

ARTICLE

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Sex-dependent habitat selection modulates risk management by meadow voles

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Abstract

Foraging involves a trade-off between food and safety. Most research into the trade-off invokes safety from predation. But danger and its associated risk arise from multiple causes that cannot be assessed solely with reference to predators. A more complete assessment of risk management requires experimental designs that attempt to modify and measure risks, regardless of the source of danger. I aimed to do so by adding shelter (mulched straw) and time-varying supplemental food (rabbit chow), while measuring foraging behavior and habitat use by a seminatural population of meadow voles. Voles foraged more intensely under safety, recognized least risk when given access to both food and shelter, but altered their risk management through time: management included a novel form of sex-dependent habitat selection in which male–male pairs occupied risky areas without shelter while female–female pairs occupied habitats sheltered by straw. The pattern is consistent with a sex-dependent evolutionary game in which female territoriality and tolerance of other females limit conflict with, and space use by, males. Voles' array of interacting strategies demonstrates that ecologists must be wary of ascribing risk only to predation, and particularly so if experiments are blind to other dangers and processes that alter foraging behavior and habitat selection.

KEYWORDS

foraging, GUD, *Microtus*, predation risk, sexual conflict

INTRODUCTION

“... if experiments are not designed to separate out trait-mediated and predation-mediated effects on dynamics, community ecologists may continue to surmise incorrectly that the important causal driver of food web dynamics is predation ...” (Křivan & Schmitz, 2004).

Numerous biotic and abiotic factors influence survival, reproduction, and dispersal, and thereby the distribution and abundance of organisms. Among these, predation risk and its attendant fear are often invoked to account, indirectly, for many patterns in the behavior of individuals, the dynamics of their populations, and the structure of ecological communities (Abrams, 1984; Blumstein, 2020; Brown et al., 1999; Holt, 1977, 1984;

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Holt & Bonsall, 2017; Laundré et al., 2001; Peacor & Werner, 2000, 2001; Zanette et al., 2011; and numerous others). The presumed importance of predation risk suffers, however, from convincing evidence (Sheriff et al., 2020, but see Allen et al., 2022 and its accompanying appendix) and from studies documenting similar behavioral and foraging responses to intra- (Morris, 2019) and interspecific competitors (Dupuch, Morris, Ale, et al., 2014; Dupuch, Morris, & Halliday, 2014; Halliday & Morris, 2013; Morris, 2009). Competitive effects include injury during aggressive interactions, limited access to resources, breeding sites and mates, and pilferage of cached foods (Dittel & Vander Wall, 2018) that reduce survival and reproductive opportunities. The fitness consequences of such chronic competition are likely to rival those of acute perils in the presence of predators. Interactions, such as those invoked in predation-risk-mediated decisions on scatter hoarding (Leaver et al., 2016; Steele et al., 2015) further blur the distinctions between risks attributed to predators and those associated with competing individuals and species.

Managing such risks is bound to vary with features such as an organism's age, sex, reproductive history, and physical condition. In particular, sex-dependent risks, including the necessity to compensate for differences in reproductive costs, are often higher for females than for males and help to account for strategies by which males in polygynous or polygamous mating systems gain access to mates (Boonstra et al., 1993; Emlen & Oring, 1977; Ims, 1988; Ostfeld, 1987; and many more). Additional examples include male harassment (e.g., Darden & Croft, 2008; Morris & MacEachern, 2010a), and in many species of mammals, including the meadow voles (*Microtus pennsylvanicus*) studied here, male-induced infanticide (Webster et al., 1981), feticide, and various forms of pregnancy terminations (the Bruce effect; Bruce, 1959; Clulow & Langford, 1971; Seabloom, 1985; Zippel et al., 2019). It is thus apparent that indirect trait-mediated effects respond to risk writ large, not just to that invoked by predators, and that the responses vary with density, habitat, and interacting strategies of risk management. Implicit in this understanding is the recognition that the adaptive behavior, abundance, and distribution of organisms emerge from a variety of simultaneous evolutionary games, not just that of risk-sensitive foraging. Assessing the outcomes of their correlated, and possibly conflicting, strategies requires field experiments that not only manipulate risk but also assess multiple responses of behavior in addition to those anticipated from species interactions or their proxies.

All biological organisms require resources and space in which to live and reproduce. They also face numerous, and oftentimes mortal, risks while doing so. It should

thus be possible to design experiments that can assess individuals' risk-dependent adaptive foraging and habitat-choice responses. Lakehead University's Habitron in northwestern Ontario, Canada (48°19'49" N, 89°47'27" W [North American Datum 83]) provides such an opportunity. The Habitron is composed of 24 vole-proof enclosures. Several of the enclosures harbor a 20-year-old closed-canopy red pine (*Pinus resinosa*) plantation with a deep litter of fallen needles, and general absence of understory plants, which is inhospitable habitat for meadow voles. Enclosures become habitable in experiments that add suitable food and ground cover for voles, and the habitat becomes heterogeneous when those treatments vary spatially. Quantifying spatial and temporal variance in foraging behavior and habitat use in the context of those experimental interventions enables an assessment of risk management by individual voles.

I begin with a short summary on the use of foraging strategies to infer risk. I briefly describe the field site, its suitability for studies on risk management by meadow voles, and outline the experiment. I detail the analyses and their results, and explore their causal linkages. I conclude by revisiting general principles responsible for trait-mediated indirect effects and their interactions in space and time.

Foraging and risk assessment

Foragers face an inevitable trade-off between the rewards of foraging and its myriad costs. Those costs can conveniently be compartmentalized into metabolism (e.g., the fitness equivalent of energy invested into finding, harvesting and digesting resources), risks of predation (probability of mortality; Lima & Bednekoff, 1999; Lima & Dill, 1990; and many others), and missed opportunities of not engaging in other activities that could otherwise enhance fitness. To the degree that metabolism, predation risk, and missed opportunities incorporate all foraging costs, an energy-maximizing individual should forage whenever the fitness thus accrued exceeds its costs, which is until

$$\text{QHR} = C + \frac{\mu F}{\frac{\partial F}{\partial e}} + \frac{\phi_t}{p \left(\frac{\partial F}{\partial e} \right)},$$

where QHR is a forager's quitting harvest rate in a resource patch, C is the metabolic cost of foraging, μ is the instantaneous probability of being killed by a predator while in the patch, F represents the fitness gained by surviving predation during the foraging period, p is the probability of survival while foraging, ϕ_t is the marginal fitness accrued by time that could be spent in

nonforaging activities, e is the net energy gain from foraging, and $\partial F/\partial e$ equates with the marginal value of energy in terms of fitness (Brown, 1988, 1992; Brown & Kotler, 2004). The equation is most often written in shorthand form

$$H = C + P + \text{MOC},$$

where H is harvest rate, P represents the cost of predation, and MOC corresponds with missed opportunities (Brown, 1988; Brown et al., 1994).

The theory is commonly tested by estimating the foraging efficiency of the final forager visiting depletable safe (often covered) versus risky (open) patches by the so-called giving-up density (GUD), a measure of the resources the forager leaves behind after foraging (Brown et al., 1994). GUDs will be higher in open patches if they are riskier than sheltered ones.

The model implicitly assumes a single foraging individual that faces no competition for its time or resources while in the patch (but competition can be estimated by assessing GUDs in the presence vs. absence of competitors). Such situations may be rare in natural settings where multiple intraspecific and interspecific competitors are likely to vie for the same resources. Experiments with voles, and another with snowshoe hares, are uniquely informative of each type of competitive effect. When offered a choice between safe covered trays versus those that were open and risky, *Myodes gapperi* foraged more intensely in the safe trays when its competitor, *M. pennsylvanicus*, was present, than when it was absent (Morris, 2009). Subsequent experiments that monitored foraging by individually marked voles confirmed the result. *Myodes*' GUDs under cover were more likely to be low when many *Microtus* were nearby than when few *Microtus* were in the area (Halliday & Morris, 2013). Dominant *Microtus* caused subordinate *Myodes* to forage more apprehensively in open risky patches.

Intraspecific competition can also reduce foraging efficiency. Winter-foraging snowshoe hares used vigilance to manage risks from both predators and competing hares (Morris, 2019). Vigilance reduces foraging efficiency that increases the forager's GUD. Thus, unless one is certain that competition (including intraspecific conflict over reproduction) has no influence on foraging behaviors attributed to predators, a parsimonious shorthand of Brown's (1988, 1992) model is to assume that

$$H = C + R + \text{MOC},$$

where R represents the marginal costs of all risks that a forager encounters while exploiting the patch. The GUD nevertheless remains a valid metric of foraging costs and their attribution to patches varying in risk and reward.

Do differences in harvest rates and GUDs translate into differences in fitness? Yes, at least for white-footed mice in southern Ontario. Long-term studies of their density-dependent habitat selection documented higher fitness in forest interior than in edge habitats. And, consistent with theory, the rodents' GUDs were higher (higher quitting harvest rates), as was the difference between safe and risky patches, in edge habitat (Morris & Davidson, 2000).

Time allocation, such as that given to foraging in safe versus risky patches, is only one of several mechanisms that foragers can use to manage risk. Other common mechanisms are apprehension (including vigilance), foraging tenacity (the ability to maintain profitable foraging under risk), and habitat selection (Brown & Kotler, 2004). Each depends on the energetic state of the forager, as does the value of missed opportunities to engage in other activities (Brown, 1988). Any successful attempt to evaluate a forager's strategy of risk management must thus incorporate potential for changes in energetic states, missed opportunities, and risk while being cognizant of the potential for each mechanism to interact with others.

METHODS

General design

Success in testing the theory requires several crucial design elements. These include abilities to (1) vary resource densities (influences state and MOC); (2) alter risks among foraging sites; (3) assess foraging in safe and risky patches; (4) evaluate habitat choice; and to do so (5) under natural conditions of predation and competition.

Study system

I conducted the experiment in one of the Habitron's smaller (25 × 25 m) enclosures during August 2021. The enclosure's closed-canopy red pine plantation shaded the needle-carpeted litter that was mostly devoid of forest-floor and understory plants. A few scraggly shrubs (e.g., *Cornus stolonifera*) persisted in ephemeral sunspots along the enclosure's 0.75 m high sheet-metal fences. Gates between enclosures were closed and the fences were buried to a depth of 0.5 m. The fences were impervious to voles and no vole entered or departed from the enclosure during the 18 days of the experiment.

Meadow voles are small, approximately 35-g, nonhibernating rodent herbivores whose high allometric metabolism implicates energy-maximizing foragers. Under normal conditions, vole diets consist primarily of

monocotyledon and dicotyledon plants with variable quantities of roots and fungi (Lindroth & Batzli, 1984). When available, meadow voles readily forage for seeds, including those embedded in artificial foraging trays. Voles construct well-traveled runways either on the surface of the ground in dense vegetation or within deep litter such as that provided by falling leaves and plant debris.

Design specifics

I partitioned the enclosure into four quadrants centered on its 12.5-m grid of permanent sampling stations and randomly allocated them to four treatments (Figure 1). I scattered mulch from six loosened bales of straw (radius ≈ 5 m) to reduce risk at two stations (Appendix S1: Figures S1 and S2; cover manipulations at larger spatial scales with straw modify population dynamics [Taitt & Krebs, 1983] and with hay, changes in small-mammal communities [Kotler et al., 1988]). One of these received

supplemental food (food with straw cover, FC); the other did not (no food with straw cover, NFC). One of the remaining stations received only supplemental food (food with no straw cover, FNC), and the remaining station served as a control (no food and no straw cover, NFNC).

I placed a pair of circular plastic foraging trays on top of 40-cm square plywood bases separated by approximately 2 m at each station then covered them with (60 × 60 × 15 cm tall) shelters to protect the trays from rain and wind. I randomly allocated a plywood (safe) and clear polyethylene (risky) lid to each pair of wooden frames. I created depleting resource patches by thoroughly mixing 8 g of whole oats in 1.5 L of sieved silica sand. Voles readily forage in the patches and their preferential exploitation of the safe patches reveals differences in the tray's foraging risks (e.g., Morris, 2020). A 2.5-cm wire mesh along the bottom margins of the shelters provided unobstructed entrance and egress by voles while excluding any larger competitors (such as red squirrels [*Tamiasciurus hudsonicus*] or chipmunks

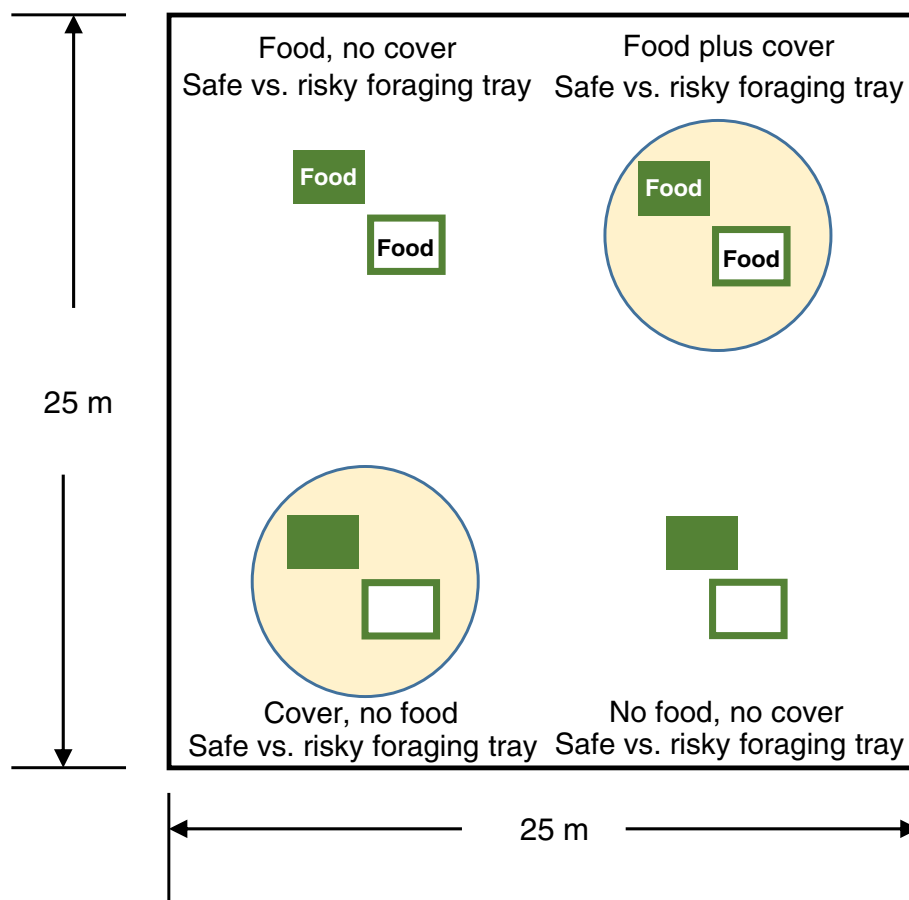


FIGURE 1 Illustration of the spatial design of a controlled field experiment assessing risk management by meadow voles (*Microtus pennsylvanicus*) in northern Ontario, Canada. Circles correspond with additional shelter provided by mulched straw, rectangles represent either safe plywood-covered foraging (green fill) trays or risky clear polyethylene-covered trays (no fill) that either were supplemented with extra food (Food) or not.

[*Tamias sciurus*]) and mustelid predators. I placed a small 9×20 cm hollowed wooden feeder on each side of the foraging trays (Appendix S1: Figures S3 and S4) and filled a 5 cm diameter \times 3 cm tall circular plastic dish with fresh water at each station.

I used the calculations in Morris and MacEachern (2010b) and Morris (2014), plus the energy content of commercial rabbit chow, to determine an adult vole's expected daily requirements if consuming only chow (6.24 g) or oats (7.07 g). I released adult voles in the center of the enclosure as they became available through weekly live trapping in nearby habitats (two males and two females on 2 August, two of each sex on 9 August). I ensured that the newly released voles would have sufficient chow by broadcasting 99.8 g of chow (5-m radius) at the two supplemental feeding stations prior to releasing voles. The broadcast pellets of chow during this training period quickly expanded and decomposed in the moist forest litter and were thus unavailable during the experiment. I filled the feeders at the food-supplemented stations with 49.9 g of chow (=199.6 g per station, sufficient for all voles to forage under a single shelter for two days) on 2 August and simultaneously placed foraging trays with oats under all shelters. I collected and replaced chow in the feeders every two days when I collected (13:30) the foraging trays, renewed the voles' drinking water, cleaned and weighed the uneaten oats (=GUDs), then recharged and returned the trays 1 h later (trays were available for foraging for 47-h intervals).

Voies were using all foraging trays when I increased the chow to 99.8 g per feeder and initiated the experiment on 14 August. This treatment enabled more than sufficient food to support all voles at a single feeder. Doing so eliminated the quantity of supplemental food as a determinant of habitat preference. Voies ate relatively small amounts of chow from feeders (maximum = 6.01 g) so I reduced the chow to 49.9 g on 18 August, then ceased supplemental feeding entirely on 22 August (reduced missed opportunities associated with foraging on "free" food). I placed eight freshly baited Longworth traps under aluminum covers at each station on the evening of 30 August, checked them at first light the following day, replaced closed traps with new ones, checked them again at mid-day, and collected all traps in the late afternoon. I failed to capture one of the voies, so I repeated the trapping procedure on 3 September.

Statistical analyses

The design included repeated measurements of GUDs at each treatment station but lacked the replication of treatments required to assess between-subject effects. I nevertheless accounted for the repeat measures in two ways.

First, I used the difference in GUDs between safe and risky trays in a one-sample *t* test to confirm that voles recognized differences in risk between them (difference >0). Next, I used the difference as the dependent variable in a general linear model (GLM) assessing differences and interactions among treatments and between the food versus no-food supplements. Using the difference in GUDs ensured a paired design such that the differences fully represented between-treatment effects. Second, I divided the presence and absence of food separately into two groupings of four equal time periods (each corresponding to one 2-day foraging interval) and included time period as a covariate in the GLM. The covariate accounted for within-treatment effects. I completed the analysis of GUDs with a Kolmogorov–Smirnov test assessing whether the model's residuals departed from a normal distribution. Analyses were conducted with MINITAB version 20 software. Data figures were completed by copying values into MS Excel or from raw data with IBM SPSS Statistics version 28.

RESULTS

Voies foraged for oats and chow

Voies consumed, on average, 26.5 g (± 6.5 SD) of oats during each 47-h foraging period. Consumption of rabbit chow over 47 h was far less (maximum = 6 g; 0.9 ± 1.6 g; mean \pm SD) but estimates of the mass eaten was compromised by absorption of moisture (maximum known gain in mass from an untouched 49.9 g tray = 0.83 g [1.7%]). Even so, the total measured consumption of oats and chow was insufficient to meet the calculated daily energy requirements of the voies.

Voies preferred to forage under safety

Voies foraged in a way that corresponded with differences in risk between foraging trays ($t = 14.58$, $p < 0.001$). All differences exceeded the null hypothesis of zero.

Risk was lowest in the food plus shelter treatment

The GLM analysis accounted for nearly 60% ($R^2_{\text{adj}} = 0.59$) of the experimental variance and revealed a clear treatment effect ($F_{3,31} = 3.54$, $p = 0.034$; Table 1). Risk, as measured by the difference in GUDs, was significantly different from (lower) the overall mean only in the food plus straw (FC) treatment ($t = -3.14$, $p = 0.005$; Figure 2).

Risk was also high when supplemental food was absent

The presence versus absence of rabbit chow had a highly significant effect on the difference in GUDs ($F_{1,31} = 12.37$, $p = 0.002$; Table 1). Risk (difference in GUDs) was low

TABLE 1 Results of a general linear model assessing a controlled field experiment on risk management by meadow voles (*Microtus pennsylvanicus*) in northern Ontario, Canada.

Source	df	F	p
Time (covariate)	1	0.73	0.40
Treatment (food and risk)	3	3.54	0.034
Food (risk and MOC)	1	12.37	0.002
Time × treatment	3	2.21	0.12
Time × food	1	4.53	0.047
Treatment × food	3	0.43	0.73
Error	19		
Total	31		

Note: The dependent variable is the difference in giving-up densities between risky and safe foraging trays; treatment is the presence/absence of supplemental food and shelter (mulched straw); food is the presence/absence of supplemental rabbit chow. Statistically significant outcomes appear in boldface. $N = 32$, $R^2_{\text{adj}} = 0.59$. Abbreviation: MOC, missed opportunities.

when supplemental food was present and high when it was absent (Figure 3).

The time course of risk varied with the presence versus absence of supplemental food

The interaction between treatment and the presence versus absence of chow was also statistically significant ($F_{1,31} = 4.53$, $p = 0.047$; Table 1). During the time when supplemental food was added, risk that was low initially increased afterwards. Intriguingly, the opposite pattern, high in the first time period and lower in the last, occurred during the period when supplemental food was absent (Figure 4), but the effect of time alone was nonsignificant (Table 1).

There was no consistent decline in vole body mass

I compared the body mass of voles when they were introduced into the enclosure with their mass at the end of the experiment. There was no change in the mass of two voles, three “lost” only 1 g, and two gained a total of 7 g. There was one outlier: a large and presumably old male that lost 10 g (27%; Appendix S2).

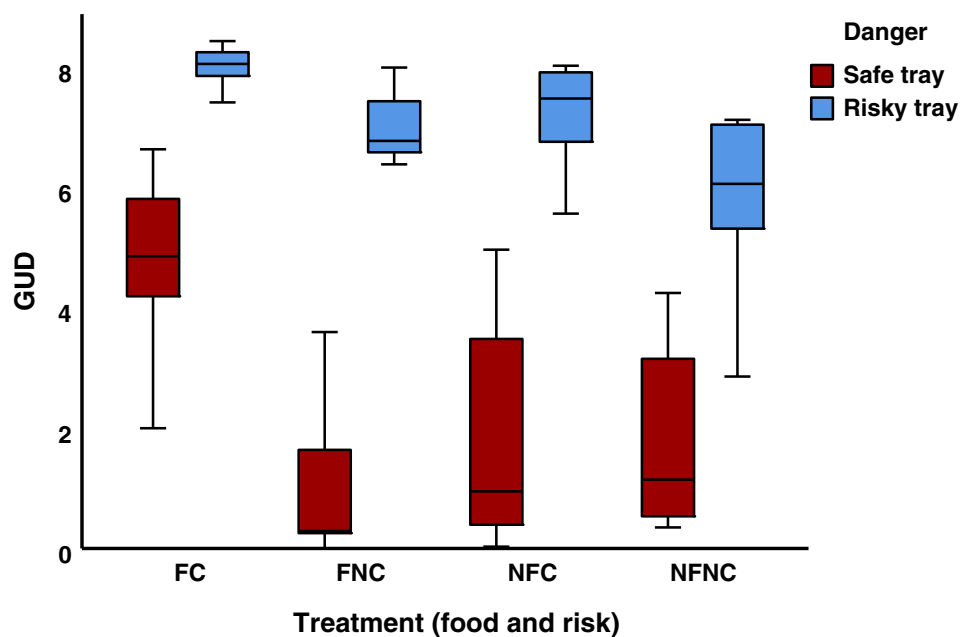


FIGURE 2 Meadow voles (*Microtus pennsylvanicus*) deemed the supplemental food with shelter (FC) treatment as less risky (difference in giving-up density [GUD] between risky and safe food patches) than all other treatments. Analysis based on paired comparisons, not mean responses as illustrated here. Boxes correspond to 25%–75% quartiles; horizontal lines, medians; and whiskers, range (1.5 times the interquartile distance). FC, rabbit chow plus straw cover; FNC, rabbit chow without straw cover; NFC, no rabbit chow with straw cover; NFNC, no rabbit chow and no straw cover.

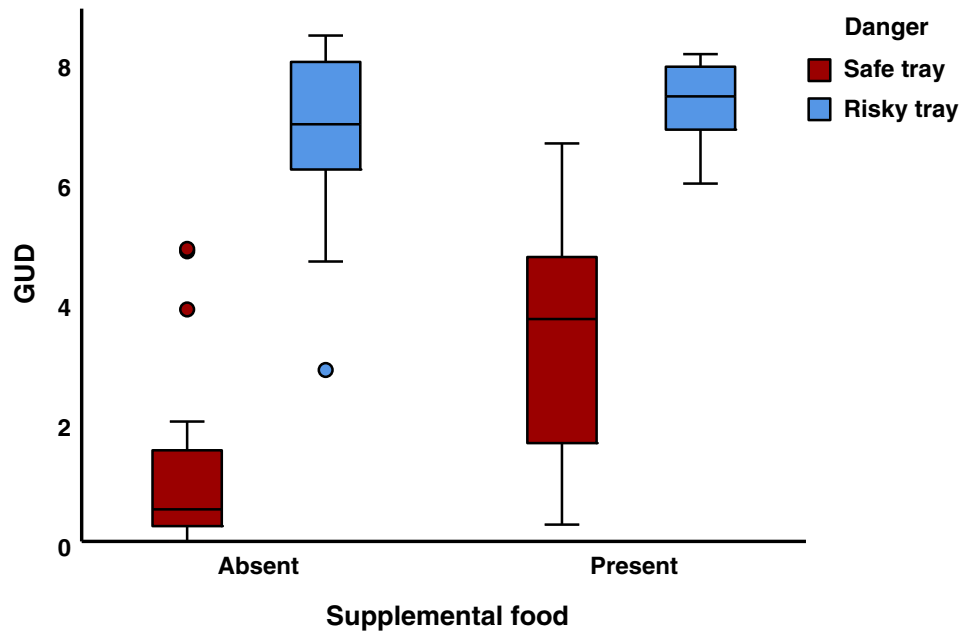


FIGURE 3 The assessment of risk (difference in giving-up density [GUD]) revealed by meadow voles (*Microtus pennsylvanicus*) foraging in risky versus safe food trays was low when supplemental food (rabbit chow) was present, and was high when supplemental food was absent. Boxes correspond to 25%–75% quartiles; horizontal lines, medians; whiskers, range (1.5 times the interquartile distance), and circles to data points \pm 1.5–3 times the interquartile distance. Analysis based on paired comparisons, not mean responses as illustrated here.

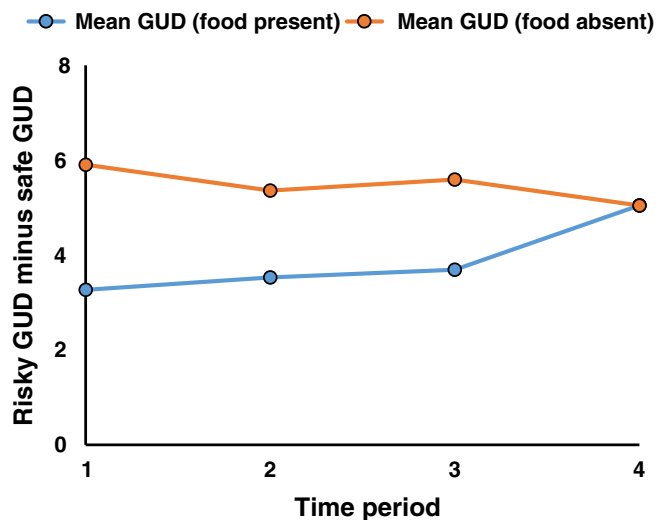


FIGURE 4 Meadow voles' (*Microtus pennsylvanicus*) assessment of risk (difference in giving-up density [GUD] between risky and safe food patches) in the presence versus absence of supplemental food (rabbit chow) depended on time since food was either added or removed. Time periods are sequential from when food was added (bottom) versus removed (top). Analysis based on paired comparisons, not mean responses as illustrated here.

Voles were distributed equally among stations but in same-sex pairs

Seven of the eight (three females and four males) voles were captured during the first live-trapping session. Six of

these were moved to another Habitron enclosure; one lactating female was released at her capture site. That female (recaptured at the same station) and the eighth vole (also a lactating female) were captured during the second round of trapping. A single deer mouse (*Peromyscus maniculatus*) was also captured overnight, and again at noon, during the second round. The mouse appeared unfamiliar with its surroundings and moved gingerly away from the trap on release. It is thus highly likely that it had only recently entered the enclosure and had no effect on the experiment's results. All but two remaining captures (one red squirrel each at a station with straw and another without; squirrels did not access food trays) were meadow voles.

Two voles occupied each station in a clear sex-dependent pattern. Male–male pairs occupied stations lacking cover, whereas female–female pairs occurred at stations with cover. I explored the likelihood of the observed distribution in MINITAB by simulating 1000 separate patterns of distribution, assuming that animals chose stations at random and independent of others. Each simulation shuffled the order of each male and female (sampled eight of eight animals without replacement), then allocated each randomly chosen animal to one of four stations (sampled four stations with replacement). I searched the entire set of simulations to identify those that yielded (1) exactly two animals at each station, (2) two same-sex animals at each station, and (3) female–female pairs at pre-allocated cover versus no-cover stations. Each of these outcomes was significant (28 simulations yielded

exactly two animals at each station; $p = 0.028$) to highly significant departure from random expectation (only 3 of the 28 yielded two animals of the same sex at each station; $p = 0.003$, and only 1 produced the observed pattern of female–female pairs at stations with cover and male–male pairs at stations lacking cover; $p = 0.001$).

DISCUSSION

Experimental treatments manipulating all combinations of supplemental food and shelter elicited clear patterns of risk management by meadow voles. Voles responded by foraging more intensely in safe patches than in risky ones. Their assessment of risk by foraging was lower at stations providing both food and shelter. When supplemental food was no longer present at any station, the voles exploited safe trays more thoroughly. Each of these patterns is fully consistent with existing theory. GUDs balance the combined metabolic, risks, and missed opportunities costs of foraging. When risk is high, the difference in GUDs between risky and safe foraging patches is also high. GUDs should be lower when missed opportunities are lower, as when voles no longer had access to rabbit chow. When risk is low with opportunity to forage freely on rabbit chow, GUDs should be high, but the difference between safe and risky patches is low (Figure 2).

But the experiment also yielded novel results. The voles' assessment of risk increased through time while supplement was being added, jumped to a higher level when supplemental feeding was suspended, and slowly declined afterwards (Figure 4). The pattern appears to represent both a rapid response to dangers associated with changes in resource renewal, followed by a prolonged period of adjustment to those changes. Might the time course correspond with a decrease in energetic state and heightened predation risk (e.g., Brown, 1988; Sinclair & Arcese, 1995)? Theory and observation suggest otherwise. A decline in energetic state increases a forager's valuation of energy and depreciates its assessment of risk. Measurements of foraging risk should have decreased through time, and especially so during the period when supplemental feeding was curtailed. Contrary to the prediction, foraging risk, although high, underwent only a modest decline with the length of time that supplemental food was unavailable. Nor was there any consistent evidence that animals' state declined during the experiment (Appendix S2). Rather, as voles learn that supplemental food is continuously available, their foraging appears to become more risk-averse. When supplemental food is removed, they appear to slowly become less risk-averse in their foraging decisions.

A logical point of departure is to ask whether theories of risk allocation (e.g., Beauchamp & Ruxton, 2011; Bednekoff & Lima, 2011; Creel, 2018; Lima & Bednekoff, 1999) can easily explain these peculiar changes in vole foraging. Animals that encounter long and sustained periods of risk, such as that induced by the absence of straw cover in the vole experiment, should forage more intensely than animals experiencing less risk (e.g., Ferrari et al., 2009; Lima & Bednekoff, 1999). Theories of risk allocation assume, however, that individual animals experience periods of both high (no cover) and low (cover) risks.

Although reasonable at the scale of the vole experiments, the pattern of sex-dependent habitat selection suggests instead that individual voles might have been socially tethered to a single level of risk. Trap-revealed habitat choice at the end of the experiment implies that males foraged under high risk while females foraged with less risk. It is doubtful that this pattern occurred throughout the experiment. All voles were released in the center of the enclosure and most likely visited multiple stations before choosing one over others. They might even have continued to use two or more stations in addition to the station where they were captured. These caveats notwithstanding, the sex-dependent captures must have, at a minimum, revealed centers of activity far different from random expectation.

It thus appears that the voles engaged in an evolutionary game of joint density- and sex-dependent habitat selection (Morris & MacEachern, 2010a). That game was resolved under conditions in which risk (presence vs. absence of straw) at preferred stations was constant through time, but the presence of supplemental food was not. Voles experiencing prolonged periods of supplemental food would normally attain a higher energetic state, forage more apprehensively, and thus allocate less foraging effort (higher GUD) to risky patches than voles in a lower state (Brown, 1988). Such state dependence might explain the apparent gradual increase in risk revealed by the difference in GUDs between risky and safe patches (Figure 4). That pattern would most likely emerge if the majority of animals had access to food supplements before sex-dependent habitat selection emerged later in the experiment. One might wonder, for example, whether the pattern of risk was associated with an apparent decline in male body mass. If so, then risk should have increased. The key point is not whether risk increased through time with food supplementation, and decreased afterward; rather whatever the time-dependent pattern was, it was different while food was supplemented than it was when supplemental food was absent.

These effects alone cannot account for the remarkable pattern of sex-dependent habitat selection. Female voles

track variation in resource abundance more closely than males (Ims, 1988; Lin & Batzli, 2004; Morris & MacEachern, 2010b), but that effect cannot account for the female–female pairing at the no food with straw (NFC) treatment in this experiment. One tantalizing possibility is that density dependence determines the number of voles (2) occupying a station while a game of cooperative and conflicting interests accounts for the apparent spatial distancing of the sexes. Cooperation emerges through the dependence of each sex on the other for successful reproduction. Conflict emerges from females' higher demands for resources, safe nesting sites for dependent offspring, and protection from marauding and potentially infanticidal (including pregnancy disruptions and feticide) males.

The conflict is partially resolved by multiple paternity (Boonstra et al., 1993) that reduces the rewards to males from infanticide in at least two different ways. (1) Infanticidal males risk killing their own progeny and (2) they are unlikely to father all offspring in a subsequent litter. Female *Microtus* typically mate during postpartum estrus (e.g., Keller, 1985). Thus vole infanticide, including pregnancy disruption in meadow voles (Seabloom, 1985; Storey, 1986), followed by induced ovulation from a nonpaternal male (Seabloom, 1985), is likely to provide the male with more mating opportunities than simply biding time while females nurse one litter and gestate another.

Infanticide is clearly detrimental to female fitness. It is thus tempting to speculate whether female–female pairs share mutual interests in reducing sexual conflict by cooperatively repelling nonpaternal males. They should do so only if males threaten current reproduction (lactating and/or pregnant females). Consistent with the speculation, one member of each female pair of voles was lactating. It is also reasonable to assume that the other might have been pregnant. Even so, a more parsimonious interpretation is that the pairings emerge simply from a greater female tolerance for other females (Parker & Lee, 2003) than for males.

Theory (Brown, 1988; Brown et al., 1999; Brown & Kotler, 2004) and example (Allen et al., 2022; Zanette & Clinchy, 2020) demonstrate that fear can manifest changes in neurobiology, physiology, behavior, and population dynamics. Many empirical studies invoke experiments that accentuate “fear,” reminiscent of attempts to measure costs of reproduction by increasing clutch size. Each can assess, indisputably, whether the manipulation induces costs. They may or may not reveal whether phenotypically plastic organisms have optimized their individual abilities to manage costs (e.g., Pettifor et al., 2001). In the case of fear, as clearly demonstrated here, we need to understand the relative success of different causes and

mechanisms that determine trade-offs between foraging versus risk. Only then can we explore their translation into life histories that are the grist of adaptive evolution (e.g., Hutchings, 2021).

Be that as it may, this relatively simple and small-scale experiment suggests that we must exercise considerable caution when ascribing cause and effect to risk-sensitive foraging. Foraging risk emerges from numerous sources in addition to predation. Foragers possess a wide spectrum of proactive and reactive responses to those risks and have a broad repertoire of interacting behavioral, physiological, and cognitive mechanisms to deal with them (Creel, 2018). Habitat selection is a particularly effective proactive mechanism by which foragers can modulate risk (e.g., Bannister & Morris, 2016; Creel et al., 2005; Lima & Dill, 1990; Valeix et al., 2009). It is thus hardly surprising that habitat selection by voles interacts with foraging behavior in ways consistent with adaptive risk management. What is surprising is that relatively few studies appear to have fully integrated adaptive habitat selection with other metrics of risk-sensitive foraging behavior.

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CONFLICT OF INTEREST

The author declares no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available from Borealis (Morris, 2022): <https://doi.org/10.5683/SP3/MNCMIL>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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