



Effect of predation risk on selectivity in heteromyid rodents

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Abstract

Variations in predation risk affect the costs of foraging and may therefore warrant different foraging decisions. One class of models (“higher requisite profit”) predicts that foragers should become more selective when predation risk increases, as low-profitability items that do not cover the increased costs are dropped from the diet. An alternative class of models (“reduced finickiness”) predicts that foragers should become less selective when predation risk increases, because selectivity requires more extensive assessment and/or search behaviour, prolonging exposure to risk. We assessed the selectivity of foraging heteromyid rodents (Merriam’s kangaroo rats, *Dipodomys merriami*, and pocket mice, *Chaetodipus* spp.) by comparing differences in “giving up densities” (GUD: the quantity of cryptic food left in a patch by animals for whom the diminishing marginal gains from foraging have dropped below the threshold for continued search) for foods of different value as a measure of selectivity in patches varying in predation risk. Data collected over two field seasons revealed that heteromyids were more selective when predation risk was highest; away from the protective cover of shrubs during the full moon. These findings support the predictions of higher requisite profit models.

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1. Introduction

If food patches vary in value, an increase in predation risk may lead foragers to be more selective in decisions about where to forage and for how long (e.g. Cerri and Fraser, 1983; Milinski, 1985; Gilliam and Fraser, 1987). This is because food qualities or encounter rates that are sufficient to warrant foraging effort under low predation risk are not profitable enough to cover the prospective fitness costs of exploiting them when risk increases, and the breadth of acceptable diet items or patch densities narrows.

We call such models “higher requisite profit” models. Supportive studies of various species have shown that the presence of either actual predators or predation risk cues such as a lack of protective cover can lead to increased selectivity with respect to the acceptable density of food patches (Milinski and Heller, 1978; Holbrook and Schmitt, 1988), with respect to the acceptable size (and hence the harvest rate) of nutritionally similar foods (Bowers, 1988, 1990), and with respect to the acceptability of seed species that differ in preference ranking (Hay and Fuller, 1981).

Other models, however, predict that foragers will be most selective when predation risk is low and will become relatively indiscriminate as risk rises (Real, 1990; Crowley et al., 1991) because economizing on search and/or assessment can reduce the duration of

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exposure. We call these “reduced finickiness” models, and they have often found support in studies of mate choice (Alatalo et al., 1988; Milinski and Bakker, 1992; Forsgren, 1992; Berglund, 1993; Hedrick and Dill, 1993; Godin and Briggs, 1996). It is perhaps unsurprising that the reduced finickiness model should be especially applicable to mate choice, because the goal in this case is seldom to maximize “consumption”, and increased selectivity would translate rather straightforwardly into increased search time. However, the prediction of reduced selectivity under predation risk has also been supported in some studies of foraging for food in fish (e.g. Cerri and Fraser, 1983; Metcalfe et al., 1987; Ibrahim and Huntingford, 1989).

In the present study, we tested the conflicting predictions of the higher requisite profit and reduced finickiness models by measuring changes in selectivity and foraging effort in relation to changing levels of predation risk, in animals foraging for foods of different nutritional value. The foragers were members of the Heteromyidae family of New World rodents, most species of which are adapted to exist in the arid American southwest. The species of interest in this study are primarily granivorous. They are an ideal family for the study of selectivity under predation risk because they preferentially select and eat seeds high in carbohydrate and low in protein, which produce metabolic water through oxidation (Schmidt-Nielsen, 1964; Price, 1983; Frank, 1988), and because they are sensitive to certain known cues of predation risk while active aboveground (e.g. Price et al., 1984; Daly et al., 1992) and during foraging (e.g. Bowers, 1988, 1990; Kotler, 1984). We measured preference by offering an abundance of two seed types that differed in percent carbohydrate and protein and comparing differences in the amount consumed (Chesson, 1983).

We looked at foraging behaviour by measuring giving up densities (GUDs), a measure that facilitates fine estimation of foraging effort (Brown, 1988). Seeds are mixed into a substrate and left for animals to exploit. As seeds in the trays are depleted, successive seeds are more difficult for foragers to detect, so harvest rate decreases with tray depletion. The seeds remaining in the substrate in a tray after the foragers have ‘given up’ are measured, and that residual amount is called the GUD: the density of seeds at which the utility of foraging was presumably too low to motivate the for-

ager to continue at that patch. GUDs provide a better estimate of foraging effort than that used in previous studies of heteromyid selectivity (e.g. Hay and Fuller, 1981; Bowers, 1988, 1990) which simply placed seeds in petri dishes with no substrate, because this tends to result in animals taking either all or nothing from the pile of seeds since there are no diminishing marginal returns.

Foraging costs for heteromyids increase with night-time illumination. As illumination increases, heteromyid activities shift to the relative safety of microhabitat under the cover of shrubs, presumably in order to minimize risk from visually hunting predators (reviews by Munger et al., 1983; Price and Brown, 1983). However, the costs of foraging under shrubs also appear to vary seasonally due to the fact that, in some areas, some snake species are less active in the winter months. Thus, heteromyids adjust their microhabitat use in ways that appear to reflect changing predation risk (Price, 1978; Bouskila, 1995).

In the present study we measured selectivity by examining changes in the difference of GUDs for the two food types in situations differing in predation risk. This measure is monotonically related to the proportion of the preferred prey in the diet.

2. Materials and methods

2.1. Study site

The study took place at Boyd Deep Canyon Desert Research Station, Palm Desert, California, USA. The scrub-brush habitat of the study site has been described in detail by Zabriskie (1979). A permanent trapping grid, with Sherman traps set at 10 m intervals in a 10 × 10 array was used in this study. The nocturnal rodent population on the study site consisted of four heteromyid species, *Dipodomys merriami*, *Chaetodipus fallax*, *Chaetodipus formosus*, *Chaetodipus penicillatus* and one cricetid species, *Peromyscus eremicus*. Leaver and Daly (2001) found that while heteromyids regularly visit the provisioned seed trays, the omnivorous *P. eremicus* visit very rarely and for short periods. On the basis of this observation, we assumed that *P. eremicus* did not contribute significantly to the data in the present study and they are excluded from further discussion.

2.2. Laboratory preference test

Seed species preferences were tested on ten *D. merriami* (five males, five females), six *C. fallax* (three males, three females), one male *C. formosus* and one female *C. penicillatus*, all of whom were trapped in the wild and held in the field station laboratory for 24 h for testing. Each animal was housed in a plastic 28 cm × 32 cm × 16 cm cage with approximately 3 cm of sand on the bottom, a tin can for shelter, a leaf of lettuce or spinach, and 3 g each of whole oats and lentils.

We predicted that lentils (61.7% carbohydrate, 24.1% protein, 1.1% fat and 33.6 calories/10 g; Price, 1983) would be the less valuable and therefore less preferred seed, while oats (68.3% carbohydrate, 13.3% protein, 7.5% fat and 38.1 calories/10 g; Arrowhead Mills), would be the preferred food due to the fact that they contain higher carbohydrate, lower protein and have higher caloric value.

After 24 h each animal was released at its point of capture and the cage contents were sifted. Oats and lentils were separated and weighed to the nearest 0.1 g in order to determine the amount consumed.

Data were analysed using two-tailed Wilcoxon signed-rank tests.

2.3. GUD trials in the field

Selectivity data were collected over two field seasons: autumn 1997 and autumn 1998. Pairs of plates were placed side by side at stations on the trapping grid. Each station was located at least 25 m from any other station. Each pair consisted of one plate containing 3 g of lentils and one plate containing 3 g of oats (all seeds were killed by microwave to prevent germination) mixed with 400 ml of sand sifted through a sieve with 1 mm openings. Each pair of plates was located in one of two microhabitat types, herein labelled “open” (at least 2 m from the nearest shrub or cactus) or “cover” (directly under the canopy of the nearest shrub or cactus).

Sixteen pairs of plates were positioned each night just before dusk and collected 2 h later. The contents of each dish were sifted and the seeds remaining in the plates were weighed to the nearest 0.01 g. Data were collected in autumn 1997 on nine full moon and seven new moon nights, and in autumn 1998, data

were collected on seven full moon and three new moon nights.

GUDs for oats and lentils were compared using a paired samples *T*-test in order to examine food preferences. A selectivity index was calculated by measuring the difference between the GUDs for lentils and oats (lentil GUD—oat GUD) at each pair of trays. Selectivity data were analysed using a two-way ANOVA (SPSS 10.0.5). Each tray location was treated as a “subject”. Microhabitat and moon phase were the two between-subject factors. Data are reported as means ± standard error (S.E.).

3. Results and discussion

3.1. Laboratory preference test

In accordance with prediction, all the rodents tested exhibited a strong preference for oats over lentils. The 10 kangaroo rats showed a unanimous preference for oats over lentils, consuming an average of 2.7 g oats and 0.3 g lentils (Wilcoxon $T = 0$, $N = 10$, $P < 0.01$). The six *C. fallax* also showed a unanimous preference for oats, consuming an average of 1.98 g versus only 0.44 g of lentils ($T = 0$, $N = 6$, $P < 0.05$). The *C. formosus* and *C. penicillatus* that were tested exhibited the same preference pattern: the former ($N = 1$) consumed 2.66 g of oats and 0.56 g of lentils and the latter ($N = 1$) consumed 2.39 g of oats and 0.20 g of lentils.

3.2. GUD trials

As predicted, GUDs also reflected a preference for oats (0.08 ± 0.02 g) over lentils (0.16 ± 0.03 ; $t_{63} = -4.11$, $P < 0.001$). It may be argued that differences in GUD may simply reflect different harvest rates due to seed size and detectability, but since the lentils are larger, and more detectable (Leaver, 2000), the fact that GUDs were higher for lentils simply serves to reinforce the conclusion that lentils were not a highly preferred food.

In accordance with the predictions of the higher requisite profit models, selectivity was highest in the situation with the highest risk of predation, in the open under the full moon (interaction of moonlight and microhabitat: $F_{1,60} = 4.34$, $P < 0.05$; Fig. 1).

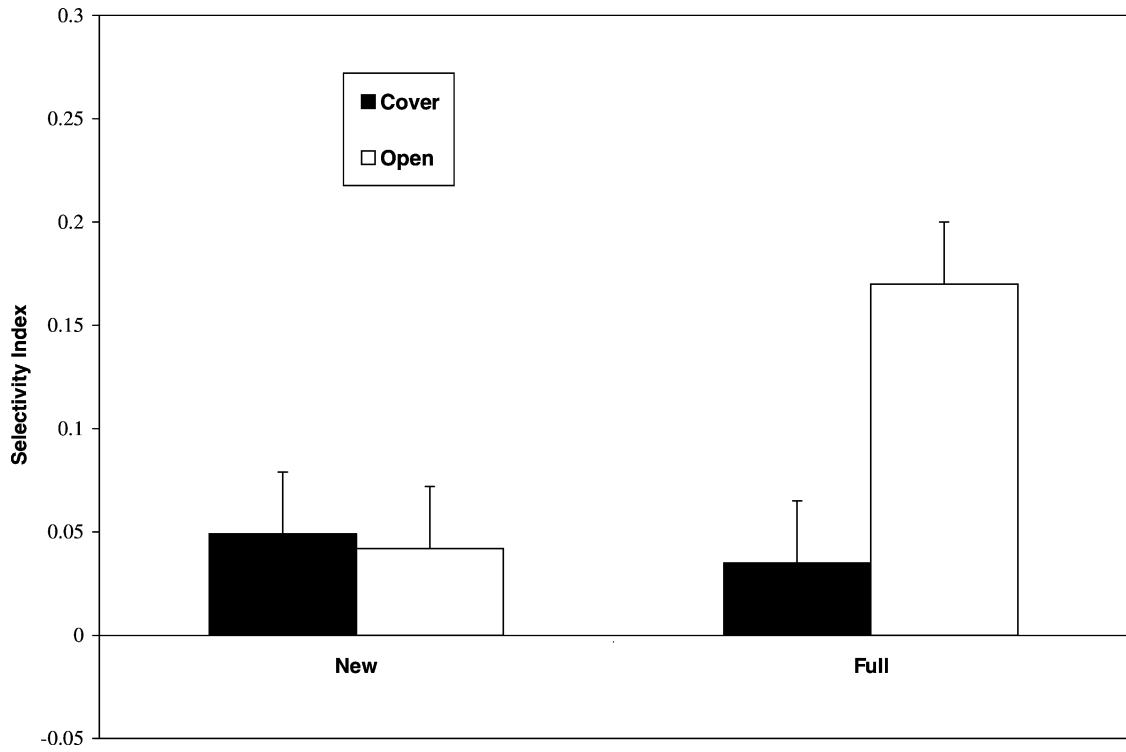


Fig. 1. Interaction of moon phase and microhabitat with selectivity (mean \pm S.E.).

Selectivity did not differ with predation risk when moonlight and microhabitat were considered independently. There was a marginally significant increase in selectivity when foraging at trays in the open (0.11 ± 0.02) versus trays under cover (0.04 ± 0.02 ; $F_{1,60} = 3.54$, NS) and no significant main effect of moon light ($F_{1,60} = 2.76$, NS) on selectivity. There was no evidence to favour the predictions of the reduced finickiness models, which is in keeping with other published studies of food selectivity in small mammals (see Section 1), all of which report evidence of increased selectivity under predation risk.

The dramatic increase in selectivity shown in the riskiest foraging situation suggests that the animals use two alternative foraging strategies (high and low selectivity) rather than a gradient of selectivity in response to increases in predation risk.

The results of the current study do not address whether kangaroo rats and pocket mice differ in their selectivity. Exclusion studies (Longland, 1994), suggest that in the absence of competitors, various het-

eromyid species show similar foraging habits, but it is not known whether this is also true for selectivity. It is possible that foraging competition from kangaroo rats forces the pocket mice to be either more or less selective than they would be without competitors, since kangaroo rats dominate access to food patches (Leaver and Daly, 2001). Future comparisons of selectivity between species might illuminate selectivity strategies as possible mechanisms of co-existence.

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