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Source: *Ecoscience*, 21(1):61-68. 2014.

Published By: Centre d'études nordiques, Université Laval

DOI: <http://dx.doi.org/10.2980/21-1-3689>

URL: <http://www.bioone.org/doi/full/10.2980/21-1-3689>

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# Male and female voles do not differ in their assessments of predation risk <sup>1</sup>

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**Abstract:** A forager's willingness to trade off safety for food varies with its energetic state. Animals in a low energetic state should accept higher risk than animals with larger energy reserves. In mammals, energy expenditure by females on gestation and lactation may exceed the relatively low cost of sperm production by males. It follows, if reproductive costs are indeed higher for females than for males, that reproductive females may be more likely than males to trade safety for food. Thus, we evaluated the use of safe *versus* risky foraging patches by male and female meadow voles using putatively safe and risky habitats. We also used behavioural trials to assess whether sexual differences in personality could account for any differences in patch use. Voles preferred to forage in safe patches over risky ones. There was no difference between male and female voles, or between reproductive and non-reproductive individuals, in their respective use of safe *versus* risky foraging patches. Personality also had no effect on patch choice. The results are consistent with recent studies on other species that have failed to find differences in reproductive costs between the sexes. Experiments on foraging behaviour might thus provide simple and repeatable tests for sexual differences and similarities in reproductive costs.

**Keywords:** cost of reproduction, giving-up density, *Microtus pennsylvanicus*, optimal foraging theory, patch residence time, personality, predation risk.

**Résumé:** Les réserves énergétiques d'un animal déterminent le compromis qu'il fera entre sa sécurité et son accès à la nourriture. Les animaux dont les réserves énergétiques sont basses devraient accepter un niveau de risque plus élevé que ceux dont les réserves sont plus grandes. Chez les mammifères, la dépense énergétique des femelles pour la gestation et la lactation peut excéder celle relativement faible des mâles pour la production de sperme. Ainsi, si les dépenses énergétiques liées à la reproduction sont plus élevées chez les femelles que chez les mâles, les femelles gestantes ou lactantes seront probablement plus enclines que les mâles à compromettre leur sécurité pour une meilleure alimentation. Nous avons donc évalué l'utilisation de parcelles d'alimentation sécuritaires et risquées par des campagnols des champs mâles et femelles en utilisant des habitats censés être soit sécuritaires ou risqués. Nous avons aussi effectué des tests comportementaux pour évaluer si des différences de personnalité reliées au sexe pourraient entraîner une utilisation différente des parcelles. Tous les campagnols ont préféré s'alimenter dans des parcelles sécuritaires plutôt que risquées. Il n'y avait aucune différence entre les sexes ou entre des individus reproducteurs ou non dans leur utilisation de parcelles d'alimentation sécuritaires ou risquées. La personnalité n'avait pas non plus d'effet sur le choix du type de parcelle. Ces résultats sont compatibles avec des études récentes sur d'autres espèces qui n'ont pas trouvé de différence entre les sexes dans les dépenses énergétiques liées à la reproduction. Des expériences sur le comportement de quête alimentaire peuvent donc constituer des tests simples qu'il est possible de répéter dans le but d'évaluer les différences et ressemblances entre les sexes dans les dépenses liées à la reproduction.

**Mots-clés:** coût de la reproduction, densité résiduelle de ressources (GUD), *Microtus pennsylvanicus*, personnalité, risque de prédation, temps passé dans la parcelle, théorie de la quête optimale de nourriture.

**Nomenclature:** Linnaeus, 1753; Duchesne, 1766; Aiton, 1789; Lambert, Bauer & Don, 1803; Palisot de Beauvois, 1812; Ord, 1815.

## Introduction

Foragers exploiting resource patches that differ in predation risk face an inevitable trade-off between securing food and avoiding predation (Gilliam & Fraser, 1987; Brown, 1988; Lima & Dill, 1990; and many others). Such foragers use strategic behavioural adaptations to deal with the trade-off, such as preferentially foraging in safe *versus* risky patches (Brown, 1988; 1992; 1999; Kotler *et al.*, 2002; Kotler, Brown & Bouskila, 2004; Morris, 2009) and habitats (Gilliam & Fraser, 1987), and increasing apprehension

and vigilance during risky periods (Kotler *et al.*, 2002; 2010) or while exploiting risky patches (Dall, Kotler & Bouskila, 2001; Kotler *et al.*, 2002). Each strategy depends on the forager's energetic and life-history state (Brown, 1988; 1992; Brown & Kotler, 2004). Organisms in a lower energetic state (*i.e.*, lower energy reserves or higher energetic requirements) should accept more risk than organisms in a higher energetic state (Brown & Kotler, 2004; Berger-Tal *et al.*, 2009). Organisms in different life-history states (*i.e.*, juvenile *versus* adult) have different future fitness expectations, and are thus also willing to accept different amounts of risk when obtaining energy (Brown & Kotler, 2004; Wolf *et al.*, 2007).

Less is known about sex-based differences in the trade-off between food and safety, and how foraging strategy

<sup>1</sup> Rec. 2014-04-08; acc. 2014-07-14.

Associate Editor: Dennis L. Murray.

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DOI 10.2980/21-1-3689

varies with reproductive state. Female rodents, for example, face high energetic costs of gestation and lactation during the breeding season (Millar, 1977; 1978; Innes & Millar, 1981; Johnson, Thomson & Speakman, 2001; Morris & MacEachern, 2010) that often restrict their activities to small foraging territories (*e.g.*, Madison, 1980; 1985). Males may accrue lower direct costs of reproduction (*e.g.*, cost of sperm relative to eggs), but nevertheless expend prodigious amounts of energy competing with other males, defending territories, and travelling through large home ranges in search of receptive females (Madison, 1980; 1985; Wolff, 1985). We explore how state might alter foraging decisions between the sexes and then test the predictions with controlled field experiments on male and female meadow voles (*Microtus pennsylvanicus*).

#### STATE-DEPENDENT PATCH USE

Optimally foraging individuals should discontinue foraging in patches when the fitness gain from foraging equals the fitness costs (*e.g.*, Brown, 1988). Accordingly, researchers can use the food remaining in a patch (the giving-up density, GUD) to estimate the forager's quitting-harvest rate and thus the metabolic, predation, and missed opportunities costs of foraging (Brown, 1988; 1992). Giving-up densities increase with increasing costs. The theory has been confirmed repeatedly by studies focused on the trade-off between food and safety; GUDs are consistently higher in risky patches than in safe patches (Brown, 1988; 1992; Brown, Morgan & Dow, 1992; Kotler & Blaustein, 1995; Brown, 1999; Brown & Kotler, 2004; Verdolin, 2006; Halliday & Morris, 2013).

Although an individual's GUD represents an appropriate payoff obtained by foragers maximizing harvest rates (Brown, 1988), it is difficult to measure in the field, and especially so if multiple foragers use the same patch. Fortunately, GUD is closely related to another, more easily estimated foraging metric, patch-residence time (PRT). PRT is estimated using Holling's (1959) disc equation:

$$\text{PRT} = (1 - \alpha^{-1}) \cdot \ln(N_0 \cdot N_f^{-1}) + h(N_0 - N_f) \quad [1]$$

where  $\alpha$  is the instantaneous search rate,  $N_0$  is initial food density,  $N_f$  is final food density after foraging (GUD), and  $h$  is the time required to handle and process each food item before resuming search for another (Kotler & Brown, 1990). Assuming that all foragers are equally efficient, the derivative of the amount of food consumed with respect to PRT yields the quitting-harvest rate of the final forager visiting the patch. PRT is thus a reliable indicator of the payoff from foraging, and differences in PRT between safe and risky patches can be used to evaluate the trade-off between food and safety.

Individual foragers with a high valuation of energy (*e.g.*, those in a low energetic state, or those with otherwise high energetic demands) should place a higher premium on consuming food than individuals with a low valuation of energy (Brown, 1988; 1992; Kotler *et al.*, 2010). The mean energetic costs of gestation and lactation by females during the breeding season, for example, may exceed the mean energetic reproductive costs of males (such as searching for mates and competing with other males). If so, then females

would value energy more than males would, and would be expected to forage longer in resource patches (longer PRT), and to forage more equally between safe and risky patches, than males. Individuals using risky patches or habitats can minimize costs either by foraging less (lower GUD and PRT) or foraging longer with more vigilance (*e.g.*, similar GUD but higher PRT; Dall, Kotler & Bouskila, 2001; Kotler *et al.*, 2010). However, individuals with greater energy requirements still need to forage longer, and thus accept more risk, in order to maintain their energetic state than do individuals with lower energy requirements.

#### PERSONALITY AND PATCH USE

Differences in risk-taking behaviours might also yield differences in foraging strategies (*e.g.*, Kurvers *et al.*, 2010; Michelena *et al.*, 2010). If risk-taking behaviour depends on sex, then it could cause or accentuate sex differences in PRTs and GUDs. If, on the other hand, variation in risk taking is high and not linked to sex, then the additional noise associated with risk-related personalities might obscure differences associated with energetic state.

With these concepts in mind, we hypothesize that higher energetic costs cause females to consume more food, and accept more foraging risk, than males. Female voles should thus forage longer and more equally in both safe and risky patches, and predation risk will have less effect on female than male patch use. We also hypothesize that patch use between males and females is associated with underlying sex-related differences in personality that will cause females to forage more in risky patches than males. We test these hypotheses and predictions with 1) a field experiment assessing PRTs of female and male voles foraging in patches and habitats with different levels of predation risk and 2) a test for sex differences in vole personalities.

## Methods

#### STUDY SITE AND SPECIES

We conducted all research in vole-proof enclosures near Thunder Bay, Ontario, Canada (48°19'49"N, 89°47'27"W; NAD83; Lakehead University Habitrón). Enclosures contained more or less evenly spaced 3- to 4-m-tall red and jack pine (*Pinus resinosa*, *P. banksiana*) in an old-field matrix of forbs, including native (*e.g.*, bluejoint [*Calamagrostis canadensis*]) and introduced grasses (*e.g.*, timothy [*Phleum pratense*]), goldenrod (*Solidago* spp.), yarrow (*Achillea millefolium*), dandelion (*Taraxacum officinale*), strawberry (*Fragaria virginiana*), and red clover (*Trifolium pratense*), as well as patches of raspberry (*Rubus idaeus*). Vigorous growth by forbs ensured high abundance of food and cover for meadow voles (*e.g.*, Reich, 1981).

#### FORAGING EXPERIMENT

We used four 25- × 25-m enclosures grouped into 2 pairs of replicates. The 2 enclosures in each pair were connected by a ground-level gate (9.25 cm diameter) that allowed voles to move freely from one enclosure to the other (Figure 1). We placed 4 pairs of circular plastic foraging trays (diameter = 40 cm, depth = 3 cm) containing 8.0 g of whole oats mixed in 1.5 L of sifted silica sand (50–100 grain; 145–254 μm) in each enclosure. Each pair

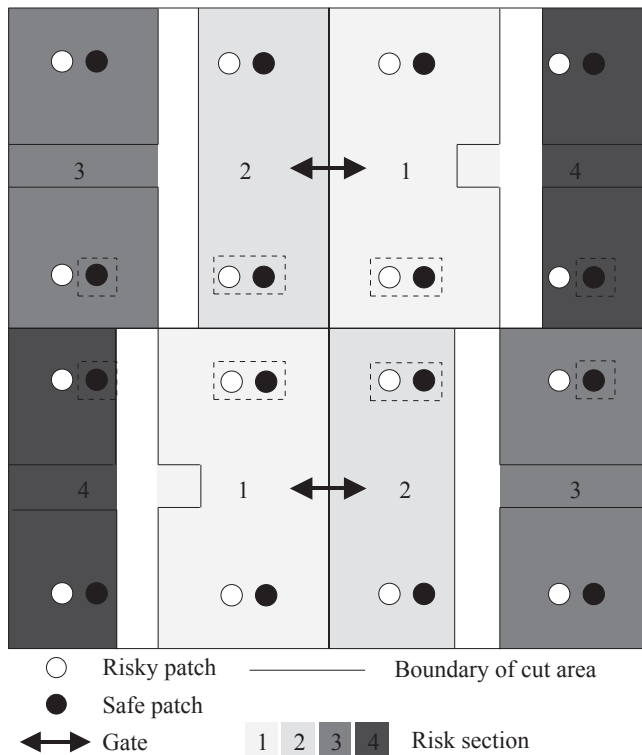


FIGURE 1. A schematic of experimental manipulations assessing patch use of male and female meadow voles at the Lakehead University Habitron in Northern Ontario, Canada. Numbers refer to replicated “sections” within enclosures (shading) varying in cover from highest (1) to lowest (4). Filled and open circles signify covered (safe) and open (risky) foraging trays. Trays within box symbols (dotted lines) were monitored by a radio-frequency identification system, which identified the unique passive integrated transponder within each vole.

consisted of a “safe” tray placed underneath a 60- × 60-cm square plywood cover mounted on top of 10-cm-tall wooden walls (with a 3 cm gap at ground level to allow voles access to the tray while excluding songbirds that would otherwise forage on the oats) as well as a “risky” tray placed under a 60- × 60-cm transparent polycarbonate cover with 10-cm steel supports at each corner. We attached 2- × 2-cm plastic garden mesh to the steel supports of each risky cover to exclude birds from the trays without inhibiting voles from foraging. We used our battery of 12 remote radio frequency identification (RFID) antennae (Vantro Systems, Burnsville, Minnesota, USA), to measure the time that voles with RFID transponders (Trovan 100) spent foraging (PRT) in 3 of the trays within each enclosure (1 pair of safe and risky trays and an additional safe tray; 12 trays in total). Although we could not monitor all trays, foraging voles had access to an equal number of paired safe and risky trays in each enclosure.

We implanted RFID transponders in 26 male and 26 female *Microtus* and placed 13 individuals of each sex in each pair of enclosures on 27 July 2009; each individual of each sex acted as a replicate within each pair of enclosures in a nested design. Juvenile recruitment increased the populations by the end of the experiment to 77 and 41 animals respectively. We assessed reproductive condition before and after the experiment to confirm that

13 of the 26 female voles and 19 of the 26 male voles were reproductively active (females with a perforate vagina, active mammary glands, or distended abdomen indicating pregnancy; males with scrotal or palpable testes). Voles forage throughout the day, so we placed the foraging trays in the enclosures at 18:00 and collected them at 12:00 on the subsequent day. After collection, we sifted uneaten oats from the sand, removed any feces, hulls, and other material from the sample, and weighed the cleaned oats to the nearest 0.01 g (= GUD). We then recharged the trays with seeds before returning them to the enclosures. We repeated this process for 4 d in succession, providing us with 4 estimates of foraging in each tray every 7 d. We separated the 3 “time blocks” (control = week 1, week 2, week 3) by leaving recharged trays in the enclosures for 3 d before the next period of data collection; we did not include these “week-end” data in our analyses. We downloaded PRT data from the RFID recording system periodically, and calculated the total time that each vole spent in each foraging tray during each foraging period (from 18:00 to 12:00 on the following day; 18 h total). Increases in population size through time could influence GUD, but not expected differences in PRT between marked male and female voles.

We modified risk by mowing strips of vegetation (width = 2.5 m, height between 5 and 10 cm) using a weed trimmer in each enclosure 1 week after placing voles in the enclosures (3 August 2009). Our mowing pattern created 4 sections with different amounts of available natural vegetation around each station in each enclosure (Figure 1). We reasoned that the reduction in cover would simultaneously increase the risk in each enclosure and differentially alter risk among the pairs of safe and risky foraging trays in each section. This manipulation of risk would allow us to further assess differences in risk allocation between female and male voles. At least 1 tray in each section was monitored by RFID antennae.

We continued collecting GUD and PRT data for 2 more weeks (until 16 August 2009). In order to analyze the data as a balanced design, we grouped the data by week (sampling from 4 consecutive days) into 3 treatments comprising a control (week 1, uncut vegetation) and 2 experimental time periods (weeks 2 and 3, cut vegetation).

#### PERSONALITY

In a subsequent experiment we quantified the personality of 17 male and 38 female meadow voles live-trapped elsewhere in the Habitron. These voles were all originally captured in the wild or were the first generation offspring of animals living in other enclosures. We released these voles from the live traps 1 at a time into the centre of a 30- × 50-cm plastic hole-board open-field box. We then videorecorded their behaviour for 5 min in order to quantify exploratory behaviour (File & Wardill, 1975; Takeda, Tsuji & Matsumiya, 1998). We introduced a novel object (2.6- × 4.7-cm cylindrical metal “thumb counter”) to the test arena immediately following the 5-min hole-board test and recorded the behaviour of each vole for an additional 5 min. We used the video to quantify 9 variables that we used to summarize the voles’ personalities.



## DATA ANALYSES

We conducted all analyses of the PRT and GUD data with linear mixed effects models in R (pkg: nlme; fcn: lme; Pinheiro *et al.*, 2010). We transformed GUD (square root) and PRT ( $\log_{10}$ ) to meet the assumption of normality and compared competing models using the bias-corrected Akaike's Information Criterion ( $AIC_c$ ) (pkg: qpcR; fcn: AICc; Spiess, 2010). We considered the model with the lowest  $AIC_c$  to be the "best" model as long as the difference in  $AIC_c$  ( $\Delta AIC_c$ ) between models was  $>2$ ; when  $\Delta AIC_c < 2$ , we chose the most parsimonious (fewest parameters) model (Akaike, 1973; Bozdogan, 1987). We confirmed model fit by checking the normality and homogeneity of residuals from the "best" model.

We first analyzed GUD ( $n = 384$ ) to determine if voles consumed more oats from safe than risky patches and if GUDs varied as the amount of risk changed at different scales: fixed effects = patch ( $n = 2$ ), section (areas of vegetation created by cutting vegetation;  $n = 4$ ), treatment (weeks 1–3;  $n = 3$ ), and all two- and three-way interactions among patch, section, and treatment; random effects = station (the location of the patch;  $n = 16$ ) nested within pair (replicate of enclosures;  $n = 2$ ) nested within day (the 18-h foraging period;  $n = 12$ ).

We analyzed PRT (the total time that an individual spent in 1 foraging patch during each 18-h foraging period) to determine if male and female voles allocated their foraging effort differently: fixed effects = sex (male or female;  $n = 2$ ), patch (covered or open), and the interaction between sex and patch; random effects = individual ( $n = 45$ , 1 male was never recorded at trays and was assumed to have perished) nested within station ( $n = 8$ ) nested within pair ( $n = 2$ ) nested within day ( $n = 12$ ). We repeated this analysis using only the 32 animals exhibiting clear evidence of reproductive activity. The analysis using reproductive individuals eliminates the possibility that shared patterns emerging from both analyses were caused by non-reproductive individuals.

We used principal components analysis in R (pkg: psych; fcn: principal; Revelle, 2014) to summarize the personalities of voles according to the variables that we collected during behavioural trials. We compared this

principal components analysis to a second analysis with a varimax rotation.

Two principal components met our criterion of eigenvalues  $>1$ . We calculated the scores and used them as dependent variables in a multivariate analysis of variance (in R, pkg: stats; fcn: aov; R Core Team, 2012; sex = independent variable) in order to determine whether males and females exhibited different personality scores. We removed data for 1 female from this analysis because she was disturbed by the observer during the trial. We repeated the principal components analysis using only females, and again using only males, in order to determine whether the PC axes (personalities) were similar or different between sexes.

## Results

## FORAGING EXPERIMENTS

Voies exhibited patterns in giving-up densities that were more complicated than expected from theory. The final model included the main effects of section, treatment, and patch as well as all two-way interactions (Table I). GUDs were lower in safe than risky patches (mean  $\pm$  SE: GUD in risky =  $4.11 \pm 0.17$  g; mean GUD in safe =  $2.10 \pm 0.17$  g;  $t_{1,189} = 8.2$ ,  $P < 0.0001$ ). GUDs declined as the treatments progressed from the uncut control to the cut vegetation treatments (mean GUD in control [week 1] =  $4.71 \pm 0.23$  g; mean GUD in week 2 treatment =  $2.57 \pm 0.19$  g; mean GUD in week 3 treatment =  $2.03 \pm 0.19$  g;  $t_{1,10} = 3.34$ ,  $P < 0.01$ ), which is the opposite of what was predicted by theory. We interpret this temporal pattern in mean GUD as likely emerging from increased numbers of juveniles foraging in the trays.

Although all two-way interactions were significant (Figure 2a,b), they did not follow the patterns created by the amount of vegetation removed among the sections (Figure 1). Differences between the control and cut vegetation treatments were inconsistent among sections (Figure 2a). For example, mean GUDs were higher in sections 2 and 3 than in sections 1 and 4 during the control period, but this difference disappeared during the 2 cut periods. Mowing the vegetation thus appeared to have greater

TABLE I. Competing models (top) and parameter values of the selected model (bottom) assessing square-root transformed giving-up densities (GUDs) of meadow voles (*Microtus pennsylvanicus*) foraging in safe and risky patches at the Lakehead University Habitron in Northern Ontario, Canada.  $\Delta AIC_c$  = the difference between Akaike's information criterion ( $AIC_c$ ) for the "selected" model (bolded) and alternative models;  $K$  = the number of parameters in each model; patch = safe versus risky foraging tray; treatment = control (week 1) versus cut vegetation (weeks 2 and 3); and section = areas with the least (1) to most (4) cut vegetation.

Model	$K$	$AIC_c$	$\Delta AIC_c$
<b>GUD = patch + section + treatment + patch <math>\times</math> section + patch <math>\times</math> treatment + section <math>\times</math> treatment</b>	<b>10</b>	<b>711.95</b>	<b>0</b>
GUD = patch + section + treatment + patch $\times$ section + patch $\times$ treatment + section $\times$ treatment + patch $\times$ section $\times$ treatment	11	717.27	5.32
GUD = patch + section + treatment	7	735.18	23.23

Parameter	Value (SE)	DF	$T$	$P$
Intercept	2.85 (0.26)	189	11.06	<0.0001
Patch	-0.95 (0.12)	189	8.24	<0.0001
Section	-0.23 (0.07)	178	3.47	<0.001
Treatment	-1.04 (0.31)	10	3.34	<0.01
Patch $\times$ section	0.18 (0.04)	189	4.92	<0.0001
Patch $\times$ treatment	-0.33 (0.09)	189	3.80	<0.001
Section $\times$ treatment	0.17 (0.08)	178	2.26	0.02

effect in some enclosures than it did in others. As predicted by theory, GUDs were lower in safe than risky patches (Figure 2b), and this pattern was consistent across sections.

Patterns were much clearer for patch-residence times. The time that adult voles spent in safe patches was

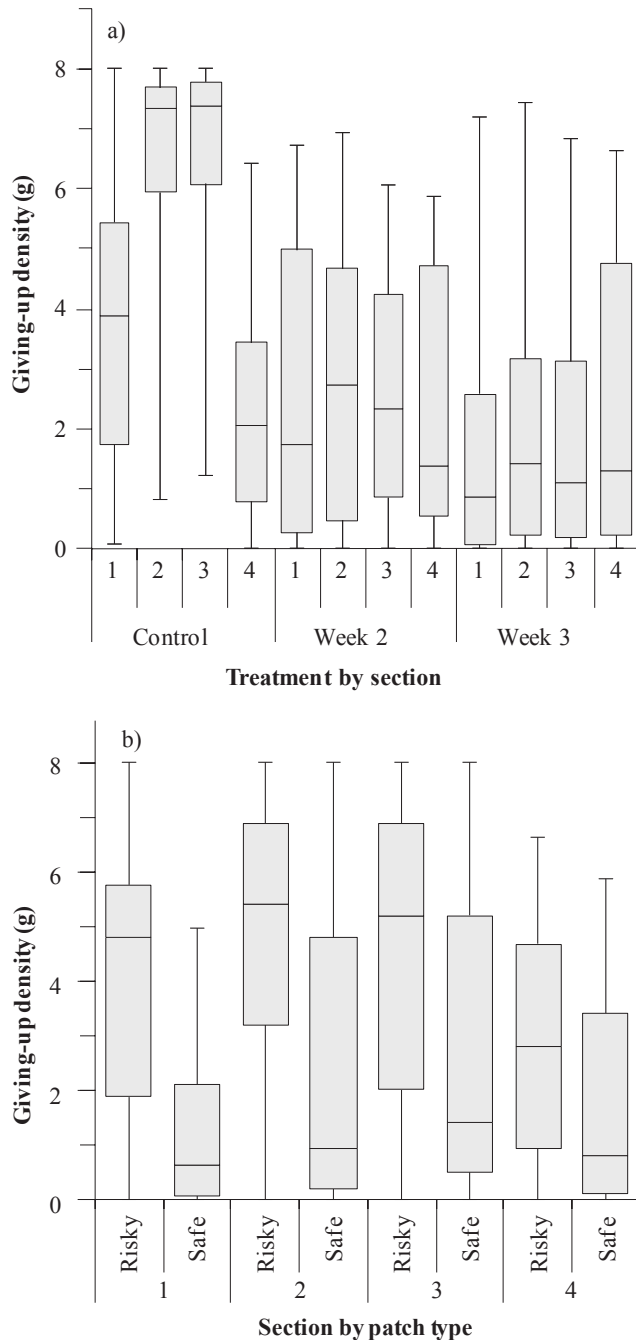


FIGURE 2. Box plots of giving-up densities (GUDs) for meadow voles (*Microtus pennsylvanicus*) foraging in safe and risky patches in enclosures at the Lakehead University Habitron in Northern Ontario, Canada. a) GUDs in 4 sections differing in the amount of available cover (1 = most cover, 4 = least cover) through time (week 1 = control). b) GUDs in safe and risky patches in 4 sections varying in cover (1 = most cover, 4 = least cover). Boxes represent the interquartile range, and the line within the box represents the median value. Whiskers represent the respective minima and maxima.

nearly 3 times greater than in risky patches (Table II; mean PRT in safe =  $834.07 \pm 75.20$  s; mean PRT in risky =  $299.77 \pm 85.38$  s;  $t = 11.01$ ,  $P < 0.0001$ ; Figure 3). There was no apparent difference between sexes in PRT (Figure 3; Table II), although a closely competing and far less parsimonious model included sex, patch, and their interaction (Table II). The pattern with PRT was confirmed when the analysis was restricted to animals known to be reproductively active (Table II). Reproducing males and females preferred safe over risky patches, but there was no difference in patch choice between sexes. There were no competing models (Table II), which suggests that the effect of patch and its interaction with sex, in our first analysis of sexual differences in PRT, was not associated with any potential differences in reproductive costs.

PERSONALITY

Two principal components (PCs) accounted for 68% of the shared variance among the behavioural variables (Table III). The first component represented a cline from latent and indifferent individuals (negative loadings on number of grooms, time to approach the novel object, and time to head dip; positive loadings on rears, lines crossed, head dips, tubes examined, and time spent at the novel object) to the opposite of active and curious animals. PC2 varied along a gradient from courageous (negative loadings on head dips, tubes examined) to fearful animals (strong positive loading on time taken to peer into holes; Table III). The solution was not improved by varimax rotation. There was no significant difference in either personality axis between males and females (PC1:  $F_{1, 54} = 2.45$ ,  $P = 0.12$ ; PC2:  $F_{1, 54} = 1.18$ ,  $P = 0.28$ ). The absence of differences between sexes was confirmed when we analyzed male and female behaviour separately. All analyses yielded similar PC loadings (Table III).

Discussion

We found no evidence for differences between male and female voles in the trade-off between food and safety. We thus reject both hypotheses; our experiments provided no evidence for differences in patch use by female and male voles, or of innate differences between the sexes in personality traits. There is little doubt, however, that direct and indirect costs of lactation and gestation in small mammals (Millar, 1977; 1978; Innes & Millar, 1981; Johnson, Thomson & Speakman, 2001; Speakman, 2008) magnify the valuation of energy by female rodents. High energy valuation by female meadow voles is consistent with their rapid switch from habitat with depleted resources to one in which resource abundance was augmented (Morris & MacEachern, 2010). What has been less apparent, however, is whether suspected differences in reproductive costs between the sexes are associated with differential foraging in safe versus risky patches. On this point our data are clear. Female and male voles did not differ in their mean use of safe versus risky patches even though safe patches were foraged much longer, and their resources depleted more completely, than were risky ones. We interpret this result as indirect evidence supporting roughly equivalent valuations of energy for male and female meadow voles.

TABLE II. Competing models (top) and the parameter values of the selected model (second) assessing  $\log_{10}$ -transformed patch residence times (PRTs + 1) of male and female meadow voles (*Microtus pennsylvanicus*) foraging in safe and risky patches at the Lakehead University Habitron in Northern Ontario, Canada. The same final model for the subset of voles that were confirmed to be reproductively active during the experiment is displayed at the bottom of the table, and was similarly selected using  $AIC_c$ .  $\Delta AIC_c$  = the difference between Akaike’s information criterion ( $AIC_c$ ) for the “selected” model (bolded) and every other model;  $K$  = the number of parameters in each model; patch = safe versus risky foraging tray; sex = male or female forager; and treatment = control (week 1) versus cut vegetation (weeks 2 and 3). \* represents a competing but less parsimonious model.

Model	$K$	$AIC_c$	$\Delta AIC_c$	
<b>PRT = patch</b>	<b>7</b>	<b>1792.74</b>	<b>0</b>	
PRT = sex + patch + sex × patch	9	1792.10	-0.54*	
PRT = sex + patch	8	1796.76	4.02	
PRT = sex + patch + treatment + sex × patch + sex × treatment + patch × treatment + sex × patch × treatment	13	1805.50	12.76	
Parameter	Value (SE)	df	$T$	$P$
Intercept	2.16 (0.06)	354	34.38	<0.0001
Patch	0.69 (0.06)	259	11.01	<0.0001
Model	$K$	$AIC_c$	$\Delta AIC_c$	
<b>PRT = patch</b>	<b>7</b>	<b>1153.43</b>	<b>0</b>	
PRT = sex + patch + sex × patch	9	1156.25	2.82	
PRT = sex + patch	8	1157.33	3.90	
PRT = sex + patch + treatment + sex × patch + sex × treatment + patch × treatment + sex × patch × treatment	13	1172.74	19.31	
Parameter	Value (SE)	df	$T$	$P$
Intercept	2.06 (0.07)	220	31.11	<0.0001
Patch	0.62 (0.08)	169	8.20	<0.0001

Similar valuations of energy between males and females, and consequent similarities in foraging strategies, could emerge if many of our monitored animals were not reproducing during the study. Such an effect cannot account for the absence of differences in risk assessment between males and females when we restricted the analysis to only those animals in obvious reproductive condition. Although we caution against over-interpreting these results, and recommend using only reproductively active animals in future tests, our data are nevertheless intriguingly consistent with recent literature documenting similar energetic costs of reproduction between free-ranging male and female mammals. Energy expenditure by male red squirrels measured by doubly labeled water during the reproductive season is approximately equal to that of reproducing females ( $2.2 \times$  resting metabolic rate; Lane *et al.*, 2010). We speculate, therefore, that one might be able to replace the expensive, time-consuming, and demanding logistics of estimating reproductive costs with the doubly labeled water technique by using simpler estimates based on foraging theory. It would be particularly interesting, for example, to evaluate whether the GUDs and PRTs of male and female red squirrels would be similar if they were given an opportunity to forage in safe and risky patches during the reproductive season.

The clear patterns in PRT, which demonstrate that females and males forage similarly and that all individuals forage longer in safe than risky patches, reflect the main pattern in GUDs. GUDs were lower in safe than risky patches. The voles thus appeared to use the increased patch residence time to remove more resources from the patches

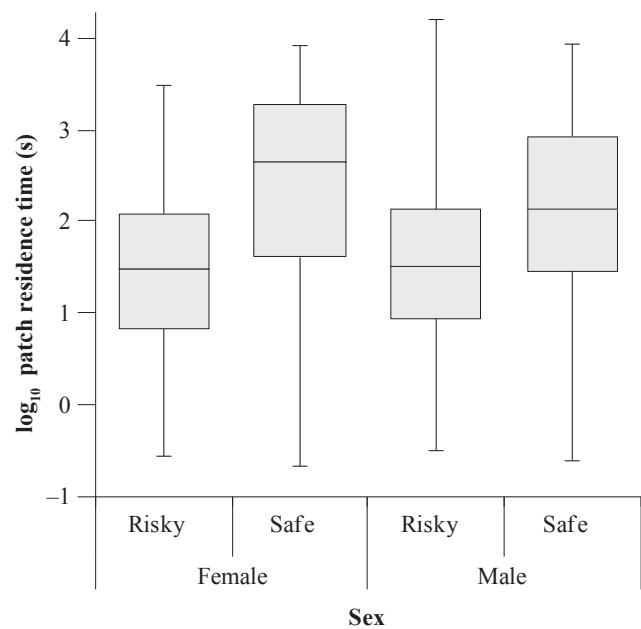


FIGURE 3. Mean patch residence times ( $\log_{10}$ -transformed PRTs) of male and female meadow voles (*Microtus pennsylvanicus*) foraging in safe and risky patches at the Lakehead University Habitron in Northern Ontario, Canada. Boxes represent the interquartile range, and the line within the box represents the median value. Whiskers represent the minima and maxima.

rather than increase vigilance. We do not currently know whether the apparent absence of increased vigilance is characteristic of meadow voles or occurred because vigilance was ineffective under the conditions of our experiment.

Table III. Principal component loadings of 9 behavioural variables quantified on all 17 male and 37 female meadow voles (*Microtus pennsylvanicus*) in a hole-board test and a novel object test, and the same analysis based on only females and only males.

Variable	Description	All		Female		Male	
		PC1	PC2	PC1	PC2	PC1	PC2
Rears	Number of times the vole moved both of its forefeet off the ground.	0.79	0.47	0.79	0.50	0.79	0.42
Interior lines	Number of grid lines crossed on the interior of the arena in 5 minutes.	0.78	-0.11	0.85	-0.24	0.68	-0.02
Head dips	Number of times the vole's head completely entered the tubes in the holes-board test.	0.75	-0.43	0.82	-0.42	0.63	-0.49
Tubes examined	Number of tubes examined in the hole-board test.	0.75	-0.40	0.81	-0.20	0.64	-0.63
Perimeter lines	Number of grid lines crossed on the perimeter of the arena in 5 minutes.	0.73	0.45	0.66	0.57	0.81	0.37
Time at novel object	Time (s) spent at the novel object.	0.71	-0.03	0.69	-0.16	0.81	0.19
Time to head dip	Time (s) until the first head dip.	-0.35	0.77	-0.27	0.80	-0.50	0.68
Grooms	Number of distinct grooming events.	-0.73	-0.35	-0.78	-0.27	-0.61	-0.42
Time to novel object	Time (s) until the vole reached the novel object.	-0.76	-0.07	-0.70	-0.27	-0.82	-0.02
Proportion of variance explained		0.51	0.17	0.53	0.18	0.50	0.18

The apparent absence of differences in reproductive costs is mirrored by a similar absence of differences in personality. Such an effect is rather crucial to any analysis of foraging differences related to reproductive costs. Contrary to our prediction that differences in personality cause females to accept more risk than males, we found no difference in personality between the sexes. Even so, tests for reproductive costs must necessarily account for innate behavioural differences before concluding that differential valuations of risk are associated with differences in reproductive cost. It is clear that there is much to be learned from assessing habitat and patch use between sexes, and among individuals in different energetic states.

### Acknowledgements

We thank A. Bannister, D. Brazeau, D. Durston, K. McKinnon, S. Moreth, M. Moses, and S. Vijayan for their help during long hours in the Habitron. We are grateful to Canada's Natural Sciences and Engineering Research Council (NSERC) for its continuing support of D. Morris' research program in evolutionary ecology. The Lakehead University Habitron was built with the assistance of the Canada Foundation for Innovation, Ontario Innovation Trust, NSERC, and Buchanan Forest Products Ltd. All work presented here complies with the current laws of Canada. All field methods were approved and certified by Lakehead University's Animal Care Committee, which follows the guidelines of the Canadian Council for Animal Care.

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