OIKOS 100: 459–468, 2003

Foraging of multimammate mice, *Mastomys natalensis*, under different predation pressure: cover, patch-dependent decisions and density-dependent GUDs

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Mohr, K., Vibe-Petersen, S., Lau Jeppesen, L., Bildsøe, M. and Leirs, H. 2003. Foraging of multimammate mice, *Mastomys natalensis*, under different predation pressure: cover, patch-dependent decisions and density-dependent GUDs. – Oikos 100: 459–468.

Patch use under predation risk often results in a change of feeding behaviour in the prey animals. However, such changes only appear if the animals are able to assess under which predation pressure they live. We investigated patch use of *Mastomys natalensis* under different conditions of avian predation pressure.

In replicated maize field plots in Morogoro, Tanzania, avian predators were allowed under natural conditions (control), attracted with perches and nest boxes or kept out with nets. During four one-week periods in late 1999, we measured rodent feeding decisions with the giving-up density (GUD) method. Trays with known amounts of millet seeds in sand were placed in pairs, one of them under a cover, the other one in the open. *M. natalensis* mice were expected to give up sooner in the open trays than in those with cover. We hypothesised that *M. natalensis* mice could assess the ambient predation pressure leading to larger difference in GUD between covered and non-covered trays in the plots where predators were attracted. We also made video recordings of the rodent activity at a pair of trays in each treatment.

The GUD-values were significantly lower for the covered trays but predation pressure did not affect this difference. The video observations showed that in the control and netted plots the animals visited trays equally frequently regardless of the cover, while the visits in the predator-attracted plots occurred significantly more often in the covered trays. We conclude that *M. natalensis* can assess the ambient predation pressure and adapt its behaviour at a feeding patch. However, the variation in predation pressure in our experiment was not obvious from the GUD. Moreover, we found a strong relation between rodent density and GUD, which may mask variations in perceived predation pressure. Similar GUD values may be reached in different ways and we present models to investigate whether animals' decision to forage at a food patch is only affected by the seed density at that patch, not by that at a neighbour patch.

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Predators are important to a prey population in more than one respect. Clearly they exert a direct effect by catching and subsequently killing the prey, but predators may also indirectly affect prey by changing their activity pattern (Hendrie et al. 1998, Banks et al. 1999, Eilam et al. 1999), foraging behaviour, growth rate (Gotthard 2000), and reproduction (Desy et al. 1990, Lima and Dill 1990, Holmes 1991, Herman and Valone 2000).

In order to balance food quality/quantity and predation risk, several prey species indeed show the ability to modify their use of a feeding patch when subjected to

Accepted 3 September 2002

ISSN 0030-1299

changes in predation pressure (Holmes 1984, Brown 1988, Brown et al. 1988, Kotler 1992, Hughes and Ward 1993). Such modifications could be seen as e.g.: 1) changes in the amount of food intake due to less time spent and/or reduced foraging effort at a given "risky" patch and/or 2) tendency to forage in covered feeding patches even though food may be less abundant or of poorer quality than in open patches and/or 3) changes in harvest rates and apprehension or vigilance (Brown et al. 1988, Kotler et al. 1992, 2002).

One of the most common rodents in Eastern Africa is *Mastomys natalensis* (Smith, 1834, Fiedler 1988a, Leirs et al. 1996). They occur all over the continent in natural grasslands, thicket, cultivated areas, and human habitations, and are significant pests in agriculture. There is an interest in finding new, ecologically based management strategies to solve this problem (Makundi et al. 1999). Attracting predators may be one possible solution (Duckett 1976, 1991, Van Gulck et al. 1998, Banks 2000).

Here we examine the patch use of *Mastomys natalensis* under different predation pressures. For this purpose we use the giving-up density method (Brown 1988), which measures the particular density of food left in a certain feeding patch when the animal ceases to forage (GUD). Brown et al. (1988) have demonstrated that an increasing risk of predation leads to an increase in the GUDs for several desert rodent species. We modified the original GUD approach in such a way that it could be used to compare predation pressure in different populations. We also used direct video observations of the prey's feeding behaviour at feeding patches, in order to see behavioural effects that might not be reflected in the GUD.

Materials and methods

Study area

All experiments were carried out from late October 1999 until December 1999 at the campus of the Sokoine University of Agriculture, Morogoro, Tanzania. The study areas consisted of 10 maize field plots 70 × 70 m, separated from each other by at least 100 m of fallow grassland or by a rodent-proof fence. Since March 1998, the plots had been subjected to three different treatments manipulating the ambient predation pressure. Four of these plots excluded avian predators (with nets covering the areas), two plots attracted predators (by means of raptor perches and nest boxes) and four control plots allowed natural predation. Apart from the predation treatments, two of the netted plots and two of the control plots were enclosed by rodent proof fences. While the netting obviously made predation by raptors impossible, we have no quantitative data about the success of the predator attraction. However, we often observed raptors using the perches as well as raptor and owl pellets under the perches. Also, the nest box at one of our perch areas was occupied by a barn owl pair with, four young at the time of the present study. We are thus confident that we did our study in at least two, probably three, levels of predation pressure.

All study plots were similar with regard to amounts of the available food and vegetation cover etc. All plots had been grown as maize fields during the 1998 and 1999 cropping seasons, all with the same standardised planting density, planting date, fertiliser scheme, harvest time etc. and were harvested in August 1999. At the start of the present study, very late in the dry season, there were no more crops available in the field, only dry empty maize stalks of which the majority had fallen down by that time; as a result, vegetation cover was poor in all plots. Multimammate mice were by far the most common small mammals in the study area. Between October and December 1999, a total of 1518 individual animals were captured at least once during an ongoing capture–recapture-study in the study plots. Of these, 1432 (94.3%) were *Mastomys natalensis*. 53 (3.5%) were *Tatera robusta*, 25 (1.5%) were *Lemniscomys striatus* (a day-active animal) and 8 animals (0.5%) were *Crocidura* spp. shrews. The video-recordings (below) showed one single instance of a Tatera visiting a seed tray.

GUD experiment

GUD reflects the feeding decision of a single animal, the last one to visit the patch. However, we suspected that very high or very low rodent densities could affect the availability of food in the area and through that, the marginal value of energy. This in turn would affect the marginal rate of substitution of predation risk and energy and thus the GUD.

Indeed, the net cost of being exposed to predation can change with population density even if the risk of predation remains unchanged. Also, higher densities of prey animals may reduce the individual risk of being taken by a predator. Finally, small variations in vegetation height and vegetation density (i.e. natural cover) between and within our 10 plots could influence the animals' foraging behaviour and thus the GUD at specific stations. For these reasons we used a modified GUD method.

We placed feeding trays in pairs. One tray in each pair was covered by a roof to provide *M. natalensis* with a feeding patch protected from avian predators, the other tray was left in the open. We expected that the GUD would be lowest in the covered trays (GUDc), as the animals would feel more secure under cover and therefore would continue harvesting towards a lower density of food than in the non-covered trays (GUDn). If the difference between GUDc and GUDn represents the animals' perceived relative safety under cover, we expected GUDn−GUDc to be largest in predation plots and smallest in netted plots.

At the centre of each plot, 3 pairs of plastic feeding trays (20 × 30 × 4 cm) were placed in a triangular pattern. The distance between each pair was approximately 10 m. The distance between two feeding trays in a pair was about 1 m and the roof, constructed from corrugated iron, above one of the trays in each pair was approximately 30 cm above the ground. The short distance between the two trays was used to ensure that surrounding conditions (i.e. environment, food availability, rodent density, weather conditions etc.) would be similar for both trays in a pair. In each tray 8 g millet seeds in a matrix of 1 litre of sieved sand were offered once a day before dusk. We chose a small grain size to obtain a finer resolution of GUD and minimising the possibility that animals would behave differently under different treatments (e.g. eating locally under low predation pressure, taking grains along under higher predation pressure) without this being clear from the GUD. Multimammate mice do not normally hoard their food and in a preliminary pilot test in the lab, we verified that they indeed consumed the small millet seeds locally. Millet seeds have also been used in a number of earlier experiments (Brown 1988, Brown et al. 1988, Kotler 1992, Hughes and Ward 1993).

The GUD in each tray was measured for four consecutive nights of forage: every morning the trays were emptied and the contents were sieved. The remaining millet seeds were weighed before trays were replaced in the study plots by dusk with a new concentration of millet seeds and sand. The experiment was carried out simultaneously in all plots to minimise possible effects of varying weather and moonlight conditions. The experiment was repeated 4 times: 1) 2–5 November, 2) 9–12 November, 3) 23–26 November (not on 25.11 due to heavy rainfall), 4) 30 November–3 December. The first period was preceded by a pilot period of 2 days with the trays containing millet ad lib.

During the first two periods of the experiment, we observed that the mice in some instances kicked out a large amount of sand while searching for seeds. Obviously, this could result in a different concentration of millet seeds per liter of sand (thus, a different GUD). During the second fortnight of the experiment, we therefore weighed not only the remaining seeds, but also the remaining sand, in order to calculate a density-corrected GUD. However, taking the kicked out sand into account did not change the GUD values significantly (Wilcoxon, $p = 0.16$). Therefore, we used the original GUD values.

GUD values were ln-transformed and the effect of treatment, cover, and time (and the relevant interactions) were examined by analysis of variance with density as a covariant. Treatment (predators attracted, control and predators excluded), period (1–4), cover (cover, non-cover), and the interactions were entered as fixed factors. Plot (nested in treatment) and feeding stations (nested within plot) were added as random effects to account for the various local conditions, which possibly could influence the animals, foraging decisions. Days, nested in period, were also added as a random effect to account for possible temporal variation within periods. All mixed model regressions in these analyses were calculated using the PROC MIXED module (SAS 8.0; Littell et al. 1996). Degrees of freedom of the fixed effects F-test were adjusted for statistical dependence using Satterthwaite formulas. All non-significant interactions were removed stepwise.

Population density was used as a covariate, using closed-model population size estimates from an ongoing long-term study (Vibe-Petersen, unpubl.). The values used for our analyses were estimated from capture sessions in that study on 27 October 1999 and 24 November 1999 and interpolated (Table 1). Pearson product-moment correlation was used to investigate the correlation between population density and GUD or visiting frequency.

Behavioural observations

Rodents were videotaped during their foraging activity period. One pair of feeding trays in a treatment plot (predators attracted, control, and predators excluded) was monitored at a time by a video camera. Video recordings were repeated three times per treatment, always with several days between recording nights. Recordings were conducted approximately from 7 pm to 10 pm, when foraging activity of *M. natalensis* mice peaks (Leirs, unpubl. telemetry data).

Table 1. Population size of *Mastomys natalensis* in the 10 study areas during the four periods of GUD-experiments. Values were estimated from 3 consecutive nights CMR.trapping on 26–28 October, 23–25 November and 21–23 December1999, and were further interpolated from a cubic spline.

	Period 1 2/11–5/11	Period 2 9/11–12/11	Period 3 23/11–26/11	Period 4 30/11–3/12
CO1	12	23	40	46
CO10	152	156	157	153
CE5	110	135	155	151
CE9	128	128	128	128
NO4	123	133	143	145
NO6	148	138	129	125
NE3	72	92	112	117
NE8	82	92	104	107
PR2	50	62	78	83
PR7	112	123	131	128

On 10 November, 6 December, 17 December (predation area), 11 November, 2 December, 10 December (control area), and 9 November, 8 December, 18 December (netted area).

In our analysis of the video tapes, we recorded the number of visits rather than the length of feeding; most visits were very short and it was difficult to accurately time them; also, very often, several individuals foraged together in the seed trays, and due their fast movements and the quality of the infra-red recordings it was difficult to keep track of single individuals. The frequency of visits was obtained by freezing the video picture and counting the number of *M. natalensis* mice present in each tray (covered, and non-covered) at 1-min intervals. Preliminary scanning of the videotapes showed that visits generally lasted a few seconds. Therefore, each observation of a *M. natalensis* mouse in a tray was considered a separate visit. Number of visits was compared between treatments separately for the covered and the non-covered tray, using a Kruskal–Wallis test carried out in Statistica (StatSoft Inc. 1995). Furthermore, the number of cases where the highest number of rodents found in the covered tray was counted, based on the 1-min interval video-frames. A binomial test was used to reveal if the incidence of more rodents in the covered tray was influenced by treatments. Differences between the number of visits in the covered and non-covered trays were tested in a Chi^2 test.

Results

Comparing open and enclosed plots within the same predation treatment showed no significant difference in GUD: open vs enclosed netted plots (Kruskal–Wallis test $p = 0.116$, $n = 170$); open vs enclosed control plots ($p = 0.960$, $n = 132$), therefore fencing treatments were pooled in the further analysis

GUD

Mean GUD values per plot were 0.37–2.2 g, though one of the control plots differed by a mean GUD exceeding 6g/l. A simultaneous study (Vibe-Petersen, unpubl.), showed that population size in that particular plot was very low in comparison with the others (Table 1). Therefore, data from this plot were excluded from further analysis.

Differences between GUD in covered and non-covered trays were small but highly significant (Table 2, Fig. 1). The GUDs in all treatments decreased markedly over time (Fig. 1). Clearly the periods affect the GUD (Table 2), resulting in a lower remaining seed density in period 4 than in period 1.

Treatments (predation, control, and net) had a significant influence on the GUD; GUD, being lowest in the predation plots, highest in the control plots and with the netted plots in between, but there was no significant interaction between cover and treatment, thus the effect of cover was similar regardless the predation pressure (Table 2). Density was highly significant as a covariate, affecting the GUD negatively, but interacted also with period. Fig. 2 shows the significant correlation ($p < 0.001$) relation between GUD and density during the first period. Even without the points at the lowest population density, there is a negative correlation (GUDc: r^2: 0,27; GUDn: r^2: 0,42; both significant $p < 0.01$) However, the difference between GUDs from the non-covered and covered tray (GUDn–GUDc) was not significantly correlated with the population density ($r^2 = 0.0002$; $p = 0.86$).

Video observations

The number of visits in the non-covered trays was affected by treatment ($p < 0.001$) whereas visits in the covered trays were not significantly affected by treatment ($p = 0.07$). Incidence of more animals in the cov-

Table 2. Effects of cover, treatment, period and density on GUD. F (with its numerator and denominator degrees of freedom in subscript) and p-values from generalised linear modelling in a stepwise reduced model. For each categorical value of the fixed effects and for the covariate density, parameter solutions and their associated standard errors and probability are listed.

Effects	F	p	category value	estimate	st.error	p
Cover	$7.84_{1,\ 744}$	0.0052	cover	−0.1356	0.0484	
			non-cover	0		
Treatment	$7.51_{2,\ 5.69}$	0.0254	control	0.6777	0.1750	0.0071
			net	0.3903	0.1453	0.0401
			predation	0		
Period	$10.74_{3,\ 32}$	<0.0001	1	2.9130	0.5353	<0.0001
			2	2.1516	0.5333	0.0002
			3	2.4553	0.5846	0.0001
			4	0		
Density	$76.48_{1,\ 14.1}$	<0.0001		−0.0085	0.0034	0.0169
Density × Period	$11.01_{3,\ 695}$	<0.0001	1	−0.0148	0.0029	<0.0001
			2	−0.0154	0.0029	<0.0001
			3	−0.0145	0.0032	<0.0001
			4	0		

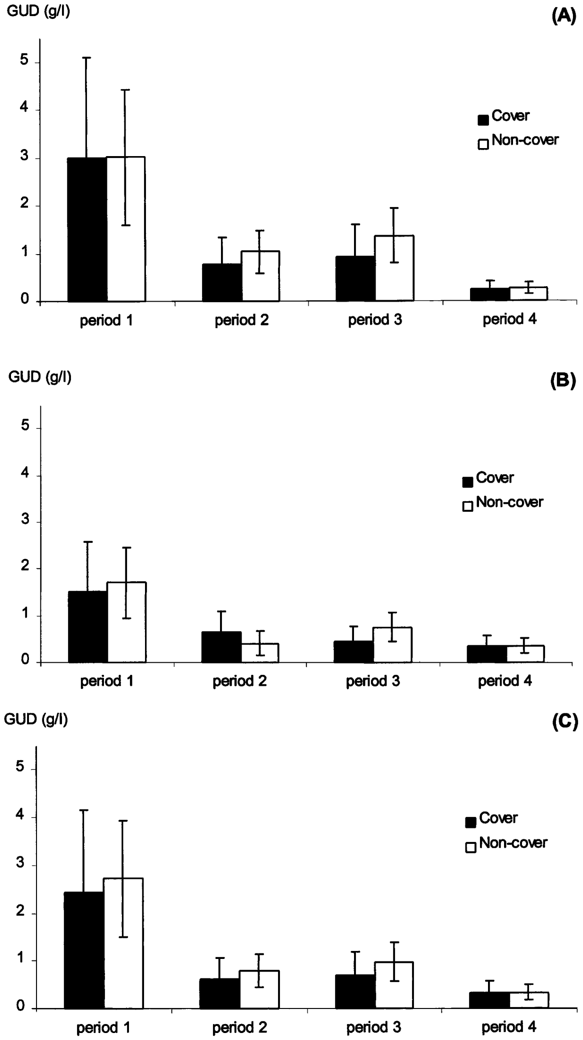

Fig. 1. **(A)**: Predation, **(B)**: Control, **(C)**: Net. Mean GUD values ± s.d. (g/l) per treatment and per period.

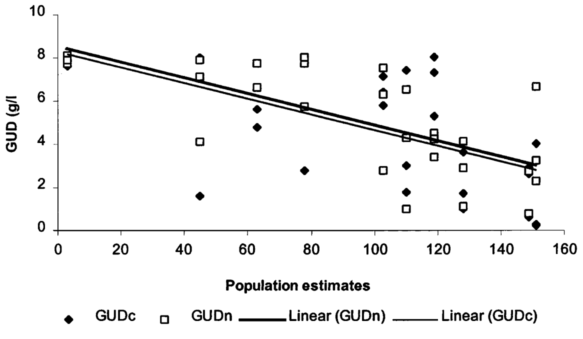

Fig. 2. Correlation between population estimates (Vibe-Petersen, in prep.) and GUD. r = 0.603 for the covered tray, and r = 0.713 for the non-covered tray (p < .001).

ered trays, as well as difference between the number of visits in the covered versus the non-covered trays, also tended to be affected by treatment.

Of the observations in the netted plot, 48.4% ± 8.6 had more animals in the covered trays than in the non-covered trays; control plot recordings showed 50.4% ± 10.4 incidents with most rodents in the covered tray. Recordings from the predation plot showed a higher preference for the animals to visit the covered tray by 59.7% ± 2.6 incidents. A binomial test showed that only in the predation plot the difference between the animals' preferences was significant (p = 0.014).

Observations made in control and netted plots revealed no difference between visits in covered and non-covered trays (control: 51.7% covered tray; 48.3% non-covered tray; $\chi^2 = 0.85$; p = 0.36; n = 855; net: 49.7% covered tray; 50.3% non-covered tray; $\chi^2 = 0.02$; p = 0.89; n = 784) whereas in the predation plot the frequency of visits in the covered trays was significantly higher than in the non-covered tray (58.4% covered tray; 41.6% non-covered tray; $\chi^2 = 24$; p = 0.01; n = 864) (Fig. 3).

Recordings showed a preference by the mice to visit the covered tray in all three recording sessions in the predation plot (respectively, 58.1%, 60.1%, and 55.1% of the total number of visits).

Neither the frequency of visits in the covered trays nor that in the non-covered tray was significantly correlated with the population size of *M. natalensis* mice ($r^2 = 0.036$, p = 0.65, and $r^2 = 0.09$, p = 0.42, respectively). The distributions of the visiting frequencies in the two trays are shown for each treatment in Fig. 4.

Discussion

Our first hypothesis was that placing a cover over a feeding patch would provide a foraging *M. natalensis* with a lower perceived risk of predation than when foraging in an open patch. Therefore, we expected lowest GUDs and a higher number of visits in the covered feeding patches.

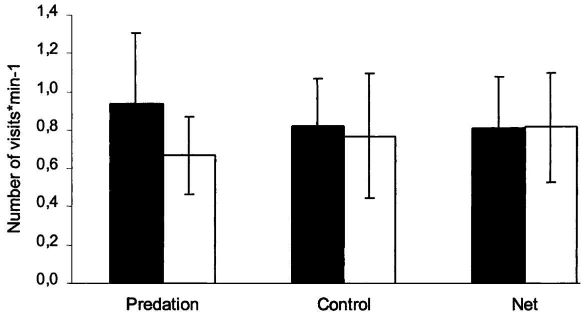

Fig. 3. Mean number of visits per minute in covered (black bars) and non-covered (white bars) trays in the three treatments: predation, control, and net. Statistics on differences between mean visits per minute in the covered and the non-covered tray showed: $\chi^2 = 24$, $p < 0.001$ for predation plots; $\chi^2 = 0.85$, p = 0.36 for control plots, and $\chi^2 = 0.02$, p = 0.89 for net plots.

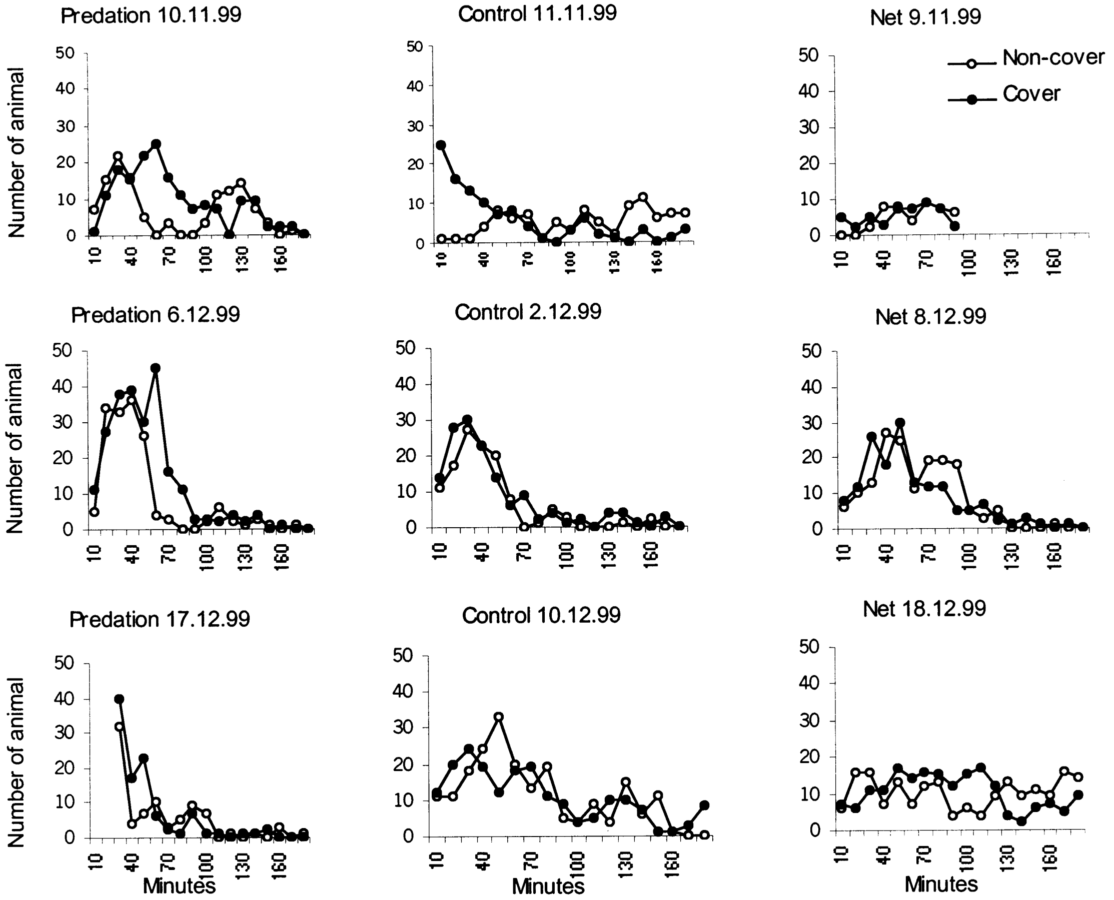

Fig. 4. The accumulated number of visits (during 10 min) in the covered (black dots) and non-covered tray (open circles), respectively. In each of the three treatments, three video tapes of 180 min each have been recorded.

This was confirmed by our GUD results for all plots and by our video observations in the predation plot. The effect of cover was not surprising as several studies showed that rodents quit foraging earlier in a risky patch (Brown 1988, 1992, Brown et al. 1992, Jacob and Brown 2000) and that prey animals prefer to forage in a microhabitat that is considered safe (Price et al. 1984, Kotler et al. 1991, Banks et al. 1999). Microhabitats providing the highest safety for a prey animal are not the same to all animals e.g. quadrupedal animals tend to forage in bushy microhabitats, whereas bipedals may prefer open areas; however, in response to the presence of a barn owl, both quadrupedals and bipedals shifted to the bushy microhabitat (Brown et al. 1988). Voles (*Microtus socialis*), which forage in relatively open spaces showed a behavioural response when exposed to owl calls, whereas common spiny mice (*Acomys cahirinus*) which forage in rock crevices (relatively protected from aerial predation), did not change their behaviour when exposed to owl calls (Eilam et al. 1999). *M. natalensis* lives in open grass- and farmland and its activity was affected by the presence of cover in this study. Also Leirs et al. (1996) found that *M. natalensis* avoided open spaces during low densities. Owls' hunting success is indeed dependent on microhabitat and is higher in open areas (Kotler et al. 1988, Longland and Price 1991, Rohner and Krebs 1996).

The cover effect on GUD was similar for all plots while visiting frequency was not affected by cover in the control and netted plots. We offer possible explanations for this later, however, first we consider the possible dependency between feeding trays in a pair.

A first type of dependency would be that trays were so close to each other that the roof over the covered tray might provide some protection for the non-covered tray. However, we found a significant cover effect on the GUDs. If trays in a pair had been farther apart, perhaps the difference in GUD-values would have been larger, which maybe would have shown differences between treatments. However, the risk of noise in our results due to different surroundings for each tray would also have been larger.

Another possible type of dependency would arise if animals foraging at two neighbouring patches would continuously compare the two patches and always try to choose the one that gives the best yield in relation to

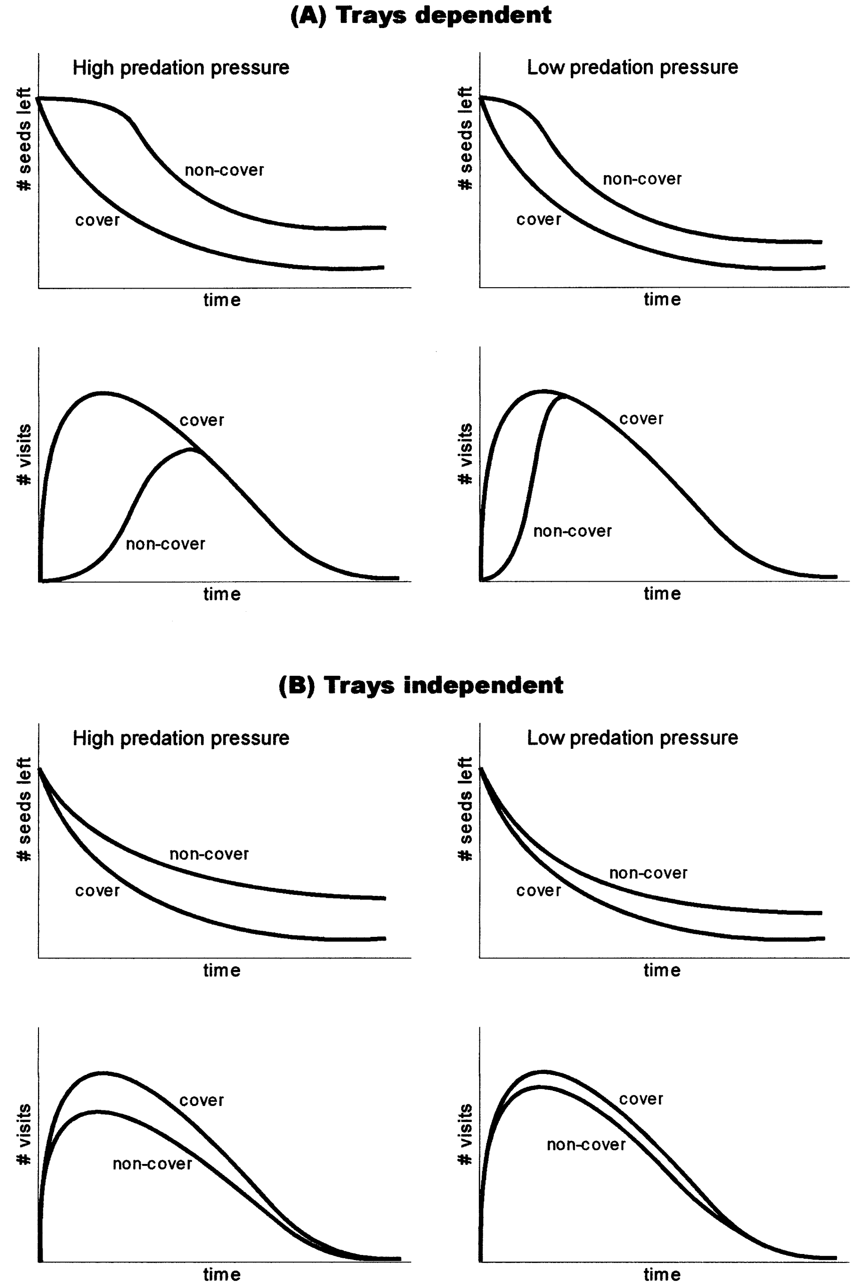

Fig. 5. Theoretical curves, showing the removal of seeds and number of visits in covered and non-covered trays, under two hypothesis of dependency between trays. A: decisions to feed in a given tray are made taking also into account what the conditions are in the other tray; B: feeding decisions are made independently for each tray). In each panel, top graphs show the decrease of seeds available in the tray until the GUD is reached, bottom graphs show the number of visits in both trays. Graphs to the left show the curves under high predation pressures, curves to the right under low predation pressure.

the predation risk. If this was true, we expect that early in the foraging period the animals mostly visit the covered tray and the amount of seeds reduces quickly; in the non-covered tray, the animals visit less often and seeds disappear very slowly (Fig. 5A). Then, the amount of seeds in the covered tray becomes so low, that the balance yield/predation risk becomes equal in the two trays (in the non-covered trays, the risk of predation is higher, but the seed density, and thus harvest rate, is higher as well). From that moment, we expect the animals to visit both trays equally often. The net benefit decreases with time, but remains equal in both trays (when one tray becomes less beneficial than the other, the animals move to the other tray and level out the difference). This continues until the amount of seeds is so low that it no longer outweighs the risk of predation and the GUD is reached (the curves become horizontal). Since the predation risk is higher in the non-covered trays, the GUD here is higher.

In an alternative model, animals consider the two trays independently and their decision to forage in one of the trays is only affected by the seed density at that particular patch, not by the density at the neighbour patch (Fig. 5B). Then we expect that animals visit both trays frequently immediately after the start of the experiment. Indeed, the density of seeds is so high that it outweighs the predation risk considerably, even in the non-covered trays. The number of visits increases fast (animals accidentally pass by and then stay because of the high benefit), thus the amount of seeds decreases fast in both trays (maybe somewhat slower in the non-covered trays). After some time, however, the benefit starts falling, and number of visits decreases. This occurs faster in the non-covered trays due to the larger risk of predation. Thus, under the hypothesis of dependency, we expect a peak of visits first in the covered trays, then in the non-covered trays. In the alternative hypothesis, we expect a quick rise of visits in both trays, but the rise is prolonged in the covered trays; thus the peak of visits there occurs later than in the non-covered trays.

Note that GUD does not provide any information about dependency, since GUD only gives the end-value of the foraging process, not the pattern during the night, which was pointed out in a study by Price and Correll (2001). In all cases, we expect that the discussed differences are clearer in areas where predation risk is considerable. The video data for the predation plots (Fig. 4) agree with the alternative hypothesis, i.e. a later and higher peak of visits in the covered trays than in the non-covered trays, suggesting that the exploitation of two neighbouring patches happens indeed in an independent way. The absence of a clear difference in the netted area was due to the lower predation risk there.

Why was there a GUD-difference between the covered trays and non-covered trays in all plots, while the video shows a difference in number of visits in the predation plots only? A difference would be observed if (1) the visits in the covered trays lasted longer than visits in the non-covered trays, resulting in the removal of more food per visit, or (2) the visits in the open trays were less effective for seed removal e.g. due to increased scanning for predators (Cassini 1991). In both cases, an equal number of visits, as seen on the video, would still result in a higher GUD in the open trays. We did not compare visit duration or activities during a visit from our video observations, but visits were always very quick, hopping in and out, and differences would be difficult to detect. The third explanation (3) is that foraging continued after the video recording session was stopped and that this foraging continued for a longer period in the covered tray.

The videotapes lasted for three hours (7–10 pm) and from Fig. 4 we see that towards the end of the tape, the number of visits in both trays had dropped to almost 0, indicating that at that time the full trajectory of our theoretical curves in Fig. 5B had been realised already. The difference in the number of visits for the whole tape was then proportional to the area between the two curves. That area is large under conditions of high predation risk, much smaller under conditions of low predation risk. We assume that in the latter case, it may not be large enough to be statistically detected in our limited sample.

Our second hypothesis was that if cover causes a difference between GUDs in a pair of trays, this difference would be larger in predation plots and smaller in net plots due to the relatively lower predation risk under cover in the predation plot. Also the relative preference to visit the covered tray was expected to be highest in predation plots and lowest in net plots. As expected, with regards to the number of visits there was an interaction between cover and treatment. This preference for foraging in the covered trays in the predation plot, but not in the other treatments, is consistent with the hypothesis that *M. natalensis* experiences the relative risk of the cover/non-cover patches differently in the predation plot. The GUD results also revealed a difference in feeding decisions in the different treatments, although not the one expected, since the predicted effect of treatment on GUD pointed to lowest GUD in the predation areas, and highest in the control area (Table 2). This suggests that *M. natalensis* not only chooses to exploit the covered feeding tray most in the predation treatment, but also prefers to exploit chosen feeding sites more as opposed to exposing themselves by searching for new sites. Making up ones mind about the discrepancy between this suggestion and our initial hypothesis needs further experimental studies.

We know from previous studies that perceived risk of predation alters prey behaviour. Risk of predation also indirectly affects prey animals in various ways (Desy et al. 1990, Lima and Dill 1990) and is often seen as a foraging cost (Kotler et al. 1992, Kotler 1997, Meyer and Valone 1999). For example Bolbroe et al. (2000) found that presence of least weasel odour changed voles behaviour, reducing consumption of distant food and decreasing their overall activity.

Assuming that a forager is behaving optimally, its GUD is the result of balancing between food gain and metabolic costs of foraging, predation cost of foraging and missed opportunity cost of not engaging in alternative activities (such as reproducing, grooming, foraging elsewhere etc., Brown 1988). If the density of the mice increases, competition for food resources also increases, the marginal rate of substitution of energy intake and the chance of not being taken by a predator changes and the missed opportunity costs of not feeding in other places than our trays decreases. This would result in a lower GUD and it is therefore not surprising that population density affects the GUD. The correlation between population density and GUD (or rather the population density's influence on the missed opportunities) makes this technique in its simple form not suitable for the comparative investigation of perceived predation pressure in different populations. The difference between the GUD in covered and non-covered trays (GUDn−GUDc) might be a more robust measure, as it is not affected by population density.

We conclude that *Mastomys natalensis* mice detect differences in predation pressure and change their feeding strategies accordingly. Direct behavioural observations were complementary to GUD data in interpreting the observed differences.

It is important to stress that the same GUD can be reached in different ways because GUD is affected both by risk of predation but also by the marginal value of energy provided in the trays. Therefore GUD values may not reveal all the relevant information about the use of a food patch. The density dependence of GUDs means that care should be taken when investigating perceived predation risk in areas where different densities of resources or missed opportunities costs may prevail.

Acknowledgements – We thank Hannu Ylönen for advice at the start of the work and Roger Pech and Burt Kotler for their comments on an earlier draft of the manuscript. KM obtained a travel grant from the Danish Council for Development Research (RUF). Many thanks go to the late Patrick Mwanjabe (Rodent Control Centre), Robert Machang'u and Rhodes Makundi (Rodent Research Unit at Sokoine Univ. of Agriculture) and the staff at SUA for assistance with the fieldwork. We also thank the staff at the Mammal Dept of the Danish Pest Infestation Laboratory for assistance with earlier laboratory experiments and Jan Scheirs (Univ. of Antwerp) for his statistical advice.

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