Bureau of Land Management (Shoshone Field Office, Shoshone, ID) near Magic Reservoir, located 20 miles south of Hailey, ID (43°3’N, 114°8’W). I conducted feeding trials at active mounds in March 2010, December 2010, January 2011, August 2011, and November 2011. I conducted the trials for at least 3 days. I classified active mounds as having one or more clearly open burrow holes, at least five fresh fecal pellets, and evidence of fresh browsing by pygmy rabbits. However, even with video monitoring, estimating the number of individual rabbits visiting each station was difficult. I constructed feeding stations using 30.5x27x30.5cm transparent storage stations, and feeding stations provided two levels of cover: low predation risk feeding stations were fitted with dark blue felt, simulating dense cover, while high predation risk feeding stations were left transparent

(Figure A.1). Feeding stations were arranged <1.5m away from active burrow holes and station openings faced burrow entrances to increase encounter rates by pygmy rabbits.

Within each station, I offered several types of sagebrush that varied in quality in an attempt to determine if one type was selected: sagebrush grown in a greenhouse (greenhouse sage), sagebrush harvested in spring months (spring sage), and sagebrush harvested in the winter that showed signs of browsing (winter sage). I classified the quality of sagebrush according to concentration of toxins, highest protein, and water content based on previous analyses (Forbey, unpublished data). I inserted sagebrush sprigs into holes in plastic platforms and anchored platforms to the ground with stiff wire to ensure no movement during foraging events. I positioned motion-sensitive game cameras (Moultrie Gamespy D55-IR Megapixel Digital Infrared Game Camera and Bushnell Trophy Cam Infrared Camera model 119653C) such that both the feeding stations and burrow entrances were visible to cameras (Figure A.2). Game cameras served to confirm pygmy rabbit foraging (rather than other potential herbivores) and collect behavioral data. I set cameras to record 15-second videos, with a one min time lapse between recordings. Cameras also recorded one photo at the start of 15s video recording, but almost no behavioral observations could be derived from photos so only video data was analyzed.

Before I inserted sagebrush into plastic holders, I weighed the samples to the nearest tenth of gram. I deployed feeding stations and game cameras in the afternoon, a lower period of rabbit activity (personal observation), for 24h. After 24h, remaining sagebrush was checked for characteristic clip marks, weighed and discarded, and new sagebrush was inserted. To prevent possible directional bias, cover treatments were switched every 24h.

Video Behavioral Observation

The following behavioral observations were recorded during a single feeding trial I conducted in November 2011. I classified behaviors on videos *post hoc* as enter, inside, vigilance, browse, sniff, or dig. I defined 'enter' as the rabbit being inside of the feeding station for less than two seconds. I identified ‘inside’ as the rabbit entering the feeding station for two seconds or longer. I identified ‘vigilance’ as the rabbit's head being up, ears alert for two seconds or longer. Rabbits displaying vigilance behaviors would occasionally adopt an upright posture with forelegs not touching the ground. Finally, I classified ‘Browse’ as the rabbit browsing on offered foods or wild food sources in the background.

Results

Pygmy rabbits failed to feed from feeding stations. However, a compilation of 120 hours of camera deployment showed that rabbits are comfortable in and around feeding stations.

Although the mean amount of time spent while inside covered feeding stations (n=8, 7.8s±1.98) and transparent feeding stations (n=15, 8.6s+0.9) was not significantly different (t_{21}=-0.41, *P*=0.68), pygmy rabbits did visit transparent stations (130s±2.3) almost twice as often as dark stations (63s+1.8, Figure A.3). The most common sequence of behaviors observed is as follows: the rabbit entered the feeding station, sniffed the surroundings, become distracted by an unknown cue, which led to vigilance, and finally exited from the camera view.

Conclusions

Despite the failure of wild pygmy rabbits to respond to field-based feeding trials, some success was noted. Pygmy rabbits appeared unafraid of the feeding stations and refuted my hypothesis that more time would be spent under dark cover stations. With this limited data set, it’s difficult to hypothesize as to why rabbits appeared to prefer transparent feeding stations. This might be due to pygmy rabbits relying on, among other senses, visual cues for estimating potential for predation risk, thus preferring to forage where possible predators can be easily spotted. Other factors, like smell of boxes or movement of cloth in dark cover boxes might also be responsible for the use of transparent cover stations. In addition, a greater number of feeding station deployment days might also allow the rabbits more time to acclimate, thus possibly increasing the chances of feeding.

While pygmy rabbits appeared to accept the feeding stations, very little foraging was recorded. There are many possibilities for why offered sagebrush was not sampled. For one, the sagebrush offered might not offer an ideal food source on a nutrient or chemical level. Some samples had been frozen for more than 6 months, so some unknown degradation of samples not visible to researchers might have taken place. Sagebrush samples, even if fresh, might not represent a quality food item to pygmy rabbits. With particular respect to feeding trials conducted in warm months, sagebrush samples were subject to extreme desiccation, which might lower the dietary value of the sagebrush. Finally, samples offered might not have been representative of the proper nutrient and chemical composition required of a pygmy rabbit during a specific season. For example, pygmy rabbits eat more forbs and grasses than sagebrush during spring and early summer (Green and Flinders 1980), so offering sagebrush of unknown quality while food resources were abundant was most likely a disadvantage for feeding trial success.

The methodology behind wild pygmy rabbit feeding trials can be improved. Most importantly, a highly desirable food source must be determined. Also important is careful consideration for the appropriate season. Feeding trials would most likely be futile during a period of food surplus (e.g., spring and early summer) and successful during a period of moderate food scarcity (e.g., fall and winter). Conducting feeding trials in extreme scenarios of food shortage might skew data but would provide insight into how foraging patterns shift temporally. In addition, deploying a valuable food sources into the habitat will only work if the forager encounters it. A researcher should take care to deploy food resources in or along areas trafficked by the forager. Once a valuable food item and appropriate season is identified, a researcher can introduce other variables that potentially influence the value of food, like cover, distance, or predation risk. Finally, the parameters of the optimal foraging theory (Charnov 1976) should be considered according to species life history. For instance, is the animal a central place forager? Does the food item require energy expenditure to obtain (i.e., handling time)? What energy gains or losses can be expected of some food item at some distance (i.e., travel time)?

In conclusion, field-based pygmy rabbit feeding trials were unsuccessful. However, insight into pygmy rabbit interaction with equipment and success with behavioral observation via game cameras provide a valuable starting point for future research.

Appendix Figures

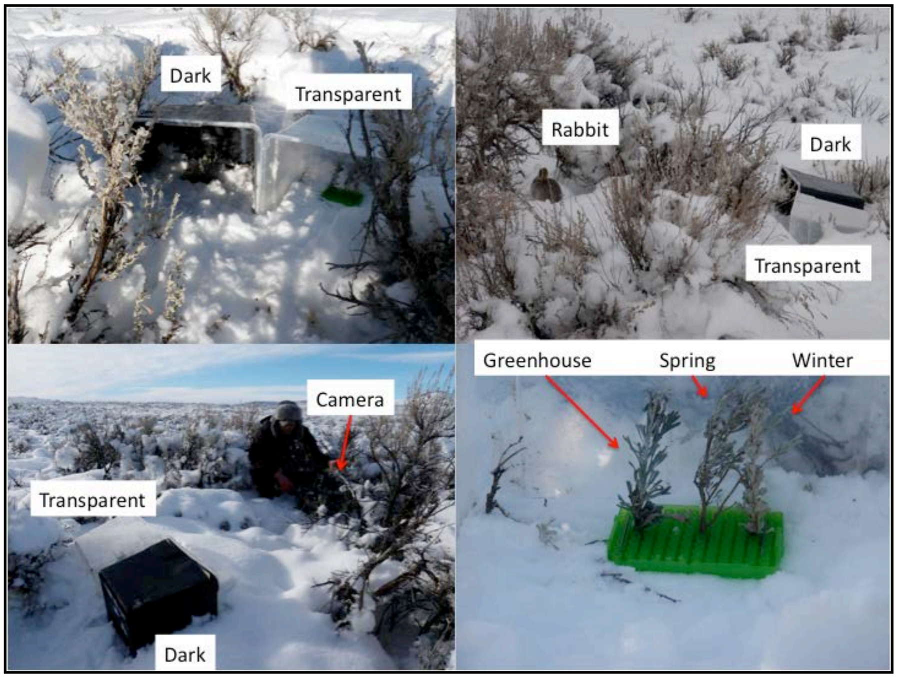

Figure A.1 The top left, top right and bottom left images show the dark and transparent feeding stations set up on active pygmy rabbit burrows and ≤ 1.5m away from an open burrow hole. The bottom right image displays the three sprigs of sagebrush anchored by plastic holders. The bottom left image also includes a researcher placing a motion-sensitive wildlife trail camera.

Figure A.2 A pygmy rabbit emerges from a burrow (bottom center) to investigate feeding stations. The transparent feeding station on the right represents high predation risk, and the feeding station on the left represents low predation risk.

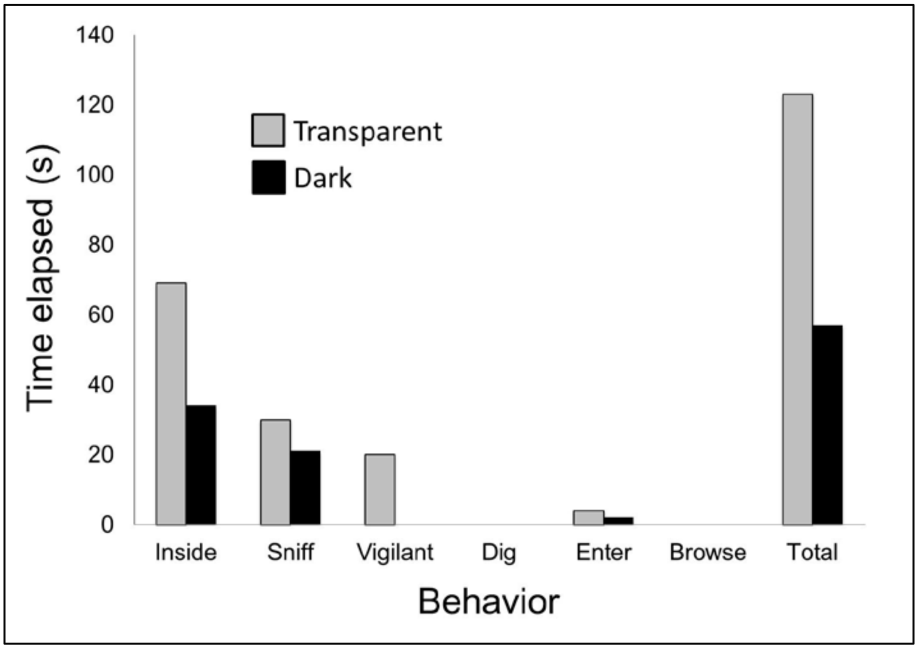

Figure A.3 Time (s) spent on specific behaviors by pygmy rabbits captured by video over the course of a 3 day feeding trial in November, 2011. Light gray bars represent behaviors recorded while a rabbit was in or around a transparent feeding station, and black bars represent behaviors recorded while a rabbit was in or around a dark feeding station.

APPENDIX C

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