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Understanding tradeoffs between food and predation risks in a specialist mammalian herbivore

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Understanding habitat use by animals requires understanding the simultaneous tradeoffs between food and predation risk within a landscape. Quantifying the synergy between patches that provide quality food and those that are safe from predators at a scale relevant to a foraging animal could better reveal the parameters that influence habitat selection. To understand more thoroughly how animals select habitat components, we investigated tradeoffs between diet quality and predation risk in a species endemic to sagebrush *Artemisia* spp. communities in North America, the pygmy rabbit *Brachylagus idahoensis*. This species is a rare example of a specialist herbivore that relies almost entirely on sagebrush for food and cover. We hypothesized that pygmy rabbits would forage in areas with low food risk (free of plant secondary metabolites, PSMs) and low predation risk (high concealment). However, because of relatively high tolerance to PSMs in sagebrush by pygmy rabbits, we hypothesized that they would trade off the risk of PSM-containing food to select lower predation risk when risks co-occurred. We compared food intake of pygmy rabbits during three double-choice trials designed to examine tradeoffs by offering animals two levels of food risk (1,8-cineole, a PSM) and predation risk (concealment cover). Rabbits ate more food at feeding stations with PSM-free food and high concealment cover. However, interactions between PSMs and cover suggested that the value of PSM-free food could be reduced if concealment is low and the value of high concealment can decrease if food contains PSMs. Furthermore, foraging decisions by individual rabbits suggested variation in tolerance of food or predation risks.

When acquiring food, herbivores must consider many factors, such as the nutritional quality of forage, potentially toxic plant secondary metabolite (PSM), and availability of cover for protection from predators and thermal stress (Werner and Hall 1988, Dearing et al. 2000, Bakker et al. 2005, Hebblewhite and Merrill 2009). However, foraging patches might not always have a sufficient mixture of these factors. Therefore, the resulting selection of foraging patches by an animal is often a tradeoff between the costs and benefits perceived by the herbivore (Lima and Dill 1990, McArthur et al. 2014).

Foraging patterns of herbivores are influenced by both the risk of PSMs and predation. The potential risks of PSMs include reduced intake (Boyle and McLean 2004, Marsh et al. 2005, Sorensen et al. 2005, Shipley et al. 2006), which can result in death (Reichardt et al. 1984) as well as numerous post-ingestive consequences such as direct toxicity to cells (Koppel et al. 1981, Forbey et al. 2011, Kohl et al. 2015), reduced digestibility and uptake of nutrients (DeGabriel et al. 2009, Au et al. 2013, Kohl et al. 2015), and increased energetic costs associated with detoxification (Sorensen et al. 2005). Moreover, concentrations of PSMs can pose large-scale constraints to herbivores by influencing habitat selection (Karban and Agrawal 2002, Moore et al. 2005, Frye et al. 2013, Ulappa et al. 2014). For example, koalas *Phascolarctos cinereus* selectively foraged from *Eucalyptus* trees that contained both lower concentrations of PSMs and higher digestible nitrogen (Moore et al. 2005). Similarly, greater sage-grouse *Centrocercus urophasianus* (Frye et al. 2013) and pygmy rabbits *Brachylagus idahoensis* (Ulappa et al. 2014) foraged from individual sagebrush *Artemisia* spp. plants that contained lower PSMs and higher protein. Furthermore, numerous studies have demonstrated that herbivores decrease foraging activity in response to elevated predation risk (Brown and Kotler 2004, Willems and Hill 2009, McArthur et al. 2012). To minimize the risk of predation, animals often select habitat patches that provide higher levels of concealment cover, which have been shown to reduce perception of risk (Brown 1988, Camp et al. 2012).

However, the risk of PSMs and predation are not encountered in isolation. As a consequence, herbivores must make habitat tradeoffs based on these simultaneous risks (Lima and Dill 1990, Brown and Kotler 2004, McArthur et al. 2014). For example, PSMs had a greater effect on foraging patterns of brushtail possums *Trichosurus vulpecula* (Kirmani et al. 2010) and fox squirrels *Sciurius niger* (Schmidt 2000) than perceived risk of predation. Moreover, brushtail possums left patches of food containing both risks of PSMs and predation sooner (i.e. higher giving up density) than patches with predation risk alone (Kirmani et al. 2010). Tradeoffs between PSMs and predation risk have yet to be investigated in a dietary specialist, where higher tolerance to PSMs may influence tradeoffs differently than in generalists.

Our objectives in this study were to examine the influence of the risk of a potentially toxic PSM, perceived predation risk, and the tradeoff between the two risks on selection of foraging patches by a small, specialist mammalian herbivore, the pygmy rabbit *Brachylagus idahoensis*. Sagebrush *A. tridentata*, which is high in PSMs (including monoterpenes; Shipley et al. 2006, Frye et al. 2013, Ulappa et al. 2014), comprises the majority of the diet of pygmy rabbits (Green and Flinders 1980, Weiss and Verts 1984, Thines et al. 2007). The classes of PSMs in sagebrush (e.g. monoterpenes, phenolics and sesquiterpene lactones) can disrupt cellular function (Wink 2008, Forbey et al. 2011), inhibit digestive enzymes (Kohl et al. 2015), irritate mucous membranes (Hedenstierna et al. 1983), cause diuresis (Dearing et al. 2000), and compromise energy budgets (Sorensen et al. 2005). In addition, pygmy rabbits experience high rates of predation from a diverse suite of terrestrial and avian predators (Estes-Zumpf and Rachlow 2009, Crawford et al. 2010), and they use burrows and sagebrush as concealment cover to reduce predation risk (Green and Flinders 1980, Camp et al. 2012). To test responses by the rabbits to the potential risk of toxicity and predation, we conducted three choice experiments. In the first trial, we offered food with and without PSMs under constant low predation risk (high concealment). In the second trial, we offered PSM-free food under two levels of predation risk (high concealment and low concealment). In the third experiment, we manipulated risks of PSMs and predation simultaneously to identify tradeoffs in foraging behavior. We predicted that pygmy rabbits would choose the lowest risk of potential toxicity from PSMs when low predation risk (high concealment) was held constant and would choose the lowest risk of predation when low food risk (PSM-free) was held constant. Because pygmy rabbits specialize on sagebrush diets containing high levels of PSMs and we used the highest concentration of a PSM that pygmy rabbits can tolerate in captivity without losing body mass (Shipley et al. 2012), we expected them to avoid risk of predation at the expense of consuming food with PSMs when offered a choice between foods with a PSM under high concealment versus PSM-free food under lower concealment. These experiments represent the first step in understanding the complex tradeoffs that a dietary specialist makes when responding simultaneously to predation risk and food quality. Such tradeoffs between habitat components have broad ecological implications, especially for interpreting fine-scale patterns of habitat selection and space use by specialist herbivores.

Methods

During summer and fall of 2010, we live-trapped 10 adult (> 300 g) pygmy rabbits (five females, five males) from three sagebrush-dominated sites in Idaho, USA, including Magic Valley (43°3′N, 114°8′W), Raft River Valley (42°8′N, 115°8′W) and Lemhi Valley (45°2′N, 113°8′W). Rabbits were transported to the Small Mammal Research Facility at Washington State University (WSU), Pullman, WA, for feeding experiments. Rabbit trapping was conducted under an Idaho Dept of Fish and Game collection permit (100310 to JSF and 010813 to JLR).

During the non-testing phase, rabbits were housed indoors within 65 × 65 × 40 cm individual pens and fed a daily basal diet of water and commercial rabbit chow (Purina Rabbit Chow Professional Natural AdvantEdge pellets, Purina Mills LLC, Gray Mills, MO, USA) ad libitum with approximately 15 g of fresh mixed greens and greenhouse-grown sagebrush *Artemisia tridentata* spp. The rabbit chow was the same chow used throughout experimental trials and was similar in fibre (36%) and nitrogen (3.4%) to sagebrush leaves (30% fibre and 2.5–4.5% nitrogen, Camp et al. 2015). Rabbits were maintained at approximately 15°C with a 10:14 light/dark cycle (i.e. winter cycle). Work with captive rabbits was approved by WSU's Institutional Animal Use and Care Committee (IACUC protocol no. 3994). For the food risk trial, individual rabbits were housed in the same indoor pens used during the non-testing phase. For the two trials involving predation risk, individual rabbits were housed outdoors in a 5.5 × 3.4 m wire enclosure with a semi-transparent roof at 3 m. Temperature during outdoor trials ranged from 18°C to –2°C, with intermittent rain and snow. Rabbits were provided with a waterproof nest box (40 × 23 × 13 cm) filled with 2 cm of pine shavings and access to a dark plastic tube 13 cm in diameter that simulated the burrow. Given the rural setting of the research facility, unquantified, but confirmed evidence of great-horned owls *Bubo vigrinianus* and diurnal raptors suggests that pygmy rabbits were exposed to random and unavoidable auditory predator cues. Coyotes *Canis latrans* were also seen occasionally, so black fabric was wrapped around the pens to reduce exposure to visual predation cues. Rabbits that failed to eat ≥ 20 g of chow at any point in any trial were removed from that trial and replaced with another rabbit in subsequent trials. Thus, not all trials contain the same individuals, but individuals within each trial remained the same.

To examine the response of pygmy rabbits to risks of PSMs and predation, we conducted three risk trials that measured food intake under different types of risk. In the food risk trial, we examined the rabbits' choice of feeding stations (ceramic bowls) containing PSM-free food versus PSM-containing food, both under constant high level of concealment. In the predation risk trial, we examined the rabbits' choice of feeding stations containing PSM-free food placed under dark (low predation risk) versus transparent (high predation risk) concealment. Finally, in the risk tradeoff trial, we examined the rabbits' choice between feeding stations with high food risk (PSMs) and low predation risk (dark concealment) versus feeding stations with low food risk (PSM-free) and high predation risk (transparent concealment).

During the food risk trial conducted from 6–9 December 2010 and 9–12 February 2011, rabbits were housed indoors in the same pens used during the non-testing phase described above. Indoor pens provided constant, consistent concealment, and the small pen size helped reduce factors that may influence diet choice in an outdoor setting (i.e. weather, predator cues). In each pen, two feeding stations were placed equidistant from each other and from a nest box refuge. Feeding stations each contained 35 g wet weight of food, which exceeded the average daily intake of rabbit pellets by pygmy rabbits during the non-testing phase. The PSM-free feeding station contained unaltered rabbit food and the toxic feeding station contained the same rabbit pellets of the same nutritional value except that pellets were mixed with 5% 1,8-cineole by dry mass (hereafter cineole, Alfa Aesar, stock no. A12269). Cineole is a monoterpene naturally found in sagebrush consumed by pygmy rabbits (Kelsey et al. 1982, Shipley et al. 2006, Ulappa et al. 2014). The total monoterpene content in sagebrush can be as high as 4% (White et al. 1982, Shipley et al. 2006) and cineole ranges from 1–13% of the total oil depending on taxa (Frye 2012) resulting in a maximum concentration of cineole lower than what we used in our study. However, our goal was to assess the relative risk of consuming a PSM compared to perceived predation risk using a simplified system where cineole represented the dietary risks associated with the suite of monoterpenes in sagebrush. In previous no-choice intake trials, pygmy rabbits began reducing food intake when cineole was increased above 5% in rabbit pellets (Shipley et al. 2012). Thus, 5% cineole represents the upper threshold of a PSM in our artificial diet that is tolerated by pygmy rabbits but does have risks (e.g. reduced intake and body mass) at concentrations above 5%. The PSM-containing food was prepared fresh each morning of the trial by thoroughly mixing 300 g pellets with 15 g of liquid cineole in a glass jar and storing it at –20° C until used. To reduce volatilization of cineole, PSM-containing pellets were refreshed every 12 h during the trials. In preliminary experiments, we found that only 1% of cineole volatilized from food pellets over a 12 h period under our experimental conditions (Utz 2012). During indoor trials, no covers were placed over individual feeding stations, but the small pen size (65 × 65 × 40 cm) provided a constant level of concealment when rabbits selected between PSM-free and PSM-containing feeding stations.

During the predation risk trial conducted from 26 October to 8 November 2010, rabbits were presented with two feeding stations with 35 g of PSM-free food under 31 × 27 × 31 cm plastic boxes. One feeding station was placed under a dark concealment box (completely covered with black contact paper to simulate low predation risk) and the other under a transparent concealment box (simulating high predation risk). Concealment boxes had one lengthwise side cut away as an opening for entry by the rabbits, and feeding stations were placed equidistant from each other, the nest box refuge and burrow tube. The transparent and concealed box allowed us to specifically test for concealment without the confounding effect of structure (i.e. presence of a box) associated with a food patch. Preliminary trials indicated that foraging patterns of pygmy rabbits were not influenced by olfactory cues. During the four day preliminary trial, we found that intake of PSM-free food associated with urine from a coyote (e.g. predator cue, <www.predatorpee.com>, 15.45 g ± 2.54) did not differ from intake of food associated with urine from captive mule deer (e.g. neutral olfactory cue 11.62 g ± 2.23) that were housed at Washington State University Wild Ungulate Facility in Pullman, WA. ($t_5 = 1.42$, $p = 0.21$, Utz 2012). Therefore, the predation risk trial focused on visual cues associated with two levels of concealment without the addition of olfactory cues.

During the risk tradeoff trial conducted from 15 November 2010 to 29 January 2011, rabbits were housed in the same outdoor pens and feeding station setup as in the predation risk trial. During this trial, however, rabbits were offered a choice between a feeding station with PSM-containing food (as described in the food risk trial) under the dark concealment box and PSM-free food placed under the transparent concealment box.

Before each of the three trials, rabbits were allowed to acclimate for two days to the experimental enclosures followed by four treatment days. To remove effects of any potential bias for one side of a pen over another, we assigned the food and cover treatments to feeding stations randomly on the first day of each treatment and switched the location of treatments between stations every 24 h during the four treatment days of each trial. Water was provided ad libitum for non-testing, acclimation and treatment days.

We estimated food consumed from each feeding station during the treatment trials as the difference between food offered and rejected. We measured the fresh mass of food pellets offered every 12 h when PSM-containing food was offered (food risk and risk tradeoff trials) and every 24 h for the predation risk trial, and corrected it for dry matter by drying a subsample at 100°C for 24 h. Food rejected at each feeding station also was dried before weighing.

Statistical analyses

The risk trials first required that we test if the average intake during the two-day acclimation periods differed among the three trials using a one-way ANOVA. Because the three trials were conducted at different times, the results for each trial could have been influenced by the effect of time. However, average intake by rabbits during the acclimation period before each trial was the same, providing evidence that time did not matter in terms of responses of rabbits during each trial.

Next, we analyzed data within a trial using a repeated measures ANOVA to test if there was an effect of time (within-subject effect), treatment (between-subject effect) or time × treatment interaction on daily intake by the rabbits. For the food risk trial, the treatment was the level of PSM (PSM-containing or PSM-free). For the predation risk trial, the treatment was the level of concealment (transparent or dark concealment). For the risk tradeoff trial, the treatment was the combination of food and predation risk (dark concealment with PSM or transparent without PSM). We removed one rabbit from the study because it would not maintain body mass on trials. Data were tested for normality and equal variance prior to analyses. Because the data for the three risk trials did not meet the assumption of compound symmetry required for repeated measures ANOVA, we used Greenhouse–Geisser adjusted p-values. All statistical analyses were performed using SAS ver. 9.2 software of the SAS Inst. 2008.

Results

During the acclimation periods, animals ate an average of 32.3 ± 3.1 g for the food risk trial, 24 ± 3.3 g for the predation risk trial, and 29.2 ± 2 g for the tradeoff trial. There was no significant difference in the average intake among the three acclimation periods ($F_{2,21} = 2.08, p = 0.15$). Within each of the three trials, the pattern of intake across four days was consistent over time. During the food risk trial, we found no within-subject effect of time ($F_{3,48} = 1.26$, $p = 0.30$) or time × treatment ($F_{3,48} = 0.87$, $p = 0.41$). However, the between-subject effect of treatment (PSM-containing versus PSM-free) was significant ($F_{1,16} = 30.48$, $p < 0.0001$). Pygmy rabbits ($n = 9$) consumed more than three times the amount of PSM-free food ($\bar{X} = 35.4 \pm 3.4$ g) than the PSM-containing food ($\bar{X} = 11.6 \pm 2.43$ g) when predation risk was constant (Fig. 1). Likewise, during the predation risk trial, we found no within-subject effect of time ($F_{3,51} = 0.39$, $p = 0.67$) or time × treatment ($F_{3,51} = 0.90$, $p = 0.41$), but the between-subject effect of treatment (transparent versus dark concealment) was significant ($F_{1,16} = 30.04$, $p < 0.0001$). Pygmy rabbits ($n = 9$) consumed more than twice the amount of food from feeding stations placed under the dark concealment (low predation risk, $\bar{X} = 27.22. \pm 2.6$ g) than the transparent concealment (high predation risk, $\bar{X} = 9.6 \pm 1.5$ g), when food lacked PSMs (Fig. 1).

When given a choice of higher risk of toxicity associated with higher concealment versus higher risk of predation associated with a PSM-free food in the risk tradeoff trial ($n = 9$), pygmy rabbits did not demonstrate a clear preference. We found no within-subject effect of time ($F_{3,48} = 0.37$, $p = 0.78$), time × treatment ($F_{3,48} = 3.13$, $p = 0.06$), nor treatment ($F_{1,16} = 2.20$, $p = 0.16$). On average, pygmy rabbits ate comparable amounts of PSM-free food under high predation risk ($\bar{X} = 26.40 \pm 4.0$ g) and PSM-containing food under low predation risk ($\bar{X} = 17.0 \pm 3.8$ g, Fig. 1). However, individual animals varied in their aversion to risk of PSMs relative to risk of predation (Fig. 2). Of the nine rabbits used in the trials, three consumed relatively more PSM-containing food under low predation risk, whereas six consumed relatively more PSM-free food under high predation risk.

Discussion

As expected, pygmy rabbits in our study preferred to feed under less risky conditions. When given a choice between PSM-containing or PSM-free food, pygmy rabbits preferred the PSM-free food. When given a choice to feed under high concealment or low concealment, they preferred the high concealment. However, when offered a choice between patches with high PSM/low predation risk and patches with low PSM/high predation risk, individual rabbits varied in their choices ranging from consuming 80% of their diet from one patch type to 80% from the other.

Although the natural diet of pygmy rabbits consists of plants with high levels of a variety of interacting PSMs and nutrients (i.e. sagebrush), rabbits in our study clearly

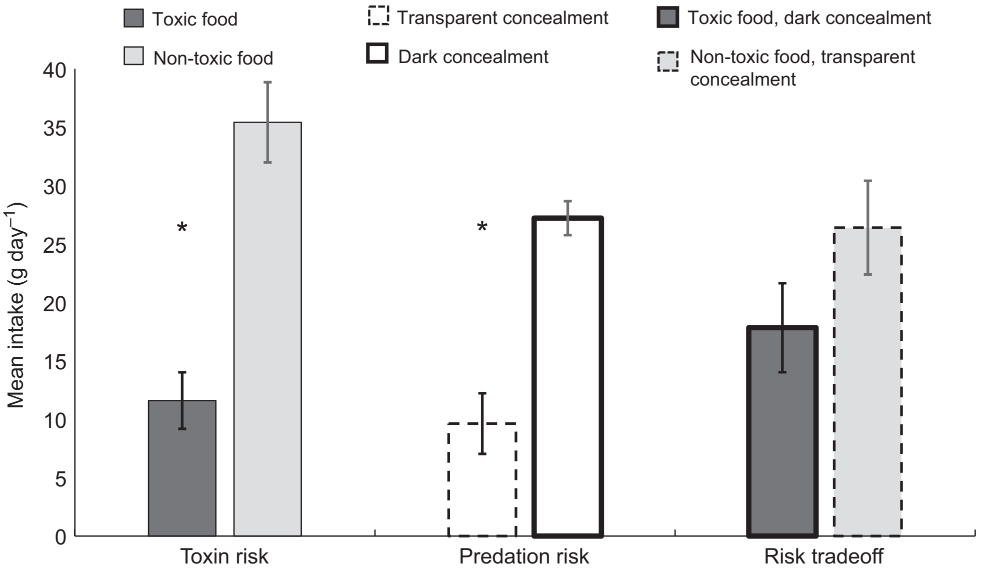

Figure 1. Daily intake (mean ± SEM, grams dry weight day^{-1}) of food by pygmy rabbits during three choice treatment trials. Dark gray bars represent foods with high food risk (high PSM), dashed borders represent concealment with high predation risk (low concealment), and asterisks denote significance between the two treatments within a trial. The food risk trial provided rabbits the choice of PSM-containing food (5% cineole by dry weight) or PSM-free food (no cineole added) under constant concealment. The predation risk trial provided rabbits with the choice of PSM-free food under high predation risk (transparent concealment) or under low predation risk (dark concealment). The risk tradeoff trial provided rabbits with a choice of PSM-containing food under low predation risk or PSM-free food under high predation risk.

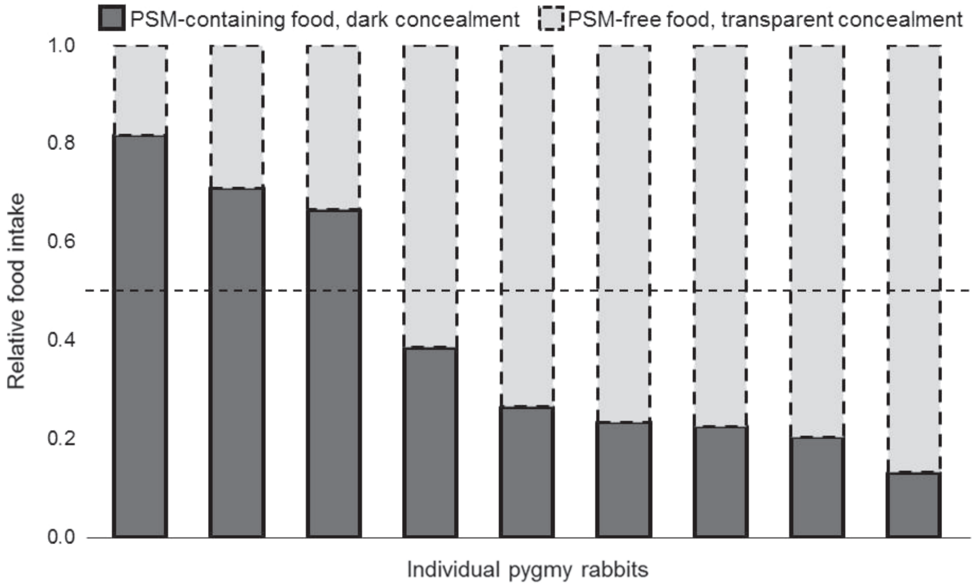

Figure 2. Relative intake of each choice treatment on the tradeoff risk trial for individual rabbits when rabbits were offered a choice to feed under low predation risk (dark concealment) that contained food with PSMs or high predation risk (transparent concealment) that contained PSM-free food. The dashed horizontal line represents equal intake of both treatment choices.

detected and avoided risk of a single measure of potential toxicity when risk of predation was constant. Pygmy rabbits consumed greater than three times more PSM-free food than food mixed with 5% of the monoterpene cineole during the food risk trial. Avoidance of PSMs is consistent with other studies involving both captive and free-ranging vertebrate herbivores. Specifically, captive trials demonstrate that intake of food by vertebrate herbivores such as brushtail possums (Boyle and McLean 2004, Marsh et al. 2005), woodrats *Neotoma* spp. (Sorensen et al. 2005), pygmy rabbits (Shipley et al. 2012), cottontails *Sylvilagus nuttalli* (Shipley et al. 2012), and snowshoe hares *Lepus americanus* (Reichardt et al. 1984) decreases with increasing concentrations of PSMs and that PSMs are avoided when higher quality food options are available. Similarly, free-ranging herbivores give up patches of artificial food with higher concentrations of PSMs sooner than patches with lower concentrations of PSMs (Kirmani et al. 2010, McArthur et al. 2012, Bedoya-Pérez et al. 2014a). Selection of artificial diets lower in concentrations of PSMs is consistent with recent field data showing the odds of browsing by pygmy rabbits and sage-grouse on a sagebrush plant increased with decreasing concentrations of monoterpenes (Frye et al. 2013, Ulappa et al. 2014). Our results provide a functional basis for using PSMs, specifically monoterpenes, as predictors of suitable habitats and use for a specialist mammalian herbivore.

Furthermore, pygmy rabbits consumed twice as much food under high concealment cover than low concealment. While the mechanism of selecting greater concealment could be associated with preference for dark places rather than lower predation risk, our results are consistent with other studies that have demonstrated that animals prefer to forage under higher levels of refuge from visual predators. For example, small mammals are known to forage during a new moon phase (i.e. darkness) rather than during a full moon phase (Kotler et al. 2010), even in the absence of predators (Yunger et al. 2002). Although foraging animals also respond to olfactory cues (Monclús et al. 2005), our preliminary trials indicated that captive pygmy rabbits in our facility might not be sensitive to the manipulation of olfactory cues of predators. 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 with predators (Powell and Banks 2004). Certainly, the strength, timing, and type of predator cue used can influence responses by prey (Embar et al. 2011, Nersesian et al. 2012). However, our results showing that pygmy rabbits respond to visual predation cues are consistent with observations of free-ranging pygmy rabbits that had lower perceptions of risk with higher levels of concealment from shrubs (Camp et al. 2012). Our results suggest that shrub cover is another important component, in addition to presence and concentration of PSMs, for determining selection of functional habitat by pygmy rabbits.

In contrast to our expectations, when offered the choice between two types of risks commonly experienced simultaneously by small mammalian herbivores (potential predation and toxicity), the population of pygmy rabbits we studied did not demonstrate a clear preference. Specifically, we hypothesized that the relatively high tolerance of pygmy rabbits to PSMs in sagebrush compared to other species would result in higher avoidance of predation risk at the expense of consuming food with PSMs. For example, in no-choice diet trials, food intake by pygmy rabbits begins to decline above 5% cineole, but was 3–5 times higher than that of cottontails (Shipley et al. 2012). Even though individuals in our study made consistent choices to avoid risks when encountered singly, our experimental population consumed, on average, the same amount of PSM-containing food under low predation risk as PSM-free food under high predation risk. This implies that individual animals might perceive and respond to risks differently based on the relative level (e.g. dose) of risks encountered as well as the physiological (e.g. detoxification capacity, stress hormones, metabolism, McArthur et al. 2014), ecological (e.g. competition), or evolutionary (e.g. life history strategy, niche specialization) status (Wolf et al. 2007, Stamps 2007, Biro and Stamps 2008, Réale et al. 2010, Montiglio et al. 2014) of the forager (Bedoya-Perez et al. 2013). Furthermore, individual responses to a specific risk might reflect individual 'personality' in risk-related behavior. For example, the degree of boldness of individual brushtail possums *Trichosurus vulpecula* affected foraging at risky, high-quality food patches and at safe patches when the concentration of PSMs was low (Mella et al. 2015). Thus, personality may influence the way in which pygmy rabbits weigh the relative risks of potential predation and toxicity.

In our study, like those of Kotler and Blaustein (1995), Nersesian et al. (2011) and McArthur et al. (2012), we only measured the animals' responses to one level of food and predation risk. Further experimentation using titration experiments would provide estimates of the rate at which animals make tradeoffs between two risks (i.e. marginal rate of substitution, Brown and Kotler 2004, Camp et al. 2015). The point at which two risks (e.g. predation and toxicity) are equal is defined as the "tipping point" (Nersesian et al. 2011) or "equivalence point" (Camp et al. 2015). On either side of this point, foragers will shift avoidance behaviors towards one risk or the other. Although a gradient in levels of PSM and predation risk is required to quantify tipping point (McArthur et al. 2012), our study suggests that 5% cineole in an artificial diet may present a similar perceived risk as the low concealment of a transparent box. Moreover, the link between individual personality, physiological mechanisms of tolerance to PSMs and stress, and relative aversion between food and predation risks should be investigated in the field, where other habitat conditions (e.g. temperatures, nutrients, predator densities, competition) can influence perception and response by animals to both risks.

Our study evaluates how risks might shape foraging decisions by a specialist mammalian herbivore. Our experimental trials reduced the complexity experienced by free-ranging animals and demonstrated a clear evaluation of how individuals dealt with both types of risk in isolation. Certainly, variation in other measures of food (e.g. other PSMs, fiber or crude protein, Au et al. 2013, Bedoya-Pérez et al. 2014b, Camp et al. 2015) and predator (e.g. type of refuge or predator, Embar et al. 2011, Nersesian et al. 2012) risks that we did not manipulate can influence foraging responses by herbivores. However, our relatively simple trials that isolated one measure of potential toxicity (a monoterpene) and one perceived predation risk (visual predator cues) demonstrated that tradeoff scenarios for a specialist mammalian herbivore are complex, even under controlled conditions. This work provides the foundation for evaluating behavioral consistency in risk aversions and responses to a range of risks to gain a better understanding of how and at what level (i.e. tipping point) animals respond to and trade off multiple risks. Integrating risks of high PSMs and low concealment at different spatial scales and response to these risks by individuals and populations could improve our ability to conserve and manage habitats for pygmy rabbits and other wildlife.

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