Preference in patchy landscapes: the influence of scale-specific intake rates and variance in reward

Kate R. Searle, a N. Thompson Hobbs, b Bruce A. Wunder, b and Lisa A. Shipley c
a Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, Colorado 80523, USA, b Department of Zoology, Colorado State University, Fort Collins, Colorado 80523, USA, and c Department of Natural Resources, Washington State University, Pullman, Washington 99163, USA

Understanding the responses of foragers to patchy distributions of resources has formed a fundamental challenge in behavioral ecology. Two currencies have been used to assess the patch preferences of herbivores—intake rate maximization and risk sensitivity. We wished to understand if small mammalian foragers, collared lemmings (Dicrostonyx groenlandicus), choose patches to maximize food intake rate or to reduce risk of starvation in “variable” environments. Moreover, we examined the possibility that maximizing intake rate depends on the spatial scale of patchiness. We designed an experiment offering two alternative patches of food, varying the predictability of food rewards and the “potential intake rate” at different spatial scales. Collared lemmings did not consistently select patches that maximized their intake rate at either scale studied. Instead, they chose patches offering the least variation in food reward over the course of the experiment. Collared lemmings used prior knowledge gained from previous foraging bouts to assess food variability. We interpret these results as evidence for risk-averse foraging strategies, which are predicted for continuous foragers aiming to minimize risk of starvation. Key words: collared lemmings, maximization of intake rate, patch selection, risk-sensitive foraging. [Behav Ecol 17:315–323 (2006)]

Foraging decisions ultimately determine the energy balance of animals and in so doing influence body mass, reproductive success, and survival. Most food resources are aggregated in patches, so a key component of successful foraging is deciding how to respond to these aggregations (Bailey et al., 1996; Bergman et al., 2001; Dumont et al., 2002; Hobbs, 1999; Johnson et al., 2001; Laca and Ortega, 1995; Ritchie, 1998; Senft et al., 1987; WallisDeVries et al., 1999). Foraging herbivores encounter food resources that are arranged in hierarchies where patches of plant tissue at fine scales are often nested within larger, coarse scale patches (Bailey et al., 1996; Hobbs, 1999; Senft et al., 1987). This patchiness creates two dimensions of variability that may shape foraging choices. The first dimension is scale-dependent rates of energy gain (Fortin et al., 2002). Patchily distributed resources can offer high intake rates averaged over fine scales of time and space and low intake rates at coarse scales, and vice versa. At fine scales, intake rate is controlled by bite size because small bites require longer handling times per gram ingested (Gross et al., 1993a; Laca et al., 1994a,b; Spalinger and Hobbs, 1992). At coarse scales, intake rate is controlled by search time to locate bites and patches of bites (Hobbs, 1999; Spalinger and Hobbs, 1992). Therefore, a landscape in which large bites are aggregated would allow an animal higher intake rates at fine scales but lower intake rates at large scales than smaller, more dispersed bites or patches (Figure 1). Thus, it is possible that herbivores respond to particular scales in the patch hierarchy. Revealing such responses will allow us to identify scales of heterogeneity that are “functionally” important to the foraging herbivores (Bailey et al., 1996; Hobbs, 1999; Kotliar and Wiens, 1990; Senft et al., 1987).

The second influence on foraging choices in patch hierarchies is predictability of resources. Patchy distributions of resources force variability in encounter rates with resources relative to uniform or random distributions (Adler et al., 2001). This variability means that foragers must consider the uncertainty of obtaining food along with the average rate of intake. Foraging animals may choose strategies that minimize the risk associated with different feeding options rather than those that maximize intake rate. Risk-sensitive foraging applies when animals are affected by the variance in the payoff obtained from alternative foraging options to a greater extent than by the average payoff (Kacelnik and Bateson, 1996). For example, two landscapes may allow animals to achieve the same average food intake rate over time or space, but in one intake rate is “constant” over time and space and in the other intake rate varies from high to low over time or space. Temporal and spatial variability in intake rate may be caused by events such as weather and seed dispersal or if some patches are empty of food because they were previously grazed. Therefore, herbivores foraging in patch hierarchies may be influenced by features of plants that control the average rate of intake or may be more strongly influenced by the predictability of intake than by its average. If the responses of animals are shaped by average rates of food intake, then herbivores may be sensitive to variability in intake rate expressed at different spatial scales. To determine how a herbivore responds to patches offering different average intake rates at different scales and to patches offering constant or variable intake rates, we tested three competing hypotheses about the way that herbivores evaluate and select food patches:

1. Herbivores prefer patches where average intake rate is greatest at fine spatial scales as a result of brief handling time.
We offered a range of patch geometries to experimental animals to assure that our hypotheses made distinct, competing predictions about the animals’ behavior. Pairs of food options (patches) of forage containing fresh alfalfa were offered in a foraging arena, a 3.6 × 3.6 m² of plywood with borders, 30 cm high (Figure 3). Each food option was a patch containing twenty feeding stations, and each patch contained the same total forage mass. The total mass provided in each patch was approximately a single “meal” for a collared lemming, the amount of food required to fill the gut. We estimated the gut capacity of collared lemmings to be similar to that of prairie voles (1 g dry matter [DM], Zynel and Wunder [2002]) and thus provided lemmings with 1.65 g DM of food in each patch.

Five combinations of two patch types, variable and constant, were offered to experimental animals (Table 1). We assumed that potential intake rate in one patch did not influence the intake rate in the other patch making up the pair. In the constant patch, patch characteristics were not varied among successive combinations of paired patches so that potential intake rate at the feeding station and patch scales remained constant across all patch combinations. However, in the variable patches, we manipulated bite size to force an increasing large advantage in potential intake rate at the feeding station scale (Figure 4A). This was achieved by increasing bite size within feeding stations while maintaining the same total mass in all feeding stations in all patches, by reducing the number of bites within the feeding station (Table 1). At the same time, we manipulated the encounter rate with feeding stations in the variable patch to force a greater potential intake rate at the patch scale when bite sizes were small and a lower potential intake rate at the patch scale when bite sizes were large (Figure 4B). If collared lemmings seek to maximize intake rate at the feeding station scale, we should observe a gradual increase in preference for the variable patch as bite size increased (Figure 4C, dashed line). If collared lemmings seek to maximize intake rate at the larger patch scale, we should observe switching in preference between patches at intermediate bite sizes (Figure 4C, dotted line). To determine whether lemmings preferred predictable patches, we designed the experiment such that one food option (the constant patch) remained constant in terms of food intake rate at both spatial scales, and the alternative option (the variable patch) varied in intake rate at two spatial scales over the five patch combinations that were offered. Collared lemmings were thus exposed to two sources of variation in food reward in the variable patch throughout the course of the experiment. First, the presence of empty feeding stations in two of the variable patch types (bite size = 0.008 and 0.025 g, Table 1) meant that collared lemmings experienced variability in food reward.

### Methods

#### Experimental design

We investigated patch choices of collared lemmings (*Dichrototonyx groenlandicus*), given three alternatives: maximization of food intake at fine scales, maximization at coarse scales, and minimization of variance in food intake. Explaining these alternatives requires defining some terms. We define a “bite” as a dry mass of forage that could be consumed with a single cropping motion. To manipulate bite size during the experiment, bites were precut to a specific dry mass of plant tissue and placed in a pile within each “feeding station.” A feeding station consists of a collection of bites that can be consumed without requiring the animal to move its feet. A patch is a spatially aggregated collection of feeding stations. Potential intake rate is the approximate maximum dry mass of forage that could be obtained per unit time spent foraging, at either the feeding station scale or the patch scale.

### Table 1

<table>
<thead>
<tr>
<th>Order of presentation of patch (date)</th>
<th>Patch type</th>
<th>Bite mass $S$ (g DM)</th>
<th>Number of bites per feeding station</th>
<th>Potential feeding station intake rate (g DM/min)</th>
<th>Number of empty feeding stations in variable patch</th>
<th>Area of patch (m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 (21–28 August)</td>
<td>Constant</td>
<td>0.0025</td>
<td>33</td>
<td>0.067</td>
<td>—</td>
<td>5.0</td>
</tr>
<tr>
<td>3 (3–12 September)</td>
<td>Variable</td>
<td>0.0025</td>
<td>33</td>
<td>0.067</td>
<td>0</td>
<td>0.85</td>
</tr>
<tr>
<td>4 (15–30 September)</td>
<td>Variable</td>
<td>0.004</td>
<td>20</td>
<td>0.077</td>
<td>0</td>
<td>0.85</td>
</tr>
<tr>
<td>5 (16–31 July)</td>
<td>Variable</td>
<td>0.006</td>
<td>14</td>
<td>0.083</td>
<td>0</td>
<td>0.85</td>
</tr>
<tr>
<td>2 (30 July–9 August)</td>
<td>Variable</td>
<td>0.008</td>
<td>10</td>
<td>0.088</td>
<td>30</td>
<td>5.0</td>
</tr>
</tbody>
</table>

Feeding station intake rates were estimated using functional response for lemmings feeding on fresh alfalfa. Number of empty feeding stations used to manipulate patch intake rate in the variable patch and total patch area for each patch.
within these trials. Second, as potential intake rates were manipulated in the variable patch over the course of the experiment, the animals experienced variability among trials. If collared lemmings seek to maximize predictability of food reward, we should observe a consistent preference for the constant patch relative to variable one (Figure 4C, solid line).

Feeding stations were contained within $14 \times 14$-cm tetrahedral houses with two entrance holes on opposite sides (Figure 2). Houses reduced visibility of food and provided a secure place for animals to feed. To create foraging risk food was hidden, so foragers would not be able to precisely determine the payoffs from alternative options at the time of forming a patch choice (Bateson, 2002). In both patch types, there were 20 $14 \times 14$-cm tetrahedral houses, all of which contained food. In the variable patch type, houses containing food were interspersed with 30–60 houses without food (Table 1). In the constant patch, houses were interspersed with 30–60 $14 \times 14$-cm canopies that provided cover from above but were open on all sides, allowing animals to see that they did not contain food (Figure 2).

Because bite size controls intake rate within feeding stations, whereas encounter rate can control intake rate when feeding stations are sufficiently far apart or difficult to locate (Gross et al., 1993a,b; Spalinger and Hobbs, 1992), we manipulated bite size to control potential intake rates at the feeding station scale and presence or absence of food in houses to control potential intake rate at the patch scale. We created different bite sizes of alfalfa using hole punches to make discs of alfalfa leaves of varying size and mass, the largest of which could still be consumed by a lemming without breaking into pieces before processing in the mouth. Bite size in the constant patch was always 0.0025 g DM. We used five different bite sizes in the variable patch that were each paired with a constant patch in the trials to create a total of five patch combinations. The dry masses of the variable patch bite sizes were 0.0025, 0.004, 0.006, 0.008, and 0.025 g and will henceforth be used to refer to the five patch combinations that were presented to collared lemmings in the course of the experiment (Table 1). Pilot experiments using methods described by Gross et al. (1993b) allowed us to estimate the effect of these different bite sizes on potential intake rate at the feeding station scale (Table 1). This was achieved by fitting

![Figure 2](https://academic.oup.com/beheco/article-abstract/17/2/315/213245/fig2)

**Figure 2**
Tetrahedral house (left) and canopy (right) used to construct food patches for collared lemmings in the foraging arena. The houses were used to provide cover for feeding stations and also reduced potential intake rate at the patch scale when left empty. Canopies were used to provide cover in patches that did not contain empty houses such that total cover remained equal in both the constant and variable patches in all trials.

![Figure 3](https://academic.oup.com/beheco/article-abstract/17/2/315/213245/fig3)

**Figure 3**
Collared lemmings were released into this foraging arena, which consisted of two distinct food options. The constant patch provided potential intake rates that did not vary in successive patch combinations throughout the experiment at either the feeding station or patch scale. The variable patch offered differing potential intake rates at the feeding station and patch scales in successive patch combinations. Each patch consisted of feeding stations containing food, feeding stations containing no food, or canopies used when necessary to achieve the same total cover in each patch. Each feeding station containing food had approximately 0.08 g DM fresh alfalfa. Bite size within feeding stations was manipulated in the variable patch to create different feeding station intake rates in successive patch combinations. Spacing between feeding stations in the variable patch was manipulated to provoke different patch intake rates in the successive patch combinations. (A) specifically represents patch combination 1, with 0.0025 g DM bite size in the constant patch and 0.008 g DM bite size in the variable patch, 30 additional feeding stations containing no food in the variable patch, and 30 canopies in the constant patch to compensate for the additional cover. (B) specifically represents patch combination 3, with 0.0025 g DM bite size in the constant patch and 0.0025 g DM bite size in the variable patch.
a functional response model to observed feeding station intake rates against bite size, averaged over the seven experimental animals. Potential intake rate at patch scales was manipulated by alternating the proportion of houses that contained food in the variable patch. This increased the variance in encounter rate with feeding stations over the 10-min trial period and permitted control over the average intake rate. A higher percentage of empty houses in the variable patch forced lower intake rates against bite size, averaged over the seven experimental animals. The proportion of empty feeding stations (x) explained only 35% of the variation in patch intake rate (y) (y = -0.24x + 0.246, r² = .35). Likewise, bite size explained only 17% of the patch intake rate (y) (y = a × bite size + b, r² = .17). Consequently, we were not confident that we could accurately predict potential patch intake rates using these models. Instead, we made every effort to induce changes in patch intake rate using the maximum changes in bite size and proportion of houses containing feeding stations within the confines of our experimental design. To test our ability to alter patch intake rates as desired by the experimental design, we measured intake rate at the patch scale during our experiments, calculated as the mass consumed from each patch divided by the time spent in each patch.

**Observations**

All trials were conducted at Colorado State University, using seven male collared lemmings (weight x 65 g). Trials were conducted in the arena, with the two food options (constant patch and variable patch) occupying opposite sides of the arena (Figure 3). A trial consisted of observations of a single collared lemming for 10 min. An observer located in the same part of the room during all trials recorded the amount of time an animal spent in either of the two food options during this 10-min foraging bout. The trial was not possible for animals to see the observer during experiments due to the sides of the arena, and every effort was made to remain as still as possible. We weighed all remaining food at the beginning and end of each trial to establish how much mass was eaten from each patch during the trial. Any brief periods of inactivity were removed from the total time recorded. If animals were inactive for more than 3 min, trials were discarded. We accounted for changes in DM of plants that occurred due to desiccation during the trial using reference samples. Animals were acclimated to feeding in houses and foraging in the arena before trials began.

We offered collared lemmings five paired patch combinations in random order (0.008, 0.025, 0.0025, 0.004, and 0.006 g), over the summer and fall of 2003 (Table 1). For each of the five paired patch combinations, we repeated trials four times with each of the seven collared lemmings (in random order) to evaluate if animals used past experience to better match their preference to the most profitable patch. Because of this, we always kept the constant patch and variable patch in the same locations within the arena throughout the experiment.

Between trials, animals were housed individually and fed a pelleted grain-alalfa rabbit ration ad libitum, with free access to tap water. Animals were fasted for 4–8 h before trials and so were maintained in negative energy balance during all trials. The animals lost weight during the days when trials were run (up to approximately 10% body mass) but recovered lost weight overnight after trials were completed and animals had ad libitum access to food.

**Analysis**

Observed patch intake rates for each food option (one constant patch and one variable patch making up one paired patch combination) offered were calculated as the mass removed from a patch divided by the time spent in a patch over the course of one trial. To determine how patch selection varied over the course of the experiment, we used two measures of patch selection: the mass removed from the constant patch and variable patch and the amount of time spent foraging in the constant patch and variable patch. To explain variation in these responses, we used log ratios of the response variables (Illius et al., 1999). For the mass removed from each patch, we calculated the natural logarithm of the ratio of the mass removed from the constant patch over the mass removed from the variable patch under the five patch combinations. Because we applied a stopping rule, only allowing the animals to feed for 10 min, we could not treat the time spent in each patch or mass consumed from each patch as independent. Instead, we treated pairs of the time spent in each patch as scaled compositional data and analyzed the natural logarithm of the ratio of the time spent in each patch (Illius et al., 1999). We converted the absolute time spent in each patch to a proportion.
If animals spent no time in a patch, the corresponding log ratio could not be formed, and hence when animals spent no time in a patch, we adjusted the time spent in that patch to 1 s before converting to a proportion. ANOVAs were conducted using the corresponding log ratios (SAS V8, 2002, SAS Institute, Cary, NC). Preference within paired patch combinations was examined across all repetitions in a single-factor ANOVA, using contrasts to assess changes in preference among paired patch combinations over the course of the experiment. Evidence of learning within a paired patch combination was examined using a single-factor ANOVA to look at changes in preference among repetitions within a paired patch combination. Because the analyses produced very similar results when using the mass consumed or the proportion of time spent per patch, we have limited the results and discussion to the analysis of the proportion of time spent per patch.

RESULTS

In three out of 129 trials, the foraging animal chose to spend no time in one of the food options, and in each of these cases, the corresponding log ratio was formed by adjusting the time spent in the unutilized food option to 1 s. Elston et al. (1996) demonstrated that the significance levels of explanatory variables are robust to substituting appropriate small values for the missing log ratios, but actual estimates of preference can be highly sensitive to the substituted value. However, because it is only recommended that this issue be addressed in cases where more than 10% of trials have an unutilized option (Elston et al., 1996), we did not think it necessary to perform additional analyses.

Observed patch intake rates averaged over the four repetitions for each of the five paired patch combinations did not vary significantly in the constant patch ($F_{1,125} = 1.93, p = .11$) and increased or declined with increasing bite size in the variable patch (Figure 5). We take this as evidence that our treatments exerted the desired effect on intake rates in the five paired patch combinations offered over the course of the experiment.

In our experiment, collared lemmings did not select patches that maximized potential intake rate at either the feeding station or patch scale. Instead, collared lemmings spent more time in the constant patch in all trials (Figures 6–8). Collared lemmings increased the proportion of time spent in the constant patch compared to the variable patch (Figures 6–8). In subsequent trials, they spent a larger proportion of the total foraging time in the constant patch compared to the variable patch (Figures 6–8). Collared lemmings increased the proportion of time spent in the constant patch between the first and fifth paired patch combinations ($F_1125 = 17.31, p < .0001$). In the first patch combination (0.008 g), collared lemmings spent more time in the variable patch than the constant patch (Figures 6–8). In subsequent trials, they spent a larger proportion of the total foraging time in the constant patch compared to the variable patch (Figures 6–8). Collared lemmings increased the proportion of time spent in the constant patch compared to the variable patch (Figures 6–8). In subsequent trials, they spent a larger proportion of the total foraging time in the constant patch compared to the variable patch (Figures 6–8). Collared lemmings increased the proportion of time spent in the constant patch compared to the variable patch (Figures 6–8). In subsequent trials, they spent a larger proportion of the total foraging time in the constant patch compared to the variable patch (Figures 6–8).
DISCUSSION

Collared lemmings did not consistently choose food options that maximized potential intake rate at either the feeding station or patch scale. Rather, they showed a strong preference for the food option where resources were predictable over the course of the experiment. This behavior suggests that collared lemmings are risk-averse foragers, preferring to minimize the variance in intake rate rather than maximizing the expected intake rate at any particular spatial scale.

Foraging animals experience variability in food encounter rate when food is distributed patchily. In our experiment, one patch remained constant in terms of food intake rate at both spatial scales, whereas the alternative patch varied in intake rate at two spatial scales over the five patch combinations that were offered. Throughout the experiment, collared lemmings were exposed to two sources of variation in food reward in the variable patch. First, the presence of empty feeding stations in two of the variable patch types (bite size = 0.008, 0.025 g, Table 1) meant that collared lemmings experienced variability in food reward within trials. Second, as potential intake rates were manipulated in the variable patch over the course of the experiment, the animals experienced variability among trials. The strongest preference for the constant patch occurred in later trials, when food reward did not vary within the patches at the feeding station scale because all houses contained feeding stations in each patch. This preference demonstrates clear risk-averse behavior at the patch scale. Because the source of the variation at the patch scale lay in differences between alternative paired patch combinations, the collared lemmings evidently used information from past patch combinations to assess variability in food reward in present patches, otherwise the need to sample the two patches would have weakened the preference for the constant patch. Collared lemmings seem capable of remembering variation in food reward over several days and of applying this knowledge to immediate

Figure 7

Mean proportion of time seven collared lemmings spent in patches containing constant bite sizes (black bars) and patches where bite size varied between pairings (gray bars), by consecutive repetitions (trial numbers 1–4). Error bars represent 1 SE. Asterisks (*) indicate a significant difference in the proportion of time spent in the constant patch versus the variable patch in each successive trial within a paired patch combination, defined by those cases where the 90% confidence interval of the corresponding log ratio did not bridge zero.
patch-choice decisions. Collared lemmings thereby based their patch preferences on a longer time scale than previously demonstrated for other small mammal species (e.g., immediate experience was more important than past experience for common shrews, *Sorex araneus*, choosing between feeding stations; Barnard et al., 1985).

The risk-sensitive behavior we observed in collared lemmings may be explained first by their ecology as small herbivores. Small herbivores have a limited capacity to store energy (Barnard and Brown, 1985; Lawes and Perrin, 1995). After a threshold is met, additional gains of energy have little value. When an animal must meet some critical requirement, natural selection may well operate strongly on the animal’s ability to assure this requirement is met (Caraco, 1980; Lawes and Perrin, 1995; Stephens, 1981; Stephens and Krebs, 1986). Because the supply of resources is inherently stochastic over time and space, we expect behaviors that result in secure acquisition of this critical requirement to dominate in such species. Collared lemmings experience winter conditions for at least 8 months of the year (Reid and Krebs, 1996). Higher metabolic costs induced by cold temperatures may diminish energy for body growth after maintenance requirements are met (Reid and Krebs, 1996). This implies the existence of a critical level of resources that must be reached because growth to a larger body mass and more rounded shape are adaptive for energy conservation (Malcolm and Brooks, 1993) and reproduction in cold environments (Collier et al., 1975). Collared lemmings are therefore likely adapted to foraging in such a way as to minimize the probability of falling below this critical level of resources to ensure survival and enhance reproductive success.

According to models developed by Houston and McNamara (1985, 1986), the optimal diet policy for continuous foragers that are able to forage during both day and night is to take all prey items encountered that result in a net energy gain. Adaptations to this model have further demonstrated that the optimal prey choice for continuous foragers does not depend on energy reserves as it does for foragers that have a limited time available for foraging activities (Barnard et al., 1985). When two food options are presented with the same mean reward rate, but different variances, then the option with the smaller variance should always be chosen (Barnard et al., 1985). In essence, continuous foragers should always exhibit risk-averse behavior when choosing between alternative food options. We found that collared lemmings preferred patches that offered predictable resources over those that offered greater average

**Figure 8**
Preference shown by collared lemmings for each patch type, by consecutive repetitions (trial numbers 1–4), where bite size varied between pairings. Preference is expressed as log ratios of the proportion of time an individual spent foraging in each patch. Values are the mean log ratio averaged over all individual lemmings in that trial. Zero values mean no preference was evident, positive values indicate preference for the constant patch, and negative values indicate preference for the variable patch. Error bars are 90% confidence intervals formed on the log ratios of each paired patch combination over all individual collared lemmings in that trial.
returns. Furthermore, the strength of the preference for the constant patch consistently increased as the experiment progressed. Collared lemmings are known to forage continuously throughout the day and night, with males exhibiting two peaks in movement (0800 and 2000 h) and females showing a single peak at 1400 h in the Canadian Arctic (Brooks, 1993; Predavec and Krebs, 2000). Because collared lemmings are continuous foragers in their natural environment, risk-averse behavior is predicted under natural conditions. In addition, because collared lemmings eat a diet of mostly vegetation, their food supply is relatively abundant, even in winter, and as such, individuals may not expect to be deficient in energy at the end of the day (Lawes and Perrin, 1995). In this case, animals may not be adapted to reliably perceive or predict circumstances under which risk-prone behavior may be optimal. The cost of being risk prone under the wrong conditions is large compared to the benefit under the right conditions (Houston and McNamara, 1985), hence animals should be expected to show risk-averse behavior.

The distribution of food resources into patches creates opportunities for alternative foraging strategies, where animals may either seek to maximize scale-dependent intake rate or minimize the variance in encounter rates with food rewards. Other small mammal species have been observed to forage in a risk-sensitive manner. However, variation in food amount and energy budgets has led to inconsistent results in several small mammal species (Table 2). We have shown that collared lemmings appear to be risk-sensitive foragers, exhibiting risk-averse behavior when under negative energy balance. This behavior can be explained in the light of their specific ecology, as small, continuous foragers, preferring a diet of vegetation and faced with high predation risk.

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REFERENCES


Table 2

Results from previous work on risk-sensitive foraging in small mammals

<table>
<thead>
<tr>
<th>Species</th>
<th>Positive energy budget</th>
<th>Negative energy budget</th>
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<tr>
<td></td>
<td>Risk averse</td>
<td>Risk prone</td>
</tr>
<tr>
<td>Rats</td>
<td>*</td>
<td>0</td>
</tr>
<tr>
<td>Round-eared elephant shrew</td>
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<td>0</td>
</tr>
<tr>
<td>Common shrew</td>
<td>*</td>
<td>0</td>
</tr>
<tr>
<td>Collared lemmings</td>
<td>*</td>
<td>0</td>
</tr>
</tbody>
</table>

Studies where support for risk-averse or risk-prone behavior under either positive or negative energy budgets are denoted by ‘*.’ Studies where species were found to be indifferent are denoted by ‘0.’


