Feeding Decisions as an Anti-Predation Strategy in the African Multimammate Rat (*Mastomys natalensis*)

M.Sc. thesis by

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Abstract

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 asses under which predation pressure they live. We investigated whether *Mastomys natalensis* changes its feeding decisions 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 periods of one week each in late 1999, we measured rodent feeding decisions with the giving-up density (GUD) method. Trays with known concentrations of millet seeds in sand were placed in pairs, one of them under a cover, the other one in the open. Since rodents give up foraging in a feeding patch when the risk of being taken by a predator starts outweighing the expected benefit of searching for food items, they were expected to give up sooner in the open trays than in those with cover. Under the hypothesis that the rodents could assess the ambient predation pressure the difference in GUD between covered and non-covered trays would be larger in the plots where predators were attracted. During the same research period, we also made video recordings of rodent activity at a pair of trays in each treatment.

The GUD-values were significantly lower under the covers, as expected, however, predation pressure did not affect this difference or the actual GUD-values. The video observations, on the other hand, showed that in the control and net 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. The variation in predation pressure in our experiment was not reflected in the GUD. We found a strong relation between rodent density and GUD, which may overshadow perceived variations in predation pressure.

Introduction

In Africa, damage by rodents is an important cause of field harvest losses and farmers often list rodents as one of their most significant crop pests (Fiedler 1988b, Howard 1988). Much of the food crop agriculture is undertaken by resource-limited smallholder farmers, and localised pest problems, as is typical for rodent damage, may therefore have a severe impact on individual households.

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, making them 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, Duckett 1991, Van Gulck *et al.* 1998, Banks 2000).

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 the prey by changing its activity pattern (Hendrie 1998, Banks *et al.* 1999, Eilam *et al.* 1999), the prey's foraging behaviour, their growth rate (Gotthard 2000), and reproduction (review by Lima and Dill 1990, Desy *et al.* 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 changes in predation pressure (Holmes 1984, Brown 1988, Brown *et al.* 1988, Kotler 1992, Hughes & Ward 1993). Such modifications could be seen as *e.g.*: 1) Changes in the amount of food intake due to for instance 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 (Brown *et al.*1988, Kotler *et al.* 1992).

Here we examine if *Mastomys natalensis* rats change their feeding strategies under different predation pressures. For this purpose we will use the giving-up density method (Brown 1988), which measures the particular density of food left in a certain often manipulated location (feeding patch) when the animal ceases to forage (GUD). Even though the feeding patch usually is used by several individuals, the GUD always represents the decision of the last animal foraging in a particular patch. Brown *et al.* (1988) have demonstrated that an increasing risk of predation leads to an increase in the GUDs for several desert rodent species. Furthermore, we also use direct video observations of the prey's actual feeding behaviour.

Materials/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 70x70 m (farmed as normal maize fields) separated from each other by at least 100 m of fallow grassland or by a rodent proof fence. The field plots were subjected to three different treatments with regard to the ambient predation pressure. Four of these plots excluded avian predators (with nets covering the areas), two field plots attracted predators (by means of raptor perches and nest boxes) and four control field plots allowed predators on a natural basis. Apart from the predation treatments, two of the net plots and two of the control plots were enclosed by rodent proof fences (see set-up in Vibe-Petersen *et al.* submitted) but this did not affect our study (see results) and is irrelevant for our approach. Therefore, this experiment will only take into account the treatments concerning predation pressure (*i.e.* predators excluded in net areas (N), predators attracted in predation areas (PR), predators allowed in control areas (C)).

The 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 anyhow could affect the availability of food in the area and thereby affect the animals' motivation to feed, hence, the GUD. Very high rodent densities could lead to increased feeding motivation and by that decrease GUD. Furthermore, variation in vegetation height and density (*i.e.* natural cover) within our 10 field plots could influence the animals' foraging behaviour and thus the GUD. For this reason 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. Surrounding conditions were similar for the two trays. 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 net plots.

To ensure that the rodents consumed the food offered at the spot of the manipulated patch (instead of removing the seeds for hoarding), the rodents were offered millet seeds, which are too small in size for the rodents to hoard (personal obs.) Millet seeds have also been used in a number of earlier experiments (Brown 1988, Brown *et al.* 1988, Kotler 1992, Hughes & Ward 1993).

At the centre of each plot, 3 pairs of plastic feeding trays (20x30x4 cm) were placed in a triangular pattern. The distance between each pair was approx. 10 m. The distance between two feeding trays in a pair was about 1 m and the roofs were approx. 30 cm above ground level. In each tray 8 g millet seeds in a matrix of 1 litre of sieved sand were offered once a day before dusk.

The GUD in each tray was measured for four consecutive nights of forage: Every morning the trays were emptied, the contents sieved and the remaining millet seeds weighed, before trays were replaced in the field plots with a new concentration of 8g seeds/l 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 an acclimatisation period of 2 days with the trays containing millet *ad. lib* in place.
During the first two periods of the experiment, we observed that the rats in some instances kicked out quite a large amount of sand while searching for seeds. Obviously, this could result in a different concentration of millet seeds per litre 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.

Effect of treatment, cover, and time (and the relevant interactions) were examined by variance analysis. GUD values were ln-transformed and analysed in ANOVA model selection. In the initial model, treatment (predators attracted, control and predators excluded), period (1-4), cover (cover, non-cover), and the interactions were entered as fixed factors. Field and feeding stations (nested within field) 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 Satterhwaite formulas. All non-significant interactions were removed stepwise.

We investigated relations between GUD and population density, using closed-model population size estimates from Vibe-Petersen (submitted). Population estimates on 27.10.99 and 24.11.99 were used, as these were the estimates closest to our study period. Pearson product-moment correlation was used to test for correlation and significance in population density with regard to both GUD and visiting frequency (see below).

The behavioural observations

Nine videotapes of the rodents during their foraging activity period were recorded. 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. The recording sessions were carried out approx. from 7 pm to 10 pm, which is the time of day rodents' foraging activity peaks (Leirs, unpublished telemetry data). Video recordings were carried out on the following days: 10 November, 6 December, 17 December (predation area), 11 November, 2 December, 10 December (control area), and 9 November, 8 December, 18 December (net area).

The frequency of visits over time was obtained by freezing the picture and counting the number of rodents present in each tray (covered, and non-covered) at 1-minute intervals. Preliminary scanning of the videotapes showed that visits generally lasted a few seconds only. Therefore, each observation of a rat in a tray was considered a 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).

Based on scannings of the videotapes the number of incidents where the highest number of rodents was found in the covered tray was counted. A binomial test was carried out in Statistica in order to reveal if incidents of more rodents in the covered tray were influenced by treatments.

Difference between number of visits in the covered and non-covered tray were tested independently by a Chi^2 test.

Results

Comparing open and enclosed fields within the same predation treatment showed no significant difference: open vs. enclosed net plots (Kruskal-Wallis test p=0.116, n=170); open vs. enclosed control plots (p=0.960, n=132).

GUD

Mean GUD values per plot were all between 0.37 to 2.2 g millet/l sand, though one of the control fields differed by a mean GUD exceeding 6g/l. A simultaneous study (Vibe-Petersen, submitted), showed that population size in that particular field plot was very low in comparison with the others. At the time when our GUD experiment started, the estimated population consisted of 3 animals, versus a range of 45-151 animals in the rest of the plots. The *M. natalensis* population increased over time. The estimated population in this control plot consisted of 73 animals at the time this experiment ended, still well below the populations of the remaining field plots (101-136). Therefore, data from this plot were excluded from further analysis.

Differences between GUD in covered and non-covered trays are not large, but consistent (table 1, fig. 1).
Mean GUDs from the covered feeding trays were generally lower than the GUDs from non-covered trays, and a Wilcoxon test for matched pairs shows that the differences between GUDc and GUDn within each treatment are significant or close to (predation: T=1011, p=0.062, n=87; control: T=2133.5, p=0.013, n=132; net: T=3716, p=0.016, n=176) (note the differences in n, due to the different number of treatment replicates).
The actual GUDs in all treatments decreased markedly over time (fig. 1). Clearly the periods affect the animals' GUD (table 1), resulting in a lower remaining seed density in period 4 than in period 1.

Treatments alone (predation, control, and net) had no significant influence on the GUD (table 1), but the interaction treat*period (table 1) proved to be significant. This significant interaction is caused partly by an effect of period in the predation and net plots (table 1) and partly by an effect of treatment in period 4, GUDs being lowest in PR plots (table 1).
We suspected the period effect to be caused mainly by the increase in rodent population. A test for dependency between GUD and population density revealed a highly significant negative correlation. The correlation between the GUDs and the population estimates was significant (p<0.001) both at the start (27.10.99) and at the end (24.11.99) of the study period for the covered and the non-covered trays

(fig. 2 shows data for 27.10.99). However, the difference between GUDs from the non-covered and covered tray (GUDn-GUDc) is not significantly correlated (r^2=0.0002; p=0.86) with the population density.

Video observations

The actual 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).

Incidents of more animals in the covered trays, as well as difference between the number of visits in the covered versus the non-covered trays, also tend to be affected by treatment.

48.4% ±8.6 of the observations in the net plot (mean of pooled data from three video tapes) 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. The binomial test showed that only in the predation plot the difference between the animals' preferences was significant (p=0.014). The p-values for the net plot and the control plot were p=0.1 and p=0.16, respectively.

Observations made in control and net plots revealed no difference between visits in covered and non-covered trays (control distribution: 51.7% covered tray; 48.3% non-covered tray; χ^2=0.85; p=0.36; n= 855 and net distribution: 49.7% covered tray; 50.3% non-covered tray; χ^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 (distribution: 58.4% covered tray; 41.6% non-covered tray; chi2 χ^2=24; p=0.01; n=864) (fig. 3).

The cover effect found in the predation treatment was unaffected by period as the behavioural recordings show a preference by the animals 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 nor in the non-covered tray was significantly correlated with the rodent population size (r^2=0.036, p=0.65, and r^2=0.09, p=0.42, respectively).

Discussion

Our first hypothesis was that placing a cover over a feeding patch would provide a foraging *M. natalensis* with a more secure feeling than when foraging in an open patch. If this was true, we expected this effect to be reflected in the animals feeding decisions resulting in lowest GUDs in the covered feeding patches and a higher number of visits in the covered tray in the video observations.

This hypothesis was confirmed by our GUD results for all plots. Also our video observations showed that cover had an effect on the animals' visiting frequency, at least in the predation plot. The results on cover effect are not surprising as several studies reveal that rodents quit foraging earlier in a risky patch (Brown 1988, 1992, Brown *et al.* 1992, Jacob & Brown 2000) and that most prey would rather forage in a microhabitat that is considered safe rather than in a risky microhabitat (Price *et al.* 1984, Kotler *et al.* 1991, Banks *et al.* 1999). Microhabitats providing the greatest safety for a prey animal are not the same to all animals *e.g.* quadrupedal animals tend to forage in bushy microhabitats, whereas bipedals 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 as confirmed by our results its activity is affected by the presence of cover. Also Leirs *et al.* (1996) found that *M. natalensis* avoided open spaces during low densities. Rohner & Krebs (1996) reported that owl hunting success is indeed higher in open areas.

The cover effect on GUD is similar for all plots while the video recorded visiting frequency was not affected by cover in the control and net plots. We offer three possible explanations for this. This 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 hard to observe. 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.

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 relative higher level of security offered by the 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. Contrary to our expectations treatment had no effects on the difference in GUD between covered and open trays but with regard to video observations there was interaction between cover and treatment: Only in the predation plot was there a clear preference for visiting the covered tray. This preference for foraging in the covered tray in the predation plot suggests that *M. natalensis* in the predation plot experience the relative risk of the cover/non-cover patches differently than in the other plots. Thus, even though the GUD results do not reveal a difference in feeding decisions in the different treatments, the video results indicate that animals in the predation plots are more aware of the risk. We know from previous studies that risk of predation alters prey's behaviour. Risk of predation also indirectly affects prey animals in various ways (see review by Lima & Dill 1990, Desy *et al.* 1990) and is often seen as a foraging cost (Kotler *et al.* 1992, Kotler 1997, Meyer & 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. Herman & Valone (2000) found that addition of predator odour reduced foraging behaviour of Kangaroo rats.

The general impression of the results was that the absolute levels of GUD were unaffected by treatment while the actual number of visits was affected by treatment. We suggest that the main reason for seeing a treatment effect in the video recordings and for the previously mentioned failures to see treatment effects on GUD are that populations sizes in our experiment had an influence on the motivation to use our trays and thereby on the GUDs. This influence causing GUDs to vary from 3 g/l to almost zero could overshadow influences from perceived variations in predation pressure, which should exist according to our video observations. The significant treatment effect (in period 4) showing lower GUD in the predation plot is also most likely due to variations in population density or the near zero GUD values.

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 rodents increases, competition for food resources also increases and therefore 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 not suitable for the 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, however, not as robust as observing the behaviour.

We conclude that *Mastomys natalensis* rats do detect differences in predation pressure - and change their feeding strategies accordingly. This is reflected by the behavioural observations from the preference of visiting the covered tray in plots having predators attracted. The same conclusion could not have been made solely from the GUD results.

Table 1: Effects of cover, treatment, and period on GUD.
F and p-values comes from generalised linear modelling.

Effects	**F**	**P**
Cover	6.92	0.009**
Treatment	0.58	0.567
Period	5.14	0.018*
Cover*Treat	0.31	0.736
Treat*Period	3.62	0.002**
Cover*Period	0.28	0.843
Treat*Period*Cover	0.93	0.473

Effects of each period and treatment on GUD.
F and p-values comes from generalised linear modelling.

Effects	**F**	**P**
Period effect on C plots	2.57	0.108
Period effect on N plots	5.56	0.014*
Period effect on PR plots	6.33	0.009**
Treatment effect on period 1	0.95	0.401
Treatment effect on period 2	0.46	0.637
Treatment effect on period 3	0.52	0.601
Treatment effect on period 4	3.56	0.044*

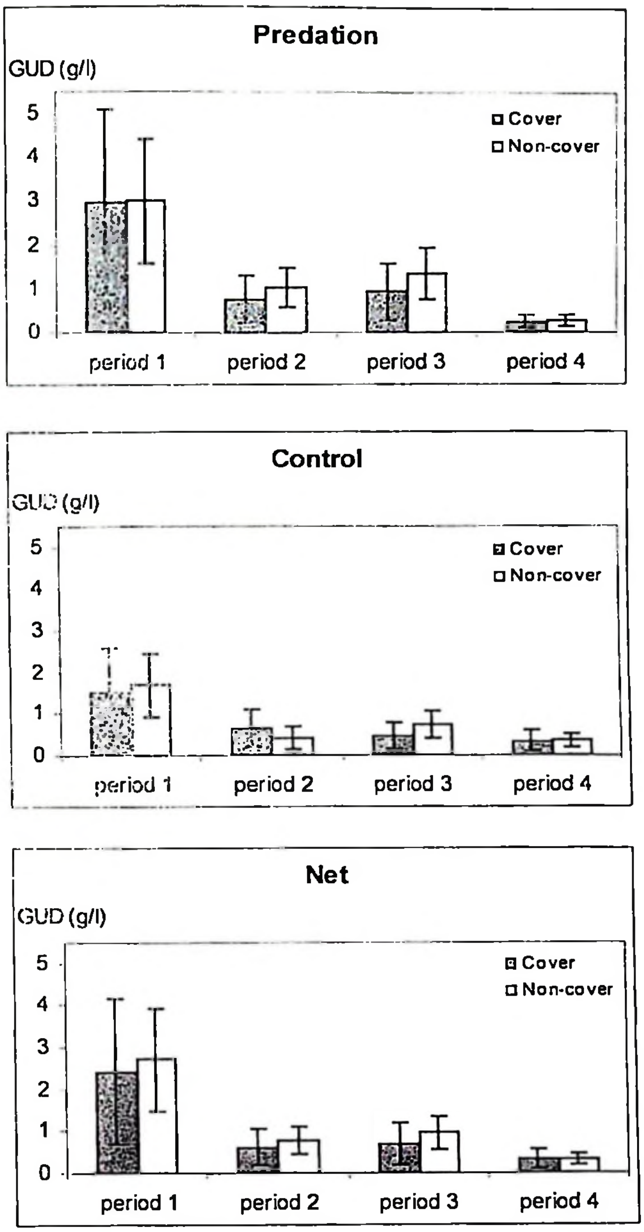

Figure 1. Mean GUD values ± s.d. (g/l) per treatment and per period.

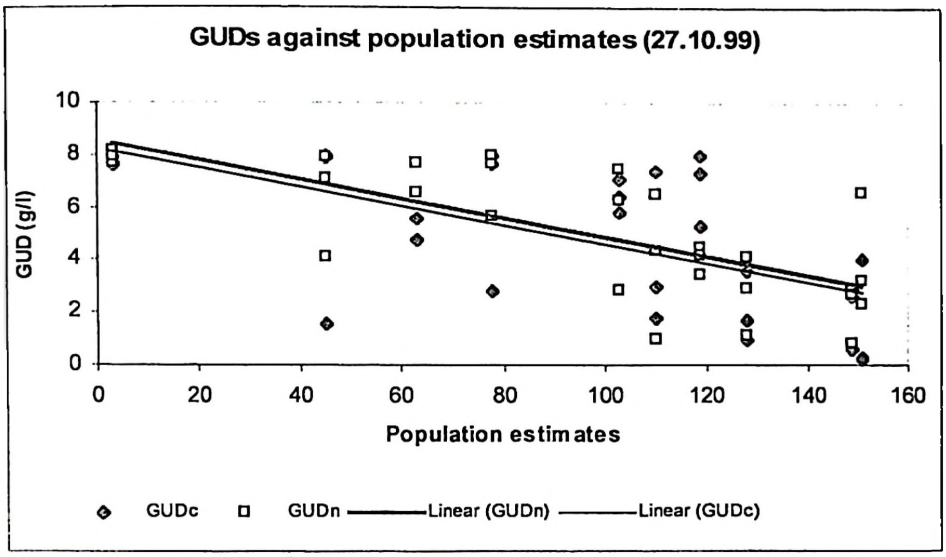

Figure 2. Correlation between population estimates (Vibe-Petersen, in prep.) and GUD ($p<0.001$). $r^2= 0.364$ for the covered tray, and $r^2=0.508$ for the non-covered tray.

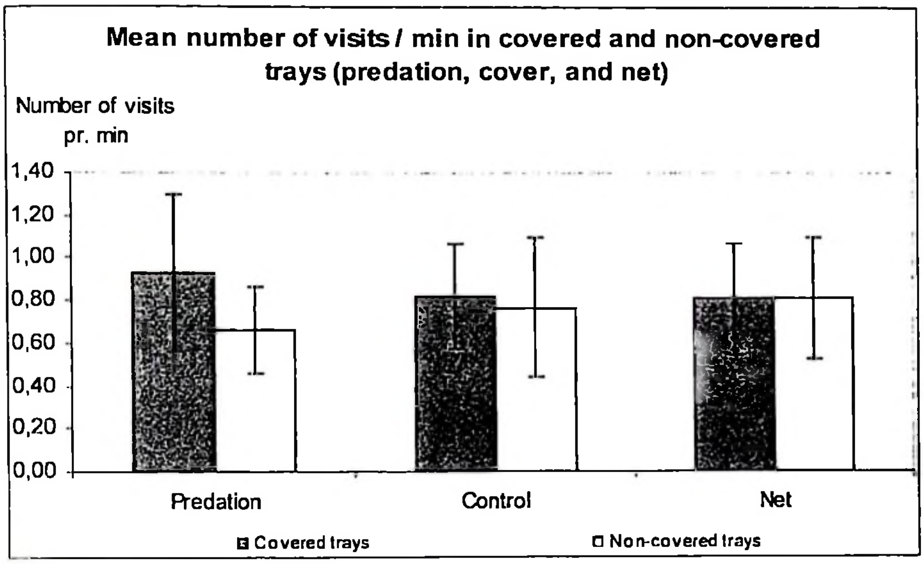

Figure 3. Mean number of visits per minute in covered and non-covered trays in the three treatments: predation, control, and net. Statistics on differences between mean visits per minute in the covered and the non-covered tray showed: $\chi^2=24$, $p<0.001$ for predation plots; $\chi^2=0.85$, $p=0.36$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

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