

12-1-2015

Modeling Trade-Offs Between Plant Fiber and Toxins: A Framework for Quantifying Risks Perceived by Foraging Herbivores

Meghan J. Camp
Washington State University

Lisa A. Shipley
Washington State University

Timothy R. Johnson
University of Idaho

Jennifer Sorenson Forbey
Boise State University

Janet L. Rachlow
University of Idaho

See next page for additional authors

Authors

Meghan J. Camp, Lisa A. Shipley, Timothy R. Johnson, Jennifer Sorenson Forbey, Janet L. Rachlow, and
Miranda M. Crowell

Modeling trade-offs between plant fiber and toxins: a framework for quantifying risks perceived by foraging herbivores

MEGHAN J. CAMP,^{1,5} LISA A. SHIPLEY,¹ TIMOTHY R. JOHNSON,² JENNIFER SORENSEN FORBEY,³ JANET L. RACHLOW,⁴
AND MIRANDA M. CROWELL¹

¹*School of the Environment, Washington State University, Pullman, Washington 99164 USA*

²*Department of Statistical Science, University of Idaho, Moscow, Idaho 83844 USA*

³*Department of Biological Sciences, Boise State University, Boise, Idaho 83725 USA*

⁴*Department of Fish and Wildlife Sciences, University of Idaho, Moscow, Idaho 83844 USA*

Abstract. When selecting habitats, herbivores must weigh multiple risks, such as predation, starvation, toxicity, and thermal stress, forcing them to make fitness trade-offs. Here, we applied the method of paired comparisons (PC) to investigate how herbivores make trade-offs between habitat features that influence selection of food patches. The method of PC measures utility and the inverse of utility, relative risk, and makes trade-offs and indifferences explicit by forcing animals to make choices between two patches with different types of risks. Using a series of paired-choice experiments to titrate the equivalence curve and find the marginal rate of substitution for one risk over the other, we evaluated how toxin-tolerant (pygmy rabbit *Brachylagus idahoensis*) and fiber-tolerant (mountain cottontail rabbit *Sylvilagus nuttallii*) herbivores differed in their hypothesized perceived risk of fiber and toxins in food. Pygmy rabbits were willing to consume nearly five times more of the toxin 1,8-cineole in their diets to avoid consuming higher levels of fiber than were mountain cottontails. Fiber posed a greater relative risk for pygmy rabbits than cottontails and cineole a greater risk for cottontails than pygmy rabbits. Our flexible modeling approach can be used to (1) quantify how animals evaluate and trade off multiple habitat attributes when the benefits and risks are difficult to quantify, and (2) integrate diverse risks that influence fitness and habitat selection into a single index of habitat value. This index potentially could be applied to landscapes to predict habitat selection across several scales.

Key words: *Brachylagus idahoensis*; *equivalence point*; *fiber*; *marginal rate of substitution*; *method of paired comparisons*; *monoterpene*; *mountain cottontail*; *plant secondary metabolite*; *pygmy rabbit*; *sagebrush*; *Sylvilagus nuttallii*.

INTRODUCTION

Understanding factors that shape habitat use and selection of resources by animals is a central focus of ecology. When selecting habitat patches, animals must acquire adequate energy and nutrients from food while avoiding risks such as toxic plant secondary metabolites, predation, and thermal stress (Werner and Hall 1988, Bakker et al. 2005, Dearing et al. 2008, Hebblewhite and Merrill 2009). Habitats vary in levels of resources and risks, forcing animals to make fitness trade-offs when selecting patches (e.g., Sih 1980, Lima et al. 1985, Houston et al. 1993, Rachlow and Bowyer 1998, Grand 2002). Optimization approaches have been used to predict decisions that animals make about which foods to eat (MacArthur and Pianka 1966, Estabrook and Dunham 1976, Mittelbach 1981, Shipley et al. 1999, Simpson and Raubenheimer 1999), which patches to feed in (e.g., Charnov 1976, Brown 1988), or how much

time to spend searching for food (e.g., Naef-Daenzer 2000), as a function of characteristics of animals and available resources, by weighing costs and benefits of alternative choices in terms of a common currency related to animal fitness (Pyke et al. 1977, Brown 1988).

The economic concept of the marginal rate of substitution (MRS), the rate at which a consumer is willing to give up one good in exchange for another while maintaining the same level of utility, has been used by behavioral ecologists to convert costs and benefits of foraging decisions into a single currency or fitness function (Caraco 1979). For example, Brown (1988) used the MRS in models predicting “giving up densities” (GUD), the amount of food left in a depletable food patch after the forager has quit harvesting the patch, to determine how much additional energy gain it would take at a patch to get a forager to accept a higher risk of predation. Subsequent models have incorporated MRS when foragers face a variety of additional costs such as toxins (Schmidt et al. 1998, Schmidt 2000), distance to water (Shrader et al. 2008), and the time lost to alternative fitness-enhancing activities (Brown 1999, Fedriani and Boulay 2006, Hochman and Kotler

Manuscript received 16 December 2014; revised 29 April 2015; accepted 13 May 2015. Corresponding Editor: T. J. Valone.

⁵ E-mail: meghan.camp@email.wsu.edu

2006). Although the concept of MRS has been central to optimal foraging theory, few studies have actually quantified the MRS between competing costs and benefits and compared them among animal species, except Schmidt (2000), who quantified MRS using the ratio of quitting harvest rate or the marginal value of two patches exploited by the same forager. However, most studies have relied on qualitative predictions about fitness or animal decisions, or indirect measures of MRS (Brown 1988, Jacob and Brown 2000, Druce et al. 2006, Bedoya-Pérez et al. 2014, Wheeler and Hik 2014).

Choice experiments provide a means for quantifying an animal's MRS between the benefits and costs associated with foraging or between competing risks. Researchers have used behavioral titration experiments in which the energy reward or predation risk was continuously altered until a point of equivalence (i.e., indifference point) was identified (Todd and Cowie 1990, Kotler and Blaustein 1995, Nersesian et al. 2011, Kralik and Sampson 2012). In economic theory, the MRS corresponds to the slope of the indifference curve passing through bundles of goods that consumers are willing to exchange to obtain the same level of utility (Mankiw 2011). Therefore, the slope of a model fit to a series of equivalence points predicts the rate at which the forager will trade off one resource or risk for another (i.e., MRS). We use the term equivalence point rather than indifference point because the equivalence point is where the animal perceives the low reward/low risk option and the high reward/high risk option or two competing risks as equal. Under some circumstances, risk titration from a foraging animal can be a more useful behavioral indicator of an animal's perceptions of risk than actual measures of fitness (Brown and Kotler 2004), which are difficult to accurately measure, especially in long-lived species. Previous research has demonstrated that animals titrate marginal costs and marginal benefits between the risk of predation and potential energy gain by increasing the marginal value of resource patches with high predation risk until the high predation risk and low predation risk microhabitats were of identical value to foragers (i.e., animals harvested the same amount out of each patch; Kotler and Blaustein 1995). Other studies have measured individual equivalence points for the risk of food toxicity and predation for foraging herbivores (Nersesian et al. 2011, McArthur et al. 2012). However, most titration studies have estimated only one equivalence point for a particular trade-off (but see Kralik and Sampson 2012), which limits their usefulness for understanding how animals make trade-offs in natural landscapes where risks exist over a range of values, and precludes measuring the MRS of one risk for the other.

In this study, we sought to measure the MRS between competing risks (commonly referred to as "costs" in optimal foraging theory) and used it to quantify trade-offs between risks using behavioral titration experiments and concepts of economic decision theory. To do this,

we used the method of paired comparisons (PC) to estimate utility, and the inverse, relative risk, to create a model predicting relative risk from combinations of two variables. The method of PC elicits binary choices from a subject for any number of paired items in a series of discrete choice sets (David 1988). The method determines the subject's preference order among the various items by asking it to choose the item in each pair that best meets a given criterion (Kendall and Smith 1940, Kingsley and Brown 2013). If the subject's preferences obey the principles of utility theory (transitivity and comparability), the result will be a relative ranking of the items in the choice set (Kendall and Smith 1940), similar to the utility model that Caraco et al. (1980) applied to foraging theory. In contrast to foraging models that assume an animal has preferences among deterministic values of resources, Caraco et al. (1980) demonstrated that utility theory allows preferences to be extended over probability distributions. As in previous foraging models, Caraco (1980) assumed that animals should act in a way that maximizes their fitness, but utility replaces time and energy as the surrogates of fitness and the optimal strategy maximizes expected utility. Because utility, as a function of a random variable, ranks the variable on a relative scale (Keeney and Raiffa 1993), it allows animals to reveal habitat preferences on a single scale representing an integrated response to a variety of risks and rewards in their environment (Rappaport 1971, Caraco 1980, Caraco et al. 1980, Lima et al. 1985, Real and Caraco 1986). In our modeling approach, we used the inverse of utility, which we refer to as "risk," with the expectation that animals should minimize risk.

The PC method makes trade-offs and indifferences between items explicit by forcing subjects to make choices between two items or conditions; thus, the ratio of the coefficients of the two variables estimates the MRS. This method can be used to determine how animals evaluate and trade off habitat attributes where the benefits and risks faced are difficult to quantify or reduce to a common currency, and to integrate diverse risks that influence fitness and habitat selection into a single index of habitat value. The outcome is a relative risk model that allows us to predict the overall perceived risk at habitat patches with multiple types of risks.

Specifically, we evaluated how two species of herbivores, the pygmy rabbit (*Brachylagus idahoensis*) and the mountain cottontail rabbit (*Sylvilagus nuttallii*, hereafter, cottontail), that differ in their tolerance for fiber and toxins in food, make trade-offs when selecting food patches. Plant fiber is risky to herbivores because it reduces the extent and rate at which nutrients can be extracted from food (i.e., digestibility reducer; Hoover and Heitmann 1972, Van Soest 1994, Iason and Van Wieren 1999). Defensive plant toxins (i.e., plant secondary metabolites such as terpenes, alkaloids, and phenolics) are risky because they impose a physiological cost as they are absorbed, metabolized, and excreted by

the animal (Freeland and Janzen 1974, Sorensen et al. 2005b, Torregrossa and Dearing 2009, Shipley et al. 2012). These costs range from small reductions in the nutritional benefits of food (Robbins et al. 1991, DeGabriel et al. 2009) to serious consequences where over-ingestion of a toxin or even small doses of some types could result in toxicosis or death (Freeland and Janzen 1974, Fowler 1983).

Although pygmy rabbits and cottontails inhabit the same sagebrush (*Artemisia* spp.) ecosystems in the intermountain western United States, they vary in their reliance on sagebrush for food. The pygmy rabbit is a dietary specialist, consuming primarily sagebrush, especially during the winter (Thines et al. 2004), whereas the mountain cottontail is considered a generalist and consumes <4% sagebrush in sagebrush communities (MacCracken and Hansen 1984). Although sagebrush leaves are relatively high in digestible protein and low in fiber compared to grasses and forbs in the community (Thines et al. 2004), they contain high levels of toxins, (e.g., monoterpenes; Kelsey et al. 2006). Moreover, pygmy rabbits are more tolerant of (e.g., consume higher concentrations of toxins) sagebrush than cottontails, and cottontails can tolerate (e.g., digest) higher fiber concentrations than pygmy rabbits (Demment and Van Soest 1985, Shipley et al. 2012). Therefore, we predicted that (1) pygmy rabbits would have a higher MRS of a toxin (i.e., 1,8-cineole, a major monoterpene in sagebrush; Kelsey et al. 2006) for fiber than cottontails; (2) high-toxin patches would have a higher relative risk for cottontails than pygmy rabbits; and (3) high-fiber patches would have higher relative risk for pygmy rabbits than cottontails.

We tested these hypotheses using a series of paired-choice experiments to titrate the equivalence curve. We then used the method of PC to quantify the relative risk at food patches based on concentrations of fiber and toxins, calculate the MRS of toxin for fiber, and model the indifference curves for each species, which depicted combinations of fiber and toxins in food that the rabbits would perceive as equally risky. Finally, we used our model to predict and compare the relative risk of consuming high-toxin, low-fiber sagebrush leaves and low- or no-toxin, high-fiber sagebrush stems and grasses for each rabbit species. We predicted that consuming stems and grasses would be riskier for pygmy rabbits than cottontails and consuming leaves would be riskier for cottontails than pygmy rabbits.

METHODS

Capture and maintenance of study animals

We captured pygmy rabbits in Camas and Lemhi Counties in Idaho, USA, and Beaverhead County in Montana, USA, and mountain cottontail rabbits in Whitman County, Washington, USA (Idaho Wildlife Collection Permits #010813 and 100310, Washington Scientific Collection Permit #13-102, Montana Scientific Collection Permit #2014-062, Washington State Univer-

sity Institutional Animal Care and Use Committee Protocol #4398). While they were not participating in experiments, rabbits were housed individually on pine shavings in 1.2×1.8 m mesh cages located in a barn at the Small Mammal Research Facility at Washington State University, Pullman, Washington. Rabbits were fed ad libitum a basal diet of water, commercial rabbit pellets (Purina Professional Rabbit Chow, Purina Mills, St. Louis, Missouri, USA; 36% NDF, neutral detergent fiber), greenhouse-grown or commercially produced greens, and wild-grown sagebrush. Rabbits were provided with a nest box and a 3 m long, 4 cm diameter tube or a wooden hutch for security cover.

Preference trials

First, to establish that pygmy rabbits and cottontails respond to differences in fiber and toxin concentrations in food, we conducted a series of preliminary preference trials in which 5–7 pygmy rabbits (for both sexes pooled, body mass = 412 ± 67 g, $\bar{x} \pm SD$) and cottontail rabbits (for both sexes pooled, body mass = 1127 ± 65 g) were offered two food patches containing different levels of fiber or toxin. To create diets that varied in fiber concentrations from 36% to 50% dry mass (DM), we added rice hulls (77% NDF) to a basal diet consisting of a completely balanced herbivore pellet (Purina Professional Rabbit Chow, Purina Mills, St. Louis, Missouri, USA; 36% NDF) using a pellet mill (PM605, Buskirk Engineering, Ossian, Indiana, USA). Grasses, forbs, and sagebrush consumed by free-ranging pygmy rabbits and mountain cottontails range from about 30% to 78% NDF (Thines et al. 2004). We measured fiber content of each diet using NDF analysis (Goering and Van Soest 1970) with filter bags, sodium sulfite, and alpha amylase (Ankom Fiber Analyzer^{200/220}, Ankom Technology, Fairport, New York, USA). We created toxin diets by adding 1,8-cineole (a major monoterpene in sagebrush, hereafter, cineole) in levels ranging from 0% to 5% DM to the basal diet. Monoterpenes in sagebrush leaves typically range from 1% to 4% by dry mass (Kelsey et al. 2006). We mixed the cineole with the basal diet daily by misting the pellets with an olive oil sprayer (Misto, Lifetime Brands, Garden City, New York, USA) to achieve consistent distribution of the cineole on the pellets. The nontoxic diets were not misted.

The preference trials were conducted during May–June 2013 in 3.8×3.6 m covered, outdoor pens constructed of chain-link fence with a 2-cm mesh. During each 24-h trial, each animal was offered a choice of two food patches (food bowls) that each contained more than the animal's normal daily intake of food. First, we examined the rabbits' preference for fiber by offering two food patches, each with a different level of fiber (36%, 39%, 44%, 47%, 50%). During a series of 10 trials, rabbits were offered all combinations of fiber levels. Next, we conducted a series of trials in which rabbits were offered two food patches with different concentrations of cineole (0%, 1%, 2%, 3%, 4%, 5%)

mixed with the basal diet (36% NDF). During a series of 10 trials, rabbits were offered all combinations of cineole concentrations. The order of each combination of fiber or toxin concentration offered was determined using a Latin squares design, and the patch location for each diet within the pen was determined from a coin flip. To control for variable weather and moon phase, pygmy rabbit and cottontail trials were conducted simultaneously within an array of nine pens.

We allowed the rabbits three days of acclimation in the trial pens before beginning the series of trials. To minimize their perception of predation risk, the food bowls were placed on rubber mats, 3 m apart, under 0.46-m³ dark acrylic boxes with 10 cm diameter holes as entryways. We corrected fresh mass of food pellets offered by the dry matter content once for each level of fiber and cineole by drying a 10-g sample at 100°C for ≥24 h. We weighed the food remaining each morning, dried the refusals at 100°C for ≥24 h, and calculated intake as the difference between DM offered and refused. We compared the proportion of total intake between the two food patches to a $\mu = 0.50$ (equal consumption from each patch) using a one-sample *t* test.

Equivalence point trials

To evaluate trade-offs that individuals make between the risk of fiber and toxins, we conducted a series of titration trials to obtain the equivalence points for combinations of fiber and toxin concentrations using nine pygmy rabbits and nine cottontail rabbits during June–November 2013. For five levels of fiber content (36%, 39%, 44%, 47%, 50%), we conducted 3–6 trials per animal in which a patch with the food of the specified fiber concentration without cineole (i.e., toxin-free patch) was paired with a second patch of food containing the basal diet (the lowest fiber content, 36%) and varying amounts of cineole (i.e., toxin patch, 0%–15%). Our goal was to find the concentration of cineole that resulted in equal intake between the two food patches (toxin-free and toxin) for each level of fiber concentration (i.e., equivalence points). To do this, we titrated the amount of cineole in the paired bowl over 3–6 trials per level of fiber to produce an adequate linear fit ($R^2 > 0.60$, $P < 0.05$) between the proportion of the toxin diet eaten and the concentration of cineole for each level of fiber for each animal. We estimated the equivalence points by fitting a linear model in which the dependent variable was the proportion of the toxin diet eaten and the independent variable was the concentration of cineole. We then solved for the concentration of cineole where the proportion of the toxin diet consumed by each animal was 0.5, indicating equal preference for the toxin-free and toxin diet.

To estimate the marginal rate of substitution of cineole for fiber, and compare it between pygmy rabbits and cottontails, we used analysis of covariance (ANCOVA; PROC GLM, SAS Version 9.3. SAS Institute 2011). The dependent variable was the concen-

tration of cineole in the toxin food patch and the independent variables were fiber concentration in the toxin-free patch, rabbit species, and the fiber × species interaction.

Relative risk model

Using the method of PC and data collected from eight pygmy rabbits and eight cottontails during the preference and equivalence trials, we created a model predicting the relative risk of patches containing different levels of cineole and fiber. We assumed that

$$E(R_{ijk}) = \beta_{0i} + \beta_{1i}F_{ijk} + \beta_{2i}T_{ijk} \quad (1)$$

where $E(R_{ijk})$ denoted the expected “risk level” of the *k*th food patch for the *i*th animal on the *j*th trial and F_{ijk} and T_{ijk} were the concentration of fiber, *F*, or toxin, *T*, in the food in the *k*th food patch presented to the *i*th animal in the *j*th trial. β_{1i} is the rate at which an increase in fiber increases relative risk and β_{2i} is the rate at which an increase in toxin increases relative risk. Because we offered two food patches ($k = 1, 2$), let $Y_{ij} = R_{ij1} - R_{ij2}$ denote the difference in the risk of each patch. Then, from Eq. 1, we have

$$E(Y_{ij}) = \beta_{1i}(F_{ij1} - F_{ij2}) + \beta_{2i}(T_{ij1} - T_{ij2}). \quad (2)$$

We quantified Y_{ij} as the difference in intake between the two bowls divided by the total intake during each trial. We used a regression analysis to provide estimates of β_{1i} and β_{2i} for each animal (R Development Core Team 2008). We tested whether the mean values of β_{1i} and β_{2i} were significantly different than zero using a one-sample *t* test. We compared β_{1i} and β_{2i} within species and between species using a two-sample *t* test. We then created indifference curves for each species that depicted food patches in terms of *F* and *T* in food that the rabbits would perceive equally risky. These are defined by the expression

$$T_1 = T_2 - (\bar{\beta}_1/\bar{\beta}_2)(F_1 - F_2) \quad (3)$$

where $\bar{\beta}_1$ and $\bar{\beta}_2$ are the average values of the estimate coefficients for each species. This equation defines, for each species, all pairs of potential food patches between which an average animal would be indifferent (i.e., equal risk). We then calculated the MRS of toxin for fiber as β_{1i}/β_{2i} and compared the MRS between species using a two-sample *t* test.

Finally, we used the modeled indifference curves to predict the relative risk level of sagebrush leaves and stems and native grasses in the winter as perceived by pygmy rabbits and cottontails. We used the values reported by Crowell (2015) for NDF and total monoterpene content of leaves (30% NDF, 2.48% monoterpenes) and stems cut at ≤3 mm diameter (77% NDF, 0.39% monoterpenes) from Wyoming big sagebrush (*A. tridentata wyomingensis*) collected in January near Leadore, Idaho, USA, where a portion of our rabbits were caught. We used the NDF value reported by Thines et al. (2004) for monoterpene-free bluebunch

TABLE 1. Proportion (mean ± SE) of the total food eaten by pygmy rabbits (*Brachylagus idahoensis*) and mountain cottontail rabbits (*Sylvilagus nuttallii*) that was consumed from the patch containing the lower fiber concentration (columns) when simultaneously offered a second patch of food containing the higher fiber concentration (rows).

Rabbit species	Fiber in higher-fiber patch	Proportion eaten from lower-fiber patch, by fiber level			
		36% fiber	39% fiber	44% fiber	47% fiber
Pygmy	39%	0.76 ± 0.10*			
	44%	0.78 ± 0.10*	0.75 ± 0.07*		
	47%	0.90 ± 0.06*	0.88 ± 0.07*	0.64 ± 0.09*	
	50%	0.88 ± 0.07*	0.79 ± 0.09*	0.88 ± 0.07*	0.72 ± 0.07*
Cottontail	39%	0.81 ± 0.08*			
	44%	0.85 ± 0.03*	0.77 ± 0.05*		
	47%	0.84 ± 0.07*	0.60 ± 0.11	0.52 ± 0.05	
	50%	0.88 ± 0.03*	0.71 ± 0.17	0.59 ± 0.08	0.62 ± 0.08

Note: Asterisks indicate proportions significantly greater than 0.5 at α=0.05, using a one-tailed *t* test.

wheatgrass (*Pseudoregneria spicata*, 76% NDF) collected in winter in habitat supporting both pygmy rabbits and cottontails near Ephrata, Washington, USA. We converted the total monoterpene values of sagebrush into 1,8-cineole equivalents (1.18 for pygmy rabbits and 1.28 for cottontail rabbits; J. Nobler, unpublished data), estimating a cineole equivalent of 2.80% for pygmy rabbits and 3.20% for cottontails for sagebrush leaves, and a cineole equivalent of 0.43% for pygmy rabbits and 0.49% for cottontails for sagebrush stems. We calculated the relative risk for the sagebrush leaf and stem patches using Eq. 1, where *F* was the fiber concentration in the stems or leaves and *T* was the cineole concentration in the stems or leaves, and then plotted the value in relation to the indifference curves.

RESULTS

Preference trials

Both pygmy rabbits and cottontail rabbits avoided risks of fiber and toxins by typically consuming a greater proportion of diets with lower levels of fiber (Table 1) and cineole (Table 2). However, cottontails were less discriminant among higher levels of fiber than were pygmy rabbits.

Equivalence point trials

The concentration of cineole that the rabbits perceived as equally risky to the concentration of fiber in food patches increased with fiber content of the toxin-free patch ($F_{3,71} = 44.71, P < 0.0001$) and varied with rabbit species ($F_{3,71} = 69.99, P < 0.0001$). Moreover, there was an interaction between fiber and rabbit species ($F_{3,71} = 28.80, P < 0.0001$). These results indicate that animals were making a trade-off between the risk of fiber and toxins, but that the rate of the trade-offs (i.e., MRS) differed between pygmy rabbits and cottontails (Fig. 1). As fiber in the toxin-free diet increased, the amount of cineole in the toxin diet that both species perceived as equivalent also increased. The slope of the regression line (i.e., MRS) was steeper for pygmy rabbits ($\bar{x} = 0.68, SE = 0.13$) than cottontails ($\bar{x} = 0.12, SE = 0.01$; Fig. 1), indicating that they traded off the risk of toxicity to avoid the risk of starvation at a faster rate than did cottontails.

Relative risk model

Using data from 905 paired-choice trials ($\bar{x} = 54$ trials per animal), the model predicting relative risk value at a food patch for pygmy rabbits was $E(R) = (0.07F) + (0.10T)$ (mean $R^2 = 0.55$), and for cottontails was $E(R) =$

TABLE 2. Proportion (mean ± SE) of the total food eaten eaten by pygmy rabbits (*Brachylagus idahoensis*) and mountain cottontail rabbits (*Sylvilagus nuttallii*) that was consumed from the patch with the lower 1,8-cineole concentration (columns) when simultaneously offered a second patch of food containing the higher 1,8-cineole concentration (rows).

Rabbit species	Cineole in higher-cineole patch	Proportion eaten from lower-cineole patch, by cineole level			
		0%	1%	2%	3.5%
Pygmy	1%	0.77 ± 0.06*			
	2%	0.81 ± 0.05*	0.76 ± 0.08*		
	3.5%	0.78 ± 0.07*	0.63 ± 0.12	0.76 ± 0.03*	
	5%	0.86 ± 0.05*	0.80 ± 0.06*	0.83 ± 0.03*	0.58 ± 0.08
Cottontail	1%	0.90 ± 0.06*			
	2%	0.81 ± 0.04*	0.61 ± 0.10		
	3.5%	0.78 ± 0.03*	0.83 ± 0.07*	0.73 ± 0.05*	
	5%	0.87 ± 0.02*	0.90 ± 0.05*	0.88 ± 0.02*	0.62 ± 0.08

Note: Asterisks indicate proportions significantly greater than 0.5 at α=0.05, using a one-tailed *t* test.

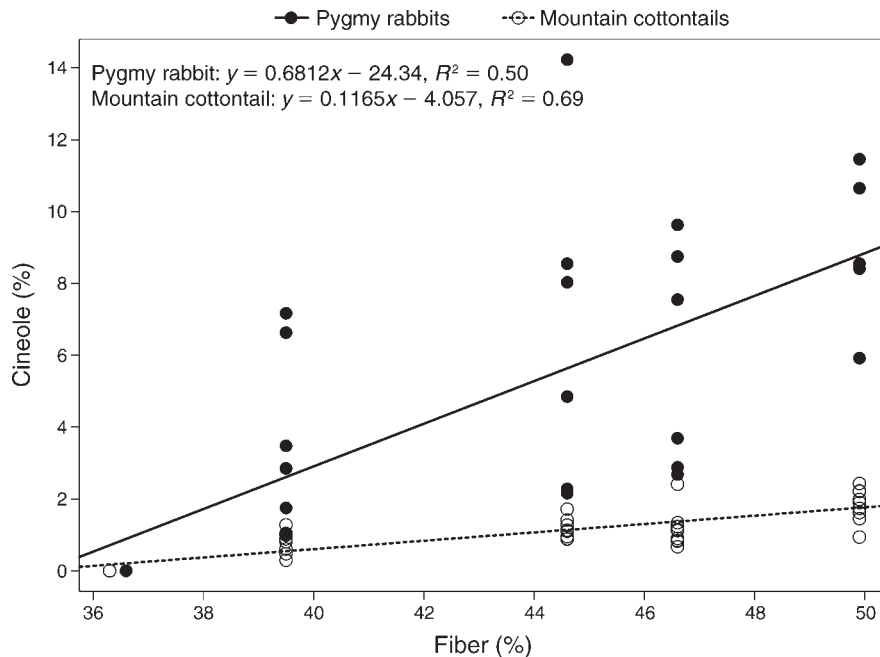


FIG. 1. Equivalence points (equal dry matter intake) between 1,8-cineole (a major monoterpene toxin in sagebrush) and fiber levels in paired food patches for nine pygmy rabbits (*Brachylagus idahoensis*, solid circles, solid lines) and nine mountain cottontail rabbits (*Sylvilagus nuttallii*, open circles, dashed lines) and the associated equivalence curves. Increasing axes from the origin indicate increasing risk, and the slopes of the curves indicate the marginal rate of substitution of cineole for fiber.

(0.05F) + (0.33T) (mean $R^2 = 0.55$), where E(R) was the expected relative risk level, F was fiber (% NDF), T was toxin (% cineole; Fig. 2A, B), and the coefficients were the average estimated values within each species. Relative risk increased with both fiber (for pygmy rabbit, $t_8 = -11.14$, $P < 0.0001$; for cottontail, $t_7 = -8.14$, $P < 0.0001$) and cineole (for pygmy rabbit, $t_8 = -14.51$, $P < 0.0001$; for cottontail, $t_7 = -8.79$, $P < 0.0001$) for both species. However, risk increased faster with fiber for pygmy rabbits ($t_{14} = 2.35$, $P = 0.03$; Fig. 2A), and with cineole for cottontail rabbits ($t_{14} = -5.67$, $P < 0.001$; Fig. 2B). For pygmy rabbits, the slope for fiber ($\bar{x} = 0.07$, SE = 0.007) was not significantly different than that for cineole ($\bar{x} = 0.10$, SE = 0.008; $t_{16} = 2.07$, $P = 0.06$). However, for cottontails the slope for fiber ($\bar{x} = 0.05$, SE = 0.006) was shallower than that for cineole ($\bar{x} = 0.33$, SE = 0.04), indicating that cineole was riskier than fiber for cottontails ($t_{14} = 6.9$, $P > 0.001$). The estimated MRS of cineole for fiber (i.e., β_{1i}/β_{2i}) was greater for pygmy rabbits ($\bar{x} = 0.86$, SE = 0.17) than cottontails ($\bar{x} = 0.15$, SE = 0.02; $t_{15} = 3.81$, $P = 0.002$), and similar to that estimated from our equivalence curves. Using Eq. 1, sagebrush leaves were 2.3 times less risky than stems and mature grass for pygmy rabbits (ratio of risk for the stems and risk for the leaves: $2.3 = 5.7/2.5$), but only 1.5 times less risky for cottontails (Fig. 2C, D).

DISCUSSION

We developed a novel framework for quantifying and comparing the trade-offs (i.e., MRS) and relative risks

faced by animals when selecting food patches based on two risks that operate in different ways: an incremental decrease in nutrient digestibility for plant fiber and a more acute toxicity from monoterpenes above a certain threshold value (Sorenson et al. 2005a, Wiggins et al. 2006). We did this by finding where two species of rabbits perceived the risks of fiber and toxins as equivalent across a range of risk values (i.e., the equivalence curve; Fig. 1) using behavior (amount of food eaten in the patch) as the common currency. We then used the PC method to model the relative risk posed by fiber and toxins and to construct indifference curves for these risks. Pygmy rabbits were willing to consume nearly five times more cineole in their diets to avoid consuming higher levels of fiber than were mountain cottontails. Fiber posed a greater relative risk for pygmy rabbits than cottontails and cineole a greater risk for cottontails than pygmy rabbits. For cottontails, the risk of incremental increases in the concentration of cineole was higher than the risk of incremental increases in the concentration of fiber, whereas for pygmy rabbits, fiber and cineole were equally risky. These differences in risk trade-offs probably reflect differences in body size and physiology between the rabbit species.

First, pygmy rabbits are less than half the size of mountain cottontails, and thus are expected to have a higher mass-specific metabolic rate (Kleiber 1975) and a higher energy requirement to gut size ratio (Demment and Van Soest 1985). In fact, pygmy rabbits required ~36% greater daily digestible energy intake in relation

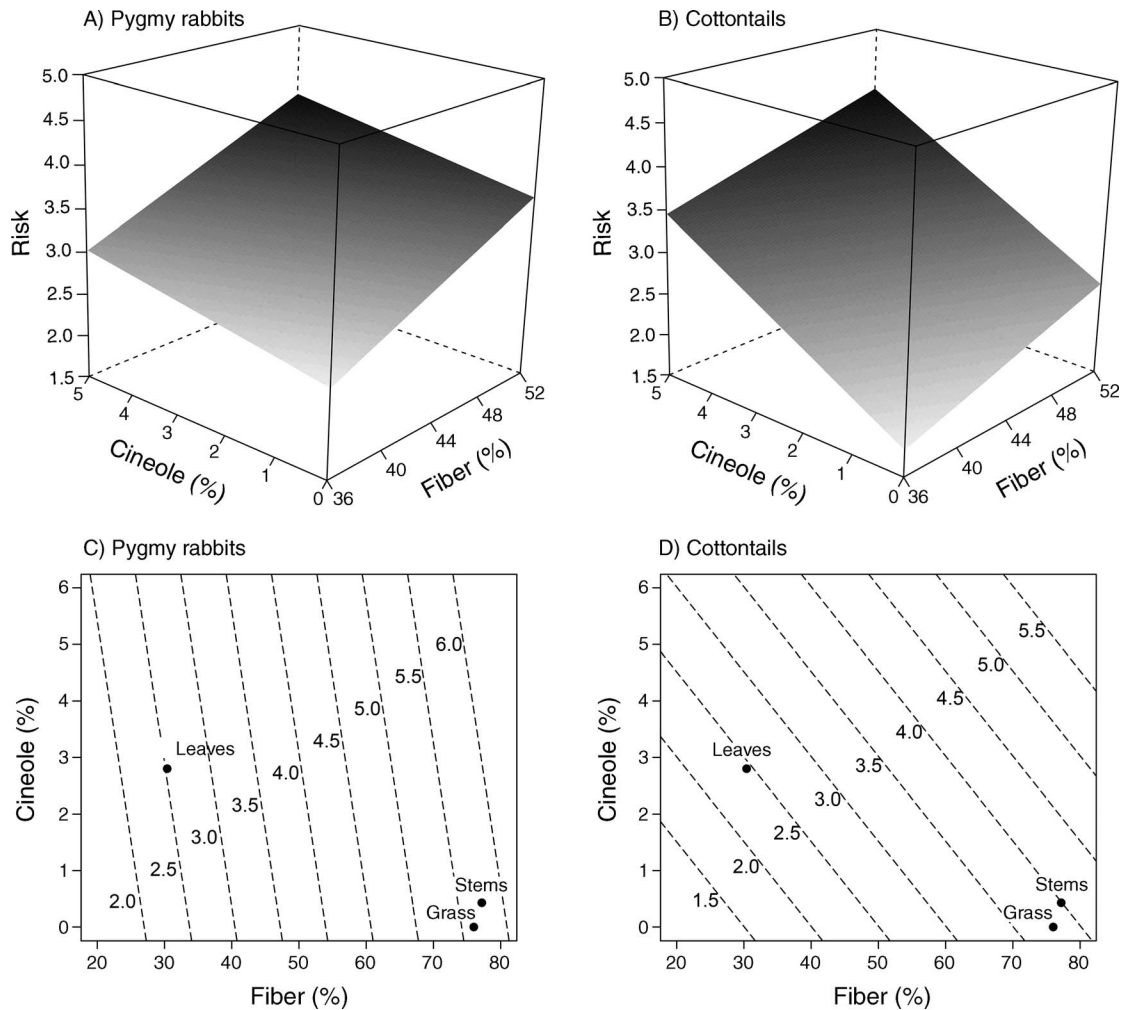


FIG. 2. (A, B) Predicted relative perceived risk values at patches with a range of 1.8–cineole values for pygmy rabbits (*Brachylagus idahoensis*) and mountain cottontail rabbits (*Sylvilagus nuttallii*), and (C, D) the associated indifference curves for pygmy rabbits and cottontails. The risk values were predicted using the model $E(R) = (0.07F) + (0.10T)$ for pygmy rabbits and $E(R) = (0.05F) + (0.33T)$ for cottontails, where $E(R)$ was the expected relative risk level, F was fiber, and T was toxin. The indifference curves were predicted using the equation $T = (R - \beta_1 F) / \beta_2$, where β_1 and β_2 are the average values of the estimate coefficients for each species. Each isoline depicts the combinations of fiber and toxin concentrations in food that the rabbits perceive as equally risky. Numbers next to the isolines are the risk levels (R); slopes of the isolines were obtained by solving for T and F at different risk levels (R). The predicted relative risk levels of sagebrush (*Artemisia tridentata wyomingensis*) stems and leaves and mature bluebunch wheatgrass (*Pseudoregneria spicata*) are shown on the indifference curves.

to their metabolic body mass ($\text{mass}^{0.75}$) to maintain their body mass than did cottontails (Shipley et al. 2006). In addition, pygmy rabbits have a smaller gut volume (which scales in proportion to body mass) than cottontails, and therefore would be expected to have a lower capacity to digest the cellulose in plant fiber (Demment and Van Soest 1985), which requires mechanical breakdown of cell wall and fermentation by microorganisms (Iason and Van Wieren 1999). When consuming the same diets ranging from 29% to 55% NDF, pygmy rabbits only digested 50–90% of the amount of NDF as did cottontails (Shipley et al. 2006). Fiber reduces the amount of nutrients that animals can acquire from plants, while increasing the time needed to

digest food and reducing the rate at which animals can consume food (Iason and Van Wieren 1999). For example, domestic rabbits that were fed a high-fiber diet had a larger mass-specific cecal volume and a lower body mass compared to rabbits on a low-fiber diet (Hoover and Heitmann 1972). Therefore, the risk of starvation is higher for the smaller pygmy rabbit consuming high-fiber diets than for the larger cottontail.

On the other hand, the risk of toxicity probably was lower for pygmy rabbits than cottontails because pygmy rabbits are better able to minimize systemic exposure to toxins found in sagebrush (Shipley et al. 2012). Exposure to consumed toxins can be reduced by minimizing absorption into the bloodstream and maximizing the

rate of detoxification (Sorensen et al. 2006). Several mechanisms, such as efflux transporters, allow excretion of toxins in the feces, thereby decreasing concentrations of toxins in the blood (Hunter and Hirst 1997). For example, P-glycoproteins in the gut epithelial cells actively transport toxic compounds out of the gut cell and reduce delivery to circulation (Sparreboom et al. 1997). Plant toxins such as monoterpenes can also be detoxified in the liver through alternative metabolic pathways such as conjugation or oxidation (Dearing and Cork 1999, Marsh et al. 2006). In a comparative study in which pygmy rabbits and cottontails were fed 1,8-cineole, pygmy rabbits excreted two times more conjugated cineole metabolites in urine than did cottontails (Shiple et al. 2012). An average of 28% of the ingested cineole was recovered as cineole metabolites in the urine and 3.8% as metabolites in feces of pygmy rabbits, whereas no metabolites were found in the feces of cottontails (Shiple et al. 2012). Similarly, Stephen's woodrats (*Neotoma stephensi*), which specialize on juniper (*Juniperus monosperma*), had a greater capacity to limit exposure to plant toxins by excreting more alpha-pinene, a monoterpene found in juniper, in their feces than did the generalist white-footed woodrat (*Neotoma albigula*, Sorensen and Dearing 2003, Sorensen et al. 2004).

The rate and extent of detoxification, in turn, determines the amount of toxic food that an animal can consume (Marsh et al. 2005). Herbivores maintain systemic toxin levels behaviorally by regulating total food intake, meal size, timing of consumption, and mixing diets (Sorensen et al. 2005a, Wiggins et al. 2006). Pygmy rabbits, with their higher capacity to detoxify monoterpenes, were able to maintain their daily intake of rabbit pellets as the concentration of cineole increased over 5%, whereas mountain cottontails began to reduce intake when cineole concentration was only 1% (Shiple et al. 2012). Likewise, the specialist Stephen's woodrat maintained its intake on diets containing up to 4% phenolic resin found in creosote bush (*Larrea tridentata*), whereas the generalist white-throated woodrat reduced its intake at concentrations of 2% (Torregrossa et al. 2012). Therefore, the risks of toxins in food, including increased energy expenditure (Sorensen et al. 2005b), reduced nutrient digestibility (Robbins et al. 1987, DeGabriel et al. 2009), and toxicosis or death from overexposure (Freeland and Janzen 1974) can be especially high for generalist herbivores like cottontails that lack specific adaptations for eliminating and detoxifying plant toxins. Furthermore, variability in how individual animals perceive, tolerate, and respond to risk of toxicity in specialist herbivores might explain the larger variance in the equivalence curve for pygmy rabbits than cottontails (Fig. 1). Individuals may differ physiologically (e.g., detoxification capacity, stress hormones, metabolism; Maltby 1999, Montooth et al. 2006) or behaviorally (e.g., boldness; Mella et al. 2014). For example, individual brushtail possums (*Trichosurus*

vulpecula) varied in measures of boldness, and boldness influenced foraging at patches with high predation risk and patches with low predation risk only when food toxins were low (Mella et al. 2014). However, Simpson and Raubenheimer (1999) found that locusts that were dietary specialists (*Locusta gregaria*) were more likely to minimize the error of overeating one nutrient and undereating another than were generalist locusts (*Schistocerca gregaria*), presumably because the generalists would be more likely to later encounter and consume a plant with a complementary imbalance to the present food, allowing the ingested excess from the current food to balance the deficit in the subsequent one.

In this study, we also demonstrated how our model could be applied to understanding diet choices of pygmy rabbits and cottontails observed in the field. Our relative risk model predicted that consuming sagebrush leaves, with low fiber and high monoterpenes, is relatively less risky than consuming sagebrush stems and mature grasses, and that stems and grasses were relatively more risky for pygmy rabbits than for cottontails. These predictions are supported by observations from both field and captive studies that pygmy rabbits consume a greater proportion of sagebrush relative to grasses and a greater leaf to stem ratio of sagebrush than do cottontails (Crowell 2015). In fact, cottontails often discard the leafy tips of sagebrush branches uneaten. Most herbivores, especially browsers, are highly selective foragers within habitats (Hofmann 1989). For example, snowshoe hares (*Lepus americanus*) selectively fed on the mature internodes over the juvenile internodes when feeding on Alaska green alder (*Alnus crispa*, Clausen et al. 1986). This preference was correlated with the higher levels of toxins in the juvenile internodes (Clausen et al. 1986). Using the relative risk levels of fiber and monoterpenes in leaves and stems, our model predicted that pygmy rabbits and cottontails should select different forages and different parts of sagebrush plants when sharing sagebrush landscapes. The difference in the foraging strategies between these two species provides insight into a possible mechanism for coexistence in sagebrush habitats.

Clearly, fiber and toxin concentrations are not the only risks faced by herbivores when selecting food patches or habitats. Like GUD models (Brown 1999, Schmidt 2000, Fedriani and Boulay 2006, Hochman and Kotler 2006, Shrader et al. 2008), our model framework easily allows addition of any number of additional risks (e.g., predation, thermal stress) or even benefits (e.g., nutrient content, food density). For each risk (or benefit) included in the model, its β depicts its contribution to overall risk of that patch or habitat, and the ratio of the β 's for any two risks estimates the MRS for one risk over the other. Exploring three-way, four-way, and n -way interactions can elucidate complex foraging behavior of herbivores. For example, Schmidt (2000) found that the MRS for predation risk, as measured by the ratio of GUDs in safe and risky habitats, did not vary with the

level of oxalates (defensive compounds), whereas MRS for tannins (digestibility reducers) increased with missed opportunity cost and decreased with metabolic cost. He concluded that foods containing plant defenses that act as digestibility reducers will be relatively less depleted under higher predation risk than will foods without defenses, whereas foods containing defensive toxins that affect fitness directly and not through diminished physiological uptake of energy will be depleted without bias to predation risk or foraging costs.

Unlike classic patch theory (e.g., marginal value theorem; Charnov 1976) and most GUD models (Schmidt 2000, Price and Correll 2001, Brown and Kotler 2004, Searle et al. 2008), our model framework does not assume a decelerating gain function at a food patch caused by monotonically decreasing harvesting rates as the patch is depleted. In our experiments, we offered food patches with equal harvesting rates and linear gain functions over 24-h trials (M. Camp, *unpublished data*) by providing food patches that exceeded the rabbits' daily intake, packaged in uniformly small bites of pellets in a bowl. However, our model framework could be used to assess relative risks associated with time spent harvesting food (e.g., increased exposure to predation and thermal stress, reduced time for other fitness-enhancing activities) and MRS of harvesting rate for other perceived risks altering bite size, cropping, chewing, or searching time in one patch (MacArthur and Pianka 1966, Brown 1988, Gross et al. 1993). In addition, in our model we assumed a linear relationship for fiber and toxins with relative risk, and that fiber and toxins acted independently on perceived risk. Nevertheless, the model could be modified to include a nonlinear relationship between the response and explanatory variables by adding polynomial functions and interactions between risks. For example, risks of tannins depend on protein content of food (Simpson and Raubenheimer 1999), risks of monoterpenes depend on the environmental temperature (Dearing et al. 2008), and risks of feeding away from a burrow depend on the amount of concealment cover (Crowell 2015).

Like Raubenheimer and Simpson (1993), we did not make any a priori judgments about the relative importance of different food properties or nutritional requirements of animals and allowed the animal to indicate how it prioritized their ingestion. Because our model uses the animal's behavior (i.e., its choice between two patches) as the currency, this choice can be measured in a variety of ways. Although we used dry matter intake at a feeding patch as our response variable, other measures of choice could be used. For example, the time spent in a nonfood patch can be used to quantify the perceived risk of nonfood patches such as nesting or loafing areas, and to determine which perceived risks most strongly influence selection of different types of habitat patches. Finally, our model differs from many resource selection models (Manly et

al. 1993) that are based on discrete choices (i.e., presence or absence) because it produces a continuous response variable (i.e., the relative amount of food consumed) that is a quantitative proxy to relative risk. Although we used a series of controlled titration experiments with captive animals to provide data for our relative risk model, the method of PC could be applied in field experiments in which animals could be presented with two food patches at a time and the habitat properties at each food location could be measured.

In summary, animals face multiple risks in their environments that vary in time and space. Many previous approaches to understanding habitat use have not fully incorporated or quantified trade-off strategies that animals with different tolerances to habitat features use to reduce risk, or are limited by inflexible assumptions and statistical techniques. Our application of the method of PC to foraging behavior is useful for quantifying trade-offs that animals make among risks. Furthermore, it allows animals to reveal habitat preferences on a single scale, representing an integrated response to a variety of risks in their environment. This approach could be useful for identifying and mapping relative risk levels at habitat patches across landscapes by creating a spatially explicit "landscape of risk," and the predicted relative risk of habitat patches across the landscape could be compared with measures of intensity of use by free-ranging animals (Searle et al. 2008, Willems and Hill 2009). The application of the method of PC to ecological questions in both controlled captive experiments and in field studies provides a more realistic approach to understanding how animals balance competing risks through trade-offs.

ACKNOWLEDGMENTS

We thank R. Kelsey (Pacific Northwest Research Center, U.S. Forest Service) for conducting the hydro-distillation of sagebrush leaves and stems, and J. Nobler (Boise State University) and J. Fleugel (Washington State University) for logistical and lab support. We appreciate the suggestions on a previous version of the manuscript provided by B. Kotler (Ben-Gurion University of the Negev). This research was funded by National Science Foundation (NSF; DEB-1146368 to L. A. Shipley; DEB-1146166 to J. L. Rachlow; DEB-1146194 to J. S. Forbey), Bureau of Land Management (BLM; #L09AC16253 to J. S. Forbey; #L09AC15391 to J. L. Rachlow), and USDA National Institute of Food and Agriculture (NIFA; Hatch Project 1005876 to L. A. Shipley).

LITERATURE CITED

- Bakker, E. S., R. C. Reiffers, H. Olf, and J. M. Gleichman. 2005. Experimental manipulation of predation risk and food quality: effect on grazing behaviour in a central-place foraging herbivore. *Oecologia* 146:157–167.
- Bedoya-Pérez, M. A., D. D. Issa, P. B. Banks, and C. McArthur. 2014. Quantifying the response of free-ranging mammalian herbivores to the interplay between plant defense and nutrient concentrations. *Oecologia* 175:1167–1177.
- Brown, J. S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioral Ecology and Sociobiology* 22:37–47.

- Brown, J. S. 1999. Vigilance, patch use and habitat selection: foraging under predation risk. *Evolutionary Ecology Research* 1:49–71.
- Brown, J. S., and B. P. Kotler. 2004. Hazardous duty pay and the foraging cost of predation. *Ecology Letters* 7:999–1014.
- Caraco, T. 1979. Time budgeting and group size: a theory. *Ecology* 60:611–617.
- Caraco, T. 1980. On foraging time allocation in a stochastic environment. *Ecology* 61:119–128.
- Caraco, T., S. Martindale, and T. S. Whittam. 1980. An empirical demonstration of risk-sensitive foraging preferences. *Animal Behaviour* 28:820–830.
- Charnov, E. L. 1976. Optimal foraging, the marginal value theorem. *Theoretical Population Biology* 9:129–136.
- Clausen, T. P., P. B. Reichardt, and J. P. Bryant. 1986. Pinosylvin and pinosylvin methyl ether as feeding deterrents in green alder. *Journal of Chemical Ecology* 12:2117–2131.
- Crowell, M. M. 2015. Food and fearscape: responses of specialist and generalist rabbits to food and predation risks. Thesis. Washington State University, Pullman, Washington, USA.
- David, H. A. 1988. The method of paired comparisons. Second edition. Hodder Arnold, London, UK.
- Dearing, M. D., and S. Cork. 1999. Role of detoxification of plant secondary compounds on diet breadth in a mammalian herbivore, *Trichosurus vulpecula*. *Journal of Chemical Ecology* 25:1205–1219.
- Dearing, M. D., J. S. Forbey, J. D. McLister, and L. Santos. 2008. Ambient temperature influences diet selection and physiology of an herbivorous mammal, *Neotoma albigula*. *Physiological and Biochemical Zoology* 81:891–897.
- DeGabriel, J. L., B. D. Moore, W. J. Foley, and C. N. Johnson. 2009. The effects of plant defensive chemistry on nutrient availability predict reproductive success in a mammal. *Ecology* 90:711–719.
- Demment, M. W., and P. J. Van Soest. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *American Naturalist* 125:641–672.
- Druce, D. J., J. S. Brown, J. G. Castley, G. I. Kerley, B. P. Kotler, R. Slotow, and M. H. Knight. 2006. Scale-dependent foraging costs: habitat use by rock hyraxes (*Procapra capensis*) determined using giving-up densities. *Oikos* 115: 513–525.
- Estabrook, G. F., and A. E. Dunham. 1976. Optimal diet as a function of absolute abundance, relative abundance, and relative value of available prey. *American Naturalist* 110: 401–413.
- Fedriani, J. M., and R. Boulay. 2006. Foraging by fearful frugivores: combined effect of fruit ripening and predation risk. *Functional Ecology* 20:1070–1079.
- Fowler, M. E. 1983. Plant poisoning in free-living wild animals: a review. *Journal of Wildlife Diseases* 19:34–43.
- Freeland, W. J., and D. H. Janzen. 1974. Strategies in herbivory by mammals: the role of plant secondary compounds. *American Naturalist* 108:269–289.
- Goering, H. K., and P. J. Van Soest. 1970. Forage fiber analyses (apparatus, reagents, procedures, and some applications). *Agriculture Handbook* 379. USDA Agricultural Research Service, Washington, D.C., USA.
- Grand, T. C. 2002. Alternative forms of competition and predation dramatically affect habitat selection under foraging–predation-risk trade-offs. *Behavioral Ecology* 13:280–290.
- Gross, J. E., L. A. Shipley, N. T. Hobbs, D. E. Spalinger, and B. A. Wunder. 1993. Functional response of herbivores in food-concentrated patches: tests of a mechanistic model. *Ecology* 74:778–791.
- Hebblewhite, M., and E. H. Merrill. 2009. Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. *Ecology* 90:3445–3454.
- Hochman, V., and B. P. Kotler. 2006. Effects of food quality, diet preference and water on patch use by Nubian ibex. *Oikos* 112:547–554.
- Hofmann, R. R. 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. *Oecologia* 78:443–457.
- Hoover, W. H., and R. N. Heitmann. 1972. Effects of dietary fiber levels on weight gain, cecal volume and volatile fatty acid production in rabbits. *Journal of Nutrition* 102:375–379.
- Houston, A. I., J. M. McNamara, and J. Hutchinson. 1993. General results concerning the trade-off between gaining energy and avoiding predation. *Philosophical Transactions of the Royal Society of London B* 341:375–397.
- Hunter, J., and B. H. Hirst. 1997. Intestinal secretion of drugs: the role of P-glycoprotein and related drug efflux systems in limiting oral drug absorption. *Advanced Drug Delivery Reviews* 25:129–157.
- Iason, G., and S. E. Van Wieren. 1999. Digestive and ingestive adaptations of mammalian herbivores to low-quality forage. Pages 337–369 in H. Olff, V. K. Brown, and R. H. Drent, editors. *Herbivores: between plants and predators: 38th Symposium of the British Ecological Society*. Blackwell Science, Oxford, UK.
- Jacob, J., and J. S. Brown. 2000. Microhabitat use, giving-up densities and temporal activity as short- and long-term anti-predator behaviors in common voles. *Oikos* 91:131–138.
- Keeney, R. L., and H. Raiffa. 1993. *Decisions with multiple objectives: preferences and value trade-offs*. Cambridge University Press, Cambridge, UK.
- Kelsey, R. G., J. R. Stephens, and F. Shafizadeh. 2006. The chemical constituents of sagebrush foliage and their isolation. *Journal of Range Management Archives* 35:617–622.
- Kendall, M. G., and B. B. Smith. 1940. On the method of paired comparisons. *Biometrika* 31:324–345.
- Kingsley, D. C., and T. C. Brown. 2013. Value learning and the willingness to accept–willingness to pay disparity. *Economics Letters* 120:473–476.
- Kleiber, M. 1975. *The fire of life: an introduction to animal energetics*. Krieger, Huntington, New York, USA.
- Kotler, B. P., and L. Blaustein. 1995. Titrating food and safety in a heterogeneous environment: when are the risky and safe patches of equal value? *Oikos* 74:251–258.
- Kralik, J. D., and W. W. L. Sampson. 2012. A fruit in hand is worth many more in the bush: steep spatial discounting by free-ranging rhesus macaques (*Macaca mulatta*). *Behavioural Processes* 89:197–202.
- Lima, S. L., T. J. Valone, and T. Caraco. 1985. Foraging-efficiency–predation-risk trade-off in the grey squirrel. *Animal Behaviour* 33:155–165.
- MacArthur, R. H., and E. R. Pianka. 1966. On optimal use of a patchy environment. *American Naturalist* 100:603–609.
- MacCracken, J. G., and R. M. Hansen. 1984. Seasonal foods of blacktail jackrabbits and Nuttall cottontails in southeastern Idaho. *Journal of Range Management* 37:256–259.
- Maltby, L. 1999. Studying stress: the importance of organism-level responses. *Ecological Applications* 9:431–440.
- Mankiw, N. G. 2011. *Principles of microeconomics*. Sixth edition. Cengage Learning, Mason, Ohio, USA.
- Manly, B. F. J., L. McDonald, and D. Thomas. 1993. *Resource selection by animals: statistical design and analysis for field studies*. Springer Science & Business Media, New York, New York, USA.
- Marsh, K. J., I. R. Wallis, and W. J. Foley. 2005. Detoxification rates constrain feeding in common brushtail possums (*Trichosurus vulpecula*). *Ecology* 86:2946–2954.
- Marsh, K. J., I. R. Wallis, S. McLean, J. S. Sorensen, and W. J. Foley. 2006. Conflicting demands on detoxification pathways influence how common brushtail possums choose their diets. *Ecology* 87:2103–2112.
- McArthur, C., P. Orlando, P. B. Banks, and J. S. Brown. 2012. The foraging tightrope between predation risk and plant

- toxins: a matter of concentration. *Functional Ecology* 26:74–83.
- Mella, V. S. A., A. J. W. Ward, P. B. Banks, and C. McArthur. 2014. Personality affects the foraging response of a mammalian herbivore to the dual costs of food and fear. *Oecologia* 177:293–303.
- Mittelbach, G. G. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. *Ecology* 62:1370–1386.
- Montooth, K. L., K. T. Siebenthal, and A. G. Clark. 2006. Membrane lipid physiology and toxin catabolism underlie ethanol and acetic acid tolerance in *Drosophila melanogaster*. *Journal of Experimental Biology* 209:3837–3850.
- Naef-Daenzer, B. 2000. Patch time allocation and patch sampling by foraging great and blue tits. *Animal Behaviour* 59:989–999.
- Nersesian, C. L., P. B. Banks, and C. McArthur. 2011. Titrating the cost of plant toxins against predators: determining the tipping point for foraging herbivores. *Journal of Animal Ecology* 80:753–760.
- Price, M. V., and R. A. Correll. 2001. Depletion of seed patches by Merriam's kangaroo rats: are GUD assumptions met? *Ecology Letters* 4:334–343.
- Pyke, G. H., H. R. Pulliam, and E. Charnov. 1977. Optimal foraging: a selective review of theory and tests. *Quarterly Review of Biology* 52:137–154.
- R Development Core Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>.
- Rachlow, J. L., and R. T. Bowyer. 1998. Habitat selection by Dall's sheep (*Ovis dalli*): maternal trade-offs. *Journal of Zoology* 245:457–465.
- Rapport, D. J. 1971. An optimization model of food selection. *American Naturalist* 105:575–587.
- Raubenheimer, D., and S. J. Simpson. 1993. The geometry of compensatory feeding in the locust. *Animal Behaviour* 45:953–964.
- Real, L., and T. Caraco. 1986. Risk and foraging in stochastic environments. *Annual Review of Ecology and Systematics* 17:371–390.
- Robbins, C. T., A. E. Hagerman, P. J. Austin, C. McArthur, and T. A. Hanley. 1991. Variation in mammalian physiological responses to a condensed tannin and its ecological implications. *Journal of Mammalogy* 72:480–486.
- Robbins, C. T., T. A. Hanley, A. E. Hagerman, O. Hjeljord, D. L. Baker, C. C. Schwartz, and W. W. Mautz. 1987. Role of tannins in defending plants against ruminants: reduction in protein availability. *Ecology* 68:98–107.
- Schmidt, K. A. 2000. Interactions between food chemistry and predation risk in fox squirrels. *Ecology* 81:2077–2085.
- Schmidt, K. A., J. S. Brown, and R. A. Morgan. 1998. Plant defenses as complementary resources: a test with squirrels. *Oikos* 81:130–142.
- Searle, K. R., C. J. Stokes, and I. J. Gordon. 2008. When foraging and fear meet: using foraging hierarchies to inform assessments of landscapes of fear. *Behavioral Ecology* 19:475–482.
- Shipley, L. A., T. B. Davila, N. J. Thines, and B. A. Elias. 2006. Nutritional requirements and diet choices of the pygmy rabbit (*Brachylagus idahoensis*): a sagebrush specialist. *Journal of Chemical Ecology* 32:2455–2474.
- Shipley, L. A., E. M. Davis, L. A. Felicetti, S. McLean, and J. S. Forbey. 2012. Mechanisms for eliminating monoterpenes of sagebrush by specialist and generalist rabbits. *Journal of Chemical Ecology* 38:1178–1189.
- Shipley, L. A., A. W. Illius, K. Danell, N. T. Hobbs, and D. E. Spalinger. 1999. Predicting bite size selection of mammalian herbivores: a test of a general model of diet optimization. *Oikos* 84:55–68.
- Shrader, A. M., B. P. Kotler, J. S. Brown, and G. I. H. Kerley. 2008. Providing water for goats in arid landscapes: effects on feeding effort with regard to time period, herd size and secondary compounds. *Oikos* 117:466–472.
- Sih, A. 1980. Optimal behavior: can foragers balance two conflicting demands? *Science* 210:1041–1043.
- Simpson, S. J., and D. Raubenheimer. 1999. Assuaging nutritional complexity: a geometrical approach. *Proceedings of the Nutrition Society* 58:779–789.
- Sorensen, J. S., and M. D. Dearing. 2003. Elimination of plant toxins by herbivorous woodrats: revisiting an explanation for dietary specialization in mammalian herbivores. *Oecologia* 134:88–94.
- Sorensen, J. S., E. Heward, and M. D. Dearing. 2005a. Plant secondary metabolites alter the feeding patterns of a mammalian herbivore (*Neotoma lepida*). *Oecologia* 146:415–422.
- Sorensen, J. S., J. D. McLister, and M. D. Dearing. 2005b. Plant secondary metabolites compromise the energy budgets of specialist and generalist mammalian herbivores. *Ecology* 86:125–139.
- Sorensen, J. S., M. M. Skopec, and M. D. Dearing. 2006. Application of pharmacological approaches to plant–mammal interactions. *Journal of Chemical Ecology* 32:1229–1246.
- Sorensen, J. S., C. A. Turnbull, and M. D. Dearing. 2004. A specialist herbivore (*Neotoma stephensi*) absorbs fewer plant toxins than does a generalist (*Neotoma albigula*). *Physiological and Biochemical Zoology* 77:139–148.
- Sparreboom, A., J. van Asperen, U. Mayer, A. H. Schinkel, J. W. Smit, D. K. Meijer, P. Borst, W. J. Nuijten, J. H. Beijnen, and O. van Tellingen. 1997. Limited oral bioavailability and active epithelial excretion of paclitaxel (Taxol) caused by P-glycoprotein in the intestine. *Proceedings of the National Academy of Sciences USA* 94:2031–2035.
- Thines, N. J., L. A. Shipley, and R. D. Saylor. 2004. Effects of cattle grazing on ecology and habitat of Columbia Basin pygmy rabbits (*Brachylagus idahoensis*). *Biological Conservation* 119:525–534.
- Todd, I. A., and R. J. Cowie. 1990. Measuring the risk of predation in an energy currency: field experiments with foraging blue tits, *Parus caeruleus*. *Animal Behaviour* 40:112–117.
- Torregrossa, A.-M., A. V. Azzara, and M. D. Dearing. 2012. Testing the diet-breadth trade-off hypothesis: differential regulation of novel plant secondary compounds by a specialist and a generalist herbivore. *Oecologia* 168:711–718.
- Torregrossa, A.-M., and M. D. Dearing. 2009. Nutritional toxicology of mammals: regulated intake of plant secondary compounds. *Functional Ecology* 23:48–56.
- Van Soest, P. J. 1994. *Nutritional ecology of the ruminant*. Comstock Publishing Associates, Ithaca, New York, USA.
- Werner, E. E., and D. J. Hall. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate–predation risk trade-off. *Ecology* 69:1352–1366.
- Wheeler, H. C., and D. S. Hik. 2014. Giving-up densities and foraging behaviour indicate possible effects of shrub encroachment on arctic ground squirrels. *Animal Behaviour* 95:1–8.
- Wiggins, N. L., C. McArthur, and N. W. Davies. 2006. Diet switching in a generalist mammalian folivore: fundamental to maximising intake. *Oecologia* 147:650–657.
- Willems, E. P., and R. A. Hill. 2009. Predator-specific landscapes of fear and resource distribution: effects on spatial range use. *Ecology* 90:546–555.